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Research Article

Relationship Between Genetic Variation and Diversity of Tree Species in Tropical Forests in the El Ocote Biosphere Reserve, Chiapas, Mexico

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Abstract

Knowledge of the genetic diversity of species in a biological community is useful for assessing the ecological and evolutionary processes that define the structure and dynamics of that community. We investigated the potential relationship between the trans-specific genetic diversity (or genetic diversity across tree species) and the diversity of tree species in a tropical subdeciduous forest. The nucleotide variation of the concatenated regions ITS 1 and ITS 3 (ITS1-3) was used to determine the trans-specific genetic diversity of 19 species of trees in five local communities at El Ocote Biosphere Reserve (REBISO), Chiapas, Mexico. Tree diversity was obtained by counting individual trees within 0.1 ha circular plots in each locality. The relationship between trans-specific genetic diversity and species diversity was established through simple linear regressions between genetic diversity parameters and community diversity. A correlation matrix was built with genetic distances (Kimura's two-parameter model) and differences in species diversity between communities. A significant relationship was observed between nucleotide diversity (π) and species richness (*Sp*), and a negative association between haplotype diversity and gamma diversity (γ). Our results show species-rich and genetically diverse tree communities and a weak association between trans-specific genetic variation and species diversity in tree communities at REBISO. This research suggests a possible ecological and genetic relationship within each community. Genetic diversity values may provide an important degree of variation upon which environmental selection pressures could operate, which may be helpful to face the current environmental modifications associated with climatic change.

Keywords

conservation genetics, natural protected area, REBISO, species diversity, tropical forest

The recognition of tree species diversity and the clustering factors (species assemblages) represent basic knowledge for managing and conserving focal species or their plant communities (Lowe et al., 2018). The current species assemblages and the distribution of each species have resulted from evolutionary processes that occurred over millions of years, which can eventually be recognized through genetic information. The current genetic diversity is the result of selection and random evolutionary processes experienced by previous generations; this genetic variability determines the evolutionary potential of species within the prevailing ecological conditions at a given time.

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With regards to tree community assemblages, the relative importance of random processes versus deterministic interactions between species, mediated by local environmental conditions, is an issue not completely solved to date (Genung et al., 2011; Stroud & Losos, 2016). The inclusion of an evolutionary genetics approach to the ecological approach in the study of communities has been proposed to gain a deeper insight on how communities are assembled, since evolution results from the interaction with ecological processes; this approach allows understanding how evolutionary forces influence natural communities and how intra- and interspecific ecological processes influence genetic variation (Genung et al., 2011). The species in a community experience common environmental factors that delineate the evolutionary trajectory they share (Fitzpatrick & Keller, 2015), considering that populations co-occur in a given space and time (Laroche et al., 2015; Robinson et al., 2010). If the species in a community are spatially arranged according to common evolutionary processes or ecological dynamics, a link should be expected between species diversity in a community and genetic diversity within the populations involved.

The relationship between genetic diversity and species diversity within a community has been little investigated due to the methodological complexities involved in relating evolutionary processes at the population level to those at the community level (Genung et al., 2011; Fitzpatrick & Keller, 2015; Lowe et al., 2018; Vellend et al., 2014). However, the study of genetic diversity related to species diversity in a community can (1) assess the eco-evolutionary dynamics that shape communities, which can be altered by environmental pressures and climatic conditions, (2) determine the degree of conservation and evolutionary potential of the community, and (3) identify potential threats, as well as develop management strategies to protect the genetic and species diversity (Bailey et al., 2009; Frey et al., 2016; Laroche et al., 2015; Lowe et al., 2018; Messmer et al., 2012).

The elements that make it possible to describe the genetic diversity of populations are the frequencies of genotypes and alleles within a population, whereas those used for estimating diversity in an ecological community are the number of species and their relative abundance (Vellend, 2005). Each of these individual components of diversity has been addressed separately in conventional studies; however, establishing the relationship between them offers a better understanding of the processes and mechanisms involved in the assembly of communities (Vellend & Geber, 2005; Wehenkel et al., 2006). Deepening the current knowledge of community assembly processes can improve management decisions for species and community conservation.

The estimators of genetic diversity and species diversity can be related to one another in three ways: (1) positively, as a result of the simultaneous effects of genetic drift and natural selection acting concurrently on all species (Odat et al., 2009; Vellend, 2004, 2005); (2) influence of genetic diversity on species diversity, since the former controls the demographic dynamics, while the genetic variation of a dominant species determines the biotic conditions of the environment experienced by the rest of the species in the community (Vellend, 2006); and (3) positive effect of species diversity on the differential selection regime within populations; therefore, genetic diversity may change according to the diversity and relative abundance of species that coexist in a community (Vellend, 2005; Vellend & Geber, 2005).

A species-genetic diversity correlation (SGDC) has been observed in insects, fish, and plants, using the genetic structure of the dominant species as a predictor of species diversity within its community (e.g., Avolio et al., 2012; Blum et al., 2012; Bossart & Antwi, 2016; Crawford & Rudgers, 2012, 2013; Csergö et al., 2014; Finn & LeRoy, 2011; Fridley & Grime, 2010; He et al., 2008; Papadopoulou et al., 2011; Simental-Rodríguez et al., 2014; Wehenkel et al., 2006; Wei & Jiang, 2012). An alternative approximation to relate intraspecific genetic variation to species diversity in a community may involve correlating an estimator of the genetic diversity of species selected at random (trans-specific genetic diversity) with an estimator of species diversity in their community (e.g., Frey et al., 2016; Wehenkel et al., 2006), assuming that individuals are characterized by trans-specific genetic traits and, therefore, by taxonomic relationships regardless of their identity (Gregorius et al., 2003).

