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Influence of forest type and host plant genetic relatedness on the canopy arthropod community structure of *Quercus crassifolia*

Efraín Tovar-Sánchez[1*], Erwin Martí-Flores[1], Leticia Valencia-Cuevas[1] and Patricia Mussali-Galante[2]

Abstract

Background: *Quercus crassifolia* is an oak species with characteristics of foundation species, which is a canopy dominant element of different forest types that supports a wide diversity of associated species. Therefore, it is an excellent system to address important ecological questions. We analyzed the effect of individual genetic relatedness of the host plant, forest type (*Abies*-*Quercus*, *Quercus*-*Pinus*, and *Quercus* forest), and season (dry vs. rainy) on the canopy arthropod community structure. Thirty oak canopies were fogged (five individuals/season/forest type).

Results: We identified 442 arthropod species belonging to 22 orders. The highest values of density, diversity, and richness were recorded during the rainy season for each forest type. Also, the non-metric multidimensional scaling (NMDS) analysis showed a separation of the host tree species for each forest type. During the rainy season, the highest values of density, diversity, and richness in each forest type were recorded. A separation of host tree was found for each forest type. In general, diversity and richness of canopy arthropods showed the following pattern: *Abies*-*Quercus* > *Quercus*-*Pinus* > *Quercus*, while density showed an inverse pattern. An increase of the diversity of canopy arthropods is significantly related to an increase of host plant genetic diversity, independently of the type of forest and of the season.

Conclusions: In terms of conservation, if arthropod species respond to genetic differences among host plants, it becomes important to conserve genetic diversity of foundation species, since it is fundamental to preserve diversity of their associated arthropod communities.

Keywords: *Quercus*; Foundation species; Individual genetic diversity; Microsatellites; Forest type; Arthropods community

Background

Efforts toward conservation strategies have focused on the preservation of charismatic animals like mammals, birds, and other terrestrial vertebrates. Most of these species have been described, their ecologies known, or threats to their habitats often documented. This information has been used to implement management and conservation programs (Leather et al. 2008). In contrast, efforts toward arthropod conservation have been limited because most of the species have not been described or their life history and roles that they play within communities are unknown (Stork 1998). Despite this, it has been documented that this phylum contains the highest species diversity on earth (from 2.5 to 3.7 million of species Hamilton et al. 2010); additionally, insects play important ecological roles and are involved in processes that maintain forest ecosystems.

Therefore, efforts to conserve biological diversity should include the protection of the arthropod fauna. Fortunately, in recent years, several hypotheses have been proposed about the conservation of biodiversity, including habitat conservation, diversity hotspots, biogeographic crossroads, and the conservation of ecosystem processes (Bangert et al. 2005). Coupled with this perspective of integrating conservation, unification and simplification of the principles that govern communities can be of great value to improve the ability to generate conservation strategies (Wimp et al. 2004).

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* Correspondence: efrain_tovar@uaem.mx
[1]Departamento de Sistemática y Evolución, Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Av. Universidad 1001, Col. Chamilpa, Morelos, Cuernavaca CP 62209, Mexico
Full list of author information is available at the end of the article

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Natural communities have been considered complex ecological systems, where its structure and functioning are determined by the interaction of different factors, whose effects are spatially and temporally variable (Bailey and Whitham 2007). One such factor is the heterogeneity of forests, for example, the forest canopy can be structurally more complex when it consists of more than one tree species (Sobek et al. 2009). This suggests that tree species communities with high levels of species richness will increase the habitat heterogeneity, resulting in more resources and conditions. In this sense, there are studies that have reported a positive relationship between plant diversity and arthropod species richness (Sobek et al. 2009).

Oak canopies represent an ideal system to study their associated communities, since they can be physically delimited. It has been documented that canopies support a great diversity of organisms (Nadkarni et al. 2004). In particular, arthropods are considered the main component of the canopy-associated communities in terms of abundance and species diversity (Stork and Hammond 1997). To study canopy arthropod communities, it is important to conduct studies at local scales. This approach minimizes the effects of other factors (e.g., geological history, topography, climate, forest age, altitude, and disturbance) that may also modify community structure parameters.

In the last 20 years, various studies have documented that genetic variation of foundation species ('species that structure a community by creating locally stable conditions for other species and by modulating and stabilizing fundamental ecosystem processes', Dayton 1972) can have an extended effect beyond the individual leading to interactions with other species to produce community and ecosystem phenotypes (Whitham et al. 2006). For example, studies with eucalyptus (Dungey et al. 2000), willows (Hochwender and Fritz 2004), cottonwoods (Wimp et al. 2004), and oaks (Tovar-Sánchez and Oyama 2006a, b) have demonstrated that plant genetics can influence the associations and interactions of communities associated with these species.

To evaluate the genetic relatedness effects of the host plant on the arthropod community structure, the majority of studies have been done at an intra-specific level (among populations or patches of mixed genotypes vs. monocultures; Hochwender and Fritz 2004), in hybrid complexes (among different genetic classes: parentals, F1 hybrids, and backcross hybrids; Wimp et al. 2004; Tovar-Sánchez and Oyama 2006a, b), and few studies have been conducted at the intra-individual level (Tovar-Sánchez et al. 2013). Therefore, studies that address the influence of intra-individual genetic variability on canopy arthropod community are valuable because they explore other factors that may play a significant role in community assemblage. Moreover, most of the studies have been conducted under experimental conditions (Hochwender and Fritz 2004) rather than on natural systems (Ferrier et al. 2012).

