Belg. J. Zool., 143(Supplement): 159-185 December 2013

Summary of our present knowledge of the spider communities of the Galápagos archipelago. First analysis of the spider communities of the islands Santa Cruz and Isabela

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ABSTRACT: A synthesis is given of 30 years of galapagoan spider fauna research, including an historical overview of spider sampling in the archipelago. A total of 11,437 specimens originating from 688 sampling localities are analyzed. In total 175 spider species are reported of which 152 could be identified or were described as new. The remaining 23 species could only be identified to morpho-species level and they may be new to science and thus endemic. Two basic conclusions could be made from this first analysis of the existing data. 1° Single islands or island groups can be characterized by a specific spider community, and 2° the well-differentiated climax vegetation zones of Isla Santa Cruz can also be characterized by a specific spider community.

KEY WORDS: Araneae, climax vegetation zones, zoogeography, species composition

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INTRODUCTION

The islands

The Galápagos Archipelago consists of thirteen large islands, six smaller islands and over forty islets. These islands are well isolated from the South American mainland and lie at a distance between 960 and 1180 km from the Ecuadorian coast. The islands are spread over 304 km east to west and 341 km northwest to southeast. The total land area is about 7.856 km² spread over a surface of 45,000 km² of sea. (Jackson, 1985; Peck, 2006)

Age

All the islands are volcanic. They have arisen over the Galápagos hot spot on the Nazca Plate. Their maximum emergence age is estimated to be between 4 (Isla San Cristóbal) and 0.07 (Isla Fernandina) million years, their minimum emergence between 2.9 (Isla Santa Fé) and 0.035 (Isla Fernandina) (Geist et al., 2013) million years.

Climate

The islands lie at the edge of the Central Pacific dry zone. There are two seasons: the rainy-warm season from about December to May characterized by being sunny with average daytime temperatures about 29°C with occasional short thunderstorms, and the dry-cool season, also called “garua” – a wet fog-drip environment – from about May to December with an average August daytime temperature of about 22°C. The prevailing winds and rain are from the South making the northern slopes much dryer.

In some years, the drought is broken in the early months of the year by warm water coming from the east and bringing a lot of rain. This phenomenon is called “El Niño” and occurs at regular times.

The average archipelago rainfall at sea level is less than 75mm per year, but in “El Niño” years it can easily exceed 3264mm (Jackson, 1985; Peck, 2006).

Vegetation zones

The climax vegetation (Figure 1), which can still be encountered in its original composition only on Isla Santa Cruz, consists of seven well-differentiated vegetation zones: the Littoral zone (with its mangroves, sandy beaches and dunes with creeping vines, grasses, succulent shrubs and saltbushes), the Arid zone (with deciduous trees such as *Bursera graveolens*, shrubs such as *Croton scouleri* and cacti, for example *Opuntia* and *Jasminocereus*), the Transition zone (a deciduous wood dominated by the endemic *Pisonia floribunda* and *Psidium galapagensis* and overwhelmed with epiphytes, mostly lichens), the *Scalesia* zone (a cloud-forest dominated by the composite *Scalesia pedunculata*, which are covered with epiphytes such as mosses, liverworts, ferns, orchids, peperonias and bromelias), the *Zanthoxylum* or Brown zone actually known as the Culture zone (altered by human activities into agricultural fields, pastures and orchards), the *Miconia* zone (a dense shrubby belt of *Miconia robinsoniana*), the Fern sedge zone or Pampa zone (ferns, grasses and sedges with some *Sphagnum* patches). The altitudinal boundaries of these vegetation zones differ strongly between southern and northern slopes due to the drier conditions along the northern slope (Figure 1, Table 1) (JACKSON, 1985; PECK, 2006).

The higher Isabela volcanoes, Cerro Azul, Volcán Darwin, Volcán Wolf and the island of Fernandina have an inversion zone situated around 1000-1200m, a cloudy region above which there is an arid summit zone with the same vegetation (cacti f. i.) as the coastal arid zone. More details are found in BAERT et al. (2008).

Four islands have human settlements: Volcán Sierra Negra (Isla Isabela), Isla Santa Cruz, Isla Floreana and Isla San Cristóbal.

In this paper I provide an initial approach to determine whether single islands or island groups can be characterized by a specific spider community and whether the well-differentiated climax vegetation zones of the central island Santa Cruz can also be characterized by a specific spider community. I likewise examine the five uninhabited volcanoes of Isla Isabela where the vegetation has not yet evolved into climax situation.

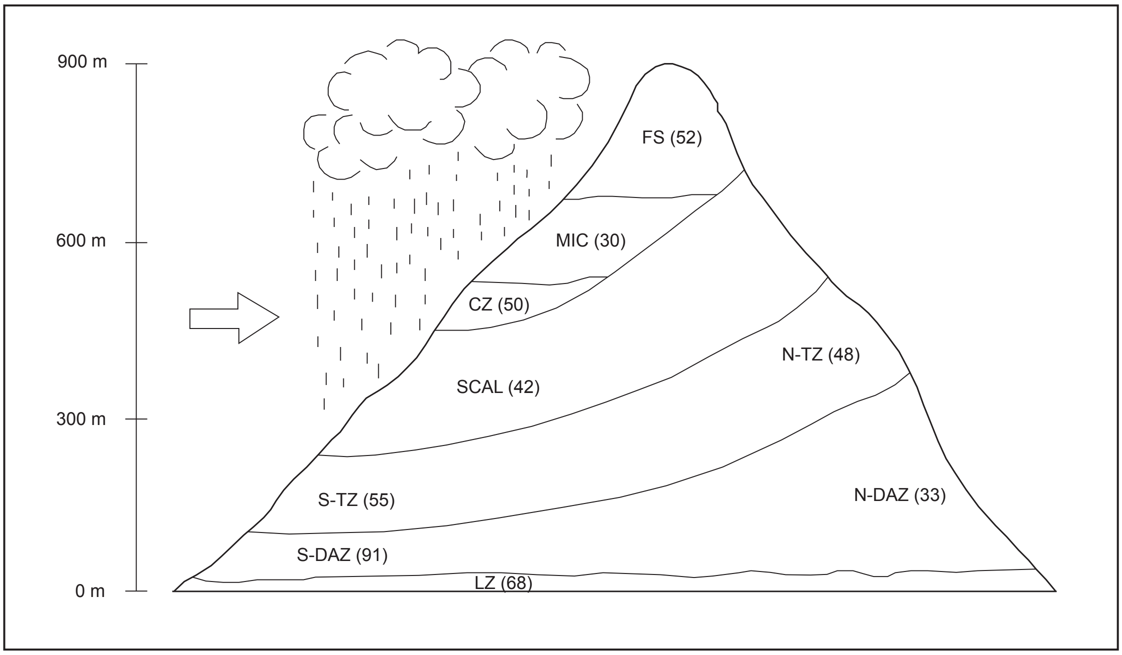


Fig. 1. – Climax vegetation zones for the island of Santa Cruz with indication of the number of species per zone. LZ = Litoral zone; DAZ = Arid zone; TZ = Transition zone; SCAL = *Scalesia* zone; CZ = Culture zone ; MIC = *Miconia* zone ; FS = Fern-Sedge zone or pampa ; N = North ; S = South. (After JACKSON, 1985, figure 10 based on C.D.R.S. museum exhibit)

TABLE 1

The altitudinal boundaries of the climax vegetation zones along the southern and northern sides of Isla Santa Cruz. Rainfall only measured along southern slope.

VEGETATION ZONE	CODE	SOUTH	RAINFALL (S)	NORTH
Littoral zone	LZ	0-5m	No measurements	0-5m
Low Arid zone (*Opuntia*)	DAZ	5-20m	75 mm/y	5-50m
High Arid zone (*Bursera* forest)	HAZ	20-110m	No measurements	50-250m
Transition forest	TZ	110-250m	No measurements	300-560m
Culture zone	CZ	140-500m	No measurements	none
***Scalesia* zone**	SCAL	550-620m	1040 mm/y	570-650m
***Miconia* zone**	MIC	500-620m	1694 mm/y	none
Fern-sedge zone	FS	600-875m	No measurements	650-875m

HISTORICAL BACKGROUND OF THE GROWTH OF OUR SPIDER KNOWLEDGE

The first spider species described from Galápagos was *Gasteracantha insulana*, described by THORELL in 1859 (now known as *G. cancriformis* (Linnaeus, 1767)). BUTLER (1877) noted six species from the Petrel expedition of 1875. In the scientific results of the explorations made by the U.S. Fish Commission Steamer Albatross, MARX (1890) mentioned 10 species of which one was an immature *Agelena* Walckenaer 1805 and three were cited as new species (*Segestria aequatoria, Loxosceles galapagoensis* and *Filistata oceanea*) but not described (catalogued thus as Nomina Nuda).

BANKS (1902) published from the Hopkins-Stanford Galápagos expedition (Snodgrass-Heller 1898-1899) a list of 38 species, of which 20 were described as new to science. He added in 1924 (BANKS, 1924) two species from the Williams Galápagos expedition (Beebe & Wheeler 1923). After the study of the material collected during the Norwegian Zoological Expedition (Wollebaek 1925) he added three more species (BANKS, 1930), bringing the total to 43 species.

A second checklist was published by ROTH & CRAIG in 1970 after the study of various collections: American Museum of Natural History of New York (AMNH), British Museum of London (BM), Museum of Comparative Zoology of Harvard (MCZ), Zoologisk Museum of Oslo (ZMO), California Academy of Sciences (CAS) with the collections made during the Californian Academy of Sciences Expeditions (1905-06 Williams expedition and the Galápagos International Scientific Project 1964 collections made by Cavagnero & Schuster) and the collection made by N. & J. Leleup in 1964-65 and deposited at the Royal Belgian Institute of Natural Sciences of Brussels (RBINS). Seventy six species were cited in this checklist.

In 1982 a study of the spider fauna was initiated by the author and Jean-Pierre Maelfait. Their first checklist was published in 2000 (BAERT & MAELFAIT, 2000) after a thorough study of all spider material available at that time. This material consisted of all previous spider collections made during the above-mentioned expeditions and which were deposited in the collections of the AMNH, BM, CAS, MCZ and ZMO. More recent collections were made by S. Jacquemart (RBINS 1974-75), H. Franz (Austria 1975), H. & I. Schatz (Austria 1985-88), S. Peck (Canada 1985-96) and many collaborators of the Charles Darwin Research Station, Galápagos). The author and several Belgian colleagues collected an important amount of material during their visits to the islands between 1982 and 2010.

The checklist published in 2000 contained 115 species. In their work on the distribution and habitat preference of the spiders of Galápagos (Baert et al., 2008), they noted 149 morphospecies (of which 121 could be named). The Belgian team visited the islands several times during the last 30 years (1982, -86, -88, -91, -96, -97, -98, 2000, -02, -09, -10).

Recently (end 2010 - beginning 2011) an opportunity arose for the author to study the collections made by S. Riechert (1967-1974) and Prof. W. Reeder (1975-1980), material deposited at the Texas Memorial Museum. The number of species rose to 174. The species *Nephila clavipes* and *Cyclosa conica* cited in Roth & Craig (1970), being (in my opinion) dubious findings or identifications, are not taken into account.

Recently, in 2011, Henri Herrera, a CDRS collaborator, found a new *Galapa* pholcid while sampling the island of Floreana, bringing the number of spiders to 175.

The increase in the number of known spider species is visualized in Figure 2.

MATERIAL AND METHODS

Study of all the material enumerated above resulted in a data base containing 11,437 specimens, derived from 5160 sampling units distributed over 688 sampling localities scattered over the whole archipelago. Figure 3 gives an overview of all spider samples taken and Table 2 gives, for each sampling team and sampling individual, the period of sampling, the number of sampling units, the number of sampling days and the sampling methods used.

