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ORIGINAL RESEARCH ARTICLE

Stingless bee distribution and richness in El Salvador (*Apidae*, *Meliponinae*)

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This is the first complete inventory of stingless bees in El Salvador. It includes the spatial distribution of wild and managed colonies and the relationships between their occurrence and vegetation cover, altitude and temperature. Applying a stratified sampling, we located wild colonies (n = 477) and managed colonies (n = 686) of stingless bees in tropical forests, agricultural fields and urban areas. Each stratum (14) was a department (political division) of El Salvador. We made maps of the distribution of the most common wild and managed species. We analysed spatial distribution of colonies through the Clark and Evans Index (CEI). For the estimation of diversity between departments, the Shannon-Wiener diversity index (H) was calculated. The relationship between species richness and vegetation cover was analysed through the chi-square test. Linear regression was used to evaluate the effects of altitude and temperature on species richness. We concluded that: (a) there are at least 20 species, six subgenera and 10 genera of stingless bees in El Salvador; (b) the departments with highest levels of diversity were Santa Ana (H' = 2.55), Chalatenango (H' = 2.41), Morazán (H' = 2.31) and La Libertad (H' = 2.22); (c) the most abundant wild species, was *Tetragonisca angustula* (n = 156, relative abundance = 32.70%) and was found in each department in clustered pattern (CEI = .26, p < .001); (d) *Melipona beecheii* (n = 405, relative abundance = 59.04%) was the most frequent managed species, mainly found in a clustered pattern (CEI = .28, p < .001) in the northern and the western part of El Salvador; (e) the species richness is associated with the vegetation cover: increased with coniferous forest (X^2 = 336.1, p < .001), fruit trees (X^2 = 41.8, p < .001), and with temperature (r = .86, p = .0015) but decreased with altitude (r = −.87, p = .001).

Distribución de abejas sin aguijóns y riqueza en El Salvador (*Apidae, Meliponinae*)

Este es el primer inventario completo de abejas sin aguijón en El Salvador. Se incluyó la distribución espacial de colonias silvestres y domesticadas, además de la relación entre la riqueza de especies con la cobertura vegetal, altitud y temperatura. Se aplicó un muestreo estratificado a las colonias silvestres (n = 477) y colonias domesticadas (n = 686) de las abejas sin aguijón localizadas en bosques tropicales, zonas agrícolas y zonas urbanas. Cada estrato (14) fue un departamento (división política) de El Salvador. También se elaboraron mapas de la distribución de las colonias silvestres y domesticadas más frecuentes. La distribución espacial de las colonias fue analizada a través del índice de Clark y Evans (CEI). La diversidad para cada departamento se calculó por medio del índice de Shannon-Wiener (H'). La relación entre la cobertura vegetal y la riqueza de especies se analizó con chi-cuadrado. Se aplicó regresión lineal para relacionar la altitud y la temperatura con la riqueza de especies. Las conclusiones fueron: a. hay por lo menos 20 especies, seis subgéneros y diez géneros de abejas sin aguijón en El Salvador; b. los departamentos con los más altos niveles de diversidad fueron Santa Ana (H' = 2.55), Chalatenango (H' = 2.41), Morazán (H' = 2.31) y La Libertad (H' = 2.22); c. la especie silvestre más abundante fue *Tetragonisca angustula* (n = 156, abundancia relativa = 32.70%) y se encontró en cada departamento en grupos (CEI = 0.26, P < 0.001); d. la especie doméstica más frecuente fue *Melipona beecheii* (n = 405, abundancia relativa = 59.04%) localizada principalmente al norte y el oeste de El Salvador también en grupos (CEI = 0.28, P < 0.001); y e. la riqueza de especies está relacionada con la cobertura vegetal: se incrementó en el bosque de coníferas (X^2 = 336.1, P < 0.001) y árboles frutales (X^2 = 41.8, P < 0.001), disminuyó con la altitud (r = -0.87, P = 0.0010) y aumentó con la temperatura (r = 0.86, p = 0,0015).

Keywords: stingless bees; meliponiculture; species richness; diversity; relative abundance; GIS; El Salvador

Introduction

El Salvador is the smallest country in Central America. It has an area of 20,935 km^2 and a high population density: 273 inhabitants per km^2. It is located between geographic coordinates 13°09′–14°25′ N and 87°43′–90°08′ W (Flores, 1980). The highest altitude is 2,733 m above sea level (m.a.s.l.). The weather is tropical, with an average annual temperature of 23.2 °C, a relative humidity of 74.9% and a precipitation of 1,841.8 mm. (Engels, Urbina, Sloot, & Castillo, 1998). The natural vegetation and cultivated trees cover 34.16% of the territory. Stingless bees (*Apidae*, *Meliponinae*) are a group of eusocial

