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Genetic Diversity of Tropical Bats and Its Relationship With Ecological Role in a Tropical Semievergreen Rain Forest in El Ocote Biosphere Reserve, Chiapas, Mexico

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Abstract

Species that are functionally equivalent but with little taxonomical relationship may display similar genetic patterns if the ecological function evolves genetically in the same way. This study investigated the levels of genetic diversity in the *D-Loop* gene of random samples collected from 21 bat species inhabiting El Ocote Biosphere Reserve (REBISO, for its acronym in Spanish), and whether the genetic diversity pattern could be associated with the ecological role. Genetic differences between functional groups, localities, and species were evaluated through generalized linear models using the Gaussian distribution error family for nucleotide diversity (π) and the Poisson family for haplotype diversity (h) and segregating sites (s). To study the clustering pattern of species based on nucleotide variation, genetic distances (Kimura's two-parameter model) between functional groups were calculated, and a Principal Components Analysis on genetic diversity parameters was run. Most of the species analyzed (20) maintained genetic diversity levels ranging from medium to high in all genetic diversity estimators. According to genetic distances, the species with the same ecological function shared a greater number of nucleotide substitutions, with some exceptions. The Principal Components Analysis did not detect any genetic structure in relation to the ecological function. Our study found no association between the diversity of the *D-Loop* gene and ecological function; nonetheless, it confirms the importance of REBISO as a reservoir of bat species richness and genetic diversity in Mexico.

Keywords

conservation, community genetics, tropical bats, REBISO

Introduction

Genetic diversity determines the evolutionary potential of a species and its ability to cope with changes in its environment (Frankham, Ballou, & Briscoe, 2002). Community genetics aims at understanding how within-species variation, species diversity, and environmental factors interact to shape community assemblages (Lamy, Laroche, David, Massol, & Jarne, 2017). Genetic diversity within communities can correlate with species diversity, both within and between trophic levels, in at least three ways (Avolio, Beaulieu, Lo, & Smith, 2012). First, intraspecific genetic diversity can influence the species diversity, structure, and functioning of communities through a *genetic-feedback mechanism* (see Genung et al., 2011; Whitlock, 2014). Second, genetic diversity and ecological function can be associated through parallel responses to selection pressures and eco-evolutionary dynamics over time (Hughes, Inouye, Johnson, Underwood, & Vellend, 2008; Whitlock, 2014). Third, ecological interactions (e.g., competition,

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depredation, reproduction) determine demographic changes (birth, death, and movement of different biological types) affecting the dynamics of both populations and communities, hence establishing levels of species diversity and genetic structure within the community (Moreira, Abdala-Roberts, Parra-Tabla, & Mooney, 2014; Vellend & Geber, 2005). When competitive interactions dominate in a community, these increase the species diversity of one group while reducing the diversity in others by occupying the available niche space (Vellend, 2008). These conditions, together with the life history of the species (i.e., social structure, mating, behavior), may contribute to define the levels of genetic diversity (Lamy et al., 2017).

Understanding the relationship between genetic diversity and ecological function is key; if genetic diversity is a structuring driver in communities and ecosystems, it deserves to be included in ecological models constructed to explain the distribution, diversity, and abundance of species. In addition, the genetic diversity contained within species may determine the responses of communities and ecosystems to anthropogenic environmental change. Gaining knowledge on genetic diversity at the community level allows anticipating and managing the potential shifts in community structure and function that may arise as correlated responses. Also, the study of genetic diversity at a community level may provide useful information to evaluate the evolutionary potential, establish models for inferring evolutionary pathways within the community, and identify potential threats for a group of species, which can be useful to support strategies aimed at the conservation of priority species, communities, and ecosystems (Crawford & Rudgers, 2013).

The ecological function of a species is likely the result of natural selection, which drives adaptive differentiation (Hughes et al., 2008; Vellend, 2006; Whitham et al., 2006). The divergence between species is reflected in genetic relationships and ecological attributes, which in turn determine taxonomic groups (Aguirre, Montaño-Centellas, Gavilanez, & Stevens, 2016). However, the same ecological function can be observed in species with no apparent taxonomic relationship (He, Lamont, Krauss, Enright, & Miller, 2008; Symstad, 2000; Vellend & Geber, 2005). Species with little taxonomic relationship but with similar ecological functions may display similar genetic diversity patterns if the evolutionary processes that drive the diversification of species and their role occur concomitantly and in the same way (Avolio et al., 2012; Hoehn, Tscharntke, Tylianakis, & Steffan-Dewenter, 2008). Alternatively, species may be unrelated because of different evolutionary processes, by differences in their original gene pool, and because intrinsic ecological processes affect differentially the genetic diversity of each species (Aguirre et al., 2016; Freeland, 2005).

In theory, communities with high species diversity show a better ecosystem functioning than those with lower levels (Hoehn et al., 2008). The composition of a community depends on the survival and reproduction of the species, and these in turn are determined by genotypic composition. If evolution via natural selection promotes the coexistence of species, the loss of genetic diversity within species could hinder this process. This may lead to the loss of species (He et al., 2008; Vellend, 2006; Vellend & Geber, 2005), with negative effects on the community, particularly when the remaining species cannot assume or replace the ecological role that is lost along with the species (Cottontail, Wellinghausen, & Kalko, 2009; Crutsinger et al., 2006; Mooney et al., 2009; Park, 2015; Vellend, 2005; Vellend & Geber, 2005).

Tropical ecosystems are characterized by the highest species richness, biomass, and productivity levels (Ricklefs, 2004; Sahu, Sagar, & Singh, 2008). The expansion of human settlements and the need to increase productive areas in tropical regions has led to accelerated deforestation and habitat fragmentation, resulting in the loss of species and natural communities (Galindo-González & Sosa, 2003; Ripperger, Tschapka, Kalko, Rodríguez-Herrera, & Mayer, 2013). Bats are one of the most abundant and diverse mammal groups in tropical forests, displaying a great variety of behavioral, morphological, and ecological attributes; in these environments, bats play a key role in pollination, insect predation, and seed dispersal (Burns & Broders, 2014; Cosson, Pons, & Masson, 1999; Fenton et al., 2001; Fenton & Ratcliffe, 2010; Gorresen & Willig, 2004; Meyer, Struebig, & Willig, 2016). Bats are classified into five functional groups (trophic guilds) in relation to feeding habits and food preference: insectivorous, frugivorous, hematophagous, nectarivorous, and carnivorous (Calonge, 2009; Duckworth, Kent, & Ramsay, 2000; Merritt, 2010; Patterson, Willig, & Stevens, 2003; Reich, Walters, & Ellsworth, 1997; Reid, 2009; Soriano, 2000). The diverse functionality of bats involves ecological relationships with a wide range of species from other biological groups, both plants and animals (Medellín, Arita, & Sánchez, 1997).

There are approximately 140 species of bats in Mexico, accounting for about 13% of the total number of bat species worldwide (Ceballos & Ehrlich, 2002; Medellín et al., 1997). In El Ocote Biosphere Reserve (REBISO, for its acronym in Spanish), one of the main remnants of tropical forest in Mexico, 48 bat species have been recorded (accounting for 34% of the total number of bat species recognized in Mexico; Navarrete, Alba, March, & Espinoza, 1996). However, their genetic diversity has not been explored. The importance of bat species richness (Espinoza et al., 1999; Hernández-Mijangos, Gálvez-Mejía, Díaz-Negrete, & Cruz-Durante, 2008; Navarrete et al., 1996; Riechers, 2004, 2009) and the role of bats in the recovery of disturbed areas (Preciado-Benítez, Gómez, Navarrete-Gutiérrez, & Horváth, 2015) have been recognized to some extent. The current lack of information coupled with the continued habitat loss and fragmentation in El Ocote (Flamenco-Sandoval, Martínez, & Masera, 2007) call for the need to conduct research on this taxonomic group characterized by a high functional diversity.

Although some studies have correlated genetic diversity with species diversity (e.g., Avolio et al., 2012; Blum et al., 2012; Csergö, Hufnagel, & Höhn, 2014; Wei & Jiang, 2012), few have been conducted in México (outside the REBISO; e.g., Simental-Rodríguez et al., 2014; Wehenkel, Bergmann, & Gregorius, 2006) and none has related genetic diversity with the ecological function of species as intended in this research. The aim of this study was to determine the genetic diversity of a random sample of bat species in a semievergreen tropical forest at REBISO and explore whether this genetic diversity is correlated with the ecological role they play in the ecosystem. Considering that natural selection acts over all genomes and leads to an increased frequency of the genotypes governing the function of an organism in the community, our expectation was to find a positive relationship, that is, similar levels of genetic diversity across species with similar ecological functions, regardless of their taxonomic affinity. Measures of genetic diversity related to ecological function in a bat community can be further trait to estimate the conservation status and get an insight on their vulnerability to environmental changes.

