Antagonistic Interactions Between Fusaria Species and Their Host Plants Are Influenced by Host Taxonomic Distance: A Case Study From Mexico

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Interactions between cultivated and wild plants with their fungal pathogens have strong ecological, evolutionary and economic implications. Antagonistic interactions, however, have been scantily studied in an applied context by using ecological networks, phylogeny and spatial ecology concurrently. In this study, we describe for the first time, the topological structure of plant-fungi networks involving species of the genus *Fusarium* and their native and introduced (exotic) cultivated host plants in Mexico. For this, we based our study on a recent database describing the attack on 75 native and introduced plant species, including 35 species of the genus *Fusarium*. Host plant species varied in their degree of phylogenetical relatedness (Monocots and Dicots) and spatial geographical distribution. Therefore, we also tested whether or not plant-*Fusarium* networks are phylogenetically structured and highlighted the spatial correlation between pathogens and their host plants across the country. In general, the pathogen-plant network is more specialized and compartmentalized in closely related taxa. Closely related hosts are more likely to share the same pathogenic *Fusarium* species. Host plants are present in different ecosystems and climates, with regions having more cultivated plant species presenting the highest number of fusaria pathogens. From an economic standpoint, different species of the same taxonomic family may be more susceptible to being attacked by the same species of *Fusarium,* whereas from an ecological standpoint the movement of pathogens may expose wild and cultivated plants to new diseases. Our study highlights the relevance of interaction intimacy in structuring trophic relationships between plants and fusaria species in native and introduced species. Furthermore, we show that the analytical tools regarding host distribution and phylogeny could permit a rapid assessment of which plant species in a region are most likely to be attacked by a given fusaria.

Keywords: ecological networks, exotic species, *Fusarium*, plant-pathogen interactions, phylogenetically structured networks, spatial distribution

INTRODUCTION

Fungal pathogens are recognized as the major causal agents of plant diseases and comprise an important threat to wild and cultivated plant species worldwide (Burdon, 1991; Anderson et al., 2004; Benítez-Malvido, 2012). They represent an essential component of biodiversity in natural plant populations and communities and have strong socioeconomic implications in agroecosystems (Burdon, 1991; Desprez-Loustau et al., 2007, 2015). Several fungal species are known for their economic importance as they cause great losses to several agricultural crops and in forestry elsewhere (Anderson et al., 2004; Geiser et al., 2004, 2013). Some of those species belong to the filamentous ascomycete fungi genus *Fusarium* (Sordariomycetes: Hypocreales: Nectriaceae). The genus is cosmopolitan and includes pathogens that cause diseases in domesticated animals, humans and plants (Leslie and Summerell, 2006). Additionally, a considerable number of fusaria species are toxin-producing plant pathogens of agricultural and medical importance (Summerell et al., 2010). Disease symptoms in plants caused by *Fusarium* range from foliage blights, branch and stem cankers, floral and vegetative malformation, crown, root and stem rots, as well as vascular wilts (Ploetz, 2006; Ma et al., 2013). There are several fusaria species that cause diseases in staple food crops worldwide (Geiser et al., 2013; Ma et al., 2013), including the following: ear rot of maize (Desjardins et al., 2002), *Fusarium* head blight (O'Donnell et al., 2000), sudden death syndrome of soybeans (Aoki et al., 2005) and wilt diseases of several others (O'Donnell et al., 1998a,b; Skovgaard et al., 2001). Although pathogenic species of *Fusarium* have been found globally infecting plants in many horticultural, forest, and ornamental crops, taxa from this genus can be recovered from plants and soil as endophytes and saprobes (Wang et al., 2004; Ploetz, 2006; Summerell et al., 2010; Ma et al., 2013). In fact, recent studies with native plants and soil substrates in natural undisturbed ecosystems indicate that the number of non-pathogenic *Fusarium* species may be far greater than those causing diseases (Wang et al., 2004; Summerell and Leslie, 2011).

The number of species in the genus has varied from nine to more than 1,000 based on different studies conducted by specialists (Wollenweber and Reinking, 1935; Snyder and Hansen, 1945; Booth, 1971; Gerlach and Nirenberg, 1982; Nelson et al., 1983; Summerell and Leslie, 2011). Recently, Leslie and Summerell (2006) described in detail 70 *Fusarium* species; however, there are approximately 300 phylogenetically distinct species in 20 monophyletic *Fusarium* complexes that require further studies for assigning formal species names (Geiser et al., 2013; Ma et al., 2013; O'Donnell et al., 2013). Some fusaria species are native to a particular region and attack native/or local plants, e.g., *Fusarium mexicanum*, a pathogen of mango that has been found only in Mexico (Otero-Colina et al., 2010), whereas other species are cosmopolitan and attack native and introduced plant species in all regions of the world, e.g., *Fusarium verticillioides*, a pathogen of maize (Leslie and Summerell, 2006; Summerell et al., 2010).

Because of *Fusarium* worldwide distribution, the agricultural, economic and health importance of the genus, and of the continuous development of research databases, *Fusarium* species represent exceptionally rich organisms for studying pathogenic plant-fungal interactions in distinct natural and anthropogenic systems (Geiser et al., 2004, 2013; Park et al., 2010; O'Donnell et al., 2013). Approximately 80% of the economically important plants had at least one disease caused by *Fusarium* (Leslie and Summerell, 2006). Consequently and due to the high diversity of *Fusarium* species and of their plant hosts, different fungal and plant species can interact with each other which generates complex ecological networks within a given environment (Pires and Guimarães, 2013; Benítez-Malvido and Dáttilo, 2015).

In the last decades, some studies have found non-random structures in ecological networks (Bascompte et al., 2003; Bascompte and Jordano, 2007; Olesen et al., 2007). For instance, in modular (i.e., compartmentalized) networks there are subgroups of species that interact more frequently among themselves than with species from other subgroups in the network (Olesen et al., 2007). Over the years, studies have shown that antagonistic networks (i.e., one species benefits at the expense of another) tend to be more modular compared to mutualistic networks of free-living species because of a high level of specialization and dependence among species (Prado and Lewinsohn, 2004; Rezende et al., 2007, 2009; Benítez-Malvido and Dáttilo, 2015). Currently, however, the challenge ahead is to understand the proposed mechanisms underlying the modular pattern of these antagonistic networks.

It is broadly accepted that species are not independent entities within the natural environment and share an evolutionary history among them (Rezende et al., 2007; Bascompte and Jordano, 2013). This indicates that the current architecture of species interactions is not only dependent on recent ecological processes, but also on ancient evolutionary distances (Ives and Godfray, 2006; Bellay et al., 2011; Gilbert et al., 2012). In this sense, we know that both chemical and morphological traits of plants are often phylogenetically related (Farrell, 2001), and therefore, it is possible to expect that the architecture of antagonistic networks involving plants and pathogens can have a phylogenetic signal (Gilbert and Webb, 2007; Vacher et al., 2008). In other words, closely related host plants could more likely share pathogenic species with similar abilities to feed on their host plants (Gilbert and Webb, 2007; Vacher et al., 2008; Gilbert et al., 2012; Benítez-Malvido and Dáttilo, 2015). In addition to the phylogenetic signals, other ecological mechanisms can drive the organizational patterns in interaction networks, such as relative abundance, forbidden links, competition, spatial or temporal segregation, among others (reviewed by Bascompte and Jordano, 2013). Despite recent advances in our understanding of ecological networks, the organizational patterns and mechanisms structuring antagonistic networks involving cultivated and non-cultivated plant species and their pathogens is still poorly understood; see Benítez-Malvido and Dáttilo (2015), however.