El Ocote Biosphere Reserve (REBISO, for its acronym in Spanish) is part of the Natural Protected Areas of Mexico and has been acknowledged as a high-biodiversity area (hotspot) of Mesoamerica, as well as one of the main remnants of subdeciduous tropical forest (Flamenco-Sandoval et al., 2007). REBISO is part of the Mesoamerican biological corridor for wildlife that connects two of Mexico's important tropical forests, Chimalapas and Uxpanapa (Flamenco-Sandoval et al., 2007; Orihuela-Belmonte et al., 2013; Ruiz-Montoya et al., 2017). Previous studies on trees in the region have addressed the impact of changes in land use (Flamenco-Sandoval et al., 2007) and forest fires (Maldonado et al., 2009; Velasco et al., 2012), as well as leaf litter production (Rivera et al., 2013), carbon-flow dynamics in soil and vegetation (Orihuela-Belmonte et al., 2013), and exploitation of timber and non-timber resources (Marquez-Reynoso et al., 2017).

The objective of the present study was to evaluate whether the trans-specific genetic diversity of a set of

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tree species is correlated with species diversity in forest communities at REBISO. Assuming that the coexistence of species in a community is driven by common evolutionary and ecological processes that determine the assembly of communities (Vellend & Geber, 2005) and that the REBISO has a high diversity of tree species (Ramírez-Marcial et al., 2017), we expected to observe a positive correlation between trans-specific genetic diversity of species selected at random and species diversity in their respective communities. This study contributes to the understanding of the eco-evolutionary processes that determine communities and their conservation.

Methods

Study Area

El Ocote Biosphere Reserve is located at the northwest of the state of Chiapas, Mexico, between coordinates 16°45'42''-17°09'00'' N, 93°54'19''-93°21'20'' E, being considered as one of the last remnants of subhumid tropical vegetation in southern Mexico (Figure 1). REBISO comprises an area of approximately 101.3 km^2 and includes a high environmental heterogeneity due to variations in topography, humidity, and climate, which lead to different types of vegetation (Flamenco-Sandoval et al., 2007). The vegetation is dominated by tree species like *Brosimum alicastrum* (Ramón, Breadnut tree), *Mortoniodendron ocotense* (Jicalpeste), *Manilkara zapota* (Chicozapote, Naseberry), and *Bursera simaruba* (Chacá, Gumbo-limbo) (Breedlove, 1981; Rzedowski, 1978). The climate is warm and humid with abundant rainfall in summer, mean annual temperature above 22 °C, and mean annual precipitation between 1500 and 2500 mm (García, 1980; Orantes-García et al., 2013).

Sampling Design

We sampled five locations at REBISO, considering each as a local community: Nuevo San Juan Chamula, Veinte

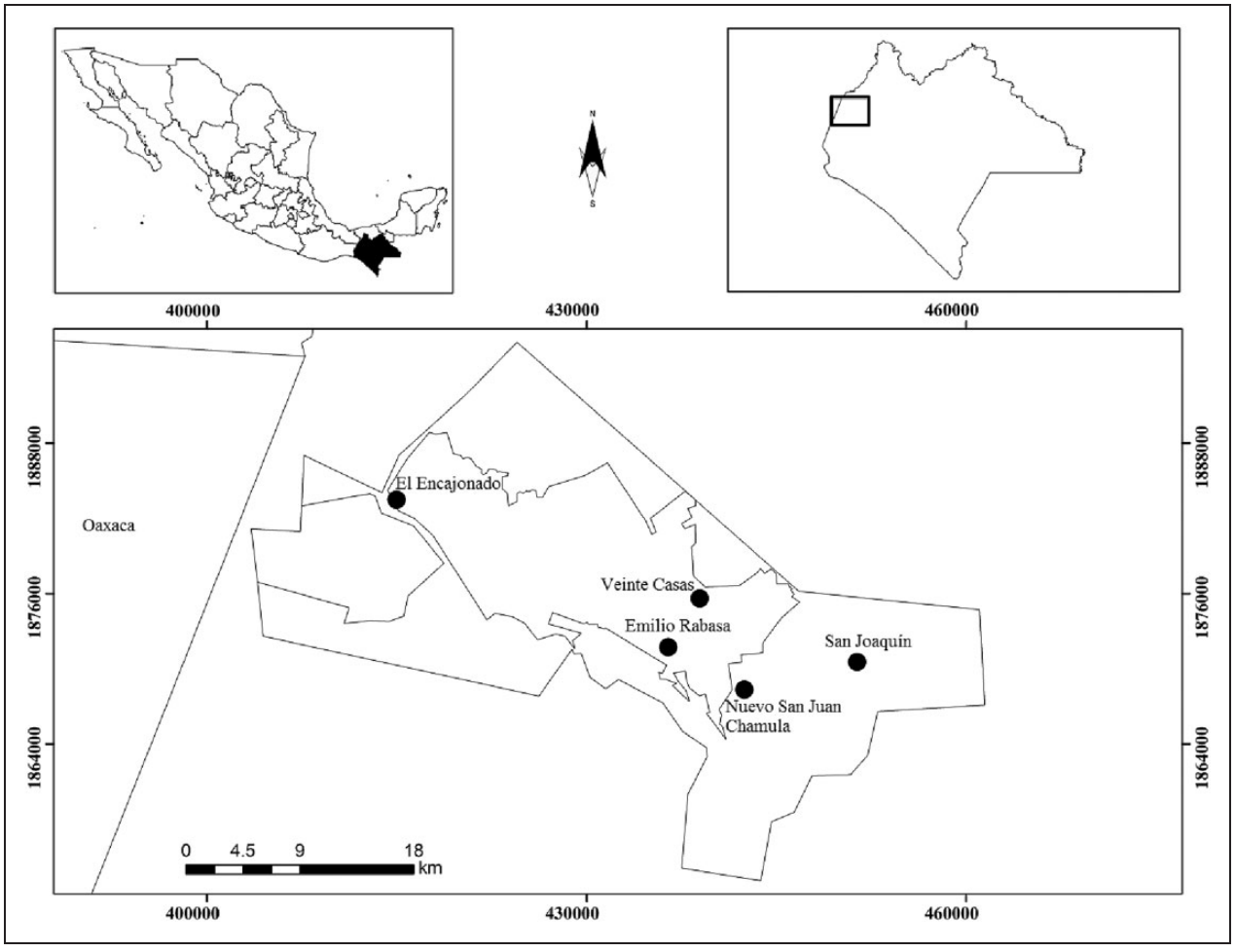


Figure 1. Sampling Localities for the Study of Genetic Diversity and Species Diversity of Tree Communities at Selva El Ocote Biosphere Reserve, Chiapas, Mexico. Inner polygons in the bottom panel represent core areas.

