CENTRO AGRONOMICO TROPICAL DE INVESTIGACION Y ENSEÑANZA

PROGRAMA DE ENSEÑANZA PARA EL DESARROLLO Y LA CONSERVACION

ESCUELA DE POSGRADUADOS

BIRDS, DUNG BEETLES AND TREES IN A FRAGMENTED LANDSCAPE OF CAÑAS, GUANACASTE: RELATIONSHIPS BETWEEN TREE 'COVER AND BIODIVERSITY.

POR

EUGENIO WILBER SABIDO

CATIE

Turrialba, Costa Rica
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Tesis sometida a la consideración de la Escuela de Posgrado, Programa de Educación para el Desarollo y la Conservación del Centro Agronómico Tropical de Investigación y Enseñanza como requisito parcial para optar el grado de:

Magister Scientae

Por

EUGENIO WILBER SABIDO

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2001

Esta tesis ha sido aceptada en su presente forma por el Programa de Educación para el Desarollo y la Conservación y la Escuela de Posgrado del CATIE y aprobada por el Comité Consejero del Estudiante como requisito parcial para optar por el grado de:

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To my Mother,
Norvea and Carissa

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Key words: biodiversity, Cañas, Costa Rica, forests, pastures, silvopastoral systems, tree cover.

Abstract

Agriculture has altered the natural vegetation cover and fragmented the Central American corridor. Central America has roughly 63% of its total land devoted to intensive agriculture or silvicultural activities and at least 38% is covered by pastures. This deforestation has left an elaborate myriad of fragmented forest patches within an agricultural landscape. Despite the apparent potential for forest fragments, isolated trees and other tree resources to conserve at least part of the original biodiversity, few studies have examined the role of tree cover in the conservation of biodiversity within fragmented landscapes.

I examined the relationships between tree cover and biodiversity in the Pacific region of Costa Rica in Cañas, Guanacaste, in a fragmented landscape (approximately 8,865 ha) dominated by pastures, which is typical Pacific cattle region. Using aerial photos, I characterized the tree cover and landuse within the area and identified three habitats; forest patches, pasture with trees (silvopastoral systems) and open pastures (pastures without trees) and chose – replicas of each habitat. I conducted tree inventories and biodiversity surveys on birds, small mammals and dung beetles forests, pastures with trees and open pasture sites; 24 sites total). These groups of organisms represented a gradient of dispersal capabilities from low (dung beetles) to high (birds). To determine the importance of each habitat for biodiversity conservation, I compared the species richness, abundance and diversity of each group (birds, mammals, dung beetles) among habitats. I also examined the influence of tree cover at different spatial scales on the species richness and abundance of these organisms.

The differences in local and landscape tree cover greatly influenced the abundance, species richness and diversity of dung beetles and birds among habitats. Dung beetle species richness and diversity was higher in forest and pastures with trees than in open pastures, whereas pastures with trees had the higher abundances of dung beetles than either forests or open pastures. Bird species richness and abundant was greater in forests and pastures with trees than in open pastures, however there were no differences between bird species richness and abundance between forests and pastures with trees. At the landscape scale, dung beetles showed no response to the surrounding tree cover, while the bird species richness and abundance responded positively to

increased tree cover at increasing landscape scales. These differences suggest that organisms of different dispersal capabilities perceive tree cover at different scales and may therefore be affected differently by the distribution of tree cover in a given landscape.

The study demonstrates the importance of tree cover at both local and landscape scales in determining the abundance, species richness and composition of organisms present. It also shows the importance of forest fragments, remnant trees and silvopastoral systems for the conservation of biodiversity in agricultural landscapes. Pastures with trees in them hold potential to support a substantial number of plant and animal species, although less than that of forests. Finally, this study shows that the conservation value and importance of each habitat differs among organisms since each habitat type and its associated tree cover affects groups of organisms differently.

Sabido, E. W. 2001. Aves, escarabajos estercoleros y árboles en un paisaje fragmentado de Cañas, Guanacaste: relaciones entre cobertura arbórea y biodiversidad.

Palabras clave: biodiversidad, bosques, Cañas, cobertura arbórea, Costa Rica, potreros, sistema silvopastoríl.

Resumen

La agricultura ha alterado la cubierta de vegetación natural y ha fragmentado el corredor centroamericano. Aproximadamente el 63% del total de tierras de América Central está dedicado a actividades intensivas de agricultura o silvicultura y al menos el 38% está cubierto por pastos. Esta deforestación ha dejado un gran número de parches de bosque fragmentados dentro del paisaje agrícola. A pesar del claro potencial de los fragmentos de bosque, árboles aislados y otros recursos arbóreos para conservar al menos una parte de la biodiversidad original, pocos estudios han examinado el papel de la cobertura arbórea en la conservación de biodiversidad dentro de paisajes fragmentados.

Dirigí la investigación en la región del Pacífico de Costa Rica, en Cañas, Guanacaste. El área de estudio donde trabajé, de 8,865 ha aproximadamente, es típica del paisaje en esta región del Pacífico. Mediante el uso de fotos aéreas caractericé la cobertura arbórea y el uso del suelo dentro del área y fue útil para identificar tres hábitat, parches de bosque, pastos con árboles (sistemas silvopastoriles) y pastos abiertos (pastos sin árboles) dentro de parcelas de 100 ha anteriormente establecidas sistemáticamente por toda el área. Realicé un inventario de árboles en sitios dentro del bosque y el pasto con árboles (24 sitios). Estos grupos representaban un gradiente de habilidades de dispersión desde baja movilidad (escarabajos estercoleros) a alta (aves). Para calcular la importancia de cada hábitat para la conservación de la biodiversidad compare la riqueza de especies, abundancia y diversidad para cada grupo (árboles, escarabajos estercoleros, aves) dentro de cada hábitat. Examine el efecto de la cobertura arbórea a diferentes escalas sobre la riqueza de especies y abundancia de estos organismos.

Encontré que la cobertura arbórea influye enormemente la abundancia, riqueza de especies y diversidad de escarabajos estercoleros y aves entre los hábitat. La riqueza de especies de escarabajos estercoleros y su diversidad fueron mas altas en bosques y potreros con árboles que en potreros sin árboles. La riqueza de especies de aves y su abundancia fueron mas altas en bosques y potreros con árboles que en potreros sin árboles, pero no hubieron diferencias entre la

riqueza de especies de aves y su abundancia entre bosques y potreros con árboles. A nivel de paisaje, los escarabajos estercoleros no demostraron ninguna respuesta a la cobertura arbórea, mientras la riqueza de especies de aves y su abundancia mostraron un respuesta positiva a un aumento en cobertura arbórea a nivel de paisaje conforme se aumentaban las escalas de medición. Estas diferencias demuestran que organismos con ciertos grados de movilidad perciben la cobertura arbórea a diferentes escalas y en fin son afectadas diferente de acuerdo a la distribución de la cobertura arbórea a través del paisaje.

Este estudio demuestra la importancia de la cobertura arbórea a nivel local y a nivel de paisaje para determinar la abundancia, riqueza de especies y composición de organismos presentes. También demuestra la importancia de los fragmentos de bosque, árboles remanentes y sistemas silvopastoriles para la conservación de la biodiversidad en el paisaje agrícola. Los potreros con árboles poseen el potencial de sostener una alta población de especies de flora y fauna pero aun menos que el bosque. Finalmente, este estudio demuestra el valor de conservación y la importancia de cada hábitat es distinta para cada organismo ya que cada tipo de hábitat y su cobertura arbórea influyen cada grupo de organismos de diferentes maneras.

1.0 INTRODUCTION

The Central American isthmus emerged about three million years ago, creating a biological corridor connecting the Northern and Southern continents. This isthmus is one of the world's most dynamic and important biological highways and a critical link between the northern and southern biotas of the American continent. It is also home to many endemic species and unique ecosystems with high biological diversity, making it one of the world's most important ecological hot spots. Presently about 70 million hectares of forest exist in Central America which provide habitat to roughly 7 % of the planet's biodiversity (CCAD, 1998).

Agriculture has altered the natural vegetation cover and has fragmented the corridor throughout the Central American region (Saunders *et al.*, 1991). From 1956 to the present, over 15.6 million hectares of natural forest were cleared due to cattle ranching, agriculture and forestry activities (Kaimowitz, 1996). During the same period, pasturelands in Central America have increased from 3.5 million hectares to 9.5 million hectares, and the number of cattle has gone from 4.2 million heads to 9.6 million heads (FAO, 1994). At present, Central America has roughly 63% of its total land devoted to intensive agriculture or silvicultural activities (CCAD, 1998) and at least 38 % of Central America is covered by pastures (FAO, 1994). This deforestation has left an elaborate myriad of fragmented forest patches within an agricultural landscape (Saunders *et al.*, 1991; Dunning *et al.*, 1995).

The reduction and fragmentation of forested areas poses a threat to the biodiversity of the region (Guevara *et al.*, 1998). Deforestation results in the loss of habitat for many plant and animal species, particularly forest specialists (Laurance and Bierregaard, 1997). Ecosystem fragmentation causes large changes in the physical environment (Saunders *et al.*, 1991) and may restrict some species to unfavorable habitat conditions within remnant patches (Ingham and Samways, 1996), especially those that require large tracts of continuous forest. The isolated patches or forest islands are less likely to support some animal populations, especially those species that cannot easily move across the agricultural landscape (Lande, 1988). This lack of dispersal results in the isolation of species in single patches, increasing the probability of extinction within the patch (Dunning *et al.*, 1995). In addition to diminishing the diversity in the area, these modified habitats may be the source for invasive species within forest fragments (Janzen, 1983).

In order to conserve biological diversity within fragmented landscapes, it is important to reestablish the linkages between natural habitats to facilitate animal movement, provide habitat to the remaining species within the region, and develop sustainable land use practices that are compatible with conservation goals. A first step towards developing conservation strategies for fragmented landscapes is to understand the role of forest patches, isolated trees and other remnant natural vegetation as habitats and movement corridors for both plant and animal species.

Numerous studies have suggested the importance of forest fragments, remnant trees and silvopastoral systems for the conservation of biodiversity in agricultural landscapes (Laurence *et al.*, 1997; Harvey and Haber, 1999; Harvey *et al.*, 2000, Estrada *et al.*, 2000). Despite the apparent potential for forest fragments, isolated trees and other tree resources to conserve at least part of the original biodiversity, few studies have examined the role of tree cover in the conservation of biodiversity within fragmented landscapes. The few that have examined the relationships between tree cover and biodiversity have focused on individual elements of the landscape (e.g. windbreaks, forest fragments or isolated trees) rather than landscape tree cover and, often have been conducted at small spatial scales (Harvey and Haber, 1999; Guevara *et al.*, 1998).

Most attempts to relate biodiversity indices with tree cover (abundance, diversity and distribution) have focused on single taxa, making it difficult to generalize these results to other biodiversity groups. However, since organisms differ in their ability to tolerate the agricultural matrix and mobility, it is likely that they will react differently in a fragmented landscape (Daily *et al.*, 2001; Daily, *in press;* Halffter, 1991; Klein, 1989). In order to fully understand the importance of tree cover for the conservation of biodiversity, it is important to characterize tree cover at both local and landscape levels, and to examine the roles of trees in the conservation of a variety of biodiversity groups at multiple scales.

To conserve biodiversity within the fragmented landscapes characteristic of Central America, it will be necessary to use an integrated landscape approach that both addresses the socioeconomic needs of local populations and ensures the conservation of biodiversity within the landscape. This landscape approach requires a clear understanding of the relationships between the abundance, arrangement and distribution of natural habitats in the landscape and the abundance and diversity of different organisms.

In this thesis, I characterized the tree cover within fragmented, pastoral landscapes and examined the relationships between different habitats (representing a gradient of tree cover) and organisms of different dispersal capabilities (birds, small mammals and dung beetles) at different spatial scales. By identifying the contribution of tree cover to biodiversity conservation within fragmented landscapes, this information will contribute to the development of management strategies and guidelines that promote long-term biodiversity conservation within fragmented landscapes.

The investigation also serves as a pilot project for the FRAGMENT project funded by the INCO Grant of the European Union and headed by Celia Harvey[1]. The FRAGMENT project will assess the functional roles of trees in sustaining farm productivity and conserving regional biodiversity within fragmented landscapes, and will seek to develop innovative decision-making tools for the sustainable management of fragmented landscapes in both Costa Rica and Nicaragua. This thesis serves as a pilot study for the FRAGMENT proposal, creating baseline data and serving to validate the proposed landscape characterization and biodiversity assessment methodologies.

[1]Departamento de Agricultura y Agroforesteria, Tropical Agriculture Research and Higher Education Center (CATIE), Turrialba, Costa Rica and is the scientific coordinator of the FRAGMENT project (INCO-DEV Project # ICA4-CT-2201-10099).

1.2 Objectives

1.2.1 General objective

To determine how the tree cover in silvopastoral systems influences the abundance, diversity and distribution of fauna (dung beetles, small mammals, birds) in a fragmented landscape in Cañas, Guanacaste, Costa Rica.

1.2.2 Specific research objectives

To characterize and compare the abundance and diversity of the tree component in a fragmented landscape

To characterize and compare the fauna (dung beetles, small mammals and birds) present in habitats of differing tree cover (forest patches, pastures with trees, open pastures) within a fragmented landscape

To explore relationships between tree cover (abundance and diversity) and biodiversity indicators and determine if organisms of different dispersal capabilities react differently to tree cover in a fragmented landscape

1.3 General hypothesis

The arrangement, density and species richness of tree cover within a fragmented landscape influences the abundance and diversity of animal species (beetles, small mammals, birds)

1.3.1 Specific Hypotheses

Organisms of varying dispersal capabilities will be affected differently by tree cover in fragmented landscapes.

The distribution of organisms of varying dispersal capabilities will be affected by tree cover within varying spatial scales in the landscape.

2.0 REVISION OF LITERATURE

2.1 History of Landuse in Central America

In order to meet growing global and local market demands much of the Central American land mass is increasingly being exploited. Escalating population densities, poverty, improper use of natural resources and land scarcity have intensified pressures and demands upon the remaining natural resources and ecology of the region (Halladay & Gilmour, 1995). New areas for intensive production have increased over the past decades and agricultural and pastoral activities now cover about 63% of Central America's total land area (CCAD, 1998; McNeely, 1995). The integration of conservation and sustainable development is now seen as the best strategy to alleviate the pressures placed upon the remaining natural resources by escalating human demands (Kremen *et al.*, 1994). The development and implementation of improved agricultural systems that maximize crop productivity and conserve and protect the remaining natural resource base is therefore necessary.

In Central America, tropical deforestation associated with the expansion of the agricultural areas was perceived as necessary in order to promote economic growth and modernization (Sader *et al.*, 1991). The rapid conversion of forests to pastures for intensive beef production was favored by an increase in beef prices of more than 30% between 1964 and 1973 (Ibrahim *et al.*, 2000). Deforestation was especially high during the 1980's when forests were cleared at a rate of 439,000 hectares annually to meet increased foreign demand (mostly from the USA) for cheap low-grade beef (Schelhas, 1991). In the 1990's, deforestation in Central America decreased to 320,000 ha annually (1990 – 1994) due to an already depleted forest cover now estimated at 19 million ha and to declining market prices for beef products (Kaimowitz, 1998).

Cattle ranching and livestock are often considered major contributors to environmental degradation and destabilizing factors in landuse (Ibrahim *et al.*, 2000). It has been estimated that greater than 70% of established pastures in Central America are in an advanced state of degradation (Ibrahim, 1994). This can be attributed to the mismanagement of livestock and the use of unimproved pasture systems that are both inefficient and unsustainable (Ibrahim *et al.*, 2000).

In Central America, cattle ranching, agriculture and forestry activities threaten the existence of plant and animal species through the conversion of natural landscapes into mosaics of pastures, agricultural fields and forest fragments (Harvey *et al.*, 2000). The loss of forest cover is alarming; however there is a tendency towards less deforestation and the recuperation of degraded areas (Pomareda & Steinfeld, 2000; Ibrahim *et al.* 2000).

2.2 History of Landuse in Costa Rica

In Costa Rica, the conversion of forests to pastures has been driven by several factors. These include a large land base (pastures covered only 630,000 ha or about 35% of its farmlands in the 1950's), a Creole cattle stock, local knowledge about cattle raising and the high yielding African jaragua grass (*Hyparhenia ruffa*) (Hall *et al.*, 2000). In addition, there were credit programs for purchasing cattle, promoted by the government and funded by international development banks, and a high demand for beef products in North America (Hall *et al. 2000*; Leeuwen and Hofstede, 1995; Sanchez-Azofeifa, 2000). Furthermore, cattle ranching was seen as a status symbol, providing economic security to small landowners (Ibrahim *et al.* 2000) further giving stimulus for the clearing of forests for cattle production. These factors coupled with the fact that cattle rearing did not require much labor or expensive imported materials and could be implemented in a variety of climatic and edaphic conditions contributed to high rates of deforestation in Costa Rica.

In Costa Rica, deforestation rates were highest during the 1970's and 1980's when internationally funded credit programs were prevalent (Ibrahim *et al.*, 2000). The undisturbed forested areas were reduced from 3,420,000 ha in 1940 to 870,000 ha in 1983 or from 67% to 17% of the national area (Hall *et al.*, 2000). During the period from 1986/1987 to 1996/1997, deforestation occurred at a rate of 16,424 ha annually (Alfaro and Reiche, 1997). A survey in 1994 indicated that the areas under pasture and cattle population now cover 45.8% of the total land area (FAO, 2000). Pastures are primarily being abandoned due to soil degradation in addition to low market prices (Pomareda & Steinfeld, 2000). They eventually become brushy, wooded areas and may even develop into secondary forest (Ibrahim *et al.*, 2000). However, an increase in world meat prices would provide enough incentive for these areas to be cleared immediately (Morales, 2000).

2.3 Cattle production systems in Costa Rica

Traditionally, cattle farmers in Costa Rica retained little tree cover on their farms. Costa Rican cattle farmers inherited methods of forest clearing and management of pastures from the early Spanish colonizers whose traditional way of preparing land involved complete removal of all existing vegetation (Leeuwen and Hofstede, 1995; Ibrahim *et al.*, *2000*). Except for the precious and hard timber tree species, forests did not have much value for farmers; instead they were seen as obstacles for development (Leeuwen and Hofstede, 1995). Consequently, many farmers left few trees standing when clearing forests for pastures.

Today, however, there is an increasing tendency for cattle farmers to recognize the multiple economic and ecological benefits derived from trees and forest patches and farmers are increasingly leaving some tree cover on their farms (Harvey and Haber, 1999; Leeuwen and Hofstede, 1995). These trees can be an important source of income for farmers and in Costa Rica trees are common within the agricultural landscape. A high percentage of timber trees come from pastures and it is foreseen that the majority of timber may be extracted from pastures in the future (Ibrahim *et al.*, 2000). The integration of trees within pastures has served to diversify cattle production areas and is a practice being increasingly adopted by cattle farmers (Pezo and Ibrahim, 1996), however, the acceptance and adoption of technologies by farmers depends on prices of timber products and the incentives paid for the environmental services they provide (Ibrahim *et al.*, 2000).

The farmer's attitude towards tree cover influences the choice of existing land practices and the impact of development and improvement of these systems on the farm (Leeuwen and Hofstede, 1995; Harvey and Haber, 1999). In order to change perceptions of farmers and have them integrate conservation and development, production systems must be sustainable and economically viable, additionally; alternative sustainable uses for forest resources must be found (Hall *et al.*, 2000; Ibrahim *et al.*, 2000). In the end, the level of deforestation and degree to which relict trees are left in the landscape will be determined by the value that tree cover represents to the farmer.

2.4 Tree cover within cattle farms in Costa Rica

Most farming systems in Costa Rica include some form of agroforestry practice that contributes partially to the economic stability of the farms and to the conservation of biodiversity (Ibrahim *et al.*, 2000). Silvopastoral systems (systems in which there are close interactions between several perennial woody species, pasture and livestock) are present in most farms as live fences or isolated trees (Ibrahim *et al.*, 2000; Pezo and Ibrahim, 1996) In cattle farms, live fences (trees planted in lines to delimit pastures or properties) are the most common forms of silvopastoral systems (Souza *et al.*, 2000). Live fences serve as multipurpose trees by holding barbed wire, providing fodder and shade to cattle (Souza *et al.*, 2000; Budowski, 1993; Paap, 1993; Sauer, 1978; Harvey, 2000). Farmers may also utilize the fruits, firewood and lumber produced by trees for household use (Guevara *et al.*, 1992; Budowski, 1993; Harvey and Haber, 1999). These trees may also serve as windbreaks that protect the animals and farm from wind damage; in addition the trees in pastures play an important conservation role (Guevara *et al.*, 1986). In general, farmers understand the role trees play within the production systems (Harvey and Haber, 1999; Stokes, 2001), and like having trees within their farms as long as the trees do not affect production negatively (Paap, 1993; Stokes, 2001).

Farmers are now more aware of the ecological and economic value of trees within pastures (Ibrahim *et al.*, 2000) and the density of valuable timber trees has increased in pastures in recent years, due mostly to natural regeneration and little or no silvicultural treatments (Souza *et al.*, 2000). Farmers often leave trees for wind protection, watershed protection, timber, firewood and fence posts, wildlife protection, and for aesthetic reasons (Harvey and Haber, 1999). In addition to aiding in the conservation of biodiversity and providing a social service, these landscape elements also fix carbon dioxide, conserve soils, and protect cattle from wind and rain (Harvey and Haber, 1999; Pezo and Ibrahim, 1996; Torres, 1987).

2.5 Importance of tree cover for biodiversity conservation

It is well established that the presence of tree cover can help conserve biodiversity in a fragmented landscape (Guevara *et al.*, 1998; Estrada *et al.*, 2000). Forest fragments serve as habitats and resources for a variety of plant and animal species (Guevara *et al.*, 1998; Estrada *et al.*, 2000). Similarly, isolated trees, windbreaks and livefences within pastures and agricultural areas provide perching, nesting and roosting sites for migratory and resident birds, as well as foci for seed dispersal and plant recruitment (Guevara *et al.*, 1998; Harvey, 2000). The presence of forest fragments and remnant trees may also enhance the connectivity of the landscape and may provide stepping-stones or corridors that facilitate animal movement (Guevara *et al.*, 1998; Debinsky & Holt, 2000). Artificially managed arrangements of trees such as live fences and windbreaks in silvopastoral systems may also provide habitats or perform as corridors, or travel lanes (Johnson, 1991; Fritz, 1993; Estrada *et al.*, 2000).

Numerous studies have emphasized the potential of silvopastoral systems in promoting the conservation of biodiversity. For example, in Monteverde, Costa Rica, 190 species of trees were found in pastures, and of these about 94 % provided fruits to birds, bats, and other animals (Harvey and Haber, 1999). Birds normally deposit ingested fruit seeds under their perches and roosting sites. Due to favorable microclimatic conditions (i.e. low light, high humidity) underneath tree canopies, a variety of tree species may germinate and establish under remnant trees in pastures (Guevara *et al.*, 1998; Harvey and Haber, 1999). Trees have been shown to serve as foci for the dissemination of seeds by birds within pastures, thus promoting natural regeneration (Harvey, 2000), and provide habitats and resources for birds and other animals (Guevara *et al.*, 1986; Guevara *et al.*, 1992; Guevara and Laborde, 1993).

Remnant trees, hedges or livefences may also serve as stopping points for fauna across the landscape or as travel lanes to move from point to another (Dix, 1991; Harvey, 1999; Estrada *et al.*, 2000). However, the distance and degree of isolation between individual trees (or tree patches) are important in determining movement across the landscape (Dunning *et al.*, 1995). It is important to consider whether agroforestry systems such as live fences and isolated trees are important to biodiversity even if pasture or large-scale agricultural systems surround them.

2.6 Biodiversity

It is difficult to aptly describe biodiversity; a simple, comprehensive and fully operational definition is unlikely to be found (Noss, 1990). Biological diversity, or biodiversity as it is commonly referred, is the key to the maintenance of the world, as we know it (Wilson 1992; Wilson, 1988) and "the control of biological diversity is not just a central problem to evolutionary biology; it is one of the key problems to science as a whole..." (Wilson, 1988). The Convention on Biological Diversity (1992) describes biodiversity as "the variability among living organisms from all sources including *interalia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems". Biodiversity is further defined as the composition of natural variation found in genes, species and communities and ecosystems (Wilson 1988).

Biodiversity is determined and constituted by three primary attributes: structure, function and composition (Noss 1990). Each attribute plays a role at various hierarchical levels of organization, namely regional-landscape, community-ecosystem, population-species and genetic. Each is dependent on and interconnected to each other such that a change in one causes an effect in another. According to Noss (1990) composition identifies and describes the variety of species and genetic diversity in a collection; structure gives the physical organization or pattern of a system ranging from habitats to landscapes; and function relates to ecological and evolutionary processes such as gene flow, disturbances and nutrient cycling. Due to the interrelationships that occur between attributes, biodiversity monitoring should not be limited only to one level but should be performed at various levels (Noss 1990).

2.6.1 Biological Monitoring

Biological monitoring uses the response of sensitive species called *indicators* to assess changes in the environment (Noss, 1990). Several criteria are applied in the selection of appropriate indicators for monitoring ecosystem changes and the biodiversity. For instance, the species richness within a particular community (or ecosystem) may be used as an indicator of other biodiversity values (i.e. ecological diversity). Indicators are used to quantify and simplify information on the significance and value of the species (or ecosystems) under investigation.

2.6.2 Biological Indicators

Biodiversity indicators are monitoring tools used primarily to measure changes across time and space, to indicate the overall status and trends of biodiversity components (i.e., genes, species and ecosystems; Convention on Biological Diversity, 1992) and to identify biodiversity threats. Indicator species show the overall state of what is being monitored (Kelly & Harwell, 1990) and are used because their presence reflects that of other species in the community. They may also reflect chemical and/or physical changes in the environment (Landres *et al.*, 1988; Noss, 1990).

2.6.2.1. Criteria for Selection of Indicators

Relying on single species indicators is inadequate since no single indicator possesses all of the desirable characteristics. Instead, effective monitoring requires that a series of complementary indicators be used (Kelly & Harwell, 1990; Noss, 1990). It is impossible to describe the general status of ecosystems using only a few components and processes; therefore it is necessary to use several types of available information at multiple levels of organization and multiple spatial and temporal scales (Noss, 1990). To accurately assess biodiversity, the most reasonable approach is to use a suite of measures, each of which is an indicator of a particular aspect of an ecosystem (Kelly & Harwell, 1990).

The selection of indicators is important to ensure that the indicators are valid, reliable and easily monitored. According to Noss (1990) and Kelly & Harwell (1990), indicators should be cost effective, easy to collect and measure, present in different conditions, sensitive to changes within the ecosystem, independent of sample size and economical to implement and monitor over time.

2.7 Indicators used in the investigation

In this study, three known biodiversity indicators (dung beetles, birds and small mammals) were used to examine the relationships between farm scale, tree cover and biodiversity. These three groups represent a gradient of dispersal capabilities from low mobility (dung beetles) to high mobility (birds).

2.7.1 Dung beetles

Dung beetles (Coleoptera: Scarabaeidae: Aphodiinae, Scarabaeinae and some Geotrupinae) appear to have excellent potential as an indicator taxon. They can be easily sampled and identified (using taxonomic keys), respond well to habitat modification and play important roles in nutrient cycling and seed dispersal. They also reduce populations of pestiferous flies and gastrointestinal parasites associated with cattle, and may be a major source of food for birds and small mammals (Mathews, 1984; Klein, 1989; Halffter, 1991). Dung beetle base their diet on the consumption of mammalian dung; consequently, the biomass of the dung beetle community should also correlate with mammalian biomass and productivity (Spector and Forsyth, 1998).

Pitfall traps or pit traps can be used to inventory dung beetle diversity within each habitat-patch type. Any variety of pitfall traps may be constructed and used. Containers such as jars, cans or cups sunk into the ground with the lip of the container level with the surface of the soil are the most common type. Cattle dung, horse or pig manure and human excrement is placed on the cup to attract the dung beetles. As the dung beetles arrive at the dung, they fall into the cup and cannot escape.

