

EDGE CONTRAST AND SPILLOVER EFFECTS IN A CLOUD FOREST BIRD
COMMUNITY

By

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To Dr. Ian Giddy

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Abstract of Thesis Presented to the Graduate School
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Tropical cloud forest supports tremendous biological diversity, which is threatened by habitat loss and fragmentation. Nonetheless, some forms of anthropogenic disturbance may lessen the effects of habitat loss and fragmentation on wildlife. For example, while clearing forest for pasture reduces the habitat available to cloud forest species, vegetation within pastures may ameliorate that loss. I documented edge effects that occurred from forest birds spilling over into pastures in a cloud forest landscape in Ecuador, and tested whether and how vegetation structure in pastures influences the spillover of birds.

I collected data on the spatial distribution of avian diversity at two private reserves containing pasture fragments that ranged in vegetation structure and composition. In some pastures trees were sparse, while in others tree density was high. Pastures contained old growth trees left uncut, young regrowth trees, or plantations of native or non-native species. I sampled 17 pastures for birds using standard point count techniques and sampled vegetation in these areas.

Distance from edge had a highly significant and consistent negative effect on bird diversity in pastures. The effect was best described by an edge measure that

incorporated the effects of multiple edges within pastures. All types of trees were positively associated with diversity, with the number of remnant trees having the most positive effect. My results suggest that remnant trees have a greater positive effect on diversity than any form of reforestation, and reduce the negative effects of forest loss and fragmentation by increasing diversity and reducing edge effects within pastures. This outcome provides guidance to help improve pasture management in this biodiversity hotspot.

CHAPTER 1 REVIEW OF THE EFFECTS OF FOREST FRAGMENTATION ON TROPICAL BIRD COMMUNITIES

Habitat loss and fragmentation and the impacts of each on biological diversity have long been prominent issues in the field of ecology (e.g., Fahrig 2003, Harrison and Bruna 1999, Tscharntke et al. 2002). Forests worldwide have been cleared and fragmented by human land use, and these ongoing processes represent a major threat to the biological diversity of forest systems (Turner 1996).

The sensitivity of the highly diverse avifauna of tropical forests to forest fragmentation provides a striking example of this problem. A large body of work has focused on the ways that bird communities are impacted by processes that occur within forest fragments, especially those driven by elements of landscape pattern such as reduced patch size, increased patch isolation, and the proliferation of edges (e.g., Brooks et al. 1999, Graham and Blake 2001, Laurance et al. 2002). Another group of studies has sought to quantify the presence of forest birds in non-forest habitats, relating it to the structure and composition of vegetation there (Daily et al. 2001, Waltert et al. 2005, Sekercioglu et al. 2007). A smaller number have combined the two approaches by considering how vegetation outside of forest patches influences the edge effects acting inside them (Restrepo and Gómez 1998). Fewer still have examined how bird diversity in non-forest habitats varies according to both land use and the proximity of forest edges (Tubelis et al. 2004). Given that the effects of deforestation are long-lasting, and that more forest will inevitably be lost, it is important to understand how former forest lands now dominated by human use can contribute to the conservation of tropical birds, and the significant component of regional biodiversity that they represent.

While the loss of total forest area has obvious negative consequences for forest-dependent species, forest birds also respond to the pattern of a fragmented landscape in three basic ways. The size of remaining forest patches plays a crucial role, as many species are area-limited and cannot persist in patches when the area falls below a certain threshold (Boulinier et al. 2001). As a rule, species richness within fragments declines with decreasing area (Rompré et al. 2009). The distance between patches is important, because it limits the ability of individuals to disperse from one patch to another. When patches become too isolated from each other, as predicted by island biogeography (MacArthur and Wilson 1967), local extinctions are not compensated by colonization, and species richness declines over time. The shape of clearings or remaining forest patches is also relevant, due to the edge effects that penetrate into forest from adjacent open areas. It is well-documented that the survival, and especially breeding success, of birds near forest edges can suffer as a result of increased predation, parasitism, and changes in microclimate (Paton 1994, Flaspohler et al. 2001). Such edge effects are likely to leave a reduced core area of habitat within each patch in which forest-dependent species are able to thrive (Laurance and Yensen 1999, Ewers and Didham 2007). Patches that are narrow or convoluted in shape will have less core area than more regularly-shaped patches of the same size. This consequence may be exacerbated by the cumulative effects of multiple edges within fragments. Malcolm (1994) found that proximity to multiple edges best explained the structure of vegetation in rainforest patches. Fletcher (2005), in a temperate grassland system, found that bobolink (*Dolichonix oryzivorus*) abundance in patches declined as a function of both the nearest and next-nearest edges.

The effects of patch area and isolation in a fragmented landscape are themselves affected by the structure and composition of vegetation in the deforested matrix (Laurance 2008). The nature and intensity of edge effects that act within forest patches are largely determined by the contrast between the forest and the matrix vegetation; matrix that is floristically and structurally more similar to the forest should lessen edge effects (Ries and Sisk 2004, Ries et al. 2004). In a study of understory birds in fragmented cloud forest, Restrepo and Gómez (1998) found that patterns of bird abundance with respect to distance from forest edges was significantly influenced by the age of regenerating matrix habitats. In both lowland (Stouffer et al. 2006) and montane (Renjifro et al. 2001) tropical forest systems, it has been found that the abundance and diversity of birds inside forest fragments is significantly and positively related to their presence outside of forest. This may be due to forest birds exploiting resources in the matrix, in which case forest and matrix might be considered supplementary habitats in the landscape (Dunning et al. 1992). The ability of matrix habitat to expand the resource base of a forest fragment could lead directly to higher populations of birds there, and perhaps allow more species to coexist. When matrix habitat has value for forest species, their positive response in fragments may be described best by an effective area model (Sisk et al. 1997) that considers the ecological extent of forest in the landscape to be greater than its structural area. An increased presence of forest birds in the matrix may indicate a greater degree of connectivity in a fragmented landscape. The readiness of birds to enter the matrix and their rate of movement there are both strongly influenced by the nature of the matrix habitat (Castellon and Sieving 2006). It has been shown that bird species which more

frequently cross gaps in a fragmented landscape are more likely to persist in isolated fragments (Lees and Peres 2009).

The paucity of bird species present in deforested habitats relative to the pre-disturbed forest has been documented by many studies, particularly in the lowland tropics. However, some studies have found that a substantial portion of forest species can utilize human-dominated landscapes under a range of conditions. In a study of bird diversity in mixed land-use types in a foothill region of Costa Rica, Daily et al. (2001) encountered 45% of forest bird species outside of the forest. Sekercioglu et al. (2007) estimated that 75% of forest birds in Costa Rica use deforested habitats to some extent. In Ecuadorian cloud forest, O'Dea and Whittaker (2007) even found that the species richness of birds in the edge and young successional habitats of fragmented landscapes is higher than that of intact forest. More typical results are those that show that bird diversity outside of forest increases as the vegetation becomes more forest-like, that is, more structurally complex and floristically diverse. In various studies, bird diversity in land-use areas has been found to be most strongly associated with tree density (Waltert 2005), canopy cover (Soh 2006), and tree species richness (Harvey 2006).

When high levels of forest bird diversity occur in any area of active land-use, the proximity of intact forest is likely to play an important role. The forest may serve as a source habitat for forest species, with individuals that emigrate or make forays from it accounting for many of the species that are detected in non-forest areas (Blake and Loiselle 2001). The appearance of a distance effect may depend on the scale of clearing in the landscape. Daily et al. (2001) found that bird diversity in an intensively

fragmented landscape did not vary significantly as a function of distance to the nearest intact forest, which was at least several kilometers away. On a smaller scale, Luck and Daily (2003) observed a significantly greater number of bird species at isolated fruiting trees in areas that were closer to forest than in areas of comparable land use that were farther away. In small agricultural plots (typically not more than a couple hectares) embedded in the New Guinean rain forest, Marsden et al. (2006) found that only a handful of bird species decreased significantly in abundance, indicating that the forest bird community was highly resilient to clearing at that scale.

The response of forest birds to converted forest land varies widely from species to species, and among trophic guilds, even when there is no significant change in species richness or abundance. Gomes et al. (2008), for example, found that bird species richness did not decline significantly across a gradient of increasing habitat disturbance, because the loss of forest species was effectively compensated by the addition of species associated with open habitats. Species that exhibit the strongest negative responses to edge effects inside the forest are, not surprisingly, among the least likely to be found outside it. It has consistently been shown that the terrestrial insectivores are the foraging group most intolerant of forest conversion (Becker et al. 2008, Tschardt et al. 2008). Frugivores seem to be relatively resilient, sometimes even increasing in abundance in secondary and edge habitat, but some studies have distinguished between small and large frugivores, and found that the larger species are more dependent on forest (Renjifo 1999, Welford 2000). Small arboreal insectivores and omnivores, as well as nectarivores (primarily hummingbirds) tend to fare relatively well in land-use areas. However, Becker et al. offer an example of how species-specific

responses can be: the tawny-bellied hermit (*Phaethornis syrmatophorus*), a hummingbird, is highly dependent on intact cloud forest because it feeds almost exclusively on the flowers of epiphytes that do not grow outside it. Social interactions among birds may also influence the extent to which they use open habitats. Poulsen (1994) found that some Ecuadorian cloud forest species only left the forest when traveling with a mixed species flock, and that flock associations generally made birds more likely to cross forest edges.

The preponderance of research on the effects of forest loss and fragmentation on birds in the tropics has been done in lowland rainforest. Montane cloud forests have received less attention in this regard, and there is less agreement among the results of the studies that have been done. Cloud forest regions differ significantly from their lowland counterparts in terms of topography, climate, bird communities, and past and present human land use. It is therefore reasonable to expect cloud forest birds to react differently to fragmentation than do their lowland counterparts. Some have proposed that cloud forest bird communities are generally more sensitive to forest clearing because a greater proportion of species are rare or restricted to small ranges (Soh 2006). Others suggest the opposite, hypothesizing that the high rate of natural disturbance in cloud forests, largely due to landslides, has resulted in species that are better adapted to forest gaps and edges (Restrepo and Gómez 1998). Given that the natural extent of cloud forest is far less than that of lowland rainforest, and that it is being lost at a greater rate (O'Dea and Whittaker 2007), it is imperative to understand the unique ways in which cloud forest birds are affected by the conversion of forest to human uses.

Forest fragmentation studies have mostly been conducted in regions where large scale land use has left only scattered patches of forest surrounded by a human-dominated matrix. Few have considered the reverse situation, in which relatively small areas of cleared land are embedded in intact forest. This is understandable, since the survival of forest species in a heavily cleared landscape would seem to be more tenuous. However, the perforation of forest by small-scale land use should not be dismissed as a conservation issue. Small clearings may still substantially degrade the quality of the landscape as habitat for forest birds, as was found by Rodewald and Yahner (2001). Alternatively, the proximity of forest may allow land use to occur in such a way that the disruption of forest bird communities is small even relative to the area of forest that is removed. The perforation pattern of forest fragmentation may be characteristic of at least some cloud forest regions. Whereas in the relatively level terrain of lowland areas, forest often remains only in the small percentage of the landscape that is impractical for land use, in the mountains where cloud forests are found the proportions may be reversed, with clearings established where the topography permits.

Within even a single category of land use, such as the grazing of livestock, there is a wide range of variation in the scale and pattern of forest clearing, and in the nature of the vegetation that replaces it. A predictive model that considers the separate, additive, and possibly interactive effects of these factors would be a valuable tool for comparing the impact of different landscapes, prioritizing areas for conservation action, and recommending land use practices that most effectively balance productive use with the maintenance of native biological diversity.

CHAPTER 2 EDGE CONTRAST AND SPILLOVER EFFECTS IN A CLOUD FOREST BIRD COMMUNITY

Introduction

An enormous amount and wide variety of natural habitat has been converted to human land-use forms, and this ongoing process represents a major threat to global biological diversity (Hoekstra et al. 2005). The conversion of habitat is often uneven, resulting either in a landscape where fragments of habitat are surrounded by a converted matrix, or where continuous habitat is perforated by land-use areas (Rodewald and Yahner 2001). While the overall loss of natural habitat has an obvious potential to negatively affect biodiversity, and may be responsible for many of the responses that are observed (Fahrig 2003), the pattern of habitat fragmentation is also relevant (Ewers and Didham 2006). The detrimental effects of reduced habitat patch size and increased patch isolation have been documented across many taxa (Bender et al. 1998, Prugh et al. 2008). Small patches jeopardize species that require a minimum contiguous area of habitat, and it has been shown that decreasing patch size is associated with a long-term decline in species richness (Laurance et al. 2002). The isolation of patches hinders the dispersal of individuals among them, increasing the risk of local extinctions and threatening the persistence of metapopulations (Hanski 1998). Although these processes were historically placed within the neutral framework of island biogeography (MacArthur and Wilson 1967), it has become evident that the nature of the matrix must be considered (Ricketts 2001). A more hospitable matrix habitat may increase the ecological effective area of patches (Sisk et al. 1997), and can reduce isolation by facilitating the movement of dispersing individuals (Castellon and Sieving 2006).

