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Vegetation analysis and culturable endophytic fungal associations in agarwood from different forest types in Marumana, Papua, Indonesia

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Abstract. *Salosa YY, Kuswinanti T, Raya I, Martanto EA. 2025. Vegetation analysis and culturable endophytic fungal associations in agarwood from different forest types in Marumana, Papua, Indonesia. Biodiversitas 26: 4874-4885. Aquilaria filaria* is a tree species valued for producing agarwood, a resinous heartwood formed in response to pathogenic fungal infections. Despite its ecological and economic significance, detailed studies on the habitat ecology of *A. filaria* in Papua remain scarce. This study investigated variation in vegetation stands containing *A. filaria* and identified pathogenic fungi associated with its infection. Fieldwork was conducted from January to March 2023 across 40 plots (50 × 50 m) established along two 1-km transects designed to capture gradients of human disturbance. Vegetation was surveyed using the Braun-Blanquet method and analyzed by TWINSPAN classification. Fungal isolation from infected stems (50% of representative *A. filaria* trees per plot) employed a modified direct-plating method on half-strength potato dextrose agar, with taxonomic identification based on morphological keys. A total of 97 plant species and 198 *A. filaria* individuals were recorded, yielding 600 wood fragments across three disturbance gradients. Dominant families included Euphorbiaceae and Moraceae. Pathogenicity tests revealed four major fungal genera: *Trichoderma*, *Fusarium*, *Penicillium*, and *Aspergillus niger*. Colonization rates increased from 70% in undisturbed to 90% in heavily disturbed sites, while fungal load, expressed as colony counts per fragment, rose from 1.76 to 2.96 across the same gradient. Diversity, measured by the Shannon-Wiener Index, declined from 1.08 in undisturbed to 0.68 and 0.67 in moderately and highly disturbed sites, respectively. These findings provide new insights into how forest disturbance reshapes vegetation structure and fungal assemblages in *A. filaria* habitats, highlighting the need to preserve forest complexity while balancing ecological resilience with economic goals.

Keywords: *Aquilaria filaria*, identification, pathogenic fungi, vegetation composition

INTRODUCTION

Papua in Indonesia is widely recognized for its exceptional biodiversity, with new species continually being documented (Barri et al. 2019). Its complex geological history and diverse topography have shaped a wide range of ecological niches, significantly contributing to the region's high biological richness (Sosanika et al. 2022). Forest structure and species distribution vary considerably across forest types, influenced by ecological factors such as soil, climate, and disturbance regimes (Katovai et al. 2015). High tree species diversity has been reported in several subdistricts, particularly within families such as Meliaceae and Myrtaceae (Robiansyah 2018). However, this rich biodiversity is increasingly threatened by deforestation. Effective conservation efforts must therefore integrate ecological characteristics and topographical variation (Katovai et al. 2015; UNDP 2017). Despite its ecological importance, much of Papua remains understudied and ecologically undocumented (Katovai et al. 2015; Robiansyah 2018). In particular, vegetation-fungus interactions, which play central role in maintaining forest ecosystem processes, have received little attention. Understanding the ecological dynamics of Papuan forests, especially the links between vegetation composition and microbial communities, is essential for conserving biodiversity and sustaining forest-dependent species.

Within this context, the genus *Aquilaria* is both ecologically and economically important. Notably, *Aquilaria filaria* and *Aquilaria malaccensis* yield agarwood—resinous heartwood prized in traditional medicine, perfumery, and incense (Wu et al. 2017; Ramli et al. 2022; Thi et al. 2024). Its major bioactive constituents, especially sesquiterpene terpenoids, underpin reported sedative, antimicrobial, anti-inflammatory, and antidepressant effects in traditional Chinese medicine (Wang et al. 2021). Rising global demand has driven unsustainable harvesting and habitat loss, causing marked declines in wild *Aquilaria* populations (Tajuddin and Deep 2019). Consequently, all recognized *Aquilaria* species are listed under CITES Appendix II to regulate international trade (Wu et al. 2017). Sustainable management therefore hinges on coupled conservation and cultivation approaches (Thompson et al. 2022). Yet key ecological determinants—host plant associations, soil microbiota, and microclimate—strongly shape *Aquilaria* distribution and health but remain poorly documented in

Papua. Integrating knowledge of fungal pathogen dynamics with vegetation structure is essential to improve agarwood production and bolster forest resilience.

Fungal infection is key to agarwood formation, stimulating resin production through host defense mechanisms, though some fungi can cause decay, depending on virulence and host condition. Fungal genera such as *Fusarium*, *Aspergillus*, *Penicillium*, and *Trichoderma* have been identified in *Aquilaria* species (Subowo 2016; Chhipa and Kaushik 2017). *Fusarium solani* is particularly effective in artificial inoculation trials (Zhang et al. 2022), but success varies by fungal strain and host species (Subowo 2016). Despite these insights, little is known about the natural fungal composition and ecological patterns in *Aquilaria* habitats, especially in relation to forest structure and human disturbance. Studies in Indonesia, including Papua, have identified species like *F. solani*, *F. tricinctum*, *F. moniliforme*, and *F. sambucinum* in association with agarwood formation (Santoso et al. 2010; Destri et al. 2020). Understanding these fungal-*Aquilaria* relationships is essential for refining induction techniques, boosting resilience, and guiding conservation efforts. Joint analyses of vegetation and fungal communities can enhance habitat-based management (Rasool and Mohamed 2016). Furthermore, accurate species identification is required to support both conservation measures and regulatory enforcement (Lee and Mohamed 2016).

Among *Aquilaria* species, *A. filaria* is native to Papua and is particularly vulnerable due to its low population density and germination rate (Destri et al. 2020). Its persistence is further threatened by overexploitation, habitat fragmentation, and limited ecological data. Arbuscular mycorrhizal fungi associated with *Aquilaria* roots have been shown to enhance plant health and may offer opportunities for conservation interventions (Wijayanti and Turjaman 2020). In addition, environmental factors such as rainfall and temperature influence phenological processes, including flowering and fruiting (Borogayary et al. 2018). Thus, a holistic understanding of *Aquilaria*'s ecological requirements, incorporating vegetation structure and microbial interactions, is critical for in situ and ex situ conservation efforts in Papua. However, ecological studies in this region remain scarce, highlighting the need for localized assessments. Targeted and sustained conservation strategies are therefore essential for ensuring the long-term survival of *A. filaria*, given its ecological role and high economic value. This study aimed to assess variation in vegetation stands containing *A. filaria* and to identify the pathogenic fungi associated with infected trees.

