SATELLITE DETECTION OF BIRD COMMUNITIES IN TROPICAL COUNTRYSIDE

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Abstract. The future of biodiversity hinges partly on realizing the potentially high conservation value of human-dominated countryside. The characteristics of the countryside that promote biodiversity preservation remain poorly understood, however, particularly at the fine scales at which individual farmers tend to make land use decisions. To address this problem, we explored the use of a rapid remote sensing method for estimating bird community composition in tropical countryside, using a two-step process. First, we asked how fine-grained variation in land cover affected community composition. Second, we determined whether the observed changes in community composition correlated with three easily accessible remote sensing metrics (wetness, greenness, and brightness), derived from performing a tasseled-cap transformation on a Landsat Enhanced Thematic Mapper Plus image. As a comparison, we also examined whether the most commonly used remote sensing indicator in ecology, the Normalized Difference Vegetation Index (NDVI), correlated with community composition.

We worked within an agricultural landscape in southern Costa Rica, where the land comprised a complex and highly heterogeneous mosaic of remnant native vegetation, pasture, coffee cultivation, and other crops. In this region, we selected 12 study sites (each <60 ha) that encompassed the range of available land cover possibilities in the countryside. Within each site, we surveyed bird communities within all major land cover types, and we conducted detailed field mapping of land cover.

We found that the number of forest-affiliated species increased with forest cover and decreased with residential area across sites. Conversely, the number of agriculture-affiliated species using forest increased with land area devoted to agricultural and residential uses. Interestingly, we found that the wetness and brightness metrics predicted the number of forest- and agriculture-affiliated species within a site as well as did detailed field-generated maps of land cover. In contrast, NDVI and the closely correlated greenness metric did not correlate with land cover or with bird communities. Our study shows the strong potential of the tasseled-cap transformation as a tool for assessing the conservation value of countryside for biodiversity.

Key words: agriculture; agroecology; biodiversity; conservation value; Costa Rica; countryside biogeography; Kauth-Thomas; Landsat; NDVI; Normalized Difference Vegetation Index; remote sensing; tasseled cap.

INTRODUCTION

Protected areas alone are unlikely to preserve more than a small fraction of the earth’s biodiversity (Daily 2001, Rosenzweig 2003, Rodrigues et al. 2004). They are, and are likely to remain, too small, too isolated, and too vulnerable to human impacts, including climate change (Hales 1989, van Schaik et al. 1997, Chundawat et al. 1999, Thapar 1999, Schneider and Root 2002, Burns et al. 2003, Tellez-Valdes and Davila-Aranda 2003, Carroll et al. 2004). As a result, researchers are focusing increasingly on characterizing the conservation potential of unprotected, human-dominated countryside (e.g., Hutton and Giller 2003, Stephens et al. 2003, Peach et al. 2004), especially given projected expansion and intensification of agriculture (Tilman et al. 2001). In this study, we define countryside habitats as “active agricultural plots, plantation or managed forest, fallow land, gardens, and small remnants of native vegetation embedded in landscapes devoted primarily to human activities” (Daily et al. 2001).

Agricultural intensification is a key driver of land cover homogenization which, in turn, drives declines in biodiversity (Estrada et al. 1997, Krebs et al. 1999, Benton et al. 2003, Perfecto et al. 2003). Nevertheless, much of the world’s countryside, particularly under low-intensity production systems, can support a large proportion of native biotas, for several decades at least.
From a conservation science perspective, the challenge now is twofold: (1) to understand the conditions that sustain biodiversity (Vandermeer and Perfecto 1997, Sekercioglu et al. 2002); and (2) to assess the presence of these conditions in countryside relatively easily, such as through remote sensing. These challenges are heightened by the high degree of land cover heterogeneity that characterizes the countryside across much of the tropics today (e.g., Daniels 1996, Estrada et al. 1997, Daily et al. 2001). While this heterogeneity is thought to confer conservation value for many species, it is difficult to integrate systematically into conservation planning because the responses of organisms to land cover heterogeneity are complex and poorly understood (Gaston 2003).