Another crucial element of pattern in fragmented landscapes is the proliferation of habitat edges. Edges are conduits by which the influence of a land-use matrix can penetrate the remaining natural habitat, altering and often degrading it (Murcia 1995). Edge effects have been widely studied and a variety of mechanisms have been documented. Among the most prevalent are changes to the microclimate of near-edge relative to interior areas (Didham and Lawton 1999), resultant changes in vegetation growth (Malcolm 1994), and an influx of predators and parasites (e.g., Paton 1994). Edge effects conspire with patch shape to determine core habitat area. In more irregularly shaped patches, which have a large amount of edge relative to their area, a smaller proportion of habitat is left unaffected (Laurance and Yensen 1991, Ewers and Didham 2007). It has also been shown that the effects of multiple edges can be additive (Fletcher 2005), indicating that irregularly shaped patches experience edge effects of greater intensity. Edge effects, like the effects of patch size and isolation, are strongly influenced by the nature of the matrix. Edge effects are typically stronger when there is greater contrast between the natural habitat and the matrix, in terms of the structure and composition of the matrix (Fletcher and Koford 2003, Ries et al. 2004). Harmful edge effects can thus be mitigated by managing land-use areas to more closely resemble the natural habitats they replace.

Edges are potential barriers to the movement of organisms; even a road through continuous habitat may significantly alter movement behavior (Laurance et al. 2004). However, it is also common for individuals originating on one side of a habitat edge to cross to the other, in either temporary forays or permanent dispersal. When there is a prevalent directionality to such movement it is termed spillover (Lidicker 1999, Rand et

al. 2006), or a halo effect (Brudvig et al. 2009). Organisms that originate in the matrix may spill over into natural habitats, as was documented in the case of agriculturally subsidized insects by Rand et al. (2006). The opposite also occurs, with organisms spilling from natural habitat into the matrix (Brudvig et al. 2009). In the first instance, at least when the organisms in question exert a negative influence, a higher rate of spillover is linked to greater degradation of the natural habitat. In the second instance, increased spillover may result from an improvement in the quality of the natural habitat which allows for larger populations of the species that spill over. Or, it may be evidence that the matrix has become more attractive to organisms based in the natural habitat. Like other edge effects, spillover attenuates with increasing distance from the edge (Tschardt et al. 2008). Spillover in different contexts can be compared on the basis of the diversity or abundance of individuals at given distances, or the rate at which these measures decline. It is reasonable to expect that the magnitude of spillover is governed by edge contrast, but this relationship has rarely, if ever, been tested. If edge contrast can be manipulated to promote the spillover of species from natural habitat to land-use areas, it could be a valuable tool for increasing the diversity and abundance of such species across fragmented landscapes.

Montane cloud forests of the humid tropics are an excellent system for examining the relationship between edge contrast and spillover. Cleared areas in cloud forest landscapes are predominately dedicated to a single form of land-use, the grazing of livestock (Gunter et al. 2007). Nonetheless, the nature of the vegetation within actively grazed pastures is highly variable. The contrast between pasture and forest can be quantified in terms of variation in vegetation structure and/or composition. For example,

pastures in cloud forest often contain remnant, old-growth trees (Harvey and Haber 1999); those with the most remnant trees are likely to be most similar in terms of composition to adjacent forest. Pastures that lack remnant trees may contain natural regrowth trees or plantations of either native or non-native species, and their compositional contrast from the forest varies accordingly. Due to the complex mountain terrain where cloud forest occurs, pastures are often embedded in continuous forest and vary widely in size and shape.

While the consequences of fragmentation have been extensively studied in lowland rain forests, cloud forests have received much less attention in this regard. Like their lowland counterparts, cloud forests support a tremendous level of biodiversity (Martínez-Morales 1995). Compared to lowland forests they contain a greater proportion of rare and range-restricted species (O’Dea and Whittaker 2007), such that cloud forest communities may be more vulnerable to habitat fragmentation (Soh et al. 2006). However, it is also possible that cloud forest species may actually be more resilient because they are adapted to a high rate of natural disturbance (Cresswell et al. 1999), driven mostly by landslides that result from the steep terrain and saturated soils (Dykes and Welford 2007). Therefore, from a conservation standpoint, land-use areas within a cloud forest landscape may represent a risk that must be mitigated or an opportunity that can be leveraged. Cloud forest birds are an ideal taxon for this type of study because they are conspicuous, diverse, mobile, and have well-known habitat preferences.

My objectives were to document patterns of bird diversity within pastures embedded in cloud forest and to examine how the configuration of pastures and the

structure and composition of the vegetation they contain influence these patterns. I predicted that the species richness of forest birds declines with increasing distance from the forest edge, indicating an effect of spillover from the forest. I expected that spillover is mediated by edge contrast, both in terms of its magnitude (an additive effect) and its rate (an interactive effect). The magnitude of spillover should be higher, and the rate at which it attenuates lower, when pasture habitat is structurally more similar to the forest.

Methods

Study Areas

I addressed my objectives in cloud forest landscapes within the Chocó-Andes region of northwest Ecuador, where forest clearing exceeds the national average by 30 percent, and which has been recognized as a high priority area for biological conservation by organizations such as Conservation International, BirdLife International, and the World Wildlife Fund (O’Dea and Whittaker 2007). All range-restricted bird species in this area are considered to be threatened or near-threatened (Cresswell et al. 1999).

Field work was conducted at two small, private reserves, the Bellavista and Santa Lucía Cloud Forest Reserves (approximate areas of 900 and 1,800 hectares, respectively). They are located on the western slope of the Andes mountain range, less than 20 kilometers apart, and together span an elevational range between 1,800 and 2,400 meters above sea level. Both are approximately 80 percent forested. At Santa Lucia, most forest is primary, while at Bellavista most is secondary. Larger expanses of continuous forest exist in the areas surrounding the reserves; Santa Lucía borders the 6,000 hectare Maquipucuna private reserve and Bellavista falls in the buffer zone of the 19,000 hectare Mindo-Nambillo Protected Forest. Both reserves contained pastures at

the time they were established (Bellavista in 1991 and Santa Lucía in 1999). Some of these pastures were abandoned and allowed to regrow, while others are still actively grazed. Cows are the principal type of livestock. They are sold for meat, with the income supplementing that which is earned through ecotourism. A small number of mules and horses also occur in pastures.

Vegetation within pastures is highly variable (Table 1). Some of the pastures contain remnant trees, particularly at Santa Lucia. Some, subject to less frequent or less intense grazing, have regenerated some degree of tree cover through natural succession. Some have been partially planted with either native Sangre de Drago trees (*Croton magdalensis*) or non-native Aliso trees (*Alnus acuminata*). Aliso are useful for timber, and because they are nitrogen fixers are also planted to improve the quality of the soil. Sangre de Drago provide effective shade for cattle, can be used for timber, and their sap has value owing to the medicinal value attributed to it. This variation among pastures results in different degrees of edge contrast with the surrounding forest.

A total of 17 pastures were mapped and used in bird and vegetation surveys, nine at Bellavista and eight at Santa Lucía (Figures 1 and 2). Pastures ranged in size from slightly less than 0.5 hectare to almost nine hectares (mean = 3.7 hectares; Table 2). Most were highly irregular in shape. The transition from forest to pasture at the forest edge was abrupt in nearly all cases. A total of 102 survey sites were established in pastures (54 at Bellavista and 48 at Santa Lucia). The maximum distance of any pasture site to the nearest forest edge was 77 meters. Thirty-two sites were placed in forest (16 at each reserve) in order to distinguish true forest species from those that prefer open habitat.

Bird Surveys

I established survey sites in all accessible pastures at both reserves, and mapped the boundaries of all pastures using a handheld GPS unit. Each pasture was sampled proportional to its area, with survey points spaced 75 meters apart. In pastures too small to accommodate more than one point, a single point was placed near the center of the pasture. In larger pastures, I placed an initial point near a corner, roughly 20 meters from the forest edge. Additional points were placed at 75 meter intervals along a line crossing the pasture at its longest axis, until the opposite edge was reached. This process was repeated with multiple lines when the size or shape of the pasture permitted it. Finally, I placed a small number of points in the spaces left empty by the line method. These spaces resulted from the highly irregular shapes of the pastures, and generally accommodated a single point whose location was strictly constrained by adjacent points and forest edges. I also established survey sites at 75 meter intervals along five different trails inside the forest. The distance of 75 meters between points (less than that used in most studies) was chosen because it reflected the small scale of forest clearing in the study area, and the variation in pasture vegetation that occurred over short distances. In this landscape, closely-spaced points were necessary to test the hypothesis that bird diversity in pastures varied as a function of both local vegetation and distance from edges. This distance is much less than the 150-200 meter spacing that is typically employed to ensure statistical independence of surveys, and thus risks spatial autocorrelation. To address this issue I included in the model selection process a model which explicitly considered the potential for spatial autocorrelation among closely spaced points (see below).

I surveyed birds using a standard fixed-radius point count method. I recorded all birds seen or heard within 25 meters of the point count site during a 10 minute period, with the exception of flyovers. The survey period was divided into four equal intervals during data collection, but detections in the full period were pooled for all analyses. I estimated the distance of each bird from the survey point at the time of detection using a laser rangefinder, which ensured accurate delineation of birds inside or outside of the count area. Surveys were conducted between 6:00 and 11:00 in the morning, except in weather conditions that would significantly impede visibility (i.e., fog or steady rain), and therefore bias the detectability of birds. All survey sites were visited four times in 2009, during a period that encompassed the rainiest part of the year (January-April) and a relatively dry season (May-July).

I collected data to characterize the vegetation within 25 meters of each point count site. All trees in this area were assigned to one of eight categories: 1) remnant trees, 2) aliso (all were planted), 3) sangre de drago (either planted or occurring through natural regrowth), 4) any other “hardwood” species that had grown naturally after clearing, 5) *Cecropia*, 6) palms, 7) tree ferns, and 8) standing dead trees. Remnant trees were recognized by their large size and particularly by their columnar shape, with a broad, straight trunk and few branches clustered near the top. Within each of these categories I counted the number of trees in three classes of diameter at breast height: 1-10 cm, 10-30 cm, and greater than 30 cm. I estimated the representative height of trees in each category, and the percent of the survey area covered by the canopy of each. When shrubs were present, I estimated their height and percent coverage. I also estimated the height and coverage of the three basic components of ground cover,

grasses, ferns, and broad-leafed herbaceous plants. Canopy foliage density was quantified by taking four densitometer readings (facing in the cardinal directions) at the center of the survey plot. Epiphyte load on each of the eight tree categories was assigned a value from 0 (none) to 5 (heaviest relative to all observed trees).

Analysis

Edge distances and pasture configuration. Survey points were overlaid on pasture polygons (derived from GPS field mapping) to quantify the position of the points relative to the surrounding pasture and forest edges. Edge effects have been quantified in numerous ways. Here, I contrast four different measures to describe the potential for edge effects: 1) nearest distance to edge, 2) a cumulative measure that incorporates the effects of multiple edges (Fletcher 2005), 3) pasture shape, and 4) area of pasture surrounding each point. The shortest distance between each survey point and a forest edge was found using the Near tool in ArcGIS. Following a method proposed by Mancke et al. (2000), three additional edge distances were measured at 90° , 180° , and 270° from the nearest edge line. For understanding how multiple edges influence spatial patterns, a simple arithmetic average of these distances is inappropriate, because, intuitively, the distance to the nearest edge should have a stronger influence than other distances. As a potential solution, I computed the harmonic means of the four measurements. The harmonic mean is heavily weighted by the shortest distance, and therefore is always less than the arithmetic mean except when all distances are equal (Fig. 3). It is a simple metric that allows for the influence of multiple edges while attributing the dominant effect to the nearest edge.

The relative irregularity of pasture shape is potentially important because pastures with more edge may experience a greater total influx of forest birds, resulting

in more observed spillover at all points irrespective of distance from edges. Pasture shape was represented by a shape index (Patton 1975) derived from the ratio of a pasture's perimeter to its area (Shape index = $\text{Perimeter} / 200 (\pi \cdot \text{Area})^{0.5}$), where perimeter is in meters and area is in hectares). A perfectly circular pasture would result in a score of 1.0, with increasingly irregular shapes generating higher scores. The relative amount of forest and pasture surrounding a survey point may also influence the spillover of birds it receives, with a greater area of forest likely containing more birds that are available to spill over. I used a GIS buffer analysis to determine the area of pasture within 150 meters of each survey point.

Vegetation. I performed a principal component analysis (PCA) in SAS (PROC FACTOR) to transform the raw vegetation data into a series of uncorrelated components. Eleven vegetation variables were input in the PCA: trees counts in the three size classes and six identity categories (*Cecropia* trees, palms, and tree ferns were consolidated into a single category), as well as the mean epiphyte load score and the shrub cover. I used the Varimax rotation method to increase the interpretability of the components. All components with eigenvalues greater than 1.0 were used in models as local vegetation predictors of bird species richness and abundance (McGarigal et al. 2000). To determine whether vegetation in pastures varied as a function of distance from forest edges, I used a general linear model with the harmonic mean of multiple edge distances as an explanatory variable and each principal component as a response variable.

