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Water availability outweighs heat and human pressure in shaping threatened plant hotspots in Kenting, Taiwan: Implications for island biodiversity conservation

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ABSTRACT: Effective biodiversity conservation requires the identification of species-rich hotspots, especially for threatened taxa. This study identified threatened plant hotspots in Kenting National Park, Taiwan, and examined the environmental and anthropogenic factors that shaped their distribution. Field surveys and herbarium records documented 140 taxa, including 18 Critically Endangered (CR), 35 Endangered (EN), 81 Vulnerable (VU), and 6 potentially threatened species (VU* suggested by authors), with 32.14% endemic to Taiwan. Six major hotspots were delineated, with the Nanjen–Chufongbi–Jialeshuei region exhibiting the highest diversity. Nonparametric correlation analysis revealed water-related variables, particularly mean annual precipitation (ρ = 0.420*) and winter precipitation ratio (ρ = 0.399*), as primary positive drivers of hotspot distribution, followed by energy-related variables (mean annual temperature and warmth index, both ρ = –0.308*), altitude (ρ = 0.320*), and human activities (ρ = –0.137*). Habitat fragmentation, invasive species such as *Leucaena leucocephala* (Fabaceae), and localized human disturbance were identified as major threats to hotspot integrity. Beyond the Kenting context, this study provides a transferable framework for identifying and managing threatened plant hotspots across tropical and subtropical island ecosystems, offering strategic insights for broader biodiversity conservation efforts.

KEY WORDS: Anthropogenic factors, environmental factors, hotspot conservation, rare plant, threatened plant species.

INTRODUCTION

Island plants rank among the most threatened organisms globally (Caujapé-Castells *et al.*, 2010), highlighting the strategic conservation importance of islands. Despite covering only about 5% of the Earth's land surface, islands harbor approximately one-quarter of all known extant vascular plant species (Kreft *et al.*, 2008; Schrader *et al.*, 2024). The vascular plant diversity index on islands significantly surpasses that of continental regions (Kier *et al.*, 2009). Due to smaller population sizes, narrow geographic ranges, and unique traits stemming from prolonged evolutionary isolation, island species are particularly susceptible to anthropogenic disturbances (Frankham, 2001). Together, these factors render islands uniquely valuable yet highly vulnerable reservoirs of biodiversity. (Caujapé-Castells *et al.*, 2010).

Conservation of biodiversity is typically approached from two perspectives (Carta *et al.*, 2019). The first prioritizes species and areas based on extinction risk, employing criteria such as range size, population trends, and demographic attributes (IUCN, 2019). The second emphasizes biodiversity hotspots, focusing on areas with high concentrations of range-restricted species and extensive habitat loss (Myers, 1988, 1990; Myers *et al.*, 2000). Synthesizing insights from both frameworks facilitates more effective allocation of resources toward priority areas, thereby enhancing the implementation of targeted conservation strategies and maximizing biodiversity outcomes (Fang *et al.*, 2011; Lu, 2016a). Global policy frameworks now center on the Kunming–Montreal Global Biodiversity Framework (Secretariat of the Convention on Biological Diversity, 2022), which establishes 23 action-oriented targets for 2030 and four long-term goals for 2050. Target 3 (“30×30”) requires conserving at least 30 % of terrestrial, inland water, and coastal/marine ecosystems by 2030 through protected areas and other effective area-based measures (Convention on Biological Diversity, 2022).

Effective protected-area management combines systematic zoning in core conservation areas, buffer zones, and sustainable-use sectors with adaptive management informed by continuous monitoring, reinforcing habitat connectivity and resilience in island contexts (Williams *et al.*, 2009; Worboys *et al.*, 2015). In Taiwan, the National Parks Act (Ministry of Interior, R.O.C., 2010) establishes zoning into core conservation areas, buffer zones, and experimental-use sectors. It also requires regular plan reviews, long-term monitoring, and adaptive management to ensure habitat protection and species recovery. These measures are reflected in Kenting National Park's co-management framework, which actively involves local stakeholders in decision-making and stewardship (Kenting National Park, 2017; Ministry of Interior, R.O.C., 2010).

While these policy frameworks set the stage, actual species distributions also reflect long-term interactions between organisms and their environment (Sterner *et al.*, 1986; Boenigk *et al.*, 2015). Two key forces shape these patterns: contemporary environmental conditions and historical contingencies (Ye *et al.*, 2022). While historical factors introduce stochasticity, current environmental conditions are often the dominant determinants (Trakhtenbrot *et al.*, 2005; Turner, 2015). Variables such as moisture availability, energy input, and habitat heterogeneity strongly influence plant species richness (Hsieh and Shen, 1994; Hawkins and Porter, 2003; Ye *et al.*, 2022). Meanwhile, human activities, including land use change, habitat fragmentation, and biotic invasions, have profoundly reshaped species distribution patterns (Laanisto *et al.*, 2015; Marco and Santini, 2015; Xu *et al.*, 2019; Wang *et al.*, 2022; Ye *et al.*, 2022). In particular, globalization has accelerated the spread of invasive species, compounding the threats to native and threatened flora (van Kleunen *et al.*, 2015; Gossner *et al.*, 2016; Chang-Yang *et al.*, 2022; Lin *et al.*, 2022;). Therefore, conservation research must incorporate both environmental and anthropogenic drivers. These considerations underpin the present study conducted in Kenting National Park, Taiwan.

Although ongoing studies have led to the discovery of previously unrecorded threatened plant taxa in Kenting National Park (Chian *et al.*, 2017; Chang *et al.*, 2019; Chen *et al.*, 2022; Lin *et al.*, 2025), comprehensive and systematic surveys have been lacking since the initial work by Hsu *et al.* (1985). To address this gap, we conducted extensive field surveys and compiled herbarium records from multiple institutions across Taiwan. This study aimed to identify distributional hotspots of threatened plant species within Kenting National Park and to evaluate the environmental and anthropogenic factors influencing their occurrence. The relationships between these variables and the spatial patterns of threatened species were analyzed and discussed in detail.

Based on identified threat patterns, we propose a list of species recommended for priority conservation (see Appendix B), aiming to maximize biodiversity gains while minimizing conservation costs. The findings not only offer a scientific basis for local conservation policymaking but also contribute insights relevant to broader strategies for conserving rare or threatened plant species and their associated hotspots globally.

MATERIALS AND METHODS

Geographic and biogeographic setting

Taiwan Island is located approximately 130-200 km east of Fujian Province in mainland China and about 360 km north of Luzon Island in the Philippines. It spans between 21°45'N and 25°37'N latitude and 119°18'E and 122°06'E longitude. The island's climate ranges from tropical to subtropical (Hsieh and Shen, 1994). Owing to its considerable size, significant isolation from continental landmasses, and complex topography (Hsieh *et al.*, 1994), Taiwan harbors a highly diversified and phytogeographically important vascular flora. According to Hsieh (2002), Taiwan is home to 4,216 native vascular plant species, of which 1,041 are endemic, resulting in an endemism rate of 24.7%. A global assessment by Kier *et al.* (2009) reported that Taiwan's species endemism richness reaches 306 per 10,000 km², a figure at least 20 times higher than that of China, placing Taiwan among the top eight regions worldwide in terms of species endemism richness.