Here we integrate the comprehensive information available in the literature on the *Fusarium* attacking different native and introduced cultivated plant species in Mexico (Fernández-Pavía et al., 2015), to determine characteristics of the community structure and the role of phylogenetic signals in plant-pathogen interactions (Gilbert et al., 2012). In addition, we used spatial

ecology tools to determine if the distribution and number of host-*Fusarium* associations changes across the country (Turner et al., 2001; Wu and Hobbs, 2002). We postulated that if phylogeny imposes restrictions on plant-pathogen interactions, we expect to find subsets of species interacting more with one another within a larger group of species (i.e., modular pattern), leading to network architecture associated with the probability of sharing a pathogen decreases with increasing taxonomic distance between host plants.

Considering the virulence of several *Fusarium* species and the potential risk of infection of native and introduced crops across the country, the usage of phylogenetic relatedness and spatial ecology concurrently in the analysis of host-*Fusarium* interactions across Mexico, could improve the effectiveness of disease risk analysis. This approach permits a quick evaluation of which plant species (or crops) in a particular region of the country are most likely to interact with a particular fungal pathogen (see Gilbert et al., 2012). Increasing human impact on natural ecosystems, the accidental movement of pathogens together with their host plants, large-scale intensive agriculture and forestry and climate change have been associated with the emergence of new plant diseases elsewhere (Gilbert, 2002; Anderson et al., 2004; Desprez-Loustau et al., 2007, 2015). In this sense, the documentation of plant-*Fusarium* interactions and their distribution in Mexico, is essential considering its status as a biologically mega diverse country, which is the center of origin and/or diversification and domestication of several plant species, and considering that contemporary human activities are leading to global climate change and to the accelerated destruction of several natural ecosystems (Espejo-Serna et al., 2004; Espejo-Serna, 2012; Gernandt and Pérez-de la Rosa, 2014; Bufford et al., 2016).

MATERIALS AND METHODS

The Data Set

The most current list of *Fusarium* pathogens in Mexico was used to evaluate the host range of 53 necrotrophic (tissue-killing) and biothrophic (relying on a living host) *Fusarium* species on a diversity of native and introduced plant species that differed in their degree of taxonomic relatedness, including dicots, monocots and gymnosperms (Fernández-Pavía et al., 2015; **Table 1**). Currently, a total 198 seed plant species have been recorded of being attacked by the genus *Fusarium* across the country, including the generic names based on sexual stages linked to *Fusarium* (e.g., *Albonectria, Gibberella, Haematonectria, Nectria,* and *Neocosmospora* (Rossman, 1996; Kvas et al., 2009; **Table 1**). From this list, only 75 plant species, morpho species and varieties in which the species of fusaria are named, were further considered in our study (Cruz-Miranda, 2011; Gómez-Gómez, 2016; SAGARPA, 2017; **Table 1**).

After a careful depuration of the data set, we firstly mapped the spatial distribution of 75 plant-*Fusarium* interactions in mainland Mexico (**Figure 1**). We conducted spatial autocorrelation tests in ArcMap to see if the patterns of the variables pathogen richness and plant richness are clustered or

follow a different spatial trend (e.g., random or dispersed). We also conducted a geographically weighted linear regression to look at the dependency of fusaria richness on plant richness. Secondly, because the data set included one taxonomic family of gymnoperms (Pinaceae) with 21 species all of which are infected only by *Fusarium circinatum* and therefore, to avoid any biases in the phylogenetic and ecological network analyses we focused only on flowering plants. For the construction of plant-*Fusarium* networks, we considered only the 35 plant species, morphospecies and varieties in which the identity of *Fusarium* species has been described in detail. In the other 163 plant species, the taxonomic identity of the *Fusarium* species is not yet known and/or is still in debate. All of those fusarial species included in our study are listed in some of the main fungi world data sets (Leslie and Summerell, 2006; MycoBank http://www.mycobank.org/quicksearch.aspx; Species Fungorum http://www.speciesfungorum.org/Names/Names.asp). For the network and phylogenetic analysis we included 13 native species to the country and 22 introduced species with well described fusaria species. The fusaria infecting the native and introduced flora are diverse, including plant species from all continents and climates which could have lead to novel potential interactions (**Table 1**).

The Structure of Plant-*Fusarium* Antagonistic Interactions

Initially, the *Fusarium*-plant antagonistic interactions were defined as an adjacency matrix A, in which A_{ij} represents an interaction between the *Fusarium* species i and the plant species j (Bascompte et al., 2003). We then constructed a bipartite network with the full set of species with the *bipartite* package (Dormann et al., 2009) in the R software version 3.3.3 (R Development Core Team, 2016). Afterwards, we also constructed one network for native plant species and a second for introduced species interacting with *Fusarium*. Thus, in these networks, *Fusarium* and plant species are depicted as nodes, and their interactions are represented by links describing the use of plant species by fusaria species. For each bipartite network we calculted the following descriptors (Dormann et al., 2009; Blüthgen, 2010): (1) network size was defined as the total richness (plant and fusaria species); (2) connectance (C) as the fraction of recorded interactions relative to the total possible interactions; (3) nestedness ($NODF$) describes the topological pattern related with how interactions are established, it assigns a number between 1 and 0 considering if the majority of the specialist species interact exclusively with more generalist species that also interact with them in return or if there is no such pattern; (4) number of links per species; (5) number of compartments: these are network subgroups that are not connected to another subgroup, related to (6) the modularity (M) that measures the level at which the species tend to be organized in subgroups of species that interact more frequently among themselves than with other members of the network.

In addition, we also calculated the niche overlap (NO) using the Morisita–Horn index (Horn, 1966) defined as follows: $NO = \frac{2 \sum p_{ij} p_{ik}}{\sum P_{ij}^2 + P_{ik}^2}$ where, $p_{ij} = $ corresponds to the proportion of species

TABLE 1 | List of different native and introduced cultivated plant species attacked by species of the genus *Fusarium* in Mexico.