Bird species richness. I defined as pasture species all birds for which 95 percent of their detections occurred in pasture (as opposed to forest surveys), and

which were recorded on at least four surveys in pastures. The threshold of four detections was applied to prevent rare forest species that were found by chance only in pasture from being incorrectly characterized as preferring open habitat. I assigned all non-pasture species to a foraging guild based on descriptions of their foraging habits by Ridgely and Greenfield (2001). Omnivores included all tanagers, as well as jays and thrushes. Frugivores included toucans, trogons, cotingas, and manakins. I divided insectivores into five categories: aerial capture species (flycatchers), gleaning species (e.g., warblers and vireos), epiphyte specialists (e.g., furnariids), bark specialists (woodpeckers and woodcreepers), and terrestrial foragers (antpittas and tapaculos). Ground doves and quail were categorized as terrestrial omnivores. Hummingbirds comprised their own nectarivorous guild. Also following the descriptions of Ridgely and Greenfield (2001), I classified species according to the vertical strata of forest in which they are most often found (canopy, mid-level, understory, and terrestrial), and whether they commonly associate with mixed species flocks. Based on the findings of previous studies of the response of tropical bird guilds to habitat disturbance (e.g., Kattan et al. 1994, Renjifro 1999, Thiollay 1999 and Gomes et al. 2008), I predicted that terrestrial and understory insectivores would be least likely to occur in pasture, whereas frugivores, nectarivores, flocking and canopy species would spill over from the forest at higher rates.

I computed a first-order jackknife species richness estimate of forest bird species richness (pasture species were excluded) for each site based on the species observed during each of the four survey visits, using the program EstimateS (Palmer 1990). A jackknife estimate increases in proportion with the number of species that are observed

only once, linking the estimated total to the number of rare species. I used this method because there was a high degree of species turnover at each site over time, making it likely that many species went undetected. To further understand the turnover of forest species in pastures, I used EstimateS to compute a Bray-Curtis similarity index comparing the species composition at each site with that of all forest sites combined. I included all species in this analysis, because the goal of this analysis was to address whether species dissimilarity of the entire community changed in pastures due to variation in spillover effects.

Model selection. I used general linear models in SAS (PROC MIXED, using maximum likelihood estimation) to determine the effects of edge proximity and local vegetation on bird species richness in pastures. I tested a series of models in order to identify the most parsimonious combination of explanatory variables. The AICc criterion was used as the basis for model selection. I chose this criterion because it is more conservative than AIC, and has been shown to perform better in cases where the sample size is small (Hurvich and Tsai 1995). The jackknife estimate of bird species richness was first modeled separately as a function of each landscape measures. The same was done for the vegetation principal components. The landscape measures and vegetation components that produced the lowest AICc scores, as well as any that were within 2.0 AICc units of the minimum (Westphal et al. 2003), were identified as candidate variables. These were then used in combination, and the most parsimonious of the combined models was selected. I next added interaction terms to this model, between the landscape and vegetation variables, to assess whether the strength of the edge effect varied according to the vegetation context. Finally, I addressed the potential

for spatial autocorrelation by extending the best model selected to include modeling the residuals with a compound symmetric variance-covariance structure that assumed constant correlation among sites within pastures (Littell et al. 2006). The same model selection process was also applied separately to each of the foraging guilds, using the raw number of species observed per site as the response variables, to determine if these groups respond in unique ways to pasture habitat and edges. In each of the models judged to be most parsimonious, I compared the effects of the retained variables based on whether their regression coefficient 95% confidence intervals overlapped zero. Those that did not were considered to have the strongest effects.

Model predictions. The model determined to be the most parsimonious predictor of bird species richness was used to compare predicted species richness under hypothetical scenarios defined by different levels of the retained variables. I produced two plots of species richness as a function of the retained landscape measure across the full range of that measure that occurred in the study area. For the first plot the retained vegetation components were maximized (i.e., I used the loadings from those sites at which the highest loading of the given component occurred). For the other plot the mean loadings (effectively zero) were used.

Site classification. All pastures sites were divided post hoc into four approximately equal groups based on the total number of trees in the medium and large size categories (dbh greater than 10 cm) and the harmonic mean of multiple edge distances. Large and medium trees were chosen because these two variables were highly loaded in the first and second vegetation principal components, and thus explained the greatest portion of variation in vegetation among the sites. I first divided

all sites into two halves at the median number of trees. Both halves were then divided at the median harmonic mean distance. Each of the resulting groups therefore represented a unique combination of the high and low ranges of these measures present in the study area: many trees close to the forest edge, many trees far from the edge, few trees close to the edge, and few trees far from the edge.

I used an ANOVA to determine whether average per site bird species richness varied significantly among the four groups of pasture site and the combined forest sites, and a Tukey test to make pairwise comparisons, applying an α of 0.05 in both cases. I also produced sample-based species accumulation curves for each of the groups (from the Mao Tau output in EstimateS), using the full set of species observed during all visits at each site. This was done due to the evident high rate of species turnover across sites. Groups might be equivalent in terms of the average species richness at each site (alpha diversity), but differ significantly in terms of the cumulative number of species (beta diversity). Finally, I compiled species lists for each group in order to compare species composition among them, with the aim of documenting how the relative proportions of each foraging guilds change with increasing distance from the forest or decreasing number of trees in pasture.

Results

Vegetation structure. Only two pasture sites had no trees. The average number of trees of any type per site was 20 (maximum = 60). Thirty sites contained at least one remnant tree. Aliso trees were present at 21 of the sites, and Sangre de Drago were present at 42 sites. All but four sites contained naturally occurring regrowth trees. Few standing dead trees were present, and these typically occurred in the same areas where remnant trees were found. Thirty-seven sites contained shrubs, including the two

sites without trees. The ground cover was almost entirely grass, which ranged in height from a few centimeters to over one meter depending on the intensity of recent grazing.

Principal component analysis. In the first principal component, the two variables with the highest loadings were the largest trees and remnant trees (Table 3). These were strongly correlated, since nearly all remnant trees were in the large size class, and most large trees were remnants. Based on the highest loaded variables, the second component was representative of aliso trees and trees in the medium size class. Small trees, regrowth hardwoods, and the combined *Cecropia*, palm, and tree fern category were all loaded at similarly high levels in the third component. In the fourth component, sangre de drago trees were highest loaded, followed by shrub cover. The fifth component was representative primarily of the epiphyte score. No components had a significant level of correlation with distance from forest edges (Fig. 4).

Bird communities. In all bird surveys, 122 species were observed among 2,774 individual detections (Appendix). Ninety-five species were detected in pasture (102 sites), while 91 were detected in forest (33 sites). Twenty-seven species were recorded only in forest, while 16 were found only in pasture. Twenty-one species were designated as “pasture species”. Because it was common for many of the species recorded at each site to be observed only once, the jackknife estimate of species richness was often substantially higher than the cumulative number of species observed. The Bray-Curtis similarity index between the species observed at each pasture site and the bird community pooled from all forest surveys was very closely correlated with species richness ($r = 0.914$). This is not surprising because the species composition at a pasture site is largely a subset of the species found in the forest. Because of the strong

correlation between species richness and species composition similarity, only the richness estimate was used in models.

Models. The edge distance and pasture area variables had negative effects on bird species richness, whereas pasture shape had a positive effect (Table 4). The harmonic mean of multiple edge distances was the best-fitting of the landscape measures. All vegetation components had positive effects on bird species richness, and when combined in a model all except the third (small and regrowth trees) had strong effects. Numerous reduced models with combinations of these variables were more parsimonious than the model with all components, and the most parsimonious included only the first (remnant trees) and fifth (epiphyte load) components. The combination of these two components with the harmonic mean of multiple edge distances was found to be the most parsimonious of all models tested. The addition of pairwise interaction terms between edge distance and the principal components increased the AICc score substantially, from which I concluded that there were no meaningful interactive effects of vegetation and edge distance on bird species richness. The model which assumed and accounted for spatial autocorrelation within pastures also produced a higher AICc score, and a very low within-pasture correlation coefficient (0.088), strongly indicating that there was not a significant degree of spatial autocorrelation among the sites.

Fig. 5 illustrates the rate of spillover predicted by the best model. One line shows the effect of the most favorable vegetation conditions (based on sites with the highest loadings for first and fifth components) while the other does not include an effect of vegetation (based mean component loadings, which are zero). At middle distances,

species richness predicted under the favorable conditions is roughly twice that predicted from the mean loadings.

The model determined to be the best predictor of species richness was also the best fit for the observed number of omnivore and nectarivore species, but different combinations of predictor variables were selected for the other foraging guilds (Table 5). In the case of omnivores, the fifth component (epiphyte load) did not have a strong effect, and in the case of nectarivores, no variable had a strong effect. In the model selected for frugivores, the first component (remnant trees) had a strong effect, but so did the second (medium-sized trees). Remnant trees did not have a strong effect on the number of aerial, gleaning, or epiphyte-specialist insectivores; instead, the components representing the aliso and sangre de drago plantation species were most important predictors. Bark insectivores were the only guild for which the harmonic mean of multiple edge distances was not the best of the landscape measures. Instead, pasture shape was selected, and had a strong positive effect. The harmonic mean and the first and second components had strong effects for both canopy and mid-level species, whereas for understory species the fourth component (sangre de drago and shrub cover) was most important. No variable had a strong effect in the model selected for flocking species, whereas the harmonic mean and the first, second, and fifth components did in the case of non-flocking species.

Site group comparisons. Excluding pasture species, 86 species were observed in forest, 65 in the most trees/nearest-to-edge pasture group, 56 in the most trees/farthest-from-edge group, 45 in the fewest trees/closest-to-edge group, and 41 in the fewest trees/farthest-from-edge group (Fig. 6). Average per site species richness

shows a similar declining trend (Fig. 7), indicating that the diversity of birds in pastures decreases with greater distance from forest edges when the number of trees is held constant, and is higher at a given distance when more trees are present. The variation in species richness across the groups was highly significant (p-value <0.0001 with alpha of 0.05), but not all of the pairwise comparisons were significant. Per site species richness in forest was significantly higher than in any pasture group except the group with many trees and small edge distances. That group had a significantly higher species richness than both of the groups (many and few trees) whose sites were farther from edges. None of the other groups differed significantly from each other.

In addition to differences in species richness among the site groups, there were evident differences in species composition (Fig. 8). Terrestrial birds were almost non-existent outside of the forest. The number of frugivore species declines sharply with both increasing distance from forest edges and decreasing number of pasture trees; The declining trends for omnivores, nectarivores, and the four insectivore categories are weaker. It appears that the height at which birds typically occur in the forest is positively related to their tendency to spill over into pasture (Fig. 9), as canopy species maintain the most constant level across the pasture groups, and species associated with the successively lower strata decline with increasing severity. The difference between flocking and non-flocking species is striking. The number of flocking species is nearly as high or higher in pasture compared to the forest, whereas the number of non-flocking species is much lower outside of the forest and declines with both increasing distance and decreasing number of trees

Discussion

I found clear evidence that the diversity of forest birds in pastures embedded in cloud forest is subject to a significant edge effect, driven by the spillover of birds from the forest into the pasture. Bird diversity declines with increasing distance from the forest edge as fewer individuals of fewer species venture so far from the forest. The importance of the nearest edge in determining diversity at a given point in a pasture is demonstrated by the heavy weight that the harmonic mean calculation places on the shortest of distances to multiple edges. However, the fact that the multiple edge measure was a better predictor of species richness than the nearest distance alone indicates that the size and shape of a pasture also have biologically meaningful effects, since the multiple edge measure inherently considers those conditions. The fact that the pasture shape index was positively related to species richness may simply mean that sites in an irregularly shaped pasture are more likely to be close to multiple edges. It is also possible that a greater density of edges results in a greater total spillover of birds into a pasture, elevating the average species richness at all sites. However, the stronger performance of multiple edge measure compared to the shape index emphasizes the importance of incorporating distance effects in species richness models.

The importance of multiple edges is likely due, at least in part, to the additive effects of spillover from those edges. It may also be the case that the proximity of opposing edges influences a bird's decision to enter a pasture at a given point. Poulsen (1994) showed that cloud forest birds are more likely to enter gaps at points where the distance to the opposite edge was shorter. Furthermore, Bélisle and Desrochers (2002) showed that forest birds cross open areas when doing so represents a significant

shortcut compared to going around them. An irregularly shaped pasture, especially one that is long and narrow, should therefore encourage more birds to enter it. However, it is important to consider the potential negative effects of edges inside the forest. While increasing edge density might promote the diversity of birds in pastures, this gain could be offset by losses inside the forest, particularly among the most sensitive forest-interior species. It would be useful to have a study that simultaneously documents patterns of bird diversity on both sides of forest edges, enabling a comparison of the effects of land-use practices in both elements of the landscape, and an assessment of which type of edge effect has the stronger influence on landscape-wide bird diversity.

