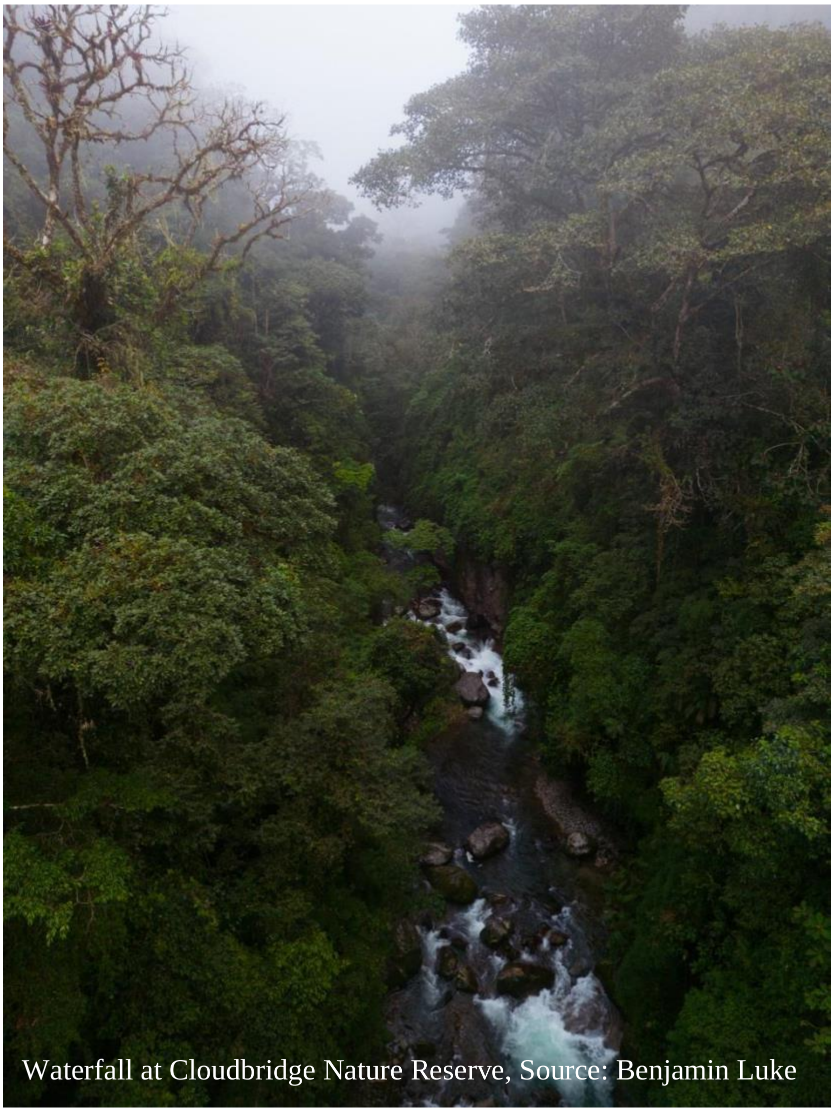
Exploring Ectomycorrhizal Communities: A Comparative Study of Forest Types in Costa Rica



Waterfall at Cloudbridge Nature Reserve, Source: Benjamin Luke

Internship report

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Abstract

This project involves the diversity and characteristics of ectomycorrhizal fungi in different forest stands at the Cloudbridge Nature Reserve in Costa Rica. It is done as a part of the IFEM study programme at the University of Sustainable Development Eberswalde. This study aimed to identify and catalogue the exploration types of ectomycorrhizal fungi in planted, natural regrowth, and old-growth forests, and to assess the fungal species richness and abundance in each category of the forest age. A robust sampling design was adopted for the study wherein a total of ninety soil samples were collected from nine plots. Under the microscope, the exploration type is characterised and separated, by their morphological features as: contact type, short-distance fringe type, medium-distance fringe, medium-distance mat-forming, medium-distance smooth and long-distance fringe type. The frequency of the exploration types will be recorded for each plot at each forest stand. Even though the statistical analysis showed no significant difference among forest categories, observations did show that contact type was the most abundant within all types of forests. This study offers baseline data and provides insight into ecological dynamics concerning EM fungi within this diversity hotspot.

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1. Introduction

1.1 Mycorrhizal fungi

When talking about mycorrhizae, one is referring to the symbiotic associations between fungi and the roots of most terrestrial plants. They play a significant role in the health and productivity of ecosystems (Smith & Read, 2008). There are two types of mycorrhizas, the Arbuscular Mycorrhizae (AM) and the Ectomycorrhizae (EM). AM are formed by fungi from the Glomeromycota phylum, a monophyletic group of soil-borne fungi. The AM penetrates the root cells of the host plants, to facilitate nutrient exchange. There are different forms of AM, some forming a symbiosis association with only one family of plants, such as Orchid mycorrhizae, only building connections with plants from the family Orchidaceae (Taylor et al., 2015).

On the other hand, there is only one kind of EM which is typically associated with woody plants. EM from a sheath or mantle around the root surface enhances nutrient uptake, as well as protecting against pathogens. Both types of mycorrhizae enhance plant resilience to environmental stressors for example drought or soil salinity (Smith & Read, 2008). By improving soil structure and promoting microbial diversity, fungi are contributing to soil health and ecosystem stability (Treseder, 2004), while playing an exemplary role in carbon cycling when assisting in the transfer of carbon from plants to the soil (Johnson et al. 2003).This has a direct effect on plant growth which improves immensely when forming mycorrhizal associations (Brundett, 2009). In return, the host plant provides the mycorrhizae with glucose, since the fungi itself is not able to practise photosyntheses.

Also, when facing global challenges such as climate change and soil degradation, it is important to understand the function of mycorrhiza in forest ecosystems and their potential applications as a tool in sustainable agriculture (van der Heijden et al. 2015). Additionally, mycorrhizae and their influence have rarely been studied yet, which makes it even more important to practise more research.