MATERIALS AND METHODS

Study area

Fieldwork was conducted from January to March 2023 in the Marumana Forest, Ayamaru, West Papua, Indonesia (Figure 1). The study focused on both primary and selectively logged secondary forests to capture variation in vegetation structure and fungal associations. Preliminary surveys indicated that *Aquilaria filaria* was mainly distributed along the shores of Lake Ayamaru, extending several hundred meters inland, and represents a lowland tropical forest type. Administratively, Marumana Forest is a community forest managed by local customary authorities. Human activities in the area include selective logging, hunting, and non-timber forest product collection, especially agarwood. Vegetation stands containing *A. filaria* and associated fungi were documented.

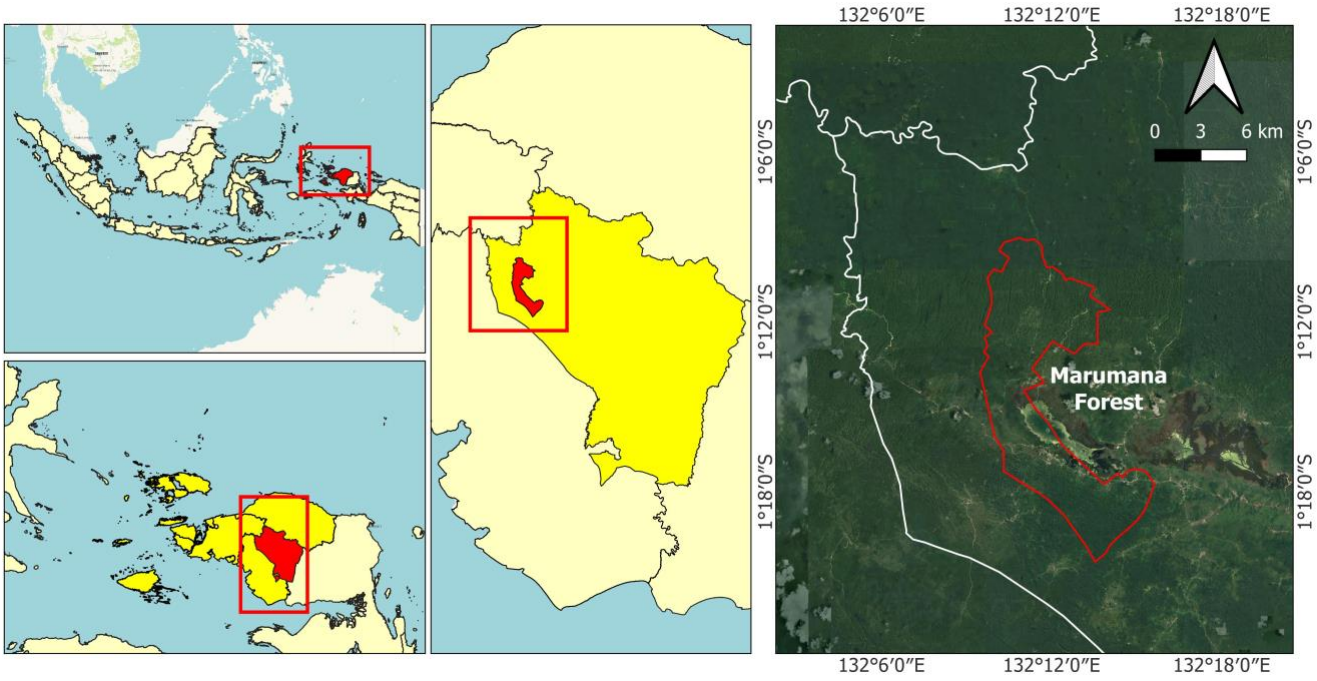


Figure 1. The study site at Marumana Forest, Ayamaru, Papua, Indonesia

Sampling design

Forty sample plots, each measuring 50 m × 50 m, were established systematically along two transects of approximately 1 km each: one in primary forest and the other in selectively logged secondary forest. These transects covered topographical gradients from foot-slopes to hilly slopes (Figure 2.A). Plot placement was determined by topography and accessibility while maintaining spatial independence. Within each plot, four horizontal line transects (3 m × 50 m) were laid out following the Gentry method (Figure 2.B). Along these transects, indicators of anthropogenic disturbance, such as felled trees, deadwood, and resin-harvesting scars, were recorded.

Plots were further subdivided into nested sampling units to capture different vegetation layers. Trees with DBH ≥10 cm were recorded across the entire 50 m × 50 m plot. Saplings (2-9.9 cm DBH) were inventoried within five 10 m × 10 m subplots, and seedlings (<2 cm DBH) within ten 2 m × 2 m quadrats. In addition, qualitative information on *A. filaria* distribution, harvesting practices, and disturbance history was collected through informal consultations and interviews with local inhabitants. To assess vegetation variation more intensively, additional surveys were conducted along two 1-km transects: one in primary forest and one in selectively logged forest. Four sampling sites were established along each transect, consisting of plots measuring 100 m × 8.5 m. These were subdivided into relevés for detailed vegetation assessments, yielding 20 relevés per transect. The distance between adjacent sampling sites ranged from 50 to 70 m, ensuring spatial independence while capturing local variation. Figure 2 illustrates the distribution of plots along the disturbance gradient across both forest types.

Environmental parameters measurement

Soil samples were collected from the upper 0-20 cm layer at five random points within each plot and composited to represent the site condition. Soil pH was measured in a 1:2.5 soil-to-water suspension using a digital pH meter. Soil moisture content was determined gravimetrically by oven-drying fresh soil samples at 105°C until constant weight. Soil organic matter and nitrogen content were analyzed using the Kjeldahl method, while relative air humidity was measured in situ with a digital hygrometer during the sampling period. Soil Cation Exchange Capacity (CEC) was determined using the ammonium acetate method at pH 7, following standard soil analysis procedures.

Vegetation structure and anthropogenic pressure measurements

Vegetation data were collected using the Braun-Blanquet phytosociological method (Westhoff and Maarel 1973), with species cover-abundance estimated according to the modified scale of Barkman et al. (1964). Tree height was measured with a Hagameter, and diameter at breast height (DBH, 1.3 m above ground) was measured using a caliper. Vertical forest structure was documented by constructing profile diagrams based on field measurements of tree height and crown diameter. The abundance of *A. filaria* individuals, including seedlings, was also recorded. To assess disturbance, Gentry transects were employed within each relevé (Figure 2) to quantify deadwood, evidence of logging, and agarwood harvesting. Disturbance levels were classified into three categories based on proximity to settlements and main roads and observable anthropogenic impacts: undisturbed (>3 km) with minimal signs of tree felling, moderately disturbed (1-3 km) with occasional tree removal, and highly disturbed (<1 km) showing frequent logging, tree felling, or other human activities. Each line transect (3 m × 50 m) was evaluated for coarse woody debris volume using the line-intersect method, and harvesting scars were mapped using GPS-based tools.

