Habitat-species association in the Hispaniolan solenodon (*Solenodon paradoxus)*; a quantitative study of an endangered Caribbean mammal.

Rocío A. Pozo Rodríguez

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"A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science and the Diploma of Imperial College London"

"Soli was always friendly, never aggressive, always hungry, never bad-tempered, always busy and never boring"

Walter Poduschka, 1975.

Declaration of own work

I declare that this thesis

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is entirely my own work and that where material could be construed as the work of others, it is fully cited and referenced, and/or with appropriate acknowledgement given.

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Name of student: **Rocío A. Pozo Rodríguez**

Name of Supervisors: **Richard Young/ Samuel Turvey/ Jose Nuñez-Miño**

Abstract

The Hispaniolan solenodon (*Solenodon paradoxus*) is one of the last endemic mammal survivors in the Caribbean. The species is categorised as endangered on the IUCN Red List (IUCN, 2010) and is found exclusively on the island of Hispaniola. Additionally, *S. paradoxus* is additionally listed as one of the top ten species within the Evolutionarily Distinct and Globally Endangered (EDGE) mammal group, devised by the Zoological Society of London (ZSL), due to its genetic distinctiveness. Little is known about the species, with its endangered status allocated essentially due to habitat loss. Additionally, little information is available concerning the species basic biology due to its secretive habits, with ignorance of its habitat associations hampering conservation planning.

This study assesses the habitat associations of the solenodon using quantitative data. This is undertaken at two different scales within the Dominican Republic: in the buffer zone of the Sierra de Bahoruco National Park, in an area of fragmented forest and agriculture (local scale), and; across three protected areas and two additional external locations in the south-western and eastern Dominican Republic (national scale).

Significant differences were found in solenodon occurrence patterns in forested areas at both scales. Within occupied areas, dry and broadleaved forest were the habitats most heavily used by the species at the local and national scales, respectively. The study found that habitat type, elevation and the relative proportions of ‘rockiness’ and soil depth were the most effective environmental variables of use in predicting solenodon presence. These findings will contribute to the better understanding the species’ distribution patterns across Hispaniola, and assist in the development of meaningful management programs to ensure the conservation of its occupied habitats.

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1. Introduction

1.1 Problem statement

Habitat fragmentation and degradation, overexploitation, introduction of invasive species and global climate change are the main drivers of biodiversity loss (Brook, *et al.,* 2008). Global population growth rates and unsustainable land use have had negative impacts on natural resources, and species extinction is one of the principal consequences.

Extinctions are estimated to be taking place at a rate of about 100 or more species a day; a conservative projection of species loss is more than 20% of the planet's biodiversity within the next decade or two (Wilson, 1992). A major impediment facing wildlife conservation is the lack of information about basic biology and ecology of endangered species. In this respect, many studies had highlighted the importance of developing knowledge about species-habitat associations (Gaylard & Kerley, 2001; Merrick *et al.*, 2007; Jackson & Robertson, 2011) as indicators of species distribution and habitat preferences. Extinction or survival of threatened species will depend on their level of dependence to specific ecological processes associated with their habitat (Harmon *et al*., 2005). Therefore, knowledge of species-habitat associations is fundamental to the improvement of conservation management plans.

The Hispaniolan solenodon (*Solenodon paradoxus*), an endangered small mammal species from the Caribbean, represents a big challenge to conservationists because little is known about the species and no conservation plans exist for it. A lack of information about their basic biology, and an absence of previously undertaken robust species-habitat studies, hampers conservation planning. Most studies on the species have focused on its taxonomic and morphological aspects (Wible, 2008 & 2010; Turvey, 2010) whilst only a few have touched upon their distribution and ecology (Ottenwalder, 1985, 1991, 2001; Roca *et. al*, 2004). Opportunistic distributional data, based on dead reported individuals (Woods, 1976 & 1981) and interviews with local people in remote regions of Hispaniola (Verrill, 1907; Turvey *et al.*, 2008; Secades, 2010), are both scarce and patchy.

Solenodons is found on Hispaniola, one of the islands of the West Indies and part of one of the most important biodiversity hotspots in Central America; supporting exceptionally diverse ecosystems, but also devastated by deforestation and human encroachment (Myers, 1988). Hispaniola comprises the most ecologically and geographically diverse island in the Greater Antilles group, and also one of the most threatened ecosystems in the region (Schubert, 1993). The extent of moist and dry forests in the Dominican Republic and Haiti has been drastically reduced through human activity (i.e. agriculture, charcoal production and mining). This, in addition to the effect of introduced invasive species, is the greatest threat to native flora and fauna on the island.

The Hispaniolan mammal fauna originally comprised of up to 25 endemic terrestrial species (Woods, 1981). Of these, only two mammals survive on the island: the Hispaniolan hutia (*Plagiodontia aedium)* and the Hispaniolan solenodon. Both are considered endangered by the IUCN Red List (IUCN, 2010) and distributed exclusively on the island of Hispaniola.

The Hispaniola and Cuban solenodon (*Atopogale cubana*) are the sole members of the family Solenodontidae and the only insectivores endemic to the Greater Antilles. They are probably the most ancient members of the West Indian mammalian fauna (Ottenwalder, 2001). Solenodons coprise the only surviving members of the mammalian order Eulipotyphla in the region, and their genetic divergence (more than 70 million years ago) makes them highly distinct from other extant mammals (Roca *et al*., 2004). Therefore, the Zoological Society of London (ZSL) has classified solenodon species in the top ten list of Evolutionarily Distinct and Globally Endangered (EDGE) mammal groups.

Recently, solenodon populations are believed to have declined throughout their distribution due to habitat fragmentation and the impact of exotic species, especially introduced mongooses, feral dogs (Woods, 1981; Ottenwalder, 1985 & 1991; Secades, 2010) and cats (Varona, 1983). In 1991, Ottenwalder concluded that the south Hispaniolan solenodon (*S. paradoxus woodi)* was the most endangered of the geographic populations. The range and status of solenodon in Haiti was unknown for more than 100 years, until 1973 when Woods reported the species in southern Haiti and then declared the subspecies "functionally extinct" again in 1981 (Ottenwalder, 1991). Finally, after more than 20 years of "extinction" Turvey *et al.* (2008) rediscovered *S. paradoxus* in the southwest of Haiti.

The species has been extremely vulnerable for the last 30 years, because of the human impact in their habitat. Considering that habitat degradation is increasing worldwide, it is essential to design conservation strategies and prioritize knowledge of the ecological and geographic distribution (Hirzel *et al*., 2006) of solenodons to improve the species' status.

This project is par of a Darwin-Initiative funded project known as "The Last Survivors" (http://www.thelastsurvivors.org/), made up of a collaboration between Durrell Wildlife Conservation Trust, ZSL, Sociedad Ornitológica de la Hispaniola and the Dominican Republic National Zoo; has been working since 2009 in the Dominican Republic and Haiti. The project seeks to increase knowledge about the current conservation status of the Hispaniolan solenodon and Hispaniolan hutia.

1.2 Aims and Objectives

The objective of this study was therefore to investigate solenodons' habitat associations with strong evidence-based data, collected through accurate individual presence detection.

The aim of was to characterise the habitats occupied by solenodons and to assess the extent to which its populations are using habitats modified by human activity. Surveys were carried out at two different scales. At the local scale, within the buffer zone of the Sierra de Bahoruco National Park in an area of fragmented forest and agriculture, and then, at the national scale, across three protected areas and two extra locations within the south-western and eastern Dominican Republic. These sites encompassed a broad range of elevation, forest types and human impacts. We also assessed the effectiveness of using field signs to detect the presence of the species.

1. Objectives: local scale
    - 1.1 To characterize solenodon denning and foraging habitats.
    - 1.2 To explore if the presence and abundance of solenodon foraging signs (nose pokes) are a reliable indicator for the occupancy by the species.
    - 1.3 To investigate whether distance to human settlements is an influencing factor in the location of den sites.
    - 1.4 To develop a model, based on environmental variables, to assess solenodon occurrence within a human-forest mosaic landscape subject to different levels of disturbance.
2. At the National level:
    - 2.1 To determine solenodon occupied habitat and its environmental characteristics.
    - 2.2 To develop a model, based on habitat characteristics, of use in estimating solenodon habitat use at the macro scale.

This is the first time that solenodons' habitat occupancy will be estimated based on the actual presence of the species. Details concerning the data collected, relative to the number of environmental variables and sample size, have not been previously developed. Also, it is the first study to build models at two different temporal and spatial scales, which in terms of conservation will generate a stronger output, as local environmental variability will be analysed in a greater context. This will increase accuracy and provide unbiased conclusions.

1.3 Thesis structure

This research study contains 5 chapters: introduction; background; methods; results, and; discussion.

- **Background** introduces the study species and its natural history, and includes a review of habitat association studies of solenodon. Finally, the study site is described at the national and local scales.
- **Methods** explain the fieldwork methodology used in the study, detailing the environmental variables measured in the field and the habitat modelling process at both scales.
- **Results** comprise the obtained outputs at the local and national scales, including explicatory graphs and tables.
- **Discussion** examines the results in a broader context, taking into account previous studies and the current environmental and social situation on Hispaniola. Additionally, some points are criticized and optional studies suggested for future conservation management.

2. Background

2.1 Family Solenodontidae

The order Eulipotyphla is made up of two families: the Nesophontidae, which went extinct during the Holocene, and the Solenodontidae, which used to be represented throughout the West Indies by numerous species (Honacki *et al.* 1982). Nowadays the genus *Solenodon* constitutes the only group of insectivores in the Caribbean and is made up of two species: *Atopogale cubana* (Peters, 1861) and *Solenodon paradoxus* (Brandt, 1833) exclusively found in Cuba and Hispaniola respectively.

Little is known about the ecology and basic biology of solenodon species because of the limited number of studies undertaken upon them, their secretive habits and endangered conservation status (IUCN, 2010). Most of the available literature refers to the anatomy and taxonomy of the Solenodontidae (Ottenwalder, 2001; Wible, 2008 & 2010). Additionally, a high proportion of the studies have been conducted with captive individuals (Mohr, 1936; Eisenberg, 1975; Poduschka, 1977) due to the species' unclear distribution, nocturnal behaviour and, thus, low probability of being observed in its native environment.

However, recent research has revealed new knowledge about solenodon species (Turvey *et. al*, 2008 & 2010; Roca *et. al*, 2004) highlighting them as a global conservation priority and underlining the importance of increasing the understanding of these species to conserve wild populations.

2.1.1 Natural history of Solenodontidae

Solenodons are mainly nocturnal mammals and the largest native insectivore (≈1 kg in weight) in the West Indies (Roca *et. al*, 2004). They usually live in family groups of 3 or 4 individuals in dens within coral-limestone rocks, hollow trees and logs (Ottenwalder, 1991).

Solenodon species have a wide diet, mainly constituted by arthropods, molluscs and annelids; although reptiles, amphibians, feathers and mouse bones have been reported in the species faeces (Peña, 1977; Ottenwalder, 1991; Eisenberg, 1975). The scavenging behaviour of solenodon leaves characteristics holes in the ground called "*nose pokes*" by "The Last Survivors" project teamwork. These are small holes in the leaf litter and soil mark where individuals searched or scavenged for food.

Information about solenodon reproduction is scarce. It has been suggested by Ottenwalder (1991) that solenodon species must be monogamous because of their ecological characteristics (*k* selected strategy, long pregnancies and precocial young), but initial field research suggests that several females and males share more than one den (Kennerley R., *pers.comm*). The only observed gestation lasted for 84 days (Ottenwalder, 1991). Two yearly litters have been suggested for the species with an inter-birth period of 145 days (Ottenwalder, 1991). The lactation period has been estimated to be 60-90 days long, with no indicators of reproductive seasonality (Ottenwalder, 1991).

2.1.2 Solenodon distribution and habitat occupancy

Few studies have been undertaken on solenodon species. The available literature is limited and extremely old in terms of species geographical distribution and habitat associations. *S. paradoxus* was discovered in 1833, but it was not found again until 1907 when Hyatt Verrill captured three individuals in the Dominican Republic. Since then several studies have reported the species in different parts of Hispaniola and its suggested conservation status has varied from scarce to extinct (Woods, 1976 & 1981; Peña, 1977; Ottenwalder, 1985, 1991 & 2001; Turvey *et al.*, 2008).

