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State of knowledge of the Glomeromycota of Costa Rica

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ABSTRACT

Introduction: Arbuscular mycorrhizal fungi (AMF) play a pivotal role in plant nutrition and soil stability, also play an important role for sustainable agriculture and the restoration of degraded areas. In Costa Rica, research has been conducted on the diversity of AMF in select ecosystems. However, a comprehensive compilation of these studies is currently lacking.

Objective: To compile an updated list of arbuscular mycorrhizal fungi (AMF) in Costa Rica, organised by vegetation types and life zones. This will facilitate a more comprehensive understanding of their diversity and serve as a foundation for future research in taxonomy, distribution, ecology and biotechnological applications.

Methods: A comprehensive literature search was conducted in Google Scholar, Scopus and Web of Science, utilising Spanish and English terms related to arbuscular mycorrhizal fungi (AMF) and Costa Rica, spanning the period from 1971 to 2024. The selection criterion included studies that identified species based on morphological or molecular criteria. The following information was integrated into a database.

Results: We compiled 57 studies published from 1975-2024 and after screening 549 initial records, 115 records corresponding to species level were confirmed. 60 AMF species belonging to five orders were identified, representing 16 % of the global diversity known as Glomeromycota. The families Glomeraceae (23 species) and Acaulosporaceae (19 species) were the best represented. Furthermore, it was observed that studies have been conducted in only four of the 12 life zones described for Costa Rica, and include agroecosystems and trap crops (consortia) or pure crops (monospecific).

Conclusions: It is evident that there has been a degree of advancement in the comprehension of the ecology, diversity and distribution of AMF. Nevertheless, further ecological and taxonomic research is required, encompassing both morphological and molecular analyses, to facilitate the expansion of knowledge concerning the distribution and diversity of AMF in Costa Rica.

Keywords: Arbuscular mycorrhizal fungi; distribution; ecological diversity; taxonomy; life zones.

RESUMEN

Estado del conocimiento de los Glomeromycota de Costa Rica

Introducción: Los hongos micorrícicos arbusculares (HMA) son clave para la nutrición vegetal y la estabilidad del suelo, también juegan un papel importante en la agricultura sostenible y la restauración de áreas degradadas. En Costa Rica, su diversidad ha sido estudiada en algunos ecosistemas, pero a la fecha no hay una compilación integral.

Objetivo: Compilar una lista actualizada de hongos micorrícicos arbusculares (HMA) en Costa Rica, organizada por tipos de vegetación y zonas de vida, que amplíe la comprensión de su diversidad y sirva de base para estudios futuros en taxonomía, distribución, ecología y aplicaciones biotecnológicas.

Métodos: Se realizó una búsqueda bibliográfica en Google Scholar, Scopus y Web of Science, empleando términos en español e inglés relacionados con hongos micorrícicos arbusculares (HMA) y Costa Rica, en el periodo 1971-2024. Se incluyeron únicamente estudios que identificaran especies basándose en criterios morfológicos o moleculares, integrando la siguiente información en una base de datos.

Resultados: Compilamos 57 estudios publicados entre 1975-2024 y después de depurar 549 registros iniciales, se confirmó que 115 registros corresponden al nivel de especie. Se identifican 60 especies de HMA pertenecientes a cinco órdenes, lo que representa el 16 % de la diversidad global conocida como Glomeromycota. Las familias Glomeraceae (23 especies) y Acaulosporaceae (19 especies) fueron las mejor representadas. Además, se observó que los estudios se han llevado a cabo únicamente en cuatro de las 12 zonas de vida descritas para Costa Rica, además de algunos estudios en agroecosistemas, cultivos trampa (consorcios) y cultivos puros (monoespecíficos).

Conclusiones: Se ha avanzado en el conocimiento de la ecología, diversidad y distribución de los HMA, sin embargo, es necesario continuar realizando investigaciones ecológicas y taxonómicas que incluyan tanto análisis morfológicos como moleculares, con el fin de ampliar el conocimiento sobre la distribución y diversidad de los HMA en Costa Rica.

Palabras clave: Hongos micorrícicos arbusculares; distribución; diversidad ecológica; taxonomía; zonas de vida.

INTRODUCTION

Arbuscular mycorrhizal fungi (AMF) are a fungal group that is widely distributed in most terrestrial ecosystems (Schüßler et al., 2001), which are associated with 72 % of vascular plants (Brundrett & Tedersoo, 2018). AMF belonging to the phylum Glomeromycota were previously classified within the Zygomycota (Morton & Benny, 1990), but in recent decades, they have been recognized as an independent and ancient phylum of the kingdom Fungi (Schüßler et al., 2001). These fungi are obligate symbionts of terrestrial plants and play an important role in nutrient uptake, particularly phosphorus absorption, improving plant growth and the tolerance to different types of stress (Brundrett & Tedersoo, 2018; Smith & Read, 2010; Wang & Qiu, 2006). They also contribute to soil stabilization (Rillig & Steinberg, 2002), and facilitate plant establishment and recruitment through multiple hyphal networks that connect plant-plant (Van der Heijden & Horton, 2009; Van der Heijden et al., 2015). They also play an important role in agroecosystems because of their biotechnological use as biofertilizers (Jeffries & Barea, 2012). This highlights their importance for sustainable agriculture and the restoration of degraded areas (Carrillo-Saucedo et al., 2022).

The phylum Glomeromycota includes approximately 371 species distributed in three classes, five orders, 16 families, and 48 genera (Goto & Jobim, 2024; Wijayawardene et al., 2022). A number of compilations of AMF diversity have been made at multiple levels, providing valuable information on their biogeographic distribution and ecological roles. At the biogeographic region level, Stürmer and Kemmelmeier (2021) documented 221 AMF species in the Neotropics, representing 69% of the global diversity described for the phylum Glomeromycota. The study encompassed 11 biomes and 52 ecological regions, emphasizing the ecological significance of AMF in diverse ecosystems, including tropical rainforests and grasslands. However, it should be noted that the study did not include data for Costa Rica.

Research has been published from Mexico and Peru, two countries which are characterised by high biodiversity. In Mexico, Álvarez-López-tello et al. (2023) and Polo-Marcial et al. (2021) identified 160 AMF species, highlighting that the majority of studies have been conducted in agroecosystems and xerophytic shrublands, with Oaxaca identified as a prominent biological hotspot. In Peru, Vega-Herrera et al. (2023) reported 93 species classified according to natural regions (Amazon, Andes and Coast), reflecting the ecological heterogeneity of the country and the predominance of families such as Glomeraceae and Acaulosporaceae. At the ecosystem-specific level, Marinho et al. (2018) addressed AMF diversity in Costa Rica's tropical forests. This research highlighted that tropical rainforests, a representative ecosystem of the country, harbour a significant proportion of AMF species, underscoring their ecological importance in processes such as enhancing nutrient uptake and soil stabilisation. Notably, Costa Rican specimens have played a pivotal role in the taxonomic classification of novel species, underscoring the country's significance in mycological research. For instance, *Acaulospora foveata* and *A. tuberculata* were described using paratypes collected in Costa Rica (Morton, 1990), while *Acaulospora splendida* was identified with a holotype from the country (Sieverding et al., 1988). Beyond these contributions, however, there is no compilation that comprehensively analyses the AMF species of Costa Rica.

