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Effect of host-plant genetic diversity on oak canopy arthropod community structure in central Mexico

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Abstract

Background: Recently it has been proposed that the genetic diversity of foundation species influences the structure and function of the community by creating locally stable conditions for other species and modulating ecosystem dynamics. Oak species are an ideal system to test this hypothesis because many of them have a wide geographical distribution, and they are dominant elements of the forest canopy. In this study we explored the response of canopy arthropod community structure (diversity and biomass) to the level of genetic diversity of *Quercus crassipes* and *Q. rugosa*, two important canopy species. Also, we examined the effect of oak species and locality on some community structure parameters (diversity, biomass, rare species, and richness of arthropod fauna) of canopy arthropods. In total, 160 canopies were fogged in four localities at the Mexican Valley (ten trees per species per locality per season).

Results: *Q. crassipes* registered the highest number of rare species, diversity index, biomass, and richness in comparison with *Q. rugosa*. We found a positive and significant relationship between genetic diversity parameters and canopy arthropod diversity. However, canopy arthropod biomass registered an inverse pattern. Our results support the hypothesis that the genetic diversity of the host-plant species influences the assemblage of the canopy arthropod community.

Conclusions: The pattern found in our study provides a powerful tool when trying to predict the effects of the genetic diversity of the host-plant species on different community structure parameters, which permits assignment of a new conservation status to foundation species based on their genetic diversity.

Keywords: Arthropods community; Canopy; Foundation species; Genetic diversity; *Quercus*

Background

In the last decade, various studies have documented that genes can have an extended effect beyond the individual, leading to interactions with other species to produce community and ecosystem phenotypes (genetic diversity of foundation species, Whitham et al. 2006). Foundation species have been defined as 'species that structure a community by creating locally stable conditions for other species and by modulating and stabilizing fundamental ecosystem process' (Dayton 1972). This emphasis

on foundation species, which are a small subset of the total species in an ecosystem, is because different studies have showed that the analysis of their genetic attributes can reveal strong and predictable effects on communities and ecosystems (Whitham et al. 2003, 2006). For example, studies in cottonwoods (Wimp et al. 2004), eucalyptus (Dungey et al. 2000), oaks (Tovar-Sánchez and Oyama 2006a,b), and willows (Hochwender and Fritz 2004) have evidenced that plant genetics can influence the associations and interactions of the communities associated with these species. The associated communities that have showed a response to the genetic differences within foundation species included taxa as diverse such as soil microbes (Schweitzer et al. 2008),

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aquatic invertebrates (Le Roy et al. 2006), mycorrhizal fungi (Stultz et al. 2009), understory plants (Adams et al. 2011), lichens (Lamit et al. 2011), and foliar arthropods (Wimp et al. 2004; Tovar-Sánchez and Oyama 2006b; Tovar-Sánchez et al. 2013). Likewise, ecosystem processes like nutrient cycling (Schweitzer et al. 2008), primary production (Crutsinger et al. 2006), and ecosystem stability (Keith et al. 2010) are affected by the genetics of foundation species.

Most of the evidence that indicates that the genetic diversity within the foundation species of terrestrial and aquatic habitats affecting the distributions of their associated species come from studies under experimental conditions (e.g., Wimp et al. 2007; Keith et al. 2010; Bangert et al. 2012). Nevertheless, it has been suggested that these studies do not show the potential consequences of different levels of genetic diversity in natural settings (Hughes et al. 2008) and may overestimate the importance of host-plant genetic attributes for structuring the communities (Tack et al. 2010, 2011). However, there are several studies in which the results obtained in experimental gardens have been corroborated in natural conditions [e.g., eucalyptus (Whitham et al. 1999; Dungey et al. 2000), and willows (Wimp et al. 2004, 2005)]. These results suggest that a genetic perspective of the community may be applicable, but there is still little understanding about the relative importance of a genetically-based trait variation within the foundation species and other factors for structuring communities in natural conditions (Wimp et al. 2007). These kinds of studies are valuable because they offer a realistic approach to processes that occur under natural conditions and the ability to span relatively large spatial or temporal scales, even when it is difficult to control variables related to the spatial location of host plants that can influence the abundance, distribution, and diversity of the species associated (Vellend and Geber 2005).

In general, both in natural and experimental conditions, the genetic diversity of the host plant has been analyzed under the assumption of the following gradient of genetic diversity [parental < F1 < backcrosses (Whitham et al. 1994; Wimp et al. 2005, 2007; Tovar-Sánchez and Oyama 2006b; Adams et al. 2011)] or considering that genetic diversity increases when more than one genotype is present (Bailey et al. 2006). In contrast, few studies have evaluated the relationship between some measures of host-plant genetic diversity on community metrics (Wimp et al. 2004; Tovar-Sánchez and Oyama 2006b; Tovar-Sánchez et al. 2013).

Canopy arthropod communities have been widely used to evaluate the influence of the genetic diversity of host plants on their associated communities (Whitham et al. 1999; Hochwender and Fritz 2004; Wimp et al. 2004, 2007; Bangert et al. 2006; Tovar-Sánchez and Oyama

2006b; Keith et al. 2010; Tack et al. 2010; Castagnyrol et al. 2012; Tovar-Sánchez et al. 2013). This preference is probably because the canopy is a habitat that can be physically delimited as their arthropod communities are considered the main component in terms of abundance and species diversity (Stork and Hammond 1997). Recently made estimates suggest that the global average richness of this group is of 6.1 million species (Hamilton et al. 2013). Additionally, arthropods play an important role in ecological terms, acting as pollinators, prey, parasites, parasitoids, herbivores, and detritivores (McIntyre et al. 2001).