Methods

Study Area

REBISO is a Protected Natural Area located to the northeast of the state of Chiapas, Mexico, between 16°45′42″ and 17°09′00″ N, and 93°54′19″ and 93°21′20″ W (Figure 1). The prevailing climate in El Ocote is warm and humid with abundant summer

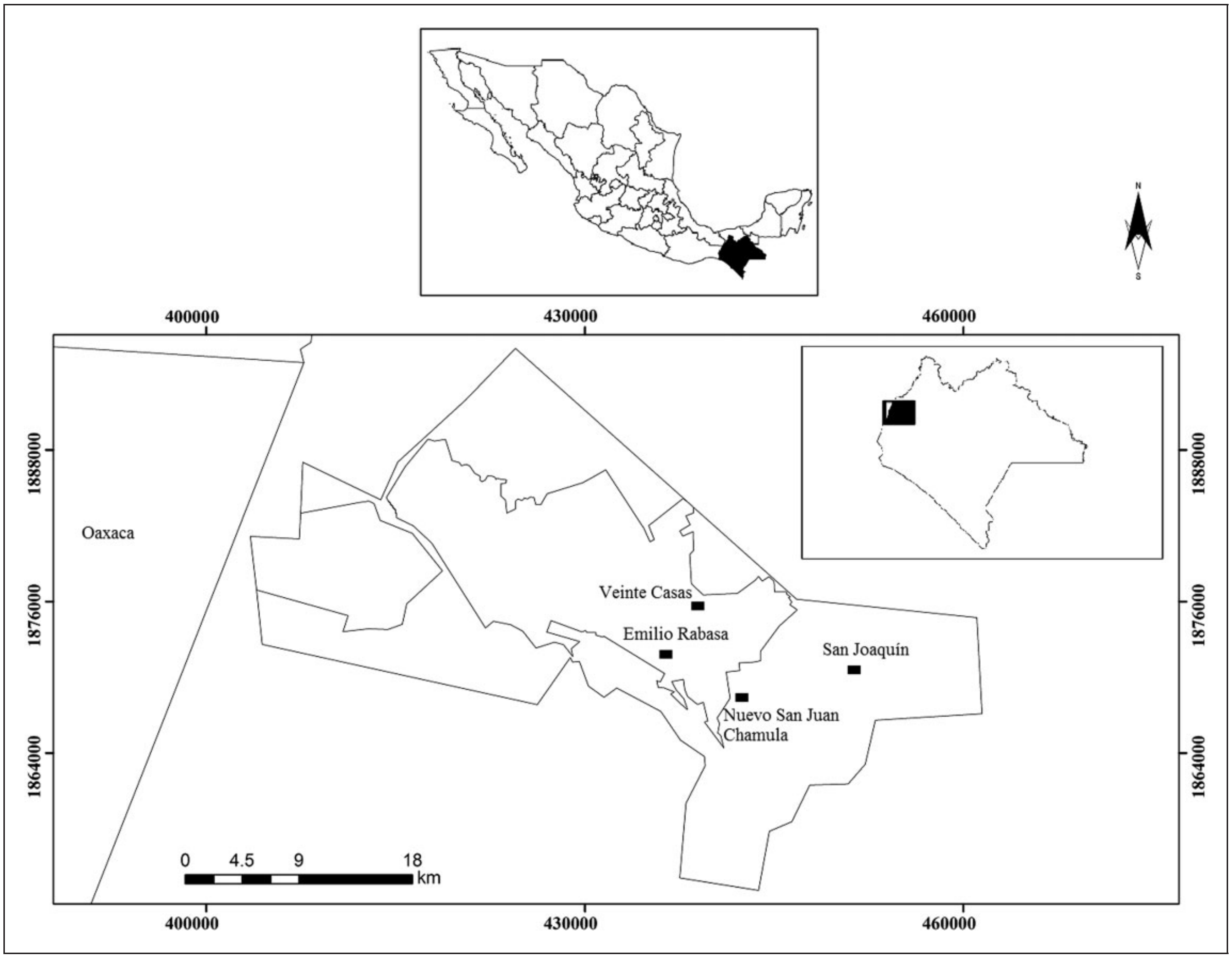

Figure 1. Location of the four sampling localities in El Ocote Biosphere Reserve for the sampling of tropical bats.

rainfall, with a mean annual precipitation of 2,145 mm and a mean annual temperature of 23.3°C (Secretaria de Medio Ambiente y Recursos Naturales-Comisión Natural de Áreas Naturales Protegidas, 2001). The study was conducted at localities within the core of REBISO, which are sites with semievergreen tropical forest (Veinte Casas, Emilio Rabasa, Nuevo San Juan Chamula and San Joaquín; Figure 1).

Fieldwork

Unlike conventional population genetics studies, which focus on obtaining a large sample size for different populations of a given species, our sampling design aimed at sampling the functional diversity of bats inhabiting the semievergreen tropical forest at REBISO. To this end, we focused on obtaining largest number of species with different ecological roles, thereby recording the genetic diversity associated with the ecological function of the species in the community. Two sampling sites were established; in each locality, bats were sampled over six consecutive nights with similar weather conditions and lunar phase, from January 2015 to September 2015 (4 Localities × 2 Sampling Sites × 6 Nights). In each sampling site, four mist nets (12 m × 2.5 m, 6 m × 2.5 m) were placed between the vegetation and near water bodies, at an average height of 2 m. In relatively open areas, nets were placed at 10 m height (Cosson et al., 1999; Preciado-Benítez et al., 2015). All nets remained open after sunset for seven hours (6p.m.–1a.m.). The specimens captured were identified taxonomically according to Medellín and Sánchez (2008) and Reid (2009). For each specimen, the biological characteristics (i.e., body size, sex, age, and reproductive status) and geographical location were recorded, and a tissue sample from the uropatagium was collected for genetic analysis; afterward, the specimen was released. Tissue samples were preserved in 1.5 ml vials containing 96% ethyl alcohol. Bat sampling was conducted under the collection license SGPA/DGVS/14214/15 issued by the Mexican Secretariat of Environment and Natural Resources (Secretaria de Medio Ambiente y Recursos Naturales).

DNA Extraction and Amplification

Genomic DNA was extracted through the cellular lysis method followed by purification with phenol/chloroform-isoamyl alcohol (Hamilton, Pincus, Di Fiore, & Fleicher, 1999). Genetic diversity was determined based on the control region of mitochondrial DNA (*D-Loop*); this gene is found in all vertebrates and is characterized by high substitution rates, allowing the comparison of the same genomic region between species to describe genetic structure at the intraspecific level (Piaggio, Navo, & Stihler, 2009). The *D-Loop* region was amplified with markers *D-Loop-E* (5′-CCTGAA GTAGGAACCAGATG-3′) and *D-Loop-P* (5′-CCCCA CCATCAACACCCAAAGCTGA-3′; Wilkinson & Chapman, 1991). Amplifications were performed in a C1000 Touch^{TM} thermal cycler (Bio-Rad) using a total volume of 50 µl. The amplification process consisted of an initial denaturation at 94°C × 4 min, 35 cycles at 94°C × 1 min (denaturation), 5°C × 1:30 min (alignment) and 72°C × 1 min (extension), and a final extension at 72°C × 10 min. To evaluate the amplification of the *D-Loop*, the PCR products were visualized through 2% agarose gel electrophoresis with a 100 base pair (bp) control marker (Ladder, PROMEGA). Positively amplified reactions were sequenced in Macrogen Inc, Korea, through capillary electrophoresis (Sanger) sequencing using the ABI PRISM® BigDyeTM Terminator Cycle Sequencing Kits and the ABI Prism® 3730XL Analyzer.

Analysis

The sequences obtained were edited with the program Chromas Pro v. 1.5 (McCarthy, 1996) and were aligned with the program Clustal X v. 2.1 (Thompson, Gibson, Plewniak, Jeanmougin, & Higgins, 1997). The genetic diversity parameters by species were obtained with the software DnaSP v. 5 (Librado & Rozas, 2009), based on the Kimura two-parameter substitution model (Kimura, 1980). The Tajima index (D) was estimated for each species (Tajima, 1989) to identify some of the demographic evolutionary processes associated with genetic diversity (e.g., bottleneck).

Genetic diversity was associated with three potential explanatory variables: ecological function, locality, and species. To assess the influence of each of these variables on genetic diversity (i.e., number of haplotypes [h], nucleotide diversity [π], segregating sites [s]), Generalized Linear Models were built with the software R v. 3 (R Core Team, 2013). According to the nature of the genetic parameters and their distribution, we used the Poisson error distribution family for Generalized Linear Model constructed for h and s, while for π the Gaussian family was used. All models were evaluated with the Akaike Information Criterion (AIC; Akaike, 1974) using the statistical package mentioned earlier.

