Landscape-level effects on avifauna within tropical agriculture in the Western Ghats: Insights for management and conservation

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ABSTRACT

A critical handicap to tropical biodiversity conservation efforts in agroecosystems is the unknowns regarding the influence of landscape-scale factors on the persistence of species. To address these uncertainties, we explored two essential landscape-scale questions, within India's biologically-rich Western Ghats, examining two nearby human-dominated landscapes that dramatically differed in their pattern of land cover. First, how does the proximity of intact forest patches affect bird community composition within agricultural landscapes? Second, can simple remote sensing-derived measures (brightness, wetness, and NDVI) be used to estimate native bird species composition within those landscapes? In both landscapes, as distance to intact forest decreased, the similarity in bird community composition between agricultural areas and intact forest increased. This suggests that the retention of tropical forest bird communities within human-dominated landscapes critically depends on the maintenance of nearby intact forest. In an answer to the second question, the remote sensing measures correlated with forest-affiliated avian species richness in only one of the two landscapes, reflecting an ecological difference between the two in the response of forest bird species to local agricultural conditions. In the landscape where a correlation was found, there was high variation in vegetative structure, which strongly impacted both the remote sensing measures and forest bird species richness. In the other landscape, forest species richness strongly correlated with changes in tree species composition in the agriculture, a factor that could not be detected by the remote sensing metrics. In order to successfully conserve biodiversity in tropical agricultural landscapes, our findings show that it is essential to conserve intact forest within those landscapes and to understand the effect of local agricultural practices on species.

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1. Introduction

It has become apparent that the current biodiversity crisis will not be solved with protected areas alone, due to concerns of isolation, insufficient coverage, uncertain ecological performance, and likely vulnerability to large-scale human impacts like climate change (Rosenzweig, 2003; Gaston et al., 2008; Lee and Jetz, 2008). Consequently, much conservation attention has focused on lands outside of protected areas that form the vast majority of almost all landscapes, with recent findings strongly suggesting that species persistence depends largely on the quality of these unprotected lands (e.g. Debinski and Holt, 2000; Prugh et al., 2008). Human pressures are rapidly intensifying on the native ecosystems that comprise these unprotected lands (Wackernagel et al.,

2002), with agricultural expansion and intensification driving much of the ecosystem conversion and degradation (Jha et al., 2000; Barve et al., 2005; Foley et al., 2005; Kareiva et al., 2007). Because agriculture so commonly displaces native ecosystems (Tilman et al., 2001), understanding the conditions under which agricultural landscapes can sustain native species is one of the most essential questions in conservation today (Sutherland et al., 2009).

A frequent hallmark of agricultural landscapes is extremely complex mixtures of land covers (e.g. Estrada et al., 1994; Fischer et al., 2009), especially within areas that experience relatively low agricultural intensity (Vandermeer et al., 1998; Fischer et al., 2008). The standard landscape metrics and the standard methods of structuring landscape used in conservation sometimes do not capture the full complexity of agricultural landscapes (Franklin and Lindenmayer, 2009). The effect of this landscape complexity on species communities remains poorly understood (Turner, 2005). In fact, the unknowns surrounding the interactions between

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species and landscape complexity form some of the largest barriers to effective species conservation in agricultural regions (Lindenmayer et al., 2008; Prugh et al., 2008).

We address the role of landscape context within the Western Ghats a biodiversity hotspot located in the vicinity of much of the west coast of India (Fig. 1; Myers et al., 2000). The need for new conservation solutions within the Western Ghats is pressing, with the region experiencing some of the highest population densities and highest pressures on native ecosystems of any hotspot (Shi et al., 2005; Haberl et al., 2007). Here, we reanalyze the data from two recent investigations within Western Ghats' agricultural landscapes (Anand et al., 2008; Ranganathan et al., 2008) to address two questions essential for effective conservation within tropical agricultural landscapes.

First, how does landscape composition affect species persistence within complex agricultural landscapes? It is well established, across multiple taxa, that the preservation of significant patches of native vegetation is essential for native species persistence within tropical agricultural landscapes (Daily et al., 2001; Ricketts et al., 2001; Fischer et al., 2009). However, the effect on species persistence of the *placement* of these native vegetation patches within complex agricultural landscapes remains an important topic of conservation research (Chazdon et al., 2008). To determine the importance of fine-scale differences in the placement of native patches on species composition within the larger agricultural landscape, we assessed the influence of distance to remnant vegetation patches on bird species composition within nearby agricultural habitats.

Second, how accurately can we estimate bird species richness with simple remote sensing-derived measures within these agricultural landscapes? Assessing species and vegetation patterns within complex agricultural landscapes often requires considerable time, expertise, and expense (Danielsen et al., 2005). Remote

sensing could potentially alleviate these concerns by allowing for inexpensive and quick measures of these landscapes. In a complex tropical agricultural landscape within Costa Rica, Ranganathan et al. (2007) found that two easily-calculated remote sensing measures (brightness and wetness) strongly correlated with landscape-level tree cover and therefore by association also closely tracked the species richness of forest-affiliated birds. These remote sensing measures are components of the tasseled cap transformation (also known as the Kauth–Thomas transformation), developed to estimate agricultural yields, and are strongly associated with soil and vegetation properties (Crist and Kauth, 1986; Phua and Saito, 2003; Cohen and Goward, 2004). We test the broad applicability of remotely-sensed brightness and wetness by investigating, in the two study areas within the Western Ghats range, whether they correlate with vegetative measures and various measures of bird species richness and composition.