The effects of the foundation species' genetic characteristics on the arthropod community structure have been detected in metrics as a composition (Bangert et al. 2005; Wimp et al. 2005; Bailey et al. 2006), richness (Dungey et al. 2000; Bangert et al. 2005, 2006, 2008; Crawford and Rudgers 2013) and species diversity (Wimp et al. 2004; Tovar-Sánchez and Oyama 2006b; Ferrier et al. 2012; Tovar-Sánchez et al. 2013). In general, the studies have reported that unique arthropod communities were associated with different genotypes of the host plant (Bangert et al. 2006; Ferrier et al. 2012) and that the richness and species diversity increases as the genotype number also increases [e.g., genotypic diversity (Wimp et al. 2005; Ferrier et al. 2012)] when the genetic diversity of the population increases (Wimp et al. 2004; Tovar-Sánchez and Oyama 2006b; Tovar-Sánchez et al. 2013), or when the individual genetic diversity level increases (Tovar-Sánchez et al. 2013). These patterns have been explained considering that an increase in the host-plant genetic diversity can generate changes in their morphological (Lambert et al. 1995; González-Rodríguez et al. 2004; Tovar-Sánchez and Oyama 2004), phenological (Hunter et al. 1997), and plant architecture (Martinsen and Whitham 1994; Whitham et al. 1999; Bangert et al. 2005), as well as in their secondary chemistry (Fritz 1999; Wimp et al. 2004). These characters constitute a wide array of resources and conditions that can be exploited by their associated herbivores. These results suggest that the effects of genetic diversity on community function can be equal or greater in magnitude compared to species diversity (Hughes et al. 2008), emphasizing the important role that genetic diversity can play in ecological processes. The incorporation of these types of studies into the field of biodiversity research is a logical extension of the theory underlying previous diversity studies, recognizing that genetic diversity is one of the fundamental levels of biodiversity (Hughes et al. 2008).

Knowledge of mechanisms that may be driving the associations between arthropods and plants plays a key role in our understanding of the impact of plant genetic diversity on dependent arthropod communities; however, these mechanisms remain poorly understood

(Wimp et al. 2007). It has been suggested that phenotypic traits that affect arthropod communities as phenology, physical defenses, and foliar chemistry are features that have a genetic basis (Johnson and Agrawal 2005; Bangert et al. 2006) but have only rarely been linked to both plant genetics and arthropod community structure (Wimp et al. 2007). Also, these attributes can vary between host-plant species (Foss and Rieske 2003; Forkner et al. 2004; Marquis and Lill 2010), affecting both the quantity and quality of resources available to arthropods (Murakami et al. 2007). Understanding the strength of these associations is important as they provide a mechanistic approach to comprehend the relationship between plant genetic diversity, environment, and arthropod community structure.

Oaks (Fagaceae, *Quercus*) are an ideal system to study the effects of host-plant species genetic diversity on their associated canopy communities because of their high levels of genetic variation (e.g., Tovar-Sánchez et al. 2008; Valencia-Cuevas et al. 2014, 2015); many of their species show a wide geographical distribution and canopy dominance (Valencia 2004), and constitute the habitat of different species. Therefore, some of them can be considered as foundation species. Unfortunately, there are a few studies that have analyzed the influence of the oak host genetic diversity on their canopy arthropods community. In addition, the results of these studies have been contrasting. For example Tovar-Sánchez and Oyama (2006b), reported a positive and significant relationship between population genetic diversity of seven hybrid zones from the *Q. crassipes* × *Q. crassifolia* complex in Mexico and the canopy endophagous insect community diversity. Similarly, the *Q. castanea* and *Q. crassipes* plants that were genetically more diverse supported higher richness, diversity, and species density of the canopy ectophagous insects (Tovar-Sánchez et al. 2013) in central Mexico. In contrast, Tack et al. (2010, 2011) found that genetic diversity has little influence on the endophagous insect community associated to *Q. robur* in Finland. Similar results were reported by Castagneyrol et al. (2012), who found that the host-plant genetic attributes (genetic diversity, relatedness, and genetic identity) did not have a significant effect on the phytophagous insect community structure (endophagous and ectophagous) associated to *Q. robur* canopy in France. The contrasting results of these investigations show the need for further studies that help us understand the importance of the genetic diversity of oak populations on canopy arthropod communities.

The aims of this study were to analyze the canopy arthropod community structure of *Quercus crassipes* and *Q. rugosa* from a genetic perspective, to answer the following questions: 1) Does the genetic diversity of host-plant species affect the arthropod community structure in terms of species diversity and biomass? 2) Does

the canopy arthropod-community structure vary between oak host species and localities? We predict that more genetically diverse host plants should support more diverse communities because they offer a wider array of resources and conditions to be exploited.

Methods

Study sites and oak species

The Mexican Valley has a well delimited biogeographical area of 7500 km² covering several states of Central Mexico surrounded by the main Mexican Sierras. Altitude ranges from 2,230 m to 2,500 m at the bottom and 3000 m to 5450 m in mountain areas. The most important vegetation types in the Mexican Valley are *Abies*, *Pinus* and *Quercus* forests (Rzedowski and Rzedowski 2001). To minimize geological historic and environmental site effects, we chose four localities [Parque Nacional El Chico (PNECh) in Hidalgo State, Parque Ecológico de la Ciudad de México (PECM) in Mexico City, and Jilotepec and Juchitepec in Mexico State] (Figure 1) that have the following common traits: it has the same geological history [the Mexican Valley is part of the Trans-Mexican Volcanic Belt (Rzedowski and Rzedowski 2001), and its formation process began during the Quaternary-Pliocene (Ferrusquia-Villafranca 1998)], weather (temperate subhumid), altitude (between 2540 m to 2720 m), vegetation type (mature oak), tree age (between 10 m to 13 m), and soil type (volcanic origin or derived from igneous and sedimentary rocks). These areas present almost no local disturbance inside the forest because they are under protection standards or because its rocky substrate prevents agriculture and livestock (Table 1).

