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Invasion of *Celtis tala* forests by *Ligustrum lucidum* in Argentina: impact on soil properties and the arbuscular mycorrhizal community

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1 **Invasion of *Celtis tala* forests by *Ligustrum lucidum* in Argentina: impact on soil**
2 **properties and the arbuscular mycorrhizal fungi community**

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Abstract

The arrival of invasive plants can cause drastic changes to ecosystems, such as the displacement of native plant communities and the disruption of ecological functions. *Ligustrum lucidum* is an invasive tree species that has been registered in numerous regions worldwide. We analysed the effect of the expansion of *L. lucidum* on the edaphic properties and mycorrhizal fungal communities in forests of *Celtis tala* located in central-western Argentina. Sampling sites were established along a gradient of invasion, in which we measured the forest structure and soil physical-chemical factors and identified the fungal species using morphological techniques. The analysis of the variance revealed severe changes in the tree structure and a decrease in the concentrations of organic matter and nitrogen in the invaded sites. Thirty-two Glomeromycota species were identified, belonging to 6 families. The abundance of *Dentiscutata cerradensis* decreased with the invasion, whereas *Funneliformis mosseae* and *Septoglomus constrictum* increased. The alpha diversity of the arbuscular mycorrhizal communities showed no differences between sites. The beta diversity decreased at invaded sites, indicating a tendency towards convergence and reduced variability in these communities in the presence of the exotic species.

Key words: Glomeromycota, biological invasions, diversity, exotic tree, arbuscular mycorrhizas

1. Introduction

Biological invasions are one of the greatest threats to the integrity of native ecosystems. The dispersion of exotic plants can affect not only the structure of native plant communities but also the ecosystem functions and microbial soil communities, including the arbuscular mycorrhizal fungi (AMF) (Egidi and Franks 2018). These microorganisms belong to the phylum Glomeromycota (Schüßler et al. 2001), and are one of the most important and widely distributed symbiotic plant associations (Tanner and Gange 2013). AMFs are obligate mutualists that are associated with the roots of 80% of the terrestrial plant species. They play a key role in the uptake of phosphorus and other nutrients, water intake, pathogen protection and resistance against various abiotic stress factors, such as drought and toxicity (Smith and Read 2008).

Interaction between AMF and plant communities has been described as codependent since the composition of one guild affects the composition of the other (Kokkori et al. 2020). AMF fungi have the ability to determine plant community structure by affecting the relative abundance of plant species and plant-species diversity. Mycorrhization can favour the growth of some plant species, be neutral or generate a negative response, influencing their performance and competitive ability (Francis and Read 1995). At the same time, the composition of the plant community can determine the composition and diversity of the AMF communities given that different plants can host distinct AMF species. Furthermore, AMF are entirely dependent on plant hosts for carbon and have unequal growth rates on different plant species (Hawesman and Hawkes 2009). In the last decade, the role of these microorganisms in invasion processes has gained increasing attention (Egidi and Frank 2018). The arrival of invasive plants can affect the

AMF abundance and diversity, and thus, these changes can not only be negative for native plants but also accelerate the invasion (Reinhart and Callaway 2006, Shah et al. 2009). If the invasive plant is little or not dependent on mycorrhizas, the abundance of these microorganisms will decrease, impairing the competitive capacity of native plants (Goodwin 1992). On the other hand, if the invading plant is dependent on mycorrhizas and establishes a positive interaction with certain fungal species, a positive feedback will be established that will favour the development of both the invasive plant and the fungus (Bever 2003).

Invasion by exotic plant species can alter ecosystem functions at local and regional scales, causing natural habitat degradation, biodiversity loss, and changes in litter input, decomposition rates, community structure and metabolic activities of soil microorganisms and soil nutrient cycles (Vilà et al. 2011). In particular, changes in soil chemical characteristics caused by the invasion of plant species have been widely documented. The plant nutrient uptake, as well as the radical exudates and the litter they produce, determine the nutrient retention and its cycling in the long term (Weidenhamer and Callaway 2010). Many invasive plants have larger leaf areas, higher concentrations of leaf nutrients and higher growth rates than native ones (Hughes and Uowolo 2006). In nutrient-poor ecosystems, the increase in nutrient cycling rates by exotic species can play an important role in their invasion success (Enoky and Drake 2017).

