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Genetic variation in foundation species governs the dynamics of trophic interactions

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Abstract

Various studies have demonstrated that the foundation species genetic diversity can have direct effects that extend beyond the individual or population level, affecting the dependent communities. Additionally, these effects may be indirectly extended to higher trophic levels throughout the entire community. *Quercus castanea* is an oak species with characteristics of foundation species beyond presenting a wide geographical distribution and being a dominant element of Mexican temperate forests. In this study, we analyzed the influence of population (He) and individual (HL) genetic diversity of *Q. castanea* on its canopy endophagous insect community and associated parasitoids. Specifically, we studied the composition, richness (S) and density of leaf-mining moths (Lepidoptera: Tischeridae, Citheraniidae), gall-forming wasps (Hymenoptera: Cynipidae), and canopy parasitoids of *Q. castanea*. We sampled 120 trees belonging to six populations (20/site) through the previously recognized gradient of genetic diversity. In total, 22 endophagous insect species belonging to three orders (Hymenoptera, Lepidoptera, and Diptera) and 20 parasitoid species belonging to 13 families were identified. In general, we observed that the individual genetic diversity of the host plant (HL) has a significant positive effect on the S and density of the canopy endophagous insect communities. In contrast, He has a significant negative effect on the S of endophagous insects. Additionally, indirect effects of HL were observed, affecting the S and density of parasitoid insects. Our results suggest that genetic variation in foundation species can be one of the most important factors governing the dynamics of tritrophic interactions that involve oaks, herbivores, and parasitoids.

Key words: community structure, introgressive hybridization, red oaks, tritrophic interactions.

An important question in modern ecology is how genetic variation within dominant species can be an important driver of ecological processes (Whitham et al. 2006; Johnson and Stinchcombe 2007;

Hughes et al. 2008). In this sense, an increasing number of reports have documented the effect of intra-specific genetic variation within foundation species on their associated communities. There is an

emphasis on foundation species, which are a small subset of the total species in an ecosystem, because it has been suggested that they should capture most of the variation in the community structure and ecosystem processes. Additionally, it could be nearly impossible to perform the studies of all species in the system had to be studied (Whitham et al. 2003, 2006). Studies performed with this perspective suggest that the genetics of the foundation species can have strong organizational effects at the community and ecosystem levels (see review Whitham et al. 2012). The effect of the host plants' genetic characteristics on the associated communities has focused on specific genotypes within a species (e.g., *Oenothera*, Johnson and Agrawal 2005; *Populus*, Shuster et al. 2006; Schweitzer et al. 2008; *Solidago*, Crutsinger et al. 2008) or hybrid systems (e.g., *Eucalyptus*, Dungey et al. 2000; *Salix*, Hochwender and Fritz 2004, *Quercus*, Tovar-Sánchez and Oyama 2006). In the latter systems, the genetic diversity levels of host plants involved in hybridization events may be increased (Tovar-Sánchez et al. 2008; Ortego et al. 2014; Valencia-Cuevas et al. 2014).

Canopy arthropod communities have been widely used to evaluate the influence of the genetic diversity of host plants on their associated communities (Wimp et al. 2004; Bangert et al. 2006; Tovar-Sánchez et al. 2013). In particular, endophagous insects include gall-forming wasps (Cynipidae) and leaf mining moths (Wimp et al. 2007). This preference is probably because they are species with specific organ and tissue specialization (Stone et al. 2002), suggesting that this group represents a good model to evaluate the influence of host plant genetic diversity on associated communities.

To date, most the studies in the field of community genetics have analyzed the influence of genetic diversity and similarity on host plant communities. In particular, these studies have reported that species diversity increases as the genetic diversity of host plant populations increases (Dungey et al. 2000; Wimp et al. 2004, 2005; Tovar-Sánchez and Oyama 2006; Crawford and Rudgers 2013), and genetically similar host plants support similar communities (Bangert et al. 2005, 2008; Barbour et al. 2009). Several studies have demonstrated that an increase in the host plant genetic diversity can generate changes in their morphology (Lambert et al. 1995; González-Rodríguez et al. 2004; Tovar-Sánchez and Oyama 2004) and phenological traits (Hunter et al. 1997) as well as their secondary chemistry (Fritz 1999; Wimp et al. 2004). These characteristics constitute a wider array of resources and conditions that can be used by their associated communities. On the other hand, similarities in host plant communities have been explained as due to genetically similar host plants expressing similar physical, chemical, and phenological characteristics (Bangert and Whitham 2007), suggesting that genetic differentiation through the geographic distribution of host plants can result in variation in the associated communities (Bangert et al. 2005, 2006, 2008; Barbour et al. 2009). In addition, it has been suggested that the ecological relevance of host plant intraspecific genetic diversity can have a cascading effect (Abrahamson 1997; Whitham et al. 2003; Johnson and Stinchcombe 2007; Crutsinger 2016), extending throughout the community (Crutsinger et al. 2006; Whitham et al. 2006; Moreira and Mooney 2013).

In particular, galls induced by cynipid wasps are structures that have extraordinary ecological value because the host communities are structured in several trophic levels. These communities sometimes form very complex networks that consist of gall inductor, parasitoid, and inquiline insects (Askew 1984). Particularly, gall wasps are frequently associated with a diverse parasitoid community. In these communities, the majority of the associated parasitoids only attack oak gall wasps (Askew 1980; Stone et al. 2002).