Genetic distances between species were obtained with the Kimura two-parameter method (Kimura, 1980), with 1,000 bootstrap replicates using the program MEGA v. 6 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013). For this purpose, sequences were tested for similarity with the software TCS v. 1.21 (Clement, Posada, & Crandall, 2000). The clustering pattern was studied from dendrograms obtained through the Neighbor-Joining method (Saitou & Nei, 1987) using the PAUP program v. 4.0 a (Swofford, 2002). In addition, an analysis of genetic distances was carried out considering the four functional group, that is, frugivores, hematophages, insectivores, and nectarivores, assigning each species to one of these groups to get the genetic relationship between functional groups. Finally, the relationship between genetic structure and functional ecology was assessed through a Principal Components Analysis (PCA) with the software Statistica v. 8 (StatSoft, 2007); to this end, a colinearity analysis was performed between the three genetic diversity parameters (nucleotide diversity, segregating sites, number of haplotypes) through Pearson's correlations with the program R v. 3 (R Core Team, 2013).

Results

We analyzed 281 sequences from 21 bat species belonging to three taxonomic families (Phyllostomidae, Vespertilionidae, and Mormoopidae; Table 1). Of these, 11 were frugivores, four nectarivores, five insectivores, and one hematophage (Table 1). All sequences comprised 396 bp. GenBank accession numbers for these sequences are MF803983-MF804264 (Appendix). The composition of the *D-Loop* region showed 32.5% thymine, 12.6% cytosine, 31.6% adenine, and 23.4% guanine.

Eptesicus furinalis (Argentine brown bat, an insectivore) showed the lowest genetic variation ($s=0$,

Table 1. Taxonomic Classification, Acronyms, Common Names, and Functional Group of 21 Bat Species Inhabiting El Ocote Biosphere Reserve.

Family	Subfamily	Species	Species acronym	Common name	Functional group
Phyllosdomidae	Carollinae	*Carollia sowelli* (Baker, Solari y Hoffmann, 2002)	Cso	Sowell's short-tailed bat	F
	Desmodontinae	*Desmodus rotundus* (E. Geoffroy S.H., 1810)	Dro	Common vampire bat	H
	Glossophaginae	*Anoura geoffroyi* (Gray, 1838)	Age	Geoffroy's tailless bat	N
		Glossophaga morenoi (Martínez y Villa, 1938)	Gmo	Western long-tongued bat	N
		Glossophaga soricina (Pallas, 1766)	Gso	Pallas's long-tongued bat	N
		Hylonycteris underwoody (Thomas, 1903)	Hun	Underwood's long-tonguet bat	N
	Phyllostominae	*Micronycteris microtis* (Miller, 1898)	Mmi	Common big-eared bat	I
	Stenodermatinae	*Artibeus jamaicensis* (Leach, 1821)	Aja	Jamaican fruit-eating bat	F
		Artibeus lituratus (Olfers, 1818)	Ali	Great fruit-eating bat	F
		Centurio senex (Gray, 1842)	Cse	Wrinkle-faced bat	F
		Dermanura phaeotis (Miller, 1902)	Dph	Pygmy fruit-eating bat	F
		Dermanura tolteca (de Saussure, 1860)	Dto	Toltec fruit-eating bat	F
		Enchisthenes hartii (Thomas 1892)	Eha	Velvety fruit-eating bat	F
		Platyrrhinus helleri (Peters, 1866)	Phe	Heller's broad-nosed bat	F
		Sturnira parvidens (Goldman, 1917)	Spa	Little yellow-shouldered	F
		Sturnira hondurensis (Goodwin, 1940)	Sho	Highland yellow-shouldered bat	F
		Uroderma bilobatum (Peters, 1866)	Ubi	Tent-marking bat	F
Mormoopidae		*Mormoops megalophylla* (Peters, 1864)	Mme	Ghost-face bat	I
		Pteronotus parnellii (Gray, 1843)	Ppa	Common mustached bat	I
Vespertilionidae	Myotinae	*Myotis keaysi* (J. A. Allen, 1914)	Mke	Hairy-legged Myotis	I
	Vespertilioninae	*Eptesicus furinalis* (d'Orbigny y Gervais, 1847)	Efu	Argentine brown bat	I

Note. N = nectarivore; F = frugivore; I = insectivore; H = hematophage.

$\pi = 0.00$, and $h = 1$). *Artibeus jamaicensis* (Jamaican fruit-eating bat) showed the largest number of segregating sites (s) and haplotypes (h) ($s = 176$, $\pi = 39$), while *Micronycteris microtis* (Common big-eared bat, an insectivore) showed the highest nucleotide diversity ($\pi = 0.27$) (Table 1). Haplotype diversity (Hd) was high in most species ($Hd = 0.94$–1.00), except for *E. furinalis* ($Hd = 0.00$) and *Desmodus rotundus* (Common vampire bat; $Hd = 0.51$).

The Tajima test (D) was performed only in 11 of the 21 species analyzed due to the insufficient sample size for the analysis. We found a significant negative relationship between nucleotide diversity (π) and nucleotide variation by sequence (θ) in *A. jamaicencis* ($D = -2.68$, $p < .001$), *A. lituratus* (Great fruit-eating bat; $D = -2.09$, $p < .001$), and *D. rotundus* ($D = -2.32$, $p < .001$) (Table 2).

The genetic diversity measure, which included segregating sites (s), nucleotide diversity (π), and number haplotypes (h), was variable both across species and across localities within individual species (Figure 2(a) to (c)). Segregating sites displayed a wide variation from 0 to 160 (Figure 2(a)). Nucleotide diversity was also heterogeneous within and between both species and functional groups, ranging from 0.00 to 0.27 in *E. furinalis* and *M. microtis*, respectively (Figure 2(b)). The number of haplotypes was reduced for hematophagous, nectarivorous, and insectivorous species (Figure 2(c)). Species that could be sampled in more than one locality, like *A. jamaicensis* and *Carollia sowelli*, showed different level of s, π, and h per locality (Figure 2(a) to (c)). The best Generalized Linear Models identified by AIC was the species-by-locality interaction for all three genetic diversity parameters; however, none reached statistical significance (Table 3).

The clustering analyses showed a random grouping of species based on functional groups. A visual examination reveals two small groups of insectivores, a small group of nectarivores, a large group of frugivores, two groups with two species, and finally three isolated individual species (Figure 3). *Glossophaga soricina* (Pallas's long-tongued bat, a nectarivorous species) was clustered together with *C. sowelli* (Sowell's short-tailed bat), a frugivorous species (Figure 3). The analysis of genetic distances by functional group revealed the closest genetic relationship

Table 2. Genetic Diversity of 21 Tropical Bat Species Inhabiting El Ocote Biosphere Reserve Based on the Mitochondrial DNA Control Region (*D-loop*).

Species	N	s	π	h	Hd	D
Anoura geoffroyi	3	38	0.07	3	1.00	NA
Artibeus jamaicensis	99	176	0.02	39	0.97	-2.68^{***}
Artibeus lituratus	16	110	0.06	12	0.96	-2.09^{***}
Carollia sowelli	42	68	0.04	34	0.99	-0.77^{a}
Centurio senex	4	9	0.01	4	1.00	-0.53^{a}
Dermanura phaeotis	5	82	0.10	5	1.00	-1.10^{a}
Dermanura tolteca	28	22	0.01	16	0.94	-1.27^{a}
Desmodus rotundus	14	84	0.04	5	0.51	-2.32^{***}
Enchisthenes hartii	4	53	0.08	4	1.00	-0.64^{a}
Eptesicus furinalis	3	0	0.00	1	0.00	NA
Glossophaga morenoi	2	81	0.24	2	1.00	NA
Glossophaga soricina	2	3	0.009	2	1.00	NA
Hylonycteris underwoody	2	3	0.009	2	1.00	NA
Micronycteris microtis	3	127	0.27	3	1.00	NA
Myotis keaysi	2	34	0.09	2	1.00	NA
Mormoops megalophylla	3	8	0.02	3	1.00	NA
Platyrrhinus helleri	2	10	0.03	2	1.00	NA
Pteronotus parnellii	6	36	0.05	6	1.00	0.49^{a}
Sturnira parvidens	10	21	0.02	8	0.96	-0.52^{a}
Sturnira hondurensis	29	95	0.06	21	0.96	-0.74^{a}
Uroderma bilobatum	2	46	0.13	2	1.00	NA

Note. N = Sample size; s = segregating sites; π = nucleotide diversity; h = number of haplotypes; Hd = haplotype diversity; D = Tajima's test; NA = not analyzed.

aNot significant, $p > .10$.

