IMPACTS OF INTRODUCED PLANTS ON THE GROUND DWELLING BEETLE FAUNA IN THE HIGHLANDS OF THE GALÁPAGOS ISLANDS

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Forord

Jeg fikk ideen til temaet i denne oppgaven under en studietur til Galápagos våren 2004. Der fikk jeg en inngående innføring i problematikken rundt introduserte planter på øygruppa. Jeg hadde lyst til å skrive en masteroppgave innen entomologi, og bestemte meg for å undersøke om de introduserte planteartene hadde noen innvirkning på insektfaunaen på Galápagos.
Fred Midtgaard sa ja til å være min veileder og sammen bestemte vi at jeg skulle innsnevre temaet til introduserte planters innvirkning på billefaunanen.

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Impacts of introduced plants on the ground dwelling beetle fauna in the highlands of the Galápagos Islands

Abstract

Introduced plant species are common on the Galápagos Islands and their amounts might influence diversity and composition of ground dwelling beetles. I compared diversity and composition of ground dwelling beetles in sites with varying amount of introduced plants, within the *Scalesia* zone, *Miconia* zone and fern-sedge zone in the highlands of Santa Cruz (the Galápagos Islands). I also did a comparison between the *Scalesia* zones of three biogeographically isolated islands; Santa Cruz, the Sierra Negra volcano in the south of Isabela, and the Wolf volcano in the north of Isabela. These three islands have varying amounts of introduced plants. This comparison was done in order to elucidate any large scale differences in the beetle fauna within the *Scalesia* zone. The sampling was done from March to May 2006. The amount of introduced plants was used as an indicator of human caused habitat alteration. In the comparison between the three islands, the number of endemic beetle specimens and the number of endemic beetle species were highest in sites without introduced plants. In the comparison within the *Scalesia* zone of Santa Cruz, no such correlation was apparent. However, the number of beetle specimens in total (endemic, indigenous and introduced) was highest in sites with more introduced plants. This suggests that the number of non endemic beetles increases in disturbed habitats and that the fragments of undisturbed *Scalesia* forest on Santa Cruz may be too small to support a rich endemic beetle fauna. In the *Miconia* zone and the fern-sedge zone on Santa Cruz there were no relationships between introduced plants and number of beetles, or number of beetle species. Other factors such as vegetation cover, amount of the introduced fire ant, *Wasmannia auropunctata,* and soil depth were also correlated with the amount of beetle specimens in the *Scalesia* zone, in the comparison between all three islands. There were more beetle specimens in areas where *W. auropunctata* was absent, total vegetation cover was low and the soil was deep. Both the Wolf volcano and Santa Cruz have considerable conservation value due to differences in species composition of the beetle fauna between the islands. Wolf also holds a unique conservation value due to its very pristine condition.

Introduction

The Galápagos Islands are situated 1000 kilometres west of mainland Ecuador. They consist of 13 primary islands; Darwin, Wolf, Pinta, Marchena, Genovesa, Fernandina, Isabela, Santiago, Baltra, Santa Cruz, Santa Fe, San Cristobal and Floreana (Fig. 1). Only Isabela, Floreana, Santa Cruz and San Cristobal are inhabited. The islands are products of outpouring from the Galápagos hotspot; an oceanic volcano now situated near the western islands. In general the south eastern islands appear to be the oldest whereas the northern and western islands appear to be the youngest (Simkin 1984). My study was done on Santa Cruz and Isabela. Isabela is one of the westernmost islands, whereas Santa Cruz is located approximately in the centre of the Galápagos Archipelago. The youngest islands, such as Isabela, lack rocks dated older than 0, 7 million years, whereas the more central islands, like Santa Cruz, contain rocks in the 0.7-1.5 million years range (Desender *et al.* 1992).

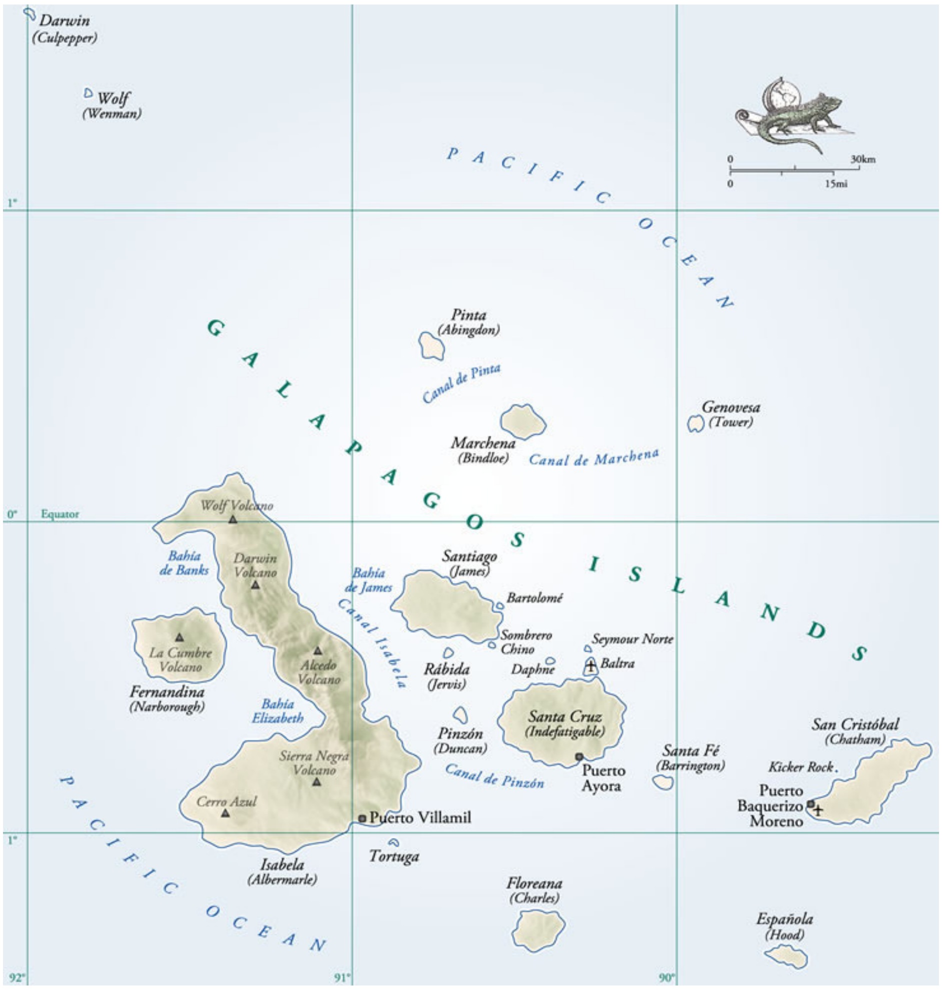

Fig. 1: Map of the Galapagos Islands

The Galápagos Islands were officially discovered in 1535, when the Bishop of Panama, Fray Tomas de Berlanga, and his ship were carried to the islands by the ocean currents, while on a journey from Panama to what is now Peru. Later pirates, scientists and whalers have visited the islands, though permanent settlement only dates from 1893 at Villamil on Isabela, whereas Puerto Ayora on Santa Cruz was founded by a group of Norwegians in 1926. Small settlements remain on the four larger islands, Isabela, Floreana, Santa Cruz and San Cristobal, with a resident population of over 12,000 in 1990 (Jackson 1993). The Galápagos Islands were declared as a national park in 1959 (Jackson 1993) and is now called the Galápagos National Park (GNP).

There are mainly four vegetation zones in the Galápagos; the dry zone, the transition zone, the moist zone and the highland zone (Stewart 1911, 1915, Bowman 1961, Itow 1965, 1971, 1990, 1992, Wiggins and Porter 1971, Itow and Weber 1974, van der Werff 1978, 1979, 1980, Hamann 1979, 1981). In the moist zone the soils are deep and fertile. Prominent in the moist zone are trees of *Scalesia* spp*, Psidium galapageium* and *Zanthoxylum fagara,* shrubs of *Psychotria rufipes* and *Tournefortia rufo-sericea* and epiphytes like *Peperomia galapagoensis* and *Asplenium auritum.* Because *Scalesia* is often monodominant, the zone is also called the *Scalesia* zone. There are 15 species, four subspecies and two varieties in the genus *Scalesia* (Itow 1995). The life span of *Scalesia* is estimated to be about 15 years at the most (Hamann 1979).

Fig. 2: *Scalesia microcephala* var. *cordifolia.* Photo: Bente Støa

In the highland zone, treeless vegetation prevails. This zone is divided in two; the *Miconia* zone and the fern-sedge zone (Bowman 1961, Itow 1992). The *Miconia* zone is only present on the windward south side on the islands of Santa Cruz and San Cristobal. On Santa Cruz, where this study was done, the *Miconia* zone is present in an altitudinal range of 450-600 MASL. The shrub *Miconia robinsoniana* is monodominant with some undergrowth of ferns. The fern-sedge zone is found above 600 MASL. In this zone, ferns such as *Pteridium aquilinum, Blechnum polypodioides* and *Nephrolepis cordifolia* and sedges such as *Rhynchospora rugosa* and *Scleria hirtella* are dominant (Itow 1992).

I collected the beetles in March, April and May because most adult beetle species in the Galápagos Islands are present or active during the rainy months from January to June (Peck 2006). I carried out my study in the *Scalesia, Miconia* and fern-sedge zones. These are the zones most influenced by introduced plants, because of the proximity to the agricultural zone. Most weed originate, establish and spread from the agricultural zones in the humid highlands of the four largest islands. Introductions are more frequent and conditions more favourable here than in the semiarid lowlands. A number of introduced plants have spread from the agricultural zones into the GNP and have changed the composition of species and community structure (Buddenhagen *et al.* 2004). There were reported 77 alien plant species in 1971 (Wiggins and Porter 1971) and 260 alien plant species in 1987 (Lawesson 1987). Today approximately 550 plant species are known as introduced to Galápagos by humans. Of these species, 221 have naturalized, with 100 of these becoming established in intact, native vegetation. Approximately 40 are recognized as having an effect on native vegetation (Charles Darwin Research Station Herbarium Database 2003, S. Henderson, unpublished data in Buddenhagen *et al.* 2004). The number one threat to the fern-sedge zone and the *Miconia* zone on Santa Cruz is the red quinine tree, *Cinchona pubescens.* In 1999 it had a range of more than 11,000 ha (Jäger 1999), covering almost 10 % of the islands` area. Renteria (2002) found that 54 % of the area infested was in the agricultural zone and the rest inside the GNP, occupying an altitudinal range of 180 to 860 MASL. The invasion of the red quinine tree has resulted in complete structural change to the vegetation from low, open scrub, fern brake and grasslands, to a closed forest canopy of 5-8 metres (Buddenhagen *et al.* 2004).

Fig. 3: *Miconia robinsoniana*, with a dead tree of *Cinchona pubescens* behind. Photo: Bente Støa

S. pedunculata forest has almost been destroyed and pasture lands go up to about 450 MASL on the south side of Santa Cruz (Moll 1998). The remnant on Los Gemelos is one of the largest remnants of *S. pedunculata* forests in the GNP (Itow 1995).
Agricultural plants like *Psidium guajaba, Rubus niveus* and *Pennisetum purpureum* is threatening the *Scalesia* forest.