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insects from the tropics living in permanent colonies, where they store pollen and honey. The main characteristics are the presence of a vestigial sting, reduced veins in the forewings and composite eyes without pilosity (Nates-Parra, 2001). These bees are classified in two tribes: *Meliponini* and *Trigonini* (Wille, 1983). The *Meliponini* tribe has just one genus and approximately 40 species. The *Trigonini* tribe has several genera and subgenera, and over 50 supraspecific groups (Ramirez and Ortiz, 1995). The stingless bees in the Neotropical region embrace 13 genera, 10 subgenera and 271 species (Nates-Parra, 2001). Meliponiculture (the keeping of stingless bees) has a long history, being practiced in Mesoamerica by the ancient Maya culture (Biesmeijer, 1997). Stingless bees are pollinators of many wild plant species, and seem to be a good future alternative in commercial pollination (Slaa, Sanchez, Malagodi, & Hofstede, 2006). They are known to visit the flowers of approximately 90 crops, and are considered effective pollinators for at least nine of them (Heard, 1999). Stingless bees are appreciated for honey production, which is used by farmers as food and medicine. According to the Salvadorian farmers, the medicinal properties of this honey depend on the bee species: honey of *Melipona beecheii* is used for treatment of gastritis and skin burns; pure honey of *Tetragonisca angustula* or diluted with water, is used for conjunctivitis, cataracts and throat infections (Ruano Iraheta, 1999).

Information about the number of species of stingless bees, their distribution and management in this country is very limited. There is an inventory of 13 species of stingless bees that were captured mostly in the western part (Departamento de Protección Vegetal – FAO, 1993). In addition, De Jong (1999) presented a list of 16 species, also collected in the west, near the border with Guatemala. The current situation of meliponiculture is similar to other Neotropical countries like México, where their habitat is rapidly being removed, causing danger of extinction. Furthermore, competition from colonies of *Apis mellifera*, inappropriate management and lack of economic incentive for stingless beekeepers (Villanueva, Roubik, & Colli-Ucan, 2005) also hinder the development of this culture.

The objectives of this study were: (a) to identify the species of stingless bees present in all the country; (b) to determine the most abundant species; (c) to find their geographic distribution within Salvadorian boundaries; and (d) to find out the relationships between species richness and vegetation cover, species richness and altitude, and species richness and temperature.

Materials and methods

The study lasted from May 2005 until May 2007. A stratified sampling was applied across the 14 departments of El Salvador, with each of the departments as a stratum. The sampling places were tropical forests, protected areas (vegetation cover on volcanoes and some places near to water bodies or to the coast), agricultural fields and urban areas. The selection in each stratum was based on preliminary information from agronomists, biologists, farmers and forest guards. Samples from 70 places were taken using active searching of flow of foragers, tube entrance, and exposed nests where the bees were manually captured for identification and placed in plastic containers. To reduce data bias, two members of the research team looked for nests in an area of 100 m^2 (10 m 10 m plots) over 3 min and compared the findings. The total area sampled per day was 1,800 m^2. Wild colonies were searched for, focusing the same efforts on trees, holes in the ground and walls. For managed colonies, the samples were taken directly from boxes or trunks in the houses and backyards belonging to the farmers. Nine stingless bee species were identified using the entomological key of Roubik (1992) and 11 were identified directly by Dr Roubik. Species diversity was analysed using Shannon-Wiener diversity index (H') (Moreno, 2001) based on the number of wild colonies of each species found in each department. We tested diversity using software PAST 2.02.

The species richness is the number of species for a region. In this study species richness was estimated for each department and for the whole country. The relative abundance (RA) is a percentage of the total, and was also estimated for each species of stingless bees to compare the number of colonies between departments. We used Global Position System Garmin model Geko 101 in each sampling place, to obtain data of latitude, longitude and altitude above sea level (m.a.s.l.). The digital cartography based on data from the Ministry of Environment and Natural Resources of El Salvador (MARN). The collected data were systematized using the software Arc-GIS 9.3 to develop a map of distribution of the most abundant species. This map was compared with an existing map of important vegetation cover (Figure 1) to relate the type of vegetation in the presence of a particular species of stingless bees and to check for sources of food or threats from the use of pesticides in areas with cultivated crops.

The spatial distribution of wild and managed colonies of *T. angustula* and *M. beecheii* was analysed by applying the index of Clark and Evans (1954, CEI), which shows colony aggregations, whether they are randomly or uniformly distributed (Biber and Weyerhaeuser, 1998). The CEI was estimated using R software version 3.1.1 (R Development Core Team, 2014). The relationship between species richness and vegetation cover in each department was analysed through the chi-square test (Bonilla, 2000) and software PAST 2.02. The software SAS 8.01 (SAS, 2002) was used to apply a linear regression analysis to find relationships between species richness and altitude. Ten different altitude ranges were defined: 0–250, 251–500, 501–750, 751–1000, 1001–1250, 1251–1500, 1501–1750, 1751–2000, 2001–2250 and 2251–2500 m.a.s.l. The same statistical analysis was applied to find the relationship between species richness and temperature, matching values corresponding to the ranges of altitude indicated. A simple average difference