$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

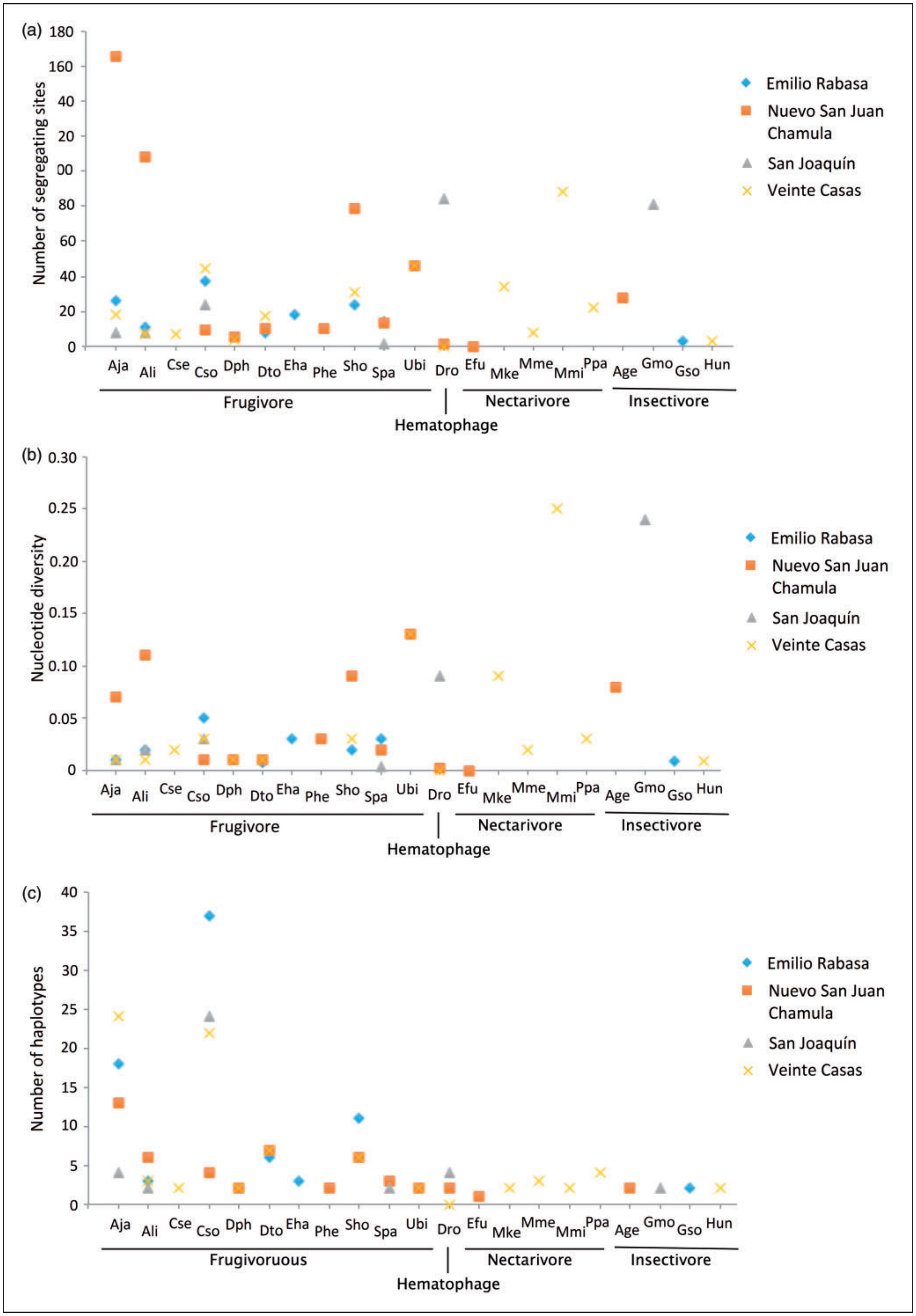

Figure 2. Distribution of the genetic diversity based on the mitochondrial DNA *D-Loop* region, of 21 bat species according to the ecological role, in four localities of El Ocote Biosphere Reserve.

Table 3. Generalized Linear Models to Explain the Genetic Diversity of 21 Tropical Bat Species Inhabiting El Ocote Biosphere Reserve.

Model		AIC
1	**$\pi \sim$ species $\times$ locality**	**-2560.60^{a}**
2	$\pi \sim$ locality $\times$ functional group	-59.05^{a}
3	$\pi \sim$ species $+$ locality	-68.22^{a}
4	$\pi \sim$ locality $+$ functional group	-44.98^{a}
5	**$h \sim$ species $\times$ locality**	**139.91^{a}**
6	$h \sim$ locality $\times$ functional group	239.40^{a}
7	$h \sim$ species $+$ locality	217.99^{a}
8	$h \sim$ locality $+$ functional group	231.47^{a}
9	**$s \sim$ species $\times$ locality**	**258.61^{a}**
10	$s \sim$ locality $\times$ functional group	339.68^{a}
11	$s \sim$ species $+$ locality	361.42^{a}
12	$s \sim$ locality $+$ functional group	360.90^{a}

Note. The best model according to AIC is highlighted in **bold**. π = nucleotide diversity (Gaussian family); s = segregating sites (Poisson family); h = number of haplotypes (family = Poisson); AIC = Akaike Information Criterion (Akaike, 1974).
aNot significant, $p > 0.10$.
$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

between frugivores and nectarivores (0.205), followed by hematophages and frugivores (0.331), frugivores and insectivores (0.347), nectarivores and hematophages (0.349), and nectarivores and insectivores (0.371); the greatest genetic distance occurred between insectivores and hematophages (0.470).

In the PCA, the first three components accounted for 100% of the genetic variation. Variables in the first and third components made a similar contribution: segregating sites (s) showed the greatest contribution (0.57, 0.43), followed by the number of haplotypes (h) (0.25). In the second component, both nucleotide diversity (π) (0.55) and the number of haplotypes (h) (0.45) accounted for virtually all the variation. The three components were positively related to the three genetic diversity variables, that is, segregating sites (s), number of haplotypes (h), and nucleotide diversity (π). The PCA showed no relationship between genetic structure and functional groups (Figure 4).

Discussion

When genetic diversity is high, the capacity of a species is better suited to respond to environmental selective pressures and stochastic events (Frankham et al., 2002). The levels of genetic diversity detected in this study suggest that 20 of the 21 species analyzed probably maintain genetic diversity levels that may contribute to their conservation if changes in the local habitat continue at the current rate (Flamenco-Sandoval et al., 2007; Frankham et al., 2002). With the exception of *E. furinalis* ($\pi = 0.000$), the genetic diversity of the bats studied lied within the range reported in previous studies of some species. For example, in *A. jamaicensis* and based on the same mitochondrial gene (*D-Loop*), a range of $\pi = 0.009$–0.23 was reported (Carstens, Sullivan, Dávalos, Larsen, & Pedersen, 2004; Llaven, Ruiz, García, Lesher, & Machkour, 2017; Redondo, Brina, Silva, Ditchfield, & Santos, 2008; Ruiz, Vargas-Miranda, & Zúñiga, 2013).

The lack of genetic variation observed in *E. furinalis* (an insectivore) in REBISO ($\pi = 0{,}000$, $s = 0$, $h = 1$) is worth noting; this may be associated either with a likely recent bottleneck or with sweeping selection. Both processes lead to a drastic decrease in genetic diversity levels (Kaplan, Darden, & Hudson, 1989; Perfectii, Picó, & Gómez, 2009). *Glossophaga morenoi* and *M. microtis* showed the highest genetic diversity ($\pi = 0.24$, 0.27, respectively). According to the IUCN Red List, *M microtis* is a generalist bat characterized by high tolerance to disturbance and high local abundance (Miller, Reid, Arroyo-Cabrales, Cuarón, & de Grammont, 2008), moreover, Téllez-Girón and Ceballos (2005) consider that this bat is a common species in undisturbed areas in Mexico, which account for the high genetic diversity levels observed in REBISO. The case of *G. morenoi* (Western long-tongued bat) is worth noting, since its endemism (Arita, 2005) would suggest a lower genetic diversity relative to species such as *A. jamaicensis* (Ortega & Steers, 2005), contrary to what we found in REBISO. However, populations of *G. morenoi* with high local abundance have been recently reported in protected areas in southern Mexico (Arroyo-Cabrales, Álvarez-Castañeda, Cuarón, & Grammont, 2015), which may explain the high levels of genetic diversity found in REBISO populations.

Hd was high in 19 species ($Hd = 0.94$–1.00), indicating a lower genetic diversity in *D. rotundus* and *E. furinalis* (Arboleda, 2008; Castillo-Cobián, 2007). *Desmodus rotundus* showed an intermediate value of unique haplotypes ($Hd = 0.51$) that may be related to its migratory habits, high flight capacity (>100 km), and high tolerance to anthropogenic environments (Burns & Broders, 2014; Castro-Castro, Muñoz-Flores, & Uieda, 2016). All these features can facilitate gene flow between populations of the REBISO localities studied and others outside the Reserve (Burns & Broders, 2014).

