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Research article

Populations of *Nepenthes* natural hybrids might overcome secondary forest in Ban Thung Tuek, Ko Kho Khao, Phangnga Province, Thailand

Napat Jantaraprasit[a], Chatchai Ngernsaengsaruay[a,b], Raweewan Thunthawanich[a,*]

[a] *Department of Botany, Faculty of Science, Kasetsart University, Bangkok 10900, Thailand*

[b] *Biodiversity Center, Kasetsart University (BDCKU), Bangkok 10900, Thailand*

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Abstract

Importance of the work: Niche-specific adaptations were highlighted through addressing the ecological dynamics and adaptive strategies of *Nepenthes* in *Melaleuca cajuputi*-dominated secondary forests.

Objectives: To assess the community structure and distribution of *Nepenthes* across environmental gradients.

Materials & Methods: Three 20 m × 50 m plots were established across a gradient from peat swamp forest to dry land, subdivided for detailed analysis of the tree, sapling and *Nepenthes* populations, including the Importance Value Index for plant community analysis.

Results: Two species, one variety, and two natural hybrids were identified: *Nepenthes andamana* and *N. mirabilis* var. *globosa* and two *Nepenthes* natural hybrids: *N. mirabilis* × *N. andamana* and *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis*. Distinct habitats were identified fostering diverse plant communities, with *Melaleuca cajuputi* as the dominant tree species. All *Nepenthes* species and natural hybrids exhibited varied distribution and abundance, influenced by habitat conditions. The highest abundance was for *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis*, mainly in intermediate and dry zones, with major implications for species survival and distribution under varying environmental conditions and anthropogenic pressures.

Main finding: Habitat-driven diversity in *Nepenthes* was uncovered, emphasizing the importance of ecological tolerance. The prevalence of *N. mirabilis* hybrids indicated genetic introgression risks, urging the need for focused conservation efforts to preserve species.

* Corresponding author.
E-mail address: fscirwt@ku.ac.th (R. Thunthawanich)

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Introduction

Nepenthes L. (family Nepenthaceae) is a genus of carnivorous plants known for its unique insect-trapping pitchers, predominantly found in the rich and diverse ecosystems of Southeast Asia (Biswal et al., 2018). The genus comprises 213 species worldwide (Plants of the World Online, 2024), with 16 species (including two varieties) reported in Thailand (Nuanlaong et al., 2022). Although the center of distribution for *Nepenthes* has not yet been confirmed due to its complex phylogenetic tree, the high occurrence of endemic species suggests that Borneo, Sumatra and the Philippines are major candidates. Phylogenetic analysis indicated that all species are related to *N. pervillei* Blume from the Seychelles in East Africa, with *N. danseri* Jebb & Cheek from Waigeo Island in East Indonesia identified as the ancestor of Southeast Asian *Nepenthes* diversity (Murphy et al., 2020). Beyond the role of *Nepenthes* spp. as food and ornamental plants, *Nepenthes* extracts are sources of antioxidant, antidiabetic, antibacterial, antifungal, hepatoprotective, antiosteoporotic and anti-inflammatory agents (Sanusi et al., 2017). In addition, these plants have inspired innovations such as bio-inspired polymers, slippery liquid-infused porous surfaces and unidirectional liquid-spreading structures (Miguel et al., 2018). The diverse applications of *Nepenthes* underscore their critical importance and the need for ongoing conservation and research efforts.

Conservation efforts for *Nepenthes* are spearheaded by the International Union for the Conservation of Nature, which has evaluated 169 species, with 30 being classified as critically endangered, 21 as uncertain and the status of the remainder ranges from endangered to least concern (Cross et al., 2020). In Thailand, all *Nepenthes* species are protected under the Plant Variety Protection Act 2021 of Thailand, aligned with the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), with unauthorized import or export of these plants being punishable by imprisonment for up to 3 mth, a fine not exceeding THB 3,000 or both (Ministry of Agriculture and Cooperatives, 2021).