Costa Rica, with its great biodiversity and diverse geography, offers ideal conditions for a wide diversity of AMF. Its geography, with mountain ranges that create numerous microclimates and a rich variety of ecosystems, contributes to this diversity (Lobo et al., 2021). The life zone classification system, developed by Leslie Holdridge (1979), identifies 12 life zones in Costa Rica, which reflects its ecological diversity.

Studies on the Glomeromycota in Costa Rica began in 1975 with an ecological survey developed by Janos (Janos, 1975), this study was the first of its kind in the country to address the associations between AMF and various tree species in tropical forests. Initially, research focused on the biotechnological potential of AMF and their impact on plant phenology, and the first taxonomic records were published years later (Blanco & Salas, 1997; Fischer et al., 1994; Sieverding et al., 1988). Most studies have focused on the impact of AMF on plants rather than on their taxonomic identification or geographic distribution (Aldrich-Wolfe, 2007; Fischer et al., 1994; Picone, 2000; Salas & Blanco, 2000; Sharrock et al., 2004; Shepherd et al., 2007; Sieverding et al., 1988). This analysis is grounded in scientific literature available in English and Spanish. The bibliographic search encompasses articles from the period between 1971 and 2024.

The objective of the present study was to compile an updated list of AMF of Costa Rica, organized by vegetation type and life zone. These new records broaden our knowledge of the diversity of AMF in Costa Rica and provide a basis for making decisions about future studies on the taxonomy, distribution, ecology and biotechnological applications of the Glomeromycota of Costa Rica.

MATERIALS AND METHODS

We conducted a literature search of AMF recorded in Costa Rica using the following databases: Google Scholar, Scopus, and Web of Science. The terms used in the search were: "arbuscular", "vesicular", "mycorrhizal", "Glomeromycota", and each family and genus of AMF, which were included in combination with the words "native" and "Costa Rica" both in Spanish and English, and we also included articles published between 1971 and 2024 to compile a checklist of AMF.

We included articles that employ identification criteria based on the morphological and/or molecular characteristics of arbuscular mycorrhizal fungi up to species level and taxon descriptions and integrated the information in a database with the reported species name, associated plant species, locality where it was reported, ecological data, molecular data, life

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zone, soil type, and the phenotypic characteristics of the glomerospores considered in the determination of the species.

To generate the AMF checklist, we ordered the AMF species according to the taxonomic classification proposed by Błaszkowski (2012), Oehl et al. (2008) and Oehl et al. (2011), including additional taxa proposed by Błaszkowski et al. (2015), Błaszkowski et al. (2017), Błaszkowski et al. (2018), Corazón-Guivin et al. (2019), Goto et al. (2012), Jobim et al. (2016), Marinho et al. (2018) and Symanczik et al. (2018). We used the life zone classification by Leslie Holdridge (1979), which considers 12 life zones (Tropical dry forest, tropical moist forest, tropical wet forest, premontane moist forest, premontane wet forest, premontane rainforest, lower montane moist forest, lower montane wet forest, lower Montane rain forest, montane wet forest, montane rain forest and subalpine rain paramo).

In order to illustrate the distribution of AMF species across the various life zones identified in Costa Rica, a Sankey diagram was constructed utilising the RStudio's ggsankey package. This diagram, based on presence/absence data, aims to graphically show the associations between AMF species and life zones, indicating where the species have been recorded. Furthermore, a network diagram was constructed using the RStudio igraph package, with the objective of visualising the connections between life zones and Glomeromycota species.

Rarefaction and extrapolation curves: We performed rarefaction and extrapolation curves based on individuals and sampling coverage to estimate the state of knowledge about the AMF community (species richness) in different life zones in Costa Rica (Chao & Jost, 2012). Individual-based curves consider the number of individuals collected in each sample, while sample coverage-based curves assess the proportion of the total species community expected to have been captured as a function of sampling effort. In order to predict the expected number of total species and to assess the required sampling effort, data per life zone were used considering their sampling coverage (Chao & Jost, 2012; Chao & Lee, 1992). Rarefaction curves were constructed both for observed data and to extrapolate the expected number of species beyond the original sample size, allowing estimation of expected richness with increased sampling effort. The corresponding graphs were generated using the RStudio iNEXT package.

RESULTS

We compiled and analyzed 57 articles that addressed aspects related to arbuscular mycorrhizal fungi (AMF) in Costa Rica published from 1975 to 2024 (Despite the fact that our research has been conducted since 1971, the first documented report was not published until 1975). It is important to note that not all of these studies focused on the identification or geographic distribution of species; only 28 % included taxonomic records (published from 1988 to 2024), while 38 % examined the ecology (the analysis of the biological, functional and ecological interactions between arbuscular mycorrhizal fungi (AMF) and abiotic and biotic factors present in these ecosystems) of AMF, 14 % investigated their physiological effect on host plants, and 19 % mentioned the Glomeromycota of Costa Rica in terms of their potential use and importance for ecosystems but without exploring any aspect in detail or providing specific data (Fig. 1).

Following a screening process, we included a total of 549 records of AMF species in our database. Of these records, 434 were only determined at a genus level or designated as related species and were thus eliminated. As a result, we kept 115 records of AMF species with a confirmed identification, which corresponded to a total of 60 species classified into three classes, five orders, ten families, and 17 genera of Glomeromycota in Costa Rica (Table 1 and Table 2).

The class Archaeosporomycetes is represented by the order Archaeosporales, the family Ambisporaceae, the genus *Ambispora,* and three species (Table 1 and Table 2).

Table 1
Taxonomic classification of the arbuscular mycorrhizal fungi from Costa Rica.

