Generalizability of neotropical bird abundance and richness models

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Abstract

Predicting the consequences of land-cover change on tropical biotas is a pressing task. However, testing the applicability of models developed with data from one region to another region has rarely been done. Bird faunas were sampled along 3.0-km routes in southern Costa Rica (Coto Brus) to develop statistical models to describe the abundance and richness of groups as a function of land-cover characteristics. The relative value of the land-cover models was assessed by comparing them with null models. The generalizability of the models was tested with data from north-western Costa Rica (Monteverde) to determine whether the models were applicable to another area that has undergone significant land-cover change in the last 60 years. The richness and abundance of understory, open-country and edge non-insectivore groups showed clear relationships with land-cover variables, and the land-cover models had lower prediction errors than the null models for Coto Brus. With one exception, useful models for canopy birds, edge insectivores and hummingbirds could not be developed. The land-cover models of abundance of canopy insectivores, understory insectivores and non-insectivores, and edge non-insectivores were generalizable to Monteverde whereas the land-cover models of abundance of open-country birds and species richness for any of the groups were not better than null models for Monteverde. The results indicate that land-cover models that describe the abundance or richness of various bird groups provide useful predictions in the area where the data were collected and that models of abundance of some canopy, understory and edge birds may perform well in areas that are similar in elevation, life zones and land use to the area from which data were collected. Land-cover models of the abundance of other groups, and of the richness of the majority of groups, may be less generalizable to other areas, or it may be difficult to develop models at all.

Introduction

It is difficult to overstate the importance of developing predictive ecological models (Peters, 1991; Côté & Reynolds, 2002; Kolar & Lodge, 2002). If models developed for one area, taxonomic group or ecosystem are generalizable to other areas, groups or ecosystems, the need for data collection may be reduced, saving resources that could be better expended in other ways. Recent work indicates that species vary in the extent to which statistical models based on environmental variables successfully predict species occurrences (Fleishman, Mac Nally & Fay, 2003). Determining the types of species that lend themselves to accurate and generalizable modeling of their abundance and richness helps us to use our resources most efficiently. If, for example, models of the abundance of a particular group are easily transferable between areas, conservation strategies can be developed. If this is not the case, area-specific studies of the habitat requirements of the group may be necessary.

Land-cover change in many tropical regions is occurring quickly (DeFries et al., 2002), resulting primarily from conversion of forest to pasture and crops (Achard et al., 2002). Given the high species richness and the dearth of resources available for conservation in many developing tropical countries (Balmford et al., 2003), these areas may particularly benefit from information regarding the types of species that lend themselves to the development of generalizable models that describe abundance and richness as functions of land-cover characteristics. Testing whether such models are applicable to areas separate from where data were collected has not yet been undertaken in tropical systems.

Studies in temperate areas have documented the influence of land-cover characteristics on bird abundances at the species or guild level (Pearson, 1993; McGarigal &
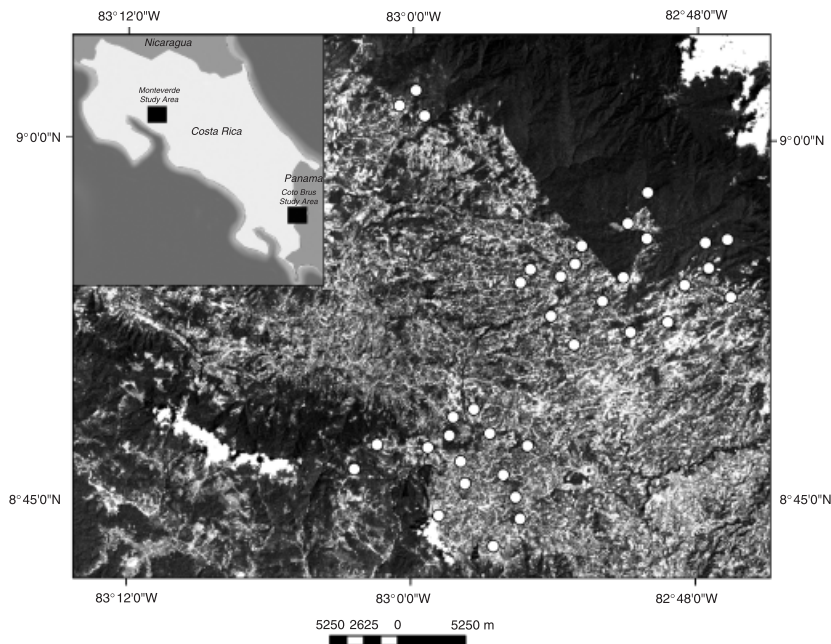
Figure 1 Approximate midpoints of routes in our Coto Brus study area. The routes are shown over a Landsat image. The darkest areas are old second growth/mature forest, for example in the upper right corner of the image, where the Talamanca Mountains and Las Tablas Protected Zone are located, and in the lower left of the image, where the Coastal Range is located. Shades of gray in the central part of the image are pasture, agriculture, residential areas and roads.