2.7.2 Birds

Birds are one of the best and most commonly used monitors of habitat modification (Wilson, 1991). Conservation biologists and ornithologists have used changes in bird populations and communities and changes in bird behavior and reproductive ability to 1) examine the long-term affects of habitat fragmentation and introduced species, 2) monitor water quality, 3) indicate the health of marine fishery stocks, and 4) identify environmental pollutants. Birds are easy to study, identify and detect, and they return to traditional breeding sites yearly. Because they have been studied extensively, changes in their populations and communities, behavior and reproductive success can easily be detected (Wilson, 1991; National Audubon Society, 1999).

Birds may be monitored through various techniques done separately or in combination. These bird census techniques include point counts which combine visual identification and bird-call identification, mist netting which is a capture and release method and nest counts which is conducted during breeding season.

2.7.3 Small mammals

Small mammals may also be used as indicators of habitat diversity. They affect the faunal and floral community structure directly and indirectly through mechanisms such as seed dispersal, vegetation alteration, seed predation and burrowing (Pendleton, 1984). Small mammals are generally monitored through capture and release methods, the most common of which are setting traps baited with food The trap sizes and arrangement may vary depending on mammal size and population density.

3.0 METHODOLOGY

3.1 Bio-physical description of the study area

The study was conducted approximately 12 kilometers south of the Canton of Cañas in the Guanacaste Province, Costa Rica (Figure 1) in the vicinity of Lajas (El Coco) and Gotera (Rio Lajas watershed) and Higuerón (Río Higuerón watershed). The study area is located on the Abangares (3146 I) and Cañas (3147 II) cartographic maps at the following coordinates, N-413965, E-25061393 (lower left corner) and N-422459.07, E-260059.63 (upper right corner) (Figure 2)[2]. Within the study area, the elevation ranges from 100 to 250 meters above sea level (Morales, 1999). The area was chosen by the Tree Resources Outside Forests (TROF) project and encompasses approximately 87 km^2 (8,788 ha). The study area is typical of the fragmented landscapes within the drier areas of the Pacific lowlands of Costa Rica that are devoted mainly to cattle ranching and sugar cane production.

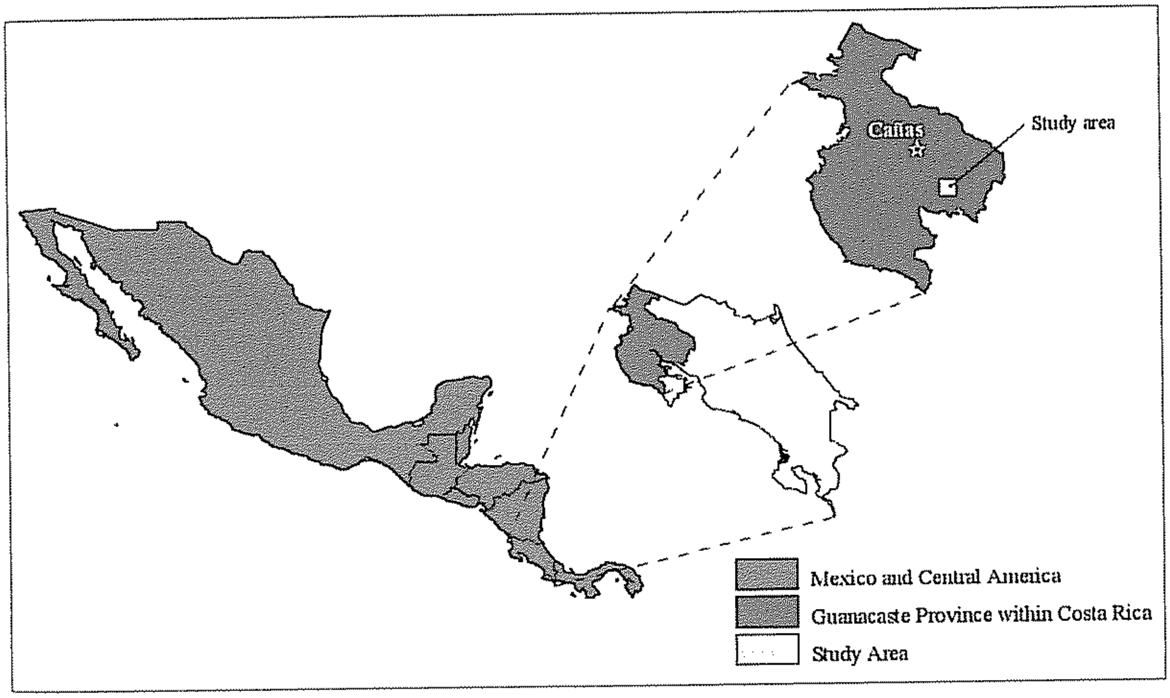


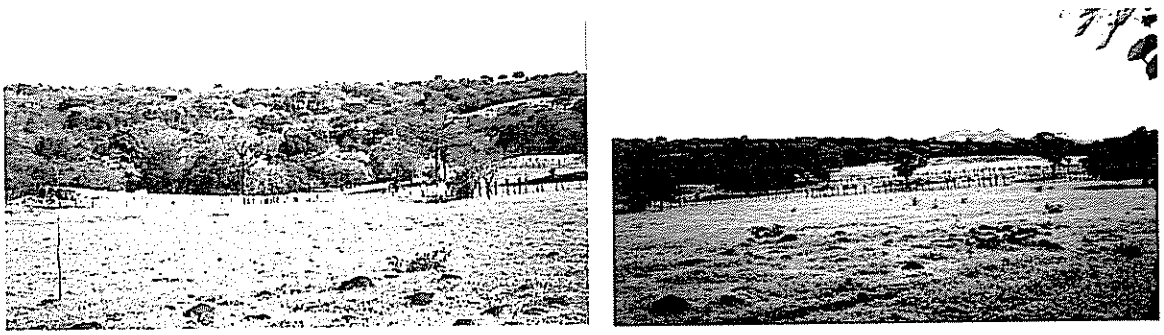
Figure 1. Location of the study area in Cañas, Guanacaste

[2] The coordinate system parameters used were Lambert Projection, Clarke 1866 Spheriod and NAD27 Datum.

Figure 2. Aerial photograph of the study area (8,755.5 ha) within Cañas, Guanacaste.

The area is classified as a Tropical Dry forest (Holdridge, 1967). The climate is characterized by abundant sunshine, large fluctuations in temperature, low relative humidity (mean evaporation rate of 238 cm per year), and extremely variable precipitation that last from May to November. The average maximum temperature is 32°C during the summer months and the average maximum is 23°C during the winter months (December and January). The effective growing season, with favorable precipitation and temperatures, is generally July through September. The mean annual rainfall at this time varies from approximately 1000 to 2500 mm per year (Ingenio Taboga, 2001).

The hotter temperatures occur during the dry season at which time at least 80 percent of the trees lose their leaves and stand leafless for three to five months (Janzen, 1988b). The Guanacaste area is extremely windy from December to April (Ingenio Taboga, 2001). The differences between the rainy and dry season months are very apparent (Figure 3). During the dry season, the vegetation is extremely dry and straw colored throughout the entire landscape especially within the pasture areas (Figure 3a). As the first rains start the vegetation begins to green and a lush green covers the landscape as the season advances (Figure 3b).



(a) Dry season (taken in February) (b) Rainy season (taken in June)

Figure 3. Photographs of study area at different times during the investigation

The study was conducted from February to July 2000 during the dry season. During the five-month study, 540 mm of rainfall were recorded (Ingenio Taboga, 2001) and the rains were mostly intermittent. The first rains were heavy downpours accompanied by thunder and lightning.

3.2 Physical description of field sites

There are roughly 100 cattle farms within the 8,788 ha study area dedicated mostly to beef production. All the farms (10) visited are held by private owners and managed by a local administrator. Although the owners make all the administrative and operative decisions, the administrator generally does the maintenance of the farm and livestock. Farm size within the study area ranges from 8 ha to >1000 ha (Stokes, 2001; farmers, pers. comm.), however there are some farms in excess of 2000 ha. In the larger farms (>1000 ha), cattle production is coupled with other agricultural practices such as sugarcane, watermelon and/or corn production and in some cases forestry plantations of *Gmelina arborea*. Extraction of several tree species dispersed throughout farms, such as Mahogany (*Swietenia macrophylla*), Cedar (*Cedrela odorata*) and Laurel (*Cordia alliodora*) for timber and Guácimo (*Guazuma ulmifolia*) for fence posts is common (pers. observation).

An African introduced grass, Jaragua (*Hyparrhenia rufa*) is common in most pastures, although those farms that have dual-purpose production have introduced high yielding varieties of *Brachiaria*. All farms have some type of live fences comprised of one or a combination of species like "pochote" (*Bombacopsis quinata*), "indio desnudo" (*Bursera simarouba*), "jocote" (*Spondias purpurea*) or "tempate" (*Jatropha curcas*) planted in single rows to hold barbed wire. These live fences delimit the farm boundaries and enclose cattle.

The majority of the farms utilize Brahman cattle stock because of their high meat yield and tolerance of the hot, drier climates. Creole and Semental cattle also occur but less frequently, and are usually mixed with herds of Brahman cattle. Most cattle farmers within the study area belong to the local cattle-owners association (Asociación Ganadera de Cañas) whose members can buy and sell cattle in auction sales at preferential rates. All transactions pertaining to cattle are done at the auction, however cattle may also be sold onsite at the farms.

The Guanacaste Area is predominantly a cattle raising area dedicated mostly to meat and some milk production, however forest fragments, riparian forests and abundant tree cover still remain within most farms. Those farms that have rivers and streams running through them have a buffer zone of riparian forest on either side of these water bodies as dictated by Costa Rican law (Zeledón, 1992). Although there is no local organization within the study area that overlooks the conservation of tree resources within the area, some farm owners with areas larger than 25 ha have allocated a certain portion of their land for forest regeneration (pers. obs).

Riparian forests and naturally regenerated areas are important to the cattle owners especially at the end of the dry season when the pastures are extremely dry. Farmers usually allow the cattle to wander inside these areas to forage on the younger saplings and other palatable species and to escape from the sun. The cattle are introduced to these areas in extreme conditions such as long, dry summers and when the pastures do not provide enough nutrients for the cattle. However, the cattle are left there only for short periods of about a week (pers. comm.).

3.3 Characterization of tree components at the landscape and local level

3.3.1 Background

The research was based on a Randomized Complete Block design (Steel *et. al.*, 1997) and on a randomized sampling scheme. The research was comprised of two phases: the landscape characterization, and the biodiversity survey. The first phase consisted of the characterization of the tree cover in the study area through the interpretation of aerial photographs and the selection of field sites for biodiversity inventories. The second phase consisted of biodiversity surveys (of birds, small mammals and dung beetles) and tree inventories within the plots established for that purpose.

3.3.2 Phase I: Landscape characterization

In order to assess the tree cover within the landscape, I used an aerial photograph taken on December 22, 1997 which I obtained through the TROF project. The photograph was georeferenced[3] but not orthorectified[4], thus some distortions might have been present at the time of interpretation. However, due to the size of the study area and scale used, these distortions are acceptable. In future studies however, it would be a good idea to delimit the areas using a stereoscope. Although the photograph was taken in 1997 few modifications have taken place at both the landscape and local levels (personal observations).

In order to interpret the aerial photograph I used ESRI's (Environmental Systems Research Institute) ArcView 3.1 whose editing features permit the creation and manipulation of spatial

[3] Georeferencing is the process of assigning (or correcting) a coordinate system for your data

[4] This is a process performed to rectify or remove errors in digitized (scanned) photos. The displacement of points is caused by tilt, relief and central projection (perspective) of the camera.

features known as coverages or layers[5]. I prepared some coverages using ESRI's PC Arc/Info 3.5.1 (which offers the same type of creation and manipulation as ArcView, but with less functionality and interface) when ArcView's tools were insufficient or lacking. I used both shapefiles (ArcView coverages) and PC Arc/Info vector coverages depending on necessity. I characterized the photo on the basis of tree cover and landuse, following the methods employed by the TROF project (Morales, pers. comm.).

3.3.3 Stratification of the 10,000 ha landscape using visual interpretation

3.3.3.1 Characterization of tree cover within study area

In order to calculate the percentage of vegetation cover of the entire study area, I overlaid a 1 km x 1 km grid (100 ha plots) on the entire 10,000 ha study area. Within each 100 ha, I systematically arranged 100 points. I then printed each 100 ha plot with the grid overlain and recorded the number of times points fell on vegetation within the 1 km^2 square for each of the 100, 100 ha plots. This allowed me to calculate the percentage of tree cover for each plot and consequently the entire study area.

3.3.3.2 Identification of landuse types

In order to create a coverage of the landuse types, I digitized the aerial photographs online in ArcView. Online digitizing entails tracing the outlines of the areas of interest while having the image onscreen on the computer. I delineated polygons representing homogeneous vegetation areas and distinguished between polygons based on differences in composition and texture and prior knowledge of the areas. The selected minimum mapping unit was 0.2 hectares, though I was sometimes able to discern and delineate even smaller areas.

I decided to digitize through visual interpretation because of the clarity of the photograph and the availability of on-ground information of the landscape composition collected by the TROF project. Although I would have liked to have done stereoscopy with the aerial photograph, the photo stereo-pairs of the study area were unavailable at the time. Since the relief of the study area is not strong (elevation varies between 0 and 150 m), it is unlikely that significant errors were introduced by this method.

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[5] Coverages or layers within PC Arc/Info and ArcView contain spatial information linked to a database which contains the feature attributes. The file structure differs in both software, and is interchangeable from PC Arc/Info to ArcView but need conversion for use from ArcView to PC Arc/Info.

Through the online digitizing process, I was able to stratify the 10,000 ha study area into four landuse types: *pastures without trees*, *pastures with trees*, *forest/secondary growth* and *agricultural areas*. I classified the landuse types depending on tree cover. I called areas totally devoid of trees and devoted to cattle rearing '*open pastures*', areas with trees and devoted to cattle rearing '*pastures with trees*' and forest patches composed of mostly secondary vegetation '*forest/secondary growth*' (Figure 4a). I also identified agricultural areas that were comprised of sugar cane and rice production areas; however I did not conduct any biodiversity inventories within these sites.

3.3.4 Selection of study sites (experimental blocks)

I randomly selected eight 100 ha plots (blocks) and used these as the experimental blocks for the biodiversity inventories. Four of these blocks were characterized by high tree cover; the other four were characterized by medium tree cover. I did not choose the 100 ha plots with low tree cover as these were generally agriculture and usually lacked the three landuse types (open pastures, pastures with trees,) necessary for biodiversity monitoring (Figure 4a).

3.3.5 Placement of the habitat-patch plots (treatments)

I positioned 3 habitat-patch types (open pastures, pastures with trees, forest/secondary growth) within each of the eight 100 ha blocks (for a total of 24 habitat-patches). Because the natural structure of the landscape features varied greatly and did not allow for arbitrary positioning of the habitat plots, I placed the habitat-patch plots manually and subjectively within each landuse type (Figure 4b).

Using a GPS (Global Positioning System), compass and a hardcopy aerial photograph of the study area, I located and marked the center of each habitat-patch in the field. I was then able to use the center within each habitat-patch as the starting point to install the traps and nets to conduct the biodiversity inventories on tree diversity and fauna (dung beetles, birds and small mammals)

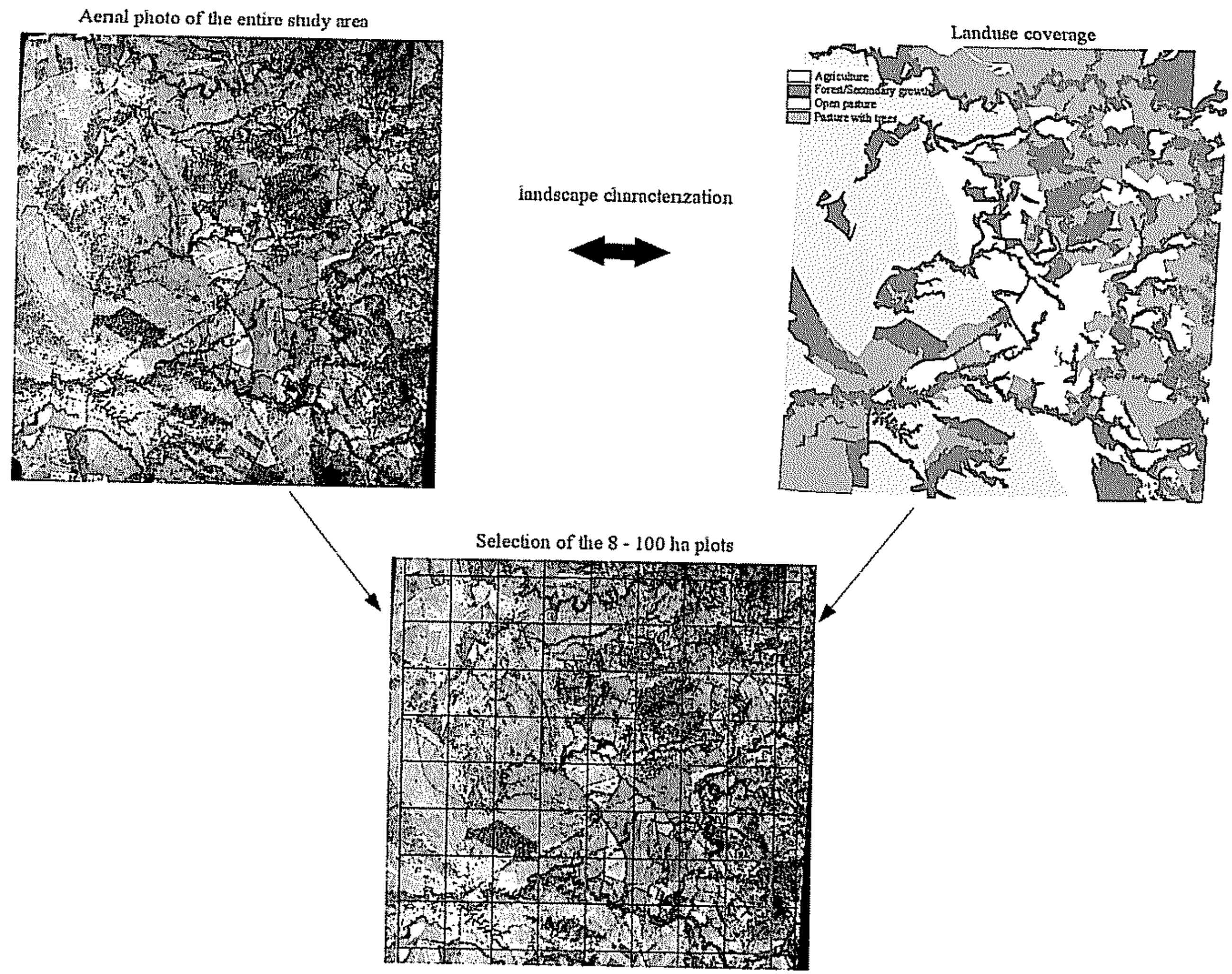

Figure 4a. Placement of the 8-100 ha plots after the characterization of tree cover and landuse.

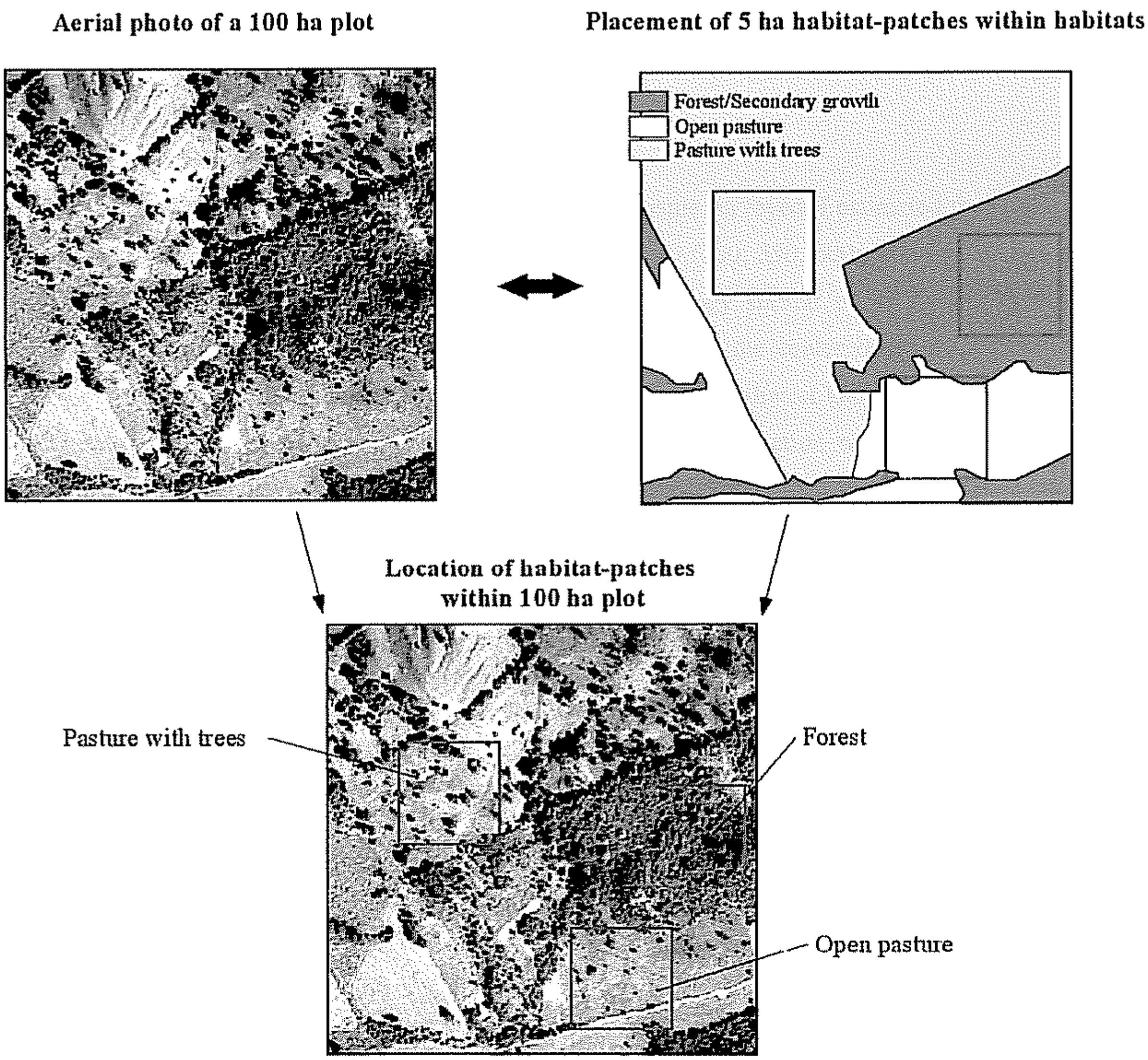

Figure 4b. Placement of the 5 ha habitat-patches within each habitat type (open pastures, pastures with trees, forest/secondary growth) at the 100 ha level.

3.4 Phase II: Biodiversity assessment

I randomly chose the order in which the eight 100 ha sites and the three habitat-patches within them were sampled. The three habitat-patches (open pastures, pastures with trees, forest/secondary growth) within a single 100 ha plot, were sampled within a three-week period and each patch surveyed only once. To minimize possible differences due to seasonality, all the organisms (birds, small mammals and dung beetles) were sampled at the same time within each habitat-patch.

3.4.1 Tree cover within concentric circles

In order to assess the effect of tree cover upon the organisms surveyed, I estimated the degree of tree cover within three concentric circles with varying radii (100, 350, 600m) from the center of each of the 24 of the habitat-patches. Using a methodology similar to the TROF Project's assessment of tree cover, I placed points at every 20m from the center of each habitat-patch moving in a North, South, East, West, Northeast, Southeast, Southwest and Northwest direction (Figure 4). I recorded the number of times points fell on vegetation within each circle and calculate the percentage of tree cover for each. In the 100 m circle, percentages were based on 41 points, in the 350 m, percentages were based on 137 points and in the 600 m, percentages were based on 241 points. Using this method, I was able to calculate the % tree cover in 3.1 ha (100 m radius), 38.5 ha (350 m) and 113.1 ha (600 m) surrounding each site and examined the relationships between tree cover and bird/beetle diversity.

3.4.2 Tree inventories

In each of the 16 habitat-patches with trees (8 pasture with trees habitat-patches, 8 forest/secondary growth habitat-patches), I placed Modified-Whittaker plots (Figure 6) to assess the diversity and density of trees present. The open pasture habitat-patch was excluded because (by definition) these sites lacked trees.

In the forest habitat-patches, I placed two Modified-Whittaker plots 50m north and south from the center (Figure 7). Within the open pasture habitat-patches, I placed four Modified-Whittaker plots, because the dispersed nature of the trees made it necessary to include a greater sample area. These plots were located 50m North, South, East and West from the plot center (Figure 8). I used a compass, tape measures and markers to locate and mark the plots.

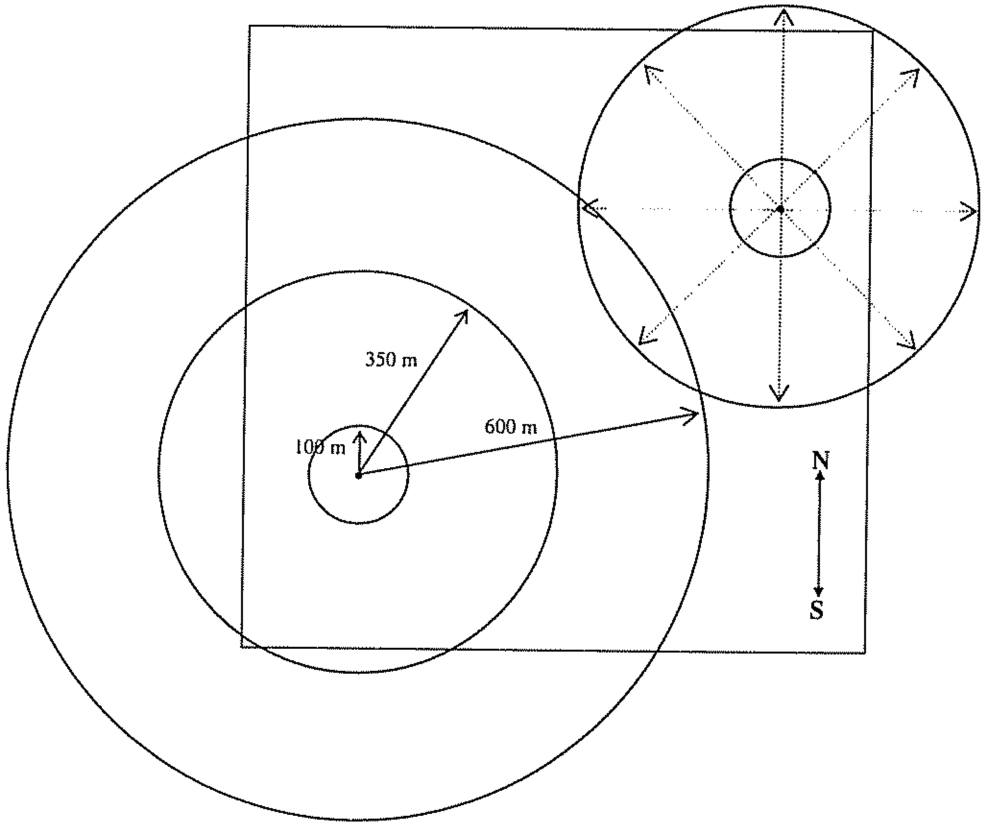

Figure 5. Position and distances of concentric circles used to calculate the % tree cover in the surrounding landscape at different scales. Dashed arrows indicate direction in which points were placed to calculate tree cover.

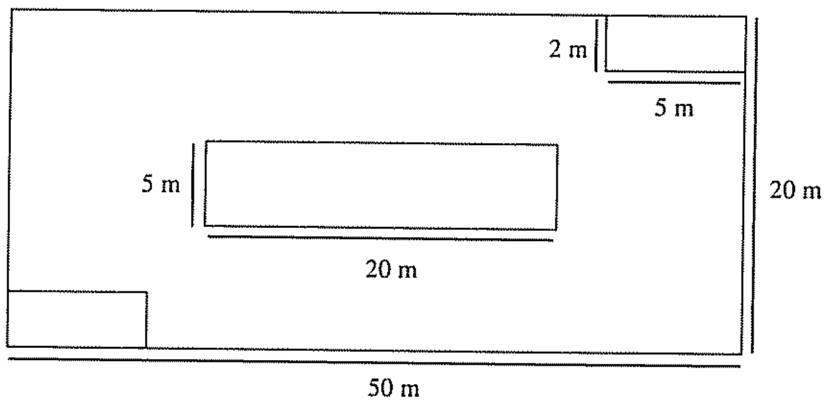

Figure 6. Diagram of the Modified-Whittaker plot used to assess tree density and diversity.