The talaes, which are located in the northwest of Buenos Aires province (Argentina), constitute a forested physiognomy dominated by *Celtis tala* Gill. ex Planch (Celtidaceae) and *Scutia buxifolia* Reiss. (Rhamnaceae) (Parodi, 1940). Currently, the composition and structure of these forests are modified due to the invasion of *Ligustrum*

lucidum W.T. Aiton (Oleaceae), commonly known as glossy privet (Franco et al. 2018). This species has invaded numerous regions worldwide. In Argentina, it was introduced at the beginning of the 20th century, used mainly as an ornamental and in living fences. It commonly forms dense spots and dominates all strata (Haene et al. 2003). In the talaes, it reaches the upper stratum in a short time (approximately 10 years) and generates a continuous coverage that exceeds the maximum height of the native species, causing high mortality (Plaza Behr et al. 2016).

Both the native species and *L. lucidum* have been registered as hosts of arbuscular mycorrhiza in the talaes (Francchia 2009, Velazquez 2010). Up to date, the study of this invasion phenomenon has focused on aboveground processes, whereas the soil interactions and their relationship with the composition of these forests have not been yet explored. Our aim was to assess the effect of the invasion of *L. lucidum* on the edaphic factors and the AMF spores community by analysing its composition and structure along a gradient of *L. lucidum* invasion.

2. Materials and Methods

2.1 Sampling

The study was carried out at the private reserve “El Destino”, located in "Parque Costero del Sur" Biosphere Reserve, Buenos Aires province, Argentina (35°11'S, 57°17'W). The climate of this region has an annual mean temperature between 15 and 17 °C. Rainfall varies between 850 and 1065 mm per year, with maximum occurrences during fall and spring. Sampling was carried out during 2016 and 2017, on cords that have a tree structure with a spatial gradient in the proportion of *L. lucidum*. Along this gradient, we

established the sampling units with the following proportions of tree species: native forest of *C. tala* and *S. buxifolia* (NAT), native forest with the presence of *L. lucidum* (MIX) and monospecific *L. lucidum* forest (INV). Three 100 m transects were established parallel to each other, each with three sites representative of the three vegetation situations. At each site, five soil subsamples were collected at a depth of 15 cm to form a composite sample (approximately 400g). In each sampling unit, we assessed the forest structure, the edaphic factors and the species composition of AMF. A total of 54 samples were collected for characterization of AMF community (2 years x 3 transects x 3 situations x 3 sites) (Fig. 1). Samples were stored in polyethylene bags at 4°C until processing (up to 2 weeks).

2.2 Vegetation structure

At each sampling site, the structure of the tree community was described in 100m² square plots. In each plot, we identified the species and measured the diameter at breast height (DBH) of each individual > 5 cm in diameter. We used this data to calculate the basal area (m²/ 100 m²) and density (individuals/ ha) of each species.

2.3 Soil analyses

We determined the pH, electrical conductivity (EC), cation exchange capacity (CEC) and exchangeable bases (IRAM-SAGyP 2004), Calcium, (Ca⁺²) and Magnesium (Mg⁺²) by complexometry with EDTA (ethylene diamine tetraacetic acid) and Sodium (Na⁺¹) and Potassium (K⁺¹) by flame photometry. Assimilable phosphorus (P) was quantified using the methodology of Bray Kurtz N1 (IRAM-SAGPyA 2010). Organic carbon was quantified by the Walkley and Black method (1934) and was used to calculate the organic matter (OM) content by multiplying by the conventional factor of $1.724 \times C$

(%). The total nitrogen (N) determination was performed by the Kjeldhal method (Bremner and Mulvaney 1982). The different textural fractions were determined using the Bouyoucos hydrometer method (1962).