Quercus crassipes Humb. & Bonpl. (*Lobatae*) and *Q. rugosa* Née (*Quercus*) are abundant species in the four study sites. Both can be recognized easily in the field from its leaf characteristics such as shape, size, coloration, and pubescence. *Q. crassipes* include trees up to 17 m tall and 1 m in trunk diameter. Leaves are deciduous, coriaceous, narrowly elliptic, and lanceolate. It flowers in May and bears fruits from September to January. It is distributed within the southeast part of the Sierra Madre Oriental and the Trans-Mexican Volcanic Belt (TVB), between 1900 m to 3500 m a.s.l. *Q. rugosa* includes large trees of up to 20 m in height with a trunk diameter of 1 m. Leaves are evergreen or semi-deciduous at maturity; they are thick and rigid, strongly rugose, and obovate to elliptic-obovate. The flowering season is in August. Fruits are produced annually (November to March). This species is distributed in the major Mexican mountain ranges [SMOr, Sierra Madre Occidental (SMOc), Sierra Madre del Sur (SMS), Sierra Norte de Oaxaca (SNO), Sierra de Chiapas (SCH), and TVB], at an altitude of 1800 m to 2900 m (Rangel et al. 2002).

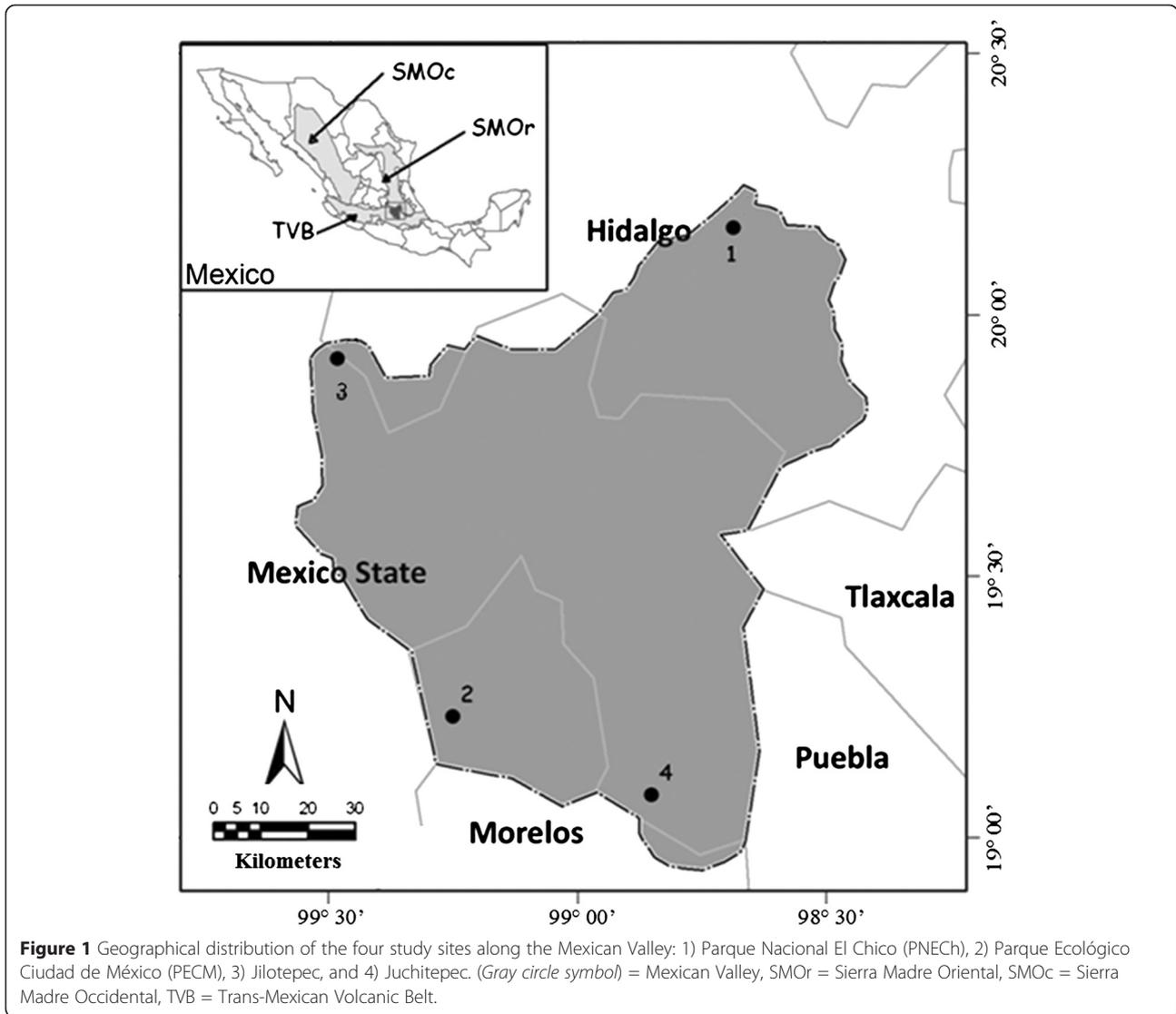


Figure 1 Geographical distribution of the four study sites along the Mexican Valley: 1) Parque Nacional El Chico (PNECh), 2) Parque Ecológico Ciudad de México (PECM), 3) Jilotepec, and 4) Juchitepec. (Gray circle symbol) = Mexican Valley, SMOr = Sierra Madre Oriental, SMOc = Sierra Madre Occidental, TVB = Trans-Mexican Volcanic Belt.