Most studies on distribution of the species have been based on either sporadic expeditions to collect individuals for *in situ* studies in zoos or reports of dead individuals from specific areas of Hispaniola (e.g. Poduschka, 1977). The first records of solenodon distribution were made by Hyatt Verrill (1902) who reported solenodon in the north of Hispaniola, in the semi-arid portion of the island, near to the Atlantic coast. Mohr (1938) collected specimens and assembled information about the presence of the species in the north of the Dominican Republic, in addition to Miller (1929) and Allen (1942) who affirmed solenodon was distributed in "stony forest" in the northeast of the country.

Further studies were published in the 1970's and 80's. Woods (1976) found two carcasses in Haiti at an altitude of 750m. The same author, in 1981, declared that solenodon was "functionally extinct" in most of Haiti, following a wide-scale survey. In 1977 Peña described two populations of solenodon, one in the north and northeast of Hispaniola and another in the southwest, near to Barahona Province.

The distribution and habitat occurrence of solenodon has previously been studied at the macro scale. The first large-scale study was developed by Ottenwalder (1985), who determined the distribution and habitat of solenodon in the Dominican Republic. He carried out a national mapping analysis, along with local interviews and collation of historical data, to gather information about the type of habitats where solenodon were found. Ottenwalder concluded, *"solenodons have a wide range in the Dominican Republic, but nowhere are they frequently seen".* He did not collect environmental variables in the field, and his work based its final conclusions on direct observations and through use of the geomorphological classification proposed by the Organization of American States.

In 1991 the same author re-defined solenodon distribution in Hispaniola based upon historical and morphological characteristics of the species. No habitat characteristics were included in this study and the conclusions were made on anatomic differences between surviving and extinct solenodon species. Finally, in 2001 Ottenwalder included new distributional records for all species of solenodon in the Dominican Republic and Cuba, gathering data from field surveys and paleontological specimens. His results showed that the Hispaniolan solenodon exhibits a large distribution and a large number of surviving, although fragmented, populations (Ottenwalder, 2001).

2.2. Habitat associations in endangered mammals

Habitat is defined as an ecological area that is inhabited by a particular species (Abercrombie, 1966). From this simple definition, the complex interaction between species and environment determines the presence or absence of specific populations. Landscapes are composed of different types of habitats that constitute a dynamic matrix of ecological interactions. Through evolutionary processes, organisms may respond to this variation by becoming either niche specialists or generalists (Elena & San Juán, 2003; Harmon *et al*., 2005). Therefore, highly specialized species are often limited to a particular type of landscape, being dependant on the ecological process associated with it (Harmon *et al.,* 2005). Changes in those environments could determine the extinction or survival of threatened species. Because of this, great effort has been made in conservation to determine the habitat characteristics and environmental variables associated with the distribution of endangered species.

Several studies have surveyed habitat associations in threatened species (Wassens *et al*., 2010; Gray *et al.* 2010; Wilson *et al.* 2011; Boer *et al.*, 2010). These approaches have been used on endangered small mammal populations (Bias & Morrison, 2006; Merrick *et al*., 2007; Jackson *et al.* 2008) to achieve conservation targets.

Endangered small mammals are difficult to find in the field, particularly in the case of nocturnal cryptic species with secretive habits (Gaylard & Kerley, 2001; Jackson & Robertson, 2011). Gathering information on such species by direct observations can be unfeasible in the short term. In these cases, indicators of the animal's presence or absence (e.g. nest sites, foraging signs and footprints) have been used to complement high-tech conservation tools (e.g. camera traps and radio collars) to collect environmental variables for species-habitat associations (Bias & Morrison, 2006; Merrick *et al.*, 2007; Jerosch *et al.*, 2010).

Statistical modelling has strongly supported habitat association studies using environmental data analysis. The use of predictive habitat distribution models has rapidly increased in ecology (Guisan & Zimmermann, 2000; Pearce & Boyce, 2006). A wide array of models have been developed to cover aspects as diverse as biogeography, conservation biology and climate change research on habitat management (Guisan & Zimmermann, 2000). These methodologies have shown strong results, predicting occurrence probability in endangered small mammal populations at different scales (Jackson *et al.* 2008; Jackson & Robertson, 2011).

2.3 Study site

This study, undertaken as part of “The Last Survivors” project, worked at two different scales (national and local). Therefore both study sites will be described.

2.3.1 National scale: Dominican Republic

The Dominican Republic (19’00’’N, 70’40’’W) is part of the island of Hispaniola, in the Caribbean (Fig. 1). Hispaniola is the second largest island (77,914 km²) of the Greater Antilles and the Dominican Republic occupies the eastern two-thirds of the island (48,67 km²), situated between Haiti, the Caribbean Sea, and the North Atlantic Ocean.

Despite its relatively small area, the physiographic complexity of the Dominican Republic exhibits considerable heterogeneity and variability in local climatic regimes (Ottenwalder, 1985), representing ecologically and geographically one of the most diverse countries in the Greater Antilles (Schubert, 1993).

The climate is tropical maritime with little seasonal variation in temperature, but with seasonal variation in rainfall; highly influenced by marine phenomena. This creates two regular rainy seasons (April-June and September-November) and one dry season (December-March). The Dominican Republic’s geographic elevation varies from -46 m at Lago Enriquillo, to 3,175 m at Pico Duarte.

The Dominican Republic is part of the insular Caribbean Biodiversity Hotspot. Four distinct eco-regions are present (two of them are maritime and two terrestrial). The terrestrial eco-regions in the Dominican Republic correspond to:

a) The *wet forests* (also called broadleaf forest) of Hispaniola. These originally comprised more than half (~60%) of the original vegetation on the island, to an altitude of about 2,100 meters. In the Dominican Republic, wet forest covered most of the eastern half of the country, ending at the higher elevations of the mountains and continuing across the entire island of Hispaniola, only being absent in the south. Despite their degradation, these wet forests still maintain an exceptionally diverse insular biota. This eco-region is found in Los Haitises, the Cordillera Central, and Sierra de Bahoruco National Park.

b) The *pine forests* of Hispaniola. These are located on slopes with shallow soils at higher elevations in the central mountain systems of the Dominican Republic. This eco-region is found mainly in mountainous areas of the Cordillera Central and Sierra de Bahoruco. The pine forests of Hispaniola contain several endemic species of plants and animals that have been assigned an internationally high conservation priority.

About 28.5% of the Dominican Republic is protected (Figure 1). In 2003 the number of protected areas was around 47, and a further 37 were added in 2009 (Schubert, 1993; Earth-Trends, 2003). Of these, 12 are National Parks, with Sierra de Bahoruco, Jaragua, Los Haitises and Del Este National Parks represening the largest parks in the country.

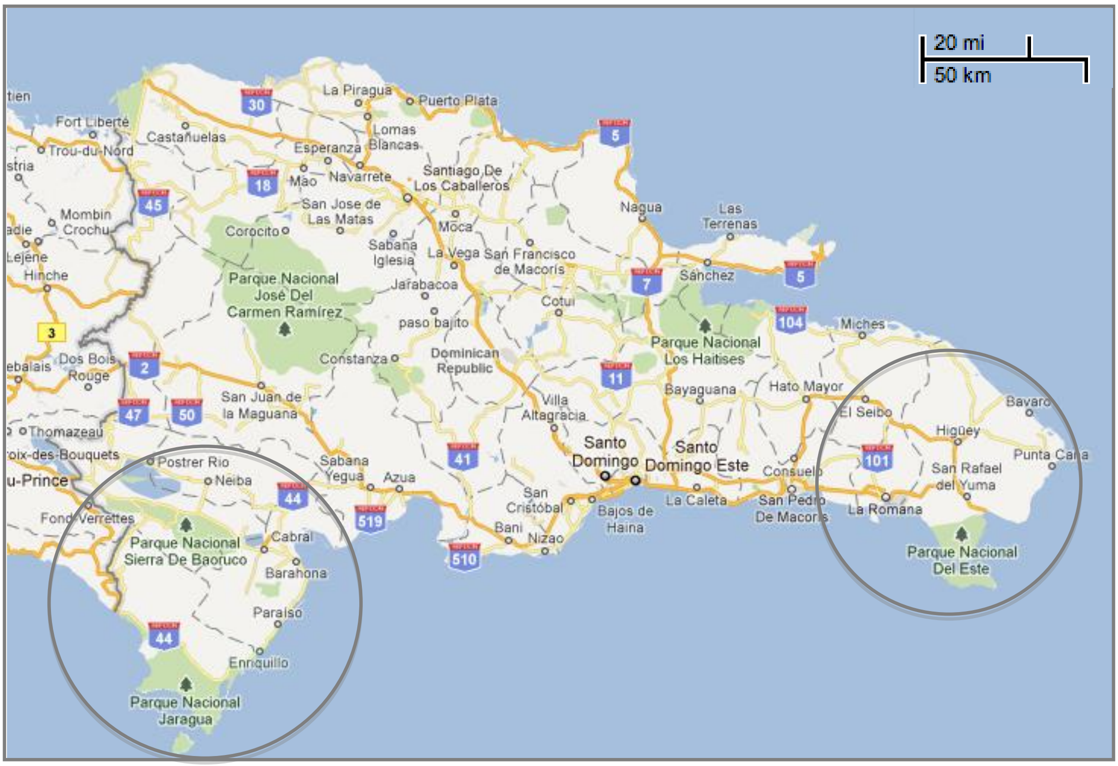


Figure 1. Survey areas (grey circles) on Hispaniola, Dominican Republic. Source: ©2011 Google-Map data ©2011 Google.

2.3.2 Local scale: Mencia

The study site was located within the buffer zone of the Sierra de Bahoruco National Park, in the area surrounding the village of Mencia (10’21’’N, 44’30’’W) in Pedernales Province (Fig. 2). Sierra de Bahoruco is a protected area with the highest biodiversity and percentage of endemism in the Dominican Republic.

The area is composed of fragments of unprotected forest and agriculture zones near to the border with Haiti, in the southwest of the Dominican Republic. The human population mainly depends on subsistence agriculture and charcoal production. These represent important threats to native fauna, together with the high rates of associated deforestation and introduction of invasive species.

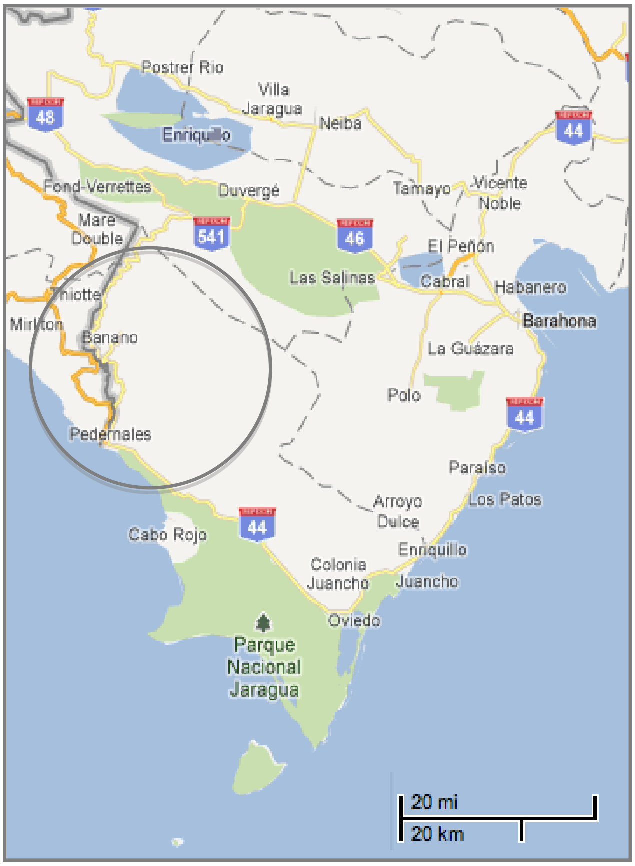


Figure 2. Map of the Pedernales Province, in the southwest of the Dominican Republic. The grey circle shows the location of Mencia. Source: ©2011 Google-Map data ©2011 Google.