The beetle fauna of the Galápagos contains 56 families, 297 genera and 486 species, of which 266 species are endemic, 110 species are indigenous (occurring naturally in the Galápagos, but also in other places) and 110 species are introduced (Peck 2006). The beetles are the insect order with the largest number of introduced species of the Galápagos. The introduced insect species occur in greatest diversity on the four large islands with permanent human inhabitants; Santa Cruz (76 introduced insects species), San Cristobal (25 introduced insect species), Isabela (22 introduced insect species) and Floreana (13 introduced insect species). The modes of introduction of beetle species have been; in plant debris, animal dung and soil around plants (35 species), in dry stored agricultural and food products (33 species), on or in living plants (14 species), in dry wood, dunnage, pallets, packaging materials, construction materials and logs (13 species), in fresh or spoiled fruits and vegetables and food products (seven species) and on ships in general (seven species) (Peck 2006). In an attempt to limit future introductions of alien arthropods the (GNP) has now evolved a program of agricultural quarantine control and inspection of goods and materials coming into the Galapagos (Causton et. al. 2000).

There is no evidence of any archipelago-wide extinction of an insect species (Peck 2006). However, in 1999, Desender *et al.* studied the impact of introduced feral goats on terrestrial invertebrates on the Alcedo volcano on Isabela. Introduction of feral goats led to mayor habitat alteration, and transformed former forest and scrub in the highlands into grassland. The study showed a decrease of high altitude specialist species and an increase of more xerophilic species in overgrazed sites. There have also been done studies on other organisms which have decreased significantly, or even suffered extinction, because of habitat alteration and human influence in the Galápagos Islands. The giant tortoises, *Geochelone nigra*, are perhaps amongst the most renowned. They once thrived throughout the Galápagos archipelago. But today three island populations are extinct, only one individual from the island of Pinta survives and several populations are critically endangered (Burns *et al.* 2003). At least half of the species of 12 endemic rodent species; the Galápagos rice rats (*Nesoryzomys* spp and *Oryzomus* spp), has gone extinct since the introduction of the black rat (*Rattus rattus)* to the Galápagos (Clark 1984, Dowler *et al.* 2000). The Warbler finch, *Certhidea fusca,* now seems to be extinct on Floreana Island. The cause of decline is uncertain, but native *Scalesia* vegetation, which is the main breeding location for the Warbler finch, has been cleared for agriculture and further degraded or destroyed by feral cattle, donkeys and alien plants. Consequently it is likely that habitat alteration has caused the decline of this species (Grant *et al.* 2005). Another example of a species which has declined because of human caused habitat alteration is the Mangrove finch, *Cactospiza heliobates.* This critically endangered finch has disappeared from Fernandina Island, and is now confined to the Island of Isabela (Dvorak *et al.* 2004).

The hypotheses tested in my study are if there is any positive correlation between numbers of introduced plant- and beetle species, and if the number of endemic ground dwelling beetles is reduced in areas with a high proportion of introduced plants. The amount of introduced plants is here used as an indicator of human influence and habitat alteration. This is the first study on the Galápagos Islands exploring the relationship between introduced plants and beetle fauna.

Method and study area

Study area

I collected beetles in the highlands of two islands of the Galápagos; Santa Cruz (Appendix 1) and Isabela (Appendix 2, Appendix 3). Most of the fieldwork was done on Santa Cruz, which is the most inhabited island of the Galápagos. It is located approximately in the centre of the archipelago and is of intermediate age (0.7-1.5 million years old). The localities in the *Scalesia* zone on Santa Cruz were situated near "Los Gemelos" (Appendix 1). These are two volcano craters in the highlands of Santa Cruz, surrounded by *Scalesia* vegetation. The craters are situated in an altitude of 560-580 MASL, close to the road leading from the port, Puerto Ayora, on the south side of the island, to the airport on Baltra, on the north side of the island. Tourists are often taken to "Los Gemelos" to see the *Scalesia* vegetation, as this is one of the few places where this type of vegetation still exists on Santa Cruz. The *Scalesia* species in this area was *S. pedunculata.* This site was less invaded by exotic plants than many other places in the highlands, though some introduced plants, like *Hyptis perfinato, R. niveus* and *Sida rhombifolia,* were growing there. I estimated the percentage of exotic plants to be 0-5 in the first two localities. The third locality was situated about a kilometre south of "Los Gemelos". This was on the border between the agriculture zone and the *Scalesia* zone, in an open, almost monodominant forest of *S. pedunculata.* The area was being treated with herbicides against the plague *R. niveus*. Where I placed the last trap group there was, however, a lot of this introduced species, because this site still not had been treated. In the first two trap groups there were 0 % and 1 % introduced plants, and in the third group there was 35 % *R. niveus.* The fourth locality in the Scalesia zone was located about one kilometre north of "Los Gemelos". The site was heavily invaded by agricultural plants like *P. purpureum, Cedrela odorata, R. niveus* and *Passiflora edulis.* I also observed the introduced plant *S. rhombifolia*. The percentage of introduced plants was estimated to be 20-40 %.

The *Miconia* zone began at approximately 400-550 MASL (Wiggins and Porter 1971) and consisted mainly of the endemic shrub *M. robinsoniana,* interspersed with different types of club mosses and ferns, the most notable being *P. aquilinum* (McMullen 1999). The localities in the *Miconia* zone were situated above the agriculture zone in the highlands, near Media Luna, 450- 600 MASL (also a volcano crater) (Appendix 1). This area had been heavily invaded by the tree species *C. pubescens,* but after several eradication programs, much of the area was now free from this invasive plant. In the first three localities there were 0-1 % introduced plants, but in the last locality, which was located on the limit between the agriculture zone and the *Miconia* zone, there were almost 100 % introduced plants. These were mainly *C. pubescens* and *P. guajava.*

Fig. 4: Fern-sedge zone on Cerro Crocker, with a forest of *Cinchona pubescens* in the background. Photo: Bente Støa

The fern-sedge zone began at an elevation of approximately 525-550 MASL (Wiggins and Porter 1971). It consisted primarily of club mosses, ferns, sedges and grasses. The first locality in the fern-sedge zone was located on the path to "Puntudo" past Media Luna, whereas the next three were located on Serro Crocker (864 MASL). This was the highest point of the island (Appendix 1). This area had also been heavily invaded by *C. pubescens*. This species had been eradicated in some sites, yet other sites were still heavily invaded. In my study the first and the third locality in the fern-sedge zone had 0-1 % introduced plants, whereas the second locality had 50 % introduced plants and the fourth locality had 10-30 % introduced plants. The introduced plants were mainly *C. pubescens.*

On Isabela I studied four localities in the south, on the Sierra Negra volcano (Appendix 2) and four localities in the north, on the Wolf volcano (Appendix 3). These two volcanoes were biogeographically like two distinct islands and will in this article be referred to as two islands. The Sierra Negra volcano was heavily disturbed by agricultural and introduced plants, whereas the Wolf volcano was considered the most pristine place in Galápagos. It also holds the highest peak of the Galápagos Islands (1707 MASL).

On Sierra Negra the first two localities were situated in "El Bosque de los Niños", a remnant of a *Scalesia cordata* forest, which was now heavily invaded by *P. guajava.* This fruit tree was out competing *Scalesia* in most of the *Scalesia* zone on Sierra Negra. I also found large amounts of the introduced herb species *Kalanchoe pinnata* and *Priva lappulacea* in these two localities. The next two localities were on a farm, with planted *S. pedunculata*. This was a highly unnatural habitat, more like arable land, with little vegetation except from *S. pedunculata.* The Wolf volcano has had very little human impact. The *Scalesia* species on this volcano was *Scalesia microcephala* var. *cordifolia.* I did not observe any introduced plants there. It also had a generally higher biodiversity of plants than the other islands. The localities studied were located from 500-1032 MASL on the north eastern side of the volcano.

Table 1: Description of localities

Locality	Island	Vegetation zone	Site	Coordinates
1	Santa Cruz	*Scalesia*	Los Gemelos	90º23'2''W, 0º37'30''S
2	Santa Cruz	*Scalesia*	Los Gemelos	90º23'2''W, 0º37'30''S
3	Santa Cruz	*Scalesia*	South of Los Gemelos, on the limit to agriculture zone	90º23'2''W, 0º37'30''S
4	Santa Cruz	*Scalesia*	One kilometre north of Los Gemelos along the Puerto Ayora-Baltra highway	90º23'2''W, 0º37'30''S
5	Santa Cruz	*Miconia*	North west of Media Luna, along the trail	90º19'49''W, 0º39'41''S
6	Santa Cruz	*Miconia*	West of Media Luna, along the trail	90º19'49''W, 0º39'41''S
7	Santa Cruz	*Miconia*	On the border between National Park and agriculture zone, south of Media Luna	90º19'49''W, 0º39'41''S
8	Santa Cruz	*Miconia*	100 metres south of the National Park border	90º19'49''W, 0º39'41''S
9	Santa Cruz	Fern-sedge	Along the trail to Puntudo	90º19'49''W, 0º38'10''S
10	Santa Cruz	Fern-sedge	About 600 metres south east of Serro Crocker	90º19'35''W, 0º38'38''S
11	Santa Cruz	Fern-sedge	About 200 metres south east of Serro Crocker	90º19'35''W, 0º38'38''S
12	Santa Cruz	Fern-sedge	About 500 metres north east of Cerro Crocker	90º19'35''W, 0º38'38''S
13	Sierra Negra	*Scalesia*	Bosque de los Niños, some kilometres south of Santo Tomas	91º2'W,0º50'S
14	Sierra Negra	*Scalesia*	Bosque de los Niños, some kilometres south of Santo Tomas	91º2'W,0º50'S
15	Sierra Negra	*Scalesia*	Garden with planted *S. pedunculata*	91º2'W,0º50'S
16	Sierra Negra	*Scalesia*	Garden with planted *S. pedunculata*	91º2'W,0º50'S
17	Wolf	*Scalesia*	Campamento 500, 500MASL	91º22'39''W, 01º05'32,8''S
18	Wolf	*Scalesia*	Campamento Pega Pega, 1032 MASL	91º21'50,5''W, 0º03'34,7''S
19	Wolf	*Scalesia*	Campamento Pega Pega, 1032 MASL	91º21'50,5''W, 0º03'34,7''S
20	Wolf	*Scalesia*	Campamento Pega Pega, 1032 MASL	91º21'50,5''W, 0º03'34,7''S

The coordinates are only approximates. Coordinates for localities 1-4 are from the point between the two craters of Los Gemelos, coordinates for localities 5-8 are from Media Luna, coordinates for localities 10-12 are from Serro Crocker, coordinates from localities 13-16 are from the centre of the agriculture zone on Sierra Negra, coordinates from locality 17 are from campamento 500 on the Wolf volcano and coordinates from localities 18-20 are from campamento Pega Pega on the Wolf volcano.

Sampling methods

I used pitfall traps to collect beetles. I activated them three times in each locality on Santa Cruz; once in week 13 (March), once in week 16 (April) and once in week 20 (May). The traps were active for three consecutive days in each period. Every time I reactivated the traps, I moved them a few metres so that vegetation would remain unaffected, and earlier trampling would not affect the results. I collected beetles in four localities in the *Scalesia* zone, four localities in the *Miconia* zone and four localities in the fern-sedge zone, in the highlands of Santa Cruz. On Sierra Negra I collected beetles in four localities in the *Scalesia* zone. Here I only collected once, in week 14 (April). On Wolf I also collected from four localities in the *Scalesia* zone. This was done only once, in week 18 (May). Also on Sierra Negra and Wolf the traps were left out for three consecutive days before emptied. In each locality I placed three groups of traps at intervals of approximately ten metres. Each group consisted of 3x3 traps, with three metres between each trap. This made it a total of 108 traps per zone on each island (four localities x three groups x nine traps = 108 traps). The traps were plastic cups with a diametre of seven centimetres and a depth of nine centimetres. I dug the traps into the ground and filled them halfway up with freshwater and a drop of detergent. In order to avoid rainwater in the traps, I placed a plate with a diametre of 16 centimetres on sticks ten centimetres above each trap. For each trap group, I noted percentage of introduced plants, other human influences and vegetation cover (ground cover, field cover, bush cover and tree cover). I also did a qualitative estimation in the field of the amount of the introduced ant species *Wasmannia auropunctata* ("No *Wasmannia",* "some *Wasmannia"* or "much *Wasmannia"*). This was based on observations of the locality and not pit fall trap material. A qualitative measure of soil depth, where code 1 meant almost no soil above the lava rocks, code 2 meant thin soil and code 3 meant thick soil, was also conducted in the field.