Molecular data

Leaves with no apparent damage were collected from twenty individuals per species in each study site [*Q. crassipes* (*n* = 80) and *Q. rugosa* (*n* = 80)]. Leaf tissue was frozen in liquid nitrogen and transported to the laboratory for DNA extraction. Total DNA was extracted and

purified by using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA). DNA quantification was done by fluorometric analysis, 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 randomly amplified

Table 1 Locality name, state, geographic coordinates, altitude, annual precipitation, slope, and *Quercus* species

Locality	State	Latitude (N), longitude (W)	Altitude (m)	Annual precipitation (mm)	Slope (°)	<i>Quercus</i> species
PNECh	Hidalgo	20°10', 98°41'	2540	1,200.2	14	<i>Q. crassipes</i> , <i>Q. rugosa</i> , <i>Q. mexicana</i> , <i>Q. laurina</i> , <i>Q. crassifolia</i> , <i>Q. deserticola</i> , and <i>Q. greggii</i> .
PECM	Mexico City	19°15', 99°11'	2620	1,084.9	11	<i>Q. crassipes</i> , <i>Q. rugosa</i> , <i>Q. castanea</i> , <i>Q. laeta</i> , and <i>Q. laurina</i> .
Jilotepec	Mexico State	19°55', 99°29'	2570	754.3	8	<i>Q. crassipes</i> , <i>Q. rugosa</i> , <i>Q. laeta</i> , and <i>Q. crassifolia</i>
Juchitepec	Mexico State	19°05', 98°51'	2720	729.9	9	<i>Q. crassipes</i> , <i>Q. rugosa</i> , and <i>Q. greggii</i> .

polymorphic DNA (RAPDs) and microsatellite markers (SSRs).

For RAPDs, sixty 10-base pair (pb) primers of random sequence (Kits A, B, C; Operon Technologies, Alameda, California, USA) were tested. Eighteen of them were selected based on the amplification results and reproducibility. The selected primers produced a total of 121 polymorphic bands. PCR reactions were done in a PTC-100 Programmable Thermal Controller (MJ Research Inc.) as follows: 10 ng of DNA template, 50 mM KCl, 10 mM Tris-HCl (pH 8.4), 2 mM MgCl₂, 0.1 mM of each dNTP, 0.2 mM of each primer, and 1 U of *Taq* polymerase in a final volume of 25 µl. Reaction conditions were the following: an initial 2 min denaturation step at 94°C, followed by 45 cycles at 94°C for 1 min, 1 min at 36°C, followed by an annealing temperature at 72°C for 30 s and a final extension at 72°C for 7 min. DNA fragments were separated through electrophoresis on agarose gels at 2.8%, stained with ethidium bromide, and developed on an UV light table. The molecular weight of the DNA fragments was estimated by comparison with a 1 kb DNA ladder.

Microsatellites primers (Ccmp3, Ccmp4, and Ccmp41) were obtained from Weising and Gardner (1999). PCR reactions were done as follows: 15 ng of DNA template, 50 mM KCl, 20 mM Tris-HCl (pH 8.4), 2 mM MgCl₂, 0.13 mM of each dNTP, 25 mM of each primer, and 0.8 U of *Taq* polymerase in a final volume of 25 µl. Reaction conditions were 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 at 72°C for 8 min. Annealing temperature differed for each primer pair. 50°C for Ccmp3, 48°C for Ccmp4, and 55°C for Ccmp41. PCR products were resolved on polyacrilamide gels at 6% (7 M urea) at 60 W for 3 h in order to determine the polymorphic primers. We measured the length of the amplified microsatellites fragments by running an aliquot of each PCR product on an automatic sequencer ABI 3100 (Applied Biosystems CA, USA) at 35 W for 80 min to 90 min using gene scan ROX-2500 (Applied Biosystems, CA, USA) as size standard. Alleles were scored using the Gene Mapper ver. 3.7 Software (Applied Biosystems, CA, USA).

Canopy arthropod communities

The arthropod community structure was surveyed in forty trees of both species. Ten individuals per species were vouchered and fogged during rainy (August 2005) and dry (February 2005) seasons on each locality. Sampling was done seasonally, which allowed having a representative annual sample of the canopy arthropodofauna, as suggested by previous studies, which have demonstrated that seasonality modifies both composition and

richness in oaks (Tovar-Sánchez and Oyama 2006a; Tovar-Sánchez 2009). The individual trees sampled in this study had a height between 10 m and 13 m (mean ± d.e., 11.0 ± 0.13 m).

Arthropods were collected by fogging the entire canopy of a single tree with 750 ml of non-persistent insecticide (AqualPy, AgrEvo, Mexico). This insecticide is composed of 30 g pyrethrin/l and 150 g piperonyl-butoxide/lL at a concentration of 30% v/v. Fallen arthropods from each fogged tree were collected in ten plastic trays (each 0.32 m² area) located randomly under the crowns. Canopies of trees selected for fogging were isolated from other trees as far as possible, by avoiding overlapping. A measure of the exploited canopy volume was estimated by multiplying the difference between the total height and the height to the lowest branch with denser leaf cover of each tree by 3.2, which is the area of collecting trays (Tovar-Sánchez 2009). The arthropods were separated into morphospecies and after sorted to major orders. All samples were sent to arthropod specialists for taxonomic identification. Abundance of each morphospecies was also counted.

The biomass of canopy arthropods associated to *Q. crassipes* and *Q. rugosa* was calculated using the model proposed by Tovar-Sánchez (2009) for oaks in the Mexican Valley. A sample of six individuals/taxa was chosen and then put in a drier at 40°C until constant weight. Weight was determined on an analytical scale.

