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Systematics and Biodiversity (2016), **14(3)**: 261–275

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Research Article

Distribution patterns of endemic flora to define hotspots on Hispaniola

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(Received 22 November 2014; accepted 30 November 2015)

Nineteen areas on the island of Hispaniola (Haiti and the Dominican Republic) were studied with the aim of determining the distribution pattern of the endemic flora in these areas, and their variability with altitude. The main concentration of endemic species occurs in mountains with a medium altitude and in certain mountain sites (palaeo-islands), which coincide with hotspots; a lower number of endemics are found in low-lying areas (coldspots), due to the degradation of their habitats. A total of 1,582 endemic species were studied and were distributed in 19 areas. The whole island is of outstanding interest for its richness in endemics; it has 2,050 endemic species, representing 34.16% of its total flora. The territory in the study is home to 1,284 genera of which 31 are endemic to the island, including monotypical genera such as *Tortuella abietifolia* Urb. & Ekman, and endemic genera such as *Hottea*, containing seven endemic species. The sites with the highest rate of endemics are area A16 in the central range with a total of 440 endemic species, of which 278 are exclusive to the territory; and the Sierra de Bahoruco, la Selle, La Hotte and Tiburón in area A12, where we found 699 plants of which 482 are endemic and exclusive to the area; and A13 with 173 and 129 respectively. This work highlights the exceptional floristic diversity in endemic species and genera and analyses their distribution patterns as a tool for conservation in this area of the world, whose high endemicity rate makes it one of the most significant hotspots in the Caribbean.

Key words: biodiversity, biogeography, Caribbean, Dominican Republic, endemicity, Republic of Haiti

Introduction

Hispaniola (Dominican Republic and Republic of Haiti) is located between parallels 17–19° N. The island belongs to the Greater Antilles group – part of the Antillean Arc – and has an area of 76,484 km^2, making it the second largest island after Cuba with 110,861 km^2.

Mollat, Wagner, Cepek, and Weiss (2004) published a recent study of the geological formations on the island. The mountains on Hispaniola are estimated to date from the Cretaceous (130 million years ago) and the Oligocene–Miocene (Tertiary) periods. The island of Hispaniola is the result of the union-separation-union of various orographic units formed in different geological eras. These combined territories extend from the central to the eastern mountain range, and date from the Cretaceous period. The formation of these first territories was followed by the northernmost range dating from the Oligocene-Miocene period, and the Sierra de Bahoruco, La Selle and La Hotte with Neiba, Matheux, Negras and Martín García. The Cordillera Central range contains the highest altitudes – not only in Hispaniola but in the Antilles as a whole – and includes the peaks of Pico Duarte (3,175 m), La Polona (3,087 m), La Rusilla (3,038 m) and Pico del Yaque (2,761 m).

We studied the endemic flora of Hispaniola based on our own research and a series of publications containing studies on geology, flora and vegetation (Borhidi, 1991; Cano, Veloz Ramirez, & Cano-Ortiz, 2010b, 2011; García & Clase, 2002; García, Mejía, & Zanoni, 1994; García, Mejía, Peguero, & Jiménez, 2001; García, Mejía, Peguero, Salazar, & Jiménez, 2002; Guerrero, Jiménez, Höner, & Zanoni, 1997; Höner & Jimenez, 1994; May, 1997, 2000, 2001; May & Peguero, 2000; Mejía & Jiménez, 1998; Mejía, García, & Jiménez, 2000; Mejía, García, &

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ISSN 1477-2000 print / 1478-0933 online
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http://dx.doi.org/10.1080/14772000.2015.1135195

Jiménez, 1998; Peguero & Salazar, 2002; Salazar, Peguero, & Veloz, 1997; Samek, 1988; Slocum, Mitchell, Zimmerman, & Navarro, 2000; Trejo-Torres & Ackerman, 2001; Velóz & Peguero, 2002; Zanoni, Mejía, Pimentel, & García, 1990). This study of the endemic areas of Hispaniola is based on earlier geological works by Liogier (2000) and Mollat et al. (2004). López Almirall (1998) studied the endemics in Cuba at the district level, and then assigned them to 86 botanical families; of these 86 with district-level taxa, 20 have over 70% of the infraspecies richness. According to Borhidi (1991), Cuba has 6,300 species in a larger area than Hispaniola, and with lower altitudes. Liogier (2000) made a comparative analysis of species density in Cuba and Hispaniola, and found 0.064 species per km^2 in Hispaniola, and 0.05 in Cuba. Recently Hernández Valdés and Castañeira Colomé (2006) reported that over 50% of the autochthonous spermatophyte flora in Cuba is endemic, fundamentally due to the serpentine outcrops. The island has an abundant representation of the families *Poaceae*, *Arecaceae*, *Araceae*, *Bromeliaceae* and *Orchidaceae*, the latter with over 30 genera, among which we have described the new species *Psilochilus crenatifolius* Kolan., given by Kolanowska (2013) in the San José de las Matas district (Dominican Republic). Other well-represented families are *Leguminosae*, *Malpighiaceae*, *Euphorbiaceae*, *Sapindaceae*, *Malvaceae*, *Cactaceae*, *Myrtaceae*, *Solanaceae*, *Bignoniaceae*, *Rubiaceae* and *Asteraceae*. Less abundant groups include the *Zingiberaceae* family, comprising 14 of the 1,300 species gathered by Uma and Muthukumar (2014), and 13 species of the genus *Paspalum*, together with the 49 collected by Lonchi-Wagner, Welker, and Waechter (2012) for grasslands in the mountains in eastern Brazil. The island has 1,284 genera, of which 31 are endemic: *Zombia*, *Leptogonum*, *Arcoa*, *Neobuchia*, *Fuertesia*, *Sarcopilea*, *Salcedoa*, *Vegaea*, *Coeloneurum*, *Theophrasta*, *Haitia*, *Stevensia*, *Samuelssonia*, *Hottea*, *Anacaona* and *Tortuella*, among others; and some of these genera are monotypes. These territories form one of the most important hotspots in the Caribbean (Francisco-Ortega et al., 2007; Francisco-Ortega et al., 2008; Maunder et al., 2008; Santiago-Valentín & Francisco-Ortega, 2008).

Materials and methods

This study considered 19 areas previously established by Cano and Cano-Ortiz (2012). The previous study included 1,582 endemic species obtained from the bibliography and from our own sampling. The influence of Central and South America on Hispaniola was highlighted by Acevedo-Rodríguez and Strong (2008), and included in Cano, Veloz Ramirez, Cano-Ortiz, and Esteban (2009a) (Fig. 1), where we used 58 genera and 675 species of *Melastomataceae*. For the authorship of the taxa we followed Liogier (1996−2000) and Martín and Cremers (2007). The bioclimatology of the island was studied following Cano, Veloz Ramirez, Cano-Ortiz, and Esteban (2009b) using thermotypes and ombrotypes. These bioclimatic concepts