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Casas, El Encajonado, San Joaquin, and Emilio Rabasa (Figure 1). The sampling in each locality was carried out in three to eleven 0.1 ha circular plots (see Ramírez-Marcial et al., 2017). In each plot, the presence of individual trees of each species with a diameter at breast height (DBH) > 5 cm was recorded (see Ramírez-Marcial et al., 2017). Trees were identified to species, with taxonomic nomenclature standardized using the Taxon stand package enabled in R (Cayuela et al., 2012). Also, vegetative tissue (young leaves with no apparent damage) was obtained from individual trees of some species in the same vegetation plots sampled. In the case of trees with hard-to-reach young leaves (very tall tree > 5 m high), a sample of vascular tissue (cambium) from the trunk was obtained. Samples were labeled and preserved in 1.5 ml vials containing CTAB buffer and stored at -4°C until processing.

Species Diversity

Species diversity was described based on the number and abundance of tree species by calculating diversity parameters for each local community. Three conventional alpha diversity estimators were obtained per locality or local communities: species richness (*Sp*), the exponential of Shannon's diversity index (exp*H*), and the inverse of Simpson's index (*InvIS*). Species richness is the number of species recorded in each community, while exp*H* and *InvIS* are estimators of the true diversity that take into account the abundance of species. The index exp*H* places more weight on species evenness and *InvIS* on the dominant species. These three estimators are deemed indicators of the effective number of species in a community (Jost, 2006).

Further, beta, and gamma diversity were obtained to metacommunity scale (including all sites sampled, i.e., plots, and communities). At the highest sampling level, e.g., metacommunity (REBISO), the components of diversity are (Whittaker, 1960): $\beta_m = \gamma$ - α_m; at every lower level in the hierarchy (plots), the components are: $\beta_i = \alpha_i + 1 - \alpha$. So, this means an additive partition of diversity: $\gamma = \alpha_i$ - $\sum \beta_i$, where γ is the regional diversity considering the total number of individuals found in a given area and belonging to a species; α_i is species richness within the community (*Sp*), and β_i is the turnover of species between communities (Marcon & Hérault, 2015). All these diversity components were obtained with the program R v. 3 (R Development Core Team, 2015), using the vegan (Oksanen, 2015) and entropart packages (Marcon & Hérault, 2015).

Genetic Diversity

Genomic DNA was extracted using the CTAB method (Doyle, 1990) and visualized through electrophoresis in 1% agarose gel to determine viability. DNA was extracted from all samples; however, the genetic analysis was conducted only for those species represented by samples including > 2 individuals across all communities. This resulted in a set of 19 species (Table 1) out of the 192 recorded in the sampling events conducted by Ramírez-Marcial et al. (2017). In samples of these 19 species, two nuclear ribosomal DNA sequences were amplified: forward ITS 1 (5′-TCCGTAGGTGA ACCTGCGG-3′) and ITS 3 (5′-GCATCGATGAAGA ACGCAGC-3′) (White et al., 1990).

The amplification was conducted in a final volume of 50 μl, with Master Mix (*Taq* DNA Polymerase; Promega) solution in a C1000 Touch^{TM} Thermal Cycler (Bio-Rad). The PCR reactions involved an initial denaturation at 95 °C × 3 min, then 35 denaturation cycles at 95 °C × 30 s for subsequent denaturation, 57 °C (ITS 1–2) and 52 °C (ITS 3–4) × 30 s for annealing, and 72 °C × 2 min for extension; the final extension was conducted at 72 °C × 10 min (White et al., 1990). The final product of the reactions was visualized by electrophoresis in 2% agarose gel with a 100 base-pair (bp) control marker (ladder, Promega). Reactions were sequenced in Macrogen Inc., Seoul, Korea, through the sequencing protocol developed by Applied Biosystems.

We selected the Internal Transcribed Spacer (ITS) as a molecular marker for being a non-coding region with a relatively high rate of nucleotide substitutions, which makes it possible to efficiently estimate genetic variation at the population level (Nagy et al., 2012; Ornelas et al., 2016; Pérez-Crespo et al., 2017). As ITS is an easy-to-replicate universal region in botany and mycology, even with degraded DNA, due to its high number of copies in the genome, its use facilitated estimating the intraspecific genetic variation of various tree species simultaneously. However, these were not phylogenetically close, a characteristic that allowed obtaining the genetic diversity of the same molecular region for all the species of a community that were analyzed, which would not have been possible with other markers, such as microsatellites. Although ITSs are widely used in the construction of phylogenies, some studies have used them for estimating intraspecific genetic diversity (e.g., Ba & Rivera-Ocasio, 2015; Coronado et al., 2019; Liu et al., 2019; Ornelas et al., 2016; Pérez-Crespo et al., 2017).

However, ITS has been seriously questioned on two grounds, which may challenge the information obtained: (1) ITSs are highly variable non-coding regions that accumulate nucleotide substitutions and mutation events; the latter involve a high risk of false-positive homologies and an increased risk of incorrect genetic relationships; (2) ITSs have low phylogenetic resolution in comparisons between genera or at upper taxonomic levels, due to the high rate of substitutions that produces

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Table 1. Species and number of individuals at the community level for the analysis of genetic diversity of trees at Selva El Ocote Biosphere Reserve with markers ITS 1 and ITS 3.