The Tajima test suggest that *A. jamaicensis*, *A. lituratus*, and *D. rotundus* are undergoing a population expansion, a condition that may result from their high tolerance to disturbed environments and their ability to use various types of habitats (Ortega & Steers, 2005; Steers & Flores, 2005; Suzán, 2005). The recent changes in land use and human activities that have transformed much of REBISO into crop and livestock areas

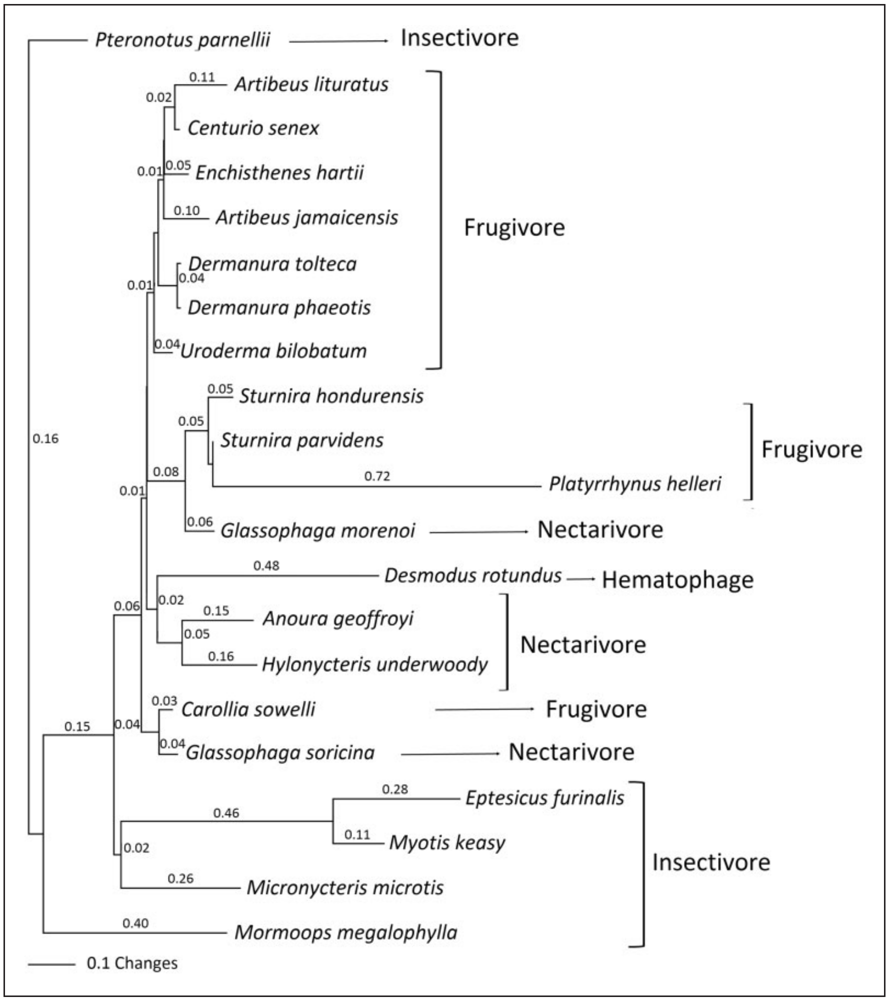

Figure 3. Kimura's two-parameter genetic distances (Kimura, 1980), with 1,000 bootstrap replicates, of 21 tropical bat species from El Ocote Biosphere Reserve, built by the Neighbor-Joining method (Saitou & Nei, 1987) based on the mitochondrial DNA *D-Loop* region.

(Flamenco-Sandoval et al., 2007) have probably favored the populations of both *D. rotundus* and *Artibeus* spp., as evidenced by their high abundance and association with crop areas (Barquez, Perez, Miller, & Diaz, 2015; Miller, Reid, Arroyo-Cabrales, Cuarón, & de Grammont, 2016).

These findings should be interpreted with caution, as the genetic diversity values for bat species reported here could be modified if further studies include a larger sample size by species (in terms of both individuals and populations) using a different molecular marker. The smaller the number of individuals captured, the lower the possibility of obtaining genetic variants; thus, a small sample size may lead to underestimate the genetic diversity of at least some species. Initially, we were interested to obtain a diversity genetic measure for several bats species for which no specific molecular markers have been developed to date. For this reason, we selected the *D-Loop* for its suitability to be reproducible and variable across mammal species (Freeland, 2005; Hernández-Baños, Honey-Escandón, Cortés-Rodríguez, & García, 2007). This gene allowed having a genetic diversity measure to be correlated with ecological community factors, such as species richness and locality.

We found no significant correlation between genetic diversity based on variations in the *D-Loop* gene and functional group. It is possible that the relationship between the genetic diversity of a species and its ecological function within a community is mediated by geographical distribution and ecological interactions.

Kimura's two-parameter genetic distances clustered species sharing the same ecological function, with a few exceptions (*G. soricina*, *G. morenoi*, *C. sowelli*, and *P. parnellii*), indicating that the number of nucleotide substitutions in these lineages is similar between species that coincide in feeding habits. The Kimura two-parameter genetic distances obtained in this study are consistent with those reported by Simmons, Seymour, Habersetzer, and Gunnell, (2008), who mention that

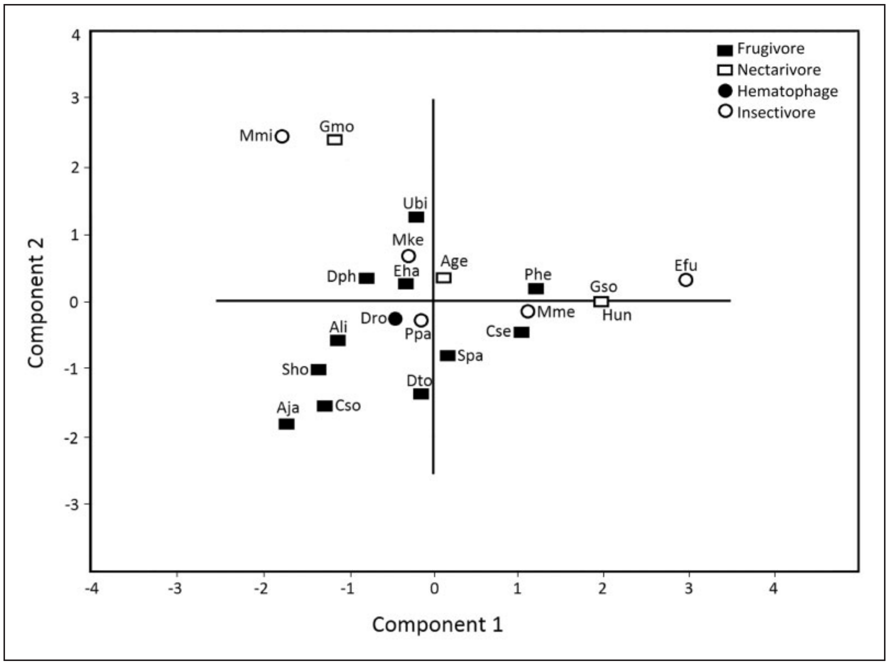

Figure 4. Principal Components Analysis of the genetic diversity of 21 tropical bat species from El Ocote Biosphere Reserve.

insectivory is the ancestral feeding habit in the Chiroptera, while frugivores and nectarivores evolved subsequently.

The close relationship between frugivores and nectarivores may be due to the fact that they occasionally share food resources during periods of resource scarcity (fruits, nectar), according to the composition of the habitat and landscape heterogeneity (Calonge, 2009; Pedro & Taddei, 1997; Vleut, Levy-Tacher, de Boer, Galindo-González, & Vázquez, 2013; Vleut, Levy-Tacher, Galindo-González, & de Boer, 2015). In addition, frugivorous and nectarivorous bats are essentially tropical (Fleming, Geiselman, & Kress, 2009), a condition that could determine a converging evolutionary history of these functional groups (Hughes et al., 2008).

Within a community, species interact in time and space regardless of their taxonomic affinity (Martínez, 1996); these interactions may lead to feedback evolutionary processes (Genung et al., 2011). As a result, the evolutionary history of each species exerts a crucial effect on the genetic structure and diversity of communities (Vellend, 2005, 2006; Vellend & Geber, 2005), in ways not yet unveiled for the bat community in the tropical forest of REBISO. One possibility is that the evolutionary processes that govern the levels of genetic diversity are independent of their role in the ecosystem (Vellend, 2005; Vellend & Geber, 2005), and are probably determined by the historical, biological and behavioral characteristics of each species (Lamy et al., 2017). These factors can explain the genetic distances observed, with two different groups of frugivores, as well as isolated individual species.

An aspect that could influence genetic diversity at the community level is intra- and interspecific competition, which interferes with the strength of natural selection and is expected to increase genetic diversity (Vellend, 2008). Another factor of importance is the life history of the species (e.g., behavior, dispersal, feeding, and reproduction), as it determines the geographical distribution, population dynamics, and genetic polymorphism (Arboleda, 2008; Burns & Broders, 2014; Hedrick, 2000). Population size, flight capacity for searching food and colonization of new sites, reproduction (i.e., polygamous vs. monogamous), and tolerance to disturbance are all characteristics that influence the competitive ability (Meyer et al., 2016) and responses to selective pressures of individual species. These characteristics are unique to each species and may facilitate evolutionary processes (genetic drift and genetic flow) with different intensity and frequency over time (Moreira et al., 2014), leading to variable levels of genetic diversity and preventing the identification of parallel ecological-evolutionary processes between functional groups (Vellend & Geber, 2005; Whitlock, 2014).