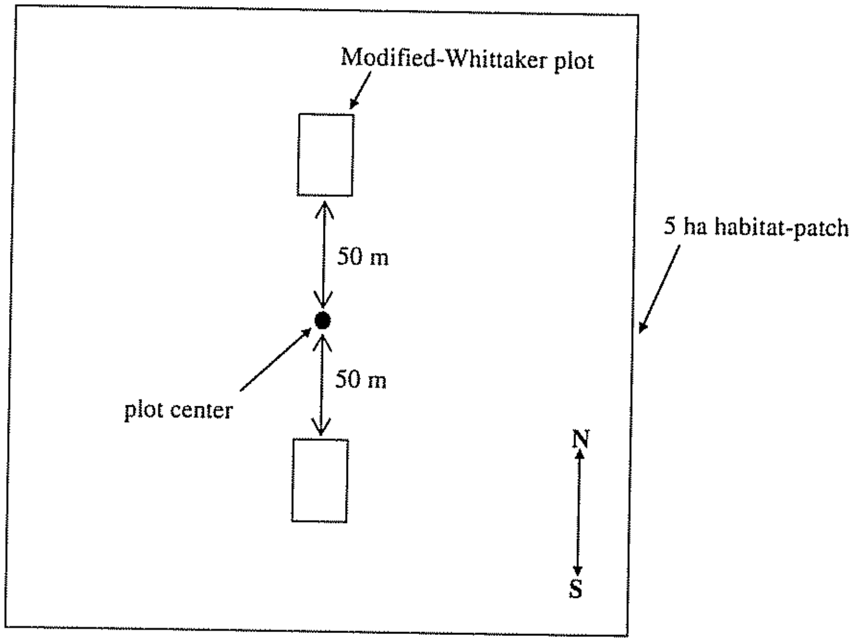

Figure 7. Location of the Modified-Whittaker plots within the forest/secondary growth patches.

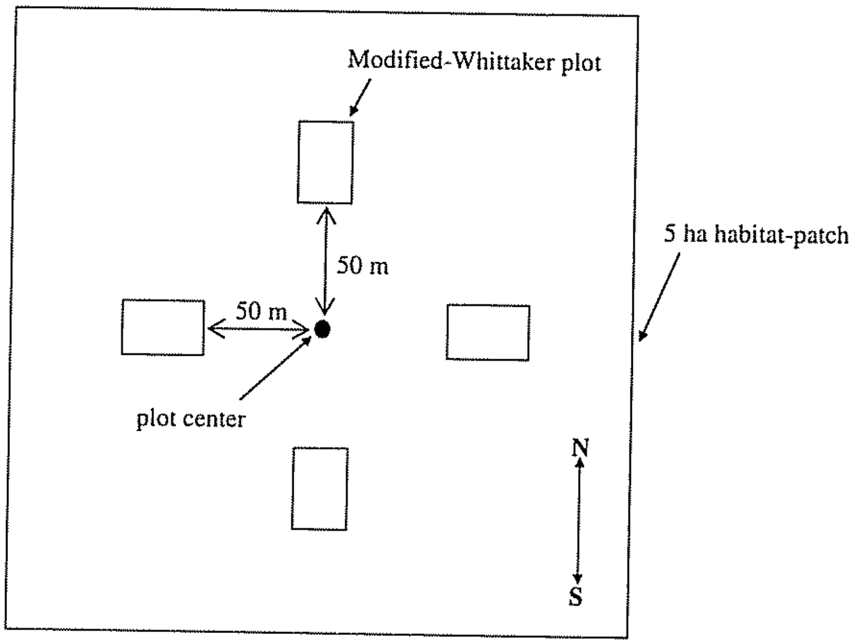

Figure 8. Location of the Modified-Whittaker plots within the pasture with trees.

I hired a local forester (Jaime Apu from MINAE) to help with the tree inventories. Within each Modified-Whittaker plot (and subplots), we inventoried all the trees above 10 cm in dbh (diameter at breast height) and determined the species, dbh and height I collected samples for the unknown species, which were later identified by Nelson Zamora of INBio (Instituto Nacional de Biodiversidad).

3.4.3 Bird trapping and identification

To characterize the avian diversity, I mist-netted birds in each habitat-patch for 4 consecutive days. Within each habitat-patch, I placed four standard sized mist nets (12 m x 2.5 m, 16 mm mesh size) at 50 m from each other along a 200 m transect running North-South (Figure 9). I used aluminum poles approximately 3 m high to keep the nets upright (Sutherland, 1996; Ralph *et al.*, 1996; Figure 10).

The nets were placed every morning at 6 in the morning and remained up for 3.5 hours consecutively during the day, with inspections every 15 minutes. I increased the frequency of inspections if there were a high number of captures in any given day. I opened and closed the nets in the same order every day. After capturing a bird, I put it into a bag for processing at another location. I identified the species using field guides and birding manuals and books (Sutherland, 1996; Ralph *et al.*, 1996) and determined their weight (using 100 g pesolas) and wing-span (with a metric ruler). I mist-netted each habitat-patch for a total of 56 net hours and each habitat for 168 net hours.

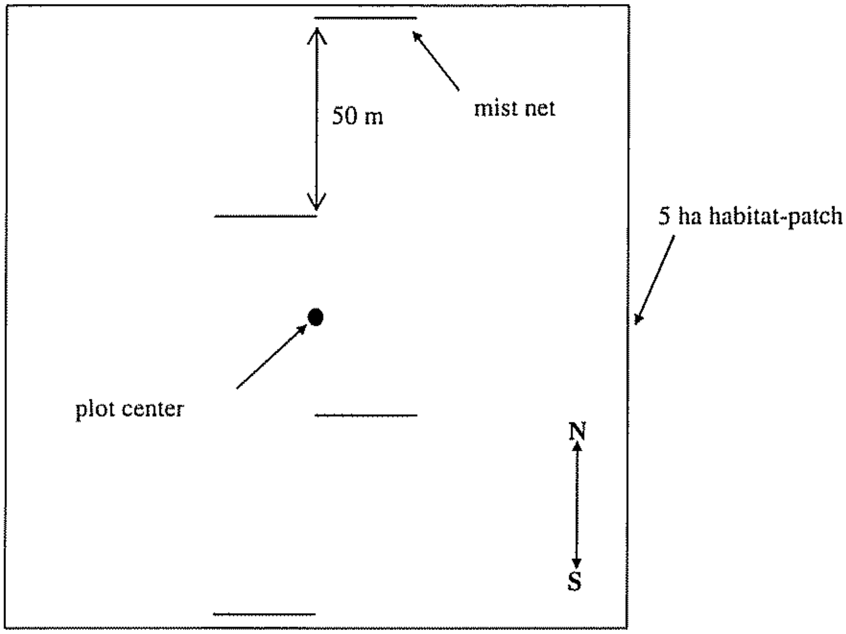

Figure 9. Location of the mist nets within each habitat-patch

Figure 10. Mist net within an open pasture

3.4.4 Dung beetle trapping and collection

In order to sample dung beetles within habitats of varying tree cover, I used pitfall traps consisting of 255 ml plastic cups placed in holes in the ground (with the lip of the cup left flush with the ground surface) and covered by a 15 cm^2 wire mesh. The mesh size was large enough to allow the passage of the larger beetles (pers. obs.). I half-filled the cups with a 93% alcohol solution to preserve the insects when they fell into the cup. About 10 grams of fresh cattle dung was placed on the wire mesh and replaced daily (Figure 11) to attract beetles. Care was taken not to have dung or dirt fall into the solution to avoid sample contamination.

Within each of the 24 habitat-patches, I placed a total of 12 pitfall traps along two transects (North-South and West-East) which crossed each other at the center of the habitat-patch (Figure 12). All traps were located 25 m apart. I sampled each habitat-patch for 4 days at the same time I conducted the bird and small mammal censuses. At the end of the 4-day sampling period, I emptied the traps and sifted through them for beetle specimens. I then cleaned and placed the specimens in alcohol until they dried. I later took the samples for identification by a specialist[6] at the National Institute for Biodiversity (INBio) and mounted them for future use in related studies.

Figure 11. Baited pitfall trap used during the research to capture beetles.

[6] Angel Solis, specialist on Scarabaeinae, Instituto Nacional de Biodiversidad (INBio), Costa Rica

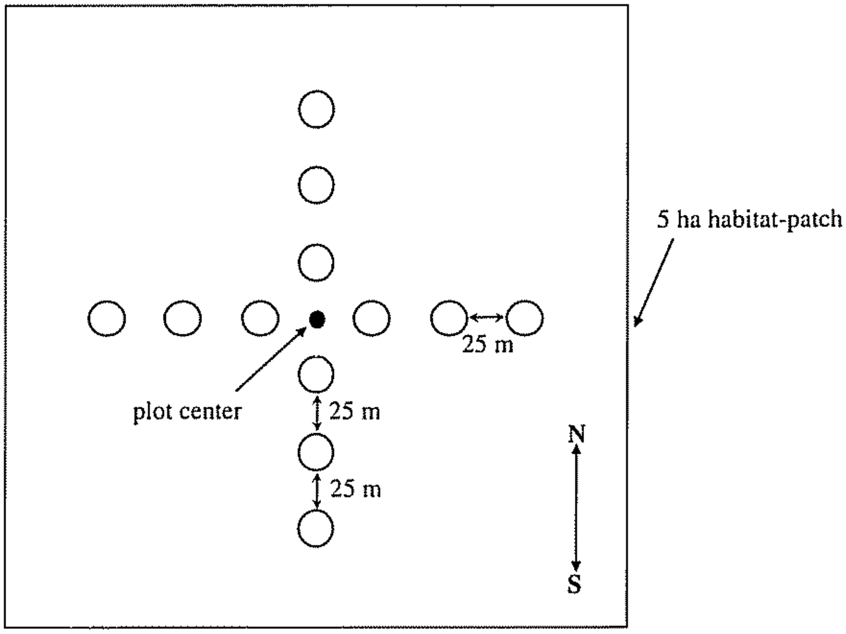

Figure 12. Arrangement of pitfall traps within habitat-patches.

3.4.5 Small mammal trapping

In order to census small mammals present within the habitat-patches I placed 49 Sherman traps in a 5 m x 5 m grid arrangement, covering an area of roughly 900 m^2 (Figures 12 and 13). I set up the traps at sunset and left them within the habitat-patch for four consecutive nights, checking each morning for captures and checked and baited the traps with food (a mixture of oats, vanilla and peanut butter) daily. I used metallic ventilated 6 oz. stainless steel Sherman traps (3" x 3.5" x 9") which are frequently used to capture small mammals. I identified the mammals trapped with the help of taxonomical keys (Emmons and Feer, 1997), and determined their weight (using 100 and 600 g pesolas) and sex before releasing them.

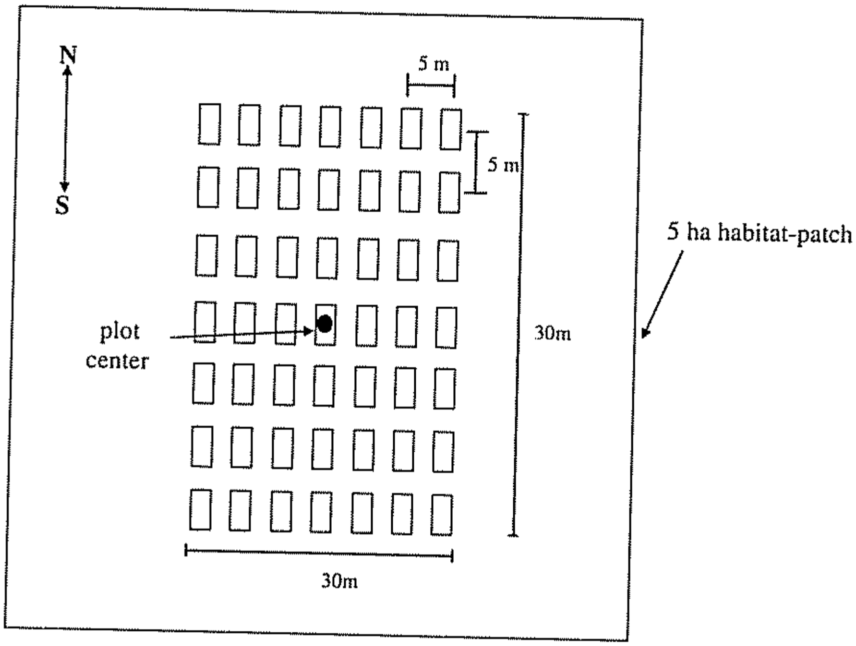

Figure 13. Arrangement of the sherman traps within the habitat-patches.

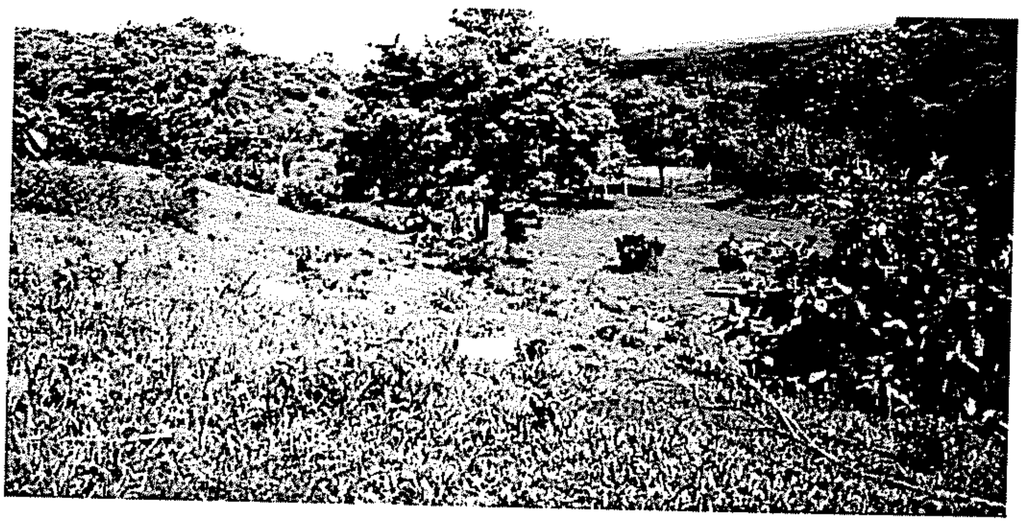

Figure 14. Sherman traps within a pasture with trees.

3.4.6 Statistical analyses

3.4.6.1 Tree data

For each habitat-patch, I calculated the total species richness (S), the total # of individuals and tree density. I also calculated Shannon's diversity (*H*) and Equitability (E_H) indices on the species present within each patch. Shannon's diversity index is commonly used to characterize species diversity in a community and is calculated by $H' = \ p_i \ln p_i$ where p_i is the proportion of S made up of the *i*th species. The equitability index ($E = H / H_{max}$ where H_{max} = total number of species) is used to compare the relative species abundance in terms of equitability or uniformity and the degree to which the relative abundance of individuals of different species are similar (Magurran, 1988).

I then performed paired t-tests on S, abundance and diversity indices to determine if any significant differences existed among the two habitats. I also calculated the Importance Value Index (IVI) with the help of Hugo Brenes[7]. The IVI's rank the importance of the species by taking into consideration the number of individuals, the frequency with which it is found within the plots and its dominance (basal area). Those species with the highest indices are the most abundant and in most cases dominate.

3.4.6.2 Bird data

I characterized the # of bird species captured and the total # of bird individuals captured within each habitat-patch. I also characterized all birds on the basis of their feeding guild (frugivores, nectarivores, granivores, omnivores, insectivores) and their preferred habitat. For each habitat I then calculated the # of individuals and spp. wtihin each guild. I then calculated Shannon's diversity (*H*) and Equitability (E_H) index for each habitat-patch.

3.4.6.3 Beetles

For each habitat-patch, I calculated the dung beetle species richness (S), # of individuals (abundance) and Shannon's diversity (*H*) and Equitability (E_H) index.

3.4.6.4 Mammal data

I was unable to characterize any data for the mammals because of the low capture rate (I only caught 18 rats in 96 trapping nights).

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[7] Information personnel in the Department of Forest Management and Biodiversity Conservation, CATIE.

3.4.6.5 Comparison of biodiversity in forest, pasture with trees and open pastures

In order to determine if any significant differences existed in the tree diversity between forests and pasture with trees, I performed paired t-tests on tree species richness and diversity.

To determine if any significant differences existed between fauna in the three habitats, in terms of bird or beetle species richness, abundance and diversity, I performed an analysis of variance on the species, individuals and diversity indices for each habitat (open pastures, pastures with trees, forest/secondary growth).

I utilized a Randomized Complete Block design as the experimental design, whose lineal model was:

$$Y_{ij} = \mu + \beta_i + t_j + e_{ij}$$

Y = the value of the y'th observation

= the overall mean of the habitats (treatments)

β_i = the effect of the block i (100 ha plot)

t_j = the effect of the treatment j

$_{ij}$ = correspond to the random components of the model: the experimental error

I used the Statistical Analysis System (SAS, ver. 8) package to perform all the statistical analyses. In order to obtain a normalized curve for the data collected, I performed a square root transformation on # of species and # of individuals per habitat-patch. I then analyzed the transformed response variables using an Analysis of Variance (ANOVA) and discriminated among means using Duncan's Multiple Range test (SAS Institute, 1988; Steel, Torrie, Dickev 1997). The treatments included the three habitats (forest, pasture with trees, open pastures) and the response variables were the # of species, # of individuals and Shannon's diversity and Equitability indices within each habitat.

3.4.6.7 Species richness and abundance vs. tree cover

To determine the response of the organisms inventoried (birds and beetles) to varying degrees of tree cover, I explored the relationships between their species numbers and abundance and tree cover at various distances around the sample area (scales: 100m, 350m, 600m) using Pearson's Correlations (r). I also performed linear regressions to further determine the relationship between species number and % tree cover.

3.4.6.8 Species-area curves

For trees, birds and beetles, I calculated species-area curves to determine how the number of species increased with an increase in the area sampled and at what size the sample areas are large enough to include all the species within the study area. The species area curves are calculated by $S = c A^z$ where S = number of species; c = a constant measuring the number of species per unit area, A = area of the habitat and z = a constant measuring the slope of the line describing the relationship between S and A (m)[8].

[8] The number of species recorded in a habitat is related to the size of area sampled. As the sample area is increased, species numbers increase accordingly. After the number of species ceases to increase even after increases in area it is determined that all species have been accounted. I used the EstimateS program, ver. 6.0 to calculate species-area curves. The program generates the species-area curves based on 100 cumulative randomizations of the *H* values.

4.0 RESULTS

4.1 Characterization of the landscape

4.1.1 Tree cover

The tree cover within the entire study area (8788.5 ha) was estimated at approximately 36.6%. However, because the research excluded the agricultural areas (low forest cover areas), the tree cover within the sample area (6262.8 ha) was about 45.4%. The tree cover includes 18 forest fragments, which are generally found in areas with an elevation greater than 80 masl. The tree cover is further increased by the presence of trees (isolated trees, live fences and tree patches) within the production areas.

4.1.2 Landuse within the study area

Several production systems are found within the area, including livestock management for beef production (and to a lesser extent dairy production), sugar cane and rice production (Figure 15). Within the entire study area of 8788.5 ha, agricultural areas (including sugar cane and rice fields) occupy 28.7% of the total area (8788.5 ha) followed by forest/secondary growth (FO, 25.7%), pastures with trees (PT, 25.8%) and open pastures (PA, 19.8%; Table 1).

In the 6262.8 ha sample area (excluding agricultural areas), forest/secondary growth occupies 36.1% and pastures account for 64% of the land area (pastures with trees 36.2% and open pastures 27.8%).

Table 1. Area under different land use within the study area.

Landuse	Area (ha)
Forest/Secondary growth	2258.4
Pastures with trees	2265.9
Open pastures	1738.5
Total	6262.8

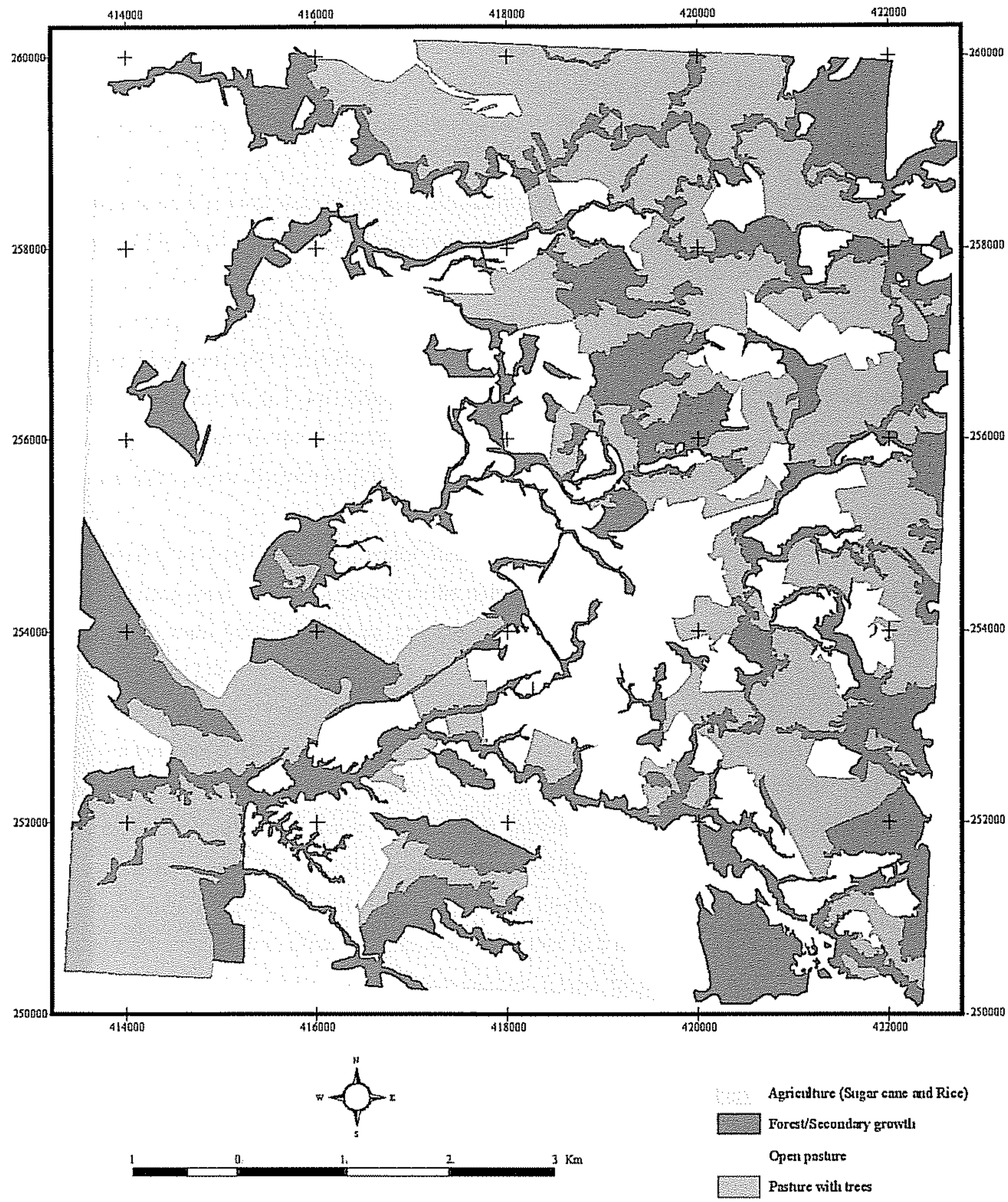

Figure 15. Landuse areas within the study area (8788.5 ha) in Cañas, Guanacaste.

Agricultural areas are found on the west and southwest sector of the study area and comprise approximately 2525.7 ha (Figure 15). Mechanized agriculture is practiced in these intensively managed areas, which contain few trees, riparian forests or forest patches.

Forest/secondary growth areas cover approximately 2258.4 ha and are found scattered throughout the study (Figure 16). These areas are comprised of both fragments and riparian forests that form a continuous network of forested areas across the agricultural landscape (Figure 17). The 18 forest fragments total about 1267.9 ha and range in size from 13.3 to 122.1 ha (mean = 70.4 ha). The remaining area (990.5 ha) is comprised of riparian forest. The forest fragments present an irregular arrangement and are infrequent within the landscape; however the riparian forests interconnect them across the landscape forming linear corridors (Figure 17). The riparian forests cover an approximate distance of 100 km and greatly enhance landscape connectivity.

The pastures with trees include pasture areas with dispersed trees or tree patches and/or live fences. These areas are found mostly to the north and eastern sector of the study area and are interspersed with forest and open pastures (Figure 18). The pastures with trees cover approximately 1738.5 ha.

The open pastures (OP) are located mostly in the central sector of the study area (Figure 19) and form a boundary between the agricultural areas to the west and the forests and pasture with trees to the east. Open pastures cover an area of approximately 2266 ha. Riparian forests run through these areas and create visible corridors or links between the agricultural areas and the pastures with trees and forest areas. Within the open pastures, there are small areas of Trasbala (*Digitaria decumbens* var. trasbala) utilized for hay production that lack trees and are not grazed. Like the pastures with trees, the open pastures possess live fences to delimit farm properties and to partition areas for cattle grazing. However, the areas partitioned for cattle grazing have no trees within them.

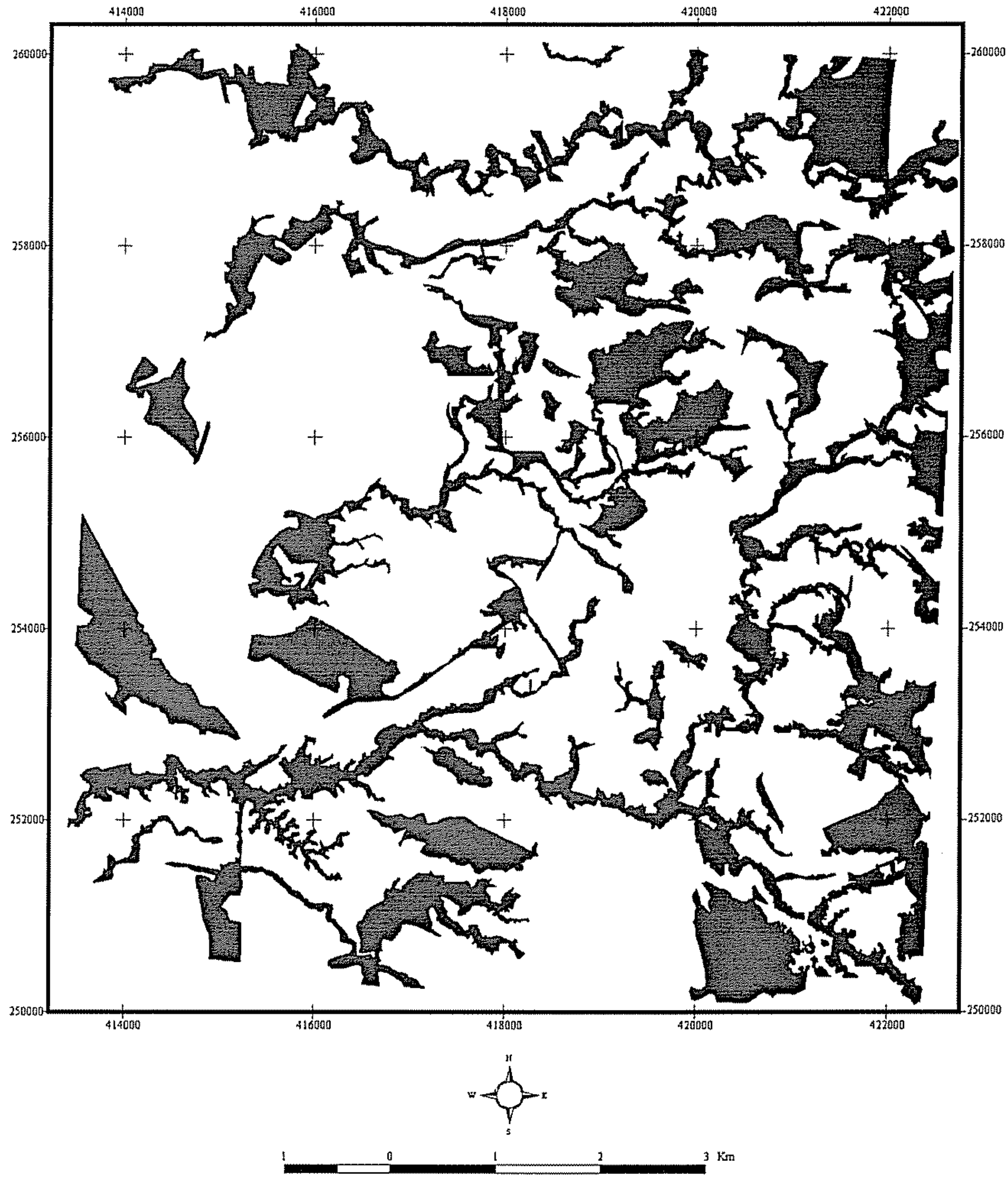

Figure 16. Location of forest areas within study area in Cañas, Guanacaste.