Taxonomy and plant identification

The nomenclature of tree species, including local and botanical names, followed established references such as New Guinea Vegetation, Flora for Schools in Indonesia, Keanekaragaman Flora Taman Wisata Alam Gunung Meja Papua Barat, and Flora Malesiana (Paijmans 1976; Van Steenis 1989, 2005; Lekitoo et al. 2008). Unidentified specimens were collected and identified at the Herbarium Manokwariense, Universitas Papua, through comparison with reference collections and expert consultation.

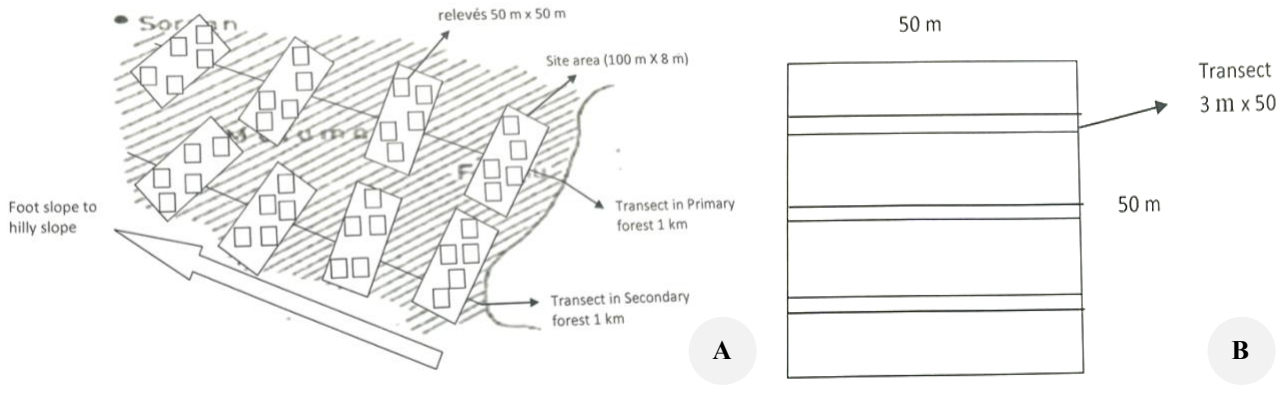


Figure 2. A. Plot selection map, and B. Gentry transects for measuring anthropogenic pressure

Fungal isolation and identification

Fungal isolation and identification were conducted morphologically in the Microbiology Laboratory, Universitas Papua, using a modified direct-plating technique on half-strength potato dextrose agar (½ PDA) following Pitt and Hocking (2022). Wood fragments (0.5 cm × 0.5 cm) were aseptically excised from the main stem at breast height (±1.3 m) of *A. filaria* using a sterilized chisel and knife. Samples were taken from living tissue at shallow depth (<1 cm) to minimize damage, with approximately 50% of representative trees per plot targeted. Each fragment was immediately placed into sterile zip-lock bags, labeled, and transported to the laboratory for fungal isolation. Sampling was conducted in 40 plots (50 × 50 m each), with three replicates per forest-level disturbance (undisturbed, moderately disturbed, and disturbed). Fragments were surface-sterilized in 70% ethanol for 1 min and 1% NaOCl for 3 min, rinsed three times with sterile distilled water, and placed on 90 mm Petri dishes containing ½ PDA supplemented with 50 mg L^{-1} streptomycin. Plates were incubated in the dark at 28±2°C for 7 days. Pure cultures were obtained via hyphal-tip transfer and maintained on PDA slants at 4°C. Both infected and uninfected stem samples were processed across the three disturbance-defined vegetation communities. Agarwood tissue fragments (0.5 cm × 0.5 cm) were washed, air-dried, treated with 5% NaHCl, rinsed with distilled water, and inoculated onto PDA. The number of fungal colonies emerging per fragment was recorded, and morphologically distinct colonies (morphotypes) were coded and counted. Isolate frequency (%) and relative abundance (%) were calculated against the total number of fragments and colonies (Safaie et al. 2024), respectively, and compared among disturbance categories. Colony counts were also used to estimate fungal load per fragment, allowing semi-quantitative assessment of fungal community composition relative to host condition and disturbance level. Morphotypes were identified to genus or species whenever possible, based on macroscopic characteristics (color, margin, texture) and microscopic traits (conidial shape, septation, size) examined under a Leica DM500 microscope (100×). Identifications were made using the taxonomic keys of Cannon and Kirk (2008) and cross-checked with published reports on pathogenicity and agarwood-associated fungal taxa.

Data analysis

Vegetation data were classified into plant communities using TWINSPAN (Two-Way Indicator Species Analysis), hierarchical dichotomous method based on Correspondence Analysis (CA) ordination. Diagnostic species groups were used to characterize communities, enabling differentiation based on indicator species presence. Species cover-abundance was quantified on an ordinal scale, and a synoptic differential table was constructed to summarize species occurrence, frequency, and mean characteristic cover within each cluster, providing insight into ecological significance. Fungal diversity within each plant community was calculated using the Shannon-Wiener Index (H′), which incorporates both species richness and evenness. The index was computed as the sum of the products of each species proportion (p_i) and the natural logarithm of that proportion across all species in the community.

RESULTS AND DISCUSSION

Vegetation structure and composition of *Aquilaria filaria* habitats

Across all vegetation communities containing *A. filaria*, a total of 97 plant species were identified and recorded. Species richness varied considerably along the disturbance gradient, reflecting differences in forest structure and human influence. These species were grouped into three distinct vegetation communities: (i) *Pometia pinnata* - *Parkia speciosa* (undisturbed), (ii) *Freycinetia* sp. - *Schefflera* sp. (disturbed), and (iii) *Habenaria* sp. - *Spathiostemon javensis* (moderately disturbed). Community delimitation was based on indicator species, canopy structure, edaphic factors, and anthropogenic disturbance levels. To illustrate overall patterns, only the ten most species-rich families are presented in Table 1. Together, these families accounted for 40% (39 of 97) of all species recorded across the three communities. This emphasis on dominant taxonomic groups follows standard practice in ecological reporting (Rodrigues et al. 2019).

