Review

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Resilience and Adaptation: Plant Ecology in Indonesia's Geothermal Environments

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Abstract

Geothermal ecosystems are defined by extreme environmental conditions, such as elevated temperatures, high concentrations of toxic chemicals, and fluctuations in abiotic stressors, which shape plant survival and adaptation. These unique ecosystems, found across various geothermal regions globally, support specialized plant communities that have developed distinctive morphological, physiological, and ecological adaptations. Indonesia, located on the Pacific Ring of Fire, is one of the world's richest geothermal nations, offering an important yet underexplored context for studying vegetation in geothermal zones. This review examines the environmental conditions of geothermal ecosystems, the adaptive strategies of vegetation, and patterns of plant diversity within Indonesian geothermal fields. It also explores ecological succession, community dynamics, and the potential use of geothermal vegetation as environmental indicators for biomonitoring. Despite growing interest, significant research gaps remain, particularly in long-term monitoring and the integration of molecular-level studies. Addressing these gaps is essential for enhancing scientific understanding and informing conservation and sustainable geothermal energy development in tropical regions. This review highlights the ecological significance of geothermal vegetation and underscores the need for research to support both biodiversity preservation and responsible energy exploitation.

1. Introduction

Geothermal environments worldwide, such as those in Iceland, New Zealand, and the United States, are increasingly acknowledged as distinctive ecosystems shaped by extreme abiotic conditions [1]. These areas are characterized by elevated soil temperatures, high sulfur and heavy metals levels, and a broad spectrum of pH values [2, 3]. Such environmental challenges make geothermal zones valuable natural laboratories for exploring plant adaptation, resilience, and ecological responses to thermal and chemical stress [4–6].

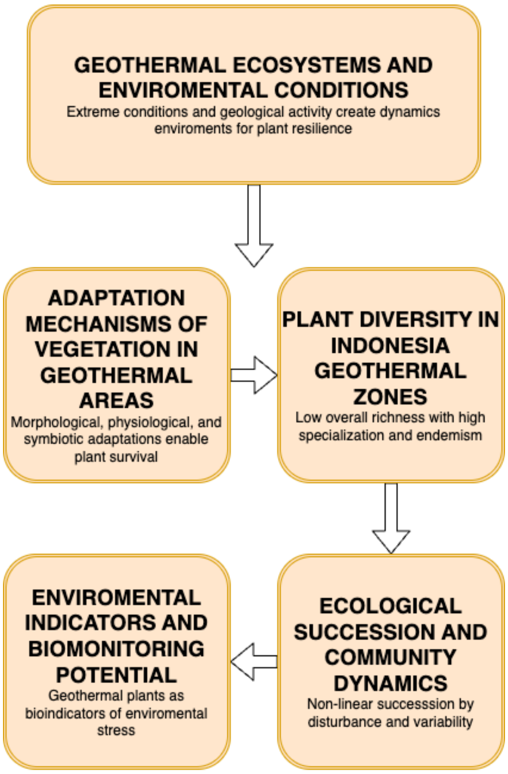

Figure 1. Conceptual model of geothermal ecosystem dynamics and plant adaptation.

Situated along the Pacific Ring of Fire, Indonesia holds more than 40 percent of the world's geothermal energy reserves, positioning it as a global leader in geothermal potential [7–9]. Indonesia has intensified its investment in geothermal energy development in light of rising energy demands and international efforts to reduce carbon emissions [10–13]. As this expansion continues, there is a growing need to understand the ecological dynamics within these geothermal landscapes, particularly concerning native plant communities directly influenced by geothermal activity [14, 15]. Despite the growing interest in geothermal energy, ecological studies of plant life in these areas remain scarce, particularly in comparison to research conducted in temperate geothermal ecosystems.

Much of Indonesia's geothermal activity occurs in volcanic regions, notably Java, Sumatra, and Sulawesi. These areas exhibit elevated ground temperatures, frequent gas emissions, and soils enriched with minerals and metals, leading to the emergence of distinct microhabitats. The complex interactions between these environmental variables and plant life influence community structure and biodiversity patterns, although many of these ecological mechanisms remain poorly understood [16–19]. Research on vegetation in geothermal environments is essential due to the substantial physiological and ecological stress these areas impose on plant communities. Abiotic stressors such as high temperatures, acidic conditions, and metal toxicity serve as strong selective forces that shape plant traits, limit species distributions, and affect community dynamics. Gaining insight into how plants respond and adapt to such stressors contributes to broader ecological theory and provides practical guidance for conservation and land-use planning in geothermal regions [20–22].