1.2 Cloudbridge Nature Reserve

1.2.1 Ecological significance

Costa Rica and its reserves are habitats for uncountable plant, animal and fungi species. One of these habitats is cloud-forest, which only make up about 1% of all forests in the world. These ecosystems are characterised by their high moisture and because of their low-hanging clouds. The nature reserve Cloudbridge is located in a cloud forest and is the home of unique biodiversity, including nearly 300 bird species, tropical trees, epiphytes and of course fungi (Max King, personal communication, 08.10.2024). Ellusive mammals can be found here such as tapir, puma and the jaguar. The Talamanca Mountains are estimated to harbour almost 4% of all the terrestrial species on Earth (UNEP-WCMC., 2025). The area boasts exceptional biodiversity, with 10,000 flowering plants and over 4,000 non-vascular plants. There are approximately 1,000 fern species and about 900 species of lichen. It supports viable populations of many rare, vulnerable and endangered species (UNESCO World Heritage Centre., 2025). On top of that, the area contains the largest remaining natural forest in central America (UNEP-WCMC., 2025) and is part of the largest protected area in Central America, which includes La Amistad International Park, a UNESCO World Heritage Site (Cloudbridge, 2025).

1.2.2 Forest types

When talking about Cloudbridge, it is important to mention that this reserve consists of old-growth forests, but mainly out of 10- to 30-year-old forests, partly of natural regrowth and partly planted. More precisely the young natural regeneration is a maximum of 30 years old, whereas the youngest forest type, the planted forest isa maximum age of 21 years old. It consists of areas where active reforestation efforts have taken place (Womack, B. H. 2023). This is because the area previously has been used as agricultural land and cattle farming with areas started to be replanted shortly after the establishment of Cloudbridge in 2002. Some areas were allowed to regenerate naturally, while others were actively reforested through tree planting initiatives. Cloudbridge is located in an ecotone, a transitional area between two biological communities, which contributes to its diverse forest composition (Womack, B. H. 2023).

This diversity of forest types is valuable, since it allows researchers to study forest regeneration and succession processes. Furthermore, it makes it possible to compare different forest types and their ecological characteristics, as well as it demonstrates the effectiveness of various reforestation and conservation strategies (Hance, J. 2023, March 23).

1.3 Objectives

The primary aim of this project is to investigate the diversity and characteristics of EM fungi in different forest stands within the Cloudbridge Nature Reserve in Costa Rica.

One of the desired outcomes would be to roughly identify and catalogue the exploration types of EM fungi present in the three distinct forest stands. So, the planted, the natural regrowth, and the old-growth forest and then assess the richness and abundance of EM in each forest age category.

1.4 Hypothesis

For this research project, two hypotheses to clarify the outcome have been proposed:

Null Hypothesis:

The proportion of EM exploration types do not differ between old-growth, young-growth, and planted forest stands, in a tropical mountain cloud forest (Kevin Beiler, 2025).

Exploration Strategy Hypothesis:

The functional traits of EM fungi, such as exploration strategies, will vary among the different forest types, with planted areas showing a higher prevalence of long-distance foraging types due to lower nutrient availability compared to natural regrowth and old-growth forests (Yang, Y., Zhang, Y., & Liu, S. 2022).

2. Methodology

2.1 Study area

Study plots were established in the Cloudbridge Nature Reserve, within the Talamanca Mountains of Costa Rica (9°31'42.0" N 83°36'47.0"W). The reserve is approximately 257 hectares of recovering tropical montane cloud forest, from 1550m to 2000m above sea level

(Womack, B.H. (2023). The site is situated within the Tropical Premontane Wet Forest to Lower Montane Wet Forest life zones, according to the Holdridge life zone classification system (Schembre, C. (2009)).
The climate is marked by high rainfall, ranging from 3500mm to 4000mm per year, with a strong wet season between May and November. Temperatures range from 15°C to 22°C, with quite modest seasonal difference. The region is often blanketed in cloud and low-lying mist, adding to its high humidity and cloud forest conditions (Phillips, K. (2024)).

Each of the plots was intentionally located on the same side of a mountain to minimise variability in environmental conditions and microclimate. Uniform conditions within the plots and management of environmental variance, as much as possible, was the primary intention with the aim to decouple the effect of forest age and management method on ectomycorrhizal diversity from that of other variables. Locating the plots for sampling at the same worksite/mountainside also simplified the access logistics.