These effects have been assessed in terms of species richness, similarity, and diversity. For example, Wimp et al. (2004), Tovar-Sánchez and Oyama (2006b), and Ferrier et al. (2012) found that greater genetic diversity of the host plant favors richness and diversity of the associated communities, because more genetically diverse host plants offer a wider range of resources and conditions. Likewise, Bangert et al. (2005) found that genetically similar host plant species will hold more similar communities, due to a major similarity in physical, chemical, and phenological characteristics. In terms of conservation, if arthropod species respond to genetic differences among host plants, it becomes important to conserve genetic diversity of foundation species, since it is fundamental to preserve diversity of their associated arthropod communities (Bangert et al. 2005; Tack and Roslin 2011).

Mexico contains 161 species of oaks (*Quercus*, Fagaceae) from which 68% of these appear to be endemic (Valencia 2004). In consequence, Mexico is considered one of the centers of diversification of the genus (Valencia 2004). In general, oaks represent an ideal system to study the effects of host plant genetic relatedness on their associated canopy communities, because they are dominant elements of temperate forest canopies and their genetic diversity levels are high (Dutech et al. 2005). Likewise, it has been documented that oaks are involved in important ecosystem processes as nutrient recycling and water balance (Madritch and Hunter 2002). This information invites us to think that most oak species can be considered as foundation species.

Mexican temperate forests are threatened by deforestation activities (≈314,000 ha/year, FAO 2006), resulting in a significant loss of habitat. When the foundation species are the habitat, a loss of genetic diversity will result in a loss of habitat that could have a potential effect on species across multiple trophic levels and major taxonomic groups (Bangert et al. 2005). The consideration of genetic diversity conservation can be a general and efficient approach to conserving processes (evolutionary and ecological) and diverse assemblages of plants and animals.

Quercus crassifolia is an excellent system to study the mechanisms that regulate its associated arthropod communities, due to its wide geographical distribution and its association with different types of forests, and it is a dominant canopy element in temperate forests which supports a wide diversity of flora and fauna.

As a consequence, and because there are no studies that analyze simultaneously the influence of genetic relatedness of foundation species and forest type on their associated arthropod fauna, the goal of this study was to evaluate the effect of individual genetic relatedness of *Q. crassifolia* on the canopy arthropod community structure in terms of composition, species richness, diversity, and density. Also, we determined if the arboreal community structure changes between forest types. We predict that the host plant with the highest levels of intra-individual genetic diversity and the highest level of surrounding arboreal species richness should support more diverse arthropod communities, because they offer a wider array of resources and conditions to be exploited.

Methods

Study site

The study areas are situated at the Parque Nacional El Chico (PNECh), which was decreed as a protected natural area in 1898. It possesses a surface of 2,739 ha and is located at the Austral portion of Transmexican Volcanic Belt (TVB) (20° 10′ N, 98° 41′ W, CONANP 2006). The altitude oscillates between 2,600 to 3,050 m. Mean annual temperature oscillates between 12°C and 18°C, and more than 90% of the annual precipitation of 1,479.5 mm falls from April to October (CONANP 2006).

Inside the PNECh, the principal forest types are *Abies*, *Quercus*, *Abies-Quercus*, *Pinus, Quercus-Pinus*, *Juniperus* forest and grassland (CONANP 2006). Because it has been documented that canopy arthropod community structure varies spatially (Tovar-Sánchez et al. 2003), we chose three forest types (*Quercus*, *Quercus-Pinus,* and *Abies-Quercus*) within the PNECh to minimize historic and environmental site effects. We presume that because these three forest types are located within the same geographic area, with similar geological and evolutive events, the influence of these factors should be reduced when assessing their associated arthropod communities. Therefore, these sites have the same geological history, weather (temperate subhumid), altitude (between 2,550 and 2,750 m), forest age (mature forest), tree height (between 10 and 13 m), soil type (volcanic origin), and degree of disturbance (no local disturbance inside the forest). In addition, in the three forest types, *Q. crassifolia* is a canopy representative element.

Quercus forest is located at an altitude of 2,750 m, and various arboreal species are found in this type of forest: *Quercus alpenses*, *Q. crassifolia*, *Quercus glabrescens*, *Quercus greggii*, *Quercus laurina*, *Quercus mexicana*, and *Arbutus glandulosa*.

Quercus-Pinus forest is situated at an altitude of 2,550 m, and it is shaped by the following arboreal species: *Q. affinis*, *Q. crassifolia*, *Q. glabrescens*, *Q. greggii*, *Q. laurina*, *Pinus rudis*, *Pinus teocote*, *Abies religiosa*, *A. glandulosa*, *Arbutus xalapensis,* and *Ilex tolucana*.

Abies-Quercus forest is located at an altitude of 2,720 m, where the following arboreal species are found: *A. religiosa*, *Q. affinis*, *Q. crassifolia*, *Q. glabrescens*, *Q. greggii*, *Quercus potosina*, *Quecus rugosa*, *Alnus arguta*, *A. xalapensis*, *A. glandulosa*, *Buddleia cordata*, *Cercocarpus macrophyllus*, *Cornus disciflora*, *Garrya laurifolia*, *I. tolucana*, and *Vibornum elatum*.

Hence, a gradient of arboreal species among forest types is observed: *Abies-Quercus* ($n = 16$) > *Quercus-Pinus* ($n = 11$) > *Quercus* ($n = 7$).