Identification of species

After the collection of beetles, I brought them to the Department of Terrestrial Invertebrates at the Charles Darwin Research Station where I, with some help from scientists at the station, identified them to lowest possible taxonomic level using "The beetles of the Galápagos Islands, Ecuador: Evolution, Ecology, and Diversity (Insecta: Coleoptera)" (Peck 2006). There were some difficulties identifying the smallest beetles to species level, because of insufficient equipment. Consequently, Osoriinae morphospecies 1 was only identified to subfamily level. All beetles were left at the CDRS after identification. I identified the plants in the field using "Flowering plants of the Galápagos" (McMullen 1999).

Environmental variables

In order to compare beetle fauna composition in localities with varying degree of introduced plants across all three islands, I divided the localities into categories of no, some and much influence by introduced plants (Table 2).

Table 2: Localities divided in categories of no, some and much influence by introduced plants

Locality	No influence	Some influence	Much influence	Percentage of introduced plants	Vegetation zone
1		x		1	*Scalesia*
2		x		0-5	*Scalesia*
3		x		0-35	*Scalesia*
4			x	20-40	*Scalesia*
5	x			0	*Miconia*
6*					*Miconia*
7		x		1	*Miconia*
8			x	100	*Miconia*
9		x		0-1	Fern-sedge
10			x	50	Fern-sedge
11	x			0	Fern-sedge
12*					Fern-sedge
13			x	60-80	*Scalesia*
14			x	60	*Scalesia*
15*					*Scalesia*
16*					*Scalesia*
17*					*Scalesia*
18	x			0	*Scalesia*
19	x			0	*Scalesia*
20	x			0	*Scalesia*

*To obtain an equal number of traps in each category, only three localities from the *Scalesia* zone, one locality from the *Miconia* zone and one locality from the fern-sedge zone were chosen to represent each category in the species composition comparison. Localities 6, 12, 15, 16 and 17 were not counted here.

Data analysis

I used Spearman Rank Correlation analysis to examine how percentage of introduced plants was related to the number of beetle specimens, number of beetle species and the Shannon Wiener index of beetle diversity, and to see if vegetation covers were related to number of beetle specimens and number of beetle species. For the comparison between Santa Cruz, Sierra Negra and Wolf, I divided the number of beetle specimens and the number of species from Santa Cruz by three, because I activated the traps three times on Santa Cruz and only one time on Sierra Negra and Wolf. Spearman Rank Correlation analysis was used to see if there were any covariations between vegetation covers and introduced plants. To determine if there was correlation between *W. auropunctata* and introduced plants, I used logistic regression analysis. Kruskal Wallis` analysis was used to determine whether the number of beetle specimens was affected by *W. auropunctata* or soil thickness in the *Scalesia* zone. I used the Mann Whitney test to find correlation between *W. auropunctata* and number of beetle specimens in the *Miconia* zone. Significance level $P<0.05$ was used in all the statistical analyses.

Results

I collected 1268 specimens from 35 beetle species and 14 beetle families during the study (Table 3). The most abundant species were *Platynus albemarli* (353 specimens), *Osoriinae* morphospecies 1 (295 specimens), *Blapstinus pubescens* (202 specimens), *Calosoma granatense* (160 specimens), *Anchonus galapagoensis* (65 specimens), *Stomion laevigatum* (41 specimens), *Blapstinus desenderi* (39 specimens), *Mordellistena galapagoensis* (28 specimens) and *Pterostichus leleuporum* (23 specimens). The most abundant families were Tenebrionidae (seven species and 287 specimens), Curculionidae (five species and 72 specimens), Staphylinidae (four species and 300 specimens) and Carabidae (three species and 536 specimens). I found three introduced species, eight indigenous species and 22 endemic species (Table 3). From the *Scalesia* zone on Santa Cruz there were two introduced, two indigenous and 14 endemic species. In the *Miconia* zone and the fern-sedge zone, all species found were endemic.

Differences between islands

Beetle fauna composition differed between the three islands (Table 3). On Santa Cruz the most abundant species were *A. galapagoensis* (62 specimens), *C. granatense* (37 specimens) and *M. galapagoensis* (28 specimens). On Sierra Negra two species were abundant: B. *pubescens* (180 specimens) and *C. granatense* (28 specimens). On Wolf *P. albemarli* (353 specimens), *C. granatense* (95 specimens), *S. laevigatum* (41 specimens) and *B. desenderi* (39 specimens) dominated the beetle fauna. The only species that was abundant on all three islands was *C. granatense.* I also found *A. galapagoensis* on all three islands, though only one specimen on Sierra Negra, and two specimens on Wolf. Most of the species in this study were restricted to one island. However, *Osoriinae* morphospecies 1 (Santa Cruz and Wolf), *B. pubescens* (Santa Cruz and Sierra Negra) and *Euscepes postfasciatus* (Santa Cruz and Sierra Negra) were found on two islands (Table 3).

Table 3: List of all beetle species found in the study

Species	Santa Cruz	Sierra Negra	Wolf	Introduced/ indigenous/ endemic	Trophic level	Family
Osoriinae morphospecies 1	292		3	Endemic	Saprophage	Staphylinidae
Anchonus galapagoensis	62	1	2	Endemic	Herbivore	Curculionidae
Pterostichus leleuporum	23			Endemic	Scavenger	Carabidae
Ataenius arrowi	17			Endemic	Scavenger	Scarabaeidae
Calosoma granatense	37	28	95	Indigenous	Predator	Carabidae
Mordellistena galapagoensis	28			Endemic	Herbivore	Mordellidae
Blapstinus pubescens	22	180		Endemic	Scavenger	Tenebrionidae
Dinoderus minutus	3			Introduced	Scavenger	Bostrychidae
Hypothenemus eruditus	2			Indigenous	Herbivore	Curculionidae
Galapaganus ashlocki	2			Endemic	Herbivore	Curculionidae
Anchastus vandykei	3			Endemic	Predator	Elateridae
Allecula galapagoensis	1			Endemic	Herbivore	Tenebrionidae
Nitidulidae	1			?	?	Nitidulidae
Polynoncus seymourensis	1			Endemic	Scavenger	Trogidae
Psyllobora bisigma	1			Endemic	Predator	Coccinellidae
Bythinoplectus peregrinus	2			Endemic	Predator	Staphylinidae
Dipropus puberulus	2			Indigenous	Predator	Elateridae
Bythinoplectus caecus	1			Endemic	Predator	Staphylinidae
Cycloneda sanguinea	1			Indigenous	Predator	Coccinellidae
Diomus anthony	1			Indigenous	Predator	Coccinellidae
Aeolus galapagoensis	1			Endemic	Predator	Elateridae
Lissohypnis pecki	2			Endemic	Predator	Staphylinidae
Euscepes postfasciatus	1	1		Introduced	Herbivore	Curculionidae
Estoloides galapagoensis	1			Endemic	Scavenger	Cerambycidae
Sericoderus sp	1			Indigenous	Predator	Corylophidae
Lobopoda galapagoensis		2		Indigenous	Herbivore	Tenebrionidae
Polytus mellerborgii		1		Introduced	Herbivore	Curculionidae
Longitarsus lunatus		1		Endemic	Herbivore	Chrysomelidae
Perepitragus solieri		1		Indigenous	Scavenger	Tenebrionidae
Platynus albemarli			353	Endemic	Predator	Carabidae
Stomion laevigatum			41	Endemic	Scavenger	Tenebrionidae
Blapstinus desenderi			39	Endemic	Scavenger	Tenebrionidae
Horistonotus williamsi			4	Endemic	Predator	Elateridae
Ammophorus obscurus			1	Endemic	Scavenger	Tenebrionidae
Polynoncus galapagoensis			1	Endemic	Scavenger	Trogidae
Total number of beetle specimens	508	215	539			
Total number of species	25	8	10			

I found nine herbivore species, 13 predator species and 11 scavenger species in this study. In the *Scalesia* zone I recorded six herbivores, four predators and eight scavengers. I only found one herbivore (*A. galapagoensis*) in localities not influenced by introduced plants. I collected two herbivores, one predator and one scavenger in the *Miconia* zone, and three herbivores, two predators and three scavengers in the fern-sedge zone. On Santa Cruz the predators dominated, whereas Sierra Negra had more herbivores and Wolf had more scavengers (Table 3). However, pit fall traps tend to catch proportionally less herbivores than predators, so herbivores could have been underrepresented in this study.

If we look at the number of beetles caught per trap, Wolf appears to have the most abundant beetle fauna (5 beetles per trap), followed by Sierra Negra (2 beetles per trap) and Santa Cruz (0.5 beetles per trap) (Table 4). However, these numbers are somewhat misleading, as they include the traps from the *Miconia* zone and the fern-sedge zone on Santa Cruz, although these zones had a poorer beetle fauna than the *Scalesia* zone. Moreover the traps from localities 15 and 16 will bias the number towards more beetle richness on Sierra Negra. These localities were from a garden with a high number of beetles. Nonetheless, almost all the beetles were from only two species; *B. pubescens* and *C. granatense.* If we overlook these misleading numbers, Wolf still has got the most abundant beetle fauna, but is followed by Santa Cruz (Table 5). These numbers correspond better for comparisons between the three islands, as they all originate in (originally) similar habitats.

Table 4: Beetle specimens per trap from the different islands, all localities included

	Santa Cruz	Sierra Negra	Wolf
No. beetle specimens	484	215	539
No. traps	972	108	108
Beetle specimens per trap (no. beetle specimens/no. traps)	0.5	2	5

Table 5: Beetle specimens per trap from the different islands, only localities from originally *Scalesia* forest

	Santa Cruz *	Sierra Negra **	Wolf
No. beetle specimens	441	4	539
No. traps	324	54	108
Beetle specimens per trap (no. beetle specimens/no. traps)	1.36	0.07	5

*Localities 5-12 are excluded, because they are not from *Scalesia* forest
**Localities 15 and 16 are excluded, because they come from a garden with planted *Scalesia pedunculata*

Differences caused by varying degree of introduced plants

Beetle richness and composition in the *Scalesia* zone

The Spearman Rank correlation analysis identified a significant, negative correlation between percentage of introduced plants and number of beetle specimens in the *Scalesia* zone (Table 6). There was also a significant negative correlation between percentage of introduced plants and number of beetle species (Table 6). When only endemic species were counted, the P-value was even stronger (Table 6, Fig. 5). There was a non-significant negative trend between percentage of introduced plants and the Shannon Wiener index of beetle diversity (Table 6).

