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# Natural Hybridization Between *Quercus crassipes* and *Q. crassifolia* (Fagaceae) Is a Key Process to Ensure the Biodiversity of Their Associated Lichen Community

**Leticia Valencia-Cuevas [1], Jennie Melhado-Carboney [2] and Efraín Tovar-Sánchez [3,*]**

[1] Escuela de Estudios Superiores del Jicarero, Universidad Autónoma del Estado de Morelos, Carretera Galeana-Tequesquitengo s/n, Comunidad El Jicarero, Jojutla 62915, Morelos, Mexico; leti70477@yahoo.com.mx
[2] Maestría en Biología Integrativa de la Biodiversidad y la Conservación, Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Av. Universidad 1001, Col. Chamilpa, Cuernavaca 62209, Morelos, Mexico; dualidadsimbiotica@hotmail.com
[3] Centro de Investigaciones en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Av. Universidad 1001, Col. Chamilpa, Cuernavaca 62209, Morelos, Mexico
* Correspondence: efrain_tovar@uaem.mx

**Abstract:** Lichens are organisms whose dynamics take place on terrestrial substrates such as rock, dead wood, living plants, and soil. Living trees are used for lichens as structural support to access light. However, little is known about how the genetic traits of a host tree influence which lichen species grow on it and, consequently, the community structure of this funga. In this study, we investigated how the genetic diversity GD of host oak taxa (*Quercus crassifolia*, *Q. crassipes* and their putative hybrid: *Q.* × *dysophylla*) influence the community structure of the associated epiphytic lichen community in two hybrid zones (HZs) in Central Mexico. The lichen community was composed of 76 species, 27 genera and 14 families. We found significant differences in lichen composition between genetically distinct individuals and oak taxa in each HZ. Lichen diversity in *Q.* × *dysophylla* was intermediate and significantly different between parents in both HZs. We conclude that genetic differences between host oaks promoted significantly different lichen communities and that hybrids may act as ecological islands, accumulating lichen species from both parental species and their own novel species. Consequently, the conservation of HZs due to their high GD may be a strategy to ensure biodiversity conservation of oak-associated lichen communities.

**Keywords:** epiphytes; interspecific gene flow; temperate forest; red oaks; species diversity

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## 1. Introduction

Identifying the driving factors of community diversity and the ways in which this is maintained are vital topics in ecology. Recently, intraspecific genetic variation in host plants and its consequences for biodiversity [1–4] have provoked the interest of the ecological community. This happens because foundation plants play a crucial role in shaping a community by creating locally stable conditions required by many other species. Also, these species are locally abundant and regionally common and modulate core ecosystem processes such as energy and nutrient fluxes or water balance [5,6]. Some tree species, such as alnus, eucalyptus, oaks, poplars, pines, and willows, have been proposed as foundation species [7–10]. From this perspective, many empirical studies and common gardens have evidenced that intraspecific genetic variation is a major driver of phenotypic

variation, which, in turn, has consequences that extend well beyond the population level in host species [7,11].

Several studies support the influence of the foundation tree genetics on different community attributes (e.g., species diversity, abundance, and composition), in assemblages as diverse as canopy arthropods, epiphytic plants, aquatic invertebrates, and soil microorganisms [7]. Two patterns have been detected: (1) the diversity of associated communities is positively and significantly related to the GD of host tree species [12,13], and (2) genetically more similar hosts support more similar associated communities [14,15]. Furthermore, it has been reported that genetic effects can be stronger than environmental effects in shaping communities [16] and that such effects can extend to the third trophic level and beyond [17].

Oak species (*Quercus*: Fagaceae) 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 [18]. They also constitute the habitat for an important diversity of species, a fact that suggests that some oak species have attributes of foundation species [19]. Moreover, oaks have high genetic variation levels as a result of their life-history characteristics [20] and hybridization events [8,19,21].

Natural hybridization is an important evolutionary process that occurs commonly among oaks [22,23]. This phenomenon is present in localized areas, often in transitional areas between different environments known as hybrid zones. These hybrid zones are unique ecological systems where genetically distinct populations or species meet, interbreed, and produce offspring with new genetic combinations known as hybrids [18]. Therefore, these hybrid zones are places of high ecological and evolutionary activity [18]. Furthermore, there is evidence that shows that hybridization events in trees can have significant effects on the GD levels of enrolled populations [8,19,24]. The high GD of hybrid plants can promote variation in the expression of phenotypic traits in comparison with their parental species [25–27]. Consequently, modifications in genetic, morphological, or chemical traits among genetic categories (hybrids and parental species) can potentially influence the communities of associated species [7]. In fact, several studies have demonstrated the effect of host species genetics on the structure of associated communities within hybrid zones [3,7,28–30]. However, to date, most studies that have evaluated the effect of the genetics of the host plants involved in hybridization events on community structure have emphasized the response of organisms that feed directly on the plant as phytophagous insects. Nevertheless, other groups dwelling directly on trees as lichens have remained relegated.

Lichens play a role in the evolution of terrestrial life, ecosystem function, and the maintenance of biodiversity [31]. These organisms include at least one fungus (mycobiont) and an alga or cyanobacterium (photobiont) living in symbiosis. Lichens colonize bark, rocks, and soil and occur in all terrestrial ecosystems, covering about six percent of the earth's land surface [32]. As epiphytic organisms, lichens depend on the physical and chemical characteristics of their host plants [33], which may be altered in hybrid zones. Genetic variation in host traits can, therefore, influence the lichen community, particularly due to hybrid plants providing novel substrates or microhabitats for lichens, influencing their distribution, abundance, and diversity [33–36]. For example, the importance of genetic variation in physical and chemical bark characteristics as a habitat for lichens has been documented. Research within *Populus angustifolia* revealed that bark roughness, condensed tannins, and bole circumference varied among host tree genotypes. Also, it was documented that bark roughness (a genetically based trait) positively influences the cover of dominant lichen *Xanthomendoza galericulata* [34]. Additionally, it has been documented that genotype variation in the bark texture of *P. angustifolia* drives lichen community

assembly across multiple environments [36]. Similar results were reported by Davies and colleagues [33] on the community composition of epiphytic taxa (23 lichen species, two mosses, and one liverwort) growing associated with different genotypes of *Populus tremula* in two experimental gardens in Scotland.

In the habitats where the oaks are distributed, a variety of lichen communities that grow on them have been observed [37]. Some of these species are host-plant specific, as they find a suitable substrate in oaks and colonize the most suitable part of the tree [38]. However, from what we know, the influence of the genetic characteristics of hybridizing oaks on their lichen communities is still unknown.

Lichens are an excellent model for testing the effects of plant genetics on associated communities for almost three reasons: (1) they are diverse and widespread organisms in temperate forests; (2) lichens are trophically disconnected from their hosts, which may cause lichens to be sensitive to a different set of plant traits and more likely to exhibit neutral responses to plant genotype; (3) as stationary organisms with slow dynamics confined to tree boundaries, lichens allow for extensive sampling and clear documentation of their interactions [34–36]. For these reasons, the relation of oak–lichen (host-associated species) is an ideal system to evaluate the influence of host oak taxa GD on changes in the structure of the associated lichen community.