Species	Family	Common names	Community				
			EE	NS	VC	SJ	ER
Mariosousa centralis (Britton & Rose) Seigler & Ebinger	Fabaceae	Guache	4				
Astrocaryum mexicanum Liebm. ex Mart.	Arecaceae	Mexican forest palm or Chocho				2	
Allophylus psilospermus Radlk	Sapindaceae	Estiquilla, Estiquillo		3			
Brosimum alicastrum Sw. var. *alicastrum*	Moraceae	Breadnut tree, Ramón	1		5		
Bursera simaruba (L.) Sarg.	Burseraceae	Gumbo-limbo, Palo mulato, Chacá	7				1
Citharexylum affine M.Martens & Galeotti	Verbenaceae	Bride tail				2	
Cordia alliodora (R. & P.) Oken	Boraginaceae	Spanish elm, Aguardientillo	9				
Dendropanax arboreus (L.) Decne. & Planch.	Araliacear	Angelica tree, Zapotillo	1			2	
Garcia nutans Vahl	Euphorbiaceae	False tungoiltree, Avellano					3
Heliocarpus appendiculatus Turcz.	Malvaceae	Jonote		10			
Manilkara zapota (L.) P. Royen	Sapotaceae	Naseberry, Sapodilla, Chicozapote					15
Maytenus purpusii Lundell	Celastraceae	Purppus' spike thorn					3
Mortoniodendron ocotense Ishiki & T. Wendt	Malvaceae	Jicalpeste			2		
Oreopanax geminatus Marchal	Araliaceae	Coleto				2	
Protium copal (Schltdl. & Cham.) Engl.	Burseraceae	Copal					2
Psychotria chiapensis Standley	Rubiaceae	Cafecillo			8	1	
Trichilia moschata Sw. subsp. *matudae* (Lundell) Penn	Meliaceae	Spoon stick		4			
Zanthoxylum acuminatum (Sw.) Sw.	Rutaceae	Lagarto tree					2
Zanthoxylum caribaeum Lam.		Prickly yellow, Chichón	7				
N_{com}			29	17	15	9	26
N_{sp}			6	3	3	5	6

N_{com} = number of individuals subjected to genetic analysis by community, N_{sp} = Number of species subjected to genetic studies by local community. EE = El Encajonado, NS = Nuevo San Juan Chamula, SJ = San Joaquín, VC = Veinte Casas, ER = Emilio Rabasa.

high homoplasy, a condition that masks the phylogenetic relationships of evolutionary events (Nagy et al., 2012). Therefore, to rule out incorrect genetic diversity levels, the quality of all the sequences obtained by Macrogen Inc. was reviewed with the program CHROMAS v. 1.45 (McCarthy, 1996).

Low and double signals were verified; also, the identity of the species was checked according to the GenBank. Sequences were reviewed considering three criteria: (1) the signal of electropherograms should be well-defined (>90%) and with no double peaks, (2) the signal of electropherograms should correspond to the nucleotide emitted (>90%), and (3) the identity of each sequence should correspond to the tree analyzed through BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Dubious sequences (i.e., electropherograms with a low signal, double peaks, and identity of erroneous sequences) were removed from the analyses, and those considered as reliable were aligned with the program Clustal X v. 2.1 (Thompson et al., 1992) after eliminating the first 30 nucleotides, which correspond to unstable signals from the equipment and the concatenation of ITS regions 1 and 3 (ITS 1–3). The sequences of each ITS region were deposited at GenBank (accession numbers MN077170- MN077362; Online Appendix 1).

Genetic diversity was estimated for each species sampled in each community (or locality) to report the values of conventional genetic diversity for sequences. This was based on segregating sites (s), which are the sites where the sequences differ; nucleotide diversity (π), i.e., the number of different nucleotides per site between two sequences taken at random; number of haplotypes (h), indicating the polymorphism given by nucleotide changes in the analyzed region; and haplotype diversity (Hd), which measures the uniqueness of a haplotype in a given population in relation to sample size (Nei & Li, 1979; Nei, 1987). Subsequently, trans-specific genetic diversity was estimated at the community level. To this end, the sequences of species corresponding to each community (sample location) were grouped together, and all the genetic diversity parameters were calculated using the software DnaSP v. 5 (Librado & Rozas, 2009).

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Estimating trans-specific genetic diversity allows making comparisons between communities, even when species are not present in all of them and belong to different taxonomic families, because it focuses on determining the variation of a given genetic attribute (e.g., genetic diversity of an identical or homologous gene) at different organization levels (Gregorius et al., 2003; Wehenkel et al., 2006). It is important to consider that this estimate does not detect the genetic structure of species or differences between species (Frey et al., 2016); thus, it is restricted to the description of trans-specific genetic diversity, with limited power to infer intra-specific evolutionary processes.

Alternatively, we obtained a genetic similarity matrix irrespective of the identity of species, expecting a complete match between haplotypes and species, as well as shared sequences between species derived from ancestry. Sequences were grouped and analyzed across communities with the Kimura's 2-parameter model using the software MEGA v. 6 (Tamura et al., 2013). In this model, evolutionary distance per site is defined as $K = -(1/2) \ln \{(1 - 2P - Q) \sqrt{1 - 2Q}\}$, where Q is the fraction of nucleotide sites showing type I (transition, i.e., homologous sites are occupied by different nucleotide bases, with both being purines or pyrimidines) and P showing type II (transversion, i.e., one of the two nucleotides is a purine and the other is a pyrimidine). The evolutionary rate per year is $k = K/(2T)$, where T is the time since the divergence of the two sequences (Kimura, 1980). Genetic distances were grouped together using the neighbor-joining method (Saitou & Nei, 1987), which represents the similarity between individuals, using the program PAUP v. 4 (Swofford, 2002).