Table 6: Spearman Rank correlation analysis on the effect of introduced plants on beetle fauna in the *Scalesia* zone, Santa Cruz, Sierra Negra and Wolf

	n	rs	df	P
Percentage of introduced plants vs. number of beetle specimens	36	-0,7251	34	<0,001
Percentage of introduced plants vs. number of beetle species	36	-0,4856	34	0,003
Percentage of introduced plants vs. number of endemic beetle specimens	36	-0,7261	34	<0,001
Percentage of introduced plants vs. number of endemic beetle species	36	-0,604	34	<0,001
Percentage of introduced plants vs. Shannon Wiener index of beetle diversity	36	-0,2622	34	0,123

n= number of trap groups (of nine traps in each group) in the analysis

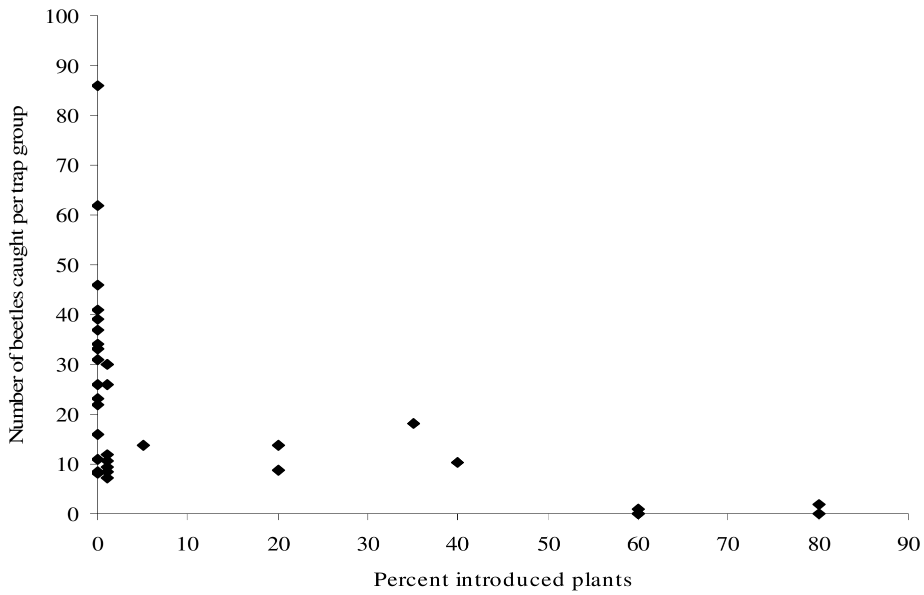

Fig. 5: Effect of introduced plants on the number of endemic beetle specimens in the *Scalesia* zone on Santa Cruz, Sierra Negra and the Wolf volcano.

In the Scalesia zone within Santa Cruz, the number of beetle specimens was significantly positively related to percentage of introduced plants (Table 7, Fig. 6). But there was no relationship between introduced plants and number of beetle species or between percentage of introduced plants and the Shannon Wiener index of beetle diversity (Table 7).

No relationships between percentage of introduced plants and number of beetle specimens, or number of beetle species were observed when only endemic species were counted (Table 7).

Table 7: Spearman Rank correlation analysis on the effect of introduced plants on beetle fauna in the *Scalesia* zone within Santa Cruz

	n	rs	df	P
Percentage of introduced plants vs. number of beetle specimens	12	0,7601	10	0,004
Percentage of introduced plants vs. number of beetle species	12	0,4097	10	0,186
Percentage of introduced plants vs. number of endemic beetle specimens	12	0,42	10	0,178
Percentage of introduced plants vs. number of endemic beetle species	12	-0,02	10	0,953
Percentage of introduced plants vs. Shannon Wiener index of beetle diversity	12	0,0582	10	0,861

n= number of trap groups (of nine traps in each group) in the analysis

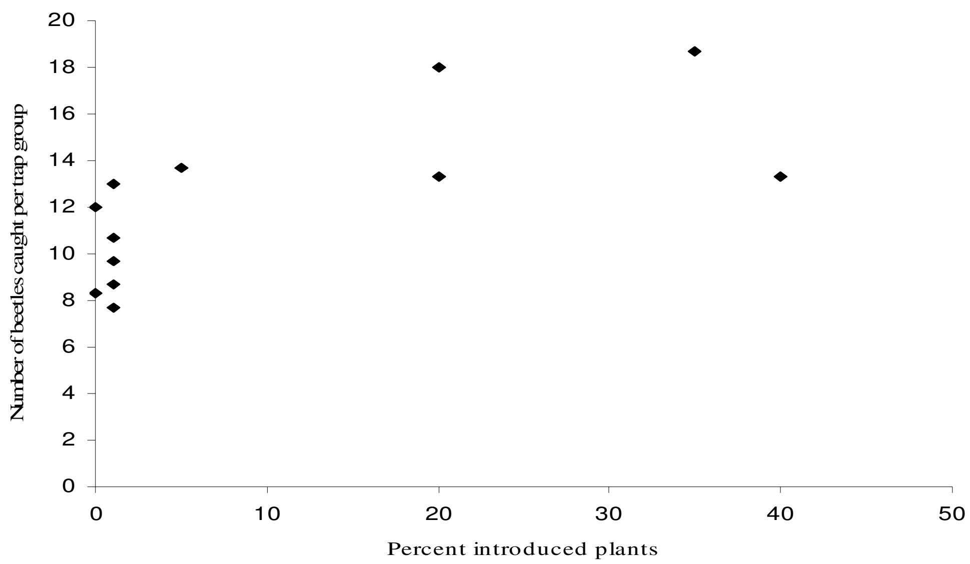

Fig. 6: Effect of introduced plants on the number of all beetle specimens in the *Scalesia* zone within Santa Cruz

The most abundant species in the "no influence" category (Table 2) were *P. albemarli* (353 specimens), *C. granatense* (88 specimens), and *B. desenderi* (21 specimens). In the "some influence" category Osoriinae morphospecies 1 was the dominant species (57 specimens) followed by *A. galapagoensis* (26 specimens). Osoriinae morphospecies 1 (22 specimens) also dominated in the "much influence" category, followed by *C. granatense* (11 specimens) (Table 8). *B. pubescens* (eight specimens) and *Polytus mellerborgii* (one specimen) were exclusively found in the "much influence" category. *P. leleuporum* (three specimens), *Hypothenemus eruditus* (two specimens), *Allecula galapagoensis* (one specimen), *Galapaganus ashlocki* (one specimen) and *Anchastus vandykei* (one specimen) were only present in the "some influence" category. Finally *P. albemarli* (353 specimens), *B. desenderi* (21 specimens), *S. laevigatum* (10 specimens), *Horistonotus williamsi* (4 specimens), *Ammophorus abscurus* (one specimen) and *Polynoncus galapagoensis* (one specimen) were restricted to the "no influence" category in my study. The only two species found in all three categories were Osoriinae morphospecies 1 and *A. galapagoensis* (Table 8).

Table 8: Beetle species composition in the *Scalesia* zone with much, some and no influence by introduced plants

Species	Much influence	Some influence	No influence
Osoriinae morphospecies	22	57	3
Calosoma granatense	11		88
Blapstinus pubescens	8		
Anchonus galapagoensis	3	26	1
Ataenius arrowi	1	9	
*Dinoderus minutus**	1	1	
Mordellistena galapagoensis	1	1	
*Polytus mellerborgii**	1		
Pterostichus leleuporum		3	
Hypothenemus eruditus		2	
Allecula galapagoensis		1	
Anchastus vandykei		1	
*Euscepes postfasciatus**		1	
Galapaganus ashlocki		1	
Platynus albemarli			353
Blapstinus desenderi			21
Stomion laevigatum			10
Horistonotus williamsi			4
Ammophorus obscurus			1
Polynoncus galapagoensis			1
Sum beetle specimens	48	103	482
Sum beetle species	8	11	9

*Introduced species

Only three of the species collected in the *Scalesia* zone were introduced. These were *P. mellerborgii,* present in the "much influence" category, *Dinoderus minutus* present in the "much influence"- and the "some influence" categories and *E. postfasciatus* present in the "some influence" category. I did not record any introduced species in the "no influence" category. I found two introduced species on Santa Cruz (*D. minutus* and *E.* postfasciatus) and two introduced species on Sierra Negra (*E. postfasciatus* and *P. mellerborgii*). The introduced species were absent on Wolf.

Beetle richness and composition in the *Miconia* zone

There were non-significant trends between percentage of introduced plants and number of beetle specimens (P= 0.11), percentage of introduced plants and number of beetle species (P= 0.11) and percentage of introduced plants and the Shannon Wiener index of beetle diversity (P= 0.13) in the *Miconia* zone. These results did not change when only endemic species were counted. However, the sample size was too low to say anything about the effect of introduced plants on the beetle fauna in this vegetation zone (Table 9).

In the "much influence" category one specimen was caught, whereas five specimens from two species were found in the "some influence" category, and five specimens from five species in the "no influence" category. All species found were endemic. The species collected in the "much influence" category was *B. pubescens.* This species was not observed in localities from any of the other categories. *A. galapagoensis* and *Lissohypnis pecki* were found both in the "some influence" category and the "no influence" category. *M. galapagoensis,* an unidentified Nitidulidae and Osoriinae morphospecies 1 were present only in the "no influence" category (Table 9).

Table 9: Beetle species composition in *Miconia* zone with much, some and no influence by introduced plants

Species	Much influence	Some influence	No influence
Blapstinus pubescens	1		
Anchonus galapagoensis		4	1
Lissohypnis pecki		1	1
Mordellistena galapagoensis			1
Nitidulidae			1
Osoriinae morphospecies			1
Sum beetle specimens	1	5	5
Sum beetle species	1	2	5

Beetle richness and composition in the fern-sedge zone

There were no significant relationships between percentage of introduced plants and number of beetle specimens, percentage of introduced plants and number of beetle species or percentage of introduced plants and the Shannon Wiener index of beetle diversity in the fern-sedge zone. These results did not change when only endemic species were counted. Also in the fern-sedge zone, the sample size was very low (Table 10).

In the fern-sedge zone I collected ten specimens from five species in the "much influence" category, one specimen from the "some influence" category, and 35 specimens from eight species in the "no influence" category. *M. galapagoensis* and *P. leleuporum* were the most abundant species in the *Miconia* zone. *M. galapagoensis* was present in all three categories and *P. leleuporum* only in the "much influence" category and the "no influence" category. *B. pubescens* (one specimen) and *Bythinoplectus peregrinus* (one specimen) were found only in the "much influence" category, whereas Osoriinae morphospecies 1 (one specimen), *A. vandykei* (one specimen), *A. galapagoensis* (one specimen), *G. ashlocki* (one specimen) and *Polynoncus seymourensis* (one specimen) in this study were restricted to the "no influence" category (Table 10).

Table 10: Beetle species composition in the fern-sedge zone with much, some and no influence by introduced plants

Species	Much influence	Some influence	No influence
Pterostichus leleuporum	4		13
Mordellistena galapagoensis	3	1	15
Ataenius arrowi	1		1
Bythinoplectus peregrinus	1		
Blapstinus pubescens	1		
Osoriinae morphospecies			2
Anchastus vandykei			1
Anchonus galapagoensis			1
Galapaganus ashlocki			1
Polynoncus seymourensis			1
Sum beetle specimens	10	1	35
Sum beetle species	5	1	8

Differences between vegetation zones

Species composition differed between the three vegetation zones studied on Santa Cruz. The most abundant species in the *Scalesia* zone was Osoriinae morphospecies 1 (291 specimens). *A. galapagoensis* dominated in the *Miconia* zone (14 specimens), whereas *M. galapagoensis* was the dominant species in the fern-sedge zone (19 specimens). Only three species were found in all three zones; *A. galapagoensis, M. galapagoensis* and *B. pubescens.* The *Scalesia* zone had the most diverse beetle fauna in the study (439 beetles from 19 species), whereas the *Miconia* zone had the less diverse beetle fauna (22 beetles from seven species). In the fern-sedge zone 47 beetles from 11 species were collected.