2. Methods

2.1. Study areas

The two studies reanalyzed here were conducted within complex agricultural landscapes in the Western Ghats of Karnataka state, India (Fig. 1). Ranganathan et al. (2008) performed their study within the coastal foothills of the Western Ghats in Uttara Kannada district (14.43°N, 74.45°E; hereafter arecanut landscape: AL). The study area formed a rough rectangle, 20 km long north–south and 15 km wide west–east, with the north–south boundaries defined respectively by the Agnashini and Sharavati Rivers and the west–east boundaries defined respectively by the coast and the Western Ghats range. The study area had high conservation value, likely harboring almost all of the pre-cultivation bird species pool (Ranganathan et al., 2008). This study area contained a complex mixture of forest and agricultural land covers. There were two types of forest cover present. The first was relatively intact forest, officially designated as Reserved Forest by the state government, where extractive activities were generally prohibited (hereafter: intact forest). The second was heavily modified forest, designated as Minor Forest by the government, where non-timber forest products were permitted to be extracted (hereafter: production forest). While these forests were interspersed through the study area, they tended to be concentrated in the eastern half of it.

Among the five agricultural land covers present in the study area, arecanut (also known as betelnut) palm plantations were the most structurally complex, generally consisting of a heterogeneous mixture of arecanut, coconut, banana, pepper, and other crops, grown with a traditional multi-cropping method. Cashew plantations consisted largely of monocultures of relatively short (3–4 m tall) cashew trees. Extensive regions of the study area were covered by sparsely vegetated shrublands, characterized by very thin soils, annual grass, and scattered trees and shrubs. Large extents of rice and peanut cultivation were also present in the study area.

Within this study area, birds and vegetation were surveyed within all land covers except rice and peanut, which were largely devoid of birds during the sampling season. Six fixed 200 m transects (hereafter "sites") were established within each land cover (a total of 30 sites), with each site at least 1 km away from all others. Each site was surveyed for birds seven times from March to June 2004. A survey consisted of a slow 30-min walk down the 200 m line, between the hours of 06:00 and 09:00, noting all birds within 50 m of the line. Birds that were deemed to be just flying over the line were ignored. At total of 114 bird species were detected during the study.
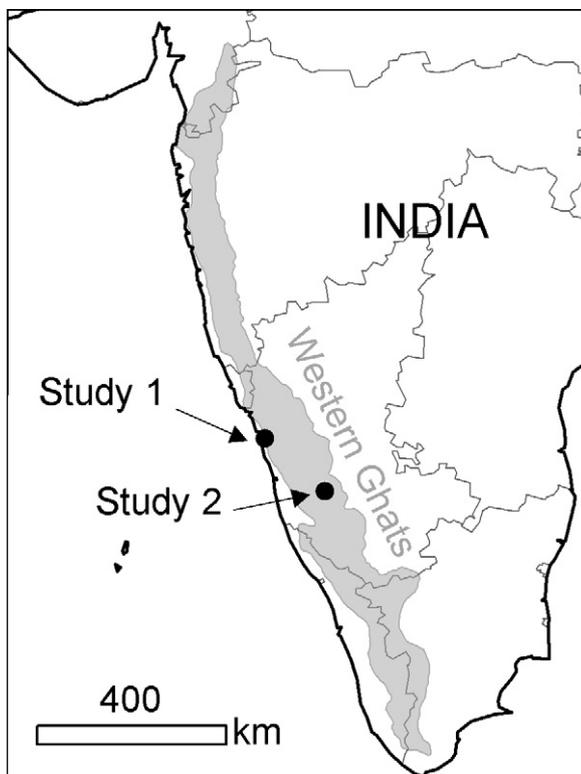
Fig. 1. Location of study landscapes within the Western Ghats mountain range of the state of Karnataka, India: study 1: arecanut landscape [AL] (Ranganathan et al. (2008), study 2: coffee landscape [CL] Anand et al. (2008).

Vegetation measures were also recorded at each site. A densiometer was used to record canopy cover at 20 m intervals down the line at each site (11 densiometer readings), which were then averaged by site. Along each site, two randomly placed 20 m by 20 m quadrats were positioned. Within a quadrat, the height, girth, and species identification of all trees with diameter breast height >10 cm were recorded. Height was estimated into four categories: 0–5 m, 5–10 m, 10–20 m, 20–30 m. Within each quadrat, a sub quadrat was taken (10 m by 10 m) where shrubs were measured. The height and species identification of each shrub was noted. Vegetation measurements for all quadrats and subquadrats were averaged by site.