Plant family	Plant species	Common name (English/Spanish)	Origin	No. of pathogen species recorded	States of Mexico recorded[a]
Agavaceae	*Agave sisalana*	Sisal/henequén	Native	1	Qro, Tamps
	Agave tequilana	Blue agave/agave azul	Native	1	Jal
Amaryllidaceae	*Allium cepa*	Onion/cebolla	Introduced	2	Ags
Amaryllidaceae	*Allium sativum*	Garlic/ajo	Introduced	1	Qro, Tlax
Fabaceae	*Arachis hypogaea*	Peanut/cacahuate	Introduced	1	NE
Asparagaceae	*Asparagus officinalis*	Asparagus/espárrago	Introduced	3	Gto
Brassicaceae	*Brassica oleracea*	Cabbage/col	Introduced	1	Mex
Brassicaceae	*Brassica oleracea* var. *italica*	Broccoli/brócoli	Introduced	1	Gto
	Capsicum annuum	Chili pepper/chile	Native	5	Gto, Mich, Oax
	Capsicum frutescens	Chili pepper/chile	Native	2	Pue
	Capsicum sp.	Chili pepper/chile	Native	2	Chih
	Carica papaya	Papaya/papayo	Native	3	Col, Gro, Tab
	Carthamus tintoreus	Safflower/cártamo	Introduced	1	BC, Chih, Son
	Cereus schotii	Cactus/órgano	Native	1	Son
	Cicer arietinum	Chickpea/garbanzo	Introduced	2	BCS, Gto, Mich, Sin, Son
	Citrullus vulgaris	Watermelon/sandía	Introduced	2	Gto, Mich, More, Sin, Son, Ver
	Coffea arábica	Coffee/cafeto	Introduced	1	Chis, Mor, Nay, Pue, Ver
	Cucumis melo	Melon/melón	Introduced	1	Col, NE
	Cucurbita pepo	Marrow/calabaza	Native	1	Dgo, Mor, NE, Pue, Son, Ver
	Dianthus caryophyllus	Carnation, clove pink/clavel	Introduced	8	BC, DF, Mex, Pue
	Dioscorea sp.	Air potato/barbasco	Native	3	Oax
	Fragaria chiloensis var. *ananassa*	Strawberry/fresa	Introduced	4	Gto, Mex, Mich
	Gladiolus grandifloras	Sword lily/espadilla	Introduced	2	Pue
	Gladiolus sp.	Sword lily/gladiola	Introduced	4	DF, Jal, Mor, Pue, Son
	Glycine max	Soybean/soya	Introduced	1	Sin, Son
	Gossypium hirsutum	Cotton/algodonero	Native	1	Chih, Coah, Mich, NE, NL, Sin, Son
	Hibiscus sabdariffa	Hibiscus/jamaica	Introduced	1	Gro
	Hordeum vulgare	Barley/cebada	Introduced	1	NE
	Lilium sp.	Lily/lírio	Introduced	1	Mex
	Linum usitatissimum	Flax/linaza	Introduced	1	NE, Sin, Son
	Mangifera indica	Mango/mango	Introduced	5	Camp, Chis, Col, Gro, Gro, Jal, Mich, Sin
	Medicago sativa	Alfafa/alfafa	Introduced	1	NE
	Megathyrsus maximus	Buffalograss/pasto	Introduced	1	SLP
	Musa sapientum	Banana/plátano	Introduced	1	Col, Gro, Qro, Mich, Nay, SLP, Tab
	Narcissus biflorus	Cemetery ladies/Narciso	Introduced	1	DF
	Nicotiana tabacum	Tobacco/tabaco	Introduced	2	Oax, Ver
	Persea americana	Avocado/aguacatero	Native	1	Gro, Mich
	Phaseolus vulgaris	Bean/frijol	Native	3	Ags, BC, Coah, Dgo, Gto, Hgo, Jal, Mex, Mich, Mor, Nay, NL, Pue, Qro, Sin, SLP, Son, Tab, Tamps, Tlax, Ver, Zac
	Physalis ixocarpa	Green tomato/tomate verde	Native	1	Gto, Mex, Mich, Mor
	Pinus arizonica var. *stormiae*	Pine/pino	Native	1	NE
	Pinus ayacahuite	Pine/pino	Native	1	NE
	Pinus cembroides	Pine/pino	Native	1	NE
	Pinus devoniana	Pine/pino	Native	1	NE
	Pinus discolor	Pine/pino	Native	1	NE
	Pinus douglasiana	Pine/pino	Native	1	NE
	Pinus durangensis	Pine/pino	Native	1	NE
	Pinus engelmannii	Pine/pino	Native	1	NE
	Pinus estevezii	Pine/pino	Native	1	NE
	Pinus greggii	Pine/pino	Native	1	NE
	Pinus halepensis	Pine/pino	Introduced	1	NE
	Pinus hartwegii	Pine/pino	Native	1	NE

(Continued)

Plant family	Plant species	Common name (English/Spanish)	Origin	No. of pathogen species recorded	States of Mexico recorded[a]
	Pinus leiophylla	Pine/pino	Native	1	NE
	Pinus maximinoi	Pine/pino	Native	2	Mich
	Pinus michoacana	Pine/pino	Native	2	Mich
	Pinus montezumae	Pine/pino	Native	4	Mich
	Pinus oocarpa	Pine/pino	Native	3	Mich
	Pinus patula	Pine/pino	Native	1	NE
	Pinus pringlei	Pine/pino	Native	1	NE
	Pinus pseudostrobus	Pine/pino	Native	3	Mich
	Pinus radiata	Pine/pino	Introduced	1	NE
	Pinus teocote	Pine/pino	Native	1	NE
	Saccharum officinarum	Sugarcane/caña de azúcar	Introduced	3	Gro, Gto, Jal, Mich, Mor, Nay, NE, Oax, Pue, Sin, Tamps, Ver, Yuc
	Salix alba	White willow/sauce	Introduced	1	Chih, DF
	Solanum lycopersicum	Tomato/jitomate	Native	1	BC, BCS, Gto, Mex, Mich, Mor, Pue, Sin, SLP
	Solanum tuberosum	Potato/papa	Introduced	2	Ags, DF, Dgo, Gto, NE
	Sorghum bicolor	Sorghum/sorgo	Introduced	1	Gto, Jal, Mich
	Sorghum sp.	Sorghum/sorgo	Introduced	1	Gto
	Sorghum vulgare	Sorghum/sorgo	Introduced	1	Mich
	Theobroma cacao	Cocoa/cacao	Native	1	Chis, Tab
	Triticosecale sp.	Triticale/tritricale	Introduced	4	Mex, Mich
	Triticum aestivum	Bread wheat/trigo	Introduced	6	Jal, Mex, Mich, Pue, Tlax
	Vanilla planifolia	Vanilla/vainilla	Native	1	Pue, Ver
	Vicia fabae	Fava bean/haba	Introduced	1	Mex
	Vitis vinífera	Grape/vid	Introduced	1	Ags, Hgo, Zac
	Zea mays	Corn/maíz	Native	13	Col, Gto, Hgo, Mex, Mich, Pue, Sin, Ver, Yuc

*The enlisted plants included species, morpho species of known genera (e.g., Bursera sp., Senna sp., and Tabebuia sp.) and cultivated varieties (Gladiolus sp. and Sorghum sp.) (after Fernández-Pavía et al., 2015 and **Supplementary Material**).*

[a]*Abbreviations for the states of Mexico: Ags, Aguascalientes; BC, Baja California; BCS, Baja California Sur; Camp, Campeche; Chis, Chiapas; Chih, Chihuahua; Coah, Coahuila; Col, Colima; DF, Distrito Federal; Dgo, Durango; Gto, Guanajuato; Gro, Guerrero; Hgo, Hidalgo; Jal, Jalisco; Méx, Estado de México; Mich, Michoacán; Mor, Morelos; Nay, Nayarit; NL, Nuevo León; Oax, Oaxaca; Pue, Puebla; Qro, Querétaro; SLP, San Luis Potosí; Sin, Sinaloa; Son, Sonora; Tab, Tabasco; Tamps, Tamaulipas; Tlax, Tlaxcala; Ver, Veracruz; Yuc, Yucatán; Zac, Zacatecas. NE means not determined.*