One major factor contributing to Taiwan’s high plant diversity is its unique biogeographic position. The island is located at the boundary between the Paleotropical and Holarctic floristic kingdoms (Good, 1964; Takhtajan, 1986; Chao *et al.*, 2010). Wallace's Line passes through the southeastern offshore region of Taiwan, marking a transition between the Oriental and Australasian biogeographic zones (Wallace, 1876; Kano, 1933; Lin, 1974). The Hengchun Peninsula, located at the southernmost tip of Taiwan, rightly lies within this transitional zone (Kano, 1933; Lin, 1974). Ecotonal areas such as this are often recognized for their high species richness. Due to environmental complexity, these transition zones can support diverse ecosystems where numerous species coexist and compete for space (Gosz, 1993; Walker *et al.*, 2003).

Established in 1984 within the core area of the Hengchun Peninsula, Kenting National Park is the first national park in Taiwan (21°56’40.2”N, 120°46’58.9”E). It is also the only region on the island with a true tropical climate (Yang and Lee, 1993; Hsu, 1997). The Park's unique geographical location and varied topography have contributed to the development of a wide range of complex habitats, which in turn has resulted in highly fragmented ecosystems. Additionally, drift plants carried by ocean currents have further contributed to the formation of tropical coastal forests in this region (Kuo *et al.*, 2014). As a result, these characteristics have made Kenting a critical refuge for numerous threatened plant species (Kenting National Park, 2017). The Park covers 17,678.98 ha of land and 14,891.16 ha of coastal area, including marine waters within one kilometer from shore, totaling 32,570.14 ha.

Local climate and anthropogenic influences

The study area within the Kenting National Park is confined to its terrestrial portion (Figure 1A). According to the gridded observational data from TCCIP (2024) for the period 1960–2020, the climate in this region is classified as tropical monsoon forest. The annual average

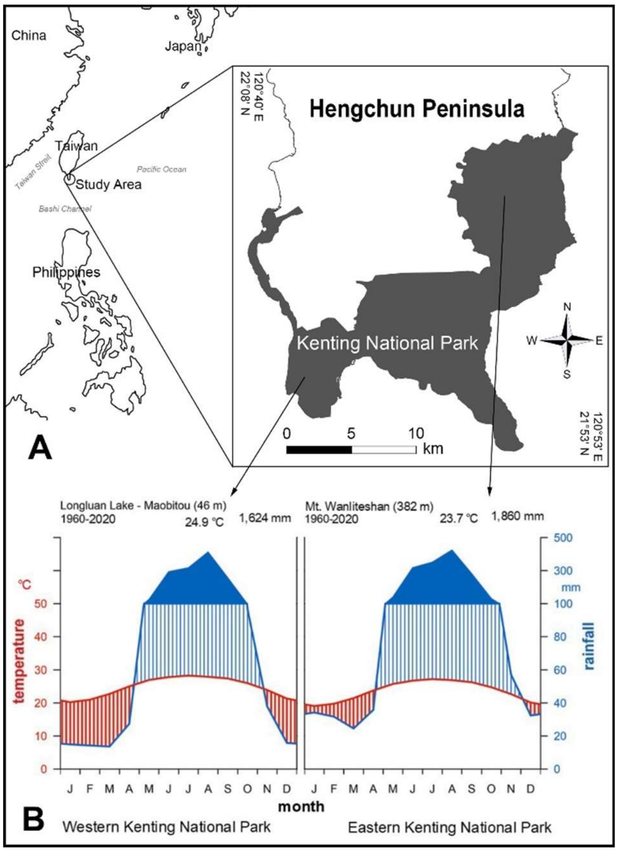

Fig. 1. Geographic setting and climatic patterns of Kenting National Park, located on the Hengchun Peninsula in southern Taiwan. **A.** Map showing the location of the park within East Asia. **B.** Climographs for the western and eastern regions of the park, based on long-term climate records (1960–2020). Monthly averages of temperature and precipitation were obtained from TCCIP (2024).

rainfall is 1,680 mm, ranging from 18.0 mm in March to 405.2 mm in July, and the annual average temperature is 24.4°C, varying from 19.5°C in January to 27.7°C in July. The dry season spans from October to April, while the remaining months constitute the wet season (Figure 1B). This area exhibits distinct seasonal changes; it is frequently affected by typhoons and southwestern airflows from July to September, and the northeast monsoons prevail from October to March (Kuo *et al.*, 2017). Notably, a rainfall gradient exists across the park, with the eastern region receiving a higher annual precipitation (1,860 mm, Figure 1B) than the western region (1,624 mm, Figure 1B), suggesting orographic and monsoonal influences. From a human activity perspective, the Hengchun Township (136.8 km^2) has an average population density of 216 persons/km² (Ministry of the Interior, R.O.C., 2024), along with approximately 2 million tourist visits annually (Kenting National Park, 2017), subjecting the study area to considerable anthropogenic pressure.

Field survey

Between April 2020 and February 2024, field surveys were conducted along roads and trails within Kenting National Park (Appendix A, Figure S1) using a transect-based approach to record the occurrences of threatened plant species. Sampling was conducted by subpopulation for each threatened taxon, and the geographic coordinates of each population were recorded using the WGS84 coordinate system. A species checklist, including all confirmed threatened and potentially threatened plant taxa (Appendix B), was generated using Checklister v.0.5.2-a2, a software developed by Lin (2018).

Herbarium resources

The study integrated data from previous works (Hsu *et al.*, 1985; Lu, 1996; Lu *et al.*, 2000, 2001; Lu and Kuo, 1997; Lu and Chiou, 1998; Lu and Mou, 1999) and field surveys to compile a preliminary list of threatened and potentially threatened plants within Kenting National Park. Initially, a large volume of information was collected and verified from specimen labels housed in major herbaria across Taiwan, including CHIA, HAST, PPI, TAIE, TAIF, TCF, TNM, and TNU. Herbarium acronyms follow the guidelines of the Index Herbariorum (Thiers, 2025).

Subsequently, records pertaining to threatened plants, as well as potentially threatened species suggested by the authors, discovered within Kenting National Park were extracted for further processing. Records associated with non-wild materials, such as street trees and cultivated plants, were excluded. Duplicate specimen records were also eliminated based on matching taxon name, collection date, collector, and collection number, as some specimens from the same subpopulation may have been collected multiple times.

Finally, coordinate information for each record was established. Coordinates originally recorded on specimen labels were used unless obvious errors were detected. For records lacking coordinates, approximate locations were assigned based on valid locality descriptions provided on the labels.