The first challenge, assessing the sustainability of countryside biodiversity, has emerged as an important new research focus. So far, researchers have characterized some of the conditions in countryside that foster native species, such as habitat elements that increase the structural and floristic diversity of the countryside, like border vegetation and tall trees (Hinsley and Bellamy 2000, Hughes et al. 2002, Wickramasinghe et al. 2003, Harvey et al. 2004). Findings vary widely by taxon and structural and floristic diversity of the countryside, like habitat elements that increase the conservation value for many species, it is difficult to integrate systematically into conservation planning because the responses of organisms to land cover heterogeneity are complex and poorly understood (Gaston 2003).

The second challenge, assessing the presence of important habitat elements, incurs the problem of measuring biodiversity directly. Even for taxa censused relatively easily, such as birds, this requires considerable expertise, time, and expense (Danielsen et al. 2005). Remote sensing could potentially alleviate this limitation by allowing for time- and cost-effective assessments of the conservation value of countryside. Remote sensing has been used widely in conservation efforts, most commonly through the creation of land cover maps that are then compared against distributions of species (Fuller et al. 1998, Saveraid et al. 2001). Many studies have taken this approach to examining the connection between various aspects of biodiversity and remote sensing, generally at relatively broad spatial scales (U.S. states and larger) and for a small subset of countryside habitats (Brooks et al. 1997, Fraser 1998, Johnson et al. 1998, Oindo 2002, Hurlbert and Haskell 2003; but see Wheatley et al. 2005).

Despite the advances achieved in conservation through image classification, it is often extremely difficult, expensive, and time consuming to classify land cover accurately, which limits its value for a "crisis discipline" (Seto et al. 2004, Baraldi et al. 2006). To overcome this problem, many easily calculated remote sensing metrics have been used in the literature, with the most common by far being the Normalized Difference Vegetation Index (NDVI; Kerr and Ostrovsky 2003, Pettorelli et al. 2005). NDVI is an index of vegetation productivity that has correlated strongly with many ecological conditions, such as land cover, land degradation, and species richness of many taxa (e.g., Tucker et al. 1985, Thiam 2003, Fairbanks and McGwire 2004, Seto et al. 2004, Foody 2005, Debinski et al. 2006). There are numerous limitations to the use of NDVI, however, particularly in the tropics where the index is known to saturate (Boyd et al. 1996, Steininger 1996, Kerr and Ostrovsky 2003).

It would be useful to broaden the basket of simple remote sensing metrics commonly used by conservation biologists, and we seek to do so in this study by exploring the utility of the tasseled-cap transformation (also known as the Kauth-Thomas transformation) for countryside work. Originally developed to estimate agricultural productivity, the tasseled-cap transformation acts on Landsat data to produce three metrics: greenness, wetness, and brightness (Crist and Cicone 1984, Crist and Kauth 1986). These three metrics are linked closely to properties of vegetation and soil: brightness is driven by soil reflectance, which in turn is closely related to soil surface structure and organic matter content; wetness is directly associated with soil and canopy moisture; and greenness is linked strongly to the amount of vegetation present (Phua and Saito 2003, Cohen and Goward 2004). All three metrics have been found to correspond with many factors meaningful for conservation biologists, such as land cover, successional stage, and forest status (Cohen and Spies 1992, Cohen et al. 1995, Helmer et al. 2000, Rogan et al. 2002, Aguilar 2005). As greenness is known to be closely associated with NDVI (Huang et al. 2002, Xu et al. 2003, Dunham et al. 2005), it can be expected that this metric will have limited utility in the tropics; brightness and wetness, however, represent untapped possibilities.