Class (3)	Order (5)	Family (10)	Genus (17)	Species (60)
Archaeosporomycetes	Archaeosporales	Ambisporaceae	*Ambispora*	3
Glomeromycetes	Glomerales	**Glomeraceae**	*Dominikia*	**1**
			Funneliformis	**3**
			Glomus	**6**
			Rhizoglomus	**7**
			Sclerocystis	**1**
		Entrophosporaceae	*Entrophospora*	5
	Diversisporales	Diversisporaceae	*Diversispora*	1
			Sieverdingia	1
		Acaulosporaceae	*Acaulospora*	**18**
			Kuklospora	**1**
	Gigasporales	Gigasporaceae	*Gigaspora*	5
		Scutellosporaceae	*Scutellospora*	1
		Racocetraceae	*Cetraspora*	1
			Racocetra	2
		Dentiscutataceae	*Dentiscutata*	3
Paraglomeromycetes	Paraglomerales	Paraglomeraceae	*Paraglomus*	1

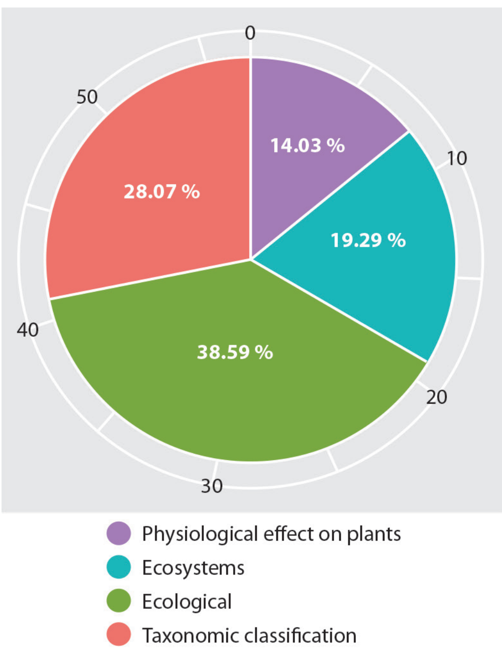

Fig. 1. Percentage distribution of studies on arbuscular mycorrhizal fungi (AMF) in Costa Rica (1975–2024) categorized by topics: taxonomic classification, ecological aspects, ecosystems, and physiological effects on plants.

The distribution of AMF studies included only four of the 12 identified life zones (Table 2, Fig. 2 and Fig. 3) (Holdridge, 1979): tropical moist forest, premontane wet forest, tropical wet forest and tropical dry forest; as well as agro-ecosystems and trap crops (consortia) or pure cultures (monospecific) (Fig. 2 and Fig. 3). Table two shows detailed data of the hosts (plant species) colonized by the 60 AMF species reported in Costa Rica from 1988 to 2024.

As demonstrated in Table 2, the Glomeromycota species with the highest number of reported hosts can be organised as follows (in decreasing order): *Acaulospora scrobiculata* (29 hosts), *Acaulospora foveata* (28 hosts), *Glomus clavisporum* (26 hosts), *Ambispora leptoticha* (21 hosts), *Acaulospora spinosa* (20 hosts), *Acaulospora denticulata* (19 hots), *Funneliformis monosporus* (17 hosts), *Acaulospora elegans* con (16 hosts), *Glomus macrocarpum* (17 hosts), *Acaulospora mellea* (15 hosts), *Glomus microcarpum* (14 hosts), *Rhizoglomus clarum* (14 hosts), *Acaulospora tuberculata* (13 hosts), *Paraglomus occultum* (12 hosts), *Acaulospora laevis* (12 host), *Rhizoglomus aggregatum*

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Table 2
Checklist of the reported arbuscular mycorrhizal fungi in Costa Rica from 1988 to 2024.

Species	Life Zone or adapted/ modified system	Associated plant species	Reference number
Archaeosporales			
Ambispora appendicula (Spain, Sieverd., N.C. Schenck) C. Walker	Greenhouse and premontane wet forest	*Brachiaria decumbens, Cajanus bicolor*	2, 4, 16
Ambispora gerdemannii (S.L. Rose, B.A. Daniels & Trappe) C. Walker, Vestberg & A. Schüssler	Tropical wet forest	*Carapa guianensis, Dalbergia tucurensis, Dipterix panamensis, Mimosa púdica, Pentaclethra macroloba, Sinarouba amara, Solanum* sp., *Vochysia ferruginea*	6
Ambispora leptoticha (N.C. Schenck & T.H. Nicolson) Walker, Vestberg & A. Schüssler	Premontane wet forest, tropical dry forest and tropical wet forest.	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Carapa guianensis, Casearia aculeata, Cordia alliodora, Chomelia spinosa, Dalbergia tucurensis, Dipterix panamensis, Enterolobium cyclocarpum, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Pentaclethra macroloba, Sinarouba amara, Spondias mombin, Tabebuia spp., Vochysia ferruginea, Vriesea werkleana*	5, 6
Diversisporales			
Acaulospora bireticulata (F.M. Rothwell & Trappe)	Agroecosystem and tropical wet forest	*Carapa guianensis, Cedrela odorata, Dalbergia tucurensis, Dipterix panamensis, Mimosa pudica, Pentaclethra macroloba, Sinarouba amara, Solanum* sp., *Vochysia ferruginea*	6, 15
Acaulospora colossica (P.A. Schultz, Bever & J.B. Morton)	Tropical wet forest	*Inga paterno, Tabebuia ochraceae*	12
Acaulospora denticulata (Sieverd. & S. Toro)	Tropical dry forest	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Casearia aculeata, Chomelia spinosa, Cordia alliodora, Enterolobium cyclocarpum, Licania arborea, Lonchocarpus* spp., *Luekea spp., Lysoma seemannii, Spondias mombin, Tabebuia* spp.	5
Acaulospora elegans (Trappe & Gerd)	Tropical dry forest	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Casearia aculeata, Chomelia spinosa, Cordia alliodora, Enterolobium cyclocarpum, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Spondias mombin, Tabebuia* spp.	5
Acaulospora excavata Ingleby & C. Walker	Agroecosystem	*Cedrela odorata*	15
Acaulospora foveata Trappe & Janos	Agroecosystem, greenhouse, tropical dry forest, tropical moist forest and tropical wet forest	*Allium cepa L., Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Carapa guianensis, Casearia aculeata, Cedrela odorata, Ceiba pentandra, Chomelia spinosa, Cordia alliodora, Dalbergia tucurensis, Dipterix panamensis, Enterolobium cyclocarpum, Hyeronima alchorneoides, Jatropha curcas, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Mimosa pudica, Pentaclethra macroloba, Psidium guajava L., Sinarouba amara, Solanum* sp., *Spondias mombin, Tabebuia* spp., *Vochysia ferruginea*	3, 5, 6, 10, 15, 16