The *Quercus* forest is located at 6.3 linear km from the *Quercus-Pinus* and *Abies-Quercus* forests. The *Quercus-Pinus* and *Abies-Quercus* forests are separated by a distance of 3.5 linear km.

Study species

Q. crassifolia Humboldt and Bonpland is a red oak (section *Lobatae*) that includes large trees up to 23 m in height with a trunk diameter of 1 m and deciduous leaves. *Q. crassifolia* can differ easily from other red oaks by its leaf characteristics such as ovate, obovate, or elliptic shape with a coriaceus upper surface, the lower surface is yellow tomentose, orange or brown, presenting from one to ten teeth (Romero et al. 2002) and not glandular sessile fasciculate and the solitary unicellular trichomes. This species presents a broad geographical distribution in Mexico, occupying the major mountain ranges at an altitude of 2,500 to 2,800 m (Romero et al. 2002).

Canopy arthropod community

Canopy arthropod community structure of *Q. crassifolia* at the PNECh was determined by sampling ten trees in each forest type, five trees during dry season (February 2005) and five trees during rainy season (August 2005). Sampling was done seasonally, which allowed having a representative annual sample of the canopy arthropod fauna, as suggested by previous studies, which have demonstrated that seasonality modifies both composition and richness of the canopy arthropod fauna (Tovar-Sánchez et al. 2003; Tovar-Sánchez and Oyama 2006a; Tovar-Sánchez 2009). We selected individual oaks of 10 to 13 m (mean ± SE, 11.42 ± 0.17 m) in height and between 20.21 and 32.64 m^2 (mean 24.89 ± 3.27 m^2) of crown cover. Crowns that do not overlap with any other tree within the oak forest were sampled. Arthropods were collected by fogging with 750 ml of non-persistent insecticide (AquaPy, AgrEvo, Mexico City) the entire canopy of a single tree. AquaPy is composed by 30 g/l of natural pyrethrine, synergized with 150 g/l of piperonyl-but-oxide. Fogging activity was done between 0400 h and 0430 h (lasting approximately 1:30 min) in order to avoid denaturalization of the insecticide by solar radiation, avoiding windy or rainy days. Arthropods fallen from each fogged tree were collected in ten plastic trays (1 m^2 area per tray) that were randomly distributed under tree crowns. The arthropods were kept in 70% ethanol except adult organisms of Lepidoptera, which were kept in glassine paper bags. The arthropods were separated into morphospecies. Abundance of each morphospecies was also counted. In this study, 'arthropod morphospecies' will be referred as 'arthropod species.'

Molecular data

Leaves with no apparent damage were collected from ten individuals of *Q. crassifolia* in each forest type. Total DNA was extracted and purified by using the DNAeasy Plant Mini Kit (Qiagen, Valencia, CA, USA). DNA quantification was done by fluorometric analysis (Eppendorf, Biophotometer, Hamburg, Germany), and DNA quality was visualized by comparing the intensity of bands with known standards of lambda DNA on agarose gels at 0.8%. Genetic analyses were performed using nuclear microsatellite markers (nSSRs).

We chose six nuclear microsatellites primers (OC11, OE09, CO8, FO7, QpZAG110, and QrZAG11) that detected polymorphisms in *Q. crassifolia*. Forward primers were labeled with a fluorescent tag: HEX (green), NED (yellow), or FAM (blue). PCR reactions were done as follows: 15 ng of DNA template, 50 mM KCl, 20 mM Tris-HCl (pH 8.4), 2 mM $MgCl_2$, 0.13 mM of each dNTP, 25 mM of each primer, and 0.8 U of Taq polymerase, in a final volume of 15 µl. Reaction conditions were as follows: an initial denaturation step at 95°C for 5 min, followed by 30 cycles at 94°C for 1 min, 1 min at the appropriate annealing temperature, followed by 30 s at 72°C, and a final extension step at 72°C for 8 min. Annealing temperature differed for each primer pair: 53°C for OC11 and OE09, 50°C for CO8, 58°C for FO7, 48°C for QpZag 110, and 53°C for QrZag 11. PCR products were resolved on agarose gels at 2% to 180 V for 1.5 h. Depending on the strength of the bands on the agarose test gel, these were diluted 1:10 to 1:90 with water. Polymorphic fragments were sequenced on an automatic sequencer ABI-PRISM 3100 (Applied Biosystems Inc., Foster City, CA, USA) using 9.5 ml of formamide, 0.5 ml of ROX 500 used as a size standard, and 1 ml of each PCR product. Alleles were scored using the Gene Mapper ver. 3.7 Software (Applied Biosystems, Foster City, CA, USA).

Statistical analysis

Three-factor ANOVAs were conducted (model type III, Zar 2010) to determine the effect of forest type (*Quercus*, *Quercus-Pinus,* and *Abies-Quercus*), season (dry and rainy), individual genetic relatedness of host plant (internal relatedness (IR)), and interaction of forest type × season on canopy arthropod density. Density values of canopy arthropods were log-transformed ($X' = \log_e X + 1$) (Zar 2010). Two-factor ANOVAs were conducted (model type III, Zar 2010) to determine the effect of forest type (*Quercus*, *Quercus-Pinus,* and *Abies-Quercus*), season (dry and rainy), and interaction of forest type × season on canopy arthropod diversity and richness species.