The composition of bird communities in agricultural landscapes is often driven by vegetation structure (Hinsley and Bellamy 2000, Soderstrom and Part 2000, Daily et al. 2001, Hughes et al. 2002, Luck and Daily 2003, Harvey et al. 2005). Accordingly, we expected the tasseled-cap metrics and NDVI to be associated with community composition to the extent that the metrics reflect the vegetation structure important for those communities. Forest-affiliated species and agriculture-affiliated species should be associated with vegetation structure (though in opposite ways), while habitat generalist species should have little association with it. Consequently, we expected only forest- and agriculture-affiliated species to correlate with the remote sensing metrics. Further, even with these two species categories, we did not expect all four remote sensing metrics to behave equally: as NDVI and the linked greenness measure tend to saturate, neither metric should have reflected vegetative structure nor, consequently, bird communities.
In this study of tropical countryside, we addressed the twin challenges of understanding the conditions that sustain biodiversity and of assessing these conditions using simple remote sensing measures. We posed three questions. First, how did avian communities found within tropical countryside vary with fine-grained changes in land cover? Second, what grain size was most relevant for the composition of countryside birds? Third, did variation in community composition correlate with the tasseled-cap remote sensing measures or NDVI? For this last question, we expected that forest and agriculturally affiliated species would correlate only with brightness and wetness.

METHODS

Study area

We conducted our study in the Valle de Coto Brus region of southern Costa Rica (Fig. 1) from June–September 2002. The study area has an elevation range of 750–1250 m, receives mean annual rainfall of 3420 mm, and occurs mostly in the tropical premontane rainforest Holdridge Life Zone (Tosi 1969). Although the area has experienced >3000 yr of human disturbance, land clearing and agriculture associated with native human populations lapsed to minimal levels by AD 1500 (Clement and Horn 2001). After >400 yr of relatively little human disturbance, the area underwent rapid deforestation in the 1950s and 1960s, resulting in the complex and heterogeneous pattern of land cover there today (see Plate 1). Remaining forest comprises mostly thin riparian zones and small forest fragments (generally <35 ha), with the largest forest fragment (Las Cruces) covering 235 ha. We defined our study area as a 15 km radius circle centered on the Las Cruces fragment. Within this circle, 25% of the area is forested, 23% is in pasture, and 15% is under coffee cultivation, with the remaining land under banana, yucca, and other crops. Landholdings are relatively small, typically 0.1–10.0 ha.
Field surveys

We measured patterns of bird diversity and land cover at 12 sites, each defined as the area circumscribed by a 300 m radius from the boundary of a small, discrete, central forest fragment (Fig. 1; average fragment area $3.1 \pm 0.6$ ha, average site area $54.2 \pm 2.9$ ha; measurements are expressed as mean $\pm$ SE). All forest fragments were separated from all others by at least 1 km. Differences in site area largely resulted from differences in forest fragment shape. We selected sites to represent the range of land cover possibilities present within the study circle.

Characterization of the bird community

We censused bird communities using fixed 50 m radius point-count stations (hereafter “station”). We placed six stations at each of the 12 sites, one station in each of the following land cover types at each site (in order of decreasing structural complexity): forest, riparian strips, high vertical-structure agriculture (e.g., coffee cultivation containing shade trees), abandoned fields, low vertical-structure agriculture (e.g., annual crops), and active pasture. All stations were separated by a minimum of 150 m. Four sites did not contain an abandoned-fields point count, and one site did not contain low vertical-structure agriculture. Thus we had 67 stations in total, and all sites contained at least five stations, with no repeats in station type within a site. We positioned all stations within 200 m of the central forest fragment.

Ten-minute point counts were taken eight times at each station over the course of the study. As this study took place during the summer, no migrants were detected. However, this omission likely had only a minor effect on the results, as only 16% of the species in the region are migratory (G. C. Daily, unpublished data). We conducted point counts between 05:00 and 09:00, recording all birds that were seen and heard within a 50 m radius of the center point, except individuals flying high over the area. We partitioned the bird species pool into subsets based on habitat affinity, where affinity was determined from an independent and long-term bird census that was conducted by one of the authors (G. C. Daily) in the same geographical area as this study. We resolved habitat affinity based on the relative frequency of observations of birds in forest and agricultural habitats in this unpublished data set. Birds that were observed three or more times and $>90\%$ of the time in forest were classified as forest-affiliated; those observed three or more times and $>90\%$ of the time in agricultural habitats were classified as agriculture-affiliated; birds observed at least once in both forest and agricultural habitats but not falling into these categories were classified as generalists; the remainder were left as unclassified.