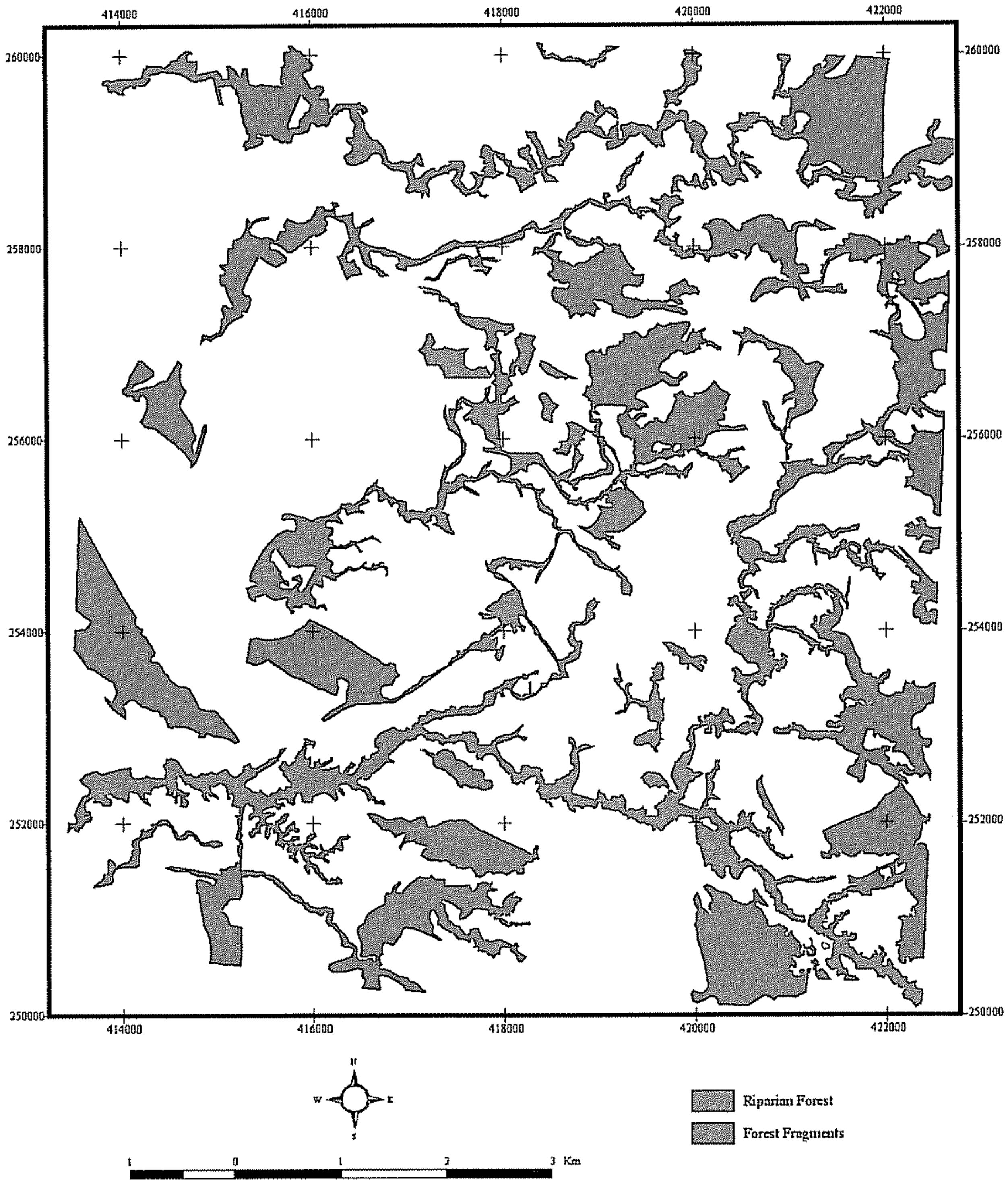

Figure 17. Riparian and forest areas within the study area in Cañas, Guanacaste.

Figure 18. Location of pastures with trees in Cañas, Guanacaste.

4.2 Diversity present in forest habitats

4.2.1 Tree diversity in forests

The forest habitats contribute greatly to the tree diversity present in the landscape. I found 43 species of trees in 25 families within forest habitats (Annex 1). This represented 86% of the tree species and 79% of the individuals identified in this study. In the forest habitats, six species represented 60% of the trees surveyed (Table 2). The most abundant species was guácimo (*Guazuma ulmifolia*), which contributed 23% of the total trees inventoried, followed by laurel (*Cordia alliodora*, 12%) and *Eugenia salamensis* (8.7%; Annex 2). In some forest sites *G. ulmifolia* represented 30-35% of the trees.

Three of the tree species found in the forest habitats, (*Acosimum panamense, Lonchocarpus rogosus, Samanea saman*) are classified as 'Scarce' in Costa Rica and *Swietenia macrophylla* as 'in danger of Genetic Erosion' (Poveda Alvarez and Sanchez-Vindas, 1999). However, only a few individuals represented each of these species.

Table 2. The top six most abundant tree species found within forest habitats, their frequency (occurrence within 8 sites) and percentage out of 311 individuals.

Family	Scientific Name	Common Name (sp)	Frequency	Total	%
Sterculiaceae	*Guazuma ulmifolia*	Guácimo	7	71	22.8
Boraginaceae	*Cordia alliodora*	Laurel	8	38	12.2
Myrtaceae	*Eugenia salamensis*	Moridero, Fruta de pava	6	27	8.7
Sapindaceae	*Cupania guatemalensis*	Manteco	6	20	6.4
Tiliaceae	*Apeiba tibourbou*	Peine de mico	4	15	4.8
Tiliaceae	*Luehea candida*	Guacimo molenillo	6	12	3.9
	remaining 38 species			123	40

The frequency distribution of tree diameters showed that 86% of the trees in forest areas had diameters between 10-30 cm, while only 14% had diameters above 30 cm (Figure 19). The distribution suggests that the forest patches sampled are mostly secondary forests in the process of regeneration and that many of the larger trees have been eliminated through harvesting.

According to the Index of Value Importance (IVI; Annex 3), the most important species in the forest habitat are *G. ulmifolia, E. salamensis, C. alliodora* and *Ochroma lagopus*. Of the eight forest patches inventoried, *G. ulmifolia* held the top index for 5 of the sites. The importance of the species is calculated taking into consideration the number of individuals, the frequency with which it is found within the plots and its dominance (basal area), therefore those species with the highest indices are the most abundant and in most cases dominate.

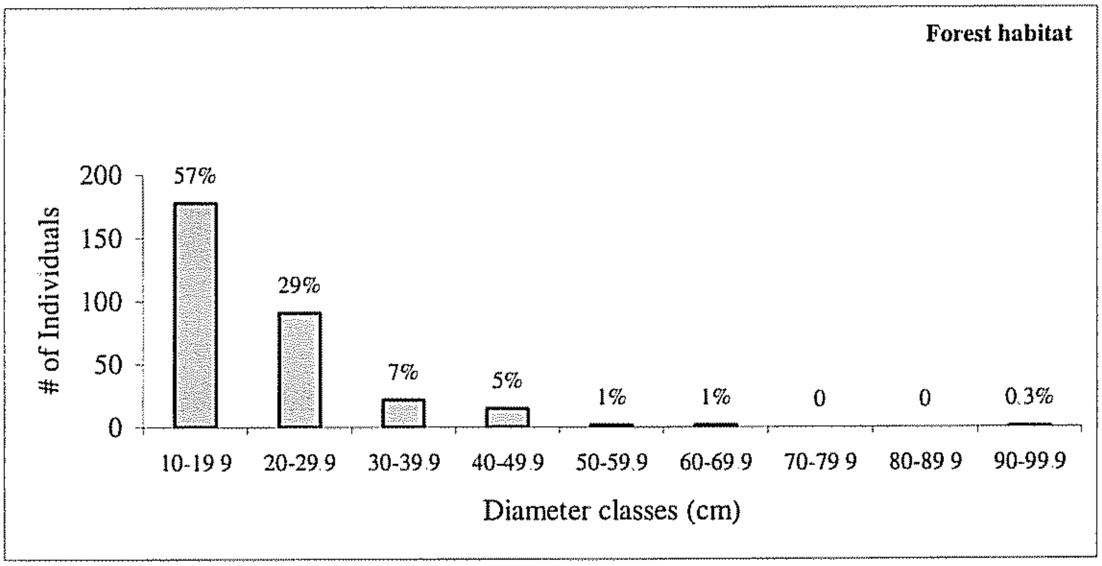

Figure 19. Frequency distribution of tree diameters in forest habitats. Data represents the inventories from 8 forest sites (total area sampled = 3.2 ha).

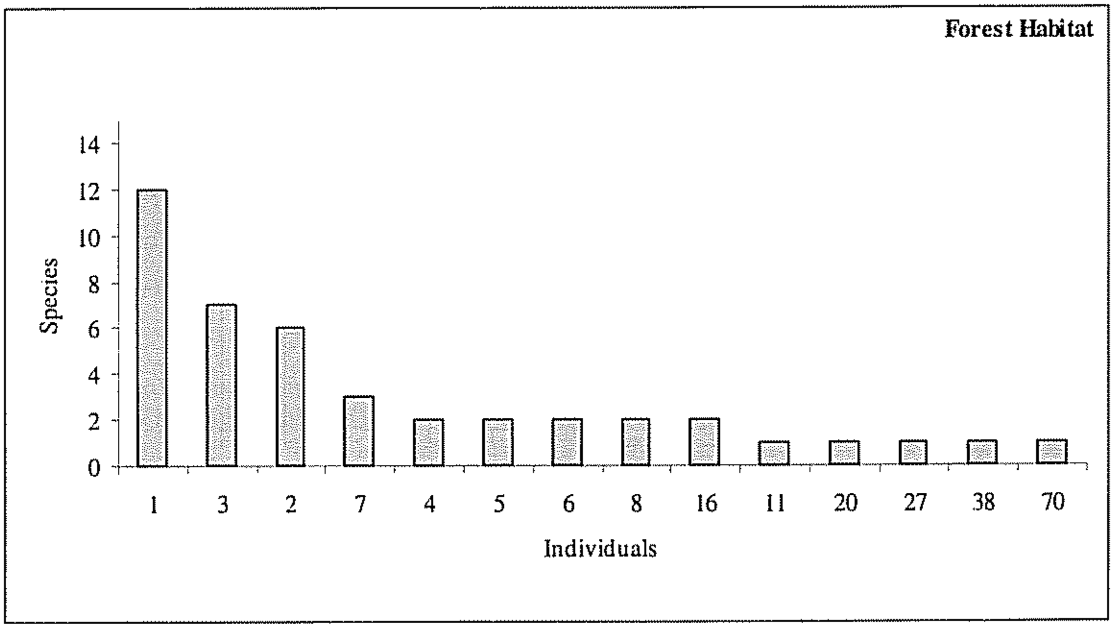

Figure 20. Relative abundance of the tree species (>10cm dbh) in forest habitats. Data represents the inventories from 8 forest sites (total area = 3.2 ha).

Few individuals represented most of the species within the forest habitats. The majority of the species (84%) found in the forest habitat were represented by <10 individuals and only 16% were represented by >10 individuals (Figure 20; Annex 4).

The Shannon biodiversity indices for the eight forest plots ranged between 1.5 and 2.6 with a mean of 2.18 (Table 3). The equitability values ranged from 0.14 to 0.19 with a mean of 0.17.

Table 3. Shannon's biodiversity (H) and equitability (E_H) indices for the forest habitats.

Site	H	E_H
1	2.53	0.15
2	1.52	0.19
3	2.21	0.14
4	2.23	0.14
5	2.17	0.18
6	2.03	0.18
7	2.66	0.15
8	2.09	0.19
Mean	2.18	0.17
SD	0.34	0.023

4.2.2 Bird diversity in forests

I captured a total of 91 individuals representing 17 species in 10 families within the forest habitats. This represented 45% of the birds and 49% of all species captured within the study area. Eleven of these species were exclusively forest dwelling birds and the remaining 6 species are typical of pasture and forest habitats. The majority of the species captured within the forest habitats were insectivorous (13; but six of these species also consumed fruits), 3 were nectarivores and 1 was an omnivore (Table 4; Annex 5).

Table 4. The five most abundant bird species found within forest habitats, their habitat and guild preferences. Guilds include: I=insectivores, F=frugivores, O=omnivores, N=nectarivores. Habitat preferences include: FO=forest habitats, PT=pasture with trees.

Common Name	Species	Individuals	Guild	Habitat
Long-tailed manakin	*Chiroxiphia linearis*	23	I/F	FO
Banded wren	*Thryothorus pleurostictus*	19	I	FO
Olive sparrow	*Arremonops rufivirgatus*	18	O	FO
Cinnamon hummingbird	*Amazilia rutila*	9	N	FO
Tropical gnatcatcher	*Polioptila plumbea*	4	I	PT/FO
	Remaining 12 species	18		

The majority of the bird species (76%) in the forest habitat were represented by <5 individuals; 8 species were represented by only one individual (Figure 21). Long-tailed manakins (*Chiroxiphia* *linearis*), banded wrens (*Thryothorus pleurostictus*) and olive sparrows (*Arremonops rufivirgatus*) were the most abundant species with 23, 19 and 18 individuals respectively (Table 4). These three species accounted for 66% of the birds captured in the forest habitats (Annex 6).

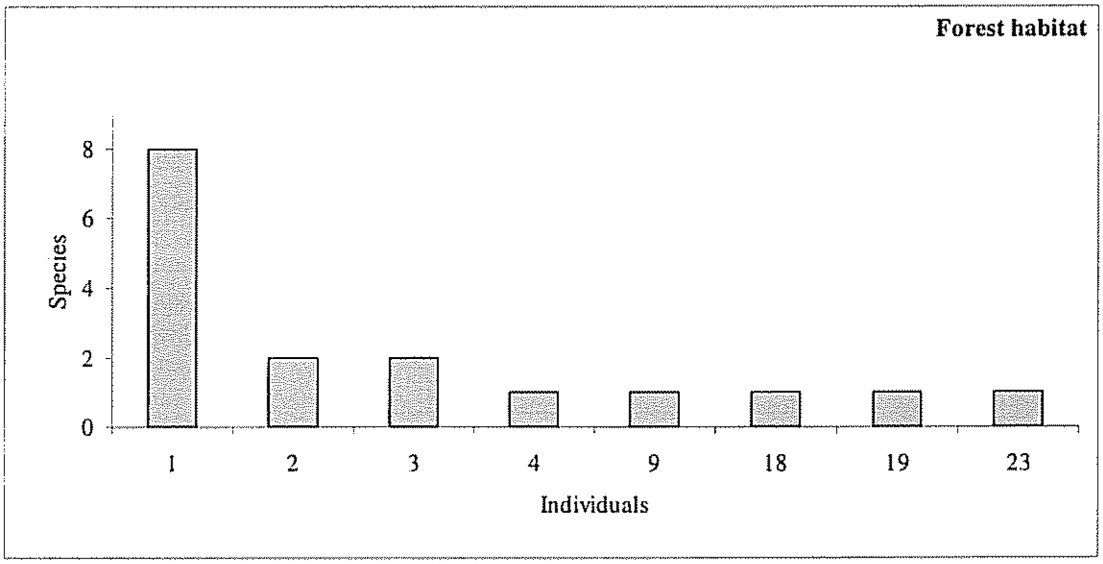

Figure 21. Relative abundance of bird species in forest habitats.

4.2.3 Beetle diversity in forests

In the forest habitats, I captured 737 dung beetles (Order: Coleoptera, Family: Scarabaeidae, Subfamily: Scarabaeinae) representing 12 species of dung beetles. These individuals represent 22% of the total individuals captured and 70% of the species identified (Annex 7).

I captured >2 species throughout all the forest habitat-patches sampled; one site had 10 species of dung beetles and also the largest number of individuals (292) captured. *Onthophagus landolti* and *Onthophagus acuminatus* represented 60% of the individuals captured in the forest habitats. *Onthophagus landolti* and *Ateuchus rodriguezi* were present in seven of the eight sites sampled (Table 5; Annex 8). The biodiversity indices ranged from 0.89 to 1.88 and the equitability indices between 0.18 and 0.29 (Table 6).

Table 5. The top five most abundant dung beetle species found within forests and the frequency with which it was found. f = # of sites (of 8 total sites).

Species	# of individuals	*f*
Onthophagus landolti	338	7
Onthophagus acuminatus	103	2
Copris lugubris	58	5
Onthophagus batesi	53	4
Dichotomius centralis	44	5
other 7 species	245	

Table 6. Shannon's diversity (H) and equitability (E_H) indices on dung beetles captured in all the forest sites.

Site	H	E_H
1	1.66	0.17
2	1.65	0.21
3	1.46	0.29
4	0.94	0.31
5	1.06	0.27
6	1.88	0.24
7	0.89	0.18
8	1.65	0.28
Mean	1.39	0.24
SD	0.13	0.05

4.3 Diversity present within pasture with trees

4.3.1 Tree diversity

I identified 80 individuals, 17 species and 12 families of trees within the pastures with trees (Annex 9). This represents 20% of all the trees identified and 33% of the total tree species in the study area. Two species, *G. ulmifolia* and *Acrocomia aculeate*, dominated the pastures contributing 39% and 15% respectively of the individuals within the pasture with trees habitat (Table 7; Annex 10).

The pastures with trees contained only one species classified as 'scarce', *Samanea saman*, that was represented by 4 individuals.

Table 7. The top six most abundant tree species found within pastures with trees, their frequency (occurrence within 8 sites) and percentage out of 311 individuals.

Family	Scientific Name	Common Name	frequency	total	%
Sterculiaceae	*Guazuma ulmifolia*	Guacimo	3	31	38.8
Arecaceae	*Acrocomia aculeata*	Coyol	3	12	15.0
Boraginaceae	*Cordia alliodora*	Laurel	2	6	7.5
Bignoniaceae	*Tabebuia rosea*	Roble	3	5	6.3
Fabaceae	*Samanea saman*	Cenizaro	2	4	5.0

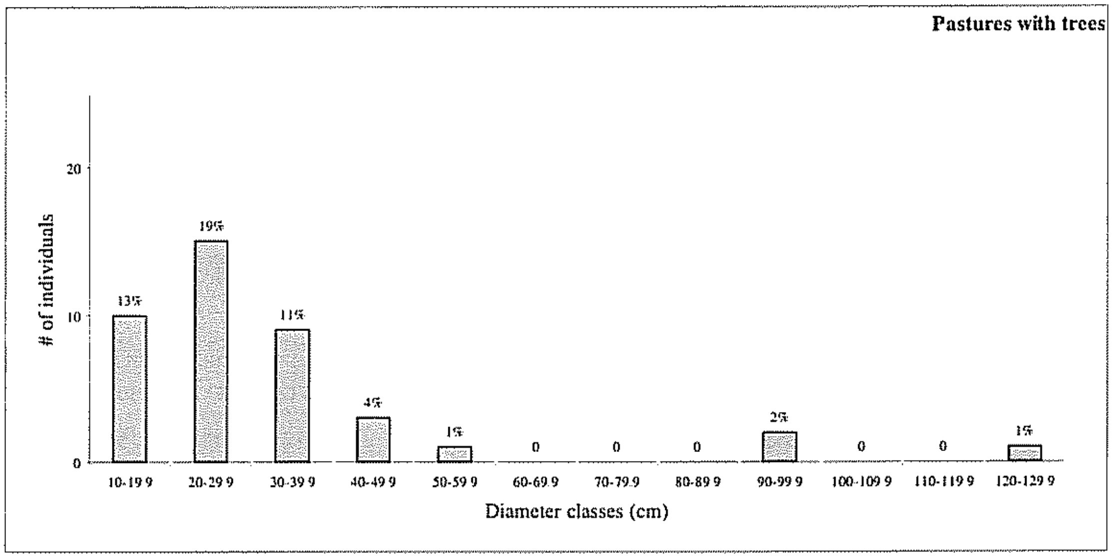

Figure 22. Frequency distribution of tree diameters in pastures with trees. Data represents the inventories from 8 pasture with trees sites (total area = 3.2 ha). Percents represent the % of total trees within a given diameter class.

The frequency distribution of tree diameters showed that 61% of the individuals had diameters between 10 and 30 cm; 39% of the individuals had diameters >30 cm (Figure 22). There were only 7 large trees (dbh > 40cm) within the pastures with trees representing *Licania arborea* (1), *S. saman* (1), *Andira inermis* (1), *G. ulmifolia* (2), and *Ficus spp* (1).

Guazuma ulmifolia had the highest IVI in three sites and *A. aculeata* in two and *Licania arborea, Maclura tinctoria, Ceiba pentandra,* in the other three (Annex 11). These two species also had the largest diameters in two sites in which they were dominant.

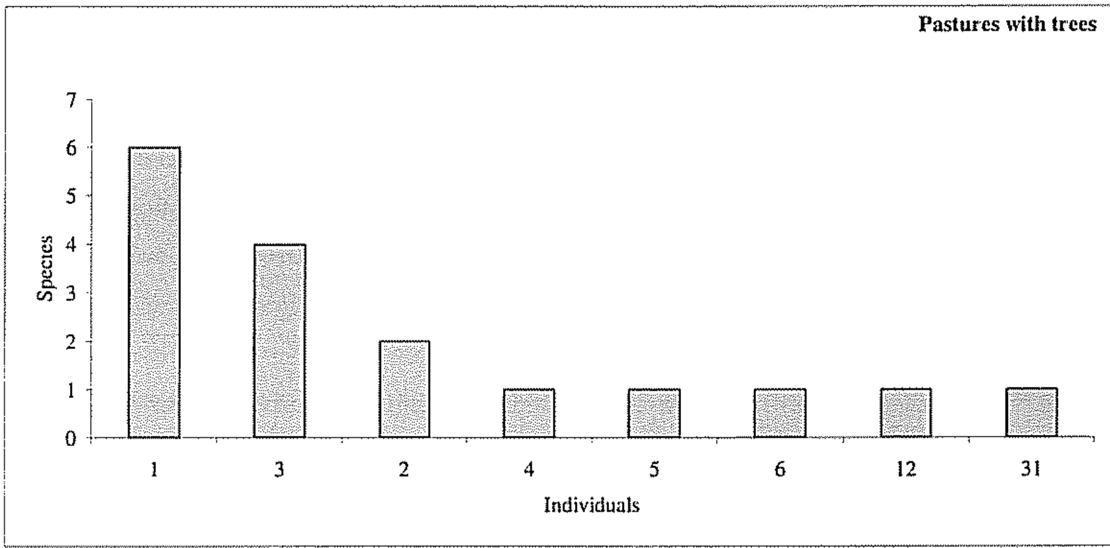

Figure 23. Relative abundance of tree species (>10cm dbh) in pastures with trees habitats. Data represent the inventories from 8 pastures with trees sites (total area surveyed = 3.2 ha).

In pastures with trees, two species, *G. ulmifolia* and *A. aculeata* were the most abundant, representing 54% of the individuals (Annex 10, 12). The remaining 15 species were represented by < 6 individuals (Figure 23). The Shannon biodiversity indices for the pasture with tree habitats ranged from 0.56 to 1.8 and the equitability indices from 0.16 to 0.34 (Table 8).

Table 8. Shannon's diversity (*H*) and equitability (E_H) indices on beetles captured in all the pastures with trees sites.

Site	*H*	E_H
1	0.64	0.32
2	1.09	0.16
3	0	0.00
4	1.21	0.30
5	1.8	0.26
6	0.45	0.23
7	1.01	0.34
8	0.56	0.28
Mean	0.845	0.23
SD	0.55	0.04

4.3.2 Bird diversity in pastures with trees

I captured 66 individuals representing 20 species and 9 families within pastures with trees. The birds captured within pastures with trees represented 33% of the total individuals captured and 57% of the total species captured. The 20 species captured included forest species (6), pasture species (6) and species that frequent both habitats (8). The majority of the species captured were frugivores and granivores (2) or insectivores and frugivores (7); three were omnivores and the rest were a combination of guilds (8; Annex 13).

The majority of the species (17) captured within pastures with trees were represented by 5 or less individuals (85%); 9 species were represented by only one individual (Figure 24). The most common species were the common ground-dove (*Columbina passerina;* with 17 individuals or 26% of the individuals), blue-black grassquit (*Volantinia jacarina;* 8 individuals) and the striped-headed sparrow (*Aimophila ruficanda;* 6 individuals). These top three species accounted for 47% of the individuals found within pasture with trees (Annex 14).

The Shannon diversity indices for bird diversity in pastures with trees ranged from 1.23 to 1.46 (Table 16) and the equitability indices from 0.19 to 0.31 (Table 17).

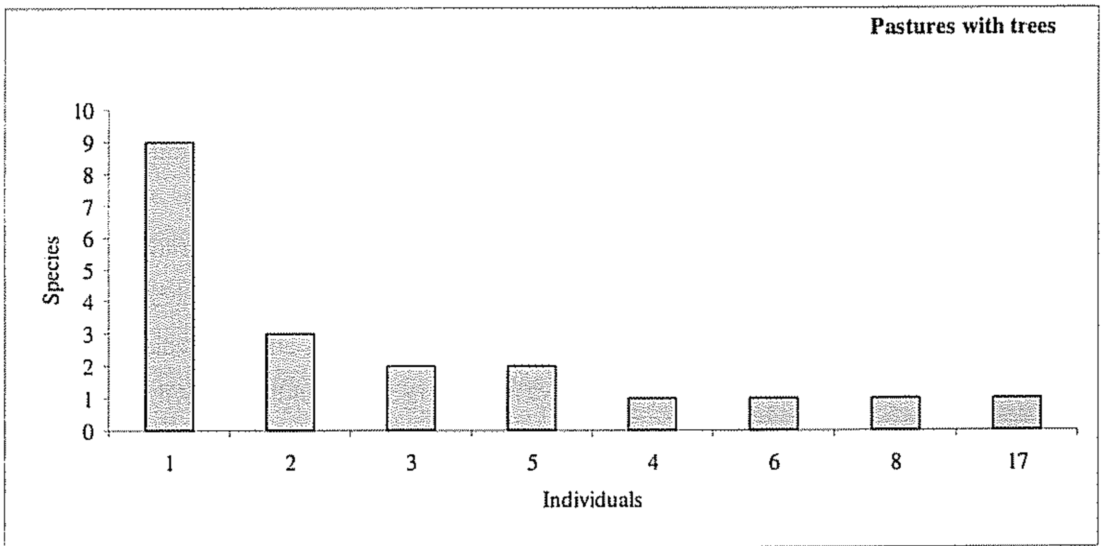

Figure 24. Relative abundance of the bird species in pastures with trees habitats. Data represents the avifauna captured in 8 pastures with trees sites (total mist netting effort = 448 net hours).

4.3.3 Beetle diversity

I captured 1,943 dung beetles representing 11 species within the pastures with trees habitat (Annex 15). This represented 58% of the total individuals and 70% of the species captured in the study. Three species, *Canthon indigaceus, Onthophagus hoepfneri* and *Onthophagus marginicollis*, accounted for 1,637 dung beetles or 84% of the individuals captured within this habitat (Table 9).

Table 9. The top five most abundant dung beetle species captured within pasture with trees and the frequency with which they were found throughout the pasture with trees habitat (out of 8 sites).