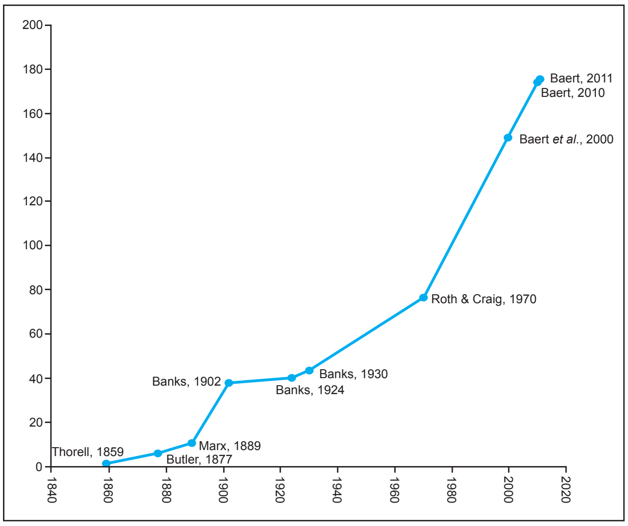


Fig. 2. – Rate of increase in the number of spider species. Y-axis: number of publications; X-axis: years of publication.

The character of the samples was not uniform; they were taken by different collectors using different sampling methods according to the arthropod group they studied. Each method yields specific species: pitfall traps capture soil surface active species, sieving captures soil and humus inhabiting species while sweeping and beating captures vegetation inhabiting species. The sample efforts were also not balanced between sites, dates or methods. The samples were taken in different years, in different periods of the year and thus during different climatic situations. Certain sampled sites were more frequently sampled forging the quantitative data. This is due to the accessibility of the islands. The island of Santa Cruz, being the starting place of all research (residential place of the Charles Darwin Research Station) with a fairly good network of "roads" and paths by which many places can easily be visited, is by far the most thoroughly sampled island. There is only one main road to the top of the other inhabited islands (San Cristóbal, Floreana and Volcán Sierra Negra of Isla Isabela). Inhabited islands are *de facto* more frequently sampled. All other islands or volcanoes are only accessible along a unique western, eastern or southern oriented path (Figure 3). Coastal habitats are also easily accessible (Figure 3).

The quantitative data can therefore not be used, only presence or absence of the species, terms that do not take into account the differences in density of the species, knowing that (some) species may have a wide distribution but may differ in density according to their preferential habitat type. I therefore used Cluster analysis based upon Sorensen's similarity index (Multivariate Analysis of Ecological Data, PC-ORD 6).

TABLE 2

Years of sampling, number of sampled sites and sampling methods used per individual collector and/or collecting team. (Bt= beating, FIT = Flight intercept traps, FIT/PF = FIT combined with big soil trap, Hc = handcatches, Ls = litter & soil sifting, M = Malaise trap, PF = Pitfall, Pt = pan trap, Sw = sweeping).

Name of collector	**Years of sampling**	**Number of sites**	**Collecting days**	**Sampling methods**
Collections	<1963	appr. 110		arbitrary catches
Leleup N.	1964-1965	26	60	arbitrary catches
Riechert S.	1967-1974	86		arbitrary catches
Jacquemart S.	1973-74	45	68	arbitrary catches
Franz H.	1975	37	68	arbitrary catches
Reeder W.G.	1975-1980	825	333	Hc, Sw, Bt, Ls
Schatz H. & I.	1985-1988	267	214	Ls, Hc
Peck S. & J.	1985-1996	639	399	FIT/PF, Ls, M, Sw, Bt
Abedrabbo S.	1986-1997	394	resident	M,PF(4 years), Hc
Heraty J.	1991	51	61	Pt, Hc
Hernandez	1991-1992	9	55	arbitrary catches in caves
Roque L.	1997-2002	96	resident	arbitrary catches
CDRS	1980-2010	691	resident	arbitrary catches
Baert L., Maelfait J.-P. & Co	1982-2010	1413	367	PF, Hc
Herrera H.	2011	22	resident	arbitrary catches

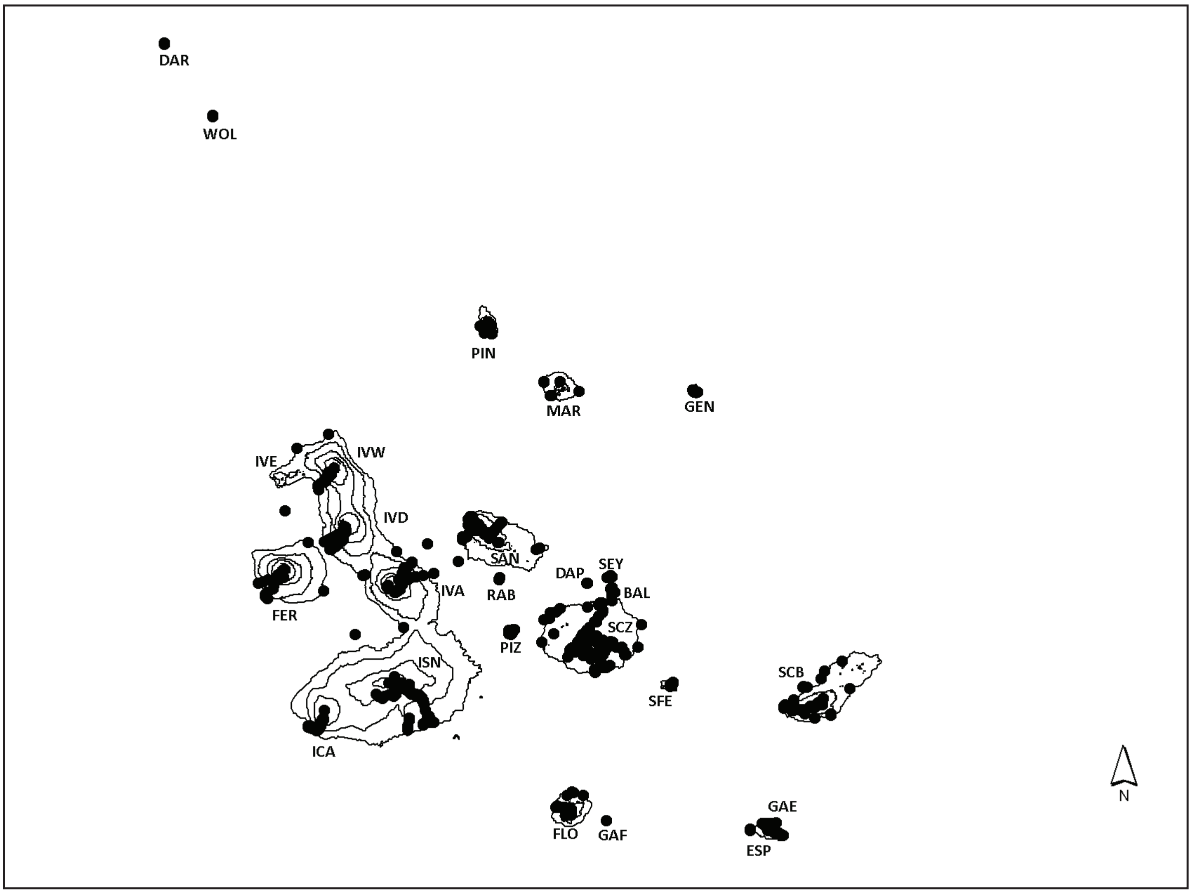


Fig. 3. – Distribution of all samples included in this study. For the island name abbreviation see Table 5.

TABLE 3

Number of species of the 32 spider families known from the archipelago with indication of the genera showing a kind of adaptive radiation.

Families (32)	**Number of Species**	**Unknown Species**	**Genera with Adaptive radiation**
THERIDIIDAE	23	4	
SALTICIDAE	13	4	*Sitticus*
PHOLCIDAE	13	1	*Aymaria,Galapa*
OONOPIDAE	11	9	
LINYPHIIDAE	11	3	
ARANEIDAE	10		
GNAPHOSIDAE	10		*Camillina*
LYCOSIDAE	7		*Hogna*
TETRAGNATHIDAE	5		
ZORIDAE	4		*Odo*
THOMISIDAE	3		
PRODIDOMIDAE	3		
DICTYNIDAE	3		
ANYPHAENIDAE	3		
ULOBORIDAE	2	1	
SPARASSIDAE	2		
SICARIIDAE	2		
SCYTODIDAE	2		
OECOBIIDAE	2		
OCHYROCERATIDAE	2		
MIMETIDAE	2		
CORINNIDAE	2		
PHILODROMIDAE	2		
TITANOECIDAE	1		
SYMPHYTOGNATHIDAE	1		
SELENOPIDAE	1		
SEGESTRIIDAE	1		
OXYOPIDAE	1		
NESTICIDAE	1		
MYSMENIDAE	1		
FILISTATIDAE	1	1	
DESIDAE	1		
THERIDIOSOMATIDAE	1		

RESULTS

Species composition and zoogeographical relationships

The known Galápagos spider fauna currently totals 175 species, distributed over 32 families (Table 3), of which 79 species (52%) seems to be "at present" endemic to one or more islands of the archipelago, 45 species (29.6%) are native to the American mainland (28 of these can be found in North America, 24 in Mexico, 26 in central America, 40 in South America and 22 in the West-Indies), 15 species are cosmopolitan (9.9%), 12 species are pantropical (7.9%), 1 species is holarctic and 23 species are still identified only to morpho-species and may be endemics. Some genera (Table 3) show a kind of adaptive radiation. They either speciated on different islands (lycosid *Hogna* Simon 1885, zorid *Odo* Keyserling 1887, pholcids *Galapa* Huber 2000 and *Aymaria* Huber 2000, and gnaphosid *Camillina* Berland 1919) and/or on the same island according to altitude (lycosid *Hogna*, salticid *Sitticus* Simon 1901) or in sympatry in the same habitat on the same island (gnaphosids *Camillina cruz* Platnick & Shadab 1982/*galapagoensis* Platnick & Shadab 1982).

Mimetus eperoides Emerton 1882 is native to the USA. *Tetragnatha lewisi* Chickering 1962 (?, uncertain identification), a species native to Jamaica (West indies), has been sampled by Stewart Peck in 1992 floating on the sea surface between North Isabela (South of Volcán Ecuador and west of Volcán Wolf and Darwin) and Fernandina, some 10 km from the coast.

Fourteen species are native to Latin America (Table 4). Most of these species are native to the north-western countries Ecuador, Peru, Venezuela and Bolivia, countries lying nearest the archipelago. World distribution is after Platnick (2013).

The number of species (endemic or not) present on each island and the abbreviations of the island names are given in Table 5. The species distribution over the islands of the archipelago is given in Table 8.

The relationship of the number of species with surface area (Figure 4) and altitude (Figure 5) gives a positive linear relationship when put in a log-graph, but shows, when put in a normal graph, a positive linear relationship for the non-inhabited volcanoes and islands, showing there is a disproportionally higher number of species for the smaller islands with human settlements (Santa Cruz, Floreana, San Cristóbal and the Isabela Volcán Sierra Negra) or islands which are or were subject to human interactions (Santiago and the Isabela Volcán Alcedo). These islands are encircled in the graph.

Spider communities within the archipelago

Can single islands or island groups be characterized by a specific spider community? A Cluster analysis based upon Sorensen's similarity index revealed (Figure 6) that four distinguishable groups of islands/volcanoes can be divided in a total of eight smaller sub-groups.