We utilized raw species counts for our analysis, as opposed to estimated species richness, for two reasons.
First, a major reason for using an estimator is to account for unequal sampling effort (Colwell and Coddington 1994), but our sampling effort was identical at each station. Second, the results produced by the large number of species estimators can vary widely as a consequence of the different assumptions made by each about the relationship of detected to undetected species (e.g., Chazdon et al. 1998, Longino et al. 2002, Melo 2004, O’Hara 2005). As we had no means of evaluating the validity of the assumptions underlying the various estimators for our study community, it was not possible to determine which estimators would be appropriate. Furthermore, applying more than one metric would introduce a multiple-test problem. Although the use of raw species richness has its own issues, involving questions of evenness and completeness of sampling, we judged this measure to be the most parsimonious means of approaching the data.

Characterization of land cover

We mapped land cover and measured vegetation attributes at each site. We separated the land cover visually into relatively homogeneous parcels (hereafter “parcel”; e.g., coffee with tall banana, pasture with shrubs). We assigned each parcel one of the following land cover classifications: forest, riparian strips, tree plantation, abandoned fields, active pasture, coffee, other cultivation (mostly annual crops), marsh, or residential. We mapped the boundaries of all parcels using hand-held geographic positioning system devices and entered the information into a geographic information system. As tree plantations and marshes were very minor components of the landscape, together comprising 1.4% of site area, they were omitted from the analysis, leaving six land cover types in consideration.

Remote sensing

We used two Landsat Enhanced Thematic Mapper Plus (ETM+) images of the study site (level 1G corrected, path 14, row 54), captured on 31 January 2001 and 21 January 2003. We selected these two particular images because they were the temporally closest cloud-free images that bracketed the time of ground sampling (June–September 2002). These images were captured during the dry season, and no cloud-free images in the wet season were available. For these images we calculated the three tasseled-cap metrics as well as NDVI (Huang et al. 2002, Pettorelli et al. 2005).

Data analyses

We performed all statistical analyses with Patch Analyst 3.1 (Rempel and Carr 2003), the statistical computing language known as “R” (R Development Core Team 2005), and a community ecology package developed for R (Oksanen et al. 2005). We first evaluated patterns of similarity across stations, using the following approach. We determined a cumulative species list for each station, which formed the basis of the species analysis. For each station, we calculated total species richness, as well as species richness within each of the three habitat affinity groups. We grouped station types, using Tukey’s honestly significant difference test as a means of comparing patterns of richness across types. To evaluate compositional differences across station types, we calculated Jaccard similarity coefficients, based on species observed, for all pairs of stations. Using those coefficients, we performed a nonmetric multidimensional scaling to graphically evaluate the compositional similarity of stations. We calculated the probability of obtaining the observed level of clustering between station types by chance, using an analysis of similarity (ANOSIM).

We next determined the effect of site-scale land cover variation on observed richness patterns at two scales: station and site. At the finer station scale, we calculated the correlation between species richness and total site proportion of each land cover type, for each of the four categories of richness at each station type. At the site scale, we pooled species across all stations of each site and then tested the correlation between the four richness categories and land cover.

Lastly, we evaluated whether the four remotely sensed metrics effectively correlated with the observed variation in species richness caused by site-scale land cover variation. As a first step in this process, we determined whether the metrics were a proxy for any of the measured land cover types. We calculated the mean metric for each site and tested the correlation between this and total site proportion of each land cover type. Next, we assessed the correlation between the metrics and observed species richness at each station, using two metric statistics: the mean and standard deviation (the latter calculated as the standard deviation of all pixels within a sampling unit). We circumscribed a 500 m wide radius around each station and divided this area into five nested disks of increasing width (100–500 m width, 100-m increment; 500 m was the largest possible radius that did not cause overlap between stations of the same type across sites). For each disk of each station, we calculated the correlation between that statistic and species richness of each station type, across all four measures of species richness.

RESULTS

Response of avian communities to fine-grained variation in land cover

We found a total of 166 bird species in our sites: 55 forest-affiliated species, 65 agriculture-affiliated species, 28 generalist species, and 18 unclassified species (Appendix A). The number of species detected varied with land cover; species richness declined with declining vegetation height diversity (Fig. 2). Forest and riparian stations thus had the greatest total species richness and the vast majority of forest-affiliated species; these stations were not significantly different from each other
in total or agriculture-affiliated richness, but they differed in forest-affiliated and generalist richness (by Tukey’s honestly significant difference test). Conversely, open pasture contained the fewest species in total, and agriculture-affiliated species constituted 82% of that total. The birds found within the remaining three station types (abandoned fields, high and low vertical-structure agriculture) contained mostly agriculture-affiliated species, with some representation by generalist species.