However, information about the effects of the foundation host plant genetic diversity on this trophic level is scarce. Understanding the processes for structuring host–parasitoid communities is important because parasitoids and their insect hosts comprise approximately one-third of the animal species and more than 50% of the terrestrial animal species (May 1988). Parasitoids also play a major role in regulating their insect host populations.

Scientific evidence has demonstrated that predators depend on herbivores. The distribution, abundance, and performance of parasitoids and predators should also somewhat depend on the quality of their host plants (Giles et al. 2002; Harvey et al. 2003). If there is high variation among plant genotypes for predation (Fritz 1995), there could be a heritable plant trait that is subject to natural selection (Hare 2002). In this sense, Whitham et al. (2003) proposed that associated communities can change in response to natural selection, which acts on plants if there are genetic correlations between the plant traits and their associated communities. Therefore, tritrophic-level interactions represent a good model for examining the interacting species and ecosystem processes in which the direct and indirect effects of plant genetics are analyzable (Price 1997). Considering that natural communities are complex ecological systems with structures and functions based on the interaction of different factors (Bailey and Whitham 2007), multifactorial studies that include genetic factors and at least one ecological factor may be useful.

Oaks are dominant elements of forest canopies. These trees have a wide geographical distribution and are involved in important ecosystem processes, such as nutrient recycling and water balance (Madritch and Hunter 2002). This information inspires us to think that most oak species have attributes of foundation species. A foundation species has been defined as "those that structure a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes" (Dayton 1972; Ellison et al. 2005). Moreover, oaks have high genetic diversity levels as a result of their life-history characteristics (e.g., Tovar-Sánchez et al. 2008; Lorenzo et al. 2009). However, few studies have evaluated the influence of the host oak species genetic diversity on canopy arthropod communities. In addition, the results of these studies differ (Tovar-Sánchez and Oyama 2006; Tack et al. 2010, 2012; Castagneyrol et al. 2012; Tovar-Sánchez et al. 2013). Furthermore, it is unknown whether the oak genetic diversity may indirectly extend to higher trophic levels throughout the community.

In addition, the associated insect communities have been considered complex systems with structures and functions that are determined by the interaction of both genetic and ecological factors (Tovar-Sánchez et al. 2015a). One important ecological factor for oak canopy insect communities is the habitat heterogeneity (Valencia-Cuevas and Tovar-Sánchez 2015). In habitats like oak forests, tree communities define the physical structure. For example, the forest canopy can be structurally more complex when it consists of more than one tree species or more host plant species individuals (Sobek et al. 2009). This complexity may result in greater availability of resources and conditions for insect communities.

Our previous studies showed that *Quercus castanea* is an oak species involved in hybridization events with other red oaks (Valencia-Cuevas et al. 2015), which promotes an increase in its genetic diversity levels (Valencia-Cuevas et al. 2014). In addition, *Q. castanea* possesses characteristics of foundation tree species (Ellison et al. 2005). In this study, we characterized the canopy endophagous insect community (gall and miner insects) and associated parasitoids to *Q. castanea* while addressing the following

hypotheses: (1) if more genetically diverse host plants offer a wider array of resources and conditions to be exploited by insects, then an increase of *Q. castanea* genetic diversity will favor more diverse endophagous insect communities; 2) if parasitoids depend on herbivores, and the herbivore species richness directly depends on the genetic attributes of the plant, an increase in the host plant genetic diversity will have indirect positive effects on the parasitoid community richness; and 3) if associated oak insect communities are complex systems whose structure and function are determined by the interaction of several factors, the structure of the canopy endophagous community insects and associated parasitoids can be shaped by both genetic and ecological factors.

Materials and Methods

Species description
Quercus castanea Neé (*Lobatae*: red oaks) includes trees from 5 to 15 m in height with a trunk diameter of 30–60 cm. These trees can be easily recognized in the field by their leaf characteristics. The flowering season is from April to May and fruiting is from August to December (Valencia 1995; Vázquez 2006). The trees are located between 1,180 and 2,600 m a.s.l., and they are distributed along all major Mexican mountain ranges (Valencia 2004). They are frequently found in perturbed areas with a xerophytic shrub type of vegetation, which is also localized in mountain cloud forests (Rzedowski and Rzedowski 2001). Furthermore, *Q. castanea* is a red oak species that possesses characteristics associated with a foundation tree species (Ellison et al. 2005). For example, *Q. castanea* is the most widely distributed species within the red oak group in Mexico (Valencia 2004); it is a dominant element of the temperate forests where it resides (Valencia-Cuevas et al. 2014) and it acts as the habitat for different species (Tovar-Sánchez et al. 2013).

Study sites and sampling
Trees that are morphologically recognized as "pure" *Q. castanea* were sampled from six populations (20 trees/site), one allopatric population of *Q. castanea* (population 1) and five sympatric stands between *Q. castanea* and other red oak species (populations 2–6, Figure 1) through the central part of the TVB. All chosen sites share the following common traits: geological history [all localities belong to the central portion of TVB with a formation process that occurred in a single geological event that began during the Quaternary–Pliocene (Challenger 1998)], weather (sub-humid temperate), altitude (between 1,800 and 2,500 m), vegetation type (mature oak), and soil type (volcanic origin or derived from igneous and sedimentary rocks). Additionally, these areas present almost no local disturbance inside the forest because they are under Mexican protection standards. This homogeneity among study sites could be useful to minimize the influence of environmental and spatial factors on insect endophagous and parasitoid communities that are associated with the *Q. castanea* canopy.