2.4 Characterization of the AMF community

The isolation and identification of the AMF morphospecies present in the rhizosphere were carried out by wet sieving of 100 g of soil using sieves of different mesh sizes (450-105-75-30 μm), followed by decanting (Gerdemann and Nicolson 1973) and sucrose density gradient centrifugation (Walker et al. 1982). The term “morphospecies” has been chosen to refer to AMF species (Robinson-Boyer et al. 2009) when their identification is based on the morphological traits and ontogeny of spores. Isolated spores were transferred to Petri dishes, and inspected under a dissecting microscope. Spore phenotypic characteristics such as hyphal attachment, spore size, color, and shape were used to distinguish different morphotypes. Spores of each morphotype were mounted permanently on slides in polyvinyl-lacto-glycerol (PVLG) and PVLG mixed with Melzer’s reagent (1:1, v/v) and examined under an optical microscope (Leitzdia lux 20EB) coupled with an Olympus SP-350 camera. Spores were identified to genus and species level based on the analysis of their spore wall structure, Melzer’s reaction and other taxonomically informative characteristics and comparisons with those originally described (Błaszkowski 2012), and online references of species description of INVAM at the West Virginia University, USA (<http://invam.wvu.edu>). Gigasporoid spores differentiating two or more germinal walls and glomoid spores that could not be attributed to species were placed in the genera *Scutellospora* and *Glomus*, respectively. The assignment of AMF morphotypes to families and genera followed the consensus classification of AMF phylogeny (www.amf-

phylogeny.com). The abundance of each morphospecies was referred to as the number of spores in 100 g of dry soil. The diversity of the AMF communities studied was estimated by the morphospecies richness (S), Pielou's evenness (J') and the Shannon-Wiener diversity index (H').

2.5 Statistical analyses

We performed permutational multivariate analyses of variance (PERMANOVA) to determine differences between the different situations (NAT, MIX and INV) on the forest structure, soil properties and the composition of the AMF community. PERMANOVA is non-parametric statistical method for ecological multivariate data sets (Anderson 2001), which was performed on Euclidean distance for soil and vegetation matrixes and on Bray-Curtis distance for AMF morphospecies matrix. Bray-Curtis constitutes an appropriate distance measure for compositional data (Anderson 2001). Number of randomizations was 4999. Soil and vegetation matrixes were standardized.

A principal coordinate analysis (PCOA) for the morphospecies/site matrix was performed using the Bray-Curtis coefficient, with a base 10 logarithmic transformation and considering only those morphospecies present in $\geq 10\%$ of the samples. The two first axes of the PCOA were used to visualize the position and dispersal trends of vegetational situations in the compositional space. Standard deviation ellipses were plotted. An analysis of multivariate homogeneity of group dispersions (PERMDISP; Anderson, 2006) was conducted to test for differences in multivariate dispersions in AMF community composition between the three vegetation situations.

One-way ANOVAs were performed to compare the forest structure, the number of spores, and diversity indexes between the three vegetation situations. In all cases, normality and homoscedasticity of variances were checked with Shapiro-Wilk and Levene's tests. The Tukey's test was used to compare between significantly different means.

Pearson's correlation was used to analyse the relationship between plant community and AMF morphospecies abundances and between plant community and soil variables.

All analyses were carried out with R "vegan" package (Oksanen et al. 2020), Infostat (Di Renzo et al. 2016) and MVSP 3.2, considering $\alpha = 0.05$.

3. Results

3.1 Vegetation structure

At NAT, we recorded predominantly *C. tala*, *S. buxifolia* and *J. rhombifolia*, and a few specimens of *L. lucidum*. At MIX, we found a greater number of *L. lucidum* specimens than of native species, which in some cases were dead. At INV, we mostly recorded specimens of *L. lucidum*. The structure of the tree community differed between sites (PERMANOVA, Pseudo-F = 2.8457, $p = 0.0088$). As shown in Fig. 2, the densities of native species and *L. lucidum* were significantly different between sites ($F = 3631$, $p < 0.001$; $F = 79.98$, $p < 0.001$, respectively). Differences of statistical significance were also found in the basal areas of native species and *L. lucidum* between sites ($F = 255.65$, $p < 0.0001$; $F = 2819$, $p < 0.001$, respectively).