Ko Kho Kao in Phangnga province, Thailand offers a unique microcosm of *Nepenthes* diversity, being the exclusive habitat to endemic species of *N. mirabilis* var. *globosa* and *N. andamana* (Catalano, 2010a, b). The island's *Nepenthes* population is further characterized by an abundance of natural hybrids, presenting a rich morphological diversity. However, the devastating 2004 Tsunami left a mark on the island's natural habitats, disrupting ecosystems and impacting the delicate balance that allows these specialized plants to thrive (Kamthonkiat et al., 2011; Kongapai et al., 2016). Compounding the challenges posed by such catastrophic events are the persistent threats of deforestation and wild plant collecting. These activities not only erode the physical spaces occupied by *Nepenthes* but also disrupt the ecological dynamics crucial for their survival and reproduction. Given the precarious situation faced by *Nepenthes* populations on Ko Kho Khao, there is an urgent need to assess their current status.

Devising effective conservation strategies necessitates understanding the distribution, abundance and community structure of these plants across different environmental gradients. Therefore, the current study aimed to provide insights into the ecological dynamics that have shaped the existence of *Nepenthes* in this unique setting. The results from this research should contribute valuable information toward the conservation efforts for these notable plants, based on the systematic examination of *Nepenthes* spp. and their interactions with the surrounding ecology.

Materials and Methods

Study area

This study was conducted in the secondary forest of Ban Thung Tuek, Ko Kho Khao, Takuapa district, Phangnga province, Thailand (8.9096 N, 98.2756 E). The area is characterized by a mosaic of peat swamp forest and coastal forest lands, providing a unique habitat for diverse plant communities, including *Nepenthes* species and natural hybrids (Fig. 1).

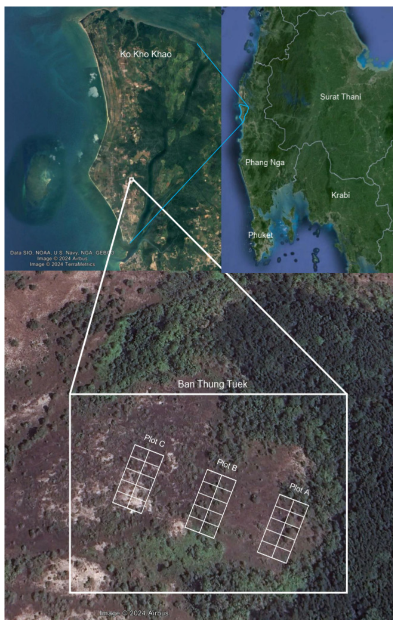

Fig. 1 Modified Google Earth map of Ban Thung Tuek-community forest showing three studied plots located in middle of lower part of island

Plot design

The community structure and distribution of *Nepenthes* were assessed based on establishing three main plots, (each 20 m × 50 m). These plots were strategically placed to capture the gradient from the peat swamp forest to the drier land areas (coastal forest). Plot A was located closest to the peat swamp forest, serving as a reference for forest-like conditions. Plot B was in an intermediate zone, representing a transitional habitat, while Plot C was in a dry land area for comparative purposes. Each main plot was subdivided into 10 subplots (10 m × 10 m) to facilitate detailed community analysis.

Tree community analysis

The collected specimens were examined based on consulting taxonomic literature (Larsen, 1972; Tagawa and Iwatsuki, 1979; Parnell and Chantaranotahi, 2002; Catalano, 2010a, b; Berg et al., 2011; Pteridophyte Phylogeny Group I, 2016; Christenhusz et al., 2017; Handayani and Hadiah, 2019; Nuanlaong et al., 2022) and an online platform (Plants of the World Online, 2024).

Each subplot focused on the tree community, specifically targeting trees with a diameter at breast height over bark (DBH) exceeding 4.5 cm that was recorded to analyze the structure and composition of the tree community across the different habitat gradients.

A 4×4 m^2 area was designated to each subplot to study the sapling and shrub community, characterized by individuals with a DBH less than 4.5 cm that was recorded. to understand the understory dynamics within the study area.

A 1×1 m^2 area was used in the same corner of each subplot dedicated to sapling and shrub analysis to specifically investigate the *Nepenthes* populations. This focused approach facilitated the assessment of the density and age structure of *Nepenthes* within the broader plant community context.

Species with reproductive parts at the time of study were deposited at the Department of Botany, Faculty of Science, Kasetsart University, Bangkok, Thailand.

Data analysis

The Importance Value Index (IVI) was determined, following the methodology outlined by Hakizimana et al. (2016), to quantify the ecological importance of the tree and sapling species. The IVI combines Relative Frequency (RF), Relative Abundance (RA) and Relative Dominance (RD) to provide a comprehensive measure of species importance within the community.