A/ The low islands with only an Arid zone as vegetation zone split into two subgroups:
  (1) a sub-group consisting of the most south-eastern island Española and its satellite island of Gardner with four species with restricted occurrence on both islands: *Goeldia obscura* (Keyserling, 1878) known only from Colombia and Peru and three endemics to these islands: *Hogna espanola* Baert & Maelfait 2008, *Odo maelfaiti* Baert 2009 and *Sitticus vanvolsemorum* Baert 2011;
  (2) a second sub-group consisting of the small islands lying around the central island of Santa Cruz: Santa Fé, Seymour Norte and Pinzón.

B/ Within the second group we have:
  (3) a subgroup consisting of the northernmost islands Pinta, Marchena and Genovesa;

(4) while the northern Isabela volcanoes Wolf and Darwin (with easterly-located Beagle crater IBC) and the westernmost youngest island Fernandina cluster together in a second sub-group. Those volcanoes and Fernandina have a summit upper Dry zone above the inversion zone 1100-1200m. All those islands and volcanoes have a maximum emergence age less than 0.5myr (GEIST et al., 2013).

C/ A third group of islands/volcanoes consists of the central archipelago islands, which further splits into three sub-groups:

(5) the south-southeastern islands Floreana and San Cristóbal, which have human settlements and are strongly altered by human impact. Both have endemics restricted to them: Floreana has *Aymaria floreana* (Gertsch & Peck 1992), *Desis galapagoensis* Hirst 1925 and *Galapa* sp. n., while San Cristóbal has *Camillina*

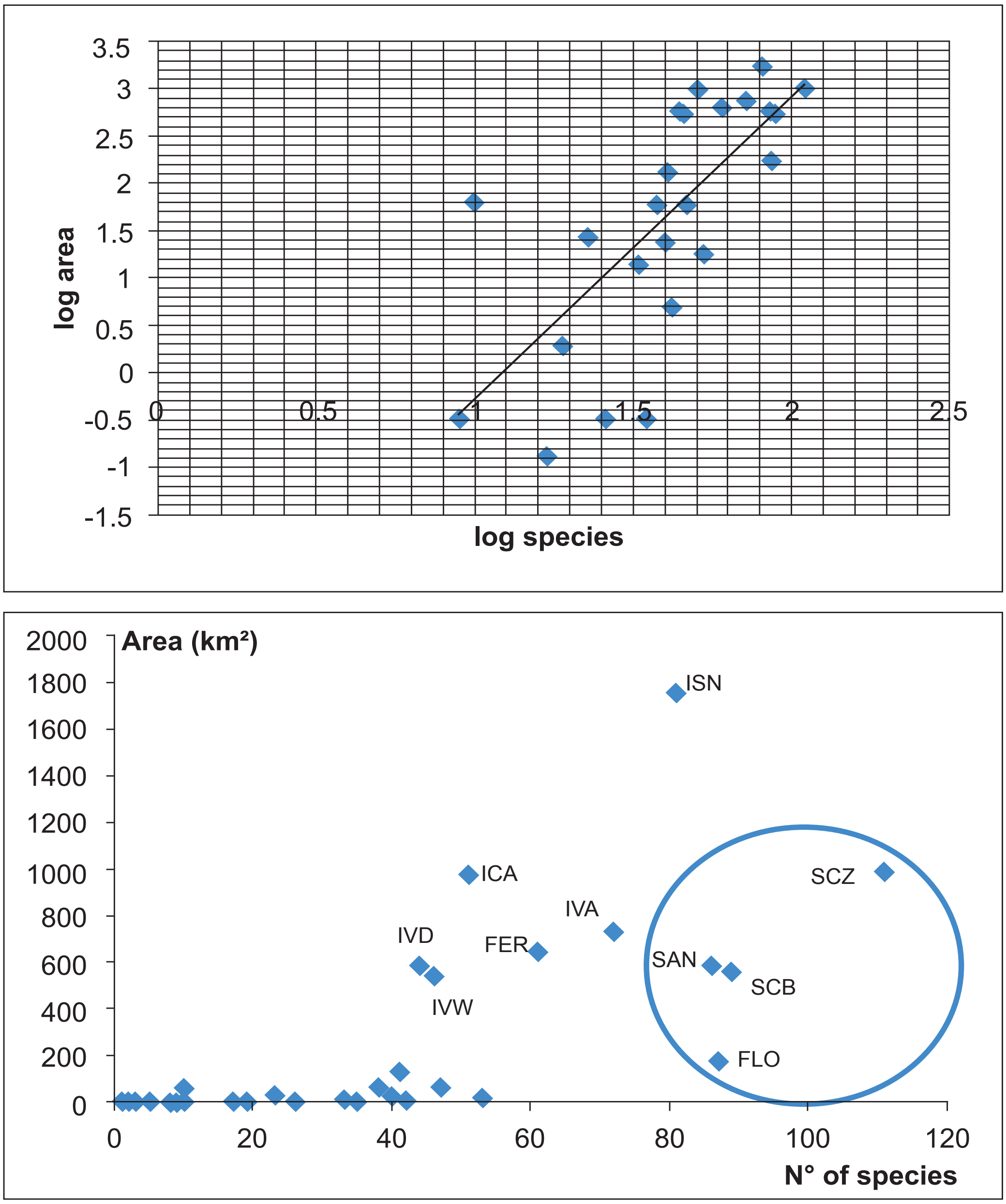
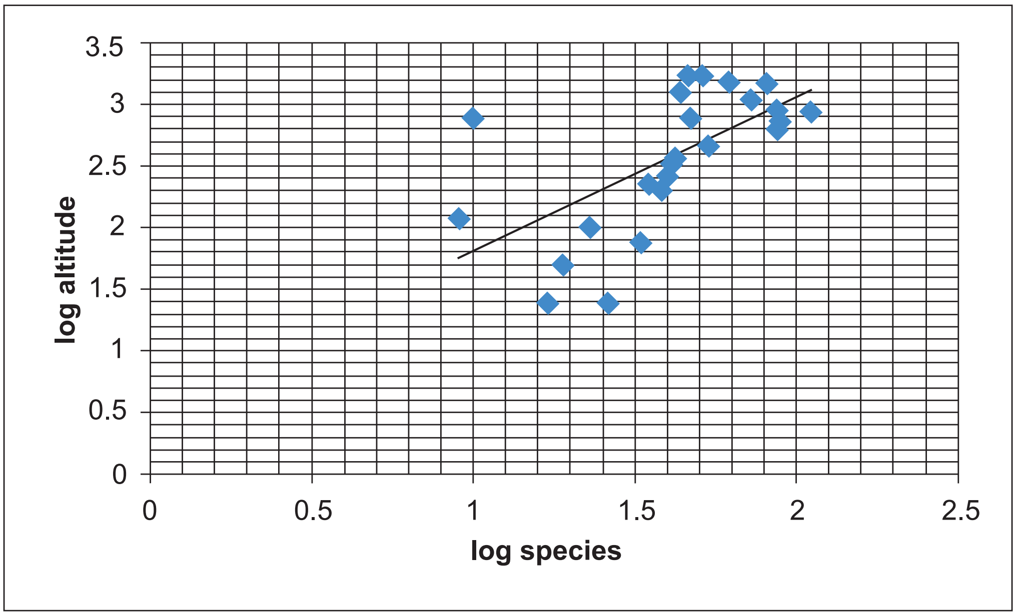


Fig. 4. – Number of species related to area (km²). Upper graph: log area/log number of species. Lower graph: area (km²)/ number of species. Encircled area: inhabited islands (SANtiago: failed colonization but great damage due to imported domestic animals).

sandrae Baert 1994, *Escaphiella cristobal* Platnick & Dupérré 2009 and *Hogna junco* Baert & Maelfait 2008;

(6) the centrally-located islands Santa Cruz, Santiago and the two eastern Isabela volcanoes Sierra Negra and Alcedo. The islands of Santa Cruz and the Isabela volcano Sierra Negra are inhabited. Colonization of Santiago failed due to the harsh environment, but the island vegetation has been altered by the introduction of donkeys, pigs, feral goats and horses. The vegetation of Volcán Alcedo has also been strongly influenced by human impact through the introduction of donkeys, pigs, feral goats and horses;

(7) the southwestern Isabela volcano Cerro Azul with a centrally-located pasture with wild cows between 700 and 900m of altitude and an extra upper Arid zone above the inversion zone 1100-1200m.



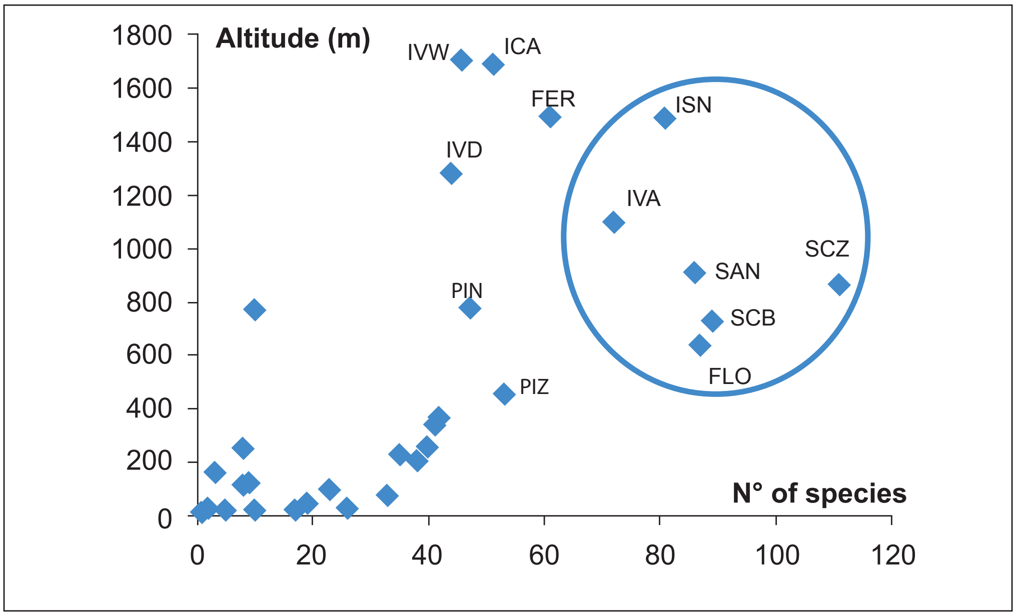


Fig. 5. – Number of species related to altitude (m). Upper graph: log altitude/log number of species. Lower graph: altitude (m)/ number of species. Encircled area: inhabited islands and the island Santiago (SAN) and the Volcán Alcedo (IVA), both greatly damaged due to imported domestic animals.

TABLE 4

Distribution of the 14 species native to Latin America (after PLATNICK, 2013).