Species-Genetic Diversity Correlation

The relationship between genetic diversity and species diversity was explored using two procedures: (1) correlating species diversity *vs*. genetic diversity through simple lineal regressions of the species diversity indices ($\exp H$, *InvIS*, *Sp*, beta, and gamma) and trans-specific genetic diversity parameters (s, π, h, Hd) (Avolio et al., 2012; Blum et al., 2012; Vellend, 2004; Wei & Jiang, 2012), using the software R v.3 (R Development Core Team, 2015); and (2) contrasting community dissimilarity indexes *vs*. genetic distances through a Mantel's test using the program PASSaGE v. 2.0.11.6 (Rosenberg & Anderson, 2011) with 1000 permutations (Odat et al., 2009; Papadopoulou et al., 2011). To this end, a simple Mantel test was first performed to explore the relationship between genetic distances (Kimura's 2-parameter method) and tree species dissimilarity indexes (pairwise differences of communities of the estimators of species diversity). The same test was used for assessing whether trans-specific genetic and species diversity could be affected by geographic distances or differences in elevation between sites. Accordingly, correlations of these variables with genetic distances and species dissimilarity indices were conducted between communities. Finally, to assess the relationship between genetic distances and tree communities regardless of the potential effects of geographic distances or altitudinal differences, a partial Mantel test was conducted (Odat et al., 2009).

Results

Species Diversity

The highest tree species diversity was found in San Joaquin ($Sp = 27$, $\exp H = 20.65$) and the lowest in Emilio Rabasa ($Sp = 17$, $\exp H = 10.96$). The inverse Simpson's index (*InvIS*) detected high dominance in Emilio Rabasa (about eight species) and the highest in San Joaquin (about 16 species) (Table 2).

The analysis within communities showed the highest gamma (γ) diversity at Emilio Rabasa ($\gamma = 97$ species), a locality that also showed the highest turnover rate ($\beta = 5$ species). These findings contrast with those for San Joaquin, a locality that showed the lowest beta diversity ($\beta = 2$ species) and the lowest total number of species ($\gamma = 60$ species). The analysis of the metacommunity, including five communities, yielded a richness of 20 species, beta (β) diversity of 4 species, and gamma (γ) diversity of 87 species.

Genetic Diversity

A total of 96 sequences were analyzed, corresponding to 19 tree species distributed in the five REBISO communities, which showed the quality needed for the analysis. GenBank accession numbers for these sequences are MN077267-MN077362 for ITS 1–2 and MN077167-MN077262 for ITS 3–4 (Online Appendix 1). This analysis revealed 53 unique haplotypes across the 19 species, with none of them shared among these species.

The lowest genetic diversity levels were detected in *Mariosousa centralis* ($s = 1$, $\pi = 0.001$, $Hd = 0.50$), *Manilkara zapota* ($s = 3$, $\pi = 0.001$, $Hd = 0.47$), and *Maytenus purpusii* ($s = 1$, $\pi = 0.0011$, $Hd = 0.47$). The highest nucleotide diversity levels occurred in *Mortoniodendron ocotense* ($\pi = 0.11$), *Zanthoxylum caribaeum* (Prickly yellow; $s = 80$, $\pi = 0.081$), *Protium copal* (Copal; $\pi = 0.078$) and *Bursera simaruba* ($s = 92$) (Table 3).

The lowest average genetic diversity values were recorded in Nuevo San Juan Chamula ($\pi = 0.18$, $s = 198$) and Emilio Rabasa ($Hd = 0.78$), and the highest in San Joaquin ($s = 307$, $\pi = 0.30$) and El Encajonado ($Hd = 0.94$) (Table 2).

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Table 2. Genetic diversity and diversity of tree species in five communities (Com) at Selva El Ocote Biosphere Reserve, based on the concatenation of ITS 1–2 and ITS 3–4 (1–4) regions of nuclear ribosomal DNA.

	Genetic diversity					Species diversity					
Com	N_{sec}	s	π	h	Hd	N_p	Sp	β	γ	exp$H$	$InvIS$
ER	26	249	0.22	11	0.78	10	17	5	97	10.96	7.79
SJ	9	307	0.30	6	0.92	3	27	2	60	20.65	15.50
VC	15	252	0.22	8	0.83	9	19	4	74	14.86	11.35
EE	29	214	0.24	16	0.94	9	20	3	71	14.36	10.29
NS	17	198	0.18	12	0.93	11	19	3	61	13.07	10.59

N_{sec} = number of sequences analyzed, s = segregating sites, π = nucleotide diversity, h = number of haplotypes, Hd = haplotype diversity, N_p = number of plots sampled, Sp = species richness, β = beta diversity, γ = gamma diversity, exp$H$ = Exponential of Shannon's index, $InvIS$ = inverse of Simpson's index, ER = Emilio Rabasa, SJ = San Joaquín, VC = Veinte Casas, EE = El Encajonado, NS = Nuevo San Juan Chamula.

Table 3. Genetic Diversity of 19 Tree Species at Selva El Ocote Biosphere Reserve Based on the Concatenation of the Nuclear Region of Ribosomal ITS 1 and ITS 3 (1–3) DNA.

Species	N	s	π	h	Hd
Mariosousa centralis	4	1	0.001	2	0.50
Astrocaryum mexicanum	2	1	0.002	2	1.00
Allophylus psilospermus	3	17	0.020	3	1.00
Brosimum alicastrum	6	6	0.003	3	0.60
Bursera simaruba	8	92	0.049	8	1.00
Citharexylum affine	2	1	0.002	2	1.00
Cordia alliodora	9	10	0.006	6	0.83
Dendropanax arboreus	3	3	0.004	3	1.00
Garcia nutans	3	36	0.041	3	1.00
Heliocarpus appendiculatus	10	5	0.003	5	0.80
Manilkara zapota	15	3	0.001	4	0.47
Maytenus purpusii	3	1	0.001	2	0.67
Mortoniodendron ocotense	2	68	0.106	2	1.00
Oreopanax geminatus	2	1	0.002	2	1.00
Protium copal	2	49	0.078	2	1.00
Psychotria chiapensis	9	20	0.009	5	0.86
Trichilia moschata	4	8	0.008	4	1.00
Zanthoxylum acuminatum	2	1	0.002	2	1.00
Zanthoxylum caribaeum	7	80	0.081	2	0.57

N = number of sequences analyzed, s = segregating sites, π = nucleotide diversity, h = number of haplotypes, Hd = haplotype diversity.