McComb, 1995; Schmiegelow, Machtans & Hannon, 1997; Estades & Temple, 1999; Villard, Trzcinski & Merriam, 1999; Lichstein, Simons & Franzreb, 2002). Land-cover characteristics also influence the richness and composition of temperate bird assemblages (Pearson, 1993; Drapeau *et al*., 2000). Studies in tropical systems are more limited, but indicate that land-cover characteristics affect the abundance of some species (Graham & Blake, 2001), the richness of some guilds (Pearman, 2002), and the composition of species assemblages in forest remnants (Stouffer & Bierregaard, 1995*a*; Renjifo, 2001) and at fruiting trees (Luck & Daily, 2003).

Our objectives in this study were (1) to develop statistical models to describe the abundance and richness of avian groups as a function of land-cover characteristics, using data from sampling routes in southern Costa Rica (Coto Brus), and (2) to compare the accuracy of the predictions of the land-cover models with predictions from null models generated for Coto Brus and another area in north-western Costa Rica, Monteverde. We classified species into groups according to their primary habitat (forest understory, forest canopy, forest edge or open) and whether they were insectivores or not. We considered hummingbirds as a distinct group. The resulting groups, with the exception of hummingbirds, should be found in all areas of the humid tropics. We used land-cover categories that are applicable to many areas of the humid tropics, particularly coffee-growing regions (see Methods).

Expectations

Within each of the groups, except for hummingbirds, we considered insectivores and non-insectivores separately, with the expectation that insectivores would show stronger relationships to land-cover variables than non-insectivores because insectivores appear to be more susceptible to disturbances (e.g. Canaday, 1996) and because non-insectivores often travel widely in search of food (e.g. Blake & Loiselle, 1991). We predicted that forest cover would be positively associated with the abundance and richness of understory and canopy birds because these groups are particularly sensitive to forest conversion and loss (Kattan, Alvarez-López & Giraldo, 1994; Stouffer & Bierregaard, 1995*a*; Thiollay, 1995; Pearman, 2002; Lindell, Chomentowski & Zook, 2004). We also expected, based on our observations, that understory and canopy bird abundance and richness would be positively affected by the amount of tall woody agricultural vegetation around sampling routes [HIW variable (2–5 m woody cover), see above].

We expected the abundance and richness of forest edge birds to be positively associated with forest cover, forest edge per ha and the diversity of land covers around a route because edge-adapted species often use resources from more than one land-cover type (Ries *et al*., 2004). Previous work has shown that many tropical open-country species are specialists on particular habitat types (Estrada, Coates-Estrada & Meritt, 1997; Garcia, Finch & Chavez-Leon, 1998), leading to the prediction that more open landscapes with a greater diversity of land covers will have greater open-country species abundance and richness. We predicted that hummingbird abundance and richness would be greatest along routes with the highest diversity of land-cover types and the greatest amount of forest edge because (1) forest fragments surrounded by second growth had higher abundances of hummingbirds than intact forest in the Amazon (Stouffer & Bierregaard, 1995*b*), (2) hummingbird species richness increases in areas with greater amounts of edge (Thiollay, 1999) and (3) hummingbird species vary in the land-cover types they prefer (Stiles & Skutch, 1989).

Table 1 Average proportions of the major land-cover types surrounding routes in both study areas (see Methods)

Category	Coto Brus	Monteverde	Monteverde percentages as reported by Harvey & Haber (1999)
0–1 m non-woody (pasture)	0.28 (0.16)	0.50 (0.21)	0.60
1–2 m woody (coffee/sugarcane/ young second growth)	0.41 (0.14)	0.04 (0.03)	
2–5 m woody (coffee/sugarcane/ second growth)	0.06 (0.04)	0.12 (0.04)	0.15
Forest	0.22 (0.28)	0.29 (0.20)	0.25

Values are mean (SD).
The value in the third row under the Harvey & Haber column is for both the 1–2 m woody and 2–5 m woody categories combined.

We expected that the species richness of all groups would increase with increasing elevational range along a route (Stiles, 1983). The expectations stated in this paragraph and the preceding one are summarized in Table 2.

We expected that the land-cover models would produce more accurate predictions for all groups in both regions than the null models. We also expected that the land-cover models for understory birds developed from data in Coto Brus would more successfully predict abundances and richnesses of those same groups in Monteverde compared with models for other groups, based on the strong relationships we anticipated finding between forest cover and the abundance and richness of understory birds. We expected the abundance and richness of the other groups to be less closely tied to one land-cover variable because these groups track resources (Stiles & Skutch, 1989) and should be more flexible in the land covers they use. Finally, we expected that the land-cover models that were generated with data from Coto Brus would generally produce more accurate predictions for Coto Brus than for Monteverde.

Methods

Study areas

Our southern study area, in the province of Coto Brus (Fig. 1), at *c.* 8°50′N, 82°55′W, has undergone significant deforestation since the 1950s (Manger, 1992). The study area includes the Coto Brus valley, a patchwork of coffee, pasture, forest patches, roads and residential areas. The valley is flanked by Amistad National Park, which, together with Panama's Amistad National Park, contains the largest tract of forest in Central America (UNEP World Conservation Monitoring Centre website, 2001).