Family	Species name	Known distribution in Latin America
Anyphaenidae	*Anyphaenoides octodentata* (Schmidt 1971)	VENEZUELA, PERU, ECUADOR
Anyphaenidae	*Anyphaenoides pacifica* (Banks 1902)	TRINIDAD to CHILE
Theridiidae	*Cryptachaea dromedariformis* (Roewer 1942)	PERU, ECUADOR
Theridiidae	*Cryptachaea orana* Levi 1963	ECUADOR
Salticidae	*Euophrys vestita* (Taczanowski 1878)	PERU
Theridiidae	*Faiditus sullana* (Exline 1945)	PERU
Oonopidae	*Gamasomorpha wasmanniae* Mello-Leitao 1939	ARGENTINA
Titanoecidae	*Goeldia obscura* (Keyserling 1878)	COLOMBIA, PERU
Salticidae	*Helvetia albovittata* (Simon 1901)	BRAZIL, PARAGUAY, ARGENTINA
Linyphiidae	*Neocautinella neotenica* (Keyserling 1886)	ECUADOR, PERU, BOLIVIA
Linyphiidae	*Neomaso patagonicus* (Tullgren 1901)	CHILE, ARGENTINA
Theridiidae	*Steatoda andina* (Keyserling 1884)	VENEZUELA to CHILE
Theridiidae	*Theridion calcynatum* Holmberg 1876	VENEZUELA to ARGENTINA
Theridiidae	*Theridion volubile* Keyserling 1884	VENEZUELA, ECUADOR, PERU

D/ The fourth cluster (8) comprises the far northernmost isolated small islands Wolf and Darwin. *Camillina isla* is endemic to both islands while the salticid *Habronattus encantadas* Griswold 1987 is endemic to Darwin and a philodromid species endemic to Wolf (this cluster is not shown in Figure 6).

Spider communities of Isla Santa Cruz

A second important question is whether the well-differentiated climax vegetation zones can be characterized by a specific spider community?

As already mentioned above, the only island where the seven well-differentiated climax vege-

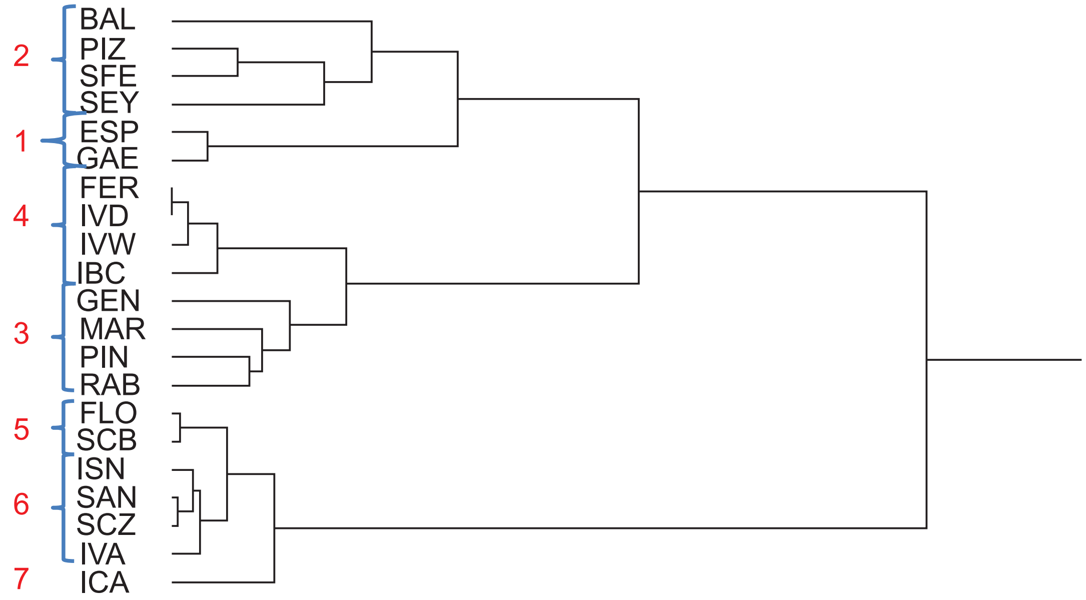


Fig. 6. – Cluster diagram based upon species composition for the archipelago. (explanation of the ciphers: see text).

TABLE 5

Number of species (N° Sp = total, End = endemics, Non-end. = non-endemics, Sp. ? = unknown species) for each island. (percentage calculated without taking into account the unknown species) (Surf = Island surface; Alt. = Island altitude; * = inhabited by man).

Island	Code	N° Sp.	Non-End.	End.	% End.	Sp. ?	Surf. (Km²)	Alt. (m)
BALTRA* (airport)	BAL	23	15	8	34.8		27	20?
BARTOLOME	BAR	8	5	2	25	1	1.2	114
CHAMPION	CHA	2	1	1	50		0.3	15
COWLEY	COW	1	0	0	0	1	0.3	15
DAPHNE	DAP	9	6	3	33.3		0.32	120
DARWIN	DAR	3	0	3	100		1.1	168
EDEN	EDE	5	1	4	80		0.32	25
ESPANOLA	ESP	39	17	21	55.3	1	60	206
FERNANDINA	FER	61	27	31	53.4	3	642	1494
FLOREANA *	FLO	87	41	38	48.1	8	173	640
GARDNER nr ESPANOLA	GAE	26	10	14	58.5	2	0.32	25
GARDNER nr FLOREANA	GAF	1	1	0	0		0.32	25
GENOVESA	GEN	33	15	17	53.1	1	14	76
ISABELA BEAGLE CRATER	IBC	35	14	20	58.8	1	0.32	225
ISABELA VOLCÁN CERRO AZUL	ICA	52	29	21	42	2	975	1689
GUY FAWKES	IGF	1	0	1	100		0.3	15
ISABELA (ICA+ISN+IVA+IVD+IVW+IVE)	ISA	107	54	46	43	7	4652.4	#
ISABELA VOLCÁN SIERRA NEGRA*	ISN	81	46	31	40.3	4	1755	1490
ISABELA VOLCÁN ALCEDO	IVA	72	29	37	56.1	6	732	1097
ISABELA VOLCÁN DARWIN	IVD	44	20	24	54.5		585	1280
ISABELA VOLCÁN ECUADOR	IVE	9	1	8	88.9		62.4	775
ISABELA VOLCÁN WOLF	IVW	46	20	25	55.5	1	543	1707
MARCHENA	MAR	41	15	24	61.5	2	130	343
PLAZA NORTE	NPL	10	4	6	60		1.2	25
PINTA	PIN	47	15	30	66.7	2	60	777
PINZON	PIZ	53	20	28	58.3	5	18	458
RABIDA	RAB	41	17	22	56.4	2	4.9	367
SANTIAGO	SAN	86	43	37	46.3	6	585	907
SAN CRISTOBAL*	SCB	89	44	36	45	9	558	730
SANTA CRUZ*	SCZ	111	53	50	48.5	8	986	864
SEYMOUR NORTE	SEY	19	8	10	55.6	1	1.9	50
SANTA FE	SFE	40	13	26	66.7	1	24	259
PLAZA SUR	SPL	17	6	11	64.7		0.13	25
WOLF	WOL	8	2	6	75		1.3	253

tation zones (Figure 1) are still present is Isla Santa Cruz, although it has the highest number of human residents. These human settlements are centralized in the coastal "city" Puerto Ayora, two villages, Bellavista & Santa Rosa situated in the Culture zone between 200 and 400m of altitude, and a few farms distributed in between. A cluster analysis was therefore performed only upon the data available from this island.

The following segregations into vegetation zones were obtained:

- The Dry Arid Zone (DAZ) divided into (Figure 7):
  - the coastal DAZ around the CDRS and Tortuga Bay;
  - the DAZ along the northern side of the island (50-300m);
  - the DAZ along the southern (W to E) side of the island;
  - the cave fauna that is linked with this vegetation zone due to the presence of species bound to this dry arid zone;
- The upper vegetation zones (Figure 8):
  - the Transition zone (TZ) linked with the Culture zone (CZ);
  - the *Scalesia* zone (SCAL);
  - the Fern Sedge zone (FS). The few *Miconia* samples (MIC) are linked with this FS zone.

Figure 1 and Table 7 show the number of species for each vegetation zone. By far the richest zone is the DAZ along the southern side of the island with 91 species. The Littoral zone (LZ) has a high number of species because they share their specific species with those of the adjacent DAZ. The proportion of endemics/non-endemics seems to vary little around 50% with the zone richest in endemics being the *Miconia* zone and the poorest the southern Transition zone.

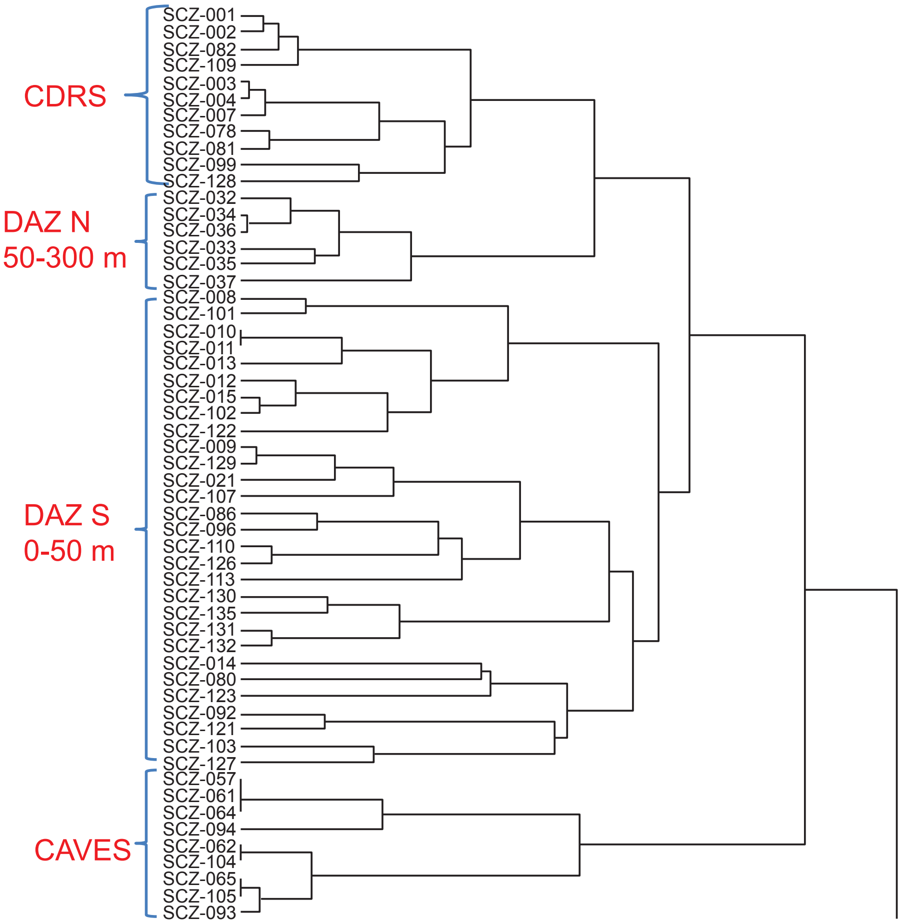


Fig. 7. – Cluster diagram based upon species composition of the arid zone (DAZ) of Isla Santa Cruz.

Different spider communities specific to certain vegetation zones of Isla Santa Cruz can be recognized. These are given in Table 7.

Spider communities of Isla Isabela

Which spider communities can be found on an island where the vegetation has not yet evolved to its climax?

Isla Isabela, the greatest archipelago island, consists of six volcanoes, North of Perry Isthmus: Volcán Ecuador, Volcán Wolf, Volcán Darwin, Volcán Alcedo; South of Perry Isthmus: Volcán Sierra Negra and Volcán Cerro Azul.

Volcán Sierra Negra, which is inhabited, is omitted in this analysis as it shows a more or less comparable succession of vegetation zones to the climax vegetation found on the more western inhabited islands of Santa Cruz, San Cristóbal and Floreana. These zones are, however, more strongly altered by human activity on this volcán.

I used for the analysis only data from the five remaining volcanoes Cerro Azul, Alcedo, Darwin, Wolf and Ecuador to determine if these volcanoes uninhabited by humans and all younger than 0.15 myr, can be differentiated by their spider fauna.

We climbed up the volcanoes along different slope directions: Cerro Azul along the southwestern slope, Alcedo along the eastern slope and Ecuador, Wolf and Darwin along their eastern slope. We had to clear the paths on Wolf and Darwin ourselves.