Nepenthes age classification

The distribution patterns of *Nepenthes* were further elucidated based on the categorization of individuals into three age classes: juvenile (non-reproductive vegetative phase; Fig. S4), mature (showing less than five active or showing decayed inflorescences from previous seasons; Fig. S5) and large mature (exhibiting at least five active inflorescences; Fig. S6). This classification provided insights into the reproductive status and potential growth stages of *Nepenthes* within the study area.

Results

Study site habitat characterization

The study site predominantly resembled a grassland ecosystem with sparse tree coverage, transitioning into a dense peat swamp forest at the edges. The soil composition was primarily sandy with notable amounts of black decaying plant matter. Among the tree species, *Melaleuca cajuputi* Maton & Sm. ex R. Powell (Myrtaceae) and *Syzygium antisepticum* (Blume) Merr. & L. M. Perry (Myrtaceae) were the most common, with the former being more predominant. The ground layer varied from nearly open to densely covered by *Dapsilanthus disjunctus* (Mast.) B. G. Briggs & L. A. S. Johnson (Restionaceae), with other grass species predominantly found in the more humid zones, such as Plot A (Fig. S1).

Tree community composition

Three tree species were identified across the plots: *Ficus* sp. (*Moraceae*) and *Melaleuca cajuputi*, and *Syzygium antisepticum* (Myrtaceae). Plot A had the highest tree abundance, dominated by *M. cajuputi*, which covered approximately 70% of the area. In contrast, Plot B contained only a single *M. cajuputi* tree, while Plot C had a sparse distribution of all species that covered only about 30% of the area. The IVI confirmed *M. cajuputi* as the dominant species across all plots (264.48%, 300% and 174.15% for Plots A, B and C, respectively) categorizing the forest as an *M. cajuputi*-dominated secondary forest (Fig. 2, Table S1).

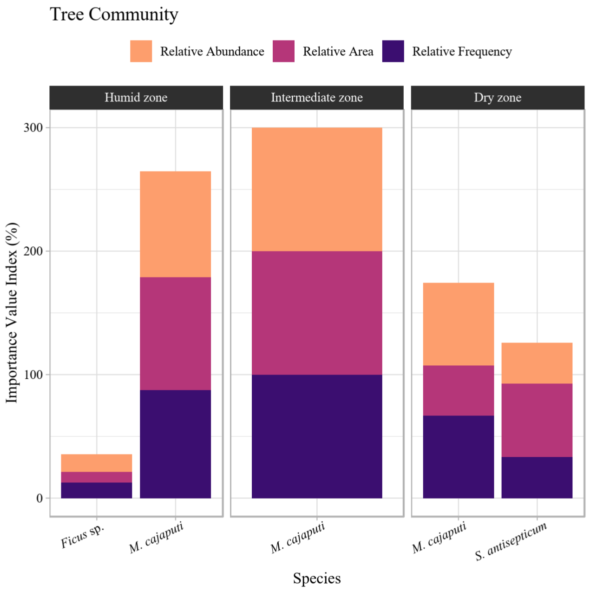

Fig. 2 Comparison of Importance Value Index components for tree species across different environmental zones (Plots A–C from left to right, respectively), showing *Melaleuca cajaputi* as dominant species in all zones

Sapling community dynamics

The sapling layer contained four species: *Melaleuca cajuputi*, *Syzygium antisepticum*, *Syzygium grande* (Wight) Walp. and an unidentified *Syzygium* species. *M. cajuputi* was the most abundant sapling across all plots, with a frequency range of 30–40%. Despite the overall sparse distribution, the sapling community had a slightly higher species diversity than the tree layer. The IVI and relative area coverage consistently highlighted *M. cajuputi* as the leading species within the sapling community (Fig. 3, Table S2).

During the study period, only *M. cajuputi* was vouchered as *N. jantaraprasit 01*. The remainder of the specimens were vegetative parts, with most of them being common species, so they were easily identified. Unfortunately, on a few morphological characters of the *Ficus* sp. and *Syzygium* sp., specimens were obtained, limiting identification to the genus level.

Nepenthes diversity

Two species and one variety were identified:

1. *Nepenthes andamana* M. Catal. – This species is an endemic to Peninsular Thailand in Phangnga province and is distinguished by its thick and narrow leaf blades. The petiole base clasps three-quarters of the stem circumference. The lid is small orbicular to reniform and the peristome typically exhibits a striking white coloration, contributing to its unique visual appeal (Fig. S7).