*Quercus crassifolia* H. and B. and *Q. crassipes* H. and B. (Fagaceae) are two red oak species (Lobatae) that overlap at the Transmexican Volcanic Belt (TVB) and in the southeastern part of the Sierra Madre Oriental in Central Mexico. When they meet, they form hybrids known as *Quercus* × *dysophylla* Benth pro sp. [26]. Previously, each of these species was characterized by leaf morphology and genetic markers (random amplified polymorphic DNA; RAPDs), and it was reported that the geographic proximity of hybrid plants to the allopatric site of a parental species increases their morphological and genetic similarity with the latter [26]. Also, Tovar-Sánchez and Oyama [29] determined that the composition, abundance, and diversity of the community of endophagous insects (gall-forming wasps and leaf miner moths) were affected by the host oak genetic categories (parental species or hybrid) and the genetic diversity at the stand level (HZ). In addition, the hybrid plants supported intermediate levels of infestation of gall-forming and leaf-mining insects compared to their putative parental species. Finally, greater GD in HZs was associated with greater diversity in the endophagous insect community.

In this study, we investigated the influence of host oak GD (hybrid vs. parental) on the composition, cover, species richness, and diversity of the lichen community associated with the *Q. crassifolia* × *Q. crassipes* complex in two hybrid zones. Specifically, (a) does the composition of the lichen community change between oak host taxa independently of HZ? and (b) is there a relationship between the GD of the oak host (at the individual and oak taxa host level) and the species richness, diversity, and coverage of the lichen community associated with this oak complex?

## 2. Materials and Methods

### *2.1. Oak Species*

*Quercus crassipes* and *Q. crassifolia* are two dominant red oak species of the temperate forests of Mexico, which can be differentiated easily through their foliar morphology. *Q. crassipes* is distinguished by its narrowly elliptic or lanceolate leaves with entire margins and 3 mm long short teeth at the apex, its smaller size, and its densely white-gray tomentose underside. In contrast, *Q. crassifolia* has obovate or oblong–obovate leaves with a yellow-orange or brown, woolly tomentose underside; the margins may be entire, wavy, or toothed, with 1–10 short teeth (for details, see work by Tovar-Sánchez and Oyama [30]). However, when they occur in sympatry at the TVB and in the southeastern part of the

Sierra Madre Oriental in Central Mexico, they can form individuals with intermediate morphology (*Quercus*× *dysophylla* Benth pro sp.) [26]. Hybrids were identified by means of leaf morphology and genetic markers. Seven zones in which hybridization occurs naturally between these two species (Cantera, Canalejas, Tlaxco, Acajete, La Esperanza, Agua Blanca, and Palo Bendito) were documented previously [26].

### 2.2. Study Sites

This study was carried out in two HZs selected from the *Q. crassipes* × *Q. crassifolia* complex in the TVB: Canalejas, State of Mexico (2570 m a.s.l., 19°58′ N–99°35′ W) and Tlaxco, Tlaxcala (2600 m a.s.l., 19°42′ N–98°04′ W). These zones were selected for this study due to their degree of conservation, ease of access, and security. In each zone, 30 trees [*Q. crassipes* (*n*= 10), *Q. crassifolia* (*n* = 10) and hybrids, *Q.* × *dysophylla* (*n* = 10)] were labeled. Individuals used in this study were previously taxonomically identified by means of leaf morphology and genetic markers (RAPDs and SSRs) [26]. We selected individuals ranging between 8 and 10 m (mean 8.7 m) in height and between 28.5 and 37.2 $m^2$ (mean 31.3 $m^2$) for crown cover. Crowns that do not overlap with any other tree within the oak forest were sampled.

### 2.3. Molecular Data

Genetic analyses were performed using four nuclear microsatellite markers (nSSRs): quru-GA-OC11, quru-GA-OE09 [39], QpZAG110 [40], and QpZAG11 [41] that showed to be polymorphic in this oak species complex. PCR reactions were set up as follows: 15 ng of DNA template, 50 mM of KCl, 20 mM of Tris-HCl (pH 8.4), 2 mM of MgCl2, 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. The 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 for QpZAG 110 was 44 °C, while for QpZAG11, quru-GA-OC11, and quru-GA-E09, it was 53 °C. PCR products were resolved on polyacrylamide gels at 6% (7 M urea) at 60 W for 3 h to determine the polymorphic primers. The length of the amplified microsatellite fragments was measured by running an aliquot of each PCR product on an automatic sequencer ABI 3100 (Applied Biosystems, California, USA) at 35 W for 80–90 min using gene scan ROX-2500 (Applied Biosystems, CA, USA) as size standard. Alleles were scored using Gene Mapper ver. 3.7 Software (Applied Biosystems, CA, USA).

### 2.4. Lichen Community

The lichen collection was carried out during the months of February and March 2015. In each of the trees, the lichen coverage was measured through a 50 × 20 cm plastic micro-square, subdivided into the points equidistantly every centimeter (1000 $cm^2$) that corresponds to 100% of the coverage of the micro-quadrant [42]. The quadrant was placed on the trunk of the tree 1 m high from the base (to avoid the inclusion of edaphic lichens), oriented toward the north face of the trunk [43]. The coverage of each lichen species was quantified by counting the points of intersection of the grid that covers the thallous.

For the determination of the lichen individuals at the species level, the taxonomic keys of Hale [44–47] and Nash III et al. [48–50] were used. Also, an optical microscope was used to observe characters at the cellular level. In some cases, it was necessary to analyze the secondary metabolites through the thin layer chromatography (TLC) method [51].

### 2.5. Statistical Analysis

Differences in lichen community composition among three host oak taxa (*Q. crassipes*, *Q. crassifolia*, and *Q.* × *dysophylla*) and HZs were tested using non-metric multidimensional

scaling (NMDS) based on the presence of 76 lichen species. NMDS was conducted to generate a dissimilarity matrix among host oak taxa and the two HZs using the Bray–Curtis dissimilarity coefficient [52]. Bootstrap analysis and ANOSIM were employed to test for differences among groups (host oak taxa and HZs) using 9999 random reassignments and determining whether the generated dissimilarity matrix significantly differed from a matrix obtained by chance [53].

An analysis of similarity percentages (SIMPER) was used to determine the lichen species responsible for the largest contribution to the Bray–Curtis dissimilarity in species abundance among host oak taxa and HZs. Also, the SIMPER analysis results were used to select the ten species that contributed the most to the dissimilarity among oak taxa and HZs. Also, similarity in lichen composition among host oak genetic categories was estimated using Jaccard's index.

Two-way analysis of variance (ANOVA) was performed to determine the effect of the host oak taxa (*Q. crassipes*, *Q. crassifolia,* and *Q.* × *dysophylla*) and site (HZ) on the relative cover of the lichen species and lichen species' richness. In the cases in which significant differences were found, post hoc comparisons were made using the Tukey test.

Furthermore, to determine the lichen diversity in each host oak taxa and HZ, the Shannon–Wiener diversity index (*H'*) was estimated. Then, this index was compared among pairs of taxa and HZs with a randomization test (delta, $\delta$) to evaluate if there are statistical differences in the diversity values. This test re-samples the distribution of species abundance produced by a summation of the two samples 10,000 times [54].