Anand et al. (2008) conducted their study in Chikmagalur district of Karnataka state (13.32°N, 75.77°E) in the central Western Ghats (hereafter coffee landscape: CL). The study area formed a rough rectangle, approximately 30 km long north–south and 20 km wide east–west. Coffee plantations spanned 870 km^2 in the district covering over 10% of its land area and producing close to 25% of all the coffee grown in the Western Ghats (Coffee Board of India, 2005). Individual coffee plantations were typically small (over 90% of the holdings are smaller than 0.1 km^2) although there were a few large corporate holdings spanning up to 5 km^2 (Coffee Board of India, 2005). Coffee in the region was entirely grown under a shade canopy.

Apart from coffee plantations, the landscape featured tropical moist deciduous forest, montane evergreen forest, grasslands, paddy and mustard fields, lakes and reservoirs. The study area was bounded on the west by the Bhadra Tiger Reserve, a 493 km^2 protected area, and on the east by the foothills of the Bababhudan Hills, an eastern offshoot of the Western Ghats. The study area was of significant importance to bird conservation (being flanked by two important Bird Areas: the Bhadra Tiger Reserve and the Kemmangundi and Bababudan Hills) and was known to harbor 25 species that were endemic to moist forests of peninsular India, including 13 out of 16 known Western Ghats endemics (Islam and Rahmani, 2004).

Within this landscape, birds were surveyed in 11 sites, positioned in the coffee plantations with each site separated from the others by at least 2 km. The sites were arrayed to maximize variation in two parameters: distance to contiguous forest and proportion of non-native trees in the canopy of coffee plantations. Birds were surveyed from December 2005 to May 2006: twice at each site during the winter season (December–February) and twice at each site during the summer season (March–May). Sampling was conducted using variable circular plots (Williams et al., 2002). Nine to twelve 5-min point counts were conducted per site between 0630 and 0915 h on two successive mornings each season. Points were located at random at least 150 m apart, along small trails and gaps/partitions between coffee bushes. In cases where points fell on wide paths or roads, sampling was carried out 20–30 m off the road within the plantation. All species seen and heard within a 70 m radius of the point were recorded. Birds flying under the canopy or within 10 m of the canopy were also recorded. Data on swifts and swallows were not collected during sampling. Although these methods were not suited for sampling raptors and nocturnal species, Oriental honey buzzard (*Pernis ptilorhyncus*), Crested serpent eagle (*Spilornis cheela*), three species of Accipiter, and Eurasian eagle owl (*Bubo bubo*) were often recorded during point counts. A total of 102 bird species were recorded during sampling.

Vegetation composition and structure were sampled at each bird point count station using circular plots at two scales. At a finer scale (10 m radius) all trees over 30 cm circumference breast height were identified to genus, and whenever possible to species. Within these plots, five canopy height and canopy cover estimates (one at the centre and at four points along the periphery of the plot) were made using a laser range finder and canopy densiometer.

ter respectively. Along with canopy cover, measures of habitat complexity were made by recording the presence or absence of foliage within a 0.5 m radius imaginary cylinder above the observer, in the height classes (in meters): 0–1, 1–2, 2–3, 3–4, 4–5, 5–6, 6–7, 7–8, 8–16, 16–32, >32. The average number of height classes per plot that contained leafy vegetation was used as a measure of vertical stratification. The number of trees below 10 m in height was recorded as a measure of the structure of the mid-storey of the canopy. A larger-scale measure of species composition was obtained in plots of 30 m radius centred at the point count station. The proportion of silver oak trees (*Grevillea robusta*; non-native trees widely used as shade cover in the region) was estimated by counting the number of silver oak trees over 10 m in height within a 30 m radius plot, and dividing by the total number of trees over 10 m height in the plot. For the present study, vegetation measurements for all circular plots were averaged by site.

2.2. Statistical methods

2.2.1. Space

As a first step in investigating the role of landscape context in determining species composition, we examined the role that geographic space alone played for patterns of species overlap across sites. We examined each of the two studies separately (AL: 30 sites, CL: 11 sites). For all pairs of sites we calculated the distance and the Jaccard overlap in bird species composition, for both total species and that subset of species primarily affiliated with forested habitats (with forest species determined by using: Daniels, 1997; Grimmett et al., 1999; Kazmierczak and van Perlo, 2000; Islam and Rahmani, 2004). These measures were then correlated using Spearman's rank correlation. It should be noted, for both studies, that total species richness and forest species richness were correlated (weakest correlation: Spearman's rho 0.7910, $p < 0.00001$).

As the data from every site was used multiple times, these pairwise measures were not independent and therefore the p-value associated with these correlations was inaccurate. We calculated the true probability of receiving our correlation results by chance with a randomization approach. We conducted 10,000 trials, where we randomized the association between pairwise distance and Jaccard overlap, and then counted the number of trials where the p-value of the Spearman rank correlations was lower than or equal to the p-value of the correlations with non-randomized data. For each trial, we randomly shuffled the number associated with each site and calculated pairwise distances, which were then correlated against the non-shuffled Jaccard overlap data. To preserve the relationship between total and forest-affiliated species, the correlation of distance with both measures was calculated within a single trial.