2. *Nepenthes mirabilis* (Lour.) Druce var. *globosa* M. Catal. – It is found exclusively in Phangnga and Trang provinces, Thailand. This variety is recognized by its very long terrestrial tendrils and markedly globose pitchers, some of which lack the distinctive pitcher hip. Its aerial pitchers have a conical shape with partially deformed wings, showcasing a deviation from typical pitcher morphology in Thai *Nepenthes* (Fig. S8).

In addition, two *Nepenthes* natural hybrids were identified.

1. *Nepenthes mirabilis* (Lour.) Druce × *Nepenthes andamana* M. Catal. – It is a natural hybrid and is characterized by broader, thinner leaves with bases that clasp the stem. The pitchers are vividly colored, ranging from red to magenta, particularly noticeable on the peristome and the underside of the lid. This hybrid demonstrates a blend of traits from its parent species, with a more extensive color palette and modified leaf structure (Fig. S9).

2. *Nepenthes mirabilis* (Lour.) Druce var. *globosa* M. Catal. × *Nepenthes mirabilis* (Lour.) Druce var. *mirabilis* (Lour.) Druce – Another notable hybrid, it exhibits more bloated pitchers (both terrestrially and aerially) than *N. mirabilis* var. *mirabilis*. Unlike *N. mirabilis* var. *mirabilis*, the pitcher wings are more pronounced and extended, though the pitchers do not reach the extreme globosity of *N. mirabilis* var. *globosa.* The lower half of the pitcher shows a marked change in circumference, creating a prominent hip. This hybrid's morphology presents a combination of the traits of both parents, with some unique deviations such as the columnar shapes and the partially deformed wings in aerial pitchers (Fig. S10).

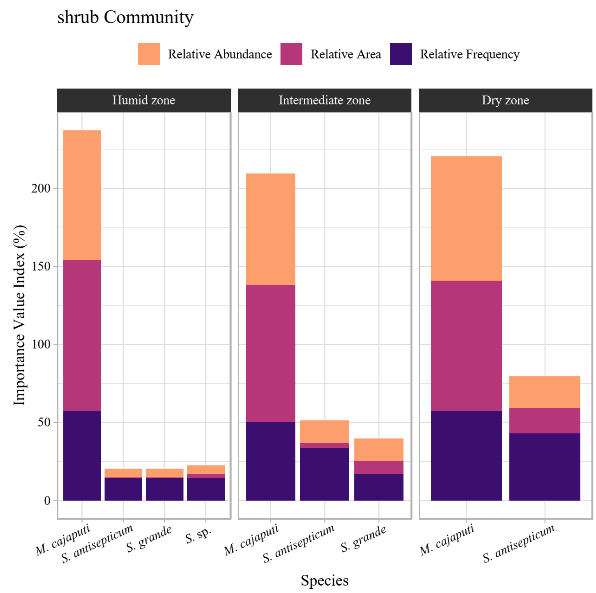

Fig. 3 Comparison of Importance Value Index components for sapling species across different environmental zones (Plots A–C from left to right, respectively), showing *Melaleuca cajaputi* as dominant species in all zones

Nepenthes population distribution

Plot A contained 10 *Nepenthes* individuals, comprising one species, *N. mirabilis* var. *globosa* and two natural hybrids. The juvenile stage of *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis* had the highest abundance (four individuals, 40% of the plot's population), with 20% frequency.

In contrast, Plot B had substantially increased *Nepenthes* abundance (32 individuals), dominated by 29 juveniles of *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis*. Despite the high individual count, the frequency remained at 20%, indicating that while numerically dominant, this hybrid's presence was spatially restricted within the plot. The other hybrid was *N. mirabilis* × *N. andamana* presenting in both the juvenile and mature stages.

Plot C was very different to the other plots, with only six individuals of a single species (*N. andamana*) encompassing all developmental stages. The total frequency of all stages was 40%, indicating a well-established, albeit small, population spanning multiple life stages, suggesting stable environmental conditions conducive to the long-term survival of *N. andamana*.

The natural hybrid *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis* was the most abundant, accounting for 60.4% of all individuals and being found exclusively in Plots A and B. Only *N. andamana* was present in Plot C, representing the sole *Nepenthes* species found in that plot. The age distribution indicated that, except for *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis*, all species exhibited all developmental stages (Fig. 4, Table S3).