In addition, the number of associated species with *Q. castanea* in each sympatric locality ranged from one to five. These species were as follows: *Q. candicans*, *Q. crassifolia*, *Q. crassipes*, *Q. laurina*, *Q. mexicana*, *Q. scytophyla*, and *Q. urbanii* (Appendix 1). The *Q. castanea* local density (ind/ha) in each site was as follows: Corredor Biológico Ajusco Chichinautzin (CBACh: 51.7), Parque Nacional El Tepozteco (PNT: 56.7), Parque Ecológico de la Ciudad de México (PECM: 149.0), Parque Barranca de Tarango (PBT: 161.6), Parque Las Peñas (PLP: 186.7) and Parque Nacional El Huixteco
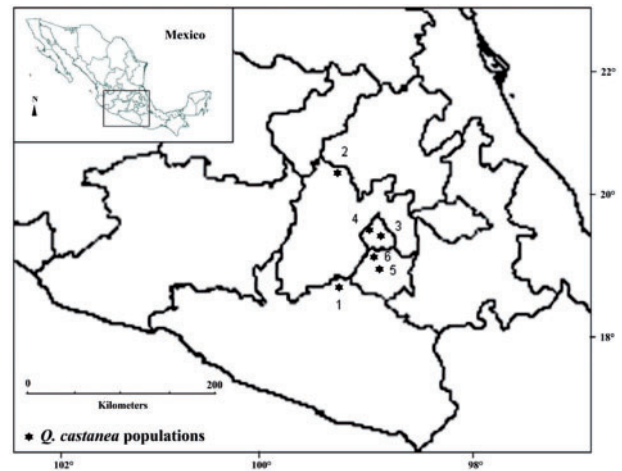

Figure 1. Spatial localization of six *Q. castanea* populations showing a natural gradient of nuclear genetic diversity in the central part of the Transmexican Volcanic Belt, according to Valencia-Cuevas et al. (2014). 1) Parque Ecológico El Huixteco (PEH, *He*: 0.873a); 2) Parque Las Peñas (PLP, *He*: 0.611d); 3) Parque Barranca de Tarango (PBT, *He*: 0.765b); 4) Parque Ecológico de la Ciudad de México (PECM, *He*: 0.832c); 5) Parque Nacional El Tepozteco (PNT, *He*: 0.611d); and 6) Corredor Biológico Ajusco Chichinautzin (CBACh, *He*: 0.621d). Different letters show that the mean values for each locality differ at $\alpha = 0.05$ (Tukey's test).

(PEH: 366.3). Three transects of 1,000 m in each locality were created. At each 50 m, the nearest individual morphologically recognized pure "*Q. castanea*" was sampled.

Molecular data
The 120 individuals (20 individuals per site) that were morphologically recognized as pure *Q. castanea* were previously analyzed by 14 microsatellite (SSRs) primers (six nSSRs and eight cpSSRs). We found an increase in the individual and population genetic diversity of *Q. castanea* populations analyzed here (Valencia-Cuevas et al. 2014) as a result of the interspecific gene flow with other red oaks species (Valencia-Cuevas et al. 2015).

Canopy endophagous insect communities and associated parasitoids
The endophagous insect and parasitoid community structure associated with *Q. castanea* was analyzed in the same 120 individuals as in Valencia-Cuevas et al. (2014). These individuals were 8–10 m (9.12 ± SE 0.17 m) in height and accounted for 18.3–20.1 m² (19.20 m² ± SE 0.17 m²) of canopy cover. Tree canopies selected for sampling were, as far as possible, spatially delimited from others by avoiding overlaps. Insect communities were sampled using four randomly selected branches (50 leaves per branch) in the middle part of the crown. Galls and mining leaves collected in each host tree were separated into the morphospecies level, placed in previously vouchered plastic containers (e.g., locality, host category, etc.) and transported to the laboratory where the insects emerged. Wasps and their parasitoids were identified to the finest taxonomic level.

Statistical analysis
Genetic diversity of host plant
To evaluate the influence of the *Q. castanea* genetic diversity on canopy endophagous communities and parasitoids, the parameter *He* (expected heterozygosis) was used to analyze the genetic diversity at

the population level, as reported by Valencia-Cuevas et al. (2014). Additionally, the *Q. castanea* individual genetic diversity was estimated using homozygosity by the loci index (*HL*), a microsatellite-derived measure that improves heterozygosity estimates in natural populations by weighting the contribution of each locus to the homozygosity value based on the allelic variability (Aparicio et al. 2006). The *HL* is calculated as follows: $HL = (\Sigma E_h)/(\Sigma E_h + \Sigma E_j)$, where E_h and E_j are the expected heterozygosity of the loci that an individual bears in homozygosis (*h*) and heterozygosis (*j*), respectively, forms. This index varies between 0, when all loci are heterozygous, and 1, when all loci are homozygous. The *HL* was estimated using CERNICALIN, an Excel spreadsheet that is available on request. These parameters (*He* and *HL*) were used because they are frequently employed to evaluate the influence of both the population and individual genetic diversity on the community structure (e.g., (Tovar-Sánchez and Oyama 2006); Tovar-Sánchez et al. 2013).