It is important to underline that the limitations of the local geographical scale used may have not captured the genetic variation contained within each individual species to an extent that would allow an accurate identification of the genetic diversity patterns associated with functional groups (Jackson & Fahrig, 2014). Furthermore, the limited resources for fieldwork in this study, as well as the rarity and geographical distribution of hematophagous bats likely resulted in that our total sample failed to capture a number of hematophagous species equivalent to those recorded for nectarivorous, frugivorous, and insectivorous bats, likely lowering the statistical power of the comparisons between functional groups.

Social structure, mating systems, and past and current environmental conditions (Burns & Broders, 2014; Hedrick, 2000) are all important aspects to consider to explain the genetic structure of communities (Hoehn et al., 2008; Vellend, 2008); therefore these aspects should be included in subsequent analysis. Likewise, knowing the demography, niche breadth, and niche overlap between both species and functional groups will allow a better assessment of the association between genetic diversity and ecological function to unveil how these interactions influence genetic diversity patterns (Hedrick, 2000; Hughes et al., 2008; Vellend, 2008; Whitlock, 2014).

Implications for Conservation

A high genetic diversity was observed in the bat assemblages inhabiting REBISO, although some species may be more vulnerable than others to changes in their habitat (Ávila-Flores & Fenton, 2005; Bilgin, Karatas, Coraman, Disotell, & Morales, 2008; Meyer et al., 2016), in particular those with limited mobility or specialized ecological requirements (Martins, Ditchfield, Meyer, & Morgante, 2007). This may be the case of *E. furinalis*, which showed extremely low genetic diversity values. Although our results may be limited due to the low sample size of *E. furinalis* ($N = 3$), we suggest monitoring this species in REBISO. Local human activities can severely affect the isolation of populations and population size, both of which reduce genetic diversity and increase species vulnerability (Ripperger et al., 2013). Therefore, *E. furinalis* should be considered as priority species warranting close monitoring in REBISO.

El Ocote Biosphere Reserve is a key biological corridor for the fauna of moist tropical forests that harbor Neartic and Neotropical species and facilitates the genetic flow between two natural areas of paramount importance in Mexico and the world: Uxpanapa, Veracruz and Chimalapas, and Oaxaca (Flamenco-Sandoval et al., 2007). This research highlights the ecological relevance of El Ocote for its high bat species richness (Mendoza-Sáenz, 2016; Riechers, 2004, 2009) and genetic diversity.

Unfortunately, the changes in land use at REBISO are the primary factor of habitat loss and transformation (Flamenco-Sandoval et al., 2007), leading to the disruption of functional connectivity and the decreased evolutionary potential and survival of species and communities at a regional scale (Frankham et al., 2002; Hedrick, 2000; Hoehn et al., 2008; Jackson & Fahrig, 2014). All of this undermines the environmental services provided by the ecosystem, with important effects on the local human populations that subsist and benefit from these resources. Therefore, maintaining the biodiversity and ecological functionality of REBISO requires preserving the species diversity and genetic diversity of tropical bats through the control of the loss of habitat caused by changes in land use and human activities. This research is the first of its kind in REBISO, contributing to conservation based on the knowledge of biodiversity, and gives rise to a number of different questions about the patterns of genetic diversity and community genetics of tropical bats.

Appendix. List of Samples of 21 Species of Tropical Bats From El Ocote Biosphere Reserve, Chiapas, Mexico

Species	Locality	Laboratory code	GenBank accession number
Pteronotus parnellii	Emilio Rabasa	Ppa02TR1	MF803983
Artibeus lituratus	San Joaquín	Ali02TS2	MF803984
Dermanura tolteca	Nuevo San Juan Chamula	Dto04TN2	MF803985
Artibeus jamaicensis	Emilio Rabasa	Aja09TR1	MF803986
Centurio senex	Nuevo San Juan Chamula	Cse01TN1	MF803987
Artibeus jamaicensis	Emilio Rabasa	Aja05TR1	MF803988
Carollia sowelli	San Joaquín	Cso04TS2	MF803989
Desmodus rotundus	Veinte Casas	Dro02TV2	MF803990
Eptesicus furinalis	Nuevo San Juan Chamula	Efu01TN1	MF803991
Dermanura tolteca	Nuevo San Juan Chamula	Dto02TN2	MF803992
Carollia sowelli	Veinte Casas	Cso03TV3	MF803993
Pteronotus parnellii	Nuevo San Juan Chamula	Ppa01TN3	MF803994

(continued)

Continued

Species	Locality	Laboratory code	GenBank accession number
Desmodus rotundus	Nuevo San Juan Chamula	Dro02TN2	MF803995
Artibeus jamaicensis	Emilio Rabasa	Aja04TR1	MF803996
Artibeus lituratus	Nuevo San Juan Chamula	Ali05TN2	MF803997
Dermanura tolteca	Nuevo San Juan Chamula	Dto05TN2	MF803998
Carollia sowelli	San Joaquín	Cso06TS1	MF803999
Myotis keaysi	Veinte Casas	Mme04TV3	MF804000
Eptesicus furinalis	Nuevo San Juan Chamula	Efu03TN1	MF804001
Artibeus jamaicensis	Veinte Casas	Aja05TV2	MF804002
Carollia sowelli	Veinte Casas	Cso29TV2	MF804003
Artibeus lituratus	Nuevo San Juan Chamula	Ali03TN2	MF804004
Artibeus jamaicensis	Veinte Casas	Aja13TV3	MF804005
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja12TN2	MF804006
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja05TN1	MF804007
Carollia sowelli	Veinte Casas	Cso05TV3	MF804008
Myotis keaysi	Veinte Casas	Mke02TV2	MF804009
Artibeus jamaicensis	Veinte Casas	Aja45TV2	MF804010
Uroderma bilobatum	Veinte Casas	Ubi01TV1	MF804011
Artibeus jamaicensis	Emilio Rabasa	Aja29TR1	MF804012
Artibeus jamaicensis	Veinte Casas	Aja01TV1	MF804013
Artibeus jamaicensis	Veinte Casas	Aja06TV3	MF804014
Myotis keaysi	Veinte Casas	Mke01TV2	MF804015
Micronycteris microtis	Emilio Rabasa	Mmi01TR1	MF804016
Dermanura phaeotis	Veinte Casas	Dph22TV2	MF804017
Carollia sowelli	Veinte Casas	Cso04TV3	MF804018
Sturnira hondurensis	Veinte Casas	Sho24TV2	MF804019
Carollia sowelli	Emilio Rabasa	Cso02TR1	MF804020
Glossophaga morenoi	San Joaquín	Gmo01TE1	MF804021
Sturnira hondurensis	Veinte Casas	Sho26TV2	MF804022
Sturnira hondurensis	Nuevo San Juan Chamula	Sho03TN3	MF804023
Carollia sowelli	Veinte Casas	Cso21TV2	MF804024
Dermanura tolteca	San Joaquín	Dph01TS2	MF804025
Glossophaga soricina	Emilio Rabasa	Gso01TR1	MF804026
Sturnira hondurensis	Nuevo San Juan Chamula	Sho01TN3	MF804027
Sturnira hondurensis	Veinte Casas	Sho22TV2	MF804028
Sturnira hondurensis	Veinte Casas	Sho20TV2	MF804029
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja02TN3	MF804030
Artibeus jamaicensis	Veinte Casas	Aja44TV2	MF804031
Dermanura tolteca	Veinte Casas	Dto03TV3	MF804032
Artibeus jamaicensis	Veinte Casas	Aja02TV1	MF804033
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja10TN2	MF804034
Carollia sowelli	Veinte Casas	Cso23TV2	MF804035
Pteronotus parnellii	Veinte Casas	Ppa02TV3	MF804036
Artibeus jamaicensis	Veinte Casas	Aja37TV2	MF804037
Artibeus jamaicensis	Emilio Rabasa	Aja13TR1	MF804038
Dermanura tolteca	Veinte Casas	Dto03TV1	MF804039
Artibeus jamaicensis	Veinte Casas	Aja42TV2	MF804040
Dermanura tolteca	Veinte Casas	Dto05TV3	MF804041