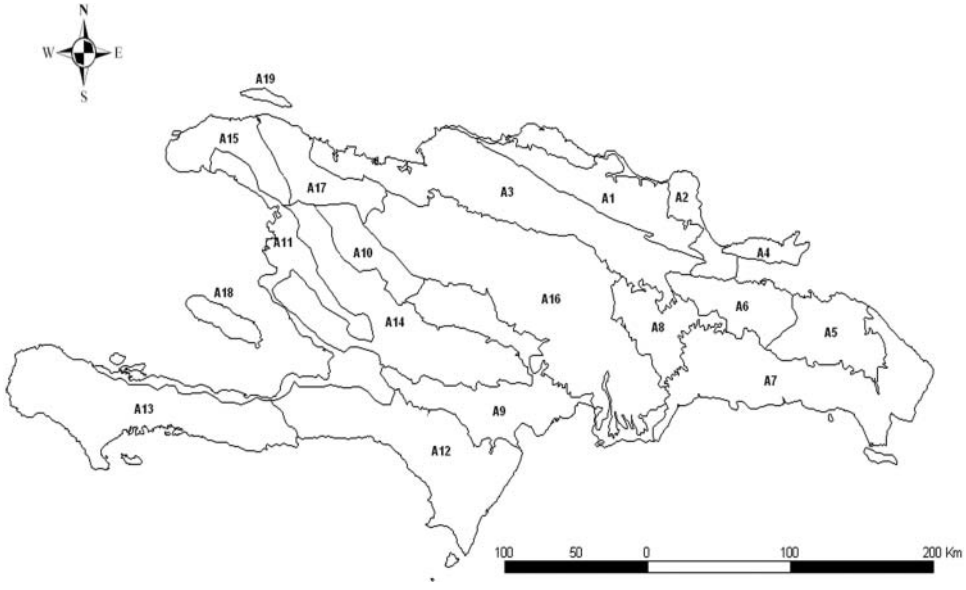


Fig. 1. Study areas of Hispaniola (Dominican Republic and Republic of Haiti). A1. – Cordillera Septentrional. A2. – Coastal-Atlantic Unit. A3. – Cibao Valley. A4. – Samana Peninsula. A5. – Cordillera Oriental. A6. – Los Haitises. A7. – Eastern Coastal Plain. A8. – Sierras of Yamasa and Prieta. A9. – Azua-Lago Henriquillo. A10. – Central Plain (Haiti). A11. – Port-au-Prince-Gonaivë. A12 – Bahoruco-La Selle. A13 – Massif de La Hotte and Tiburón. A14. – Massif of Matheux and Montañas Negras. A15. – Northwest Haiti. A16. – Cordillera Central Oriental (Dominican Rep.). A17. – Cordillera Central Occidental (Rep. of Haiti). A18. – Gonaive Island. A19. – Tortuga Island (from Cano et al., 2009a).

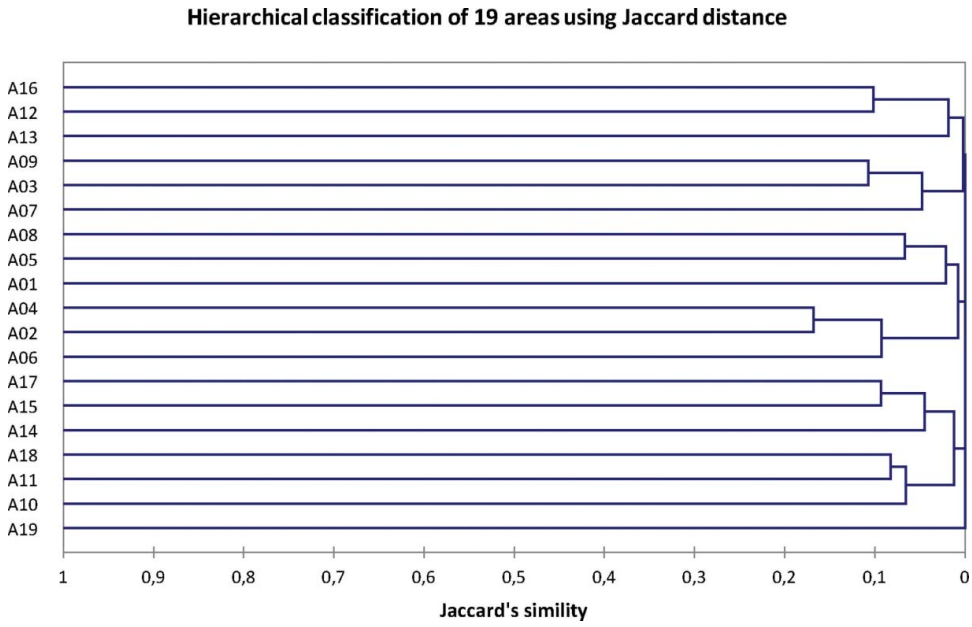


Fig. 2. Jaccard analysis based on endemic species in the sample study areas (from Cano et al., 2010a).

describe the relationship between climate factors and the living beings that inhabit the territory, and, together with the bioclimatic indices of thermotypes and ombrotypes, were established by Rivas-Martínez, Sánchez Mata, and Costa (1999). The map of the 19 biogeographic areas takes into account their geological history, substrate and the presence/absence of the 1,582 endemics. To observe the endemic rate we use the cosmopolitanism index (Rapoport, Ezcurra, and Drausal, 1976): C = (Σ(r·Yr/n)-1)/rmax-1 = 0.018494943; whose result is 19; this near-zero indicates that the 19 areas have a high rate of endemics. We applied a Jaccard clustering to determine the greater or lesser similarity between the areas (Fig. 2). We calculated the Shannon index in order to determine the biodiversity of the study areas, and applied the formula described in Shannon and Weaver (1959) to the abundance indices of the inventories described above. This analysis separated the inventories taken on serpentines (22) from those on other substrates (88), and analysed the 110 inventories as a whole. They were then linearly correlated with the altitude variable, divided into 50 intervals, and the inventories were assigned to each interval by clustering with the K-means method, both with Shannon's index and with the total number of species and endemics.

For the Jaccard and Shannon Pearson values we used the statistical software XLSTAT 2009. We applied Jaccard and Pearson analyses to the 1,582 endemic species to determine the relationship between the 19 study areas. We consider that the sample of 1,582 (77.17%) endemic species out of a total of 2,050 is sufficiently representative for a comparative analysis between areas. An analysis of series was done to find the areas with the greatest diversity of endemics, based on the number of times each of the 1,582 species appeared in each of the 19 areas. This means that a particular species may be in 1, 2, 3 or more areas, according to the cosmopolitanism index (Rapoport et al., 1976) (Table 1). For the relationship between altitude and number of endemics, 110 samples were taken at different sites and at different heights on the island over an area of 100−2000 m^2. We followed the phytosociological methodology of Braun-Blanquet (1979) for the vegetation field sampling. The plot size was selected homogeneously based on the physiognomy, dynamism, and structure of the vegetation.

Results

The study of the 19 areas described by Cano, Veloz Ramirez, and Cano-Ortiz (2010a) in six biogeographic sectors faithfully represents the total areas existing on the island at the district level. The comparative analysis between these 19 district areas reveals a low correlation between them, as in all cases the Pearson correlation value is near zero, and the maximum degree of similarity between areas A04 and A06 is 28.5%. When Shannon's index was applied to the 110 samplings, we obtained a group found at altitudes of over 1,000 m, with Shannon values (H) ranging between 3.34 and 4.28; whereas the rest of the plots sampled at altitudes below 1,000 m have a Shannon index of between 3.91 for plots located on serpentines, and the lowest value of 1.03 (Tables 2 and 3) (Shannon & Weber, 1959). The correlation analysis with altitude, using the average values of Shannon's

Table 1. Vegetation data in the 110 samples.