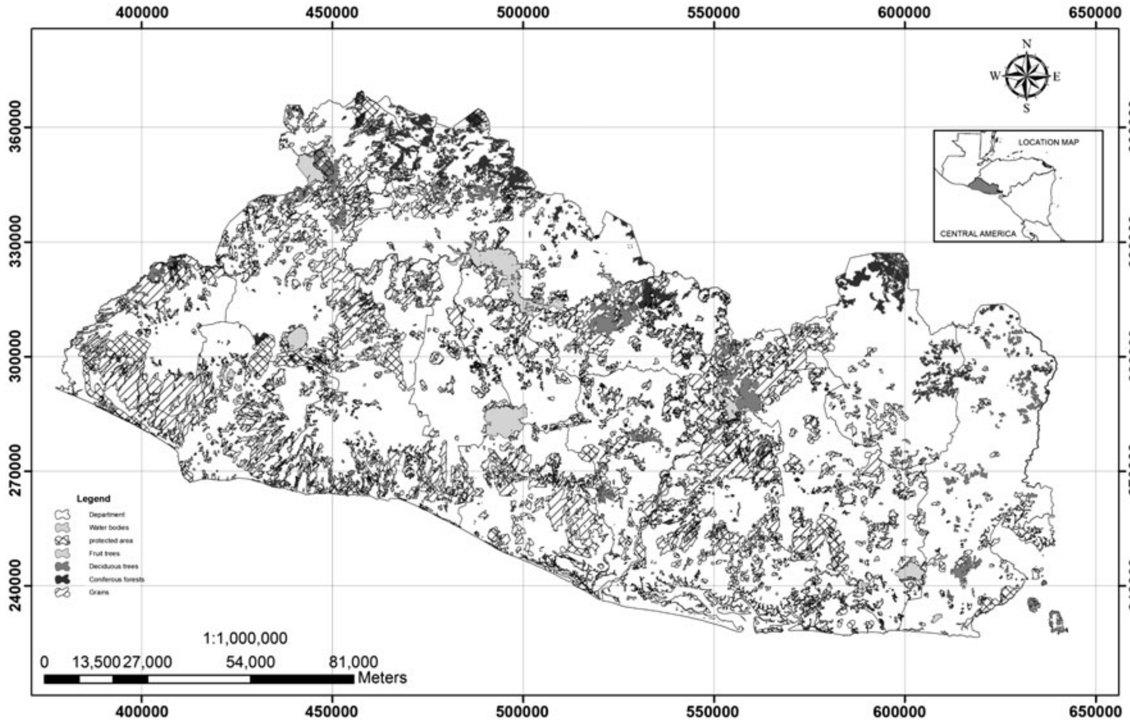

Figure 1. Important vegetation cover for stingless bees and location map of El Salvador.

was used for comparing temperatures between departments. Temperature data of sampling places was based on historic register (annual average) from nearby meteorological stations in each department (two to seven stations per department).

Results

Species richness, diversity and RA

In collaboration with Dr Roubik, 20 species were identified (Table 1) from six subgenera and 10 genera. There were 18 species from the *Trigonini* tribe, and two species from the *Meliponini* tribe. No new species were found, but *Plebeia moureana*, *Plebeia jatiformis*, *Frieseomelitta nigra*, and *Trigonisca* sp. were reported for the first time from El Salvador in this study.

The Shannon-Wiener diversity index revealed superior diversity for Santa Ana ($H' = 2.55$), Chalatenango ($H' = 2.41$), Morazán ($H' = 2.31$) and La Libertad ($H' = 2.22$). The lowest diversity index was found in La Unión ($H' = 1.42$). *T. angustula* was the most abundant wild colony ($n = 156$, RA = 32.70%), followed by *Nannotrigona perilampoides* ($n = 51$, RA = 10.69%) and *Trigona fulviventris* ($n = 49$, RA = 10.27%). The less abundant wild colonies were those of *Trigona fuscipennis* ($n = 4$, RA = .84%) and *Melipona yucatanica* ($n = 3$, RA = .63%). The most abundant managed colonies were from *M. beecheii* ($n = 405$, RA = 59.04%) *T. angustula* ($n = 221$, RA = 32.22%) and *N. perilampoides* ($n = 17$, RA = 2.48%). The less abundant managed colonies were *P. moureana* (n = 2, RA = .29%) and *Tetragona mayarum* ($n = 1$, RA = .15%). *Tetragona dorsalis* from Central America is *T. mayarum.*