Species	# of individuals	*f*
Onthophagus hopfneri	795	6
Canthon indigaceus	599	6
Onthophagus marginicollis	243	6
Phaneus demon	141	5
Copris lugubris	55	6
other 11 species	110	

Three dung beetle species, *Canthon mutabilis, Phaneus eximius, Agomopus lampros* were captured exclusively in the pastures with trees habitat. *Dichotomius annae, C. indigaceus, Copris lugubris, O. hoepfneri, O. marginicollis* and *A. rodriguezi* were present in six of the eight sites sampled (Annex 16).

The biodiversity indices for the beetles within the pastures with trees habitats ranged between 0 and 1.84 (mean = 1.05) while the equitability indices ranged from 0.9 to 0.23 (mean = 0.13)

4.4 Diversity present within open pasture habitats

4.4.1 Tree diversity

No inventories were conducted within the open pastures, since by definition these did not possess trees.

4.4.2 Bird Diversity

In the open pastures, I captured 43 birds representing 8 species in 5 families. The birds captured in open pasture represented 22% of the total individuals and 23% of the species identified. All the species except one, cinnamon hummingbird (*Amazilia rutila)* a forest species, are commonly found in pastures (either open or pasture with trees). Five feeding guilds were identified from the species captured within the open pastures: frugivores/granivores (3 spp.), insectivores/frugivores (1 spp.), insectivores/granivores (1 spp.), insectivores (1 spp.) or nectarivores (2 spp.; Annex 17)).

The majority of the species (6) were captured infrequently with <10 individuals/spp.. Only two species, *V. jacarina* and *C. passerina*, were caught frequently and represented 38% and 23% of the individuals captured within open pastures (Table 10; Figure 25; Annex 18).

Table 10. The top five most abundant bird species within open pastures and their guild and habitat associations (Skutch and Stiles, 1989). F=frugivores, G=granivores, I=insectivores, N=nectarivores; PA=open pasture species, PT=pasture with trees species, FO=forest species.

Common Name	Species	Individuals	Guild	Habitat
Blueblack grassquit	*Volantinia jacarina*	12	F/G	PA
Common ground dove	*Columbina passerina*	10	F/G	PA/PT
Plain breasted ground dove	*Columbina minuta*	7	F/G	PT
Gray-crowned yellowthroat	*Geothlypis poliocephala*	7	I	PA
Steely-vented hummingbird	*Amazilia saucerrottei*	2	N	PT/FO
	remaining 3 species	5		

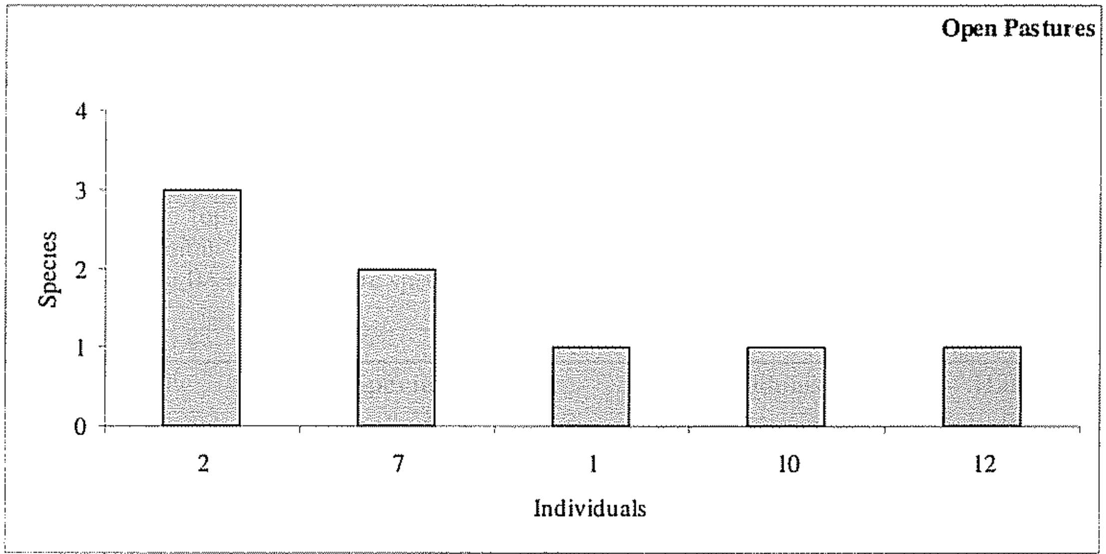

Figure 25. Relative abundance of the bird species in open pastures. Data represents the avifauna captured in 8 open pastures sites (total mist netting effort = 448 net hours).

4.4.3 Beetle diversity

I captured 661 dung beetles representing 7 species within the open pastures (Annex 19). The dung beetles captured represented 20% of the individuals and 39% of the species captured in the open pastures. *Canthon indigaceus* and *Onthophagus hoepfneri* accounted for 439 dung beetles or 66% of the individuals captured; while the remaining 5 species represented only 222 dung beetles or 44% of the individuals captured within open pastures (Table 11; Annex 20).

Table 11. The top five most abundant dung beetle species captured within open pastures and the frequency (*f*) with which they were found throughout the open pasture sites (out of 8 total sites).

Species	# of individuals	*f*
Canthon indigaceus	266	4
Onthophagus hopfneri	173	4
Onthophagus marginicollis	93	4
Dichotomius annae	61	4
Phaneus demon	59	4
other 2 species	9	

The Shannon diversity indices for dung beetles in open pastures ranged between 0.89 and 1.63 with a mean of 0.71, while the equitability indices ranged between 0.2 and 0.28 with a mean of 0.13 (Table 12).

Table 12. Shannon diversity (*H*) and equitability indices (E_H) for dung beetles found within open areas.

Site	H	E_H
1	1.63	0.27
2	0.43	0.02
3	0	0.00
4	0	0.00
5	0	0.00
6	1.38	0.28
7	0.89	0.22
8	1.39	0.28
Mean	0.71	0.13
SD	0.24	0.05

4.5 Comparison of the diversity between the three habitats

4.5.1 Tree diversity

The forests had a higher total number of tree species (44) than pastures with trees (17) and many more trees (311 vs 80) despite a larger sample area in pasture with trees (Table 13). The forest habitats had a significantly greater number of trees (paired t-test, t=3.99; $P<0.05$) and species (paired t-test, t=5.61; $P<0.05$) than pasture with trees (Table 13; Figure 26).

Table 13. Summary of the tree inventories conducted on forest and pasture habitats. FO=forest, PT=pastures with trees

Habitat	No. of sites	No of plots	Area/plot (ha)	Area sampled (ha)	Total families	Total species	Total Individuals
FO	8	16	0.1	1.6	25	44	311
PT	8	32	0.1	3.2	12	17	80

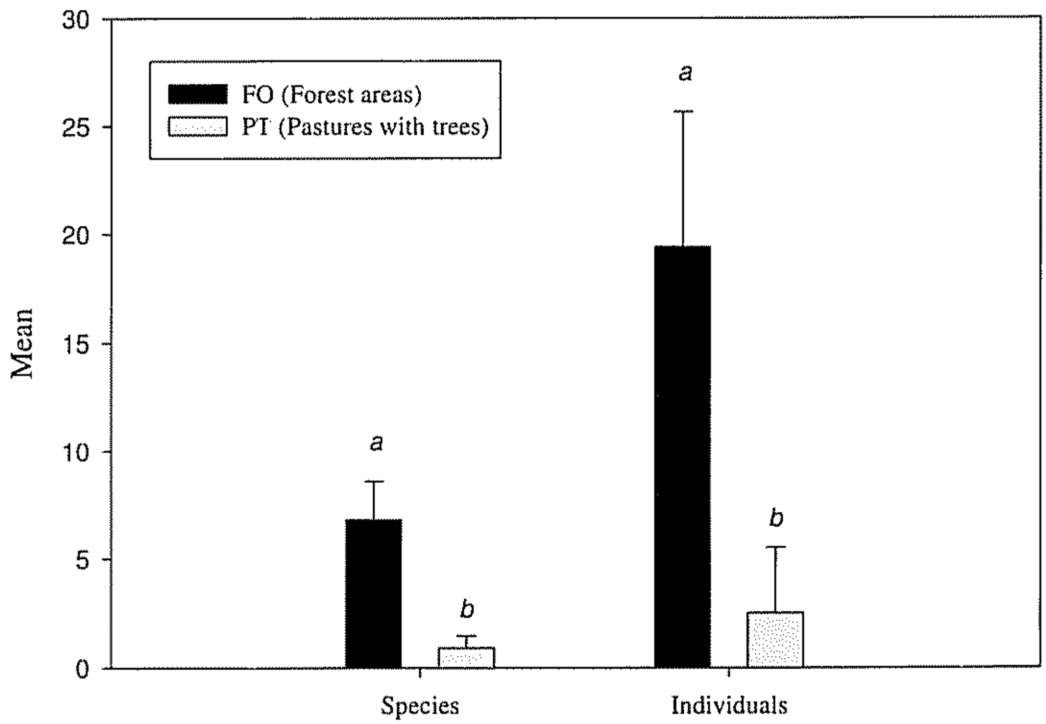

Figure 26. Comparison of the mean # of spp./plot and mean tree density in forests and pastures with trees. The forest data represent 16, 0.1 ha plots and pasture data represent the mean of 32, 0.1 ha plots.

The forests had significantly greater Shannon diversity indices (*H*) than pastures with trees (paired t-test, t=5.65; P<0.05). The forest habitats had a mean *H* of 2.18 compared to a mean H of 0.85 in pastures (Table 14); there was greater variation in the Shannon index values in pastures with trees than in forest habitats. The distribution of individuals among species or equitability (E_H) was similar in both pastures with trees and forest habitats (paired t-test, t=1.803; P>0.05), an increase in the area sampled would probably show greater variation in pastures with trees. It is important to note that some sites were given a value of 0 for *H* (and E_H) because only one individual was identified, thus diversity was calculated to be 0 (Table 15).

Table 14. Comparison of biodiversity indices (*H*) of tree diversity between forests and pastures with trees.

Site	forest	pastures with trees
1	2.53	0.64
2	1.52	1.09
3	2.21	0
4	2.23	1.21
5	2.17	1.8
6	2.03	0.45
7	2.66	1.01
8	2.09	0.56
Mean	2.18*a*	0.85*b*
SD	0.34	0.55

Table 15. Equitability values (E_H) of tree diversity between forest and pasture with trees.

Site	forest	pastures with trees
1	0.15	0.32
2	0.19	0.16
3	0.14	0.00
4	0.14	0.30
5	0.18	0.26
6	0.18	0.23
7	0.15	0.34
8	0.19	0.28
Mean	0.16*a*	0.23*a*
SD	0.023	0.12

The forest and pasture with trees habitats differed in species composition. *Guazuma ulmifolia* and *C. alliodora* were the most common species in forests while *G. ulmifolia* and *Acrocomia aculeata* were most abundant species in pastures with trees. Of the 52 total tree species identified, I found 36 species exclusive to forests but only 9 to pastures with trees; 8 tree species were found in both habitats.

The species-area curves indicated clear differences in the species richness between the two habitats (Figure 27). Tree species richness was higher in forests than in pastures with trees at every scale. The species-area curves also indicated that the area sampled was not sufficient to capture all the species present since in both curves, the slopes do not reach an asymptote.

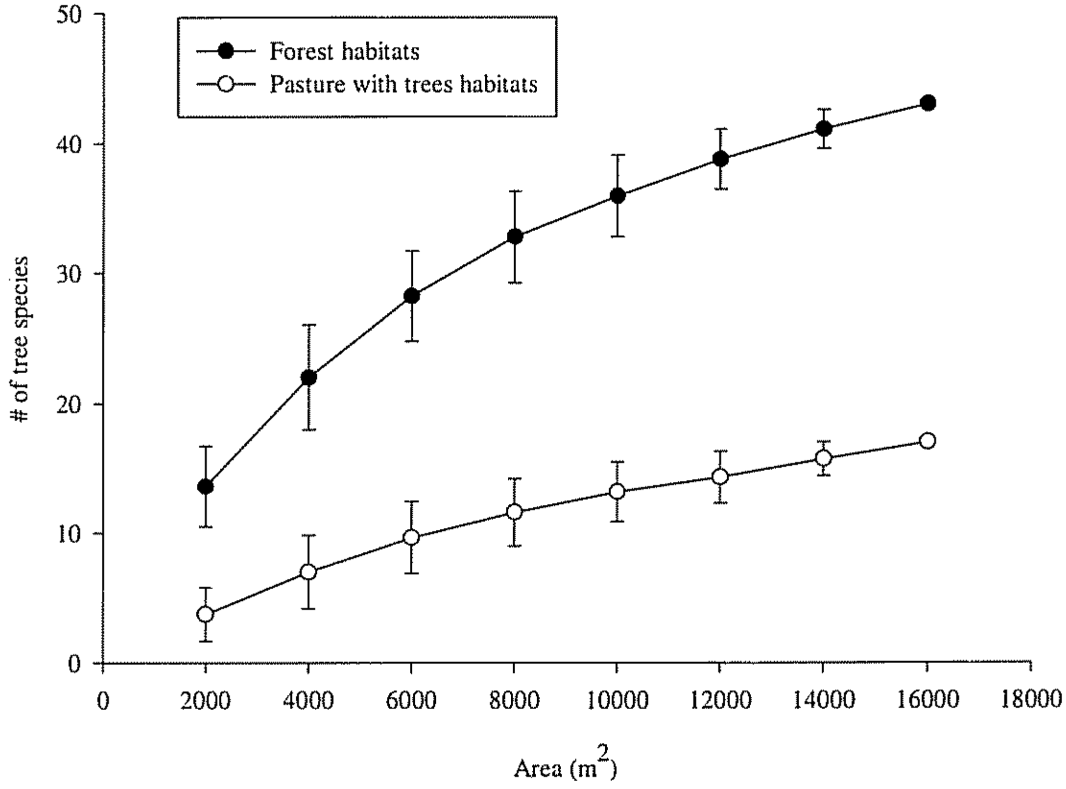

Figure 27. Species-area curves for all forest and pasture with trees habitats. Each curve was based on tree inventories conducted within Modified Whittaker plots located in the two habitats. Bars represent standard deviations.

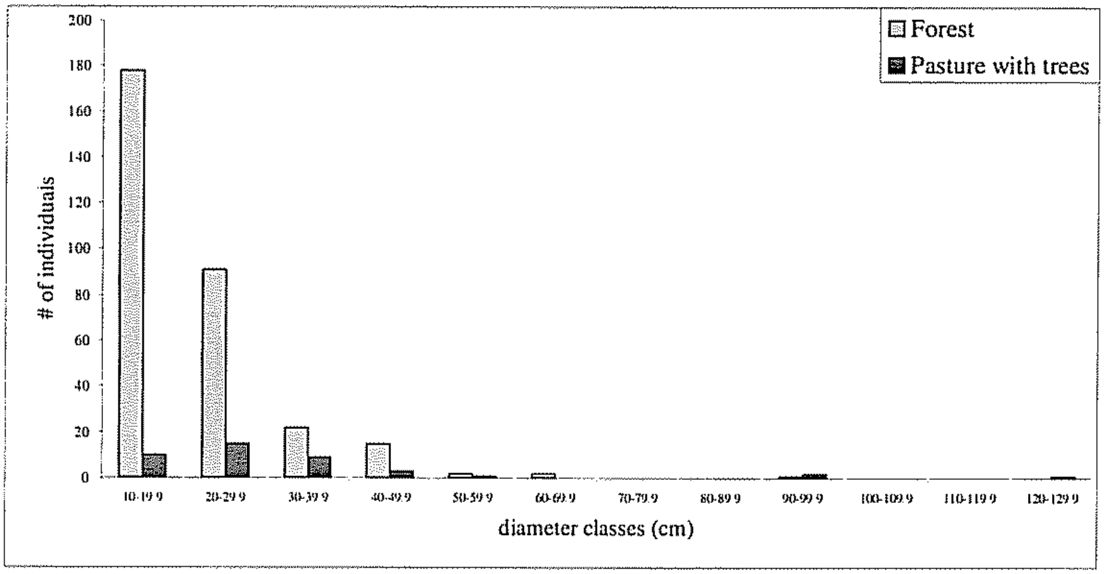

Figure 28. Frequency distribution of tree diameters in pastures with trees and habitat patches. Data represents the inventories from the cumulative data on 8 forest and 8 pasture with trees sites (total area for forests = 1.6 ha and pastures with trees = 3.2 ha).

The range of tree diameters was similar in both forests and pasture with trees (10 – 40 cm), however the diameter classes were more unevenly distributed in forests than in pastures with trees (Figure 28). There were fewer individuals in the smaller diameter classes in pastures with trees than in forests, suggesting regeneration, albeit very limited, in pastures in trees.

4.5.2 Bird diversity

There were no significant differences in either mean number of bird species/site (ANOVA, $F_{3,18}$ = 2.96, P > 0.078) or individuals (ANOVA: $F_{3,18}$ = 3.13, P > 0.068) between the three habitats (Figure 29). The p-values suggest differences (but not significant) between pairs of habitats but not across all three. There was significant difference in the mean Shannon diversity (Table 16) between habitats (ANOVA: $F_{3,18}$ = 4.02, P < 0.05; Table 3); these differences however, are marginal and are between pairs of habitats and not across all three. The equitability indices (Table 17) suggest a higher distribution of individuals within species identified in forests (mean = 0.30) than in both pastures with trees (mean = 0.20) and open pastures (mean = 0.18), however these differences are not significant among habitats.

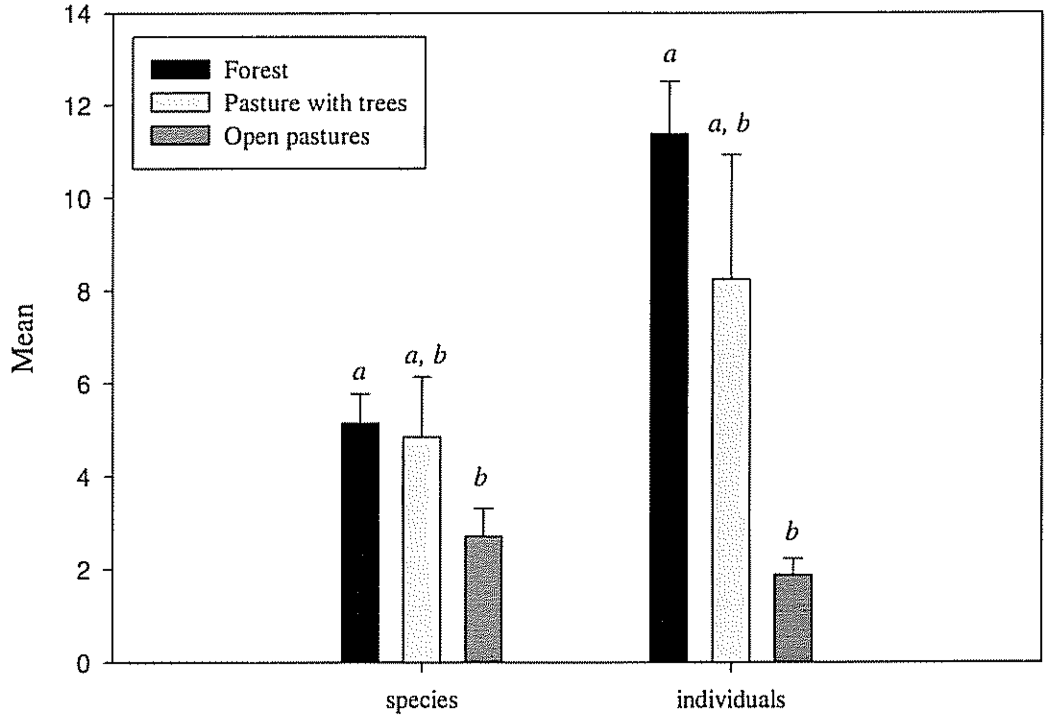

Figure 29. Mean # of bird species and individuals within forest, pasture with trees and open pastures. Bars show standard error. Means with different letters are significantly different ($P < 0.05$).

Table 16. Shannon diversity (*H*) indices for birds captured in all habitats. FO=forest, PT=pasture with trees, PA=open pastures. Means with different letters are significantly different ($P < 0.05$).

Site	FO	PT	PA
1	1.09	1.46	0.96
2	1.7	2.3	0
3	1.47	1.33	1.16
4	1.98	0	0.97
5	1.68	1.23	0
6	1.28	0	1.04
7	0.73	0.5	0
8	1.37	1.24	0.64
Mean	1.41*a*	1.00*a,b*	0.60*b*
SD	0.39	0.79	0.51

Table 17. Shannon's equitability indices (E_H) for the birds captured in all habitats. FO=forest, PT=pasture with trees, PA=open pastures

Site	FO	PT	PA
1	0.36	0.29	0.24
2	0.28	0.19	0.00
3	0.29	0.33	0.23
4	0.25	0.00	0.32
5	0.28	0.25	0.00
6	0.32	0.00	0.35
7	0.24	0.25	0.00
8	0.34	0.31	0.32
Mean	0.30	0.20	0.18
SD	0.04	0.13	0.16

Table 18. Bird species and individuals captured within all habitats and their guild and habitat associations. Within the feeding guilds, I=insectivores, F=frugivores, O=omnivores, N=nectarivores, G=granivores and within habitat guilds, FO=forest species, PT=pastures with tree species and PA=open pasture species.

Common Name	Species	Individuals	Guild	Habitat
Forest: 91 individuals, 17 species				
Long-tailed manakin	*Chiroxiphia linearis*	23	I/F	FO
Banded wren	*Thryothorus pleurostictus*	19	I	FO
Olive sparrow	*Arremonops rufivirgatus*	18	O	FO
Cinnamon hummingbird	*Amazilia rutila*	9	N	FO
Tropical gnatcatcher	*Polioptila plumbea*	4	I	PT/FO
Yellow-olive flycatcher	*Tolmomyias sulphurescens*	3	I/F	FO
Yellow-green vireo	*Vireo flavoviridis*	3	I/F	FO
Great crested flycatcher	*Myiarchus crinitus*	2	I/F	PT/FO
Kentucky warbler	*Opornis formosus*	2	I	FO
Steely-vented hummingbird	*Amazilia saucerrottei*	1	N	PT/FO
Rufous-naped wren	*Campylorhynchus rufinucha*	1	I	FO
Swainson's thrush	*Catharus ustulatus*	1	I/F	ALL
Fork-tailed emerald	*Chlorostilbon canivetii*	1	N	FO
Yellow warbler	*Dendroica petechia*	1	I	PT/FO
Common puaraque	*Nyctidromus albicollis*	1	I	PT/FO
Long-billed gnatwren	*Ramphocaenus melanurus*	1	I	FO
Yellow crowned tyranulet	*Tyrannus elatus*	1	I/F	PT
Pasture with trees: 66 individuals, 20 species				
Common ground dove	*Columbina passerina*	17	F/G	PA
Blueblack grassquit	*Volantinia jacarina*	8	F/G	PA
Striped-headed sparrow	*Aimophila ruficanda*	6	I/G	FO
Banded wren	*Thryothorus pleurostictus*	5	I	FO
Yellow-green vireo	*Vireo flavoviridis*	5	I/F	FO
Groove billed ani	*Crotophaga sulcirostris*	4	O	PT
White-collared seedeater	*Soporophila torqueola*	3	I/G	PA
Barred antshrike	*Thamnophilus doliatus*	3	I	FO
Rufous-tailed hummingbird	*Amazilia tzacatl*	2	N	PT/FO
Great crested flycatcher	*Myiarchus crinitus*	2	I/F	PT/FO
Yellow-olive flycatcher	*Tolmomyias sulphurescens*	2	I/F	FO
Grasshopper sparrow	*Ammodramus savannarum*	1	I/G	PA
Inca dove	*Columbina inca*	1	G	PA
White-tipped dove	*Leptotila verreauxi*	1	G	PT/FO
Boat billed flycatcher	*Megarhynchus pitangua*	1	I/F	PT/FO
Sulphur-bellied flycatcher	*Myiodynastes luteiventris*	1	O	FO
Social flycatcher	*Myiozetetes similis*	1	I/F	PA/PT
Indigo bunting	*Passerina cyanea*	1	O	PA/PT
Plain colored tanager	*Tangara inornata*	1	I/F	PT/FO
Yellow-crowned tyrannulet	*Tyrannulus elatus*	1	I/F	PT
Open pastures: 43 individuals, 8 species				
Blueblack grassquit	*Volantinia jacarina*	12	F/G	PA
Common ground dove	*Columbina passerina*	10	F/G	PA/PT
Plain breasted ground dove	*Columbina minuta*	7	F/G	PT
Gray-crowned yellowthroat	*Geothlypis poliocephala*	7	I	PA
Steely-vented hummingbird	*Amazilia saucerrottei*	2	N	PT/FO
Cinnamon hummingbird	*Amazilia rutila*	2	N	FO
Clay colored robin	*Turdus grayi*	2	I/F	PT/FO
Grasshopper sparrow	*Ammodramus savannarum*	1	I/G	PA

Of the 35 bird species captured, no species were found in all three habitats (Figure 30), 5 were found in both forest and pastures with trees, 2 in forest and open pastures and 3 in pastures with trees and open pastures.

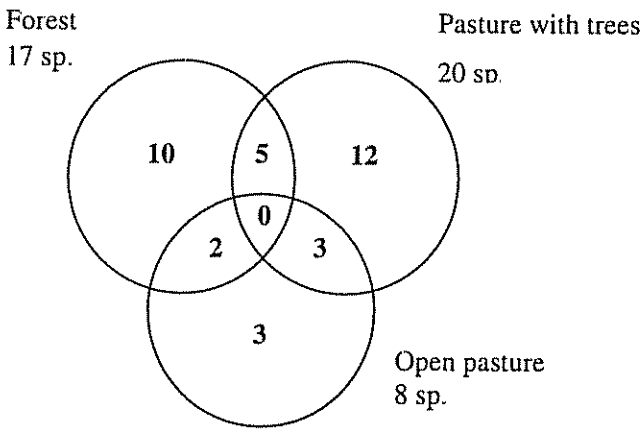

Figure 30. A Venn diagram showing the species distribution between the three habitats. Data represent information on all bird species captured and identified within all habitats.

The three habitats differed in species composition (Table 18), however there were close associations between habitat type and the feeding and habitat preferences of the birds species found within them (Figure 31; Annex 21). Species characterized as forest dwellers and insectivores were found mostly in forests, these bird species that preferred forests had diets that primarily included insects along other food types (i.e. fruits or grains). The species found in the pastures had mixed diets that included grains, fruits and insects, or a combination diet of insects and either grains or fruits (Figure 31b). Only three species (15 individuals) were exclusively insectivorous and of those three, two preferred forest habitats while the other was an open pasture species (Figure 31a, 31d). The nectarivores were found in all three habitats but in low numbers.

The forest bird species were found in all three habitats; they were concentrated in forest habitats, but a considerable number (7 of 15 species) were also captured in pastures with trees and open pasture habitats (Figure 32). The bird species recorded in pastures were generalist species capable of living in a combination of habitats, these species were found in both pastures with trees and open pastures but rarely in forest habitats (Figure 32b, 32c). Their dietary requirements probably restricted them from entering the forest habitats. Open pasture species were also present in pastures with trees, 4 of 5 open area species were found in pasture with trees (Figure 31c).