Species	Life Zone or adapted/ modified system	Associated plant species	Reference number
Acaulospora laevis Gerd. & Trappe	Agroecosystem, premontane wet forest and tropical wet forest	*Cedrela odorata, Coffea* sp., *Inga paterno, Vriesea werkleana*	14, 15
Acaulospora longula (Spain & N.C. Schenck)	Premontane wet forest	Not specified	2
Acaulospora mellea Spain & N.C. Schenck	Agroecosystem, greenhouse, tropical moist forest and tropical wet forest	*Carapa guianensis, Cedrela odorata, Ceiba pentandra, Cordia alliodora, Dalbergia tucurensis, Dipterix panamensis, Hyeronima alchorneoides, Jatropha curcas, Mimosa pudica, Pentaclethra macroloba, Sinarouba amara, Solanum* sp., *Vochysia ferruginea*	6, 8, 10, 15, 16
Acaulospora minuta Oehl, Tchabi, Hount., Palenz., I.C. Sánchez & G.A. Silva	Agroecosystem	*Coffea* sp.	14
Acaulospora morrowiae Spain & N.C. Schenck,	Tropical moist forest	*Cedrela odorata, Ceiba pentandra* *Cordia alliodora, Hyeronima alchorneoides, Zea mays*	6, 8, 10
Acaulospora rehmii Sieverd. & S. Toro	Agroecosystem and greenhouse	*Cedrela odorata, Jatropha curcas*	5, 15, 16
Acaulospora rugosa J.B. Morton	Greenhouse and premontane wet forest	*Jatropha curcas, Vriesea werkleana*	2, 16
Acaulospora scrobiculata Trappe	Agroecosystem, greenhouse, premontane wet forest, tropical dry forest, tropical moist forest and tropical wet forest	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Carapa guianensis, Casearia aculeata, Cedrela odorata, Ceiba pentandra, Chomelia spinosa, Coffea* sp., *Cordia alliodora, Dalbergia tucurensis, Dipterix panamensis, Enterolobium cyclocarpum, Hyeronima alchorneoides, Jatropha curcas, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Mimosa pudica, Pentaclethra macroloba, Sinarouba amara, Solanum* sp., *Spondias mombin, Tabebuia* spp., *Termilania amazonia, Vochysia ferruginea, Vriesea werkleana*	2, 5, 6, 8, 10, 13, 14, 15, 16
Acaulospora spinosa C. Walker & Trappe	Agroecosystem, greenhouse, premontane wet forest, tropical dry forest and tropical moist forest	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Casearia aculeata, Cedrela odorata, Ceiba pentandra, Chomelia spinosa, Cordia alliodora, Enterolobium cyclocarpum, Hyeronima alchorneoides, Jatropha curcas, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Spondias mombin, Tabebuia* spp., *Vriesea werkleana*	5, 6, 7, 8, 15, 16
Acaulospora spinosissima Oehl, Palenz., Sánchez-Castro, Tchabi, Hount. & G. A. Silva	Agroecosystem	*Cedrela odorata*	15
Acaulospora splendida Sieverd., Chaverri & I. Rojas	Greenhouse	*Quercus costaricensis*	1
Acaulospora tuberculata Janos & Trappe	Agroecosystem, greenhouse and tropical wet forest,	*Carapa guianensis, Cedrela odorata, Dalbergia tucurensis, Dipterix panamensis, Jatropha curcas, Mimosa pudica, Pentaclethra macroloba, Sinarouba amara, Solanum* sp., *Vochysia ferruginea*	6, 15, 16
Kuklospora colombiana (Spain & N.C. Schenck) Oehl & Sieverd	Agroecosystem	*Cedrela odorata*	15

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Species	Life Zone or adapted/ modified system	Associated plant species	Reference number
Sieverdingia tortuosa (N.C. Schenck & G.S. Sm.) Błaszk., Niezgoda & B.T. Goto.	Tropical moist forest	*Cedrela odorata, Ceiba pentandra, Cordia alliodora, Hyeronima alchorneoides*	8, 10
Diversispora versiformis (P. Karst.) Oehl, G.A. Silva & Sieverd	Greenhouse and premontane wet forest	*Tithonia diversifolia, Vriesea werkleana*	11
Entrophosporales			
Entrophospora claroidea (N.C. Schenck & G.S. Sm.) Błaszk., Niezgoda, B.T. Goto & Magurno	Greenhouse, ropical moist forest and premontane wet forest	*Brachiaria decumbens, Cajanus bicolor, Ceiba pentandra, Vriesea werkleana*	8
Entrophospora colombiana Spain & N.C. Schenck	Premontane wet forest, tropical wet forest	*Carapa guianensis, Dalbergia tucurensis, Dipterix panamensis, Mimosa pudica, Pentaclethra macroloba, Sinarouba amara, Solanum* sp., *Vochysia ferruginea, Vriesea werkleana*	2, 6
Entrophospora etunicata (W.N. Becker & Gerd.) Błaszk., Niezgoda, B.T. Goto & Magurno	Agroecosystem, premontane wet forest and tropical moist forest	*Cedrela odorata, Coffea* sp., *Cordia alliodora, Hyeronima alchorneoides, Vriesea werkleana, Zea mays*	9, 14
Entrophospora infrequens (I.R. Hall) R.N. Ames & R.W. Schneid.	Greenhouse	*Brachiaria decumbens, Cajanus bicolor*	4
Entrophospora lutea (L.J. Kennedy, J.C. Stutz & J.B. Morton) Błaszk., Niezgoda, B.T. Goto & Magurno	Tropical moist forest	*Termilania amazonia*	13
Glomerales			
Funneliformis geosporum (T.H. Nicolson & Gerd.) C. Walker & A. Schüssler	Agroecosystem, premontane wet forest and tropical wet forest	*Carapa guianensis, Cedrela odorata, Dalbergia tucurensis, Dipterix panamensis, Mimosa pudica, Pentaclethra macroloba, Sinarouba amara, Solanum* sp., *Vochysia ferruginea, Vriesea werkleana*	2, 15
Funneliformis monosporus (Gerd. & Trappe) Oehl, G.A. Silva & Sieverd	Tropical dry forest	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Casearia aculeata, Chomelia spinosa, Cordia alliodora, Enterolobium cyclocarpum, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Spondias mombin, Tabebuia* spp.	5
Funneliformis mosseae (T.H. Nicolson & Gerd.) C. Walker & A. Schüssler	Agroecosystem, premontane wet forest	*Cedrela odorata, Vriesea werkleana*	2, 15
Glomus brohultii (Sieverd. & Herrera)	Premontane wet forest	Not specified	2
Glomus clavisporum (Trappe) R.T. Almeida & N.C. Schenck	Agroecosystem, tropical dry forest, tropical moist forest and tropical wet forest	*Allium cepa L., Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Carapa guianensis, Casearia aculeata, Cedrela odorata, Chomelia spinosa, Cordia alliodora, Dalbergia tucurensis, Dipterix panamensis, Enterolobium cyclocarpum, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Pentaclethra macroloba, Psidium guajava L., Sinarouba amara, Spondias mombin, Tabebuia* spp., *Vochysia ferruginea*	3, 5, 6, 15