The second study area, Monteverde, *c.* 10°19′N, 84°49′W, in north-western Costa Rica, is on the Pacific slope of the Tilarán Mountains and elevations are similar to those in Coto Brus. The area comprises similar land-cover

Table 2 Response variables and the explanatory variables in potential models

Response variables	Explanatory variables in potential models
Canopy insectivore abundance	FOR HIW
Canopy insectivore richness	FOR ELEV HIW**r**ELEV
Canopy non-insectivore abundance	FOR HIW
Canopy non-insectivore richness	FOR ELEV HIW**r**ELEV
Understory insectivore abundance	FOR HIW
Understory insectivore richness	FOR ELEV HIW**r**ELEV
Understory non-insectivore abundance	FOR HIW
Understory non-insectivore richness	FOR ELEV HIW**r**ELEV
Edge insectivore abundance	FOR FEDG**r**FOR DIV**r**FOR
Edge insectivore richness	FOR ELEV FEDG**r**FOR DIV**r**FOR
Edge non-insectivore abundance	FOR FEGD**r**FOR DIV**r**FOR
Edge non-insectivore richness	FOR ELEV FEDG**r**FOR DIV**r**FOR
Open insectivore abundance	PAS DIV**r**PAS
Open insectivore richness	PAS ELEV DIV**r**PAS
Open non-insectivore abundance	PAS DIV**r**PAS
Open non-insectivore richness	PAS ELEV DIV**r**PAS
Hummingbird abundance	DIV FEDG
Hummingbird richness	DIV FEDG ELEV

Explanatory variables describe aspects of land-cover characteristics within 60-m buffers around bird sampling routes. The explanatory variables were used in all combinations during model selection. For example, for canopy insectivore abundance, models were (1) FOR, (2) HIW and (3) FOR and HIW. Hence, there were three models compared when there were two potential explanatory variables, seven models with three explanatory variables and 15 models with four explanatory variables. FOR, forest cover; HIW, 2–5 m woody cover; ELEV, elevation range; FEDG, forest edge per ha; DIV, diversity of land covers; PAS, 0–1 m non-woody cover; see descriptions in text. Explanatory variables described with a small bold **r** in the middle, for example HIW**r**ELEV, refer to the residuals of the first variable fit as a function of the second; see Methods.

types as Coto Brus, although in different proportions (Table 1). Intensive settlement of the area began in the 1940s (Burlingame, 2000). The area also includes a large expanse of forest, over 20 000 ha in extent (Powell & Bjork, 1995). The majority of the areas sampled in both Coto Brus and Monteverde fall into the premontane and lower montane wet forest life zones (*sensu* Holdridge, 1967; Hartshorn, 1983; Haber, 2000).

Bird sampling

We sampled the bird species along 37 3.0-km routes in Coto Brus (Fig. 1). The first point for one route in each of the areas where sampling occurred was located randomly, and the other routes were located systematically from this first route with the constraints that all points within a route fall between 900 and 1750 m, that routes be far enough apart to ensure non-overlap of buffers (see below) and that each route be accessible by dirt road or trail. Parts of the study area without sampling routes did not fit these criteria (Fig. 1). Thirty-seven was the maximum number of routes

that we could find in the study region that fit these constraints.

We sampled birds along eight routes in Monteverde chosen to represent a range of different proportions of land-cover types. The number of routes was constrained by funding and weather considerations. All routes fell within elevations from 1000 to 1660 m and met the same criteria as described above.

We located sampling points every 200 m along a route for a total of 15 points per route. For seven of the Coto Brus routes, points ended up being roughly 250 m apart. To keep all routes approximately the same length, we used data from only the first 12 points of these routes in the analyses. We used 50-m fixed-radius sampling plots for the point counts and they lasted 6 min. The counts for each route were conducted on one morning between sunrise and 1000 h standard time on clear days with little or no wind. All species seen or heard within 50 m were recorded. All counts were conducted by Jim Zook (J. Z.), who has numerous years' experience conducting point counts in Costa Rica. Sampling in Coto Brus took place between 24 November 2000 and 10 January 2001. Sampling in Monteverde took place between 16 November 2001 and 29 November 2001.

Assignment to groups

We assigned species to groups that included their primary habitat type and their diet. Primary habitat types included (1) forest understory, (2) forest canopy, (3) forest edge or (4) open country (cf. Stiles, 1985). We assigned species to these categories using the observations of Stiles (1983, 1985), Stiles & Skutch (1989) and Karr *et al.* (1990), and personal observations. In cases where species use two or more of these habitat types, we assigned species to one type based on their relative dependence on a particular habitat type given the alternatives. Diet categories included (1) insectivores or (2) non-insectivores which included frugivores, insectivore-frugivores and omnivores. We assigned species to diet types using the observations of Stiles & Skutch (1989), Karr *et al.* (1990) and Pearman (2002). The resulting groups are in Table 2. We did not include neotropical migrants in these analyses. The assignment of species to groups is available from the first author. For each group we developed explanatory models for both the number of individuals detected per point along a route, the abundance, and the number of species detected per point along a route, the richness. Sample sizes per route per group were small enough that it was not possible to use richness estimators (Boulinier *et al.*, 1998). Species and family assignments follow the American Ornithologists' Union (AOU) check-list and supplements (American Ornithologists' Union, 1998, 2000, 2002).