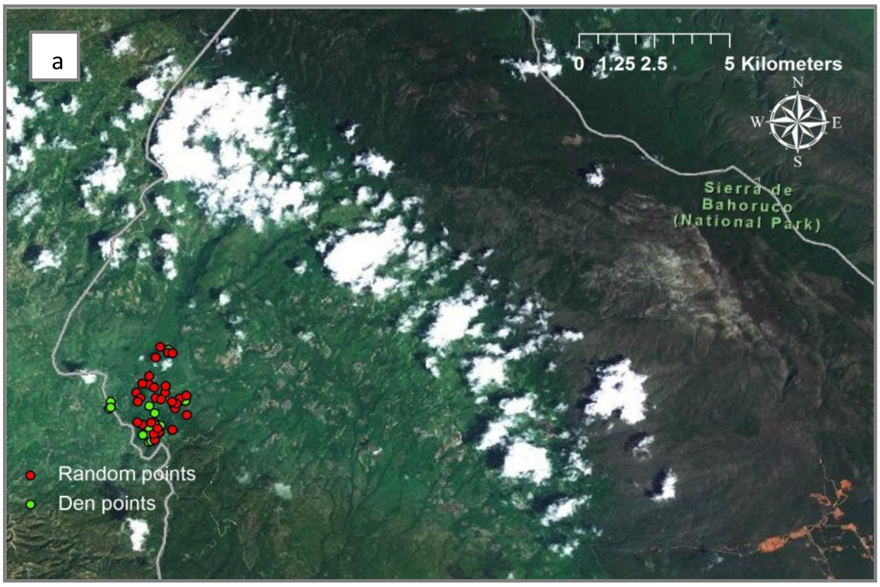
3. Methods

Local scale study

The local scale survey was undertaken in the area surrounding the village of Mencia (18°10’15’’N 71°44’49’’W) in the south west of the Dominican Republic near to the border with Haiti.

Habitats present within the study area were mapped using Global Positioning System (GPS) receivers (Garmin eTrex® H), with tracks used to delineate different habitat patches (see Appendix 1). A total of seven habitats were defined: forest (humid, semi-humid and dry), dry scrub, agricultural areas (coffee and bean plantations) and pastures. From these, five categories were created: humid forest (HF), semi-humid forest (SHF), dry forest (DF), dry scrub (DS) and agricultural/pastoral areas (A/P). Forest types were classified in the field based on three different categories: vegetation structure, tree species and soil characteristics (see Appendix 2). Agricultural areas and pastures were grouped as high human impact areas. Finally, dry scrub was left as a single category type due to its unique characteristics in relation to the other groups.

Sample sites were classified as either den sites or random points (Fig. 3). Both were assessed using standardised survey methods to determine habitat characteristics within each plot.



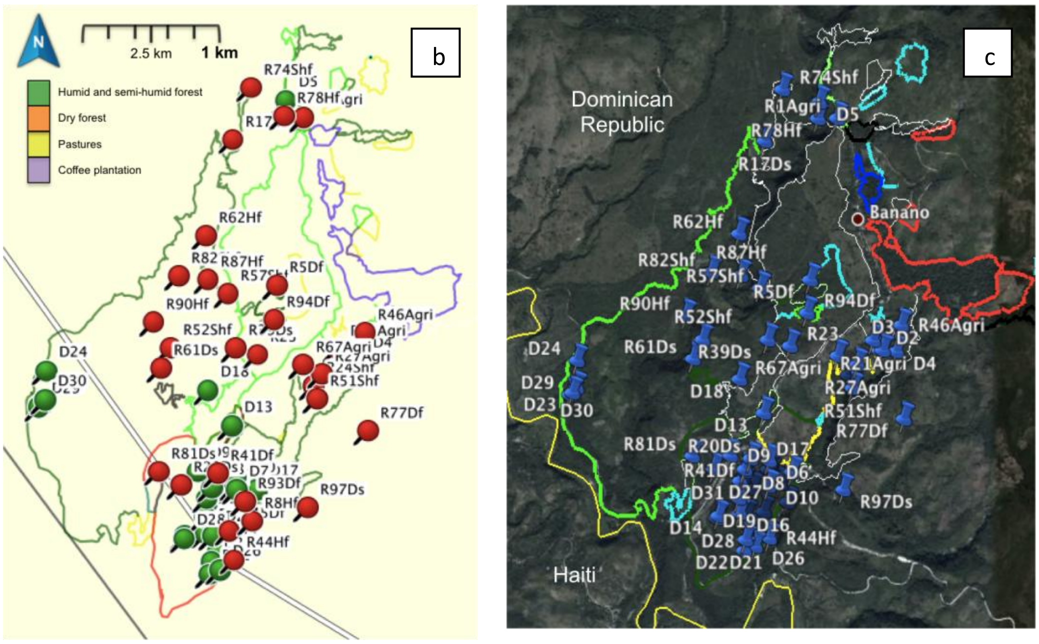


Figure 3. Maps of the location of the study site. **a)** shoews the buffer zone of Mencia, next to Sierra de Bahoruco National Park. Red plots represent the GPS location of random points; in green are represented the GPS location of den sites. **b)** ilustrates the location of den sites (green dots) and random points (red dots) in the mapped area at the local scale (see Appendix 1). Source: Base Camp© version 3.2.1 (3.2.1). **c)** shows the location of den sites (green dots) and random points (red dots) in the mapped area at the local scale (see Appendix 1) in a satellital image. Source: ©Google Earth version 6.0.3.2197.

3.1 Survey design

In order to determine which habitat characteristics are associated with solenodon presence, surveys were carried out within two types of sites:

- **Random Points:** one hundred random points were generated within a 25 km² area using Microsoft Excel version 14.00 (100825). Once they were classified in terms of their habitat type (five available habitats), thirty random points (six in each habitat) were randomly selected using the same method, which correspond to the surveyed random points.

- **Den sites:** thirty confirmed solenodon dens were surveyed between the 29th of April and the 20th of June 2011. These dens were found after tracking radio-collared individuals (TW-3 medium mammal tags, Biotrack Ltd.) during the day when they were resting, to discover the location of active dens. Solenodons were radio-tracked once every two nights to record the GPS location of the individual. This allowed us to register the UTM co-ordinates of inhabited solenodon den sites. Camera traps (Moultrie i60 infrared cameras) were then strategically placed outside the den entrance to confirm presence of solenodon within those dens. Once solenodon presence was confirmed, a new GPS waypoint was recorded and surveyed as one den site. Seven radio collars were used on ten individuals from February to June 2011 by Ros Kennerley (PhD candidate, University of Reading) and “The Last Survivors” fieldwork team to gather information about the species home range, habitat use, family group size, and den sites.

Random points and den sites were surveyed using the same methods, combining the habitat measurements detailed below, in addition to field sign collection.

3.1.1 Environmental variables

Each plot was delineated as having a diameter of 40m. UTM co-ordinates, date and time were recorded at each plot, along with the following environmental variables: habitat type, elevation, type of soil, topographical characteristics and most common tree species. Signs of solenodon presence, along with indicators of human impact, were also recorded.

3.1.1.1 Habitat measurements

Five habitat measurements were taken: ‘rockiness’, vegetation density and heterogeneity, soil depth, canopy openness and tree biomass.

GPS random points and den locations were recorded as the central point of the plot. From there a 20m rope, marked at 2m intervals along its length, was extended from the centre (Fig. 3). A 2.5m pole, with 50cm marked intervals, was then placed at each 2m marker along the rope. A measure of ‘rockiness’ was then taken based upon whether the pole was touching rock, soil, live plant material (e.g. roots), dead plant material (e.g. logs) or water. A total of ten measurements by transect (4 transects in total, 20m each) were surveyed in each plot (Fig. 3).

A 28cm metal spike was then inserted into the ground within a 1cm circumference of each of the contact points described above (approximately every 2m), in order to estimate soil depth.

Vegetation density and heterogeneity were calculated in terms of foliage height diversity (MacArthur & MacArthur, 1961; Willson, 1974). Each contact made by non-grass species within the five 50cm sections, comprising the full pole height, was recorded. This was undertaken at 2m intervals along the transect length, at 90 degrees from the previous position, in order to produce four perpendicular measures for each plot (Fig. 4).

This gave a total of forty measures per plot of 'rockiness' and soil depth, along with forty measures of vegetation density at 5 increasing heights from the ground.

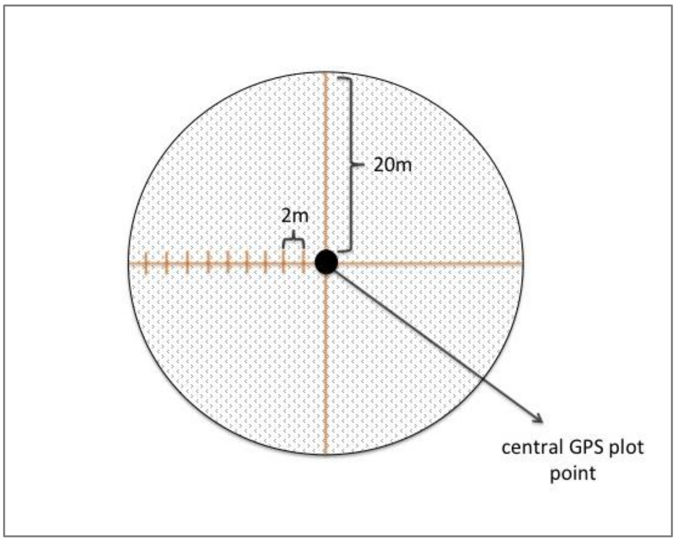


Figure 4. Diagram of data plot collection. The figure shows the length of each transect and the sub-division within them.

Canopy openness was measured using a canopy scope (Brown *et al.*, 2000). This was constructed from a clear compact disc case with twenty-five evenly spaced black dots drawn on it. The scope was held up vertically, 20cm from the researcher's eye, with the number of dots masking light shining through the canopy then counted. This was done four times per plot at a 10m distance from the plot centre, halfway along the transect rope used for the measures previously described.

The ten trees with a circumference >10cm closest to the centre of the plot were identified with a vernacular and scientific name and their circumference recorded.

This provided measures of mean tree circumference and forest relative biomass through Tree Basal Area (TBA) (Hédl *et al.* 2009). The equation provided below was utilised to calculate TBA per plot, with ΣDBH equal to the sum of the 10^{th} nearest trees diameter at breast height in cm;

$$\text{TBA (m}^2\text{)} = \pi \times (\Sigma\text{DBH}/200)^2$$

3.1.2 Human impact indicators

The following human impact indicators were recorded: number of logged trees; presence/absence of domestic species (cattle, chickens, dogs and cats); presence of human settlements (roads, houses, charcoal ovens, etc.), and; nearest environment type to the surveyed plot (forest patch, agricultural areas or pasture). The presence of domestic animals was determined by direct observation as well as searching for faeces and tracks.

The nearest environment to the habitat patch was classified in the field using the same categories which were previously defined and corroborated in Google Earth (version 6.0.3.2197) based on the local habitat type developed map.

Distance to the nearest human settlements (DHS) was estimated using Google Earth (version 6.0.3.2197) as a variable, relative to habitat fragmentation effects in solenodon populations. DHS was recorded as the minimum distance from the plot centre to the nearest road, agricultural zone (plantations and pastures), local houses and/or charcoal exploitation sites.

3.1.3 Solenodon field signs

Twenty minutes were spent searching for the different field signs of solenodon within each plot area (1,600 m²). “Nose pokes”, a description devised by the Last Survivors’ Project work team for the most common sign of species presence (Figure 5a), were searched for. These are small conical holes in the soil created when solenodon digs whilst looking for food (primarily insects and other invertebrates).

Figure 5. Solenodon field signs: a) solenodon "nose poke"; b) solenodon faeces.

The second field sign searched for was solenodon dung, which was generally found either on the soil surface, on fallen logs or on top of rocks (Figure 5b). Solenodon dung is very distinctive because of its "goat-like" smell, in addition to the usual presence of a large proportion of chitinous millipede body ring sections within it.

The third field sign comprised solenodon dens. These were typically found in small limestone caves (Ottenwalder, 1991). In order to investigate the activity status of each den, the entrance was examined for the absence of spider webs across it in addition to the presence or absence of the strong "goat" smell associated with the species. Further evidence of species presence included small paths leading up to den entrances and small scratch marks from solenodon claws on the surface of rocks or vegetation at the den entrance.

National scale study

Five large-scale study sites were selected across the Dominican Republic: Sierra de Bahoruco (19'20''N, 30'23''W), Jaragua (47'07''N, 30'04''W) and Del Este (09'00''N, 41'00''W) national parks, Punta Cana (31'57''N, 21'59''W) and Isla Catalina (21'15''N, 00'26''W). Because of the very different features present in the protected areas, two different stratified random sampling approaches were used by "The Last Survivors" project. Sierra de Bahoruco National Park is located in a mountainous area Sampling was thus stratified according to altitude, with random sampling points divided within 400m altitudinal bands. Both Jaragua National Park and Del Este National Park are located in lowland areas and stratified sampling was therefore undertaken according to vegetation type. From these five zones 221 random points were surveyed (Fig. 6), with habitat information collected across the Dominican Republic since October 2009.

