# Unraveling Gorse's (Ulex europeaus) Invasion: Insights from Colombia's Mountain Ecosystems

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# Unraveling Gorse's (*Ulex europeaus*) Invasion: Insights from Colombia's Mountain Ecosystems

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**Abstract**

*Ulex europaeus* (gorse), a perennial woody shrub native to western continental Europe and the British Islands, has become one of the most invasive shrubs worldwide. Despite its widespread impact, gorse's success in tropical ecosystems remains poorly understood. This study investigates if land cover has a differential effect on gorse germination and growth rate in the mountain ecosystems of Colombia, emphasizing the role of soil composition and mycorrhizal associations in different land covers. In this study we sampled six land covers: páramo, grasslands, burnt grasslands, a forest with a ca. 15-yr old restoration process and a <5 yr-old restoration effort. Soil samples had differences in terms of organic carbon, nitrogen, and phosphorus levels between land covers. A principal component analysis highlighted the significance of pH, exchange acidity, and base saturation percentage in explaining soil variation. Seed bank analysis uncovered viable gorse seeds in all land covers, showcasing its adaptability to both established ecosystems, in a restoration process and burned grasslands. Given that mycorrhizal associations may play a crucial role in nutrient uptake, contributing to gorse's ecological success, we used DNA-based analysis and qualitative methods to explore the arbuscular mycorrhizae associated with gorse. We found 11 different species, three of which belong to *Diversispora*. Our study sheds light on the complex interactions that could aid in gorse’s spread in the mountain ecosystems of Colombia. Understanding the impacts of soil composition, seed banks, and mycorrhizal associations on gorse colonization contributes to broader knowledge of invasive species dynamics. This knowledge is crucial for informing targeted conservation efforts in tropical environments, ultimately aiding in the conservation of biodiversity and ecosystem resilience.

*Keywords*
Invasive species, mycorrhizal colonization, páramo, seed bank, soil composition

## Introduction

Invasive species are a conservation threat that have caused species extinctions worldwide (Sodhi & Ehrlich, 2010). Most invasive species establish populations and significantly impact ecosystems. They also compete with native species, often escaping from their native herbivores, pathogens, and parasites in their new geographic ranges. Given that species invasions can have damaging consequences for the local flora and fauna, deepening our understanding of their biology is strategical to deal with them effectively (Foxcroft et al., 2013). One of the most invasive shrubs in the world is *Ulex europaeus* (gorse) (Broadfield & McHenry, 2019; Lowe et al., 2000); native to western continental Europe and the British Islands, it is now found in 50 temperate and tropical countries, causing important economic and environmental impacts (Christina et al., 2020; Roberts & Florentine, 2021). Gorse is a perennial woody shrub from the legume family (Fabaceae), that can grow up to 7 m, with spines along its branches, and can form nitrogen fixing nodules (Díaz & Vargas, 2009; Clements et al., 2001). Although gorse has reached all continents, it has been most successful in regions where temperature oscillates between 4 °C and 22 °C (Atlan et al., 2015a; Fenner, 1995) and annual rainfall between 500 and 1500 mm (Broadfield & McHenry, 2019).

Several life history traits have contributed to gorse's successful establishment. Gorse can produce up to 18,000 viable seeds annually (Markin et al., 1996), and is able to survive and germinate after many decades (> 30 years) in seed banks (Clements et al., 2001; Hill et al., 2001; Udo et al., 2017). Gorse also has few constraints on recruitment, such as low seed predation and herbivory (Mason et al., 2016); it reaches maturity in ca. 18 months; germinates and grows quickly; and easily establishes mutualisms with pollinators and soil microorganisms (i.e., nitrogen-fixing bacteria). Moreover, above and belowground dispersal has been aided by livestock, birds and water, which has increased gorse's expansion in the naturalized range (Bowman et al., 2008; Broadfield & McHenry, 2019; Christina et al., 2020; Clements et al., 2001; Hill et al.,1996, 2001; Kariyawasam & Ratnayake, 2019; Sixtus et al., 2013; Udo et al., 2017). Germination is induced by scarification, heat exposure from fire and soil acidity (Ivens, 1983; Udo et al., 2017). Therefore, agroecological disturbances have also fostered environments that encourage further invasions. For instance, soil disruptions, fire and modifying the vegetation cover are related to an increase in seed germination (Hornoy et al., 2012). Fire has not been related with a destruction of the seed bank (e.g., Mason et al., 2016; Udo et al., 2017).

Gorse was introduced into the highland ecosystems of Colombia and has threatened these ecosystems for decades, just as it has in many other countries (Atlan et al., 2015b). The goal of introducing gorse was to enclose a water reservoir close to Bogotá, as a cost-effective fencing measure (Bagge, 2014; Camargo Joya, 2020; Díaz & Vargas, 2009), but a few years later it was found in Andean forests and the páramos (cold weathered ecosystems) of Sumapaz, Chingaza and Pisba. The páramo is unique for its high biodiversity (Diazgranados & Castellanos Castro, 2021; Diazgranados & Castellanos-Castro, 2017; Hernández-Lambraño et al., 2017) and for being a natural reservoir (Buytaert et al., 2006; Rada et al., 2019). However, it is also one of the most fragile, threatened ecosystems by climate change, land use cover change and invasive species (Buytaert et al., 2006; Hernández-Lambraño et al., 2017; Mollot et al., 2017; Mooney, 2005). Therefore, managing gorse's expansion into highland ecosystems has become one of the top environmental priorities of Colombia due to its threat to páramo biodiversity. In addition, the widespread use of fire for the expansion of agriculture in the páramo has aided in gorse's dispersal, while having long lasting seed viability makes gorse hard to eradicate (Richardson & Hill, 1998; Roberts & Florentine, 2021; Tarayre et al., 2007; Udo et al., 2017).