i used by species j and p_{ik} = corresponds to the proportion of species i of the total resource pool used by species k. Note that in this case i and j can be either plant or fungi, and therefore, we have the niche overlap (or niche partitioning) for both *Fusarium* and the hosts. The Morisita-Horn's index varies from 0, when there is no overlap of resources used, to 1, when there is complete resource overlap.
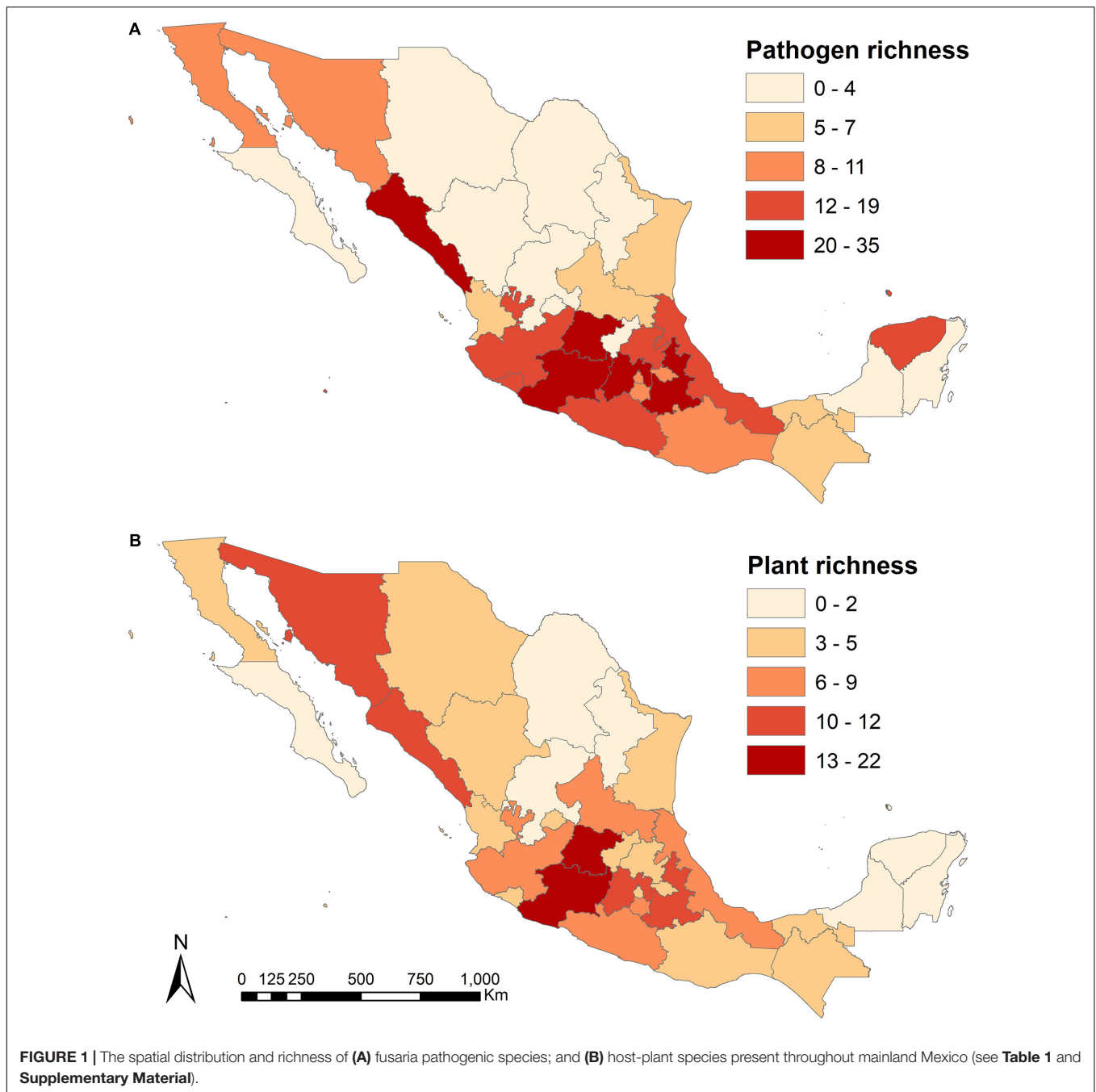
Similarly, robustness was calculated to evaluate vulnerability to extinction in the *Fusarium* species in the different networks. This descriptor refers to the area below the extinction curve created by the fraction of species that survive following the removal of a given species, calculated as the exponent a of the function $y = 1 - x^a$.

Additionally, we tested for differences in the number of species of fusaria between native and introduced cultivated plants using a t-test. Finally, we used a Spearman correlation to test if the states of Mexico with a higher number of species of cultivated plants corresponded to states with more species of fusaria pathogens. Both t-tests and correlation were performed in the R software version 3.3.3 (R Development Core Team, 2016).

Phylogenetic Relatedness Structuring Plant-*Fusarium* Interactions

To test if the degree of phylogenetic relatedness among host plant species influences host-pathogen interactions we followed the next steps. Firstly, we built a phylogenetic tree including angiosperms species being attacked by identified fusaria species across Mexico (**Figure 2**). For the tree construction, we used as a backbone the megaphylogeny generated at the species level by Zanne et al. (2014), which is based on sequences for seven-gene regions available in the GenBank[1] and fossil data. This phylogeny includes 98.6 and 51.6% of the families and genera, respectively, of all extant seed plants in the world. We specifically used the updated and expanded version of the Zanne et al. (2014) phylogeny provided by Qian and Jin (2016), which is the largest and most up-to-date time-calibrated species-level phylogeny of seed plants. At the end, we obtained an ultrametric tree (**Figure 2**) with branch lengths in units of time (millions of years).
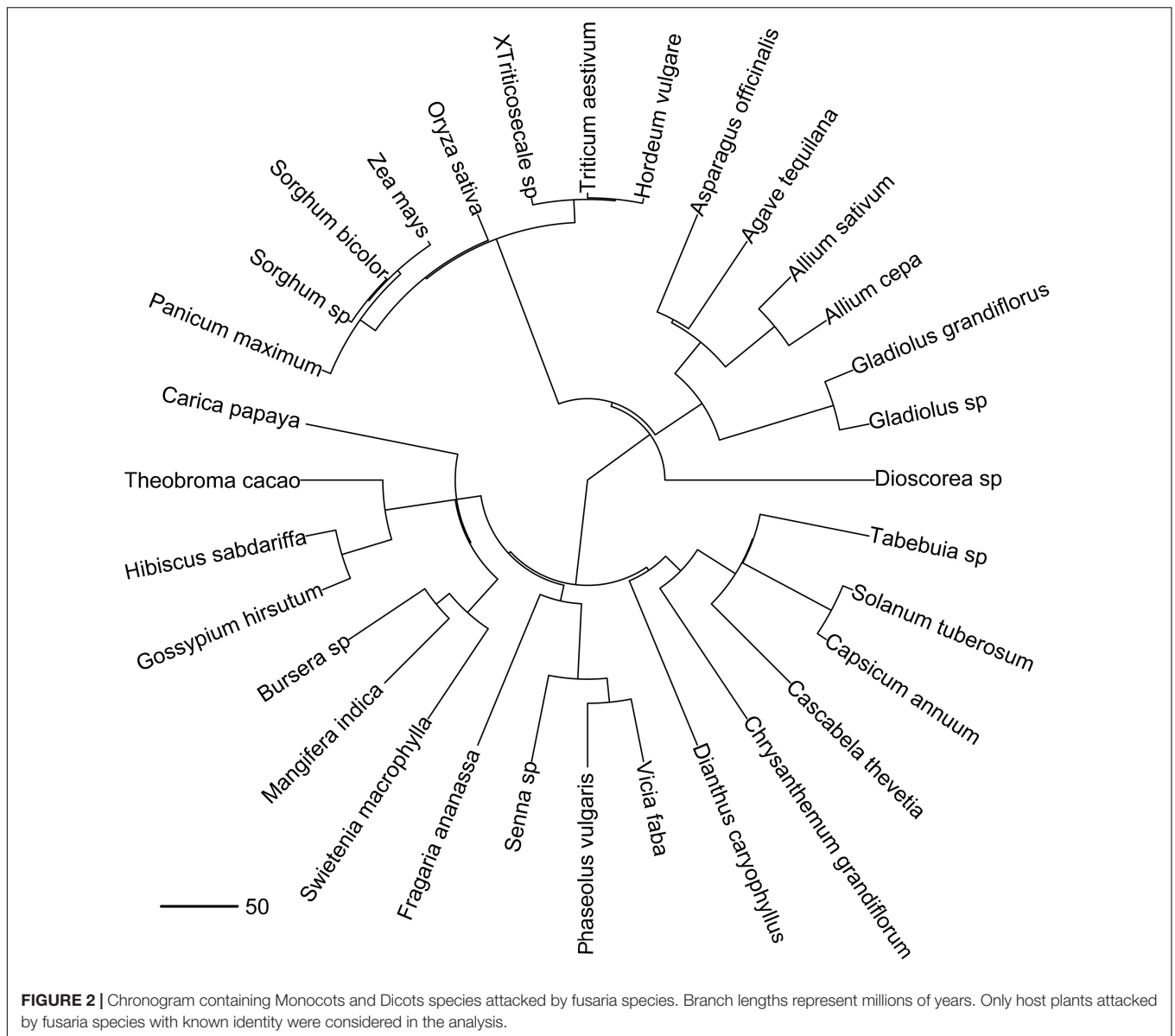
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[1]http://www.ncbi.nlm.nih.gov/genbank/