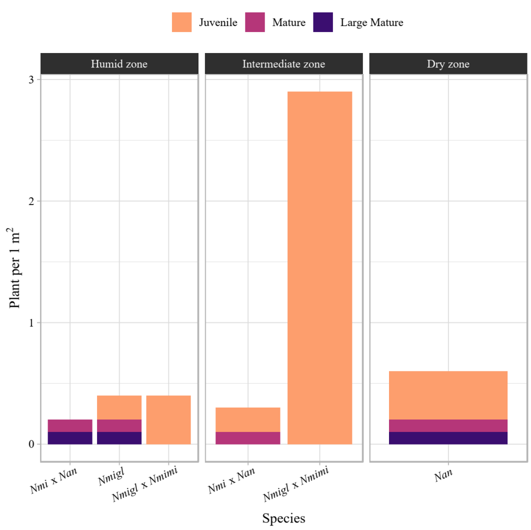

Fig. 4 Comparison of *Nepenthes* individuals and their growing stages across different environmental zones (Plots A–C from left to right, respectively), where Nmi × Nan = *N. mirabilis* × *N. andamana* , Nmigl = *N. mirabilis* var. *globosa*, Nmigl × Nmimi = the natural hybrid *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis* and Nan = *N. andamana*, with *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis* having highest number of individuals (mainly in plot B), however, it was the only species not developing all growing stages

Discussion

Ecological dynamics and hybridization in Nepenthes populations

The results from the current study provided major insights into the ecological dynamics of the *Melaleuca cajuputi*-dominated secondary forests on Ban Thung Tuek and Ko Kho Khao, alongside the adaptive strategies of *Nepenthes*. The observed variations in habitat across the three plots highlighted the intricate relationship between soil moisture, humidity levels and plant community composition, underscoring the diversity of shrub and tree species that characterize these environments.

Nepenthes natural hybrids, which are of considerable interest among scientists and plant collectors, display a morphological mixture of their parent species' characteristics (Cheek and Jebb, 2001; Yulita and Mansur, 2012; Scharmann et al., 2021; Victoriano, 2021). These hybrids can display striking pitcher colors that are influenced by the parental role of each species in reproduction, according to DNA marker analysis (Yulita and Mansur, 2012). Furthermore, genetic studies have shown that introgression and hybridization are pivotal in the *Nepenthes* speciation because most phylogenetic clades within *Nepenthes* exhibit DNA admixture from other clades, complicating the understanding of *Nepenthes* phylogeny within a traditional bifurcated phylogenetic tree (Scharmann et al., 2021).

However, many hybrid populations do not reach the abundance levels of their parent species, despite the parents having similar flowering periods. This phenomenon could be linked to the complexities of hybrid fertility and viability. Even artificial cross-pollination among these species typically results in low seed yields, highlighting potential reproductive barriers and the selective pressures influencing hybrid survival (Victoriano, 2021).

Adaptive strategies of Nepenthes across habitat gradients

Two species, one variety, and two natural hybrids were identified. Although *Nepenthes mirabilis* var. *mirabilis* was absent in the current study areas, its widespread distribution was observed along the margins of peat swamp forests and in secondary forests dominated by *Melaleuca cajuputi*. This could have been responsible for the occurrence of its natural hybrids.

The distinct habitat characteristics of Plot A, with its high humidity and soil moisture, have fostered a unique microenvironment for species requiring damp conditions, as evidenced by the abundant fern diversity and substantial decayed plant matter in the soil. Similarly, the prevalence of *N. mirabilis* var. *mirabilis* along the edge of the peat swamp forest, with its presence declining deeper into the jungle, suggested its preference for highly humid environments (Cheek and Jebb, 2001). This species' distribution pattern highlighted the nuanced habitat preferences within the genus *Nepenthes* and demonstrated the importance of microhabitat variability in shaping plant community structures.

In contrast, Plot C's open land and sandy soil, characterized by minimal shading and the prevalence of drought-tolerant species, such as *Dapsilanthus disjunctus*, highlighted the adaptive resilience of the flora in response to drier conditions (Fig. S2). The presence and distribution of *Nepenthes* species and natural hybrids, particularly *N. andamana* and *N. mirabilis* var. *globosa*, illustrated the critical role of ecological tolerance in species survival and distribution. The adaptation of *N. andamana* to sandy, heat-prone environments, evidenced by individuals with fire-burnt leaves, suggested a notable resilience and a potential mechanism for regeneration, which is classified in the *Nepenthes* section Pyrophytae (fire tolerance with rootstock *Nepenthes*), according to Nuanlaong et al. (2022). This adaptability, coupled with the lack of competition from other *Nepenthes*, may explain the successful establishment of *N. andamana* across all growth stages within its niche.