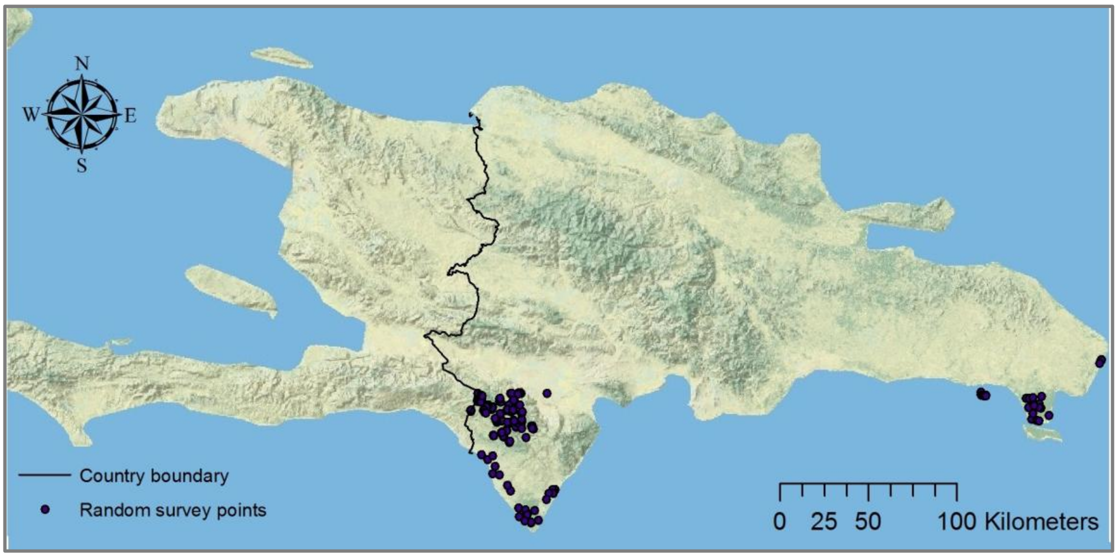


Figure 6. Location of 221 random points (black dots) included in the national analysis undertaken within the southeast and southwest of the Dominican Republic.

Fieldwork survey methods (i.e. habitat measurements and recording of solenodon field signs) were applied in the same manner at the national scale as described for the local scale surveys. Human impact variables were not recorded at this level however.

3.2 Analyses

Two levels of analysis were carried out: one at the local scale using the previously detailed field data, and the second at the national scale using data from the 221 random points. Data were managed with Microsoft Excel and analysed using R v.2.11.1 (R Development Core Team, 2010).

Three response variables were measured at the local scale: solenodon presence at the dens sites (Spres), solenodon nose poke presence (SNPp) and solenodon nose poke abundance (SNPn). Solenodon presence was a strong indicator of solenodon denning areas because of the accuracy of the radiotelemetry/camera trap methods used, whilst solenodon nose poke presence and abundance were considered indicators of solenodon foraging zones.

To investigate which explanatory variables (habitat type, elevation, vegetation density and heterogeneity, percentage of 'rockiness', soil depth, percentage of canopy openness and tree biomass) can best predict two response variables (presence of solenodon and solenodon foraging signs) at the local scale, two multi-variable models with binomial distribution error response were developed using Generalized Linear Models (GLMs).

To select the number of explanatory variables considered in the model, each response variable was initially plotted independently, and then subsequently in relation to each explanatory variable, to understand how they behaved. Moreover, a matrix of explanatory variable interactions was plotted to determine which ones were correlated. In the case of two different variable correlations explaining the same variance, one of the variables was removed from the model. Furthermore, a tree analysis (TA) and random forest model (RFM) were required to confirm explanatory variables that must be considered to estimate Spres (based on confirmed den sites) and SNPp as response variables. Both GLMs were designed to correlate habitat characteristics with solenodon occupancy in denning and foraging areas at the local scale, and to study the response of the species to habitat loss in a human-forest mosaic landscape.

One response variable was measured at the national scale: solenodon presence (Spres) was estimated in relation to solenodon nose poke presence (SNPp). At this scale a similar modelling process was carried out to develop a multi-variable GLM using solenodon nose poke presence as an indicator of solenodon presence within and outside protected areas. No tree and/or random forest analysis were needed because of the large sample size and relatively small quantity of explanatory variables included in the modelling process.

Maximal models were simplified when appropriate by deleting non-significant terms. Significance was determined for all analyses at p=0.01 (p>0.1 “n.s.”; p<0.05 “.”; p<0.01 “*”; p<0.001 “**”; p<0.0001“***”) and model selection was based on Akaike’s Information Criterion (AIC), in addition to an Analysis of Deviance for Generalized Linear Model Fits (anova).

4. Results

4.1 Local scale: Mencía

4.1.1 Solenodon denning habitat characteristics

A total of sixty plots were surveyed. Of these 53.3% were solenodon-occupied plots in dry forest (n=16), followed by semi-humid forest (33.3%, n=10) and humid forest (10%, n =3). Just one den was found in dry scrub (3.3% occupancy) and no dens were found in agricultural land or pastures (Table 1).

Table 1. The five habitats surveyed (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas to find *S. paradoxus* denning areas. Environmental variables mean are compared between the different habitat categories.

	Habitats				
	DF (n=16)	**SHF (n=10)**	**HF (n=3)**	**DS (n=1)**	**A/P (n=0)**
%	**53.3**	**33.3**	**10.0**	**3.3**	**0**
Variable					
Elevation (m)	344.97	341.13	341.62	382.00	-
Vegetation density	0.65	0.65	0.66	0.65	-
Rockiness (%)	30.6	34.8	24.3	68	-
Soil depth (cm)	7.00	7.08	7.41	2.58	-
Canopy openness (%)	47.57	44.13	43.54	55.00	-
Tree diameter (cm)	30.41	33.81	30.48	22.30	-
TBA (m^2)	8.14	10.63	7.20	3.91	-

Mean elevation in occupied areas was 344.9m, with the highest altitude in dry scrub (DS) plots (382.0m). The mean vegetation density index was relatively high (0.65) for occupied habitats. The mean percentage of 'rockiness' was 30.6%, varying from 6.0% in DF to 68.0% in DS plots. Soil depth was similar between forest areas (mean= 7.16cm), with a depth of 2.58cm measured within DS den plots, with a total mean of 6.99cm. Canopy openness within solenodon occupied habitat was relatively high (47.5%); although a lower index was detected in a SHF plot (10%) and the greatest exposure recorded was within a DF plot (100%). The mean tree circumference close to the plot centre point was 30.4cm; the highest and lowest means were shown in

SHF plots (33.81 cm) and DS plots (22.30 cm), respectively (Table 1). Mean TBA was calculated as 8.1 m² for occupied habitats.

4.1.2 Solenodon foraging areas habitat characteristics

Fifty of the sixty surveyed plots recorded the presence of solenodon nose pokes. Of these, 42% were located in DF plots (n=21), 28% in SHF plots (n=14), followed by 14% in HF plots (n=7) and 8% in DS and A/P zones respectively (n=4 in both groups) (Table 2).

Table 2. The five habitats surveyed (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas) to find *S. paradoxus* foraging areas. Environmental variables mean are compared between the different habitat categories.

	Habitat				
	DF (n=21)	**SHF (n=14)**	**HF (n=7)**	**DS (n=4)**	**A/P (n=4)**
%	**42.0**	**28.0**	**14.0**	**8.0**	**8.0**
Variable					
Elevation (m)	356.88	361.29	369.24	371.75	407.75
Vegetation density	0.62	0.62	0.61	0.62	0.33
Rockiness (%)	28.9	29.1	29.4	26	35.5
Soil depth (cm)	7.24	7.31	7.05	9.35	6.03
Canopy openness (%)	53.52	50.98	48.78	57.75	95.00
Tree diameter (cm)	32	34	37.0	22.5	35
TBA (m²)	10.22	11.03	14.86	4.64	10.06

Mean elevation in SNPp areas was 359.84m, with higher altitude in agriculture/pastures plots (407.75m). The mean vegetation density was 0.61 for habitats exhibiting solenodon nose pokes. The percentage of 'rockiness' recorded was 30.5%, with a relatively uniform distribution (26.0% in dry scrub to 35.5% in agriculture/pastures zones). Soil depth was once again similar between forest areas (mean=7.2), with 9.35cm measured in dry scrubs plots and 6.03cm in agriculture/pastures sites, with a total soil depth mean of 7.40cm for all habitats. Canopy openness was relatively high (61.21%) in zones exhibiting solenodon foraging signs; the maximum value was recorded for agriculture/pastures plots (95%). The tree mean circumference was 32.9 cm, with similar indices in forested and agricultural zones (Table 2). Mean TBA within species foraging areas was calculated as 10.16 m².

4.1.3 Solenodon signs as indicators of species presence

Occurrence of SNPp was 83.3% in surveyed plots (50/60). Of this, 41.1% were from individuals using dry forests (21/50); 27.4% in semi-humid forests (14/50); 13.7% in humid forests (7/50) and 8% in dry scrub (4/50) and agriculture/pasture zones (4/50), respectively (Table 3).

Table 3. Solenodon response variables expressed in number (n) and percentage (%) in the five habitat categories surveyed (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas).

		Habitat				
Response variable		**DF**	**SHF**	**HF**	**DS**	**A/P**
Solenodon presence (S.pres)	n	16	10	3	1	0
	%	53.33	33.33	10	3.33	0
Solenodon nose pokes presence (SNPp)	n	21	14	7	4	4
	%	41.18	27.45	13.73	8.00	8.00
Number of solenodon nose pokes (SNPn)	n	1305	529	43	180	462
	mean	57.76	54.47	49.86	45.00	109
	%	18.27	17.23	15.77	14.24	34.48

Total abundance of Solenodon nose pokes varied between habitat types (Fig. 7). These values differed significantly (chi-squared = 19.4722, df = 1, p<0.001) between different areas.

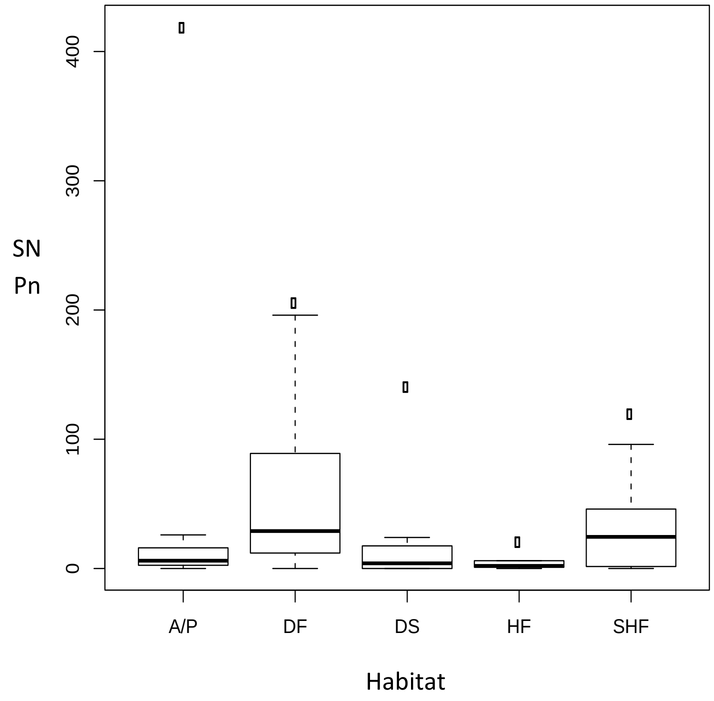


Figure 7. The frequency distribution of the number of solenodon nose pokes (SNPn) in the five habitat categories (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas).

Total nose poke means by plot were higher in agriculture/pastoral zones than in any other type of habitat (plot mean = 115.5), followed by dry forests (plot mean = 62.1), dry scrub (mean = 45), semi-humid forest (mean = 37.7) and humid forest (mean = 6.1) (Fig. 8). The differences between habitats were highly significant (chi-squared = 41.0915, df = 1, p<0.001).