The invasive ecology of gorse has been well documented in temperate first-world countries (Bateman & Vitousek, 2018; Udo et al., 2017). However, very little is known about the ecological factors that have aided the establishment and spread of gorse in the tropics. Gorse has successfully invaded tropical ecosystems that have climatic conditions that resemble its native range. In addition, the high biodiversity of the tropics and the high endemicity of ecosystems such as the páramo (Podwojewski & Poulenard, 2005; Waltert et al., 2011) has exacerbated the severity of the risk posed by gorse. As far as we are aware of, there is only one study that has explored seed morphology and germination patterns of gorse in Colombia across an elevational gradient (Osorio Castiblanco, 2019). However, we currently do not know if land cover type (e.g., native forest vs. pastures) affects gorse's germination, and if there are any differences between establishment in the Andean Forest (lower elevation) versus páramo (higher elevation). In this study, we examined six land covers with different degrees of human intervention, collecting soil samples for physicochemical and seed bank analyses in each land cover. We also recorded germination and seedling growth rate, and tested if the distance from the nearest adult individual had any effect. With these data we hypothesized that *U. europaeus* had higher germination and growth rate in disturbed ecosystems (e.g., grasslands, burned grasslands, forests in the process of restoration) compared to established ecosystems (páramo and forests). We also hypothesized that growing close to an adult could be beneficial due to the associations with nitrogen fixing bacteria. We also explored the interaction between gorse and soil

microorganisms such as mycorrhizae in three of the disturbed land covers. Our hypothesis was that gorse associates with a wide diversity of arbuscular mycorrhizae fungi, which could aid in its establishment (Aslani et al., 2019; Bunn et al., 2015; Zubek et al., 2016).

## Materials and methods

### Study site

Samples were collected in Encenillo Natural Reserve, located in Guasca, Colombia (Fig. 1). This reserve has 206 ha, between the elevations of 2800 to 3200 m, with an annual mean temperature of 12 ºC (between 4 to 21 ºC), and an annual mean rainfall of 1300 mm (Porras Rey, s. f.). The reserve used to be a quarry, but later converted into a protected area in 2006 (Gutiérrez-Fernandez et al., 2021). There are two main ecosystems in Encenillo: Andean Forests and páramo. There are also several areas where active restoration of Andean Forest is underway. In these areas, some companies from the private sector have financially compensated for their industrial activities by planting designated areas with native plants, as well as supporting control plans against invasive species, including gorse (see below).

We sampled six land covers: a forest with a 15-yr old restoration process (RF), forest with recent (< 5 yr) restoration (IRF), grassland (GL), forest border (BF), burned grasslands (BGL) and páramo ecosystem (PR) (Fig. 1). The highest site was PR at an elevation of 3205 m. Most sites, except for IRF (at 2931 m.a.s.l.), were at or above 3000 m.a.s.l. In each land cover, we chose three sexually mature flowering adult individuals, with a height of at least 50 cm (except for BGL as there were no individuals; see below for sampling used in this land cover). We made a 5 m long transect starting from the base of the individual (Fig. 2). For the transects we did not use a set direction. The priority was to sample within the chosen land cover, avoiding a cluster of gorse individuals. Gorse growing in the PR site occurred at the edge of the land cover, separating the páramo from a grassland. The case of the BGL land cover was different from the other five sites. The reserve has been trying to eradicate gorse by uprooting adult individuals and burning them afterward. To understand if this measure is effective, we sampled three areas where adults were uprooted and started the transects from those points randomly. All samples were collected during the rainy season (March-May 2022).