Differences in canopy arthropod species composition between forest types were tested using non-metric multidimensional scaling (NMDS) based on the presence of 422 arthropod species. NMDS is a robust ordination technique for community analysis. NMDS was used to generate a dissimilarity matrix between forest types by season using the Bray-Curtis dissimilarity coefficient. Differences in canopy arthropod community species composition between forest types were quantified with the Bray-Curtis similarity coefficient that was calculated on the square root-transformed species by sample abundance data matrix.

Analysis of similarity (ANOSIM) was used to evaluate the differences between arthropod community composition and forest type by season. ANOSIM was employed to test for differences among groups using 1,000 random reassignments and determining whether the generated dissimilarity matrix is significantly different than chance (Warwick et al. 1990).

The diversity of canopy arthropod community associated to *Q. crassifolia* at each oak tree was estimated using the true Shannon diversity index (exp(H′)) (Jost 2006). Thereafter, the index was compared between forest types with a randomization test as described by Solow (1993), this test re-samples 10,000 times from a distribution of species abundances produced by a summation of the two samples.

Individual genetic relatedness of *Q. crassifolia* was quantified using the IR parameter (Amos et al. 2001). IR is based on the relatedness measure of Queller and Goodnigth (1989), except that at each locus, two alleles rather than two pairs of alleles are compared. Over several loci, the resulting values are approximately normally distributed and centered on zero, with negative values suggesting relatively outbred individuals and high positive values being suggestive of inbreeding. IR values were computed using EXCEL (Microsoft INC.) macro written in Visual Basic provided on the William Amos website (http://www.zoo.cam.ac.uk/directory/william-amos, Department of Zoology, Cambridge University, UK). For this study, IR values were multiplied by (–). Thus, IR values below zero denote inbred individuals and values above zero denote outbred individuals. Diversity index (H') and species richness (S) variables were correlated with each other. Therefore, the relationship between individual genetic relatedness of *Q. crassifolia* in each forest type and the arthropod H' was tested by regression analyses.

The softwares used for statistical analysis were STATISTICA 8.0 (StatSoft Inc 2007), Species Diversity and Richness 3.03 (Henderson and Seaby 2002), and PC-ORD 4.28 (McCune and Mefford 1999).

Results

Composition of arthropods

In total, 17,485 individuals were collected, 15,073 during rainy and 2,412 during dry season. Canopy arthropod composition of *Q. crassifolia* is formed by 422 species belonging to 22 orders (Araneae, Arthropleona, Astigmata, Coleoptera, Cryptostigmata, Dermaptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Mecoptera, Mesostigmata, Neuroptera, Opiliones, Orthoptera, Pseudoscorpiones, Prostigmata, Psocoptera, Symphypleona, Thysanoptera, and Trichoptera).

Relative abundance of species grouped into arthropod orders changed between seasons and between forest types (Figure 1). During dry season, the most abundant groups were Hymenoptera, Cryptostigmata, and Diptera, whereas Arthropleona, Coleoptera, and Cryptostigmata were the most common groups during rainy season, independently of the forest type (Figure 1). For forest type, Cryptostigmata, Arthropleona, and Hemiptera were the most common groups in *Quercus* forest, whereas Arthropleona, Coleoptera, and Cryptostigmata were the most abundant groups in *Quercus-Pinus* forest. Finally, Hymenoptera, Cryptostigmata, and Coleoptera were the most common groups in *Abies-Quercus* forest (Figure 1).

In general, we found significant differences in canopy arthropod community composition associated to *Q. crassifolia* among forest types (ANOSIM $R = 0.4823$, $n = 39$, $P < 0.001$) (Figure 2), being these communities significantly different from one another on all three forest types. Within a forest type, we found significant differences in canopy arthropod community composition between different seasons, also, the differences among categories (forest types) were significant after correcting the critical value of alpha for inflated type II errors ($P < 0.02$ for all comparisons) (*Quercus*: ANOSIM $R = 0.4802$, $P < 0.001$; *Quercus-Pinus*: ANOSIM $R = 0.5137$,