To evaluate the influence of GD of each host oak taxa on associate lichen communities, the expected heterozygosity (*He*) was utilized. Also, individual genetic diversity was estimated using homozygosity by the loci index (*HL*), a microsatellite-derived measure that improves heterozygosity estimates in natural populations by weighing the contribution of each locus to the homozygosity value based on the allelic variability [55]. This index varies between zero, when all loci are heterozygous, and one, when all loci are homozygous. Homozygosity via the loci index was estimated using CERNICALIN, an Excel spreadsheet that is available upon request [55]. These parameters (*He* and *HL*) were used because they are commonly utilized to assess the influence of genetic diversity on the community structure (e.g., [3,13]). To determine the relationship between GD and the lichen community composition, we related two NMDS axes for each HZ to individual genetic diversity (*HL*) using a Pearson correlation coefficient [56]. To determine the influence of host oak taxa (independent variable) and its genetic diversity (covariable) on diversity, richness, and associated lichen coverage, covariance analyses (ANCOVA) were performed using general linear models (GLM).

These statistical analyses were carried out in STATISTICA 8.0 [57], Species Diversity and Richness version 3.03 [58], and Past 4.01 [59].

## 3. Results

### *3.1. Composition of Lichens Associated with Quercus crassifolia* × *Q. crassipes Complex in Two Hybrid Zones*

The lichen community associated with the *Quercus crassifolia* × *Q. crassipes* complex was composed of 76 species contained in 27 genera belonging to 14 families (Table 1). The most representative lichen families in terms of the number of genera were Parmeliaceae (9) > Physciaceae (3) > Arthoniaceae (2) = Candelariaceae (2) = Lecanoraceae (2) (Table 1).

**Table 1.** Composition of lichens (families, genera, and species) associated with *Quercus crassifolia* × *Q. crassipes* complex in two hybrid zones. Canalejas, Mexico State and Tlaxco, Tlaxcala.

| Family | Species | Host Oak Taxa | | | Hybrid Zone | |
|---|---|---|---|---|---|---|
| | | *Q. crasf* | *Q.* × *dys* | *Q. crasp* | Canalejas | Tlaxco |
| Acarosporaceae | *Strangospora moriformis* (Ach.) Stein | | X | X | | √ |
| Arthoniaceae | *Herpothallon* sp. | X | | X | √ | √ |
| | *Sporostigma* sp. | X | X | | | √ |
| Candelariaceae | *Candelaria concolor* (Dicks.) Arnold. | | X | X | | √ |
| | *Candelariella vitelina* (Hoffm.) Müll. Arg. | | | X | | √ |
| Cladoniaceae | *Cladonia coniocraea* (Flörke) Spreng | | | X | | √ |
| | *Cladonia ochrochlora* Flörke | X | | | | √ |
| Collemataceae | *Leptogium azureum* (Sw. ex Ach.) Mont. | X | | | | √ |
| | *Leptogium burnetiae* C.W. Dodge | X | X | X | | √ |
| | *Leptogium chloromelum* (Sw. ex Ach.) Nyl. | | X | | | √ |
| | *Leptogium corticola* (Taylor) Tuck | | X | X | | √ |
| | *Leptogium digitatum* (A. Massal.) Zahlbr. | X | X | X | | √ |
| | *Leptogium laceroides* B. de Lesd | | | X | | √ |
| | *Leptogium phyllocarpum* (Pers.) Mont. | | X | | | √ |
| Graphidaceae | *Graphis scripta* (L.) Ach. | | X | | | √ |
| Lecanoraceae | *Japewia* sp. | | X | | | √ |
| | *Lecanora albella* (Pers.) Ach. | X | X | | √ | |
| | *Lecanora albellula* Nyl. | X | X | X | | √ |
| | *Lecanora allophana* Nyl. | | X | | | √ |
| | *Lecanora caesiorubella* Ach. | | | X | | √ |
| | *Lecanora densa* (Sliwa & Wetmore) Printzen | | X | | √ | |
| | *Lecanora horiza* (Ach.) Lindasy | | X | | | √ |
| | *Lecanora hybocarpa* (Tuck.) Brodo | X | | | | √ |
| | *Lecanora laxa* (Sliwa & Wetm.) Printzen | | X | X | √ | |
| | *Lecanora neaosonorensis* Lumbsch & T. Nash | | | X | √ | |
| | *Lecanora symmicta* (Ach.) Ach. | X | | | | √ |
| | *Lecanora tropica* Zahlbr. | | | X | | √ |
| | *Lecanora zosterae* (Ach.) Nyl. | | X | | | √ |
| Lobariaceae | *Sticta beavoisii* Delise | X | X | X | | √ |
| | *Sticta kunthii* Hook. F | X | | | | √ |
| | *Sticta fuliginosa* (Hoffm.) Ach. | X | | X | | √ |
| Parmeliaceae | *Cetrelia* sp. | | | X | | √ |
| | *Everniastrum sorocheilum* (Vain.) Hale | | | X | | √ |
| | *Everniastrum* sp. | X | X | | √ | |
| | *Flavoparmelia caperata* (L.) Hale | X | X | X | √ | √ |
| | *Flavopunctelia flaventior* (Nyl.) Hale | X | X | X | √ | √ |
| | *Flavopunctelia praesignis* (Nyl.) Hale | X | X | X | √ | √ |
| | *Hypotrachyna pulvinata* (Fee) Hale | X | X | | | √ |
| | *Hypotrachyna revuluta* (Flörke) Hale | | | X | √ | |
| | *Hypotrachyna rockii* (Zahlbr.) Hale | | | X | √ | |
| | *Hypotrachyna* sp. | | X | X | | √ |
| | *Phaeophysica* sp. | X | X | X | | √ |
| | *Parmotrema alidactilatum* Estrabou & Adler | X | X | | √ | |
| | *Parmotema apoteciada* (Taylor) Hale | | | X | | √ |
| | *Parmotrema arnoldii* (Du Rietz) Hale | X | | X | √ | |
| | *Parmotrema crinitum* (Ach.) M. Choisy | X | X | | | √ |
| | *Parmotrema eurysacum* (Hue) Hale | X | X | X | √ | √ |
| | *Parmotrema hypoleucium* (Steiner) Hale | X | X | X | √ | √ |
| | *Parmotrema reticulatum* (Taylor) M. Choisy | X | X | X | | √ |
| | *Parmotrema stuppeum* (Taylor) Hale | X | | | √ | |
| | *Punctelia hypoleucites* (Nyl.) Krog, | | X | X | √ | |
| | *Punctelia perreticulata* (Räsänen) G. Wilh. | X | X | X | √ | |

