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*Chapter 6*

# CONTRIBUTION OF HOMEGARDENS, AGROSILVOPASTORAL SYSTEMS, AND OTHER HUMAN-DOMINATED LAND-USE TYPES TO THE AVIAN DIVERSITY OF A BIOLOGICAL CORRIDOR IN COSTA RICA

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## ABSTRACT

As a result of the limitations of protected areas in providing habitat for many wildlife species, in the last two decades efforts have shifted to studying wildlife conservation in human-dominated landscapes. The present study was carried out in the Path of the Tapir Biological Corridor, Costa Rica. The corridor, an 82,000 ha area of fragmented forests, encompasses 55 rural communities with more than 10,000 people. Deforestation and development are the main threats to biodiversity in the region. The main objective of this study was to estimate the contribution of ten habitat types: forested areas (wildlife refuges and biological reserves), agroforestry systems (homegardens and agrosilvopastoral systems), and other human-dominated land uses on the conservation of bird species in the corridor. Bird data was obtained using point counts along a whole year. Each habitat type had a total of 20 sampling points (200 points total), and each sampling point was visited three times during the summer and three times during the winter seasons. The bird species were categorized by habitat preference, habitat and feeding guilds, and endangered status. We identified a total of 21,015 bird individuals that corresponded to 293 species. Forest fallows (155 species), forest edges (154), homegardens (148), and agrosilvopastoral systems (143) were the land uses with the most species. On the other hand, villages (104 species), oil palm plantations (107), residential tourism projects (111), and tree plantations (115) had the lowest bird species richness

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values. Biological reserves (124 species) and wildlife refuges (121) had intermediate species richness values. But, they both provided habitat to 68 forest-dependent species that were not found in any other habitat type, and to 19 species (70%) of the species of conservation concern, thus they are a priority habitat for conservation in the region. It is also relevant to highlight the importance of homegardens and agrosilvopastoral systems as habitat for 70% of the avian diversity of the region, including the endangered Scarlet Macaw (*Ara macao*). Biodiversity conservation should always include primary and old-secondary forests (e.g., those forests located in wildlife refuges, biological reserves, or isolated forest fragments) as these are the most important habitat type for wildlife at the landscape level. However, the results of this research also show that the matrix, especially agroforestry systems and tree plantations, are important to ensure wildlife conservation in the biological corridor in the short and long term.

## INTRODUCTION

The establishment of protected areas is one means of counteracting some of the threats to biodiversity such as habitat loss and fragmentation [1, 2]. As a result of this approach, in the last three decades there has been an exponential growth in the number of protected areas worldwide, particularly in tropical countries where biodiversity is greatest [3, 4]. However, most of the world's biodiversity exists outside protected areas [5], particularly because of the socio-economic and political constraints that limit the amount of land allocated to protected status. Protected areas, therefore, do not necessarily hold the extent of habitat needed by most living species, forcing wildlife to seek habitat and refuge beyond the artificial boundaries of parks [2, 5, 6, 7]. Costa Rica, even though it is one of the most diverse countries of the world [8], and has one of the most significant systems of protected areas [9], is not an exception. Fragmentation and isolation of Costa Rican protected areas are jeopardizing biological conservation [6, 10]. Therefore, given the limitations of the protected areas system, there is a pressing need to study biodiversity and improve management not only within the protected areas' boundaries, but also in the fragmented landscape matrices that surround them.

The present study was carried out in the fragmented and human-dominated Path of the Tapir Biological Corridor in Costa Rica, which is one of the most diverse areas of Central America [11], but whose biodiversity is at risk due to deforestation and development. The main goal of this study was to assess the contribution of ten different habitat types to the conservation of bird species in the region. The ten land-use types were: biological reserves, wildlife refuges, homegardens, agrosilvopastoral systems, forest edges, forest fallows, tree plantations, oil palm plantations, local villages, and residential tourism projects. Aside from the contribution of habitat types to the overall avian diversity of the region, we also evaluated the contribution of these habitat types to species of conservation concern. The manuscript also provides a theoretical background to understand the effects of fragmentation and human-dominated landscapes, including agroforestry systems, on the conservation of wildlife.

### Landscape Fragmentation and Land Use Change Effects on Wildlife Species

Destruction or alteration of natural habitat by humans, resulting in land-use change, represents one of the most serious threats to biodiversity worldwide [9], along with climate change, and invasive species [12]. Due to this loss of natural habitats there is a challenge of maintaining and conserving biodiversity in fragmented landscapes now dominated by human land use [13]. Habitat fragmentation has two main components: (1) a reduction in the area covered by a habitat type or natural habitat generally, in a landscape; and (2) a change in habitat configuration, with the remaining habitat left in smaller and more isolated patches [14]. As a consequence of these processes, Anderson and Jenkins [15] mention that fragmentation may lead to: (1) elimination or dangerous reduction of populations of large, wide-ranging species, including many top carnivores; (2) unraveling of entire biological communities—as, for example, when the decline of top carnivores in fragmented habitats results in the "release" of smaller predators and herbivores, leading to overpredation or overgrazing that may eventually eliminate species or destabilize communities; (3) destruction or degradation of remaining habitat through the intrusion of edge effects such as altered microclimate or invasive species; and (4) disruption of key ecological processes dependent on increasingly rare animal agents—such as pollination, seed dispersal, predator-prey interactions, and nutrient cycling.

The response of wildlife species to habitat destruction and fragmentation is influenced by the species' home range area, body size, food resources and foraging patterns, nesting and shelter requirements, as well as tolerance to habitat disturbance and sensitivity to altered microclimates [13]. Based on these animal characteristics, the species vulnerable to fragmentation can be organized into six groups [9]:

(1) Wide ranging species: species such as large carnivores and migratory ungulates that roam a large area in the course of their daily or seasonal movements. Also animals of heterogeneous landscapes such as amphibians and turtles are vulnerable to fragmentation because they depend on distinct habitats for different phases of their life cycles.
(2) Non-flying species: species with poor dispersal abilities may not travel far from where there were born, or may be stopped by barriers such as a road or a clear-cut. Examples are carrion beetles in Amazonian forests being fragmented by pasture development [16], and arboreal mammals, peccaries, and many insect bats that are unwilling to enter the matrix [17].
(3) Species with specialized requirements: Species with specialized habitat or resource requirements are often vulnerable to extinction, especially when those resources are unpredictable in time or space. For example, the great green macaws (*Ara ambigua*) nest and forage more than 90% of the time in almond trees (*Dipteryx panamensis*), and the decrease of these trees has had a negative impact of the macaws populations in Costa Rica [18].
(4) Large-Patch or Interior Species: Some species occur only in large patches of forests, and are absent from small patches with little or no true interior habitat. For example, in Central Amazonia, many forest understory birds—including army ant followers, solitary species, members of mixed-species flocks, and terrestrial species—strongly avoid forest edges [19].
(5) Species with low fecundity: A species with low reproductive capacity cannot quickly rebuild its population after severe reduction caused by a number of factors. For example, large mammals such as the tapir and jaguar have low fecundity in comparison with small mammals like rodents.

(6) Species vulnerable to human exploitation or persecution: Some species are actively sought by people for food, furs, medicine, pets, or other uses, whereas other species, such as snakes and large predators, may be killed on sight. For example, as a result of hunting, species such as the jaguar and peccaries have decreased their populations in Corcovado National Park in Costa Rica in the last two decades. Jaguar populations changed from 150 individuals in 1990 to only 30 individuals in 2004 and peccaries from 2000 in 2000 to only 400 in 2004 [20].

Due to the concerns about the effects of habitat fragmentation and isolation on wildlife conservation, there have been an increasingly large number of studies on single species or assemblages in fragmented landscapes throughout the world [21; see also a large list of papers summarized by Bennett 13] However, most of those studies have focused on the fragments themselves ignoring species distribution in surrounding sites such as agricultural or other human-dominated areas [22]. Thus, there is a need to study the importance of the landscape matrix for biological conservation.