Among the dominant families, Euphorbiaceae and Moraceae were the richest (5 species each). Euphorbiaceae occurred only in disturbed and moderately disturbed habitats, suggesting a preference for or tolerance of altered environments, while Moraceae was distributed across all sites. Calophyllaceae, Meliaceae, and Myristicaceae (4 species each) were mainly associated with disturbed and moderately disturbed communities, indicating adaptability to modified conditions. Rubiaceae and Anacardiaceae were absent in the moderately disturbed community, whereas Orchidaceae showed the opposite trend, occurring only in undisturbed and moderately disturbed sites. The “Others” category, encompassing 37 families with fewer representatives, contributed the majority of overall richness (57 species), with the highest concentration in the disturbed community (39 species). Species richness was greatest in the *Freycinetia* sp. - *Schefflera* sp. (disturbed) community (60 species), followed by the *Habenaria* sp. - *S. javensis* (moderately disturbed) community (26 species) and the *P. pinnata* - *P. speciosa* (undisturbed) community (11 species). This pattern highlights the influence of disturbance on species turnover and compositional variability.

Community of *Pometia pinnata* - *Parkia speciosa* (undisturbed)

The *Pometia pinnata* - *Parkia speciosa* community was represented by four relevés (37-40) located in the primary forest (Figure 3). This assemblage contained 11 differential species, including *Pometia pinnata*, *Parkia speciosa*, *Hydriastele costata*, *Osmoxylon globulare*, *Corymborkis veratrifolia*, *Dendrobium* sp., *Syzygium* sp., *Ficus* sp., *Freycinetia* sp., *Schefflera* sp., and *Timonius* sp. The coexistence of canopy trees, understory shrubs, and epiphytic orchids indicates a structurally complex community, with diverse microhabitats and resource niches. Canopy openness

averaged 13.5%, maintained primarily by large-diameter trees. The community was located ca. 3 m from the Kali Siwa watercourse, in low-lying primary forest at 270 m above sea level. The forest floor was covered by a 2.3 cm litter layer. Environmental conditions included high relative humidity (71%), elevated soil moisture (26.2%), alkaline soil pH (7.55), and relatively high nitrogen content in soil organic matter (1.3%). Anthropogenic disturbance was minimal. The site lies ~0.5 km from the main road, and an average of three dead trees per relevé was recorded, mostly from natural senescence or windthrow. Indigenous cultural protection strongly limited human interference: the forest is designated as "Wahyu," a sacred site believed to be an ancestral passage, thereby restricting activities such as logging and resin harvesting.

Community of *Freycinetia* sp. - *Schefflera* sp. (disturbed)

The *Freycinetia* sp. - *Schefflera* sp. community, represented in Figure 4, was the most species-rich, comprising 80 taxa across multiple genera. Prominent species included *Homonoia* sp., *Coleus scutellarioides*, *Nephrolepis biserrata*, *Decaspermum fruticosum*, *Syzygium* sp., and *Rhus* sp., alongside timber and hardwood species such as *Diospyros ebenum* and *Rhus taitensis*. Additional representatives included *Flueggea* sp., *Morinda citrifolia*, *Eugenia* sp., *Dracena angustifolia*, *Ixora* sp., *Artocarpus altilis*, and *Casuarina* sp. Ferns such as *Dicranopteris pedata* and *Selaginella doederleinii* were also recorded.

The genus *Ficus* was particularly diverse, with species such as *F. benjamina*, *F. trachypison*, and *F. annulata*, accompanied by *Mussaendopsis* sp. and *Alectryon* sp. Other notable trees included *Brassica* sp., *Lithocarpus* sp., *Carallia brachiata*, *Semecarpus papuana*, *Alstonia* sp., *Nuxia* sp., *Macaranga tanarius*, *Noronhia macrophylla*, and *Maesa* sp.. Tall canopy elements such as *Palaquium* sp., *Prunus arborea*, *Terminalia* sp., and the tree fern *Sphaeropteris glauca* were also present. The understory was characterized by *Freycinetia* sp., *Garcinia* sp., *Myristica pseudoargentea*, and *Buchanania macrocarpa*, complemented by shrubs and small trees including *Clerodendrum* sp., *Cryptocarya* sp., *Dianella* sp., and *Diospyros* sp. Additional plants documented in this assemblage included *Euodia* sp., *Horsfieldia sylvestris*, *Pandanus furcatus*, *Pentas* sp., *Haplolobus lanceolatus*, *Alstonia macrophylla*, *Glycosmis* sp., *Timonius* sp., *Adina* sp., and *Aglaia odorata*. Species such as *Calophyllum inophyllum*, *Calophyllum procerum*, *Elaeocarpus* sp., *Flagellaria indica*, *Pometia coriacea*, *Diospyros lolin*, *Drypetes* sp., *Leea* sp., *Sterculia* sp., and *Garcinia picrorhiza* further contributed to the diversity of this community. Vegetation height ranged from 10 to 50 m, reflecting a mix of species persisting after logging and newly established recruits. Canopy openness was relatively high (17.58%), resulting in increased daytime temperatures, with a mean of 21.69°C. The forest floor was covered by a 3.4 cm litter layer. Most relevés representing this community were sampled in secondary forest, although relevés 23, 24, and 36 were derived from primary forest stands. Synecologically, this community occurred at an average elevation of 268.5 m above sea level, approximately 371 m from the main road. The soil was notable for its high cation exchange capacity (34.4 cmol(+)/kg), suggesting relatively high nutrient retention and fertility compared to other communities.