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Continued

Species	Locality	Laboratory code	GenBank accession number
Carollia sowelli	Nuevo San Juan Chamula	Cso02TN2	MF804042
Artibeus jamaicensis	Veinte Casas	Aja44TV3	MF804043
Artibeus jamaicensis	Veinte Casas	Aja11TV3	MF804044
Artibeus jamaicensis	Emilio Rabasa	Aja22TR1	MF804045
Dermanura tolteca	Nuevo San Juan Chamula	Dto03TN2	MF804046
Artibeus jamaicensis	Veinte Casas	Aja15TV3	MF804047
Artibeus jamaicensis	Emilio Rabasa	Aja03TR1	MF804048
Dermanura tolteca	Nuevo San Juan Chamula	Dto04TN1	MF804049
Artibeus jamaicensis	Veinte Casas	Aja05TV3	MF804050
Dermanura phaeotis	Nuevo San Juan Chamula	Dph01TN2	MF804051
Dermanura phaeotis	Veinte Casas	Dph21TV2	MF804052
Enchisthenes hartii	Emilio Rabasa	Eha01TR1	MF804053
Artibeus jamaicensis	Veinte Casas	Aja18TV3	MF804054
Artibeus lituratus	Nuevo San Juan Chamula	Ali06TN2	MF804055
Carollia sowelli	Veinte Casas	Cso02TV2	MF804056
Carollia sowelli	Veinte Casas	Cso22TV2	MF804057
Carollia sowelli	San Joaquín	Cso33TS2	MF804058
Artibeus jamaicensis	Veinte Casas	Aja04TV1	MF804059
Artibeus jamaicensis	Emilio Rabasa	Aja18TR1	MF804060
Artibeus jamaicensis	Veinte Casas	Aja41TV2	MF804061
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja01TN2	MF804062
Artibeus jamaicensis	Veinte Casas	Aja03TV3	MF804063
Artibeus jamaicensis	Veinte Casas	Aja16TV3	MF804064
Artibeus jamaicensis	Emilio Rabasa	Aja14TR1	MF804065
Artibeus jamaicensis	Emilio Rabasa	Aja23TR1	MF804066
Centurio senex	Veinte Casas	Cse01TV1	MF804067
Glossophaga soricina	Emilio Rabasa	Gso02TR1	MF804068
Carollia sowelli	Veinte Casas	Cso01TV3	MF804069
Carollia sowelli	Veinte Casas	Cso08TV3	MF804070
Carollia sowelli	Emilio Rabasa	Cso03TR1	MF804071
Carollia sowelli	Emilio Rabasa	Cso10TR1	MF804072
Artibeus jamaicensis	Veinte Casas	Aja19TV3	MF804073
Artibeus jamaicensis	Veinte Casas	Aja08TV3	MF804074
Carollia sowelli	Veinte Casas	Cso24TV2	MF804075
Carollia sowelli	Veinte Casas	Cso26TV2	MF804076
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja14TN2	MF804077
Dermanura tolteca	Emilio Rabasa	Dto03TR1	MF804078
Artibeus jamaicensis	Emilio Rabasa	Aja30TR1	MF804079
Carollia sowelli	Emilio Rabasa	Cso04TR1	MF804080
Carollia sowelli	Emilio Rabasa	Cso05TR1	MF804081
Artibeus lituratus	Emilio Rabasa	Ali01TR1	MF804082
Sturnira hondurensis	Veinte Casas	Sho02TV2	MF804083
Artibeus jamaicensis	Veinte Casas	Aja03TV2	MF804084
Carollia sowelli	Emilio Rabasa	Cso07TR1	MF804085
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja11TN2	MF804086
Carollia sowelli	Veinte Casas	Cso03TV2	MF804087
Carollia sowelli	Veinte Casas	Cso20TV2	MF804088

(continued)

Continued

Species	Locality	Laboratory code	GenBank accession number
Carollia sowelli	Veinte Casas	Cso28TV2	MF804089
Desmodus rotundus	San Joaquín	Dro07TS2	MF804090
Carollia sowelli	Veinte Casas	Cso01TV2	MF804091
Carollia sowelli	Veinte Casas	Cso03TV1	MF804092
Carollia sowelli	Veinte Casas	Cso04TV2	MF804093
Artibeus jamaicensis	Emilio Rabasa	Aja17TR1	MF804094
Artibeus jamaicensis	Veinte Casas	Aja01TV2	MF804095
Artibeus jamaicensis	Veinte Casas	Aja17TV3	MF804096
Artibeus lituratus	Nuevo San Juan Chamula	Ali04TN2	MF804097
Artibeus jamaicensis	Emilio Rabasa	Aja27TR1	MF804098
Dermanura tolteca	Emilio Rabasa	Dto04TR1	MF804099
Artibeus lituratus	Emilio Rabasa	Ali01TR3	MF804100
Dermanura tolteca	Veinte Casas	Dto04TV3	MF804101
Artibeus jamaicensis	Emilio Rabasa	Aja08TR1	MF804102
Dermanura tolteca	Veinte Casas	Dto05TV1	MF804103
Dermanura tolteca	Nuevo San Juan Chamula	Dto22TN2	MF804104
Sturnira parvidens	Emilio Rabasa	Spa04TR1	MF804105
Desmodus rotundus	San Joaquín	Dro03TS2	MF804106
Sturnira hondurensis	Emilio Rabasa	Sho05TR1	MF804107
Eptesicus furinalis	Nuevo San Juan Chamula	Efu02TN1	MF804108
Artibeus jamaicensis	Emilio Rabasa	Aja19TR1	MF804109
Artibeus jamaicensis	Veinte Casas	Aja32TV2	MF804110
Artibeus jamaicensis	Emilio Rabasa	Aja07TR1	MF804111
Artibeus jamaicensis	Veinte Casas	Aja45TV3	MF804112
Artibeus jamaicensis	Veinte Casas	Aja40TV2	MF804113
Carollia sowelli	San Joaquín	Cso22TS2	MF804114
Dermanura tolteca	Emilio Rabasa	Dto02TR1	MF804115
Artibeus jamaicensis	Veinte Casas	Aja39TV2	MF804116
Dermanura tolteca	Veinte Casas	Dto30TV2	MF804117
Sturnira parvidens	San Joaquín	Spa01TS2	MF804118
Sturnira parvidens	Nuevo San Juan Chamula	Spa01TN1	MF804119
Sturnira hondurensis	Emilio Rabasa	Sho03TR1	MF804120
Centurio senex	Emilio Rabasa	Cse01TR1	MF804121
Sturnira parvidens	San Joaquín	Spa02TS2	MF804122
Sturnira hondurensis	Emilio Rabasa	Sho12TR1	MF804123
Carollia sowelli	Veinte Casas	Cso06TV2	MF804124
Carollia sowelli	Emilio Rabasa	Cso08TR1	MF804125
Carollia sowelli	Veinte Casas	Cso09TV3	MF804126
Sturnira hondurensis	Emilio Rabasa	Sho01TR1	MF804127
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja04TN1	MF804128
Dermanura tolteca	Nuevo San Juan Chamula	Dto05TN1	MF804129
Centurio senex	Veinte Casas	Cse02TV1	MF804130
Artibeus lituratus	Nuevo San Juan Chamula	Ali02TN2	MF804131
Enchisthenes hartii	Emilio Rabasa	Eha02TR1	MF804132
Dermanura phaeotis	Nuevo San Juan Chamula	Dph02TN2	MF804133
Sturnira parvidens	Nuevo San Juan Chamula	Spa02TN2	MF804134
Sturnira hondurensis	Emilio Rabasa	Sho20TR1	MF804135

(continued)