Geographic location of species

Wild colonies ($n = 477$) were found in each of the departments of El Salvador, whereas managed colonies ($n = 686$) appeared in 12 of the 14 departments (Table 2). In San Vicente and La Unión, we did not find managed colonies, but some farmers stated that in previous years to the field work of this study some had kept colonies of *T. angustula* in trunks or boxes, but these were abandoned by the bees. Most of the wild colonies of the *Trigonini* tribes were found in the central area of El Salvador (San Salvador, $n = 125$, RA = 26.21%; La Libertad, $n = 60$, RA = 12.58%; La Paz $n = 55$, RA = 11.53%), being *T. angustula* and *N. perilampoides* the most predominant species. Wild colonies of *T. angustula* according the index of Clark and Evans (CEI = .26, $p < .001$, $n = 156$), presented a clustered distribution around the country (Figure 2). We observed similar distribution in managed colonies of *T. angustula* (CEI = .33, $p < .001$, $n = 221$). The scant wild colonies of the *Meliponini* tribe were found only in Santa Ana ($n = 4$, RA = .84%), Chalatenango ($n = 4$, RA = .84%), Ahuachapán ($n = 2$, RA = .42%) and Cuscatlán ($n = 2$, RA = .42%). Wild colonies of *M. beecheii*, the most predominant *Meliponini* species showed no definite pattern of distribution ($p = .66$) due to low number of colonies found ($n = 9$), but as expected, they coincided with the location of the majority of managed colonies of

Table 1. Inventory of stingless bee species in alphabetic order with number of colonies and RA.

Scientific name	Wild colonies (*n*)	Managed colonies (*n*)	Relative abundance of wild colonies (%)	Relative abundance of managed colonies (%)
Cephalotrigona zexmeniae[a]	7	3	1.47	.44
Frieseomelitta nigra[a]	6	1	1.26	.15
Geotrigona lutzi[a]	5	0	1.05	.00
Lestrimelitta sp.[b]	6	0	1.26	.00
Melipona beecheii[b]	9	405	1.89	59.04
Melipona yucatanica[a]	3	8	.63	1.17
Nannotrigona perilampoides[b]	51	17	10.69	2.48
Oxytrigona mediorufa[a]	14	0	2.94	.00
Partamona bilineata[a]	13	0	2.73	.00
Plebeia jatiformis[a]	11	7	2.31	1.02
Plebeia moureana[a]	15	2	3.14	.29
Scaptotrigona mexicana[a]	5	3	1.05	.44
Scaptotrigona pectoralis[b]	40	9	8.39	1.31
Tetragona mayarum[b]	24	1	5.03	.15
Tetragonisca angustula[b]	156	221	32.70	32.22
Trigona corvina[b]	34	0	7.13	.00
Trigona fulviventris[b]	49	0	10.27	.00
Trigona fuscipennis[b]	4	0	.84	.00
Trigona nigerrima[a]	5	9	1.05	1.31
Trigonisca sp.[a]	20	0	4.19	.00

[a]Identified by D. W. Roubik.
[b]Identified by C. E. Ruano.

Table 2. Species richness, number of colonies, Shannon-Wiener index and temperature (annual average) for each department of El Salvador.

Departments	Species richness	Wild colonies (*n*)	Managed colonies (*n*)	Shannon-Wiener index (*H*′)	Temperature (°C)
Ahuachapán	8	23	15	1.73	23.3 ± 3.43
Santa Ana	14	29	103	2.55	21.1 ± 4.52
Sonsonate	8	17	8	1.84	22.9 ± 5.04
Chalatenango	14	35	479	2.41	21.3 ± 6.01
La Libertad	12	60	1	2.22	22.8 ± 3.53
San Salvador	13	125	4	1.98	23.2 ± .14
Cuscatlán	8	21	5	1.84	24.1 ± 2.62
La Paz	12	55	1	1.71	25.7 ± .11
Cabañas	6	9	2	1.68	25.0 ± 2.12
San Vicente	9	25	0	1.99	25.9 ± 1.82
Usulután	10	22	7	2.07	23.9 ± 2.54
San Miguel	9	26	35	1.88	27.6 ± 2.10
Morazán	11	17	26	2.31	21.1 ± 5.48
La Unión	5	8	0	1.42	27.0 ± 1.24

M. beecheii in the northern (Chalatenango $n = 347$, RA = 50.58%) and in the western (Santa Ana $n = 55$, RA = 8.02%) part of El Salvador. The pattern of distribution of managed colonies of *M. beecheii* was clustered (CEI = .28, $p < .001$, $n = 405$).

Species richness and vegetation cover

Santa Ana and Chalatenango presented the highest species richness, with La Unión, the lowest. The species richness is related to vegetation cover in protected areas ($X^2 = 254.5$, df = 13, $p < .001$, $n = 14$), deciduous forest ($X^2 = 155.5$, df = 13, $p < .001$, $n = 14$), Coniferous forest ($X^2 = 336.1$, df = 13, $p < .001$, $n = 14$), fruit trees ($X^2 = 41.8$, df = 13, $p < .001$, $n = 14$), and cereals ($X^2 = 27.0$, df = 13, $p = .013$, $n = 14$). There was insufficient evidence to assert which type of vegetation is in some way influencing the nesting and food availability for stingless bees. However, vegetation cover with coniferous forest and fruit trees increased species