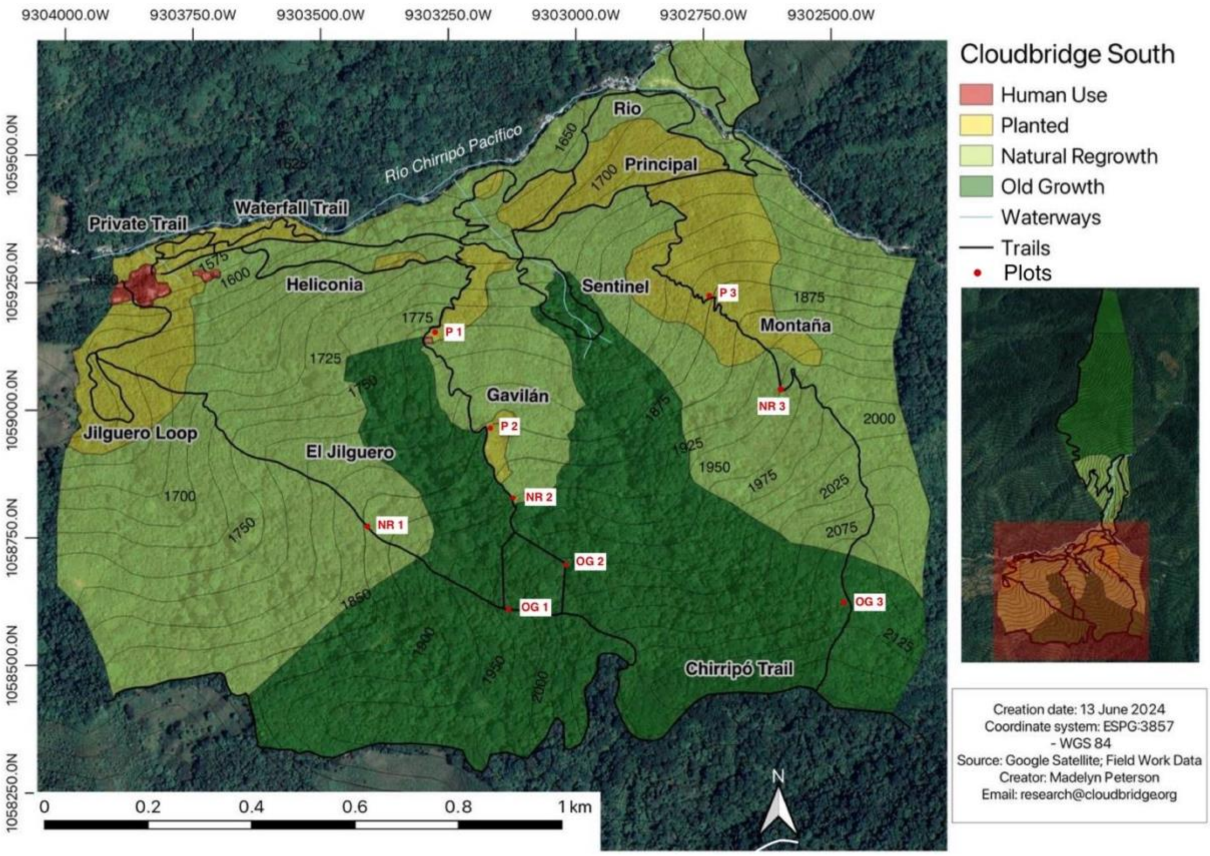


Figure 1. Map of Cloudbridge South with marked plots, Modified from: Madelyn Peterson (Google Satellite; Field Work Data)

2.2 Sampling design

For this study a Sampling design was chosen to investigate the diversity and exploration strategies of ectomycorrhizal fungi in forests of varying ages. Nine special plots were created for the study, meaning the plots were permanently established. Three plots are assigned to each of three forest stands representing different age categories: Planted (Yellow), Natural Regrowth (light green) and Old Growth (dark green) (Fig. 1). This design evaluates all EM communities across the entire study area repeatedly and thoroughly. Measuring tape and marking tape were used to set up the plots.

Approximating 10 meters by 10 meters in dimension, the plots provide a sufficient sampling area while minimising overlap. Five samples were collected from each plot at four corners and the centre. At each of the five designated sampling points, two soil samples were collected; one from the uppermost 7cm of soil and another from a depth of 20-30cm. Stratified sampling eases a study of potential variations in EM communities and detailed analysis across different soil depths.

A total of ninety samples, collected from nine plots, comprised the study's thorough dataset; each plot yielded ten individual samples (five sampling points at two different depths). A sampling intensity of exactly 90 samples guarantees strong statistical analysis and sufficient catch of the diversity and distribution of EM communities across all spatial and vertical forest stand gradients. Its advanced design eases precise detection of complex patterns and subtle variations in EM diversity and exploration types. This methodology should offer meaningful understandings into how EM communities change with forest age and sampling across multiple age categories will greatly simplify this (Kevin Beiler, 2024).

2.3 Ectomycorrhizal sampling techniques

Sampling was done only in the wet season to ensure that fungal activity is at its peak and samples are homogeneous. With the help of a spade, a square of soil was extracted in order to standardise the volume of all samples. Soil samples were then stored in labeled plastic bags and taken to the laboratory. In the laboratory, root samples were gently separated from soil over a mesh to eliminate bulk soil particles. The roots were soaked in a water bath for a few minutes to gently loosen soil and then rinse the roots very gently to remove loose soil from among the roots to minimise destruction to fungal structures. The procedures were repeated for each set of 10 samples collected at each plot. Samples were kept in a cooling box or refrigerator throughout the process, to prevent deterioration of fungal structures. This technique offers minimum disturbance of fungal structures and provides efficient separation of roots from soil with minimum loss of ectomycorrhizal integrity (Kevin Beiler, 2025).

Figure 2. Labeled bags in the field before taking samples, Source: Carlotta Voigt

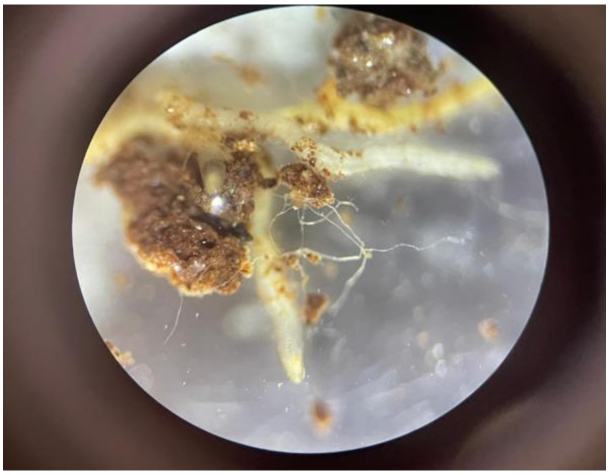
2.4 Identification and classification of exploration types

A light microscope with magnifying glasses was used for inspecting root samples for EM structures such as fungal hyphae and mantle layers. Fungal species were identified based on their morphological features, colour, texture, and structure of the mycorrhizal mantle along with associated hyphae. Every sample was recorded at each step. Fine roots were sorted and counted using scalpels and scissors, and they were prepared for microscopic analysis.