**Table 1.** *Cont.*

| Family | Species | Host Oak Taxa | | | Hybrid Zone | |
|---|---|---|---|---|---|---|
| | | *Q. crasf* | *Q.* × *dys* | *Q. crasp* | Canalejas | Tlaxco |
| | *Usnea ceratina* (Ach.) | X | | X | | √ |
| | *Usnea ceratinatum* (Ach.) | X | X | | | √ |
| | *Usnea filipendula* Stirton | X | X | | | √ |
| | *Usnea florida* (L.) Weber ex F.H.Wigg. | | | X | | √ |
| | *Usnea glabrata* (Ach.) Vainio | X | X | X | | √ |
| Physciaceae | *Diriniaria* sp. | X | | | √ | |
| | *Heterodermia granulifera* (Ach.) Culb. | | X | X | √ | √ |
| | *Heterodermia hypoleuca* (Mühl.) Trevis | | | X | √ | |
| | *Heterodermia japonica* (M. Satô) Swinscow | X | | X | √ | |
| | *Heterodermia leucomela* (L.) Poelt | X | X | X | | √ |
| | *Heterodermia obscurata* (Nyl) Trevis | X | X | | | √ |
| | *Heterodermia pseudospeciosa* (Kurok.) Culb | X | | X | √ | √ |
| | *Heterodermia tremulans* (Müll. Arg.) W. Culb. | | | X | | √ |
| | *Physcia erumpens* Moberg | | X | | | √ |
| Pertusariaceae | *Pertusaria californica* Dibben | | | X | √ | |
| Ramalinaceae | *Ramalina asahinae* W.L. Culb. | X | X | X | | √ |
| | *Ramalina celastri* (Sprengel) Krog & Swinsco | X | X | X | | √ |
| | *Ramalina complanata* (Sw.) Ach. | | X | X | | √ |
| | *Ramalina* sp. | X | | | | √ |
| Stereocaulaceae | *Lepraria incana* (L.) Ach | X | | | √ | |
| | *Lepraria lobificans* (B. de Lesd.) R.C. Harris | | X | | √ | |
| | *Lepraria* sp. | | X | | √ | |
| Teloschistaceae | *Teloschistes chrysophthalmus* (L.) Th. Fr. | | | X | √ | |
| | *Teloschistes flavicans* (Sw.) Norman | | X | X | | √ |

Note: *Q. crasf* = *Quercus crassifolia*, *Q.*× *dys* = *Quercus* ×*dysophylla*, *Q. crasp* = *Quercus crassipes*, X = lichen species present in host oak taxa, √ = lichen species present in each hybrid zone.

Considering the number of lichen species that exist, the most important genera associated with the *Quercus crassifolia* × *Q. crassipes* complex were *Lecanora* (12) > *Parmotrema* (8) > *Heteroderma* (7) = *Leptogium* (7). In particular, the presence of 47 species was recorded in *Q. crassipes*, 45 species in *Q.* × *dysophylla,* and 40 species in *Q. crassifolia* (Table 1). The most important lichen family associated with the host oak taxa (*Quercus crassifolia*, *Q. crassipes,* and *Q.* × *dysophilla*) due to the number of genera that it contains was Parmeliaceae. Finally, the dominant lichen species in the three genetic categories in terms of cover were *Flavoparmelia caperata*, *Flavopunctelia flaventior,* and *F. praesignis*. In this study, we also found unique lichen species associated with each host oak taxa and registered the next pattern: *Q. crassipes* ($n$ = 15) > *Q.* × *dysophilla* ($n$ = 9) = *Q. crassifolia* ($n$ = 9) (Table 1).

In HZ, the lichen community associated with Canalejas was composed of 28 species contained in 13 genera belonging to seven families. In addition, the lichen community associated with Tlaxco was composed of 56 species containing 23 genera belonging to 12 families. For details, see Table 1.

In general, we found significant differences in lichen composition among three host oak taxa in the Canalejas HZ (ANOSIM R = 0.9943, $p < 0.0001$, Figure 1) and in the Tlaxco HZ (ANOSIM R = 0.9902, $p < 0.0001$), showing that the communities on *Quercus crassifolia*, *Q.* × *dysophilla,* and *Q. crassipes* are significantly different from each other (Figure 1).