Inventory no.	Order no.	UTM_X	UTM_Y	Altitude (m.)	Area	% Coverage	Average vegetation height (m)	Number of native	Number of endemic	Substrate
Inv0106	60	343898	2302285	300	2000	100	8	42	16	
Inv0206	61	343898	2302285	300	1000	80	3	51	8	
Inv0306	62	384190	2058733	182	2000	100	10	37	11	
Inv0406	63	392342	2068910	140	2000	90	4	20	11	
Inv0506	64	490861	2033796	13	200	40	12	4	0	
Inv0606	65	490861	2033796	10	200	60	25	4	0	
Inv0706	66	490285	2834062	15	2000	95	5,5	33	5	
Inv0806	67	489200	2034829	8	2000	90	5	38	3	
Inv0906	68	490488	2037546	24	2000	100	6	42	3	
Inv1005	3	340283	2106095	1473	2000	100	10	19	17	
Inv1006	69	516924	2033776	69	1000	100	12	49	7	
Inv1105	4	340288	2106283	1441	500	100	4	20	13	
Inv1106	70	519492	2027853	4	1000	100	4,5	30	5	
Inv1205	5	340165	2106429	1465	2000	100	20	20	16	
Inv1206	71	517200	2000026	29	500	60	8	32	6	
Inv1305	6	339971	2105962	1373	500	100	9	31	7	
Inv1306	72	489524	2092418	519	2000	70	14	49	1	
Inv1405	7	339590	2105699	1377	1000	100	9	25	9	
Inv1505	8	339203	2105784	1251	1000	100	15	21	11	
Inv1506	74	486735	2092513	541	2000	100	12	19	2	
Inv1705	9	339203	2105784	1200	500	100	7	21	9	
Inv1706	76	398581	2061827	109	500	100	5,5	36	11	Serpentines
Inv1805	10	321806	2082834	2058	1000	100	19	11	13	
Inv1806	77	398246	2062093	102	500	90	5,5	36	13	Serpentines
Inv1905	11	325399	2078286	2336	1000	75	9	4	9	
Inv1906	78	397232	2062450	110	500	100	5	39	17	Serpentines
Inv2005	12	326681	2076397	2290	1000	90	20	4	9	
Inv2006	79	397231	2062447	106	500	100	5	35	16	Serpentines
Inv2105	13	331098	2069273	2383	1000	100	20	10	11	
Inv2106	80	398451	2063175	113	500	100	3,5	29	14	Serpentines
Inv2206	81	272603	2176209	47	500	70	3,5	20	1	
Inv2305	14	267592	2002124	1207	2000	100	25	36	11	
Inv2306	82	273593	2176232	83	500	80	4,5	25	5	
Inv2405	15	268161	2002764	1239	2000	100	25	34	19	
Inv2406	83	273241	2177242	139	500	40	4,5	21	3	
Inv2505	16	268152	2002964	1233	2000	100	20	27	16	
Inv2506	84	273458	2178554	163	500	70	4,5	19	2	
Inv2605	17	268736	2000217	1140	2000	100	15	30	10	
Inv2606	85	267694	2177030	166	500	85	6	15	1	
Inv2705	18	229587	2006325	1358	2000	80	15	13	18	
Inv2706	86	265559	2177065	160	500	75	6,5	16	2	
Inv2805	19	229143	2006087	1343	2000	85	15	14	23	
Inv2806	87	265579	2177120	162	500	100	6	14	3	
Inv2905	20	227793	2005430	1286	2000	85	15	7	21	
Inv2906	88	262945	2180508	94	500	70	4,5	22	4	
Inv3005	21	225980	2005665	1203	2000	85	15	4	22	
Inv3006	89	262882	2181400	121	500	65	6,5	33	5	
Inv3105	22	219951	1995921	144	500	60	6	29	18	

(*continued*)

Table 1. (*Continued*)

Inventory no.	Order no.	UTM_X	UTM_Y	Altitude (m.)	Area	% Coverage	Average vegetation height (m)	Number of native	Number of endemic	Substrate
Inv3106	90	222565	2200698	16	500	60	3	30	7	
Inv3205	23	219738	1993286	104	500	50	6	23	16	
Inv3206	91	222610	2200836	3	500	70	3,5	30	7	
Inv3305	24	219223	1990191	15	600	50	9	21	17	
Inv3306	92	222986	2200769	26	300	90	1	9	1	
Inv3405	25	219663	1988966	13	1000	60	6	7	2	
Inv3505	26	249877	1969945	1	500	100	7	7	0	
Inv3506	94	223543	2201543	21	800	80	4	30	8	
Inv3605	27	249877	1969945	0	500	100	7	7	0	
Inv3606	95	223546	2201547	25	300	100	1	13	3	
Inv3705	28	278689	2014182	0	500	70	7	7	0	
Inv3706	96	243245	2197512	169	1000	90	7,5	30	8	
Inv3805	29	278689	2014182	0	500	100	7	4	0	
Inv3805bis	30	278689	2014182	0	500	100	7	3	0	
Inv3806	97	238370	2202751	27	500	80	4,5	37	8	
Inv3905	31	278689	2014182	0	500	100	7	5	0	
Inv3906	98	235750	2201393	70	500	80	5,5	34	5	
Inv4005	32	278689	2014182	0	500	100	7	8	0	
Inv4006	99	234500	2201316	53	500	80	4	32	4	
Inv4105	33	283638	2043825	160	600	60	5	26	9	
Inv4106	100	234505	2201316	71	300	80	1	20	3	
Inv4205	34	275855	2035891	209	1000	80	4	19	6	
Inv4206	101	232308	2200291	58	500	75	3,5	17	8	
Inv4305	35	340420	2031565	218	1000	90	10	27	6	
Inv4306	102	228383	2200317	8	500	70	4	21	6	
Inv4405	36	353122	2025661	118	1000	85	7	21	8	Pine forests on serpentines
Inv4406	103	225402	2156162	200	1000	80	7,5	27	9	Serpentines
Inv4505	37	489790	2039255	38	1000	100	9	51	3	Pine forests on serpentines
Inv4506	104	226716	2157562	250	1000	70	10	32	9	Serpentines
Inv4605	38	490159	2037558	39	1000	100	8	37	4	Pine forests on serpentines
Inv4606	105	229337	2158209	172	1000	60	8,5	32	7	Serpentines
Inv4705	39	490586	2038122	36	1000	100	5	29	3	Pine forests on serpentines
Inv4706	106	227746	2158156	245	1000	60	10	31	8	Serpentines
Inv4805	40	516942	2032979	42	2000	95	17	44	7	
Inv4806	107	318408	2192458	41	500	80	5	22	12	Serpentines
Inv4905	41	517849	2031060	8	2000	90	3	34	2	
Inv4906	108	318034	2192804	95	1000	95	7	24	7	Serpentines
Inv5005	42	517877	2031096	8	2000	100	19	41	1	
Inv5006	109	318034	2192804	100	300	90	0,8	14	5	Serpentines
Inv5105	43	516780	2030824	1	500	80	5	14	1	
Inv5106	110	318198	2192601	69	1000	70	2,5	27	9	Serpentines
Inv5205	44	565493	2050559	14	2000	100	18	38	1	
Inv5206	111	318595	2192785	18	1000	80	5	22	8	Serpentines
Inv5305	45	564945	2051672	12	2000	100	20	38	1	
Inv5306	112	367683	2171293	64	1000	85	3,5	28	3	Serpentines
Inv5405	46	478610	2041154	0	2000	100	12	8	0	
Inv5406	113	367771	2171272	89	1000	60	4	27	6	Serpentines
Inv5505	47	267385	2176805	84	1000	60	4	20	2	

(*continued*)

Table 1. (*Continued*)