The EM observed were sorted according to their morphological features in exploration types dividing the foraging into short and long distance. Short-distance foraging is made by dense short roots; long-distance foraging is realised by extensive hyphal networks. The abundance of every exploration type was recorded for each plot, and on all forest stands.

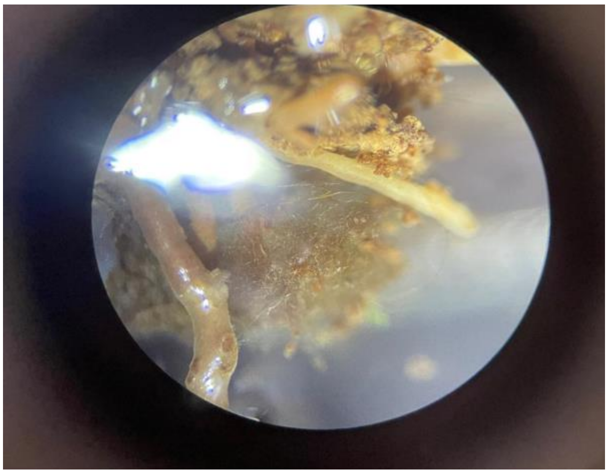
The mycorrhizae observed were separated into six types of exploration types (Kevin Beiler, 2024):

Contact type:



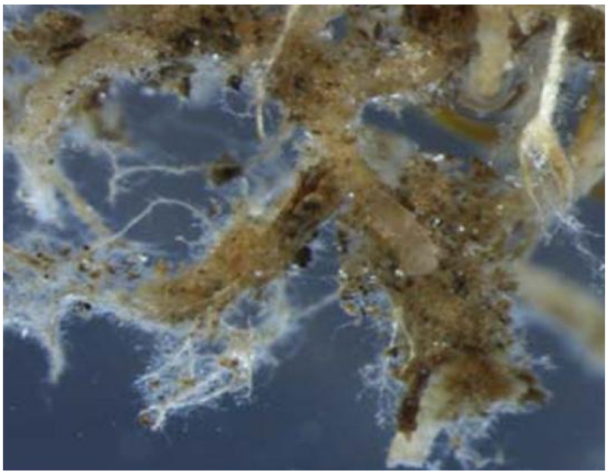
- Dense, smooth, hydrophilic mantles with few emanating hyphae
- Close contact with surrounding substrate

Short-distance fringe type:



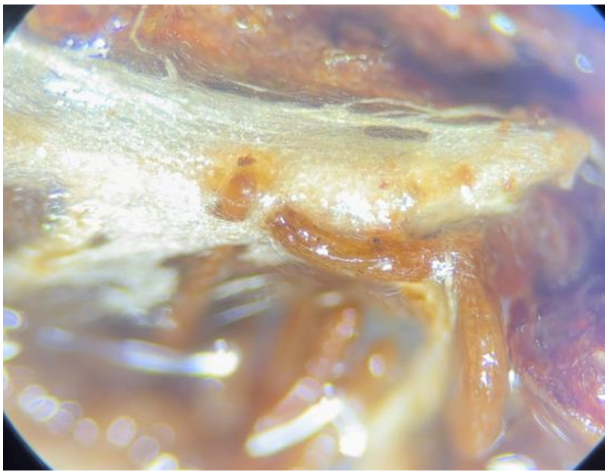
- Lack rhizomorphs, but with frequent hyphal projections
- Emanate a short distance into surrounding substrate

Medium-distance fringe:



- Form interconnected hyphal networks
- Rhizomorphs repeatedly divide and fuse

Medium-distance mat-forming:

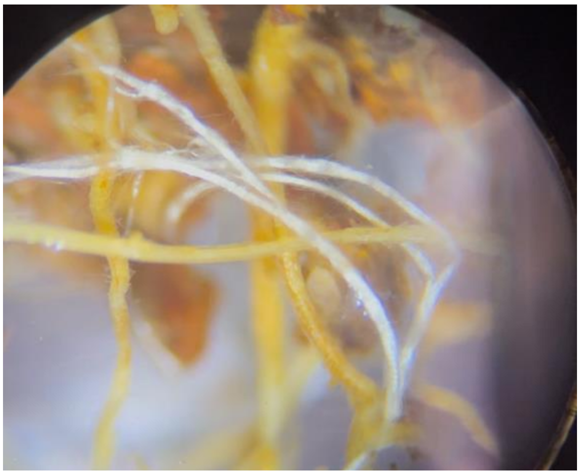


- Form dense hyphal mats
- Aggregate into a homogeneous mass

Medium-distance smooth:

- Rhizomorphs with smooth mantles and margins

Long-distance fringe type:



- Highly differentiated rhizomorphs with hollow vessel-like transport tubes
- Associated with enhanced organic nitrogen uptake

This classification system will allow a comprehensive analysis of the structure and distribution of EM communities in the area of interest, given that different strategies of nutrient acquisition and carbon allocation are represented. Such strategies affect the fungi's ability to colonise new roots, form common mycorrhizal networks, and adapt to various environmental conditions (Defrenne et al., 2019).

3. Results and Analysis

3.1 Comparison of ectomycorrhizal diversity across forest types

The results show sharp differences in the distribution of the different exploration types of EM among these forest stands.

The contact type was the most abundant in all forest types, being highest in planted forests with a number of 864 EM, followed by natural regrowth with 636 and old-growth forests with 523. The short-distance exploration type increased considerably in old-growth forests to 98, against the planted with 38 and natural regrowth with 18. Long-distance exploration types were most frequent in the planted forests at 717, followed by natural regrowth with 497, while in old-growth forests, this type was less frequent with 230.