Figure 3. Undisturbed community, close to the Siwa water stream

Table 1. Top ten species-rich plant families recorded in the three *Aquilaria filaria* vegetation communities

Plant family	Community 1 (Undisturbed)	Community 2 (Disturbed)	Community 3 (Moderately disturbed)	Total species
Euphorbiaceae	0	2	3	5
Moraceae	1	3	1	5
Calophyllaceae	0	2	2	4
Meliaceae	0	2	2	4
Myristicaceae	0	2	2	4
Myrtaceae	1	2	1	4
Rubiaceae	1	3	0	4
Anacardiaceae	0	3	0	3
Clusiaceae	0	2	1	3
Orchidaceae	2	0	1	3
Others (37 families)	4	39	14	57
Total	11	60	26	97

Community of *Habenaria* spp. - *Spathiostemon javensis* (moderately disturbed)

Twenty seven plant species were identified within the *Habenaria* spp. - *Spathiostemon javensis* community (Figure 5), representing a diverse assemblage spanning multiple families and growth forms. Several tree species of ecological and economic value were prominent, including *Didymocheton mollissimus*, *Endospermum moluccanum*, *Hopea* sp., *Sundacarpus amarus*, and *Vatica rassak*, all characteristic of tropical lowland rainforests, and widely recognized for their timber. Species with ethnobotanical significance were also present, such as *Cinnamomum culitlawan* and *Cinnamomum burmanni*, valued for their aromatic bark, alongside *Garcinia* sp. and *Flacourtia inermis*, both of which have traditional uses. The understory was characterized by shade-tolerant taxa, including *Habenaria* sp., *Begonia* sp., *Leea aculeata*, and *Vitex* sp., while transitional or secondary forest elements were represented by *Spathiostemon javensis*, *Aglaia* sp., and *Cynometra* sp. Additional notable records included *Gymnacranthera farquhariana* and *Horsfieldia sylvestris* (Myristicaceae), together with *Glochidion* sp. (Phyllanthaceae), which highlight the floristic complexity of this community. The genus *Artocarpus* was represented by *Artocarpus heterophyllus*, a widely cultivated fruit tree in Southeast Asia, reflecting human influence on the forest composition. Other taxa included *Calophyllum* sp., *Pimelodendron amboinicum*, *Tristaniopsis* sp., *Terminalia* sp., and two species of *Haplolobus* (*H. lanceolatus* and *H. celebicus*). Collectively, the species composition indicates a mixture of primary and secondary forest elements, emphasizing the ecological heterogeneity of this moderately disturbed habitat and the importance of continued botanical documentation. Structurally, this community exhibited the highest canopy cover among all vegetation types examined, averaging 87.74%. Synecologically, it occupied the highest elevation in the study area (286.58 m a.s.l.) on moderately sloping terrain (mean slope 21°). The soils were predominantly clay (40.8%) with relatively low moisture content (10.63%), yet they displayed the highest recorded pH (KCl = 7.20). A substantial litter layer averaging 5.9 cm indicated both stability and relative maturity of the forest system.

Population structure of *Aquilaria filaria* under different disturbances

The population assessment of *A. filaria* across the three disturbance gradients revealed clear differences in abundance, demographic composition, and mortality patterns (Table 2; Figure 6). A total of 198 individuals were recorded, with the highest abundance observed in the disturbed forest (132 individuals), followed by the moderately disturbed forest (65 individuals), and the undisturbed forest, where only a single adult tree was recorded. These results suggest that disturbance strongly influences the regeneration and recruitment processes of *A. filaria*.

In the undisturbed *Pometia pinnata* - *Parkia speciosa* community, located ~0.5 km from the main road, cultural protection by Indigenous communities restricts human activity. The area, regarded as “Wahyu” (a sacred ancestral passage), remains largely free of anthropogenic disturbance, with tree mortality arising mainly from natural causes such as windthrow and senescence, reflected in an average of three naturally dead trees per relevé. The population structure showed an absence of seedlings and saplings, with only one adult tree present. This scarcity of younger cohorts indicates limited regeneration under intact canopy cover, despite otherwise favorable conditions for seed dispersal and establishment.

Figure 4. In a disturbed area, the forest floor is mostly covered by *Selaginella doederleinii*

Figure 5. Moderate disturbed community, mostly on the slope and at higher altitudes, the forest floor covered by *Begonia* sp.

The disturbed *Freycinetia* sp. - *Schefflera* sp. community supported the largest *A. filaria* population (132 individuals), dominated by seedlings. Canopy openings created by intensive logging provided recruitment opportunities but also increased seedling and sapling mortality due to harsher microclimatic conditions and physical damage. The high number of dead trees in this community highlights the destabilizing effects of logging, which simultaneously enhances germination niches while undermining long-term survival. This dual effect highlights disturbance as a driver of both regeneration and mortality dynamics.

In the moderately disturbed *Habenaria* spp. - *S. javensis* community, 65 individuals of *A. filaria* were recorded, with a relatively balanced distribution across seedlings, saplings, juveniles, and adults. This indicates ongoing regeneration despite some anthropogenic pressure, notably the selective harvesting of agarwood from an adult tree. Mortality in this community was comparatively low and largely attributable to natural causes, suggesting that moderate disturbance levels may support both regeneration and adult persistence, although long-term viability could be jeopardized by targeted exploitation of reproductive individuals.

Overall, these findings demonstrate that disturbance plays a pivotal role in shaping *A. filaria* population dynamics. While heavy disturbance (logging) may stimulate seedling recruitment, it also increases mortality risks, whereas cultural protection in undisturbed sites can safeguard adult trees but limit regeneration. Moderately disturbed systems appear to provide a balance between these extremes, supporting both regeneration and persistence. Such insights are essential for conservation planning, particularly for designing management strategies that integrate traditional protection systems with sustainable use practices to ensure the long-term survival of this ecologically and economically valuable species.

Fungus - *Aquilaria filaria* association

Associations between agarwood formation in *A. filaria* and fungal colonization were documented across disturbance gradients, based on three relevés in the Marumana forest (Table 3; Figure 7), while micromorphological and colony characteristics of fungi are detailed in Table 6. The dominant fungal taxa identified were *Trichoderma* spp., *Fusarium* spp., *Penicillium* spp., and *Aspergillus niger*. The distribution of these taxa varied with disturbance level and edaphic conditions. The undisturbed *P. pinnata* - *P. speciosa* community, situated at lower altitudes on wet soils with lower C/N ratios and farther from roads, was associated primarily with *Fusarium* spp., *Penicillium* spp., and *A. niger*. In contrast, the disturbed *Freycinetia* sp. - *Schefflera* sp. community, occurring on sandy soils with high Cation Exchange Capacity (CEC), was dominated by *Trichoderma* spp. and *Fusarium* spp. The moderately disturbed *Habenaria* sp. - *S. javensis* community, established on higher-elevation clayey soils, was characterized by associations with *Trichoderma* spp. and *Penicillium* spp. (Table 3).

Fungal colonization intensity in *A. filaria* wood increased with disturbance level (Tables 4, 5; Figure 8). A total of 29, 37, and 132 trees were sampled in the undisturbed, moderately disturbed, and disturbed communities, respectively, yielding 90, 114, and 396 wood fragments. The proportion of colonized fragments rose from 70% in the undisturbed forest to 90% in the disturbed forest, with intermediate values in moderately disturbed stands. Similarly, the total number of fungal colonies increased more than sevenfold along the gradient, from 158 in the undisturbed forest to 1,173 in the disturbed forest. Average colony counts per fragment followed the same pattern (1.76, 2.40, and 2.96, respectively), with the highest fungal load recorded in the disturbed community (Table 4).