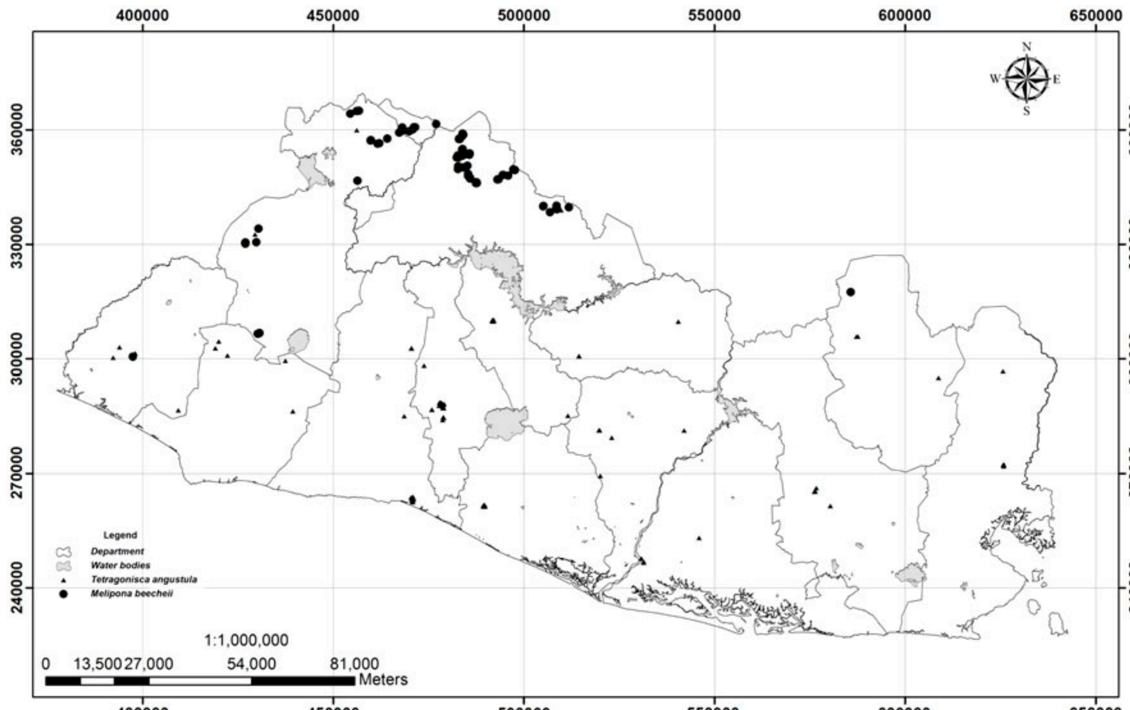

Figure 2. Geographic location of wild colonies of *T. angustula* and managed colonies of *M. beecheii.*

Table 3. Total area of different vegetation cover by department in El Salvador.

Departments	Protected areas (km^2)[a]	Deciduous forest (km^2)[b]	Coniferous forest (km^2)[b]	Fruit trees (km^2)[c]	Cereals (km^2)[c]
Ahuachapán	73.89	22.36	.00	25.83	382.54
Santa Ana	65.06	42.16	64.29	9.88	457.58
Sonsonate	247.31	.67	1.18	9.54	249.49
Chalatenango	4.15	57.21	190.17	1.78	208.98
La Libertad	28.46	34.70	.00	16.44	366.82
San Salvador	.98	12.41	.00	10.51	161.87
Cuscatlán	6.53	7.82	.00	10.15	180.59
La Paz	17.28	17.43	.00	23.97	199.74
Cabañas	53.45	115.15	33.69	1.60	229.16
San Vicente	10.25	64.74	.00	4.03	259.15
Usulután	209.22	11.36	.00	13.78	361.92
San Miguel	19.69	36.35	.00	2.43	293.41
Morazán	2.90	11.27	136.10	2.96	173.05
La Unión	219.65	204.89	19.74	.75	289.08

[a]MARN (2014).
[b]Cisneros Velásquez, García Gómez, and Gómez Morales (2012).
[c]MINEC (2009).

richness, conversely the others type of vegetation decreased it (Table 3).

Species richness and altitude

The maximum altitude at which a stingless bee colony was found (*M. beecheii*) was 2,260 m.a.s.l.; whereas the lowest altitude (*T. fuscipennis*) was at 2 m.a.s.l. The range of altitude for *M. beecheii*, the largest among the species found (10.7 mm long) was between 640 and 2,260 m.a.s.l. The subterranean nest species *G. lutzi*, (6.0 mm) was found between 570 and 1,367 m.a.s.l. The altitude range for *T. angustula* (4.7 mm) was from 10 to 1,373 m.a.s.l. The smallest species, *Trigonisca* sp. (3.2 mm), was found between 17 and 964 m.a.s.l. The majority of the species (19) were found within the range of 501 and 750 m.a.s.l. and gradually decreased. There were two species (*T. corvina* and *M. beecheii*) at an altitude higher than 1750 m.a.s.l. and just one (*M. beecheii*) at more than 2,250 m.a.s.l. The linear regression analysis showed a highly negative correlation ($r = -.87$, $p = .001$) between species richness and altitude. The model developed was: $y = -.0079x + 19.27$ (Figure 3).