Differences between months

I collected 170 beetles from 15 species in March, 257 beetles from 13 species in April and 89 beetles from 13 species in May (Table 12). In this comparison all localities on Santa Cruz were counted. The beetles found on Sierra Negra and Wolf were not counted, as I only collected beetles there once. The most pronounced differences between March, April and May were the changes in number of Osoriinae morphospecies 1 and *C. granatense.* Numbers of Osoriinae morphospecies 1 increased significantly in April, compared to March and May, whereas *C. granatense* disappeared completely in May. Other species which decreased from April to May were *A. galapagoensis, P. leleumporum, M. galapagoensis* and *B. pubescens.*

Table 11: Species differences between months, only Santa Cruz

Species	March, Santa Cruz	April, Santa Cruz	May, Santa Cruz
Osoriinae morphospecies 1	79	165	60
Anchonus galapagoensis	29	23	8
Pterostichus leleuporum	12	9	2
Ataenius arrowi	12	2	3
Calosoma granatense	11	24	
Mordellistena galapagoensis	10	15	3
Blapstinus pubescens	6	12	4
Dinoderus minutus	2		1
Hypothenemus eruditus	2		
Galapaganus ashlocki	2		
Anchastus vandykei	1		2
Allecula galapagoensis	1		
Nitidulidae	1		
Polynoncus seymourensis	1		
Psyllobora bisigma	1		
Bythinoplectus peregrinus		2	
Dipropus puberulus		1	1
Bythinoplectus caecus		1	
Cycloneda sanguinea		1	
Diomus anthony		1	
Aeolus galapagoensis		1	
Lissohypnis pecki			2
Euscepes postfasciatus			1
Estoloides galapagoensis			1
Sericoderus sp			1
Total number of beetle specimens	170	257	89
Total number of species	15	13	13

Vegetation cover

Scalesia

There were more beetle specimens in sites with low ground cover, low field cover, low tree cover and low total cover in the *Scalesia* zone (Table 12). Number of beetle species was significantly negatively correlated with ground cover (P=0,002), tree cover (P=0,007) and total cover (P=0,048).

The Spearman Rank correlation analysis identified significantly positive covariations between the percentage of introduced plants and ground cover (P= 0,001), field cover (P=0,007), tree cover (P= 0,032) and total cover (P= 0,024). There were no such covariations between the percentage of introduced plants and bush cover.

Table 12: Spearman Rank analysis on the effect of vegetation cover on number of beetle specimens in the *Scalesia* zone, Santa Cruz, Sierra Negra and Wolf

	n	rs	df	P
Ground cover vs. number of beetle specimens	36	-0,495	34	0,002
Field cover vs. number of beetle specimens	36	-0,4218	34	0,01
Bush cover vs. number of beetle specimens	36	0,2679	34	0,11
Tree cover vs. number of beetle specimens	36	-0,4506	34	0,006
Total cover vs. number of beetle specimens	36	-0,4396	34	0,007
Ground cover vs. number of beetle species	36	-0,509	34	0,002
Field cover vs. number of beetle species	36	-0,008	34	0,968
Bush cover vs. number of beetle species	36	-0,185	34	0,279
Tree cover vs. number of beetle species	36	-0,443	34	0,007
Total cover vs. number of beetle species	36	-0,331	34	0,048

n= number of trap groups (of nine traps in each group) in the analysis

In the *Scalesia* zone within Santa Cruz, there was no correlation between vegetation cover and number of beetle specimens. The lowest P-value was between ground cover and number of beetle specimens (P= 0.49). Neither were there any correlations between percentage of introduced plants and vegetation cover.

Miconia

There was a marginally significant negative correlation between ground cover and number of beetle specimens (P= 0.05) in the *Miconia* zone. There were no significant correlations between number of beetle specimens and field cover, bush cover, tree cover or total cover. No significant correlations between vegetation cover and percentage of introduced plants were found.

Fern-sedge

There was a significant positive correlation between ground cover and number of beetle specimens (P= 0.03) in the fern-sedge zone. Apart from this, there were no significant correlations between vegetation cover and number of beetle specimens, or between vegetation cover and percentage of introduced plants.

Wasmannia auropunctata

W. auropunctata was present in most localities, except in the fern-sedge zone on Santa Cruz and the three upper localities on the Wolf volcano; 18, 19, and 20 (Table 13).

Table 13: Amount of *Wasmannia,* and soil depth in each locality

Locality	Amount of *Wasmannia*	Soil depth
1	Some	3
2	Some	3
3	Some	3
4	Some	3
5	Some	2
6	Much	2
7	Much	2
8	Some	2
9	No	2
10	No	2
11	No	2
12	No	2
13	Much	1
14	Much	1
15	Some	3
16	Some	3
17	Some	2
18	No	3
19	No	3
20	No	3

1= almost no soil above lava rocks, 2= thin soil, 3= thick soil

There was a significant, positive relationship between the amount of *W. auropunctata* and percentage of introduced plants ($P<0,001$) (Fig. 7), and a significant, negative relationship between the amount of *W. auropunctata* and number of beetle specimens ($P<0,001$) (Fig. 8) in the *Scalesia* zone. There was no significant correlation between *W. auropunctata* and number of beetle specimens in the *Miconia* zone ($P=0.07$).

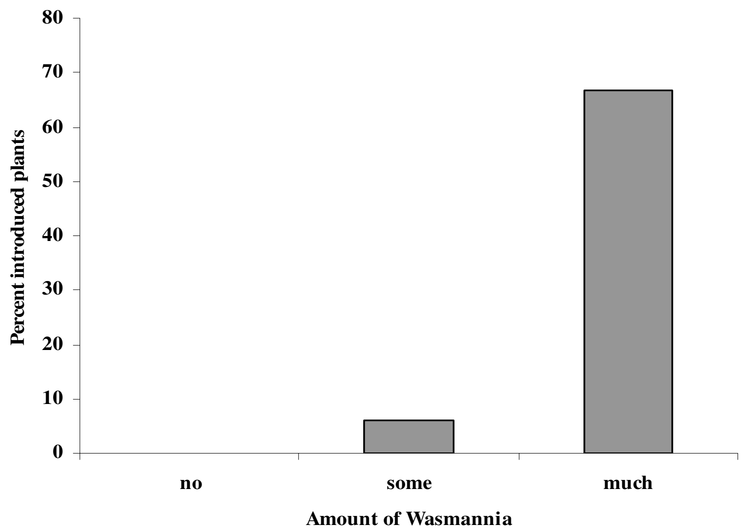

Fig. 7: Percentage of introduced plants in relation to amount of *W. auropunctata*

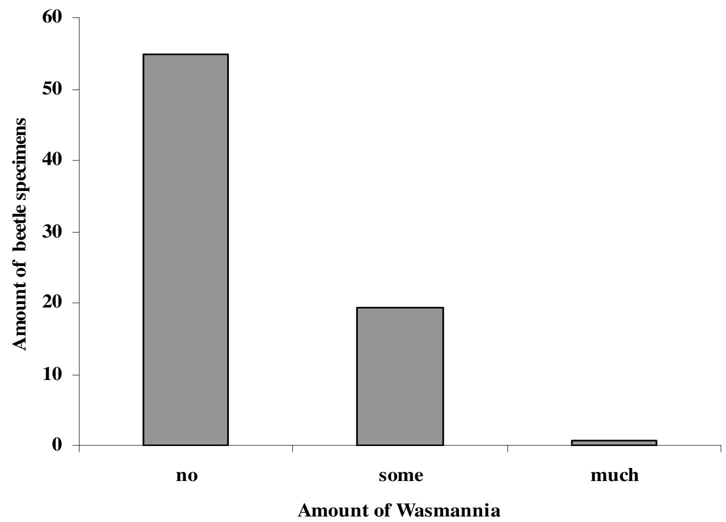

Fig. 8: Number of beetle specimens in relation to amount of *W. auropunctata*

Soildepth

There was a significant negative correlation (P= 0,001) between soil depth and number of beetle specimens in the *Scalesia* zone. Soil depth in the *Miconia* zone and the fern-sedge zone was more or less the same in all localities, so I did not conduct any analysis comparing soil depth and number of beetles in these zones. The soil depth in different localities can be seen in Table 13.

Discussion

The hypotheses tested were if there would be a positive relationship between the numbers of introduced plants and beetle species, and if the number of endemic ground dwelling beetles would be reduced in areas with a high proportion of introduced plants. The current study shows, that on a large scale (between different islands), this is verifiable. However, this does not mean that introduced plants are directly changing the beetle fauna, but that the beetle fauna is changed in areas with more introduced plants. This is probably due to a combination of factors having to do with different kinds of human influence on nature. Nevertheless, because introduced plants often are found in connection to other human caused influences and activities, they can be an effective indicator of human caused disturbance. In other studies, human activities have also shown to influence the insect fauna. In a study of the Hawaiian island Lanai, done by Hobdy (1993), he describes how introduced plants are choking out and replacing native species. None of Lanais` native insect species have been documented as suffering extinction, though they are becoming increasingly rare and the increasing rate of disturbance to native vegetation communities, especially in under storey and ground litter levels, is threatening many species.

My results confirm that there was a strong, negative correlation between percentage of introduced plants and number of beetle specimens in the *Scalesia* zone on Santa Cruz, Sierra Negra and Wolf (Table 6). I got the same P-value ($P<0,001$) when only endemic species were counted. There was also a significant negative correlation between number of species and percentage of introduced plants. This correlation was even stronger when only endemic species were counted (Table 6). In the analysis including the *Scalesia* zone within Santa Cruz, there was an opposite trend, showing a positive correlation between percentage of introduced plants and number of beetle specimens. No such correlation was found between number of beetle species and percentage of introduced plants. Neither did I find any significant correlations between introduced plants and number of beetle species or number of beetle specimens, when only endemic species were counted (Table 7). This clearly shows that the increased number of beetle specimens in localities with more introduced plants on Santa Cruz, is a result of increase in introduced or indigenous species, rather than endemic species. The reason for the lack of negative correlation between percentage of introduced plants and number of beetle specimens within Santa Cruz can be that the small fragments of *Scalesia* forest, which remain on Santa Cruz, are too small to support a rich beetle fauna. This situation can be applicable to the island biogeography model (MacArthur and Wilson 1967), in which habitat fragments resemble islands in an inhospitable, human-dominated sea. Habitat fragmentation reduces the area of original habitat and limits dispersal and colonization. As species go extinct within individual fragments through natural, successional and metapopulation processes, new species will be unable to arrive due to barriers to colonization, and the number of species present in the habitat fragment will decline over time. Species that are able to live in and move across disturbed habitat will increase in abundance in small, isolated fragments of original habitat (Primack 2002). Several studies have been done about the effect of habitat fragmentation on insects, with varying results. In their study about ant communities in forest fragments in the Amazonia, Vasconcelos *et al.* (2006) found that fragments supported fewer ant species than continuous forest. Fragments also had fewer rare species and fewer ant genera. Larger fragments supported more species than small fragments. Benedick *et al.* (2006) studied the difference between butterfly diversity in forest remnants and intact forest in northern Borneo. They found that species richness and diversity were positively related to remnant size and negatively related to isolation. Yet species richness and diversity in the largest forest remnants were no different from those in intact forest. In a study from southern Finland, Halme & Niemelä (1993) investigated carabid beetles in fragments of coniferous forest. In this study abundance and species richness were lowest in contiguous forest, and highest in the fragments surrounding. Still some specialized forest carabids were caught exclusively in contiguous forest, and only the most generalized forest species were obtained from small forest fragments.