2.2.2. Land cover and space

We investigated the role that land cover, particularly forest cover, plays in determining bird species composition across the landscapes. In each landscape, we calculated the ecological distance between the communities found in intact forest sites and in other sites. For CL, we calculated the Bray–Curtis species composition distance between each coffee site and the average composition of forest sites. We modeled these composition coefficients with respect to the minimum distance to forest cover.

For AL, Bray–Curtis species composition distances were calculated to compare compositional differences between intact forest sites and other sites. For each site not in intact forest, a compositional distance was calculated to the average composition of all intact forest sites. This compositional distance could not be compared to distance to forest cover, as was the case for CL, due to a lack of a current and accurate vegetation map for AL. As an alter-

native, we used four measures to approximate distance to forest cover for AL non-intact forest sites: (1) distance to the nearest intact forest site, (2) average distance to all intact forest sites within the study landscape, (3) distance to the nearest production forest site (necessarily, only arecanut, cashew, and shrubland sites considered), and (4) average distance to all production forest sites within the study landscape (using same sites as with 3). We used two measures of forest cover (distance to intact forest and distance to production forest) in order to investigate the role that forest in differing conditions plays in maintaining intact forest communities. Using linear regression, we contrasted these four forest distance measures against the species composition distances for AL.

2.2.3. Remote sensing and space

For each of the study areas, we used the Landsat Enhanced Thematic Mapper Plus image that was acquired closest in time to bird sampling and that was also cloud free (CL: path 145, row 51, acquisition January 19, 2006; AL: path 146, row 50, acquisition December 4, 2003). For these images we calculated two components of the tasseled cap transformation, brightness and wetness (Huang et al., 2002). These two tasseled cap metrics were found to be ecologically significant by Ranganathan et al. (2007), as they correlated with percent tree cover, a parameter closely associated with the number of forest-affiliated bird species within agricultural habitats. Additionally, we also used the same Landsat data to calculate, as a comparison, the more commonly used remote sensing metric Normalized Difference Vegetation Index (NDVI; Pettorelli et al., 2005). For a given sampling circle around each site, successively defined by a 100 m and 500 m radius about the site, we calculated the mean value for brightness, wetness, and NDVI. As all sites across studies were at least one kilometer away from each other, none of the circles overlapped. Using Spearman rank correlations, we calculated the correlation between these metrics and forest bird species richness.

We further investigated the role of geographic and remote sensing distance between sites in explaining spatial patterns of compositional dissimilarity between sites by another approach. In each study, three measures were calculated for all pairs of sites: Bray–Curtis distance in overall bird species composition, geographic distance, and remote sensing distance. For both AL and CL, the remotely sensed distance between sites was based on the mean values and their standard deviations for brightness, wetness, and NDVI using sampling circles defined by a 100 m and 500 m radius about the site. Thus the remotely sensed distance between sites using this approach takes into account our knowledge of site heterogeneity within the two landscapes in addition to the mean response. We calculated a Mantel's correlogram for geographic distance against overall compositional distance and another for remote sensing Euclidean distance against overall compositional distance.

Ranganathan et al. (2007) found, in a complex Costa Rican tropical agricultural landscape, a strong correlation between vegetative structure and remote sensing measures (brightness and wetness). We examined whether this correlation held true for our two study areas in the Western Ghats range, using the following approach. For both AL and CL, we calculated the mean value and standard deviation for brightness, wetness, and NDVI for each site, using sampling circles 100 m in radius that were centred on each site. We used these remote sensing measures to generate a pair-wise dissimilarity matrix across all pairs of sites at both AL and CL. Similarly, for both study areas, we used the measured vegetation variables to construct a pair-wise dissimilarity matrix across all pairs of sites. We compared these two dissimilarity matrices using a Mantel's test, a technique commonly used to assess the correlation of matrices composed of non-independent pair-wise distances.

3. Results

3.1. Space

For AL, bird compositional similarity across sites decreased with increasing distance, indicating species turnover across the study area. When all species were considered, pairwise Jaccard overlap across sites negatively correlated with pairwise distance (Spearman's rho: −0.2079, randomization-based p: 0.0158). However, with just the subset of forest-affiliated species, there was no correlation between overlap and distance (randomization-based p: 0.8730). For CL, there was no strong correlation between species overlap and distance across sites, with either species category (all species: randomization-based $p = 0.5337$; forest-affiliated species: randomization-based $p = 0.1088$).

However, the use of an alternate statistical technique, Mantel's correlograms, showed a somewhat weaker relationship between geographic space and species turnover in AL than CL. For AL, there was a weak relationship between geographic distance between sites and bird species compositional distance (Fig. 2a; overall Mantel's correlation: 0.159, $p = 0.077$). In contrast, CL showed a stronger relationship between the two (Fig. 2c; overall Mantel's correlation: 0.413, $p = 0.018$). The Mantel's correlograms however indicate that the effect of spatial proximity is restricted to about 2 km or less for both landscapes and there is no evidence for a spatial decay effect (Fig 2).