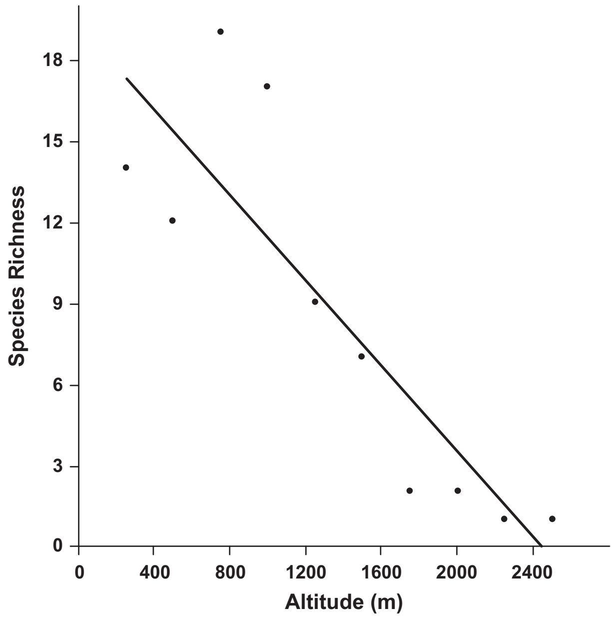

Figure 3. Relationship between species richness vs. altitude.

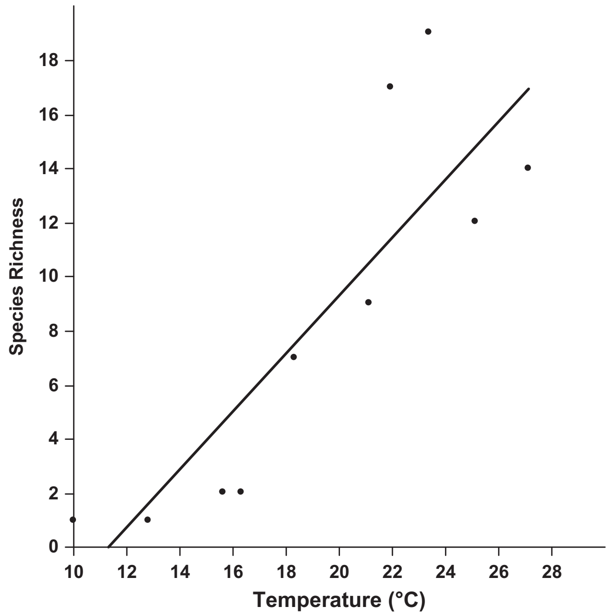

Figure 4. Relationship between species richness vs. temperature.

Species richness and temperature

The largest difference in temperature in ranges of altitude was 17.2 °C (between 0 and 2,500 m.a.s.l.), but every 250 m the temperature decreased by an average of 1.9 ± .82 °C. The highest average temperatures of each department corresponded to San Miguel (27.6 ± 2.10 °C) and La Unión (27.0 ± 1.24 °C). The lowest average temperatures were Santa Ana (21.1 ± 4.52 °C), Morazán (21.1 ± 5.48 °C) and Chalatenango (21.3 ± 6.01) (Table 2). The linear regression analysis showed a highly positive relationship ($r = .86$, $p = .0015$) between species richness and temperature. The analysis showed this model: $y = 1.067x - 12.07$ (Figure 4).

Discussion

The newly found species in El Salvador have been already reported in neighbouring countries: *P. Jatiformis* and *Trigonisca* sp in México, Guatemala, Costa Rica and Panamá; *F. nigra* in Mexico, Belize, Guatemala, Costa Rica (Camargo & Pedro, 2007) and Panamá (Roubik, 1993); and *P. moureana* in México (Ayala, 1999) and Guatemala (Yurrita and Enriquez, 2005). The number of species of stingless bees in El Salvador (20) is smaller in comparison to other Neotropical countries: over 50 species identified in Costa Rica (Ortiz, 1998), 46 species in México (Ayala, 1999), 32 species in Guatemala (Yurrita and Enriquez, 2005) and 20 species in drier lowland forests of Panamá (Roubik, 1993). The lower number of species in El Salvador does not have an obvious explanation, however it is probably associated with the smaller area, the limited original vegetation (reduced to less than 3%), deforestation (annual rate is 4.6%) and intensive farming. Some farmers stated that until the 1970s there were some stingless bee species of the *Meliponini* tribe (probably *M. solani, M. costaricensis* or *M. melanopleura*) in the eastern departments (San Miguel, Morazán and La Unión), but we have not found any of these species during our study, which might indicate that now they are extinct or threatened with extinction.

