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ORIGINAL ARTICLE

Ecological factors affecting the distribution of the *Amanita* genus (poisonous mushrooms) in the Central Highlands, Vietnam

Factores ecológicos que afectan la distribución del género *Amanita* (hongos venenosos) en las Tierras Altas Centrales de Vietnam

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ABSTRACT

The *Amanita* genus, a member of the Amanitaceae family, thrives in Vietnam's Central Highlands and exhibits remarkable diversity and abundance. These *Amanita* fungi species predominantly inhabit pine forests, mixed forests, and grassy areas. Because most species in this genus are toxic, the impact of ecological factors on their emergence and development must be understood. This study aims to build the correlation between ecological factors, namely light, humidity, altitude, temperature, and habitat. Our findings reveal that fungi within this genus primarily inhabit higher-altitude zones (ranging from 500 to 800 m). Their optimal growth temperature lies between 19 and 22 °C, with a light intensity of 800-1000 lux and relatively high humidity levels, ranging from 85% to 90%. These factors significantly influence the frequency of these fungi's occurrence. These insights serve as a foundation for identifying the distribution area of these toxic mushrooms and improving their recognition. This research enhances our understanding of *Amanita* biodiversity in this region and provides valuable insights into the specific environmental conditions that support their growth and conservation.

Keywords: Amanitaceae, biodiversity, conservation, ecological factors, poisonous mushrooms.

RESUMEN

El género *Amanita*, miembro de la familia Amanitaceae, prospera en las tierras altas centrales de Vietnam y exhibe una diversidad y abundancia notables. Estas especies de hongos *Amanita* predominan en bosques de pinos, bosques mixtos y áreas herbáceas. Debido a que la mayoría de las especies de este género son tóxicas, es necesario comprender el impacto de los factores ecológicos en su surgimiento y desarrollo. Este estudio tiene como objetivo construir la correlación entre los factores ecológicos, específicamente la luz, la humedad, la altitud, la temperatura y el hábitat. Nuestros hallazgos revelan que los hongos de este género habitan principalmente zonas de mayor altitud (entre 500 y 800 m). Su temperatura óptima de crecimiento se sitúa entre 19 y 22 °C, con una intensidad luminosa de 800-1000 lux y unos niveles de humedad relativamente altos, que oscilan entre el 85% y el 90%. Estos factores influyen significativamente en la frecuencia de aparición de estos hongos. Estos conocimientos sirven como base para identificar

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el área de distribución de estos hongos tóxicos y mejorar su reconocimiento. Esta investigación mejora nuestra comprensión de la biodiversidad de *Amanita* en esta región y proporciona información valiosa sobre las condiciones ambientales específicas que apoyan su crecimiento y conservación.

Palabras clave: Amanitaceae, biodiversidad, conservación, hongos venenosos, factores ecológicos.

INTRODUCTION

The *Amanita* genus encompasses hundreds of fungus species in the Amanitaceae family, situated within the Agaricales class of the kingdom Fungi. This genus comprises approximately 600 species, among which some of the most poisonous have gained worldwide recognition (Benjamin 1995). Advances in science and technology facilitating the identification and study of toxic fungi have led to the discovery that certain *Amanita* species pose a threat to humans. Characteristically, *Amanita* species feature white spores, a volva, and a ring. Notably dangerous species are *Amanita bisporigera*, *A. ocreata*, *A. verna*, and *A. virosa* (Menolli *et al.* 2009). These fungi develop into white fruiting bodies, commonly found in forested areas during humid periods such as the summer and fall. *A. phalloides*, another poisonous species that inhabits jungles, has caps in shades of green or brown and appears during the summer or early fall. In grasslands and fields, *A. muscaria*, recognized for its toxicity, emerges during the summer; this species induces hallucinations and is employed as a fly repellent in certain regions (Zhao *et al.* 2007). Other toxic members of the species include *A. brunnescens* and *A. pantherina*. However, some *Amanita* species, including *A. caesarea*, *A. rubescens*, and *A. vaginata*, are considered edible (Kiet 2013).

An array of scientific publications have examined *Amanita*. Benjamin (1995) and Tulloss (2009) explored the diversity of the Amanitaceae family and developed taxonomic keys (Benjamin 1995, Tulloss 2009). Karadelev *et al.* (2011) unveiled 27 *Amanita* species, including *A. boudieri*, *A. curtipes*, *A. ovoidea*, and *A. vittadinii* (Karadelev *et al.* 2011). Santi *et al.* (2012) assessed the impact of *A. phalloides* on the human liver, revealing toxicity linked to two toxin groups: phallotoxin and amatoxin (Santi *et al.* 2012). Beyond studying toxicity, researchers have examined fungal diversity, including the composition of poisonous mushrooms and the fungal flora of Eastern Africa (Ryvarden & Johansen 1980). Notably, these studies often focus on three poisonous mushrooms, predominantly saprophytic wood-dwelling species.

In Vietnam, research on the *Amanita* genus is limited. Kiet (1981, 2011, 2013) has conducted extensive research on large mushroom diversity, describing 37 *Amanita* species (Kiet 1981, 2011, 2013). Minh (2012) explored the biology and toxicity of poisonous mushrooms in Bac Kan, proposing preventive and emergency measures against toxic mushroom poisoning (Minh 2012). Dung (2015) analyzed mushroom poisoning cases in Cao Bang and revealed samples containing amatoxin, which causes liver damage, paralysis, and multi-organ failure (Dung 2015). Hao (2011) examined mushroom poisoning causes, toxins, symptoms, and potential treatments (Hao 2011). In central Vietnam, Dung (2003) authored a book on Tay Nguyen's large mushrooms, mentioning five *Amanita* species (Dung 2003). In addition, Bao (2008) studied fungal biology (Bao 2008), and Hien (2018) investigated the species distribution and toxicity of Amanitaceae in the Central Highlands of Vietnam (Hien 2018).