## Importance of the Landscape Matrix for Wildlife Conservation

Assessing the conservation potential of human-dominated landscapes requires investigation of the activities, movement, and persistence of species not only in remnants of native habitats but also in the full array of countryside habitats [14, 23, 24], known also as the matrix. The matrix can be defined as the most widespread habitat within which other elements are embedded, and it can be either the original habitat type (e.g., a primary forest now surrounded by a matrix of agroforestry) or a modified one (e.g., an agricultural plantation surrounded by a matrix of pristine forest) [15]. In anthropogenically modified landscapes, some of the matrix or all of it may be human-modified communities such as agricultural fields of various types, agroforestry systems, clear-cut forests, pastures, tree plantations, fallow land, and towns [7, 25].

As part of the landscape, the matrix plays different roles for wildlife conservation:

(1) Matrix regulating the movement of organisms: the matrix has a significant effect on connectivity in forest landscapes and in determining the quantity of successful movements among habitat patches [7, 26, 27], acting as a selective filter (not an absolute barrier) for the movement of species across the landscape [26]. The type of vegetation cover in the matrix determines the pore size of the matrix movement. For example, tall secondary forests are analogous to a filter with a large pore size that allows more faunal movement because of its structure similar to primary forest. On the contrary, a matrix maintained in pasture has a fine pore size that may impede much faunal movement [26].

(2) Matrix as a resource: this is the case when the matrix can provide abundant food resources that can be exploited by some species. In addition, the matrix may also offer access to some resources that are rarely needed by a species, perhaps seasonally, such as forage plants rich in a scarce mineral, a favorable hibernation site, or access to a pollinator [7].

(3) Matrix as secondary habitat: it is possible that the matrix may serve as secondary habitat for some populations [7, 27]. This situation is called a source-sink axis [28]. The source population is one in which reproduction is adequate to balance mortality and usually to export surplus individuals, as well. Such a population supplies the residents with a secondary habitat. Sink populations are those living in a secondary habitat [7]. If sink populations produce enough offspring those may supplement populations in reserves [7, 27].
(4) Matrix as a sink or stopper: the matrix may function as a dispersal sink when the matrix is large relative to the size of patches, it does not support a resident population of a target species, and when few other habitat patches are available to dispersers [7]. In addition, the matrix may act as a "stopper" when it is a complete barrier to dispersal [7].

Several studies addressing the effect of the landscape matrix on wildlife conservation have been conducted in the tropics [22, 24, 25, 26, 29, 30]. Even though the authors mentioned above clarify that there is no substitute for native forest habitat, they also highlight the importance of human-dominated landscapes (e.g. agroforestry systems, coffee plantations, pastures, tree plantations, secondary forests) for the conservation of butterflies [29], non-flying mammals [25, 26], frogs [26], moths [22], and birds [24, 26, 31, 32]. For instance, in a study of non-flying mammal species in the montane areas of Costa Rica, Daily et al. [25] found a total of 26 native species. From these 26 species, 9 (35%) were restricted to forest habitat, 14 (54%) occurred in both forest and agricultural habitats, and 3 (11%) were found only in agricultural habitats, showing that the majority of native mammals use countryside habitats. In the same region, Hughes et al. [24] found a total of 144 bird species. For this study it was estimated that 46% of those native to the region were utilizing the matrix in some manner. Moreover, it was predicted that bird richness in the matrix would decline to approximately 40% if tall trees and edge habitats were removed from the landscape. Results of the Biological Dynamics of Forest Fragments Project (BDFFP) in central Brazil also report differences in the behavior of wildlife in forest fragments and in the surrounding matrix [26]. Overall, for ants, small mammals, birds, and frogs it was found that between 8-15% of the primary-forest species were recorded in matrix habitats. In addition, for three vertebrate groups (mammals, frogs, and birds) there were positive and significant correlations between population abundance in the matrix and vulnerability to fragmentation. This suggests that species that avoid the matrix tend to decline or disappear in fragments, while those that tolerate or exploit the matrix often remain stable or increase following landscape fragmentation [26].

## Enhancing Wildlife Conservation through Biological Corridors

Minimizing the effects of isolation by enhancing landscape connectivity is one way to counter the adverse effects of fragmentation [13, 33] in addition to increasing the effective habitat area [33]. Connectivity can be defined as linkages of habitats, communities, and ecological processes at multiple spatial and temporal scales [34]. Connectivity is used to describe how the spatial arrangements and the quality of elements in the landscape affect the movement of organisms among habitat patches [35]. Among other alternatives corridors are a strategy for maintaining connectivity in fragmented landscape [36]. A number of definitions and types of corridors have been proposed over time [7, 13, 15, 35]. For instance, Forman [35] defines corridors as strips of habitat that differ from the adjacent habitat on both sides. A more detailed definition is provided by Anderson and Jenkins [15] where corridors are defined as spaces in which connectivity between species, ecosystems, and ecological processes is maintained or restored at various levels. Among the types of corridors there are four classified by Bennett [13]:

(1) natural corridors, such as waterways and streams and their associated riparian vegetations;
(2) remnant corridors, such as strips of logged forest within clear-cuts, natural woodlands along roadsides, and natural habitat retained as links between nature reserves;
(3) regenerated corridors, such as fencerows and hedges; and
(4) planted corridors, such as windbreaks or shelterbreaks and urban greenways.

Regardless the type of corridor, Forman [35], mentions that there are six main functions that corridors provide:

(1) Conduit: corridors act as conduit when it provides for movement between habitat patches, but organisms do not reside within it [37].
(2) Habitat: corridors perform as habitat when the organisms have enough resources for survivorship, reproduction, and movement [37].
(3) Filter: corridors act as filter when there is some level of permeability and some organisms and material pass through the corridor whereas others cannot [37].
(4) Barrier: Corridors may represent a barrier to animals when they are a complete blockage and none animals cross the corridor [37].
(5) Source: Corridor can work as source when animals emanate from it [37].
(6) Sink: poorly designed corridors may act as population sinks, because the large amount of edge exposes animals to predation from matrix dwellers and competition from generalist species [38, 39, cited by 37].

Although biological corridors can be a good tool for biological conservation, there is a large controversy about their efficacy [13, 36, 40]. Bennett [13] summarizes the critics in three main points:

(1) whether sufficient scientific evidence is available to demonstrate the potential conservation benefits of corridors;
(2) whether the potential negative effects of corridors may outweigh any conservation value;
(3) whether corridors are a cost-effective option in comparison with other ways of using scarce conservation resources.

Even though several disadvantages have been reported to corridors, such as serving as pathways for fire, predators, and pathogens, which can undermine conservation objectives [15, 41], and that it is clear that corridors are not the solution to all of the current conservation problems [33], many of the potential disadvantages could be avoided or mitigated if the proper design is applied to the specific requirements of the species, habitats, ecosystems, and ecological processes of concern in each case [15]. However, further research has to be carried out in order to investigate the positive or negative impacts of corridors and their elements (land-use types), especially at the landscape level.

## METHODS

### Study Area Description: Path of the Tapir Biological Corridor

The PTBC is located in southwestern Costa Rica (Figure 1) and is a part of the multinational Mesoamerican Biological Corridor (MBC). The corridor's main objective is to create a network of sites favorable to fauna and flora between the forests of the Osa Peninsula and Golfo Dulce, including Corcovado National Park. These forests connect with those located in the Los Santos Forest Reserve in the Talamanca Mountain Range. The PTBC area covers approximately 82,000 has, inhabited by 10,000 people in 55 communities. This mosaic of human-dominated land uses includes primary and secondary forests, native and exotic forest plantations, agriculture, agroforestry systems, bamboo, oil palm plantations, ecotourism projects and others.