Statistical analysis

Genetic diversity of oak host species

Genetic diversity of *Q. crassipes* and *Q. rugosa* was estimated for SSRs and RAPDs molecular markers as the average expected heterozygosity (*He*). We used this parameter of genetic diversity in order to compare the results with others studies in oaks. Genetic data were analyzed with TFPGA v. 1.3 and POPGENE v. 1.31. The data were transformed as \sqrt{x} (Zar 2010), and we used a *t*-student test to examine differences in genetic diversity between species. A Kruskal-Wallis analysis of variance was used to determine differences in oak-species genetic diversity among sites. Thereafter, a Tukey test was conducted to determine significant differences (Zar 2010). Statistical analyses were conducted using STATISTICA for Windows v. 8.0 software (StatSoft 2007).

Canopy arthropods

The diversity of the canopy arthropod community was estimated at the morphospecies level by using the Shannon-Wiener index (*H'*). This index was then compared between pairs of localities with a randomization test as described by Solow (1993). This test re-samples 10,000 times from a distribution of species abundances produced by the sum of the two samples. In addition,

rare species number (RS) was analyzed. Rare species were defined as those species represented by fewer than four individuals in the samples (Tovar-Sánchez and Oyama 2006a).

The arthropods biomass (W) was calculated according to Tovar-Sánchez (2009):

$$W = (e^{-10.644}) (L^{2.587})$$

where W is the biomass in mg (dry weight) and L is the body length in millimeters. A mean size and aggregate biomass of the morphospecies population in the sample was estimated from the number of individuals, the mean size of all others measured, and the number of individuals of the same morphospecies. This estimation was calculated for oak canopy arthropod biomass in temperate forests from the Mexican Valley.

Two-Factor Analysis of Variance (Model I fixed effects, Zar, 2010) was conducted to test differences in canopy arthropod biomass, species richness, number of rare species among localities (L), species (S), and interaction $L \times S$. Data were transformed as follows: $X' = \log X + 1$ (Zar 2010). To determine significant differences in species richness, number of rare species, and biomass between localities, a posterior Tukey test was conducted (Zar 2010). Statistical analyses were conducted using STATISTICA for Windows v. 8.0 software (StatSoft 2007).

General Linear Model (GLM) Analysis of Covariance (Model I fixed effects; Zar 2010) was performed to determine the effect of the locality (L), oak species (S), Genetic diversity, and interaction locality \times oak species ($L \times S$) on canopy arthropod biomass and Shannon-Wiener diversity index.

Diversity (H') and biomass (W) variables were not correlated with each other. In order to determine the effects of locality, oak species (*Q. crassipes*, *Q. rugosa*) and host-plant genetic diversity (expected heterozygosity estimated with microsatellite and RAPDs data) on canopy arthropods diversity index (H') and biomass, we performed a GLM. The model used a Poisson error distribution and log link function. GLM describes the effects of variables in a multivariate-model setting. This analysis has the advantages that even if a variable has a non-significant effect on a variable when subjected to univariate analysis, it may still be a significant variable in a multivariate-model setting when accounting for covariance with other factors (Hillebrand et al. 2008). We pooled the following genetic data from 20 trees within each locality: the community was quantified at the stand level and the occurrence of individual SSRs and RAPDs markers present in each locality, resulting in a unique genetic diversity value for each locality. Locality and oak species were considered as categorical fixed factors and genetic diversity a continuous factor. Statistical analyses

were conducted using species diversity and richness version 3.03. and the General Linear Model platform within STATISTICA for Windows v. 8.0 software (StatSoft 2007).

Results

Genetic diversity of *Quercus crassipes* and *Q. rugosa*

Genetic diversity analyses revealed that the expected heterozygosity was significantly higher in *Q. crassipes* than *Q. rugosa* populations [RAPDs ($t = 3.59$, $P < 0.05$); SSRs ($t = 3.45$, $P < 0.05$)] (Table 2). A Kruskal-Wallis analysis of variance showed significant differences in genetic diversity indexes (He) among populations of *Q. crassipes* and among populations of *Q. rugosa* (SSR's: $H = 11.29$, $P = 0.002$; RAPDs: $H = 9.87$, $P = 0.009$). A multiple comparison Tukey test (RAPDs) showed that *Q. rugosa* and *Q. crassipes* present the following He gradient PNECh = PECM > Jilotepec = Juchitepec. While SSRs registered the next He pattern *Q. rugosa*: PNECh > PECM > Jilotepec = Juchitepec, and *Q. crassipes*: PNECh < PECM > Jilotepec > Juchitepec.

Arthropods composition (abundance)

Canopy arthropod communities were represent by a total of 44,627 arthropods included in 614 morphospecies belonging to the following 24 orders: Araneae, Astigmata, Coleoptera, Cryptostigmata, Dermaptera, Diptera, Entomobryomorpha, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Mecoptera, Mesostigmata, Neuroptera, Opilionida, Oribatida, Orthoptera, Poduromorpha, Pseudoscorpiones, Psocoptera, Prostigmata, Symphypleona, Thysanoptera, and Trichoptera (nomenclature based on Evans 1992;

Table 2 Genetic diversity parameters for three chloroplast microsatellite loci and 18 RAPD loci, in *Quercus crassipes* and *Q. rugosa* populations

Population	N	Average expected heterozygosity	
		RAPDs	SSRs
<i>Q. crassipes</i>			
PNECh	20	0.43	0.51
PECM	20	0.46	0.58
Jilotepec	20	0.30	0.32
Juchitepec	20	0.28	0.26
Average	20	0.37 (0.03)*	0.42 (0.02)*
<i>Q. rugosa</i>			
PNECh	20	0.33	0.40
PECM	20	0.32	0.35
Jilotepec	20	0.25	0.21
Juchitepec	20	0.23	0.20
Average	20	0.28 (0.02)*	0.48 (0.07)*

Numbers in parenthesis are standard error. *Significant differences ($P < 0.05$) (t- student test).

N, sample size; (standard errors).