Infestation levels of endophagous insects

The species richness (*S*) of the canopy arthropod community and their associated parasitoids was estimated at the morpho-species level. Each host tree infestation value was estimated as [(number of galls or miners/200 leaves) × 100] over the four branches. Analysis of variance (ANOVA, Model III; Zar 2010) was used to determine differences in the average infestation levels among *Q. castanea* populations. Infestation percentage data were corrected as $X = \arcsin (\%)^{1}/_{2}$, and discontinuous data were transformed as $X = (x)^{1}/_{2} + 0.5$ (Zar 2010). Finally, a Tukey test was used to determine significant differences between the infestation mean values among populations (Zar 2010). The software used for statistical analysis was STATISTICA 8.0 (Statsoft 2007).

Influence of *Q. castanea* genetic diversity, host plant density, and red oak species richness on canopy insects

We used a multiple regression approach to examine whether the *Q. castanea* genetic diversity levels [population (*He*) and individual (*HL*)] and two ecological factors (*Q. castanea* density and red oak species richness) influence the canopy endophagous insect and associated parasitoids. Specifically, this analysis was useful to determine the relative contribution from each factor on the species richness variation and endophagous and parasitoid insect density. We used a standard least squares model with partial (type III sums of squares) error structure and the *He*, *HL*, host density, and oak richness as our factors. We excluded the variables that showed a correlation coefficient >0.6 to improve the analysis. Considering that endophagous insects are resources for parasitoids, we were interested in determining whether the density and species richness of endophagous insects can predict the density and species richness of the associated parasitoids. Therefore, we used simple linear regressions. The software used for statistical analysis were STATISTICA 8.0 (Statsoft 2007) and Species Diversity and Richness version 3.03 (Henderson and Seaby 2002).

　　We constructed one structural equation model (SEM) to estimate the causal relationships between the host plant genetic diversity (*He*, *HL*) and ecological (host plant density and red oak species richness) and community (*S* and density of endophagous and parasitoid insects) variables. Based on a previous study (Valencia-Cuevas et al. 2014) and literature review, we anticipated what causal paths may be important. For the model, we considered the host plant density and red oak species richness as independent variables. The dependent variables that we examined were the individual (*HL*) and

population (*He*) genetic diversity, *S* and density of endophagous and parasitoid insects. The model was performed with the lavaan package for R (Rosseel 2011).

Results

Endophagous and associated parasitoid insect community composition

The endophagous insect community associated with *Q. castanea* consisted of 22 species that belong to the following three orders: Hymenoptera (18 species), Lepidoptera (two species), and Diptera (two species, Appendix 2). In particular, the gall insect group (Hymenoptera: Cynipidae) was represented by eight genera (Appendix 2). In terms of the species richness, the most important genus was *Andricus* at 38.8% (seven species, Appendix 2). Meanwhile, the leaf mining insect group was represented by two families, Diptera and Lepidoptera (Appendix 2, Figure 2).

　　The parasitoid community was represented by 13 families (Figure 2). The most important family in terms of the genus and species richness was Eulophidae (Appendix 2). In addition, we found one inquiline wasp species was associated with gall inducted with *Amphibolips hidalgoensis* belonging to *Synergus* genus (Cynipidae). We also found two individuals who belong to Encyrtidae and one to Megaspilidae. Both families included hyperparasitoids species. Hyperparasitoids and inquiline insects were not included in the analysis.

Infestation levels

The mean infestation levels of endophagous insects were significantly different among the *Q. castanea* populations ($F_{5, 114} = 42.688$, $P < 0.0001$). We did not detect an infestation level pattern over the natural genetic diversity gradient that was previously recognized in *Q. castanea* populations. In general, the infestation levels had the following relationship (mean ± SE): PNT (12.98 ± 1.92) = PECM (14.78 ± 0.74) < PEH (18.61 ± 0.73) = CBACh (24.45 ± 1.22) < PLP (26.23 ± 1.52). Finally, we found that there is no relationship between the infestation levels of gall forming insects and the parasitoid density ($r^2 = 0.2$, $r = 0.13$, $P = 0.17$).

Influence of *Q. castanea* genetic diversity, host plant density, and red oak species richness on canopy insects

In general, our results showed that the *Q. castanea* genetic diversity levels (population and individual), host tree density, and red oak species richness influence the community structure of endophagous and parasitoid canopy insects (Table 1). Specifically, we found that the *HL* and oak richness had a significant positive effect on the *S* of endophagous insects, explaining 10.7% and 5.6%, respectively, of the variation of this metric. In contrast, the *He* had a significant negative effect on the *S* of endophagous insects, explaining 13.6% of the variation in this metric (Table 1).

　　We found that the *HL* had a significant positive influence on the endophagous insect density, explaining the 11.1% of the variation. In contrast, the host density had a significant negative influence on the endophagous insect density, explaining 4.1% of the variation (Table 1).