Genetic distances revealed that the tree communities in El Encajonado and Nuevo San Juan Chamula are genetically closer, while those in San Joaquin and Nuevo San Juan Chamula are the most distant ones (Figure 2).

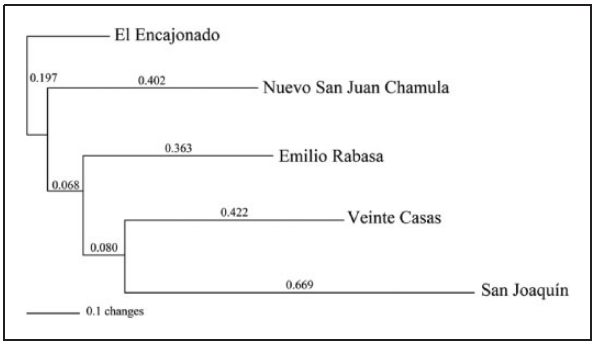


Figure 2. Clustering of Communities Using the Neighbor-Joining Method (Saitou & Nei, 1987) Based on Kimura's 2-Parameter Genetic Distances (Kimura, 1980), at Selva El Ocote Biosphere Reserve, Chiapas, Mexico.

Species-Genetic-Diversity Correlation

Linear regressions showed statistical significance between trans-specific nucleotide diversity (π) and species richness (Sp) ($r^2 = 0.90$, $P = 0.04$), as well as between haplotype diversity (Hd) and gamma diversity (γ) ($r^2 = -0.87$, $P = 0.05$) (Figure 3). Also, the regressions showed positive trends in the relationships of segregating sites (s) and haplotype diversity (Hd) with species diversity (Figure 3). Simple Mantel tests showed a non-significant relationship of genetic distances with elevation ($r^2 = -0.67$, $P = 0.93$) and with geographic distances ($r^2 = -0.43$, $P = 0.82$); likewise, a non-significant relationship was observed with the dissimilarity matrix of species richness between communities (Sp, exp$H$ and evenness; Table 4(a)). Besides, no statistical significance was observed for the relationships between genetic distances and species dissimilarity indexes with geographic distances and differences in elevation between communities (Table 4(b)).

Discussion

Tree communities at REBISO were diverse in terms of both species and intraspecific genetic diversity. However, our results partially confirmed the original expectation (i.e., a positive relationship between genetic diversity and species diversity), given that we observed a positive correlation between nucleotide diversity and species

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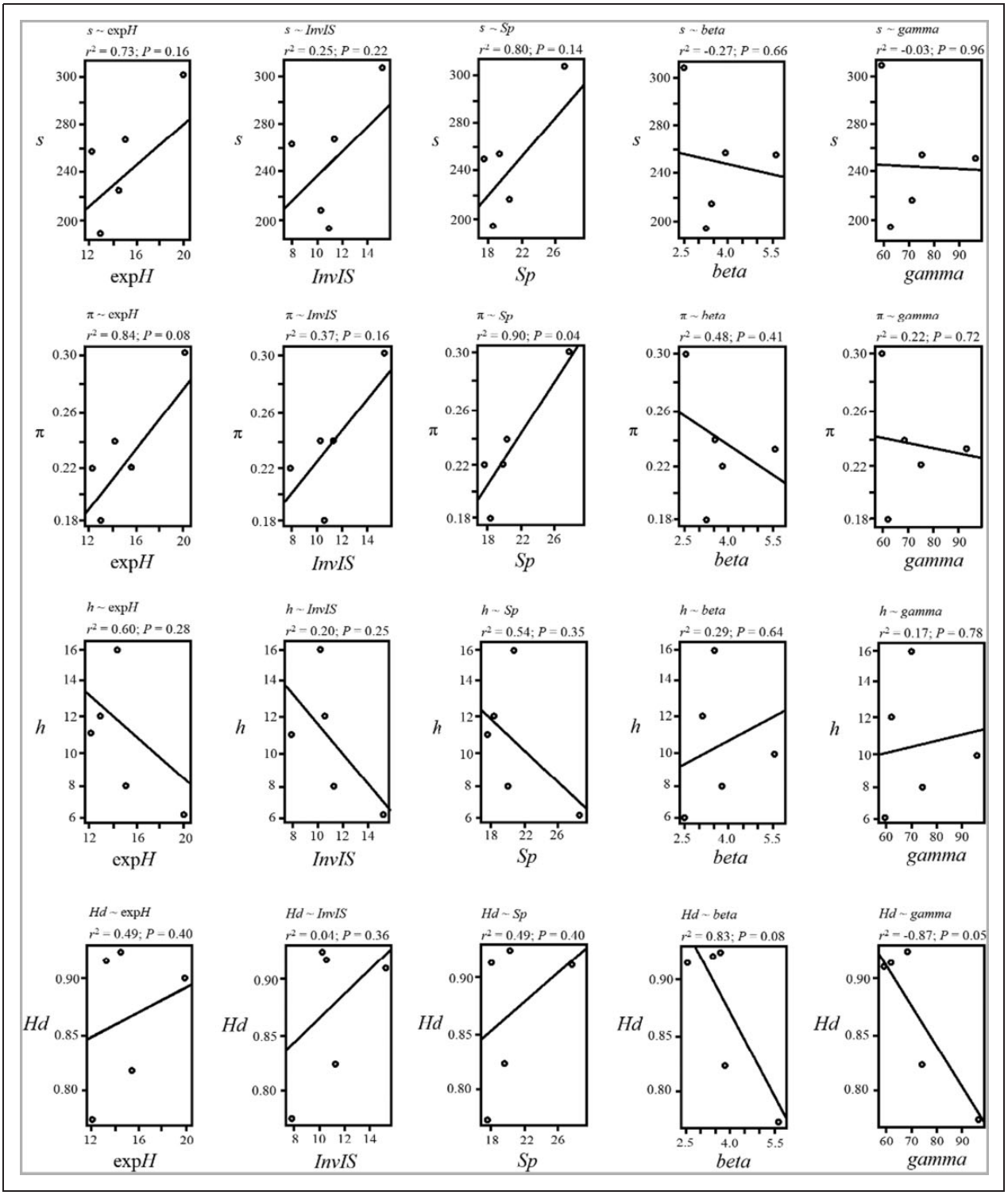