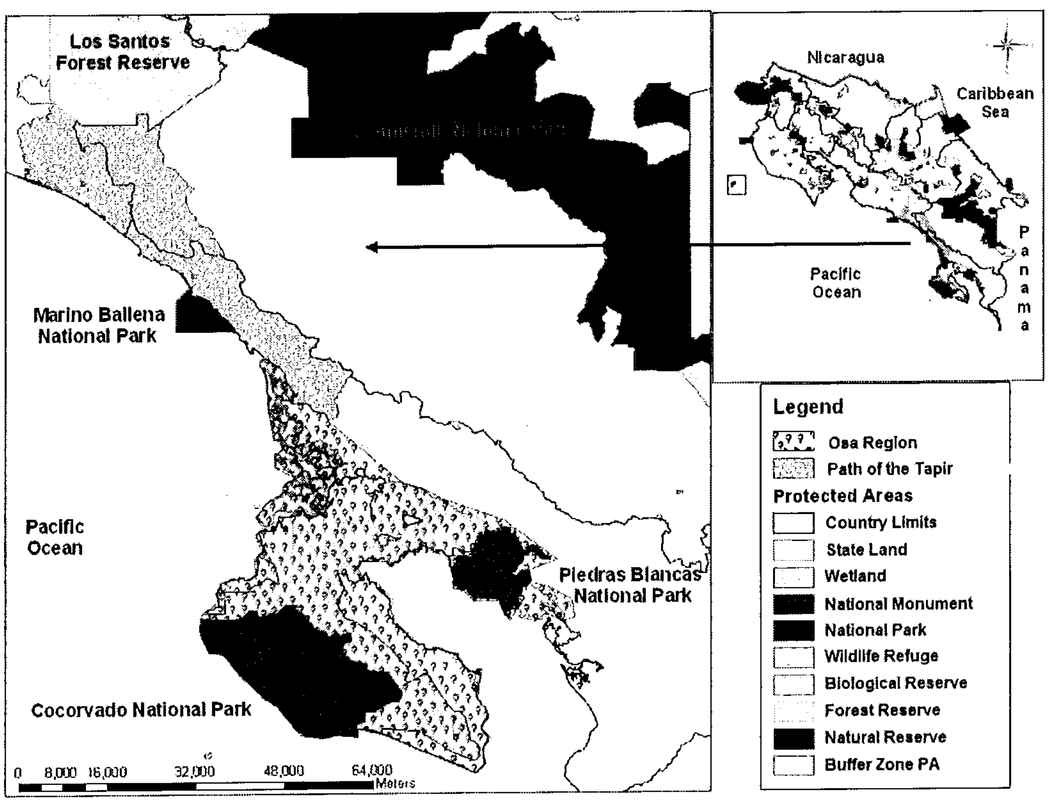



Figure 1. Location of the Path of the Tapir Biological Corridor, Costa Rica.

The corridor is composed of terrain ranging in altitude from 0 to 1100 meters above see level [11]. According to the Holdridge System (42), three life zones are represented within it: (1) The Tropical Wet Forest that comprises the entire length of the corridor, especially the lower zones; (2) The Tropical Wet Forest Transition to Premontane, represented by a small fringe at the intermediate altitudes, and (3) The Tropical Rainforest Premontane found at the highest elevation in the corridor. The climate in this region of the country is categorized as Seasonal Tropical Wet with an annual precipitation of 4,239 mm and average temperature of 27 °C. There is also a high precipitation during the rainy season of as much as 685 mm per month (maximum of 1,715 in October 1988), and a pronounced 4 to 5 months dry season with little rain (less than 100 mm) from January to May [11]. The soils in the corridor are of low in fertility, and are generally classified as Ultisols and Inceptisols. There are more than 30 rivers among which the main ones are Coronado, Higueron, Uvita, Baru, Hatillo, Savegre, and Guabo [11].

PTBC is one of Costa Rica's most diverse regions. A Rapid Ecological Assessment carried out in the region identified a total of 2700 plant species which represent 10% of the total plant diversity in the country, as well as 173 mammal, 26 amphibian, 46 reptile, and 191 bird species [11]. Moreover, 470 avian species have been registered in the area in the six most recent annual bird counts. The PTBC provides habitat to some endangered animal species such as margay (*Leopardus wiedii*), ocelot (*Leopardus pardalis*), jaguar (*Panthera onca*), scarlet macaw (*Ara macao*), spider monkey (*Ateles geoffroyi*), squirrel monkey (*Saimiri oerstedii*), great curassow (*Crax rubra*), and endemic tree species such as quira (*Caryodaphnopsis burgeri*).

## Land Use in the Path of the Tapir Biological Corridor

Current land use in the corridor has been the result of the process of local and national settlement and development policies. Between 1940 and 1960, Costa Ricans migrated from the northern part of the country toward this region, searching for new lands to clear and cultivate. Between 1960 and 1990, an expanding cattle industry was a major contributing factor to deforestation [11]. To date, deforestation rates have decreased, forest cover has increased as a result of pasture abandonment, and conservation efforts are being undertaken through the establishment of 1 National Park, 5 National Wildlife Refuges, and 27 Informal Private Nature Reserves [Ewing, J. personal communication, June 2006]. The main land uses in the region are primary and secondary forests (35,682 ha), pastures (22,243 ha), young secondary forests (13,488 ha), agriculture (4,074 ha), forest tree plantations (2915 ha), and mangroves (1,160 ha) [11].

Most local people work in agriculture, and recently ecotourism has been growing as another important source of income in the region. However, as land prices have increased, land ownership is shifting from local farmers to wealthy foreigners. Costa Ricans have either become employees of the new owners, or migrated to larger cities in Costa Rica or to the United States and Europe. This poses a new challenge for the region, as protected areas are interspersed with private lands [43]. Therefore, in order to avoid land use change and ensure connectivity among all protected areas, it is essential that the corridor's conservation plan provides adequate incentives to landowners.

Agricultural lands in the region are mostly planted with rice, oil palm, and small scale crops. Pastures for cattle have different characteristics. Some of them have living fences of native tree species as well as scattered remnant trees as shade for cattle. Tree plantations are mostly of timber species that are being planted in the Caribbean and Pacific lowlands of the country. The main species based on area planted is *Tectona grandis* (teak), an exotic species brought to Costa Rica from Asia. Second, *Terminalia amazonia* (amarillón), a native species that is being planted in medium or small scale plantations. The third species is *Gmelina arborea* (melina) also exotic to Costa Rica. Teak and melina plantations represent more than 50% of the total area of tree plantations in the country [44].

## Description of the Habitats Used for Evaluation of Bird Abundance and Diversity

Based on the predominant land uses currently present in the PTBC we selected ten different habitat types that were located up to 500 m.a.s.l. The studied habitat types were wildlife refuges, biological reserves, forest edges, forest fallows, tree plantations, oil palm plantations, homegardens, agrosilvopastoral systems, residential tourism projects, and villages. For each habitat type a total of 20 different sampling points were located along the whole corridor, based on 16 routes, using existing roads or trails.

(a) **Wildlife refuges:** We surveyed forested areas (primary or old secondary forest) within two refuges: Rancho La Merced and Hacienda Baru (10 sampling points at each refuge for a total of 20 points for this type of habitat). La Merced (329 ha) and Baru (330 ha) are private reserves and have governmental protection since 1995.
(b) **Biological reserves:** We selected two biological reserves: La Cusinga and Oro Verde (10 sampling points at each refuge). La Cusinga (250 ha) and Oro Verde (150 ha) are also private reserves, but without governmental incentives or protection. The height of the forest canopy in both the biological reserves and in the wildlife refuges was up to 35 m.
(c) **Forest edge:** twenty sampling points were located in areas along the edge of primary and old-secondary forests.
(d) **Forest fallows (young secondary forest)**: These were areas of forest regenerating in recently abandoned pasture lands (5-10 years after abandonment). Canopy height at these locations was up to 10-15 meters.
(e) **Homegardens:** These were traditional Costa Rican homegardens composed of a combination of annual/perennial crops, ornamental plants, and timber and fruit trees.
(f) **Agrosilvopastoral systems**: Most of the pastures on the region were used to raise beef cattle, and had been planted with exotic pasture species. All of the selected sites had either living fences or scattered trees that provided perches or food sources to birds.
(g) **Tree plantations:** As explained above, most tree plantations in the PTBC consist of teak (*Tectona* grandis), or amarillon *(Terminalia amazonia)*. Teak is a valuable exotic timber species that is exported to Europe and the United States. Amarillon is native to Costa Rica and it is one of the most promising species for timber production in the country. Since we did not get access to enough number of *T. amazonia* plantations to set up 20 sampling points, we located 10 points in teak and 10 in

amarillon plantations so as to have a total of 20 points for this habitat type. Plantation size varied from 2 ha to 20 ha, being teak plantations the largest ones in size.