Inventory no.	Order no.	UTM_X	UTM_Y	Altitude (m.)	Area	% Coverage	Average vegetation height (m)	Number of native	Number of endemic	Substrate
Inv5506	114	367336	2172128	12	1000	65	5,5	34	4	Serpentines
Inv5605	48	228891	2192923	16	1000	90	4	21	4	
Inv5606	115	368174	2172212	15	1000	75	3,5	22	5	Serpentines
Inv5705	49	222203	2198952	1	1000	90	3	6	0	
Inv5706	116	481397	2129511	31	500	45	4,5	16	4	
Inv5805	50	221947	2200447	1	1000	90	5	8	0	
Inv5806	117	482276	2129906	18	500	70	4,5	16	3	
Inv5905	51	220785	2188049	7	2000	90	5	15	2	
Inv5906	118	482611	2130197	40	500	60	4,5	18	4	
Inv6005	52	213308	2180654	1	1000	90	2	5	0	
Inv6006	119	482718	2130308	25	500	50	2	14	4	
Inv6105	53	219187	2178798	5	1000	100	7	5	0	
Inv6205	54	219184	2178801	12	2000	90	2	25	13	
Inv6805	59	233257	2046743	12	1000	100	5	26	9	

biodiversity index and the total number of species, shows a high correlation after the elimination of the 22 serpentine samples, with R^2 values between 0.983 and 0.945 (Fig. 3). This correlation decreases when the analysis is applied to the 110 inventories – including the 22 on serpentines – giving R^2 values of between 0.443 and 0.705 (Fig. 4). This correlation does not occur when applied exclusively to serpentine samples, which have a R^2 of between 0.004 and 0.055 (Fig. 5).

In this study, we used 1,582 endemic species to characterize the 19 previously established natural areas (A01 ... A19). The floristic relationship between the 19 study areas on Hispaniola is shown in the Jaccard and Pearson analyses. In the analysis of distances established by Jaccard, areas A12 and A16 have a distance of 0.898, representing a coincidence of only 10.2% (Cano et al., 2010a). The high number of endemic species in areas A12 and A16 – with 699 endemics as opposed to 482 exclusively endemic plants in area A12, and 440 compared with 278 in A16 (Table 4) (Figs 6, 7) – shows that these are two points with a high rate of endemicity and deserving of special conservation measures.

The high number of endemic species with a widespread distribution on the island is the reason the Pearson index reveals a low relationship between areas A12 and A16 ($r = -0.254$), as they have different geological and floristic characteristics; between A16 and A13 ($r = -0.168$); and between A12 and A13 ($r = -0.226$). In this last case, the weak relationship between both areas is due to the difference in the number of endemics; and although both zones have calcareous substrates, A13 has been subject to greater human impact and the resulting habitat loss and fragmentation. Similarly, A16 and A17 are separated with $r = -0.036$, as expected, as the Massif du Nord (A17) is a prolongation of the Cordillera Central (A16).

An analysis of the number of times a particular endemic species is repeated in each of the 19 areas reveals that series 1R presents endemics exclusive to the area. In 2R there are a number of endemics in two areas, and in 3R there are few cases in which the species are repeated. Table 4 shows that areas A12, A16, and A13 have the greatest diversity in endemic species.

The total number of endemics in the 19 areas is 2,094, and the sum of exclusive endemics is 1,162; the difference between $2{,}094-1{,}162 = 932$, indicating the significant number of endemics distributed around the island. The greatest concentrations are found in areas A12, A13, A16, whereas the remaining areas have a lower rate of endemics, with an increase in areas A04, A09. These areas continue to be of interest as they present endemic species that are exclusive to the territory, in some cases including endemic genera, as in A18 and A19 (Table 5).

The linear correlation analysis between the number of endemics and altitude shows a higher correlation after eliminating the plots on serpentines – $R^2 = 0.502$ (Fig. 8). The number of endemics increases with altitude until 1,200−1,300 m, and then decreases at greater heights. When the analysis is applied to the 110 plots the correlation is lower ($R^2 = 0.396$), and minimal and near zero in the case of plots on serpentines ($R^2 = 0.101$) (Figs 9, 10). This natural noise is due to serpentine soils (Cano, Cano-Ortiz, Del Río, Veloz Ramirez, and Esteban Ruiz, 2014b). There is no correlation between altitude and serpentines, as the species found on serpentines are edaphic and are not affected by the altitude parameter.

Table 2. Shannon (H) in altitudes <1,000 m

No. rel.	Inv0106	Inv0206	Inv0306	Inv0406	Inv0706	Inv0806	Inv0906	Inv1006	Inv1106	Inv1206	Inv1306	Inv1506	Inv1706	Inv1806	Inv1906
Altitude	300	300	182	140	15	8	24	69	4	29	519	541	109	102	110
Shannon (H)	3,932	4,119	3,819	3,543	3,693	3,743	2,138	3,595	3,680	3,897	3,466	3,793	3,839	3,901	
No. rel.	Inv2006	Inv2106	Inv2206	Inv2306	Inv2406	Inv2506	Inv2606	Inv2706	Inv2806	Inv2906	Inv3006	Inv3105	Inv3106	Inv3205	Inv3206
Altitude	106	113	47	83	139	163	166	160	162	94	121	144	16	104	3
Shannon (H)	3,734	3,707	3,034	3,320	3,219	2,913	2,720	2,877	2,782	3,240	3,564	3,857	3,609	3,676	3,517
No. rel.	Inv3305	Inv3506	Inv3706	Inv3806	Inv3906	Inv4006	Inv4105	Inv4205	Inv4206	Inv4305	Inv4306	Inv4405	Inv4406	Inv4505	Inv4506
Altitude	15	21	169	27	70	53	160	209	58	218	8	118	200	38	250
Shannon (H)	3,630	3,552	3,559	3,722	3,610	3,529	3,483	3,147	3,113	3,557	3,203	3,401	3,559	3,919	3,537
No. rel.	Inv4605	Inv4606	Inv4705	Inv4706	Inv4805	Inv4806	Inv4905	Inv4906	Inv5005	Inv5106	Inv5205	Inv5206	Inv5305	Inv5306	Inv5406
Altitude	39	172	36	245	42	41	8	95	8	69	14	18	12	64	89
ShanNon (H)	3,578	3,615	3,404	3,446	3,801	3,519	3,596	3,382	1,040	3,499	3,605	3,226	3,642	3,372	3,456
No. rel.	Inv5505	Inv5506	Inv5605	Inv5606	Inv5706	Inv5806	Inv5905	Inv5906	Inv6006	Inv6205	Inv6805	Inv0506	Inv0606	Inv5006	Inv3306
Altitude	84	12	16	15	31	18	7	40	25	12	12	13	10	100	26
Shannon (H)	3,070	3,649	3,182	3,164	2,898	3,032	2,702	3,127	2,860	3,632	3,483	3,443	2,451	3,179	2,130
No. rel.	Inv3405	Inv3505	Inv3605	Inv3606	Inv3705	Inv3805	Inv3805bis	Inv3905	Inv4005	Inv4106	Inv5105	Inv5405	Inv5705	Inv5805	Inv6005
Altitude	13	1	0	25	0	0	0	0	0	71	1	0	1	1	1
Shannon (H)	2,334	1,707	1,858	2,750	2,059	1,318	1,035	1,717	1,958	3,032	2,614	1,985	1,488	2,017	1,526
No. rel.	Inv6105														
Altitude	5														
Shannon (H)	1,498														

Table 3. Shannon in altitudes >1,000 m

No. rel.	Inv3005	Inv2605	Inv2305	Inv1105	Inv1005	Inv1205	Inv2505	Inv1305	Inv1405	Inv1505	Inv1705	Inv2805	Inv2905	Inv2705	Inv2405
Altitude	1203	1140	1207	1441	1473	1465	1233	1373	1377	1251	1200	1343	1286	1358	1239
Shannon (H)	3,347	3,681	3,830	3,464	3,566	3,557	3,781	3,557	3,458	3,424	3,357	3,533	3,367	3,431	3,972
No. rel.	Inv1805	Inv1905	Inv2005	Inv2105											
Altitude	2058	2336	2290	2383											
Shannon (H)	3,987	4,185	3,881	3,509											