FIGURE 1 | The spatial distribution and richness of **(A)** fusaria pathogenic species; and **(B)** host-plant species present throughout mainland Mexico (see **Table 1** and **Supplementary Material**).

The used taxonomic designation of species following "The Plant List[2]."

Secondly, we built two distance matrices, one considering the phylogenetic distance among host species (evolutionary distance matrix), calculated from the phylogenetic tree, and the other one considering the degree of similarity between host species in term of the pathogens that attack them (pathogen similarity matrix). The last matrix was built considering the Jaccard similarity index, calculated using an incidence dataset. Then, we tested

for the correlation between the evolutionary distance matrix and the pathogen similarity matrix through a Mantel tests. The significance of the correlation (Spearman's rank correlation, r_S) was computed through 999 permutations, considering an alpha = 0.05 level.

Thirdly, we used the non-Metric Multidimensional Scaling (MDS) ordination for mapping the relationships among host species captured in the pathogen similarity matrix. During this process, we calculated and used the stress value to evaluate how properly the resulting ordination reflects the distance among the host species showed in the pathogen similarity matrix

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[2]www.theplantlist.org

FIGURE 2 | Chronogram containing Monocots and Dicots species attacked by fusaria species. Branch lengths represent millions of years. Only host plants attacked by fusaria species with known identity were considered in the analysis.

(McCune and Grace, 2002). Then, through the "envfit" function implemented in the vegan R package (Oksanen et al., 2013), we tested for differences between Monocots and Dicots species in terms of the identity of pathogens attacking them. The "envfit" function estimates the centroids corresponding to each group of species in the ordination space and evaluates if the observed distance among centroids is greater than expected by chance – significance testing ($P \leq 0.05$) based on 999 permutation.

RESULTS

Host specificity varied among *Fusarium* species. The number of *Fusarium* species infecting a particular plant species ranged from one to 15 pathogenic fungi. Most species of plants (59% of all species considered) were attacked by one identified species

of *Fusarium*, whereas only a few were attacked by more than three species concurrently, including maize (*Zea mays*) with 15 fusaria species, followed by black bean (*Phaseolus vulgaris*) with ten species, carnation (*Dianthus caryophyllus*) with six, and mahogany (*Swetenia macrophylla*) with five fusaria species. The fusaria species with the largest number of plant hosts were *Fusarium solani*, infecting 15 hosts, and *F. verticillioides* and *F. proliferatus* with six hosts each. Furthermore, 52% of fusaria species had only one host plant species which suggests a strong host specificity. No significant differences, however, were detected in the number of species of pathogens infecting native (mean ± SD: 3.14 ± 4.2) and introduced (1.76 ± 1.2) plant species ($t = 2.58$; df = 33; $P = 0.12$). Overall, of the 31 fusaria species eleven (34%) infect native and introduced plants concurrently, 13 (41%) were found exclusively in native hosts (*F. andiyazi, F. chlamydosporum, F. crookwellense,*

F. heterosporum, F. lateritium, F. napiforme, F. nygamai, F. poae, F. pseudonygamai, F. sporotrichioides, F. subglutinans, F. temperatum) while eight (25%) only in introduced plant species (*F. brachygibbosum, F. fujikuroi, F. globosum, F. meridionale, F. sacchari, F. semitectum. F. thapsinum* and *F. tricinctum*).

Spatial Distribution of Plant-*Fusarium* Interactions

In relation to the spatial distribution of antagonistic interactions between fusaria pathogens and their host plants in Mexico (**Figure 1**), Michoacán was the state with most species of *Fusarium* ($n = 35$), followed by the states of Sinaloa ($n = 30$) and Puebla ($n = 28$, mean $\pm$ SD per state: 10.84 ± 9.23) (**Figure 1A**). Furthermore, *F. oxysporum* and *F. solani* were the pathogen species more widely distributed in the country ($n = 28$ states, which corresponds to 87% of all states). In addition, Michoacán and Guanajuato were the states with more species of cultivated plants reported with diseases caused by *Fusarium*: 22 and 16 species, respectively (mean $\pm$ SD per state: 6.51 ± 6.06) (**Table 1**; **Figure 1B**). Bean (*Phaseolus vulgaris*) and sugarcane (*Saccharum officinarum*) were the plant species more widely cultivated in Mexico in terms of locations (bean in 22 states and sugarcane in 12 states, which corresponds to 68 and 37.5% of all states, respectively). The states with more cultivated plant species had a higher number of fusaria species ($r = 0.65$; $P < 0.001$). Furthermore, the spatial autocorrelation tests showed that fusaria and plant richness are spatially clustered (fusaria richness Moran's $I = 0.134$, z-score = 1.936, $P = 0.053$; plant richness Moran's $I = 0.125$, z-score = 1.89, $P = 0.059$), and there is less than a 6% likelihood that the observed pattern could be the result of random chance. The geographically weighted linear regression suggests that there is a strong association between fusaria richness and plant richness: $R^2 = 0.696995$, R^2Adjusted $= 0.671155$.

Ecological Networks of Plant-*Fusarium* Interactions

The interaction network of *Fusarium* and their plants showed a nested arragement. When comparing native and exotic plant-*Fusarium* networks, *Fusarium* species established a more nested network with native than with exotic plant species, even when the native and the exotic networks are of similar size (**Table 2**). In both networks *F. solani* is the species with the highest number of interactions.

In the complete network we identified four modules (groups) of *Fusarium* species strongly associated with a particular set of plant species, while the native species network has two compartments and the exotic species network seven modules (**Figure 3**). The size of the modules varied significantly from small modules with very specialized interactions between one plant species and one pathogen species to modules with more than 10 plant species and more than 10 pathogens (**Figure 3**). Moreover, we found a remarkable difference in the niche overlap between *Fusarium* species and plant species, considering native and exotic plants. Native plants tended to share more pathogens among themselves ($NO = 0.34$) than pathogens sharing their

host plants ($NO = 0.12$), while exotic plants share less *Fusarium* species ($NO = 0.08$) than the pathogens associated with them ($NO = 0.19$). In addition, we observed that interactions among *Fusarium* species and plant hosts were influenced by host taxonomic distance (Mantel $r = 0.49$; $P < 0.001$). In other words, taxonomically close host plants tended to share the same pathogenic species. In terms of robustness, the complete network, considering exotic and native plants, showed a similar value than native or exotic-*Fusarium* networks on their own.