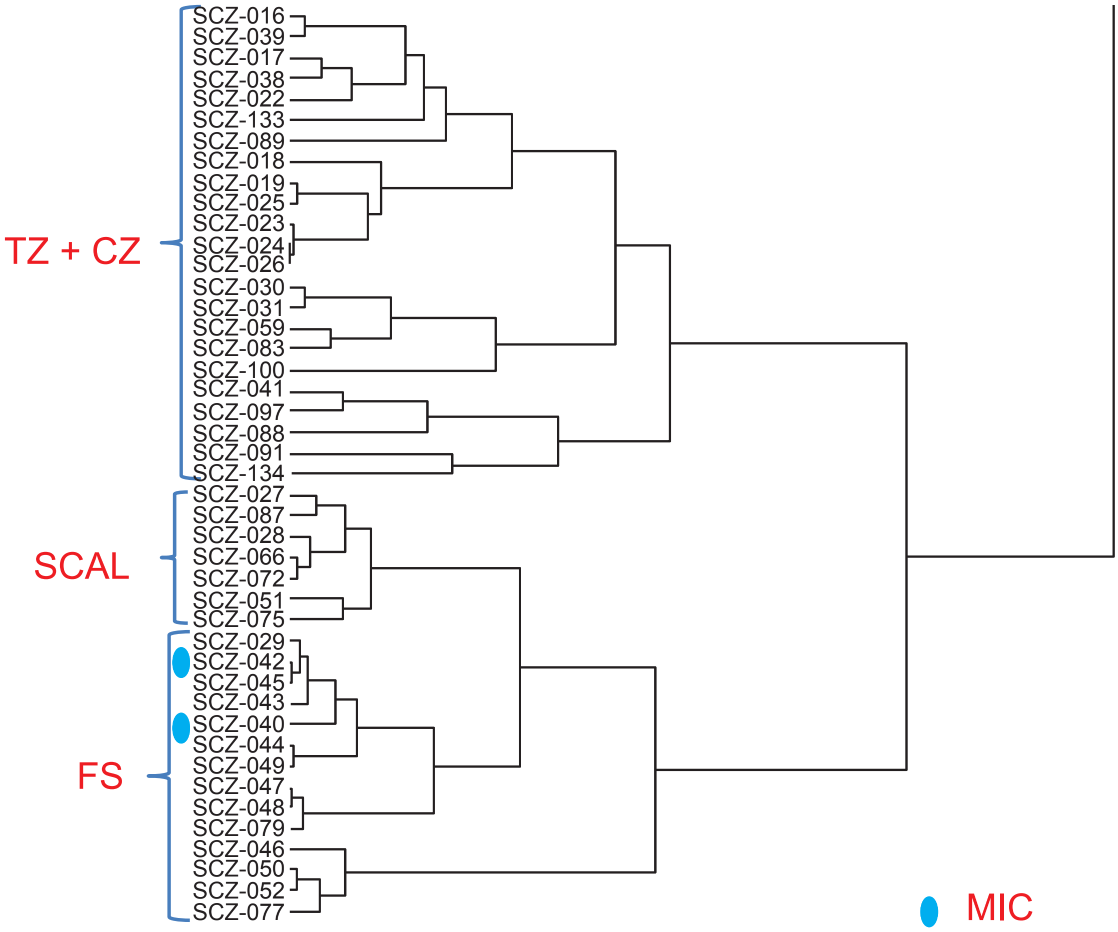


Fig. 8. – Cluster diagram based upon species composition of the higher vegetation zones of Isla Santa Cruz. (TZ: Transition zone, CZ: Culture zone, SCAL: *Scalesia* zone, FS: Fern-sedge zone, MIC: *Miconia* zone).

Where the soil is not covered with a layer of young bare lava, we find the kind of typical vegetation transect as shown in Figure 9. The transition of one vegetation zone into another is not as distinct as on the islands of Santa Cruz and San Cristóbal. A distinct pampa zone is not well developed. The tallest volcanoes (Cerro Azul, V. Darwin and V. Wolf) penetrate the upper inversion zone and they show an upper highland arid zone with arborescent cacti of the genus *Opuntia* or *Scalesia* as the dominant plants. The plant and animal species of this upper arid zone seem to be in general the ones found in the low elevation arid zone.

For the cluster analysis I divided the volcanoes into altitudinal zones of 200m (except the 100m boundary).

The analysis (Figure 10) shows that the northern volcanoes Ecuador (14), Wolf (15) and Darwin (13) have a more or less identical spider fauna. The numbers between brackets refer to the first cipher of the altitude code-number as represented in the figure. The lower arid zone of Volcán Ecuador tends to resemble more the central part of Volcán Darwin (400-1000m) while the upper arid zone of Volcán Darwin (1000-1400m) is more similar to the upper arid zone of Volcán Wolf (1200-1800m).

The lower arid zones (0-200m) of all volcanoes cluster together with all altitudinal zones of Volcán Alcedo. Volcán Cerro Azul is totally distinct from all other volcanoes, with a clear distinction between the lower (200-1000m) and the higher (1000-1600m) altitudinal zones.

DISCUSSION

A tentative comparison of the spider fauna of the Galápagos archipelago with other oceanic archipelagos or islands can be found in Baert & Jocqué (1993).

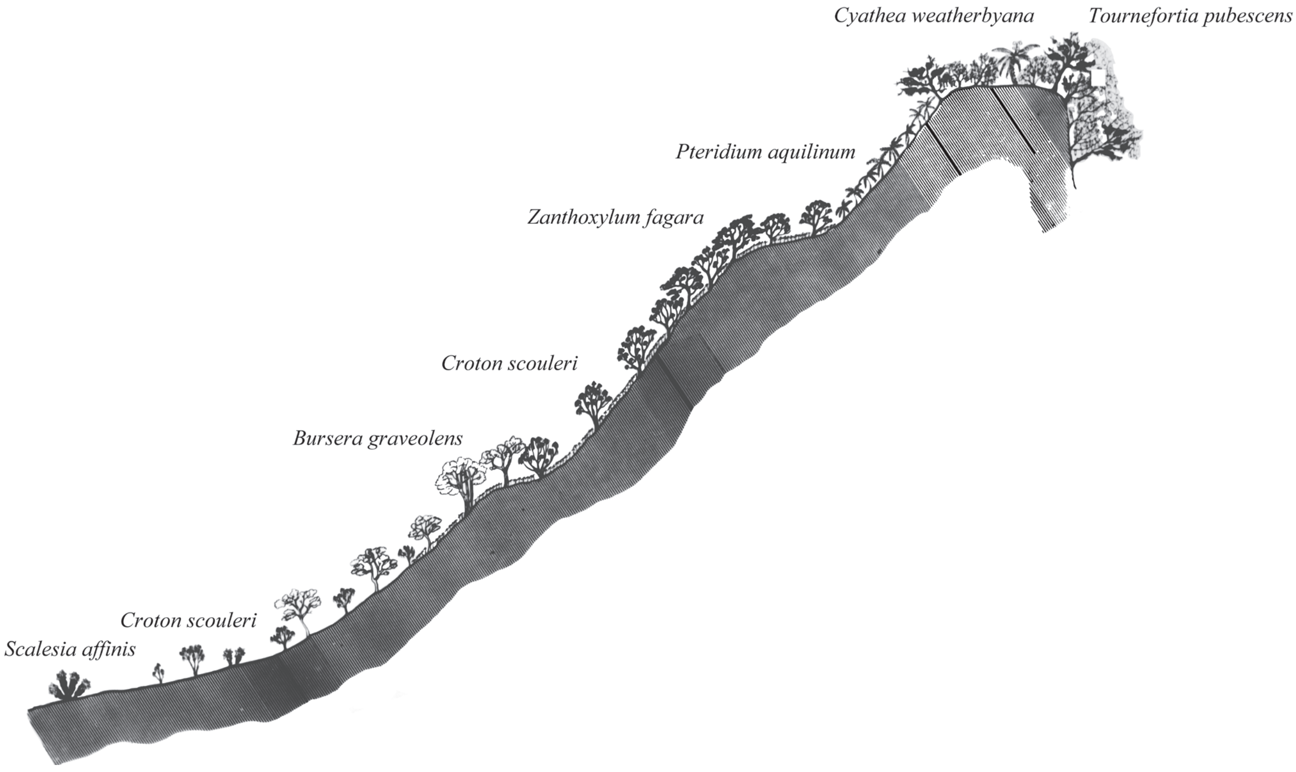


Fig. 9. – Schematic vegetation transect of the Isla Isabela volcano Alcedo (old drawing made by hand by S. Jacquemart in pre-computer times, unpublished).

Origin of the spider fauna

There are three principal mechanisms by which spiders can disperse over a long distance and thus colonize islands: 1) by rafting on flotsam; 2) through the air by way of "ballooning" or aeronautical behaviour; or 3) carried unintentionally by humans.

Rafting

The presence on the Galápagos Islands of northern, central (with Antillean elements) and southern American elements, could be explained by their special situation astride the equator. The archipelago lies in such a position that it is reached by the northern warm Niño Current in the rainy season and by the cold Humboldt Current in the dry season.

Flood debris (such as large trees, driftwood and vegetation-mats) brought by the western coastal rivers lying along the western South American coast beneath the equator and emerging into the sea are quickly picked up by the north-flowing Humboldt current, which then turns west, at the latitude of Ecuador, proceeding directly towards the Galápagos as the Southern Equatorial Current, this for at least half of the year. It takes about two to four weeks for a floating raft to reach the islands from the South American mainland (SCHATZ, 1991).

Alternatively, the Californian Current of the Northern Hemisphere runs southwards along the North American coast and reaches the Panama Basin where it is warmed up and turns towards the Galápagos, as does the Niño current, and it may also bring debris from the northerly Central and South American regions.

Furthermore, there was a broad connection between the Caribbean region and the eastern Pacific area from 48 myr ago until 3.5-3 myr ago (WOODRING, 1959; JONES & HASSON, 1965), with a sea current running from the Atlantic to the Pacific (PETUCH, 1982). The Panama isthmus rose some 3 myr ago by uplift of the Caribbean Plate, which was shoved in between the North and the South American plates. At that time the Galápagos Islands had already emerged from the