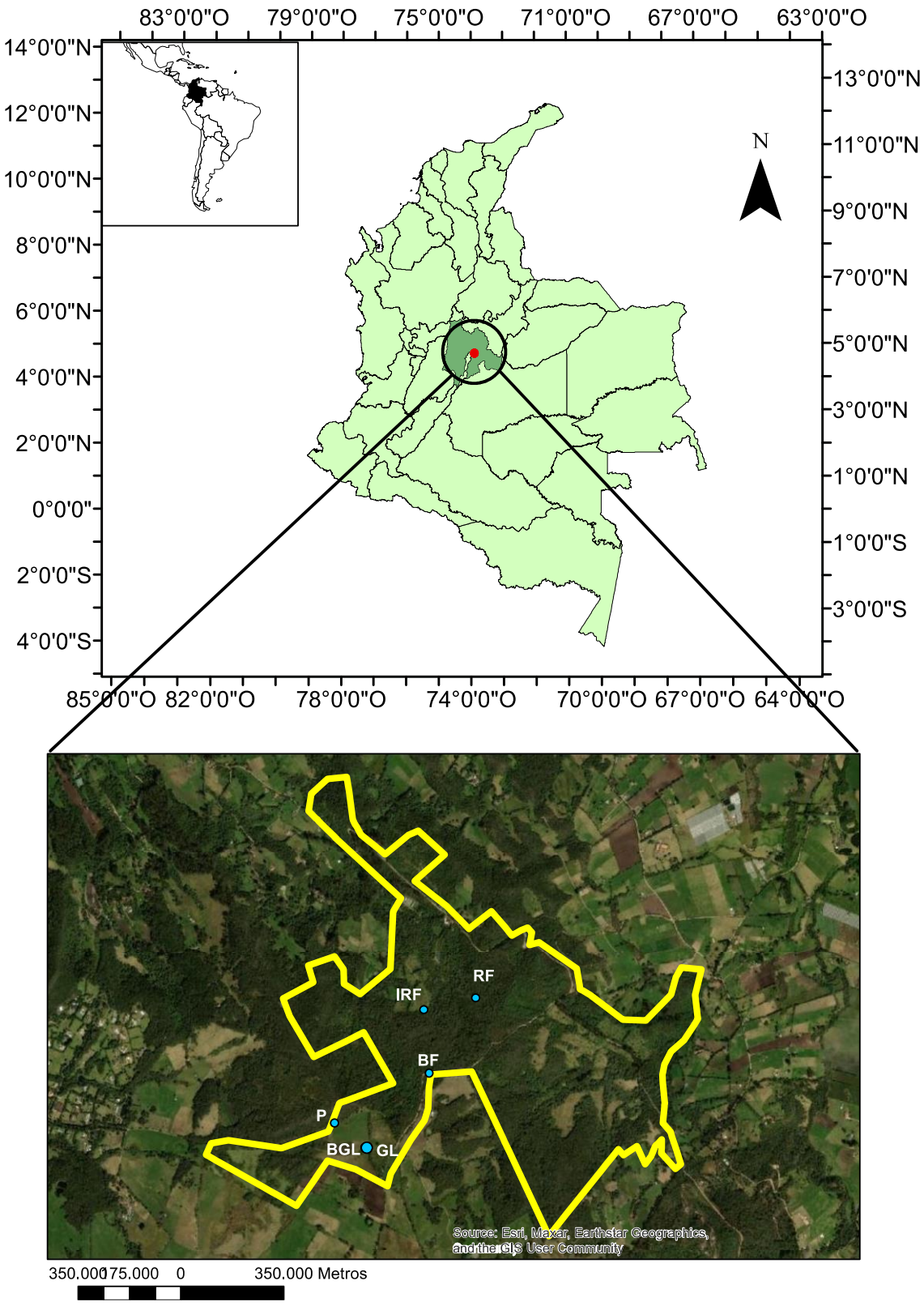


**Fig. 1.** Map of the study area. The natural reserve Encenillo is located in the Cundinamarca Department of Colombia. The reserve is delimited by a yellow line, and the sampled land covers are labeled with blue dots corresponding to: Grassland (GL), Burnt grassland (BGL),

Forest with a 15-yr old restoration process (RF), Forest with recent (<5 yr) restoration (IRF), Forest border (BF) and Páramo (PR).

**Soil samples**

We collected and analyzed one compound soil sample on each land cover. We measured P, N, and organic carbon (OC), pH, exchange acidity saturation percentage (EAS, %), base saturation percentage (BS, %) and effective cation exchange capacity (ECEC). To understand if there is an increased input in OC under gorse, we analyzed an additional 36 samples: six sampling locations, three adult individuals, and two points per individual (below the adult plant at 0 m and at 5 m)(Fig. 2). Given that gorse has associations with nitrogen-fixing bacteria, we analyzed 15 soil samples for total N content. These samples were collected below the adult individuals, except for the BGL site (no adults). To analyze soil composition, we used a Principal Component Analysis (PCA) using RStudio (RStudio Team, 2020) and the packages FactoMineR (Lê et al., 2008) and factoextra (Kassambara, 2016). Organic carbon and nitrogen were compared using an ANOVA.

**Seed banks**

We collected three soil samples along the transects: right below the adult individual (0 m), at 2.5 and at 5 m (Fig. 2). We wanted to understand if there was an influence (positive or negative) of the closest adult individual on seed density and/or germination. Before potting the soil samples in a greenhouse (Manigua Foundation, at ca. 2700 masl), we removed roots and litter and used a soil mixture of 40% rice husk and 60% black soil (soil with a high percentage of humus, P and ammonia). In the greenhouse, soil samples were kept at the same temperature and humidity. Every week we checked for germinated seeds. As soon as we identified gorse seedlings, we measured growth rate every week, for a total of 15 weeks. Growth rate (cm $week^{-1}$) was defined as the total height of the individual (cm), from the bottom to the highest leaf, divided by the total number of weeks. We measured growth rate in a subset of germinated seedlings, as many died. Additionally, given that not all seedlings germinated at the same time, the number of weeks was not the same for each seedling.

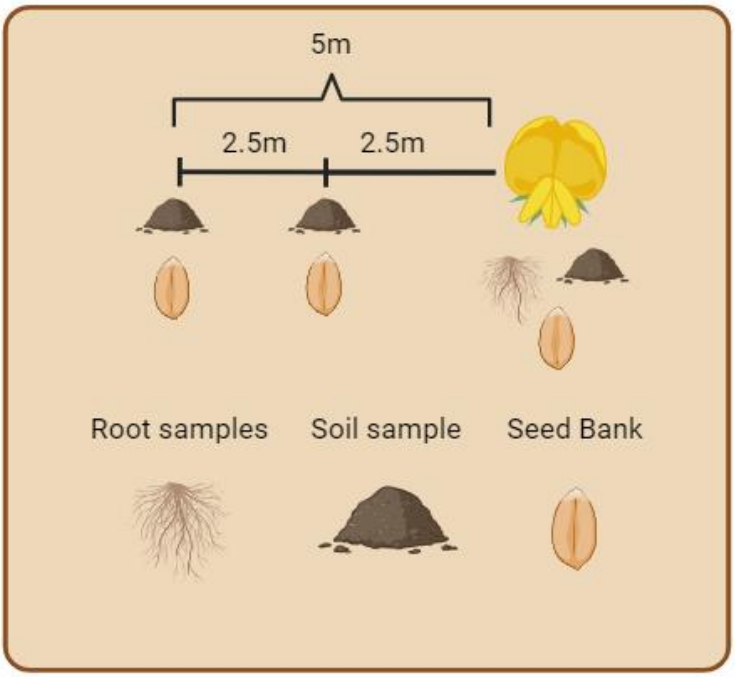


**Fig 2.** Illustration of the sample collection on each of the six land covers. For each land cover we made three transects, each one starting at the base of an adult gorse individual. The transect consisted of three sample points, one below an adult individual plant (next to the trunk), another at 2.5 m from the adult and the last one at 5 m. Soil samples were analyzed for organic carbon content.

For the data analysis, we used an NMDS including the soil variables, growth rate and germination. This analysis was made in RStudio using the package vegan and setting a seed of six for the analysis (Oksanen et al., 2018). For the germination and growth data, we tested all data for normality (Shapiro-Wilk test) and equality of variances (Levene's test) and used an ANOVA or Kruskal-Wallis test in the software JASP (JASP Team, 2024). A posthoc test (Tukey or Dunn) was applied when necessary. For these data, we compared the germination between different land covers and within each land cover, we compared the three distance points (0, 2.5 and 5 m).

**Root samples**

To study the associations between gorse and arbuscular mycorrhizae (AM), we carefully excavated two fine root (< 2 mm) samples of each adult individual used in the transects. One sample was used for DNA analysis and the other to calculate mycorrhizal colonization.