3.2. Land cover

In AL, site difference from intact forest species composition was significantly influenced by the average distance to intact forest sites ($r^2 = 0.224$, $p = 0.019$), while the distance to the nearest intact forest site was slightly weaker ($r^2 = 0.161$, $p = 0.052$). In contrast, neither the nearest distance nor average distance to production forest was an important factor on compositional difference from intact forest ($p > 0.200$). For CL, proximity to nearest forest was an important factor in determining site difference from average forest composition ($r^2 = 0.587$, $p = 0.006$).

3.3. Remote sensing surrogates

In AL, brightness, wetness, and NDVI were strongly correlated with each other, using both sampling circles of 100 m and 500 m. Brightness and wetness were negatively correlated, as were brightness and NDVI (weakest correlation across metrics and sampling circles: −0.5730, $p = 0.001$). NDVI and wetness were positively correlated (weakest correlation: 0.8580, $p < 0.0001$). In contrast, with CL no correlation was found between NDVI and the other metrics (strongest correlation across metrics and sampling circles: $p = 0.073$). Brightness and wetness were correlated here with both sampling circles (weakest correlation: −0.8454, $p = 0.002$).

In AL, the three remote sensing metrics varied across land covers where birds were sampled, in a manner similar to that found by Ranganathan et al. (2007). Sites located in the three land covers with the greatest tree cover (intact forest, production forest, and arecanut) had significantly different remote sensing means than sites located in the two land covers with the lowest tree cover (cashew and shrubland), with the former set of sites having generally lower brightness values, higher wetness values, and higher NDVI values (Fig. 3; Tukey's honest significant difference (HSD) test, $p = 0.05$). Ranganathan et al. (2007) found that, as the number of forest-affiliated species increased, wetness increased while brightness decreased and NDVI displayed no significant correlation at all. With AL, we found the same pattern between forest species richness and brightness and wetness, using both buffer radii; in
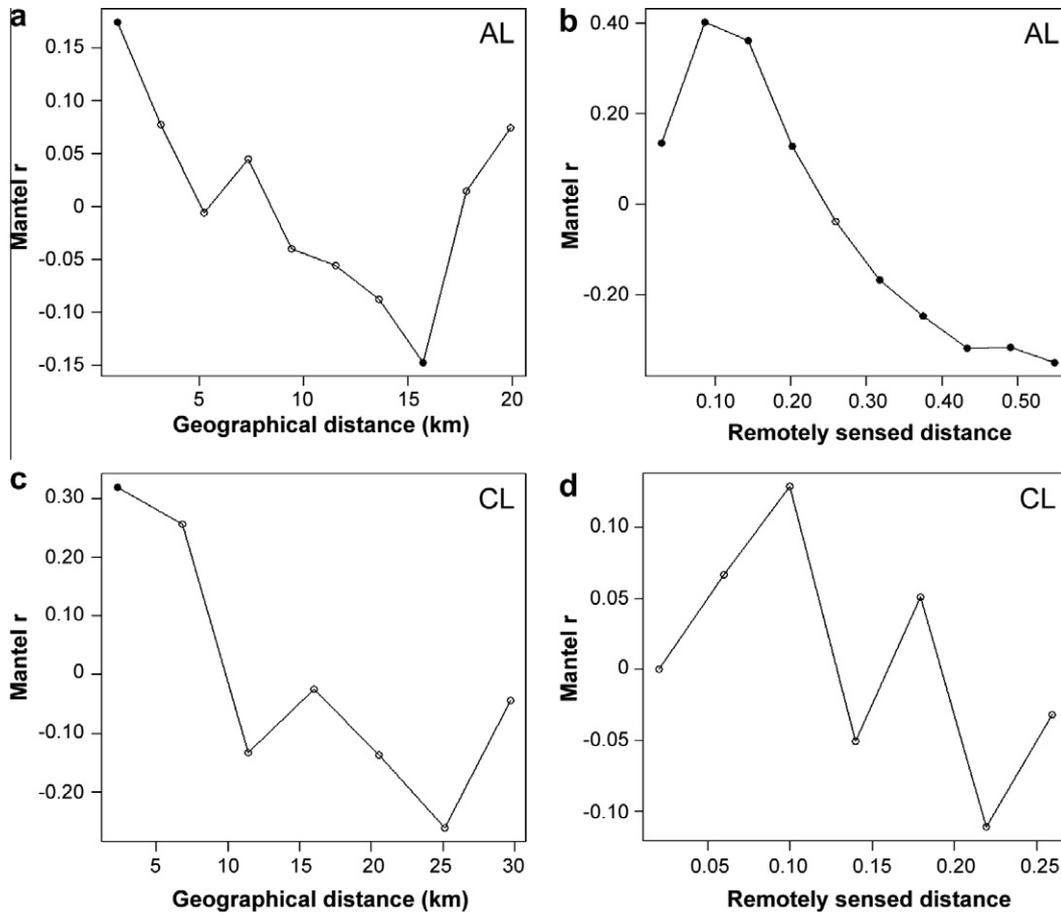
Fig. 2. Mantel correlograms for: (a) species overlap in AL and geographical distance, (b) species overlap in AL and remote sensed distance, (c) species overlap in CL and geographical distance, and (d) species overlap in CL and remote sensed distance. Filled circles indicate significance at $p = 0.05$.
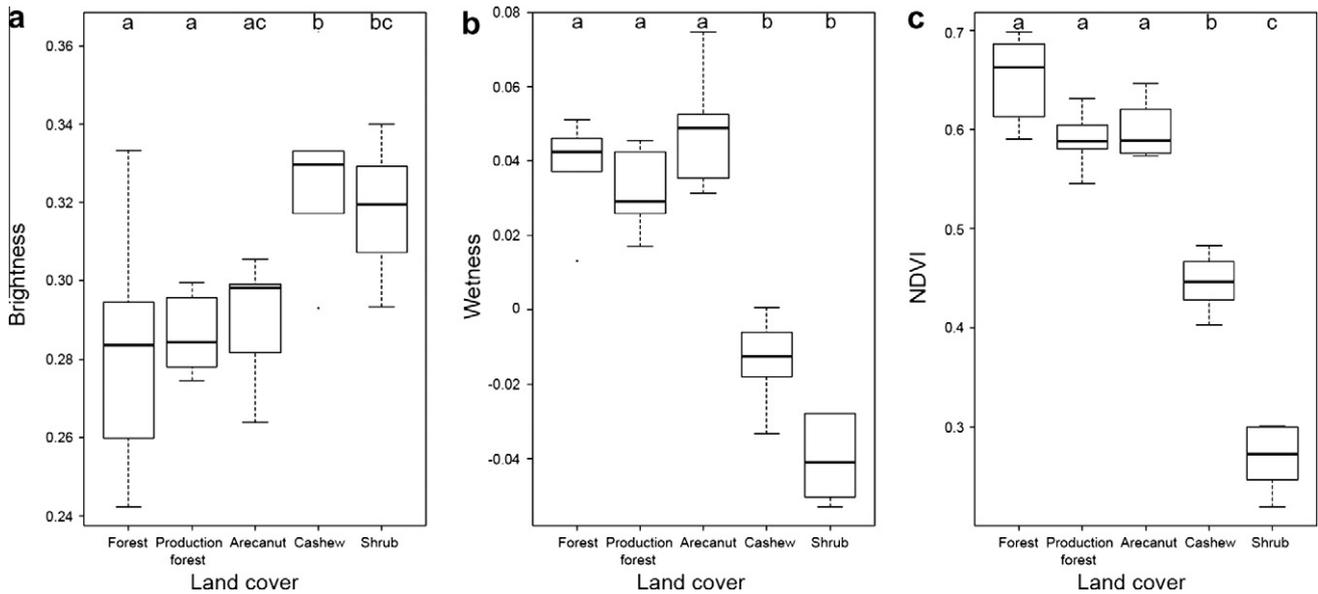
Fig. 3. Remotely sensed metrics as a function of land-cover type in AL, for: (a) brightness, (b) wetness, and (c) NDVI. The results with a 100 m buffer are shown here, with 500 m buffer results very similar. Bars with the same lowercase letter above them are not significantly different from each other, as determined by a Tukey's honest significant difference test ($p = 0.05$).