Table 2. Number of *Aquilaria filaria* individuals in different life stages per community

Community	Total	Number of *Aquilaria filaria* individuals			
		Seedling	Sapling	Juvenile	Adult
Undisturbed community	29	10	3	15	1
Disturbed community	132	83	12	33	4
Moderate disturbed community	37	21	5	4	8
Total	198				

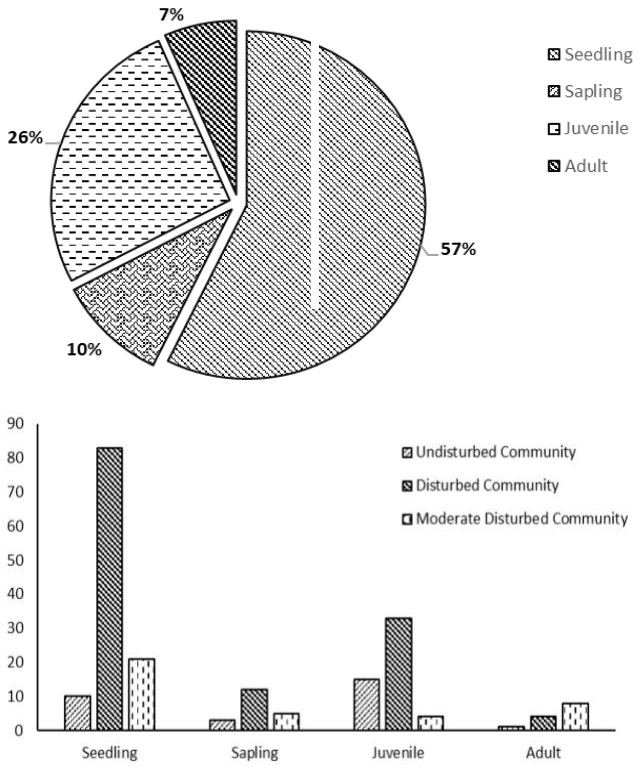


Figure 6. Percentage (above) and number (under) of *Aquilaria filaria* (per life stage) in communities with different anthropogenic pressures

Patterns of fungal composition and diversity further highlight the influence of disturbance. In the undisturbed forest, *Fusarium* spp. was most frequent (50% of isolates), followed by *Penicillium* spp. (45%) and *A. niger* (30%), yielding the highest Shannon-Wiener Diversity Index (H′ = 1.08). The moderately disturbed forest was dominated by *Trichoderma* spp. (60%) and *Penicillium* spp. (55%), but showed lower diversity (H′ = 0.68). The disturbed forest was heavily dominated by *Trichoderma* spp. (75% frequency; 704 colonies), alongside *Fusarium* spp. (65%; 469 colonies), with overall diversity remaining low (H′ = 0.67) (Table 5).

Taken together, these results indicate that disturbance not only increases fungal colonization intensity in *A. filaria* but also shifts fungal community composition toward a dominance of aggressive taxa such as *Trichoderma* spp. The higher fungal loads in disturbed habitats may accelerate agarwood induction but at the cost of reduced fungal diversity. Conversely, undisturbed sites harbor a more balanced fungal assemblage, including taxa such as *Penicillium* spp. and *A. niger*, potentially contributing to more heterogeneous agarwood formation dynamics. These findings highlight the dual role of disturbance as both a facilitator of fungal infection and a driver of fungal community homogenization in *A. filaria* habitats.

Table 3. Fungal composition of agarwood in different plant communities

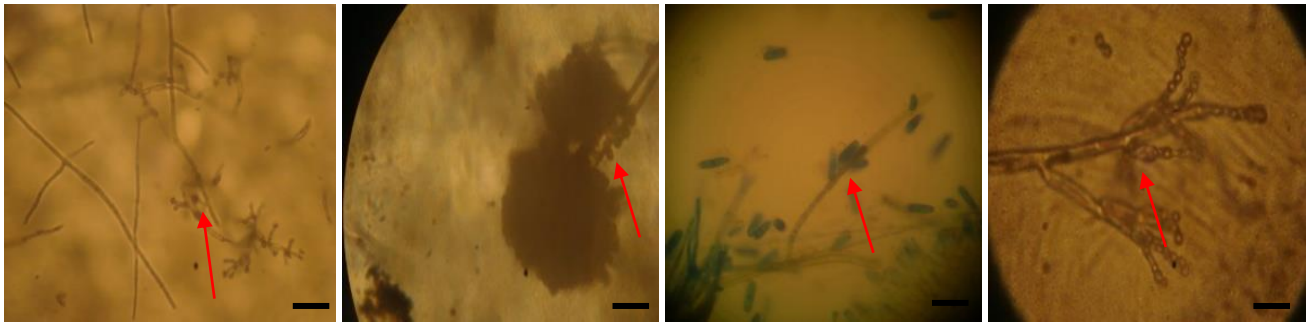
Relevés/community	Average DBH	Fungi
Pometia pinata - *Parkia speciosa* (undisturbed)	15	*Fusarium* spp., *Penicillium* spp., and *Aspergillus niger*
Freycinetia sp. - *Schefflera* sp. (disturbed)	25	*Trichoderma* spp. and *Fusarium* spp.
Habenaria sp. - *Spathiostemon javensis* (moderately disturbed)	20	*Trichoderma* spp. and *Penicillium* spp.

Table 4. Summary load of *Aquilaria filaria* colony per community

Disturbance level	Total of trees	Sampled fragments (n)	Colonized fragments (n, %)	Total fungal colonies	Colonies/fragment	Colonies/colonized fragment
Undisturbed	29	90	63 (70%)	158	1.76	2.51
Moderately disturbed	37	114	98 (86%)	274	2.4	2.8
Disturbed	132	396	356 (90%)	1,173	2.96	3.29

Table 5. Isolate frequency, relative abundance, and colony counts of *Aquilaria filaria* by disturbance gradient

Disturbance level	Taxon	Frequency (%)	Relative abundance (%)	Number of colonies (n)	Shannon-Wiener Index (H′)
Undisturbed	*Fusarium* spp.	50	40	63	1.08
	Penicillium spp.	45	35	55	
	Aspergillus niger	30	25	40	
Moderately disturbed	*Trichoderma* spp.	60	55	151	0.68
	Penicillium spp.	55	45	123	
Disturbed	*Trichoderma* spp.	75	60	704	0.67
	Fusarium spp.	65	40	469	



A **B** **C** **D**

Figure 7. Spores of pathogenic fungi (red arrow) isolated from *Aquilaria filaria* stem at a magnification of 10×10. A. *Trichoderma* spp., B. *Aspergillus niger*, C. *Fusarium* spp., D. *Penicillium* spp.