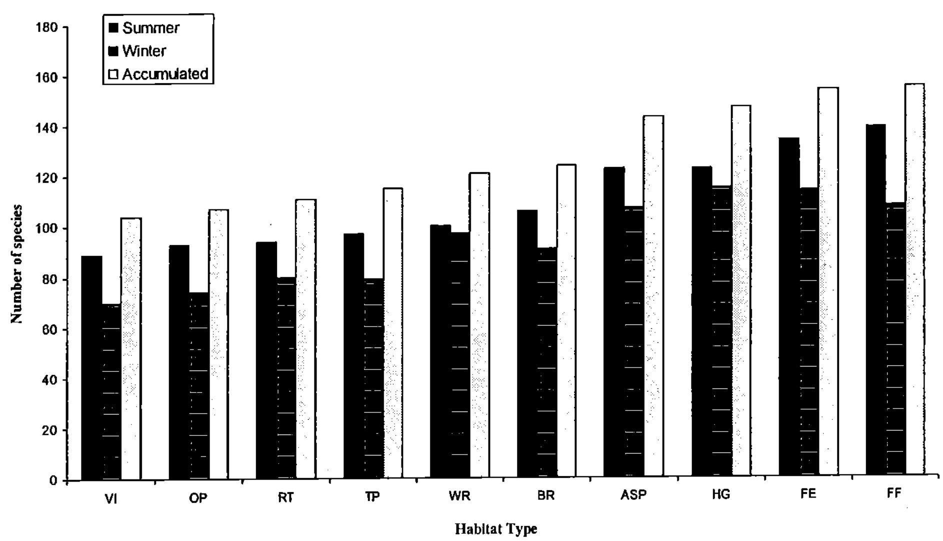
(h) **Oil palm plantations:** In the northern region of the corridor, there were hundreds of ha of oil palm plantations (*Elaeis guineensis*), which is an exotic crop to Costa Rica. We located the sampling points from recent established plantations (1.5 m tall) to mature plantations (up to 10 m height).

(i) **Villages:** We selected two main areas for sampling. The first one was the largest village or town within the corridor (Puerto Cortez). In Puerto Cortez We located 10 sampling points. The other 10 sampling points were located in the small villages along the main highway.

(j) **Residential tourism projects:** Because the Path of the Tapir is along the Central and South Pacific Coast of the country, there has been an exponential growth in the number of foreigners building summer or retirement houses in the area in the last 10 years. We located the points in areas where there were more than one house built.

## Bird Surveys

Each point was surveyed three times in the summer and three times during the rainy seasons. At each sampling point (in a 50m radius plot and during a period of 10 minutes) We recorded and identified every bird species that was seen, habitat type, tree or structure where it was found as well as type of bird activity (e.g., foraging, nesting, moving, perching). All surveys were conducted from sunrise to 9:15 am during clear days, avoiding windy situations. Field identification was conducted using the Manual of Birds of Costa Rica [45] and the Birds of Costa Rica [46], as well as an identification of their calls and songs.




BR = Biological Reserves, FE = Forest Edges, FF = Forest Fallows, HG = Homegardens, OP = Oil palm, ASP = Agrosilvopastoral systems, WR = Wildlife Refuges, RT = Residential Tourism Projects, TP = Tree Plantations, VI = Villages.

Figure 2. Accumulated number of bird species found in ten different habitat types in the Path of the Tapir Biological Corridor, Costa Rica.

## Data Analysis

For each habitat type we calculated the total abundance and species richness of birds by combining data from the two sampling periods (summer and winter) as well as comparing between both periods. We also calculated Shannon diversity index, rarefaction curves, Sorensen similarity index, and the number of shared species using EstimateS 5.0 [47]. Rarefaction curves were plotted against the number of individuals observed, using the mean of the four commonly employed abundance-based estimators (ACE, CHAO1, JACK1, and BOOSTRAP) [48]. Species were assigned dietary guilds and habitat guilds following Stiles and Skutch [45]. We compared abundance, species richness, diversity, and habitat and feeding guilds among the ten habitat types, using analysis of variance and/or Kruskal Wallis tests. We also used cluster analysis to group habitat types based on species composition. All statistical analyses were conducted in PAST v 1.90 [49].

# Results

## Bird Abundance and Diversity in the Path of the Tapir Biological Corridor

A total of 21,015 birds of 293 species were identified during 200 hours in the ten land-use types (Appendix 1). From the observed birds, 11,045 individuals (271 species accumulated) corresponded to the summer surveys and 9,970 individuals (246 species) corresponded to winter surveys (Figure 2). Even though there was a difference of 25 species in between both surveys, it is important to highlight that there were 47 species that were sighted only in the summer surveys and not in the winter season, as well as 22 species only found during the winter surveys. From the 47 species only found in summer, 35 species (75%) corresponded to migratory species. On the contrary, almost 100% of the species only registered in winter corresponded to resident species that are considered rare or uncommon species.

The most commonly observed species were (percentage from the total) *Ramphocelus costarricensis* (1064 individuals – 5.0%), *Thraupis episcopus* (754 individuals – 3.6%), *Quiscalus mexicanus* (743 – 3.5%), *Sporophila americana* (719 – 3.4%), *Troglodytes aedon* (702 – 3.3%), *Pitangus sulphuratus* (686 - 3.2%), and *Volantinia jacarina* (618 – 2.9%). Contrary to the abundance of these species, there were 121 species (41%) that had least than 10 individuals, and from this group, 23 species were sighted just once.

The majority of birds were insectivorous, accounting for 162 species and 42.4% of all observations. Frugivorous (56 species, 34.1%) and Granivorous (23 species, 13.9%) were the second and third most common guilds, respectively. Nectarivorous, Omnivorous, Carnivorous, and Piscivorous accounted by least than 10% of the observations all together. In addition, most registered birds were classified as open area specialist (55 species, 40%), followed by generalist species (100 species, 32.5%), and forest specialist (123 species, 25.6%).

**Table 1. Abundance, species richness, and diversity of birds registered in ten habitat types in the Path of the Tapir Biological Corridor, Costa Rica**

| Habitat Type | Abundance (n/census) | Species Richness (species/census) | Shannon Index |
|---|---|---|---|
| Homegardens | 562 (61.5)a | 82 (3.3)ab | 3.78 (0.03)ab |
| Agrosilvopastoral Systems | 516 (55.0)ab | 79 (3.0)ab | 3.79 (0.04)ab |
| Villages | 480 (66.5)b | 56 (2.8)bc | 3.38 (0.04)c |
| Oil Palm | 362 (21.4)c | 55 (1.2)c | 3.42 (0.03)c |
| Forest Fallows | 349 (33.6)c | 83 (5.6)a | 3.85 (0.05)a |
| Residential Tourism | 315 (34.7)c | 59 (2.7)bc | 3.63 (0.05)b |
| Forest Edges | 261 (29.9)cd | 77 (1.8)ab | 3.83 (0.05)a |
| Wildlife Refuges | 233 (19.8)cd | 67 (1.4)bc | 3.80 (0.03)ab |
| Biological Reserves | 219 (31.2)cd | 65 (2.3)bc | 3.81 (0.05)ab |
| Tree Plantations | 205 (38.3)d | 57 (2.5)bc | 3.70 (0.06)b |

Data represents means per census (N = 6) and standard errors. Different letters within same column indicate differences across land use types

## Comparison Across Sites in Bird Abundance and Diversity

There were differences in the mean abundance, species richness, and diversity of birds observed across the ten land-use types (Table 1). Agrosilvopastoral systems and homegardens were the most bird-abundant habitats, followed by the villages. On contrary, most forested habitats (tree plantations, biological reserves, wildlife refuges, and forest edges) were the least abundant ones. While forest fallows, forest edges, agrosilvopastoral systems, homegardens, and the reserves shared the highest species richness and diversity of birds, tree plantations and some open area habitats such as villages, oil palm plantations, and residential tourism projects had the lowest diversity values.