Hopkin 1997; Deharveng 2004; Triplehorn and Johnson 2005).

Community structure of canopy arthropods associated to *Q. crassipes* and *Q. rugosa*

Shannon-Wiener diversity (H'), species richness (S), number of rare species (RS), and biomass (W) total values were significantly different ($P < 0.05$) between *Q. crassipes* ($H' = 5.2$, $S = 569$, $RS = 575$, $W = 560.20$) and *Q. rugosa* ($H' = 4.4$, $S = 450$, $RS = 438$, $W = 313.25$). In addition, in all localities these parameters were higher in *Q. crassipes* than in *Q. rugosa* ($P < 0.05$) (Table 3). PNECh and Juchitepec consistently showed significant differences for H' , S , RS , and W values in both oak species. In contrast, PECM and Jilotepec had similar values, excepting H' in *Q. crassipes*, and RS for both oak species (Table 3). For *Q. crassipes* and *Q. rugosa*, the Shannon-Wiener diversity index (H') differed significantly between localities ($P < 0.05$), except from PECM and Juchitepec for *Q. rugosa*. However, some oak host individuals presented the same diversity values within and among localities for both species. In general, a statistically significant effect of the locality ($F_{3,152} = 8.151$, $P < 0.001$), the species ($F_{1,152} = 23.902$, $P < 0.001$) and interaction $L \times S$ ($F_{2,152} = 3.205$, $P < 0.001$) was detected on rare species. *Q. crassipes* had more number of rare species (less than four individuals) than *Q. rugosa*. Between localities, PNECh showed the highest number of rare species, followed by PECM, Jilotepec, and Juchitepec (Figure 2). Similar results were registered in arthropod species richness, a statistically significant effect of locality ($F_{3,152} = 16.023$, d.f. = 3, $P < 0.001$), species ($F_{1,152} = 32.007$, $P < 0.001$), and interaction $L \times S$

Table 3 Shannon-Wiener diversity index (H'), species richness (S), rare species (RS) and coefficient of variation (CV) of S and RS (in parentheses); and biomass (W) mg DW/m² (standard error in parentheses) of canopy arthropods associated to *Quercus crassipes* and *Q. rugosa* in four localities in the Mexican Valley

Locality	H'	S (CV)	RS (CV)	W
<i>Q. crassipes</i>				
PNECh	5.0 ^A	224 (10.11) ^a	173 (10.20) ^a	427.63 (0.042) ^a
PECM	4.4 ^B	202 (6.17) ^a	165 (7.39) ^a	338.15 (0.054) ^{ab}
Jilotepec	3.8 ^C	183 (9.43) ^a	124 (12.48) ^b	490.29 (0.020) ^b
Juchitepec	3.0 ^D	162 (6.57) ^b	113 (12.26) ^c	984.75 (0.040) ^c
<i>Q. rugosa</i>				
PNECh	4.6 ^A	165 (8.71) ^a	127 (8.38) ^a	200.92 (0.053) ^a
PECM	4.0 ^B	158 (6.09) ^{ab}	119 (9.86) ^b	282.89 (0.027) ^b
Jilotepec	3.5 ^B	153 (5.05) ^b	105 (12.68) ^c	354.19 (0.042) ^{bc}
Juchitepec	2.7 ^C	117 (9.43) ^c	87 (13.36) ^c	415.61 (0.027) ^c

Same letters show that the mean values for each locality did not differ at $\alpha = 0.05$ (capital letters = Solow test; lower case letters = Tukey's test).

($F_{2,152} = 3.283$, $P < 0.05$) was detected. For arthropod biomass, a statistically significant effect of the locality ($F_{3,152} = 12.952$, $P < 0.001$), the species ($F_{1,152} = 30.741$, $P < 0.001$), and interaction $L \times S$ ($F_{2,152} = 9.708$, $P < 0.001$) was registered.

Effect of genetic diversity of oak host species on canopy arthropod community

In general, the diversity (H') and biomass of canopy arthropod species differ significantly among localities, oak species and genetic diversity (He). Also, the interaction locality \times oak species was significant, independently of molecular marker used (SSRs and RAPDs). The only variable that had not a significant effect on canopy arthropod diversity was oak species (S) using both molecular markers, and the interaction locality \times oak species on arthropod biomass (Table 4).

Discussion

The hypothesis that genetic diversity of foundation species affects the community structure of the canopy arthropods was supported by our results. Also we found that the arthropod community structure was significantly different between host oak species and localities.

Genetic diversity of *Quercus crassipes* and *Q. rugosa*

In general, our study demonstrates that *Q. crassipes* had higher levels of genetic diversity than *Q. rugosa*. These high genetic diversity levels in *Q. crassipes* may be due to incipient reproductive barriers, which facilitate inter-specific crosses with closely related species. For example, Valencia (1994) proposed that a group of oaks conformed by *Q. affinis*, *Q. crassipes*, *Q. crassifolia*, *Q. laurina*, *Q. mexicana*, and *Q. rubramenta* may experience genetic exchange when they occur in sympatric/mixed stands. This last scenario has been corroborated by Tovar-Sánchez and Oyama (2004) for the *Q. crassipes* \times *Q. crassifolia* complex, González-Rodríguez et al. (2004) for the *Q. laurina* \times *Q. affinis* complex, and Valencia-Cuevas et al. (2015) for *Q. castanea*, *Q. laurina*, and *Q. crassifolia*. The species mentioned above are distributed along the Mexican Valley, a fact that may facilitate the genetic exchange with *Q. crassipes*.

Moreover, when the study sites are classified by their number of red oak species, the following pattern is observed PNECh > PECM > Jilotepec > Juchitepec, which is congruent with the genetic diversity pattern for both species (Table 2). Therefore, we suggest a possible relationship between the number of red oak species and their genetic diversity levels. This is supported by the work of Valencia-Cuevas et al. (2014), who reported an increase on the levels of *Q. castanea* genetic diversity as the local richness of the red oak community also increases.