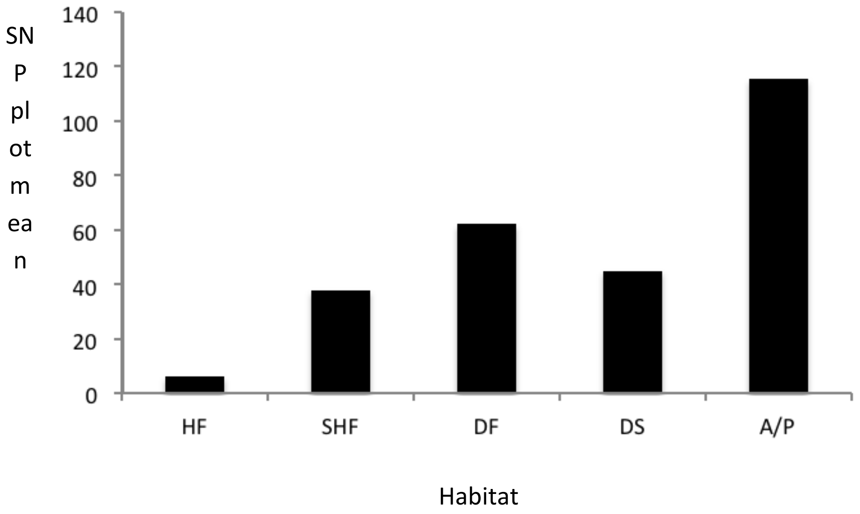


Figure 8. Solenodon nose pokes (SNP) mean plot frequencies in the five habitat categories (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas).

It is important to consider than seven plots recording presence of solenodon nose pokes were located within agriculture/pastoral zones (mean=115.5). Furthermore, one of them exhibited 419 nose pokes, which significantly increased the nose poke mean for agriculture/pastoral habitat. This plot was therefore removed from the analysis, but differences between habitats remained significant. Thus, the highest number of nose pokes was found in dry forest, followed by semi-humid forest (Fig. 9). The same situation was repeated in dry scrub where the total habitat mean was 45 SNP per plot, with one of them containing 141 solenodon nose pokes. Due to the large increase in the habitat mean this plot was removed, and habitat mean re-established (mean=13). The final graph is shown in Figure 9.

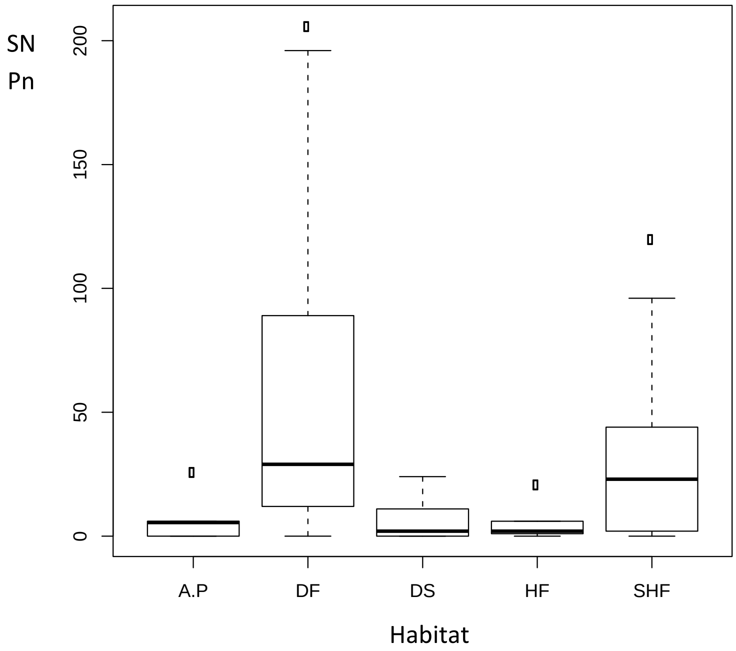


Figure 9. The frequency distribution of the number of solenodon nose pokes (SNPn) in the five habitat categories (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas), after extreme values were removed.

Comparing Spres, SNPp and SNPn plot percentages between habitats, the results show that proportions of Spres and SNPp behave consistently in all habitats (Fig. 10), with the exception of agriculture/pastoral zones (where no solenodons were found). Percentages of SNPn in relation to the presence of solenodon were proportional in humid forest, semi-humid forest and dry forest (Fig. 10). This relationship within dry scrub plots and agriculture/pastoral zones showed dramatically higher differences because of the previously explained distributions (see Fig. 9).

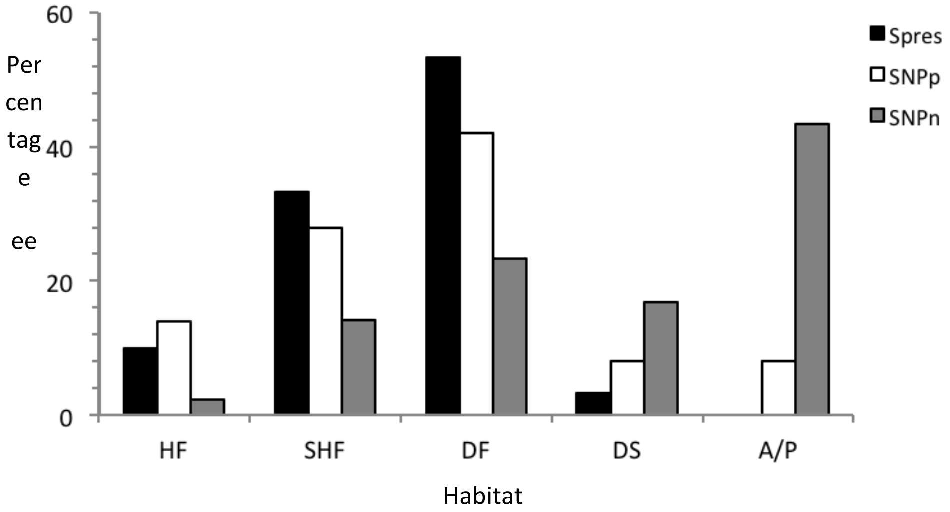


Figure 10. Proportions of solenodon presence (Spres), solenodon nose pokes presence (SNPp) and solenodon abundance (SNPn) in relation to habitat categories (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas).

Logistic regressions for both response variables were constructed (Spres~SNPp and Spres~SNPn). A positive correlation was shown between Spres and SNPp (SE = 1.092, z value = 2.307; p<0.01) and between Spres~SNPn (Fig. 11). The last correlation was not statistically significant.

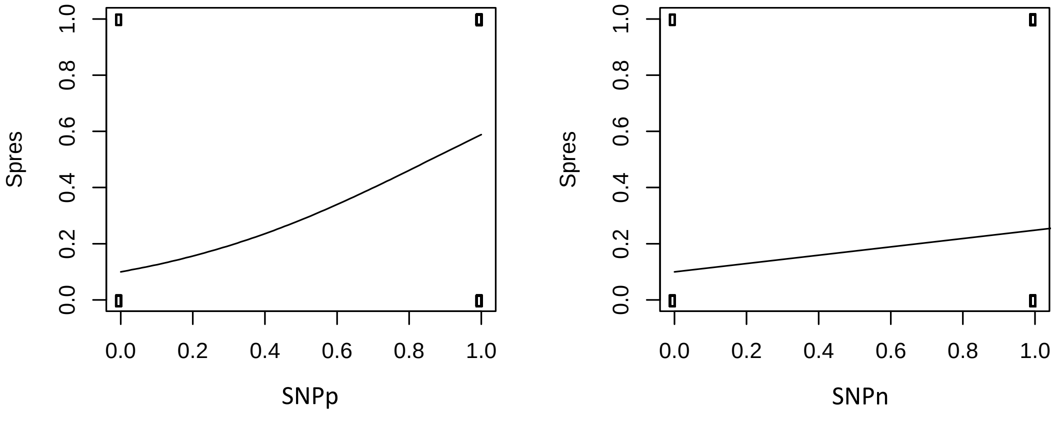


Figure 11. The fitted regression lines illustrate the relationship between solenodon nose pokes presence (SNPp) and solenodon nose poke abundance (SNPn) with the probability to find *S. paradoxus* in the same habitat type.

4.1.4 Human activities and solenodon-occupied areas

Distance to human settlements (DHS), presence of logged trees, presence/absence of domestic species, and nearest areas (NE) to the surveyed plot were studied as measurements of human disturbance in areas where solenodon are found.

The distance between solenodon occupied plots and human settlements (DHS) were estimated as 110.51m for all habitat types (total mean). The mean number of logged trees per plot was 12.3 and 80% of solenodon confirmed used areas also supported domestic animal species (Table 4).

Table 4. Human disturbance variables mean values in the five surveyed habitat types (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas).

	Habitat				
	DF (n=16)	**SHF (n=10)**	**HF (n=3)**	**DS (n=1)**	**A/P (n=0)**
%	**53.3**	**33.3**	**10.0**	**3.3**	**0**
Variable					
Distance to human settlements (m)	126.08	116.53	145.37	54.09	-
Logged trees	12.33	14.40	8.92	5.00	-
Domestic species (%)	100.0	60.0	33.3	0	-

The closest environments to solenodon occupied plots consisted of: 36.67% dry forests, 33.3% agriculture/pasture areas, 13.33% humid forests, 13.33% semi-humid forest, and 3.31% dry scrubs.

Logistic regressions of Spres and human impact variables showed a positive correlation (std. error=0.059, t value=2.344, $p<0.01$) in the probability of finding solenodon denning sites and DHS (Fig. 12). Because Spres and SNPp are positively correlated, both response variables behaved equally in relation to DHS (Fig. 12).

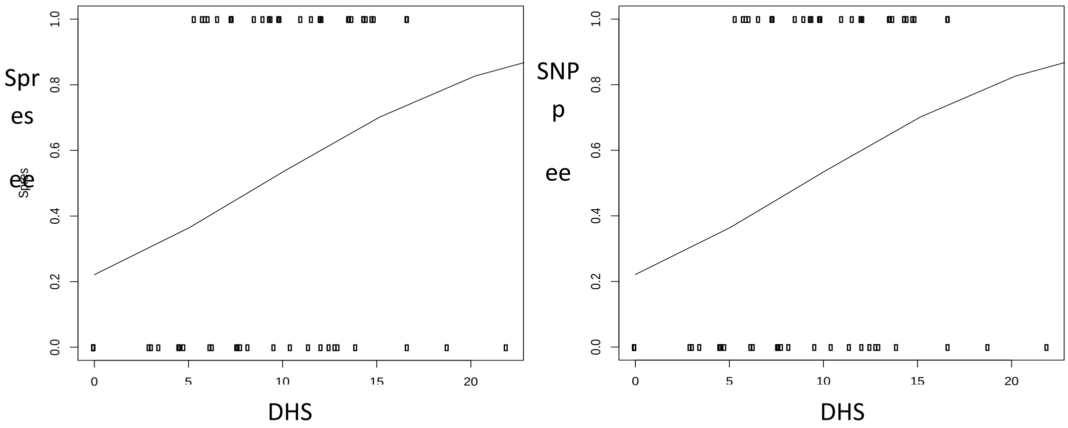


Figure 12. The fitted regression lines show the relationship between distance to human settlements (DHS) with the probability to find *S. paradoxus* (Spres) and solenodon nose pokes (SNPp) within an area.

The number of logged trees showed a negative relationship with Spres, these differences were not statistically significant. Finally, the presence of domestic animal species in solenodon used habitats was not statistically significant for the species presence in the same area.

Logistic regressions of solenodon nose poke abundance and human impact variables (DHS, logged trees and presence of domestic species) were conducted; no correlations were found.

4.1.5 Solenodon-habitat association in human fragmented forest mosaic environments: model at the local scale

A logistic regression model was constructed to investigate the relative importance of environmental explanatory variables in the probability of finding solenodon in studied plots. The selected explanatory variables used were: habitat type; elevation; vegetation density (VD); 'rockiness' (R%); soil depth; canopy openness (CO%), and; mean tree circumference (TC) were analysed by a tree modelling and random forest regression (Crawley, 2007) (see Appendix 3). The aim was to select explanatory variables to be considered in the local model and reject less important parameters.

A number of alternative models were run and non-significant variables were excluded. AICc criteria complementary to analysis of deviance for GLMs fit were used to select the minimal fixed model for solenodon occurrence. This included three factors with significant effects: habitat, elevation and TC. The best-fit model was:

Local model: Spres ~ Habitat * elevation + TC

The “Habitat * elevation” factor indicated that the probability of finding solenodon (Spres) increases in forested areas. Within the results dry forest is the most suitable habitat for solenodon distribution, followed by semi-humid forest and humid forest categories at lower elevations (Fig. 13). The tree circumference (TC) was negatively associated with the presence of the species, indicating the probability of finding *S. paradoxus* decreases as tree circumference increases (Fig. 13).