The total amount of pasture surrounding a survey site had less influence on bird diversity in pastures than did the distance of forest edges. I tested the effect of pasture area (within a 150 meter buffer of each site) because it seemed likely that more extensive tracts of forest would contain larger populations of forest birds, resulting in a greater rate of spillover into the pasture. Such a possibility is suggested by the results of Brudvig et al. (2009), who found greater spillover of plants outside of habitat patches that were connected to other patches by corridors. The relatively weak effect of forest area in the models should not be considered evidence that the forest can be more densely perforated with pastures without causing the pastures to become more species-poor. There is almost certainly a threshold of forest area in the landscape below which it can no longer function as source habitat. It is also probably that the effective area of the forest would decline at a greater rate than the total area, due to the negative effects emanating from additional edges.

Local vegetation is also a strong determinant of bird diversity in pastures. This was not surprising, given the wealth of investigations that have found bird community changes along local vegetation gradients (e.g. Luck and Daily 2003). Remnant forest trees had the strongest effect on bird richness, where a greater number of remnant trees was positively correlated with species richness. This is perhaps not surprising because they represent the kinds of trees that birds typically encounter in the forest. Remnant trees may be more likely than young regrowth trees to produce valuable fruits (Herrera and García 2009). Due to their older age, remnant trees are often composed partly of dead wood, which may contain insects that some birds consume, or cavities attractive as nest sites. Remnant trees also support a greater volume and diversity of epiphytes than do younger trees (Koster 2009). The importance of epiphytes to promoting the presence of forest birds in pastures was underscored by the fact that the fifth principal component, which represented epiphyte load independent of remnant trees, was the only other vegetation variable selected in the final model. Epiphytes multiply the resources that trees provide to birds, in terms of fruit, flowers, and insect foraging substrates.

Contrary to my prediction, I found no evidence for an interaction between matrix structure and edge effects, but rather these were independent (additive) effects on avian species richness. That is, under one set of vegetation conditions the bird diversity at any given distance from the edge may be higher than under a different set of conditions, but the rate at which diversity declines with increasing distance is the same in both. This result may be an artifact of the small size of pastures in the study area. No survey point was more than 80 meters from the nearest forest edge, and the great

majority was less than 50 meters from the edge. If I had been able to document bird species richness at greater distances, it is possible that I would have found increasing disparities among the vegetation types, and that interactions would be needed to explain the differing trends.

Comparisons among the pasture groups and forest reflect the results of the models. Perhaps the most important result of the group comparisons is the near-equality of species richness between the group with many trees far from the edge and the group with few trees close to edge. This suggests that within the range of pasture size and vegetation considered in this study, the presence of trees in pastures compensates for the loss of bird diversity that occurs with increasing distance from the forest edge, despite the lack of significant interaction between edge distance and vegetation in the models.

Species accumulation curves enable a different method of comparison among groups, as they represent not just the number of species observed at individual sites, but also the turnover of species across sites within each group. This is a potentially important distinction in cloud forest, where the high level of bird diversity and prevalence of rare species means that the species observed at any site will necessarily represent a fraction of those that occur there. In this study, the species accumulation curves and per site averages illustrate broadly similar but not identical patterns. The difference between the bird communities of the forest and the many trees/close-to-edge pasture group, which was not significant in terms of average species richness, is greater when judged by accumulation curves. This suggests that the forest contains a larger proportion of rare species, and raises the possibility that rare forest species are more negatively

affected by pastures than are more common ones. Another comparison between the accumulation curves and average species richness lends support to this idea: whereas the difference in average species richness between groups with more trees and groups with fewer trees is greater than the difference between near-edge and far-edge groups, the accumulation curves show a greater loss of species as a function of distance. This may indicate that rare species are more dependent on the forest and less likely to venture far from the edge. The sensitivity of rare species would be an intuitive result, and in keeping with studies which have shown that cloud forest species more abundant before fragmentation are more resilient afterward (Renjifro 1999). However, Restrepo and Gómez (1998) found that rare cloud forest birds occurred disproportionately in disturbed areas.

While the size and shape of pastures directly affects bird diversity by determining the distance to multiple forest edges, it may also affect it indirectly by influencing the structure and composition of vegetation in the pasture. The lack of correlation between the vegetation components and edge distance suggests that there are not significant gradients of vegetation structure within pastures. However, given that few plant species were identified in this study, there could be compositional gradients. It has been shown that the diversity of trees in regenerating pastures decreases with increasing distance from the forest edge (Gunter et al. 2007). This likely indicates a feedback process, in which the establishment of trees in pasture depends on spillover of seed-dispersing birds from the forest (Galindo-Gonzalez et al. 2000), and the tendency of birds to enter the pasture is a function by the trees that have already grown. Despite active grazing, the pastures in this study have all been colonized by forest trees to some extent, so

such a process could be at work. The configuration of pastures is also relevant to the diversity of epiphytes, which the models showed to have a strong, positive effect on bird diversity. Remnant trees typically have a heavy epiphyte load, but maintaining that condition over time requires the recruitment of new plants to replace those that suffer mortality. Koster et al. (2009) found that the diversity of epiphytes on remnant trees, like the diversity of regrowth trees, declined with increasing distance from the forest edge. Interestingly, they found that distance to the nearest equivalent tree had a stronger effect on epiphyte diversity, indicating that isolated trees can be sources of epiphyte propagules for each other if they exist at a sufficiently high density.

The differing results of the foraging guild models and comparisons among the site groups demonstrate that the effects of edge distance and vegetation are not uniform across the forest bird community. The importance of remnant tree to frugivores and bark insectivores may indicate that these trees are in fact more likely than others to provide fruit and insect-bearing bark. Because these resources are not important to the aerial, gleaning, and epiphyte insectivores, it is not surprising that remnant trees did not have a strong influence on those guilds. Instead, they were most strongly influenced by the plantation trees. These trees had no conspicuous fruit or flowers, but their spreading, open canopies provide many perches for birds that sally to catch insects. As fast growing species, the aliso and sangre de drago may produce foliage that is palatable to herbivorous insects, which would in turn attract birds that glean insects from leaves. Hummingbirds were the group seemingly least disturbed by forest clearing, as no landscape or vegetation variables had a significant effect of their diversity. This is consistent with previous studies, some of which have found that hummingbirds respond

positively to human land-use, as the flowers at which they feed often proliferate at edges and in open areas (e.g., Stouffer and Bierregaard 1995). The apparent sensitivity of frugivores contradicts the results of several studies, which have found them to be relatively resilient in the face of forest disturbance (e.g., Gomes et al. 2008). However, the frugivore guild did include some of the largest species in the area, and large species have been shown in some cases to be more negatively affected by forest clearing (Kattan et al. 1994, Renjifro 1999). The high rate of spillover by canopy and flocking species was likely driven by the tanagers, a diverse group of omnivores that included six of the 10 most commonly detected species. Most tanagers in the study area were canopy birds that usually foraged with mixed species flocks (Ridgely and Greenfield 2001). One of the most striking changes occurring at the forest-pasture boundary was the sharp reduction in terrestrial and understory species. The reliance of this category of species on intact forest has been well documented in studies throughout the tropics (Kattan 1994, Renjifro 1999, Sekercioglu et al. 2002). It is likely that they require dense undergrowth and structurally complex ground cover, conditions that are nearly universal in the forest but almost never exist in pasture.

Conclusions

The species richness of cloud forest bird communities in pastures is largely governed by the spillover of birds across forest edges. The magnitude of the spillover effect is influenced by edge contrast, with a greater number of birds entering pastures where the vegetation is more structurally similar to the forest. Spillover from multiple edges has a cumulative effect on points within pastures, and the harmonic mean of multiple edge distances is a useful metric for modeling this effect. Of all types of trees, remnant trees having the strongest positive effect on forest bird species richness in

pasture. Although pasture vegetation and edge distance do not appear to have an interactive effect, which would cause the rate at which spillover attenuates with increasing distance to vary as a function of pasture habitat, the additive effect of vegetation means that sites in the interior of pastures may receive as many or more forest species when the habitat is favorable than sites close to the edge do when habitat is poor. Within the range of pasture size, shape, and vegetation documented in the study area, it is possible for actively grazed pastures to contain a large proportion of the forest bird community. However, some species appear unlikely to leave the forest under any conditions. The results of this study support the idea that the spillover of species from target habitat into land-use areas is an important driver of diversity in fragmented landscapes.

Table 2-1. Summary of the pasture vegetation data

Vegetation variable	Minimum	Maximum	Mean
Number of trees <10 cm dbh	0	37	9.4
Number of trees 10-30 cm dbh	0	53	10.2
Number of trees >30 cm dbh	0	5	1.0
Number of remnant trees	0	7	0.7
Number of aliso trees	0	50	3.8
Number of sangre de drago trees	0	13	1.5
Number of regrowth trees	0	36	12.9
Number of palms, tree ferns, and <i>Cecropia</i> trees	0	9	1.4
Number of standing dead trees	0	3	0.3
Epiphyte load	0	9	4.1
Percent shrub cover	0	45	5.9

All vegetation variables that were entered into the principal component analysis, with the minimum, maximum, and mean values of each occurring across all survey sites.

Table 2-2. Summary of pasture dimensions and allocation of survey sites

Pasture	Area (hectares)	Perimeter (meters)	No. of survey sites
Bellavista 1 (BV-P1)	1.66	692	4
Bellavista 2 (BV-P2)	0.64	325	1
Bellavista 3 (BV-P3)	2.91	940	6
Bellavista 4 (BV-P4)	8.69	1514	14
Bellavista 5 (BV-P5)	6.74	1806	10
Bellavista 6 (BV-P6)	4.26	1711	9
Bellavista 7 (BV-P7)	1.34	534	3
Bellavista 8 (BV-P8)	3.90	895	5
Bellavista 9 (BV-P9)	1.01	464	2
Santa Lucía 1 (SL-P1)	8.89	2092	11
Santa Lucía 2 (SL-P2)	8.16	2024	11
Santa Lucía 3 (SL-P3)	4.69	1228	5
Santa Lucía 4 (SL-P4)	0.48	297	1
Santa Lucía 5 (SL-P5)	1.64	586	2
Santa Lucía 6 (SL-P6)	0.83	407	3
Santa Lucía 7 (SL-P7)	7.86	1703	9
Santa Lucía 8 (SL-P8)	2.34	1067	6

Table 2-3. Results of principal component analysis on vegetation data

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Vegetation variable	Loadings				
Remnant trees	0.890*	-0.043	0.144	-0.145	0.107
Aliso trees	-0.101	0.866*	-0.015	-0.056	-0.243
Sangre de drago trees	0.005	0.281	-0.105	0.836*	-0.121
New hardwood trees	-0.024	0.142	0.867*	-0.076	0.327
<i>Cecropia</i> , palms, tree ferns	0.269	-0.233	0.718*	0.084	-0.350
Small trees (< 10 cm dbh)	0.128	0.242	0.712*	-0.265	-0.241
Medium trees (10-30 cm dbh)	0.009	0.892*	0.160	0.086	0.132
Large trees (> 30 cm dbh)	0.920*	-0.008	0.090	-0.022	0.155
Epiphyte score	0.429	-0.133	-0.088	-0.131	0.769*
Shrub cover	-0.252	-0.417	-0.101	0.694*	0.008
Standing dead trees	0.239	0.102	0.043	-0.129	0.036
Variance explained	26.6%	19.8%	13.6%	10.1%	7.2%

All vegetation variables are tree counts except epiphyte score and shrub cover.

* Loadings of at least 0.600, indicating those variables of which each factor is most representative. Multiple variables with high loadings in one factor are correlated.