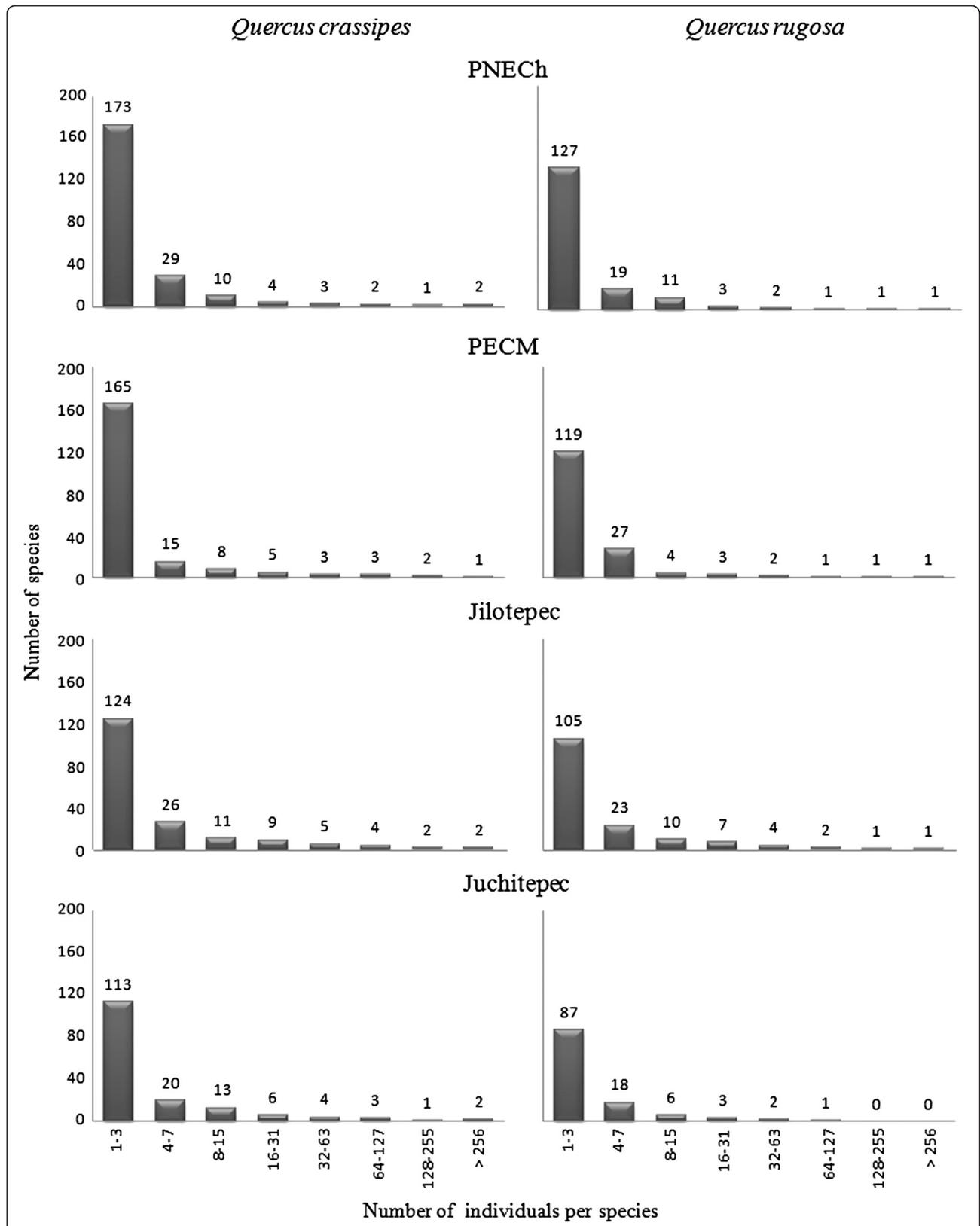


Figure 2 The number of all species per abundance class in fogging collections for *Quercus crassipes* and *Q. rugosa* in four localities in the Mexican Valley [Parque Nacional El Chico (PNECh), Parque Ecológico Ciudad de México (PECM), Jilotepec, and Juchitepec].

Table 4 Results from the General Linear Model (GLM Analysis of Covariance) testing the effects of locality (PNECh, PECM, Jilotepec, and Juchitepec), oak species (*Quercus crassipes* and *Q. rugosa*), host-plant genetic diversity (expected heterozygosity, estimated with microsatellites and RAPDs data), and the interaction L × S on canopy arthropod diversity and biomass

	Arthropod community responses							
	Shannon-Wiener diversity				Biomass			
	df	MS	F	P	df	MS	F	P
	Microsatellites							
Locality (L)	3	1.86	23.17	<0.000	3	0.46	29.01	<0.000
Oak species (S)	1	0.10	1.23	0.271	1	0.96	59.58	<0.000
Genetic diversity	1	4.50	56.18	<0.000	1	0.44	27.59	<0.000
L × S	2	1.23	15.36	<0.000	2	0.04	2.56	0.084
Residual	72	0.08			72	0.02		
	RAPDs							
Locality (L)	3	0.71	8.31	<0.000	3	0.28	17.32	<0.000
Oak species (S)	1	0.13	1.48	0.227	1	0.87	54.49	<0.000
Genetic diversity	1	9.42	109.82	<0.000	1	0.85	52.74	<0.000
L × S	2	0.73	8.53	<0.000	2	0.16	10.08	<0.000
Residual	72	0.09			72	0.02		

Particularly, the hybridization phenomenon has been documented between *Q. crassipes* and *Q. crassifolia* in Jilotepec (Tovar-Sánchez and Oyama 2006a), and possible hybrids have been observed in PNECh between *Q. crassipes* and *Q. crassifolia* (S. Valencia, Science Faculty Herbarium, Universidad Nacional Autónoma de México). In addition, there is evidence that *Q. rugosa* hybridizes with *Q. glabrescens* at the PNECh (Núñez-Castillo et al. 2011). The above statements support that *Q. crassipes* and *Q. rugosa* presents higher genetic diversity levels at the PNECh as a result of interspecific hybridization, since genetic combinations produced by introgression exceeds the possible combinations resulting from mutational processes (Anderson 1949). This may increase the genetic diversity levels.