This review aims to fill specific gaps in our understanding of tropical geothermal ecosystems by examining the adaptive strategies of plants in these extreme environments, focusing on the lack of long-term ecological data, the need for molecular-level studies, and the absence of detailed comparisons with temperate systems. This review will clarify the scope by focusing on the geothermal ecosystems of Java, Sumatra, and Sulawesi, which feature diverse environments such as acidic geothermal wetlands in Sumatra and high-altitude geothermal fields in Java and Sulawesi, each with unique plant communities. It will provide an overview of these regions' plant community dynamics, biodiversity, and ecological succession. Additionally, the review will incorporate theoretical frameworks linking plant adaptations in geothermal areas to broader ecological and evolutionary theories. Concepts like niche differentiation, adaptation to abiotic stress, and ecological resilience will be discussed, offering insights for conservation and land-use planning in geothermal zones. A conceptual overview of the ecological processes discussed in this review is presented in Figure 1. It outlines the cascading interactions between geothermal environmental conditions, plant adaptation mechanisms, species diversity, community dynamics, and the role of geothermal vegetation as bioindicators.

While much of the existing research on geothermal plant ecology focuses on temperate regions, this review highlights the need for further investigations into tropical geothermal ecosystems, particularly in Indonesia. Understanding how tropical plants adapt to geothermal stressors is essential for developing effective biomonitoring tools and conservation strategies tailored to tropical settings. By filling these knowledge gaps, this review will contribute to advancing global understanding of geothermal ecology and its relevance to sustainable development goals, particularly in the context of Indonesia's growing geothermal energy sector.

2. Geothermal Ecosystems and Environmental Conditions

Geothermal ecosystems in Indonesia are defined by highly distinctive environmental conditions that sharply contrast with those of adjacent landscapes. These areas typically experience elevated soil and air temperatures, substantial concentrations of toxic elements such as sulfur, arsenic, and mercury, and significant fluctuations in pH [3, 23–25]. These stressors arise from continuous subsurface geothermal activity, which releases hot gases and mineral-rich fluids that fundamentally alter the soil's chemical and physical properties [26, 27]. As a result, many geothermal sites present hostile conditions unsuitable for most plant species. In tropical regions like Indonesia, geothermal sites experience additional complexity due to seasonal variations, primarily driven by the wet and dry seasons. These seasonal shifts can profoundly affect the environmental conditions of geothermal ecosystems, influencing abiotic and biotic factors in ways that are not commonly observed in temperate geothermal zones.

Despite these inhospitable circumstances, certain plant species with specialized adaptations are able to establish and persist. These adaptations include thermal resistance, physiological mechanisms to tolerate heavy metal toxicity, and water-use efficiency under conditions of limited availability. The extreme selection pressures in these environments often lead to communities with low species richness but high levels of functional specialization [20, 28]. In many geothermal areas, vegetation is dominated by a small number of stress-tolerant species, making these systems ideal for studying ecological resilience and the evolution of niche-specific traits [29–31].

While geothermal ecosystems are generally harsh, they are not environmentally uniform. Many sites contain diverse microhabitats formed by features such as hot springs, fumaroles, and steaming vents. These features generate fine-scale gradients in temperature, moisture, and soil chemistry. Such microgradients often vary considerably over short distances, resulting in a patchwork of vegetation types within a single geothermal landscape. This spatial heterogeneity promotes niche diversity and provides a valuable framework for examining plant responses to subtle environmental variation [32–34].

Geothermal systems are dynamic environments, influenced by ongoing geological processes like pressure fluctuations, seismic activity, and hydrothermal flow, which can lead to rapid environmental changes. These abrupt environmental changes can significantly disrupt plant communities, leading to altered species composition, increased mortality, or shifts in successional trajectories. For this reason, geothermal landscapes offer a natural platform for investigating how vegetation responds to both immediate disturbances and long-term ecological change [15, 35, 36].

Understanding plant life in geothermal areas, especially in the face of such extreme and fluctuating conditions, provides important insights into the mechanisms of adaptation and survival. These ecosystems illustrate how abiotic stressors shape ecological processes, constrain biodiversity, and influence evolutionary outcomes [5, 37]. Research on these systems enhances ecological theory and supports conservation and management in rapidly changing environments.