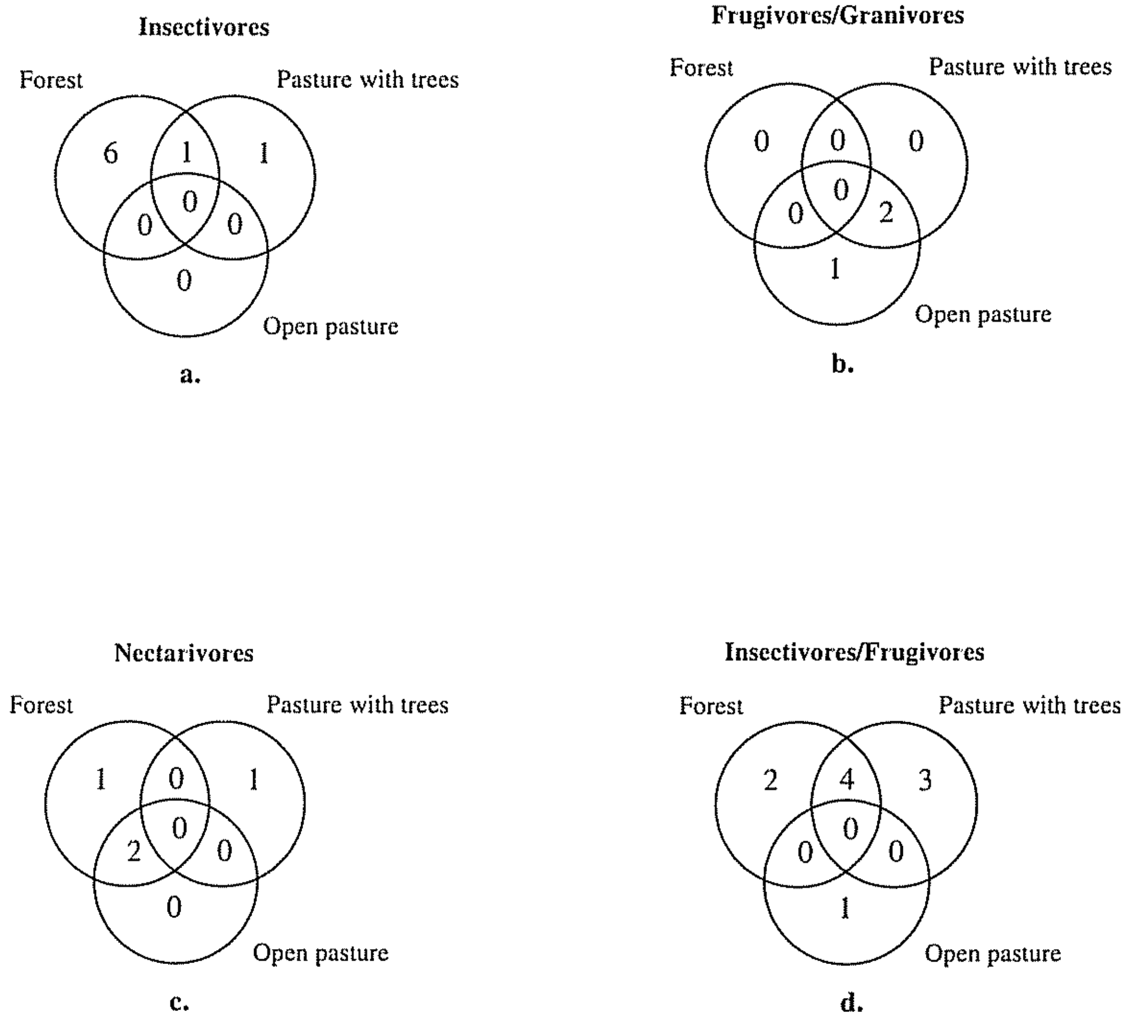

Figure 31. The distribution of bird feeding guilds between the three habitats. Data represent information on birds captured and identified within all habitats. Ten species are not included because they are poorly represented ($n = 1$). Habitat guild information was based on Stiles and Skutch (1989).

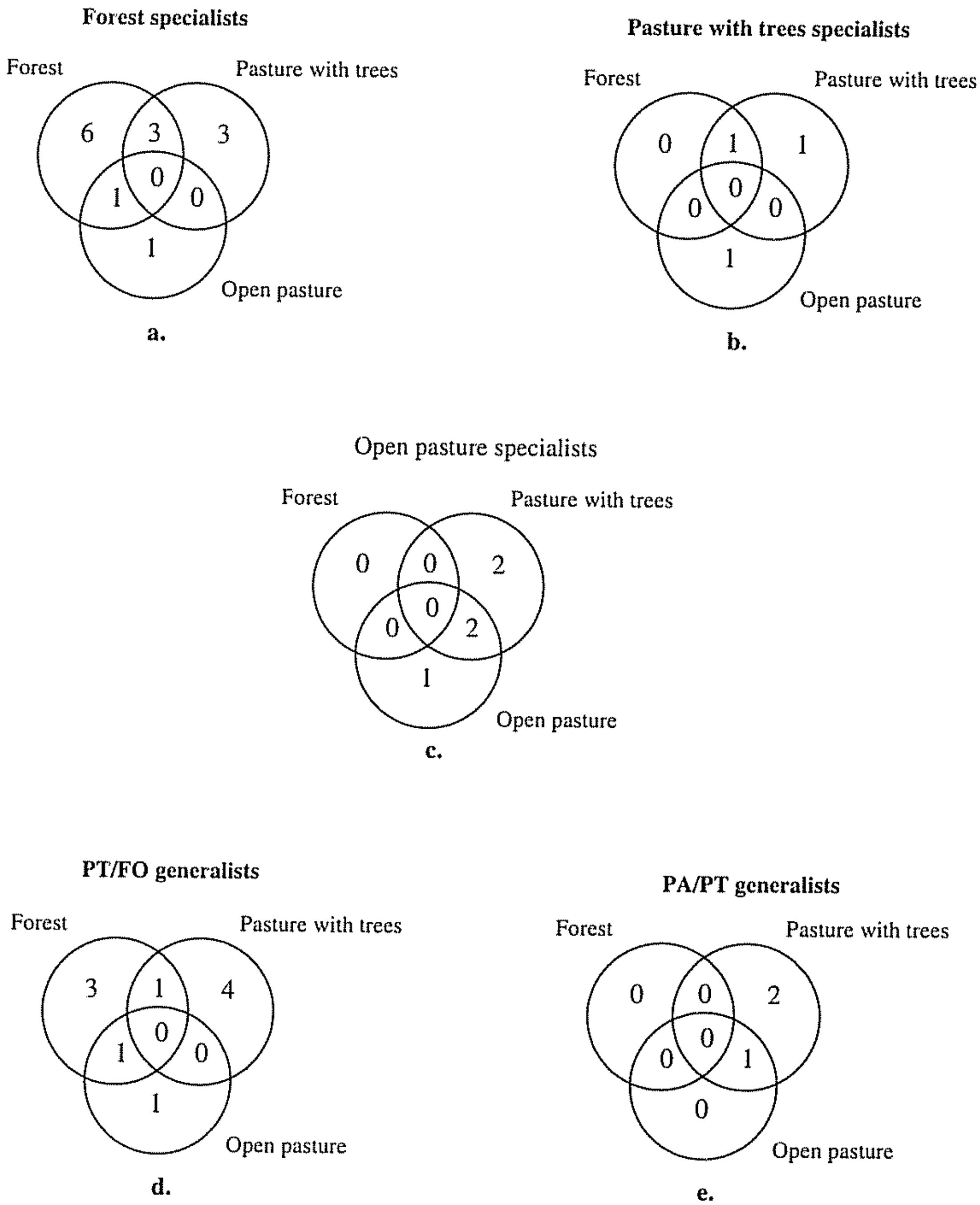

Figure 32. The distribution of bird habitat-guilds between the three habitats (a, b, c). The distribution of habitat generalists between the three habitats (d, e). Data represents information on birds captured and identified within all habitats. Habitat guild information was based on Stiles and Skutch (1989). PT/FO=species that are found in both pasture with trees (PT) and forest habitats (FO), PA/PT=species found in open pastures (PA) and pasture with trees (PT) habitats.

The species-area curves showed differences in bird species richness between the three habitats, with forests and pastures with trees having greater bird species richness than open pastures. Both forests and pastures with trees show similar tendencies in species accumulation, however the curves do not appear to reach an asymptote; this suggests that a greater area and sampling effort is necessary (Figure 33).

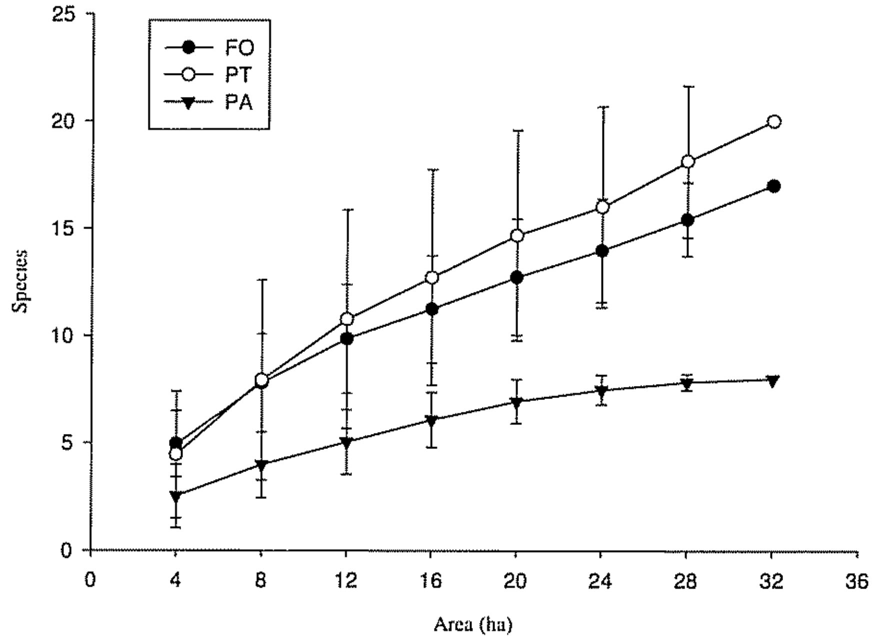

Figure 33. Species-area curves of all the bird species captured in all habitats. Each curve is based on the abundance within each habitat and the bars represent standard deviation.

4.5.3 Beetle diversity

There were significant differences in the number of species (ANOVA: $F_{3, 18} = 6.37$, $P < 0.05$) and individuals (ANOVA: $F_{3, 18} = 6.47$, $P < 0.05$), however the differences (and similarities) were between pairs of habitats and not between the three habitat types. The mean species/habitat was similar between forest and pasture with trees but lower in open pastures (Figure 34a). The mean abundance of dung beetles was higher in pasture with trees than in either forest or open habitats (Figure 34b). There was also a significant difference in the Shannon diversity indices (ANOVA: $F_{3, 18} = 6.22$, $P < 0.05$) among the three habitats. The species richness and diversity of dung beetles was higher in forest and pasture with trees than in open pastures (Table 19).

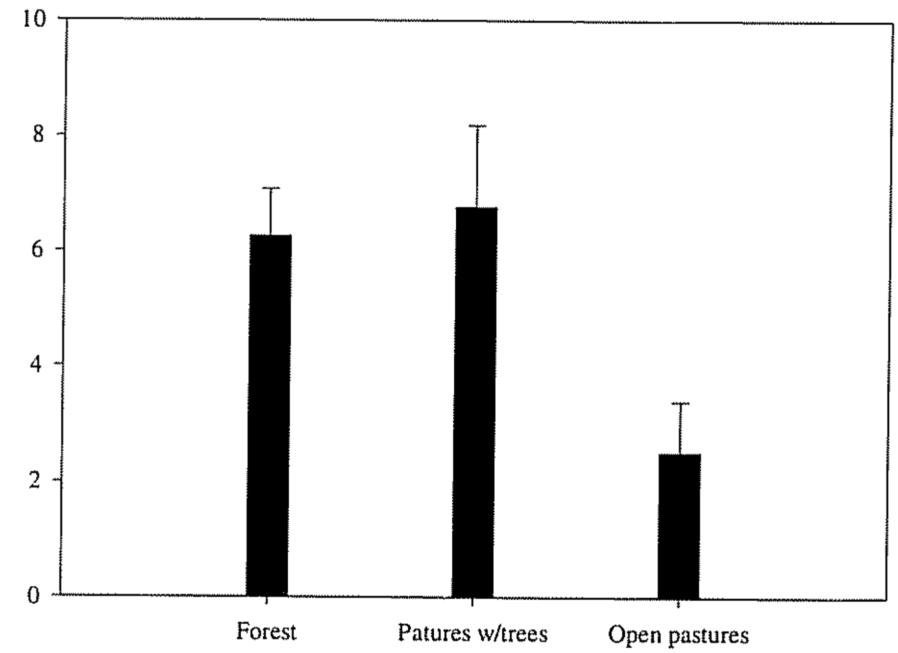

Figure 34a. Mean dung beetle species within forest, pasture with trees and open pastures. Bars show standard error. Means with different letters are significantly different ($P < 0.05$).

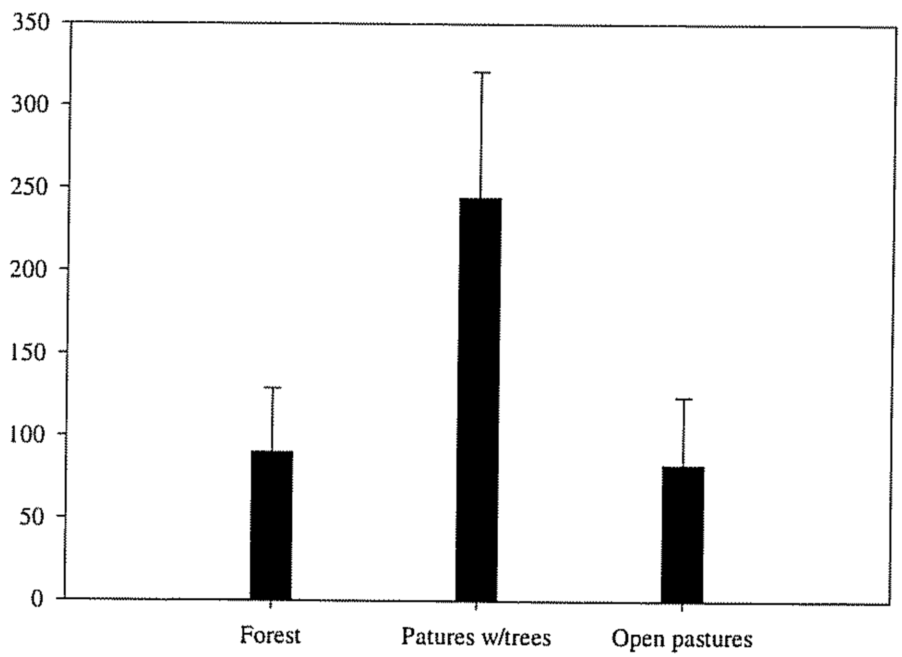

Figure 34b. Mean dung beetle individuals within forest, pasture with trees and open pastures. Bars show standard error. Means with different letters are significantly different ($P < 0.05$).

Table 19. Shannon diversity (*H*) for the beetles captured in all habitats. FO=forest, PT=pasture with trees, PA=open pastures. Means with the same letter are not significantly different.

Site	FO	PT	PA
1	1.66	1.84	1.63
2	1.65	1.58	0.43
3	1.46	0.61	0
4	0.94	0	0
5	1.06	0	0
6	1.88	1.47	1.38
7	0.89	1.46	0.89
8	1.65	1.48	1.39
Mean	1.39a	1.05a, b	0.71b
SD	0.13	0.26	0.24

The equitability indices showed that the dung beetles were more equally distributed among the species in forest habitats than in either pasture with trees or open pastures (Table 20).

Table 20. Shannon equitability indices (E_H) for the beetles captured in all habitats. FO=forest, PT=pasture with trees, PA=open pastures.

Site	FO	PT	PA
1	0.17	0.23	0.27
2	0.21	0.23	0.02
3	0.29	0.09	0.00
4	0.31	0.00	0.00
5	0.27	0.00	0.00
6	0.24	0.15	0.28
7	0.18	0.16	0.22
8	0.28	0.19	0.28
Mean	0.24*a*	0.13*b*	0.13*b*
SD	0.05	0.03	0.05

In each habitat, at least one beetle species was dominant (*O. landolti* in forest, *O. hoepfneri* in pasture with trees and *C. indigaceus* in open pastures) and represented >30% of the individuals within that habitat. Within each habitat, <60 individuals represented the majority of the species. Of the 17 dung beetle species identified, only 4 occurred in all three habitats. Five dung beetle species were found exclusively in forests (*Onthophagus championi, Uroxys sp., Dichotomius* *centralis, Canthon meridionalis* and *Onthophagus acuminatus*) and 3 exclusively in pastures with trees (*Canthon mutabilis, Phaneus eximius* and *Agomopus lampros*). No species were unique to the open pastures (Figure 35).

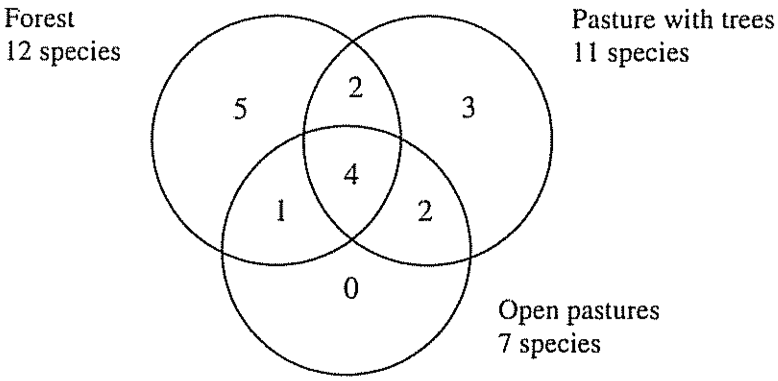

Figure 35. Venn diagram showing the species distribution among the three habitats. Data represent all the dung beetles captured within each habitat.

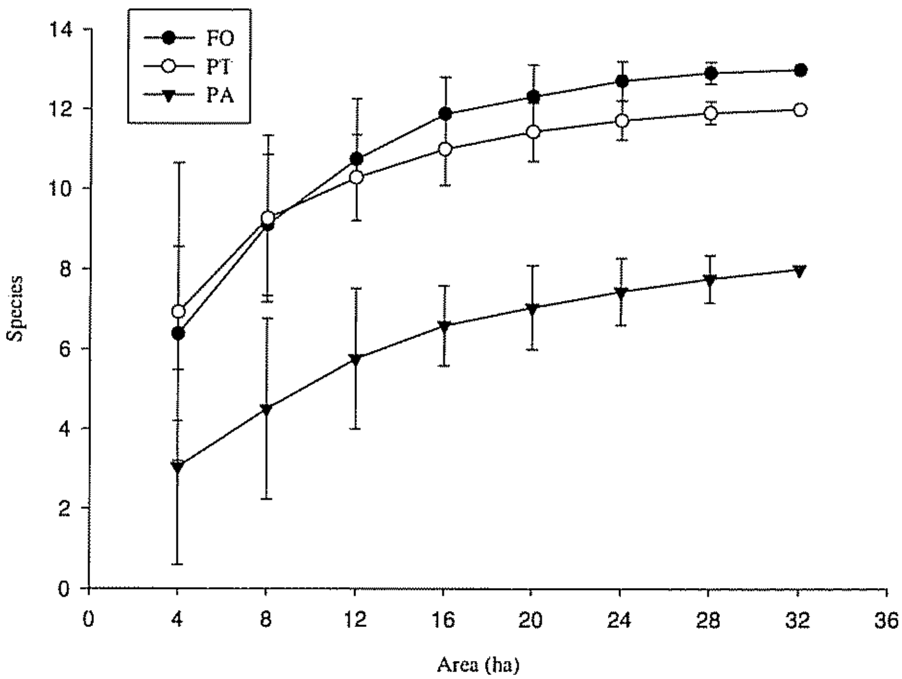

Figure 36. Species-area curves of all the beetle species captured in all habitats. Each curve is based on the abundance within each habitat and the bars represent standard deviation.

The species-area curves confirm that the beetle species richness in forest and pasture with trees is similar, whereas open pastures have much lower species richness (Figure 36). In all three habitats, the species-area curves appear to reach an asymptote, suggesting that most of the beetle species present in each of the habitats were identified and that the sampling effort was sufficient.

4.5.4 Small Mammal diversity

The numbers of small mammals (Order: Rodentia, Family: Heteromyidae and Muridae) captured were insignificant. The individuals captured belonged to two species, *Heteromys desmarestianus* and *Sigmodon hispidus*. These two species have been extensively investigated and documented at the nearby Ingenio Taboga. Investigations suggest that the abundance of these species is cyclical (Alvarez, personal communication; Ruiz, 1992), with the populations fluctuating (high-low) every 5 years. During the time I conducted my investigation populations were low, hence the low capture rates

4.6 Diversity and tree cover

4.6.1 Bird diversity

There was a strong positive correlation between the percent tree cover at all three radii distances (100, 350, 600 m) and the # of bird species at a given site, with significant correlations ($P < 0.05$) at 100 and 350 m (Table 21). Similarly, there were strong positive and significant correlations ($P < 0.05$) between the surrounding tree cover (at all 3 radii) and # of birds at a given site.

Table 21. Correlations (Pearson's *r*) between the tree cover at three radii (100, 350 and 600 m) and bird species and abundance

	100m	350m	600m
species	0.42371*	0.45081*	0.38878n.s.
individuals	0.49221*	0.46473*	0.40797*

* = signficant (P < 0.05)
n.s. = not significant (p=0.06)

4.6.2 Beetle diversity

There was no correlation between the % tree cover at 100 m (3.1 ha), 350 m (38.5) and 600 m (113.1 ha) radii and dung beetle species or abundance.

5.0 DISCUSSION

The tree cover within the study area is typical of the Cañas landscape, is highly heterogeneous and varies according to the topography. The tree cover is concentrated in forest fragments, which occur at the highest points on hills or hillocks (or montañas, as they are referred to by locals) or as strips of riparian forest along streams and rivers. These riparian forests are obligatory, and protected under Costa Rican law (which requires a buffer of at least 50 m along streams). In addition to providing additional habitat, the riparian forests greatly enhance the connectivity of the landscape, connecting individual forest patches within the landscape. The matrix surrounding the forest fragments is comprised of pastures, in which local farmers have retained remnant trees or allowed trees that serve multiple purposes for cattle production benefits and household uses to regenerate (Budowski, 1993). Live fences also border many of the pastures. The tree cover in pastures may have a buffer effect for the fauna inhabiting the forest patches by providing alternative food sources, lessening the impact of habitat and forest cover loss and enhancing landscape connectivity.

The heterogeneity of the tree cover has important consequences for the abundance, species richness and diversity of birds, beetles and other organisms at both the local and landscape scale. At the local scale, individual habitats (open pastures, pastures with trees, forests), differ in tree density, species richness and composition, with forests having much higher tree densities and species richness than pastures.

The relative importance of tree cover was noticeably different between the two groups of organisms studied (birds and dung beetles) and may in part depend on the dispersal ability of individual organisms and their dependence on tree cover. The two organisms sampled were of high mobility (birds) and low mobility (dung beetles). The differences in species richness and abundance, suggest that organisms of differing dispersal capabilities may perceive tree cover at different scales and may be affected differently by the distribution and density of tree cover in any given landscape. The local tree cover affected bird species composition (but not species richness or abundance), while tree cover at a larger scale (at 100 and 250 m radii) affected both bird species richness and abundance. In contrast, dung beetles, which are of limited mobility responded clearly to local tree cover (at the habitat scale) but showed no apparent response to the tree cover surrounding each habitat.

There are several limitations to this study. The mist netting results may not provide a true picture of the bird diversity that exists in the study area because mist nests capture only a subset of the total bird species present; therefore a combination of methodologies for avifauna data collection is necessary. The main limitation for the dung beetles was the season in which data were collected: the majority of the data was collected during the dry months and a few weeks of the rainy season (February to July, 2001). The majority of the dung beetle specimens were collected during the first weeks of the rainy season mainly because these insects easily emerge from underground because of the softened ground and food availability is high since restocking of cattle also occurs during this time. In order to reduce the effect of temporal patterns on dung beetle species numbers and abundance, and to obtain a true account of dung beetle populations, sampling should occur throughout the year to account for fluctuations in their populations during the rainy and dry seasons.

5.1 Differences in tree cover in different habitats

The tree cover varied greatly in all three habitats (open pastures, pastures with trees and forests); the open pastures completely lacked trees, and except for the occasional live fences these were the least diverse of the three habitats. Forest habitats had a significantly higher densities and species richness of trees than the pastures with trees (forests had 44 species vs. 17 in pastures with trees). The forest habitats also had steeper species-area curves indicating that their total species richness is likely significantly higher than that of pastures with trees. The forest habitats possessed higher tree diversity (mean Shannon index = 2.18) than pasture with trees (mean Shannon index = 0.85), however pastures with trees had a higher mean equitability index (0.23) than forest habitats (0.19).

Even though the forests habitats had a higher density of trees per unit area than pastures with trees, there was better distribution of individuals among species in pastures with trees and hence a higher equitability. Within the forest habitats almost 60% of the individuals were represented by a few species (*G. ulmifolia, C. alliodora, E. salamensis, Cupania guatemalensis, Apeiba tibourbou,* and *Byrsonima crassifolia*). In the pasture habitats, the pastures with trees habitats *G. ulmifolia* and *Acrocomia aculeata* represented 54% of the individuals. *Guazuma ulmifolia,* a characteristic tree species of the Pacific regions, was the dominant species (Budowski and Russo, 1993; Alvarez and Sanchez-Vindas, 1999; Madrigal *et al.*, 1999) in both forest and pasture habitats. The tree species composition differed between habitats: 36 species were found in forest habitats, 9 species only in pastures with trees and 8 species were present in both habitats.

The forest and pastures with trees had a similar range of tree diameters (10 to 99.9 cm) although the forest had much higher tree densities in all diameter classes. The presence of a few large trees within the pastures suggests that these trees are probably remnants from earlier timber harvesting operations. Tree regeneration within forests was high, as evidenced by the high abundance of small trees, which represented 57% of tree individuals (diameter 10 - 19.9 cm); in contrast regeneration within pastures was more limited, with smaller diameter trees comprising only 13% of the tree individuals (diameter 10 - 9.9 cm). Regeneration is probably higher within the forests because of higher seed input, more favorable microclimate and soil conditions, and because of limited grazing.

The differences in tree density and species richness between forests and pasture with trees reflect differences in land management (Guevara *et al.*, 1992; Guevara *et al.*, 1998, Stokes, 2001). Forests are minimally managed and only sporadically grazed and therefore retain a high plant diversity. In contrast, pastures are managed for cattle production and tree cover is limited to avoid competition with grass. Although the pasture with trees possessed a lower tree species richness, abundance and diversity than forests, the presence of trees within pastures may important be for conservation efforts, enhancing the floristic diversity and providing food resources and habitats to fauna (Harvey and Haber, 1999; Estrada *et al.*, 2000).

5.2 Bird diversity and tree cover

5.2.1 Effects of local tree cover on bird diversity

The tree cover had an effect on the species richness and abundance of birds. The forest areas and pastures with trees, both had a greater species richness and abundance than open pastures; however there was no significant difference between forests and pastures with trees. Interestingly, there were marked differences in the species composition among the three habitats. The lack of significant differences in abundance and species richness across all three habitats may be attributable to a low sampling effort and the bird identification method employed (mist-netting). Although mist-netting is an effective method for capturing understorey and low flying birds, it should be combined with other bird identification techniques to sample the entire bird community present. An increased sampling effort combined with mist net trapping and point counts, which rely on audio-visual identification, may unmask additional differences among the three habitats and better quantify species richness and abundances

There were clear differences between the bird communities present in the three habitat types. The forest habitats had the greatest diversity of avifauna (total # of spp. = 17) and a greater equitability of species while the open pastures were the least diverse (total # of spp. = 8) and had the most unequal distribution of individuals among its species. Although the pasture with trees had the highest number of species (n = 20), bird species were not recorded in two sites, which reduced its overall diversity index; its equitability value was also considerably less than forests (0.30 vs. 0.20). The results suggest that pastures with trees provide resources to a high diversity of bird species in a similar manner as the forest habitats, whereas open pastures provide resources to only to a limited number of specialized species. The species distribution among sites of the same habitat type may be affected by factors such as proximity to nesting habitat, presence of tree cover and density of tree cover and food availability.

The bird feeding guild composition differed greatly among the three habitats and was closely associated with habitat preference. The majority of the bird species found in forest habitats were forest specialists and belonged to one feeding guild (insectivores), while the bird species found in pastures with trees were generalists both in habitat and diet requirements. Most of the forest specialist species were found in the forest habitats; however, some forest specialists were also found in the other two habitats. I observed that the forest specialists may not be limited to forests since they may also need to supplement their diet with fruits and seeds, which are available in pastures with trees and in live fences, hence the high capture rates of forest specialists in pastures with trees. The generalist species are able to use forest habitats, but are also able to exploit the resources found in pastures and actively forage in them. I found five open habitat species but only one was found exclusively in open pastures; the rest were found in both open pastures and pasture with trees.

