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Effects of species ecology and urbanization on accuracy of a cover-type model: A test using GAP analysis

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ABSTRACT

Models of vertebrate distributions based on dominant vegetation cover or land-use classification are commonly used for conservation planning, but these models may be inappropriate for species that choose sites based on criteria other than land cover or within urban areas that are not adequately described by cover-type alone. We compared the accuracy of predicted occupancy of birds for a set of cover-type models—Alabama Gap Analysis Program's (ALGAP) vertebrate distribution maps—between an urban and a rural landscape in east-central Alabama. We performed analysis at two scales of investigation—0.03-km^2 point-count surveys or 28.26-km^2 landscapes—using point counts conducted during summers 2004–2006. We tested ALGAP's ability to predict the occupancy of habitat by birds grouped by life-history parameters: migrant, resident, insectivore, carnivore, and omnivore, forest dweller, and cavity nester. ALGAP performed well at the scale of entire landscapes but poorly at the scale of individual point counts. At the point-count scale, ALGAP was most accurate for species requiring interior forest conditions. At the landscape scale, ALGAP was more accurate in the rural landscape than the urban landscape, and it had higher commission errors in the urban landscape. Variation in the ability of ALGAP to predict species occupancy was likely due to (1) poor model performance when applied to species that choose sites using criteria other than cover type and (2) the inadequacy of ALGAP to describe a heterogeneous urbanized landscape. Our results highlight pitfalls of using land cover information to model species distributions in situations where it may be inappropriate.

1. Introduction

Models relating habitat to the occurrence of wildlife are commonly used to predict locations of animals based on land-cover information collected either remotely or by directly assessing the site (Morrison, Marcot, & Mannan, 1998). Cover-type models are often built using expert opinion and assume that occupancy of an area by a species depends heavily on the response of that species to the dominant vegetation (Schlossberg & King, 2009). These models are commonly used to identify biodiversity "hotspots", to prioritize areas to conserve, and to predict the responses of wildlife to management (Scott et al., 1993). Because a great emphasis is often placed on such models, it is essential to have some means to validate their accuracy. Testing models of animal distributions using independent datasets enables researchers to estimate overall accuracy and error rates (Fielding & Bell, 1997). It would be expected that cover-type models would perform with different rates of success in different contexts, such as rural or urban environments, and for different categories of birds, such as insectivores or omnivores. Thus, it is important to test models for accuracy across different groups of birds in multiple contexts. In this way researchers can assess the contexts in which models are most appropriately used, when models are prone to errors, or even when inferences from the models are likely to be misleading (McPherson & Jetz, 2007).

Weaknesses of models built to predict vertebrate distributions can often be anticipated based on the ecology of a given species (e.g., Kilgo et al., 2002; McPherson & Jetz, 2007; Mitchell, Lancia, & Gerwin, 2001), particularly when the models are built using low-resolution information such as type of cover. Distributions of species associated with fine-scale aspects of habitat that are not readily captured by satellite imagery or land cover classifications may be poorly predicted (Fielding & Haworth, 1995). For instance, models describing distributions of habitat generalists often perform poorly compared to models of specialist distributions (e.g., Hepinstall et al., 2002; Mitchell et al., 2001; Segurado & Araújo, 2004), possibly because generalists respond more to aspects of vegetation structure (Pearson, 1993) that are not captured adequately by land cover classifications or satellite imagery, or because generalists use multiple types of cover, making their distributions difficult to predict. Migratory status also affects performance of models of vertebrate distributions based on land

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cover classifications, with migrant distributions often better predicted than those of resident species in North America (Flather & Sauer, 1996; Mitchell et al., 2001), and resident species distributions better predicted than migrant distributions in southern Africa (McPherson & Jetz, 2007). The difference in ability of models to predict the distribution of migrants versus residents may arise because migrants are adapted to certain cover-types or seral stages that experience seasonal fluctuations in food availability and that are apparent from maps of land cover (Sherry & Holmes, 1995). Further, distributions of species that occupy higher trophic levels may be influenced by biotic interactions that are not captured by models making their distributions difficult to predict using habitat characteristics alone (McPherson & Jetz, 2007).