3. Adaptation Mechanisms of Vegetation in Geothermal Areas

Plants inhabiting geothermal environments, including those in Indonesia, exhibit a range of adaptations that enable them to withstand extreme and fluctuating environmental conditions. A common morphological adaptation is the development of thick or succulent leaves that store water and minimize moisture loss—an essential trait in the dry, thermally stressed soils typically found near geothermal features. In addition, some species form specialized root systems that either penetrate below heated surface layers to access cooler, moister soil strata or avoid soil zones with high concentrations of toxic elements. In Indonesian geothermal wetlands, species like certain ferns and sedges show these adaptive root systems, allowing them to thrive in areas with fluctuating temperatures and toxic soils [38, 39].

The surfaces of leaves may also be covered with fine hairs, or trichomes, which help reduce water loss and protect plant tissues from intense solar radiation and thermal stress. These structural features are essential for plant survival in geothermal conditions. Beyond morphological traits, many geothermal-adapted plants rely on physiological mechanisms to cope with environmental stress. Heat tolerance is particularly crucial, with some species able to maintain metabolic activity at temperatures that would inhibit or damage most other plants. This heat tolerance is a key adaptation in species that thrive in soils that can reach extreme temperatures [40–42].

Geothermal soils often contain elevated levels of heavy metals such as arsenic, mercury, and boron, which can pose toxic challenges. Certain plant species have evolved strategies to cope with these elements, including sequestration in cell vacuoles and complexation with organic compounds to reduce their bioavailability and toxicity. Water stress presents another significant constraint, as soils may appear moist due to steam presence but frequently lack accessible water. The combination of physiological and morphological adaptations allows plants to persist and function in these demanding environments [43–47].

Symbiotic relationships further enhance plant resilience in geothermal habitats. Mycorrhizal fungi, which form close associations with plant roots, contribute to improved nutrient and water uptake, particularly in nutrient-poor or chemically imbalanced soils. These fungi may also protect toxic metals by facilitating detoxification processes. Other beneficial microbes, such as nitrogen-fixing bacteria, can also support plant growth by enhancing soil fertility. These microbial associations are often critical for plant establishment and survival in geothermal settings [48–52].

Empirical studies from various geothermal sites highlight numerous examples of these adaptive strategies. In Indonesia, *Dicranopteris linearis* is commonly found in hot, acidic soils, demonstrating both thermal tolerance and acid resistance. Several sedge and fern species also flourish in sulfur-enriched geothermal wetlands. In New Zealand, *Pteridium esculentum* frequently occurs near steam vents, supported by a deep-root system and symbiotic microbial partners. Such cases illustrate how geothermal ecosystems foster the evolution of unique and highly specialized plant traits, many of which are seldom encountered in more stable environments [53–57].

4. Plant Diversity in Indonesia Geothermal Zones

The adaptive strategies previously discussed are central to understanding the patterns of plant diversity within Indonesia's geothermal ecosystems. Geothermal zones often support specialized plant communities adapted to survive extreme environmental pressures such as elevated temperatures and toxic soils. While species richness may be lower, these ecosystems foster unique biodiversity. In a country renowned for its exceptional biodiversity, geothermal regions represent critical habitats for rare, endemic, and stress-tolerant species [58–60].

Comparative studies of geothermal sites across Indonesia reveal significant differences in plant community composition, shaped by local environmental conditions and varying degrees of anthropogenic influence. In Java, geothermal fields such as Kawah Kamojang and the Dieng Plateau are often dominated by low-stature vegetation, including heat-tolerant grasses, pioneer ferns, and dwarf shrubs [61–64]. In contrast, geothermal wetlands in Sumatra support more diverse communities of sedges, aquatic species, and thermophilic mosses and liverworts, which flourish in moisture-rich, mineral-laden soils. These differences are largely driven by variations in soil chemistry, water availability, and disturbance levels [65–68].

Anthropogenic disturbances, particularly those linked to geothermal energy infrastructure, have significant effects on plant communities and biodiversity within geothermal zones. These impacts can be categorized into direct and indirect effects. Direct impacts include habitat destruction due to drilling, land clearance for geothermal plants, and the construction of access roads and facilities. Indirect impacts arise from the increased human presence, which leads to disturbances such as soil compaction, pollution, and increased human activity that affect local flora and fauna. As these disturbances progress, generalist or invasive species often proliferate, diminishing the ecological distinctiveness of these systems [69, 70].