　　The species richness of parasitoid insects was significantly positively influenced by the *HL* and host density, explaining 5.6% and 3.5%, respectively, of the variation. In contrast, the species richness of parasitoid insects was significantly negatively influenced by the oak richness, explaining 9.2% of the variation (Table 1).
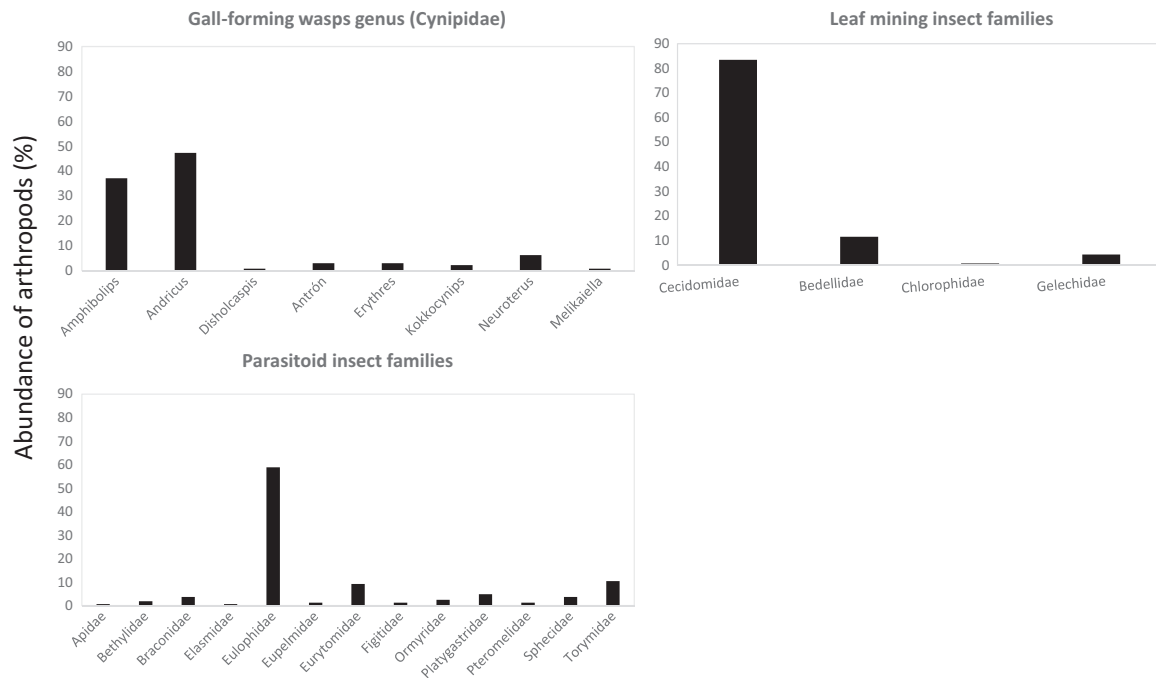
Figure 2. Canopy endophagous insects (gall-forming wasps and leaf mining insects) and parasitoid composition associated to *Q. castanea*.

Table 1. Multiple regression analysis testing the influence of 1.-individual (*HL*) and population genetic diversity of *Q. castanea* (*He*), 2.-host density, and 3.-red oak species local community richness on species richness and density of endophagous insect and associated parasitoids to *Q. castanea* in the Transmexican Volcanic Belt

	Species richness					Density				
	df	SS	*F*	*P*	% Variation	*df*	SS	*F*	*P*	% Variation
Endophagous insects										
He	1	9.934	11.983	**0.000**	6.2	1	1.260	0.475	0.490	0.4
HL	1	53.220	64.194	**0.000**	33.2	1	36.845	13.893	**0.000**	7.5
Host density	1	0.000	0.007	0.927	0.0	1	31.395	11.838	**0.000**	5.1
Oak richness	1	4.173	5.034	**0.026**	2.6	1	10.549	3.977	**0.048**	7.2
Parasitoid insects										
He	1	0.004	0.156	0.693	0.1	1	0.207	0.973	0.326	0.9
HL	1	0.328	11.095	**0.001**	8.6	1	2.219	10.384	**0.001**	9.6
Host density	1	0.111	3.764	0.055	2.9	1	1.412	6.612	**0.011**	6.0
Oak richness	1	0.207	7.005	**0.009**	5.4	1	2.066	9.673	**0.002**	8.4

We also found that the *HL* and host density had a significant positive influence on the parasitoid insect density. The relative contributions of the abovementioned factors on the variation in the parasitoid density were 5.1% and 5.9%, respectively. In contrast, the oak richness had a significant negative influence on the parasitoid insect density, explaining 10.5% of the variation (Table 1).

In general, the *HL* was the factor that explained the highest percentage of variation in the analyzed community parameters. Additionally, the proportion of the total variance explained by the plant genotype was lower for parasitoids than for endophagous insects (Table 1). When the relationship between the gall and parasitoid density was analyzed, there was no significant relationship ($r^2 = 0.02$; $P = 0.17$). In contrast, the gall and parasitoid richness showed a significant positive relationship ($r^2 = 0.12$; $P < 0.0001$).

Figure 3 shows the partial correlation coefficient for each path. In all cases, the proposed paths were significant. The only exception was the relationship between the host plant density and parasitoid density. In particular, the *He* and *HL* had a significant influence on

the *S* and density of endophagous and parasitoid insects. However, the *He* was negatively correlated with the *S* of endophagous insects. In contrast, the *HL* showed a positive influence on the analyzed community parameters. Similarly, ecological variables had a significant influence on the associated endophagous and parasitoid creatures (Figure 3; Table 2).

Finally, this model explained 25.75% and 16.24% of the *S* and density of endophagus insects, respectively. Additionally, 12% and 8.91% of the *S* and density of parasitoid insects, respectively, were explained with this model (Figure 3).