Models built using classified land cover maps derived from satellite imagery or other remotely sensed data may also be poor at predicting distributions within some types of landscapes. For example, the National Land-Cover Database (Homer, Huang, Yang, Wylie, & Coan, 2004) classifies developed areas as low, medium, and high-intensity according to amount of impervious surface. Broad classification schemes such as those used by the National Land-Cover Database often fail to adequately capture heterogeneity (Cadenasso, Pickett, & Schwarz, 2007) or vegetative cover within urbanized or residential landscapes (Pennington & Blair, 2011). Fine-scale heterogeneity may render areas unsuitable for some species (Wiens, 2000), but such subtle vegetation features may not be apparent on a map of land cover. As a consequence, fine-scale heterogeneity within an urban landscape may increase the chances of falsely classifying an area as suitable for a given species. Therefore, models built using only information from existing land cover maps may be missing key information needed to predict the distribution of some species (Cadenasso et al., 2007; Pennington & Blair, 2011).

Gap Analysis Programs (GAP) use cover-type models to identify areas of high species diversity that are not currently protected by existing conservation lands (Jennings, 2000; Scott & Jennings, 1997). GAP creates models using literature review and expert opinion, then applies these models to vegetation maps such as the National Land-Cover Database (Homer et al., 2004) to predict distributions of species (Csuti & Crist, 1998; Scott & Jennings, 1997). The maps of species distributions created by GAP therefore incorporate cover-type, patch-size, and level of urbanization, among other aspects of an area that are obtainable from satellite imagery (Silvano et al., 2007). GAP's standards call for the correct assignment of the presence or absence of a species within a sample area in 80% of judgments (Crist & Jennings, 2000; Csuti & Crist, 1998). However, a meta-analysis of cover-type models (mostly GAP) by Schlossberg and King (2009) showed that the presence or absence of a species was correctly assigned in only 71% of judgments, on average. GAP models also often perform modestly in predicting species occupancy when compared to empirical models (e.g., Howell, Peterson, & Conroy, 2008; Peterson, 2005) because GAP performs best at coarse spatial extent (1:100,000; Scott et al., 1993).

The developers of GAP acknowledge limitations of the models in predicting the distributions of species that choose sites based on criteria not available from maps of land cover (Csuti & Crist, 1998). They encourage field biologists to test GAP's predictions to determine if certain life-history or behavioral traits are associated with increased accuracy (Csuti & Crist, 1998). Knowledge of the situations in which GAP analysis is best applied would help wildlife biologists and managers to use GAP to its maximum effectiveness. Our goal in this study was to assess and contrast the accuracy of Alabama GAP (ALGAP; Silvano et al., 2007) in predicting the distribution of bird species based on aspects of species ecology such as migratory status, nesting guild, habitat specificity, area sensitivity, and trophic level, as well as to compare ALGAP's predictive abilities in an urban and rural landscape.

We tested ALGAP's predictions at the scale of the individual survey location and at the scale of entire 28.26 km^2 study-sites. We predicted that ALGAP would have higher accuracy rates and lower commission errors in a rural versus an urban landscape. We further predicted that GAP would perform most poorly when predicting distributions of species with certain life history characteristics, specifically generalists, residents, cavity nesters, and species occupying high trophic levels, which we hypothesized choose sites based on characteristics that are not apparent from maps of land cover alone. We also predicted that ALGAP would perform better at the scale of the entire study sites than at the scale of the individual point counts.

2. Materials and methods

2.1. Alabama GAP species distribution maps

The species distribution models from ALGAP are based on literature review and expert opinion. ALGAP incorporates patch size and forest edge/interior characteristics as well as cover-type into the modeling procedure (Silvano et al., 2007). ALGAP habitat models were applied to land-cover maps (Kleiner et al., 2007) to create species distribution maps for bird species within Alabama. The resulting maps are 30 m resolution binary matrices of suitable and unsuitable habitat (Silvano et al., 2007).

2.2. Study sites

Our rural landscape was centered on Tuskegee National Forest (TNF), located on the northern edge of the East Gulf Coastal Plain. Our study site was defined by a 3-km-radius circle centered in the southwest portion of the national forest (32°25.899′N, 85°38.637′W). These sites were selected for a mosquito and arbovirus study with bird surveys added later (Estep et al., 2011). TNF contained a variety of natural habitats including bottomland hardwood forest and upland longleaf pine forest. This study site contained < 0.1% urbanized area (defined as > 60% impervious surface, Donnelly & Marzluff, 2006) and 8% developed area (defined as >20% impervious surface, Homer et al., 2004). Within this study site, 373 bird survey points were established using a systematic grid with each point separated from the next closest point by roughly 250 m. Most survey points were within the national forest boundary, although several points fell within surrounding neighborhoods and farmland.