contrast to the previous findings, we found a significant positive correlation between forest species richness and NDVI (Table 1).

In contrast, for CL, there was no significant difference among coffee plantation types across all remote sensing types (Fig. 4;

Table 1
Correlation between remote sensing metrics and forest species richness in AL.

Remote sensing metric	Radius of sampling area (m)	Spearman's rho	*p*
Brightness	100	−0.473	8.3×10^{-3}
Brightness	500	−0.652	9.6×10^{-5}
Wetness	100	0.743	2.6×10^{-6}
Wetness	500	0.733	4.1×10^{-6}
NDVI	100	0.873	3.1×10^{-10}
NDVI	500	0.857	1.5×10^{-9}

HSD test, $p = 0.05$). Further, in this location there was no significant correlation between any of the remote sensing metrics and forest species richness (strongest correlation: $p = 0.1456$).

The Mantel's tests and correlograms provided an alternate nonparametric method of investigating the response of species composition to remote sensing distances (defined differently compared to the Spearman's analyses as the metrics included site heterogeneity), with broadly similar results found. In AL, remote sensing distance had a strong relationship with species compositional distance (Fig. 2b; overall Mantel's $r = 0.841$, $p = 0.001$). In contrast, with CL, there was no relationship (Fig. 2d; overall Mantel's $r = 0.131$, $p = 0.516$).

In a similar result, for AL there was a strong correlation between the vegetation measures and the remote sensing measures (Mantel's $r = 0.384$, $p = 0.003$), while there was no fit between the two for CL (Mantel's $r = 0.015$, $p = 0.237$).

4. Discussion

Studies on biodiversity in human-dominated landscapes in general, and those in the Western Ghats in particular have focused on comparing specific land use types with each other (e.g. Kumara et al., 2004; Ambinakudige and Sathish, 2009), and have rarely looked at broader scale patterns emerging from interactions between the various elements of these complex landscapes. A substantial body of literature today, however, indicates the important role played by landscape-scale patterns in determining biodiversity patterns across these landscapes (Lindenmayer and Fischer, 2006). It is also clear that strategies for effective conservation can vary greatly depending on the local characteristics of these landscapes (Fischer et al., 2008).