*DNA analysis*

We conducted an exploratory DNA analysis from three land covers (RF, IRF and GL) in a successional trajectory. Given that site heterogeneity may lead to differences in AM composition (Ettema & Wardle 2002), we sampled two replicates in the restoration land covers, IRF and RF (refered to as IRF 1 and IRF 2 and RF 1 and RF 2). We extracted the DNA using the NucleoSpin soil kit (Rischer et al., 2016) and analyzed concentration and quality in a Nanodrop. To screen for mycorrhizae, we used the SSU515F & LR5-R primers (D'Andreano et al., 2020) which amplify the regions from 18S to 28S, more specifically from the V3 region of 18S until the D3 region of 28S. These included the ITS section used to identify arbuscular mycorrhizae. The length of this amplification was of 1kb for which we used the Q5 (BioLab) enzyme, specialized in long fragments.

Once the fragments were amplified, we prepared the libraries, adapters and barcodes for sequencing using Nanopore (MinION MK1B). We demultiplexed to discard sequences with a quality lower than seven, as Nanostat recommended (Lee & Burke, 2022). We created the reference database using AM sequences from the website database MarjAM (Öpik et al., 2010) and the Centrifuge software. Once the taxonomic assignment was done, we used Rstudio Pavian (Breitwieser & Salzberg, 2020) to graph the relative abundance and we calculate the alpha diversity using the Hill numbers with the package iNEXT (Hsieh et al., 2016; Jost, 2019).

*Staining analysis*

To study mycorrhizal colonization, we stained the roots using the methodology described in Manoharachary and Kunwar (2002). We analyzed the roots by cutting sections of 0.5 cm at each end of the root (tip and end). Root colonization quantification was done by estimating the presence or absence of colonization in root segments (hyphae, arbuscules, vesicles and internal spores). The percentage of colonization was calculated as:

$$\%\, Colonization = \frac{Number\ of\ colonized\ segments}{Total\ number\ of\ segments\ examined} \times 100$$

Using a LEICA-DM750 4-100x microscope with an eyepiece graticule, we counted the number of colonized segments in each unit. After checking for normality and equality of variances, we compared the colonization percentage from all samples using a t-test (comparing the base and end of the root tip) and an ANOVA (comparing colonization between five land covers). Colonization was not conducted for the BGL land cover (no adult individuals).

## Results

### Soil composition

We found that P concentration was higher than 40 mg $kg^{-1}$ for BGL, GL and IRF, while BF, PR, RF had a concentration below 15 mg $kg^{-1}$ (Table S1). The OC analysis revealed that BF was lower than the rest of the land covers (≤ 7.5%), but there were no differences between 0 and 5 m (Table S2). BF, IRF and RF had the most acidic pH (lower than 4.5). The exchange acidity saturation was higher (> 60%) on five land covers (RF, IRF, GL, BGL and BF) compared to PR (30%) (Table S1). In the soil composition PCA (Fig. 3A), we found that PCA1 explained 67.4% of the variation and pH, EAS and BS were the principal drivers of this axis. Phosphorus was the only variable close to PCA2, which explained 15.6%.

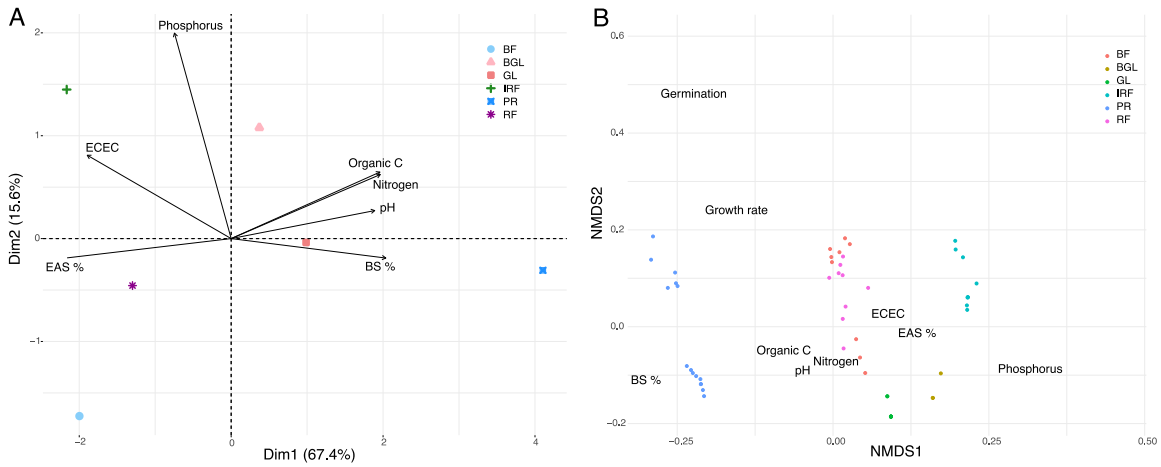


**Fig. 3.** Principal component analysis for A: soil variables, and B: Non-metric Multidimensional Scaling analysis (NMDS) with soil variables, and gorse growth rate and germination. Abbreviations: Burned grassland (BGL), Grassland (GL), Forest with a 15-yr old restoration process (RF), Forest with recent (< 5 yr) restoration (IRF), Forest border (BF), Páramo (PR), Cation exchange capacity (ECEC), Base Saturation (BS, %), and exchangeable acidity saturation (EAS, %).

For the NMDS analysis (Fig. 3B), the variables closer to NMDS1 were P (99.6%) and BS (97.8). NMDS2 had growth (96.8%) and germination (90.4%) (Table S3). We also found that RF and BF, and GL and BGL were closer, whereas P and IRF were separated from the other land covers. Nitrogen, OC, and pH grouped together, as well as EAS (%) and ECEC. Other variables such as germination, growth rate, BS (%) and P were separated from the others. Interestingly, growth rate and germination were placed far from P. For the OC analysis, we found that BF was significantly different from the other land covers ($p < 0.01$) and had the lowest concentration (mean 6.63 ± 1.22 mg $kg^{-1}$). There were also no

differences between distance from the adult individual (0 and 5 m; $p > 0.05$) in the same land cover. For the N analysis, BF had significantly lower values compared to IRF, PR and GL (Table S4).