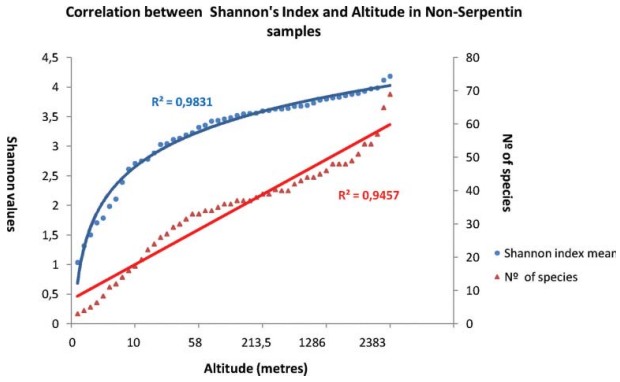


Fig. 3. Correlation between Shannon's index, no. of species, and altitude (m) in non-serpentine samples.

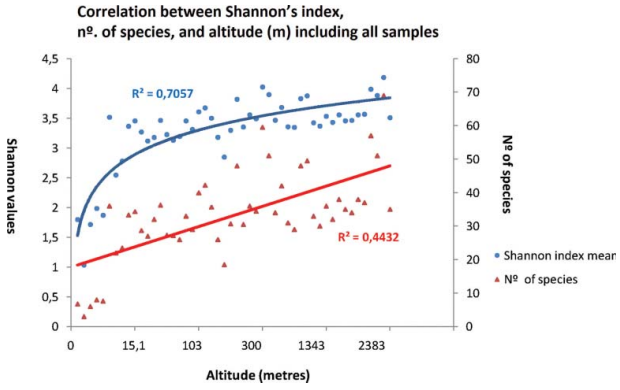


Fig. 4. Correlation between Shannon's index, no. of species, and altitude (m) including all samples.

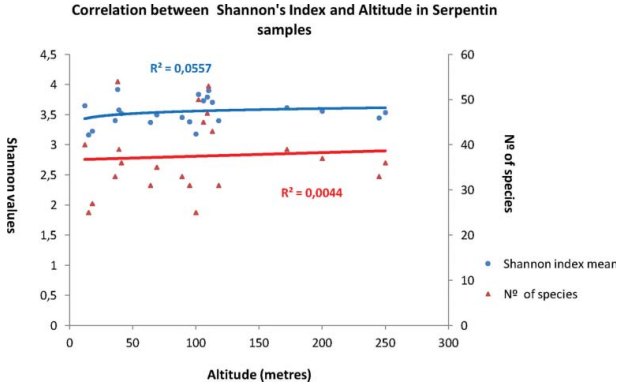


Fig. 5. Correlation between Shannon's index, no. of species, and altitude in serpentine samples.

As can be seen in Fig. 1, the Cordillera Central **A16** (Dominican Rep.) is dominated by siliceous materials, and some serpentines in the easternmost areas. The thermotype ranges from the infratropical to the supratropical, and the dominant ombrotype is humid-hyperhumid. This unit is very rich in endemics, with a total of 440 endemic species, compared with 278 that are exclusive to the area. The influence of the Alyssian winds towards the mid-mountain causes a predominance of rainforests – both broadleaf and cloud forest – with 100% coverage, and a high proportion of species in the genera *Prestoea*, *Magnolia*, *Didymopanax*, *Cyathea*; in contrast, in the high-mountain areas beyond the reach of the Alyssians there is a prevalence of *Pinus occidentalis* Sw., constituting endemic forests, as in unit A12 (Cano, Veloz Ramirez, and Cano-Ortiz, 2011), and hemicryptophytic communities of *Danthonia domingensis* Hack. & Pilg. Areas A16 and A17 in the Cordillera Central have r = −0.036; this distance is due to the lower number of endemic taxa in A17 caused by the impact of human activity in the Republic of Haiti.

Bahoruco-La Selle (**A12**) consists of calcareous mountains with sporadic presence of the supratropical thermotype and the humid ombrotype. There is a broadleaf cloud forest of *Magnolia hamorii* Howard and *Didymopanax tremulus* Krug & Urb., with 100% coverage. In the rainiest sites and in gorges there are formations of *Prestoea montana* (Cano, Veloz Ramirez, and Cano-Ortiz, 2014a). Area A12 has a high rate of endemicity with a total of 699 endemics, of which 482 are exclusive to these mountains. In basal areas such as Procurrente de Barahona, Ceitillan, and Pedernales, the ombrotype is semiarid and the thermotype is infratropical, with a predominance of dry forest with a floristic composition characterized by *Lemaireocereus hystrix* Britt & Rose, *Pilosocereus polygonus* (Lam.) Byles & Rowles, *Consolea moniliformis* (L.) Britt, *Agave antillarum* Descourt., *Cylindropuntia caribaea* (Britt & Rose) Kunth and *Melocactus pedernalensis* (Ait.) Mejía and R. García. The continuation of these sierras is the Massif de La Hotte (**A13**), an area characterized by calcareous substrates located at the end of the southwest peninsula (Haiti), with 173 endemic plants compared with 129 which are exclusive to the area. The relationship between areas A12 and A13 is r = −0.226, as they include different endemic flora and the endemic genus *Hottea*.

The rest of the areas are also of interest for conservation, as they contain endemics that are exclusive to these sites. The Sierras of Neiba, Matheux and Noires (**A14**) reveal a certain influence of the Cordillera Central due to the presence of *Podocarpus aristulatus* Parl. The absence of *Magnolia hamorii* Howard and the presence of *Pinus occidentalis* Sw. connect it with Bahoruco, as does the presence of the endemic genus *Hottea*, containing the endemics *H. crispula* (Urb.) Urb., *H. goavensis* Urb., *H. malangenis* (Urb. & Ekm.) Urb., *H. micrantha* Urb. & Ekm., *H. miragoanae* Urb., *H. neibensis* Alain and *H. torbeciana* Urb., distributed throughout biogeographic units A12, A13 and A14. Tortuga Island (**A19**) has a calcareous character and is located to the north of Haiti at a maximum altitude of 378 m; the Alyssian winds thus only affect the highest areas. Most of the territory has a dry and

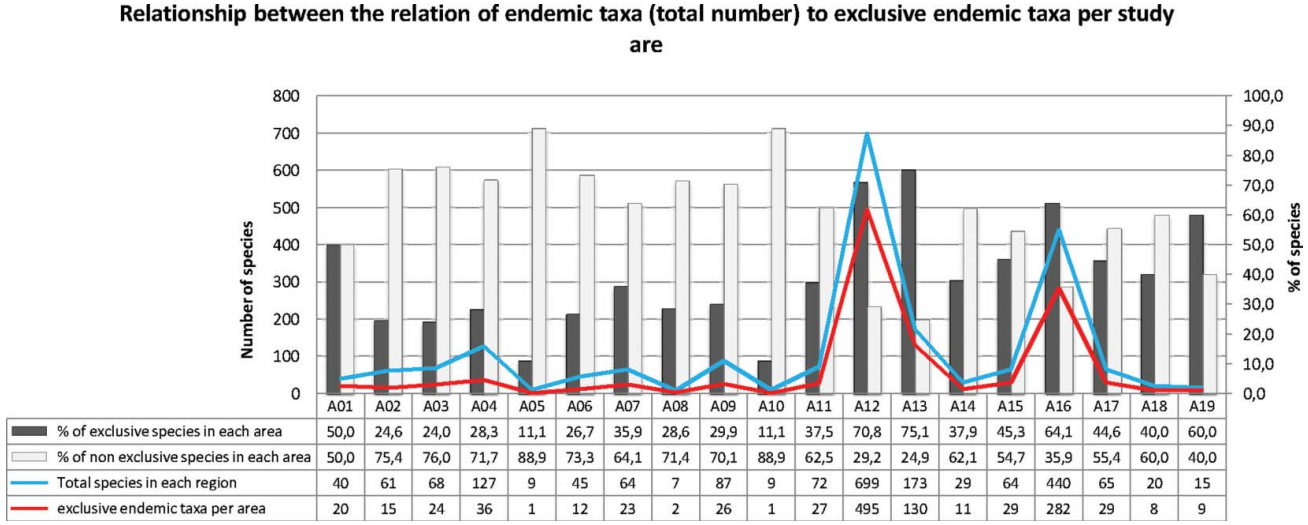
Table 4. Number of species and repetitions in the area (series 1R…6R).