Medium-distance types, namely fringe, mat-forming, and smooth, presented different features between forest types: fringe types were abundant in old growth (161) and planted forest (126), but scarce in natural regrowth (9); mat-forming types were lower and similar between forest types; smooth types occurred most in the planted forest (337), second in natural regrowth (164), and minimum in old growth (41).

3.2 Distribution of exploration types in each forest category

The distribution of exploration types in the studied forest categories can be explained by the morphological characteristics of ectomycorrhizae (Suz et al., 2008).

Mainly contact types (40.9%) and long-distance exploration types (34.0%) are found in planted forest areas. Natural regeneration has a similar dominance of contact types, 47.6%, and long-distance exploration types, 37.2%, but in stronger expression of contact types.

The biggest heterogeneity are seen in old-growth stands, especially for short-distance (9.2%) and fringe types (15.1%). This corresponds to complex mantle patterns observed in the mature ecosystems. Also, a reduction of long-distance exploration (21.6%) can be observed.

Eveness Values:

- 0.74 for planted forests

- 0.61 for natural regeneration areas

- 0.76 for old-growth forests.

3.3 Statistical analysing of findings

In this work statistical tests were conducted to compare ectomycorrhizal exploration types among the three categories of forests: planted forests (P), natural regeneration areas (NR), and old-growth forests (OG). With a level of significance being $\alpha = 0.05$, a threshold commonly used in ecological works. This value is a balance between the minimisation of Type I error (false positives) and the assurance of reasonable statistical power to find significant differences. Descriptive statistics were calculated for each forest category.

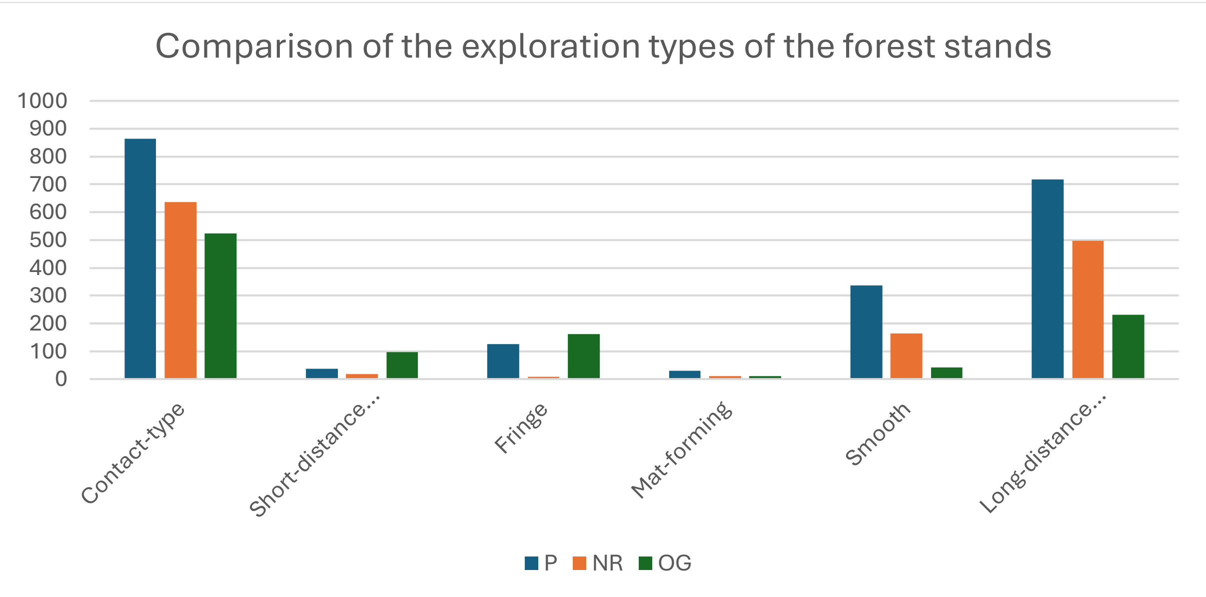


Figure 3. Comparison of the descriptive statistics of the forest stands

These descriptive statistics show some preliminary trends. Planted forests have the highest mean abundance of ectomycorrhizal exploration types with a value of 351.83, followed by natural regeneration areas with 222.5, and then old-growth forests with 177.33. Within the planted forests, however, the standard deviation is the largest at 360.44.

Friedman Test:

$$Q = (12 / [N * k * (k + 1)]) * \Sigma(R\_j^2) - 3 * N * (k + 1)$$

To compare the three forest stands with each other, the Friedman test was used, which is a non-parametric test to determine if the differences among the three categories (other than Wilcoxon-test) of forests presented above were significantly different. A non-parametric test

Mean	351.83	222.5	177.33
Median	231.5	91	129.5
Standard Deviation	360.44	276.37	187.12
Minimum	29	9	11
Maximum	864	636	523

was used here since data is not normally distributed and also because of the nature of the repeated measures in our study design.

Results of the Friedman test:

A p-value of 0.13 is larger than our significance level of 0.05, so there is no significant difference in the distribution of ectomycorrhizal exploration types across the three forest categories.

Although the omnibus test did not show significant differences, a post-hoc pairwise comparison was performed to examine possible differences among specific forest categories:

1. Total P - Total NR:

Test statistic = 1.08, Std. error = 0.58, Std. test statistic = 1.88, p = 0.061, Adj. p = 0.182

2. Total P - Total OG:

Test statistic = 0.92, Std. error = 0.58, Std. test statistic = 1.59, p = 0.112, Adj. p = 0.337

3. Total NR - Total OG:

Test statistic = -0.17 Std. error = 0.58 Std. test statistic = -0.29 p = 0.773 Adj. p = 1.000

The adjusted p-values for all pairwise comparisons are above the generally accepted significance level of 0.05. This means that none of the differences among the forest categories are statistically significant at the conventional 5% level.