**Seed banks**

A total of 134 gorse seeds germinated in all six land covers (Fig S1). Most seeds germinated in PR (62), followed by the forest covers (30 in BF, 21 in RF, 16 in IRF) and very few germinated in the pastures (4 in GL and 1 in BGL). Seeds started sprouting in week one, and the first set of leaves appeared in week six. The RF and BF had a germination peak in the 10th week, GL and BGL peaked in the 9th, whereas PR and IRF had their peak on the 7th and 8th week, respectively. Gorse germination was significantly different between land covers ($H = 14.76$; $p = 0.011$). Germination in PR and BF was significantly higher than GL and BGL ($p < 0.001$ and $p < 0.05$, respectively) (Fig S1). Although most seeds tended to germinated under the adult individuals (0 m; except for BGL), when comparing within each land cover (at 0, 2.5 and 5 m) and distances between all land covers, we found no significant differences ($p > 0.05$) (Tables S4, S5). Therefore, germination was not affected by the distance from an adult.

We measured growth rate in 28 seedlings in PR, 15 BF, 8 RF, 10 IRF and 2 in GL. Growth rate did not significantly change when comparing land cover and distance from the adult ($p > 0.01$) (Tables S4, S6).

**Roots samples**

*Mycorrhizal diversity*

We identified 11 species of arbuscular mycorrhizae, of which three belonged to the genus *Diversispora* (Fig. 4). In almost all samples we found *Gigaspora margarita* and *Geosiphon pyriformis*. *Paraglomus occultum* was found in the RF and GL, whereas *Acaulospora brasiliensis, Diversispora* spp., *Funneliformis mossaea* and *Rhizophagus cf. irregularis* were only found in the RF. Interestingly, there were composition differences between the samples in the RF land cover, where RF 2 was more similar to IRF 2. Based on these preliminary results, the Hill numbers in all the samples did not differ much except for the richness in RF 2, which was 10 effective species (the other samples had 2-3 species; Table 1). With regard to the variance (Shannon) and dominance (Simpson) the number of effective species was $2.13 \pm 0.41$ for Shannon and $1.81 \pm 0.29$ for Simpson.

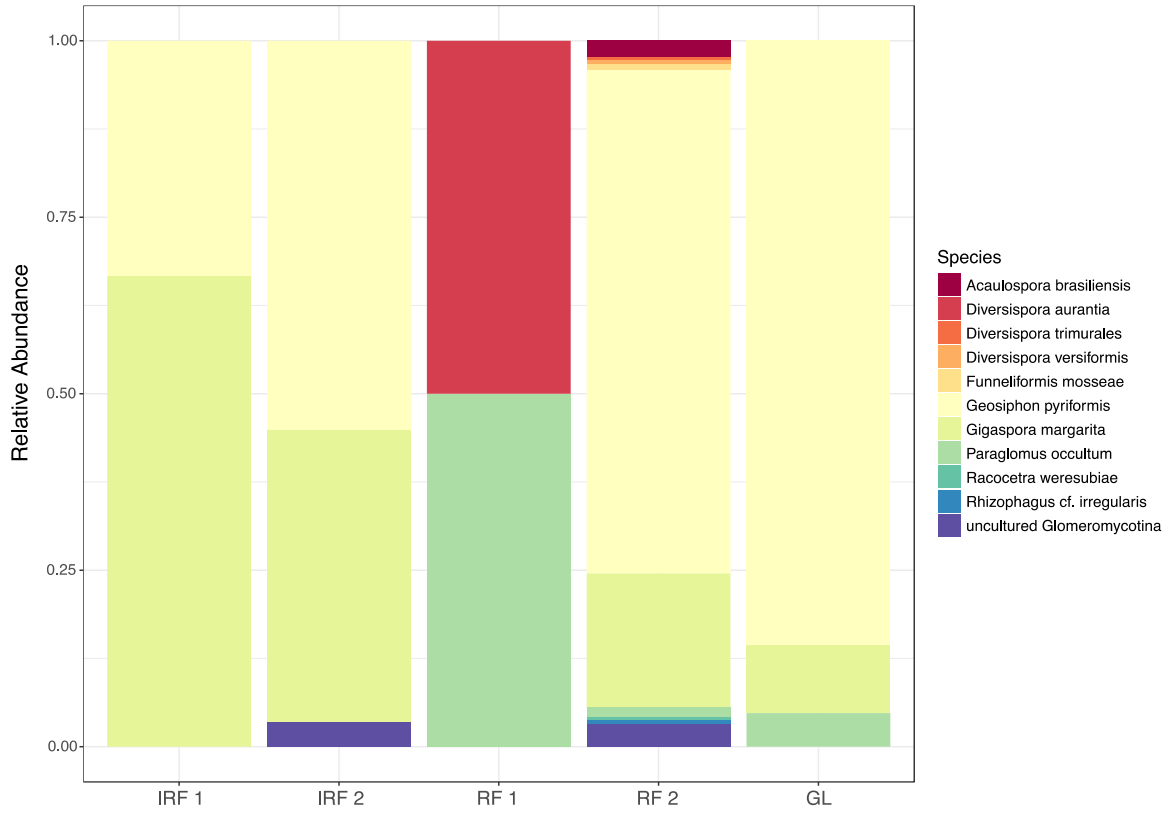


**Fig 4.** Relative abundance and taxonomic classification of arbuscular mycorrhizae found in gorse roots samples. We sampled three land covers: Forest with recent (< 5 yr) restoration (IRF), Forest with a 15-yr old restoration process (RF), and Grassland (GL). Two samples were collected from IRF and RF, which refer to IRF 1 and IRF 2 and RF 1 and RF 2, respectively.