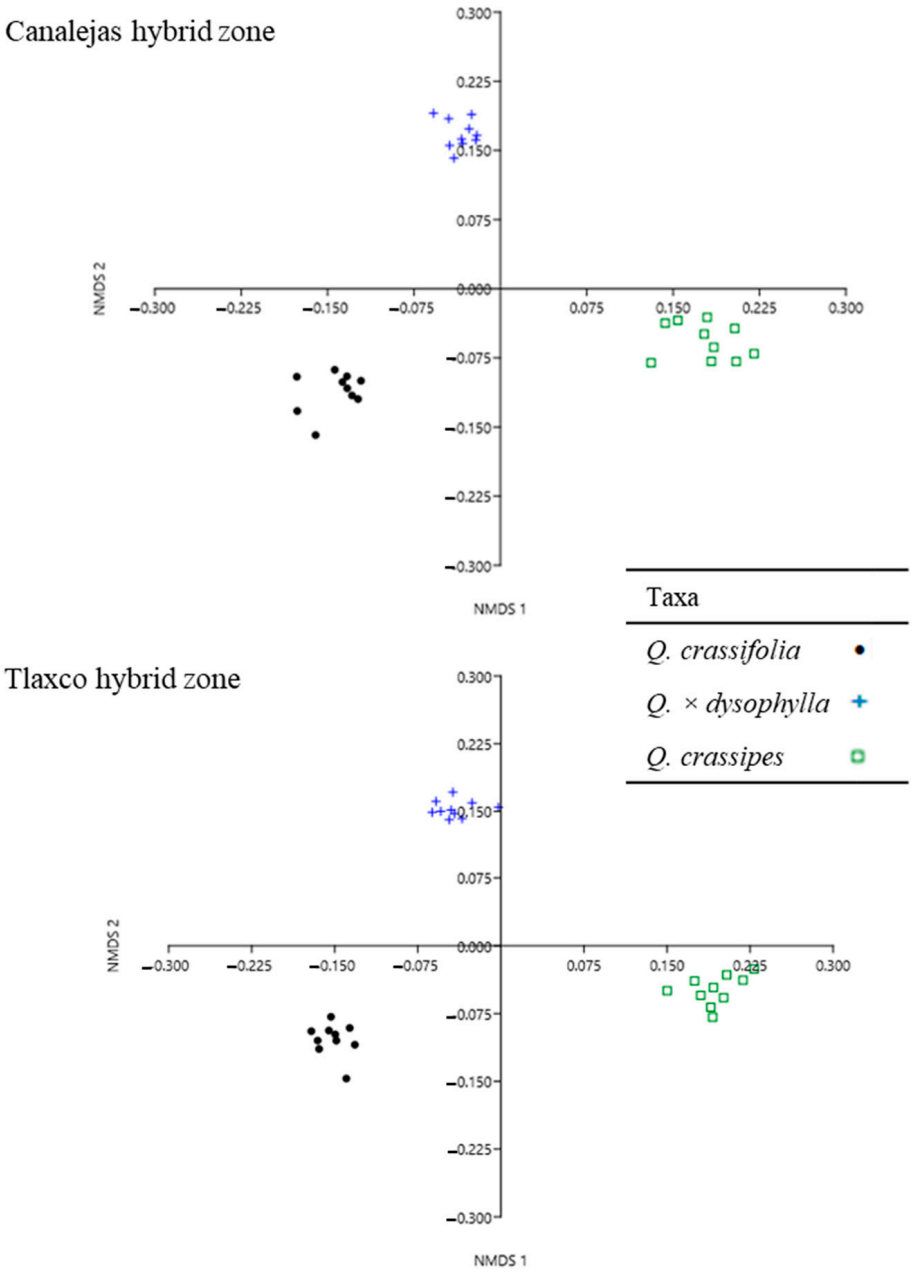



**Figure 1.** Lichen community composition differences among host oak genotypes (*Quercus crassifolia*, *Q.* × *dysophilla, and Q. crassipes*) in two hybrid zones using nonmetric multidimensional scaling (NMDS). Each point is a two-dimensional (axis 1 and axis 2) representation of the lichen species composition (10 points per host oak genotype). Distances between points reflect a dissimilarity matrix created using the Bray–Curtis dissimilarity coefficient (Faith et al., 1987 [52]). Points that are close together have lichen communities that are more similar in composition compared to points that are far apart. Data of Canalejas hybrid zone (Stress values: 0.149. Final instability, 0.0001) and Tlaxco hybrid zone (stress values of 0.128 and final instability of 0.0001) were used in this analysis.

The SIMPER analysis identified that the ten most important lichen species in terms of cover, that contributed to the dissimilarity between host oak taxa in both HZs, were *Punctelia perreticulata*, *Flavopunctelia praesignis*, *Parmotrema reticulatum*, *Heterodermia granulifera*, *Flavoparmelia caperata*, *Parmotrema eurysacum*, *Flavopunctelia flaventior*, *Punctelia hypoleucites*, and *Parmotrema hypoleucium* (Tables 2 and 3).

**Table 2.** Summary of SIMPER results for Canalejas hybrid zone: average cover of discriminating species in each host oak taxa, their contribution (%) to the dissimilarity between groups, and the cumulative total (%) of contributions (90% cut-off).

| | Cover | | Contribution | Cumulative Contribution |
|---|---|---|---|---|
| Lichen Species | *Q. crassifolia* | *Q.* × *dysophylla* | | |
| *Punctelia perreticulata* | 2.97 | 80.3 | 30.52 | 30.52 |
| *Flavoparmelia caperata* | 37.1 | 86.1 | 21.31 | 51.83 |
| *Punctelia hypoleucites* | 0 | 16.4 | 6.96 | 58.79 |
| *Parmotrema eurysacum* | 29.7 | 34.7 | 5.91 | 64.70 |
| *Herpothallon* sp. | 12 | 0 | 4.76 | 69.46 |
| *Lecanora laxa* | 0 | 9.7 | 3.78 | 73.24 |
| *Lepraria incana* | 8.8 | 0 | 3.54 | 76.78 |
| *Parmotrema hypoleucium* | 0 | 8.2 | 3.19 | 79.97 |
| *Dirinaria* sp. | 7.6 | 0 | 2.94 | 82.92 |
| *Everniastrum* sp. | 7.3 | 0 | 2.91 | 85.82 |
| *Flavopunctelia praesignis* | 10.8 | 12.9 | 2.88 | 88.71 |
| *Lecanora albella* | 7.11 | 0.5 | 2.74 | 91.45 |
| | *Q.* × *dysophylla* | *Q. crassipes* | | |
| *Flavopunctelia praesignis* | 12.9 | 120.0 | 31.45 | 31.45 |
| *Punctelia perreticulata* | 80.3 | 12.0 | 21.07 | 52.52 |
| *Flavoparmelia caperata* | 86.1 | 36.0 | 16.91 | 69.43 |
| *Parmotrema eurysacum* | 34.7 | 11.0 | 7.46 | 76.89 |
| *Punctelia hypoleucites* | 16.4 | 8.8 | 3.80 | 80.69 |
| *Parmotrema hypoleucium* | 8.2 | 16.0 | 3.55 | 84.24 |
| *Heterodermia hypoleuca* | 0 | 10.2 | 3.05 | 87.29 |
| *Lecanora laxa* | 9.7 | 0.5 | 2.81 | 90.09 |
| | *Q. crassifolia* | *Q. crassipes* | | |
| *Flavopunctelia praesignis* | 10.8 | 120.0 | 40.46 | 40.46 |
| *Parmotrema eurysacum* | 29.7 | 11.0 | 7.41 | 47.88 |
| *Parmotrema hypoleucium* | 0 | 16.0 | 6.52 | 54.40 |
| *Flavoparmelia caperata* | 37.1 | 36.1 | 5.81 | 60.21 |
| *Herpothallon* sp. | 12.0 | 0 | 4.79 | 65.00 |
| *Flavopunctelia flaventior* | 0 | 11.2 | 4.70 | 69.70 |
| *Heterodermia hypoleuca* | 0 | 10.2 | 3.86 | 73.55 |
| *Punctelia perreticulata* | 3.0 | 12.0 | 3.78 | 77.33 |
| *Punctelia hypoleucites* | 0 | 8.8 | 3.57 | 80.9 |
| *Lepraria incana* | 8.8 | 0 | 3.56 | 84.46 |
| *Dirinaria* sp. | 7.6 | 0 | 2.95 | 87.41 |
| *Everniastrum* sp. | 7.3 | 0 | 2.92 | 90.33 |

**Table 3.** Summary of SIMPER results for Tlaxco hybrid zone: average cover of discriminating species in each host oak taxa, their contribution (%) to the dissimilarity between groups, and the cumulative total (%) of contributions (90% cut-off).

| | Cover | | Contribution | Cumulative Contribution |
|---|---|---|---|---|
| Lichen Species | *Q. crassifolia* | *Q.* × *dysophylla* | | |
| *Parmotrema reticulatum* | 35.3 | 70.5 | 17.76 | 17.76 |
| *Flavopunctelia flaventior* | 11.1 | 34.2 | 11.35 | 29.11 |
| *Flavoparmelia caperata* | 47.0 | 33.3 | 10.35 | 39.46 |
| *Parmotrema crinitum* | 21.6 | 5.2 | 7.70 | 47.16 |
| *Heterodermia leucomela* | 4.0 | 19.9 | 7.51 | 54.66 |
| *Parmotrema hypoleucium* | 15.9 | 0.8 | 7.01 | 61.67 |
| *Lecanora albellula* | 0.3 | 9.5 | 4.39 | 66.06 |
| *Leptogium chloromelum* | 0 | 5.2 | 2.48 | 68.54 |
| *Leptogium burnetidae* | 1.5 | 6.4 | 2.38 | 70.91 |
| *Flavopunctelia praesignis* | 0 | 4.5 | 2.07 | 72.98 |
| *Heterodermia obscurata* | 0 | 4.3 | 2.05 | 75.03 |