Land-cover variables

We conducted a land-cover classification for Coto Brus using Landsat Enhanced Thematic Mapper (ETM) + imagery acquired on 31 January 2001, path 14, row 54 and for the Monteverde area with a scene acquired on 15 June 2001,

path 15, row 53. Images were geo-referenced using corner points included with image metadata. Principal components analyses (PCAs) were performed on Landsat ETM + bands 1 through 5 and 7. We used the first three principal components, which explained 89.9, 6.8 and 2.1% of the variation in the data, to classify the ETM image. The PCA images were clustered into 45 categories using the ISODATA algorithm (Tou & Gonzalez, 1974; Erdas Imagine 8.6, 2002). The 45 clusters were reclassified into eight categories. This reclassification was accomplished by taking locations on the ground with a global positioning system unit, recording the land-cover types at the locations, and then comparing these ground truth data with the 45 categories. Categories that were similar land covers, for example various types of 1–2 m woody vegetation, were then reclassified into one category. Pixels were classified as forest, 0–1 m non-woody vegetation, 1–2 m woody vegetation, 2–5 m woody vegetation, water, bare soil, cloud shadow or cloud.

The extensive elevational relief in the study regions and the lack of digital elevation models prevented us from carrying out systematic accuracy analyses of the land-cover classifications. However, extensive work on the ground, and comparisons of the classifications with aerial photographs, demonstrated that the classifications accurately reflected the vegetation cover types.

We constructed 60-m buffers around the routes. We chose this buffer size because (1) it is a multiple of the 30-m spatial resolution of the Landsat ETM + imagery, (2) it is slightly larger than the 50-m radius within which birds were sampled and birds detected right at the 50-m boundary were likely influenced by the vegetation structure immediately beyond the boundary and (3) previous work shows that land-cover characteristics at this scale influence the abundance and/or richness of bird species (e.g. Pearson, 1993; Graham & Blake, 2001; Pearman, 2002).

We found the union of the buffered routes and the vectorized classification grid and calculated the proportions of the following land-cover classes within the buffers for each route: FOR (forest cover), PAS (0–1 m non-woody cover, which is primarily pasture), LOW (1–2 m woody cover, which includes coffee and young second growth) and HIW (2–5 m woody cover, which includes primarily coffee and some second growth). We calculated total edge and forest edge density for each route within the buffer, EDGE and FEDG, respectively. We excluded the edges of the buffers in calculations of edge density. We also calculated a landscape diversity measure for each route within the buffer, using the formula for the Shannon diversity index, $H' = -\Sigma p_i \ln p_i$, where p_i is the proportion of the *i*th species.

Data analyses

To determine whether the land-cover variables were independent, we first conducted correlation analyses for each pair of variables. If the variables were not significantly correlated at the $P = 0.10$ value, we considered them independent. If the variables were significantly correlated, as were FOR and DIV, and we were interested in using both

variables in model selection for a particular response variable, we fitted linear models for one of the correlated variables as a function of the other. We then used the residuals from these models as the explanatory variable. This is a partial regression technique that removes any correlations between the original variables (Villard *et al.*, 1999; Lichstein *et al.*, 2002).

The potential models that were examined for each response variable are given in Table 2. Akaike's information criterion (AIC) values for each model were calculated from least-squares multiple regression models (SAS, version 8.2, 2001) following Burnham & Anderson (2002, p. 63). These values were corrected because the ratio of sample size to the number of estimated parameters was less than 40 in all cases and hence are referred to as AIC$_c$ values (Anderson & Burnham, 2002; Burnham & Anderson, 2002). We examined the residual plots for the models with the greatest weights for each response variable. Some of the plots exhibited increasing variance. To meet the assumption of constant variance and because the response variables were count data, we transformed the response variables with log transformations, first adding one to each untransformed value. We then repeated the model selection procedure. Final models were chosen based on differences between competing models in AIC$_c$ values and Akaike weights (Burnham & Anderson, 2002). For five of the 11 response variables that we consider in detail, two or three models were within two AIC$_c$ units of each other, suggesting that they were equally good models. For these cases we used the competing model with the smallest number of explanatory variables because simpler models would be more desirable in a conservation context and because the additional variables in the larger models explained small amounts of the variation in the data. The percentages of variability explained in the data (adjusted R^2) were generated by SAS (2001).

To determine whether the land-cover models we developed were useful in describing the abundance and richness of the bird groups in the Coto Brus region, we compared the prediction error percentages of these models with those for null models. We developed the null models based on the assumption that land covers do not influence the abundance or richness of the bird groups under consideration. One type of null model was the mean abundance or richness of each group across all Coto Brus routes. The second type of null model was the random assignment of the response variable values to the routes. This type of null model represents a situation where response variable values are randomly distributed across the landscape, with the constraint that the values we recorded represent the range of possible values. Mean squared prediction errors and prediction error percentages were calculated following Rawlings, Pantula & Dickey (1998).

To test the generalizability of the land-cover models developed from the data gathered in Coto Brus to the Monteverde area, we placed the land-cover data collected from the eight routes in the Monteverde area into the regression equations and compared the predicted and observed values for the response variables. We used the CLI

model option with the regression procedure in SAS to generate 95% confidence limits for the predicted values (Freund & Littell, 2000; SAS, 2001). We used the same two types of null models as described above for comparison, although for these null models we used the Monteverde means and response variable values. We then compared the prediction error percentages of the land-cover models with the percentages generated when using the null models.