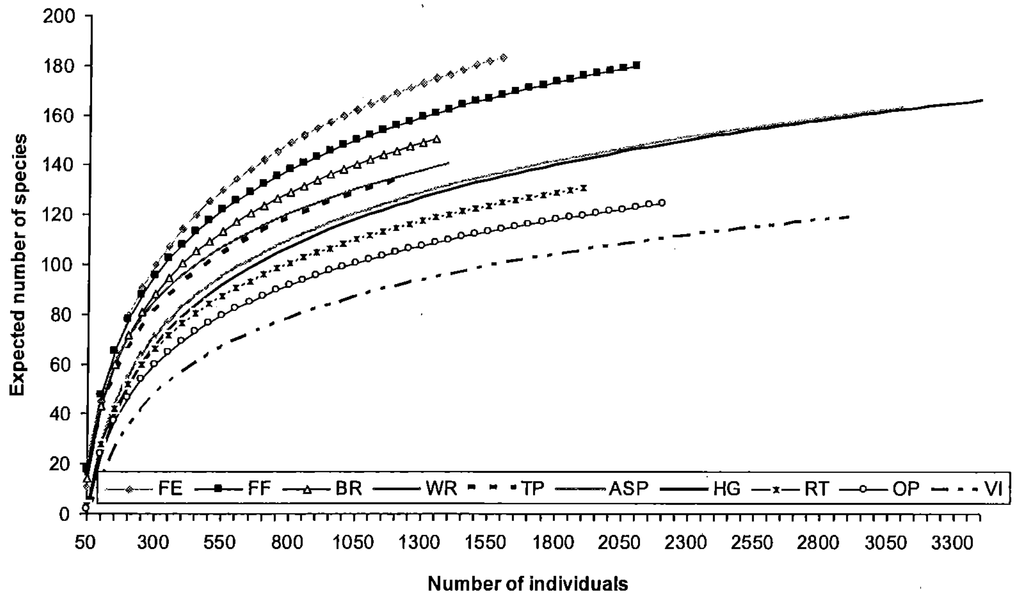
Rarefaction curves of the accumulated number of bird species confirmed some of the patterns described above (Figure 3). Forest fallows and forest edges had the highest expected number of species, followed by the wildlife refuges, biological reserves, and tree plantations. The villages, oil palm, and residential tourism projects had the lowest expected number of species. The agrosilvopastoral systems and the homegardens had intermediate results between these two extremes.

Biological reserves, wildlife refuges, and forest edges had the most similar assemblage of species (Table 2, Figure 4). This may be due to the fact that these three habitats are dominated by primary and old-secondary forest, having a majority of forest-specialist bird species. Agrosilvopastoral systems, homegardens, residential tourism, oil palm plantations were also very similar among themselves since they were dominated by generalist and open area bird species. Tree plantations and forest fallows were also very similar because they shared a high number of both generalist and forest-specialist bird species. As expected, habitats that did not share many species also differed sharply in their proportion of forest cover. For instance, biological reserves and wildlife refuges were dominated by forest-specialist species while villages had a majority of open area and generalist bird species.

**Table 2. Sorensen similarity index and shared species of ten habitat types in the Path of the Tapir Biological Corridor, Costa Rica**

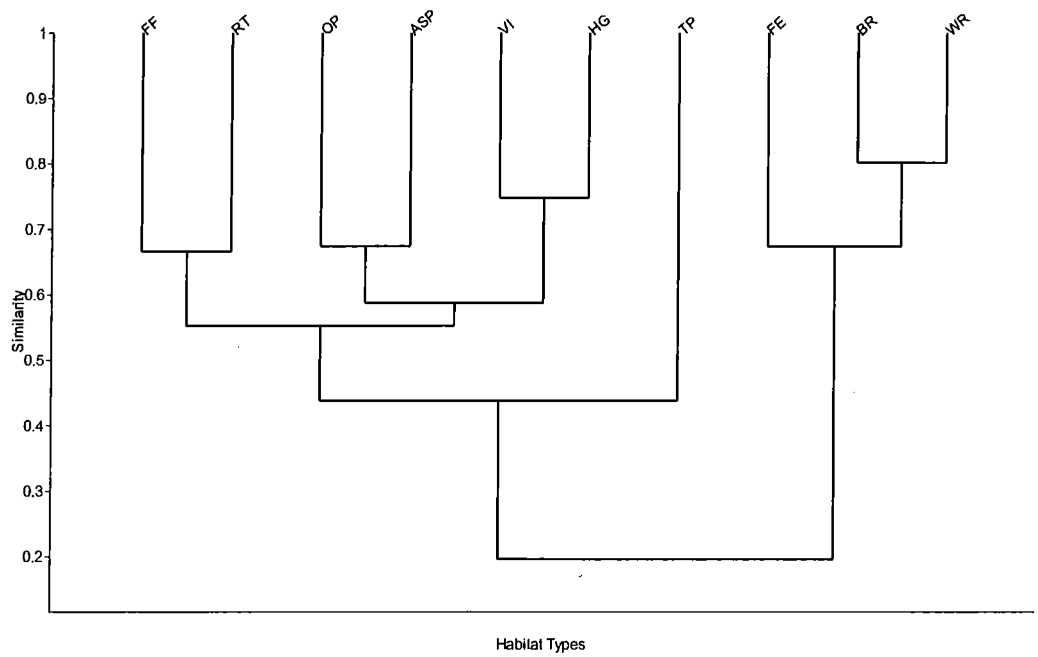
| Habitat 1 | Habitat 2 | Species 1 | Species 2 | Shared species | Sorensen Index |
|---|---|---|---|---|---|
| BR | WR | 124 | 121 | 102 | 0.833 |
| HG | RT | 148 | 111 | 102 | 0.788 |
| HG | ASP | 148 | 143 | 110 | 0.756 |
| FF | TP | 155 | 115 | 102 | 0.756 |
| OP | RT | 107 | 111 | 82 | 0.752 |
| ASP | RT | 143 | 111 | 93 | 0.732 |
| VI | RT | 104 | 111 | 78 | 0.726 |
| VI | TP | 111 | 115 | 81 | 0.717 |
| HG | VI | 148 | 104 | 90 | 0.714 |
| HG | OP | 148 | 155 | 108 | 0.713 |
| FF | RT | 155 | 111 | 94 | 0.707 |
| FE | WR | 154 | 121 | 96 | 0.698 |
| OP | ASP | 107 | 143 | 87 | 0.696 |
| FE | FF | 154 | 155 | 107 | 0.693 |
| HG | OP | 148 | 107 | 88 | 0.69 |
| VI | ASP | 104 | 143 | 84 | 0.68 |
| VI | OP | 104 | 107 | 71 | 0.673 |
| BR | FE | 124 | 154 | 93 | 0.669 |
| HG | TP | 148 | 115 | 87 | 0.662 |
| FE | TP | 154 | 115 | 88 | 0.654 |
| FF | ASP | 155 | 143 | 95 | 0.638 |
| OP | TP | 107 | 115 | 68 | 0.613 |
| ASP | TP | 143 | 115 | 77 | 0.597 |
| FF | OP | 155 | 107 | 75 | 0.573 |
| VI | FF | 104 | 155 | 74 | 0.571 |
| FE | RT | 154 | 111 | 75 | 0.566 |
| VI | TP | 104 | 115 | 61 | 0.557 |
| HG | FE | 148 | 154 | 84 | 0.556 |
| BR | FF | 124 | 155 | 73 | 0.523 |
| FF | WR | 155 | 121 | 72 | 0.522 |
| BR | TP | 124 | 115 | 61 | 0.51 |
| WR | TP | 121 | 115 | 60 | 0.508 |
| FE | ASP | 154 | 143 | 71 | 0.478 |
| FE | OP | 154 | 107 | 58 | 0.444 |
| VI | FE | 104 | 154 | 54 | 0.419 |
| WR | RT | 121 | 111 | 48 | 0.414 |
| BR | RT | 124 | 111 | 46 | 0.391 |
| HG | BR | 148 | 124 | 51 | 0.375 |
| HG | WR | 148 | 121 | 49 | 0.364 |
| ASP | WR | 143 | 121 | 40 | 0.303 |
| BR | ASP | 124 | 143 | 40 | 0.3 |
| OP | WR | 107 | 121 | 33 | 0.289 |
| BR | OP | 124 | 107 | 31 | 0.268 |
| VI | WR | 104 | 121 | 26 | 0.231 |
| BR | VI | 124 | 104 | 26 | 0.228 |

BR = Biological Reserves, FE = Forest Edges, FF = Forest Fallows, HG = Homegardens, OP = Oil palm, ASP = Agrosilvopastoral systems, WR = Wildlife Refuges, RT = Residential Tourism Projects, TP = Tree Plantations, VI = Villages




BR = Biological Reserves, FE = Forest Edges, FF = Forest Fallows, HG = Homegardens, OP = Oil palm, ASP = Agrosilvopastoral systems, WR = Wildlife Refuges, RT = Residential Tourism Projects, TP = Tree Plantations, VI = Villages.