Continued

Species	Locality	Laboratory code	GenBank accession number
Sturnira hondurensis	Emilio Rabasa	Sho04TR1	MF804136
Sturnira hondurensis	Emilio Rabasa	Sho07TR1	MF804137
Sturnira parvidens	Nuevo San Juan Chamula	Spa01TN2	MF804138
Sturnira parvidens	Emilio Rabasa	Spa02TR1	MF804139
Dermanura tolteca	Emilio Rabasa	Dto01TR1	MF804140
Desmodus rotundus	Emilio Rabasa	Dro01TR1	MF804141
Artibeus jamaicensis	Emilio Rabasa	Aja06TR1	MF804142
Platyrrhinus helleri	Nuevo San Juan Chamula	Phe07TN2	MF804143
Dermanura tolteca	Veinte Casas	Dto04TV1	MF804144
Artibeus jamaicensis	San Joaquín	Aja05TS1	MF804145
Artibeus lituratus	Emilio Rabasa	Ali03TR1	MF804146
Micronycteris microtis	Veinte Casas	Mmi03TV3	MF804147
Desmodus rotundus	Nuevo San Juan Chamula	Dro01TN2	MF804148
Desmodus rotundus	Nuevo San Juan Chamula	Dro01TN1	MF804149
Artibeus jamaicensis	Veinte Casas	Aja12TV3	MF804150
Artibeus jamaicensis	Veinte Casas	Aja43TV2	MF804151
Dermanura tolteca	Emilio Rabasa	Dto05TR1	MF804152
Anoura geoffroyi	Nuevo San Juan Chamula	Age02TN2	MF804153
Pteronotus parnellii	Veinte Casas	Ppa01TV3	MF804154
Sturnira hondurensis	Nuevo San Juan Chamula	Sho04TN2	MF804155
Pteronotus parnellii	Veinte Casas	Ppa01TV1	MF804156
Artibeus jamaicensis	Veinte Casas	Aja36TV2	MF804157
Artibeus jamaicensis	Emilio Rabasa	Aja11TR3	MF804158
Dermanura tolteca	Emilio Rabasa	Dto07TR1	MF804159
Carollia sowelli	Veinte Casas	Cso05TV2	MF804160
Desmodus rotundus	San Joaquín	Dro06TS2	MF804161
Dermanura tolteca	Veinte Casas	Dto02TV2	MF804162
Artibeus jamaicensis	Veinte Casas	Aja07TV3	MF804163
Artibeus jamaicensis	Emilio Rabasa	Aja16TR1	MF804164
Dermanura tolteca	Nuevo San Juan Chamula	Dto13TN2	MF804165
Micronycteris microtis	Veinte Casas	Mmi01TV2	MF804166
Artibeus jamaicensis	Emilio Rabasa	Aja01TR1	MF804167
Pteronotus parnellii	Veinte Casas	Ppa01TV2	MF804168
Carollia sowelli	Veinte Casas	Cso10TV3	MF804169
Artibeus jamaicensis	Veinte Casas	Aja20TV3	MF804170
Artibeus jamaicensis	Veinte Casas	Aja35TV2	MF804171
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja01TN3	MF804172
Artibeus jamaicensis	Veinte Casas	Aja03TV1	MF804173
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja02TN2	MF804174
Artibeus jamaicensis	San Joaquín	Aja06TS1	MF804175
Carollia sowelli	Emilio Rabasa	Cso09TR1	MF804176
Artibeus jamaicensis	San Joaquín	Aja01TS2	MF804177
Artibeus jamaicensis	Veinte Casas	Aja10TV3	MF804178
Artibeus jamaicensis	Veinte Casas	Aja40TV3	MF804179
Artibeus jamaicensis	Veinte Casas	Aja02TV2	MF804180
Sturnira hondurensis	Nuevo San Juan Chamula	Sho06TN2	MF804181
Desmodus rotundus	Veinte Casas	Dro20TV2	MF804182

(continued)

Continued

Species	Locality	Laboratory code	GenBank accession number
Artibeus jamaicensis	Veinte Casas	Aja01TV3	MF804183
Uroderma bilobatum	Nuevo San Juan Chamula	Ubi01TN3	MF804184
Artibeus lituratus	Nuevo San Juan Chamula	Ali07TN2	MF804185
Carollia sowelli	Nuevo San Juan Chamula	Cso01TN1	MF804186
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja04TN2	MF804187
Dermanura tolteca	Veinte Casas	Dto01TV3	MF804188
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja13TN2	MF804189
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja02TN1	MF804190
Hylonycteris underwoody	Veinte Casas	Hun02TV2	MF804191
Anoura geoffroyi	Nuevo San Juan Chamula	Age01TN2	MF804192
Anoura geoffroyi	Emilio Rabasa	Age01TR3	MF804193
Platyrrhinus helleri	Nuevo San Juan Chamula	Phe01TN1	MF804194
Desmodus rotundus	San Joaquín	Dro05TS2	MF804195
Sturnira hondurensis	Nuevo San Juan Chamula	Sho05TN2	MF804196
Hylonycteris underwoody	Veinte Casas	Hun01TV2	MF804197
Artibeus jamaicensis	Veinte Casas	Aja38TV3	MF804198
Desmodus rotundus	Nuevo San Juan Chamula	Dro02TN1	MF804199
Artibeus jamaicensis	Veinte Casas	Aja46TV2	MF804200
Dermanura tolteca	Nuevo San Juan Chamula	Dto01TN3	MF804201
Artibeus lituratus	Nuevo San Juan Chamula	Ali01TN2	MF804202
Desmodus rotundus	San Joaquín	Dro01TS2	MF804203
Artibeus jamaicensis	Emilio Rabasa	Aja01TR3	MF804205
Sturnira hondurensis	Emilio Rabasa	Sho02TR1	MF804206
Artibeus jamaicensis	Emilio Rabasa	Aja15TR1	MF804207
Dermanura tolteca	Veinte Casas	Dto02TV3	MF804208
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja03TN1	MF804209
Dermanura tolteca	Veinte Casas	Dto20TV2	MF804210
Artibeus jamaicensis	Emilio Rabasa	Aja21TR1	MF804211
Carollia sowelli	Nuevo San Juan Chamula	Cso02TN1	MF804212
Enchisthenes hartii	Emilio Rabasa	Eha03TR1	MF804213
Artibeus jamaicensis	Emilio Rabasa	Aja25TR1	MF804214
Enchisthenes hartii	Veinte Casas	Eha01TV1	MF804215
Mormoops megalophylla	Veinte Casas	Mme02TV3	MF804216
Sturnira hondurensis	Veinte Casas	Sho23TV2	MF804217
Carollia sowelli	Veinte Casas	Cso25TV2	MF804218
Sturnira hondurensis	Veinte Casas	Sho21TV2	MF804219
Sturnira parvidens	Nuevo San Juan Chamula	Spa02TN1	MF804220
Sturnira hondurensis	Nuevo San Juan Chamula	Sho01TN2	MF804221
Desmodus rotundus	Veinte Casas	Dro01TV2	MF804222
Sturnira hondurensis	Veinte Casas	Sho25TV2	MF804223
Sturnira hondurensis	Emilio Rabasa	Sho10TR1	MF804224
Sturnira parvidens	Emilio Rabasa	Spa03TR1	MF804225
Artibeus jamaicensis	Veinte Casas	Aja38TV2	MF804226
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja01TN1	MF804227
Carollia sowelli	Veinte Casas	Cso02TV1	MF804228
Dermanura tolteca	Nuevo San Juan Chamula	Dto01TN1	MF804229
Sturnira hondurensis	Emilio Rabasa	Sho06TR1	MF804230

(continued)

Continued

Species	Locality	Laboratory code	GenBank accession number
Sturnira hondurensis	Veinte Casas	Sho02TV3	MF804231
Sturnira hondurensis	Emilio Rabasa	Sho11TR1	MF804232
Sturnira hondurensis	Nuevo San Juan Chamula	Sho02TN3	MF804233
Sturnira parvidens	Veinte Casas	Spa01TV1	MF804234
Sturnira hondurensis	Emilio Rabasa	Sho09TR1	MF804235
Sturnira hondurensis	Emilio Rabasa	Sho08TR1	MF804236
Artibeus lituratus	Veinte Casas	Ali01TV3	MF804237
Glossophaga morenoi	San Joaquín	Gmo02TS2	MF804238
Artibeus jamaicensis	Veinte Casas	Aja09TV3	MF804239
Artibeus lituratus	San Joaquín	Ali01TS1	MF804240
Mormoops megalophylla	Veinte Casas	Mme01TV3	MF804241
Artibeus jamaicensis	Veinte Casas	Aja31TV2	MF804242
Artibeus jamaicensis	San Joaquín	Aja03TS2	MF804243
Artibeus jamaicensis	Nuevo San Juan Chamula	Aja3TN2C	MF804244
Desmodus rotundus	San Joaquín	Dro04TS2	MF804245
Artibeus lituratus	Veinte Casas	Ali04TV3	MF804246
Artibeus jamaicensis	Emilio Rabasa	Aja20TR1	MF804247
Artibeus jamaicensis	Emilio Rabasa	Aja28TR1	MF804248
Artibeus jamaicensis	Veinte Casas	Aja04TV3	MF804249
Artibeus jamaicensis	Veinte Casas	Aja32TV3	MF804250
Dermanura tolteca	Veinte Casas	Dto01TV1	MF804251
Carollia sowelli	Nuevo San Juan Chamula	Cso01TN2	MF804252
Artibeus jamaicensis	Veinte Casas	Aja39TV3	MF804253
Artibeus jamaicensis	Emilio Rabasa	Aja11TR1	MF804254
Artibeus jamaicensis	Veinte Casas	Aja04TV2	MF804255
Artibeus lituratus	Veinte Casas	Ali02TV3	MF804256
Carollia sowelli	Emilio Rabasa	Cso01TR1	MF804257
Artibeus jamaicensis	Veinte Casas	Aja02TV3	MF804258
Artibeus jamaicensis	Emilio Rabasa	Aja24TR1	MF804259
Artibeus lituratus	Nuevo San Juan Chamula	Ali01TN1	MF804260
Carollia sowelli	Veinte Casas	Cso06TV3	MF804261
Artibeus jamaicensis	Emilio Rabasa	Aja12TR1	MF804262
Artibeus jamaicensis	Emilio Rabasa	Aja26TR1	MF804263
Artibeus jamaicensis	San Joaquín	Aja02TS2	MF804264

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