Finally, for those response variables where the land-cover model (as opposed to the null models) did a substantially better job of prediction in both the Coto Brus and Monteverde regions, we compared whether the land-cover models did a better job of prediction in Coto Brus or whether they were equally good in both regions. In other words, were the land-cover models generalizable to a greater degree to the local area from which the data were generated or were they equally useful in another area? To make these comparisons, we matched each of the eight Monteverde routes with a Coto Brus route that had a similar level of forest cover. We then produced eight data sets from the original Coto Brus data set, each with one of the matched Coto Brus routes missing. We then used the land-cover models and these data sets to generate predictions for response variables for the missing Coto Brus route and its matched Monteverde route. We compared the differences between the observed and predicted values for the eight pairs of matched Coto Brus and Monteverde routes to determine whether they were consistently smaller for the Coto Brus routes.

Results

We recorded 11 880 registrations (individuals detected) during the study, 10 203 for Coto Brus and 1677 for Monteverde. Of the registrations, 11 827, or 99.6%, were identified to species. Of the 53 registrations that were unidentified to species, 49 were hummingbirds. Two-hundred and eighty species were recorded. The numbers of species in each group that were detected in each of the study areas are given in Table 3.

The great majority of land covers within the buffers of the routes were of the categories 0–1 m non-woody, 1–2 m woody, 2–5 m woody and forest. The mean proportions of land-cover types differed between Coto Brus and Monteverde (Table 1).

We were unable to develop regression models that explained more than 50% of the variation in the data for canopy insectivore richness, canopy non-insectivore richness and abundance, edge insectivore richness and abundance, and hummingbird richness and abundance. The final models for the 11 other response variables are given in Table 4, with relationships between some response variables and forest cover, an important explanatory variable, illustrated in Fig. 2.

The root mean squared errors (RMSE) of the predictions from the land-cover models (a measure of the average variance of the residuals from the regression line) were less than the RMSE of the predictions for the mean null models for all 11 response variables when applied to the Coto Brus data. These results indicate that the land-cover models

Table 3 Numbers of species detected in both study areas or in only one of the study areas

Group	Both study areas	Only Coto Brus	Only Monteverde	Proportion of shared species	No. of families represented in the group
Canopy insectivores	12	16	4	0.38	11
Canopy non-insectivores	14	37	9	0.23	14
Understory insectivores	8	15	3	0.31	11
Understory non-insectivores	3	12	4	0.15	10
Edge insectivores	3	8	3	0.21	10
Edge non-insectivores	14	18	1	0.42	15
Open insectivores	2	8	0	0.20	7
Open non-insectivores	5	8	3	0.31	8
Hummingbirds	6	14	7	0.22	1

Table 4 Selected regression models, based on AIC_c values

Response variable	Explanatory variables	W	K	Parameter estimate (SE)	d.f.	Partial R^2	Model-adjusted R^2
Canopy insectivore abundance	FOR	0.74	3	0.517 (0.081)	36		0.50
Understory insectivore abundance	FOR	0.53	3	0.515 (0.056)	36		0.74
	ELEV			0.118 (0.033)		0.10	
Understory insectivore richness	FOR	0.62	4	0.224 (0.033)	36	0.65	0.73
Understory non-insectivore abundance	FOR	0.69	3	0.332 (0.043)	36		0.67
	ELEV			0.108 (0.027)		0.22	
Understory non-insectivore richness	FOR	0.66	4	0.133 (0.027)	36	0.50	0.70
Edge non-insectivore abundance	FOR	0.57	3	−0.706 (0.087)	36		0.67
Edge non-insectivore richness	FOR	0.22	3	−0.315 (0.036)	36		0.68
	DIV**r**PAS			0.202 (0.038)		0.15	
Open insectivore abundance	PAS	0.80	4	0.279 (0.034)	36	0.47	0.60
	DIV**r**PAS			0.101 (0.017)		0.16	
Open insectivore richness	PAS	0.60	4	0.122 (0.015)	36	0.41	0.54
	DIV**r**PAS			0.442 (0.078)		0.26	
Open non-insectivore abundance	PAS	0.98	4	0.536 (0.070)	36	0.45	0.69
	DIV**r**PAS			0.148 (0.015)		0.26	
Open non-insectivore richness	PAS	0.62	4	0.174 (0.014)	36	0.52	0.76

All response variables were log-transformed. W is the generalized Akaike weight, a measure of the level of evidence for a model. K is the number of estimable parameters in the model, used in the calculation of Akaike's information criterion (AIC_c) values. Expansions for the other abbreviations like FOR, DIV, etc. are given in Table 2. Explanatory variables described with a small bold **r** in the middle, for example DIV**r**PAS, refer to the residuals of the first variable fit as a function of the second.

predicted the Coto Brus data better than the mean null models (Table 5). The random null models had higher prediction errors than either the land-cover models or the mean null models for every response variable.

The Coto Brus land-cover models predicted the Monteverde response variables better than either null model for the abundance of canopy insectivores, understory insectivores, understory non-insectivores and edge non-insectivores. The richness of understory insectivores, understory non-insectivores and edge non-insectivores was predicted approximately equally well by the land-cover models and the mean null models. The mean null models predicted all the open-country bird response variables with more accuracy than the land-cover models (Table 5, Fig. 3). Again, the random null models had higher prediction errors than either the land-cover models or the mean null models for the majority of the response variables.