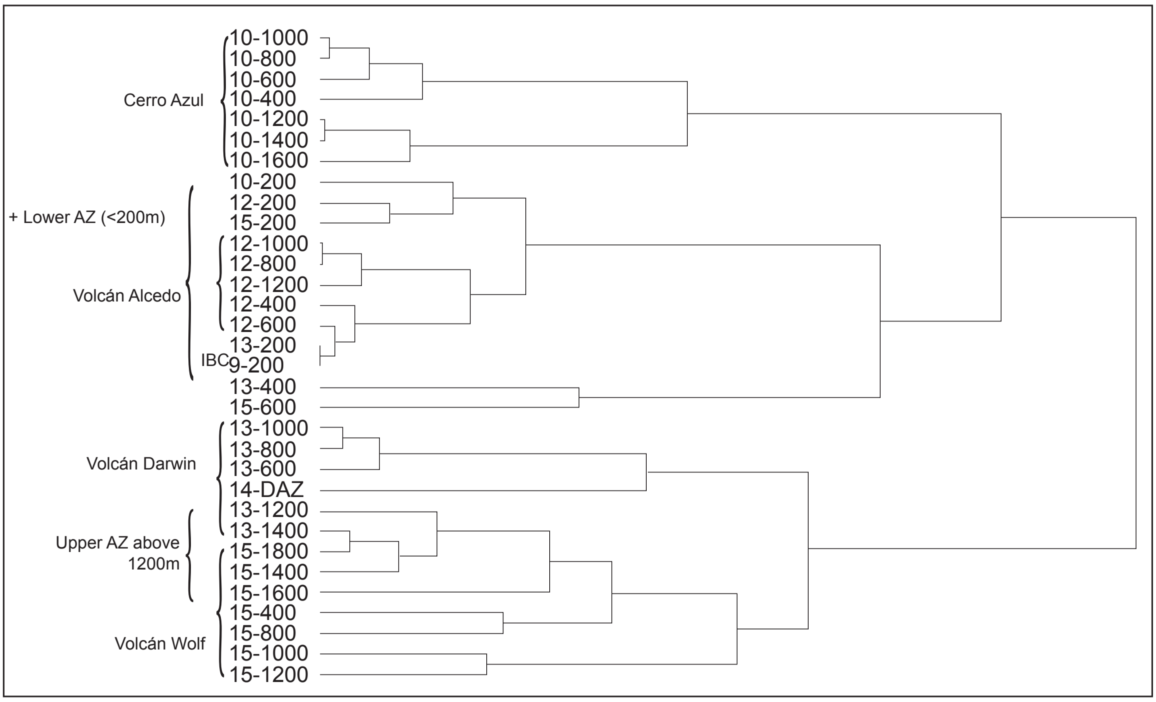


Fig. 10. – Cluster diagram based upon species composition for the Isabela volcanoes. Code 9 = Beagle crater near Volcán Darwin; code 10 = Volcán Cerro Azul; code 12 = Volcán Alcedo; code 13 = Volcán Darwin; code 14 = Volcán Ecuador and code 15 = Volcán Wolf. Sampled altitudes: DAZ (0-200m), 200m, 400m, 600m, 800m, 1000m, 1200m, 1400m and 1600m.

sea. It is plausible that many faunal elements of the Caribbean reached the islands before that time (Baert & Jocqué, 1993).

Peck (1994) probably proved, by means of net-towing along the sea surface in between the islands, that floating might have been a means of dispersion of spiders within the archipelago. He found at a distance of 10 km from the coast between N-Isabela and Fernandina an adult male of *Tetragnatha lewisi* (?) and a juvenile lycosid, along the south-western coast of Santiago a subadult male of *Olios galapagoensis* Banks 1902, between Isabela and Santiago a juvenile *Heteropoda venatoria* (Linnaeus 1767) and along the western coast of Isabela an adult male of *Frigga crocuta* (Taczanowski 1878) and a juvenile *Olios galapagoensis*. The question remains of course if those spiders, though well preserved after the catch, were still alive at the moment of capture.

Ballooning

Some spider families are known to disperse by means of "ballooning" either as juveniles (e.g. Lycosidae, Thomisidae, Araneidae) or as adults (Linyphiidae). The best airborne species belong to the family of the Linyphiidae (Bell et al., 2005).

A typical example of a spider found in the Galápagos that disperses very well by way of the air is *Erigone atra*. This species has a Holarctic distribution and is one of our commonest ballooners in the palearctic. It lives in the highest vegetation zones (the fern-sedge zone or pampa) of the southern Isabela volcanoes (Cerro Azul and Sierra Negra), Santiago, San Cristóbal and Santa Cruz where the climatic conditions are more or less the same as during European summer months. Very striking was its sudden population explosion in the pampa region of Volcán Sierra Negra after a heavy fire in 1986 (Abedrabbo, 1988) where the soil of the burned area was covered by a layer of white silk "with hundreds of small black spiders running around (Giovanni Onoré pers. comm.). This species is in Europe known to be a fast coloniser of disturbed areas.

It remains, however, a mystery how this northern hemisphere species could reach the Galápagos archipelago of which most high altitude islands lie just south of the equator. A pertinent question is: Can spiders disperse by means of the air over such long distances, knowing that to do so they probably have to reach high altitudes where the air may be too cold to survive?

A similar case has been observed with the linyphiid spider *Tenuiphantes tenuis* (Blackwall 1852), another strong palearctic "ballooner", which is also found in the southern hemisphere in New Zealand and Isla de Pascua (Rapa Nui or Easter Island) (Baert et al., 1997).

The possibility should not be overlooked that *Erigone atra* (Blackwall 1841) and *Tenuiphantes tenuis* (Blackwall 1852) might have been brought to the islands by humans during transport of goods by plane or boat.

Peck (1994b) proved there must be an interisland distribution of spiders by way of the air from sampling by means of nets hung at the top of the boat mast navigating between islands. He only captured juveniles and unfortunately did not mention even the family to which they belonged.

Dispersal by means of the air is not obvious on islands, as these are very strongly exposed to inward winds. It is, however, very probable that *Erigone atra* dispersed that way within the archipelago. Members of the family Lycosidae are also good ballooners as juveniles but we never observed such behaviour for the Galapagoan species of *Hogna*.

Human introduction

An example of a probable recent introduction and dispersal by man is the nesticid *Eidmannella pallida* (Emerton 1875) which was first captured on Isla Santa Cruz in pitfall-traps at almost the same time in September-November 1993, on top of Cerro Crocker and along the coast at Bahía Tortuga. It was captured during the 31st month of a continuous sampling, which started in April

TABLE 6

Number of species for each vegetation zone of Isla Santa Cruz with indication of the percentage of endemism for each (percentage calculated without taking into account the unknown species)(CA: Caves; L: Littoral zone; DAZ: Arid zone; TZ: Transition zone; CZ: Culture zone; SCAL: *Scalesia* zone; MIC: *Miconia* zone; FS: Fern-sedge zone; S: along southern slope, N: along northern slope).

Vegetation zone	Total number of species	Number of endemics	Number of non-endemics	Number of unknown species	% endemics
CA	17	9	8		**53**
L	68	35	31	2	**53**
DAZ(S)	91	44	42	5	**51**
DAZ(N)	33	14	18	1	**44**
TZ(S)	55	23	29	3	**44**
TZ(N)	47	23	23	1	**50**
CZ	50	24	26		**48**
SCAL	42	21	21		**50**
MIC	30	17	13		**57**
FS	52	27	25		**52**

1991. It was later observed in Puerto Baquerizo Moreno (Isla San Cristóbal) in 1996. It appeared on Volcán Alcedo (Isla Isabela) in 1997, on Isla Santa Fé and Isla Marchena in 1998, on Santiago in a PNG campsite “La Central” in 2002, and finally on Cerro Azul between 100m and 600m of altitude in 2009. It apparently followed scientists, tourists or residents during their trips to those islands (Baert et al., 2008). This is not surprising as we could always detect the theridiid spider *Nesticodes rufipes* (Lucas 1846) in every tourist or fishing boat during our sampling trips to several islands. This species is well established in the archipelago and can be found widespread on most islands in nearly all vegetation zones.

Endemism

The uninhabited islands and volcanoes (each volcano is considered as a separate entity) have a higher percentage of endemism (between 53.1 and 90%) (Table 5). The inhabited islands and the islands that have been altered in the past by human activity (Baltra & Santiago / Volcán Cerro Azul) have a higher percentage of non-endemics. Baltra is the actual airport for tourist arrival and was an important airport for The United States Army during World War II, while pigs, donkeys, horses and goats have been imported onto Santiago in the past. The area between ca. 600 and 900m of altitude on Cerro Azul is altered as a huge meadow where cattle are living freely.

The percentage of endemism of the spider fauna (52%) for the whole archipelago is more or less comparable with, for example, the 54,7% endemism of the coleopteran fauna (Peck, 2006). The relatively high number (for some islands up to nine, see Table 5) of, at the moment, still unidentifiable morpho-species (which most probably are endemic new species) for the large islands (Santa Cruz, San Cristóbal and Santiago) and the two southern volcanoes of Isabela, makes it difficult to draw adequate conclusions on that matter at present. The islands with the highest degree of endemism (with exception of the very small remote islands Wolf and Darwin) are the northernmost islands of Pinta (66.7%) and Marchena (61.5%) and the more or less centrally located small Isla Santa Fé (66.7%). There are only five islands with their own endemic species: the southern islands Española, Floreana and San Cristóbal each with three species, and the northernmost very remote small islands Wolf and

TABLE 7

Spider communities of the various vegetation zones of Isla Santa Cruz. (Abbreviations of vegetation zones: see legend of Table 6)

All vegetation zones *Eidmanella pallida* *Darwinneon crypticus* *Frigga crocuta* *Ischnothyreus peltifer* *Meioneta galapagosensis* *Neocautinella neoterica* *Notiophantes excelsa* *Neoscona oaxacensis* *Olios galapagoensis* *Aymaria conica* *Calomyspoena santacruzi* *Coleosoma floridanum* *Glenognatha maelfaiti* *Hogna albemarlensis* *Theotima galapgosensis* *Camillina galapagosis* Not in AZ *Oxyopes saltans* *Triaeris stenaspis* *Erigone miniata* Not in SCAL & MIC *Anyphaenoides octodentata* *Eustala species* *Gamasomorpha insularis* *Selenops galapagoensis* *Hasarius adansoni* *Philaeus pacificus* *Rhompaea fictilium*	LZ An unknown salticid species LZ & AZ *Cryptachaea hirta* *Latrodectus apicalis* *Escaphiella gertschi* *Gamasomorpha wasmanniae* *Oonopid species* *Phantina remota* *Sitticus tenebricus* *Lygromma anops* *Pikelinia fasciata* AZ *Cyclosa turbinate* *Mastophora rabida* *Epectris apicalis* *Leucauge argyra* *Menemerus bivittatus* *Sicarius ultriformis* *Latrodectus geometricus* *Odo galapagoensis* *Apollophanes fitzroyi* *Galapa baerti* *Modisimus solus*	AZ & TZ *Hogna hendrickxi* *Plexippus paykulli* *Neozimiris pinta* *Poecilochroa bifasciata* *Tidarren sisyphoides* A salticid species *Mecaphesa reddelli* *Tmarus galapagosensis* *Tivyna spathula* *Ariadna tarsalis* SCAL & FS *Ero gemelosi* *Faiditus sullana* Only in SCAL, MIC & FS *Laminacauda baerti* Only TZ A salticid species Only FS *Camillina Isabela* *Erigone atra* *Mermessus fradeorum* Only in caves *Metagonia bellavista* *Theridion strepitus*

Darwin each with two species (see text above). Three species are known from Isla Darwin and these are all endemic to the archipelago while eight species are known from Isla Wolf of which five are endemic to the archipelago.

Spider communities of Isla Santa Cruz

The island of Santa Cruz, being the centre where all research is organised through the Charles Darwin Research Station and the offices of the Parque Nacional de Galápagos, is by far the most thoroughly sampled and documented island of the archipelago. All scientists reside a long time there before and between their different sampling trips to the other islands. Many sites can be reached easily by car or by foot along the southern side of the island, although less along the northern side. Various types of continuous traps can be installed in different places and emptied at regular times over a long period, yielding a wealth of information.

The number of species occurring in each natural vegetation zone clearly decreases with altitude along the southern slope till ca 600m (DAZ: 91 > TZ: 55 > SCAL: 42 > MIC: 30) and increases (DAZ: 33 > TZ: 48 > FS: 52) along the northern slope, while it reaches a higher number in the upper pampa zone (FS: 52) (see Fig. and Table 6). The Culture or agricultural zone (CZ), lying in between the *Scalesia* (SCAL) and the *Miconia* (MIC) zones has, however, a higher number of spider species (50). The same, but less pronounced, decreasing trend is discernible in the number of endemic species (DAZ: 43 > TZ: 22 > SCAL: 21 > MIC: 17 < FS: 27). The upper humid zones (Transition zone, *Scalesia* zone and *Miconia* zone) have approximately the same number of endemics. The arid lowland has nearly twice the number of endemics as the higher humid zones, but in percentage it is, however, the *Miconia* zone that has the highest endemism (56.7%).