**Table 3.** *Cont.*

| | Cover | | Contribution | Cumulative Contribution |
|---|---|---|---|---|
| *Sticta beavoisii* | 4.5 | 0.2 | 2.04 | 77.07 |
| *Leptogium azureum* | 3.9 | 0 | 1.87 | 78.94 |
| *Ramalina asahinae* | 5.0 | 1.2 | 1.82 | 80.76 |
| *Lecanora symmicta* | 3.8 | 0 | 1.76 | 82.52 |
| *Usnea ceratina* | 3.3 | 0 | 1.57 | 84.09 |
| *Cladonia ochrochlora* | 2.7 | 0 | 1.30 | 85.40 |
| *Strangospora moriformis* | 0 | 2.5 | 1.18 | 86.57 |
| *Heterodermia pseudospeciosa* | 0 | 2.4 | 1.15 | 87.72 |
| *Parmotrema eurysacum* | 0 | 2.1 | 1.02 | 88.74 |
| *Teloschistes flavicans* | 0 | 1.9 | 0.96 | 89.70 |
| *Lecanora horiza* | 0 | 1.8 | 0.85 | 90.54 |
| | *Q.* × *dysophylla* | *Q. crassipes* | | |
| *Parmotrema reticulatum* | 70.5 | 21.4 | 16.66 | 16.66 |
| *Heterodermia granulifera* | 0 | 46.1 | 15.63 | 32.30 |
| *Flavopunctelia flaventior* | 34.2 | 35.2 | 7.00 | 39.30 |
| *Flavopunctelia praesignis* | 4.5 | 24.6 | 6.95 | 46.25 |
| *Flavoparmelia caperata* | 33.3 | 15.6 | 6.74 | 52.99 |
| *Parmotrema apoteciada* | 0 | 18.8 | 6.43 | 59.42 |
| *Heterodermia leucomela* | 19.9 | 3.13 | 5.69 | 65.11 |
| *Parmotrema eurysacum* | 2.1 | 14.9 | 4.31 | 69.42 |
| *Heterodermia pseudospeciosa* | 2.4 | 14.1 | 4.01 | 73.43 |
| *Lecanora albellula* | 9.5 | 0 | 3.26 | 76.69 |
| *Candelariella vitellina* | 0 | 9.7 | 3.21 | 79.90 |
| *Phaeophysica* sp. | 1.5 | 8.0 | 2.28 | 82.17 |
| *Parmotrema crinitum* | 5.2 | 0 | 1.79 | 83.96 |
| *Leptogium chloromelum* | 5.2 | 0 | 1.78 | 85.74 |
| *Heterodermia obscurata* | 4.3 | 0 | 1.48 | 87.22 |
| *Leptogium burnetidae* | 6.4 | 4.4 | 0.94 | 88.16 |
| *Ramalina complanata* | 1.1 | 3.6 | 0.90 | 89.06 |
| *Everniastrum sorocheilum* | 0 | 2.3 | 0.78 | 89.84 |
| *Cetrelia* sp. | 0 | 2.3 | 0.75 | 90.60 |
| | *Q. crassifolia* | *Q. crassipes* | | |
| *Heterodermia granulifera* | 0 | 46.1 | 15.47 | 15.47 |
| *Flavoparmelia caperata* | 47.0 | 15.6 | 10.48 | 25.95 |
| *Flavopunctelia praesignis* | 0 | 24.6 | 8.348 | 34.30 |
| *Flavopunctelia flaventior* | 11.1 | 35.2 | 8.09 | 42.39 |
| *Parmotrema crinitum* | 21.6 | 0 | 7.25 | 49.64 |
| *Parmotrema apoteciada* | 0 | 18.8 | 6.37 | 56.00 |
| *Parmotrema hypoleucium* | 15.9 | 0 | 5.28 | 61.28 |
| *Parmotrema reticulatum* | 35.3 | 21.4 | 5.27 | 66.55 |
| *Parmotrema eurysacum* | 0 | 14.9 | 4.99 | 71.54 |
| *Heterodermia pseudospeciosa* | 0 | 14.1 | 4.66 | 76.20 |
| *Candelariella vitellina* | 0 | 9.7 | 3.17 | 79.37 |
| *Phaeophysica* sp. | 0.42 | 8.0 | 2.58 | 81.95 |
| *Leptogium azureum* | 3.9 | 0 | 1.33 | 83.28 |
| *Ramalina asahinae* | 4.9 | 1.3 | 1.28 | 84.56 |
| *Lecanora symmicta* | 3.8 | 0 | 1.26 | 85.82 |
| *Ramalina complanata* | 0 | 3.6 | 1.23 | 87.05 |
| *Sticta beavoisii* | 4.5 | 1.0 | 1.19 | 88.25 |
| *Leptogium burnetidae* | 1.5 | 4.4 | 1.00 | 89.25 |
| *Cladonia ochrochlora* | 2.7 | 0 | 0.93 | 90.17 |

### 3.2. Lichen Similarity Among Host Oak Taxa in Two Hybrid Zones

The percentage of lichen species shared among host oak taxa belonging to the *Quercus crassifolia* × *Q. crassipes* complex registered the following pattern: *Q. crassifolia* vs. *Q.* × *dysophylla* (49%) > *Q. crassipes* vs. *Q.* × *dysophylla* (42.5) > *Q. crassipes* vs. *Q. crassifolia* (28.5%). Also, the Jaccard similarity index showed that 10% ($n$ = 8) of the 76 species of lichens associated in the complex were shared between HZs.

### 3.3. Species Richness and Cover of Lichens in Host Oak Taxa and Hybrid Zones

There was no significant effect of the host oak taxa (*Quercus crassifolia*, *Q.* × *dysophylla*, *Q. crassipes*) on lichen species' richness [Canalejas and Tlaxco ($F_{2,27}$ = 0.369, $p$ > 0.05) and lichen cover in both HZs ($F_{2,27}$ = 0.369, $p$ > 0.05). The seven dominant lichen species in terms of relative cover by oak taxa and hybrid zone were *Flavoparmelia caperata*, *Flavopunctelia praesignis*, *Flavopunctelia flaventior*, *Parmotrema reticulatum*, *Parmotrema eurysacum*, *Punctelia perreticulata,* and *Heterodermia pseudospeciosa*.

### 3.4. Lichenic Diversity in Hybrid Zones and Host Oak Taxa

In the Tlaxco HZ, the lichen diversity index ($H'$) recorded the following pattern: *Q. crassipes* (2.65) > *Q.* × *dysophylla* (2.34) > *Q. crassifolia* (2.28) ($\delta$ test, $p$ < 0.05), while in Canalejas HZ, the following pattern was found: *Q. crassifolia* (2.12) > *Q.* × *dysophylla* (1.79) > *Q. crassipes* (1.74) ($\delta$ test, $p$ < 0.05). As we can see, $H'$ values showed statistically significant differences between host oak taxa, and the lichen diversity in *Q.* × *dysophylla* was intermediate with respect to the parents in both HZs.

### 3.5. Host Oak Taxa Genetic Diversity

The heterozygosity (*He*) values per host oak taxa in both HZs revealed that hybrids showed higher levels than parental species (mean ± standard error): *Q.* × *dysophylla*.

(Canalejas 0.809 ± 0.04), Tlaxco 0.616 ± 0.071) > *Q. crassifolia* (Canalejas 0.601 ± 0.076, Tlaxco 0.501 ± 0.079) > *Q. crassipes* (Canalejas 0.573 ± 0.077, Tlaxco 0.487 ± 0.079). Also, Canalejas HZ showed higher levels of *GD* in comparison with Tlaxco.