Birds are not limited by mobility and can easily disperse throughout the landscape matrix in search of food resources. Consequently, the forest dwelling bird species, which were found in more than one habitat, were observed foraging elsewhere for food resources that could not be found in their habitat. This suggests that trees in pastures (pastures with trees) may provide complementary resources of food and adequate tree cover to forest bird species. On the other hand, birds typical of pasture or open habitats were rarely found within forest habitats, possibly because the forest habitats could not contribute to their diet.

The presence of bird species (including forest specialists) in both open pastures and pastures with trees suggests that many species are able to utilize all the components of the fragmented landscape, irrespective of habitat type. Daily *et al.*, 2001 and Daily and Luck (*in press*), found a similar pattern of habitat and resource utilization in the landscape components in a study conducted in Las Cruces Biological Station, Costa Rica. Similar to Estrada *et al.* (2000) and Daily *et al.* (2001), I was able to determine that generalist species (especially those that can forage within disturbed areas) use open pastures and pasture with trees for food resources, however they may not use open pastures as long-term habitats. The open pastures are likely to be unsuitable for many of the bird species captured and only the open area species reproduce within these habitats; on the other hand pastures with trees may provide the necessary resources to bird species that can survive in disturbed areas and to forest dwelling species.

5.2.2 Effects of tree cover at larger scales (3.1, 38.5 and 113.1 ha) on bird diversity

There were no strong relationships between tree cover and species numbers and abundance of birds at the local habitat scale, however, both bird abundance and species richness were positively correlated to tree cover at the 100 (13.1 ha) and 350 m (38.5 ha) radii surrounding each habitat. This suggests that bird species richness and abundance may be responding to tree cover at larger scales. A study conducted by Daily and Luck (*in press*) at Las Cruces Biological Station, Costa Rica, revealed that spatial scale and tree cover greatly influence the bird species richness and abundance.

Birds probably respond to tree cover at a larger scale because they are highly mobile organisms and are able to disperse large areas in search of habitat, resources and nesting sites and may use tree cover throughout a large area. Daily and colleagues (2001) and Daily and Luck, (*in press*) in their studies at Las Cruces Biological Station, Costa Rica, used scales (<2 km and 5 – 8 km) larger than that used in this study and similarly found that the bird response varied depending on tree cover and spatial scales. Specifically, they found that there were no significant differences at small spatial scales with increased tree cover; however, they noted differences at larger spatial scales with decreasing tree cover. They also suggest that spatial scale and tree cover influences bird response to the landscape, however they could not determine the optimum scale at which bird response to the landscape may be measured.

It is likely that the presence of forest fragments around pasture areas has increased the presence of birds within the open pastures and pastures with trees, as many organisms may be moving between habitats. This may account for the fact that there was similar species richness and abundance of birds between all three habitats.

5.3 Dung beetle diversity and tree cover

5.3.1 Effects of local tree cover on dung beetle diversity

Dung beetle species richness and abundance differed significantly among the forest, pasture with trees and open pasture habitats. The forest habitats and pasture with trees had significant more dung beetle species and a greater overall diversity (H') than open pastures; whereas, the pasture with trees had greater mean beetle abundance than either the forests or the open pastures.

Dung beetle ecology is poorly known, however the majority of species found in the forest habitats are specialized to forest conditions and are stenotopic (i.e. affected by variations in microclimatic conditions) When forests are cleared, many specialized dung beetle species usually disappear because they tend to avoid open areas due to inappropriate tree cover and habitats, low food availability, and generally inhospitable conditions that exclude the specialized species (Klein, 1989; Kirk, 1992). The microclimatic conditions of the open pastures greatly inhibit occupation by large beetle diversity even though there is ample food available, which explains why in this study, simple ecosystems such as open pastures contained significantly lower species richness than the remaining forest habitats and pastures with trees (Halffter, 1991). Tree shade is an important feature in pastures with trees, which when combined with ample food availability provides the conditions for a high beetle abundance and species richness.

The species richness and abundance of dung beetles is influenced by many factors, with habitat preference, food availability and mobility ranking among the most important. In this study, the presence of four dung beetle species (*Onthophagus hopfneri, Onthophagus marginicollis, Dichotomius annae, Copris lugubris*) in all three habitats suggests that some dung beetle species are adaptable to different habitats. In addition, the presence of dung beetle species such as *Canthon indigaceus, Onthophagus hopfneri, Onthophagus marginicollis, Dichotomius annae, Phaneus demon, Copris lugubris and Onthophagus batesi* in open pastures suggests that these species may have become adapted to the harsh conditions of open pastures and are now common in these pasture habitats.

I found five dung beetle species exclusively in forest habitats, and three in pastures with trees, however the majority (9 species) were shared in various combinations among the three habitats. This occurrence suggests movement and adaptation by dung beetles to various habitats in the landscape matrix. The presence of dung beetles species in pastures with trees suggests the ability of dung beetles to survive in man made habitats, which still retain trees and provide shade. Kirk, (1989, Santa Cruz Province, Bolivia), Halffter (1991) and Halffter *et al.*, (1992; Los Tuxtlas, Veracruz, Mexico) similarly reported the incidence of beetle species shared between pasture and forest habitats.

It is likely that a relatively high number of dung beetle species were abundant within pasture with trees because the pasture with trees were adjacent to forest areas, and may serve as buffers or forest edges, as they have intermediate microclimatic conditions between forests and pastures. This may increase the probability of survival for forest edge species to survive in pasture areas, and may account for the shared species between forest and pastures with trees habitats. Similar results were reported by Halffter *et al.*, 1992 and Estrada *et al.*, 1998 (Los Tuxtla, Veracruz, Mexico).

Interestingly, most of the dung beetles in forest habitats were represented by few species while in the pasture with trees and open pastures there was a more equal distribution among species. This pattern is typical of most tropical forests, in which there is an unequal distribution of individuals among a few species that are very abundant, and few individuals distributed among many species mainly because of increased competition for limited resources (Halffter *et al.*, 1991; Hanski, 1991 and Halffter *et al.*, 1992). In contrast this pattern is less evident in pastures with trees perhaps because of the greater availability of dung. Kohlmann and Sanchez-Colon, Halffter, (1991) and Estrada and colleagues (1998) similarly reported an even distribution of dung beetles among species and an abundance of dung beetles across all species in pastures.

5.3.2 Effects of tree cover at larger scales (3.1, 38.5 and 113.1 ha) on beetle diversity

The abundance or species richness of dung beetles within a given habitat did not appear to be affected by the tree cover surrounding the patch, at the 3.1, 38.5 or 113.1 ha distance. This suggests that dung beetles respond primarily to the local tree cover, but remain unaffected by tree cover at greater scales. Local tree cover is important because it provides a set of microclimatic conditions that include temperature, humidity, soil temperature and degree of solar incidence (Mathews, 1974; Halffter 1991; Halffer and Arellano, *in press*), that are appropriate for dung beetles; furthermore it also provides rotting fruits and leaf litter that can be used as food and/or nesting sites by some species.

5.4 Implications of the study

This study provides baseline information on the effect of tree cover at the local (habitat) and landscape level on birds and dung beetles. It is an also an important first attempt to characterize the floristic and faunistic diversity of a representative area in the Cañas, Guanacaste landscape during the dry season (February to July). However, existing data needs to be supplemented by other data collection techniques, conducted over longer temporal intervals (including both wet and dry seasons), to more accurately determine the effects of trees cover on biodiversity

The study demonstrates the importance of tree cover at both local and landscape scales in determining the abundance, species richness and composition of organisms present. It shows that the tree cover at the local, habitat scale affects both the bird and dung beetle communities, and that tree cover in the surrounding landscape affects the bird communities (but not the dung beetle community).

This study has shown the importance of pastures with trees and their contribution in supporting biodiversity within fragmented landscapes. Although pastures with trees have lower floristic diversity than forests, they nevertheless are used by a variety of dung beetles and bird species. In addition, it adds to the growing literature on the importance of forest fragments, remnant trees and silvopastoral systems in the conservation of biodiversity in agricultural landscapes (Guevara *et al.*, 1992; Budowski, 1993; Estrada *et al.*, 1998; Estrada *et al.*, 2000).

Isolated trees in pastures are especially important within fragmented landscapes for birds, since they serve as foci for the dispersion of seeds (Harvey, 2000; Guevara and Laborde, 1993), as nesting sites, food sources, perching sites, cover and stepping-stones across the landscape (Harvey *et al.*, 1999; Guevara *et al.*, 1998; Guevara *et al.*, 1992; Estrada *et al.*, 1998). In addition, trees provide the necessary cover that creates the appropriate microclimatic conditions (temperature, humidity, soil temperature) for dung beetles and for many other organisms (Halffter, 1991; Kirk, 1989; Halffter *et al.*, 1992; Klein, 1989). Dung beetles are affected greatly by changes in the microclimate, especially since decreased forest cover dries the dung and soil faster and generally creates inhospitable conditions for the specialized dung beetle species. Some species of dung beetles also utilize trees as perch sites to pick up scents and as stepping-stones in a similar manner as birds (Halffter and Arellano, *in press*).

This study suggests that both habitat types and local landscape tree cover influence the distribution of organisms and that different organism respond differently to tree cover. In order to better understand the relationships that exist, it is important to consider measuring tree cover and species richness at all scales, since as this study shows the patterns in abundance and diversity will vary with tree cover at many spatial scales.

Conservation strategies must start using an integrated landscape (and eventually an ecoregional approach) to biodiversity conservation to ensure the conservation of all species, and maintenance of the ecological processes within the landscape. Conservation strategies must now focus on monitoring sets of organisms with varied responses to the landscape matrix, as opposed to the traditional single-species monitoring approach, in order to get a better perspective of the actual state of biodiversity within fragmented landscapes. It is also important to identify the most significant threats to areas of concern and the most effective strategies to mitigate them. This approach requires a clear understanding of the relationships between tree cover at the local and large scale and the abundance, and diversity of different organisms and their response to the landscape matrix.

6.0 CONCLUSIONS

The habitats within fragmented landscapes vary in tree density, diversity and species richness. The differences in tree cover in turn affect the diversity, species richness and abundance of the organisms within the habitats. There were significant differences among habitats in the species richness, diversity and abundance of dung beetles and birds. Dung beetle species richness and diversity was higher in forest and pastures with trees than in open pastures, whereas pastures wth trees had the higher abundances of dung beetles than either forests or open pastures. Bird species richness and abundant was greater in forests and pastures with trees than in open pastures, however there were no differences between bird species richness and abundance between forests and pastures with trees. At the landscape scale, dung beetles showed no response to the surrounding tree cover, while the bird species richness and abundance responded positively to increased tree cover at increasing landscape scales.

In general the forest habitats possessed a high diversity of flora and fauna. The species richness of flora and fauna was greatest in forest habitats than in pastures with trees and open pastures. The pastures with trees possessed an intermediate diversity of bird and dung beetle generalist species and appear to provide resources to some forest specialists. Although the pastures with trees habitats possess lower tree diversity than forest habitats, they provide habitat, adequate tree cover and food resources to a great range of biodiversity and may serve as complementary habitats (to forest habitats) to some fauna. The open pastures were the most species poor of the three habitats, possessing a low species richness and abundance of bird and dung beetle species.

It is difficult to assess the effect of anthropogenic disturbance in ecosystems through the use of single species indicators. Therefore it is important to select multiple species indicators to determine the impact of anthropogenic landuse on ecosystem change in the landscape. This approach is essential to establish the best management strategy which balances economic sustainability and biodiversity conservation goals.

7.0 RECOMMENDATIONS

The relationships that exist between landscape components and biodiversity must be fully understood in order to develop conservation strategies for biodiversity management. This is especially important in fragmented landscapes in which biodiversity is under constant anthropogenic pressure. It is also necessary that research start focusing on evaluating multiple species and groups, since different species appear to react differently to the habitats and habitat modifications within the landscape. Since the tree cover appears to affect both the high and low mobility organisms differently at varying spatial scales, it is also important to focus evaluations at both local and landscape levels.

Criteria must be established when sampling species of varying dispersal capabilities and feeding and habitat guild requirements. Sampling different organisms only at the landscape level paints a false picture of the interactions that exist at the local level and vice versa. The dispersal range and mobility of the organism should be used determine the intensity and scale at which it should be sampled. The temporal patterns of the weather and spatial patterns of the landscape matrix influence the numbers of species and abundances of species identified, as does the methodology employed for fauna identification. In order to account for the temporal weather patterns, sampling throughout the year both in dry and wet weather months is important. The sampling design must utilize the maximum sampling effort and larger sample areas for high mobility organisms On the other hand, a systematic sampling design at the local habitat or microhabitat level is necessary for the low mobility species.

The methodology employed for fauna identification determines the success of any study. In order to obtain a good representation of the species diversity that exists within any given landscape, a combination of data collection methodologies should be used. In the case of birds, visual identification, vocalization and mist netting can be used. During known nesting periods, nest counts may also be conducted. In the case of dung beetles pit-fall traps in combination with beetle collection at dung mounds is recommended.

There should be more research conducted of organisms' behavior within habitats of varying tree cover, their use of the habitats and of the tree resources available to them, and of their life history. These researches should also aim to contribute supplementary data on the role of trees in the rural landscape and their contribution to biodiversity conservation.

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ANNEXES

Annex 1: Tree species identified within forest habitats, 311 individuals, 43 species, 25 families.

Family	Scientific Name	Common Name (sp)	Indiv.
Sterculiaceae	*Guazuma ulmifolia*	Guacimo	71
Boraginaceae	*Cordia alliodora*	Laurel	38
Myrtaceae	*Eugenia salamensis*	Moridero, Fruta de pava	27
Sapindaceae	*Cupania guatemalensis*	Manteco	20
Tiliaceae	*Apeiba tibourbou*	Peine de mico	16
Malpighiaceae	*Byrsonima crassifolia*	Nance	16
Tiliaceae	*Luehea candida*	Guacimo molenillo	11
Chrysobalanaceae	*Hirtella racemosa var. hexandra*	Serrecillo	8
Fabaceae	*Lonchocarpus spp.*	Chaperno	8
Fabaceae	*Caesalpinia eriostachys*	Saino	7
Bixaceae	*Cochlospermum vitifolium*	Poro poro	7
Tiliaceae	*Luehea seemannii*	Guacimo colorado	7
Fabaceae	*Enterolobium cyclocarpum*	Guanacaste	6
Papilionaceae	*Piscidia carthagenensis*	Pellejo de toro, Siete cueros	6
Mimosaceae	*Lysiloma divaricatum*	Quebracho	5
Bombacaceae	*Ochroma pyramidale*	Balsa	5
Annonaceae	*Anona reticulata*	Anona silvestre	4
Meliaceae	*Cedrela odorata*	Cedro amargo	4
Fabaceae	*Acosmium panamense*	Carboncillo	3
Mimosaceae	*Albizia niopoides*	Gallinazo, Guanacaste blanco	3
Moraceae	*Artocarpus altilis*	Fruta de pan	3
Bixaceae	*Bixa urucurana*	Achiote silvestre	3
Rubiaceae	*Calycophyllum cadidissimum*	Madroño	3
Flacourtiaceae	*Casearia corymbosa*	Cerito	3
unknown	sp. 1	unknown	3
Chrysobalanaceae	*Licania arborea*	Alchornoque	2
Papilionaceae	*Lonchocarpus rugosus*	Carao Macho	2
Lauraceae	*Ocotea veraguensis*	Canelo	2
Anacardiaceae	*Spondias mombin*	Jobo	2
Apocynaceae	*Stemmadenia donnell-smithii*	Cohón de chancho	2
Bignoniaceae	*Tabebuia ochracea*	Corteza amarillo	2
Bombacaceae	*Bombacopsis quinata*	Pochote	1
Moraceae	*Brosimum alicastrum*	Ojoche	1
Burseraceae	*Bursera simaruba*	Indio desnudo	1
Polygonaceae	*Coccoloba sp*	Papaturro	1
Papilionaceae	*Gliricidia sepedium*	Madero negro	1
Rubiaceae	Guaitil	Genipa americana	1
Moraceae	*Maclura tinctoria*	Mora silvestre	1
Mimosaceae	*Zygia longifolia*	Sotacaballo	1
Mimosaceae	*Pseudosamanea guachapele*	Gavilán, Guayaquil	1
Fabaceae	*Samanea saman*	Cenizaro	1
Meliaceae	*Swietenia macrophylla*	Caoba	1
Combretaceae	*Terminalia oblonga*	Surá	1

Annex 2: Tree species found within the forest habitats, their abundance within each site, their frequency and percentage they occupy of all the species identified within the forest habitats. The species are arranged in order of abundance; frequency refers to the occurrence of species (out of 8 sites) and total refers to abundance.

Family	Scientific Name	Common Name (sp)	individuals/site								frequency	total	%
			1	2	3	4	5	6	7	8			
Sterculiaceae	*Guazuma ulmifolia*	Guacimo	7		14	20	3	12	4	11	7	71	22.8
Boraginaceae	*Cordia alliodora*	Laurel	7	14	8	3	2	1	2	1	8	38	12.2
Myrtaceae	*Eugenia salamensis*	Moridero, Fruta de pava	1	1		1	12	5	3	4	6	27	8.7
Sapindaceae	*Cupania guatemalensis*	Manteco	3		1	5	5	4		2	6	20	6.4
Tiliaceae	*Apeiba tibourbou*	Peine de mico				7		3	3	2	4	15	4.8
Malpighiaceae	*Byrsonima crassifolia*	Nance				14	1			1	3	16	5.1
Tiliaceae	*Luehea candida*	Guacimo molenillo		1	1	3	2	2		3	6	12	3.9
Chrysobalanaceae	*Hirtella racemosa var. hexandra*	Serrecillo				3	3	2			3	8	2.6
Fabaceae	*Lonchocarpus spp.*	Chaperno	4		3				1		4	8	2.6
Fabaceae	*Caesalpinia eriostachys*	Saíno	4		2				1		3	7	2.3
Bixaceae	*Cochlospermum vitifolium*	Poro poro		1	3				2		3	6	1.9
Tiliaceae	*Luehea seemannii*	Guacimo colorado						2	1	4	4	7	2.3
Fabaceae	*Enterolobium cyclocarpum*	Guanacaste		4						2	2	6	1.9
Papilionaceae	*Piscidia carthagenensis*	Pellejo de toro, Siete cueros	2		1				3		3	6	1.9
Mimosaceae	*Lysiloma divaricatum*	Quebracho	1			2				2	3	5	1.6
Bombacaceae	*Ochroma lagopus*	Balsa							5		1	5	1.6
Annonaceae	*Anona reticulata*	Anona silvestre				1	3				2	4	1.3
Meliaceae	*Cedrela odorata*	Cedro amargo							4		1	4	1.3
Fabaceae	*Acosmium panamense*	Carboncillo				1	1	1			2	3	1.0
Mimosaceae	*Albizia niopoides*	Gallinazo, Guanacaste blanco				1		1		1	3	3	1.0
Moraceae	*Artocarpus altilis*	Fruta de pan		1			2				2	3	1.0
Bixaceae	*Bixa urucurana*	Achiote silvestre	1		1	1			1		4	4	1.3
Rubiaceae	*Calycophyllum cadidissimum*	Madroño	1		1				1		3	3	1.0
Flacourtiaceae	*Casearia corymbosa*	Cerito	2		1						2	3	1.0
unknown	*sp. 1*	unknown				3					1	3	1.0
Chrysobalanaceae	*Licania arborea*	Alchornoque	1		1						2	2	0.6
Papilionaceae	*Lonchocarpus rugosus*	Carao Macho				1		1			2	2	0.6

Annex 2: cont'd.

Family	Scientific Name	Common Name (sp)	individuals/site								frequency	total	%
			1	2	3	4	5	6	7	8			
Lauraceae	*Ocotea veraguensis*	Canelo							2		1	2	0.6
Anacardiaceae	*Spondias mombin*	Jobo	1		1						2	2	0.6
Apocynaceae	*Stemmadenia donnell-smithii*	Cohón de chancho	1		1						2	2	0.6
Bignoniaceae	*Tabebuia ochracea*	Corteza amarillo					2				1	2	0.6
Bombacaceae	*Bombacopsis quinata*	Pochote			1						1	1	0.3
Moraceae	*Brosimum alicastrum*	Ojoche	1								1	1	0.3
Burseraceae	*Bursera simaruba*	Indio desnudo							1		1	1	0.3
Polygonaceae	*Coccoloba sp*	Papaturro	1								1	1	0.3
Papilionaceae	*Gliricidia sepium*	Madero negro							1		1	1	0.3
Rubiaceae	*Genipa americana*	Guaitil				1					1	1	0.3
Moraceae	*Maclura tinctoria*	Mora silvestre		1							1	1	0.3
Mimosaceae	*Zygia longifolia*	Sotacaballo	1								1	1	0.3
Mimosaceae	*Pseudosamanea guachapele*	Gavilán, Guayaquil					1				1	1	0.3
Fabaceae	*Samanea saman*	Cenízaro		1							1	1	0.3
Meliaceae	*Swietenia macrophylla*	Caoba							1		1	1	0.3
Combretaceae	*Terminalia oblonga*	Surá			1						1	1	0.3
		Total	40	26	44	71	42	40	43	41		311	

Annex 3. Top five most important species (dbh >10 cm) within each forest site. A = # of individuals, D = dominance = basal area (m2), F = frequency = # times an individual appears in a subplot, R= relative values, IVI = index value of importance (RA+RD+RF).

Plot #				**1**				
Species	**A**	**D**	**F**	**RA**	**RD**	**RF**	**IVI**	**%IVI**
Guazuma ulmifolia	7	0.218	5	17.949	16.568	16.667	51.183	17.061
Cordia alliodora	7	0.207	3	17.949	15.723	10	43.672	14.557
Caesalpinia eriostachys	4	0.146	4	10.256	11.134	13.333	34.724	11.575
Lonchocarpus spp	4	0.131	3	10.256	9.985	10	30.241	10.08
Cupania guatemalensis	3	0.095	1	7.692	7.215	3.333	18.24	6.08
other species (12)	14	0.518	14	35.896	39.376	46.664	121.941	40.648
Total	39	1.314	30	100	100	100	300	100
				2				
Cordia alliodora	14	0.207	2	58.333	20.911	20	99.244	33.081
Enterolobium cyclocarpum	4	0.374	2	16.667	37.783	20	74.449	24.816
Maclura tinctoria	1	0.292	1	4.167	29.503	10	43.67	14.557
Samanea saman	1	0.049	1	4.167	4.958	10	19.124	6.375
Luehea candida	1	0.025	1	4.167	2.484	10	16.651	5.55
other species (3)	3	0.366	3	12.501	36.945	30	79.445	26.482
Total	24	0.99	10	100	100	100	300	100
				3				
Guazuma ulmifolia	14	0.499	3	34.146	24.22	13.636	72.003	24.001
Cordia alliodora	8	0.267	3	19.512	12.945	13.636	46.093	15.364
Caesalpinia eriostachys	2	0.144	2	4.878	7.006	9.091	20.975	6.992
Luehea candida	1	0.278	1	2.439	13.493	4.545	20.477	6.826
Lonchocarpus spp	3	0.082	2	7.317	3.974	9.091	20.382	6.794
other species (11)	13	0.791	11	31.707	38.363	49.995	120.07	40.023
Total	41	2.061	22	100	100	100	300	100
				4				
Guazuma ulmifolia	19	0.361	2	29.688	18.608	7.407	55.703	18.568
Malpighiaceae	9	0.221	3	14.063	11.392	11.111	36.566	12.189
Apeiba tibourbou	7	0.299	1	10.938	15.444	3.704	30.085	10.028
Desconocido	3	0.213	2	4.688	10.995	7.407	23.09	7.697
Sapindaceae	4	0.095	2	6.25	4.888	7.407	18.546	6.182
other species (14)	22	0.751	17	34.381	38.672	62.965	136.01	45.335
Total	64	1.937	27	100	100	100	300	100
				5				
Eugenia salamensis	12	1.345	4	32.432	34.31	17.391	84.134	28.045
Cordia alliodora	2	0.781	1	5.405	19.917	4.348	29.671	9.89
Guazuma ulmifolia	3	0.435	2	8.108	11.108	8.696	27.912	9.304
Cupania guatemalensis	5	0.176	2	13.514	4.489	8.696	26.698	8.899
Anona reticulata	3	0.132	3	8.108	3.363	13.043	24.515	8.172
other species (9)	12	1.052	11	32.433	26.812	47.828	107.071	35.691
Total	37	3.919	23	100	100	100	300	100

Annex 3 cont'd.

				6				
Guazuma ulmifolia	11	0.187	4	34.375	17.074	17.391	68.84	22.947
Eugenia salamensis	3	0.223	2	9.375	20.443	8.696	38.514	12.838
Cupania guatemalensis	4	0.055	4	12.5	5.054	17.391	34.945	11.648
Apeiba tibourbou	3	0.142	2	9.375	12.982	8.696	31.052	10.351
Albizia niopoides	1	0.161	1	3.125	14.758	4.348	22.231	7.41
other species (7)	10	0.325	10	31.25	29.691	43.48	104.417	34.806
Total	32	1.092	23	100	100	100	300	100
				7				
Ochroma lagopus	5	0.142	3	13.889	12.621	9.677	36.188	12.063
Cedrela odorata	4	0.147	3	11.111	13.093	9.677	33.882	11.294
Guazuma ulmifolia	4	0.072	4	11.111	6.444	12.903	30.458	10.153
Piscidia carthagenensis	3	0.168	2	8.333	14.927	6.452	29.712	9.904
Eugenia salamensis	3	0.106	2	8.333	9.399	6.452	24.184	8.061
other species (12)	17	0.489	17	47.225	43.516	54.841	145.576	48.525
Total	36	1.124	31	100	100	100	300	100
				8				
Guazuma ulmifolia	9	0.166	4	34.615	21.836	22.222	78.674	26.225
Enterolobium cyclocarpum	2	0.179	2	7.692	23.507	11.111	42.31	14.103
Luehea seemannii	4	0.072	3	15.385	9.524	16.667	41.575	13.858
Albizia niopoides	1	0.158	1	3.846	20.731	5.556	30.133	10.044
Luehea candida	3	0.041	2	11.538	5.42	11.111	28.069	9.356
other species (5)	7	0.146	6	26.922	18.982	33.335	79.238	26.413
Total	26	0.76	18	100	100	100	300	100

Annex 4: The five most abundant tree species within the eight forest patches inventoried. # I = number of individuals identified in the sample plot.

1	
species	**# I**
Guazuma ulmifolia	7
Cordia alliodora	7
Caesalpinia eriostachys	4
Lonchocarpus spp.	4
Cupania guatemalensis	3

2	
species	**# I**
Cordia alliodora	14
Enterolobium cyclocarpum	4
Maclura tinctoria	1
Samanea saman	1
Luehea candida	1

3	
Guazuma ulmifolia	14
Cordia alliodora	8
Caesalpinia eriostachys	2
Luehea candida	1
Lonchocarpus spp.	3

4	
Guazuma ulmifolia	19
Malpighiaceae	9
Apeiba tibourbou	7
Unknown	3
Sapindaceae	4

5	
Eugenia salamensis	12
Cordia alliodora	2
Guazuma ulmifolia	3
Cupania guatemalensis	5
Anona reticulata	3

6	
Guazuma ulmifolia	11
Eugenia salamensis	3
Cupania guatemalensis	4
Apeiba tibourbou	3
Albizia niopoides	1

7	
Ochroma lagopus	5
Cedrela odorata	4
Guazuma ulmifolia	4
Piscidia carthagenensis	3
Eugenia salamensis	3

8	
Guazuma ulmifolia	9
Enterolobium cyclocarpum	2
Luehea seemannii	4
Albizia niopoides	1
Luehea candida	3

Annex 5. Bird species and individuals captured within forest habitats (91 individuals 17 species, 10 families) and their guild and habitat associations. Within the feeding guilds, I=insectivores, F=frugivores, O=omnivores, N=nectarivores, G=granivores and within habitat guilds, FO=forest species, PT=pastures with tree species and PA=open pasture species.