4. Discussion and Conclusion

The results from this study offer insight into the distribution and diversity of ectomycorrhizal exploration types across different categories of forests within the Cloudbridge Nature Reserve. The Friedman test with a p-value of 0.13, higher than the decided level of significance 0.05, therefore the variation observed in the proportion of exploration type among three forest categories may not be considered as statistically significant. While no significant statistical differences in forest types could be evidenced via the statistical analysis performed, a few trends do deserve more elaborate discussion.

The differences among forest types point to ecophysiological adaptations of ectomycorrhizae. The dominance of hydrophilic contact types in plantations versus hydrophobic long-distance types in natural regeneration matches the spectrum of exploration types described by Suz et al. (2008). Increasing mantle complexity with age in old growth stands (from plectenchymatous to pseudoparenchymatous) reflects the maturation of ectomycorrhizal communities and confirms that forest age and soil development are crucial factors for functional diversity (Wu et al. 2013).

This gives the interesting pattern in the distribution of EM exploration types across forest categories, supplemented with evenness values: 0.74 for planted forests, 0.61 for natural regeneration areas, and 0.76 for old-growth forests. Together with the observed distribution of exploration types, these values provide a good insight into the ecology of EM fungi across different forest stages in this tropical mountain cloud forest ecosystem.

In plantations, the codominance of contact types (40.9%) and long-distance exploration types (34.0%) suggests a double adaptation to the environment of these younger, managed ecosystems. The dominance of contact types, with their smooth mantle structures, can be an opportunistic response to readily available nutrients, perhaps induced by management practices like fertilization. Meanwhile, the large proportion of long-distance exploration types with well-differentiated rhizomorphs indicates a strategy for nutrient capture in more distant or depleted soil patches, which can occur even in fertilized, young forest ecosystems. These rhizomorphs are effective at transporting water and nutrients along extensive distances.

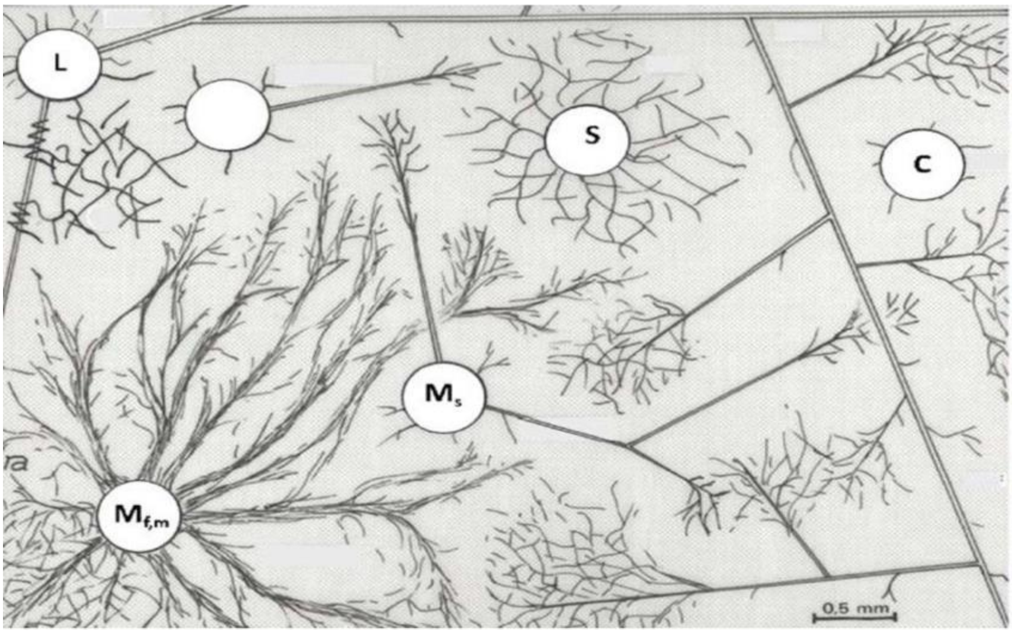


Figure 4.Exploration types of ectomycorrhizal fungi. The schematic extent of hyphae emanating from ectomycorrhizae of different exploration types is shown here for contact (C), short-distance (S), medium-distance smooth (M s), mediumdistance fringe or mat (M f,m), and long-distance (L).

Source: https://www.researchgate.net/figure/Exploration-types-of-ectomycorrhizal-fungi-The-schematic-extent-of-hyphae-emanating-from_fig2_225525336 (07.02.2024)

The evenness is high at 0.74, showing that other exploration types are relatively evenly represented, perhaps due to management practices or the developing nature of these forests. Note that these planted areas are no older than 21 years since reforestation at Cloudbridge began in 2002 (Scherer, 2023). It should also be mentioned that the numbers seen in plot P3 were markedly different from the rest, probably because this plot is situated within a stand of diseased oak trees. Most likely, the trees have been infected with a fungus or fungus-like spores, which probably have an effect on the ectomycorrhizal community in this area. On top of that oaks are known to be trees more likely to be in symbioses with many fungi's (Filipa Cox et al., 2010).