Four response variables, the abundance of canopy insectivores, understory insectivores, understory non-insectivores and edge non-insectivores, were predicted more accurately by the land-cover models than the null models for both the Coto Brus and Monteverde areas. For these four variables, the differences between predicted values and observed values were not consistently smaller for Coto Brus than for Monteverde (Table 6).

Discussion

Our expectation that we would be more likely to identify relationships between land-cover characteristics and insectivores compared with non-insectivores was not generally supported. The more significant distinctions appear to be related to primary habitat types. We were able to develop models explaining more than 50% of the variation for all the
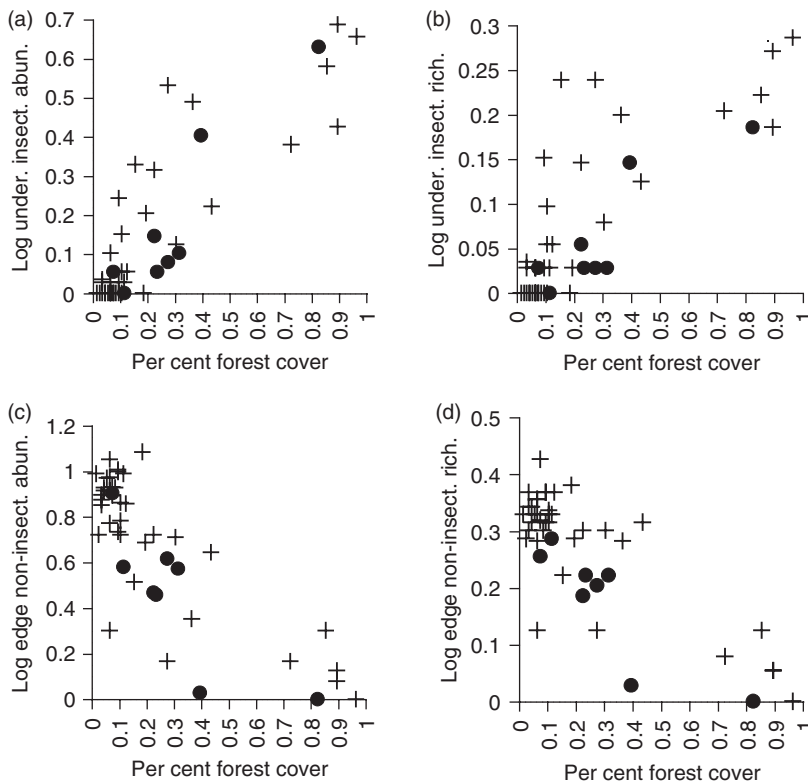
Figure 2 Relationships between four of the response variables and forest cover, the most important or only explanatory variable in the final models for these response variables. +, Coto Brus routes; ●, Monteverde routes. Abun. refers to the number of individuals detected per point. Rich. refers to the number of species detected per point, that is the species richness. The relationships between forest cover and abundance of various groups (a and c) tended to be more similar for the Coto Brus and Monteverde regions than the relationships between forest cover and richness of various groups (b and d). This pattern is reflected in the better predictability of the land-cover models compared with the null models for abundance but not for richness for Monteverde (Table 5).

understory and open-country response variables but not for most of the response variables for canopy birds, edge insectivore abundance or richness, or hummingbird richness or abundance. These findings suggest that the development of land-cover models for understory and open-country birds may be relatively straightforward compared with the development of models for other groups. These latter groups may have more complicated relationships with land-cover variables based on their use of multiple habitats over relatively short time scales (see Ries *et al.*, 2004) or they may respond to the landscape at a scale not captured in the present study. Land-cover characteristics in Brazilian and Ecuadorian Amazon were not related to the abundance or species richness of hummingbirds (Stouffer & Bierregaard, 1995*b*; Pearman, 2002). Hummingbirds may be plastic in their habitat use because they rely on resources that vary temporally and spatially and so are not clearly associated with any land-cover type (Feinsinger *et al.*, 1988; Stouffer & Bierregaard, 1995*b*). For canopy birds, environmental characteristics such as the seasonality and diversity of food resources (Karr, 1971, 1976; Blake & Loiselle, 1991) may be particularly important influences on their abundance and richness.

The land-cover models for understory insectivore and non-insectivore abundance and richness were the most satisfactory as a group, explaining between 67 and 74% of the variation in each case, through positive relationships with forest cover, concurring with previous results from tropical forests (Stouffer & Bierregaard, 1995*a*; Pearman, 2002). Land-cover models also explained most of the variation (between 54 and 76%) in the abundance and richness of

open-country birds. These findings suggest that pasture provides resources important to many open-country species and that a number of open-country species may rely on distinct habitats within the landscape so that more habitat diversity leads to more species diversity. Previous work in Mexico has shown dissimilar groups of species using non-arboreal crop types (Estrada *et al.*, 1997) and a greater proportion of specialist species using pastures and shrublands than forests (Garcia *et al.*, 1998). For both the open-country and understory groups, their reliance on particular land covers and their virtual absence from routes without these land covers likely make useful models, and hence conservation plans, easier to develop than for groups with more flexible and/or difficult-to-discern habitat requirements.