Species composition also varied across station types, in a manner similar to richness. The nonmetric multidimensional scaling revealed that census station types clustered strongly in terms of species composition (stress [a measure of goodness of fit] = 0.158; Fig. 3). Forest stations were grouped tightly and were all located within a cloud of riparian stations, which were less tightly bunched. These two census station types clustered together quite distinctively from the other types to form a “remnant vegetation” cluster. An “agriculture” cluster was evident in the largely overlapping stations for the following station types: abandoned fields, high vertical structure, and low vertical structure. Pasture stations formed their own cluster. ANOSIM results indicated that this clustering was highly significant ($R = 0.7341, P < 0.0001$).

We found that land cover variation at the intrasite scale did not affect species composition, as shown in two ways. First, we failed to reject the null hypothesis of no correlation ($P > 0.05$) between the area of the forest fragment at the center of each site and species richness (total and the three habitat affinity categories) for any station type (see Appendix B for regression coefficients). Second, the intrasite spatial composition of land cover did not affect community composition (Appendix C).

In contrast, we found that land cover variation at the scale of the site did affect composition. At this scale, species richness was affected by land cover variation only within the remnant vegetation cluster, with only one land cover (forest) significantly affecting richness. Forest-affiliated species richness rose with site-level forest extent in both forest and riparian stations (forest $r = 0.701, P = 0.011$; riparian $r = 0.715, P = 0.009$). In a related note, forest-affiliated species richness within forest and riparian stations were also correlated ($r = 0.7341, P < 0.0001$).
0.744, $P = 0.006$). Agriculture-affiliated species richness in forest stations declined with site-level forest extent ($r = -0.670, P = 0.017$). We found similar results when species were pooled by site, with the only significant relationship found between forest-affiliated species and site-level forest extent ($r = 0.722, P = 0.008$).

**Correlation of remote sensing metrics with species richness**

The pattern of significant correlations ($P < 0.05$) was identical using the 2001 and 2003 Landsat images; all correlations that were significant with the 2001 image were also significant with the 2003 image and vice versa. For simplicity, only the 2003 results are presented in this article. Standard deviation did not significantly correlate with either land cover or species richness for any metric (all $P > 0.05$). Normalized Difference Vegetation Index (NDVI) and greenness across sites were correlated ($r = 0.781, P = 0.003$), and the mean of each correlated with neither our land cover categories nor species richness (all $P > 0.05$). Mean wetness and brightness across sites were negatively correlated ($r = -0.853, P < 0.001$), and the mean of each metric at each site was closely related to percent forest extent (wetness $r = 0.818, P = 0.001$; brightness $r = -0.679, P = 0.015$; Fig. 4). Consequently, the species richness categories in the remnant vegetation cluster that were sensitive to forest extent were similarly sensitive to the mean of both remote sensing metrics (Fig. 5). Importantly, for agriculture-affiliated species in forest stations, richness was more strongly correlated with the two remote sensing measures (wetness and brightness) than the field-mapped measure (forest extent). This pattern was true for all disk sizes used in the remote sensing calculations, with wetness negatively correlated with richness and brightness positively correlated. The strength of the correlation between forest-affiliated species richness in forest stations and the remote sensing measures (positive correlation for wetness and negative correlation for brightness) rose with disk radius, with disks $\geq 400$ m radius producing correlations comparable to that of richness and forest cover. Forest-affiliated species richness in riparian stations did not vary significantly with the remote sensing measures when we used disks centered about riparian stations ($P > 0.05$); yet richness of this group did correlate positively with the measures (disk radius $\geq 300$ m) when we used disks centered about forest stations ($P < 0.05, r > 0.60$).