Species	Life Zone or adapted/ modified system	Associated plant species	Reference number
Glomus microcarpum (Tul. & C. Tul.)	Tropical dry forest	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Casearia aculeata, Chomelia spinosa, Cordia alliodora, Enterolobium cyclocarpum, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Spondias mombin, Tabebuia* spp.	5
Glomus macrocarpum (Tul. & C. Tul.)	Tropical dry forest and ropical moist forest	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Casearia aculeata, Chomelia spinosa, Cordia alliodora, Enterolobium cyclocarpum, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Spondias mombin, Tabebuia* spp., *Termilania amazonia*	5,13
Glomus rubiforme (Gerd. & Trappe) R.T. Almeida & N.C. Schenck	Tropical wet forest	*Carapa guianensis, Dalbergia tucurensis, Dipterix panamensis, Pentaclethra macroloba, Sinarouba amara, Vochysia ferruginea*	6
Glomus taiwanense (C.G. Wu & Z.C. Chen) R.T. Almeida & N.C. Schenck ex Y.J. Yao	Greenhouse	*Jatropha curcas*	16
Dominikia indica (Błaszk., Wubet & Harikumar) Błaszk., G.A. Silva & Oehl	Agroecosystem	*Coffea* sp.	14
Rhizoglomus aggregatum (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl	Tropical dry forest	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Casearia aculeata, Chomelia spinosa, Cordia alliodora, Enterolobium cyclocarpum, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Spondias mombin, Tabebuia* spp.	5
Rhizoglomus clarum (T.H. Nicolson & N.C. Schenck) Sieverd., G.A. Silva & Oehl	Agroecosystem, greenhouse, premontane wet forest, tropical moist forest and tropical wet forest	*Carapa guianensis, Cedrela odorata, Dalbergia tucurensis, Dipterix panamensis, Hyeronima alchorneoides, Inga paterno, Jatropha curcas, Mimosa pudica, Pentaclethra macroloba, Sinarouba amara, Solanum* sp., *Vochysia ferruginea, Vriesea werkleana*	6, 10, 12, 15, 16
Rhizoglomus fasciculatum (Thaxt.) Sieverd., G.A. Silva & Oehl	Agroecosystem, premontane wet forest	*Coffea* sp., *Vriesea werkleana*	14
Rhizoglomus intraradices (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl	Greenhouse, premontane wet forest, tropical moist forest and tropical wet forest	*Tabebuia ochraceae, Termilania amazonia, Tithonia diversifolia, Vriesea werkleana, Zea mays*	9, 11, 12, 13
Rhizoglomus microaggregatum (Koske, Gemma & P.D. Olexia) Sieverd., G.A. Silva & Oehl	Greenhouse	*Brachiaria decumbens, Cajanus bicolor*	4
Rhizoglomus proliferum (Dalpé & Declerck) Sieverd., G.A. Silva & Oehl	Tropical wet forest	*Vriesea werkleana*	12
Rhizoglomus vesiculiferum (Thaxt.) Błaszk., Kozłowska, Niezgoda, B.T.Goto & Dalpé	Premontane wet forest	*Vriesea werkleana*	12

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Species	Life Zone or adapted/ modified system	Associated plant species	Reference number
Sclerocystis coremioides Berk. & Broome	Agroecosystem, greenhouse, premontane wet forest, tropical moist forest and tropical wet forest	*Allium cepa L., Carapa guianensis Cedrela odorata, Dalbergia tucurensis, Dipterix panamensis, Jatropha curcas, Mimosa pudica, Pentaclethra macroloba, Psidium guajava L., Sinarouba amara, Solanum* sp., *Vochysia ferruginea, Vriesea werkleana*	3, 6, 15, 16
Gigasporales			
Dentiscutata heterogama (T.H. Nicolson & Gerd.) Sieverd., F.A. de Souza & Oehl	Greenhouse	*Brachiaria decumbens, Cajanus bicolor*	4
Dentiscutata scutata (C. Walker & Dieder.) Sieverd., F.A. de Souza & Oehl	Tropical moist forest	*Cordia alliodora, Hyeronima alchorneoides*	10
Dentiscutata nigra (J.F. Readhead) Sieverd., F.A. de Souza & Oehl	Tropical dry forest	*Astronium graveolens, Bombacopsis quinata, Bursea simaruba, Calycophyllum candidissimum, Casearia aculeata, Chomelia spinosa, Cordia alliodora, Enterolobium cyclocarpum, Licania arborea, Lonchocarpus* spp., *Luekea* spp., *Lysoma seemannii, Spondias mombin, Tabebuia* spp.	5
Gigaspora albida N.C. Schenck & G.S. Sm	Greenhouse and remontane wet forest	*Brachiaria decumbens, Cajanus bicolor, Vriesea werkleana*	4, 6
Gigaspora gigantea (T.H. Nicholson & Gerd.) Gerd. & Trappe	Premontane wet forest and tropical wet forest	*Carapa guianensis, Dalbergia tucurensis, Dipterix panamensis, Pentaclethra macroloba, Sinarouba amara, Vochysia ferruginea, Vriesea werkleana*	6
Gigaspora margarita W.N. Becker & I.R. Hall	Agroecosystem and greenhouse	*Coffea* sp., *Jatropha curcas*	14, 16
Gigaspora ramisporophora Spain, Sieverd. & N.C. Schenck	Greenhouse	*Brachiaria decumbens, Cajanus bicolor*	4
Gigaspora rosea T.H. Nicolson & N.C. Schenck	Tropical moist forest	*Zea mays*	9
Cetraspora pellucida (T.H. Nicolson & N.C. Schenck) Oehl, F.A. de Souza & Sieverd	Greenhouse, premontane wet forest, tropical moist forest and tropical wet forest	*Allium porrum, Cajanus cajans, Capsicum annum, Carapa guianensis, Cedrela odorata, Cordia alliodora, Cucumis sativus, Dalbergia tucurensis, Dipterix panamensis, Hyeronima alchorneoides, Pentaclethra macroloba, Sinarouba amara, Vochysia ferruginea, Vriesea werkleana, Zea mays*	6, 7, 10
Racocetra castanea (C. Walker) Oehl, F.A. de Souza & Sieverd	Premontane wet forest and tropical moist forest	*Cedrela odorata, Hyeronima alchorneoides, Vriesea werkleana*	10
Racocetra coralloidea (Trappe, Gerd. & I. Ho) Oehl, F.A. de Souza & Sieverd	Tropical wet forest	*Carapa guianensis, Dalbergia tucurensis, Dipterix panamensis, Pentaclethra macroloba, Sinarouba amara, Vochysia ferruginea*	6
Scutellospora calospora (T.H. Nicolson & Gerd.) C. Walker & F.E. Sanders	Greenhouse	*Brachiaria decumbens, Cajanus bicolor*	4

Species	Life Zone or adapted/ modified system	Associated plant species	Reference number
Paraglomerales			
Paraglomus occultum (C. Walker) J.B. Morton & D. Redecker	Agroecosystem and tropical moist forest, premontane wet forest and tropical wet forest	*Carapa guianensis, Cedrela odorata, Cordia alliodora, Dalbergia tucurensis, Dipterix panamensis, Hyeronima alchorneoides, Mimosa pudica Pentaclethra macroloba, Sinarouba amara, Solanum* sp., *Vochysia ferruginea, Vriesea werkleana*	6, 10, 15

Citations arranged in ascending chronological order; Sieverding et al. (1988)[1], Vargas (1990)[2], Fischer et al. (1994)[3], Blanco & Salas (1997)[4], Johnson & Wedin (1997)[5], Picone (2000)[6], Salas & Blanco (2000)[7], Lovelock et al. (2003)[8], Lovelock et al. (2004)[9], Lovelock et al. (2005)[10], Sharrock et al. (2004)[11], Shepherd et al. (2007)[12], Aldrich-Wolfe (2007)[13], Aldrich-Wolfe et al. (2020)[14], Polo-Marcial et al. (2023)[15], Solís-Ramos et al. (2023)[16].