Previous research has mainly focused on the diversity of *Amanita* without considering the influence of ecological factors, including light, temperature, humidity, and altitude, on the occurrence and growth of *Amanita* species. Therefore, this study investigated ecological factors, serving as a basis for *Amanita* species conservation efforts. To address this gap, the following hypotheses guided the present study: (1) light intensity, humidity, altitude, and temperature are significantly correlated with the occurrence and growth of *Amanita* species in Vietnam's Central Highlands and (2) Specific habitat types (pine forests, mixed forests, and grassy areas) differ in *Amanita* species composition and occurrence frequency. Based on these hypotheses, the study pursued four main objectives: (1) To quantify the relationship between key ecological factors (light intensity, humidity, altitude, temperature, and habitat type) and the occurrence frequency of *Amanita* species in Vietnam's Central Highlands; (2) To determine the optimal environmental ranges supporting *Amanita* growth; (3) To identify potential distribution zones of toxic *Amanita* species for improved early recognition and public awareness; and (4) To provide a scientific basis for incorporating ecological factor analysis into future *Amanita* biodiversity and conservation research in Vietnam.

MATERIAL AND METHODS

Study areas

The research area was conducted in conservation areas and national parks of the Central Highlands Provinces (Fig. 1), Vietnam, including (I) Ea So Conservation Area (12°53'18"N; 108°43'54"E), Dak Lak Province; (II) Yok Don National Park (12°45'00''N; 107°48'30''E), Dak Lak Province; (III) Chu Yang Sin National Park (120°14'16"N; 108°34'48"E), Dak Lak Province; (IV) KonKa Kinh National Park (14°20'00"N; 108°22'00"E), Gia Lai Province; (V) Chu Mon Ray National Park (14°18'00''N; 107°47'08''E), Kon Tum Province; and (VI) Bidup National Park (12°00'00''N; 108°75'00''E), Lam Dong Province.

In the Central Highlands, vegetation physiognomy and floristic composition are shaped by the region's distinctive geo-environmental conditions. According to Chien (1985), these conditions give rise to five principal climatic zones, each associated with a characteristic vegetation formation and further subdivided into specific ecological subtypes. The major vegetation formations include tropical evergreen forests, bamboo-dominated stands, pine (*Pinus* spp.) forests, seasonally inundated swamp forests, and various deciduous forest types—comprising non-Dipterocarpaceae and Dipterocarpaceae-dominated assemblages—as well as open-canopy forests, shrublands, and grassland ecosystems.

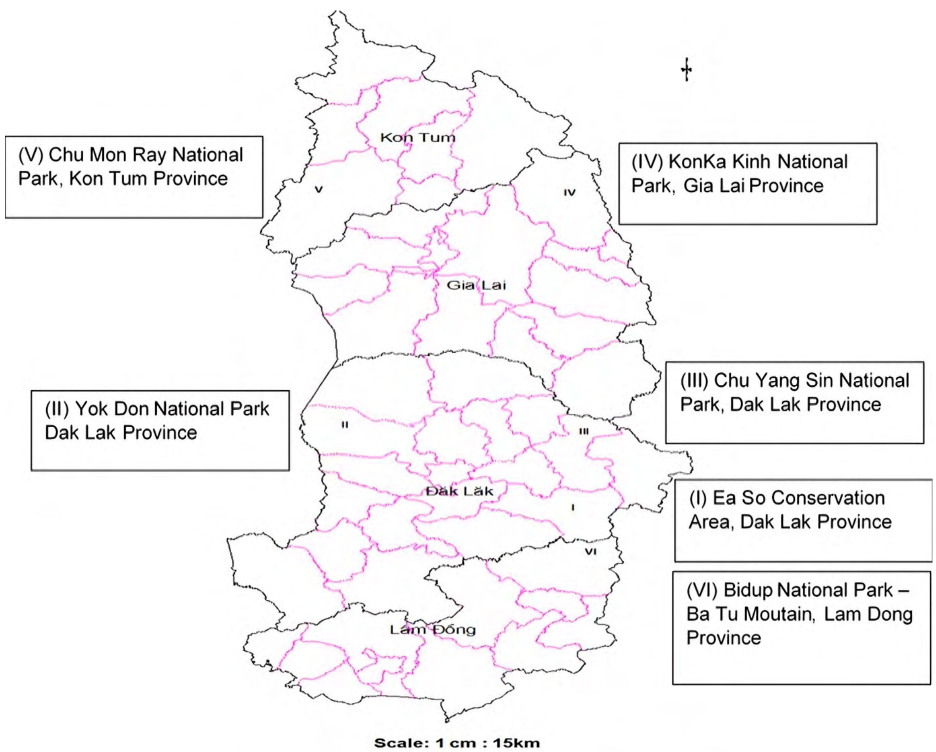

Figure 1. Collection sites of *Amanita* species in the Central Highlands, Vietnam. / Sitios de recolección de especies de *Amanita* en las Tierras Altas Centrales de Vietnam.

Sample collection

Mushroom samples were collected from June to November 2021. Samples of poisonous mushrooms of the Amanataceae family were collected along the herringbone route in different habitats (broadleaf forests, coniferous forests, and mixed forests) in the Central Highlands. During sample collection, several key characteristics of the Amanitaceae family guided sampling. These included diverse, rich colors (red, orange, and yellow); fleshy umbrella-shaped mushroom caps; large white or yellow gills; and fleshy stalks attached to the center that detach easily from the cap. In addition, the mushrooms grow saprophytically on the ground. When forming fruiting bodies in the young mushroom stage, a common sheath often connects the edge of the cap and the stem. As the mushrooms mature, this sheath splits, forming a basal sheath and a mushroom ring.

The following steps for collecting mushroom samples in the wild were followed:

1. Mushrooms were photographed in different positions (top, bottom), and characteristics that are easily lost characteristics when making specimens were recorded.

2. After collecting mushroom samples, the following symbols and brands were immediately recorded: number, date of sample collection, characteristics of the sample, location of sample collection, and sample collector.

3. Immediately after sample collection, the ecological characteristics of the sampling location, such as the coordinates, altitude, temperature, humidity, and vegetation, were described (Dung 2003, Kiet 2011).

Sample identification

Mushroom samples were identified by comparative anatomical morphology and molecular biology methods. The following steps of the identification process were carried out:

1. After being processed, the samples were arranged by family and genus.

2. The scientific names were determined.

Dichotomous keys and species descriptions from previous authors were used for identification (Teng 1964, Rolf 1986, Wieland 1986, Baier 1991, Benjamin 1995, Dung 2003, Tulloss 2009, Kiet 2013). Identification requires objectivity and careful attention to the inherent characteristics of the studied species.