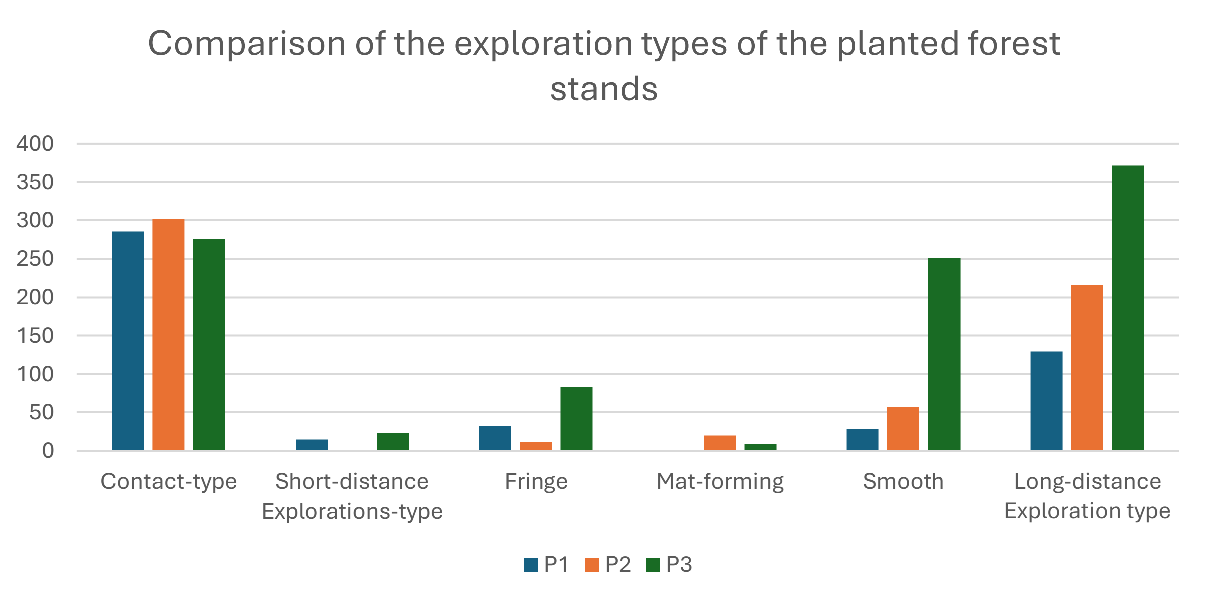


Figure 5. Comparison of the exploration types of the planted forest stands

Natural regeneration areas showed a similar pattern, but with a slight increase in contact types (47.6%) and maintained presence of long-distance types (37.2%). These could reflect transitional stages in mantle development typical for regenerating ecosystems, for example, the pseudoparenchymatous mantle types. The fringe types are rare, 0.7%, and this agrees with the general scarcity of cystidia in the early stages of the forest. The low evenness value observed here-0.61-suggests a transient stage in the development of the forest and its EM community. These represent the mix of active planting and natural regeneration approaches that have been adopted at Cloudbridge. It is important to note that NR2 had a much lighter canopy in the first and second tree layers and showed a lot of signs of peccary activity. Peccaries, which forage for roots, fungi, and other plant material, may influence the EM fungal community through their rooting activity and alteration of soil structure (Wild Expedition, 2025). This plot, compared to the rest when considering the diagrams, has a fairly lower number of mycorrhizal associations, most likely due to increased light penetration and disturbance of the soil by wildlife.

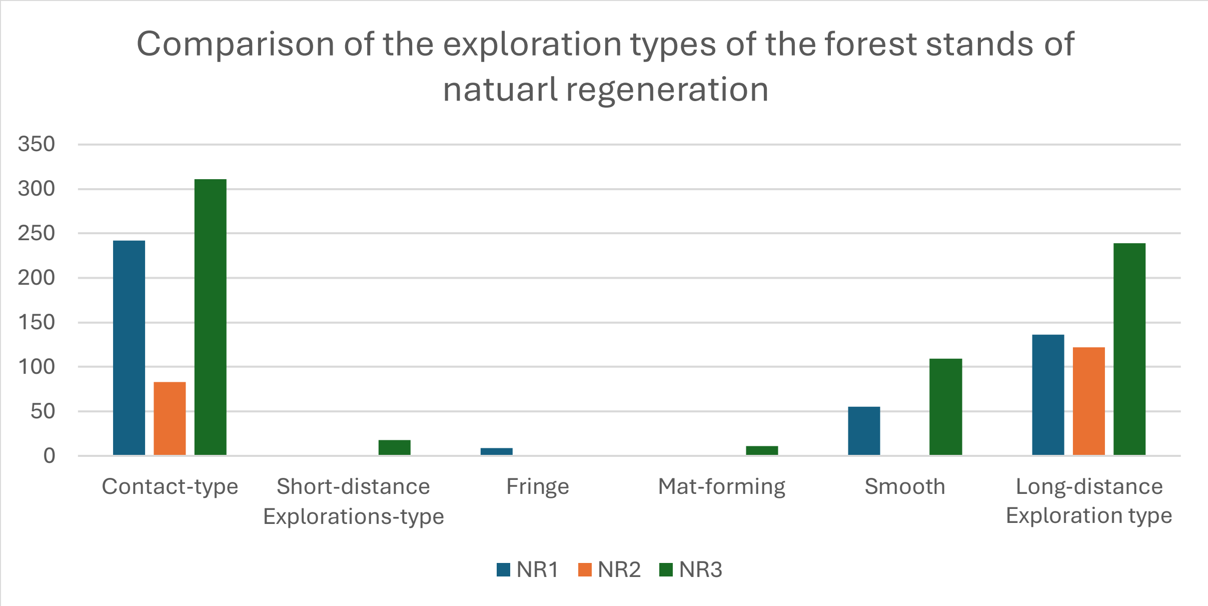


Figure 6. Comparison of the exploration types of the planted forest stands

While old-growth forests had the most even distribution of exploration types, short-distance and fringe types increased to 9.2% and 15.1%, respectively. Reduced long-distance exploration (21.6%) might be indicative of more efficient nutrient cycles in the old forests, while an increase in hydrophilic short-distance types hints at well-developed organic soil layers (Schembre, 2009). The highest evenness value of 0.76 supports this diversity and would thus suggest a more balanced distribution of the EM strategies in mature, stable ecosystems with complex soil structure and diverse microhabitats. Comparing the three plots in the old growth forest stand, no pattern could be seen.