Table 6. Micromorphological and colony characteristics of fungi isolated from *Aquilaria filaria*

Genus/species	Colony characteristics (PDA)	Micromorphological features (40×)
Trichoderma spp.	Fast-growing, white to green, cottony; later turning dark green	Branched, septate hyphae; flask-shaped phialides; conidia smooth, globose to subglobose
Fusarium spp.	Pink to violet, cottony to floccose colonies	Septate hyphae; sickle-shaped macroconidia with 3-5 septa; microconidia oval
Penicillium spp.	Velvety to powdery, blue-green colonies with white margin	Septate hyphae; brush-like conidiophores; chains of globose conidia
Aspergillus niger	Black colonies, granular to powdery texture	Conidiophores smooth, ending in vesicle; biseriate phialides; globose black conidia

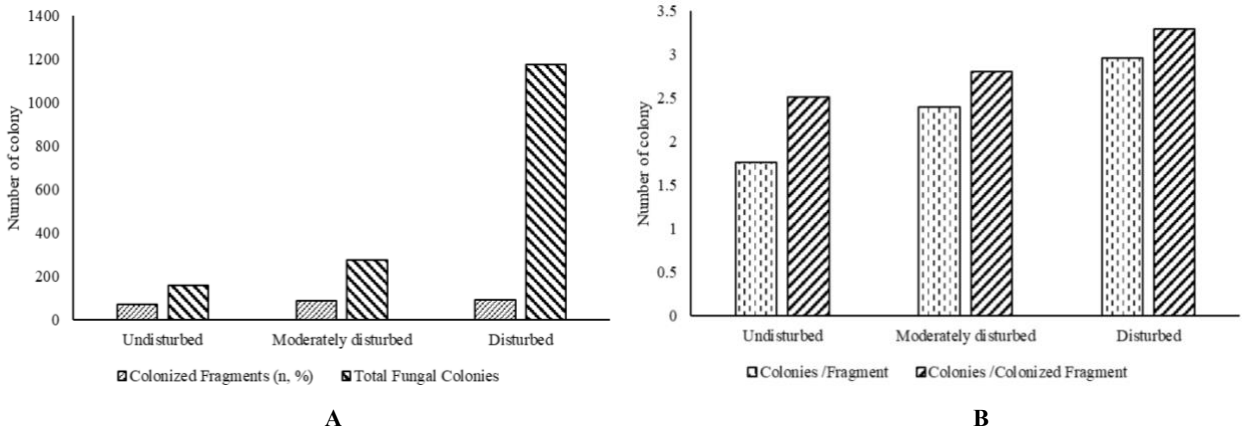


Figure 8. Quantitative assessment of fungal colonization in *Aquilaria filaria* across gradients of habitat disturbance. A. Colonized fragments and total fungal colonies, B. Colonies/fragments and colonies/colonized fragments

The composition of fungal communities shifted with increasing disturbance intensity. In the undisturbed forest, *Fusarium* spp., *Penicillium* spp., and *Aspergillus niger* were dominant, with isolate frequencies ranging from 30% to 50% and relative abundances between 25% and 40%. In contrast, *Trichoderma* spp. became the most prevalent taxon in moderately and heavily disturbed communities, with isolate frequencies of 60% and 75% and relative abundances exceeding 55%. *Penicillium* spp. remained prominent in the moderately disturbed community but declined sharply under high disturbance. Interestingly, *Fusarium* spp. maintained a substantial presence in the disturbed community, though at lower frequencies compared to *Trichoderma* (Table 5). These patterns indicate that disturbance enhances fungal colonization intensity and promotes compositional shifts toward opportunistic taxa such as *Trichoderma*, which are recognized for rapid colonization and competitive abilities under stressed conditions. In contrast, taxa such as *A. niger* appear more restricted to stable, undisturbed habitats, reflecting their narrower ecological preferences. Diversity metrics supported these observations.

The Shannon-Wiener index showed a decline in fungal diversity along the disturbance gradient. The undisturbed site exhibited the highest diversity (H' = 1.08), reflecting a more balanced community of three dominant taxa. In contrast, moderately and heavily disturbed sites showed lower values (H' = 0.69 and 0.67, respectively), each dominated by only two taxa. These results demonstrate that disturbance reduces fungal diversity, favouring disturbance-tolerant species, while stable habitats support greater richness and evenness.

Discussion

Tropical forests are among the most biologically complex ecosystems on Earth, contributing disproportionately to global biodiversity through high plant richness, endemism, and structural complexity (Liang et al. 2022). The high species richness and abundance of *A. filaria* recorded in this study highlight the exceptional biodiversity and conservation value of the investigated forest. Vegetation diversity in these habitats is shaped by environmental factors such as rainfall patterns, flood frequency, water table fluctuations, and soil water retention capacity (Koljanin et al. 2023). Globally, escalating environmental degradation has prompted nations to expand protected area networks as a means to mitigate biodiversity loss (Waheed et al. 2024). Since species-rich forests sustain critical ecological functions, their degradation results in major declines in species richness and ecosystem integrity. Bavcon et al. (2024) further note that tropical botanical ecosystems face increasing threats from agricultural intensification and land abandonment, emphasizing the urgency of long-term conservation measures.

Our findings revealed three distinct plant communities that correspond closely to disturbance regimes. The *P.*

pinnata - *P. speciosa* community characterizes undisturbed forests and supports 11 plant species. Occurring in low-lying primary forests around 270 m above sea level, it is typified by a closed canopy (13.5% openness) formed by large-diameter mature trees. This structural complexity generates stable microclimatic conditions, supporting 29 juveniles and seedlings of *A. filaria*. Human activity was minimal here, likely due to indigenous protection of sacred sites. Similar results were observed by Abdillah et al. (2023) in Riau Province, where such communities persisted despite external pressures. However, commercial logging in Papua frequently targets *Pometia* as timber (Murdjoko et al. 2016), threatening long-term forest viability and altering community composition (Osazuwa-Peters et al. 2015).