**Table 1.** Alpha diversity calculated for each sample using the Hill numbers (Richness q=0, Shannon q=1 and Simpson q=2). Land covers: Forest with recent (< 5 yr) restoration (IRF), Forest with a 15-yr old restoration process (RF), and Grassland (GL).

| Land cover | Shannon (q=1) | | Simpson (q=2) | | Richness (q=0) | |
|---|---|---|---|---|---|---|
| | Sample 1 | Sample 2 | Sample 1 | Sample 2 | Sample 1 | Sample 2 |
| IRF | 1.89 | 2.25 | 1.80 | 2.10 | 2 | 3 |
| RF | 2 | 2.60 | 2 | 1.83 | 2 | 10 |
| GL | 1.65 | | 1.34 | | 3 | |

*Mycorrhizal colonization*

Percent colonization was generally lower at the root base (7.83 ± 7.69) than the root tip (13.31 ± 10.44) but there were no significant differences between sections ($p > 0.01$). There were also no significant differences in colonization between land covers ($p > 0.01$) (Table 2; Tables S4, S6). Arbuscular mycorrhizae colonized roots in the five land covers sampled.

**Table 2.** Colonization percentage for each land cover: Grassland (GL), Forest with a 15-yr old restoration process (RF), Forest with recent (< 5 yr) restoration (IRF), Forest border (BF), Páramo (PR). Standard deviation (SD).

| **Root segment** | **GL Mean +/- SD** | **RF Mean +/- SD** | **IRF Mean +/- SD** | **BF Mean +/- SD** | **PR Mean +/- SD** |
|---|---|---|---|---|---|
| Root base | 15.44 ± 12.32 | 0.91 ± 0.82 | 6.32 ± 5.07 | 7.1 ± 6.92 | 9.37 ± 4.65 |
| Root tip | 7.66 ± 6.0 | 14.29 ± 20.39 | 13 ± 1.90 | 18.37 ± 11.33 | 13.23 ± 9.55 |

## Discussion

The invasion of gorse (*Ulex europaeus*) has raised concerns around the world due to its speed of colonization and its impact on native biodiversity (Hernández-Lambraño et al., 2017; Lowe et al., 2000; Roberts & Florentine, 2021). Our study wanted to elucidate the mechanisms contributing to gorse's success as an invasive species in Colombia by investigating gorse germination and seedling growth, as well as mycorrhizal associations in six land covers. Our first hypothesis, stating that there would be higher germination and growth rate in disturbed ecosystems was not supported by our results. Seeds were found in all land covers, with significantly higher germination in páramo ecosystem (PR) and forest border (BF) and lower in grasslands (GL) and burned grasslands (BGL). Soil characteristics, such as OC and N do not seem to have an effect on seed germination, given that OC and N were lowest in the BF land cover. Distance from the adult individual did not contribute to higher germination or growth rate. For our second hypothesis, we found that gorse associated with several species of arbuscular mycorrhizae (AM) and *Gigaspora margarita* and *Geosiphon pyriformis* were the most common and abundant. This is the first approximation to identify the AM associated with gorse, at least in the tropics.

### Soil Composition and Seed banks

The principal component analysis (PCA) highlighted the importance of pH, exchange acidity, and base saturation percentage in explaining soil variation (Bateman & Vitousek, 2018; Neina, 2019). These variations may influence gorse establishment and growth, since despite its adaptation to a wide range of acidity, gorse may benefit from less acidic soils (Grime et al., 2014). Soil composition analyses revealed differences in OC, N, and P levels between different land covers as found in other studies (e.g., Kooch & Noghre, 2020; Ngo-Mbogba et al., 2015). The site located at the border of the mature forest exhibited significantly lower

OC and N concentrations. It has been shown that higher OC availability may facilitate nutrient uptake by symbionts, such as N or phosphorus, which in turn may help gorse establish in different ecosystems (Aslani et al., 2019; Soong et al., 2019). Therefore, we need further studies exploring the AM mycorrhizae associated with gorse and evaluate if they have any effect in seedling establishment.

In our seed bank analysis, we found viable gorse seeds in most land covers. However, seeds germinated less in burned grasslands. This highlights the plant's resilience to various environments outside its native range, just like other invasive plants such as french groom (Herrera et al., 2011). However, it also highlights that burning is an effective way to control gorse's spread. In addition, these findings may also suggest that gorse may be using both methods of seed dispersal (shorter- and longer distance) as there were no differences on the gorse germination when comparing distances (Fenner, 1995). This would allow gorse to establish seed banks in different habitats.

Portilla Yela (2019) found that gorse produces fewer seeds at lower elevations but has a higher germination rate than at higher elevations. We found a different pattern where more seeds germinated at higher elevations, such as in the páramo site. It is widely recognized that higher biodiversity in an ecosystem contributes to resistance against invasive species (Gamfeldt et al., 2008). Nevertheless, we found that gorse exhibited consistent germination in páramo and forests with different restoration processes. This adaptability may be attributed to the ca. 80 years of gorse in these land covers, allowing populations to establish over time. The presence of viable gorse seeds in diverse land covers suggests the importance of understanding and managing seed banks to control proliferation.

**Mycorrhizal Associations**

Mycorrhizal associations play a crucial role in plant nutrient uptake and contribute significantly to ecosystem functioning (Philippot et al., 2013). The mycorrhizal diversity DNA analysis revealed multiple species associated with gorse roots, especially in the genus *Diversispora*. Associations with AM were suggested by several authors (Grime et al., 2014; Hume, 1993; Reid, 1973) but the information on this topic is limited and needs further research. The restored forest exhibited the highest mycorrhizal diversity, which emphasizes the importance of land covers in shaping belowground interactions (Bonfim et al., 2013). Interestingly, one of the most common species, *Gigaspora margarita* is widespread, colonizes different land covers (Fernandes et al., 2016), had not been reported in Colombia (https://redlist.info/iucn/species_view/314488/), and also associates with agricultural plants (Schenck & Kinloch, 1980). In this study we provide a first exploration of AM fungi

associated with gorse. We need further studies exploring the AM relationships in more land covers and understand if gorse associates with whichever AM is present in a given land cover. There was also high heterogeneity in the AM diversity (Fig. 4). Sampling effort and soil heterogeneity can affect AM diversity (Ettema & Wardle 2002; Whitcomb & Stutz, 2007). A study conducted in Arizona estimated that 15 samples would be needed to detect 70-80% of the AM species in a given plot (Whitcomb & Stutz, 2007).