The original *Scalesia* zone has in the past been transformed into the actual Culture zone. The observed spider species richness of the Culture zone today is certainly due to the diversification of that zone as a result of human agricultural activities, yielding a higher diversity in vegetation structure and composition than the original *Scalesia* wood. In this zone we find vegetation types varying from open meadows to very closed orchards (Baert et al., 1991).

The higher number of spider species and endemics in the lower arid zone is comparable to the situation in the beetle fauna (Peck & Kukalová-Peck, 1990). This is possibly due to the fact that the lower arid zone is the largest habitat area in the archipelago, but that it is also the normal location where the colonists arrive first (e.g. by rafting).

The number of species caught along the northern slope is less because of the lower sampling effort along this seldom-visited side of the island (the only frequently visited sites are Caleta Tortuga Negra, las Bachas and the embankment point).

Spider communities of Isla Isabela

There is a great discrepancy in the number of times the volcanoes were sampled and in the number of samples taken on each volcano. The sampling visits were, however, in the same period of the year, namely the rainy-warm season. The sampled sites were often confined to the coastal area (e.g. Tagus cove at the base of Volcán Darwin). The samples taken near the Beagle crater situated at the base of Volcán Darwin were therefore separated as IBC (= 9-200 in Fig. 10). Volcán Alcedo has been visited 13 times since 1974, Volcán Cerro Azul five times between 1986 and 2009, Volcans Wolf and Darwin three times between 1988 and 1996 and Volcán Ecuador twice in 1977-78. This is probably reflected in the number of caught species decreasing with number of visits: Alcedo: 72; Cerro Azul: 52; Wolf: 46; Darwin: 44; Ecuador: 10.

There is, however, an obvious differentiation in faunal composition between Cerro Azul, Alcedo and the northern Darwin and Wolf which are more similar.

Volcán Alcedo is by far the most thoroughly sampled along the eastern path towards the summit. Nearly half of the species, mostly species living in the lower arid zones of most islands, are distributed all along this upward transect. No clear spider communities can be discerned. More thorough sampling will be necessary to be able to do that.

However, some species show a remarkable distribution:

There are three lycosid *Hogna* species living on V. Cerro Azul: *Hogna albemarlensis* (Banks 1902) found from the coast up to 1000m of altitude, *Hogna galapagoensis* (Banks 1902) found between the altitudes of 1000-1300m and *Hogna jacquesbreli* Baert & Maelfait 2008 found in the "artificial" meadow lying between 750-1100m of altitude. The inversion line (cloud limit) lies in the vicinity of 1100m altitude. During the 1997-1998 El Niño *H. albemarlensis*

Table 8

List, and reported islands, of the known species (the species in bold are endemic to the archipelago).

Species	**BAL**	**BAR**	**CHA**	**COW**	**DAP**	**DAR**	**EDE**	**ESP**	**FER**	**FLO**	**GAE**	**GAF**	**GEN**	**IBC**	**ICA**	**IGF**	**ISA**	**ISN**	**IVA**	**IVD**	**IVE**	**IVW**	**MAR**	**NPL**	**PIN**	**PIZ**	**RAB**	**SAN**	**SCB**	**SCZ**	**SEY**	**SFE**	**SPL**	**SSU**	**WOL**
ANYPHAENIDAE																																			
***Anyphaenoides katiae* Baert 1995**																							X						X						
Anyphaenoides octodentata (Schmidt 1971)										X					X			X	X				X					X	X	X		X			
Anyphaenoides pacifica (Banks 1902)		X	X					X	X	X	X		X	X	X		X	X	X	X		X	X	X	X	X	X	X	X	X	X		X		X
ARANEIDAE																																			
Argiope argentata (Fabricius 1775)	X	X			X			X	X	X	X		X	X	X		X	X	X	X		X	X		X	X	X	X	X	X	X	X			
Argiope trifasciata Forsskal 1775)															X																				
Cyclosa turbinata (Walckenaer 1841)	X				X			X	X	X	X		X	X			X	X	X	X		X	X		X	X	X	X	X	X		X	X		
***Eustala* spec.**	X						X	X	X	X	X		X	X				X	X	X			X		X	X	X	X	X	X	X	X	X		
***Galaporella thaleri* Levi 2009**								X	X	X					X			X	X			X			X	X		X	X	X					
Gasteracantha cancriformis (Linnaeus 1758)					X				X	X			X	X	X		X	X	X	X		X			X		X	X	X	X			X		
***Mastophora rabida* Levi 2003**									X	X				X					X	X							X			X					
Metazygia dubia (Keyserling 1864)									X								X	X	X			X						X		X					
***Metepeira desenderi* Baert 1987**					X			X	X	X	X		X	X			X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X		
Neoscona oaxacensis (Keyserling 1863)	X	X			X		X	X	X	X	X		X	X	X		X	X	X	X	X	X	X		X	X	X	X	X	X	X	X			
CORINNIDAE																																			
Creugas gulosus Thorell 1878									X	X								X											X	X					X
***Creugas* spec.**										X					X							X						X		X					
DESIDAE																																			
***Desis galapagoensis* Hirst 1925**										X																									
DICTYNIDAE																																			
***Emblyna formicaria* Baert 1987**														X					X			X													
***Phantyna remota* (Banks 1924)**		X			X			X	X	X	X			X	X		X	X	X	X	X	X		X	X		X		X	X		X	X		
Tivyna spatula (Gertsch & Davis 1937)	X							X	X					X	X			X	X	X		X	X			X	X	X	X	X	X				
FILISTATIDAE																																			
***Pikelinia fasciata* (Banks 1902)**					X			X		X	X		X	X					X	X	X	X	X		X	X		X	X	X		X			X
GNAPHOSIDAE																																			
***Camillina cruz* Platnick & Shadab 1982**									X	X					X			X	X			X	X		X	X	X	X	X	X		X			
***Camillina galapagoensis* (Banks 1902)**	X								X	X				X	X		X	X	X	X		X	X		X	X	X	X	X	X		X	X		

Species	BAL	BAR	CHA	COW	DAP	DAR	EDE	ESP	FER	FLO	GAE	GAF	GEN	IBC	ICA	IGF	ISA	ISN	IVA	IVD	IVE	IVW	MAR	NPL	PIN	PIZ	RAB	SAN	SCB	SCZ	SEY	SFE	SPL	SSU	WOL
***Camillina isabela* Platnick & Murphy 1987**								X		X																			X	X					
***Camillina isla* Platnick & Shadab 1982**						X																													X
***Camillina pecki* Baert 1994**										X																			X						
***Camillina sandrae* Baert 1994**																													X						
***Poecilochroa bifasciata* Banks 1902**									X				X						X	X		X	X		X		X			X					
***Zimiromus* spec.**											X																X								
Trachyzelotes kulckzynskii (Bösenberg 1902)										X																		X	X	X					
Zelotes laetus (O.P.-Cambridge 1872)															X			X	X				X					X	X	X					
LINYPHIIDAE																																			
Erigone atra (Blackwall 1841)										X					X			X										X	X	X					
***Erigone miniata* Baert 1990**									X	X								X	X						X	X		X	X	X					
Laminacauda baerti Miller 2007															X			X	X									X	X	X					
***Meioneta albomaculata* Baert 1990**									X											X		X	X		X	X						X			
***Meioneta arida* Baert 1990**								X	X	X				X	X				X	X			X			X		X	X	X		X			
***Meioneta galapagosensis* Baert 1990**	X									X					X			X	X							X		X	X	X					
***Meioneta pinta* Baert 1990**																						X			X										
Mermessus fradeorum (Berland 1932)																		X										X		X					
Neocautinella neoterica (Keyserling 1886)									X	X					X			X	X	X								X	X	X					
Neomaso patagonicus (Tullgren 1901)																									X										
Notiohyphantes excelsus (Keyserling 1901)										X			X		X			X					X					X	X	X					
LYCOSIDAE																																			
***Hogna albemarlensis* (Banks 1902)**		X							X	X			X	X	X			X	X	X		X	X				X	X	X	X					
***Hogna espanola* Baert & Maelfait 2008**								X			X																								
***Hogna galapagoensis* (Banks 1902)**															X				X							X	X	X	X	X					
***Hogna hendrickxi* Baert & Maelfait 2008**																										X				X					
***Hogna jacquesbreli* Baert & Maelfait 2008**															X			X																	
***Hogna junco* Baert & Maelfait 2008**																													X						
***Hogna snodgrassi* (Banks 1902)**											X																		X						
MIMETIDAE																																			
***Ero gemelosi* Baert & Maelfait 1984**									X													X			X			X	X	X					
Mimetus epeiroides Emerton 1882																							X		X		X								

Species	**BAL**	**BAR**	**CHA**	**COW**	**DAP**	**DAR**	**EDE**	**ESP**	**FER**	**FLO**	**GAE**	**GAF**	**GEN**	**IBC**	**ICA**	**IGF**	**ISA**	**ISN**	**IVA**	**IVD**	**IVE**	**IVW**	**MAR**	**NPL**	**PIN**	**PIZ**	**RAB**	**SAN**	**SCB**	**SCZ**	**SEY**	**SFE**	**SPL**	**SSU**	**WOL**
MYSMENIDAE																																			
***Calomyspoena santacruzi* Baert & Maelfait 1983**								X	X	X								X	X	X		X				X		X	X	X	X	X			
NESTICIDAE																																			
Eidmannella pallida (Emerton 1875)										X					X				X				X					X	X	X		X			
OCHYROCERATIDAE																																			
***Speocera jacquemarti* Baert & Maelfait 1986**																		X	X																
***Theotima galapagoensis* Baert & Maelfait 1986**										X					X			X	X						X	X			X	X		X			
OECOBIIDAE																																			
Oecobius concinnus Simon 1893	X							X		X	X		X					X	X				X			X	X	X	X	X	X	X			
Oecobius navus Blackwall 1859																											X								
OONOPIDAE																																			
Epectris apicalis Simon 1893																		X											X	X					
***Escaphiella cristobal* Platnick & Shadab 2009**																													X						
Escaphiella gertschi Chickering 1951																		X												X					
***Escaphiella isabela* Platnick & Shadab 2009**																			X	X															
Gamasomorpha insularis Simon 1907										X					X			X											X	X					
Gamasomorpha wasmanniae Mello-Leitao 1939																										X			X	X					
Heteroonops spinimanus (Simon 1891)								X																				X							
Ischnothyreus peltifer (Simon 1891)								X										X												X					
Opopaea concolor (Blackwall 1859)														X															X						
Opopaea deserticola Simon 1891	X								X	X								X				X						X	X	X	X	X			
***Orchestina* spec.**								X		X			X					X								X		X	X	X					
***Silhouettella* spec.**																														X					
Triaeris stenaspis Simon 1891										X								X											X	X					
OXYOPIDAE																																			
***Oxyopes* spec.**									X					X	X			X	X	X		X	X		X			X		X					
PHILODROMIDAE																																			
***Apollophanes fitzroyi* Baert 2013**									X																		X	X		X	X				
***Apollophanes (?) lonesomegeorgei* Baert 2013**																																			X
PHOLCIDAE																																			
***Anopsicus banksi* (Gertsch 1939)**								X		X	X																								
***Aymaria conica* (Banks 1902)**								X	X	X					X			X		X		X		X	X	X	X	X	X	X	X	X	X		