Santa Ana, Chalatenango, Morazán and La Libertad have higher diversity of stingless bees. This can be related to larger areas with coniferous forests (except La Libertad) for nesting compared with the other departments. Furthermore, the levels of diversity found in La Libertad ($H' = 2.22$) might be related to deciduous trees (34.70 km^2) and some areas with fruit trees (16.44 km^2), despite the recent urban development of this department. Even though a large range of altitude and a very diverse vegetation are found across the four departments with the highest diversity, the annual average temperature was similar between them (21.1–22.8 °C, major difference of 1.7 °C). Macieira and Proni (2004) reported thermal limits of mortality for *Scaptotrigona postica* in Brazil outside the range of −5 °C and 41 °C. San Miguel and La Unión presented the highest temperatures (maximum 35.3 and 35.5 °C, respectively) in conformity with a lower diversity index (Table 2). However, such temperatures do not fall outside the range reported by Macieira and Proni (2004), therefore is not possible to say that the temperature itself is a factor negatively affecting the species. San Miguel and La Unión have low cover of fruit tress: 2.43 and .75 km^2, respectively (MINEC, 2009), besides the largest drought period in this region and desertification areas (1,256 and 589 km^2, respectively) according MARN (2003). Therefore, the main factor possibly is the area and type of vegetation. Some stingless bee species are probably restricted to forest, at least for nesting; and nests or individuals in deforested habitats may be subject to greater disease, parasite, or predation threats (Brosi, Daily, & Ehrlich, 2007). In one coffee farm, the surrounding forest cover was positively correlated with both bee richness and abundance. The presence of stingless bees and *A. mellifera* was most strongly related to the proximity of shade trees which are their main nest sites (Florez, Muschler, Harvey, Finegan, & Roubik, 2002).

M. beecheii were the most abundant managed colonies due to relative high honey production (2.2 ± 1.41 l per year per colony), followed by *T. angustula* and *N. perilampoides* due to the RA of wild colonies in the country. Wild colonies of the *Trigonini* tribe were commonly found in some densely populated departments such as San Salvador (1,768 inhabitants per km^2) and La Libertad (400 inhabitants per km^2). Their presence in such populated areas might be related to the low demand of these bees for sugar concentration from flower nectar (Kerr, Blum, & Fales, 1981) or any source of sugar. We observed some cases of *T. fulviventris* and *T. corvina* consuming residues of coffee and soda water in rubbish. The species *O. mediorufa* and *T. fuscipennis* even drank the sweet honeydew produced by treehoppers (*Homoptera: Membracidae*). Also, the majority of species of *Trigonini* were not selective when they needed holes to build their nests, they adapt very well to deforested areas, nesting in walls, posts and ground holes. *T. angustula, T. fulviventris,* and *N. perilampoides* were the most abundant wild colonies, probably because of the wide range of adaptation in food sources and lodging. In a study in Costa Rica, Slaa (2006) found that the probability of annual survival of *T. angustula* is better in deforested areas than in forest. On the other hand, we did not find wild or managed colonies of the *Meliponini* tribe in departments with highest deforestation and desertification process. In agreement with our findings, Brosi et al. (2007) reported that at forest edges in Costa Rica, native social stingless bees comprised more than 50% of the individuals sampled, whereas away from forests (remnant trees and open pastures) their proportion dropped to 20% of the sampled bees.

Likewise, we found no wild or managed colonies of the Meliponini tribe in the coastal zone (south of El Salvador), because it was deforested gradually during the 1930s to develop intensive agriculture with cereals and cotton, which required flat topography and constant use of pesticides (López, 1986). Agriculture expansion and intensification have been identified as major threats to bees due to logging and land clearing which diminishes bee nesting and feeding opportunities. Also, agricultural insecticides kill adult and larval bees. The sub-lethal effects are dangerous too: disrupting sensory, navigational and recognition abilities (Freitas et al., 2009). In Guatemala, Rodas, Enriquez, and Maldonado (2008) demonstrated the effect of parathion (an organophosphate insecticide widely used in Central America) on *M. beecheii* and *T. angustula.* The mortality rates for the two bee species within 24 h were 50 and 100% respectively.