The total density of tree species (*C. tala*, *S. buxifolia*, *J. rhombifolia* and *L. lucidum*) was significantly lower ($F = 25.73$, $p < 0.001$) at NAT and MIX (2177.77 ± 1442 ind/ha and 2000 ± 750 ind/ha, respectively) than at INV sites (3588.88 ± 958.4 ind/ha).

3.2 Soil properties

All sites showed similar soil texture and characteristics, corresponding to a sandy loam type with alkaline pH, moderate to high salinity, high CEC and strong Ca^{+2} saturation (Table 1). Soil properties showed differences between vegetation situations (PERMANOVA, Pseudo- $F = 4.0598$, $p = 0.0042$).

Pearson's correlation analysis showed that the content of OM, N and P correlated negatively with the density of *L. lucidum* ($r = -0.746$, $p < 0.001$; $r = -0.818$, $p < 0.001$ and $r = -0.5770$ and $p < 0.001$ respectively) and positively with the density of native trees ($r = 0.6682$, $p = 0.0001$; $r = 0.7832$, $p < 0.001$ and $r = 0.7110$, $p < 0.0001$), indicating a decreasing trend with regard to *L. lucidum* invasion.

3.3 AMF communities

We isolated a total of 9,943 AMF spores. Most samples had between 12 and 550 spores/100 g dry soil, except one sample that showed a density of 1490 spores/100 g dry soil. Although the total density of spores tended to increase in sites invaded by *L. lucidum*, the differences between sites were not significant ($F = 0.69$, $p = 0.5082$). Thirty-two morphospecies were identified, belonging to the families Glomeraceae (70.3%), Diversisporaceae (15.9%), Gigasporaceae (8.5%), Acaulosporaceae (4.4%), Pacisporaceae (0.6%), and Archaeosporaceae (0.4%) (Fig. 3).

211 *Septoglomerus constrictum*, *Diversispora spurca*, *Entrophospora infrequens*,
 212 *Sclerocystis sinuosa*, *Dentiscutata cerradensis*, *Paraglomerus albidum*, *Glomerus* sp. 1,
 213 *Acaulospora delicata*, *Claroideoglomerus etunicatum*, *Glomerus* sp. 2, *Rizophagus aggregatus*,
 214 and *Acaulospora mellea* were found in the three vegetation situations. *Rizophagus*
 215 *intraradices* was found only in sites with the presence of native trees (NAT and MIX),
 216 whereas *Acaulospora scrobiculata*, *Pacispora robigina*, *Kamienskia bistrata* and *Glomerus*
 217 *corymbosum* only at sites with the presence of *L. lucidum* (MIX and INV). The rest of the
 218 morphospecies recorded exhibited an erratic presence in the different vegetation situations.
 219 (Table 2).

220 According to PERMANOVA, the vegetation had no effect on the composition of
 221 the AMF community (Pseudo-F = 1.4011, $p = 0.1072$). Nevertheless, Pearson's correlation
 222 analysis showed that the abundance of *D. cerradensis* correlated positively with the density
 223 of the native *C. tala* ($r = 0.3640$, $p = 0.0068$), whereas the *F. mosseae* abundance correlated
 224 negatively with the density of native trees ($r = -0.288$, $p = 0.0347$) and positively with the
 225 density of *L. lucidum* ($r = 0.2975$, $p = 0.0289$). In addition, the abundance of *S. constrictum*
 226 also correlated negatively with the density of native trees ($r = -0.3348$, $p = 0.0048$) and
 227 positively with the density of *L. lucidum* ($r = 0.3556$, $p = 0.00829$). The morphospecies
 228 richness varied between 1 and 14 morphospecies per sample and showed no differences
 229 between sites. The H' index ranged between 0 and 0.84 and also showed no differences
 230 (Fig. 4)

231 The PCOA analysis showed a single point cloud distributed throughout the four
 232 quadrants (Fig. 5), with the NAT, MIX and INV points overlapped. The INV and MIX
 233 points exhibited a compact distribution within the point cloud. On the other hand, NAT

sites presented a more dispersed distribution, with a greater distance between each other. Additionally, PERMDISP analysis showed differences in the relative dispersion of plots within groups ($F = 16.634$, $p = 0.001$).