The urban landscape was the city of Auburn, AL, which is located within the East Gulf Coastal Plain roughly 20 km northeast of our rural site. Our study site was a 3-km-radius circle centered on the campus of Auburn University (32°35.517′N, 85°29.417′W). The study site contained an urban center as well as surrounding neighborhoods, parks, farmland and some forested land. Approximately 18% of it was urbanized area and 63% was developed area. We established a grid of 439 bird survey points, each separated by roughly 250 m.

2.3. Bird surveys

Birds were surveyed by trained observers using point counts (Ralph, Droege, & Sauer, 1995) in which all birds encountered within a 100-m radius were recorded. Each point was surveyed for a total of 16 min. In the rural site all points were surveyed twice using 5-min counts in 2004 and twice using 3-min counts in 2005. In the urban site points were surveyed twice using 5-min counts in 2005 and twice using 3-min counts in 2006. We used 5-min counts during one year because Farnsworth et al. (2002) recommended 5-min counts when using their method to calculate detection probabilities. We used 3-min counts the next year due to logistical constraints. During 3-min point counts, the total number of individuals of each species observed was recorded. During 5-min point counts, the number of new individuals observed during each 1-min interval of the total 5-min session was recorded so that detection probabilities could be calculated following the approach of Farnsworth et al. (2002). All counts were conducted between 0500 and 1100 CST and between 26 May and 11 August each year and care was taken so that locations were not surveyed twice at the same time or date.

3. Statistical analysis

3.1. Point scale

We assumed that a species was predicted as present by ALGAP if ≥1 pixels within a 100-m buffer of each point were predicted as suitable habitat by ALGAP's vertebrate species distribution maps (Kleiner et al., 2007). We also considered a species as present at a survey location if it was detected at that location during at least one survey, and absent if it was never detected. We then calculated accuracy as the percentage of bird survey locations where ALGAP's predictions matched presence or absence as determined by our bird surveys, commission error as the percentage of points where a species was predicted as present by ALGAP, but never detected, and omission error as the percentage of points where the species was predicted as absent, but detected.

To test the hypotheses that ALGAP's accuracy, commission error, and omission error at the scale of individual surveys are affected by urbanization or ecological factors, we built general linear models using ALGAP's accuracy, commission, and omission error rates as dependant variables. We created several binary factors indicating landscape (1 = urban, 0 = rural), migratory status (1 = migrant, 0 = resident), whether the species is associated with forest interior conditions, whether it nests in cavities, and whether it is an insectivore, carnivore, or omnivore, as well as a covariate for the number of habitats used by the species for use in model building. All ecological data was gathered from Hamel (1992). We built models representing all possible combinations of factors then ranked and compared models separately for accuracy, commission, and omission using Akaike's Information Criterion corrected for small sample size (AIC_c, Burnham & Anderson, 2002). We considered models as competitive for inference if they were within $\Delta\text{AIC}_c \leq 2$ of the best model and did not contain uninformative parameters (Arnold, 2010; Burnham & Anderson, 2002). If >1 model was competitive, we model averaged by weighting each model by its Akaike weight across all competitive models to produce final models used for inference (Burnham & Anderson, 2002). We further considered ecological factors as useful for inference if the 95% confidence intervals of their regression coefficients did not include zero (Chandler, King, & Destefano, 2009). We used an arcsine-square root transformation of all percentage variables to ensure normality.

3.2. Landscape scale

We considered a species to be predicted as present by ALGAP if any pixel within the 3-km buffer was classified as present. We then used our point-count dataset to determine the overall accuracy as well as the commission and omission error rates within each landscape assuming that a species was observed as present if it was detected during any survey. The predictive measures for the two landscapes were then compared using Fisher's exact test. We also modeled accuracy and commission errors using generalized linear models with a binomial distribution and a logit link function and the same factors and model building procedures described for the point-scale models. For all analyses, we only analyzed data from taxonomic groups which we believe were well-sampled using point counts. These groups include perching birds (*Passeriformes*), woodpeckers (*Piciformes*), doves and pigeons (*Columbiformes*), the Northern Bobwhite (*Colinus virginianus*), and the Yellow-billed Cuckoo (*Coccyzus americanus*). All point- and landscape-scale statistical operations described above were performed using R version 2.13.1 (R Development Core Team, 2011).