In addition to human influence, elevation and geothermal intensity are significant determinants of plant community composition. High-altitude geothermal areas, such as those in the mountains of Sulawesi, support montane and subalpine species that are adapted to low temperatures and nutrient-deficient soils, often exhibiting combined tolerances to both thermal and environmental stresses. Conversely, geothermal sites at lower elevations, such as those near coastal fault zones or volcanic bases, are predominantly inhabited by species that can withstand high heat, frequent disturbances, and variable moisture conditions. The intensity of geothermal activity, as indicated by factors such as soil temperature, sulfur concentrations, and steam emissions, further constrains species diversity,

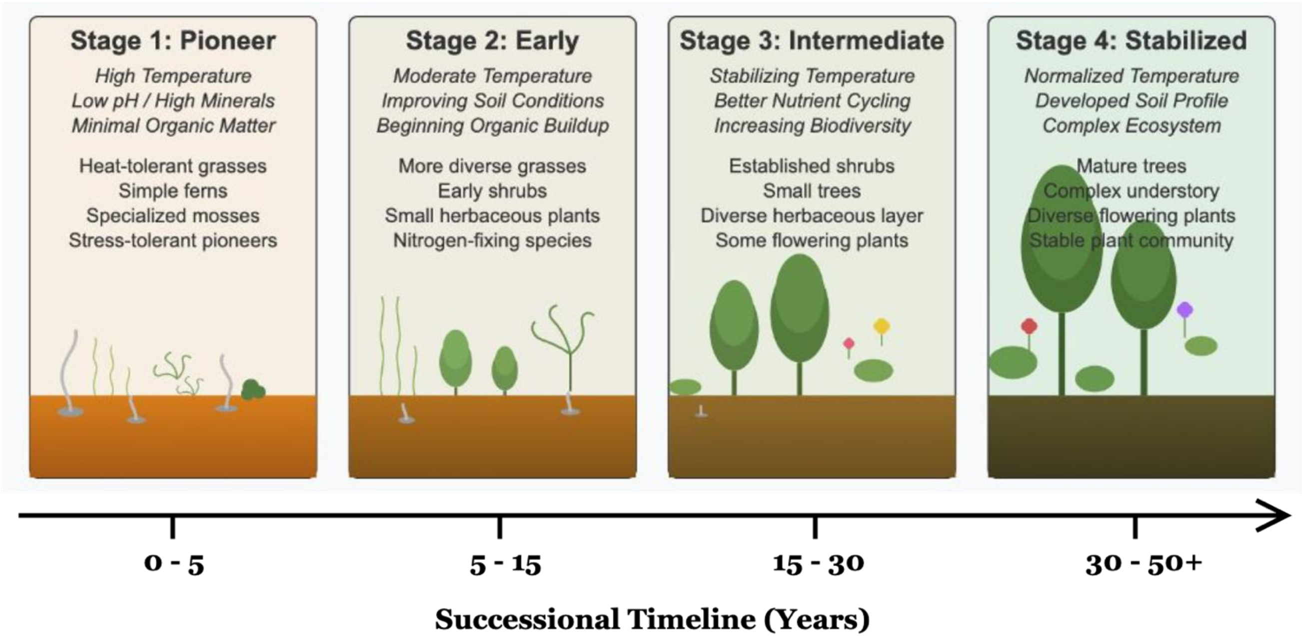

Figure 2. Successional stages in geothermal plant communities.

particularly in regions proximate to active vents and hot springs [71–76].

Several plant species identified in these geothermal areas are either endemic or exhibit highly restricted distributions. Field observations have documented ferns, mosses, and liverworts confined to specific microhabitats, such as the margins of hot springs, acidic wetlands, and fumaroles. These taxa function as ecological indicators, reflecting unique environmental conditions, and offer valuable models for exploring adaptation to extreme habitats. Their presence underscores the ecological significance of geothermal zones as sites of evolutionary innovation and resilience [77–79].