Macroscopic morphological analysis

During field collection, detailed notes were recorded for each specimen, including shape, size, color, odor, taste, and in situ chemical reactions—particularly features likely to fade or degrade during drying. Observations were conducted both with the naked eye and using a 20× or 50× hand lens (Dung 2003; Kiet 2011). Macromorphological features were documented in the following order:

Growth habit

- Solitary or clustered;
- Fused or separate at the base;
- Distinctive field characteristics.

Basidiocarp (fruiting body)

- Shape: funnel-shaped, bell-shaped, umbilicate;
- Color: yellow, reddish-brown, pale green;
- Surface: dry, slimy, smooth, hairy, or scaly.

Hymenophore (fertile surface)

- Coverage: partial or entire fruiting body;
- Location: surrounding the stipe or confined to one side.

Stipe (stem)

- Surface structures: hairs, spines;
- Shape, size, and color.

Context (flesh)

- Thickness, color, odor;
- Texture: soft, firm, tough, brittle;
- Color changes upon exposure to air.

Microscopic analysis

Microscopic examinations were primarily performed on fresh specimens. Longitudinal sections of the fruiting body, including the pileus and hymenophore, were prepared to assess tissue arrangement, thickness, color, and taste. Small tissue fragments were isolated with fine needles and mounted on slides for structural characterization or strain isolation.

Cross-sections of the hymenophore were observed under a compound microscope at 400-1000× magnification to examine basidia, basidiospores, cystidia, and other diagnostic structures. Fresh samples were mounted in distilled water to preserve natural pigmentation; dried samples were rehydrated in 3% KOH to restore cell morphology. For challenging specimens, Congo red or Cotton blue staining was applied; excess stain was removed using filter paper, followed by rinsing before microscopic observation (Dung 2003; Kiet 2011).

For detailed analysis of spore ornamentation, additional stains such as aniline in lactic acid or Melzer's reagent were employed to detect amyloid or dextrinoid reactions.

Microscopic features were recorded as follows:

Hyphal system (from pileipellis or context)

- Branching pattern, septation, clamp connections;
- Hyphal diameter;
- Wall structure (thick- or thin-walled), amyloid or non-amyloid.

Spores

- Shape, size, color;
- Wall structure and internal contents.

Basidia

- Shape, size, color;
- Number of sterigmata;
- Wall characteristics.

Cystidia and other sterile cells (if present)

- Shape, size, color.

All macroscopic and microscopic analyses were conducted at the Department of Biology, Tay Nguyen University, and the Electron Microscopy and Ultrastructure Imaging Facility, National Institute of Hygiene and Epidemiology (NIHE), Vietnam. Observations were made using an Olympus light microscope (Japan) and a Hitachi S-4800 scanning electron microscope (Japan). Color reactions were evaluated with standard color charts and 3% KOH solution.

Determination of ecological factors

The ecological factors at the site were measured using a Tiger Direct Moisture Meter HMAMT-110 (USA), a Tiger Direct Light Intensity Meter LMLX1010B (USA), a Garmin Trex Vista HCx GPS altimeter (USA), and an Extech 445703 thermometer. The humidity, light, altitude, and temperature were tracked.

Analyzing the correlation of ecological factors

Statgraphics Centurion XV is used to establish multivariable regression functions and analyze the relationship and occurrence frequency (density) of the genus *Amanita* with ecological factors.

RESULTS

Collection results of *Amanita* species

Samples of mushrooms in the Amanitaceae family were collected during the rainy season (June to November 2021) in the mountainous and forested areas of the Central Highland provinces of Vietnam. Key characteristics of Amanitaceae mushrooms guided the sampling. These included diverse, rich colors (e.g., red, orange, and yellow); fleshy, umbrella-shaped caps with a white or yellow planar layer; and fleshy, centrally attached stems that are detached easily from the caps. All mushrooms were harvested fresh, living saprophytically on the soil. During harvesting, particular attention was given to the young mushrooms forming fruiting bodies, which often have common and separate capsules connecting the cap edge to the stem. These capsules split to form a basal capsule and a mushroom ring, a prominent feature of the Amanitaceae family. After collection, the samples were processed and analyzed for morphological characteristics, such as color, shape, and size, and a microscopic analysis of the spores, mesophyll, and mycelium was performed. This served as the basis for identification using the morphological and anatomical comparative method, along with molecular biology identification methods. A total of 815 mushroom samples belonging to 25 species of the Amanitaceae family were identified.

TAXONOMY

Amanita crocea **(Quél.) Singer 1951 (Fig. S1, Supplementary data)**

Description — The cap measures approximately 8-10 cm in diameter, yellow to orange-yellow with a distinct margin, and may appear orange (or light brown) toward the center. The central region is a paler orange-yellow, occasionally creamy white. The white gills curve gradually toward the stem and display irregular deep grooves, measuring 0.2-0.3 cm in width. The stem is cylindrical, burnt yellow, 8.5-23 cm long, and 0.7-1.4 cm in diameter, bearing yellow, powdery scales. The basal sheath is white and sepal-like. The flesh is white, soft, and emits a faint odor (Fig. S1a, b). Spores are elongated and elliptical, measuring 7.5-8 × 10-12 µm, containing numerous essential oil droplets, with germ pores positioned at approximately 20-25 degrees (Fig. S1c).

Biology and ecology — This species typically grows solitarily, thrives during the rainy season, and prefers sunny, dry habitats with temperatures of 18-25 °C and relative humidity of 65-80%.

Distribution — Found mainly in several Central Highlands localities, including Đak Lak and Đà Lạt.

Current value — A highly poisonous species, potentially lethal to humans (Sanmee *et al.* 2008).

The specimen *A. crocea* (Quél.) Singer 1951 with code number TH-17-TN.009 is preserved in the Biology Department Laboratory of Tay Nguyen University.

Amanita eliae **Quél. 1872 (Fig. S1, Supplementary data)**

Description — The cap measures approximately 6-8 cm in diameter, initially egg-white, later becoming pale pink and occasionally exhibiting white patches. The center is darker, and as the fruiting body matures, the cap gradually expands, forming lighter cracks toward the margin. The cap surface is dry and non-viscous, with a folded margin. The creamy-white gills curve gradually toward the stem and possess deep grooves. The stem is cylindrical and white, measuring 7.5-15 cm in length and 1-1.5 cm in diameter at the base, which gradually swells into a spongy tubercle covered with fine hairs. The upper portion of the stem bears a characteristic ring, cream-white and more opaque than the gills, consisting of a thin, scarf-like membrane folded and hanging down, easily detaching from the gills. This structure is a remnant of the universal veil, persisting after the cap margin has separated.