Figure 3. Simple Linear Regression Between Genetic Diversity and Species Diversity of Trees at Selva El Ocote Biosphere Reserve, Chiapas, Mexico. *s* = segregating sites, π = nucleotide diversity, *h* = number of haplotypes, *Hd* = haplotype diversity, exp*H* = Exponential of Shannon's index, *InvIS* = inverse of Simpson's index, *Sp* = species richness, *beta* = beta diversity, *gamma* = gamma diversity. Rows include genetic diversity; columns include species diversity parameters, aiming to show all potential combinations to correlate the two components of diversity.

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Table 4. Correlation (r^2) of Simple (a) and partial (b) Mantel Tests Between Genetic Distances and Dissimilarity of Tree Species at Selva El Ocote Biosphere Reserve.

(a)	Altitude	Geographic distances
Species dissimilarity		
InvIS	-0.54^{NS}	-0.09^{NS}
Sp	-0.47^{NS}	0.03^{NS}
exp*H*	-0.57^{NS}	-0.10^{NS}
(b)	Genetic distances	
Species dissimilarity	Altitude	Geographic distances
InvIS	0.48^{NS}	0.70^{NS}
Sp	$0.\ 69^{NS}$	0.86^{NS}
exp*H*	0.62^{NS}	0.79^{NS}

Geographic distances and altitudinal differences between localities were the constants in the partial Mantel test. *InvIS* = differences in evenness between pairs of communities, *Sp* = differences in species richness between pairs of communities, exp*H* = differences in exponential of Shannon's diversity index between pairs of communities. $^{NS} = P > 0.10$, $^{*} = P < 0.01$, $^{**} = P < 0.05$, $^{***} = P < 0.001$.

richness and a negative correlation between haplotype diversity and gamma diversity.

Our findings regarding species diversity are consistent with the global patterns described for the diversity of trees in tropical forests (Stropp et al., 2009; ter Steege et al., 2013), showing groups of species with high local abundance and others with low densities. Some studies that describe the diversity of tropical trees recognize that this diversity pattern is due to local (i.e., ecological interactions, microenvironmental conditions) and regional (e.g., migration, extinction) processes, as well as to evolutionary processes that lead to adaptation and speciation. This may explain the variations in species diversity at various geographic scales (Fine, 2015; Ricklefs & Schluter, 1993; Stropp et al., 2009).

According to Hubert et al. (2015), dispersal (migration) is a process that either restrains or strongly favors ecological speciation, diversification, and coexistence of species in a metacommunity. Anthropogenic events (e.g., change of land use, fires; Flamenco-Sandoval et al., 2007), physical-geographic conditions, and environmental heterogeneity (Manzanilla-Quiñones & Aguirre-Calderón, 2017) that characterize the REBISO are likely to be drivers of the limited dispersal of the tree communities, thus favoring the high local diversification and high alpha diversity observed. Altogether, these conditions may promote local adaptation processes and, ultimately, speciation (Stroud & Losos, 2016). The heterogeneous arrangement of species in the metacommunity should involve a high genetic diversity, given the number of species involved and because each species has a unique genetic pool that is preserved if its populations in REBISO maintain a low gene flow.

The species studied showed a wide range of genetic diversity, with some cases of low variation (e.g., *Mariosousa centralis*, *Manilkara zapota*, and *Maytenus purpusii*). The genetic diversity recorded is likely unevenly distributed across the constituent populations, which would mean that it is not expressed at the local community level either. The small sample size for some species and the low number of species studied from a genetic standpoint, relative to the species diversity in their communities, points to the need for a greater sampling effort to achieve a more robust statistical representation.

We expected a positive relationship between species diversity and genetic diversity under the assumption that these components of diversity interact with each other to establish a community. This interaction involves intraspecific evolutionary processes such as mutation, selection, drift, and migration, in addition to processes related to ecological dynamics, i.e., the distribution and abundance of species in the community (Evanno et al., 2009; Vellend, 2004, 2005). In general, this study shows a similar pattern in both trans-specific genetic diversity and species diversity: lower genetic and species diversity in Emilio Rabasa and Nuevo San Juan, and higher genetic and species diversity in San Joaquin; however, this relationship was statistically significant only between nucleotide diversity and species richness, on the one hand, and between haplotype diversity and gamma diversity, on the other. The lack of significance in the relationship between other parameters may be due to the statistical weakness related to low sample sizes for the species genetically analyzed and the small number of communities studied. Bearing in mind the low statistical power of the study, these findings suggest that the processes involved in the formation of genetic and species communities at REBISO are complex and difficult to detect.

Evolution in response to the environment takes place at the population level (Fitzpatrick & Keller, 2015); simultaneously, there are interactions between species, as well as migration and intra-specific competition, all of which determine genetic diversity at the population level (Laroche et al., 2015; Vellend, 2005; Vellend & Geber, 2005). Factors that vary temporarily and spatially, and local conditions (resources, environmental conditions, connectivity, species, populations sizes), exert a differential effect across species, which experience genetic changes at different rates and directions. These factors may explain the lack of correlation between some genetic diversity estimators and species diversity (Evanno et al., 2009; Lamy et al., 2017; Puscas et al., 2008; Vellend, 2005; Vellend & Geber, 2005; Wei & Jiang, 2012).