For the 11 response variables for which we were able to develop reasonable land-cover models, these models gave more accurate predictions than null models for Coto Brus, indicating that the models are able to provide some guidance as to the types of land covers that influence the richness and abundance of various bird groups, in the region where the data for model development were collected. In contrast, only four of the land-cover models provided more accurate predictions for the Monteverde region than null models, suggesting that the generalizability of these models is limited to some response variables and to some bird groups. The four useful land-cover models all described abundance rather than richness. Although we chose Monteverde as our test site because of similarities in elevational range, land-cover types and life zones to Coto Brus, the two regions

Table 5 Root mean square errors of prediction of the land-cover models and the mean null models for Coto Brus (columns 2 and 3) and for Monteverde (columns 4 and 5) for the 11 response variables with land-cover model R^2 values greater than 0.50

Response variable	Root mean square error of prediction for land-cover model (per cent prediction error)	Root mean square error of prediction for mean null model (per cent prediction error)	Root mean square error of prediction for land-cover model (per cent prediction error)	Root mean square error of prediction for mean null model (per cent prediction error)
Canopy insectivore abundance	0.11 (54%)	0.16 (78%)	0.06 (32%)	0.11 (52%)
Understory insectivore abundance	0.11 (69%)	0.22 (142%)	0.09 (50%)	0.20 (111%)
Understory insectivore richness	0.05 (62%)	0.09 (125%)	0.06 (99%)	0.06 (100%)
Understory non-insectivore abundance	0.07 (74%)	0.13 (133%)	0.06 (48%)	0.11 (85%)
Understory non-insectivore richness	0.03 (57%)	0.05 (107%)	0.04 (95%)	0.04 (92%)
Edge non-insectivore abundance	0.17 (24%)	0.32 (44%)	0.25 (54%)	0.28 (63%)
Edge non-insectivore richness	0.06 (21%)	0.10 (37%)	0.09 (53%)	0.10 (56%)
Open insectivore abundance	0.08 (30%)	0.13 (50%)	0.18 (81%)	0.13 (59%)
Open insectivore richness	0.02 (34%)	0.04 (52%)	0.08 (288%)	0.01 (49%)
Open non-insectivore abundance	0.15 (26%)	0.28 (51%)	0.38 (85%)	0.21 (46%)
Open non-insectivore richness	0.03 (22%)	0.06 (47%)	0.09 (99%)	0.05 (49%)

All response variables were log-transformed. The mean null model in column 3 is the mean value of the response variable across all routes in Coto Brus ($n = 37$). The mean null model in column 5 is the mean value of the response variable across all routes in Monteverde ($n = 8$).

differ in geographical location, leading to different regional species richness patterns. For example, Monteverde has some spillover of species from the Mesoamerican dry forest in north-western Costa Rica (Stiles, 1983; Young & McDonald, 2000) whereas Coto Brus is closer to the species-rich zoogeographic regions of South America than Monteverde (Stotz *et al.*, 1996). The overall species richness for the areas in Monteverde where sampling took place is likely somewhat lower than it is for the Coto Brus region (Young & McDonald, 2000; Daily, Ehrlich & Sánchez-Azofeifa, 2001; Lindell *et al.*, 2004), which may explain why the predictions from the land-cover models tended to overestimate the number of edge and open species (Figs 2d, 3c and d). Regional richness patterns in Coto Brus and Monteverde apparently differ enough to limit the generalizability of the richness models.

In addition to regional species richness differences, a greater proportion of Monteverde is in pasture, compared with Coto Brus. Pasture is depauperate in species richness compared with other land covers in tropical regions (Estrada *et al.*, 1997). It is possible that the greater proportion of Monteverde that is in pasture depresses the species richness of particular groups, for example, forest edge species (or population sizes of these species, making them more difficult to detect) compared with Coto Brus. This line of reasoning would suggest that the species richness and abundance of open-country groups should be greater in Monteverde than in Coto Brus. However, the land-cover models developed with Coto Brus data consistently overestimated the richness and abundance of open-country groups in Monteverde, leading us to believe that the regional

species richness differences mentioned above likely account for the lack of generalizability of the richness models.

With regard to our richness models, one caveat is that our sampling design may have produced more accurate estimates of abundance than richness. Each route was sampled one time and species richness values typically increase with repeated sampling (e.g. Matthias *et al.*, 2005). It would be useful to focus future work on how many times sampling should be repeated to maximize the accuracy and precision of land-cover models that predict species richness and what degrees of accuracy and precision are lost with fewer sampling rounds. This work could then be used to determine a sampling strategy that maximizes information gain given the resources available.

The four land-cover abundance models that transferred well to Monteverde did not have prediction errors that were always greater for Monteverde than for Coto Brus (Table 6), indicating that these models were not more applicable to the local region where the data for the models were generated. Species richness differences between the regions may result in some type of density compensation within the groups we studied, hence resulting in similar abundance patterns (McGrady-Steed & Morin, 2000). This result suggests the potential usefulness of classifying species, as we did, into groups with some functional significance, for example primary diet.