Identification of Threatened plant

In this study, the identification of "threatened plants" follows the criteria established by the IUCN (2012a,b) and the Red List of Taiwan Plants Editorial Committee (2017). Threatened plants are classified into three conservation statuses: Critically Endangered (CR), Endangered (EN), and Vulnerable (VU). Based on IUCN assessment criteria, the Editorial Committee classified 989 taxa as threatened across Taiwan, representing 22.26% of the 4,442 evaluated wild vascular plant species. This update has since served as an important benchmark for threatened plant research in the region. In earlier years, however, the threatened status of plant species was determined by individual researchers without the guidance of a unified standard.

In Kenting National Park, Hsu *et al.* (1985) initially recorded 150 threatened taxa. Following reassessment according to the IUCN criteria and the 2017 Red List, only 59 taxa (6 CR, 13 EN, and 40 VU) were confirmed to meet the criteria for threatened status. Subsequent studies conducted between 1996 and 2001 (Lu, 1996; Lu and Kuo, 1997; Lu and Chiou, 1998; Lu and Mou, 1999; Lu *et al.*, 2000, 2001) collectively recorded 124 threatened taxa. Of these, 72 taxa (8 CR, 18 EN, and 46 VU) were validated according to the 2017 assessment standards.

A comparison of the reassessed datasets from Hsu *et al.* (1985) and later studies (1996–2001) indicates an increase in the number of recognized threatened taxa, from 59 to 72. This increase likely reflects the contributions of continued research efforts aimed at more comprehensively uncovering and documenting at-risk species in the region.

Analysis on Diversity Hotspots of Threatened Plants

Kernel density estimation (KDE) is a common method for estimating the relative species density of organisms (Sussman *et al.*, 2019) and identifying plant diversity hotspots (Barabesi, 2001; Colville *et al.*, 2020). It transforms point distribution data into gridded data to reflect relative density patterns (Wong *et al.*, 2014).

In this study, KDE was applied to model the distribution of threatened plants using the Heatmap tool within the Interpolation module of QGIS v3.36.3 (QGIS.org, 2024), with specified parameters for bandwidth and cell size. A bandwidth of 200 meters was selected based on the study area's geographic extent and the spatial characteristics of the occurrence data. To account for differences in conservation priority among taxa, we applied weighted KDE, where threatened statuses were weighted with different ratings: CR = 3, EN = 2, and VU = 1. This weighting scheme enhances the prominence of areas dominated by species with higher conservation status, thereby facilitating the identification of diversity hotspots.

Following modeling, the resulting 200 × 200 m grid data were resampled, and the relationship between kernel density values and sample site counts was plotted to determine an appropriate threshold for delineating threatened plant hotspots. The threshold was determined empirically from the distribution of kernel density values, following previous data-driven approaches that identify natural breaks in value distributions (e.g., Kenchington *et al.*, 2014; Li *et al.*, 2016; Li and Banerjee, 2021).

Obtaining environmental variable data

To obtain climate, topographic, and anthropogenic disturbance data for analysis, the study area was first defined on the Taiwan Digital Terrain Model (DTM) (Ministry of Digital Affairs, R.O.C., 2024) to acquire topographic information. Next, we employed the *clim.regression* tool (Lin and Chen, 2023) from TCCIP (2024) to process and aggregate meteorological data of Taiwan in 2000-2020 year period. All geospatial analyses were conducted using QGIS v3.36.3 (QGIS.org, 2024).

The climate layers included eight variables: mean annual temperature (MAT, °C), year temperature difference (TD, °C), warmth index (WI), mean annual precipitation (MAP, mm), May to September precipitation (MSP, mm), winter precipitation ratio (WPR) (Li *et al.*, 2013), summer heat moisture index (SHM), and annual heat moisture index (AHM).

The topographic layers included altitude (m), slope (°), and topographic position index (TPI) (Guisan *et al.*, 1999). TPI is calculated as the difference between the altitude of a DEM grid cell and the mean altitude of its neighboring cells. A positive TPI value indicates that the grid cell is higher than its surroundings, suggesting a topographic feature such as a summit or ridge. Conversely, a negative TPI value suggests a lower position relative to the surrounding cells, often corresponding to valleys or depressions (Weiss, 2001).

An anthropogenic disturbance layer was generated using the human population density (HPD) data from the Global Population Database (https://landscan.ornl.gov/) (Rose *et al.*, 2018). Specifically, we utilized the 2020 Taiwan region TIFF file and clipped it to the boundaries of Kenting National Park. Additionally, the study employed various land use types within the area defined by Kenting National Park Headquarters (2011) to assess the impact of human activities towards local threatened plants.

Correlation analysis between environmental layers and threatened plant hotspots

The relationship between hotspot values in each grid and environmental layers was assessed by using non-parametric Spearman's rank correlation analysis (Spearman, 1904). The analysis was conducted with SPSS version 22.

RESULTS

List of threatened and potentially threatened species from field survey and herbarium data

The area of Kenting National Park was divided into 199 grids, each measuring 1 × 1 km (Appendix A, Figure S1). The survey route in this study passed through 180 of these grids, covering approximately 90.4% of the area. By incorporating specimen records from multiple herbaria, spatial coverage was extended to 187 grids, representing about 94.0% of the total area. Field surveys documented 337 subpopulations from 99 threatened plant species. In addition, 2,215 herbarium records were reviewed, of which 371 records belonging to 123 threatened species were retained following a screening process. In total, 708 valid occurrence records (337 from field surveys and 371 from herbarium data) were used for subsequent analyses.

Based on the combined dataset, a checklist of 140 threatened and potentially threatened species was produced. These 140 species represent 75 families and 122 genera,

Table 1. Overview of threatened plant hotspots in Kenting National Park

Hotspot	Area (ha)	Altitude (m)	MAT (℃)	MAP (mm)	Taxon (family/genus/species)	Threatened plant
a. Guanshan–Longluan lake	1,032	0–150	25.3	1,475	22/27/28	CR: 4; EN: 8; VU: 15; VU*: 1
b. Mobitou cape	378	0–50	25.5	1,637	11/14/14	CR: 2; EN: 3; VU: 9
c. Yongjing	604	20–100	24.5	1,827	10/16/17	CR: 1; EN: 5; VU: 11
d. Kenting–Eluanbi cape	3,030	0–50	24.8	1,955	40/56/63	CR: 10; EN: 14; VU: 38; VU*: 1
e. Gangkou	355	0–70	25.0	2,028	9/11/11	CR: 1; EN: 2; VU: 8
f. Nanjen–Chufongbi–Jialeshuei	5,496	0–522	23.7	2,294	63/91/98	CR: 10; EN: 21; VU: 62; VU*: 6

MAT = mean annual temperature; MAP = mean annual precipitation.
Climate data compiled from TCCIP (2024).
VU* indicates taxa that have not been formally assessed but are provisionally flagged for conservation concern based on judgment by the authors.