On the other hand, the phylogenetic distance between the species studied (derived from their belonging to different taxonomic families) means that these species evolved in different ways, resulting in various genetic diversity patterns, a condition that reduces the probability of observing a causal relationship that could be

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estimated in an SGDC (Taberlet et al., 2012). This probability may decrease even further according to the genetic marker chosen. The ITS is characterized by being a region that yields little information in intergeneric analyses because it can lead to incorrect kinship relationships (Nagy et al., 2012); besides, it captures a reduced intraspecific genetic variation relative to other genetic markers (Cruz-Salazar et al., 2017).

Furthermore, evolutionary and ecological processes are probably shared between species inhabiting the REBISO, but these do not affect the DNA region revealed in the same way (Vellend & Geber, 2005). Therefore, parallel processes do not necessarily lead to similar variation patterns in all estimators of genetic diversity and species diversity (Blum et al., 2012; Lamy et al., 2017; Puscas et al., 2008; Vellend & Geber, 2005). The results reported here highlight the need to analyze the genetic structure of species, or at least of the dominant species, across broad geographic areas, to obtain additional information on species diversity (see Genung et al., 2011; Simental-Rodríguez et al., 2014). Future studies should also include other genetic markers to support the results of this research, a larger sample size for each species, and a broader spatial scale to incorporate diverse communities and increase statistical power (Yu et al., 2009).

Although the results obtained here are limited, these suggest the expected relationship between genetic and species diversity. The trends observed here could be taken as a starting hypothesis for evaluation in future studies, also considering that intrinsic factors such as the dispersal syndrome, shade tolerance, resistance to disturbance, and mating system influence the genetic diversity of plants (Hamrick et al., 1993; Zeng et al., 2012). An aspect worth highlighting is the negative relationship between haplotype diversity and gamma diversity, suggesting that the scale of the analysis influences the SGDC, since a positive relationship is evident between genetic diversity and species diversity at a local scale (community), but an inverse relationship emerges at a regional scale (metacommunity). Probably, the increased competition associated with high species diversity, coupled with the limited gene flow between communities, gives rise to a negative relationship at the metacommunity level.

High evenness implies low abundance and limited distribution of most species within a community (Elton, 1958); thus, the resources locally available are not controlled by the dominant species (Odat et al., 2009; Vellend & Geber, 2005; Vellend, 2006). Under this ecological condition, a reasonable expectation is that the community may display a low genetic diversity, mainly due to random effects (Vellend, 2005). The five REBISO localities showed evenness (*InvIS*) values ranging from 7.79 at Emilio Rabasa to 15.50 at San Joaquin. This means that San Joaquin displayed a higher species richness and a more even distribution of the abundance of the species present, i.e., a lower dominance; by contrast, Emilio Rabasa showed lower values of species richness and evenness (7.79). The more genetically diverse community (San Joaquin, $\pi = 0.30$) displayed the highest species richness and evenness. These estimators are consistent with the species richness obtained; lower evenness (higher dominance) is associated with a higher turnover rate between communities, with the highest value ($\beta = 5$) observed in Emilio Rabasa. These findings suggest that higher numbers of dominant species in a community are related to lower species richness and genotypes, leading to greater differences in species composition between communities.

Implications for Tree Conservation

Current patterns of species richness and genetic diversity in plant communities are strongly affected by historical processes that have influenced the dispersal of organisms and the colonization of habitats (Ramírez-Marcial et al., 2017; Stewart et al., 2016). It has been suggested that tropical forests within protected natural areas are in a relatively stable state; however, there is evidence suggesting that global climate change is boosting changes in species structure and composition (van der Sande et al., 2016). These may be governed by environmental changes (local factors) such as variations in resource availability, heavier drought stress, and less resilience from previous disturbances (Stewart et al., 2016).

Considering that the knowledge of genetic and species diversity makes it possible to determine the evolutionary potential of a community and predict one diversity component as a function of the other (Kahilainen et al., 2014; Messmer et al., 2012), our study can contribute to project the diversity of REBISO at a larger spatial scale. However, further studies are needed to support the evaluation of SGDC in other communities within this Reserve. Since REBISO shows a variable composition across communities, it is important to emphasize the need to protect the five communities evaluated in this study to preserve the evolutionary potential of the whole metacommunity.

Genetic diversity allows species to respond to the selection imposed by competition. When fitness depends on the extent of functional similarity between one individual and its competitors, genetic diversity can foster the coexistence of species (Vellend, 2006). Furthermore, the genetic diversity of species may influence the structure of the community and ecosystem processes (Whitham et al., 2006). Therefore, it is essential to preserve the genetic diversity contained in an ecosystem subject to conservation, such as REBISO.

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We recommend conducting further genetic studies for *Mariosousa centralis, Manilkara zapota,* and *Maytenus purpusii* due to the low genetic diversity levels observed. In addition, our results indicate that the remainder of the species studied are characterized by a relatively higher genetic variability, which might provide them with a greater capacity for adaptive response to current environmental changes. Emilio Rabasa appears to be the most vulnerable community, in contrast with San Joaquin, which shows a diverse floristic composition and a genetic pool of high evolutionary potential.

Changes in land use and deforestation deteriorate forests at REBISO (Flamenco-Sandoval et al., 2007) because these reduce population size, modify the habitat, and increase the isolation between populations. All of this may lead, in the mid-term, to lower genetic diversity and species diversity due to the effects of genetic drift, ecological drift, and decreased migration (Frey et al., 2016; Hughes et al., 2008; Vellend & Geber, 2005; Vellend, 2006). It is imperative to maintain a mosaic of forest fragments to preserve tree diversity in REBISO, which could favor migration between populations and increase genetic diversity, the functionality of the ecosystem, and the ecological and evolutionary processes that occur in this important remnant of tropical forest.

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