Table 2-4. Species richness model selection

Predictors	AICc	Δ AICc	Variables with significant effect (regression coefficients do not overlap zero)		
Pasture shape	683.1	18.6	Pasture shape (+)		
Nearest edge	678.3	13.8	Nearest edge (-)		
Pasture area	677.7	13.2	Pasture area (-)		
Harmonic mean	674.9	10.4	Harmonic mean (-)		
All veg. components	678.5	14.0	Factor 1 (+)	Factor 5 (+)	
Veg. Factors 1 & 5	675.7	11.2	Factor 1 (+)	Factor 5 (+)	
Harmonic mean, veg. Factors 1 & 5*	664.5	-----	Harmonic mean (-)	Factor 1 (+)	Factor 5 (+)
Plus pairwise interactions	669.5	5.0	Harmonic mean (-)	Factor 1 (+)	Factor 5 (+)
Accounting for spatial autocorrelation	672.7	7.7	Harmonic mean (-)	Factor 1 (+)	Factor 5 (+)

* The most parsimonious set of predictors

Table 2-5. Models selected for each foraging guild

Response variable	Predictors in most parsimonious model	Variables with significant effect (regression coefficients do not overlap zero)			
Omnivores	Harmonic mean, veg. Factors 1 & 5	Harm. mean (-)	Factor 1 (+)		
Frugivores	Harmonic mean, veg. Factors 1 & 2	Harm. mean (-)	Factor 1 (+)	Factor 2 (+)	
Aerial insectivores	Harmonic mean, veg. Factors 2, 3, 4	Harm. mean (-)	Factor 2 (+)		
Gleaning insectivores	Harmonic mean, veg. Factor 4	Harm. mean (-)	Factor 4 (+)		
Epiphyte insectivores	Harmonic mean, veg. Factor 4 & 5	Harm. mean (-)	Factor 4 (+)		
Bark insectivores	Pasture shape, veg. Factor 1	Past. shape (+)	Factor 1 (+)		
Nectarivores	Harmonic mean, veg. Factors 1 & 5	None			
Canopy Sp.	Harmonic mean, veg. Factors 1 & 2	Harm. mean (-)	Factor 1 (+)	Factor 2 (+)	
Mid-level Sp.	Harmonic mean, veg. Factors 1, 2, 5	Harm. mean (-)	Factor 1 (+)		
Understory Sp.	Harmonic mean, veg. Factors 4 & 5	Harm. mean (-)	Factor 4 (+)		
Flocking Sp.	Pasture shape	None			
Non-flocking Species	Harmonic mean, veg. Factors 1, 2, 4	Harm. mean (-)	Factor 1 (+)	Factor 2 (+)	Factor 4 (+)

Total number of detected species in each guild used as response variables

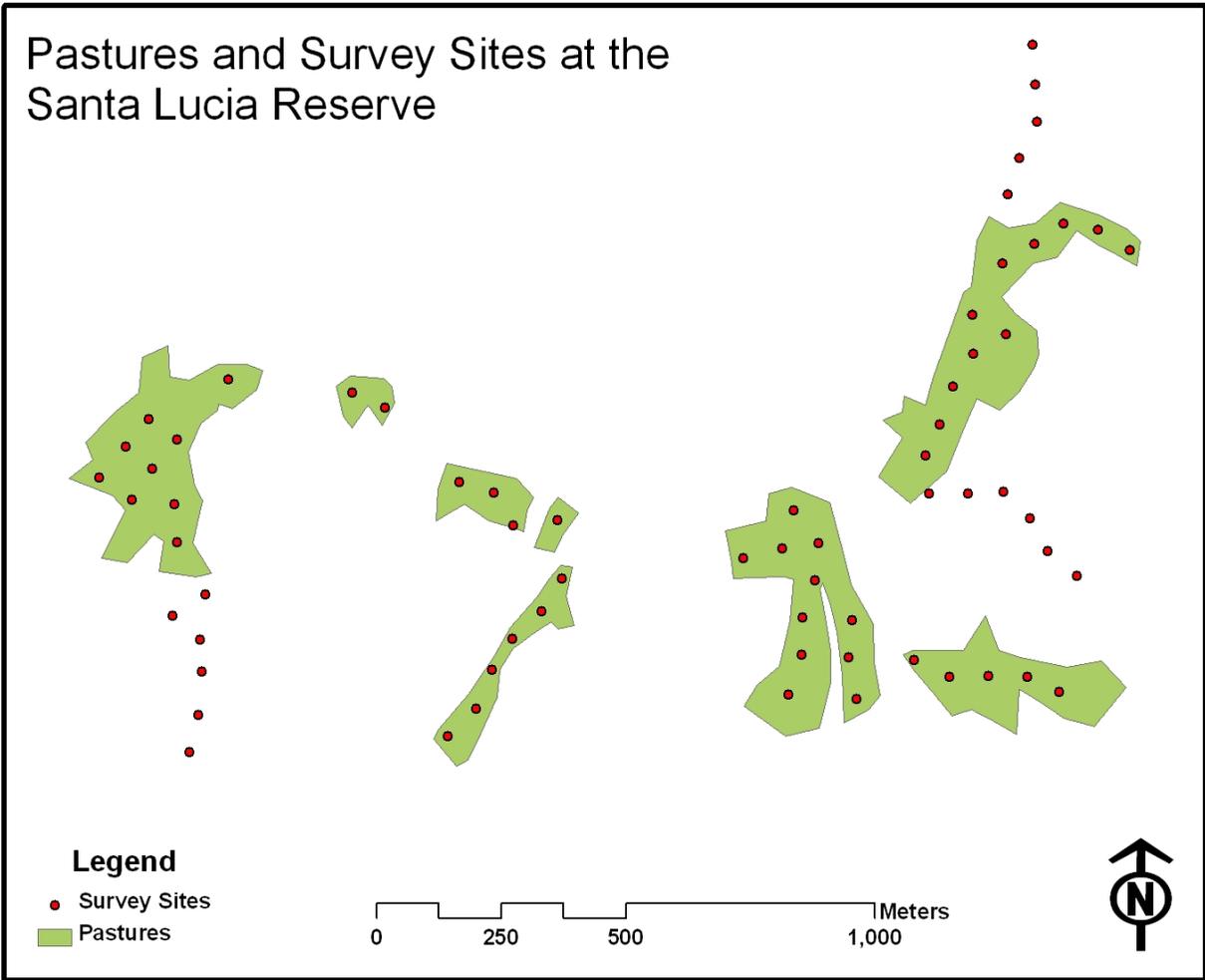


Figure 2-1. Map of the Santa Lucía Reserve.

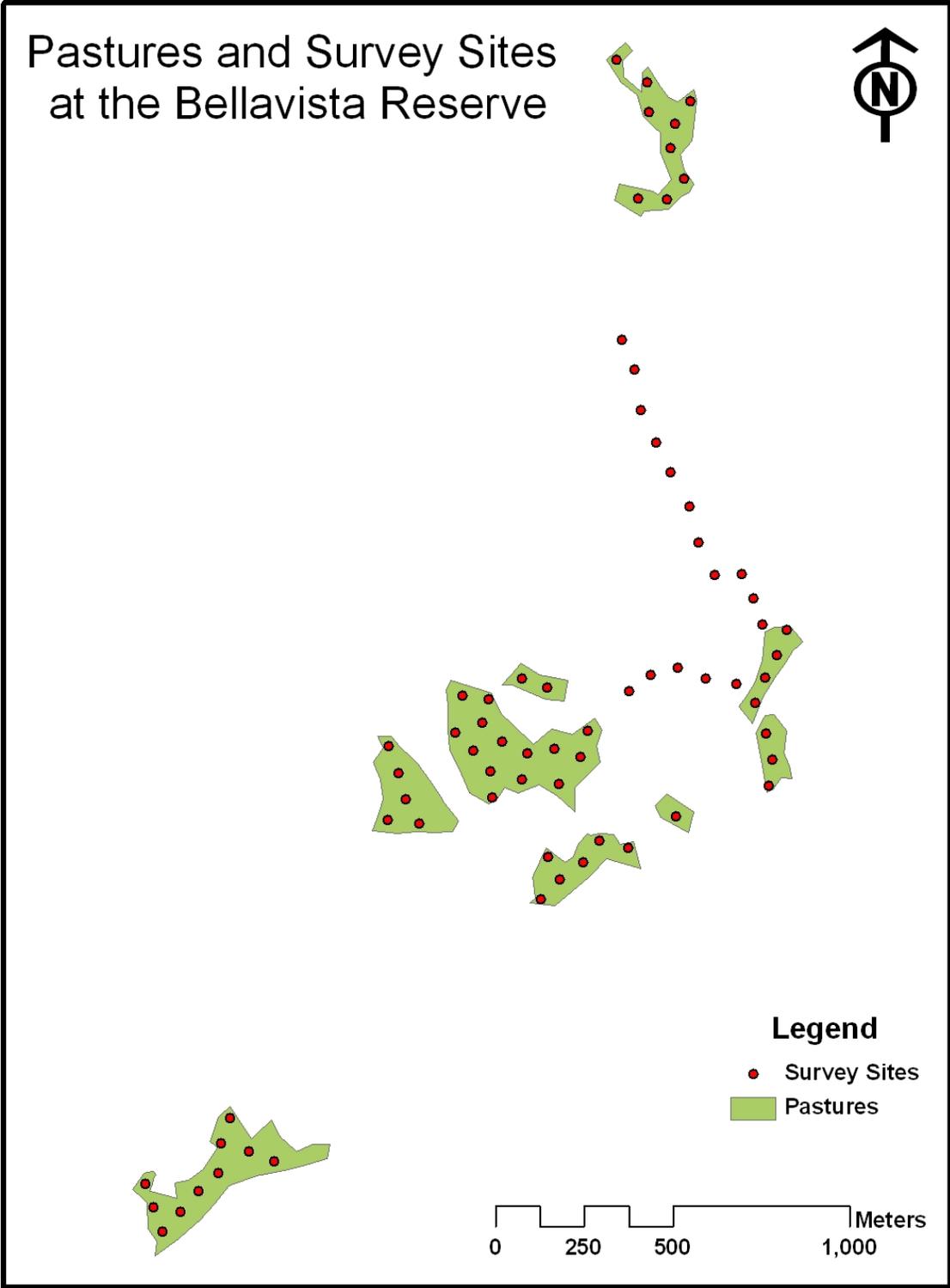
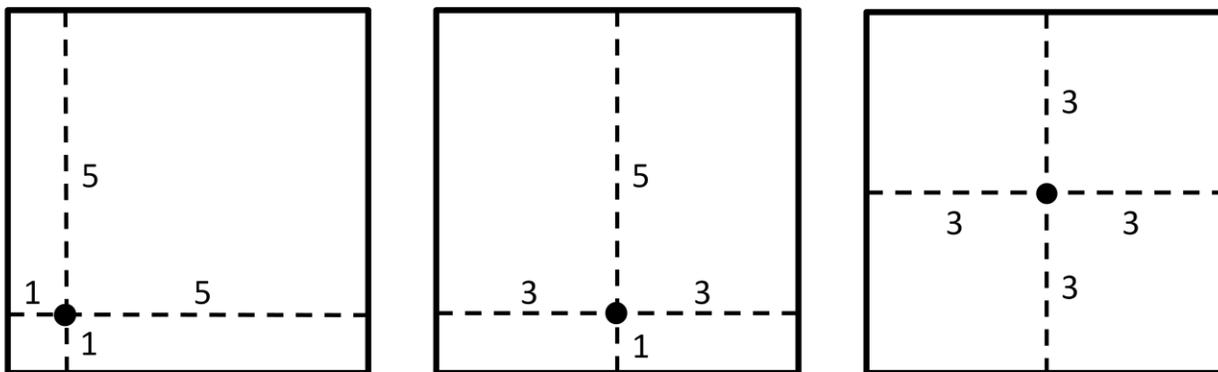


Figure 2-2. Map of the Bellavista Reserve.



Harmonic
mean: 1.67

2.14

3.00

Mean: 3.00

3.00

3.00

Figure 2-3. Different effects of multiple edge distances on the arithmetic and harmonic means.

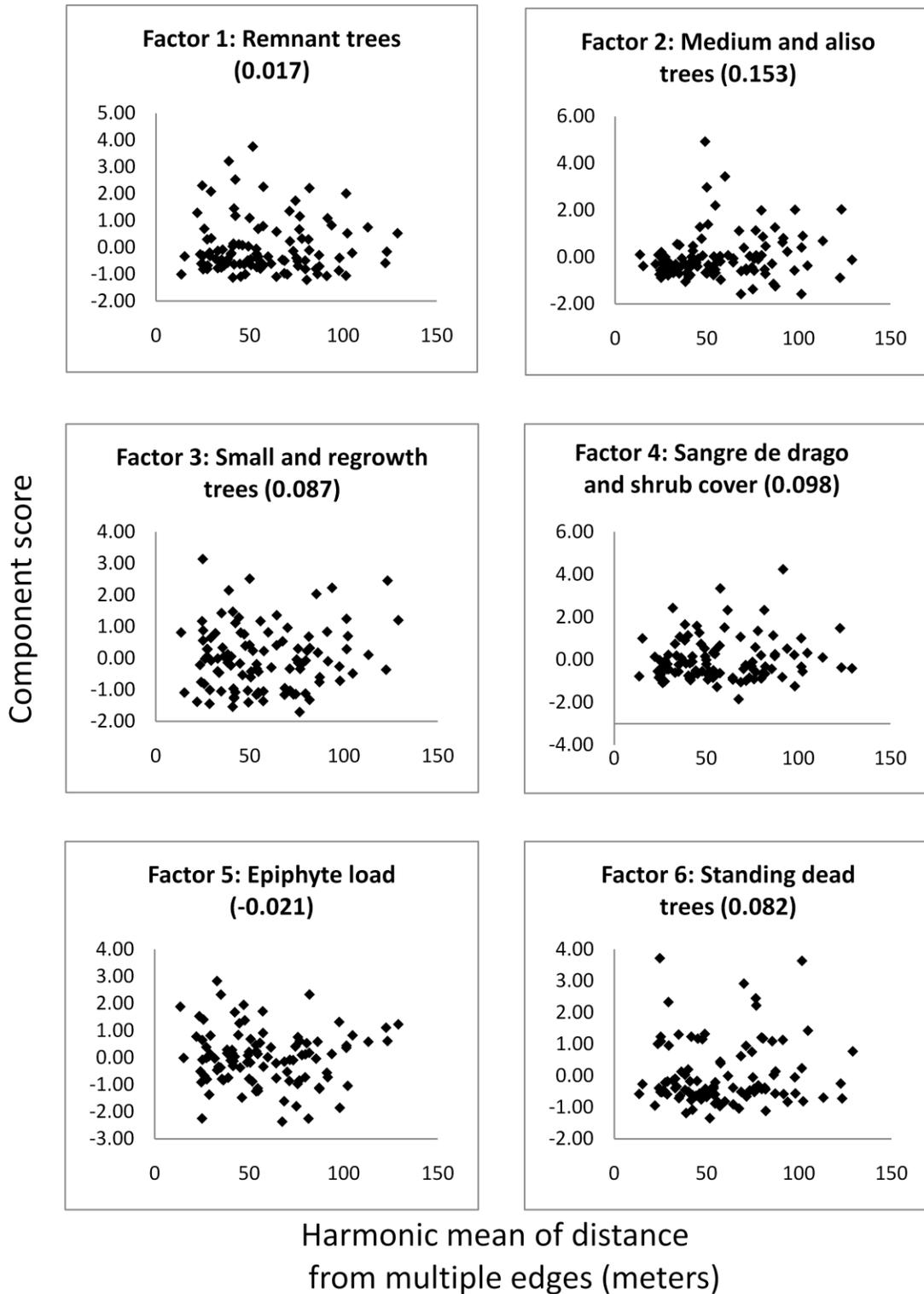


Figure 2-4. Relationship between distance from edge and pasture vegetation structure. Correlation coefficients between each vegetation principal component and the harmonic mean of multiple edge distances are given.