Safeguarding plant diversity within geothermal environments is essential for maintaining ecosystem integrity and preserving the genetic and adaptive resources that contribute to Indonesia's natural heritage. As geothermal energy development advances, it is imperative to incorporate biodiversity considerations into land-use planning, ecological monitoring, and conservation strategies. Such an approach will help ensure the protection of these rare and ecologically important plant communities for future scientific research and the benefit of future generations.

5. Ecological Succession and Community Dynamics in Geothermal Zones

Geothermal plant communities undergo succession driven by natural disturbances such as fumaroles and temperature fluctuations. Early pioneers, like heat-tolerant grasses, stabilize soil and initiate nutrient cycles. As conditions improve, less stress-tolerant but more competitive species gradually establish. Unlike typical ecosystems, geothermal succession is non-linear, with recurring disturbances creating a patchwork of communities at different developmental stages [80].

This ecological heterogeneity is further amplified by the inherently variable nature of geothermal habitats. Soil temperature, moisture availability, gas emissions, and mineral concentrations can differ significantly across short distances, creating a multitude of microhabitats. These localized environmental conditions support a diversity of plant assemblages and contribute to high species turnover across the landscape. Such spatial variability enhances ecosystem resilience by supporting a broad array of species with distinct ecological strategies [81, 82].

Both natural and human disturbances influence geothermal communities. Natural events like landslides, eruptions, and seismic activity alter habitats and restart succession cycles. Human activities such as drilling, vegetation clearing, and infrastructure development can accelerate or disrupt these processes. These interventions may facilitate invasive species spread or alter soil properties, hindering native vegetation recovery and potentially causing long-term ecological damage [83, 84].

A comprehensive understanding of how plant communities respond to disturbance and succession in geothermal environments is vital for effective conservation, restoration, and ecological monitoring. As geothermal energy development expands, particularly in biodiverse tropical regions such as Indonesia, there is an urgent need to align energy production goals with ecological stewardship. Recognizing the interplay between natural geothermal dynamics and human-induced change will be critical for ensuring the sustainable management of these unique and ecologically valuable systems. Figure 2 shows the four stages of ecological succession in geothermal environments. In Stage 1 (0-5 years), heat-tolerant plants like grasses and ferns thrive in harsh conditions. Stage 2 (5-15 years) sees improving soil conditions and the growth of grasses, shrubs, and nitrogen-fixing plants. Stage 3 (15-30 years) features established shrubs, small trees, and increased biodiversity. In Stage 4 (30-50+ years), the ecosystem matures with stable plant communities and fully developed soils.

6. Environmental Indicators and Biomonitoring Potential of Geothermal Vegetation

Geothermal plants are valuable bioindicators, reflecting shifts in environmental conditions and providing an effective method for monitoring ecosystem health. Many plant species in these habitats are highly responsive to extreme conditions such as elevated temperatures, toxic substrates, and fluctuating moisture levels. Their sensitivity makes them valuable indicators of environmental change, positioning geothermal vegetation as a promising natural tool for biomonitoring applications [85, 86].

Specific geothermal conditions, such as high sulfur content, acidic soils, or heavy metal concentrations, are closely associated with particular plant species. Mosses, ferns, and sedges commonly occupy these specialized niches and serve as bioindicators, their presence or absence reflecting shifts in geothermal activity, contamination levels, or environmental disturbance. The reappearance of pioneer species can also indicate early stages of ecosystem recovery. These plant indicators are particularly valuable in remote geothermal locations where conventional monitoring methods are difficult to implement [87–89]. Additionally, certain geothermal plants function as environmental regulators by absorbing toxic elements, including arsenic, mercury, and cadmium. These hyperaccumulating species enable scientists to monitor pollution patterns through analysis of metal concentrations in plant tissues, providing a practical alternative to traditional soil or gas monitoring in areas with limited accessibility [90–93].

To select bioindicator species for Indonesian geothermal ecosystems, focus on plants adapted to sulfur-rich soils, acidic conditions, and fluctuating moisture. These species can be identified through field surveys, historical data, and existing research, with insights from indigenous knowledge offering additional value. Plant monitoring systems face challenges from variable species responses to environmental stressors and incomplete knowledge of tolerance thresholds, especially in biodiverse regions like Indonesia. External factors such as elevation and climate further complicate identifying geothermal impacts. Incorporating traditional ecological knowledge in monitoring protocols would be beneficial, as local communities can offer historical perspectives on plant responses to geothermal conditions, helping to refine species selection and monitoring practices. Improving effectiveness requires standardized methods, deeper ecological knowledge, comprehensive bioindicator databases, and integration into geothermal management frameworks to enable early stress detection and guide restoration efforts [94–98]. Practical monitoring protocols in Indonesian contexts could include long-term vegetation surveys, remote sensing technologies, and regular sampling of hyperaccumulating species to monitor heavy metal concentrations. These methods can be standardized across different geothermal sites, allowing consistent and reliable data collection to track environmental changes over time.