Although the land-cover models produced more accurate predictions than the null models for Coto Brus and for some response variables in Monteverde, the prediction errors were not trivial in many cases. We caution that, because the mean value of the response variable has a strong influence on the per cent prediction error, those response variables with low
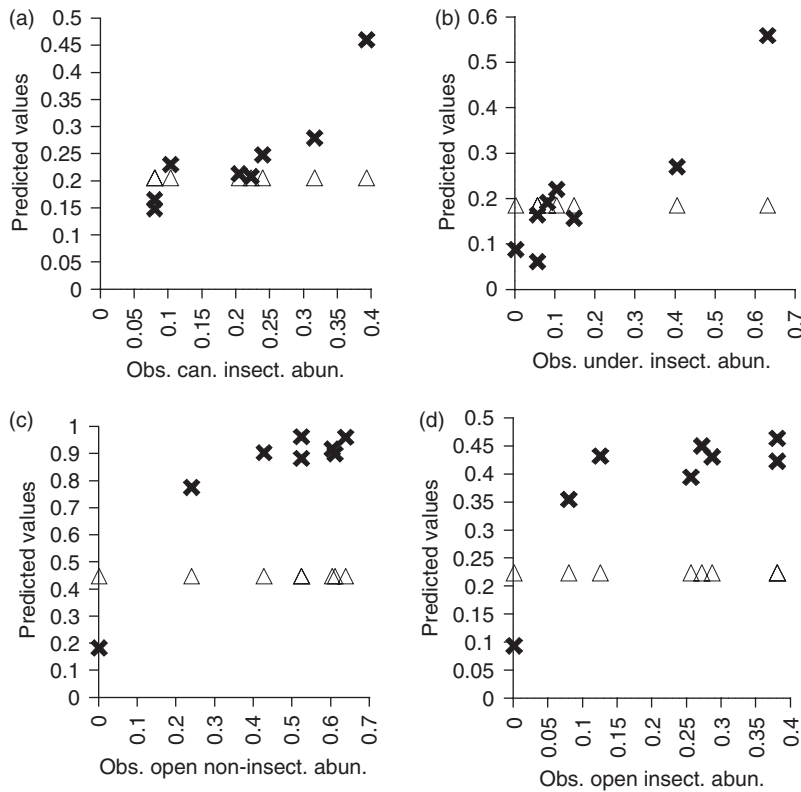
Figure 3 Relationships between the observed values (*x*-axis) and predicted values (*y*-axis) for four response variables. ✖, the predicted/observed points with the predicted values generated from the land-cover models; △, the predicted/observed points with the predicted values generated from the mean null models. The land-cover models for canopy insectivore abundance (a) and understory insectivore abundance (b) more accurately predicted Monteverde values than the mean null models. The mean null models for open non-insectivore abundance (c) and open insectivore abundance (d) more accurately predicted Monteverde values than the land-cover models.

Table 6 Relative generalizability of land-cover model predictions to the Coto Brus and Monteverde regions

Response variable	No. of differences between observed and predicted values that were smaller for the Coto Brus route than for the paired Monteverde route (out of 8 pairs of routes)	No. of differences between observed and predicted values that were smaller for the Monteverde route than for the paired Coto Brus route (out of 8 pairs of routes)
Canopy insectivore abundance	3	5
Understory insectivore abundance	3	5
Understory non-insectivore abundance	4	4
Edge non-insectivore abundance	4	4

All response variables were log-transformed.

means tended to have high errors. For example, understory non-insectivore richness and open non-insectivore richness (Table 5) have the same RMSE; however, because more of our sampling routes had low amounts of forest and hence lower species richness of understory non-insectivores compared with open non-insectivores, the per cent prediction error is higher for the land-cover model for the understory

non-insectivores. Hence the per cent prediction errors are primarily useful for comparisons between models for a given response variable. Nonetheless, the non-trivial prediction errors indicate that future work should focus on measuring land-cover variables at a number of scales and investigating whether measurement of other environmental variables could contribute to refinement of the models.

We used broad species groups and land-cover categories that could be used in other regions. Our results are somewhat encouraging in that, for some groups most at risk from deforestation, including understory insectivores and frugivores (Castelletta, Sodhi & Subaraj, 2000; Sekercioglu *et al.*, 2002), abundance models related to land-cover characteristics were the simplest to determine and had the most applicability to another region. In contrast, it may be more difficult to demonstrate clear relationships between easily measured land-cover variables and the richness of the above groups, or the abundance and richness of groups like hummingbirds, and to apply these models elsewhere. Future work should investigate the environmental variables that influence the abundance and richness of canopy birds and open-country birds, with a particular eye to the scale at which the most important explanatory variables work. It is also important to determine the range of environmental characteristics and geographical areas over which models for particular groups can be applied since the types of species that are particularly sensitive to land-cover change may vary geographically (e.g. Watson, Whittaker & Dawson, 2004). Finally, because of the logistical difficulties of sampling off trails in tropical forest and of obtaining permission from

numerous landowners in non-forest areas, we conducted our sampling along roads and trails. It would be useful to investigate the degree to which sampling along roads or trails, as compared with off roads or trails, influences the abundance and richness variables we measured.

Acknowledgements

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