4. Discussion

Our study reported for the first time the effect of the invasion by *L. lucidum* on the edaphic factors and the AMF communities in native forests.

We observed that the native tree structure of *C. tala* and *S. buxifolia* forests was modified by the invasion of *L. lucidum*. The three vegetation situations analysed, i.e. NAT, MIX and INV, showed significant differences in the tree community composition. According to Franco et al. (2018), the presence of *L. lucidum* displaces native species, preventing their regeneration due to shading and modifying severely the community, which leads to the dominance of the exotic species.

The soil of these forests is the result of quaternary deposits of shells of marine molluscs and is classified as Rendol, which is characterized by alkaline pH (<8), moderate to high salinity and strong saturation of Ca^+ (Hurtado and Ferrer 1988). These soil characteristics, which were confirmed by physicochemical analyses, were the same in the three vegetation situations and can be limiting for the fungal development since these organisms develop better in neutral or slightly acidic pH (Dumbrell et al. 2010). Oehl et al. (2010) found that even in environments with different use intensities, pH is usually one of the most important factors in determining the characteristics of AMF communities. Since all sites showed similar textural characteristics, differences in nutrient concentration can be attributed to changes in vegetation.

Our results indicated that the presence of *L. lucidum* produced a decrease in the soil OM and N contents. Although the development of invasive species in many ecosystems has been correlated with an increase in the leaf litter decomposition rate and N mineralization (Ashton et al. 2005, Liao et al. 2008, Feng et al., 2009), the invasive species *Heracleum mantegazzianum* and *Fallopia japonica* showed slow cycling of organic matter in grassland soils of Belgium (Koutika et al. 2007). It is yet unknown if the leaf litter of *L. lucidum* might present a lower decomposition rate than the native trees of the talar.

The P soil content was positively correlated with native trees and negatively correlated with *L. lucidum*, showing the same tendency as the OM and N. This could be attributed to the P uptake and retention by part of the vegetation since the sites with the lowest P availability were those with the highest total tree density (MIX and INV). Dassonville et al. (2008) observed that the decrease in the soil concentration of removable P can be associated with high productivity of underground biomass.

Thirty-two morphospecies of AMF were recovered. This number is comparable to and even greater than the number of Glomeromycota species reported for other forests in Argentina (Soteras et al. 2015) and other regions of the world (Montaño et al. 2012, Cofré et al. 2019). Among the AMF families, Glomeraceae was dominant in all sites, as previously reported for various environments (Stover et al. 2012, Brundrett and Ashwath 2013, Nunes et al. 2019). The abundance of members of this family is related to the ability to produce a large spore number in short periods of time to ensure survival, as well as their wide tolerance to various stress and disturbance factors (Daniell et al. 2001). The rest of the families showed abundances < 16%. The most abundant morphospecies were *F. mosseae*,

278 *E. infrequens*, *S. constrictum*, and *S. sinuosa*, which have been referred as generalists and
279 characteristic of calcareous soils with alkaline pH in Europe (Oehl 2010).

280 The effect of the invasion on AMF community composition was not significant. *D.*
281 *cerradensis* was the only morphospecies whose abundance was negatively correlated with
282 the abundance of *L. lucidum* and positively correlated with the presence of native *C. tala*.
283 These findings coincide with the results of Allen et al. (2013), who observed that the
284 species of Gigasporaceae family are characteristic of climax or late succession
285 communities, and is absent or non-abundant in young forests. On the other hand, *S.*
286 *constrictum* and *F. mosseae* were positively associated with *L. lucidum* and correlated
287 negatively with the density of native trees. Although we cannot affirm that these species are
288 benefiting with the development of *L. lucidum*, they might have established a positive
289 interaction that could lead to the development of symbiosis, according to the positive
290 feedback model proposed by Bever (2003).