Fragments differ from the original habitat in having a greater amount of edge for the area of habitat. The edge between forest and agriculture land will often have higher species richness than the adjacent habitats because it harbours species associated with the forest edge, the forest and the agriculture land. In my comparison between localities within the *Scalesia* zone of Santa Cruz, the localities with a higher percentage of introduced plants also had the highest numbers of beetle specimens. These localities were 3.3, 4.1, 4.2 and 4.3. Locality 3.3 was on the border between *Scalesia* forest and agriculture land. Localities 4.1, 4.2, and 4.3 were situated on the border between *Scalesia* forest and the transition zone. The higher number of beetle specimens in these localities could be explained by the edge effect, though this is not probable. There are numerous studies about how the edge effect increases species diversity (Bedford & Usher 1994, Magura *et al.* 2001), but no study has so far proved an increased number of specimens in the edge zone. In my study the species which dominated the "edge localities," were Osoriinae morphospecies 1, *C. granatense* and *B. pubescens.* Osoriinae morphospecies 1 was in general a very abundant species in all localities in the *Scalesia* zone on Santa Cruz, whereas *C. granatense* and *B. pubescens* were most abundant in localities 4.1, 4.2 and 4.3, yet also present in localities 3.1, 3.2 and 3.3. Because these two species also were found in large numbers in localities 15 and 16; in the garden on Sierra Negra, it is likely that these are opportunistic species, taking advantage of new and altered habitats. *C. granatense* is usually found in the lower vegetation zones, in more arid habitats and may be favoured, also in the Scalesia zone, when the forest is cleared for agricultural purposes, due to more open and arid conditions. For the same reason Desender *et al.* (1999) found an increase of xerophilic species in sites overgrazed by goats in their study of the impact of feral goats on the Alcedo volcano. *C. granatense* and *B. pubescens* are both winged. This makes it easier to colonize new habitats and may contribute to their success in altered habitats.

The fact that no correlations were apparent between introduced plants and beetle fauna in the *Miconia* zone and the fern-sedge zone can be due to low sample size. Very few beetles were found in these zones.

I collected three introduced, eight indigenous and 22 endemic beetle species (Table 5). As mentioned in the introduction, the beetle fauna of the Galápagos contains 266 endemic species, 110 indigenous species and 110 introduced species (Peck 2006). Hence the percentage of endemic beetles found in the present study (66.7 %) is larger than the general percentage of endemic beetles on the Galápagos (54.7 %). None of the three introduced species were found in the "no influence" category (Table 8). This suggests that introduced beetle species are mostly found in degraded habitats, though the sample size in my study is too small to conclude anything certain. It is also feasible that there would be more accidental introductions in the dry zones, because this is where all the ships etcetera unload. However, Peck (2006) claims that the introduced beetle species are more or less evenly distributed in all zones. The three introduced species collected; *D. minutus* (Fig. 9), *P. mellerborgii* (Fig. 10) and *E. postfasciatus* (Fig. 11) have probably been introduced through dry wood, woody debris and soil respectively (Peck 2006). All three species are formerly known from Santa Cruz. *E. postfasciatus* is additionally recorded on Isabela. I also collected *P. mellerborgii* on Sierra Negra, Isabela, although this species has never earlier been observed on this island. All the three introduced species are small (≤4 millimetres).

In addition to differences in the presence or absence of introduced beetle species, the species composition in general differed greatly between the three islands (Table 3). The only species that was abundant on all three islands was the carabid beetle *C. granatense* (Fig. 12). This relatively large species (13, 7-22, 9 millimetres) is indigenous and is present on all islands of the archipelago (Peck 2006). It is the only winged species of *Calosoma* on the Galápagos (Desender *et al.* 1992). Carabid beetles are generally easy to catch in pit fall traps, and some of the most common species in my study were carabids (Table 3). The medium sized carabid, *P. albemarli,* (7, 5-10 millimetres) (Fig. 15) was found in large numbers on Wolf. It is endemic to Isabela and is active from the arid to the pampa zones. A third carabid beetle, which I regularly found on Santa Cruz, was *P. leleuporum* (Fig. 14). This medium sized beetle (about ten millimetres) is endemic to Santa Cruz and is found under stones and litter in humid forest and pampa zones (Peck 2006). Species from the Tenebrionidae family are also relatively easy to catch in pit fall traps. This is especially so on the Galapagos Islands, because of the warm and sunny climate (Peck 2006). This was apparent also in my study, where three of the eight most common species were from the Tenebrionidae family (Table 3). These were *B. desenderi, B. pubescens* and *S. laevigatum. Blapstinus* (Fig. 13) is a genus of small (about six millimetres) beetles, endemic to the Galápagos Islands. *B. desenderi* is a flightless species endemic to the islands of Isabela, Santa Cruz and Santa Fe. It is present in all vegetation zones. *B. pubescens* is the only species of *Blapstinus* which can fly. This accounts for the wide distribution. It is present on most of the islands and in all vegetation zones of the archipelago (Peck 2006). *S. laevigatum* is also found on most of the islands and in most vegetation zones. Other commonly collected species in my study were Osoriinae morphospecies 1, *A. galapagoensis* and *M. galapagoensis* (Fig. 16). Osoriinae morphospecies 1 is a very small Staphylinidae, with a body size of only a few millimetres. Due to the small size, I could not identify it to species level with the equipment available. Consequently I can not say for certain that it was not in fact more than one species. But it is probably only one species, endemic and saprophage. *A. galapagoensis* is a small, endemic Curculionidae (about five millimetres). In this study it was collected on all three islands, though in very low numbers on Sierra Negra and Wolf. It is found in all vegetation zones (Peck 2006). *M. galapagoensis* is a small Mordellidae (about five millimetres). It is endemic to several islands of the archipelago and is common in all vegetation zones, though in this study I collected it exclusively on Santa Cruz.

Fig. 9: *Dinoderus minutus*

Fig. 10: *Polytus mellerborgii*

Fig. 11: *Euscepes postfasciatus*

Fig. 12: *Calosoma* sp

Fig. 13: *Platynus* sp

Fig 14: *Pterostichus* sp

Fig. 15: *Blapstinus* sp

Fig. 16: *Mordellistena* sp

The differences in beetle fauna between the three vegetation zones studied, reflects an earlier analysis in the Galápagos done by Peck & Kukalova-Peck (1990), who also recorded fewer species in the higher elevations. The diversity of beetles decreases with elevation as the area of the ecological zone decreases, even though more favourable conditions occur in the humid zones. This is probably because the lower zones have been available for colonization for a longer time period than the higher zones. The vegetation zones in the Galápagos Islands have not been stable through time. During the Pleistocene glacials, the arid zone was much larger and the moist zones much smaller than today. The moist zone, as known today, may be as young as 10 000 years (Johnson and Raven 1973).

Most of the increase in beetle number from March to April comes from the increase in Osoriinae morphospecies 1. If this species was excluded, the number of beetle specimens in March and April would be almost the same. There were clearly less beetles in May than in March and April (Table 16). Disturbance and depletion are possible factors that could influence the pit fall catches over time (Digweed *et al.* 1995). I can not rule out the possibility that depletion had an effect in this study, causing a decrease in number of beetle specimens in May. However, this is not likely, because no such effect was observed from March to April. Disturbance should not influence the catches from month to month in this study, because I moved the pit fall traps some metres between each time I placed them out, to avoid such effect. There are several beetle species present in only one of the months. Nonetheless, these are present in only one or two specimens, so this can be due to chance rather than demography. As mentioned in the methods the material from Santa Cruz was divided by three for the comparison between the three islands. This was done because collection of beetles was carried out three times on Santa Cruz and only one time on Wolf and Sierra Negra. One could argue that this would bias the results towards less beetle specimens on Santa Cruz, due to the lower numbers of beetles in May. However, in an additional analysis where only the material from March and April were counted (divided by two) I got the same P-values as for the material from all three months together. Thus the possibility that seasonality in beetle activity would influence the final results can be ruled out.

Vegetation cover only had a significant effect on number of beetle specimens and beetle species in the *Scalesia* zone. The number of beetle specimens was negatively related to ground cover, field cover, tree cover and total cover, whereas number of beetle species was negatively related to ground cover, tree cover and total cover. This could indicate that beetle fauna is richer in more open habitats, with more light. However, there were also significantly positive correlations between percentage of introduced plants and ground cover, field cover, tree cover and total cover (Table 12). Hence vegetation cover and percentage of introduced plants covaried, and the observed effect of vegetation cover on number of beetle specimens could be an effect of introduced plants on beetle specimens. This is likely because the localities with the highest ground cover were the localities on Sierra Negra, which also had a very high percentage of introduced plants. Most of the other localities had 0 % ground cover. Furthermore, most localities on Wolf, where introduced plants were totally absent, had less than 10 % tree cover. This also contributed significantly to the positive correlation between percentage of introduced plants and tree cover. Field cover was generally low on Wolf and high on Santa Cruz. This can be one reason for the elevated number of beetle specimens on Wolf, because a dense field cover could reduce beetle mobility. This is further supported by the fact that dense field cover only had an effect on specimen level and not on species level.

Another influencing factor may be the introduced fire ant, *Wasmannia auropunctata* (Fig. 17). It was brought to Santa Cruz sometime in the early part of the 20. century (Silberglied 1972, Clark *et al.* 1982) and has since spread to the other inhabited islands of the Galápagos. It is probably the most aggressive invertebrate that has been introduced to the archipelago. In 1984 it was found on the inhabited islands of Santa Cruz, Floreana, San Cristobal and the Sierra Negra volcano on Isabela, as well as on San Salvador Island, and at two isolated sites; one at Point Albemarle on the northern tip of Isabela, and another at James Bay on San Salvador Island (Lubin 1984). I found it as high as 500 MASL on the Wolf volcano, to where it has probably spread from Point Albemarle. *Wasmannia* coexists with few or no other species of ants and influences numerous other arthropods as well (Clark *et al.* 1982, Lubin 1984). In the Galápagos, *Wasmannia* occurs in most habitats, but is most abundant in the moist transition and lower humid zones and in habitats disturbed by man (pastures, fruit crops, villages) (Lubin 1984). Densities of *Wasmannia* seem to increase with increasing altitude and rainfall. The species occurs up to the lower portion of the *Miconia* zone on the south slope, but was never found in the very moist fern-sedge zone of the summit. *Wasmannia* is more numerous in the hot season. It is a generalist and feeds primarily on honeydew and invertebrates (scavenged or killed) (Clark *et al.* 1982). In the current study there was no evidence that *W. auropunctata* was limiting the beetle fauna in the *Miconia* zone. Most beetles were found in locality 6, where I also observed a lot of *Wasmannia.* In locality 8, where I observed less *Wasmannia*, I only found one beetle. In this locality vegetation structure has been totally changed from a monodominant *Miconia* forest, to agriculture land, dominated by *P. guajaba* and *C. pubescens.* These structural changes of the vegetation may be the limiting factor here. There was, however, a significant positive correlation between amount of *Wasmannia* and amount of introduced plants in the *Scalesia* zone (Fig. 7). This is in accordance with observations by Lubin (1984) that *Wasmannia* is more abundant in habitats disturbed by man. There was a negative correlation between number of beetle specimens and amount of *W. auropunctata* (Fig. 8). Because the correlation between introduced plants and *W. auropunctata* was so clear, it is hard to say which of these factors influences the beetle fauna most. But it is probably is a combination of environmental factors caused by alteration of the habitat.

Fig. 17: *Wasmannia auropunctata*

Another factor that might influence the beetle fauna is soil depth. In the *Miconia*- and fern-sedge zone, soil was thin in all localities, so no analysis could be done. There was, however, a significant, positive correlation (P= 0,001) between soil depth and number of beetle specimens in the *Scalesia* zone. In localities 13 and 14 in Bosque de los Niños, on Sierra Negra, soil was extremely thin, and the lava rocks were almost not weathered at all. The poor beetle fauna in these localities could be a result of thin soil. These localities were also heavily infested by *Wasmannia* and introduced plants. Either of these factors, or a combination, could be limiting factors.