The volva at the base is shaped like a floral receptacle. The flesh is white and soft (Fig. S1e-g). Spores are elongated and elliptical, measuring 5.4-7 × 9-11 µm, containing numerous green essential oil droplets, with the germ pore offset at approximately 20-25 degrees (Fig. S1h). The mycelium exhibits transverse septa and measures 4-6 µm in diameter (Fig. S1i).

Biology and ecology — This species typically grows solitarily, with vigorous development during the rainy season. It prefers sunny, dry environments, with temperatures of 18-25 °C and relative humidity between 65-80%.

Distribution — Found mainly in pine forests, as well as grassland and shrub areas, in the Central Highlands.

Current value — A highly poisonous mushroom, potentially lethal to humans (Wieland, 1986).

The specimen *A. eliae* Quél. 1872 with code number TH-17-TN.0010 is preserved in the Biology Department Laboratory of Tay Nguyen University.

***Amanita fulva* Fr., 1815 (Fig. S2, Supplementary data)**

Description — The fruiting body is umbrella-shaped, light brown, and approximately 8 cm in height. The cap is convex to hemispherical, bearing a brown, shield-like umbo at the center, and measuring about 9 cm in diameter. The cap surface is smooth and glossy, with distinctly striate margins. The lamellae are free, of unequal length, closely spaced, deeply grooved, and white in color. The stipe is cylindrical, light brown, approximately 7 cm long and 1.5 cm in diameter. The volva at the stipe base is white and sepal shaped. The context is white and soft (Fig. S2a, b). Basidiospores are subglobose, 10-11 µm in diameter, containing starch granules, with a germ pore offset by approximately 20-25 degrees (Fig. S2d). Basidia are unicellular, clavate, 15-17 × 20-25 µm, and contain numerous light-blue oil droplets (Fig. S2e). The hyphae are unbranched, septate, and measure 8-10 µm in diameter (Fig. S2f).

Biology and ecology — This species forms ectomycorrhizal associations with broadleaf or coniferous trees during the rainy season. It was recorded at coordinates 12°27'30.1" N, 108°21'44.5" E, at an elevation of 1,050 m, with relative humidity of 86%, temperature of 20 °C, moderate slope, and a thin litter layer (approximately 0.3 cm) composed mainly of leaves and pine cones.

Distribution — The species is mainly found in pine forests and semi-evergreen forests in the Central Highlands of Vietnam, particularly in Dak Lak and Da Lat, with a notable presence in the Langbiang mountain area, Lam Dong Province.

Current value — This is a poisonous and inedible mushroom, posing potential hazards to both humans and animals.

The specimen *A. fulva* Fr., 1815 with code number TH-17-TN.0013 (DL33) is preserved in the Biology Department Laboratory of Tay Nguyen University.

***Amanita similis* Boedijn 1951 (Fig. S2, Supplementary data)**

Description — When young, the cap is shaped like a reddish-brown olive. At maturity, it measures 10-12 cm in diameter. After separating from the universal veil, the cap is initially hemispherical, then becomes plano-hemispherical, and eventually flattens with a slightly concave center. The central surface is deep yellow, gradually transitioning from honey yellow to a goat-skin hue toward the margin. In young specimens or under humid conditions, the pileus surface is viscid and sticky, becoming shiny when dry. The context extends from the stipe into the pileus and is approximately 5 mm thick. The margin is inrolled. Lamellae are straw-yellow, deeply grooved, and curve inward toward the stipe. The stipe is yellow with zones matching the pileus coloration, forming zigzag striations as remnants of upward stipe elongation. The stipe surface is viscid when fresh but cracks upon drying, measuring 10-15 cm in length and 0.8-1.6 cm in diameter at the base, which gradually swells into a spongy bulb; the interior is hollow, forming a narrow central canal that extends to the apex. The annular zone in the upper stipe is darker yellow than the lamellae and folded downward, representing the remnant of the partial veil that persists after pileus expansion. The volva at the stipe base is gray-white, cottony, shallowly lobed, and represents the remnant of the universal veil that originally enclosed the egg-shaped immature basidiome. This structure is often buried partially in soil, and improper harvesting may leave the volva behind, obscuring critical diagnostic features. The volva measures 2-3.5 cm in diameter, with a context thickness of 2-3 cm. The pileus flesh is yellow and soft; the lamellae are easily separable from the context (Fig. 2g-i). Basidiospores are ellipsoid, measuring 6-8 × 10-12 µm, containing conspicuous oil droplets; the germ pore is positioned at approximately 20-25 degrees (Fig. 2j). Hyphae are pale yellow, 5-6 µm in diameter, and lack transverse septa (Fig. 2k).

Biology and ecology — Fruiting bodies typically appear at the onset of the rainy season. Recorded at coordinates 12°26.701' N, 108°20.445' E, altitude 790 m, relative humidity 86%, on moderate slopes with a thin litter layer (~0.3 cm) consisting mainly of leaves and pine cones.

Distribution — This species occurs predominantly in pine forests of the Central Highlands.

Current value — A poisonous species posing a significant risk to human health (Dung 2003).

The specimen *A. similis* Boedijn 1951 with code number TH-17-TN.0022 is preserved in the Biology Department Laboratory of Tay Nguyen University.