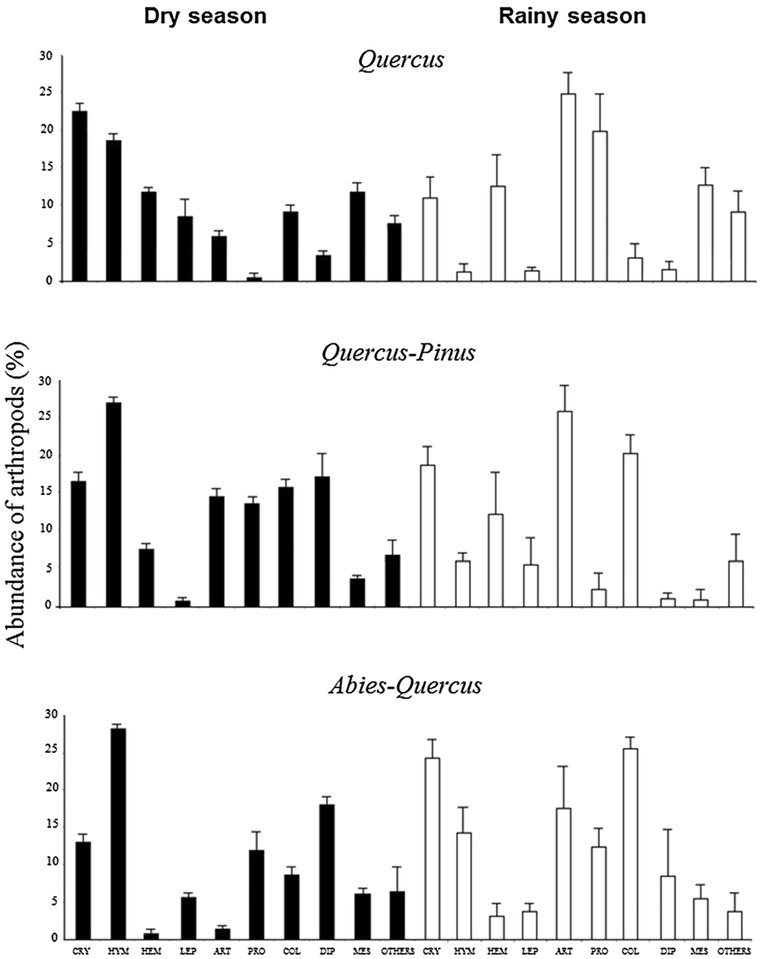

Figure 1 Canopy arthropod relative abundance (%) in *Q. crassifolia* associated to three types of vegetation association. The types of vegetation are *Quercus*, *Quercus-Pinus*, and *Abies-Quercus* at the Parque Nacional el Chico in dry (February 2005) and rainy (August 2005) seasons. ARA = Araneae, ART = Arthropleona, AST = Astigmata, COL = Coleoptera, CRY = Cryptostigmata, DIP = Diptera, HEM = Hemiptera, HYM = Hymenoptera, LEP = Lepidoptera, MES = Mesostigmata, PSO = Psocoptera, PRO = Prostigmata, SYM = Symphypleona, and others (Dermaptera, Isoptera, Mecoptera, Neuroptera, Opiliones, Orthoptera, Pseudoscorpiones, Thysanoptera and Trichoptera).

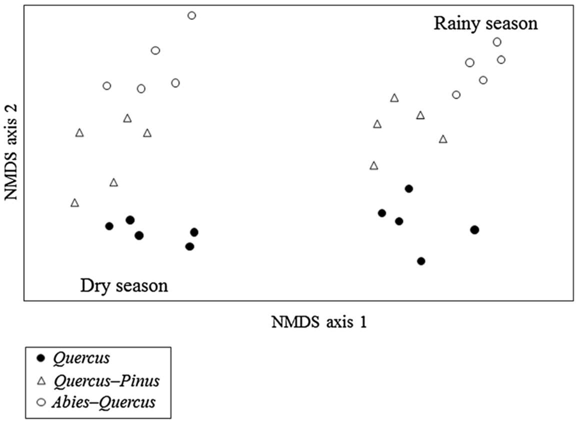

Figure 2 Arthropod community composition differences associated to canopy of *Quercus crassifolia* among forest types (*Quercus, Quercus-Pinus, Abies-Quercus*). Each point is a two-dimensional (axis 1 and axis 2) representation of arthropod species composition on an individual tree based on global, nonmetric multidimensional scaling (NMDS). Distances between points reflect a dissimilarity matrix created using the Bray-Curtis dissimilarity coefficient. Points that are close together have arthropod communities that are more similar in composition compared to points that are far apart.

$P < 0.001$; *Abies-Quercus*: ANOSIM $R = 0.6330$, $P < 0.001$). Therefore, these results indicate that canopy arthropod community composition varies in space and time.

Density of arthropods

The density of canopy arthropod species differed significantly between individual genetic relatedness ($F_{24,270} = 8.26$, $P < 0.001$), forest types ($F_{2,270} = 6.93$, $P < 0.01$), seasons ($F_{1,270} = 187.07$, $P < 0.001$) and interaction season × forest types ($F_{2,270} = 4.99$ $P < 0.01$). In general, we found that canopy arthropod densities associated to *Q. crassifolia* showed the following pattern: *Abies-Quercus* < *Quercus-Pinus* < *Quercus* for both seasons. The results showed that in each forest type, the arthropod densities increased between 4.9 and 5.9 times higher during rainy than dry season (Table 1).

Diversity of arthropods

The richness of canopy arthropod species differed significantly between forest types ($F_{2,24} = 53.64$, $P < 0.001$), seasons ($F_{1,24} = 648.12$, $P < 0.001$), and interaction season × forest type ($F_{2,24} = 175.63$, $P < 0.001$). On the other side, the diversity of canopy arthropod species did not differed significantly between forest type ($F_{2,24} = 1.93$, $P > 0.05$) and interaction season × forest type ($F_{2,24} = 1.44$, $P > 0.05$), in contrast, significant differences between seasons were registered ($F_{1,24} = 50.91$, $P < 0.001$).

In this study, we found that H' and S of canopy arthropods associated to *Q. crassifolia* showed the following pattern, according to forest type: *Abies-Quercus* [$S = 209$; $\exp(H') = 148$] > *Quercus-Pinus* [$S = 143$; $\exp(H') = 81$] > *Quercus* [$S = 116$; $\exp(H') = 55$] (Table 2). In addition, the highest values of H' and S were found during rainy season for the three forest types: *Abies-Quercus* > *Quercus-Pinus* > *Quercus* (Table 2).

Relationship between oak host plant genetic relatedness and canopy arthropod community

This study revealed that host plant IR affects significantly the diversity of canopy arthropods (H'). In general, our results showed a positive and significant relationship between genetic relatedness of *Q. crassifolia* and the diversity of canopy arthropods in dry ($r = 0.66$, $F_{1,13} = 10.17$, $P < 0.01$) and rainy season ($r = 0.73$, $F_{1,13} = 14.86$, $P < 0.01$) (Figure 3).