Fig. 5 shows that three habitat–species association groups were significantly correlated with brightness and wetness, with a habitat–species association group defined as a species group (forest-affiliated, generalist, agriculture-affiliated, total) within a point count station type (forest, riparian strips, high vertical-structure agriculture, abandoned fields, low vertical-structure agriculture, and active pasture). Those three habitat–species association groups were: agriculture-affiliated species in forest stations (significant correlations across all five disk radii), forest-affiliated species in forest stations, and forest-affiliated species in riparian stations (the latter two exhibiting significant correlations across three adjacent disk radii).

As our analysis of the relationship between species composition and remote sensing involved numerous correlations, we investigated whether our results were an artifact of multiple comparisons. Using a randomization approach, we rejected the null hypothesis that our significant results are due to the multiple comparisons (Appendix D).

**DISCUSSION**

In this study, we showed that brightness and wetness (two components of the tasseled-cap transformation) correlated strongly with avian compositional differences...
in the tropical countryside. Our confidence in our remote sensing results is heightened because all of the patterns between the remote sensing metrics and avian composition were stable across two images that were captured in the same season of different years. The underpinning of this relationship between the two components of the tasseled-cap transformation and species composition is that these metrics also correlated with landscape composition, specifically tree cover.

According to our results, however, wetness and brightness are more than just proxies for tree cover. The two metrics were imperfectly correlated with tree cover (wetness $r = 0.818$; brightness $r = -0.679$). Consequently, if wetness and brightness were mere proxies for tree cover, then tree cover should be more strongly correlated with species compositional differences than the remote sensing metrics. However, for forest-affiliated species in forest stations, all three landscape measures correlated similarly with species richness (tree cover and richness $r = 0.701$; mean wetness and richness with buffer radius $\geq 300$ m, $0.590 \leq r \leq 0.720$; mean brightness and richness with buffer radius $\geq 300$ m, $-0.720 \leq r \leq -0.590$). For agriculture-affiliated species in forest stations, the two landscape measures showed a better correlation with species richness than did tree cover (tree cover and richness $r = -0.670$; mean wetness and richness $-0.890 \leq r \leq -0.760$; mean brightness and richness $0.760 \leq r \leq 0.890$). The likely explanation for this result is that continuous measurements, like brightness and wetness, allow for finer distinctions of landscape than measurements based on categorical variables, such as mapped tree cover (DeFries et al. 1995, DeFries et al. 1999, Lambin 1999).

By contrast, NDVI and the closely correlated greenness metric were not significantly associated with either landscape composition or richness. This negative result is likely caused by the tendency of NDVI, and by extension greenness, to saturate in the tropics (Boyd et al. 1996, Steininger 1996, Kerr and Ostrovsky 2003).

There are several advantages of brightness and wetness: (1) they are sensitive to the vegetative structure important for species persistence (Cohen et al. 1995), and (2) they are easily and quickly calculated. Although the tasseled-cap transformation has been used occasionally in ecology (e.g., Cohen and Spies 1992, Price and Jakubauskas 1998, Aguilar 2005), ecologists should consider using it more widely as part of the standard set of commonly used remote sensing tools.

This study also sheds insight into the appropriate scale for conservation activities in the tropical countryside. The question of appropriate scale is often straightforward within protected areas, where the scale of conservation activities is set by the scale of the protected area. In contrast, the appropriate scale within the countryside is more ambiguous, for multiple reasons. First, from a planning perspective, there are often not defined boundaries for the countryside that obviously demarcate the scale of conservation operations. Second, from an ecological perspective, the functioning of biological communities in the countryside is generally
poorly understood (Kleijn and Sutherland 2003, Kleijn et al. 2004), making it difficult to select an appropriate scale for conservation action.

We addressed this concern in this study by simultaneously determining bird community response to land cover variation at two scales: the scale of individual habitat elements and a larger, sub-1-km² “site” scale. The smaller habitat–element scale has been well studied in earlier research (e.g., Gascon et al. 1999, Estrada et al. 2000, Daily et al. 2001, Harvey et al. 2005), and our findings mirror the conclusion of other studies that land cover type strongly influences the richness and composition of countryside bird communities. Indeed, individual habitat features in heterogeneous landscapes are often critical for avian persistence (e.g., Estrada et al. 1997, Graham 2001, Berg 2002, Luck and Daily 2003).