Discussion

In this study, we simultaneously evaluated the influence of genetic attributes of *Q. castanea* (individual and population genetic diversity) and two ecological factors (host density and red oak species richness) on two different trophic levels of the canopy arthropod community, endophagous insects, and associated parasitoids.
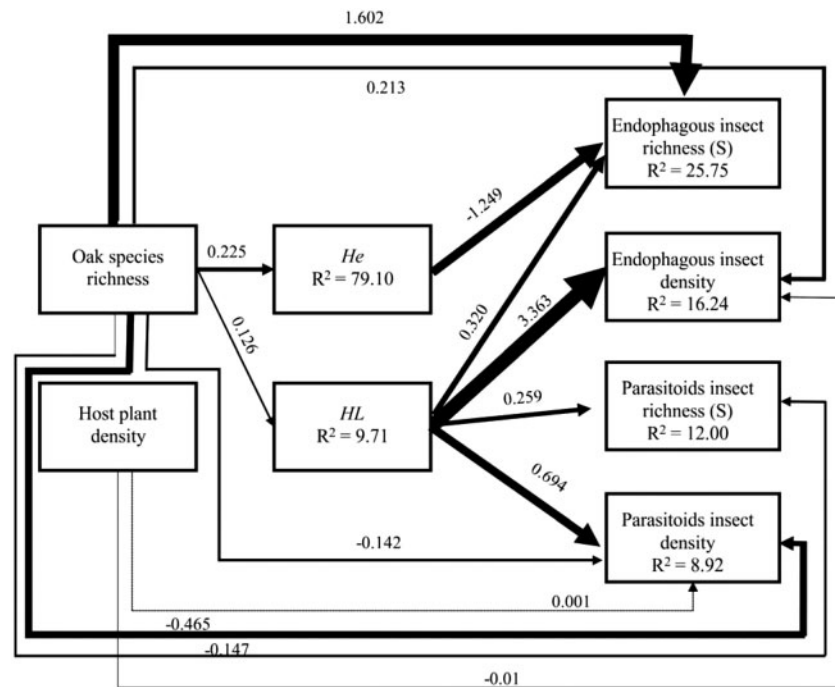
Figure 3. Path model. Solid paths are statistically different from 0 ($P < 0.05$), where dotted path is not. Path widths are proportional to the standardized regression coefficients. Only the coefficients for significant paths are shown. The R^2 of the endogenous variables are inside of the boxes.

Table 2. Coefficient value, standard errors, Z scores, and P values for the SEM

Path	Estimate	SE	Z value	P
$He \rightarrow$ S_endophagous	−1.249	0.243	−5.134	0.000
S_ oaks $\rightarrow$ S_endophagous	0.213	0.064	3.351	0.001
$HL \rightarrow$ S_endophagous	0.320	0.081	3.970	0.000
$HL \rightarrow$ endophagous density	3.363	0.952	3.531	0.000
S_oaks $\rightarrow$ endophagous density	1.602	0.761	2.106	0.035
Host plant density $\rightarrow$ endophagous density	−0.010	0.003	−3.175	0.001
$HL \rightarrow$ S_parasitoids	0.259	0.102	2.541	0.011
S_oaks $\rightarrow$ S_parasitoids	−0.147	0.041	−3.570	0.000
S_oaks $\rightarrow$ parasitoid density	−0.465	0.151	−3.082	0.002
Host plant density $\rightarrow$ parasitoid density	0.001	0.000	1.767	0.077
$HL \rightarrow$ parasitoid density	0.694	0.273	2.543	0.011
S_oaks $\rightarrow$ He	0.225	0.011	20.408	0.000
S_oaks $\rightarrow$ HL	0.126	0.037	3.440	0.001

Notes: *He*, population genetic diversity; *HL*, individual genetic diversity; S_oaks, oak species richness; S_endophagous, endophagous species richness; S_parasitoids, parasitoid species richness.

The results in this study are in accordance with those in other studies that have shown the genetic diversity of foundation species has a significant effect on the associated community (Bangert and Whitham 2007; Hughes et al. 2008; Whitham et al. 2012; Crutsinger 2016). Additionally, we found that insect communities associated with *Q. castanea* are determined by both host plant genetic attributes and ecological factors, such as the host tree density and local red oak species richness.

Studies in natural systems, as presented in this report, offer the realism of the wild; however, it is important to considerer that it is difficult to control the variables related to the spatial location of

host plants, which can influence the abundance, distribution, and diversity of the associated species, in this type of system (Vellend and Geber 2005). Therefore, common garden studies can be a useful approach for comparing the effects of the genetic diversity of *Q. castanea* and other ecological variables on the associated arthropods in both experimental settings and wild populations.