Figure 3. Rarefaction curves for bird species in ten habitat types in the Path of the Tapir Biological Corridor.




BR = Biological Reserves, FE = Forest Edges, FF = Forest Fallows, HG = Homegardens, OP = Oil palm, ASP = Agrosilvopastoral systems, WR = Wildlife Refuges, RT = Residential Tourism Projects, TP = Tree Plantations, VI = Villages.

Figure 4. Similarity of bird assemblages across ten habitat types in the Path of the Tapir Biological Corridor, Costa Rica.

From the 293 species observed, there were only 13 species that were observed in the ten habitat types and 16 species that were found in 9 land-use types, confirming the highly distinct bird assemblages in the study area. From the 13 species reported in the ten habitats, four corresponded to migratory species: *Legatus leucophaius, Vermivora peregrine, Dendroica pensylvanica,* and *Catharus ustulatus*; and nine were native species: *Ramphastos swainsonii, Pionus senilis, Leptotila verreauxi, Tangara larvata, Tityra semifasciata, Leptotila cassini, Cyanocompsa cyanoides*, and *Attila spadiceus*. Contrary to the capability of adaptation of these species to different habitat types, there were 47 species that were registered in only a single habitat type: 11 in agrosilvopastoral systems, 7 in forest edges, 6 in biological reserves, 5 in oil palm plantations, 5 in villages, 4 in homegardens, 4 in forest fallow, 2 in wildlife refuges, 1 in tree plantations, and none in the residential tourism projects. Furthermore, 25 species were only observed in either or both the biological reserves and wildlife refuges, and 21 species were only registered in the agroforestry systems.

## Species of Conservation Concern

Bird species of conservation concern are those more sensitive to be extirpated from a site following habitat loss, species with larger or heavier bodies and those foraging on insects, fruits, or both [50]. According to the Law 7317 for the Conservation of Wildlife in Costa Rica, at present, there are 80 bird species of conservation concern and 17 that are considered endangered species in the country.

We registered a total of 26 species of conservation concern and three endangered species (Table 3). Most species (20 out of 29) were forest specialist, followed by generalist (5 species) and open area species (4 species). Moreover, 55.2% (16 species) were frugivorous, 24.1% (6 species) insectivorous, 13.8% carnivorous (4 species), and 3.4% (1 species) nectarivorous. Overall, all land-use types provided habitat to at least one of the species of conservation concern, and a few of the bird species were observed in more than one habitat. For instance, forest edges, biological reserves or wildlife refuges harbored 18 of the species of concern; and the two agroforestry systems surveyed in this study provided habitat for 13 of these species, including the *Ara macaw*, one of the three endangered species found in this study.

# DISCUSSION

## Contribution of the Different Land-Use Types to Bird Diversity in the PTBC

The accumulated number of bird species observed in this study represented 34% of the avifauna registered in the whole country (293 out of 854 bird species in Costa Rica, [46]), and almost 62% of the species recorded in the Annual Christmas Count conducted in a part of the biological corridor in 2008 [Urena, N., personal communication, 2009]. However, we can assume that this number would be larger if the present study had included flyover species, wetland habitats, and the part of the corridor above 500 m.a.s.l.

**Table 3. Species of conservation concern found in ten habitat types in the Tapir of the Tapir Biological Corridor, Costa Rica**

| Common name | Scientific name | Family | Guilds |
|---|---|---|---|
| Reduced populations | | | |
| Great Black-Hawk | *Buteogallus urubitinga* | Accipitridae | F, C |
| King Vulture | *Sarcoramphus papa* | Cathartidae | F, C |
| Scaled Pigeon | *Patagioenas speciosa* | Columbidae | G, Fr |
| Turquoise Cotinga | *Cotinga ridgwayi* | Cotingidae | F, Fr |
| Yellow-billed Cotinga | *Carpodectes antoniae* | Cotingidae | F, Fr |
| Crested Guan | *Penelope purpurascens* | Cracidae | F, Fr |
| Great Curassow | *Crax rubra* | Cracidae | F, Fr |
| Wedge-tailed Grass-Finch | *Emberizoides herbicola* | Emberizidae | OA, Gr |
| Bat Falcon | *Falco rufigularis* | Falconidae | OA, C |
| Collared Forest-Falcon | *Micrastur semitorquatus* | Falconidae | F, C |
| Long-tailed Woodcreeper | *Deconychura longicauda* | Furnariidae | F, I |
| Yellow-tailed Oriole | *Icterus mesomelas* | Icteridae | G, I |
| Speckled Mourner | *Laniocera rufescens* | Incertae Sedis | F, I |
| Marbled Wood-Quail | *Odontophorus gujanensis* | Odontophoridae | F, I |
| Golden-naped Woodpecker | *Melanerpes chrysauchen* | Picidae | F, I |
| Blue-headed Parrot | *Pionus menstruus* | Psittacidae | G, Fr |
| Brown-hooded Parrot | *Pionopsitta haematotis* | Psittacidae | F, Fr |
| Crimson-fronted Parakeet | *Aratinga finschi* | Psittacidae | OA, Fr |
| Mealy Parrot | *Amazona farinosa* | Psittacidae | F, Fr |
| Orange-chinned Parakeet | *Brotogeris jugalaris* | Psittacidae | OA, Fr |
| Orange-fronted Parakeet | *Aratinga canicularis* | Psittacidae | G, Fr |
| Red-lored Parrot | *Amazona autumnalis* | Psittacidae | F, Fr |
| White-crowned Parrot | *Pionus senilis* | Psittacidae | G, Fr |
| Crested Owl | *Lophostrix cristata* | Strigidae | F, I |
| Great Tinamou | *Tinamus major* | Tinamidae | F, Fr |
| Baird's Trogon | *Trogon bairdii* | Trogonidae | F, Fr |
| Endangered species | | | |
| Mangrove Hummingbird | *Amazilia boucardi* | Trochilidae | F, N |
| Scarlet Macaw | *Ara macao* | Psittacidae | F, Fr |
| Red-crowned Ant-Tanager | *Habia rubica* | Thraupidae | F, I |

Guilds: F = forest specialist, G = generalist, OA = open area species, Fr = Frugivorous, I = Insectivorous, N = nectarivorous, Gr = granivorous, C = carnivorous

The persistence of tropical forest species in human-dominated landscapes is a fundamental challenge of tropical ecology and conservation [51]. Conservation in the PTBC is undertaken through 30 private reserves and the goal is to provide connectivity among these reserves [43]. Therefore, the contribution of agroforestry systems and other human-modified land-use types (matrix) may determine the success of the corridor in its role as connector among habitats. In the present study, the evaluated landscape matrix, including agrosilvopastoral systems, homegardens, tree plantations, oil palm plantations, villages, residential tourism projects, and the young secondary forest, harbored a total of 239 (81.5% of the observed species), highlighting its relevance for bird conservation in the corridor. However, the main forested habitats (wildlife refuges, biological reserves, and forest edges) harbored 66% of the species in the area, and were also the main habitat for species of conservation concern [24, 25, 29, 52, 53].