Discussion

The results obtained in the present study showed that the forest type had a significant effect on canopy arthropod community structure of *Q. crassifolia*. We found a different community structure among forest types in terms of composition. Also, the values of H', S, and density of arthropod fauna were higher during rainy season for the three forest types. In general, H' and S of arthropods showed the following pattern: *Abies-Quercus* > *Quercus-Pinus* > *Quercus*. Surprisingly, the density showed an inverse pattern (*Abies-Quercus* < *Quercus-Pinus* < *Quercus*). Finally, an increase of the host plant genetic diversity was significantly related to an increase of canopy arthropod diversity, independently of the forest type and season.

Effect of forest type and season on canopy arthropod community

Our results showed that the forest type has a significant effect on canopy arthropod community structure of *Q. crassifolia*. We found a different community structure among forest types in terms of composition, density, S, and H'. In general, Hymenoptera, Cryptostigmata, and Diptera were the most abundant groups collected in *Q. crassifolia* canopies during dry season. Also, we found that the majority of Hymenoptera species corresponded to the Cynipidae family, which is highly specialized to the *Quercus* genus (Stone et al. 2002). The fact that Cynipidae populations increase during dry season is probably related to its oviposition behavior or eclosion processes (Stone et al. 2002).

In our collection, Cryptostigmata was one of the most abundant groups in both seasons. These results are similar to other studies in tropical (Palacios-Vargas and Castaño-Meneses 2003) and temperate (Tovar-Sánchez 2009) forests in Mexico. Probably, the presence of arboreal epiphytes and rugose cortex (which accumulates organic matter) of *Q. crassifolia*, mainly during rainy season, favors an increase of resources and conditions that can be exploited by these organisms (Palacios-Vargas and

Table 1 Density (no. ind./m^2 ± SE) of canopy arthropods associated to *Q. crassifolia* by forest type

Tree	Forest type					
	Quercus		***Quercus-Pinus***		***Abies-Quercus***	
	Dry	**Rainy**	**Dry**	**Rainy**	**Dry**	**Rainy**
1	29.5 ± 3.2	*123.2 ± 8.9*	*17.8 ± 2.5*	137.6 ± 14.5	20.1 ± 2.8	90.8 ± 11.4
2	37.4 ± 4.1	*238.2 ± 12.3*	25.0 ± 3.3	105.3 ± 20.2	*24.7 ± 3.6*	105.3 ± 10.6
3	39.7 ± 5.3	175.9 ± 20.1	27.3 ± 4.1	138.5 ± 17.3	*13.7 ± 2.3*	112.4 ± 13.2
4	*45.2 ± 3.6*	129.8 ± 19.0	*30.6 ± 3.8*	*98.3 ± 9.7*	17.4 ± 2.7	*89.5 ± 8.3*
5	*28.6 ± 3.9*	144.5 ± 18.3	23.3 ± 3.4	*165.7 ± 31.4*	14.3 ± 3.0	*132.7 ± 12.3*
Total	33.1 ± 3.0	162.3 ± 9.3	24.8 ± 3.2	129.9 ± 16.7	18.0 ± 2.6	106.1 ± 10.3
	a	*A*	*b*	*B*	*c*	*C*

Data from dry (February 2005) and rainy seasons (August 2005). Italicized data indicated the values of the maximum and minimum densities per season. Different letters show significant differences $P < 0.05$ (Tukey test). Capital letters show significant differences between forest type in rainy season and lower case letters in dry season.

Castaño-Meneses 2003). The abundance of Cryptostigmata in each forest type registered the following pattern: *Abies-Quercus* > *Quercus-Pinus* > *Quercus.* This pattern is related to the number of arboreal species growing in sympatry with *Q. crassifolia* in each forest type, a phenomenon that is known as 'associational susceptibility' (White and Whitham 2000), in which plant species present greater abundance of herbivores when spatially associated with heterospecific neighbors (White and Whitham 2000).

On the other hand, Arthropleona, Coleoptera, and Cryptostigmata were the most abundant groups in the different forest types during rainy season. We suggest that the high abundance of Arthropleona may be due to its small body size and preference to humid habitats. Probably, the augment of the water availability and organic matter concentration in canopies during rainy season promoted an increase of conditions and resources that allowed the increase of their population size (Castaño-Meneses 2002). Contrary to the results obtained for Cryptostigmata, these results do not support the 'associational susceptibility' hypothesis, because Arthropleona, was more abundant in the *Quercus* forest, followed by *Quercus-Pinus* and *Abies-Quercus*.

We found that Coleoptera was a very abundant group during rainy season (*Abies-Quercus* > *Quercus-Pinus* > *Quercus*). Barbosa et al. (2000) suggested that during this season, there is an increase in resource availability, which is in accordance with seasonal growth of forest ecosystems. In this sense, Romero et al. (2002) document that *Q. crassifolia* is a deciduous species, which increases branch, leaves, and fruit formation and development of epiphyte plants, a fact that can favor a great possibility of resources that may be used by canopy arthropods (Tovar-Sánchez et al. 2003). Also, during rainy season, younger leaves are more abundant, nutritive, and softer and have less secondary metabolites (Coley et al. 2006). An increase in host plant nutritional quality as well as the availability of canopy resources may explain the proliferation of phytophagous beetles associated to *Q. crassifolia* canopies at the PNECh during rainy season. Similar results were observed by Wagner (2000) in the canopy of *Rinorea beniensis* in a rainy forest in Uganda. Moreover, the results obtained for the order Coleoptera support the associational susceptibility hypothesis.