In general, we found a significant positive effect of the genetic diversity levels (*HL*) of *Q. castanea* on the *S* and density of endophagous insects. This result was supported by path analysis. A similar response has been reported in phytophagous insect communities that are associated with different foundation species [e.g., poplars (Whitham et al. 2006); willows (Hochwender and Fritz 2004); eucalyptus (Dungey et al. 2000); and oaks (Tovar-Sánchez and Oyama 2006; Tovar-Sánchez et al. 2015a,b)]. For example, Tovar-Sánchez et al. (2013) reported that the *H'* variation of the *Q. crassipes* and *Q. castanea* arthropod communities was positive and significantly influenced by the individual genetic diversity of the host. Additionally, recent studies in *Q. crassifolia* (Tovar-Sánchez et al. 2015a) showed that individual genetic diversity had a significant positive influence on the *S* and *H'* of the canopy arthropods during the dry and rainy seasons, respectively. It has been proposed that increasing the genetic diversity of the host plant can generate changes in its morphological (Lambert et al. 1995; González-Rodríguez et al. 2004; Tovar-Sánchez and Oyama 2004), phenological (Hunter et al. 1997), architectural (Whitham et al. 1999; Bangert et al. 2005), and chemical (Fritz 1999; Cheng et al. 2011) characteristics. These changes can be translated into a broader mosaic of resources and conditions that can be beneficial for canopy arthropods.

Considering that the arthropod community structure could be influenced by several factors beyond the host genetic diversity (Johnson and Stinchcombe 2007; Hughes et al. 2008; Tack et al. 2012), the approach used in the present study offers a more realistic scenario than the other studies that only evaluate the role of host

plant genetic attributes on the community structure (Hersch-Green et al. 2011). Although these studies have helped demonstrate that intraspecific genetic variation can have an effect beyond an individual's phenotype, they likely do not accurately estimate its effective size. The most commonly employed method in these approaches has been the collection of multiple genotypes from diverse and often distant environments as well as to replicate these genotypes into single common environments where the environmental variation is minimized (Tack et al. 2012). As a result, these studies provide little information regarding the importance of the plant genotype or genetic variation compared with other factors that also influence multitrophic communities. In our study, we simultaneously evaluated the influence of genetic attributes of Q. castanea (individual and population genetic diversity) and two ecological factors (host density and red oak species richness) on canopy insect community in natural conditions. This experimental design allowed us to more accurately quantify the influence of the effects of three different variables on community structuring.

In contrast, some studies have not found significant effects of plant genetics on associated communities. For example, Tack et al. (2010) found that genetic diversity had little influence on the endophagous insect community structure (gallers, leafminers, and leafrollers) of Q. robur in Finland. Similar results were reported by Castagneyrol et al. (2012), who found that the genetic attributes of the host plant had no significant effect on the phytophagous insect community (endophagous and ectophagous) of Q. robur in France.

In the case of Q. castanea, previous studies have shown high genetic diversity levels (Valencia-Cuevas et al. 2014) as a result of interspecific gene flow with three of its associated red oak species in the Transmexican Volcanic Belt (Valencia-Cuevas et al. 2015). In this scenario, it is possible that the Q. castanea genetic diversity levels are sufficient for the endophagous insect community to have an observable response.

It has been proposed that the direct effects of genetically based plant traits on herbivores may also indirectly extend to the next trophic level, impacting predators and parasitoids (Johnson and Agrawal 2005; Crutsinger 2016). From this perspective, we expected that the endophagous insect species richness directly depends on the genetic attributes of the host plant, which has indirect positive effects on the parasitoid community richness. This hypothesis was supported in this study because we found that the Q. castanea genetic diversity levels influenced the canopy parasitoid insects. When the relationship between parasitoid species richness and endophagous species richness was examined, we found a significant positive relationship ($r^2 = 0.12$; $P < 0.0001$). This result demonstrates the high degree of specialization between parasitoid species and their host gall inductor species (Sanchez et al. 2013). Finally, we suggest that the genetic diversity of Q. castanea had an indirect effect on the S of parasitoid insects, which was mediated through the effects on the S of endophagous insects. These results are consistent with reports by Bailey et al. (2006) and Johnson (2008). Overall, these results show that genetic variation in plants can be an important factor governing the herbivore population dynamics and tritrophic interactions that involve plants, herbivores, and parasitoids. According to the results obtained in this study, we suggest that Q. castanea is a foundation species whose genetic diversity levels have direct effects on the endophagous insect community.

In addition, we found that ecological parameters, such as the host density and red oak species richness, influence the canopy insect community. It has been suggested that high host density should provide herbivores with substantial edible biomass and the biomass

should be easy to find (Sholes 2008). Additionally, a high resource concentration could support both more herbivore species and higher densities of each herbivore species (Root 1973; Kareiva 1983). Additionally, this effect will be the strongest for specialist herbivores (Stephens and Myers 2012). Under this scenario, we suppose that lower Q. castanea densities promote low resource concentration for endophagous insects; as a result, their densities are less favored, as seen in other systems (Ostergard and Ehrlén 2005; Sholes 2008). This hypothesis is also suggested by our path analysis in which there was a significant negative relationship between the host plant density and endophagous insect density. In contrast, the path analysis failed to show that the host density also affects the parasitoid density. In addition, we found that there is no relationship between gall forming insects and parasitoid density. Both results led us to think that the parasitoid insect densities are not mediated by resource availability (endophagous insect density), but they are probably related to the host plant or prey quality, as has been reported in other studies (e.g., Fritz et al. 1997; Harvey et al. 2003; Schädler et al. 2010). For example, Harvey et al. (2003) and Fritz et al. (1997) demonstrated differences in the performance of parasitoids, which depend on the host plant quality. From this perspective, Schädler et al. (2010) reported that parasitoid abundance may be correlated with the quality of host plants. Considering these statements, it is likely that certain performance traits of parasitoids associated with Q. castanea are affected by the quality of the host plant or endophagous insect prey, suggesting that the host plant's genetic attributes can influence parasitoid populations via plant quality or prey consumption. It is important to emphasize that we did not measure the host plant or endophagous insect quality in this study; however, addressing this issue in future work could help accept or reject these hypotheses. Moreover, the oak species richness also had a significant influence on the endophagous species richness. Previous studies in Q. crassifolia (Tovar-Sánchez et al. 2015a) revealed a phenomenon known as "associational susceptibility" (Brown and Ewel 1987) in which plant species present with greater abundance and diversity of herbivores when they are spatially associated with heterospecific neighbors. This phenomenon probably occurs in Q. castanea.