Notably, the hybrid *N. mirabilis* × *N. andamana* demonstrated a broader ecological tolerance, thriving in both humid and semi-arid zones than its parents which might have soil niche preferences (Clarke and Moran, 2016). The adaptability of the hybrid may indicate a promising future for this hybrid in the study area, potentially influencing the composition and dynamics of the local *Nepenthes* population.

The abundance of *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis* hybrids, despite the limited presence of one parent species, suggested several underlying factors, including the possibility of cross-species fertilization due to the absence of *N. mirabilis* var. *globosa* individuals, non-species-specific pollinators and the external introduction of hybrid seeds. This scenario highlighted the complex interplay of ecological and evolutionary processes driving hybridization and its potential consequences for species diversity.

The potential for genetic introgression between the hybrids and *N. mirabilis* var. *globosa* poses a major concern for the conservation of pure species, particularly in areas where hybrids are more abundant. The predominance of hybrid pollen could lead to a decline in *N. mirabilis* var. *globosa*, altering the genetic landscape and potentially impacting the ecosystem's overall diversity and resilience.

Comparative analysis of Nepenthes populations across diverse habitats

Considering all the studied plots, there was a strikingly high abundance of *Nepenthes* species and natural hybrids, with population numbers in the range 2,000–11,000 individuals/ha (IPH), being notably higher based on the data from various other *Nepenthes* habitats. For example, comparatively, the low elevation peat swamp forests in South Borneo support a relatively modest *Nepenthes* population density, with only 84–232 IPH (Mansur, 2010). This contrast becomes even more pronounced in the high elevation regions of Mount Talang, West Sumatra, where the population densities are lower still, in the range 22–400 IPH (Mansur et al., 2024). In contrast, the Kaingaran Trail of Mount Trus Madi, Sabah, Borneo, has an extraordinarily wide range of densities in the range 100–19,400 IPH (Damit et al., 2017). These numbers suggests a high variability in habitat suitability within a single geographical region, possibly influenced by factors such as microclimatic conditions, soil fertility or interspecific competition, highlighting the adaptability of *Nepenthes* across different environmental gradients.

The notably abundance of the hybrid *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis*, at 11,000 IPH, in the current study area paralleled the dense populations of *N. tentaculata* in the upper montane forests in the range 11,400–19,400 IPH (Damit et al., 2017). Despite the differences in forest types and existing *Nepenthes* diversity, the high population densities in the current study suggested that this *Nepenthes* population could robustly colonize and establish themselves in disturbed forest environments. This capability indicates a high ecological resilience and adaptability, particularly in responding to disturbed or altered habitats. Such resilience may be driven by specific adaptive traits, such as competitive root systems, efficient nutrient uptake, or favorable reproductive strategies, that allow these plants to thrive in a disturbed environment (Adam et al., 1992; Clarke and Moran, 2016).

Future directions

Given the ecological importance and potential threats identified in the current study, future research should focus on long-term monitoring of *Nepenthes* population dynamics, particularly the impacts of hybridization and genetic introgression on species diversity. Additionally, investigating the ecological impacts of human activities on these unique plant communities will be crucial for developing effective conservation strategies. Exploring the physiological and genetic mechanisms underlying the adaptive resilience of *Nepenthes* in under varying environmental conditions could further enhance understanding of plant adaptation and survival strategies in secondary forests.

In addition, the current findings have raised concerns about the impacts of human activities, such as deforestation and wild plant poaching, on the distribution and survival of *Nepenthes* species and natural hybrids. The abundance of *N. mirabilis* var. *globosa* × *N. mirabilis* var. *mirabilis* hybrids suggests a high germination rate but also shows the potential vulnerability of these hybrids to drought and anthropogenic disturbances.

Consequently, the data obtained in the current study should support the development of targeted conservation strategies to protect species and manage hybrid populations, thereby preserving genetic diversity and ecological balance. By examining the adaptive strategies of *Nepenthes* in response to varying environmental conditions, the research enhances knowledge about plant resilience and adaptation mechanisms in secondary forests.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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