Order	Family	Common Name	Species	Individuals	Feeding Guild	Habitat
Passeriformes	Papridae	Long-tailed manakin	*Chiroxiphia linearis*	23	I/F	FO
Passeriformes	Troglodytidae	Banded wren	*Thryothorus pleurostictus*	19	I	FO
Passeriformes	Emberizidae	Olive sparrow	*Arremonops rufivirgatus*	18	O	FO
Apodiformes	Trochilidae	Cinnamon hummingbird	*Amazilia rutila*	9	N	FO
Apodiformes	Sylviidae	Tropical gnatcatcher	*Polioptila plumbea*	4	I	PT/FO
Passeriformes	Tyrannidae	Yellow-olive flycatcher	*Tolmomyias sulphurescens*	3	I/F	FO
Passeriformes	Vireonidae	Yellow-green vireo	*Vireo flavoviridis*	3	I/F	FO
Passeriformes	Tyrannidae	Great crested flycatcher	*Myiarchus crinitus*	2	I/F	PT/FO
Passeriformes	Parulidae	Kentucky warbler	*Opornis formosus*	2	I	FO
Apodiformes	Trochilidae	Steely-vented hummingbird	*Amazilia saucerrottei*	1	N	PT/FO
Passeriformes	Troglodytidae	Rufous-naped wren	*Campylorhynchus rufinucha*	1	I	FO
Passeriformes	Mimidae	Swainson's thrush	*Catharus ustulatus*	1	I/F	ALL
Passeriformes	Trochilidae	Fork-tailed emerald	*Chlorostilbon canivetii*	1	N	FO
Passeriformes	Parulidae	Yellow warbler	*Dendroica petechia*	1	I	PT/FO
Columbiformes	Caprimulgidae	Common puaraque	*Nyctidromus albicollis*	1	I	PT/FO
Passeriformes	Sylviidae	Long-billed gnatwren	*Ramphocaenus melanurus*	1	I	FO
Columbiformes	Tyrannidae	Yellow crowned tyranulet	*Tyrannus elatus*	1	I/F	PT

Annex 6: Bird species found within the forest habitats, their abundance within each site, their frequency and percentage they occupy of all the species identified within the forest habitats. The species are arranged in order of abundance; frequency refers to the occurrence of species (out of 8 sites) and total refers to abundance.

Forest habitat

Order	Family	Scientific Name	Common Name (En)	individuals/site 1	2	3	4	5	6	7	8	frequency	total	%
Passeriformes	Papridae	*Chiroxiphia linearis*	Long-tailed manakin	3		2			2	13	3	5	23	25.3
Passeriformes	Troglodytidae	*Thryothorus pleurostictus*	Banded wren	3	2	2	1	1	3	4	3	8	19	20.9
Passeriformes	Emberizidae	*Arremonops rufivirgatus*	Olive sparrow	4	3	5	2		1		3	6	18	19.8
Apodiformes	Trochilidae	*Amazilia rutila*	Cinnamon hummingbird		2		3	3		1		4	9	9.9
Apodiformes	Sylviidae	*Polioptila plumbea*	Tropical gnatcatcher			1			1		2	3	4	4.4
Passeriformes	Tyrannidae	*Tolmomyias sulphurescens*	Yellow-olive flycatcher				1	2				2	3	3.3
Passeriformes	Vireonidae	*Vireo flavoviridis*	Yellow-green vireo		3							1	3	3.3
Passeriformes	Tyrannidae	*Myiarchus crinitus*	Great crested flycatcher			2						1	2	2.2
Passeriformes	Parulidae	*Opornis formosus*	Kentucky warbler				2					1	2	2.2
Apodiformes	Trochilidae	*Amazilia saucerrottei*	Steely-vented hummingbird		1							1	1	1.1
Passeriformes	Troglodytidae	*Campylorhynchus rufinucha*	Rufous-naped wren					1				1	1	1.1
Passeriformes	Mimidae	*Catharus ustulatus*	Swainson's thrush					1				1	1	1.1
Passeriformes	Trochilidae	*Chlorostilbon canivetii*	Fork-tailed emerald					1				1	1	1.1
Passeriformes	Parulidae	*Dendroica petechia*	Yellow warbler				1					1	1	1.1
Columbiformes	Caprimulgidae	*Nyctidromus albicollis*	Common puaraque				1					1	1	1.1
Passeriformes	Sylviidae	*Ramphocaenus melanurus*	Long-billed gnatwren		1							1	1	1.1
Columbiformes	Tyrannidae	*Tyrannus elatus*	Yellow crowned tyranulet			1						1	1	1.1
			Total	10	12	13	11	9	7	18	11		91	

Annex 7: Beetle species identified within forest habitats (FO), 737 individuals, 12 species.

Scientific name	Individuals
Onthophagus landolti	338
Onthophagus acuminatus	103
Copris lugubris	58
Onthophagus batesi	53
Dichotomius centralis	44
Onthophagus hopfneri	29
Ateuchus rodriguezi	29
Dichotomius annae	27
Canthon meridionalis	22
Uroxys sp.	9
Onthophagus championi	6
Onthophagus marginicollis	4

Annex 8: Beetle species found within the forest habitats, their abundance within each site, their frequency and percentage they occupy of all the species identified within the forest habitats.

Forest habitat

	individuals/site										
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**frequency**	**total**	**%**
Onthophagus landolti	143	1		4	8	4	160	18	7	338	47
Onthophagus acuminatus	56						47		2	103	14
Copris lugubris	20	12	9			2		15	4	58	8
Onthophagus batesi	15					2	5	31	4	53	7.3
Dichotomius centralis	9	3	5			6		21	5	44	6.1
Onthophagus hopfneri	13	10	5			1			4	29	4
Ateuchus rodriguezi	10	3	5		1	3	4	3	7	29	4
Dichotomius annae	16	1					10		3	27	3.7
Canthon meridionalis	7	1				1		13	5	22	3
Uroxys sp.		2	1	1	5				4	9	1.2
Onthophagus championi				5	1				2	6	0.8
Onthophagus marginicollis	3					1			2	4	0.6
Total	292	33	25	10	15	20	226	101		722	

Annex 9: Tree species identified within pastures with trees, 80 individuals, 17 species, 12 families.

Family	Scientific Name	Common Name (sp)	Indiv.
Sterculiaceae	*Guazuma ulmifolia*	Guacimo	31
Arecaceae	*Acrocomia aculeata*	Coyol	12
Boraginaceae	*Cordia alliodora*	Laurel	6
Bignoniaceae	*Tabebuia rosea*	Roble	5
Fabaceae	*Samanea saman*	Cenízaro	4
Bombacaceae	*Ceiba pentandra*	Ceiba	3
Fabaceae	*Pseudosamanea guachapele*	Gavilán, Guayaquil	3
Moraceae	Ficus spp	Higueron	3
Rutaceae	*Citrus aurantifolia*	Limón	3
Malpighiaceae	*Byrsonima crassifolia*	Nance	2
Papilionaceae	*Piscidia carthagenensis*	Pellejo de toro, Siete cueros	2
Chrysobalanaceae	*Licania arborea*	Alchornoque	1
Fabaceae	*Cassia grandis*	Carao	1
Fabaceae	*Enterolobium cyclocarpum*	Guanacaste	1
Moraceae	*Maclura tinctoria*	Mora silvestre	1
Papilionaceae	*Andira inermis*	Almendro de monte	1
Sapindaceae	*Cupania guatemalensis*	Manteco	1

Annex 10: Tree species found within the pastures with trees habitats, their abundance within each site, their frequency and percentage they occupy of all the species identified within the pastures with trees habitats. The species are arranged in order of abundance; frequency refers to the occurrence of species (out of 8 sites) and total refers to abundance.

Family	Scientific Name	Common Name (sp)	individuals/site 1	2	3	4	5	6	7	8	frequency	total	%
Sterculiaceae	*Guazuma ulmifolia*	Guacimo	3	25					3		3	31	38.8
Arecaceae	*Acrocomia aculeata*	Coyol				4	3	5			3	12	15.0
Boraginaceae	*Cordia alliodora*	Laurel		5			1				2	6	7.5
Bignoniaceae	*Tabebuia rosea*	Roble		1		3		1			3	5	6.3
Fabaceae	*Samanea saman*	Cenízaro		3		1					2	4	5.0
Bombacaceae	*Ceiba pentandra*	Ceiba					1			2	2	3	3.8
Fabaceae	*Pseudosamanea guachapele*	Gavilán, Guayaquil		2	1						2	3	3.8
Moraceae	*Ficus spp.*	Higueron	1						1	1	3	3	3.8
Rutaceae	*Citrus aurantifolia*	Limón					3				1	3	3.8
Malpighiaceae	*Byrsonima crassifolia*	Nance							2		1	2	2.5
Papilionaceae	*Piscidia carthagenensis*	Pellejo de toro, Siete cueros		2							1	2	2.5
Chrysobalanaceae	*Licania arborea*	Alchornoque					1				1	1	1.3
Fabaceae	*Cassia grandis*	Carao					1				1	1	1.3
Fabaceae	*Enterolobium cyclocarpum*	Guanacaste		1							1	1	1.3
Moraceae	*Maclura tinctoria*	Mora silvestre			1						1	1	1.3
Papilionaceae	*Andira inermis*	Almendro de monte				1					1	1	1.3
Sapindaceae	*Cupania guatemalensis*	Manteco					1				1	1	1.3
		Total	4	39	2	9	11	6	6	3		80	

Annex 11: Top five most important species (dbh >10 cm) within each pastures with trees site. A = # of individuals, D = dominance = basal area (m2), F = frequency = # times an individual appears in a subplot, R= relative values, IVI = index value of importance (RA+RD+RF).

Plot #				**1**				
Species	**A**	**D**	**F**	**RA**	**RD**	**RF**	**IVI**	**%IVI**
Ceiba pentandra	2	0.135	1	66.667	69.814	50	186.481	62.16
Ficus spp.	1	0.059	1	33.333	30.186	50	113.519	37.84
Total	3	0.194	2	100	100	100	300	100
				2				
Guazuma ulmifolia	25	0.685	3	64.103	57.948	30	152.05	50.683
Samanea saman	3	0.149	2	7.692	12.622	20	40.314	13.438
Cordia alliodora	5	0.106	1	12.821	8.933	10	31.754	10.585
Pseudosamanea guachape	2	0.118	1	5.128	9.974	10	25.102	8.367
Enterolobium cyclocarpum	1	0.079	1	2.564	6.717	10	19.281	6.427
other species (2)	3	0.045	2	7.692	3.807	20	31.499	10.54
Total	39	1.182	10	100	100	100	300	100
				3				
Maclura tinctoria	1	0.061	1	50	67.897	50	167.897	55.966
Pseudosamanea guachapele	1	0.029	1	50	32.103	50	132.103	44.034
Total	2	0.089	2	100	100	100	300	100
				4				
Acrocomia aculeata	4	0.27	2	44.444	15.479	33.333	93.257	31.086
Tabebuia rosea	3	0.142	2	33.333	8.161	33.333	74.828	24.943
Samanea saman	1	0.688	1	11.111	39.464	16.667	67.242	22.414
Andira inermis	1	0.643	1	11.111	36.895	16.667	64.673	21.558
Total	9	1.744	6	100	100	100	300	100
				5				
Licania arborea	1	1.227	1	9.091	72.969	12.5	94.56	31.52
Acrocomia aculeata	3	0.267	2	27.273	15.882	25	68.155	22.718
Citrus aurantifolia	3	0.076	1	27.273	4.537	12.5	44.31	14.77
Cordia alliodora	1	0.04	1	9.091	2.367	12.5	23.957	7.986
Ceiba pentandra	1	0.03	1	9.091	1.796	12.5	23.387	7.796
other species (2)	2	0.041	2	18.182	2.449	25	46.631	15.21
Total	11	1.682	8	100	100	100	300	100
				6				
Acrocomia aculeata	5	0.253	2	83.333	85.676	66.667	235.676	78.559
Tabebuia rosea	1	0.042	1	16.667	14.324	33.333	64.324	21.441
Total	6	0.295	3	100	100	300	100	100
				7				
Guazuma ulmifolia	3	0.431	1	50	60.953	25	135.953	45.318
Byrsonima crassifolia	2	0.032	2	33.333	4.582	50	87.915	29.305
Ficus spp	1	0.244	1	16.667	34.465	25	76.131	25.377
Total	6	0.707	4	100	100	100	300	100
				8				
Guazuma ulmifolia	3	0.124	2	75	58.376	66.667	200.043	66.681
Ficus spp.	1	0.089	1	25	41.624	33.333	99.957	33.319
Total	4	0.213	3	100	100	100	300	100

Annex 12: The five most abundant tree species within the eight pastures with trees sites inventoried. # I = number of individuals identified in the sample plot.

1	
species	**# I**
Ceiba pentandra	2
Ficus spp.	1

2	
species	**# I**
Guazuma ulmifolia	25
Samanea saman	3
Cordia alliodora	5
Pseudosamanea guachapele	2
Enterolobium cyclocarpum	1

3	
Maclura tinctoria	1
Pseudosamanea guachapele	1

4	
Acrocomia aculeata	4
Tabebuia rosea	3
Samanea saman	1
Andira inermis	1

5	
Licania arborea	1
Acrocomia aculeata	3
Citrus aurantifolia	3
Cordia alliodora	1
Ceiba pentandra	1

6	
Acrocomia aculeata	5
Tabebuia rosea	1

7	
Guazuma ulmifolia	3
Byrsonima crassifolia	2
Ficus spp.	1

8	
Guazuma ulmifolia	3
Ficus spp.	1

Annex 13: Bird species and individuals captured within patures with trees (66 individuals, 20 species, 9 families) and their guild and habitat associations. Within the feeding guilds, I=insectivores, F=frugivores, O=omnivores, N=nectarivores, G=granivores and within habitat guilds, FO=forest species, PT=pastures with tree species and PA=open pasture species.

Order	Family	Common Name	Species	Total/Strata	Feeding Guild	Habitat
Columbiformes	Columbidae	Common ground dove	*Columbina passerina*	17	F/G	PA
Passeriformes	Emberizidae	Blueblack grassquit	*Volantinia jacarina*	8	F/G	PA
Cuculiformes	Emberizidae	Striped-headed sparrow	*Aimophila ruficanda*	6	I/G	FO
Passeriformes	Troglodytidae	Banded wren	*Thryothorus pleurostictus*	5	I	FO
Passeriformes	Vireonidae	Yellow-green vireo	*Vireo flavoviridis*	5	I/F	FO
Passeriformes	Cuculidae	Groove billed ani	*Crotophaga sulcirostris*	4	O	PT
Passeriformes	Emberizidae	White-collared seedeater	*Soporophila torqueola*	3	I/G	PA
Passeriformes	Formicariidae	Barred antshrike	*Thamnophilus doliatus*	3	I	FO
Columbiformes	Trochilidae	Rufous-tailed hummingbird	*Amazilia tzacatl*	2	N	PT/FO
Passeriformes	Tyrannidae	Great crested flycatcher	*Myiarchus crinitus*	2	I/F	PT/FO
Apodiformes	Tyrannidae	Yellow-olive flycatcher	*Tolmomyias sulphurescens*	2	I/F	FO
Columbiformes	Emberizidae	Grasshopper sparrow	*Ammodramus savannarum*	1	I/G	PA
Passeriformes	Columbidae	Inca dove	*Columbina inca*	1	G	PA
Columbiformes	Columbidae	White-tipped dove	*Leptotila verreauxi*	1	G	PT/FO
Passeriformes	Tyrannidae	Boat billed flycatcher	*Megarhynchus pitangua*	1	I/F	PT/FO
Passeriformes	Tyrannidae	Sulphur-bellied flycatcher	*Myiodynastes luteiventris*	1	O	FO
Passeriformes	Tyrannidae	Social flycatcher	*Myiozetetes similis*	1	I/F	PA/PT
Columbiformes	Emberizidae	Indigo bunting	*Passerina cyanea*	1	O	PA/PT
Cuculiformes	Thraupidae	Plain colored tanager	*Tangara inornata*	1	I/F	PT/FO
Apodiformes	Tyrannidae	Yellow-crowned tyrannulet	*Tyrannulus elatus*	1	I/F	PT

Annex 14: Bird species found within the pastures with trees habitats, their abundance within each site, their frequency and percentage they occupy of all the species identified within the pastures with trees habitats. The species are arranged in order of abundance; frequency refers to the occurrence of species (out of 8 sites) and total refers to abundance.

Pastures with trees

Order	Family	Scientific Name	Common Name (sp)	individuals/site 1	2	3	4	5	6	7	8	frequency	total	%
Columbiformes	Columbidae	*Columbina passerina*	Common ground dove	1			1	7	1	4	3	6	17	25.8
Passeriformes	Emberizidae	*Volantinia jacarina*	Blueblack grassquit	3	4	1						3	8	12.1
Cuculiformes	Emberizidae	*Aimophila ruficanda*	Striped-headed sparrow	1		2			1	1	1	5	6	9.1
Passeriformes	Troglodytidae	*Thryothorus pleurostictus*	Banded wren	3	1	1						3	5	7.6
Passeriformes	Vireonidae	*Vireo flavoviridis*	Yellow-green vireo		5							1	5	7.6
Passeriformes	Cuculidae	*Crotophaga sulcirostris*	Groove billed ani					2	1		1	3	4	6.1
Passeriformes	Emberizidae	*Soporophila torqueola*	White-collared seedeater		3							1	3	4.5
Passeriformes	Formicariidae	*Thamnophilus doliatus*	Barred antshrike		3							1	3	4.5
Columbiformes	Trochilidae	*Amazilia tzacatl*	Rufous-tailed hummingbird		2							1	2	3.0
Passeriformes	Tyrannidae	*Myiarchus crinitus*	Great crested flycatcher	1		1						2	2	3.0
Apodiformes	Tyrannidae	*Tolmomyias sulphurescens*	Yellow-olive flycatcher		2							1	2	3.0
Columbiformes	Emberizidae	*Ammodramus savannarum*	Grasshopper sparrow								1	1	1	1.5
Passeriformes	Columbidae	*Columbina inca*	Inca dove		1							1	1	1.5
Columbiformes	Columbidae	*Leptotila verreauxi*	White-tipped dove		1							1	1	1.5
Passeriformes	Tyrannidae	*Megarhynchus pitangua*	Boat billed flycatcher					1				1	1	1.5
Passeriformes	Tyrannidae	*Myiodynastes luteiventris*	Sulphur-bellied flycatcher		1							1	1	1.5
Passeriformes	Tyrannidae	*Myiozetetes similis*	Social flycatcher		1							1	1	1.5
Columbiformes	Emberizidae	*Passerina cyanea*	Indigo bunting					1				1	1	1.5
Cuculiformes	Thraupidae	*Tangara inornata*	Plain colored tanager					1				1	1	1.5
Apodiformes	Tyrannidae	*Tyrannulus elatus*	Yellow-crowned tyrannulet		1							1	1	1.5
			Total	9	25	5	1	12	3	5	6		66	

Annex 15. Beetle species identified within pastures with trees (PT), 1,943 individuals, 11 species.

Species	**Individuals**
Onthophagus hopfneri	795
Canthon indigaceus	599
Onthophagus marginicollis	243
Phaneus demon	141
Copris lugubris	55
Agamopus lampros	40
Dichotomius annae	33
Ateuchus rodriguezi	26
Phaneus eximius	5
Onthophagus landolti	5
Canthon mutabilis	1

Annex 16: Beetle species found within the pastures with trees, their abundance within each site, their frequency and percentage they occupy of all the species identified within the forest habitats.

Pastures with trees **individuals/site**

Species	1	2	3	4	5	6	7	8	frequency	total	%
Onthophagus hopfneri	78	37	105			156	204	215	6	795	41
Canthon indigaceus	60	43	1			143	192	160	6	599	31
Onthophagus marginicollis	41	16	14			44	62	66	6	243	13
Phaneus demon	24	15				27	40	35	5	141	7.3
Copris lugubris	12	1	2			10	15	15	6	55	2.8
Agamopus lampros	15	4					6	15	4	40	2
Dichotomius annae	18	4	1			2	3	5	6	33	2
Ateuchus rodriguezi	12	1	1			6	4	2	6	26	1.3
Phaneus eximius						2		3	2	5	0.3
Onthophagus landolti			1		1		3		3	5	0.3
Canthon mutabilis						1			1	1	0.1
Total	260	121	125		1	391	529	516		1943	

Annex 17: Bird species and individuals captured within open pastures (43 individuals, 8 species, 5 families) and their guild and habitat associations. Within the feeding guilds, I=insectivores, F=frugivores, O=omnivores, N=nectarivores, G=granivores and within habitat guilds, FO=forest species, PT=pastures with tree species and PA=open pasture species.

Order	Family	Common Name	Species	Individuals	Feeding Guild	Habitat
Passeriformes	Papridae	Long-tailed manakin	*Chiroxiphia linearis*	23	I/F	FO
Passeriformes	Troglodytidae	Banded wren	*Thryothorus pleurostictus*	19	I	FO
Passeriformes	Emberizidae	Olive sparrow	*Arremonops rufivirgatus*	18	O	FO
Apodiformes	Trochilidae	Cinnamon hummingbird	*Amazilia rutila*	9	N	FO
Apodiformes	Sylviidae	Tropical gnatcatcher	*Polioptila plumbea*	4	I	PT/FO
Passeriformes	Tyrannidae	Yellow-olive flycatcher	*Tolmomyias sulphurescens*	3	I/F	FO
Passeriformes	Vireonidae	Yellow-green vireo	*Vireo flavoviridis*	3	I/F	FO
Passeriformes	Tyrannidae	Great crested flycatcher	*Myiarchus crinitus*	2	I/F	PT/FO
Passeriformes	Parulidae	Kentucky warbler	*Opornis formosus*	2	I	FO
Apodiformes	Trochilidae	Steely-vented hummingbird	*Amazilia saucerrottei*	1	N	PT/FO
Passeriformes	Troglodytidae	Rufous-naped wren	*Campylorhynchus rufinucha*	1	I	FO
Passeriformes	Mimidae	Swainson's thrush	*Catharus ustulatus*	1	I/F	ALL
Passeriformes	Trochilidae	Fork-tailed emerald	*Chlorostilbon canivetii*	1	N	FO
Passeriformes	Parulidae	Yellow warbler	*Dendroica petechia*	1	I	PT/FO
Columbiformes	Caprimulgidae	Common puaraque	*Nyctidromus albicollis*	1	I	PT/FO
Passeriformes	Sylviidae	Long-billed gnatwren	*Ramphocaenus melanurus*	1	I	FO
Columbiformes	Tyrannidae	Yellow crowned tyranulet	*Tyrannus elatus*	1	I/F	PT

Annex 17: Continued

Order	Family	Common Name	Species	Individuals	Feeding Guild	Habitat
Passeriformes	Emberizidae	Blueblack grassquit	*Volantinia jacarina*	12	F/G	PA
Passeriformes	Columbidae	Common ground dove	*Columbina passerina*	10	F/G	PA/PT
Passeriformes	Columbidae	Plain breasted ground dove	*Columbina minuta*	7	F/G	PT
Apodiformes	Parulidae	Gray-crowned yellowthroat	*Geothlypis poliocephala*	7	I	PA
Apodiformes	Trochilidae	Steely-vented hummingbird	*Amazilia saucerrottei*	2	N	PT/FO
Passeriformes	Trochilidae	Cinnamon hummingbird	*Amazilia rutila*	2	N	FO
Passeriformes	Turdidae	Clay colored robin	*Turdus grayi*	2	I/F	PT/FO
Passeriformes	Emberizidae	Grasshopper sparrow	*Ammodramus savannarum*	1	I/G	PA

Annex 18: Bird species found within the open pasture habitats, their abundance within each site, their frequency and percentage they occupy of all the species identified within the open pasture habitats. The species are arranged in order of abundance; frequency refers to the occurrence of species (out of 8 sites) and total refers to abundance.

Open pastures

Order	Family	Scientific Name	Common Name (sp)	individuals/site 1	2	3	4	5	6	7	8	frequency	total	%
Passeriformes	Emberizidae	*Volantinia jacarina*	Blueblack grassquit	1		11						2	12	27.9
Passeriformes	Columbidae	*Columbina passerina*	Common ground dove	1		1	3	1	1	1	2	7	10	23.3
Passeriformes	Columbidae	*Columbina minuta*	Plain breasted ground dove				4		2		1	3	7	16.3
Apodiformes	Parulidae	*Geothlypis poliocephala*	Gray-crowned yellowthroat	3		4						2	7	16.3
Apodiformes	Trochilidae	*Amazilia saucerrottei*	Steely-vented hummingbird			2						1	2	4.7
Passeriformes	Trochilidae	*Amazilia rutila*	Cinnamon hummingbird			1				1		2	2	4.7
Passeriformes	Turdidae	*Turdus grayi*	Clay colored robin				1		1			2	2	4.7
Passeriformes	Emberizidae	*Ammodramus savannarum*	Grasshopper sparrow					1				1	1	2.3
			Total	5	0	19	8	2	4	2	3		43	

Annex 19: Beetle species identified within open pastures (PA), 661 individuals, 7 species.

Scientific name	Individuals
Canthon indigaceus	266
Onthophagus hopfneri	173
Onthophagus marginicollis	93
Dichotomius annae	61
Phaneus demon	59
Copris lugubris	8
Onthophagus batesi	1

Annex 20: Beetle species found within the open pastures, their abundance within each site, their frequency and percentage they occupy of all the species identified within the forest habitats.

Open pastures	individuals/site										
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**frequency**	**total**	**%**
Canthon indigaceus	31					52	23	160	4	266	40
Onthophagus hopfneri	34					48	35	56	4	173	26
Onthophagus marginicollis	20					10	1	62	4	93	14
Dichotomius annae	7	11				16		27	4	61	9.2
Phaneus demon	13	2				11		33	4	59	8.9
Copris lugubris	8								1	8	1
Onthophagus batesi							1		1	1	0.2
Total	113	13				137	60	338		661	

Annex 21: Bird species found identified in the entire study and their habitat and feeding guild associations. The habitat guilds are: OP=Open pastures, PT=pastures with tree species, FO/SG=forests and secondary growth and GF=Gallery forests. The feeding guilds are: I=insectivores, F=frugivores, O=omnivores, N=nectarivores and G=granivores.

		HABITAT				GUILD
Common Name	**Species**	**OP**	**PT**	**FO/SG**	**GF**	
Cinnamon hummingbird	*Amazilia rutila*			X		N, I
Steely-vented hummingbird	*Amazilia saucerrottei*		X	X		N, I
Banded wren	*Thryothorus pleurostictus*			X		I
Yellow-green vireo	*Vireo flavoviridis*			X		I,F
Olive sparrow	*Arremonops rufivirgatus*			X	X	I, G, F
Long-billed gnatwren	*Ramphocaenus melanurus*			X		I
Rufous-tailed hummingbird	*Amazilia tzacatl*		X		X	N, I
White-tipped dove	*Leptotila verreauxi*		X	X		G, I
Inca dove	*Columbina inca*	X	X			G
Yellow-crowned tyrannulet	*Tyrannulus elatus*		X			F, I
Blueblack grassquit	*Volantinia jacarina*	X				G, I, F
Social flycatcher	*Myiozetetes similis*	X	X			I, F, G
Yellow-olive flycatcher	*Tolmomyias sulphurescens*			X		I, F
White-collared seedeater	*Soporophila torqueola*	X	X			I, F
Barred antshrike	*Thamnophilus doliatus*				X	I
Sulphur-bellied flycatcher	*Myiodynastes luteiventris*			X		I, F, G
Common puaraque	*Nyctidromus albicollis*		X	X		I
Kentucky warbler	*Opornis formosus*			X		I
Yellow warbler	*Dendroica petechia*		X	X		I
Common ground dove	*Columbina passerina*	X	X			F, G
Plain breasted ground dove	*Columbina minuta*		X			F, G
Clay colored robin	*Turdus grayi*		X	X		I, F, O
Long-tailed manakin	*Chiroxiphia linearis*			X	X	F, I
Striped-headed sparrow	*Aimophila ruficanda*			X		G, I
Tropical gnatcatcher	*Polioptila plumbea*		X	X		I
Groove-billed ani	*Crotophaga sulcirostris*		X	X		I, F
Grasshopper sparrow	*Ammodramus savannarum*	X				G, I
Great crested flycatcher	*Myiarchus crinitus*		X	X		I, F
Gray-crowned yellowthroat	*Geothlypis poliocephala*	X				I, F
Fork-tailed emerald	*Chlorostilbon canivetii*			X		N, I
Swainson's thrush	*Catharus ustulatus*	X	X	X	X	F, I
Rufous-naped wren	*Campylorhynchus rufinucha*			X	X	I
Indigo bunting	*Passerina cyanea*	X	X			G, F, I
Plain colored tanager	*Tangar inornata*		X	X	X	F, I
Boat billed flycatcher	*Megarhynchus pitangua*		X	X		I, G, F