(12 hosts), *Entrophospora colombiana* (12 hosts), *Gigaspora gigantea* (11 hosts), *Acaulospora minuta* (11 hosts), *Glomus rubiforme* (11 hosts), *Cetraspora pellucida* (15 hosts), *Funneliformis mosseae* (10 hosts), *Acaulospora excavata* (10 hosts), *Rhizoglomus intraradices* (10 hosts), *Sieverdingia tortuosa* (9 hosts), *Sclerocystis coremioides* (14 hosts), *Acaulospora rehmii* (9 hosts), *Acaulospora splendida* con 8 and *Ambispora gerdemannii* (9 hosts) (Table 2).

In terms of their distribution by life zones, of the 60 species identified in Costa Rica (Table 1 and Table 2; Fig. 2 and Fig. 3), 24 species (40 %) were recorded in the premontane wet forest, with three species unique to this life zone; 22 species (36 %) were reported in agroecosystems, with five unique species; 23 species (38 %) were reported in greenhouses (trap crops), with three unique species; 19 species (31 %) were reported in the tropical moist forest, with six unique species; 21 species (35 %) in the tropical wet forest, with seven unique species and 12 species (20 %) in the tropical dry forest, with five unique species (Fig. 3).

With respect to family composition in the different life zones, the families Acaulosporaceae and Glomeraceae were the most predominant, exhibiting a wide distribution and diversity in these ecosystems (Table 1). The families Ambisporaceae, Entrophosphoraceae, Racocetraceae, Dentiscutataceae, and Paraglomeraceae showed lower richness and abundance, and were even absent in 8 life zones (Table 3), which may indicate specific environmental conditions that limit their presence or a lack of sufficient studies in those areas.

Table 3

Diversity and Abundance of the reported Glomeromycota in Different Life Zones and Agroecosystems of Costa Rica from 1988 to 2024.

Life zone	Families	Genera	Species	Total Abundance
Tropical dry forest	3	4	5	**98**
Tropical moist forest	8	11	**19**	55
Tropical wet forest	7	12	**21**	**130**
Premontane moist forest	0	0	0	0
Premontane wet forest	11	14	**24**	38
Premontane rain forest	0	0	0	0
Lower montane moist forest	0	0	0	0
Lower montane wet forest	0	0	0	0
Lower Montane rain forest	0	0	0	0
Montane wet forest	0	0	0	0
Montane rain forest	0	0	0	0
Subalpine rain paramo	0	0	0	0
Agroecosystem	6	10	22	27
Greenhouse	8	10	23	39

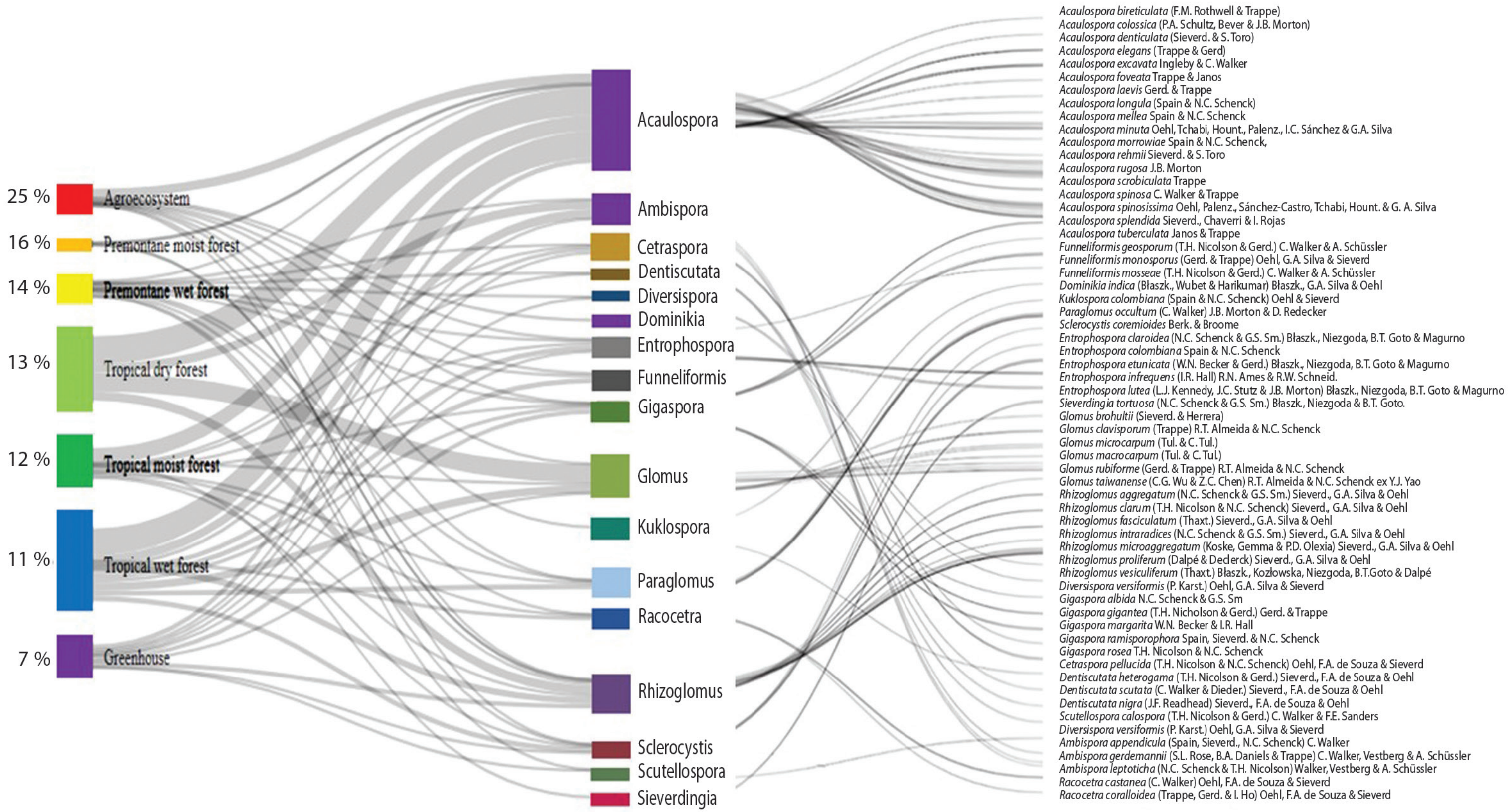

Fig. 2. Sankey diagram depicting the families of arbuscular mycorrhizal fungi identified in different life zones and production systems. The width of the bands indicates the relative proportion of each AMF genus associated with the life zones. The species of each genus are detailed on the right.