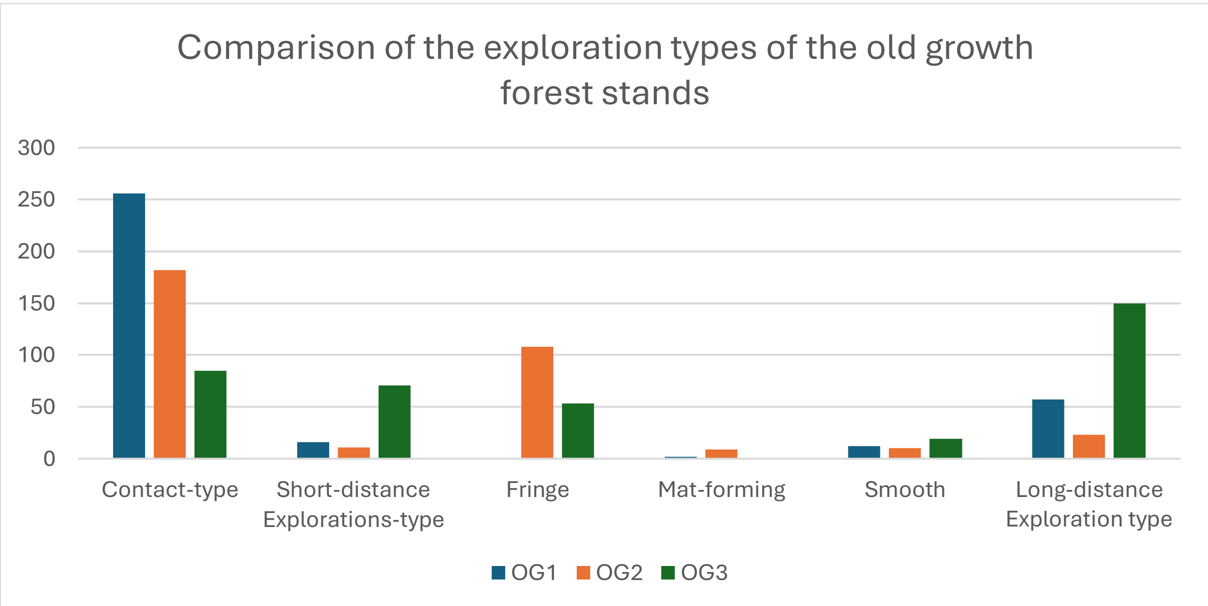


Figure 7. Comparison of the exploration types of the old growth forest stands

One influencing factor in these observed patterns could be the fast plant growth, as some of the planted trees here at Cloudbridge have reached a height of 20 meters after only 20 years. These rapid growth patterns may affect development of the communities of EM fungal communities and possibly explain some variation in exploration type between younger to older forested stands.

The results are in accordance with the general research of ECM diversity in different forest ecosystems. Estimates are that between 8,000 and 25,000 ECM fungal species exist worldwide, with approximately a third of about 6,000 macrofungal species being ectomycorrhizal in Switzerland. Generally, temperate and boreal forests have higher diversities of ECM fungi than tropical forests, with up to 60% of trees in these regions forming ectomycorrhizal associations (Averill et al., 2023).

Moreover, results of the analysis presented by Van Dorp et al. (2015) indicate that forest age structure corresponds to the frequency of ectomycorrhizal species. With an increase in the proportion of younger Douglas firs (< 50 years), the number of tubercles from Rhizopogon vesiculosus grew while the amount of its related genotypes, R. vinicolor declined. More generally, this implies differential impact on forest changes in a stand structure and regeneration among ectomycorrhizal species.

The statistical analysis did support the initial null hypothesis "The proportion of EM exploration types do not differ among old-growth, young-growth, and planted forest stands in a tropical mountain cloud forest" therefore it cannot be rejected. As mentioned, the Friedman test with a p-value of 0.13, higher than the decided level of significance 0.05. The p values obtained in post-hoc pairwise comparison reveal that the variation observed in the proportion of exploration type among three forest categories may not be considered as statistically significant. Any seeming variation in mean abundance of ectomycorrhizal exploration types across categories is not big enough to assure significant differences within the true populations. This may be related to the fact that the latter have large standard deviations, and thus a wide variability within each forest category might contribute to such a result. Thus, under this analysis, there is no sufficient evidence for rejecting the null hypothesis that, therefore, precludes from concluding on whether the proportion of EM exploration types differs significantly in old-growth, young-growth, and planted forest stands in this tropical mountain cloud forest.

These findings do, however, support the view that there is some observable variation in mean abundance between ectomycorrhizal exploration types among forest categories, though the differences are not statistically significant. The high variability within each category, as seen by the large standard deviation, may be one of many factors contributing to the nonsignificant trend.

Therefore the other hypothesis "the functional traits of EM fungi such as the strategy of exploration, will vary between different forest types, and forest plantations are more likely to host a greater number of long-distance foraging types because of low nutrient availability than in the case of natural regeneration and old-growth forest," is partly supported yet not finally proved. The findings confirm that ectomycorrhizal fungal exploration types indeed relate to forest type and, by extension, soil nutrient conditions. However, this hypothesis is only partially supported for the case of planted forests, since even though one could reasonably expect that the nutrient availability is lower in recently planted areas, the results do not directly indicate that there is a higher occurrence of long-distance foraging types in the case of planted forests compared to natural regrowth and old-growth forests.

In conclusion, while this study failed to detect significant differences in types of EM exploration between forest categories, it serves as a baseline dataset and insights into the ecological dynamics of the EM fungi within the unique setting of the Cloudbridge Nature Reserve. The evenness values and distribution patterns of exploration types across forest stages are calling for more research, like long-term projects, to be conducted to elucidate fully the relationship between these variables and their implications for forest management and conservation strategies in this biodiversity hotspot.

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