291 In this study, we analysed the effect of the invasion on the alpha and beta diversity
292 of the AMF communities. The presence of *L. lucidum* showed a non-significant effect on
293 the alpha diversity estimated using the S, H' and E indices. This indicates an unexpected
294 resilience of the fungal community against plant diversity loss. On the other hand, the
295 presence of *L. lucidum* affected the beta diversity, which was estimated using PCOA,
296 PERMANOVA and PERMDISP analysis. The results showed that AMF communities
297 differed between situations because they had different dispersions rather than different
298 compositions. The PCOA evidenced this effect by showing more compacted point clouds
299 for MIX and INV sites than for NAT sites. Therefore, we observed that the invasion of *L.*
300 *lucidum* generated less variable AMF communities, causing a convergence in its

composition and reducing the variability present in the native ecosystem. Similar results were found for the invasion of herbaceous species in Central American forests, in which the reduction in vegetation diversity did not cause losses in the AMF richness and diversity, but increased the similarity between fungal communities (Johnson and Wedin 1995).

Studies based on morphological identification of AMF are widely used all over the world (Solís-Rodríguez et al. 2020, Nunez et al. 2019, Cofré et al. 2019) and sometimes are even more efficient than modern molecular approaches (Wetzel et al. 2014). Despite morphologically described AMF species are highly intraspecifically variable, not necessarily represent root colonizing taxa, and not always sporulate during sampling, they can give a valuable approach of the AMF community of a particular place and moment. However, further DNA-based descriptions should be combined with morphospecies approach in order to deeply characterize AMF communities in the talaes and the dynamics of *L. lucidum*-AMF interaction.

5. Conclusion

The native tree structure of *C. tala* and *S. buxifolia* forests was completely modified by the invasive *L. lucidum*. In addition, the expansion of this exotic species caused changes in the soil characteristics and reduced the availability of some nutrients. Its effect on the Glomeromycota community was evidenced by the absence of *D. cerradensis* and the increase in abundance of *F. mosseae* and *S. constrictum*. Although the alpha diversity did not exhibit differences associated with vegetation, it is not possible to affirm that changes in the AMF community related to the invasion will not happen in the future. However, our results indicated that the exotic *L. lucidum* caused a decrease in the

variability of fungal communities. Future studies might further investigate the interaction between *L. lucidum* and native AMF in this ecosystem through molecular techniques and greenhouse experimental approaches. We believe that understanding the role that AMF communities play in plant invasion can potentially help predict the severity of invasion and potentially lead to successful management and restoration strategies.

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Tables

Table 1: Edaphic factors of three situations of vegetation (native, mixed and invaded). The values are expressed as means ($\pm$ standard deviation).

Soil characteristics	Vegetation		
	NAT	MIX	INV
pH (H ₂ O)	7.62 (0.18)	7.86 (0.30)	7.66 (0.40)
EC (μ S m ⁻²)	835.33 (159.20)	784.33 (247.70)	724.33 (238.11)
CEC (cmol kg ⁻²)	21.2 (5.35)	19.27 (4.05)	24.23 (6.71)
OM (%)	8.04 (1.40)	3.72 (0.09)	3.61 (0.18)
N (%)	0.50 (0.01)	0.27 (0.02)	0.21 (0.01)
P (mg kg ⁻²)	5.66 (0.58)	3.67 (2.08)	2.67 (1.15)
K ⁺ (cmol kg ⁻²)	2.10 (1.05)	1.07 (0.01)	3.70 (0.46)
Na ⁺ (cmol kg ⁻²)	0.47 (0.06)	0.2 (0.10)	0.50 (0.01)
Ca ⁺⁺ (cmol kg ⁻²)	24.60 (6.46)	27.23 (4.95)	19.03 (10.11)
Mg ⁺⁺ (cmol kg ⁻²)	10.83 (1.44)	14.13 (1.44)	13.4 (2.49)

NAT: native forest; MIX: mixed forest; INV: invaded forest.

Table 2: Number of spores per 100 g of dry soil of the morphospecies recorded in native, mixed and invaded forest sites. Values are expressed as means ($\pm$ standard deviation). (*) indicates the species present in $\geq 10\%$ of the samples. Shaded rows indicate species that were found only in one year.