Geothermal vegetation represents an effective, cost-efficient, and ecologically meaningful approach for monitoring environmental dynamics in volcanic and geothermal regions. Long-term ecological studies, interdisciplinary collaboration, and increased investment in biodiversity research are necessary to fully harness this potential, particularly in tropical areas such as Indonesia. These efforts will strengthen our ability to use vegetation as a tool for sustainable environmental management in geothermal landscapes.

7. Research Gaps and Future Directions

Although interest in geothermal vegetation is increasing, substantial gaps in knowledge persist, particularly in tropical regions such as Indonesia. While research on geothermal systems' physical and chemical properties is extensive [19], further ecological and botanical dynamics studies are needed to understand plant adaptations in these environments fully. Moreover, most investigations are short-term and localized, constraining insights into long-term dynamics and plant community responses to both geothermal fluctuations and broader environmental changes like climate variability. A key gap in geothermal plant research lies in understanding their molecular and physiological responses. Although structural traits like thick leaves and deep roots are well known, the genetic and biochemical pathways behind their tolerance to heat, acidity, and heavy metals are still largely unexplored. Advancing this knowledge could inform strategies for climate resilience, soil rehabilitation, and agriculture in extreme conditions [99–101].

Plant diversity in geothermal areas outside protected conservation zones often suffers from inadequate documentation. Sites targeted for energy development typically undergo technical feasibility assessments without comprehensive biodiversity surveys, putting potentially endemic or undiscovered plant species at risk of extinction before scientific recording. Expanding botanical inventories, particularly in underexplored regions like eastern Indonesia, is crucial for developing a complete understanding of biodiversity in geothermal ecosystems. The development of vegetation-based biomonitoring tools remains in its early stages. Although several plant species demonstrate potential as bioindicators due to their sensitivity to geothermal conditions, the field lacks standardized monitoring protocols and region-specific guidelines [102, 103]. Future efforts should focus on advancing these tools through enhanced interdisciplinary collaboration between botanists, ecologists, geologists, and engineers to create scalable, practical systems that balance environmental conservation with geothermal infrastructure needs.

Bridging these knowledge gaps calls for long-term, coordinated research integrating ecological understanding with geothermal planning. As Indonesia continues expanding its geothermal energy sector, there is a pressing challenge and a strategic opportunity to align biodiversity conservation efforts with sustainable development objectives. Investing in field-based ecological research and embedding this knowledge into policy and planning frameworks will make it possible to safeguard the unique vegetation found in geothermal environments while supporting national energy goals.

8. Conclusion

Indonesian geothermal ecosystems, shaped by extreme thermal, chemical, and geological conditions, present a unique ecological landscape where specialized plant communities thrive. These environments, though harsh, support resilient vegetation that exhibits a wide range of morphological, physiological, and symbiotic adaptations to survive and persist. While biodiversity in these regions is generally lower compared to adjacent habitats, the species found are often highly specialized and endemic and serve as critical indicators of ecological conditions.

Natural processes, such as ecological succession, and anthropogenic influences, including geothermal energy development, govern plant communities' dynamics in geothermal zones. These processes contribute to a mosaic of plant assemblages at different successional stages, enhancing ecosystem heterogeneity and resilience.

Despite their ecological significance, geothermal plant communities in Indonesia remain understudied, especially in terms of long-term ecological monitoring, genetic and physiological mechanisms of adaptation, and comprehensive biodiversity inventories. The potential of geothermal vegetation as a natural tool for biomonitoring underscores the importance of developing standardized, interdisciplinary approaches for conservation and management.

As Indonesia expands its geothermal energy infrastructure, it is imperative to integrate ecological knowledge into planning and policy. Protecting and understanding the unique flora of geothermal regions is essential for biodiversity conservation and informing sustainable development strategies in the face of increasing environmental and climatic challenges.

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