	A01	A02	A03	A04	A05	A06	A07	A08	A09	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19
1R	20	15	24	36	1	12	23	2	26	1	27	482	129	11	28	278	29	8	10
2R	12	31	26	60	1	24	32	3	38	1	19	154	30	9	17	115	24	5	5
3R	6	9	11	18	2	5	7	0	16	4	21	39	10	6	14	30	9	6	1
4R	1	1	3	7	4	4	2	1	2	1	3	4	1	1	2	5	1	0	0
5R	1	3	3	4	0	1	1	1	2	0	0	5	1	1	1	4	1	0	1
6R	1	2	0	2	1	1	0	0	3	0	0	2	0	0	0	3	0	1	0

occasionally subhumid-humid ombrotype. The relationship of A19 with areas A3 and A15 is r = −0.21 and r = −0.112. The presence of the monotypical genus *Tortuella abietifolia* Urb. & Ekman and 10 exclusive endemics points to the fact that, in spite of its small size, this island is of great interest for conservation. Unit **A09**, of recent geological formation, contains emblematic endemic plants such as *Neoabbottia paniculata* (Lam.) Britt & Rose, *Melocactus lemairei* (Monv.) Miq. and *Acacia barahonensis* Urb. & Ekman. Gonâve Island (**A18**), located in the middle of the bay of Port au Prince, has an altitude of 702 m and is practically devoid of natural vegetation due to considerable human pressure; this satellite island of Hispaniola has an infra- and thermotropical thermotype and a semiarid-dry ombrotype due to its isolation. The floristic analysis reveals the presence of endemics that are exclusive to this island such as *Mouriri gonavensis* Urb. & Ekman, *Pilea dispar* Urb., *Solanum aquartia* Dunal var. *luxurians* (O.E. Schulz) Alain, *Dendropemon gonavensis* Urb., *D. spathulatus* Urb. & Ekman, *Galactia caimitensis* Urb. & Ekman and *Isidorea gonavensis* Aiello & Borhidi; and it shares other endemic species with **A11** – Pearson's index r = 0.165 – and the same vegetation type (dry forest).

The eastern coastal plain (**A07**) is coralline in origin with species of particular concern, as they are under serious threat from tourism, namely *Pereskia quisqueyana* Alain and *Melicoccus jimenezii* (Alain) Acev. Rodr., classified as endangered by Peguero and Jiménez (2008, 2011) (Table 6, see online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2015.1135195).

The Samaná peninsula (**A04**) was isolated from the rest of the territory until 300−400 years ago (Salazar et al., 1997). It is a geomorphological unit dominated by karstic and limestone materials, schists and marbles. It has an infratropical thermotype and a subhumid-humid ombrotype, where the presence of escarpments (outcrops) gives rise to special edaphoxerophilous communities dominated by *Pilosocereus polygonus* (Lam.) Byles & Rowles, *Zamia debilis* L., *Agave antillarum* Descourt., *Eugenia samanensis* Alain, *Bursera simaruba* (L.) Sarg., *Ficus velutina* H. B. ex Willd. and *Opuntia dillenii* (Ker-Gawl) Haw. From the floristic point of view it has 127 species, of which are 36 exclusive endemics. There are several reasons for the high number of endemic species and habitats: the island's geological origin, the bioclimate – with



	A01	A02	A03	A04	A05	A06	A07	A08	A09	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19
% of exclusive species in each area	50,0	24,6	24,0	28,3	11,1	26,7	35,9	28,6	29,9	11,1	37,5	70,8	75,1	37,9	45,3	64,1	44,6	40,0	60,0
% of non exclusive species in each area	50,0	75,4	76,0	71,7	88,9	73,3	64,1	71,4	70,1	88,9	62,5	29,2	24,9	62,1	54,7	35,9	55,4	60,0	40,0
Total species in each region	40	61	68	127	9	45	64	7	87	9	72	699	173	29	64	440	65	20	15
exclusive endemic taxa per area	20	15	24	36	1	12	23	2	26	1	27	495	130	11	29	282	29	8	9

Fig. 6. Relation of endemic taxa (total number) to exclusive endemic taxa in each study area.

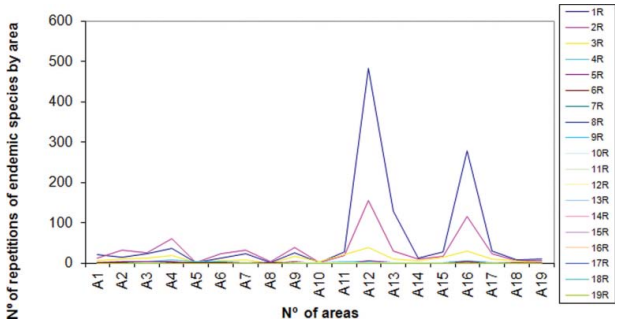


Fig. 7. Number of repetitions of endemic species in the 19 areas.

thermotypes ranging from the infratropical to supratropical, the semiarid-hyperhumid ombrotype, the origin of the flora due to migratory routes, and the isolation of its mountains.

Discussion

The geological origin of the island, the result of its union-separation-union, has produced mountains that are biogeographic islands (Liira, Jürjendal, and Paal, 2014), and given rise to the island's high diversity. The distribution and species richness in the tropical forest varies with altitude and with other patterns such as rainfall distribution, topography, geographic distance, and human impact (Eisenlohr et al., 2013), and in places altered by humans there are fewer trees to enable the presence of climbing species (Pereira Villagra, Pereira Cabral Gomes, Buruham, and Romaniuc Neto, 2013). It is difficult to establish the origin of high neotropical biodiversity (Rull, 2013); in the case of Hispaniola, its geology, topography, and geographic distance act as significant obstacles on migratory routes, which has led to its current diversity. The island's similar diversity invites comparison with the megadiversity of Mexico (Luna-Vega, Espinosa, Rivas, and Contreras-Medina, 2013).

Rumeu, Alfonso, Fernández-Palacios, and Nogales (2014) established three species of conifers for Hispaniola, two of which are vulnerable and critically endangered according to IUCN (2013); these data should be corrected, as in Hispaniola there is a representation of the families *Pinaceae* (2 species), *Araucariaceae* (1 species), *Cupressaceae* (9 species), *Podocarpaceae* (3 species) with the endemics *Podocarpus hispaniolensis* Laubenfels and *Podocarpus aristulatus* Parl.