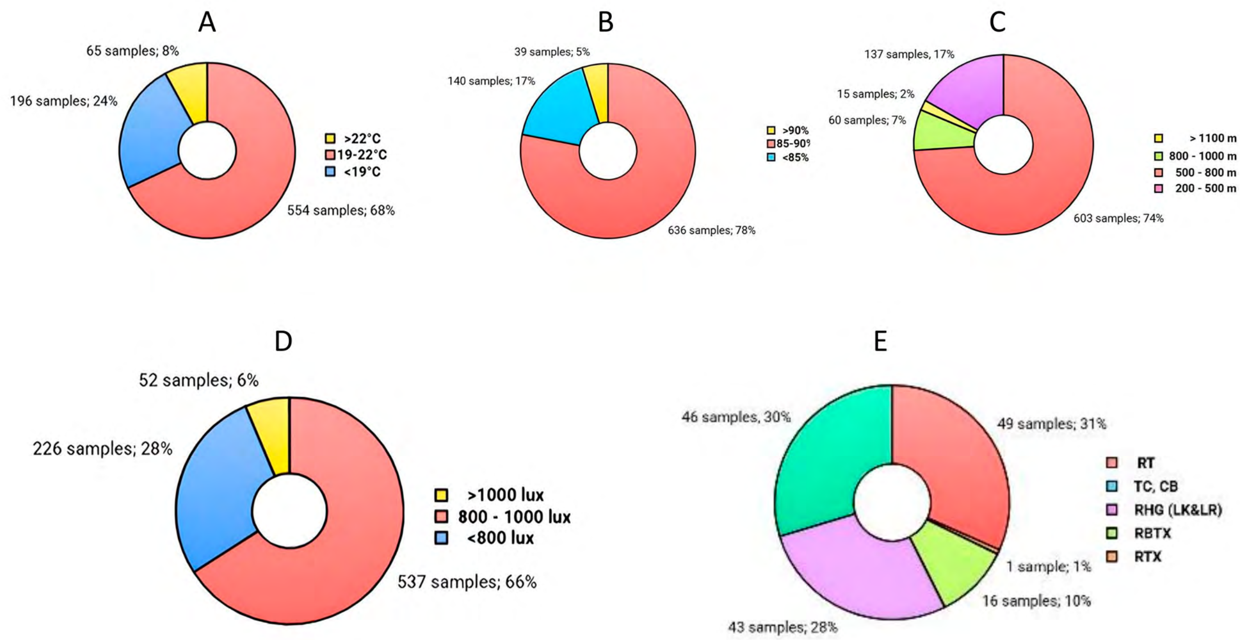

Figure 2. Density of different species by temperature (A), humidity (B), altitude (C), light intensity (D), and habitat (E). / Densidad de diferentes especies según la temperatura (A), la humedad (B), la altitud (C), la intensidad de la luz (D) y el hábitat (E)..

Amanita sp.9 (Fig. S3, Supplementary data)

Description — In the immature stage, the cap is quail-egg-shaped, enclosed within a universal veil that is white and cup-like. The immature fruiting body within the veil is entirely white. Upon emergence from the universal veil, the pileus develops from conical to umbrella-shaped. At maturity, the pileus measures 6-8 cm in diameter, convex to plano-convex, with a dark gray disc and scattered, discontinuous gray patches extending toward the margin. The pileus surface is viscid and sticky when young or under humid conditions. Context extends from the stipe into the pileus and is about 3 mm thick. The margin is inrolled. Lamellae are free, creamy white, deeply striate, and curve gradually toward the stipe. The stipe is cylindrical, white (sometimes with a faint lilac tint), viscid when fresh, 7-17 cm long, 0.7-1.25 cm wide at the base, and gradually enlarges into a bulbous, spongy base with fine hairs. The stipe interior is hollow, forming a narrow tubular canal that extends to the apex. An annulus is positioned on the upper half of the stipe, membranous, thin, more opaque than the lamellae, and folded downward, clearly separated from the gills; this represents the remnant of the partial veil after pileus expansion. The basal bulb is encased in a thin, white, cup-shaped volva with torn, lobed margins resembling kapok flower petals, representing the remnants of the universal veil; the volva is about 2 cm in diameter. Context is white, soft (Fig. S3a-c). Basidiospores are elongate-ellipsoid to ovoid, measuring 5-7 × 9-12 µm, containing abundant refractive granules; the germ pore is eccentric, oriented at an angle of 20-25 degrees (Fig. 3d). Hyphae are hyaline, branched, septate, and 2-3 µm in diameter (Fig. 3e).

Biology and ecology — Fruiting bodies occur solitarily, fruit abundantly during the rainy season, and prefer sunny, relatively dry habitats with temperatures of 18-25 °C and relative humidity of 65-80%.

Distribution — Found in semi-evergreen and mixed forests of the Central Highlands.

Current value — A poisonous species, potentially dangerous to humans.

The specimen *A.* sp.9 with code number TH-17-TN.0028 (CD279) is preserved in the Biology Department Laboratory of Tay Nguyen University.

Amanita sp.10 (Fig. S3, Supplementary data)

Description — The cap measures approximately 6-8 cm in diameter and is pale honey-yellow, with a creamy-white margin occupying 15-20% of the radius. The center is darker, gradually fading toward the margin. The cap surface is dry and non-viscid. The lamellae are white to pale pink, gradually curving toward the stipe and displaying deep grooves. The stipe is cylindrical, white, about 15 cm long, and ~1 cm in diameter at the base, gradually expanding into a spongy tubercle covered with fine hairs. White zigzag bands encircle the stipe. The stipe base is enclosed by a white, sepal-like volva. The context is white and soft (Fig. S3f-h). Basidiospores are elongate-ellipsoid, measuring 6.5-7.5 × 10-12.8 µm, containing numerous pale green oil droplets; the germ pore is eccentric, positioned at an angle of approximately 20-25 degrees (Fig. S3i). Hyphae measure 2-4 µm in diameter (Fig. S3j).

Biology and ecology — This species typically occurs solitarily, with vigorous growth during the rainy season. It thrives in sunny, relatively dry habitats at temperatures of 18-25 °C and relative humidity of 65-80%.

Distribution — Primarily found in pine forests, grasslands, and shrub-dominated areas of the Central Highlands.

Current value — Undetermined.

The specimen *A.* sp.10 with code number TH-17-TN.0030 (DL127) is preserved in the Biology Department Laboratory of Tay Nguyen University.

Amanita sp.11 (Fig. S4, Supplementary data)

Description — At maturity, the cap is umbrella-shaped with a flat to slightly concave center, creamy white to pale yellow in color. The cap measures 8-10 cm in diameter, with the central depression approximately 1 cm in radius, dark yellow in color, gradually fading toward the margin. The cap surface is covered with a layer of burnt-yellow powder that can be easily separated from the gills. The margin bears shallow, closely spaced striations. The gills, creamy white to pale yellow, radiate from the stipe to the cap margin, closely packed, thick, and uniform. The stipe is 6-12 cm long, cylindrical, tapering slightly from the base toward the cap, and similar in color to the cap. Its surface is coated with a layer of orange-yellow powder that is easily detachable. The volva is cup-shaped, representing a remnant of the universal veil from the immature, bract-like stage, and is grayish-brown in color. The flesh is creamy white to pale yellow, thick, and soft (Fig. S4a-c). Spores are broadly ellipsoid to subglobose, measuring 2.5-3.5 × 4-6 µm, containing numerous starch granules, with a germ pore positioned at approximately 15 degrees. Spores are abundant and often aggregated within the volva, making them easy to observe (Fig. S4d). The hyphae are non-branched (Fig. S4e).