Effect of genetic diversity of oak host species on canopy arthropod community

We found a significant effect of the host genetic diversity on parameters of arthropod community structure [Shannon-Wiener diversity (H') and biomass (W)]. These results are consistent with those reported by Wimp et al. (2004), who found that the cottonwood's genetic diversity (heterozygosity) (*Populus fremontii* × *P. angustifolia*) has a significant influence on the diversity (H') of their associated gall-forming insects, explaining about 60% of the variability in the community. Similarly, Tovar-Sánchez and Oyama (2006b) reported that the oak genetic diversity (Shannon-Wiener) (*Quercus crassipes* × *Q. crassifolia*) explained about 78% of the diversity (H') of associated gall-forming insects. This could be explained due to the high

level of specialization of gall-forming insects, since they have been considered as species-organ-tissue specific (Stone et al. 2002). This high level of specialization along with their tight relationship with host species may account for their high level of response to host species in comparison to canopy epiphyte insects.

Host-plant genetic diversity not only has direct impact on the associated community of herbivores, yet, its effects can be extended to the following 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 increase in their architectural complexity and nutritional quality (Bailey et al. 2004). This may favor a greater density of herbivores (Bailey et al. 2006), depredation intensity, and parasitism degree (Sarfranz et al. 2008).

Canopy arthropod community structure (H' , S , RS , and W) differed significantly between host species. *Q. crassipes* had the highest values in all the parameters mentioned. This pattern may be explained by the higher dominance and genetic diversity of *Q. crassipes* in all localities. In general, this species dominates oak forests, and its great abundance and genetic diversity may be favoring the availability of resources and conditions, resulting in a more complex arthropod assemblage. These results are supported by several studies that have showed that the increase in genetic variation in plants can generate a large amount of variation in morphological (González-Rodríguez et al. 2004; Tovar-Sánchez and Oyama 2004, López-Caamal et al. 2013), phenological (Hunter et al. 1997), architectural (Bangert et al.

2005), and chemical traits (Fritz 1999). All these features are genetically controlled given that arthropods are sensitive to these host-plant traits; it is not surprising that they would closely track the plant genetic *via* these traits (Bangert et al. 2008). A similar response has been reported in canopy cottonwoods (Wimp et al. 2004), willows (Hochwender and Fritz 2004), and eucalyptus (Dungey et al. 2000).

In general, the canopy arthropod community associated with *Q. crassipes* and *Q. rugosa* was represented by few abundant species and many rare species, which agrees with that reported in other studies (e.g., Tovar-Sánchez 2009). Particularly, the results showed that the canopy of *Q. crassipes* supports a greater number of rare species than *Q. rugosa*. Probably because the first species offers a wider range of resources and conditions as a result of their genetic diversity as already explained. This is supported by the work of Tovar-Sánchez and Oyama (2006a), who reported a greater number of rare species in hybrids of *Q. crassipes* × *Q. crassifolia* complex, where genetic diversity is increased.

These studies have suggested that the areas with more genetically diverse hosts can be considered as centers of diversity and species richness (Tovar-Sánchez and Oyama 2006a), areas of great ecological and evolutionary activity, providing new habitats for associated communities. Our results showed that the arthropod diversity (H') for *Q. crassipes* and *Q. rugosa* presents the following gradient: PNECh > PECM > Jilotepec > Juchitepec. In general, this pattern is consistent with the level of genetic diversity among localities. In addition, this pattern could be related to the number of arboreal species growing in sympatry with *Q. crassipes* and *Q. rugosa* in each locality, a phenomenon that is known as “associational susceptibility” (White and Whitham 2000), in which plant species present greater diversity of herbivores when spatially associated with heterospecific neighbors (White and Whitham 2000).

Implications for conservation

Mexico is one of the centers of diversification of the genus *Quercus* with more than 161 species (Valencia 2004). Oak and pine trees are the dominant species in most of the temperate forests of Mexico and they provide fundamental ecosystem services. In particular, some oak species can be considered foundation species. Unfortunately, deforestation rates are increasing in Mexican forests (≈ 314 thousand ha/year, FAO 2006) with potentially serious implications. From a conservation perspective, this study suggests that the maintenance of the genetic diversity of the host plants is crucial for the preservation of associated species. Also, it is a priority to assign a new conservation status for foundation species and propose strategies to safeguard mechanism to

maintain their genetic diversity. 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). This serves as a guide for future conservation efforts and provides a mechanism for 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.

Conclusions

In order to understand the assembly of natural communities, some factors such as interactions, degree of disturbance, type and quality of resources and environmental conditions have been widely studied. Recently, a genetic approach has revealed that the influence of genetic diversity extends to the community level. In this study, we found a genetic diversity effect of oak host species on canopy arthropod community, regardless of the molecular marker used as well as the host plant species type. Since oaks represent dominant trees in Mexican temperate forest, these findings may be important locally and at a landscape level. The consideration of the genetic diversity of the foundation species can be a general and efficient approach to conserving processes and diverse assemblages in nature. The development of this 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. Also, all authors read and approved the final version of the manuscript.

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