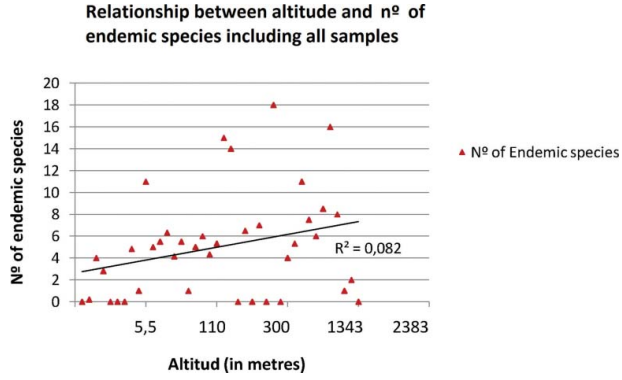


Fig. 8. Relationship between altitude and no. of endemic species including all samples.

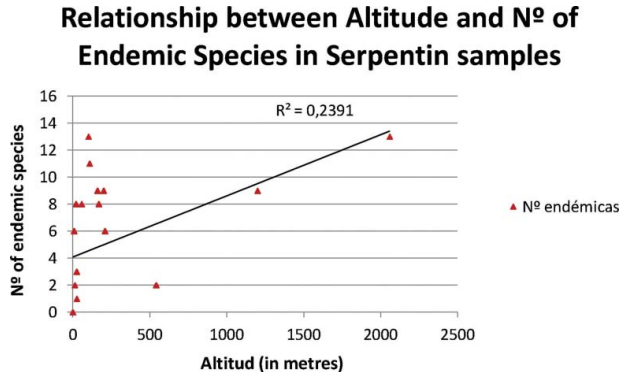


Fig. 9. Relationship between altitude and no. of endemic species in serpentine samples.

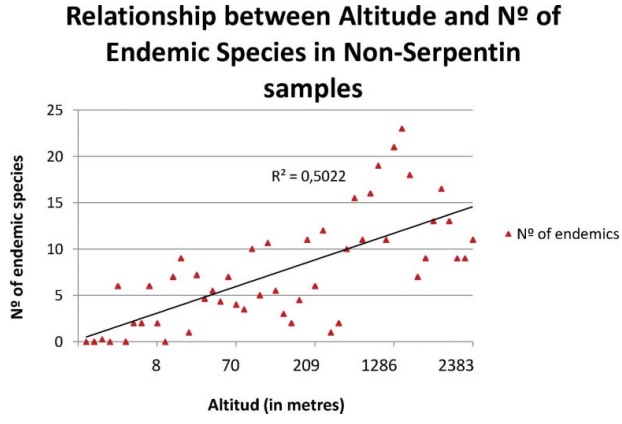


Fig. 10. Relationship between altitude and no. of endemic species in non-serpentine samples.

Table 5. Comparative analysis of the ratio of endemic taxa (total number) to exclusive endemic taxa in each study area. 1.- Number of exclusive endemic taxa per area. 2.- Total number of endemic taxa per area.

	A01	A02	A03	A04	A05	A06	A07	A08	A09	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19
1	20	15	24	36	1	12	23	2	26	1	27	482	129	11	28	278	29	8	10
2	40	61	68	127	9	45	64	7	87	9	72	699	173	29	64	440	65	20	15

Table 6. Pearson index values.

	A01	A02	A03	A04	A05	A06	A07	A08	A09	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19
A01	1	0,01	0,045	0,071	0,041	−0,003	−0,033	0,05	0,014	0,041	−0,016	−0,127	−0,056	0,008	−0,013	−0,046	−0,033	0,054	0,026
A02	0,01	1	−0,026	0,267	0,029	0,143	0,026	0,086	−0,02	−0,015	−0,044	−0,086	−0,07	−0,027	−0,024	−0,051	−0,041	−0,023	0,014
A03	0,045	−0,026	1	0,006	−0,016	−0,036	0,051	0,033	0,154	0,025	0,043	−0,088	−0,044	0,041	0,02	−0,09	0,05	0,004	−0,021
A04	0,071	0,267	0,006	1	0,194	0,285	0,069	0,015	0,021	−0,022	−0,065	−0,169	−0,104	−0,04	−0,037	−0,048	−0,061	−0,033	−0,005
A05	0,041	0,029	−0,016	0,194	1	0,088	−0,016	0,122	0,019	−0,006	−0,017	−0,033	−0,027	−0,01	−0,016	0,066	−0,016	−0,009	−0,007
A06	−0	0,143	−0,036	0,285	0,088	1	−0,035	0,046	−0,008	0,038	−0,019	−0,106	−0,048	−0,023	−0,035	−0,072	−0,016	−0,019	−0,017
A07	−0,03	0,026	0,051	0,069	−0,016	−0,035	1	−0,014	0,077	0,027	−0,014	−0,028	−0,062	−0,004	−0,026	−0,12	−0,01	−0,023	−0,02
A08	0,05	0,086	0,033	0,015	0,122	0,046	−0,014	1	−0,016	−0,005	−0,015	−0,04	−0,023	−0,009	−0,014	0,001	−0,014	−0,008	−0,007
A09	0,014	−0,02	0,154	0,021	0,019	−0,008	0,077	−0,016	1	0,092	0,027	−0,002	−0,076	0,008	−0,021	−0,088	−0,022	−0,002	0,005
A10	0,041	−0,015	0,025	−0,022	−0,006	0,038	0,027	−0,005	0,092	1	0,185	−0,05	0,027	0,052	0,155	−0,009	0,069	0,142	−0,007
A11	−0,02	−0,044	0,043	−0,065	−0,017	−0,019	−0,014	−0,015	0,027	0,185	1	−0,109	0,079	0,083	0,109	−0,095	0,031	0,165	0,01
A12	−0,13	−0,086	−0,088	−0,169	−0,033	−0,106	−0,028	−0,04	−0,002	−0,05	−0,109	1	−0,226	−0,046	−0,144	−0,254	−0,165	−0,089	−0,087
A13	−0,06	−0,07	−0,044	−0,104	−0,027	−0,048	−0,062	−0,023	−0,076	0,027	0,079	−0,226	1	−0,018	−0,041	−0,168	−0,011	−0,022	−0,034
A14	0,008	−0,027	0,041	−0,04	−0,01	−0,023	−0,004	−0,009	0,008	0,052	0,083	−0,046	−0,018	1	0,068	−0,043	0,09	0,027	−0,013
A15	−0,01	−0,024	0,02	−0,037	−0,016	−0,035	−0,026	−0,014	−0,021	0,155	0,109	−0,144	−0,041	0,068	1	−0,07	0,135	0,063	0,112
A16	−0,05	−0,051	−0,09	−0,048	0,066	−0,072	−0,12	0,001	−0,088	−0,009	−0,095	−0,254	−0,168	−0,043	−0,07	1	−0,036	−0,045	−0,061
A17	−0,03	−0,041	0,05	−0,061	−0,016	−0,016	−0,01	−0,014	−0,022	0,069	0,031	−0,165	−0,011	0,09	0,135	−0,036	1	0,005	0,013
A18	0,054	−0,023	0,004	−0,033	−0,009	−0,019	−0,023	−0,008	−0,002	0,142	0,165	−0,089	−0,022	0,027	0,063	−0,045	0,005	1	−0,011
A19	0,026	0,014	−0,021	−0,005	−0,007	−0,017	−0,02	−0,007	0,005	−0,007	0,01	−0,087	−0,034	−0,013	0,112	−0,061	0,013	−0,011	1

Echeverry and Morrone (2010) noted the panbiogeographic character of Caribbean territories and considered the evolutionary character of the taxa, as interpreted from the cladograms made by these authors. We agree on the natural character of the biogeographic range of the Province of Hispaniola proposed by Echeverry and Morrone, and also proposed by us in Cano et al. (2010a); as the geographic location of this island makes it the frontier for various migration routes, such as the route from the Bahamas and the Lesser Antilles, and to lesser extent, the Gulf of Mexico. This is due to the isolation of the taxa (clades), which have evolved and led to a high rate of endemism.