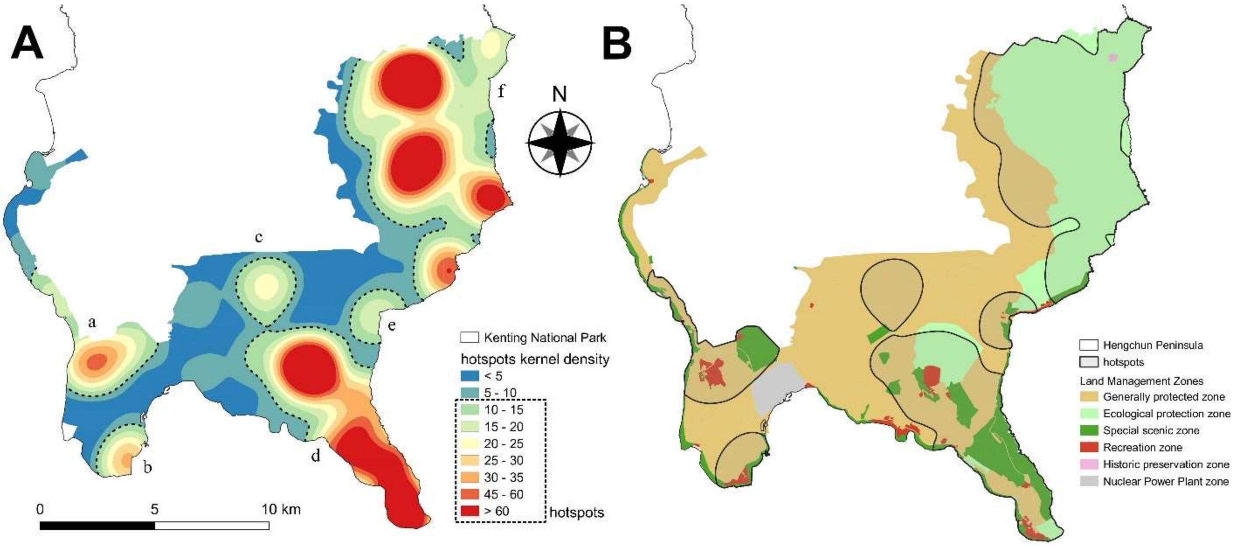

Fig. 2. Map of the Kenting National Park, Taiwan. **A.** The distribution of threatened plant hotspots across six major hotspot regions (a–f), based on weighted kernel density estimation (CR = 3, EN = 2, VU = 1). Areas with kernel density above 10 are outlined, and warmer colors indicate higher concentrations of threatened plant species: a. Guanshan–Longluan Lake, b. Mobitou Cape, c. Yongjing, d. Kenting–Eluanbi Cape, e. Gangkou, f. Nanjen–Chufongbi–Jialeshuei. **B.** Land management zones with these hotspots, using the same weighted kernel density method to highlight areas exceeding a density threshold of 10.

including 134 nationally listed threatened species (CR: 18; EN: 35; VU: 81) and six additional species proposed by the authors as potentially threatened (designated as VU*; see Discussion for justification). Among these, 45 species (32.14%) are endemic to Taiwan (Appendix B). However, only about eight of these endemic taxa are narrowly distributed or primarily confined to Kenting National Park, while most occur across multiple habitats within the park and adjacent regions. Fabaceae contributed the highest number of species (23), followed by Asteraceae and Acanthaceae, each represented by six species.

Hotspots modeling of threatened plant species

Following the modeling of threatened plant distributions (Figure 2A), the study area within Kenting National Park was subdivided into a grid of 200 × 200 m sampling units and the occurrence of threatened species within each unit was evaluated. As shown in Figure S2 of Appendix A, kernel density values increase as the number of sampling units decreases, indicating that areas with high species diversity are relatively limited in spatial extent.

Based on the distribution of sampling frequencies and the cumulative curve, a kernel density value of 10 was designated as the threshold for identifying threatened plant diversity hotspots, corresponding to a visible gap in the histogram (see the dashed line in Appendix A, Figure S2). This threshold strikes a balance between capturing a large fraction of total species occurrences and minimizing the inclusion of marginally diverse areas.

Using this threshold, six hotspots were delineated, listed from west to east as follows: (a) Guanshan–Longluan Lake; (b) Mobitou Cape; (c) Yongjing; (d) Kenting–Eluanbi Cape; (e) Gangkou; and (f) Nanjen–Chufongbi–Jialeshuei (Figure 2A, Table 1). Among them, Nanjen–Chufongbi–Jialeshuei harbors the highest diversity, with 99 species across 5,496 ha, followed by Kenting–Eluanbi Cape with 63 species in 3,030 ha. All single-population CR species and the majority of EN species were confined to these six hotspots. These results demonstrated that the designated threshold effectively identified areas of highest ecological significance for threatened plant conservation in the park.

Table 2. Comparative kernel density of threatened plants and human impact across different land management zones in the Kenting National Park, Taiwan.

Major zone / sub-zone	Grid count*	Area (m²)	Percentage (%)	Human density **	Threatened plant	
					species count	kernel density value (mean ± SD)
Generally protected zone	**2,477**	**99,080,000**	**56.92**	**1,442**	**69**	**12.54 ± 12.36**
forestry land	1,344	53,760,000	30.88	164	55	11.34 ± 12.03
river land	14	560,000	0.32	0	0	4.14 ± 6.7
Marine Biology Museum and service area	22	880,000	0.51	149	2	8.82 ± 0.8
livestock experiment land	287	11,480,000	6.59	161	7	19.06 ± 10.81
port area	5	200,000	0.11	21	0	8.8 ± 7.56
rural construction land	49	1,960,000	1.13	313	1	10.61 ± 11.04
agricultural land	672	26,880,000	15.44	398	11	11.99 ± 12.55
road land	48	1,920,000	1.10	98	8	20.06 ± 15.24
greenbelt land	5	200,000	0.11	1	5	17.6 ± 17.71
cemetery land	22	880,000	0.51	20	4	12.73 ± 14.11
school land	3	120,000	0.07	99	0	7.67 ± 3.51
government land	6	240,000	0.14	18	0	18.17 ± 22.68
Ecological protection zone	**1,349**	**53,960,000**	**31.00**	**5**	**84**	**28.11 ± 16.37**
Special scenic zone	**360**	**14,400,000**	**8.27**	**26**	**43**	**29.92 ± 15.77**
Recreation zone	**82**	**3,280,000**	**1.88**	**383**	**29**	**34.48 ± 20.76**
Youth Activity Center land	4	160,000	0.09	33	0	10.75 ± 5.5
hotel land	7	280,000	0.16	98	0	18.71 ± 17.9
parking lots	6	240,000	0.14	5	0	33.67 ± 29.84
outdoor recreation land	31	1,240,000	0.71	4	28	43.87 ± 24.5
management and service station land	2	80,000	0.05	5	0	19.5 ± 14.85
camping land	2	80,000	0.05	14	1	44.5 ± 21.92
Historic preservation zone	**3**	**120,000**	**0.07**	**0**	**0**	**16.67 ± 1.15**
Nuclear Power Plant zone	**81**	**3,240,000**	**1.86**	**122**	**0**	**3.56 ± 1.7**

* Each grid is 200 × 200 m. ** people per 1 × 1 km grid (Rose *et al.*, 2018). Kernel density values were computed using weighted KDE, with threat status weights: CR = 3, EN = 2, VU = 1. Note: Some grids without species records may show nonzero kernel density values due to interpolation from nearby occurrences. Data source: Land-use types were obtained from Kenting National Park Headquarters (2011).