Phylogenetic Relatedness Structuring Plant-*Fusarium* Interactions

We found a significant correlation between the evolutionary distance matrix and the pathogen similarity matrix ($r_S = 0.219$; $P = 0.001$), pointing out that taxonomically close host species tend to share pathogen species (**Figure 2**). This result was also consistently obtained ($r_S = 0.216$; $P = 0.001$) even after removing from the analysis the species (*Musa* sp., *Saccharum officinarum* and *Citrullus lanatus*) that differ more strongly from the rest in terms of their fusaria community, that can be potentially influencing the correlation analysis in a similar way that the outliers.

We also found that the centroids corresponding to the Monocots and Dicots species in the ordination space (**Figure 4**) were more distant from one another than expected by chance ("envfit" test, $r^2 = 0.189$; $P = 0.006$), indicating that Monocots and Dicots species tend to be affected by different pathogens. We considered only two axes for the MDS ordination, because additional dimensions did not substantially diminish the resulting stress value (3.558), which according to the Kruskal and Clarke's rule of thumb corresponds to an ordination with no real risk of drawing false inferences (McCune and Grace, 2002).
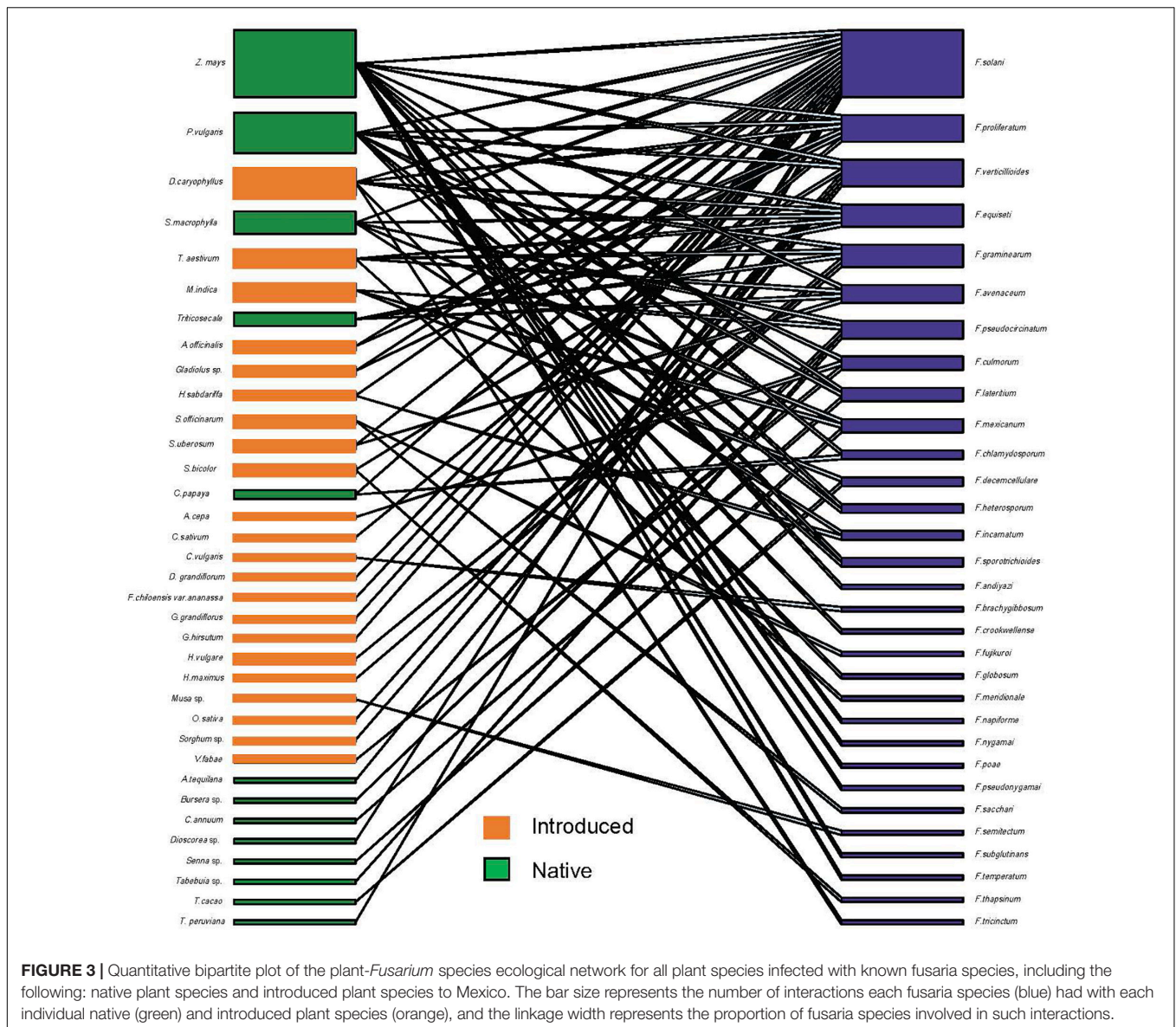
DISCUSSION

Results from this study indicated various important aspects in the plant-*Fusarium* ecological networks. Firstly, these networks tended to be specialized and compartmentalized (i.e., modular topology). Secondly, taxonomically close host plants tended to be affected by the same pathogenic fusaria species. Thirdly,

TABLE 2 | Attributes of plant-*Fusarium* ecological networks in Mexico, including the following: all plant species, native plant species only and introduces plant species only.

Network metrics	All plant species	Native plants	Exotic plants
Network size	63	36	38
Connectance (*C*)	0.07	0.14	0.09
Nestedness (*NODF*)	0.19	0.32	0.12
No. of compartments	4	2	7
No. of links per species	1.21	1.16	0.9
Robustness	0.63	0.61	0.59
Niche overlap fusaria	0.12	0.12	0.19
Niche overlap plants	0.18	0.34	0.08

See methods for details.