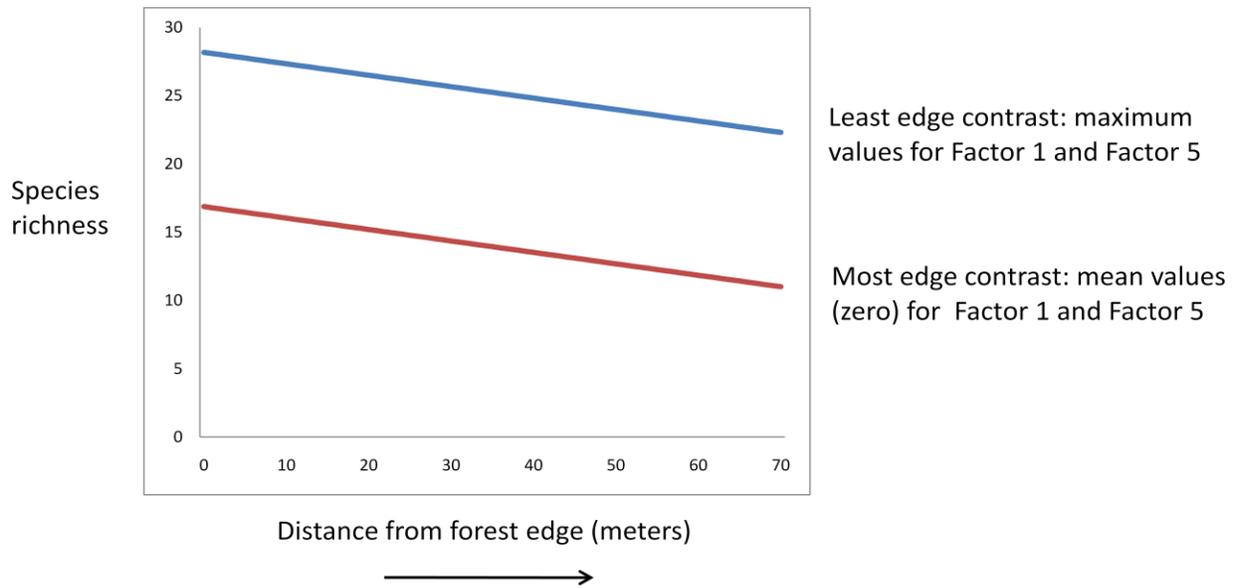


Figure 2-5. Predicted forest bird spillover given two different scenarios of pasture habitat and edge contrast.

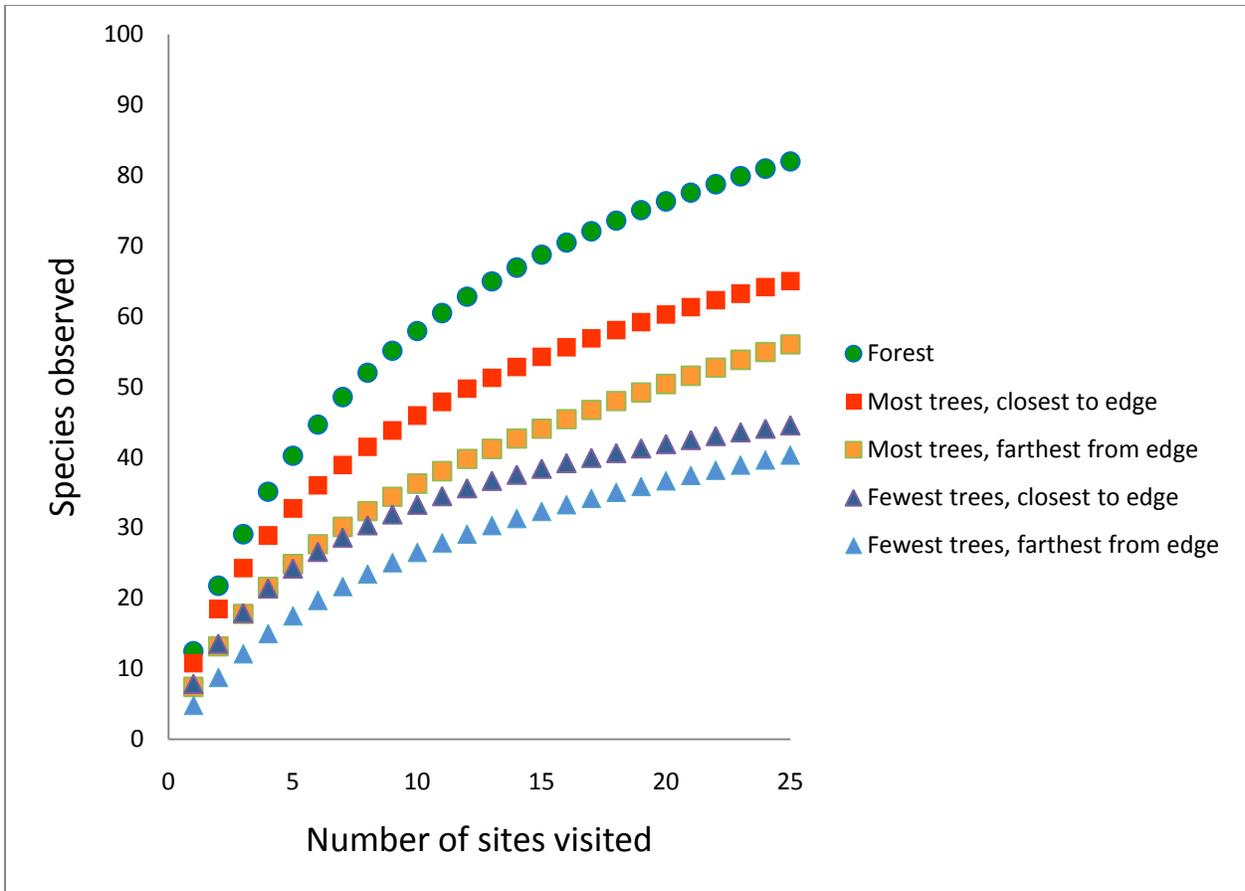


Figure 2-6. Sample-based species accumulation curves for combined forest sites and each of four pasture groups.

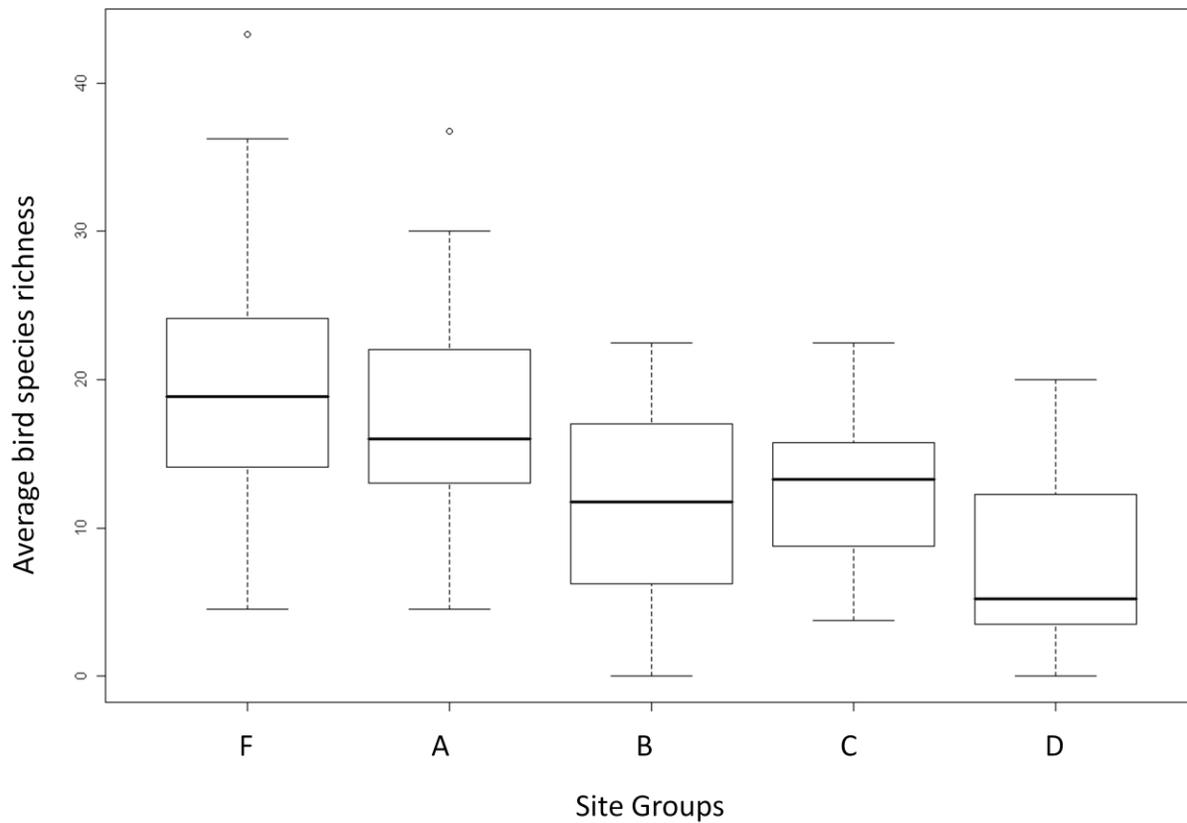


Figure 2-7. Average per site bird species richness compared across forest and pasture site groups (F=forest, A=most trees/near edge, B=most trees/far-from-edge, C=fewest trees/near edge, D=fewest trees/far-from-edge).

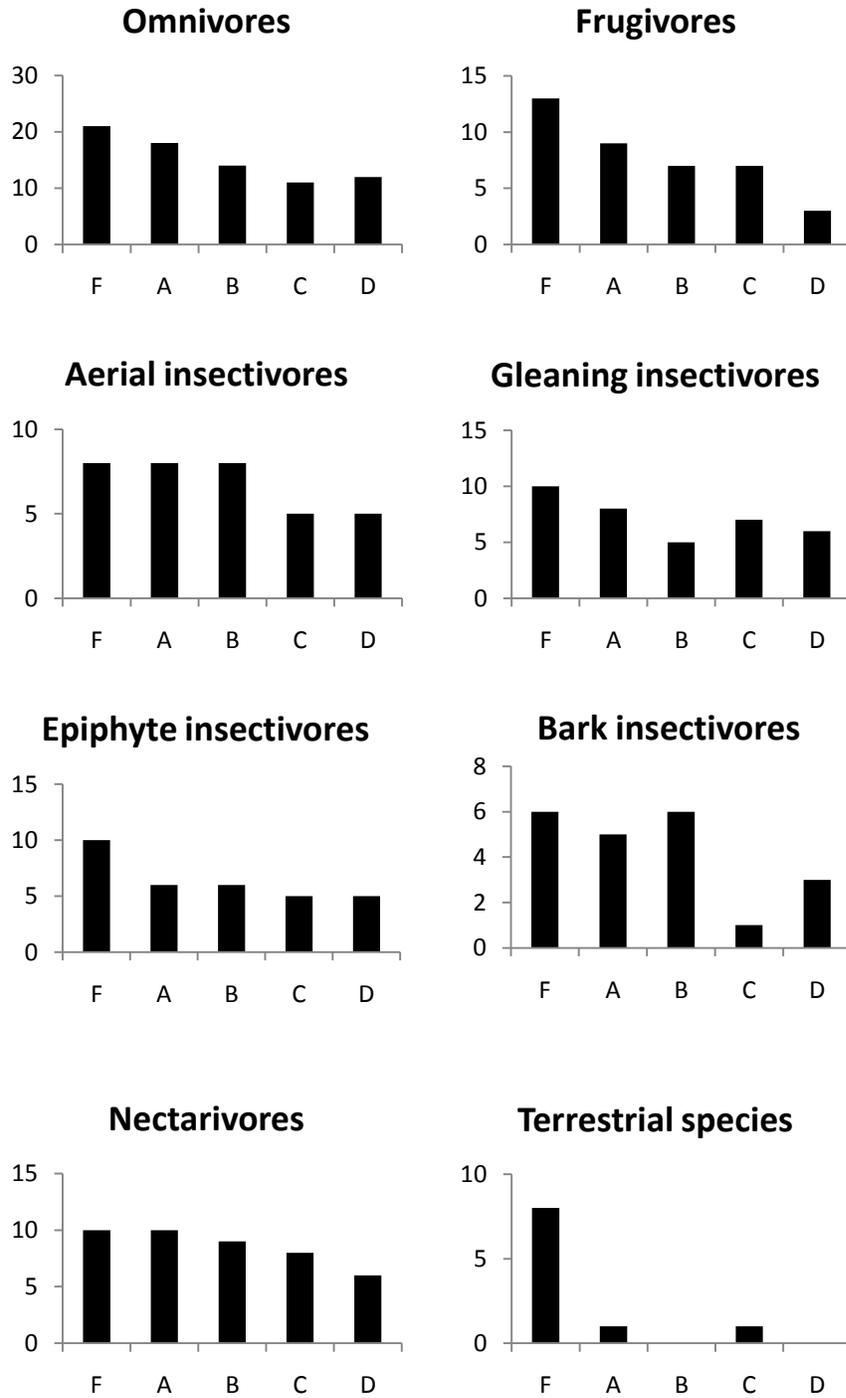


Figure 2-8. Number of species of each foraging guild detected in each of the four site groups (F=forest, A=most trees/near edge, B=most trees/far-from-edge, C=fewest trees/near edge, D=fewest trees/far-from-edge).