The distribution of hotspots of threatened plants and human impacts across different land management zones in Kenting National Park

To evaluate the potential influence of human activities on the distribution of threatened plant hotspots, kernel density values were compared across different land management zones defined by the Kenting National Park zoning plan (Kenting National Park, 2017) (Figure 2B; Table 2). The highest kernel density values were observed in the Recreation Zone (34.48 ± 20.76), Special Scenic Zone (29.92 ± 15.77), and Ecological Protection Zone (28.11 ± 16.37), suggesting these regions might serve as critical habitats for threatened plants.

Human population density was highest in the Generally Protected Zone (1,142 persons/km²), followed by the Recreation Zone (383 persons/km²). Their corresponding kernel densities were 12.54 ± 12.36 and 34.48 ± 20.76, respectively. The Generally Protected Zone, which covers 56.92% of the park, included forestry land occupying 30.88% of the total park area (kernel density: 11.34 ± 12.03). Notably, road land within this zone exhibited the highest kernel density (20.06 ± 15.24) despite covering only 1.10% of the park, suggesting a spatial overlap between linear infrastructure and plant occurrences.

The Ecological Protection Zone, covering 31% of the park area, hosted the highest number of threatened species (84 species) and exhibited a high kernel density of threatened plants (28.11 ± 16.37), with minimal human presence (5 persons/km²) (Figure 2B; Table 2). In contrast, the Special Scenic Zone (8.27% of the park) showed relatively high values for both kernel density and human activity. The Recreation Zone (1.88% of the park) displayed marked internal variation, with outdoor recreation land (43.87 ± 24.50), camping areas (44.50 ± 21.92), and parking lots (33.67 ± 29.84) exhibiting particularly high values despite low human densities (4, 14, and 5 persons/km², respectively) (Table 2).

The Historic Preservation Zone and Nuclear Power Plant Zone occupied small portions of the park (0.07% and 1.86%, respectively) and had lower kernel densities. However, the Historic Preservation Zone (16.67 ± 1.15) still exceeded several sub-zones in other zones (Figure 2B). This elevated value might reflect spatial smoothing from adjacent areas with high kernel densities, rather than local species concentration.

Table 3. Spearman's correlation (ρ) between environmental factors and kernel density values of threatened plants in Kenting National Park, Taiwan.

Environmental factors	Spearman's correlation (ρ)
Water factors	
mean annual precipitation (MAP), mm	0.420*
May to September precipitation (MSP), mm	0.399*
winter precipitation ratio (WPR)	0.374*
Energy factors	
mean annual temperature (MAT), ℃	-0.308*
warmth index (WI)	-0.308*
year temperature difference (TD), ℃	0.259*
Heat moisture index	
summer heat moisture index (SHM)	-0.390*
annual heat moisture index (AHM)	-0.419*
Habitat heterogeneity	
altitude, m	0.320*
slope,	0.162*
topographic position index (TPI)	-0.011
Human activities	
human density	-0.137*

Spearman's ρ indicates the strength and direction of monotonic relationships between each environmental variable and the kernel density of threatened plants across grids.
* Statistical significance is at the 0.01 level (two-tailed).

Correlation between threatened plant kernel density and environmental variables

The correlations between environmental variables and kernel density values of threatened plants indicated that water-related factors and certain aspects of habitat heterogeneity (e.g., altitude) were positively associated with hotspot intensity. In contrast, most temperature-related and heat–moisture indices showed significant negative associations, while human activity exhibited a weaker but still significant negative effect (Figure 3, Table 3).

Specifically, MAP and MSP were strongly positively correlated with kernel density (ρ = 0.420* and ρ = 0.399*, respectively), and WPR also showed a positive correlation (ρ = 0.374*). MAT and WI exhibited identical negative correlations (both ρ = –0.308*), while TD showed a weaker but significant positive correlation (ρ = 0.259*), suggesting a distinct pattern from other temperature-related variables. SHM and AHM showed significant negative correlations (ρ = –0.390* and ρ = –0.419*, respectively). Among habitat heterogeneity variables, altitude had a moderate positive correlation (ρ = 0.320*), slope a weaker one (ρ = 0.162*), and TPI was not significant (ρ = –0.011). Human density was weakly but significantly negatively correlated with kernel density (ρ = –0.137*) (Figure 3, Table 3).

DISCUSSION

Ecological patterns in threatened plant hotspots

The park encompasses a wide range of ecosystems and landscape types, including coastal areas, dry woodlands, monsoon forests, *Acacia confusa* and mixed-species forests, grasslands, farmlands, aquatic habitats, and barren land (Chen and Chung, 2003).

In the western region, areas such as Guanshan–Longluan Lake (Figure 2Aa) were historically cultivated with *Agave sisalana* (Agavaceae) and are now dominated by *Leucaena leucocephala* (Fabaceae) invasion, leading to forest fragmentation. Nevertheless, remnants of native forest patches persist, supporting species such as *Diospyros blancoi* (Ebenaceae) and a variety of rare plants (Chen *et al.*, 2011; Chian *et al.*, 2017; Feng *et al.*, 2009).

In contrast, the eastern region, including the Nanren Lake system (Figure 2Af), retains high landscape integrity, with well-preserved forests and multiple natural lakes supporting diverse habitats (Lai, 2004; Giletycz *et al.*, 2021; Ku *et al.*, 2023). Moreover, the Gangkou hotspot (Figure 2Ae), once the outlet of the prehistoric Manzhou Lake (9,000–6,000 years ago), still retains brackish remnants shaped by coral uplift and geomorphic changes (Giletycz *et al.*, 2021). Additionally, northeast monsoons during winter continue to shape vegetation patterns on the park's windward slopes (Hsieh *et al.*, 1992; Chao *et al.*, 2010; Ku *et al.*, 2021, 2023).