While no significant differences were observed in mycorrhizal colonization between land covers or root segments, the consistent presence of mycorrhizae across all sites suggests a potential role in facilitating gorse establishment. In particular, the hypothesis of tripartite symbiosis, involving plant's associations with both mycorrhizae and nitrogen-fixing bacteria in nodules, could explain the uniformity in mycorrhizal abundance and diversity observed among different land covers (Herrera et al., 2022; Kafle, 2018; Wilgan, 2021). We also need further studies exploring AM associations in seedlings to understand if this association could be aiding in their establishment and colonization.

Our investigation sheds light on some of the complex interactions which may be influencing gorse spread in the mountain ecosystems of Colombia. While the factors driving gorse success globally are known (Hill et al., 2008), our study reveals that we need region-specific studies to guide conservation practices. Future research is recommended to study the persistence of seed banks and its implications. This exploration might delve into factors such as the protective role of the seed coat and the response of seed dormancy to environmental changes, as suggested by Lacerda et al. (2004). Additionally, examining gorse's associations with bacteria and fungi, could uncover new species associated with gorse and elucidate whether gorse introduces novel microorganisms to ecosystems or associates with existing ones. We highly encourage further explorations on interactions and their implications for biodiversity conservation and ecosystem resilience. The presence of viable seeds in diverse land covers and associations with AM highlights the importance of understanding and managing seed banks to control the invasion, given that AM associations could be helping gorse colonize habitats. Finally, conducting comparative studies on a larger scale, and contrasting undisturbed with disturbed ecosystems, could provide valuable insights into the broader ecological implications of gorse invasion.

**Data Availability**

The raw dataset and scripts to reproduce the analyses are available at: https://osf.io/4hwxd/?view_only=141a207c444947e8abb1082efb48b27d

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## Contributions

The project was conceptualized by JSH-S and AS. Data collection methodology was developed by JSH-S, and data curation by JSH-S and AS. Data analysis methodology was performed by JSH-S. All drafts of the manuscript were written by JSH-S and AS. Both authors read and approved the final manuscript.

## Conflict of interests

We declare we have no competing interests.

**Supplementary Information**

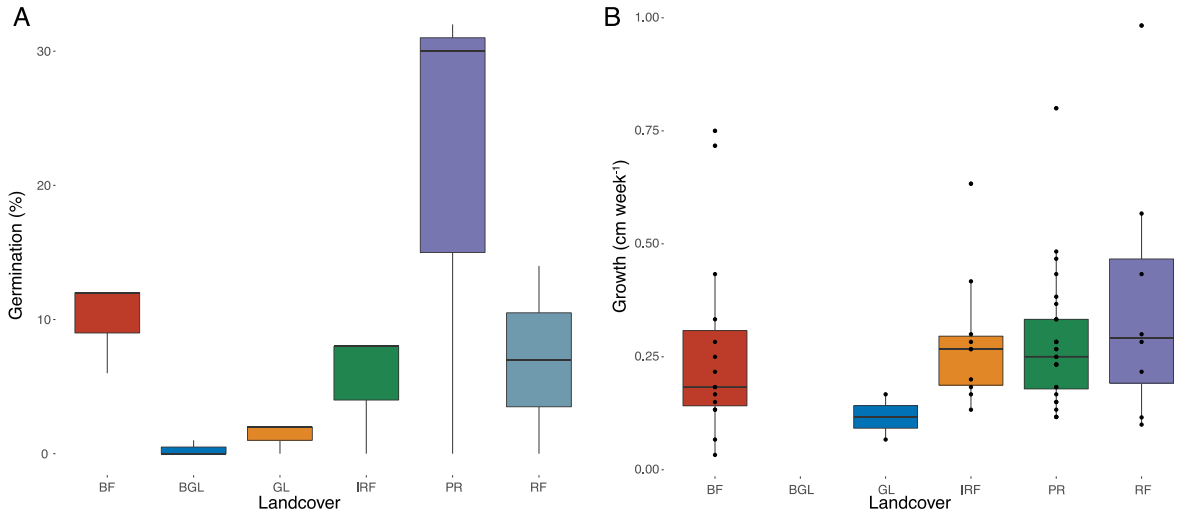


**Figure S1**. Gorse germination (%) (A) and growth rate (cm week$^{-1}$) (B) between land covers. The bottom and top of the boxplot indicates the 25th and 75th percentiles (respectively); the line within the box indicates the median value. Burned grassland (BGL), Grassland (GL), Forest with a 15-yr old restoration process (RF), Forest with recent (< 5 yr) restoration (IRF), Forest border (BF), Páramo (PR)

**Table S1**. Soil composition analysis for all the land covers sampled. Burned grassland (BGL), Grassland (GL), Forest with a 15-yr old restoration process (RF), Forest with recent (< 5 yr) restoration (IRF), Forest border (BF), Páramo (PR), Organic Carbon (OC), Nitrogen (N), Phosphorous (P), Cation exchange capacity (ECEC), Base Saturation (BS), and Exchangeable acidity saturation (EAS).

| Land cover | pH | EAS (%) | OC (%) | N (%) | P (mg kg$^{-1}$) | ECEC | BS (%) |
|---|---|---|---|---|---|---|---|
| BGL | 4.72 | 60 | 10.37 | 0.89 | 109.91 | 11.08 | 6.11 |
| BF | 4.31 | 89.51 | 8.03 | 0.69 | 10.81 | 9.63 | 2.66 |
| IRF | 4.23 | 92.03 | 9.55 | 0.82 | 155.94 | 14.06 | 1.44 |
| GL | 4.82 | 72.77 | 10.76 | 0.93 | 47.38 | 6.87 | 3.01 |
| RF | 4.14 | 95.23 | 10.45 | 0.9 | 3.76 | 13.85 | 2.28 |
| PR | 4.81 | 30.09 | 12.16 | 1.05 | 6.77 | 4.82 | 21.24 |