Species	BAL	BAR	CHA	COW	DAP	DAR	EDE	ESP	FER	FLO	GAE	GAF	GEN	IBC	ICA	IGF	ISA	ISN	IVA	IVD	IVE	IVW	MAR	NPL	PIN	PIZ	RAB	SAN	SCB	SCZ	SEY	SFE	SPL	SSU	WOL
***Aymaria floreana* (Gertsch & Peck 1992)**										X																									
***Aymaria insularis* (Banks 1902)**																		X		X					X					X					
***Aymaria jarmila* (Gertsch & Peck 1992)**										X																				X					
***Galapa baerti* (Gertsch & Peck 1992)**									X				X			X			X						X			X		X		X			
***Galapa bella* (Gertsch & Peck 1992)**													X											X	X					X			X		
***Galapa* spec.**										X																									
***Metagonia bellavista* Gertsch & Peck 1992**																														X					
***Metagonia reederi* Gertsch & Peck 1992**										X								X																	
Modisimus culicinus (Simon 1893)										X			X					X							X	X		X	X	X					
***Modisimus modicus* (Gertsch & Peck 1992)**																		X										X	X						
***Modisimus solus* Gertsch & Peck 1992**																														X					
Physocyclus globosus (Taczanowski 1874)	X									X								X											X	X					
PRODIDOMIDAE																																			
***Lygromma anops* Peck & Shear 1987**										X																				X					
***Neozimiris pinta* Platnick & Shadab 1976**								X		X									X				X		X			X	X	X		X	X		
***Neozimiris pinzon* Platnick & Shadab 1976**																										X				X					
SALTICIDAE																																			
Balmaceda estebanensis Simon 1903									X									X				X													
***Darwinneon crypticus* Cutler 1971**								X	X	X	X		X	X	X			X	X	X		X	X		X	X	X	X	X	X	X	X			
Euophrys vestita Taczanowski 1878								X						X					X							X		X							
Frigga crocuta (Taczanowski 1878)	X							X	X	X	X		X	X	X		X	X	X	X		X	X	X		X	X	X	X	X	X	X	X	X	
***Habronattus encantadas* Griswold 1987**						X																													
Hasarius adansoni (Audouin 1826)	X							X		X								X								X				X					
Helvetia albovittata Simon 1901					X			X	X	X							X		X	X		X				X		X	X	X		X	X		
Menemerus bivittatus (Dufour 1831)										X								X											X	X					
***Metacyrba insularis* (Banks 1902)**								X	X		X							X	X		X			X		X	X	X	X	X	X	X			
***Phanias distans* Banks 1924**	X							X																				X							
***Philaeus pacificus* Banks 1902**								X	X	X			X	X			X	X	X	X	X	X	X		X	X	X	X		X		X			X
Plexippus paykuli (Audouin 1826)	X							X		X								X	X											X					
***Sitticus phaleratus* Galiano & Baert 1990**	X									X			X					X	X									X	X	X		X			
***Sitticus tenebricus* Galiano & Baert 1990**										X					X				X				X		X		X			X			X		
***Sitticus uber* Galiano & Baert 1990**															X			X				X				X		X		X					
***Sitticus vanvolsemorum* Baert 2011**								X			X																								

Species	**BAL**	**BAR**	**CHA**	**COW**	**DAP**	**DAR**	**EDE**	**ESP**	**FER**	**FLO**	**GAE**	**GAF**	**GEN**	**IBC**	**ICA**	**IGF**	**ISA**	**ISN**	**IVA**	**IVD**	**IVE**	**IVW**	**MAR**	**NPL**	**PIN**	**PIZ**	**RAB**	**SAN**	**SCB**	**SCZ**	**SEY**	**SFE**	**SPL**	**SSU**	**WOL**
SCYTODIDAE																																			
Scytodes fusca Walckenaer 1837	X								X	X	X		X		X			X	X							X	X	X	X	X					
Scytodes longipes Lucas 1845										X			X					X	X	X									X	X		X			
SEGESTRIIDAE																																			
***Ariadna tarsalis* Banks 1902**	X					X			X				X						X			X	X		X	X	X	X	X	X	X	X	X		X
SELENOPIDAE																																			
Selenops galapagoensis Banks 1902									X	X					X		X	X	X	X		X				X		X	X	X					
SICARIIDAE																																			
Loxosceles laeta (Nicolet 1849)								X	X	X	X		X				X					X		X	X	X	X	X	X	X		X			
***Sicarius ultriformis* Butler 1877)**							X	X		X	X								X	X	X						X	X		X		X	X		
SPARASSIDAE																																			
Heteropoda venatoria (Linnaeus 1767)	X									X					X			X	X							X		X	X	X				X	
***Olios galapagoensis* Banks 1902**	X						X	X	X	X	X			X	X		X	X	X	X		X	X		X	X	X	X	X	X		X		X	
SYMPHYTOGNATHIDAE																																			
Anapistula secreta Gertsch 1941																		X																	
TETRAGNATHIDAE																																			
***Glenognatha maelfaiti* Baert 1987**									X	X					X			X										X	X	X					
Leucauge argyra (Walckenaer 1842)										X																	X		X	X					
***Leucauge bituberculata* Baert 1987**									X	X				X	X		X	X	X	X		X	X		X	X		X	X	X					
Tetragnatha lewisi Chickering 1962																																		X	
Tetragnatha nitens (Audouin 1826)									X						X		X	X	X									X							
THERIDIIDAE																																			
Argyrodes elevatus Taczanowski 1873					X			X	X	X	X		X	X	X		X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X		
Chrysso pulcherrima (Mello-Leitao 1917)															X																				
Coleosoma floridanum Banks 1900	X	X							X	X		X	X	X	X			X	X	X		X			X	X	X	X	X	X		X			
Cryptachaea dromedariformis (Roewer 1942)									X									X							X										
Cryptachaea hirta (Taczanowski 1873)		X							X	X				X	X			X	X	X			X		X	X	X	X	X	X					
Cryptachaea orana Levi 1963																														X					
Faiditus sullana (Exline 1945)									X	X								X		X					X		X		X	X					
Thymoites guanicae (Petrunkevitch 1930)										X																									
***Latrodectus apicalis* Butler 1877**	X								X	X			X	X	X			X	X	X		X	X		X	X		X	X	X	X	X			
Latrodectus geometricus C.L.Koch 1841										X																			X	X					

Species	**BAL**	**BAR**	**CHA**	**COW**	**DAP**	**DAR**	**EDE**	**ESP**	**FER**	**FLO**	**GAE**	**GAF**	**GEN**	**IBC**	**ICA**	**IGF**	**ISA**	**ISN**	**IVA**	**IVD**	**IVE**	**IVW**	**MAR**	**NPL**	**PIN**	**PIZ**	**RAB**	**SAN**	**SCB**	**SCZ**	**SEY**	**SFE**	**SPL**	**SSU**	**WOL**
Nesticodes rufipes (Lucas 1846)	X								X	X			X		X			X	X	X								X	X	X					
Phycosoma lineatipes Bryant 1933										X								X										X	X						
Platnickia mneon (Bösenberg & Strand 1906)																												X							
Rhompaea fictilium (Hentz 1850)									X					X	X			X	X	X		X	X					X	X	X					
Steatoda andina (Keyserling 1884)																												X							
Theridion calcynatum Holmberg 1876									X	X					X		X	X	X	X		X			X			X	X	X					
***Theridion coldeniae* Baert & Maelfait 1986**								X	X	X			X	X	X			X	X	X	X	X	X	X	X		X	X	X	X		X			
Theridion myersi Levi 1957										X																									
***Theridion strepitus* Peck & Shear 1987**																		X				X						X		X					
Theridion volubile Keyserling 1884																												X		X					
Sphyrotinus confraternus (Banks 1898)									X	X					X			X		X		X				X		X	X	X					
Tidarren sisyphoides (Walckenaer 1842)									X					X			X		X	X		X						X		X					
THERIDIOSOMATIDAE																																			
***Theridiosoma* spec.**																													X						
THOMISIDAE																																			
***Mecaphesa inclusa* (Banks 1902)**									X	X			X	X				X	X	X	X		X		X	X	X	X		X					
***Mecaphesa reddelli* Baert 2013**													X	X					X						X					X					
***Tmarus galapagosensis* Baert 2013**									X	X				X				X	X	X	X		X		X	X		X		X		X			X
TITANOECIDAE																																			
Goeldia obscura (Keyserling 1878)								X			X																								
ULOBORIDAE																																			
Uloborus segregatus Gertsch 1936															X														X	X					
Zosis geniculatus (Olivier 1789)																		X										X		X					
ZORIDAE																																			
***Odo desenderi* Baert 2009**													X										X									X			
***Odo galapagoensis* Banks 1902**								X		X	X		X													X		X	X	X		X			
***Odo insularis* Banks 1902**	X						X		X					X	X				X	X		X				X	X	X	X	X	X	X	X		
***Odo maelfaiti* Baert 2009**									X																										

had invaded the whole followed trajectory from the coastline up to the volcano rim (1530m alt.) and occurred everywhere in high densities (Baert & Maelfait, 2002). *H. albemarlensis* is known as a eurytopic species, which lives preferentially in coastal salt marsh habitats but which is able to thrive in other wet situations in the vicinity of fresh water pools, even at high altitudes. This upward migration occurs only during the extremely wet years of El Niños. When the wet El Niño circumstances disappear, *H. albemarlensis* slowly does as well (Baert & Maelfait, 2002).

The dictynid *Emblyna formicaria* Baert 1987*,* living in the vicinity of ants, is endemic to Isla Isabela. It has been found in the lower arid zone (> 200m altitude) within the Beagle Crater situated at the western foot of Volcán Darwin, between 400-600m altitude along the western flank of Volcán Alcedo but also in the upper arid zone of Volcán Wolf between 1400-1600m altitude.

It is generally known that species living in the lower arid zone of the islands also occur in the upper arid zone (zone lying above the inversion line with arborescent *Opuntia* cacti and *Scalesia* as the dominant plants) of the high altitude volcanoes of the archipelago (Fernandina, Volcán Wolf, Volcán Darwin and Volcán Cerro Azul) (Peck, 2006). Examples for spiders are: *Argiope argentata* (Fabricius 1775) together with its cleptoparasite *Argyrodes elevatus* Taczanowski 1873, *Latrodectus apicalis* Butler 1877 and *Odo insularis* Banks 1902. *Odo insularis* was found in the lower arid zones of Volcán Alcedo, Volcán Darwin and Volcán Wolf and in the upper arid zones of Volcán Cerro Azul, Volcán Alcedo and Volcán Wolf.

ACKNOWLEDGEMENTS

This work is dedicated to my two “brothers in arms”, Konjev Desender († 9/09/2008) and Jean-Pierre Maelfait († 6/02/2009), who accompanied me to Galápagos during the first 20 years (1982-2002) of this arachnological research.

Field collaboration has been given by Peter Verdijck (1996-02), Frederick Hendrickx (2002-10) & Wouter Dekoninck (2009-10) (Belgium), Stewart Peck & John Heraty (Canada), Heinrich & Irene Schatz (Austria), Sandra Abedrabbo, Sonja Sandovall, Germania Estevez, Lazaro Roque & Henri Herrera (Ecuador).

We received support from the Charles Darwin Research Station (CDRS) and the Parque Nacional de Galápagos (SPNG). Financial support was given by the Belgian State (now Belspo), FWO and Léopold III Fund. I thank Richard Kime for improving the English.

This publication is contribution number 2083 of the Charles Darwin Foundation for the Galápagos Islands.

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Received: June 11th, 2012

Accepted: November 7th, 2013

Branch editor: Artois Tom