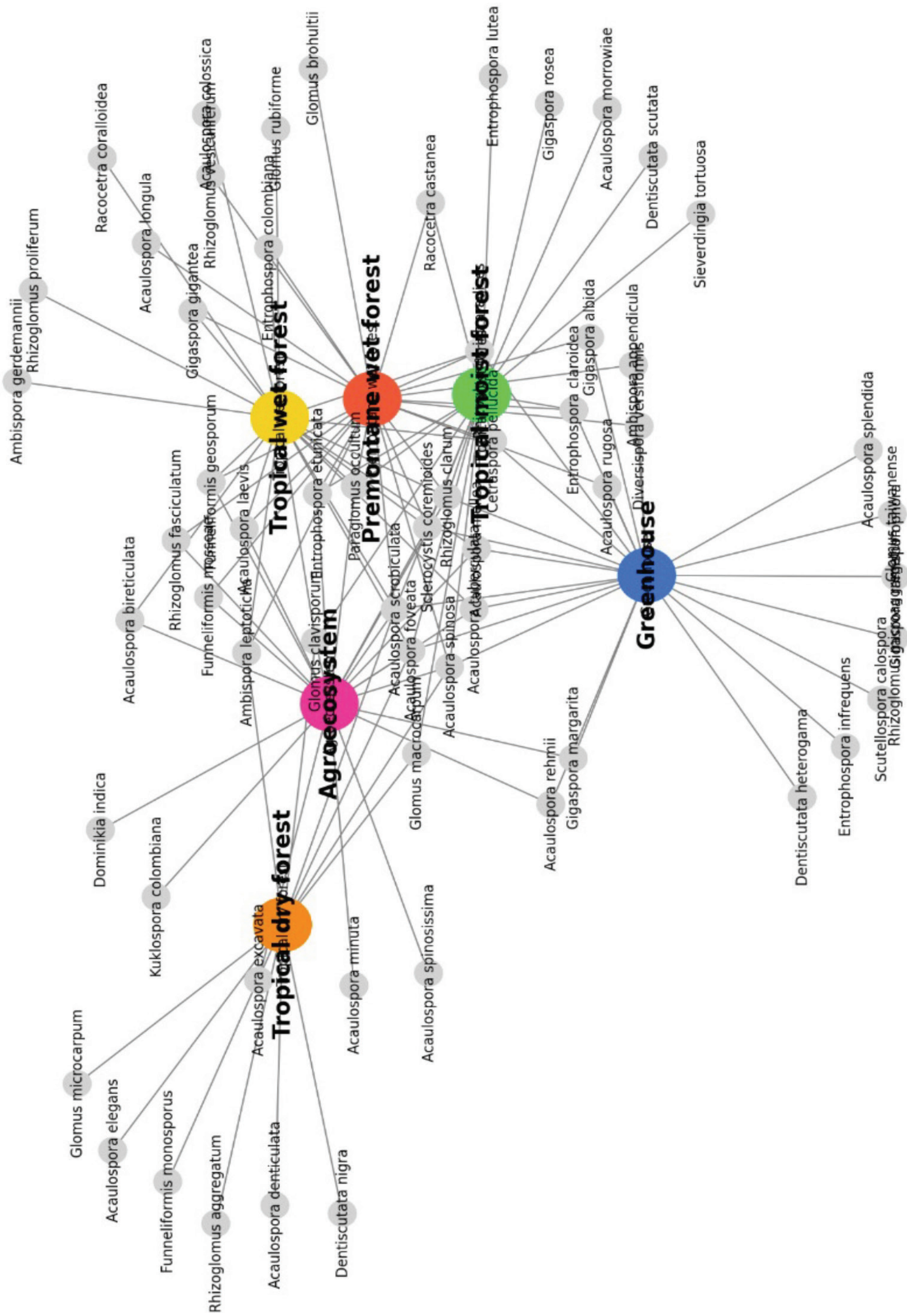

Fig. 3. Diagram of connection networks between life zones and reported Glomeromycota species in Costa Rica from 1988 to 2024. Life zones include Agroecosystem, Tropical Wet Forest, Tropical Dry Forest, Premontane Wet Forest, Tropical Moist Forest and Greenhouse.

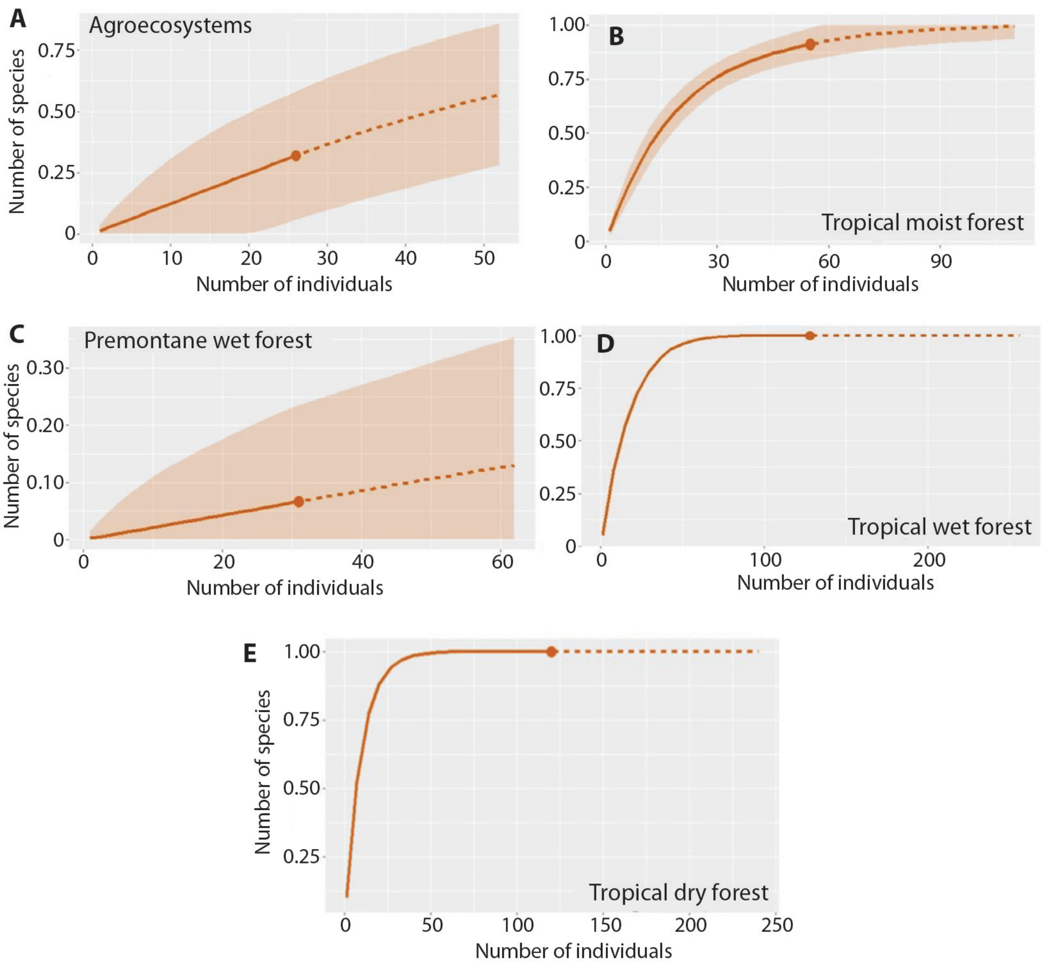

Fig. 4. Individual-based rarefaction and extrapolation curves of arbuscular mycorrhizal fungi found in four different life zones and in agroecosystems in Costa Rica from 1988-2024. a) Agroecosystem, b) Tropical moist forest, c) Premontane wet forest, d) Tropical wet forest, e) Tropical dry forest. The dashed line represents the extrapolation curve, indicating the expected number of species that could be found by increasing the sampling effort in the different life zones of our reference samples.