**Table S2**. Soil analysis composition of mean Organic carbon (OC) and Nitrogen (N) in all land covers. Burned grassland (BGL), Grassland (GL), Forest with a 15-yr old restoration process (RF), Forest with recent (< 5 yr) restoration (IRF), Forest border (BF), Páramo (PR). Distance refers to where soil samples were collected: 0 is under the adult plant or 5 m away from the adult. Nitrogen was only measured under adult individuals. Mean values are calculated for three samples. SD = standard deviation.

| Sample | Distance (m) | OC (%) | N (%) |
|---|---|---|---|
| BGL | 0 | 11.12 ± 0.91 | |
| BF | 0 | 5.76 ± 0.73 | 0.50 ± 0.07 |
| BF | 5 | 7.50 ± 0.96 | |
| IRF | 0 | 12.06 ± 1.00 | 1.01 ± 0.13 |
| IRF | 5 | 9.87 ± 1.91 | |
| GL | 0 | 11.09 ± 1.58 | 0.94 ± 0.14 |
| GL | 5 | 11.47 ± 0.83 | |
| RF | 0 | 9.24 ± 0.70 | 0.79 ± 0.06 |
| RF | 5 | 10.79 ± 1.19 | |
| PR | 0 | 12.05 ± 0.51 | 1.04 ± 0.01 |
| PR | 5 | 11.87 ± 0.30 | |

**Table S3**. Vector analysis to find which variable fits the NMDS axes (both 1 and 2). The number of permutations was 999. * shows the highest percentages that fit NMDS axes.

| Variables | NMDS 1 | NMDS 2 | r2 | Pr(>r) |
|---|---|---|---|---|
| EAS % | 0.883 | 0.469 | 0.774 | 0.001 |
| BS % | -0.978* | -0.208 | 0.837 | 0.001 |
| ECEC | 0.789 | 0.615 | 0.774 | 0.001 |
| pH | -0.536 | -0.844 | 0.683 | 0.001 |
| Organic C | -0.811 | -0.585 | 0.568 | 0.001 |
| Nitrogen | -0.809 | -0.587 | 0.574 | 0.001 |
| Phosphorus | 0.996* | 0.088 | 0.560 | 0.001 |
| Growth rate | -0.251 | 0.968* | 0.425 | 0.001 |
| Germination | -0.427 | 0.904* | 0.575 | 0.001 |

**Table S4**. Results from statistical tests used for comparing nitrogen content (N) organic carbon content (OC), germination, growth rate and mycorrhizal colonization, between land covers. Burned grassland (BGL), Grassland (GL), Forest with a 15-yr old restoration process (RF), Forest with recent (< 5 yr) restoration (IRF), Forest border (BF), Páramo (PR). Sample size (N), and degrees of freedom (df).

| Analysis | Test | Statistic value | p-value | df | N | Post-hoc |
|---|---|---|---|---|---|---|
| N content | ANOVA | 13.8 | <0.001 | 4 | 14 | BF<GL, IRF, P. BF=RF |
| OC content | ANOVA | 16.46 | <0.001 | 5 | 38 | BF<GL, RF, IRF, P, BGL |
| Germination (%) | Kruskal-Wallis | 14.76 | 0.011 | 4 | 134 | PR>GL, BGL; BF>GL, BGL |
| Growth rate (cm week$^{-1}$) | ANOVA | 0.92 | 0.46 | 4 | 63 | NA |
| Mycorrhizal colonization, root tips | T-test | -1.64 | 0.11 | 28 | 30 | NA |
| Mycorrhizal colonization land covers (root tip) | ANOVA | 0.32 | 0.85 | 4 | 15 | NA |
| Mycorrhizal colonization comparison land covers (root end) | ANOVA | 1.68 | 0.23 | 4 | 15 | NA |

**Table S5**. Number of seeds that germinated in all land covers and at 0. 2.5 and 5 m from the adult individual. Burned grassland (BGL) does not have data for distances at 2.5 and 5 m, as this land cover had no individuals. Burned grassland (BGL), Grassland (GL), Forest with a 15-yr old restoration process (RF), Forest with recent (< 5 yr) restoration (IRF), Forest border (BF), Páramo (PR).

| **Land cover** | **0 m** | **2.5 m** | **5 m** | **Total** |
|---|---|---|---|---|
| PR | 24 | 24 | 14 | 62 |
| BF | 21 | 7 | 2 | 30 |
| RF | 9 | 5 | 7 | 21 |
| IRF | 8 | 3 | 5 | 16 |
| GL | 2 | 2 | 0 | 4 |
| BGL | 1 | NA | NA | 1 |
| **Total** | 65 | 41 | 28 | 134 |

**Table S6**. Statistical data from all analysis when comparing distances data within each land cover point for germination (%), growth rate (cm week$^{-1}$) and root colonization (%). All data were tested using parametric test ANOVA (for gorse germination and growth rate) and T-test (for root colonization). For IRF gorse growth we used Kruskal-Wallis. Burned grassland (BGL), Grassland (GL), Forest with a 15-yr old restoration process (RF), Forest with recent (< 5 yr) restoration (IRF), Forest border (BF), Páramo (PR). 0, 2.5 and 5 m refer to the comparison between gorse germination at different distances from the adult individual.

| | **Germination** | | **Growth rate** | | **Root colonization** | |
|---|---|---|---|---|---|---|
| **Land cover** | **Statistic** | **p** | **Statistic** | **p** | **Statistic** | **p** |
| RF | 0.2 | 0.82 | 0.21 | 0.18 | -1.14 | 0.32 |
| IRF | 0.19 | 0.83 | 5.45 | 0.07 | -2.14 | 0.1 |
| BF | 2.85 | 0.14 | 0.84 | 0.38 | -1.47 | 0.22 |
| GL | 0.5 | 0.63 | NA | NA | 0.98 | 0.38 |
| PR | 0.24 | 0.79 | 2.22 | 0.13 | -0.63 | 0.56 |
| 0 m | 2.14 | 0.13 | | | | |
| 2.5 m | 0.56 | 0.7 | | | | |
| 5 m | 0.53 | 0.72 | | | | |