Other ecological factors might also influence the insect fauna. The use of pit fall traps is highly dependent upon a number of factors, including vagility of the organism under study, and ecological factors such as the influence of substrate type, vegetation and weather patterns (temperature, relative humidity, moon phase, recent rainfall and amount of cloud cover) on activity levels (Ahearn 1971, Thomas and Sleeper 1977, Thomas 1979). This has been shown earlier on the Galápagos Islands. Finston *et al.* (1997) found that various species of Tenebrionidae showed significant correlations with several variables, such as maximum daily temperature, the day's precipitation, and hours of sunlight during the day etcetera. These factors were not examined in the present study. Nonetheless they might have had an influence on the results.

One important difference between the results of this study and the results of similar studies elsewhere (Bedford *et al.* 1994, Benedick *et al.* 2006, Desender *et al.* 1995, Halme *et al.* 1993, Magura *et al.* 2001, Vasconcelos *et al.* 2006) is that the main effect in this study was on number of specimens rather than on number of species and/or biodiversity indexes. There were more beetles on the Wolf volcano, which was the most pristine site in this study, but there were more species on Santa Cruz. One possible explanation could be that Santa Cruz is older than Isabela. Isabela is about 0.7 million years old, whereas Santa Cruz is about 0.7-1.5 million years old. This means Santa Cruz has had more time to build up nutrients in the soil, and hence support a richer flora and fauna. Isabela is also further from the mainland than Santa Cruz. This makes it harder to colonize Isabela from the mainland. One could therefore expect a richer beetle fauna on Santa Cruz than on Isabela. However, no significant relationship has earlier been found between number of species and island age on the Galápagos Islands. There has actually been found to be a loss of species on old islands, probably caused by the loss of area and habitats and extinction of species as the island subsides and erodes in its old age (Peck 2006). Even though Santa Cruz is more species rich than Wolf, it is still important to conserve the Wolf volcano as it is today. It is a rare example of an almost unaltered habitat, where I did not observe any introduced species of plants nor beetles. However, the results of the present study also confirm the importance of conservation efforts on Santa Cruz. There are many endemic beetle species in the remnants of *Scalesia* forest on this island, and many of these species were in this study only found on Santa Cruz. On the Sierra Negra volcano I did not collect any endemic beetle species, which were not present on the other sites of the study. The localities studied on Sierra Negra were totally degraded from *Scalesia* forest to forests completely dominated by introduced plants, and have apparently lost their conservation value. On the Galápagos Islands there are in general several species endemic to only one or a few islands. To be able to conserve the entire biodiversity it is important with conservation efforts on every single island of the archipelago.

Conclusion

The hypotheses tested were if there would be a positive correlation between the numbers of introduced plant- and beetle species, and if the number of endemic ground-dwelling beetles would be reduced in areas with a high proportion of introduced plants, due to habitat alteration. This study confirmed my predictions that there would be more introduced beetles in areas with more introduced plants. I only collected three introduced species; *P. mellerborgii* (one specimen), *E. postfasciatus* (two specimens) and *D. minutus* (three specimens). These were all found in the *Scalesia* zone, in the "some influence"- and "much influence" categories. I did not observe any introduced species in the "no influence" category.

Number of endemic beetle specimens and number of endemic beetle species was significantly related to percentage of introduced plants (Table 6) in the *Scalesia* zone on Santa Cruz, Sierra Negra and the Wolf volcano. There were no such correlations between percentage of introduced plants and number of endemic beetle specimens or endemic beetle species in the *Scalesia* zone within Santa Cruz. This might be because the fragments of undisturbed *Scalesia* forest on Santa Cruz were too small to show an elevated number of beetle specimens in comparison with the disturbed *Scalesia* forests. There was, however, a significant, positive correlation between percentage of introduced plants and number of beetle specimens when all beetle species (also indigenous and introduced) were counted (Table 7). This shows that the increase in beetle specimens in more disturbed localities was mainly due to more indigenous and introduced species. There were no significant relationships between percentage of introduced plants and number of beetle specimens or percentage of introduced plants and number of beetle species in the *Miconia* zone and the fern-sedge zone. This may be due to low sample size in these vegetation zones.

In the *Scalesia* zone there were significantly more beetle specimens in sites with low ground cover, low field cover, more bush cover, low tree cover and low total cover. This is probably due to covariations of the percentage of introduced plants and ground cover, field cover, tree cover and total cover. There was no correlation between vegetation cover and number of beetle specimens in the *Scalesia* zone within Santa Cruz, in the *Miconia* zone or in the fern-sedge zone.

Amount of *W. auropunctata* and soil depth might also have influenced the beetle fauna in the *Scalesia* zone. I collected more beetle specimens in areas with no *W. auropunctata* and deep soil. However, these areas were the same areas that had few or no introduced plants, so it is hard to say which was the most determining factor.

Finally both the Wolf volcano and Santa Cruz have considerable conservation values. They both hold endemic species found few, or no other places and are important contributors to the overall biodiversity of the Galápagos archipelago.

Literature

Ahearn, G. A. 1971. Ecological factors affecting population sampling of desert tenebrionid beetles. *American Midland Naturalist* 86, 385-406.

Becker, P.1975. Island colonization by carnivorous and herbivorous Coleoptera. *Journal of Animal Ecology* 44, 893-906

Bedford, S. E. and Usher, M. B. 1994. Distribution of arthropod species across the margins of farm woodlands. *Agriculture, Ecosystems and Environment* 48, 295-305.

Benedick, S., Hill, J.K., Mustafa, N., Chey, V.K., Maryati, M., Searle, J. B., Schilthuizen, M. & Hamer, C. 2006. Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. *Journal of Applied Ecology* 43, 967-977.

Bowman, R. 1961. Morphological differentiation and adaptation in the Galàpagos finches. *University of California Publications in Zoology* 58, 1-302.

Buddenhagen, C. E., Renteria, J. L., Gardener, M., Wilkinson, S. R., Soria, M., Yanez, P., Tye. A. and Valle, R. 2004. The control of a highly invasive tree *Cinchona Pubescens* in Galàpagos. *Weed Technology* 18, 1194-1202.

Burns, C. E., Ciofi, C., Beheregaray, L. B., Fritts, T. H., Gibbs, J. P., Márquez, C., Milinkovitch, M. C., Powell, J. R. and Caccone, A. 2003. The origin of captive Galápagos tortoises based on DNA analysis: implications for the management of natural populations. *Animal Conservation* 6, 329-337.

Causton, C. E., Zapata, C. E. and Roque-Albelo, L. 2000. Alien arthropod specie deterred from establishing in the Galápagos, but how many are entering undetected? *Noticias de Galápagos* 61, 10-13.

Clark, D. A. 1984. Native land mammals. In: Perry, R. (ed) Key environments: Galápagos. Pergamon Press, Oxford, pp 225-231.

Clark, D. B., Guayasamin, C., Pazmino, O., Donoso, C. & Paez de Villacis, Y. 1982. The tramp ant *Wasmannia auropunctata*: Autoecology and effects on ant diversity and distribution on Santa Cruz Island, Galápagos. *Biotropica* 14, 196-207.

Desender, K., Baert, L. & Maelfait, J-P. 1992. Distribution and speciation of carabid beetles in the Galápagos Archipelago (Ecuador). *Bulletin de l'institut royal des sciences naturelles de Belgique. Entomologie* 62, 57-65.

Desender, K., Baert, L., Maelfait, J-P. & Verdyck, P. 1999. Conservation on Volcán Alcedo (Gálapagos): terrestrial invertebrates and the impact of introduced feral goats. *Biological conservation* 87, 303-310.

Digweed, S. C., Currie, C. R., Cárcamo, H. A. & Spence, J. R. 1995. Digging out the "digging-in effect" of pitfall traps: Influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* 39, 561-576.

Dowler, R. C., Carroll, D. S. and Edwards, C. W. 2000. Rediscovery of rodents (Genus *Nesoryzomys*) considered exinct in the Galápagos Islands. *Oryx* 34, 109-117.

Dvorak, M., Vargas, H., Fessl, B. and Tebbich, S. 2004. On the verge of extinction: a survey of the mangrove finch *Cactospiza heliobates* and its habitat on the Galápagos Islands. *Oryx* 38, 171-179.

Finston, T. L., Peck, S. B. and Perry, R. B. 1997. Population density and dispersal ability in Darwin's Darklings: Flightless beetles of the Galápagos Islands. *Pan-Pacific Entomologist* 73, 110-121.

Grant, P. R., Grant, B. R., Petren, K. & Keller, L. F. 2005. Extinction behind our backs: the possible faith of one of the Darwin's finch species on Isla Floreana, Galápagos. *Biological Conservation* 122, 499-503.

Halme, E. & Niemelä, J. 1993. Carabid beetles in fragments of coniferous forest. *Annales Zoologici Fennici* 30, 17-30.

Hamann, O. 1979. On climatic conditions, vegetation types and leaf size in the Galàpagos Islands. *Biotropica* 11, 101-122

Hamann, O. 1981. Plant communities of the Galàpagos Islands. *Danish Botanical Archive* 34, 1-163.

Hobdy, R. 1993. Lanai: A case study: The loss of biodiversity on a small Hawaiian Island. *Pacific science* 47, 201-210.

Itow, S. 1965. Preliminary note on the vegetation of the Galàpagos Islands. *Hikobia* 4, 318-323.

Itow, S. 1971. A study of vegetation in Isla Santa Cruz, Galàpagos Islands. *Noticias de Galápagos* 17, 10-13.

Itow, S. 1990. Herbaceous and ericaceous communities in the highlands of Santa Cruz, the Galàpagos Islands. *Monographs in Systematic Botany Missouri Botanical Garden* 32, 47-58.

Itow, S. 1992. Altitudinal change in plant endemism, species turnover, and diversity on Isla Santa Cruz, the Galápagos Islands. *Pacific Science* 46, 251-268.

Itow, S. 1995. Phytogeography and ecology of *Scalesia* (Compositae) endemic to the Galápagos Islands. *Pacific science* 49, 17-30.

Itow, S. and Weber, D. 1974. Fens and bogs in the Galàpagos Islands. *Hikobia* 7, 39-52.

Jackson, M. H. 1993. Galàpagos: A natural history. University of Calgary Press. pp 315.

Jäger, H. 1999. Impact of the introduced tree *Cinchona pubescens* Vahl. On the native flora of the highlands of Santa Cruz Island (Galàpagos Islands). Oldenburg, Germany: University of Oldenburg. pp 102.

Johnson, M. P. & Raven, P. 1973. Species number and endemism: The Galápagos Archipelago revisited. *Science* 179, 893-895.

Lawesson, J. E. 1987. Alien plants in the Galàpagos Islands, a summary. In: Lawesson, J. E., Hamann, O., Rogers, G., Reck, G. and Ochoa, H. 1990. Botanical research and management in Galápagos held 11-18 April 1987, at the CDRS, Santa Cruz, Gal., *Ecological Monographs in Systematic Botany Missouri Botanical Garden* 32, 15-20.

Lubin, Y. D. 1984. Changes in the native fauna of the Galápagos Islands following invasion of the little red fire ant, *Wasmannia auropunctata. Biological Journal of the Linnean Society* 21, 229-242.

MacArthur, R.H. and Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Magura, T., Tóthmérész, B. and Molnár, T. 2001. Forest edge and diversity: carabids along forest-grassland transects. *Biodiversity and Conservation* 10, 287-300.

McMullen, C. K. 1999. Flowering Plants of the Galàpagos. Cornell University Press. pp 370.