## Contribution of Agroforestry Systems to Bird Conservation in the Corridor

Agroforestry systems are becoming increasingly important land uses in the tropics due to their functions in improving food security, contributing to rural development and poverty alleviation, and providing several environmental services such as carbon sequestration and biodiversity [54, 55, 56]. The contribution of agroforestry systems to biodiversity conservation has been studied by several authors [56, 57, 58, 59, 60]. Overall, some studies have shown that certain types of agroforestry systems-- such as windbreaks, agrosilvopastoral systems, homegardens, and perennial crop-tree combinations-- can contain bird assemblages that are as abundant, species-rich and diverse as those in natural forests of the same region [60]. However management type and intensity of management practices, including fertilization, herb control, mulching, and shade, can have potentially different effects on biodiversity [61].

In addition, wildlife diversity can vary depending on wildlife species and guilds. For example, several authors have found that forest-specialist bird species tend to be less abundant, while open- area species, granivores, and generalist species populations tend to be larger in agroforestry systems than in nearby forests [56, 60]. In this study, forested habitats (wildlife refuges, biological reserves) and agroforestry systems (homegardens, agrosilvopastoral systems) shared less than 51 bird species, thus showing this difference in species composition. Biodiversity conservation in agroforestry systems can increase if there is diversification of native species and other plants that ensure structural complexity, and that provide fruits and other resources to wildlife [60].

## Role of Agrosilvopastoral Systems in Bird Species Conservation and Potential for Improvement

According to recent statistics, in the Neotropics pastures and agrosilvopastoral land represent 77% of the total of 500 million ha of agricultural land [62]. About 30% of these pastures are on poor acid soils [63], as is the case in the present study. Agrosilvopastoral systems that involve the combination of trees with pastures and livestock offer an alternative set of cattle production systems. These systems are more complex than grass monocultures and are classified based on the functions and configuration or structure of trees within the system; examples are dispersed trees in pastures; live fences in pastures; fodder banks; tree alley pasture systems; and pastures with windbreaks [64]. Agrosilvopastoral systems can provide benefits to cattle farmers by enhancing nutrient cycling, increasing the sustainability of pastures, fodder production for animals, and diversification of income (income from timber, firewood, etc.) that contributes to the economic sustainability of cattle farms [65]. In addition, due to their increased complexity relative to grass monoculture systems, agrosilvopastoral practices also have important benefits for biodiversity [66, 67, 68, 69].

For example, in many tropical pastures there are isolated trees that can be remnants of the original forest. They are conserved by farmers for their functions as shade for animals and humans, and as sources of firewood, timber and fruit. These trees and shrubs may be important in attracting birds, in comparison with tree-less grass monocultures. Crown size and shape, tree height, fruit production and other characteristics may influence the ability of trees to attract birds [70, 71]. Apparently birds prefer taller trees as perches to have a better view of the surroundings and to avert potential predators. On the other hand, results of a recent study in the Pacific region of Costa Rica suggested that crown diameter was more important than height of trees in attracting birds [69].

As shown above, a combination of several characteristics may determine the role of each tree species to attract birds to trees in agrosilvopastoral systems. Distance to forest patches and position in the matrix can also have an important influence. For example, to evaluate the contribution of living fences to improving the connectivity of the agricultural matrix, Francesconi et al. [69] examined bird species composition (forest specialists, open-area specialists, and generalist species) that use living fences as habitat in Esparza, located in the Pacific lowlands of Costa Rica. Bird species composition changed as a function of distance to the forest patch; yet species richness, number of individual birds and Shannon Diversity indices were similar between forest interiors (control) and living fences. Their results suggest that living fences near forest patches provide habitat to many bird species including forest specialists. However, fence structure and composition significantly influenced usage by birds. The authors concluded that the presence of diverse native tree species in fences and increased vegetative cover may counteract the effect of distance to the forest patch, promoting greater bird species diversity in living fences and in the landscape [69].

As seen, the specific types of agrosilvopastoral practices adopted by farmers are important for the conservation of biodiversity [72, 73]. In a long term project in landscapes dominated by cattle in Esparza (Costa Rica), Matiguas (Nicaragua), and Quindio (Colombia), intensive monitoring of birds in different land use systems over four years showed that the agrosilvopastoral practices with high tree densities in pastures and multi-strata or permanent live fences had significantly higher abundance and species richness of birds than degraded and grass monoculture pastures, with comparable values to those of forested vegetation [74]. In their study, Ibrahim et al. [74] reported that a total of 111 bird species were observed in the landscape of Esparza, Costa Rica, 170 species in Quindio, Colombia and 154 species in Matiguas, Nicaragua. Of these, a total of 60.5%, 54% and 64% of the species inventoried were dependent on the forest in Costa Rica, Colombia, and Nicaragua, respectively. Likewise, in a fragmented agricultural landscape in Cañas, Costa Rica, Cardenas et al. [75] showed that the agrosilvopastoral systems with high tree densities and permanent live fences (multi-strata fences) had more than 40 bird species, whereas grass monoculture pastures had 28 bird species.

These data indicate that it is possible to implement agrosilvopastoral systems that are compatible with production objectives and biodiversity conservation. Good farm planning is needed including a mosaic of land uses that are compatible with both the conservation of biodiversity and production objectives [68, 73]. For example, cattle farms should incorporate land uses which include establishment of fodder banks, multi-strata live fences, and pastures with high tree cover or density, as well as riparian and secondary forest [74].

The agrosilvopastoral systems evaluated as part of this study were characterized by the presence of native and exotic tree/shrub species that were either sparsed in the pasture fields as remnant trees, or were part of living fences. This vegetation may play an important role for biodiversity conservation within the corridor because it provides habitat, resources, and facilitates connectivity that is otherwise absent in the agricultural landscape of the region [66, 75, 76]. Therefore, diversifying agrosilvopastoral systems through the use of native species may be a priority to enhance connectivity along the corridor. This may be especially important because more than 20% of the PTBC is composed of open pasture lands [43].

## Role of Homegardens in Conservation of Avian Diversity in the PTBC

The homegardens, which provide the household with a basic food source as well as high value products to generate cash are important in Latin America, and are often used as tools in development projects that promote food security, especially in the poorest areas [77, 78]. In several regions of Costa Rica homegardens are important for supplying food [79]; they also serve as a buffer in times of harvest failure or economic depression [80].

As in other regions worldwide, the structure and composition of homegardens in Latin America are quite complex: they are quite diverse in vertical and horizontal structure and well as in plant species composition. Most homegardens of Latin America consist of several vertical and horizontal strata in which plants are arranged according to their adaptability to the existing light conditions and nutrient resources. The number of individual plants per stratum varies among homegardens; older, more mature homegardens display more developed tree strata. Some homegardens resemble agricultural fields with an emphasis on the herbaceous and low shrub strata, with a greater focus on agricultural crop production. Others have more trees, with architecture similar to that of the native forest of the region [80, 81, 82].

Plant species composition in homegardens is influenced by access to water, owners' economic activities, labor availability, traditional social organization, modernization processes, and economic development [81, 83]. Both exotic and native plants are used, with emphasis on fruit trees. Locally, plant species diversity of homegardens can be influenced by size of the homegardens. For example, in Nicoya, Costa Rica, Lok et al. [82] found that the size of homegardens ranged from 0.1 to 1.4 ha with an average of 0.5 ha. The smallest homegardens considered in the study had the highest plant species diversity, with 205 to 745 species and an average of 348 species per ha. In contrast, the larger homegardens had only an average of 96 species per ha, with less variability among homegardens, in comparison with the smaller homegardens that exhibited higher variability in their species diversity.

Homegardens may have positive effects on biodiversity of wildlife, as they can serve as local refuges for plants and animals that otherwise may be threatened by human or natural disturbances [78]. For example, Griffith [84] reported that during the 1998 fires in Petén, Guatemala, homegardens and other agroforestry systems may have served as critical refuge during a habitat bottleneck for many forest species. Apparently, agroforestry farms attracted birds by virtue of their complex structure – similar to that of intact forest patches – as they harbour insects, provide nesting sites, and offer protection from predators [84]. They were also attracted by the cultivated fruit trees, which may have provided some of the only food sources in the region after fire destroyed most of the surrounding vegetation.