3.3. Estimating detection probability

Our analyses of differences in accuracy and error rates between landscapes and ecological traits were potentially subject to bias if there were differences in the probability of detection of species between sites. For instance, a species may simply be more detectable in one landscape over another, biasing measures of accuracy and error rates. To address this possibility, we estimated detection probabilities for species at each site using the approach of Farnsworth et al. (2002). This approach uses a removal model, whereby the estimates of detection probability of a species during each interval of an observation session are obtained through maximization of a multinomial likelihood function conditioned on the total number of individuals of that species observed during the session (Farnsworth et al., 2002). We implemented this approach to estimation using program SURVIV (White, 1992). We fit the simplest model to the data for each species at each site; this model assumes no heterogeneity among individuals of the same species in detection. Species-site combinations for which error messages resulted from attempts to fit this simplest model were excluded from further analysis.

One-minute detection probabilities were calculated for 61 species. Extending 1-min detection probability estimates (p_1) to 16-min, the total length of time of observations at each point over the course of the study, the total detection probability—or probability of detecting an individual of a given species during our 16-min of surveying, given that it is present—for a species-site combination equals $1-(1-p_1)^{16}$ (MacKenzie et al., 2002).

To determine if inference from this study could be affected by differences in species detection rates, we compared species' detectabilities within the urban and rural landscapes and across ecological traits. We used Spearman rank correlations to determine if the difference in detectability between sites is correlated with the difference in accuracy, commission, and omission error rates. Further, using Spearman rank correlations, we tested whether a species' average detectability across landscapes (urban and rural) was correlated with overall accuracy, commission and omission error rates, as well as ecological traits. We also used a binomial test to determine whether differences in detectability caused species to be observed in one landscape over another by determining how many species were, in fact, observed in the landscape in which they were more detectable, but not in the other.

4. Results

Overall, we analyzed data for 73 focal bird species including the 59 species detected in the urban landscape and the 68 detected in the rural landscape (Appendix A). European Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*) were not modeled by ALGAP and were not included in the analysis. Overall accuracy at the scale of the point counts across species was 0.52 (SE = 0.01) commission error was 0.44 (SE = 0.04) and omission error was 0.01 (SE < 0.01). There were seven competitive models for accuracy at the point count scale. We therefore used model averaging to create the final model of accuracy at the scale of the individual point counts. The only factor in this model with coefficient confidence intervals that did not include zero was the factor forest species

Table 1
Coefficient estimates (β) and Akaike weights (w_i) for variables in models describing the relationship between the accuracy, commission error rates and omission error rate of Alabama Gap Analysis Program's maps of breeding bird distributions at the scale of individual point counts and the landscape. Models shown were built by building models containing all possible combinations of predictor variables and then model averaging across all models with ΔAICc ≤ 2 that did not contain uninformative parameters.

	β_0	Cavity	Forest	Habitats	Insectivore	Omnivore	Carnivore	Site	Migrant
Point count scale									
Accuracy									
β	0.77 (0.09)		0.22 (0.07)	−0.01 (0.01)	0.11 (0.07)	0.08 (0.09)	0.42 (0.25)	0.06 (0.06)	0.03 (0.07)
w_i	1.00		1.00	1.00	0.46	0.08	0.62	0.12	0.08
Commission									
β	0.86 (0.09)	0.21 (0.08)	−0.25 (0.07)	−0.00 (0.01)	−0.15 (0.08)	−0.07 (0.09)	−0.44 (0.25)	−0.08 (0.06)	0.11 (0.07)
w_i	1.00	1.00	1.00	1.00	0.79	0.07	0.40	0.34	0.36
Omission									
β	0.14 (0.02)	−0.09 (0.04)							
w_i	1.00	1.00							
Landscape scale									
Accuracy									
β	0.73 (0.64)			0.20 (0.06)				−1.51 (0.58)	
w_i	1.00			1.00				1.00	
Commission									
β	−1.32 (0.70)			−0.15 (0.06)				1.30 (0.62)	
w_i	1.00			1.00				1.00	

(Table 1 and Fig. 1). There were eight competitive models describing commission errors at the scale of the point counts. Model averaging of parameter estimates resulted in only two factors having coefficient confidence intervals excluding zero, revealing a positive association with cavity nesters and a negative association with forest birds (Table 1). The only competitive model for omission error at the scale of the point counts included a negative association with cavity nesters, with coefficient confidence intervals excluding zero (Table 1).