In contrast, the larger site scale has been little examined in the avian countryside literature. Features at this scale are likely to exert a strong influence on multiple elements important to bird persistence, such as foraging energetics and nest success (Benton et al. 2003). However, land cover variation at this scale did affect community components within the remnant vegetation cluster (forest and riparian strips). Specifically, forest- and agriculture-affiliated species within this cluster responded to land cover variation at a grain size of roughly 25–75 ha, as indicated by the remote sensing and field-mapped results. On the other hand, this scale was not significant for communities found in the agriculture and pasture clusters, perhaps because the birds that occur in such areas are not as sensitive to variation in these environmental factors as those constrained to forested areas.

The effect of landscape on community composition at the site scale was most evident with forest-affiliated species, the group of greatest conservation concern. Almost all observed forest-affiliated species were found in forest and riparian habitats, and in these habitats there was a strong correlation between richness and local forest extent. Forest-affiliated species at forest and riparian stations responded very similarly to landscape composition, and in both cases the landscape buffers mediating that response were centered around the forest fragments at the center of the site. These two results strongly suggest that the primary association of forest-affiliated species found within riparian areas is nearby forest fragments, accentuating the importance of maintaining remnant habitat in the countryside to maintain species of greatest conservation concern. These findings confirm the conclusion that the conservation value of riparian habitats cannot be disassociated from the landscape matrix in which they are found (Rodewald and Bakermans 2006). The forest fragments in this study were comparatively small, and yet they were disproportionately important for species richness. Conservation efforts at the local scale in tropical countryside should thus focus on maintaining forest cover, especially in forest fragments >5 ha or in smaller strips and patches close to these fragments.

The observed patterns of community composition align well with what is known about the biology of the component species. Thirteen of the species in the forest-affiliated species group belonged to largely forest-specialist families (Formicariidae [antbirds], Furnariidae [ovenbirds], Thamnophilidae [antbirds], and Ramphastidae [toucans]). The remaining species were generally dependent on forest for critical aspects of their life cycle, such as nesting (e.g., Thryothorus semibadius, Riverside Wren) and feeding (e.g., Habia rubica, Red-crowned Ant-Tanager; Skutch 2001, Maldonado-Coelho and Marini 2004). The agriculture-affiliated group comprised species that regularly nest in buildings (e.g., Trogodytes aedon, House Wren), while others feed readily within agricultural fields (e.g., Volatinia jacarina, Blue-black Grassquit; Stiles and Skutch 1989, Tubelis and Cavalcanti 2000). Generalist species richness did not vary with forest extent at the scales measured in this study; certain species in the group are relatively flexible and adaptable (e.g., Mumotus momota, Blue-crowned Motmot), while others are more commonly associated with forest but still make extensive use of highly modified habitats (e.g., Turdus assimilis, White-throated Robin; Snow 2001, Cohen and Lindell 2004).

Interestingly, we found that land cover around a station did not influence total species richness of birds at any station. This result is likely to be highly dependent upon scale. The landscape factors considered in this study are likely to impact overall landscape-level richness resulting from differential species turnover (beta diversity). We did not investigate species turnover between sites, however. We expect that forest-affiliated species, which are more likely than agriculture-affiliated or generalist species to be range limited or specialized, would turn over more quickly between regions of countryside (Gaston 2003, Lindell et al. 2004).

Our findings show the need to plan at multiple scales when designing conservation initiatives for birds in the tropical countryside, as the birds themselves respond to their landscape at multiple scales. Both scales tested here are relatively small and within the scale at which individual landholders make land use decisions. We show that conservation strategies focused on tropical countryside at this landholding scale can pay large dividends for bird conservation.

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LITERATURE CITED


APPENDIX A

Avifauna detected within the study and their habitat affinity (Ecological Archives A017-059-A1).

APPENDIX B

Association between forest fragment area and species richness (Ecological Archives A017-059-A2).

APPENDIX C

Effect of intrasite spatial composition of land cover on community composition (Ecological Archives A017-059-A3).

APPENDIX D

Effect of multiple comparisons on detection of species groups using remote sensing (Ecological Archives A017-059-A4).