Biology and ecology — This species typically occurs solitarily, fruits abundantly during the rainy season, and thrives in sunny, dry habitats at temperatures of 18-25 °C and relative humidity of 65-80%.

Distribution — Widely distributed in the Central Highlands of Vietnam, particularly in provinces such as Dak Lak and Lam Dong (Da Lat).

Current value — This is a poisonous species and may pose serious risks to human health.

The specimen *A.* sp.11 with code number TH-17-TN.0031 (DL019) is preserved in the Biology Department Laboratory of Tay Nguyen University.

Amanita sp.12 (Fig. S4, Supplementary data)

Description — The fruiting body comprises a well-developed pileus and stipe, with a distinct annulus on the stipe, which is centrally attached. The pileus is umbrella-shaped, white, and covered with evenly distributed scales on a brownish background, with the center being darker; diameter 6-9 cm. The margin is inrolled and often bears a white fringe derived from the partial veil (Fig. S4f-h). Lamellae are free, crowded, unequal in length, and white. The stipe is white, measuring 0.5-1 cm in diameter and 6-9 cm in length. The annulus is membranous, located about one-quarter of the stipe length from the apex, and flaring downward. The volva is cup-shaped. Basidia are clavate, measuring 5-7.5 × 20-25 µm (Fig. S4i). Spores are ellipsoid to broadly ellipsoid, 6-7 × 10-13 µm, smooth-walled, and with a single wall layer (Fig. S4i) Hyphae are aseptate, 2-2.5 µm in diameter (Fig. S4k).

Biology and ecology — Occurs on moist, loose soils at coordinates 12°23.109' N, 108°18.165' E, typically from May to November. The habitat is at approximately 600 m elevation, with an average temperature of 21.5 °C, relative humidity of 85%, and steep terrain, often among grasses.

Distribution — Found in semi-evergreen forests, grasslands, and shrub layers along forest edges in Dak Lak Province, Vietnam.

Current value — Undetermined.

The specimen *A.* sp.12 with code number TH-17-TN.0033 (CD279) is preserved in the Biology Department Laboratory of Tay Nguyen University.

The effect of temperature and humidity on the distribution of the *Amanita* genus

As shown in Table 1 and Fig. 2A (Supplementary data), temperature has a large effect on the development of *Amanita* species. At a temperature range of 19-22 °C, the species were most dominant (554 samples, 68%); at about 19 °C, they accounted for 24% (196 samples), while at 22 °C, they were least common (65 samples, 8%).

Table 1 and Fig. 2B (Supplementary data) provide a comprehensive overview of the distribution and percentage composition of the *Amanita* genus. Humidity emerged as a pivotal factor influencing their developmental patterns. A large majority of species (78%, 636 samples) thrived within the humidity range of 85-90%, indicating that this humidity range was the most conducive and suitable for the growth and development of *Amanita* species within the humidity spectrum examined. Approximately 17% of fungal species (140 samples) existed at a humidity below 85%, and 5% (39 samples) thrived in environments exceeding 90% humidity. Notably, humidity levels below 90% often coincided with temperatures exceeding 22 °C, an unfavorable combination for the optimal growth and development of *Amanita* species. Conversely, excessively high humidity levels surpassing 90% create an overly saturated environment, hindering essential substrate decomposition reactions and mycelium growth. Consequently, humidity ranges below 85% and above 90% are less favorable for the *Amanita* genus, resulting in a diminished population density within these conditions. This analysis highlights the 85-90% humidity range in the Central Highlands as an ideal environment for the development of *Amanita* species.

The effect of altitude and light intensity on the distribution of the *Amanita* genus

The impact of altitude on the prevalence of *Amanita* species is presented in Table 1 and Fig. 2C (Supplementary data). Across altitudes of 200 to 1100 meters above sea level, a discernible pattern emerges: the frequency of *Amanita* species exhibits a gradual decrease. These fungi were most prominent at an altitude of 500 to 800 meters, constituting a significant 74% of the observations (603 samples). Following this, 17% (137 samples) were recorded at 200 to 500 meters. The rate of occurrence diminished progressively at higher altitudes: a mere 7% (60 samples) appeared in the 800-1100-meter range, and an even more modest 2% (15 samples) were observed at altitudes surpassing 1100 meters. This phenomenon can be explained by the elevation-related augmentation of water vapor content beyond 800 meters. Coupled with a decrease in oxygen concentration, these conditions lead to heightened air humidity, often reaching 95-100%. Such conditions are unsuitable for both the mycelium and fruiting bodies characteristic of the *Amanita* genus. Consequently, the findings pinpoint the altitude range of 500-800 meters as the optimal elevation for the growth and development of the *Amanita* genus.

The findings detailed in Table 1 and Fig. 2D (Supplementary data) underscore the significant impact of light on the developmental trajectory of fruiting bodies within the *Amanita* genus. Predominantly, *Amanita* species in the Central Highlands exhibit a marked preference for lower light intensities, particularly those falling below the 800-1000 lux threshold. This category constituted a substantial 66% (537 samples) of occurrences, in contrast to the 22% (226 samples) found in light intensities lower than 800 lux and the mere 6% (52 samples) observed at light intensities exceeding 1000 lux. The formation of fruiting bodies in *Amanita* species occurred within a light intensity range of 800-1000 lux. These findings align with the observation that these fungi occur only in coniferous and sparsely forested environments. Following rain showers and the return of sunlight, species of the *Amanita* genus undergo widespread growth, supporting our results that light conditions are essential for their development.