Moreover, the most limiting factor for survival of *M. beecheii* and *M. yucatanica*, is probably the kind of vegetation. We found wild and managed colonies in major proportion in northern and western parts of El Salvador. These communities are close to forested areas that correspond to 8.73% of El Salvador embracing open vegetation predominantly tropical perennial sub mountain of conifers. The predominating trees were pine (*Pinus* spp.), oak (*Quercus* spp.) and some broadleaf trees. The keepers of stingless bees consider these tree species as the most frequent natural lodging for stingless bees. They also asserted that the preferred sources of food were cirín (*Clidemia* spp., *Miconia* spp., and *Conostegia xalapensis*), guayaba (*Psidium guajava*), manzana rosa (*Syzygium jambos*), liquidambar (*Liquidambar styracyflua*), suquinay (*Vernonia* spp.), and tatascamite (*Perymenium grande*). The importance of proper vegetation for stingless bees was demonstrated through the project "Support for reforestation and forest management by the traditional keeping of stingless bees in north-west El Salvador" (PROMABOS) that developed palynological research in El Salvador and Costa Rica to determine the source of food of stingless bees. In El Salvador, the species of plants that were important as pollen sources for *M. beecheii* were *Cestrum* sp, *Solanum asperum*, *Heliocarpus mexicanus*, *Miconia* sp. and *Ardisia compressa*. Nectar sources were *Cordia alliodora*, *Prunus* sp., *Cestrum* sp., *Solanum dyphyllum* and *Montanoa hibiscifolia*. The research in Costa Rica, included *M. beecheii* and *T. angustula*, and the results showed that the diversity of pollen collected by *T. angustula* was greater than that collected by *M. beecheii*. This is probably due to a different foraging behaviour and physical differences among these bee species, leading them to different accessibility to flowers based on differences in morphology, colour and smell of the flower and, the availability of pollen and nectar during the day (Landaverde, Sánchez, Ruano, & Smeets, 2004). Also, Biesmeijer (1997) demonstrated in Costa Rica that *M. beecheii* is very selective with pollen and sugar concentration of nectar, for this reason was less active as a forager (almost the half) in comparison with *T. angustula.* In addition, the foraging range is wider in *Meliponini* than *Trigonini* tribe. Roubik and Aluja (1983), reported more than two km of foraging range for *M. fasciata*; whereas van Nieuwstadt and Ruano Iraheta (1996) reported just 800 m for *T. angustula*. This limited range leads *T. angustula* to be less selective towards sources of pollen and nectar.

We found that *M. beecheii* limits its distribution to forested areas, in contrast to *T. angustula* which is also found in urban areas. These results coincide with those of Arce (1994), who reported also found such pattern for the two most frequent managed species of stingless bees in Costa Rica (*M. beecheii* and *T. angustula*). According to elder farmers, nowadays it is harder than before to find wild colonies of *M. beecheii*, and also the number of stingless beekeepers has decreased. The civil war in El Salvador from 1980 until 1991, and more recently, the extreme poverty, have played a role in this phenomenon, causing the migration of people living in the countryside abandoning their homes and their agricultural activities, managed stingless bees included. This tendency of decreasing meliponiculture is similar for other countries of Mesoamerica. Different to the situation of *T. angustula*, there is a large gap between wild and managed colonies of *M. beecheii* (Table 1).

In El Salvador, some keepers of stingless bees protects them from extinction by using techniques of artificial reproduction along with feeding practices (e.g. sugar syrup) during the season of lack of flowering plants from April until October. Technical assistance is provided by projects of Ministry of Agriculture (MAG) and University of El Salvador (MAG, 2003). Furthermore, there are some projects about the management and conservation of stingless bees in nearby countries like México (Reyes, 2013) and Costa Rica (Herrera Gonzalez, Aguilar Monge, and Mena Aguilar, 2013). Most of the managed colonies of *M. beecheii* were found at altitudes higher than 1,000 m.a.s.l., with relative low human population density (96 inhabitants per km^2; 3.4% of the country area). Low human population density is linked with less deforested areas, less pollution and, thus, more probability of survival for the bees. The altitude is also important for *G. lutzi,* because they need places without risk of inundation for their subterranean nests. Normally, *G. lutzi* nests in hills and mountains. The vast majority of the species was found between 501 and 750 m.a.s.l., in accordance to Nates-Parra (2001) in Colombia, and Yurrita and Enriquez (2005) in highlands of Guatemala. We found just two species of stingless bees of moderate and large size (*T. corvina* and *M. beecheii*) over 2,000 m, probably this low number of species is related to a less diverse vegetation (Flores, 1980; Jacquemyn, Micheneau, Roberts, & Pailler, 2005) covering a significantly small area (.0029%) in the whole of El Salvador. Also, this scant number of species could be limited for fresher temperatures (minimum 10.3 °C) according to the highly positive relationship founded between species richness and temperature. This coincided with Ribeiro and Barbosa (2013) who found, that temperature annual range was the main abiotic predictor affecting bee richness and diversity of bees in Brazil. Furthermore, Gouw and Gimenes (2013) stated that the flight activity of *Melipona scutellaris* and *Frieseomelitta doederleini* started with temperatures from 19 to 26 °C.

In summary, there are at least 20 species of stingless bees in El Salvador, the most frequent wild species found is *T. Angustula* and the most frequent managed species is *M. beecheii*, both found in clustered pattern. This research highlights the positive relationship of the vegetation cover (coniferous forest and fruit trees) with the species richness, diversity and geographic distribution of stingless bees. Furthermore, species richness was positively associated with temperature and negatively associated with altitude. This information has set the basis for further studies on the sustainable use and conservation of stingless bees in El Salvador. It also highlights the need to implement conservation activities in the vegetation in order to maintain and promote biodiversity.

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