Homegardens are important for bird conservation because their large plant diversity tends to attract many bird species of different guilds [56]. In spite of their many advantages in ensuring food supply and other benefits to local people, currently in the PTBC homegardens are gradually disappearing as they are displaced by increasing urbanization and tourism development [43]. Increased urbanization typically leads to reduction in species richness [85]. For instance, in this study there was decrease in bird species richness from 148 species in homegardens, to only 111 and 104 species in residential tourism projects and in villages, respectively.

In this study, the evaluated homegardens were located in areas with unpaved roads and houses of small size in relation to the garden. In contrast, point counts in villages were located along paved roads, and most of the landscape was composed of cement structures, surrounded by some native and exotic vegetation. Residential tourism projects were located either in fragmented forest landscapes, or they were surrounded by pasture lands. In addition, in these sites houses were of large size in comparison to those in the homegarden and village sites. Therefore, because birds respond to vegetation composition and structure [60, 85, 86], it may be recommended to retain more native vegetation in villages and residential projects, as well as to reduce the size of the urbanized areas so as to retain more bird diversity [85].

## Contribution of Secondary Forests and Tree Plantations to Bird Conservation

Secondary forests and tree plantations are rapidly expanding across tropical landscapes [48]. Secondary forests and tree plantations may play an important role to biodiversity conservation by increasing regional-scale species richness at the landscape level [24, 48]; improving connectivity across the landscape, and buffering existing forest fragments [87]. In the current study, forest fallows and tree plantations shared less than 73 species with either the biological reserves or wildlife refuges. Forest fallows provided habitat to 53 forest species and the tree plantations to 42 species. Even though forest fallows can provide habitat for many bird species, regaining the complex microhabitats and structures required by primary forest specialist is likely to take centuries [48, 88]. It is likely that the older the secondary forest the more forest species may inhabit the area. Therefore, allowing these forest fallows to re-grow by themselves may increase the connectivity between forested reserves in the corridor.

It has been observed that tree plantations promote the regeneration of understory species by shading out grasses, increasing nutrient richness of topsoil, allowing the growth of more sensitive tree species, and creating a microclimate that attracts seed dispersers [89, 90]. In addition, tree plantations may serve as perches, food sources and habitat for a number of wildlife species, thus contributing to increase overall biodiversity [70, 71, 91].

Use of native species, especially in mixtures, may increase wildlife populations in former degraded landscapes such as those currently present in the PTBC [92]. In this study, we found 96 bird species in the native *Terminalia amazonia* plantations and only 71 in the exotic *Tectona grandis* plantations. Although a formal statistical test was not run to compare plantations of the two species due to lack of enough sites to allow for 20 point counts in each (as explained in the Methods section), this appears to be an interesting trend. However, management intensity could also have contributed to these differences in bird diversity among the two species [61]. For example, all understory vegetation growing in the *T. grandis* was removed, as it is commonly done in teak plantations in Costa Rica and elsewhere in Latin

America. In contrast, *Terminalia amazonia* plantations were less intensively managed than *T. grandis* plantations, possibly due to the lack of well defined silvicultural guidelines for *Terminalia.* In the *T. amazonia* plantations visited in this study, most of the natural regenerated vegetation was not removed and thus remained as a part of the natural landscape. Recent studies conducted in experimental plantations of several native species in the Caribbean region of Costa Rica have also found abundant and species-diverse understory growth in unmanaged *T. amazonia* plantations [93, 94]. This understory may provide habitat and other resources to bird and other wildlife species [91, 93].

To increase bird and other wildlife abundance and diversity in the PTBC, it may be wise to encourage and promote the establishment of plantations of native species such as *T. amazonia,* instead of those of exotics such as teak or oil palm. *Terminalia amazonia* is considered a very promising native timber species for plantation in Central America due to high value and good growth, and it is already one of the most frequently planted native species by local farmers in the Caribbean region of Costa Rica [95, 96]. In Panama, the commercial company Futuro Forestal reported sales of first thinnings of young *T. amazonia* plantations from their farms in Chiriqui that achieved the same price at *T. grandis*, due in part to Forest Stewardship Council certification [97]. *T. amazonia* is apparently capable of adapting to different site conditions, with good growth even on degraded sites covered by invasive vegetation [98]. Other native tree species could be planted with similar advantages. Improved knowledge and application of management techniques (thinning, pruning) and genetic selection can also contribute to improved performance [96]. In Costa Rica, incentives such as Payments for Environmental Services (PES) are available to establish tree plantations including native species.

## Contribution of Habitat Types of the PTBC to Species of Conservation Concern

In order to evaluate the role of different habitat types to biodiversity conservation, it is important to know not only how many species are present within these habitats, but also which species are present and whether any of these are of conservation concern [60].

The nine species of the Psittacidae family registered in this study are considered of conservation concern or endangered (*Ara* macaw) as a result of habitat loss, direct hunting, and poaching for the pet trade market [45, 46]. However, most of these species were observed in more than one habitat type and the majority of them had important abundance. Of more concern are *Pionopsitta haematotis,* which individuals were only found in private reserves, and *Ara macaw*, which once resided on both the Pacific and Caribbean slopes, and now is only located in a few spots along the Pacific Coast [45, 46, 99]. In the corridor, *Ara macaw* populations were located foraging and perching mostly in homegardens, villages, and in forest edges in the southern part of the region. A few individuals were also registered in homegardens of the PTBC's northern limit; however, according to a few neighbors these birds were part of a re-introduction program back in the 1990s.

The other two endangered species *Habia rubica* and *Amazilia boucardi* were registered only once over the time of this project. *Habia rubica* is a forest-dependent species that forages in the understory of mature forests and *Amazilia boucardi* is an endemic species of the Pacific coast of Costa Rica, specifically mangrove and adjacent forests [46]. Another group of species that also depend on the conservation of forest for their survivorship in the corridor are *Buteogallus urubitinga*, *Sarcoramphus papa*, *Cotinga ridgwayi*, *Carpodectes antoniae*, *Penelope purpurascens*, *Crax rubra*, *Micastur semitorquatus*, *Deconychura longicauda*, *Laniocera rufescens*, *Odontophorus gujanensis*, *Pionopsitta haematotis*, *Lophostrix cristata*, *Tinamus major*, and *Trogon bairdii*. Unfortunately, urban and tourism development are jeopardizing the conservation of many of these species in the region, especially because forest cover is either disappearing or being fragmented around most private reserves.

## CONCLUSIONS

As highlighted recently by several researchers, a new conservation paradigm must incorporate human-modified landscapes in assessments of biodiversity and ecosystem services, planning of corridors, establishment of buffer zones, and restoration of degraded lands [100]. The current study aimed to incorporate this approach, thus we assessed biodiversity not only in private forest reserves, but also in several other habitat types that were part of this human-modified biological corridor known as Path of the Tapir.

Agroforestry systems such as agrosilvopastoral systems and homegardens are diverse habitats that if managed in the proper way may increase the current contribution to the PTBC and other fragmented habitats to wildlife conservation. Adding native tree species, especially fruit trees, in agricultural systems adjacent to forested areas may add conservation value to these habitat types, attracting bird species such as *Ara macaw* and other forest-dependent bird species.

Forest fragmentation, unplanned urbanization, monocultures, and the introduction of exotic plant species should be avoided in biological corridors in order to not jeopardize biodiversity. One example of these monocultures that should be avoided is oil palm plantations, whose diversity values were one of the lowest of all evaluated habitats. In contrast, planting native timber tree species, such as *Terminalia amazonia* and other native tree species of interest in Costa Rica and elsewhere, should be given priority to serve biodiversity and economic objectives of humans inhabiting the corridor.

At the species level, aside from the 29 species of conservation concern, special priority should be given to favoring habitat types preferred by the forest-specialist species. This is especially important with regards to frugivorous and insectivorous birds that are more sensitive to human disturbances and therefore more prone to extinction.

Finally, we need to stress that biodiversity conservation should always include primary and old-secondary forests (e.g., those forests located in wildlife refuges, biological reserves, or isolated forest fragments) as these are the most important habitat type for wildlife at the landscape level. However, the results of this research also show that the matrix, especially agroforestry systems and plantations, are important to ensure wildlife conservation in the biological corridor in the short and long term.

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