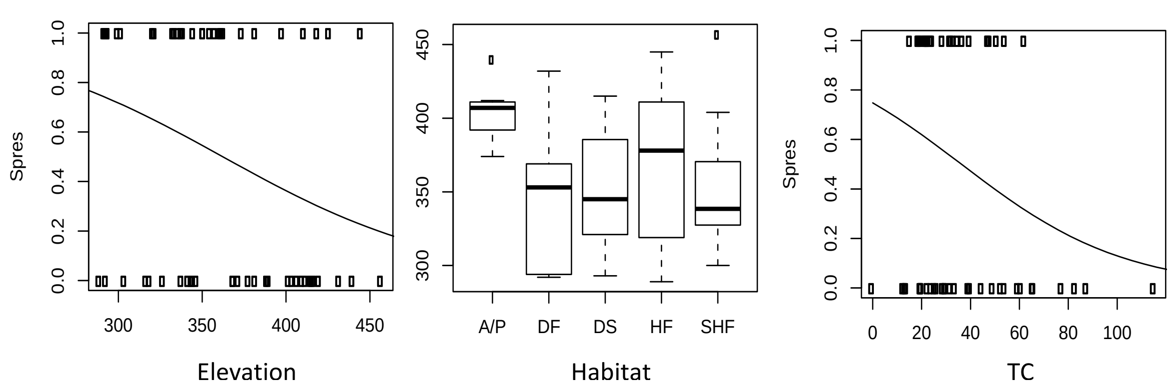


Figure 13. Regression results to local fitted model; **a)** fitted regression line illustrate the relationship between the probability to find solenodon and elevation (std. error=-0.006, t value=-2.37, p<0.01); **b)** elevation frequencies in solenodon occupy habitat (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas); **c)** fitted regression line illustrate the relationship between the probability to find solenodon and tree circumferences (std. error=-0.001, t value=-1.49, p<0.01)

4.2 Landscape scale: national database

4.2.1 Solenodon-occupied habitat characteristics

A total of 221 random points were surveyed in five locations in the Dominican Republic. In this study twenty points were excluded from analysis because of incomplete data in the national database provided**.** A total of 201 random points were therefore investigated.

Seven broad habitat types were assessed over two years: forest (cactus, broadleaf and pine); coast; crop plantations; mangrove, and; savannah. Of these, solenodon populations were present in five habitat categories: broadleaf forest (BLF); pine forest (PF); coast shore; mangrove, and; savannah. The proportion of plots where signs of solenodon were found was 38.3% (77/201); of these 64.9% were sites in BLF (50/77), 31.2% in PF (24/77) and 1.3% were in coastal, mangrove and savannah areas (1/77), respectively (Table 6). Plots exhibiting positive solenodon presence were distributed around the previously mentioned five locations within the Dominican Republic.

Table 5. The five habitats surveyed (dry forest=DF, semi-humid forest=SHF, humid forest=HF, dry scrub=DS, A/P=agriculture/pastures areas to find *S. paradoxus* at the national scale. Environmental variables mean are compared between the different habitat categories.

	Habitat				
	BLF (n=50)	**PF (n=24)**	**Coast (n=1)**	**Mangrove (n=1)**	**Savannah (n=1)**
%	**64.9**	**31.2**	**1.3**	**1.3**	**1.3**
Variable					
Elevation (m)	662.75	938.87	0.00	4.00	1782.00
Vegetation density	0.55	0.44	0.00	0.65	0.34
Rockiness (%)	27.1	32.3	100.0	0.0	0.0
Soil depth (cm)	11.34	11.82	0.00	28.00	28.00
Tree diameter (cm)	31	39	0	23	0

Five environmental variables were examined in each habitat: elevation, vegetation density (VD), 'rockiness' (R%), soil depth and tree circumference (Table 5). Canopy openness and TBA were not considered in the landscape analysis because of the strong correlation between VD and tree circumference .

Habitats used by solenodons across the DR had mean elevations of 819.2m, with the highest altitude in a single plot located in savannah (1,782m) and the lowest in coastal habitat (0.0m). The mean vegetation density was 0.54, with higher indices recorded in mangrove areas (0.65) and lower indices in coastal plots (0.0). Mean 'rockiness' comprised 28.21% in solenodon-occupied areas, varying from 100% in coastal habitats to 0% in mangroves and savannah. The mean soil depth was 11.06cm for all sites surveyed, with the minimum being in coastal sites (0.0cm) and maximum in mangroves and savannah (28cm). Lastly, mean tree circumference corresponded to 35.75cm, with 0 cm recorded at coastal points and 39cm in pine forests (PF).

One clear issue shown in the landscape results related to the extremely high variance added by coastal, mangrove and savannahs plots. Because of this, and the low number of plots within those areas (total n=3), the landscape scale study incorporated in this analysis only includes forest plots (n=74).

4.2.2 Solenodon occupancy: model at the landscape level

A minimal fitted model was constructed to investigate the national distribution of solenodon populations in suitable habitats. Initially, all explanatory variables were incorporated (habitat, elevation, VD, R%, soil depth and tree circumference) and non-significant variables removed (in this case VD and tree circumference).

At the national scale solenodon occurrence was most closely associated with habitat type, soil depth and R%, but was also strongly influenced by elevation. Logistic regression between Spres at the large scale and elevation showed a strong negative correlation (SE=0.0002, t value=-3.51, p<0.0001). Thus, high altitudes were negatively correlated with the probability of finding solenodon present within plots (Fig. 13).

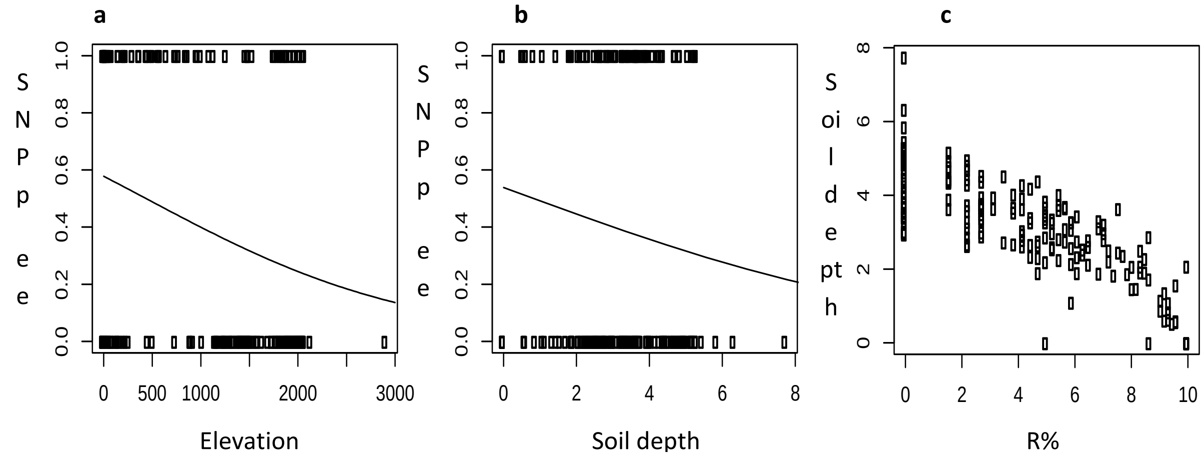


Figure 13. National fitted model regressions; **a)** the fitted regression line illustrate the relationship between the probability to find solenodon nose pokes (SNPp) and elevation; **b)** the fitted regression shows the relationship between the probability to find solenodon nose pokes (SNPp) and soil depth; **c)** correlation between R% and soil depth (values expressed in squared roots) in plots positive to solenodon nose pokes.

Again, several alternative models were run and AICc criteria used to select minimal fixed models for the probability of solenodon presence in five locations in the Dominican Republic. The best-fitted model was constituted by habitat, soil depth and R%:

Landscape model: Spres ~ Habitat + Sq.R. + Sq.S.d

The "Habitat" factor indicates a strong probability of finding the species in broadleaf forest (BLF) rather than in pine forest (PF) (SE=0.3147, z value=-3.722, p<0.0001). Solenodon presence is negatively associated with Sq.R. (squared root of R%) and positively associated with Sq.S.d (squared root of soil depth). These two variables interact negatively (i.e. plots with high percentages of R% will contain low soil depth, see Fig. 13c). Thus, both variables determine suitable environment for solenodons (i.e. regions exhibiting relatively low soil depth and a high 'rockiness' percentage).

Both models, at the local and national scales, showed solenodon occupied habitats were primarily located within forested areas, rather than in any other habitat type.

Unfortunately the criteria applied at the two scales differ in forest type, although the results are strong enough to determine that solenodon occupy forested habitats. Amongst the habitat categories, the local scale dry forest and semi-humid forest were the most used. National-level approximations of the distribution of this species showed that forest across the Dominican Republic (broadleaves and pine, mainly) were the most occupied habitats.

In relation to soil depth and R%, both variables behaved in a similar way within each habitat at the two scales (inversely proportional). Levels of soil depth differ between both scales because of the different environment characteristics in both groups of samples; furthermore their proportions were similar.

Elevation constitutes another important factor to consider in determining suitable habitat for solenodons. The small-scale analysis also included this variable in the best-fitted model, and at both scales it was negatively correlated with species presence. For this reason the probability of finding solenodon appears to be greater at mid to low altitudes.

Other explanatory variables included in solenodon predictive models are related to local habitat conditions (i.e. TC) present specifically in forested areas around Mencía.

5. Discussion

5.1 Solenodon habitat characteristics

5.1.1 Habitat and elevation

The results presented here reflect previous suggestions made by Ottenwalder (1985) that solenodon is more closely associated with older, "undisturbed", forests than any other type of habitat. These results are similar to those of previous work focusing on insectivorous mammal species (Mortellini et al., 2007).

Most forest plots where solenodon signs were detected were between 300m and 700m in elevation (e.g. within a range of 0-2,900m across the country). Although a high altitudinal distribution for the species has been described previously (Ottenwalder, 1985 & 1991), and a national-wide survey noted some solenodon signs above 1,000m, this pattern has not been observed frequently. Most records pertain to zones <1,000m in elevation (Ottenwalder, 1985, 1991 & 2001; Verrill, 1907; Woods, 1976 & 1981). The elevation factor is an important response variable at both scale studies, corresponding with forest distribution in the Dominican Republic. Broadleaf forests are distributed around the country between 0-900m (Tolentino & Peña, 1998). Above these altitudes pine forest are more frequent.

Ottenwalder (1985) described temperature, moisture and particularly soil quality as additional factors that could play a role in limiting use of higher elevations by solenodon. High elevations affect soil characteristics associated with food availability, and microclimate conditions affect survival rates of insect populations (Choi & Kim, 2002) (which are a fundamental part of the diet of solenodon). Several studies have investigated habitat selection by small mammals and their relationship with food availability (Bias & Morrison, 2006; Jackson, 2007; Jackson *et al.*, 2008; Jackson & Robertson, 2011; Merrick *et al.*, 2007). Based on these, feeding sites seem to be one of the most important variables considered in individual habitat choice.

Elevation and habitat were the most important habitat variables retained in modelling the distribution of solenodon and habitat occupancy. Both variables are closely related and depend on one another to provide the specific conditions required by solenodon. Particular environmental variables will be a consequence of the exact location (i.e. elevation) and type of forest.

5.1.2 Rockiness and soil depth

The occurrence of solenodon at a particular site increased with percentage of 'rockiness' and low soil depths, both at the local and national scales. The model at the small scale did not include 'rockiness' as a significant response variable, but the linear regression between this factor and solenodon presence showed a positive significant correlation. One reason for this interaction is related to the Solenodon's denning behaviour. Ottenwalder (1991) determined that Solenodon dens were generally located within coral-limestone rock structures, hollow trees and logs. The results of this study differ as no dens were found in trees. However, 100% of surveyed dens were located in limestone rock systems; which provides an explanation for the positive correlation of *S. paradoxus* presence and 'rockiness' percentage.

Of further interest is the close relationship between invertebrates and leaf litter microclimate (Gonzalez & Herrera, 1983). Invertebrate growth is favoured by specific soil ecosystem conditions (Choi & Kim, 2002) and the physico-chemical characteristics of the soil (Loranger-Merciris *et al.*, 2008) created in the interphase between limestone and the leaf litter (Wallwork, 1976). Coleoptera are the most important group in the diet of the solenodon (Ottenwalder, 1985). Wallwork (1976) investigated relative abundance of Coleoptera in the limestone-litter interface in the Dominican Republic and showed that snails, millipedes and woodlice need calcium carbonate (a principal component of limestone rocks) in high quantities to maintain their exoskeleton. Therefore, rocky areas may be better for solenodon's denning and foraging requirements. Consequently, as 'rockiness' and soil depth are negatively correlated response variables, the probability of solenodon populations' occurrence is higher in areas with shallow soils.