In this study, we observed significant differences in the endophagous insect infestation levels associated with Q. castanea among different localities. The occurrence of different response patterns has been attributed to differences in the host plant genetic characteristics and genetic mechanisms that determine the inheritance of resistance characteristics (Boecklen and Spellenberg 1990; Fritz et al. 1994; Strauss 1994). In a previous study, we revealed the existence of an array of homozygous and heterozygous genotypes in the Q. castanea populations that were analyzed in this research (Valencia-Cuevas et al. 2014). Therefore, we presumed that different Q. castanea genotypes inherit different mechanisms which, in turn, establish the different resistance patterns observed here. In addition, it has been reported that the host plant resistance characteristics may be differentially expressed in different environments (Fritz 1999). The Q. castanea populations in this study are distributed in the central portion of the TVB, whose formation process occurred in a single geological event that began during the Quaternary–Pliocene (Challenger 1998). This observation makes us suppose that these populations have had the same evolutionary origin, which has minimized the environmental variation among localities and the influence of such variability on the endophagous insect infestation levels among the study sites. Hence, we suggest that the variation in the expression of the resistance characteristics of Q. castanea through the localities

found in this work is related to the genetic characteristics of the host plant in each population.

In conclusion, the multifactorial approach used in this study helped to determine the influence of genetic and ecological factors on the arthropod community structure associated with *Q. castanea*, as well as to obtain a more realistic understanding of natural conditions. Therefore, the results from this study suggest that evaluating genetic variation in plant traits may be essential to understanding the ecology of oak–parasite–parasitoid interactions.

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Appendix 1. Locality name, state, and red oak species associated to *Q. castanea* in the Transmexican Volcanic Belt

Locality	State	Oak species
Corredor Biológico Ajusco-Chichinautzin	Morelos	*Q. castanea*
Parque Nacional El Tepozteco	Morelos	*Q. castanea*, *Q. crassipes*
Parque Ecológico de la Ciudad de México	Mexico City	*Q. castanea*, *Q. crassipes*, *Q. laurina*
Parque Barranca de Tarango	Mexico City	*Q. castanea*, *Q. crassipes*, *Q. laurina*, *Q. mexicana*
Parque Ecológico Las Peñas	Mexico State	*Q. castanea*, *Q. crassipes*, *Q. laurina*, *Q. mexicana*, *Q. crassifolia*
Parque Ecológico El Huixteco	Guerrero	*Q. castanea*, *Q. crassifolia*, *Q. laurina*, *Q. candicans*, *Q. urbanii*, *Q. scytophyla*

Appendix 2. Community composition of canopy endophagous and parasitoid insects associated to *Q. castanea* in the Transmexican Volcanic Belt

Orden	Family	Genus	Species
Endophagous insects			
Hymenoptera	Cynipidae	*Amphibolips*	*Amphibolips hidalgoensis*
		Andricus	*Andricus* nr *sphaericus*
		Disholcaspis	*A. nievesaldreyi*
			A. linària group
			A. tuberoses group
			A. nr *bonansaeai*
			A. sp. 1
			A. sp. 2
			Disholcaspis nr *pallens*
			D. sp 1
		Antron	Antron sp.
		Erythres	*Erythres hastata*
		Kokkocynips	*Kokkocynips doctorrosae*
		Neuroterus	*Neuroterus* nr *junctor*
			N. sp. 1
			N. sp. 2
			N. sp. 3
		Melikaiella	*Melikaiella amphibolensis*
Diptera	Cecidomyiidae		Cecidomyiidae sp.1
	Chloropidae		Chloropidae sp. 1
Lepidoptera	Bedellinae		*Bedellia* sp.
	Gelechiidae		Gelechiidae sp.
Parasitoid insects			
	Apidea		Apidea sp.1
	Bethylidae		Bethylidae sp.1
	Braconidae		Braconidae sp.1
	Elasmidae	*Elasmus*	*Elasmus* sp.
	Eulophidae	*Cirruspilus*	*Cirruspilus* sp.
		Clostocerus	*Clostocerus* sp.
		Euplectrus	*Euplectrus* sp.
		Tetrastichinae	*Tetrastichinae* sp.
			Eulophidae sp. 1
			Eulophidae sp. 2
			Eulophidae sp. 3
	Eupelmidae	*Brossema*	*Brossema* sp.
	Eurytomidae	*Eurytoma*	*Eurytoma* sp.
	Figitidae		Figitidae sp. 1
	Ormyridae	*Ormyrus*	*Ormyrus* sp.
	Platygastridae	*Scelionidae*	*Scelionade* sp.
			Platigastridae sp. 1
	Pteromelidae		Pteromelidae sp. 1
	Sphecidae		Sphecidae sp. 1
	Torymidae	*Torymus*	*Torymus* sp.