### 3.6. Influence of Genetic Diversity and Oak Host Taxa on the Structure of the Lichen Community in Two Hybrid Zones

Correlation analysis between NMDS scores axes (composition of lichens) and *HL* (individual genetic diversity) revealed significant positive correlations in both the Canalejas (NMDS axis 1 vs. *HL*: r = 0.567, $p$ = 0.001) and Tlaxco HZs (NMDS axis 1 vs. *HL*: r = 0.534, $p$ = 0.002). Also, a significant effect of GD (He) and host oak taxa on the richness and diversity of lichen species was detected. In contrast, there was no effect on the lichen cover (Table 4). Finally, a significant effect of HZ on the richness ($F_{1,56}$ = 17.332, $p$ < 0.001), and diversity of lichen species ($F_{1,56}$ = 9.056, $p$ < 0.01) was detected, but not on lichen cover ($F_{1,56}$ = 0.187, $p$ > 0.05).

**Table 4.** Effect of genetic diversity (*He*) at host oak taxa (*Q. crassifolia*, *Q.* × *dysophylla*, *Q. crassipes*) and hybrid zone on species richness, lichen cover, and Shannon–Wiener index diversity ($H'$) of associated lichen community to oaks.

| Variable | S.S. | $F_{1,56}$ | $p$ |
|---|---|---|---|
| Species richness | | | |
| Host oak taxa | 73.080 | 7.588 | <0.001 |
| Hybrid zone | 73.768 | 15.313 | <0.001 |

**Table 4.** *Cont.*

| Variable | S.S. | $F_{1,56}$ | $p$ |
|---|---|---|---|
| Lichen cover | | | |
| Host oak taxa | 106,444 | 2.656 | >0.05 |
| Hybrid zone | 14,640 | 0.7306 | >0.05 |
| Shannon-Wiener diversity | | | |
| Host oak taxa | 2.597 | 7.970 | <0.001 |
| Hybrid zone | 1.325 | 8.134 | <0.01 |

## 4. Discussion

### *4.1. Composition of Lichens Among Host Oak Taxa*

Our results evidenced that lichen communities are different among host oak taxa (*Quercus crassifolia*, *Q.* × *dysophilla*, and *Q. crassipes*) in both HZs (Canalejas and Tlaxco). Similar results have been reported in the literature. For example, bark epiphyte communities established on different genotypes of *Populus tremula* L. grown in an experimental garden in Scotland [34] and epiphytic bark lichen communities associated with *Populus angustifolia* growing in common gardens in the USA showed that different plant genotypes support different communities [36]. Also, in the literature, it has been reported that the effects of tree genotype on lichens are associated with genetic variation in physical and chemical bark characteristics) [34]. For example, differences among genotypes in bark roughness promote changes in the richness of the lichen species, total lichen coverage, and variations in community composition [36]. Moreover, lichen communities are highly responsive to microclimatic factors like humidity and bark pH [35,36]. These factors should be considered important alongside genetic traits. Research linking the genotype of host oaks with microclimatic conditions will be invaluable for a more comprehensive understanding of the assembly of epiphytic lichen communities associated with these oaks.

To our knowledge, this is the first study evaluating the effect of host oak hybridization on its associated lichen communities. In general, studies that have documented the effect of plant hybridization have focused on arthropod communities. For example, Tovar-Sánchez and Oyama evaluated the effect of hybridization of the *Q. crassifolia* × *Q. crassipes* complex on the community structure of endophagous [29] and ectophagous [30] insects. In both communities, they found significant differences in the insect species composition between parental species and hybrids, showing that these communities on each host taxa are significantly different from one another. Similar results have been reported in arthropod communities associated with the other three species involved in hybridization events, such as eucalyptus [28], willows [60], and cottonwoods [12,61]. The authors have explained that different genetically hosts support more dissimilar associated arthropod communities [14,62], suggesting that more genetically dissimilar populations have a lower similarity in their physical, chemical, and phenological characteristics. Considering the aforementioned information, we suggest that genetically dissimilar host oaks express more differences in bark characteristics (physical and chemical), promoting differences in their associated lichen communities.

### *4.2. Similarity Among Host Oak Taxa*

A greater similarity of lichen species was recorded between the hybrid host (*Q.* × *disophylla*) and each of its parental species compared to the similarity of lichen species recorded between the parental species (*Q. crassifolia* and *Q. crassipes*). This can be attributed to the fact that the hybrid host contains in its genome a mixture of genetic material from both parental species, while each parental species is genetically differentiated,

as documented in seven HZs in Mexico [26]. Also, the authors found that hybrid individuals exhibit an intermediate phenotype in foliar macromorphological characters. The same pattern was reported in *Q.* × *dysophylla* because this taxon showed an intermediate phenotype of foliar micromorphological characters compared with parental species in the same seven HZs [63]. Probably, this intermediate inherence pattern of leaf morphology (macro and micro) also occurs in the expression of important habitat attributes for lichen species establishment. In this scenario, the *Q.* × *dysophylla* host could express similar characteristics (e.g., physical and chemical bark characteristics, morphology, phenology) to both *Q. crassifolia* and *Q. crassipes*, which facilitates the presence of lichen species from the parental species. In the future, it could be interesting to measure bark characteristics (e.g., pH, roughness, and crevice depth) on each host oak taxa to test these hypotheses. Also, gene flow analyses in Canalejas and Tlaxco HZs revealed introgression between hybrid genotypes and parental species, respectively [26]. These results suggest that in both HZs, the hybrids could contain in their genetic pool an important portion of *Q. crassifolia* and *Q. crassipes* genetic material. This concurs with other reports of parental species and their hybrids [16,62].

### *4.3. Species Richness, Diversity, and Cover of Lichens Between Host Oak Taxa*

In this study, we documented that there was no effect of host oak taxa on lichen richness and cover in both HZs. However, the hybrid genotype recorded intermediate diversity values (*H'*) in its associated lichen community with respect to parental species. This response pattern coincides with the additive pattern [64] reported in the literature. The same pattern was reported in the endophagous insect communities associated with the *Q. crassifolia* × *Q. crassipes* complex [29]. It has been suggested that when this pattern occurs, it is because the hybrid host should express similar phenotypic characteristics (e.g., defense, phenology, and secondary compounds) to both parental species [65]. This fact could facilitate the establishment of the lichen species from both the parental species in the hybrid individuals, as detected here. Previous studies have reported that hybrid individuals exhibit an intermediate phenotype in macromorphological leaf traits between *Q. crassifolia* and *Q. crassipes* [26]. Specifically, in Canalejeas and Tlaxco HZs, the authors found that 88% of characters evaluated in *Q.* × *dysophylla* showed an intermediate phenotype. These results suggest that phenotypic characters in these *Quercus* species may have polygenic control with additive effects, as reported previously in other oak species [66,67]. Considering that the effects of tree genotypes on lichens are strongly associated with bark texture and chemistry [34,68], we suggest that the expression in these characters could have additive effects, as reported in macro- and micromorphological characters in this complex, promoting an additive response in the diversity pattern in the lichen communities associated with hybrids. Supporting this proposal are the studies by Orians et al. [69] and Cheng et al. [70], who found that 28.2% of the metabolites in hybrid plants (qualitative and quantitatively) are expressed in an intermediate way. However, studies evaluating phenotypic expression in the physical and chemical characteristics of the bark of the hybrid and parental taxa in this oak complex are necessary.