By contrast, the *Freycinetia* sp. - *Schefflera* sp. community is associated with heavily disturbed forests. With the highest canopy openness (17.58%) and vegetation heights of 10-50 m, it occurs at ~268.5 m elevation, close to human access routes, making it vulnerable to logging and firewood extraction. Increased canopy openness enhances light penetration and raises daytime temperatures (average 21.69°C), altering regeneration dynamics. A litter layer of 3.4 cm contributed to nutrient cycling, but the site also contained 132 *A. filaria* individuals, including many dead trees caused by logging and windthrow. This community represents a regenerating secondary forest under heavy anthropogenic pressure. Villanueva and Buot (2018) emphasize that such disturbances substantially reshape forest composition and biodiversity. Consistent with this, Nature Serve (2018) documents *Schefflera* as typical of mid- to lower-elevation forest-floor habitats with lower nutrient availability, where tropical plant diversity often peaks (de Andrade Kamimura et al. 2025). These findings highlight the combined effects of elevation and resource gradients on community composition and their importance for conservation planning.

The *Habenaria* spp. - *S. javensis* community represents moderately disturbed forest, located at the highest elevation (286.58 m) with dense canopy cover (87.74%). It is characterized by a thicker litter layer (5.9 cm), moderate slope (21°), and stable microclimatic conditions. Supporting 37 *A. filaria* individuals, including adults and one resin-bearing tree, this community appears transitional between undisturbed and disturbed conditions. Its structural characteristics provide microhabitat variability, influencing fungal colonization and regeneration (Man et al. 2022). This highlights how disturbance gradients shape both vegetation and associated fungal dynamics. Notably, although *Habenaria* and *Spathiostemon* are diverse across tropical to temperate regions (Hyam 2024), their role in shaping understory structure along fine-scale gradients remains insufficiently studied (Wang et al. 2024).

Population structure patterns of *A. filaria* closely mirrored these disturbance regimes. Undisturbed communities showed continuous regeneration across size classes, whereas disturbed sites exhibited recruitment failure and high mortality, likely due to harvesting. Moderately disturbed forests displayed intermediate regeneration, reflecting partial resilience but ongoing vulnerability. These patterns highlight the combined effects of canopy openness, soil conditions, and human activity on population viability.

Fungal communities associated with *A. filaria* also shifted markedly along the disturbance gradient. *Fusarium*, *Penicillium*, *Trichoderma*, and *A. niger* were isolated from agarwood tissues, but their distribution varied by community: *Fusarium* was absent in the moderately disturbed *Habenaria* - *Spathiostemon* forest, *Penicillium* was absent in the disturbed *Freycinetia* - *Schefflera* community, and *A. niger* occurred exclusively in the undisturbed *Pometia* - *Parkia* forest. These findings align with Koziol and Bever (2018), who showed that vegetation structure strongly shapes plant-fungal associations. Furthermore, Zhao et al. (2024) emphasize that fungal induction enhances agarwood quality by stimulating resin production and modifying chemical profiles.

Our results also highlight significant fungal richness within *A. filaria* habitats, including multiple morphotypes of *Fusarium*, *Penicillium*, *Trichoderma*, and *Aspergillus*. This suggests a complex assemblage with diverse ecological roles rather than single-species dominance. While some taxa are broadly distributed, others show host or habitat specificity, influencing resin induction and tree health (Liu et al. 2024). Preserving fungal diversity is therefore critical for both forest resilience and sustainable agarwood production (Castillo et al. 2023). Conservation strategies should integrate microbial diversity alongside host tree protection to support ecosystem function.

Fungal taxa identified in this study are known to influence agarwood formation. *Fusarium* and *Penicillium* induce stress responses in host trees, stimulating resin accumulation (Tan et al. 2019; Li et al. 2023). These fungi activate biochemical pathways involving reactive oxygen species and defense-related enzymes, promoting resin biosynthesis (Zhao et al. 2024). *Trichoderma* spp., dominant in disturbed sites, are fast-growing colonizers that produce antifungal metabolites, offering competitive advantages but also accelerating decay and degrading resin quality (Dutta et al. 2022; Liu et al. 2024). Mega et al. (2023) and Pang et al. (2024) reported similar trends in Indonesia and China, respectively, confirming the role of *Trichoderma* and *Fusarium* in resin enhancement.

Colony morphology further corroborated species identification: *Penicillium* formed white spherical conidia on branched conidiophores (Ong et al. 2024); *Fusarium* appeared as white colonies with yellow centers and septate hyphae (Brugman and Mario 2024); *Trichoderma* produced green colonies with soft hyphae and oval conidia (Tyśkiewicz et al. 2022; Provilia et al. 2023); and A. niger formed distinct black colonies (Abouamama et al. 2023). The absence of *Fusarium* in the moderately disturbed community represents a potentially novel ecological filter or host specificity not previously reported.

Quantitative analyses reinforced these results: fungal colonization increased nearly seven-fold with disturbance (Table 4, Figure 8). This is likely due to enhanced wound availability and altered microenvironments favouring opportunistic fungi (Dossa et al. 2021). Similar patterns have been reported in tropical forests of Vietnam (Cuong et al. 2024) and Indonesia (Arifah et al. 2023), where the

same genera were consistently observed. Such findings confirm the adaptability and ecological significance of these fungi across Southeast Asian forests.

Although fungal colonization enhances agarwood formation, unchecked proliferation of fast-growing taxa may compromise tree health by accelerating decay, weakening structural integrity, and reducing lifespan. This duality highlights the need for integrative management that balances resin yield with conservation objectives (Du et al. 2022). Moderately disturbed forests, where *Trichoderma* and *Penicillium* coexist, may represent a more balanced ecological niche for sustainable agarwood production.

The positive correlation between disturbance and fungal load (Figure 8) emphasizes that anthropogenic pressures reshape microbial dynamics, with cascading effects on forest regeneration and resin quality (Bahram and Netherway 2022). Accurate assessments of canopy structure are essential for designing interventions (Beeles et al. 2022), and fostering structural complexity is increasingly recognized as a baseline strategy for restoring resilience (Wang et al. 2025).

In conclusion, these findings show that disturbance not only alters vegetation and *A. filaria* demographics but also fundamentally reshapes fungal communities crucial to agarwood formation. Effective management therefore requires maintaining forest structural complexity and moderating disturbance to sustain both ecological resilience and economic value. The culture-based approach employed in this study provides valuable insights into cultivable endophytic fungi, although it likely represents only a subset of the community associated with *A. filaria*.

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