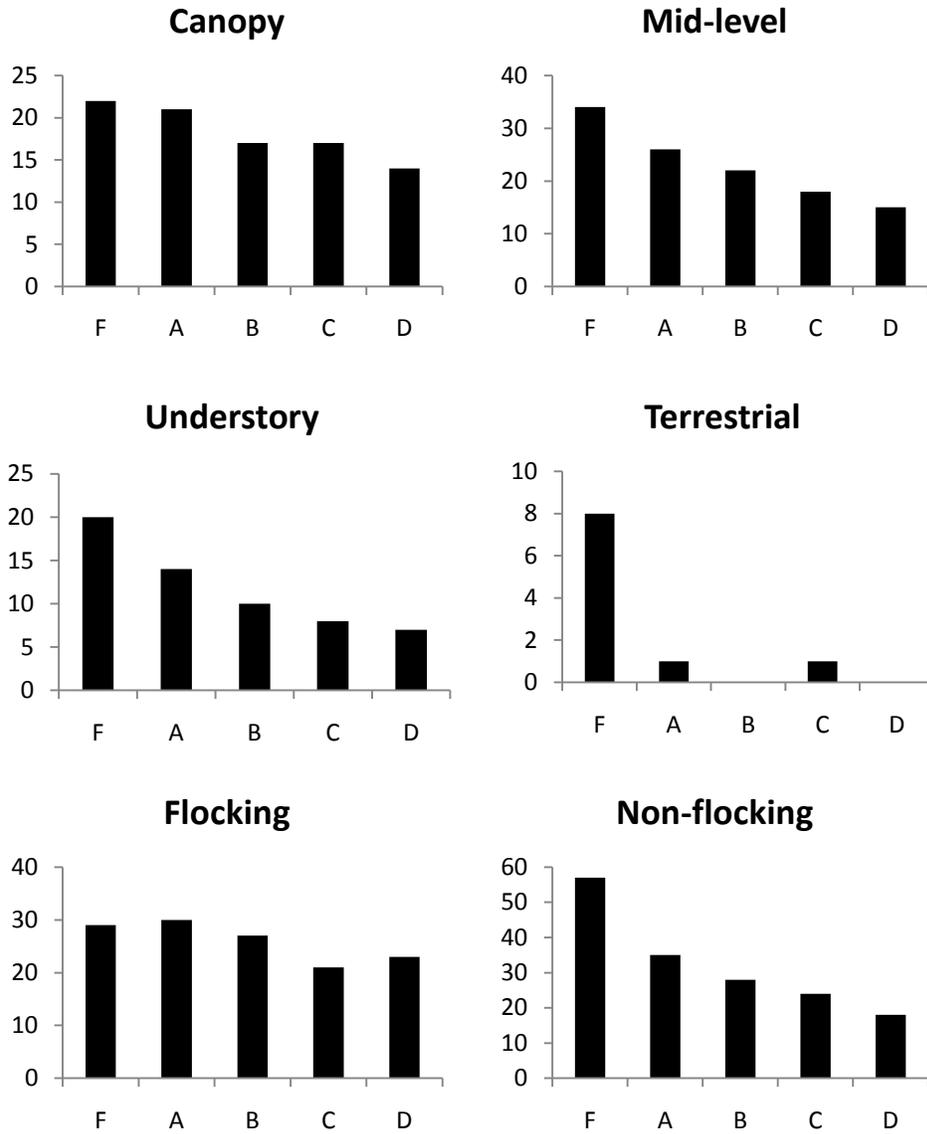


Figure 2-9. Number of species preferring each of four vertical strata of the forest, and of species that do and do not associate with mixed flocks, detected in each of the four site groups (F=forest, A=most trees/near edge, B=most trees/far-from-edge, C=fewest trees/near edge, D=fewest trees/far-from-edge).

CHAPTER 3 CONSERVATION RECOMMENDATIONS AND SUGGESTIONS FOR FURTHER RESEARCH

Conservation Recommendations

When I arrived at the Santa Lucía Cloud Forest Reserve, there was only one negative comment in the guest book. The visitor who wrote it was surprised and disappointed to see cows grazing in the reserve, and suggested that they were incompatible with Santa Lucia's mission of forest conservation. This viewpoint may be over-simplistic. The cooperative of landowners who established Santa Lucía turned to ecotourism because changing economics made it impossible for them to earn a living from livestock. But despite the success of the reserve, the income they receive from tourism is also not sufficient, and so grazing continues. The key difference is that they are now devoted stewards of the remaining forest. My research was motivated, in part, by the dual nature of the reserves at which I worked. By modeling the spillover of forest birds into pastures, I hoped to provide one means of comparing the ecological impacts of different types of pasture according to their size, shape, and vegetation, and to identify those pasture conditions that most effectively balance land-use with the conservation of forest biodiversity. To achieve this goal would require further research, but the results of my study do suggest some ways that pastures can be managed to promote greater diversity of forest birds.

The fact that spillover does appear to be a significant determinant of forest bird species richness in pastures supports the intuitive conclusion that small pastures will have higher average species richness than will larger ones. The importance of distance from forest edges means that an irregularly shaped pasture should contain higher bird species richness throughout than a more regularly-shaped pasture of equal area. The

pastures at both reserves are all relatively small and irregular, as is dictated by the terrain. The positive influence of remnant trees is encouraging because many pastures contain them, but discouraging because more remnant trees cannot be created. The plantation species may not have had a significant effect on overall species richness, but they did appear to promote the spillover of a different set of species (insectivores) than did remnant trees (frugivores and omnivores), and therefore may be complementary to them. The positive role of planted trees might be increased if species were chosen which more readily hosted epiphytes. There may be no way to manage an actively grazed pasture to promote spillover of terrestrial and understory species, but perhaps a rotation scheme that allows pastures to be abandoned for longer periods, and thereby develop dense shrub and herbaceous growth, would enable them to serve as habitat for these species at some times.

Directions for Further Study

My research could be strengthened and broadened by several lines of inquiry. First, it would be useful to more rigorously define which bird species are truly forest species, and what constitutes spillover. I have defined forest species as those that are not predominantly found in pasture. However, it may be more appropriate to consider all species that are found in forest a given distance from pasture. Some species that are abundant in pastures may in fact be gap specialists that naturally occur at low numbers in the forest. More extensive surveys within forest and an attention to variation of forest structure would be the key to identifying such species. I treated all forest birds detected in pasture as having recently originated in the forest, ignoring the possibility that some may be resident in the pasture. If some forest birds do settle in pastures, spillover could be driven by dispersal in addition to forays. Field methods that track the movements of

individual birds would enable this distinction. They would also allow for a more detailed picture of foray-based spillover by providing data about how far from forest edges birds travel, and how long they remain in pasture.

It would also be useful to quantify the resources that pastures provide to forest birds, and the risks they pose. Although I assumed that forest birds generally entered pasture to forage, and I did often observe them foraging there, I did not quantify the variety or amount of the food resources available to them, or their success at obtaining those resources. I also did not estimate the risk of predation, although I observed very few predators. Even in the absence of predation risk, birds might experience reduced fitness in pastures relative to forest if more time or energy is required to obtain food there. Such a situation would raise the possibility that pastures with a high rate of forest bird spillover represent ecological traps (Battin 2004), and have a negative effect on birds at the landscape level.

The scope of the data I was able to collect was limited by the landscape of my study areas in two major ways. First, the small size of the pastures only allowed me to document bird species richness across a relatively narrow range of distance from forest. Working in larger pastures would make it possible to more accurately describe the rate of spillover, and to more effectively test for interactive effects on spillover of edge distance and pasture vegetation. Second, access to forest was limited to a small number of trails, as the steep terrain and dense vegetation made it infeasible to walk off trail in the forest. A study design in which birds are surveyed along transects that extend from either side of the forest edge would allow for a comparison of edge effects both in

pasture and in the forest surrounding it. This would make it possible to assess the impact of pasture conditions on the entire landscape.

Finally, it is tempting to speculate that the response of cloud forest birds to pastures birds mimics their response to landslides, which were common in the study areas, and that their adaptation to the natural disturbance makes them more tolerant of the anthropogenic one. Nearly every author working in fragmented cloud forest systems has raised this possibility, but the evidence to support it is circumstantial at best.

Restrepo and Gómez (1998) noted that rare species were found disproportionately in disturbed areas. Becker (2008) concluded that the proportion of forest bird species that responded positively to fragmentation was comparable to the proportion of the landscape impacted by landslides. To effectively address the issue of landslides, it would be necessary to compare them directly with pastures on the basis of size, shape, vegetation at different stages of succession, and the species of birds they contain.

APPENDIX

LIST OF ALL BIRD SPECIES DETECTED DURING SURVEYS

All bird species detected from all surveys, ranked by total number of detections and including number of detections separately in pasture and forest. Also includes the foraging guild, vertical strata, and flocking assignments for each species, and identifies those species endemic to the Chocó-Andes region.

English common name	Scientific name	Guild	Strata	Flocking?	Endemic?	Total	Pasture	Forest
Beryl-spangled Tanager	<i>Tangara nigroviridis</i>	Omnivore	Can.	Yes		228	138	90
Dusky Bush-tanager	<i>Chlorospingus semifuscus</i>	Omnivore	Under.	Yes	Yes	195	105	90
Blue-winged Mountain-tanager	<i>Anisognathus somptuosus</i>	Omnivore	Can.	Yes		189	128	61
Masked Flowerpiercer	<i>Diglossopsis cyanea</i>	Omnivore	Mid.	Yes		158	140	18
Orange-bellied Euphonia	<i>Euphonia xanthogaster</i>	Frugivore	Mid.	Yes		112	71	41
Slate-throated Whitestart	<i>Myioborus miniatus</i>	Gleaning insectivore	Mid.	Yes		111	87	24
Golden Tanager	<i>Tangara arthus</i>	Omnivore	Can.	Yes		104	74	30
Azara's Spinetail	<i>Synallaxis azarae</i>	Epiphyte insectivore	Open			79	78	1
White-tailed Tyrannulet	<i>Mecocerculus poecilocercus</i>	Aerial insectivore	Can.	Yes		63	49	14
Golden-naped Tanager	<i>Tangara ruficervix</i>	Omnivore	Can.	Yes		63	48	15
Smoke-colored Pewee	<i>Contopus fumigatus</i>	Aerial insectivore	Open			60	59	1
Buff-tailed Coronet	<i>Boissonneaua flavescens</i>	Nectarivore	Can.			56	50	6
Violet-tailed Sylph	<i>Agelaiocercus coelestis</i>	Nectarivore	Mid.		Yes	56	36	20
White-sided Flowerpiercer	<i>Diglossa albilatera</i>	Omnivore	Open	Yes		54	53	1
Rufous-collared Sparrow	<i>Zonotrichia capensis</i>	Omnivore	Open			50	50	0
Brown-capped Vireo	<i>Vireo leucophrys</i>	Gleaning insectivore	Can.	Yes		47	35	12
Blue-and-black Tanager	<i>Tangara vassorii</i>	Omnivore	Can.	Yes		44	29	15
Grey-breasted Woodwren	<i>Henicorhina leucophrys</i>	Epiphyte insectivore	Under.			44	10	34
Speckled Hummingbird	<i>Adelomyia melanogenys</i>	Nectarivore	Under.			43	37	6
Cinnamon Flycatcher	<i>Pyrrhomyias cinnamomeus</i>	Aerial insectivore	Mid.			42	31	11