### *4.4. Influence of Host Oak Taxa Genetic Diversity in Two Hybrid Zones on the Structure of the Lichen Community*

Studies evaluating lichen communities associated with hybridizing species are very limited. In this research, we found an effect of the GD of the host oak taxa in two hybrid zones on the lichen communities associated with the *Q. crassifolia* × *Q. crassipes* complex. These results are in accordance with others that have shown that the GD of host species has a significant effect on the associated community structure [1,3,61]. Our results are important because they broaden the diversity of organisms known to be af-

fected by host tree genetics and hybridization processes. In addition, they are important as evidence of the potential for intraspecific genetic variation within foundation species to structure-dependent communities, presenting new challenges and opportunities for biodiversity management [11].

The significant positive correlation between composition of lichens (NMDS scores axes) and individual genetic diversity (*HL*) of the analyzed plants of *Q. crassifolia* × *Q. crassipes* complex in both HZs suggests that genetically different individuals support different assemblages of lichen species. Similar results were reported in vascular epiphyte communities associated with plants genetically different from *Brosimum alicastrum* [71] and different lichen species assemblages in genetically different plants of *Populus angustifolia* [31]. Several authors have suggested that genetically different individuals within a species or taxa vary in many traits, such as growth rates, physiological processes, secondary chemistry, and ontogeny, attributes that have an impact on other species [72,73]. Variations in these traits in host plants can have an influence on associated species, creating unique communities of individual plants [74], as reported here.

Additionally, lichen community responses to host taxa in this oak complex were detected. Even when we analyzed data from two different HZs, we found the same significant differences in lichen community composition among oak taxa. These findings argue that the genetic differences among host oak taxa (parental or hybrids) exert a strong organizing influence on the lichen community. These findings agree with those by Wimp et al. [1], who reported differences in arthropod community composition among four different types of cottonwood crosses (*Populus fremontii*, *P. angustifolia,* and their naturally occurring F1 and backcross hybrids). The effect of the host oak genotype on the associated epiphyte community composition has potential implications for temperate forest conservation. Forest stands in which hybridization events occur are important to consider in conservation strategies because they not only help maintain genetic diversity within oak species but also have conservation benefits for the broader community [25]. This is due to the contrasting species composition between the hybrid genotypes and their parent species.

Also, we found that as the genetic diversity (*He*) of the oak host increased (regardless of the host oak taxa), the species richness and diversity of the dependent community also increased. Similar positive relationships were reported between the genetic diversity of the host tree and arthropod community diversity associated with *Populus angustifolia* × *P. fremontii* complex [12], *Q. crassipes* × *Q. crassifolia* complex [29,30], and *Q. castanea* [3]. The increase in the host plant's genetic diversity can generate changes in morphological [11,26,66], phenological [75], and chemical characteristics [76]. These changes constitute a wider array of resources and conditions that can be used by their associated communities [77]. Our results highlight the importance of conserving genetic variation within widespread foundation oak species involved in hybridization events. This intraspecific genetic variation would be crucial to consider in Mexican temperate forest restoration, as the genetic diversity in the foundation species used to create habitat structure could greatly influence the accumulation of diverse species.

Several studies have acknowledged that phenotypic variation at the community level is determined not only by the host plant's genetic attributes but also by the environments in which individuals and species occur [61]. For example, only one-third of the variation in *Xanthomendoza galericulata* cover, a dominant bark lichen associated with *Populus angustifolia,* is explained by differences among host tree genotypes [34]. Meanwhile, a significant effect of the locality on community composition of epiphytic taxa (23 lichen species, two mosses, and one liverwort) growing associated with different genotypes of *Populus tremula* was reported in Scotland [33]. In our case, we observed a significant effect of HZ on the richness and diversity of lichen species associated with *Q. crassifolia* × *Q. cras-*

*sipes* complex. Likewise, a significant effect of the HZ was reported by Tovar-Sánchez and Oyama [29] in the community structure of canopy endophagous insects associated with the *Q. crassifolia* × *Q. crassipes* complex. These results suggest that the variation in richness and species diversity of lichen communities among hybrid zones is also influenced by locality variation factors.

The hybrid zones included in this work have similar characteristics in terms of climate, altitude, type of vegetation, geographical history, and distribution in the TVB. In this scenario, it is unlikely that these ecological factors have shaped the response of the lichen communities since, at this broad scale, both populations were in the same condition. However, at a fine scale, there could be other factors that may have an impact on lichen communities. For example, lichen communities are sensitive to microclimatic conditions such as humidity and bark pH [34–36], which should be acknowledged as potentially significant factors in genetic traits to which the lichen communities are sensitive. Also, the oak species composition of each HZ can have a strong impact on the structure of the communities associated with the host oak plants, as suggested in the hypothesis of "associational susceptibility" [78], which indicates that the number of tree species growing in sympatry with the study tree species can modify the structure of the associated communities since the potential source of new species comes from the closest hosts. Future studies connecting the host oak genotype, micro-climatic conditions, number of oak species, and lichen communities should be useful to gain a more complete understanding of epiphytic lichen community assembly.

## 5. Conclusions

Hybridization can have strong ecological and evolutionary effects on organisms linked to plants. With this study, we broaden the knowledge of the importance of hybridization events to include its effects on lichen communities, and we contribute to evidence of the diversity of organisms known to be affected by the host tree's genetic diversity. Specifically, we detected that the composition and species diversity of lichen communities associated with the *Q. crassifolia* × *Q. crassipes* complex respond to the genetic diversity of the host oak. Considering that the modern genomic approaches like RAD-seq, Genotyping-by-Sequencing (GBS), or whole-genome sequencing enable more precise detection of hybrid individuals and a more detailed understanding of genetic diversity and population structure, techniques relatively traditional such as microsatellites could be limited in resolution and may lead to inaccuracies when studying hybridization in complex taxa such as *Quercus*, where gene flow and introgression are highly dynamic processes. Future research would significantly strengthen the analysis of hybridization and genetic diversity in *Q. crassifolia* × *Q. crassipes* complex by incorporating these advanced techniques. Furthermore, considering that environmental conditions can modulate the expression of genetically variable plant traits, and these genotypes by environment interactions can affect associated communities, it could be interesting to evaluate the relative importance of genotype vs. environment to bark traits that influence lichens, as well as their interactions, for a complete understanding of epiphytic lichen community assembly associated with these oaks. From the conservation perspective, the recognition of the influence of the genetic characteristics of host oaks on associated lichen biodiversity has important implications. Oak forests where hybridization events occur may generate higher levels of accumulated lichen diversity because of the contrasting species composition among different host categories (parental species and hybrids). These findings suggest that to maintain the hybridization events between *Q. crassifolia*, *Q.* × *dysophylla*, and *Q. crassipes* in the forests where they naturally inhabit, it is important to not only favor the GD levels that allow the populations of these

taxa to respond to future environmental change but also to ensure that the populations are able to host diverse lichen communities.

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