The high biodiversity found in the mountains decreases in low-lying areas due to the impact of farming communities (Aitken, 2012), which has caused a deterioration in the local ecosystems. This includes the mangrove (Cano, Cano-Ortiz, Veloz Ramirez, Alatorre, and Otero, 2012), with a decline in the populations of *Rhizophora mangle* L., and supports the thesis of Takayama, Tamura, Tateishi, Webb, and Kajita (2013) regarding the influence of the American continent as a geographic barrier to the dispersion of the propagules of *Rhizophora* towards the Pacific. Mangrove forests are being altered due to their improper use as an energy source by the local population. This causes fragmentation, a decrease in their propagules, and hence reduced dispersion, a phenomenon also occurring in other low-lying areas used by humans, with the resulting decline in the number of endemics. It is however possible to combine conservation and development and sustain indigenous populations while regulating their activities (Kothari, 2013). This can be done by raising awareness of the value of the various biogeographic territories (Cano et al., 2010a) and analysing the diversity of the invasive species in these areas in order to outline measures for biogeographic conservation (Richardson, 2012).

The floristic analysis reveals a very diverse range of influences, and points to a significant affinity with the flora of tropical South and Central America, as a large part of the flora of Hispaniola was formed from these floras, and arrived on the island through migratory routes (Cano et al., 2009a). The isolation of the mountain chains and ranges is one of the causes of the high rate of endemics: 2,050 (34.16%) out of a total of 6,000 species (Mejía, 2006), representing 50% of the 12,000 species included in Oleas et al. (2013), and 25.6% of the endemics in the Caribbean. Global change is endangering the conservation of this endemic flora (Weller, Sunding, and Sakai, 2013) and creating the need for predictive models for its conservation (Addison et al., 2013). This biodiversity is not only due to the isolation of the flora over a period of millions of years, but also to Hispaniola's altitudinal gradient, the highest in all the Antilles. This explains the fact that the greatest number of endemic plants is found in the Cordillera Central and in the Sierra de Bahoruco, La Selle and La Hotte, where there is less habitat fragmentation.

The analysis of the results highlights areas with a greater concentration of endemics, A12, A13, and A16, possibly a case of palaeo-islands that were separated for some time. These palaeo-islands are currently linked by large warmer and drier valleys that have acted as barriers to dispersion (Dod, 1984). Our analysis of the concentration of endemics in the area coincides with that of May (2001), as the highest number of endemics is found in Sierra de Bahoruco (A12), the Cordillera Central (A16), and Massif de la Hotte (A13). However the frequent presence of calcareous patches in A17 and the serious impact of human activity – in combination with the island effect (Primack & Ros, 2002) – is leading to the extinction of habitats and species. Thus A17 is nearer the altered territories to the northwest of Haiti: A15 ($r = 0.135$). Areas A03, A09, and A12 all have arid-dry ombrotypes with similar vegetation and endemic species and a good representation of the genus *Croton*, which has a high diversity in Caribbean areas (Van Ee, Berry, Riina, and Gutierrez Amaro, 2008) and contains 14 endemic plants always located in dry environments, unlike the subgenus *Macrocroton* which was not found on the island.

The *Leguminosae* family is well represented (Lavin and Beyra Matos, 2008) in all the biogeographic areas of Hispaniola (Caribbean), with approximately 50 genera and 2,500 species; and the locally endemic species *Acacia barahonenis* Urban, *Caesalpinia buchii* Urban, *Calliandra tortuensis* Alain, and *Pithecelobium domingense* Alain.

The oldest palaeo-islands on Hispaniola correspond to the Cordillera Central (A16), Cordillera Oriental (A05 and A06), Sierra de Bahoruco (A12), and Massif de la Hotte (A13); whereas the Cordillera Septentrional (A1) and the other areas are younger. The relatively young age of these areas, in combination with their use which has led to the fragmentation of habitats, accounts for the lower concentration of endemics. It is precisely these low-lying areas that are the most altered by human activity; this leads to the modification of habitats, a decrease in the number of endemics, and an increase in the number of generalist (native) species (Table 1). Our results concur with the research of Liira et al. (2014), as the fragmentation of habitats has given rise to new small patches with a high richness in common species and a lower number of endemics.

The sampling of the 110 plots located at altitudes of between zero and 2,383 m reveals that the greatest concentration of endemics occurs at medium altitudes, with a decrease in low-lying areas and at higher altitudes. This follows the altitude distribution pattern (Eisenlohr et al., 2013) whereby the greatest richness of endemic species is found in mountain areas at medium altitudes. The mountains that act as islands show a similar pattern of distribution of flora (Pérez-García et al., 2012), and constitute a

bioclimatic ecotone as they serve as a bioclimatic transition between the tropical xeric, tropical pluvial and tropical pluviseasonal macrobioclimates (Rivas-Martínez et al., 1999). This distribution pattern is modified by the alteration of habitats, the presence of soil islands (serpentines), and by topography and geographic distance. The linear distribution pattern with altitude is due to the effects of palaeo-islands (hotspots) and habitat fragmentation (coldspots), with the highest number of endemics located in areas of bioclimatic ecotone and in soil islands at lower altitudes. Coldspots are areas in which habitat fragmentation has led to a loss of endemic species and the ingression of generalist species. Diversity may be high, but with a decrease in the number of habitat-specific and endemic plants; the only way to maintain high-quality diversity is through habitat conservation. Our results show that the mountain areas have a high rate of endemicity, and particularly the mountains in areas A12, A13, A16, and A17. The conservation of these areas should be entrusted to small indigenous populations who have a traditional knowledge of these species, as has been demonstrated in other territories with experiments in Ontario, British Columbia, and Coastal Canadian Arctic, where value is placed on the traditional knowledge of the indigenous population (Agrawal, 2009; Berkes, 2009; Robson et al., 2009).

Conclusions

Hispaniola has a high diversity concentrated in specific mountain sites and soil islands, due to the effect of palaeo- and neo-islands (soil islands). The greatest richness in endemic species occurs in mountains at medium altitudes; the increase in endemism at medium altitudes is caused mainly by the fact it is an ecotonic area from the bioclimatic point of view, since there is contact between the pluvial and the pluviseasonal bioclimate in the high mountain. The most seriously degraded areas are found below altitudes of 500 m; this decline in diversity is caused by deforestation, burning, high-density tourism, and collection of wood as an energy source (charcoal production). We therefore propose protection measures for certain specific areas.

Finally we recommend the establishment of a Biosphere Reserve in areas A12 and A13, including the Sierra de Bahoruco, La Selle, Tiburón, and La Hotte (Dominican Republic and Republic of Haiti); and A16 and A17 in the Cordillera Central belonging to both countries. The remaining areas are also highly important, and some have been declared protected nature reserves. Where this is not yet the case, we propose the following as protected nature reserves: A1 Northern Cordillera, A4 Samaná Peninsula, A6 Los Haitises, A8 Sierras of Yamasa and Prieta, A18 Gonâve Island, and A19 Tortuga Island.

Acknowledgements

We are grateful to the two anonymous reviewers who provided valuable suggestions for improvements to the first draft of this paper. This article was translated by Ms Pru Brooke-Turner (M.A. Cantab.).

Disclosure statement

No potential conflict of interest was reported by the authors.

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Associate Editor: Polly Hayes