Year	2016			2017		
AMF Species /Vegetarion	NAT	MIX	INV	NAT	MIX	INV
<i>*Septoglomus constrictum</i>	60(129)	44.9 (63.5)	242.4 (471)	47.7 (112)	31.1 (42.7)	22.7 (16.7)
<i>*Entrophospora infrequens</i>	35.9 (73.1)	23.3 (33.9)	14.9 (28.7)	1 (2)	0.8 (1.2)	3.8 (4.2)
<i>*Diversispora spurca</i>	16.2 (17)	23.2 (16.9)	33.8 (33.6)	7.2 (7.1)	8.4 (8.3)	6.6 (6.3)
<i>*Dentiscutata cerradensis</i>	56.9 (88.7)	5.8 (8.89)	7.1 (13.1)	12.7 (24.2)	1.9 (3.8)	2.3 (4.7)
<i>*Funnelformis mosseae</i>	8.9 (19.6)	16.3 (19.8)	29 (22)	2.7 (4.8)	2.1 (3.4)	5.4 (7.1)
<i>*Sclerocystis sinuosa</i>	25.2 (40.1)	12.3 (12.8)	12.6 (16.9)	11.9 (8.7)	21.6 (16.2)	15 (9.9)
<i>*Glomus sp.1</i>	7.6 (14.2)	10.9 (24.6)	14.7 (22.1)	9.4 (26.9)	3.3 (5)	4.7 (5.7)
<i>*Acaulospora delicata</i>	10.3 (16.1)	3.8 (9.2)	7.2 (7.5)	2.6 (3.8)	2.1 (3.1)	3.8 (5.2)
<i>*Claroideoglomus etunicatum</i>	14 (41.3)	0.2 (0.7)	1 (3)	1.6 (4.7)	0.0	0.0
<i>*Glomus sp3</i>	3.6 (8.4)	3.3 (5.4)	2.2 (5.1)	0.0	0.0	0.4 (1.3)
<i>Corymbiglomus corymbiforme</i>	0	1.6 (4.67)	6.7 (20)	0.0	0.0	0.4 (1.3)
<i>*Rizophagus aggregatus</i>	2 (1.7)	3 (1.9)	3.2 (1.9)	0.6 (1.7)	0.9 (1)	0.3 (1)
<i>*Paraglomus albidum</i>	0.2 (0.67)	4.9 (10.8)	1.8 (4.14)	10.3 (28.4)	2.7 (4.3)	5.4 (8.3)
<i>*Pacispora robigina</i>	0	4.7 (11)	0.2 (0.6)	0.0	0.8 (2.3)	1.3 (4)
<i>*Acaulospora mellea</i>	1.9 (4.9)	0.6 (1.7)	1.3 (4)	1.7 (5)	0.0	0.2 (0.7)
<i>*Rizophagus intraradices</i>	2.2 (6.7)	0.8 (2.3)	0	0.0	1.8 (5.3)	0.0
<i>Glomus badium</i>	0	0.2 (0.7)	0	0.0	0.8 (2.3)	0.0
<i>Kamienskia bistrata</i>	0	0	2.8 (8.3)	0.0	0.0	0.4 (1.3)
<i>*Glomus sp. 2</i>	3 (8.28)	0	9.8 (17.4)	0.0	0.0	0.0
<i>Archaespora trappei</i>	0.8 (2.3)	0.2 (0.67)	1.6 (4.7)	0.0	0.0	0.0
<i>Rhizoglomus microaggregatum</i>	15.7 (32.9)	1 (3)	0	0.0	0.0	0.0
<i>Acaulospora laevis</i>	1.1 (3.3)	0	1.2 (3.7)	0.0	0.0	0.0
<i>Glomus hoi</i>	0	0	0.1 (0.3)	0.0	0.0	0.0
<i>*Acaulospora scrobiculata</i>	0	0	0	0.2 (0.7)	0.0	10.4 (22.4)
<i>Glomus glomeratum</i>	0	0	0	2.2 (6.72)	2.8 (8.3)	0.6 (1.67)
<i>*Scutellospora sp.</i>	0	0	0	3.6 (9.9)	1.3 (2.7)	2 (6)
<i>*Glomus sp. 4</i>	0	0	0	0.0	0.0	0.4 (1.3)