Grassland-associated threatened species are primarily concentrated in areas such as Yongjing (Figure 2Ac), Chufongbi and Bitou (Figure 2Af), and parts of Eluanbi and Kenting (Figure 2Ad). These grasslands, historically managed by the Paiwan Indigenous people, have undergone abandonment in the past 50–100 years (Wang *et al.*, 2004; Wu *et al.*, 2007), resulting in forest encroachment (Chen, 1989; Hu and Wang, 1994). Today, traditional grazing remains essential to maintaining these open landscapes (Chen, 1989; Hu and Wang, 1994; Hosokawa and Syohji, 2010). Conservation management should prioritize both habitat preservation and the continuation of traditional management practices to sustain these landscapes.

Overall, Kenting National Park exemplifies a complex ecological mosaic shaped by sharp geographic gradients and contrasting climatic regimes. This west–east–grassland variation provides an empirical basis for zoned management. The distinct environmental and biotic assemblages between its western and eastern regions underscore the park's importance as a biodiversity reservoir and a critical landscape for integrated conservation planning.

Environmental factors and conservation challenges against threatened plant hotspots

Rare and threatened species prefer significantly narrower habitats on average compared to common species (Wamelink *et al.*, 2014). While these species have specific environmental preferences, their collective persistence across landscapes depends on the availability of diverse microhabitats. Therefore, maintaining broad ecological

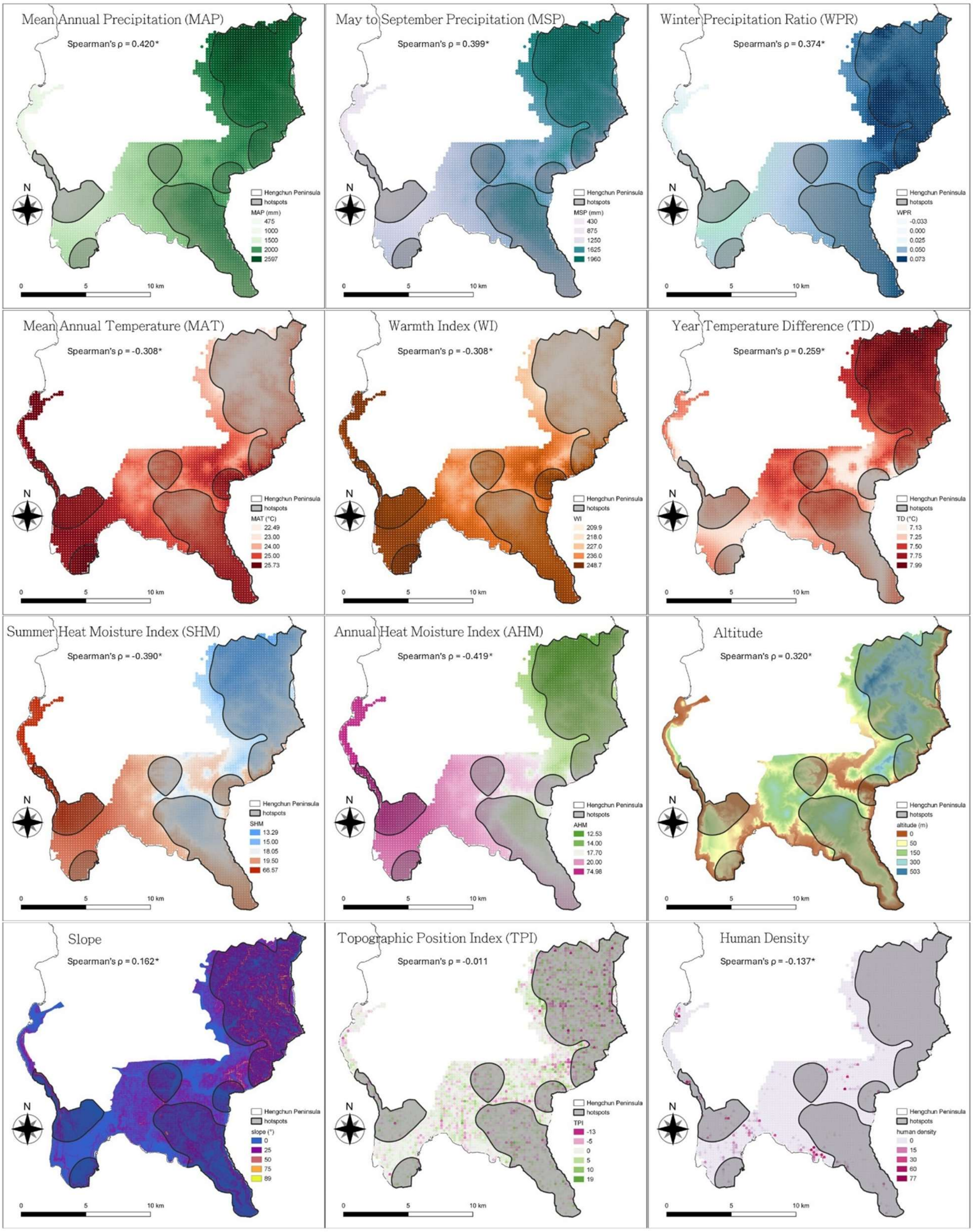

Fig. 3. Spatial distribution of environmental factors and threatened plant hotspots in the Kenting National Park, Taiwan. Kernel density values were calculated using weighted KDE with threat status weights: CR = 3, EN = 2, and VU = 1. The contour line delineates areas where the weighted kernel density of threatened plants exceeds 10. * Statistical significance is at the 0.01 level (two-tailed).

(abiotic) gradients is essential to ensure that the full range of these niche conditions is retained. Based on our results (Figure 3; Table 3), water factors, energy factors, habitat heterogeneity, and human activities all significantly influence the distribution of threatened plant hotspots. Among these, water factors show the strongest correlations, followed by energy-related variables. These findings are generally consistent with those of previous studies (Vetaas *et al*., 2019; Li *et al*., 2022; Ye *et al*., 2022).

Specifically, MAP and MSP are significantly positively correlated with hotspot distributions (ρ = 0.420* and ρ = 0.399*, respectively, Figure 3; Table 3), indicating that moderate levels of precipitation are crucial for sustaining rare species. Interestingly, even relatively dry regions such as Guanshan–Longluan Lake and Mobitou Cape still harbor extensive hotspots (Figure 2; Appendix C), that threatened species can persist under lower precipitation regimes, provided microhabitats are suitable. WPR also shows a positive correlation (ρ = 0.374*), indicating that moisture availability during the dry season may play a key role in reducing water stress and supporting local plant persistence (Lin *et al.*, 2018). Stable precipitation regimes can reduce extinction risks, as indicated by Enquist *et al.* (2019) and earlier studies (Diamond, 1984; Pimm *et al.*, 1988). In the Nanjen–Chufongbi–Jialeshuei hotspot, relatively consistent rainfall supports Taiwan's last low-altitude primary tropical monsoon rainforests and the park's most diverse and abundant threatened plants (Chao *et al.*, 2023; Chao *et al.*, 2008; Kenting National Park, 2017; Ku *et al.*, 2021).