The effect of habitat on the distribution of the *Amanita* genus

Table 1 and Fig. 2E (Supplementary data) demonstrate the profound influence of habitat on the developmental trajectory of fruiting bodies within the *Amanita* genus. Notably, *Amanita* species in the Central Highlands exhibit a distinct proclivity for specific habitats. Among the five studied forest types—pine forests (RT), evergreen forests (RTX), semievergreen forests (RBTX), coniferous forests (RHG), and grasses and low shrubby areas (TC,CB)—these fungi predominantly thrive in pine forests (49 samples, 31%), coniferous forests (43 samples, 28%), and grasses and low shrubby areas (46 samples, 30%). This habitat preference aligns with the distinctive ecological niches these fungi occupy. The presence and distribution of *Amanita* species within these specific habitats highlight the intricate interplay between their growth requirements and the distinct attributes of these environments.

The multivariable regression model predicts the occurrence frequency (density) of the *Amanita* species related to ecological factors.

Statgraphic Centurion XV software is used to analyze 99-point survey data on Excel to set up multivariate regression functions and analyze the relationship and frequency of occurrence of fungi species with ecological factors (Table 2, Supplementary data). When conducting regression analysis with 05 important ecological factors on a sample size of 99 points for mushroom species, variables that do not satisfy the condition on the relationship with the frequency of occurrence at $p > 0.05$ are excluded. The relationship detection is from simple to complex functions, from single variables to combinations of variables and variable transformations. The results obtained are summarized in Table 3 (Supplementary data).

With 05 ecological factors (variables) detected, 04 factors have an important influence on the frequency and distribution of the fungal species and can be expressed through the following equation 1:

Frequency of occurrence = C + a x l + b x m + c x h - d x t (1)

where C, a, b, c, and d, are constant.

With n = 99 and all variables tested by t-standard with the condition $p < 0.05$, it has been discovered that 4 factors, namely light (l), air humidity (m), altitude (h), and temperature (t), have a clear influence on the distribution of the *Amanita* species. Simultaneously, R^2 = 72.7894% with $p < 0.05$ shows that the relationship between the frequency of occurrence of the fungal species and the above 04 ecological factors is very close and interacts with each other as follows: The frequency of occurrence is inversely proportional to the temperature, which shows that as the temperature increases, the frequency of occurrence of fungal species will decrease. In addition, the frequency of occurrence of fungi is proportional to humidity, light intensity, and altitude above sea level. This means that the higher the altitude, the lower the air temperature and the higher the air humidity, and in this condition, the frequency of occurrence of the fungal species increases. Regression modeling helps to understand the initial ecological requirements of fungal species. This is to help detect the distribution area of the species, as well as to be the basis for the cultivation and development of the above-mentioned mushroom species.

DISCUSSION

In this study, we collected numerous mushrooms from the Amanitaceae family in the provinces of the Central Highlands of Vietnam. The Central Highlands is bordered to the north by Quang Nam province, to the east by Quang Ngai, Binh Dinh, Phu Yen, Khanh Hoa, Ninh Thuan, and Binh Thuan provinces, to the south by Dong Nai and Binh Phuoc provinces, and to the west by Attapeu province (Laos) and Ratanakiri and Mondulkiri provinces (Cambodia). This region accounts for one-sixth of Vietnam's area and includes the five provinces of Kon Tum, Gia Lai, Dak Lak, Dak Nong, and Lam Dong. The terrain of the Central Highlands is divided by various mountain ranges (e.g., the Ngoc Linh, An Khe, Chu Dju, and Chu Yang Sin ranges) with altitudes ranging from 400 to 2200 meters above sea level (Fig. 1). The climate is characterized by two distinct seasons: the rainy season from May to November and the dry season from December to April. The average annual rainfall ranges from 1500 to 3600 mm, and approximately 95% occurs during the rainy season, creating high humidity. The average yearly temperature ranges from 21 to 23 °C at altitudes of 500-800 meters and from 18 to 21 °C at higher altitude areas. The average humidity is between 80 and 86%. The ecosystem in the Central Highlands is highly diverse, comprising six main ecosystem types: tropical moist evergreen closed forest, tropical moist deciduous closed forest, tropical moist semi-deciduous closed forest, coniferous forest, mixed bamboo forests, shrub and grassland ecosystems, and field and residential ecosystems. This diversity supports a rich variety of animals, plants, and fungi, including many species listed in the Red Book and some endangered species. The natural conditions in the Central Highlands are conducive to the growth of large mushrooms in general and the Amanitaceae family in particular.

Currently, research on large mushrooms is limited. Globally, most research has focused on the toxicity or toxic components of poisonous mushrooms. For instance, Li & Oberlies (2005) studied the chemical composition of the *Amanita* genus (Li & Oberlies 2005). Wieland (1967, 1986) and Santi *et al.* (2012) investigated the toxicity of *A. phalloides* in Europe and later examined the composition of substances in the genus (Wieland 1967, 1986, Santi *et al.* 2012). Benjamin (1995) researched toxins in mushrooms and medicinal drugs (Benjamin 1995), and Kirchmair *et al.* (2011) examined the potential for kidney failure due to *Amanita* poisoning (Kirchmair *et al.* 2011). Ryvarden & Johansen (1980) focused on mushrooms in eastern Africa, identifying three poisonous species (Ryvarden & Johansen 1980). Ammarati (1985) and Baier (1991) researched mushrooms and their toxins in North America and Canada (Ammarati 1985, Baier 1991). Rolf (1986) studied large mushrooms, including some poisonous families in the southern United States (Rolf 1986). Zhao *et al.* (2007) studied light spectrum effects on the Amanitaceae family in Yunnan and Southern China (Zhao *et al.* 2007). Tulloss (2009) compiled a classification key for 48 species of the Amanitaceae family worldwide (Tulloss 2009), and Sanmee *et al.* (2008) identified 25 Amanitaceae species in Thailand, including 18 newly recorded species (Sanmee *et al.* 2008). Furthermore, genetic sequencing studies of the *Amanita* genus have also been conducted (Zhang *et al.* 2004, Froslev *et al.* 2005, Bonito *et al.* 2010, Kim *et al.* 2013, Li *et al.* 2014, Zhang *et al.* 2015). In Vietnam, most studies focus on the midland delta region; research in the Central Highlands is primarily concentrated in the Southern Central Highlands. Kiet (1981, 2011, 2013) studied large mushrooms in the North, detailing 37 *Amanita* species of large mushrooms in