In addition, we found that *H´* and *S* of canopy arthropods showed the following pattern: *Abies-Quercus* > *Quercus-*

Table 2 Shannon-Wiener diversity index (exp(*H′*)) and species richness (*S*) of the communities of canopy arthropods

Tree	Forest type											
	Quercus				***Quercus-Pinus***				***Abies-Quercus***			
	Dry		**Rainy**		**Dry**		**Rainy**		**Dry**		**Rainy**	
	S	**Exp(*H′*)**	***S***	**Exp(*H′*)**	***S***	**Exp(*H′*)**	***S***	**Exp(*H′*)**	***S***	**Exp(*H′*)**	***S***	**Exp(*H′*)**
1	13	14.88	38	40.44	*33*	22.20	54	*36.95*	*32*	24.53	77	*29.96*
2	11	*16.44*	43	22.19	*15*	*30.26*	*66*	44.70	*44*	*60.34*	83	33.11
3	*15*	8.17	41	*47.94*	18	*7.84*	49	*81.45*	42	29.96	*70*	*99.48*
4	*9*	*5.47*	*36*	*11.02*	16	22.20	*51*	66.68	33	14.88	*84*	46.52
5	13	7.39	*49*	32.45	20	18.17	53	68.72	38	*17.63*	73	47.94
Total	26	18.17	90	49.40	40	33.12	126	66.7	53	40.44	157	109.94

Associated to *Q. crassifolia* in three forest types (*Quercus*, *Quercus-Pinus*, *Abies-Quercus*) at the Parque Nacional el Chico, Hidalgo, during dry (February 2005) and rainy (August 2005) seasons. Italicized data indicated the values of the maximum and minimum diversity index and species richness per season.

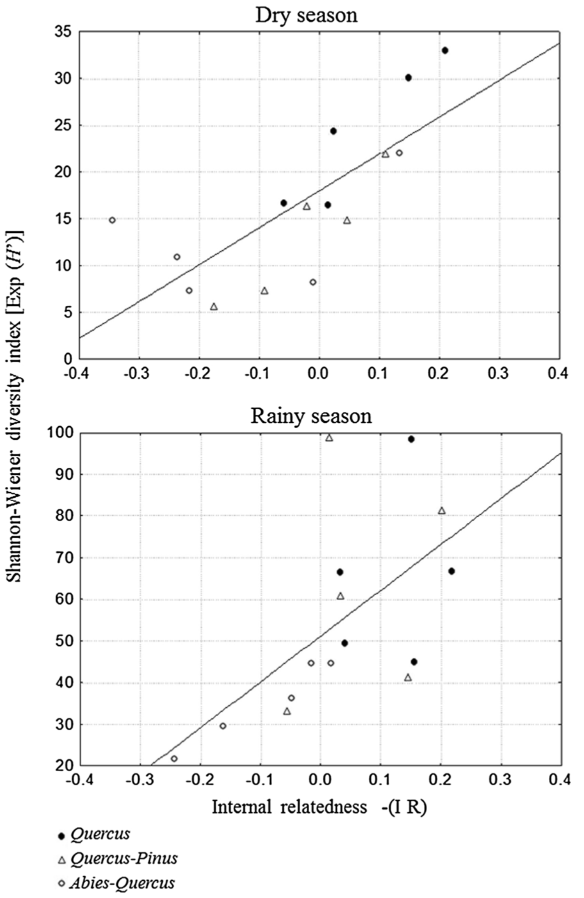

Figure 3 Correlation analyses and canopy arthropod diversity. Correlation analyses between individual genetic diversity of host plant (IR) (*Q. crassifolia*) in dry season and rainy season, and canopy arthropod diversity (Shannon-Wiener diversity index) obtained with nSSRs. $P < 0.01$.

Pinus > *Quercus.* This pattern is consistent with a gradient of tree species among forest types: *Abies-Quercus* ($n = 16$) > *Quercus-Pinus* ($n = 11$) > *Quercus* ($n = 7$), supporting once more the 'associational susceptibility' hypothesis.

In habitats such as temperate forests, tree communities are a key element for shaping the environmental physical structure. For this reason, it has been suggested that tree species richness could influence an increase in richness and abundance of canopy arthropod fauna (Lassau et al. 2005). The aforementioned pattern is also supported by the results obtained by Castaño-Meneses (2002) who evaluated the spatial distribution of the epiphyte plant *Tillandsia violaceae* inside the PNECh. The author found a major density of *T. violaceae* in *Abies-Quercus* forest. This information supports our field observations, where the epiphyte *T. violaceae* increases its density in the following gradient: *Abies-Quercus* > *Quercus-Pinus* > *Quercus*. Therefore, we propose that an increase in epiphyte abundance favors a greater heterogeneity of resources and conditions in the canopy of *Q. crassifolia*. Therefore, habitat heterogeneity predicts that structurally more complex habitats can offer a wider array of resources and conditions, which will favor more species diversity in the communities (Affeld 2008). Hence, we propose that the gradient observed for canopy arthropods associated to *Q. crassifolia* is a response to habitat heterogeneity, motivated by the richness of tree species, heterospecific neighbors (associational susceptibility, White and Whitham 2000) and epiphyte density among forest types.

Density, *S*, and *H´* values of arthropods in the different forest types were higher during rainy season. These results are similar to those reported for other temperate forests in Mexico (Tovar-Sánchez et al. 2003; Tovar-Sánchez and Oyama 2006a, b; Tovar-Sánchez 2009). It has been proposed that this pattern may be the result of an increase in resource availability during rainy season, which is in accordance with this season major productivity of forest ecosystems (Barbosa et al. 2000).