Grassland ecosystems generally respond more sensitively to precipitation changes than forests, partly due to a higher proportion of annual species (Cleland *et al.*, 2013; Li *et al.*, 2020). Annual and quasi-annual species synchronize their life cycles with rainfall variability, which often increases their rarity and vulnerability (Goldberg and Miller, 1990; Oksanen, 1996). In the park, strictly annual species (those completing their entire life cycle within one growing season) are relatively uncommon, with examples including *Eragrostis unioloides* (Poaceae, EN) and *Acmella paniculata* (Asteraceae, VU). By contrast, many herbaceous taxa combine perennial below-ground organs with annual above-ground shoots, such as *Tacca leontopetaloides* (Dioscoreaceae, CR) and *Alloteropsis semialata* (Poaceae, EN). This intermediate strategy can enhance resilience to rainfall variability by relying on perennial reserves during dry periods; yet it offers limited competitive advantage against fully perennial species and remains susceptible to intensified moisture stress.

Energy factors and habitat heterogeneity both influence the distribution of threatened plant hotspots. Among energy-related variables, MAT and WI correlate negatively with hotspot intensity (both ρ = –0.308*) (Figure 3; Table 3), suggesting that while many hotspot species favor warm conditions, excessive heat may limit their range. In contrast, greater annual temperature difference (TD) correlates positively with hotspot distribution (ρ = 0.259*), indicating that seasonal temperature variation may enhance species coexistence (Tonkin *et al.*, 2017). For example, the Nanjen–Chufongbi–Jialeshuei hotspot, characterized by high TD, supports numerous subtropical threatened species, including *Lithocarpus formosanus* (Fagaceae, CR), *Nageia nagi* (Podocarpaceae, EN), and *C. brevipedunculatum* (Lauraceae, VU). Heat–moisture balance indices also show strong negative correlations with hotspot distribution (SHM: ρ = –0.390*; AHM: ρ = –0.419*), suggesting that excessive heat relative to moisture availability constrains the persistence of threatened species. This pattern aligns with findings from other regions (Li *et al.*, 2022) and reinforces the pivotal role of moisture-related variables in shaping plant rarity under warming climates.

Habitat heterogeneity also plays a vital role. Altitude correlates positively with hotspots (ρ = 0.320*) (Figure 3; Table 3), and mid- to low-altitude areas in the study region provide stable conditions fostering threatened plants (Tang *et al.*, 2013). Although the maximum altitude of the Nanjenshan area is only about 500 m, the cooler and wetter conditions, driven by northeast monsoons, has made this area a compressed vegetation zones, thereby sustaining higher threatened plant richness than other areas in Kenting National Park (Chao *et al.*, 2008, 2010; Liao *et al.*, 2014; Ku *et al.*, 2021, 2023). Slopes show a weaker but still positive correlation (ρ = 0.162*), possibly reducing human disturbance and offering microhabitats. Conversely, TPI lacks a clear relationship with hotspots, likely due to the diverse evolutionary histories of these species.

Overall, these findings align with broader evidence that mountainous regions, with their stable climates and heterogeneous habitats, serve as refuges for rare and threatened species (Baskin and Baskin, 1988; Lavergne *et al.*, 2003; Enquist *et al.*, 2019; Rahbek *et al.*, 2019a,b). Here, the southern extent of Taiwan's Central Mountain Range also supports greater threatened plant diversity (Hsieh *et al.*, 1994; Hsieh and Shen, 1994), emphasizing the importance of diverse, moderately elevated habitats in conserving threatened plant species.

Balancing human activities and threatened plant conservation

Human activities such as agriculture and tourism development further interact with invasive species pressure, jointly shaping the spatial distribution of threatened plants. Population density is weakly but significantly negatively correlated with the distribution of threatened plants (ρ = –0.137*) (Figure 3; Table 3). Such a negative correlation reflects that, within the park, areas with higher levels of human activity tend to support fewer threatened species, most likely due to habitat modification and disturbance. Indeed, numerous studies have similarly shown that agricultural development, livestock grazing, and other anthropogenic land uses disrupt native plant communities and constrain the persistence of sensitive taxa (Lavergne *et al.*, 2005; Kier *et al.*, 2009; Laanisto *et al.*, 2015; Li, 2014; Marco and Santini, 2015; Robinson and Hermanutz, 2015; Carta *et al.*, 2019; Enquist *et al.*, 2019; Xu *et al.*, 2019).

Nevertheless, although human activity is negatively correlated with the distribution of threatened plants, its influence appears weaker than that of most environmental variables (Figure 3; Table 3). When compared with the correlation coefficients for environmental factors, this weaker influence may reflect the decline in land development following the establishment of the park, especially relative to the intensive use observed 70–120 years ago (Wang *et al.*, 2004; Wu *et al.*, 2007). Moreover, despite receiving around 2 million tourists annually (Kenting National Park, 2017), tourist impacts are predominantly localized in specific zones. Specifically, table 2 shows that certain areas, such as the Special Scenic Zone, Recreation Zone, road lands, and livestock experiment lands, support relatively high human densities while also maintaining elevated kernel densities of threatened plants (Figure 2B). Together, these findings suggest that, with appropriate management, human activity and conservation can coexist, particularly when ecological connectivity is preserved.

By contrast, in the western part of the park, particularly in hotspots such as Guanshan–Longluan Lake (Figure 2Aa) and Mobitou Cape (Figure 2Ab), the survival of rare plants remains under pressure from tourism, illegal harvesting, development, and invasive species. Such hotspots therefore require targeted management attention. Furthermore, many hotspots contain grassland landscapes shaped by historical grazing or feral cattle activity. Notable examples include Yongjing (Figure 2Ac), Eluanbi Cape (Figure 2Ad), and Chufongbi (Figure 2Af). While these grassland areas support many distinctive plant species, they face a high risk of *Leu. leucocephala* invasion in the future (Chiou *et al.*, 2013, 2016; Lu, 2016b). This vulnerability underscores the need for closer ecological monitoring (see later Discussion).

In summary, the establishment of the national park has facilitated the preservation and partial restoration of diverse habitats, supporting a balance between human activity and biodiversity conservation. Accordingly, future efforts should focus on managing hotspots vulnerable to disturbance or invasion. Implementing long-term monitoring and adaptive management will be essential to mitigate threats and foster ecological recovery.

Ecological pressures from invasive species and large herbivores

Forest disturbances, both natural and anthropogenic, have facilitated the rapid spread of invasive plants in the park, most notably *Leucaena leucocephala*, widely recognized as the Hengchun Peninsula's most aggressive invader (Chung and Lu, 2006; Feng *et al.*, 2009; Chen *et al.*, 2011; Chen *et al.*, 2012). This species expands most readily under warm, dry conditions, affecting both forests and grasslands, especially near forest edges and in areas disturbed by roads or abandoned farmland (Chen *et al.*, 2011; Chian *et al.*, 2017). Such environments are concentrated in the park's western, central, and southern sectors (Chung and Lu, 2006; Chiou *et al.*, 2013, 2016; Lu, 2016b).