English common name	Scientific name	Guild	Strata	Flocking?	Endemic?	Total	Pasture	Forest
Blackburnian Warbler	<i>Dendroica fusca</i>	Gleaning insectivore	Can.	Yes		42	40	2
Spectacled Whitestart	<i>Myioborus melanocephalus</i>	Gleaning insectivore	Mid.	Yes		38	34	4
Booted Rackettail	<i>Ocreatus underwoodii</i>	Nectarivore	Mid.			38	35	3
Collared Inca	<i>Coeligena torquata</i>	Nectarivore	Mid.			36	28	8
Montane Woodcreeper	<i>Lepidocolaptes lacrymiger</i>	Bark insectivore	Mid.	Yes		32	28	4
Russet-crowned Warbler	<i>Basileuterus coronatus</i>	Gleaning insectivore	Under.			31	11	20
Capped Conebill	<i>Conirostrum albifrons</i>	Omnivore	Can.	Yes		30	27	3
Metallic-green Tanager	<i>Tangara labradorides</i>	Omnivore	Can.	Yes		28	17	11
Tricolored Brushfinch	<i>Atlapetes tricolor</i>	Omnivore	Under.			25	24	1
Flame-faced Tanager	<i>Tangara parzudakii</i>	Omnivore	Can.	Yes		24	22	2
Black-crested Warbler	<i>Basileuterus nigrocristatus</i>	Gleaning insectivore	Open			23	21	2
Spillman's Tapaculo	<i>Scytalopus spillmanni</i>	Terrestrial insectivore	Terr.			23	4	19
Pearled Treerunner	<i>Margarornis squamiger</i>	Epiphyte insectivore	Mid.	Yes		22	15	7
Turquoise Jay	<i>Cyanolyca turcosa</i>	Omnivore	Mid.			21	13	8
Golden-crowned Flycatcher	<i>Myiodynastes chrysocephalus</i>	Aerial insectivore	Mid.			20	18	2
Blue-capped Tanager	<i>Thraupis cyanocephala</i>	Omnivore	Open	Yes		18	18	0
Grass-green Tanager	<i>Chlorornis riefferii</i>	Omnivore	Mid.	Yes		18	5	13
Three-striped Warbler	<i>Basileuterus tristriatus</i>	Gleaning insectivore	Under.	Yes		18	3	15
Brown Inca	<i>Coeligena wilsoni</i>	Nectarivore	Mid.		Yes	17	12	5
Streak-necked Flycatcher	<i>Mionectes striaticollis</i>	Aerial insectivore	Under.	Yes		17	13	4
Toucan Barbet	<i>Semnornis ramphastinus</i>	Frugivore	Can.		Yes	17	9	8
Yellow-bellied Siskin	<i>Carduelis xanthogastra</i>	Omnivore	Can.			16	16	0
Green Violet-ear	<i>Colibri thalassinus</i>	Nectarivore	Can.			16	16	0
Plumbeous Pigeon	<i>Patagioenas plumbea</i>	Frugivore	Can.			15	7	8
Lineated Foliage-gleaner	<i>Syndactyla subalaris</i>	Epiphyte insectivore	Under.	Yes		15	8	7
Green-and-black Fruiteater	<i>Pipreola riefferii</i>	Frugivore	Mid.			15	6	9
Masked Trogon	<i>Trogon personatus</i>	Frugivore	Mid.			14	8	6
Sparkling Violet-ear	<i>Colibri coruscans</i>	Nectarivore	Open			13	13	0
Red-billed Parrot	<i>Pionus sordidus</i>	Frugivore	Can.			13	9	4

English common name	Scientific name	Guild	Strata	Flocking?	Endemic?	Total	Pasture	Forest
Red-faced Spinetail	<i>Cranioleuca erythropis</i>	Epiphyte insectivore	Can.	Yes		13	7	6
Streaked Tuftedcheek	<i>Pseudocolaptes boissonneautii</i>	Epiphyte insectivore	Mid.	Yes		12	7	5
Gorgeted Sunangel	<i>Heliangelus strophianus</i>	Nectarivore	Can.		Yes	12	9	3
Andean Solitaire	<i>Myadestes ralloides</i>	Omnivore	Under.			12	3	9
Great Thrush	<i>Turdus fuscater</i>	Omnivore	Open			11	11	0
Plate-billed Mountain-toucan	<i>Andigena laminirostris</i>	Frugivore	Can.		Yes	11	6	5
Golden-headed Quetzal	<i>Pharomachrus auriceps</i>	Frugivore	Mid.			11	7	4
Strong-billed Woodcreeper	<i>Xiphocolaptes promeropirhynchus</i>	Bark insectivore	Mid.	Yes		10	4	6
Olive-crowned Yellowthroat	<i>Geothlypis semiflava</i>	Gleaning insectivore	Open			10	10	0
Tropical Kingbird	<i>Tyrannus melancholicus</i>	Aerial insectivore	Open			9	9	0
House Wren	<i>Troglodytes aedon</i>	Epiphyte insectivore	Open			9	9	0
Mountain Wren	<i>Troglodytes solstitialis</i>	Epiphyte insectivore	Mid.			9	0	9
Crimson-rumped Toucanet	<i>Aulacorhynchus haematopygus</i>	Frugivore	Can.			9	2	7
Barred Becard	<i>Pachyramphus versicolor</i>	Aerial insectivore	Can.	Yes		8	8	0
Powerful Woodpecker	<i>Campephilus pollens</i>	Bark insectivore	Mid.			8	6	2
Western Hemispingus	<i>Hemispingus ochraceus</i>	Omnivore	Under.	Yes		7	3	4
Crimson-mantled Woodpecker	<i>Colaptes rivolii</i>	Bark insectivore	Mid.			7	4	3
Flavescent Flycatcher	<i>Myiophobus flavicans</i>	Aerial insectivore	Under.			7	5	2
Long-tailed Antbird	<i>Drymophila caudata</i>	Gleaning insectivore	Under.			7	5	2
Fawn-breasted Brilliant	<i>Heliodoxa rubinoides</i>	Nectarivore	Under.			7	3	4
Lesser Elaenia	<i>Elaenia chiriquensis</i>	Aerial insectivore	Open			6	5	1
Tawny-bellied Hermit	<i>Phaethornis syrmatophorus</i>	Nectarivore	Under.			6	0	6
Golden-winged Manakin	<i>Masius chrysopterus</i>	Frugivore	Under.			5	0	5
Glistening-green Tanager	<i>Chlorochrysa phoenicotis</i>	Omnivore	Can.	Yes	Yes	5	4	1
Bluish Flowerpiercer	<i>Diglossopsis caerulescens</i>	Omnivore	Can.	Yes		5	0	5
Glossy-black Thrush	<i>Turdus serranus</i>	Omnivore	Mid.			5	2	3

English common name	Scientific name	Guild	Strata	Flocking?	Endemic?	Total	Pasture	Forest
Nariño Tapaculo	<i>Scytalopus vicinior</i>	Terrestrial insectivore	Terr.		Yes	4	0	4
Purple-throated Woodstar	<i>Calliphlox mitchellii</i>	Nectarivore	Can.			4	4	0
Chestnut-crowned Antpitta	<i>Grallaria ruficapilla</i>	Terrestrial insectivore	Terr.			4	0	4
Plushcap	<i>Catamblyrhynchus diadema</i>	Omnivore	Under.	Yes		4	0	4
Squirrel Cuckoo	<i>Piaya cayana</i>	Omnivore	Can.			4	4	0
Swallow-tailed Kite	<i>Elanoides forficatus</i>	Raptor	Open			4	4	0
Yellow-vented Woodpecker	<i>Veniliornis dignus</i>	Bark insectivore	Mid.			4	4	0
Blue-and-white Swallow	<i>Notiochelidon cyanoleuca</i>	Aerial insectivore	Open			4	4	0
Smoky-brown Woodpecker	<i>Veniliornis fumigatus</i>	Bark insectivore	Mid.			4	3	1
Roadside Hawk	<i>Buteo magnirostris</i>	Raptor	Open			4	4	0
Purple-bibbed Whitetip	<i>Urosticte benjamini</i>	Nectarivore	Mid.		Yes	3	2	1
Slaty Antwren	<i>Myrmotherula schisticolor</i>	Gleaning insectivore	Under.	Yes		3	0	3
Blue-gray Tanager	<i>Thraupis episcopus</i>	Omnivore	Open	Yes		3	3	0
Rufous Spinetail	<i>Synallaxis unirufa</i>	Epiphyte insectivore	Under.			3	0	3
Fawn-breasted Tanager	<i>Pipraeidea melanonota</i>	Omnivore	Open			3	3	0
Plain-tailed Wren	<i>Thryothorus euophrys</i>	Epiphyte insectivore	Under.			3	3	0
Chestnut-capped Brush-finch	<i>Arremon brunneinucha</i>	Omnivore	Under.			3	0	3
Band-tailed Pigeon	<i>Patagioenas fasciata</i>	Frugivore	Can.			2	1	1
Olivaceous Piha	<i>Snowornis cryptolophus</i>	Omnivore	Mid.			2	0	2
Rufous-breasted Antthrush	<i>Formicarius rufipectus</i>	Terrestrial insectivore	Terr.			2	0	2
Andean Cock-of-the-rock	<i>Rupicola peruvianus</i>	Frugivore	Mid.			2	0	2
Black-and-white Becard	<i>Pachyramphus albogriseus</i>	Aerial insectivore	Can.	Yes		2	2	0
Yellow-bellied Chat-tyrant	<i>Ochthoeca diadema</i>	Aerial insectivore	Under.			2	2	0
Yellow-bellied Seedeater	<i>Sporophila nigricollis</i>	Granivore	Open			2	2	0
Black-capped Tanager	<i>Tangara heinei</i>	Omnivore	Open	Yes		2	2	0
Empress Brilliant	<i>Heliodoxa imperatrix</i>	Nectarivore	Under.		Yes	2	2	0
White-faced Nunbird	<i>Hapaloptila castanea</i>	Gleaning insectivore	Mid.			1	0	1

English common name	Scientific name	Guild	Strata	Flocking?	Endemic?	Total	Pasture	Forest
Spotted Woodcreeper	<i>Xiphorhynchus erythropygius</i>	Bark insectivore	Mid.	Yes		1	0	1
Scaly-throated Foliage-gleaner	<i>Anabacerthia variegaticeps</i>	Epiphyte insectivore	Mid.			1	0	1
Sickle-winged Guan	<i>Chamaepetes goudotii</i>	Frugivore	Mid.			1	0	1
Dark-backed Wood-quail	<i>Odontophorus melanonotus</i>	Terrestrial omnivore	Terr.		Yes	1	0	1
Rufous-headed Pygmy-tyrant	<i>Pseudotriccus ruficeps</i>	Aerial insectivore	Under.			1	0	1
Striped Treehunter	<i>Thripadectes holostictus</i>	Epiphyte insectivore	Under.			1	0	1
Red-crested Cotinga	<i>Ampelion rubrocristatus</i>	Frugivore	Mid.			1	1	0
Sepia-brown Wren	<i>Cinnycerthia olivascens</i>	Epiphyte insectivore	Under.			1	1	0
Black-capped Tyrannulet	<i>Phyllomyias nigrocapillus</i>	Aerial insectivore	Open	Yes		1	1	0
Tyrannine Woodcreeper	<i>Dendrocincla tyrannina</i>	Epiphyte insectivore	Mid.	Yes		1	1	0
White-tipped Dove	<i>Leptotila verreauxi</i>	Terrestrial omnivore	Terr.			1	0	1
White-throated Quail-dove	<i>Geotrygon frenata</i>	Terrestrial omnivore	Terr.			1	0	1
Scaled Fruiteater	<i>Ampelioides tschudii</i>	Frugivore	Mid.			1	0	1
Ochre-breasted Antpitta	<i>Grallaricula flavirostris</i>	Terrestrial insectivore	Terr.			1	0	1
Ornate Flycatcher	<i>Myiotriccus ornatus</i>	Aerial insectivore	Mid.			1	0	1
Ashy-headed Tyrannulet	<i>Phyllomyias cinereiceps</i>	Aerial insectivore	Mid.	Yes		1	1	0
Beautiful Jay	<i>Cyanolyca pulchra</i>	Omnivore	Mid.			1	0	1
Golden-crowned Tanager	<i>Iridosornis rufivertex</i>	Omnivore	Mid.	Yes		1	1	0
Golden-olive Woodpecker	<i>Colaptes rubiginosus</i>	Bark insectivore	Mid.			1	1	0
Yellow-breasted Antpitta	<i>Grallaria flavotincta</i>	Terrestrial insectivore	Terr.		Yes	1	0	1

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BIOGRAPHICAL SKETCH

Nathan Marcy grew up in rural western Massachusetts, where he developed a deep interest in wildlife and the natural world. He received a bachelor's degree in zoology from Connecticut College in 2003. Following college he moved to Boston and worked at National Public Radio's "Living on Earth," a job he eventually left to go backpacking through Central America. A stint volunteering at a cloud forest reserve in Costa Rica convinced him to pursue a career in ecological research. After returning to the US he served as a field technician on a series of avian studies at locations across the country. He went back to the tropical cloud forest several times, in both Costa Rica and Ecuador, and conducted independent studies of the birds there. These projects lead directly to his master's thesis work at the University of Florida.