Moll, E. J. 1998. A further report on the distribution of introduced plants on Santa Cruz Island, Galápagos. School of Natural and Rural System Management. Occasional Paper Vol. 5 nr 1 1998, University of Queensland.

Peck, S.B., and Kukalova-Peck, J. 1990. Origin and biogeography of the beetles (Coleoptera) of the Galápagos Archipelago, Ecuador. *Canadian Journal of Zoology* 68, 1617-1638.

Peck, S.B. 2006. The beetles of the Galápagos Islands, Ecuador: Evolution, ecology and diversity (Insecta: Coleoptera). National Research Council of Canada. pp 313.

Primack, R. B. 2002. Essentials of conservation biology. Sinauer Associates, Inc. Publishers. pp 698.

Renteria, J. L. 2002. Ecologìa y manejo de la cascarilla (*Cinchona pubescens* Vahl), en Santa Cruz, Galàpagos. Àrea agropecuaria y de recursos naturales renovables. Loja, Ecuador: Universidad Nacional de Loja. pp 89.

Silberglied, R. 1972. The little fire ant *Wasmannia auropunctata,* serious pest in the Galápagos Islands. *Noticias de Galápagos* 13, 19-20.

Simkin, L. 1984. Geology of the Galàpagos Islands. In: Key environments Galàpagos, Pergamon Press, Oxford, pp 15-41.

Stewart, A. 1911. A botanical survey of the Galàpagos Islands. *Proceedings of the California Academy of Sciences* 4, 7-288.

Stewart, A. 1915. Some observations concerning the botanical conditions on the Galàpagos Islands. *Transactions of the Wisconsin Academy of Sciences Arts and Letters* 18, 272-340.

Thomas, D. B. 1979. Patterns in the abundance of some tenebrionid beetles in the Mojave Desert. *Environmental Entomology* 8, 568-574.

Thomas, D. B. and Sleeper, E. L. 1977. The use of pit-fall traps for estimating the abundance of arthropods, with special reference to the Tenebrionidae (Coleoptera). *Annals of the Entomological Society of America* 70, 242-248.

Van der Werff, H. 1978. The vegetation of the Galápagos Islands. Ph.D. thesis. Rijksuniversiteit, Utrecht.

Van der Werff, H. 1979. Conservation and vegetation of the Galàpagos Islands. pp 391-404. In D. Bramwell, ed. Plants and islands. Academic Press, London.

Van der Werff, H. 1980. The vegetation types of Santa Cruz and Alcedo. *Noticias de Galàpagos* 31, 11-13.

Vasconcelos, H. L., Vilhena, J. M. S., Magnusson, W. E. & Albernaz, A. L. K. M. 2006. Long term effects on forest fragmentation on Amazonian ant communities. *Journal of Biogeography* 33, 1348-1356.

Wiggins, I. L. and Porter, D. M. 1971. Flora of the Galàpagos Islands. Stanford University Press, California.

Figure list

The images in Fig. 9 to Fig. 17 were taken from the following web pages:

Fig. 9: http://www.centreinar.org.br/pragas/bostrichidae.html
Fig. 10: http://www.forestryimages.org/browse/detail.cfm?imgnum=5179010
Fig. 11:
http://www.lucidcentral.org/keys/sweetpotato/key/Sweetpotato%20Diagnotes/media/html/TheCrop/CropEcosystem/Insect%20pest%20gallery.htm
Fig. 12:
http://images.google.com/imgres?imgurl=http://tarwi.lamolina.edu.pe/~acg/Calosoma_rufipenne.jpg&imgrefurl=http://tarwi.lamolina.edu.pe/~acg/calosoma_rufipenne_dejan.htm&h=476&w=425&sz=30&hl=no&start=2&tbnid=JasFLXywD1xQaM:&tbnh=129&tbnw=115&prev=/images%3Fq%3DCalosoma%26svnum%3D10%26hl%3Dno
Fig. 13: www.lesinsectesduquebec.com/insecta/24-coleoptera/platynus.htm
Fig. 14: http://www.biology.ualberta.ca/bsc/news16_2/alvar.htm
Fig. 15:
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Fig.16:
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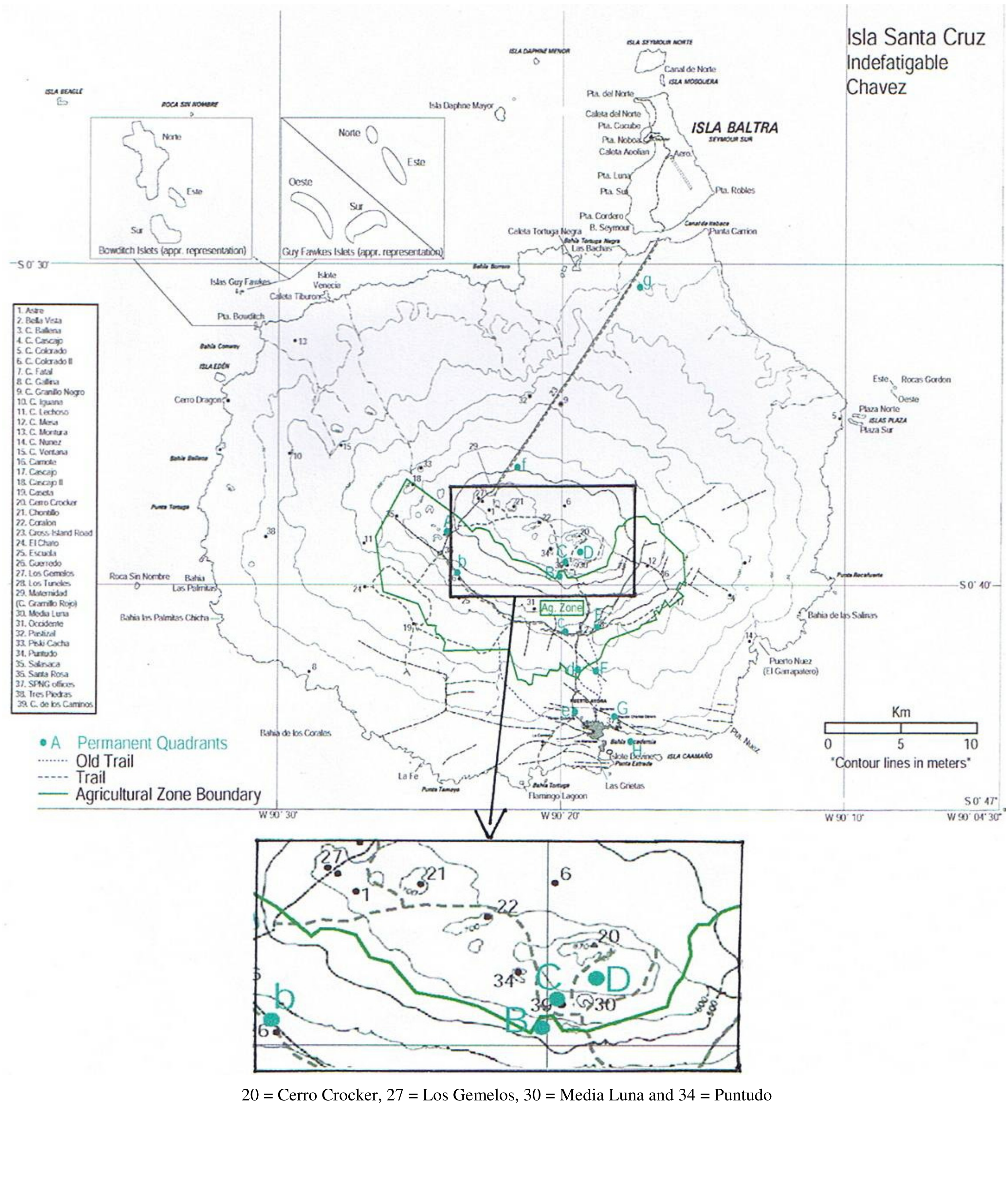
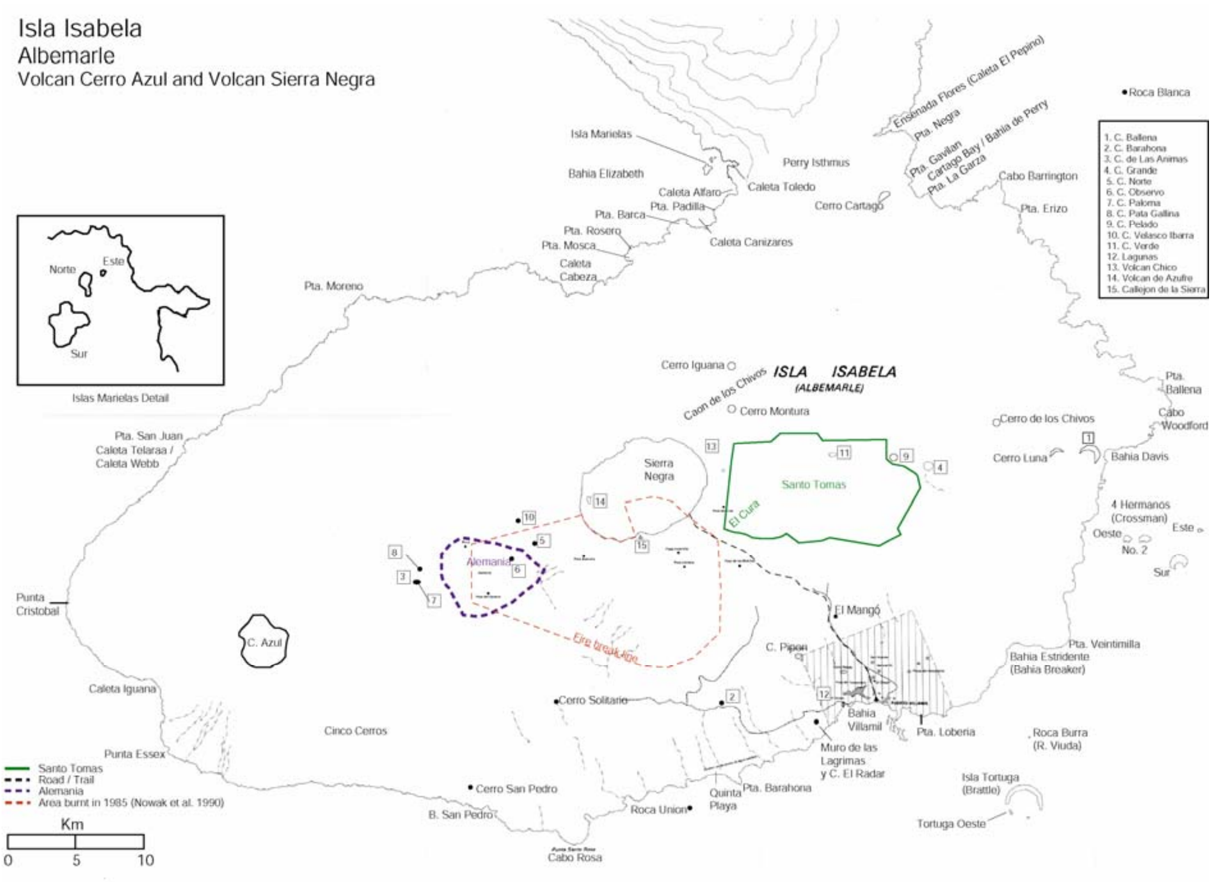
Fig. 17: http://www.tau.ac.il/lifesci/zoology/members/dayan_files/pictures/wasmannia.jpg

Appendix 1: Map of Santa Cruz Island



20 = Cerro Crocker, 27 = Los Gemelos, 30 = Media Luna and 34 = Puntudo

Appendix 2: Map of Sierra Negra, Isabela south



Appendix 3: Map of the Wolf volcano, Isabela north