FIGURE 3 | Quantitative bipartite plot of the plant-*Fusarium* species ecological network for all plant species infected with known fusaria species, including the following: native plant species and introduced plant species to Mexico. The bar size represents the number of interactions each fusaria species (blue) had with each individual native (green) and introduced plant species (orange), and the linkage width represents the proportion of fusaria species involved in such interactions.
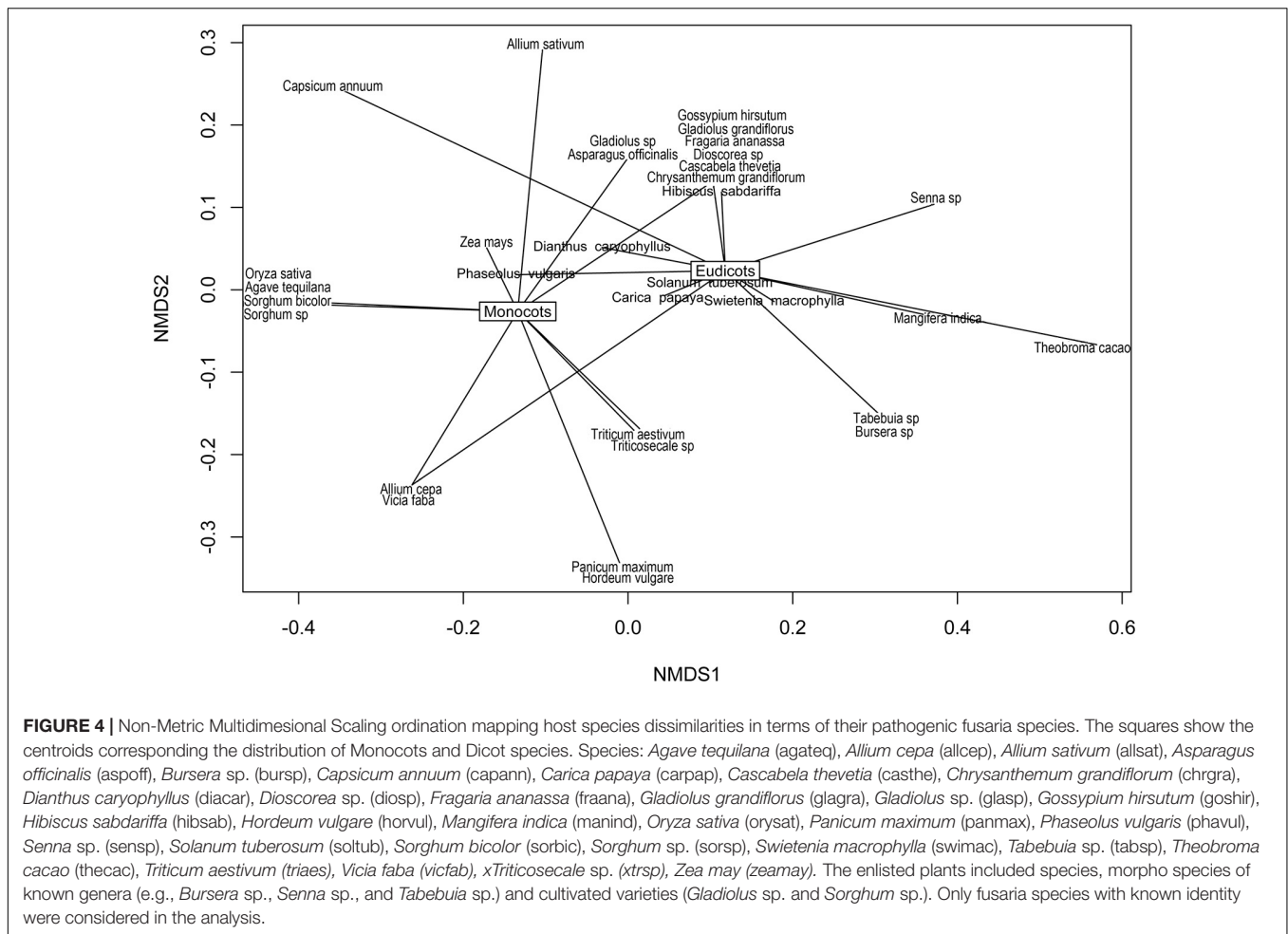
fusaria species are spread throughout Mexico's mainland occupying different ecosystems and climates. Finally, two states located in the central western region of Mexico had the highest number of cultivated plant species and fusaria species. We found that plant-*Fusarium* interactions are rich in the numer of species for both plants and pathogens. We also showed that in Mexico species of the genus *Fusarium* are ecologically diverse and affect economically important native and introduced crops. The high number of cultivated exotic plants suggests that a considerable number of fusaria species might have been introduced with their host plants to the country (Bufford et al., 2016). Our findings, however, are incomplete as many other plant species recorded as being infected by *Fusarium* (118 species) were not included in the analysis because the identity of the pathogen species involved have not yet been described.

Geographic Distribution of Hosts and Fusaria Species

The spatial analysis showed that not all plants and fusaria species are distributed everywhere; however, except for Quintana Roo, every other state presented at least one species of *Fusarium* listed as infecting a plant host (**Figure 1**). The spatial pattern of plant-fusaria interactions across Mexico could be the consequence of a complex interplay of natural and human driven factors including the following, local climate, land-use practices, agricultural intensity, differences in sampling efforts across the country, among others. Natural environmental conditions and human activities interact to create the spatial patterns in the distribution of plant-fusaria interactions observed in the country.

The spatial distribution of fusaria-plant interactions across Mexico showed a significant positive relationship with the number of introduced plant species. In other words, the greater

FIGURE 4 | Non-Metric Multidimesional Scaling ordination mapping host species dissimilarities in terms of their pathogenic fusaria species. The squares show the centroids corresponding the distribution of Monocots and Dicot species. Species: *Agave tequilana* (agateq), *Allium cepa* (allcep), *Allium sativum* (allsat), *Asparagus officinalis* (aspoff), *Bursera* sp. (bursp), *Capsicum annuum* (capann), *Carica papaya* (carpap), *Cascabela thevetia* (casthe), *Chrysanthemum grandiflorum* (chrgra), *Dianthus caryophyllus* (diacar), *Dioscorea* sp. (diosp), *Fragaria ananassa* (fraana), *Gladiolus grandiflorus* (glagra), *Gladiolus* sp. (glasp), *Gossypium hirsutum* (goshir), *Hibiscus sabdariffa* (hibsab), *Hordeum vulgare* (horvul), *Mangifera indica* (manind), *Oryza sativa* (orysat), *Panicum maximum* (panmax), *Phaseolus vulgaris* (phavul), *Senna* sp. (sensp), *Solanum tuberosum* (soltub), *Sorghum bicolor* (sorbic), *Sorghum* sp. (sorsp), *Swietenia macrophylla* (swimac), *Tabebuia* sp. (tabsp), *Theobroma cacao* (thecac), *Triticum aestivum (triaes), Vicia faba (vicfab), xTriticosecale* sp. *(xtrsp), Zea may (zeamay).* The enlisted plants included species, morpho species of known genera (e.g., *Bursera* sp., *Senna* sp., and *Tabebuia* sp.) and cultivated varieties (*Gladiolus* sp. and *Sorghum* sp.). Only fusaria species with known identity were considered in the analysis.

the number of non-native cultivated plants, the greater the number of fusaria species. The plant and fusaria species in this study have different biogeographical origins, and because of human activities they are spread all across the Mexican mainland. Mexico has been recognized as the centre of origin, diversification and domestication of some taxonomic plant families (e.g., Pinaceae and Agavaceae) and species (e.g., maize, *Zea mays*; beans, *Phaseolus vulgaris;* and squash *Cucurbita pepo,* etc.), considering the broad distribution of fusaria diseases infecting native and introduced plant species and crops, special attention should be given to plant species endemic to Mexico and to those used as staple food crops (Espejo-Serna et al., 2004; Espejo-Serna, 2012; Gernandt and Pérez-de la Rosa, 2014).

Overall, it has been estimated that Mexico holds about 11% of all known plant seed species worldwide (Espejo-Serna et al., 2004). Humans and global climate change have facilitated the introduction, proliferation and severity of plant diseases (Fraser, 2004; Qu et al., 2008; Benítez-Malvido, 2012; Bufford et al., 2016). This is of particular concern for many endemic plant species in Mexico present in ecosystems with high rates of land-use change and transformation as these actions affect the probability of the establishment of introduced pathogens and the distribution and severity of diseases in different tropical

and temperate ecosystems (Shaw and Osborne, 2011; Sturrock et al., 2011; Benítez-Malvido, 2012). Several plant species have important cultural and economic connotations including maize and several species of Agavaceae. For instance, around 40% of all Liliopsida that have been described in Mexico are endemic to the country (including *Vanilla planifolia* and several Agavaceae) (Gernandt and Pérez-de la Rosa, 2014).