Hotspots of naturally open grasslands (Yongjing, Guanshan–Longluan Lake, and Kenting–Eluanbi Cape) lie adjacent to zones of human disturbance and are therefore highly vulnerable to future *Leucaena* invasion. These grasslands have been sustained by moderate grazing, which helps maintain their open structure and underscores the need for long-term monitoring. Because cutting above-ground biomass alone cannot eradicate *Leucaena* (Peng *et al.*, 2019), current control efforts emphasize complete removal of invasive plants and reintroduction of native species. Preliminary observations suggest that disturbed vegetation can recover rapidly, often within a single growing season, through recruitment from existing seed and seedling banks. However, the long-term recovery dynamics remain uncertain and warrant continued study (Wang and Chen, 2010).

Another ecological concern is the impact of reintroduced Formosan sika deer (*Cervus nippon taiouanus*) on native vegetation. This subspecies, once widespread in lowland Taiwan, became extinct in the wild by 1969 due to overhunting and expanding human settlement (McCullough, 1974). A captive breeding program launched in 1986 has since reestablished stable wild populations in the park (Pei, 2009). Nevertheless, browsing and antler rubbing by deer exert new pressures on forest understorey, and populations of some threatened plants, especially *Helminthostachys zeylanica* (Ophioglossaceae, CR), have declined markedly, with only a few individuals remaining (Wang *et al.*, 2015, 2019; Yeh *et al.*, 2021). Fencing has been installed in selected forest areas to exclude deer from sensitive habitats (Liang *et al.*, 2020). While this approach shows initial effectiveness, its long-term outcomes require sustained monitoring and adaptive management.

Whether reintroduced deer can replicate the ecological functions historically provided by Indigenous grazing or feral cattle remains unclear. Deer browsing patterns differ from livestock grazing in timing and selectivity, which may affect seedling recruitment and species composition differently. Further research should quantify how deer browsing intensity compares with livestock grazing in maintaining species-rich grasslands and identify optimal herbivore densities for semi-natural habitat stability.

Analysis of threatened plant diversity and prioritized conservation species

A total of 140 species were documented, of which 45 are endemic to Taiwan, resulting in an endemism rate of 32.1% (Appendix B). This figure exceeds Taiwan's overall endemic rate of 26.1% (Hsieh, 2002) but is slightly lower than the 33.7% endemism reported for the country's threatened plant species (Editorial Committee of the Red List of Taiwan Plants, 2017).

Turning to the spatial distribution of CR taxa, up to ten CR species were recorded in each of the Nanjen–Chufongbi–Jialeshuei and Kenting–Eluanbi Cape hotspots within Kenting National Park, whereas the Guanshan–Longluan Lake area supports up to four CR species (Table 1, Appendix C). Among these, *Indigofera taiwaniana* (Fabaceae, CR), *I. byobiensis* (Fabaceae, CR) and *Leptaspis formosana* (Poaceae, CR) are endemic to Taiwan (Hsu, 1971; Huang and Huang, 1987; Huang and Wu, 1992) Within the park (i.e., in our survey area) they host the only known stable populations of these three species.

Although *Osteomeles anthyllidifolia* var. *subrotunda* (Rosaceae, CR) and *T. leontopetaloides* are not endemic (Yang and Liu, 2002), the populations we located in Kenting National Park represent the only stable Taiwanese populations documented to date and are likewise threatened by overharvesting. Notably, *Decalobanthus similis* (Convolvulaceae, CR), last collected by Chang (1971), went unrecorded until its recent rediscovery in 2021 (Chen *et al*., 2022); although it also occurs in the Philippines, its habitats are now under severe deforestation pressure, making the conservation of the Taiwanese subpopulation a high priority (Staples, 2022).

From a broader biogeographical perspective, Robyns (1925) observed that the genus *Sphaeranthus* typically follows the limits of the Tropics of Cancer and Capricorn. In our study area, *Sphaeranthus africanus* (Asteraceae, VU), one of the most widely distributed members of the genus, appears to mark the northern boundary of its global range. Furthermore, comparison with Hsu *et al.* (1985) suggests that the current distributions of *Mallotus tiliifolius* (Euphorbiaceae, VU) and *H. zeylanica* within the national park are contracting, underscoring the need for ongoing population monitoring and targeted habitat protection.

Finally, the Nanren Lake system supports the most diverse assemblage of wetland plant species in Kenting National Park, including several VU taxa, *Nymphoides coreana* (Menyanthaceae), *Limnophila aromatica* (Plantaginaceae), *Rotala wallichii* (Lythraceae), *Lygodium microphyllum* (Lygodiaceae) and *Diplacrum caricinum* (Cyperaceae), as well as two putatively undescribed taxa herein referred to as "Nanjen's *Hydrophila* sp." and "Pingtung's *Limnophila* sp." (see Appendix A). Historical records also indicate past occurrences of *Salix kusanoi* (Salicaceae, EN). Although many wetland species evade high-risk categories, thanks to traits such as long-distance, bird-mediated dispersal and frequent clonal reproduction (Santamaría, 2002; Li, 2014; Wang *et al.*, 2022), the combined pressures of urban expansion and climate change may yet precipitate population declines (Jain, 1990; Viana, 2017; O'Hare *et al.*, 2018). Preserving the unique biodiversity of the Nanren Lake wetlands is therefore of critical importance.

In summary, Kenting National Park harbors a rich flora characterized by high endemism, concentrations of CR taxa in key hotspots, biogeographically marginal species, and a particularly diverse wetland community. We recommend establishing an integrated monitoring program and implementing habitat-specific conservation measures to safeguard both the endemic and threatened assemblages identified in this study.

CONCLUSION

This study provides a comprehensive assessment of threatened plant distribution and conservation priorities in Kenting National Park by integrating field surveys, herbarium records, and geospatial modeling. Applying these methods, six major hotspots were identified via kernel density analysis, with Nanjen–Chufongbi–Jialeshuei exhibiting the highest species richness. Environmental driver analysis revealed that water availability (MAP and MSP) was the most influential factor, followed by energy variables, habitat heterogeneity, and human disturbance.

Conservation efforts should therefore prioritize management in these hotspots, specifically regions beyond existing reserves such as Guanshan and Yongjing. Moreover, adaptive grazing regimes in grassland areas could maintain habitat structure, and early intervention is critical for controlling invasive species such as *Leu. leucocephala*.

Finally, our framework highlights underrecognized taxa of conservation concern, namely newly recorded species and ecologically distinctive populations, underscoring the need to resolve taxonomic uncertainty and integrate field-based evidence into planning. Beyond Kenting, this kernel density–driven approach is transferable to other tropical and subtropical island ecosystems, offering strategic insights for broader biodiversity conservation efforts.

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