5.1.3 Vegetation density and tree circumference

Indices of vegetation density and tree circumference in forest sites inhabited by solenodon are directly associated with the type of forest surveyed. Tropical forest classification has been a real challenge for forest researches and no true consensus exists. Nonetheless, Whitmore (1998) described six categories of forest formations for worldwide-distributed tropical rainforests, and the Dominican Republic forests were part of the tropical semi-evergreen rainforest group (made up of both evergreen and deciduous trees). This mixture provides a constantly thick leaf litter because of the tree species' non-synchronous leafless periods. Similar leafless characteristics have been defined for broadleaf forest in the Dominican Republic (Torentino & Peña, 1998).

The importance of leaf litter is not just explained in terms of food availability. The requirement for solenodon to have a dry nest inside den caves has been previously described and any litter layer present over the rocks plays an important role in deterring water from draining into den systems (Ottenwalder, 1985). Underground conditions (i.e. temperature, moisture, oxygen and carbon dioxide) are markedly different than outside environments and their effect on subterranean species has been studied (Jackson, 2007; Jackson *et al.*, 2008; Jackson & Robertson, 2011). Endothermic species inhabiting underground conditions need to maintain a relatively constant body temperature (Warnecke & Geiser, 2010) and in this respect, solenodons are no exception. For this reason, dry conditions resulting from litter layer presence are another fundamental component of solenodon habitat.

Tree circumference is an interesting variable to analyse. Similar values were obtained at both study scales; although the variable was only relevant in predicting solenodon presence in the model constructed at the small scale. Presumably this response could be related to the fact that, at the small scale, only solenodon den sites were surveyed rather than random points, as done in the large scale study. As was previously mentioned, all dens were located in rocky areas and these stony systems are not suitable for large rainforest tree growth (Whitmore, 1998). Therefore, solenodon denning is closely related to a high percentage of 'rockiness' and this variable is negatively correlated with large tree growth. On the other hand, plots surveyed in broadleaf forest and pine forest seem to present a more random distribution of tree circumferences in their habitats. Consequently, similar mean tree circumference values were found but their spatial distribution was not grouped.

The main characteristics of habitats used by *S. paradoxus* at the large and small scale are interrelated with solenodon ecology and the species' physiological requirements. Tropical forests are characterized by their high species richness due to the large variety of niches found within them. Thus, high indexes of species endemism and specialization are present in these areas (Whitmore, 1998).

5.2 Solenodon foraging and denning areas: applied use of SNP

The foraging areas used by solenodon only differ slightly in their environmental characteristics from denning plots. Broadly speaking, at the local scale, where denning and foraging zones can be classified, foraging plots were located at higher altitudes, in more opened canopy areas with a smaller percentage of rocks and greater soil depth. These results show that solenodons are selective about their feeding patches, and the species field signs (nose pokes) observed in agricultural areas confirmed this. In 1985, Ottenwalder described, *"feeding tracks of S. paradoxus can be found anywhere the soil and litter layers are deep enough to support soil fauna"* as he found solenodons feeding in depressions between hills, where the soil and litter tended to accumulate.

Ottenwalder's results differed from those of this study at the local scale because higher altitudes were used to forage. This controversial result is mainly associated with the different scales of both projects and the lower mean elevation of the surrounding area of Mencia, compared with the sites used by Ottenwalder. An interesting point is that in both cases solenodons visited a wider area to forage. A good example is the plot mentioned in the result section 4.1.3 where more than 400 nose pokes were found in an agriculture/pasture patch. It has to be considered in this particular case that the random point was located next to a dry forest fragment. Ottenwalder (1991) observed similar behaviours in individuals foraging in crop plantations near to forested areas. It is likely that individuals live in the forest patch, because no den was found in the neighbouring agriculture/pasture plot but there was abundant evidence that they foraged within it.

The presence and abundance of solenodon field signs (i.e. nose pokes) were good indicators of the species presence. In the local study, solenodon nose pokes (SNP) were present in each plot where solenodon dens were located and, after extreme values of solenodon nose pokes abundance were removed, similar proportions were found between the number of SNP and the species occurrence. This is an important constraint when estimating species presence in terms of the number of nose pokes. Logistic regressions between species presence and both response variables (SNP presence and abundance) confirmed this limitation. Solenodon nose pokes (SNP) have been mentioned in previous works as an indicator of species presence (Ottenwalder, 1985; Turvey *et al.*, 2008), but it is the first time that correlations using their abundance has been analysed.

Other studies looking at endangered small mammals (Bias & Morrison 2006; Merrick *et al.* 2007; Jerosch *et al.* 2010) have used indirect clues to indicate species presence (e.g. nest sites, faeces, burrows) and determine habitat occupancy, with accurate results overall. Evidently, detection of occupied habitats by indirect indicators (on this case den sites, SNP presence and abundance) makes data collection and model evaluation easier and quicker than collecting data from trapped individuals in the field. Thus, SNP represents a strong field method of use solenodon surveys.

SNP presence corresponded to solenodon denning and solenodon foraging areas. From this response variable alone it was not possible to distinguish between both zones. In the case that different conservation management would be applied to those areas (e.g. to protect denning areas located in forest patch and increase local population awareness in feeding sites, like agriculture/pasture zones) a different response variable should be use. To counteract this, an index based on SNP could be developed to distinguish between denning and foraging sites. Nevertheless, further research and larger sample sizes will be needed to investigate such an index in the future.

5.3 Human activities and solenodon-occupied areas

Logistic regressions between distance to human settlements (DHS) and solenodon occurrence at the local scale suggested that areas further away from human modified habitats represent more suitable denning and foraging zones for solenodon.

Human wildlife conflict has been one of the greatest problems in conservation (Woodroffe & Ginsberg, 1998; Woodroffe *et al.*, 2005) and the main detrimental issue affecting solenodon populations. Since solenodon was first described its conservation status has been linked to human activities on Hispaniola (Verrill, 1907; Woods, 1976 & 1981; Ottenwalder, 1991; Turvey *et al.*, 2008; Secades, 2010) in terms of habitat loss, human persecution and introduced species (Ottenwalder, 1991; Turvey *et al.*, 2008; Secades, 2010).

The Dominican Republic, Haiti and Jamaica are the countries with the highest deforestations rates (4% forest loss per year) in the Caribbean islands (Brooks *et al.*, 2002) and the Dominican Republic is one of the countries with major indices of growth rate (>400%) over the last 50 years (http://esa.un.org/unup/). In addition, the highest levels of poverty in the Americas (United Nations, 2008), and subsistence agriculture as the principal activity in rural areas (Ottenwalder, 1991), makes the problem even worse.

Because habitat degradation has been increasing, solenodon presence close to human settlements is becoming more common (Secades, 2010). In 1991 Ottenwalder reported solenodons present less than 2km from crop plantations. Secades (2010) concluded that dog predation was the most important source of mortality in solenodon populations, explaining 73% of deaths in the local study area where the research took place.

Previous studies, in addition to our observations of solenodon nose pokes in agriculture/pastoral plots, were surprised by the expansiveness of solenodon territories. The results showed that solenodon avoid human settlements and habitat modified by them and, on the other hand, the species uses human modified areas to forage. These two apparently contradictory results are the consequence of the same phenomenon that reduces the species available habitat, forcing individuals to forage in less optimal sites. Similar responses have been observed in many species, particularly in large carnivores (Mondol *et al*., 2009; Inskip & Zimmermann, 2009), where evident impact to human settlements has been a justification to develop conservation management strategies to reduce human-wildlife conflict. Small mammal populations in similar conservation situations have not been as lucky as big carnivores and they have not been considered as much of a priority by the international conservation community.

5.4 Study strengths and weaknesses

This is the first time that a habitat characterisation study has been developed based on quantitative solenodon presence/absence data. This provides a large advantage when compared to previous studies where individual observations and reports from local people were the main source of data. Because of the accuracy in recording the location and exact type habitat used by the species, cameras traps and radio collars allowed us to gather data on species occurrence, not biased plot were surveyed in relation to the exact habitat used by the species . Camera trap images of solenodon using dens are provided in Appendix 4.

This is also the first study that compares two models at different geographical scales to define and predict environmental variables associated with the presence of solenodon. The method applied is extremely useful, because the small scale study can be made in detail in terms of spatially surveyed areas and these results can then be compared with national results obtained through extensive surveys across the country in a wider range of habitats and environmental conditions. From these two physical scales the same information was obtained in relation to different time scales (e.g. different habitat associations can be made between years where different weather condition affect the surveyed areas). The study in Mencia was very detailed but undertaken over a short period of time, so the results are intrinsically biased to some degree. For example, sampling was not carried out across all seasons. This weakness was decreased when local results were compared with the national database, which was collected over a period of two years.

Despite the considerable effort invested in this project the current local sample size was not large enough to answer some interesting questions, such as the potential value of using SNP abundance in future research. However, in comparison with other studies of endangered species (Jackson & Robertson, 2011; Gibson & Barrett, 2007), 30 dens is an acceptable number from which to draw relevant conclusions through habitat modelling. Also, it has to be considered that the forest habitat classification used in the field could be improved upon, by making it less subjective. At the small scale, only relative observations and local knowledge were used to define them. In order to exemplify differences between humid forest, semi-humid forest and dry forest in the surrounding area of Mencia, pictures are shown in Appendix 2.

Finally, a critical overview of the modelling process needs to be undertaken. The current study of *S. paradoxus* in the Dominican Republic has been developed based upon presence/absence data. Although significant results were obtained and the derived conclusions will serve to improve general knowledge of the species, the limitations of presence/absence data are well known (Gibson & Barrett, 2007; Gisan & Zimmermann, 2000). A common problem in many studies examining species distributions based on presence/absence data is that absence cannot be inferred with certainty (Hirzel *et al.*, 2006) and this constraint increases in rare or cryptic species (Gibson & Barrett, 2007; Jackson & Robertson, 2011). Because of previous reasons, this research as a first attempt to define and quantify the habitats used by solenodon, determined that the effects of the presence-only data on the final results are not relevant, in this particular case, considering the constraint finding the species due to its conservation status.

5.5 Final conclusions and recommendations for future conservation managements

Knowledge of the habitat requirements of endangered species is of fundamental use as a base-line to plan future conservation actions. In this study, the habitat characteristics preferred by *S. paradoxus* were not very different to those suggested by Ottenwalder (1985). However, unlike Ottenwalder's study, this is the first to quantify the habitat associations of *S. paradoxus* using robust data.

Forested areas in mid-low elevations, exhibiting a high percentage of 'rockiness', are still optimal habitats for the species; which suggests that the solenodon has not changed its habitat use for the last twenty-five years. In recent years, conservation efforts in Hispaniola have become more difficult after the earthquake in 2010. Considering that the southwest of the Dominican Republic has sustained solenodon populations for a long time (probably because of the protection afforded by Sierra de Bahoruco and Jaragua National Parks) this area needs to be protected. A buffer zone between the National Parks and the border with Haiti (Jotikapukkana *et al.*, 2010) is urgently needed, and biological corridors connecting both National Parks could represent a potential conservation management to achieve that.

Nevertheless, the social-economic situation at the Dominican Republic-Haiti border has to be considered, including local communities in the conservation programme to decrease the human-wildlife conflict generated in agricultural areas. Additionally, it would be highly advisable to use these results to explore and understand *S. paradoxus* current distribution across Hispaniola and effectively improve sampling time and conservation efforts in unexplored areas of the island, to manage international conservation prioritization.