Linking Ecology and Evolution

An evolutionary ecological perspective provides insights for the understanding of plant-pathogen interactions in a dynamic world and can provide the knowledge for sustainable management of natural, agricultural and forestry systems (Gilbert and Webb, 2007; Gilbert et al., 2012; Desprez-Loustau et al., 2015). The coupling of ecology and evolutionary biology has become an important tool for understanding the origin and proliferation of plant diseases as well as a way to slow disease emergence and severity when possible (Gilbert, 2002; Gilbert and Webb, 2007; Gilbert et al., 2012; Varki, 2012; Vander Wal et al., 2014; Desprez-Loustau et al., 2015). The plant-*Fusarium* ecological networks in Mexico are shaped by the coevolutionary history of the interacting species (see Desprez-Loustau et al., 2007, 2015; Rezende et al., 2007; Bufford et al., 2016). In some cases,

clusters reflected closely related species as in the Fabaceae. The existence of such similarities implies that besides ecological and human factors evolutionary history also explains the patterns of interactions between fusaria species and their plant hosts in Mexico. From commercial, agricultural, forestry and conservation standpoints, this means that different species of the same plant taxonomic Family may be more susceptible to being attacked by the same species of *Fusarium* in a given area (Gilbert and Webb, 2007; Gilbert et al., 2012; Benítez-Malvido and Dáttilo, 2015). In fact, it has been found that phylogenetic relatedness rather than direct contact, explains many of the emerging associations between native and exotic plant and pathogen species (Bufford et al., 2016).

Evolution of pathogen populations can occur in short time scales, especially in ecosystems under strong anthropogenic influence (Palumbi, 2001; Burdon and Thrall, 2008; Qu et al., 2008; Benítez-Malvido, 2012; Jousimo et al., 2014). By comparison, long-lived tree species and other plants are expected to adapt more slowly (Carroll et al., 2014). Some plant species in this study have been introduced and cultivated in Mexico for several decades (e.g., sugar cane, wheat, mango, etc.), and probably their pathogens have already adapted to the environment where they were introduced together with their hosts. This adaptation might explain the lack of significant difference in the number of fusarial species infecting native and exotic plant species despite that the number of fusaria species exclusively infecting introduced plant hosts doubled those infecting native hosts. There is evidence that human activities have intensified the rates of genetic change in both pathogen populations and plant populations, and therefore an evolutionary ecological perspective for disease management needs to be continuously developed (Desprez-Loustau et al., 2007, 2015; Gilbert and Webb, 2007; Soto-Plancarte, 2013; Carroll et al., 2014; Bufford et al., 2016; Santillán-Mendoza et al., 2018). In fact, host species with related pattern of interactions could be more susceptible to the same stochastic events of environmental disturbance (Bascompte and Jordano, 2013).

Disease Ecology and Management

In general, natural and/or wild plant populations rarely suffer from devastating fungal epidemics contrary to what has been observed in several native and introduced cultivated species (Hansen and Goheen, 2000; Jousimo et al., 2014). The natural regulation of diseases, however, can be hindered by exotic pathogens (Bufford et al., 2016). Pathogens are capable of adapting to new hosts after introductions or becoming more virulent in homogeneous plantations and/or crops (Soto-Plancarte, 2013). This is because frequently individuals of the same species with low genetic variation are grown close together in very large numbers (Vurro et al., 2010). A fungal pathogen may disperse rapidly and effectively under these conditions as postulated by the resource concentration hypothesis (Root, 1973). Therefore, intercropping is recommended over monocultures.

Disease epidemics, in particular those caused by introduced pathogens may cause dramatic, permanent changes in plant populations, forest community structure, species composition and consequently in the ecosystem functioning (Hansen and Goheen, 2000; Rizzo et al., 2002; Weste et al., 2002; Laidlaw and Wilson, 2003; Weste, 2003). For fusaria species host switches may have already been observed from wild to cultivated plants in Mexico (Soto-Plancarte, 2013; Bufford et al., 2016). For instance, two species of *Fusarium* have been detected and described in mango (*Mangifera indica* L.) cultivars throughout Mexico (Otero-Colina et al., 2010; Rodríguez-Alvarado et al., 2013; Soto-Plancarte, 2013). One such pathogens is *F. mexicanum* that seems to be endemic to Mexico since it has not been detected in other mango growing areas outside this country. This pathogen was placed in the American clade according to a biographic clade hypothesis for *Fusarium* species belonging to the *Fusarium fujikuroi* species complex proposed by O'Donnell et al. (1998a,b) and based on a phylogenetic analysis using five gene regions (Otero-Colina et al., 2010). A major assumption of this clade hypothesis is that there is a close association between the origin of the fusaria species and the origin of its host plant (O'Donnell et al., 1998a,b); however, some researchers have provided data that support and contradict this hypothesis (Kvas et al., 2009; Summerell et al., 2010). Mango trees were introduced to Mexico from the Philippines by the Spaniards around the end of the 1700s (Iyer and Schnell, 2009). Considering that mango is an introduced species in this country and that *F. mexicanum* has not been yet detected elsewhere, it is possible that spores (microconidia) of *F. mexicanum* were disseminated by wind or insect vectors from its original hosts to susceptible mango trees in plantations. That the original host or hosts for *F. mexicanum* could be native plants is shown by the recent finding of this pathogen in association with herbaceous, native plants of the genus *Senna* sp. and with trees of *Switenia macrophylla* (Meliaceae) located near commercial mango orchards and in suburban settings (Soto-Plancarte, 2013; Rodríguez-Alvarado, unpublished data). On the other hand, a native plant species from Mexico, *Ipomea batatas*, has been found to be infected by *F. denticulatum* in Africa; however, this plant is not reported to be a host of this fusaria in Mexico (O'Donnell et al., 1998a,b). Overall, these emerging associations between native and exotic plants and pathogens can have a negative impact on managed and natural terrestrial ecosystems (Benítez-Malvido, 2012; Bufford et al., 2016).

Host density but also identity is important for disease development and transmission. The more susceptible the plant hosts, the faster and more widespread will be the proliferation of a given disease (Beldomenico and Begon, 2009). Because the striking differences in the management, usages and commercialization of the plant hosts known to be infected by *Fusarium* in Mexico, disease control techniques should be implemented accordingly. For instance, the Pinaceae are used for timber, other species are used as ornamental plants, and some other plants are considered as staple foods or have industrial purposes. In addition, some native species from the Agavaceae with economic importance (*Agave atrovirens, A. fourcroydes, A. sisalana, A. tequilana*) are infected by unidentified fusaria species, which prevented us from including them in our analysis.

The same occurred for other important native crops with cultural and economic connotations such as tomato (*Solanum lycopersicum*), chilli pepper (*Capsicum annuum*) and trees like the cypress (*Taxodium mucronatum*).

CONCLUSION

Fungal pathogens, including *Fusarium*, represent essential components of biodiversity in natural ecosystems and have strong socio-economic implications in agroecosystems. The ecological costs of disease outbreaks constitute the loss of species and populations as well as ecosystem degradation (Hansen and Goheen, 2000; Rizzo et al., 2002; Weste et al., 2002; Laidlaw and Wilson, 2003; Weste, 2003; Anderson et al., 2004; Vurro et al., 2010). Increasing human impact on forests and other natural systems, including the unintentional movement of pathogens, plant trade, global climate change, and large-scale intensive plantations, has been associated with an unprecedented emergence of new diseases (Carroll et al., 2014). An evolutionary and spatial ecological perspective can help address these significant challenges and provide direction for sustainable management of natural and agricultural systems (Qu et al., 2008; Bufford et al., 2016). It is essential to understand fusaria disease dynamics, the identity of all fusaria pathogens that have been recorded in different plants and in different habitats, the life histories of plant hosts and the effects of the local environmental conditions on them (Benítez-Malvido, 2012). This is the first report of the distribution and diversity of plant-*Fusarium* interactions throughout Mexico.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

JB-M conceived the idea, spearheaded the writing, and edited and did literature review. GR-A provided the data, spearheaded the writing, and did literature review. MÁ-A, LÁ-C, Ed-V, and AL-N performed the data analysis, contributed to the writing, and created the figures. RG-C provided the data and did literature review. All authors secured the financial contribution. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021. 615857/full#supplementary-material

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