Vietnam (Kiet 1981, 2011, 2013). Anh (2003) described 12 *Amanita* species in Thua Thien Hue (Anh 2003), while Bao (2008) identified four *Amanita* species (Bao 2008). Dung (2003) identified five poisonous Amanitaceae species in the Central Highlands, illustrating the importance of researching both medicinal and poisonous mushrooms to promote health benefits while ensuring public safety (Dung 2003). Minh (2012) investigated the biological characteristics and toxicity of poisonous mushrooms in Bac Kan Province, identifying five *Amanita* species (Minh 2012), and Dung (2015) described nine *Amanita* species (Dung 2015). Khanh and Hai (2004) reported ten poisonous mushroom species, including five Amanitaceae species (Khanh & Hai 2004), and Hao (2011) studied fungi that cause poisoning in animals, including three *Amanita* species (Hao 2011). Notably, these reports have only focused on studying biodiversity and toxicity, overlooking ecological factors (e.g., temperature, humidity, altitude, light, and habitat) that affect the formation and development of *Amanita* species. Our results show that Central Highlands *Amanita* species thrive at altitudes of 500 to 800 meters (Table 2), with optimal temperatures ranging from 19 to 22 °C (Table 1), humidity levels of 85 to 90% (Table 1), and light intensities between 8000 and 10000 lux (Table 2). High humidity and moderate temperatures are conducive to fungal growth, reflecting conditions that are often found in various forest ecosystems. The Yanshan Mountains in northern China, characterized by lower temperatures and humidity levels and a warm-temperate continental monsoon climate, experience annual precipitation ranging from 350 to 700 mm and host a mix of deciduous broad-leaved and coniferous forests (Zhou *et al.* 2023). By contrast, the Evergreen Forest zone in Taï National Park, Côte d'Ivoire, features an upper Guinean evergreen forest with significantly higher annual rainfall ranging from 1700 to 2200 mm and a distinct wet season from March to July. Although all regions support diverse forest types, the Yanshan Mountains have a broader altitude range (200 to 2200 m), which influences the specific species composition and diversity of *Amanita*. Other regions, such as the Guinean Savanna Zone (Marahoué National Park) and the Sudano-Guinean Savanna Zone (Comoé National Park) in West Africa, present different environments, with mean annual precipitation ranges of 1100-1800 mm and approximately 1150 mm, respectively (Soro *et al.* 2019). Both environments exhibit a forest-savanna mosaic, but they differ in habitat composition and anthropogenic pressures. Marahoué faces severe deforestation and illegal farming, while Comoé is threatened by uncontrolled fires. These conditions highlight the adaptation and survival challenges *Amanita* species face in rapidly changing environments. Additionally, *A. muscaria*, primarily found in temperate and boreal regions of the northern hemisphere, thrives in podzolic soils within deciduous and coniferous forests, demonstrating its preference for acidic conditions with low nitrogen mineralization. These studies suggest that *Amanita* species have adapted well to various climates, including temperate regions with wide temperature, humidity, and height ranges, indicating their resilience and ecological significance (Quentin & Lopez 2021).

Our study is one of the first on the *Amanita* genus in the Central Highlands of Vietnam, specifically focusing on the ecological factors influencing the distribution of these poisonous mushrooms in the region. We compiled a comprehensive list of *Amanita* species, identifying 13 of 25 known species. In conclusion, the *Amanita* species found in the Central Highlands of Vietnam thrive within the temperature range of 19-22 °C, showing optimal growth and development. These fungi are adapted to relatively high humidity conditions, flourishing within the range of 85-90%, an environment conducive to their appearance, survival, and maturation. Within the altitude range of 200 to 1100 meters above sea level, the frequency of *Amanita* species tends to decline with increasing elevation. Notably, the genus is most abundant at altitudes between 500 and 800 meters, with 74% of observations occurring in this range. Light also has an impact on the distribution and appearance of these fungi. Predominantly, *Amanita* species in the Central Highlands exhibit peak growth at light intensities of 800 to 1000 lux, indicating that this range is the most suitable for these fungi. Habitat also plays a pivotal role in the development of *Amanita* species. Among the five forest types studied in the Central Highlands, these *Amanita* species predominantly inhabit pine forests, coniferous forests, grasslands, and low shrubby areas. Notably, the ecological factors of light, humidity, altitude, and temperature influence the occurrence of fungal species, and these variables are intricately connected. The relation between these variables is very close, and they interact with each other through the equation (1). Specifically, the frequency of occurrence exhibits an inverse relationship with temperature: as temperature increases, fungal species occurrence decreases. Conversely, the occurrence of fungi is positively associated with humidity, light intensity, and altitude. Higher altitudes correspond to lower air temperatures and higher humidity, providing an environment conducive to increased fungal occurrence.

In this study, we present several significant findings, including comprehensive morphological descriptions of *A. crocea* Quél. Singer 1951, *A. eliae* Quél. 1872, *A. fulva* Fr., 1815, *A. similis* Boedijn 1951, and *A.* sp. 9-sp. 12. This work is the first to examine the effects of ecological factors—specifically light, temperature, humidity, and altitude—on the occurrence and growth of *Amanita* species. Moreover, we developed a multivariate regression model to predict species occurrence frequency (density). However, species identification was based solely on macroscopic and microscopic morphological analyses, without molecular confirmation, due to limited laboratory facilities and specialized equipment. Future studies will address these limitations by incorporating molecular approaches to enhance taxonomic precision and provide a more comprehensive understanding of the ecological patterns of *Amanita* species.

CONCLUSIONS

This study is one of the first on the *Amanita* genus in the Central Highlands of Vietnam, specifically focusing on the ecological factors influencing the distribution of these poisonous mushrooms in the region. The results indicate that the *Amanita* species thrive within the temperature range of 19-22 °C, high humidity conditions (85-90%), altitudes between 500 and 800 meters, light intensities of 800 to 1000 lux, and these *Amanita* species predominantly inhabit pine forests, coniferous forests, grasslands, and low shrubby areas. These fungi have a close relationship with other plant species through symbiosis, contributing to improving soil quality and nutrient cycling in nature. Research on the effects of ecological factors such as temperature, humidity, light, and altitude facilitate the identification of ideal environmental conditions for mushroom growth, supporting the development of effective conservation strategies. By documenting *Amanita* species, this research not only enhances our understanding of *Amanita* diversity in Vietnam but also sets a precedent for future studies to explore the ecological roles of these mushrooms.

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