Although well-managed tropical agricultural systems can sustain communities that are of very high value for biodiversity conservation (Daily et al., 2001; Harvey et al., 2005; Mayfield and Daily, 2005), our comparison between two agricultural landscapes in the Western Ghats range makes very clear that local conditions govern how that value can be achieved. Ranganathan et al. (2008) found that conservation value was broadly distributed in AL, with 96% of the total species pool and 90% of the forest-affiliated species pool found outside of intact forest. Tree-dominated land covers were of especially high conservation value; in particular, arecanut plantations contained a statistically-identical set of bird species as that contained within production forest, harboring such flagships of Asian conservation as the Great Hornbill (*Buceros bicornis*) and the Malabar Gray Hornbill (*Ocyceros griseus*). In a similar finding, Anand et al. (2008) determined that the coffee plantations in CL contained species of high conservation value, particularly several range-restricted species. However, within this predominantly tree-covered system, Anand et al. (2008) detected a strong pattern of decline in encounter rates of species of conservation value at increasing distances from the intact forest, with only secondary effects caused by variation in land cover (composition and diversity of the shade canopy layer). In contrast, more open types of agriculture in AL supported relatively depauperate bird assemblages, resulting in major differences among land covers in bird species richness and community composition (Ranganathan et al., 2008).

Some of these differences in local agricultural conditions between the two study areas, which drove the different response between the two areas in the response of bird communities to agriculture, were reflected in our remote sensing analysis. In the arecanut landscape, vegetation measures correlated with our simple remote sensing measures (brightness and wetness). This is consistent with the finding of Ranganathan et al. (2007) that brightness and wetness correlated with landscape-level tree cover in a complex Costa Rican agricultural landscape. In contrast, there was no fit between the vegetation measures and the remote
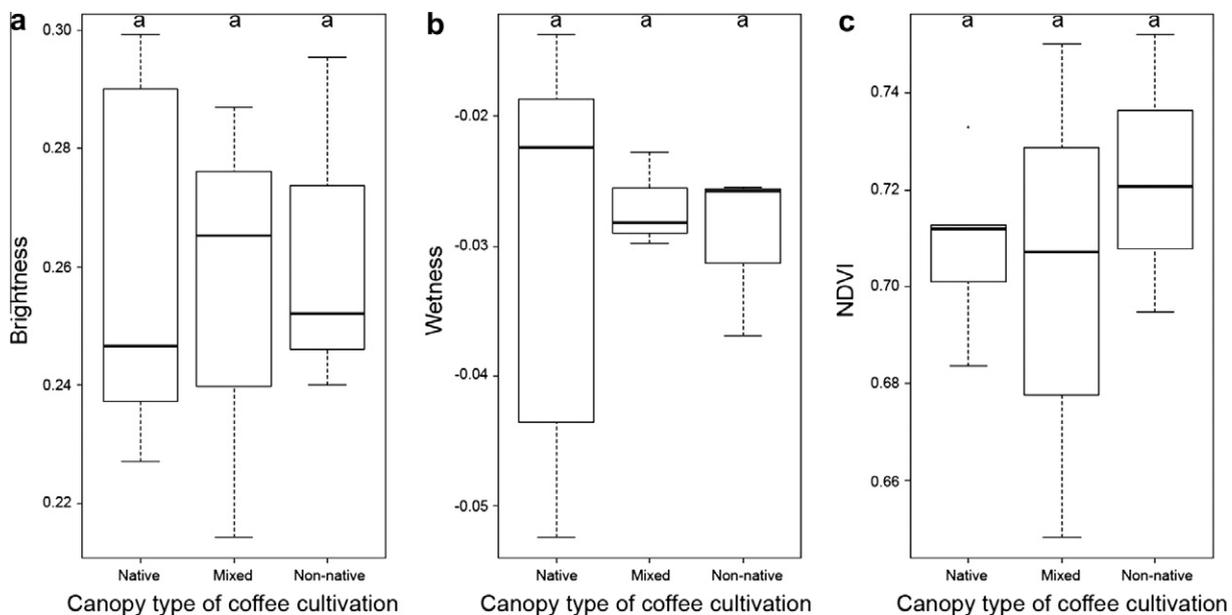
Fig. 4. Remotely sensed metrics as a function of land-cover type in CL, for: (a) brightness, (b) wetness, and (c) NDVI. The results with a 100 m buffer are shown here, with 500 m buffer results very similar. Bars with the same lowercase letter above them are not significantly different from each other, as determined by a Tukey's honest significant difference test ($p = 0.05$).

sensing measures in the coffee landscape, which was driven by a lack of variation in the vegetative structure within the area. The coffee plantations in CL contained two structural vegetation layers (a taller shade tree layer and a shorter coffee layer), both of which were specifically managed to be within a very narrow range of density and height (Coffee Board of India, 2001). The much better fit between the vegetation measures and the remote sensing in AL was driven by the much larger range of vegetative structure present in the area (from essentially bare ground to intact forest).