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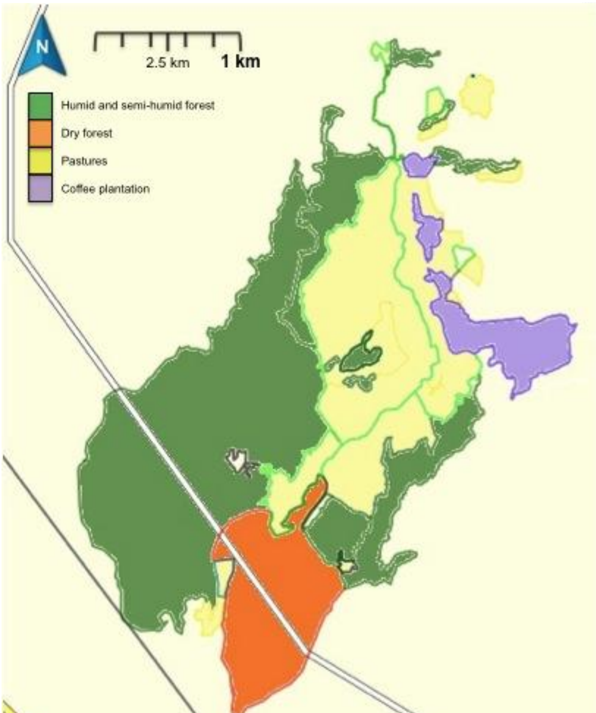
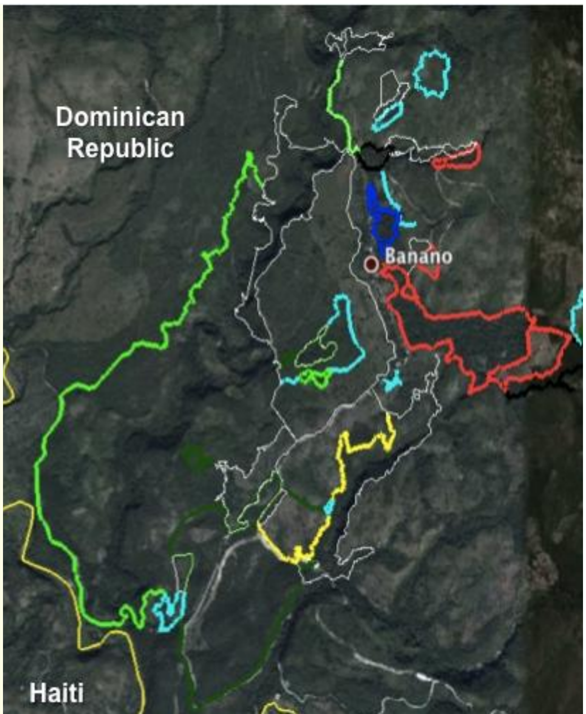
Appendix 1: Mapped area in the buffer zone of Sierra de Bahoruco National Park

Scheme A shows outline of the mapped area in the study site at the local scale. Green zones represent humid and semi-humid forest; orange represent dry forest; yellow represent pastures and violet coffee plantations. Humid and semi-humid forests were tracked within the same colour because of the gradient between both habitats, therefore the difficulties in make a limit between them. **Scheme B** shows the same mapped area in a satellital photograph. **Scheme C** illustrate the distribution of *S. paradoxus* den sites surveyed. **Scheme D** shows the same dens in waypoint in a satellital image. **Scheme E** illustrate the distribution of the 30 random points used in the study. **Scheme F** shows the same random locations in waypoint in a satellital image.

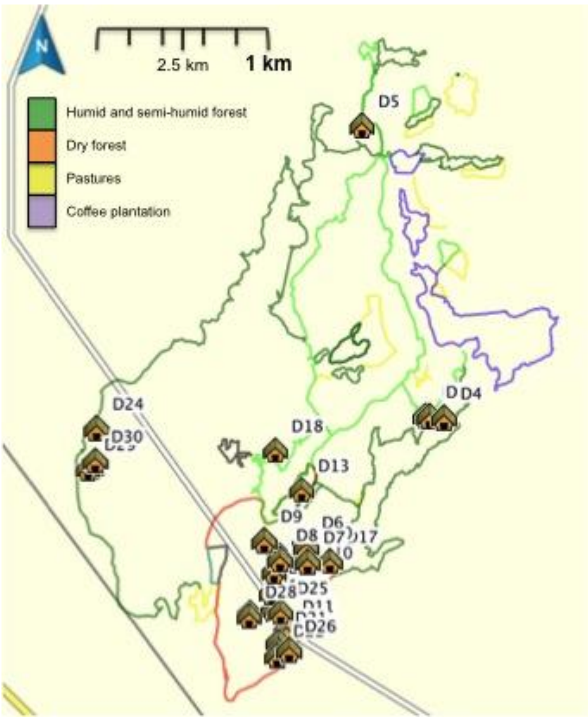
A



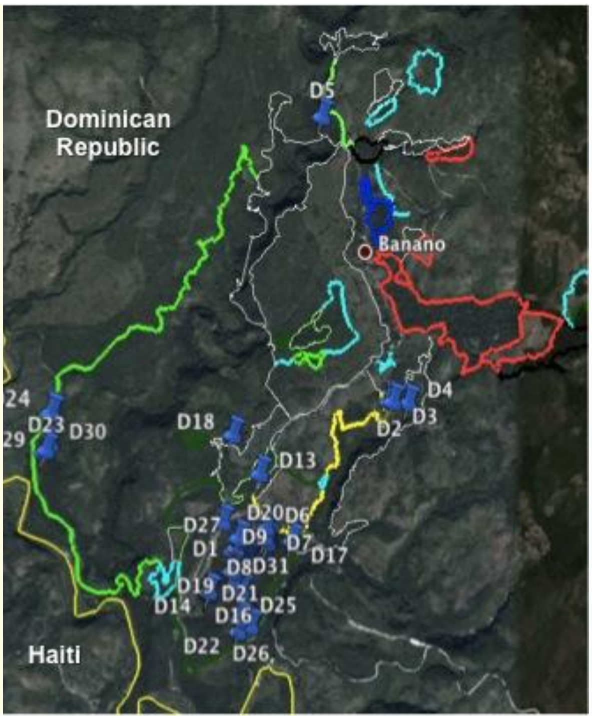
B



C


N
2.5 km
1 km
Humid and semi-humid forest
Dry forest
Pastures
Coffee plantation
D5
D4
D24
D30
D18
D13
D9
D6
D8
D7
D17
D25
D28
D26

D


Dominican Republic
Haiti
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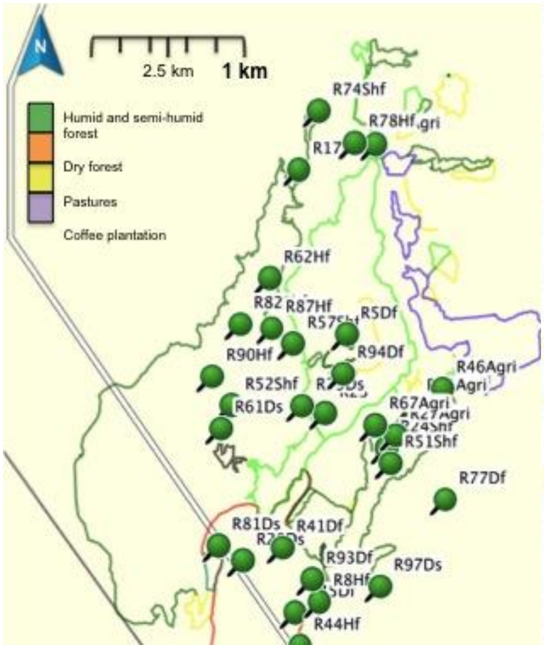
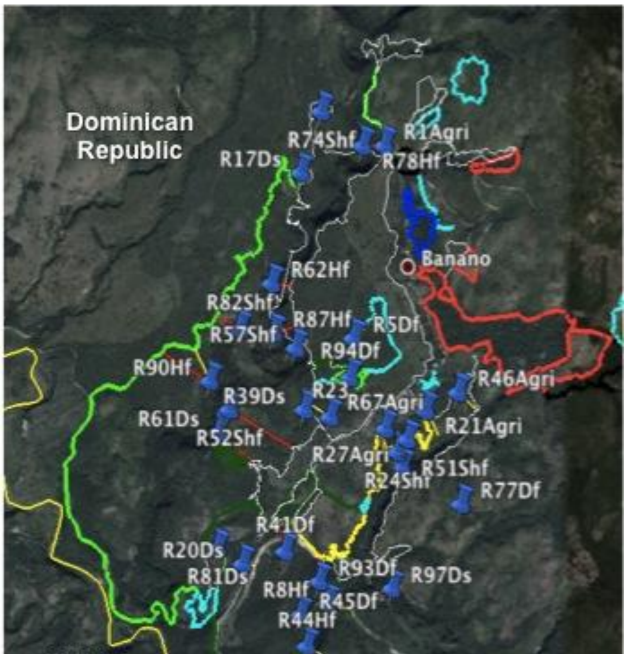
D26

F


N
2.5 km
1 km
Humid and semi-humid forest
Dry forest
Pastures
Coffee plantation
R74Shf
R78Hf
R17
R62Hf
R82
R87Hf
R5Df
R90Hf
R94Df
R52Shf
R61Ds
R46Agri
R67Agri
R51Shf
R77Df
R81Ds
R41Df
R93Df
R8Hf
R97Ds
R44Hf

G


Dominican Republic
Banano
R74Shf
R1Agri
R78Hf
R17Ds
R62Hf
R82Shf
R87Hf
R5Df
R57Shf
R94Df
R90Hf
R39Ds
R23
R67Agri
R46Agri
R61Ds
R52Shf
R21Agri
R27Agri
R24Shf
R51Shf
R77Df
R41Df
R20Ds
R81Ds
R93Df
R97Ds
R8Hf
R45Df
R44Hf

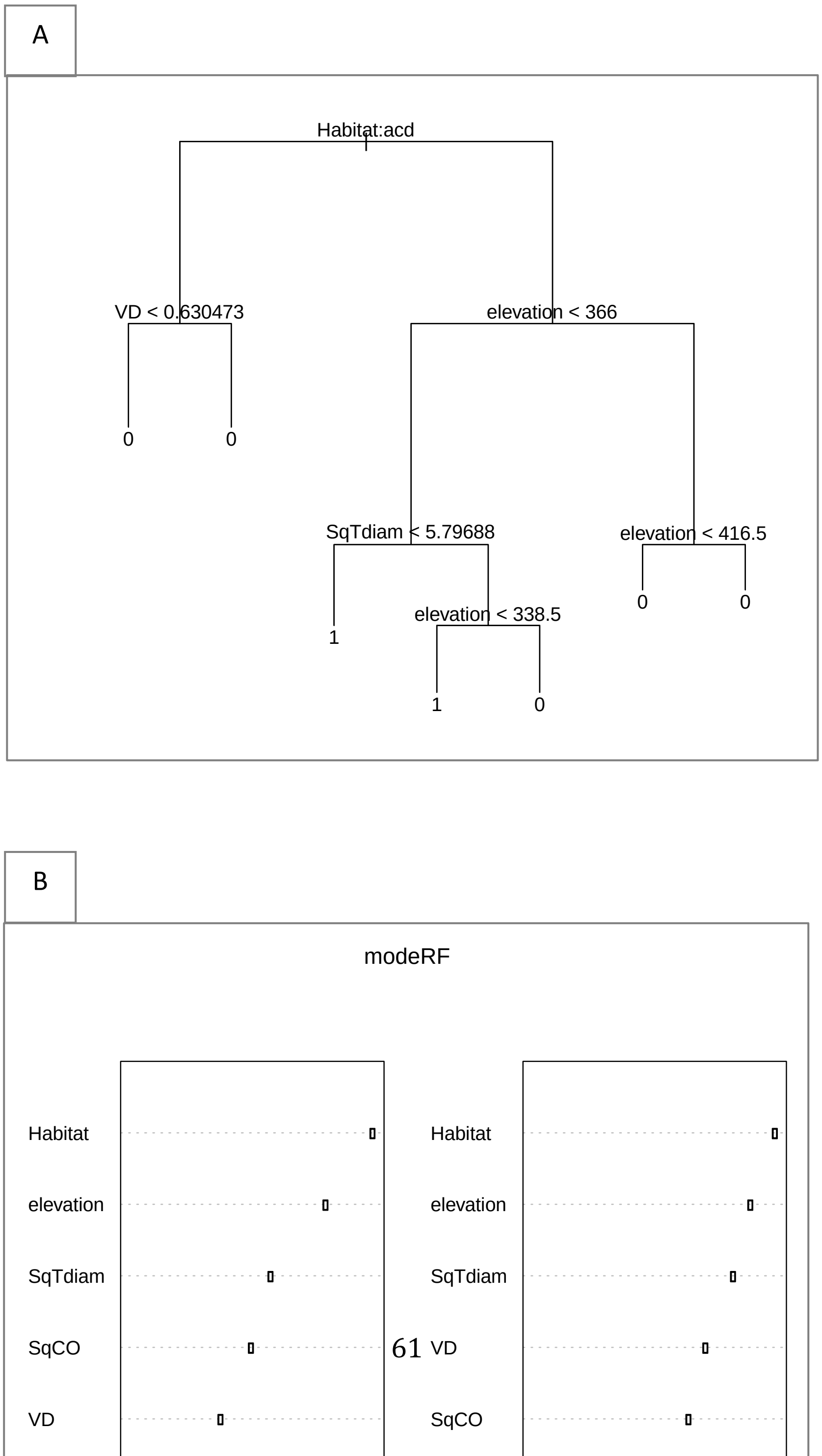
Appendix 2. Forest types in the local study.

Humid Forest: main view and canopy.

Semi-humid Forest: main view and leaf litter.

Dry Forest: main view and den site with camera trap.

Appendix 3. Tree modelling output (A) and random forest analysis result (B).



Appendix 4. Camera traps images.