In general, associated arthropod communities to different oak species are composed mainly of generalist species. Although these communities appear to be generalists, it has been documented that the taxonomic status of host-trees may be an important factor in the arthropod community structure (Tovar-Sánchez et al. 2003, Tovar-Sánchez and Oyama 2006a). In particular, special attention has been paid to gall forming (Cynipidae: Hymenoptera) and leaf mining insects (Lepidoptera: Tischeridae, Citheraniidae). Oak gall wasps are obligate parasites and are considered as organ-species-specific. Mexico has the greatest richness of oak gall wasps, with approximately 700 species included in 29 genera (Wendel 1960). Studies of the Cynipidae family in hybrid zones of *Quercus crassipes* × *Q. crassifolia* complex have shown that gall wasps are highly sensitive to host plant genetic diversity levels (Tovar-Sánchez and Oyama 2006b). Valuable insights into these processes can be gained through the investigation of distribution, abundance, and diversity of canopy insects in response to genetic diversity.

Effect of host plant genetic relatedness on canopy arthropod community

Our results showed that as the individual genetic relatedness (IR) of *Q. crassifolia* increases, the values of *H´* of the canopy arthropod communities also increases, independent of the forest type or season. In particular, during dry season, the IR of *Q. crassifolia* explains 44% of canopy arthropod diversity. Whereas, during rainy season, the IR of *Q. crassifolia* explains 53% of the canopy arthropod diversity. These results are consistent with those reported by Tovar-Sánchez et al. (2013), who found that an increase in *IR* levels of *Q. crassipes* and *Quercus castanea* favors *H*′, *S*, and density of canopy arthropods. Specifically, their results of *IR* vs. *H´* explained from 56% to 73% of the variation for *Q. crassipes* and from 68% to 84% for *Q. castanea*. Likewise, Wimp et al. (2004) found that the cottonwoods genetic diversity (*Populus fremontii* × *Populus angustifolia*) is positively and significantly related to the diversity (*H´*) of their endophagous insect community, explaining about 60% of the variability in the community. Similarly, Tovar-Sánchez and Oyama (2006b) reported that the oak genetic diversity (*Quercus crassipes* × *Q. crassifolia*) explained about 78% of the diversity (*H´*) of their endophagous insect community. However, in both studies, genetic diversity was measured at the population level. The results obtained by these studies show that canopy arthropod communities respond to the genetic diversity of host plant, independent of the biological organization level where it is measured.

In this study, we evaluated the genetic relatedness of the host plant in different forest types in one locality, this experimental design allowed us to control variables that have been documented as factors that modify the arthropod community structure. For example, forest age (Marquis et al. 2000), altitude (Summerville et al. 2003), soil type (Gering et al. 2003), climate (Price et al. 2004), and disturbances (Tovar-Sánchez et al. 2003) and spatial location (Tack et al. 2010) are among others.

Host plant genetic relatedness not only has a direct impact on their herbivore community, because its effects can be extended to higher trophic levels indirectly, by promoting a cascade effect throughout the community (Whitham et al. 2006). For example, an increase in host plant genetic diversity can promote an augment in their architectural complexity and nutritional quality (Bangert et al. 2005). This may favor herbivore density, predation intensity, and parasitism degree (Whitham et al. 2006).

These studies have suggested that the areas with more genetically diverse host plant species can be considered as centers of species diversity (Tovar-Sánchez and Oyama 2006a), areas of great ecological and evolutionary activity, providing new habitats for associated communities.

Conclusions

Recently, a genetic approach has revealed that the influence of genetic diversity in foundation species extends to the community and ecosystem levels. Our results demonstrate that the forest type and genetic relatedness of host plants have a significant effect on the canopy arthropod community structure. Interestingly, genetic diversity effect is presented in a consistent manner, regardless of forest type and season. It is now important to demonstrate these effects in other foundation species and in other spatial scales to understand their generality.

From a conservation perspective, maintaining genetic diversity of host plants and arboreal plant communities richer in species is crucial for the preservation of associated arthropod species. Also, it is a priority to assign a new conservation status to foundation species and propose strategies to safeguard mechanism to maintain their diversity. This serves as a guide for future conservation efforts and provides a mechanism of why conservation efforts may fail if they do not consider the community consequences of genetic variation in foundation species, because their extended phenotypes affect the rest of the community. Because oaks represent dominant trees in Mexican temperate forests, these findings may be important locally and at a landscape level. The development of a community genetic perspective should help us to understand the natural world, its complex interactions, and the effects of anthropogenic change.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

All authors participated in the review topic design, in the data analyses, and in the manuscript writing. T-SE: participated in experimental design, field work, data analyses and in the manuscript writing. M-FE: participated in field work and in arthropod determination. V-CL: participated in the manuscript writing and statistical analysis. M-GP: participated in the manuscript writing and statistical analysis. All authors read and approved the final version of the manuscript.

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Author details

[1]Departamento de Sistemática y Evolución, Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Av. Universidad 1001, Col. Chamilpa, Morelos, Cuernavaca CP 62209, Mexico. [2]Laboratorio de Investigaciones Ambientales, Centro de Investigación en Biotecnología, Universidad Autónoma del Estado de Morelos, Av. Universidad 1001, Col. Chamilpa, Morelos, Cuernavaca CP 62209, Mexico.

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