The analysis of the rarefaction and extrapolation curves showed differences in the species diversity captured according to the number of individuals sampled in the different life zones (Fig. 4). In the agroecosystems and premontane wet forest, it is clear that diversity showed a gradual increase without reaching an asymptote. This indicates that more sampling effort is required to capture the full diversity present. The broad confidence bands indicate uncertainty in the extrapolations (Fig. 4).

In contrast, in the tropical moist forest, tropical wet forest, and tropical dry forest, the curves reach a plateau, it is clear that most species were recorded with the current sampling (Fig. 4). The thinner confidence bands in these cases indicate more precise estimates (Fig. 4). It is important to mention that this analysis did not consider trap or pure crops (greenhouses), since they were grouped according to the life zones where the samples were extracted from the soil for the experiments. This analysis demonstrates that AMF species diversity varies significantly between life zones and modified systems. In certain regions, such as agroecosystems and pre-montane moist forests, the full diversity has not yet been documented due to inadequate sampling efforts. Conversely, in other regions, such as tropical dry forests, the sampling appears to be adequate to reflect the majority of species present. Furthermore, the confidence bands indicate divergent levels of precision in the estimates, contingent on the quality and quantity of the available data.

DISCUSSION

Since the compilation made by Blanco and Salas in 1997, where 19 species were recorded, the present checklist shows an increase of 31 % in the recorded taxa. This illustrates Costa Rica's biological potential in terms of biodiversity, since the species identified represent 16 % of the Glomeromycota species worldwide (Goto & Jobim, 2024). Of the 15 Glomeromycota families, ten are represented in the present checklist, with Glomeraceae being the most abundant, followed by Acaulosporaceae, which is consistent with the records from other, better studied megadiverse countries such as Mexico and Brazil (Jobim & Goto, 2016; Polo-Marcial et al., 2023; Stürmer & Kemmelmeier, 2021). The dominant genera is *Acaulospora*, which has a high representativeness in Neotropical ecosystems (Stürmer & Kemmelmeier, 2021), we found that in the four life zones and vegetation types studied of Costa Rica, the AMF community is dominated by *Acaulospora* spp. (Johnson & Wedin 1997; Lovelock & Ewel 2005; Picone, 2000). Some reported studies on AMF have focused on determining the physiological response of different hosts with AMF cultivated strains (Blanco & Salas, 1997; Hernández & Salas, 2009; Salas & Blanco, 2000). Studies identifying and evaluating native AMF communities are scarce, for example Polo-Marcial et al. (2023) and Solís-Ramos et al. (2023), studied the effect of AMF communities in *Cedrela odorata* and *Jatropha curcas* respectively. However, a high morphological richness of AMF has been found in tropical forests and dry grasslands (Johnson & Wedin, 1997; Lovelock & Ewel, 2005; Picone, 2000).

Among the life zones evaluated, the premontane moist forest is the best studied, since 24 of the 60 species recorded in Costa Rica are found in this life zone. This number of species highlights the unique vegetation types of the region and contrasts with the previous limited taxonomic inventories in these areas (Aldrich-Wolfe, 2007; Aldrich-Wolfe et al., 2020; Fischer et al., 1994; Johnson & Wedin, 1997; Lovelock et al., 2003, Lovelock et al., 2004; Lovelock et al., 2005; Picone, 2000; Polo-Marcial et al., 2023; Salas & Blanco, 2000; Sharrock et al., 2004; Shepherd et al., 2007; Sieverding et al., 1988; Solís-Ramos et al., 2023).

The evaluation of different areas provides relevant information for understanding the diversity of AMF in Costa Rica. Among its life zones, the premontane moist forest, lower montane rain forest, premontane rain forest, lower montane moist forest, and montane wet forest represent underexplored regions, there is no record of any Glomeromycota species. These underexplored or under-inventoried areas may host new AMF species whose value for the local flora remains unknown.

The rarefaction curves show the limited knowledge of species richness in the few (four) life zones where studies have been conducted. Given that Costa Rica is recognized by its biodiversity (Acuña, 2002), studies focused on bioprospecting for AMF diversity in understudied life zones will help to broaden the knowledge of this group, which has significant potential for applications in horticulture, production of ornamentals, sustainable agriculture and forest management, and the restoration of degraded areas. The knowledge generated will support the development of public policies for the successful conservation of biodiversity and the sustainable production in Costa Rica. For example, some species of the genera *Acaulospora*, *Glomus*, and one *Ambispora* are dominant in terms of the number of hosts and vegetation types on which they have been reported. This information makes them

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the obvious candidates for consideration in mycorrhizal inoculum production. However, further ecological and taxonomic research is required, encompassing biotechnological techniques, morphological and molecular analyses, to validate the applications of the diversity of AMF in Costa Rica

CONCLUSIONS

We compiled data on 60 AMF species found in Costa Rica from 1988 to 2024, which represents 16 % of the Glomeromycota known in the world. Twenty percent of the species reported in the studies were classified only at the genus level and the reports include only 4 of the 12 life zones of the country, which suggests a high possibility of identifying new species. If we consider the diversity of edaphoclimatic conditions, the variability in the terrain, and the different types of natural vegetation that prevail in Costa Rica, which remain to be further explored, we can expect the record of AMF species to expand as further research is conducted. It is fundamental to perform studies on the interactions with different hosts, as well as to make taxonomic inventories of AMF in the different life zones and biogeographic districts, combining morphological analyses and molecular characterizations, since this information allows a robust confirmation of taxonomic identity, the establishment of phylogenetic relationships, the determination of AMF species distribution, and complete characterizations that aid in species recognition and tracking *in situ*, in order to gain a more comprehensive view of the richness and ecology of the Glomeromycota of Costa Rica. The data presented here significantly contribute to the knowledge of the diversity and distribution of this group in the natural life zones of Costa Rica and to the understanding of the diversity and distribution of AMF worldwide, and also provide a basis for making decisions about future studies on the taxonomy, distribution, ecology, and biotechnological applications of the Glomeromycota of Costa Rica.

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