The relationship between forest-affiliated species richness and the remote sensing measures followed a similar pattern as we found with vegetation measures. In AL brightness and wetness correlated with forest-affiliated species richness. In this same landscape, Ranganathan et al. (2008) found that forest-affiliated species richness increased with vegetative complexity. Here, we found that the three land covers with the greatest vegetative complexity (intact forest, production forest, and arecanut) also had brightness and wetness values distinct from the other two land covers (cashew and shrub). As both species richness and the two remote sensing measures tracked vegetative complexity, they were consequently correlated.

In CL, there was no fit between forest-affiliated bird species richness and the remote sensing measures. This lack of fit was not just a result of the homogeneity of vegetative structure in the area, but also because of another factor that could not be detected by our remote sensing methods: variation in the species composition of the shade layer in the coffee layer. Many of the study sites in CL contained a high proportion of silver oak trees in the shade layer, a factor that can reduce conservation value for forest bird species in coffee plantations (Raman, 2006). As the remote sensing measures could track changes in vegetative structure, but not differences in composition among plant species that share a similar structure, this variation in silver oak across coffee plantations was invisible to our remote sensing methods.

One of the major points made by Ranganathan et al. (2007) was that the simple remote sensing metric most commonly used in conservation, NDVI, had no value for predicting community composition within complex tropical agriculture, while brightness and wetness did. However, here, we found that NDVI, brightness, and wetness all correlated with forest species richness only in AL. The discrepancy between these two findings is likely due to differences in climate between the study area in Costa Rica where Ranganathan et al. (2007) worked and the Western Ghats. NDVI is a measure of vegetation productivity, which in turn is often driven by rainfall (Pettorelli et al., 2005). Although both regions experience high rainfall, the studied areas of the Western Ghats experience a much more pronounced dry season than the studied area of Costa Rica (Rao, 1981; Janzen, 1983). Landsat imagery for the study regions in the Western Ghats was only available for the dry season, a time when vegetative growth would be largely confined to forested areas, in the absence of irrigation. As a consequence, within the study area of the Western Ghats, brightness, wetness, and NDVI were all likely tracking the same parameter, vegetative structure. The difference in the response of remote sensing metrics to bird species richness between the Costa Rican and Indian study areas likely is a reflection of ecological differences between the regions. However, recent improvements in the temporal, spatial, and spectral resolution of remote sensing data (and in the statistics used to analyze that data) may yet still produce more generalizable remote sensing-based surrogates for biodiversity (Krishnaswamy et al., 2009).

Although the different agricultural practices in the two study areas led the bird communities in each landscape to respond very differently to agriculture, there still was an essential commonality between the two study areas: the importance of intact forest for maintaining intact forest bird communities. In both the coffee and arecanut landscapes, agricultural sites closer to intact forest had communities with significantly greater similarity to intact forest communities. In contrast, production forests, which received much more human use than intact forests and were only found in the arecanut landscape, did not play a large role in maintaining intact forest bird communities. The distance from a study site to production forest had no impact on the similarity of the community found at that site to an intact forest community. Our findings are in line with others from the Western Ghats and around the world showing the irreplaceability of intact native tropical ecosystems for preserving native communities (Daniels et al., 1991; Barlow et al., 2007; Parry et al., 2007; Radford and Bennett, 2007; Gardner et al., 2009; Anand et al., 2010).

The comparison between our two study landscapes yields several clear management implications. The bird communities associated with intact forest are some of the communities most in need of conservation assistance (Laurence and Bierregaard, 1998). There is no substitute for preserving good-condition forest in order to maintain these kinds of communities within nearby agricultural landscapes, a finding common to both of our study areas. This similar response is encouraging for conservation planning, given the high degree of uncertainty regarding the response of species in agricultural areas to their environments (Chazdon et al., 2008; Harvey et al., 2008; Prugh et al., 2008; Tscharntke et al., 2008). Second, even with this commonality, our research indicates that the success of conservation efforts in tropical agricultural landscapes is strongly dependent on understanding local conditions. The response of a similar species pool to agriculture differed dramatically between our two study areas, because the local agricultural practices differed dramatically between the two areas. It is essential to understand the response of species to local agricultural practices, as even small differences in these practices can have a large impact in the ability of threatened species to persist, even for types of agriculture that are generally considered to be biodiversity friendly (Donald, 2004; Bisseleua et al., 2009). Third, the remote sensing measures of brightness and wetness that we tested in this analysis could well be useful in other locations, depending on whether those locations contain high variation in vegetative structure and whether that variation is meaningful for species persistence. These limitations on the use of remote sensing measures are not unique to brightness and wetness, with the much more widely used measure of NDVI also suffering from constraints on use, particularly in the tropics where the index is known to saturate (Boyd et al., 1996; Steininger, 1996; Kerr and Ostrovsky, 2003). Protected areas will continue to be critical for biodiversity conservation. However, the adoption of biodiversity-friendly agricultural practices and the maintenance of remnant forest in agroecosystems (through a framework of incentives and payments for ecosystem services) will be essential to sustain biodiversity in the mixed landscapes of the Western Ghats.

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