NAT: native forest; MIX: mixed forest; INV: invaded forest

Figure captions

Figure 1: Sampling design used to describe arbuscular mycorrhizal fungi communities, soil properties and forest structure along three transects with a *Ligustrum lucidum* invasion gradient (NAT: native forest, MIX: mixed forest and INV: invaded forest).

Figure 2: Basal area ($\text{m}^2/100 \text{ m}^2$) and density (individuals/ hectare) of native trees (*Celtis tala*, *Scutia buxifolia* and *Jodina rhombifolia*) and of *Ligustrum lucidum* in three situations of vegetation (NAT: native forest, MIX: mixed forest and INV: invaded forest). Values are expressed as means ($\pm$ standard deviation). Different letters indicate significant differences between means ($\alpha < 0.05$).

Figure 3: Arbuscular mycorrhizal fungi spores isolated from the soil of *Celtis tala* and *Scutia buxifolia* forests with presence of *Ligustrum lucidum*. a- *Entrophospora infrequens* b- *Funneliformis mosseae* c- *Septoglomus constrictum* d- *Diversispora Spurca* e- *Sclerocystis sinuosa* f- *Dentiscutata cerradensis*.

Figure 4: Species richness (S), Shannon-Wiener diversity index (H'), and evenness (E) of the arbuscular mycorrhizal fungi communities in three situations of vegetation (NAT: native forest, MIX: mixed forest and INV: invaded forest). Values are expressed as means ($\pm$ standard deviation). Different letters indicate significant differences between means ($\alpha < 0.05$).

Figure 5: Analysis of main coordinates for the abundance of Glomeromycota species at sites corresponding to three situations of vegetation: native forest (green), mixed forest (yellow), and invaded forest (red). The lines define standard deviation ellipses (native, mixed and invaded). Variance explained: 49.9%.

Figure 1: Sampling design used to describe arbuscular mycorrhizal fungi communities, soil properties and forest structure along three transects with a *Ligustrum lucidum* invasion gradient (NAT: native forest, MIX: mixed forest and INV: invaded forest).

164x113mm (96 x 96 DPI)

Figure 2: Basal area (m²/100 m²) and density (individuals/ hectare) of native trees (*Celtis tala*, *Scutia buxifolia* and *Jodina rhombifolia*) and of *Ligustrum lucidum* in three situations of vegetation (NAT: native forest, MIX: mixed forest and INV: invaded forest). Values are expressed as means ($\pm$ standard deviation). Different letters indicate significant differences between means ($\alpha < 0.05$).

434x264mm (300 x 300 DPI)

Figure 3: Arbuscular mycorrhizal fungi spores isolated from the soil of *Celtis tala* and *Scutia buxifolia* forests with presence of *Ligustrum lucidum*. a- *Entrophospora infrequens* b- *Funneliformis mosseae* c- *Septoglomus constrictum* d- *Diversispora Spurca* e- *Sclerocystis sinuosa* f- *Dentiscutata cerradensis*.

52x65mm (300 x 300 DPI)

Figure 4: Species richness (S), Shannon-Wiener diversity index (H'), and evenness (E) of the arbuscular mycorrhizal fungi communities in three situations of vegetation (NAT: native forest, MIX: mixed forest and INV: invaded forest). Values are expressed as means ($\pm$ standard deviation). Different letters indicate significant differences between means ($\alpha < 0.05$).

456x477mm (300 x 300 DPI)

Figure 5: Analysis of main coordinates for the abundance of Glomeromycota species at sites corresponding to three situations of vegetation: native forest (green), mixed forest (yellow), and invaded forest (red). The lines define standard deviation ellipses (native, mixed and invaded). Variance explained: 49.9%.

52x56mm (300 x 300 DPI)