GAP was much more accurate at the scale of the landscape than at the point count scale. The urban landscape had an overall accuracy of 0.78 and the rural landscape had an overall accuracy of 0.92 (Table 2), resulting in an average accuracy across all survey locations, regardless of landscape, of 0.80. Fisher's exact test showed a significant difference in ALGAP's accuracy between the two sites ($p = 0.04$). Commission error rates were significantly higher in the urban site (0.18) than in the rural site (0.06, $p = 0.03$, Table 2). The only competitive model for accuracy at the scale of the landscape included a positive association with number of habitats and negative association with the urbanized landscape; coefficient confidence intervals for both parameters excluded zero (Table 1). The only competitive model for commission error included a positive association with the urbanized landscape and a negative association with the number of habitats a species could use; all confidence intervals excluded zero (Table 1).

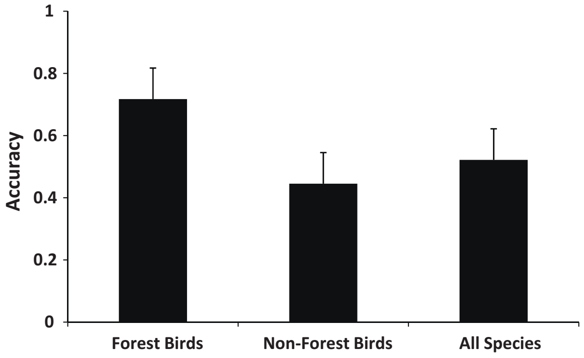

Fig. 1. Average (SE) accuracy values for Alabama Gap Analysis Program's maps of breeding bird distributions (Silvano et al., 2007) for species that do, and do not require forest interior conditions and for all species in Auburn, AL and Tuskegee National Forest, AL summer 2004–2006.

Estimates of this total 16-min detection probability averaged 1.00 (SE < 0.01, $n = 56$) for species in the rural landscape and 0.99 (SE = 0.01, $n = 46$) for species in the urban landscape. Differences in detection between landscapes were not correlated ($p > 0.05$) with differences in accuracy ($r < -0.11$), commission ($r = 0.03$), or omission ($r = -0.04$) error rates. Average detectability of species across landscapes was not correlated ($p < 0.05$) with cavity nesters ($r = -0.10$), forest birds ($r = 0.12$), migrants ($r = 0.12$), number of habitats ($r = 0.16$), insectivores ($r = -0.22$), omnivores ($r = 0.22$), carnivores ($r = 0.02$), or scavengers ($r = -0.16$). At the landscape scale, only 10 of 40 species were detected in the landscape in which they were most detectable, and not in the other landscape, significantly lower than would be expected by chance (binomial test: $p < 0.001$). We were therefore able to reject the hypothesis that observed differences in ALGAP's predictive abilities were due heterogeneity in probability of detection.

5. Discussions and conclusions

The distributions of species predicted by cover-type models such as GAP are commonly used in conservation plans and actions (Rondinini, Stuart, & Boitani, 2005; Scott et al., 1993). Although many GAP models have been tested broadly (Schlossberg & King, 2009), no study has determined whether the accuracy of these models is dependent on the ecology of target species or the type of landscape to which the models are applied. In this study we sought to determine the accuracy of GAP models when they are applied to species or landscapes that vary in how well they are characterized by land-cover maps.

In our assessment of ALGAP we found that the model performed poorly at the scale of a point count (0.03 km^2) having an average accuracy of 0.52, slightly higher than random. Therefore, ALGAP is likely of limited use at this scale. In contrast, ALGAP performed well at the scale of the entire study site (28.26 km^2) with an average accuracy across our urban and rural landscapes matching GAP's standard of 0.80 (Crist & Jennings, 2000; Csuti & Crist, 1998). In fact, both study sites had accuracy rates higher than the average reported by Schlossberg and King (0.71, 2009) with ALGAP having higher accuracy within the rural landscape (0.92), than any model reported by Schlossberg and King (2009). These observations support GAP's recommendations and past research showing similar models performing best at larger scales (Csuti & Crist, 1998; Edwards, Deshler, Foster, & Moisen, 1996; Schlossberg & King, 2009). Although these results are perhaps not surprising, it

Table 2
Contingency table for all predictions, predictions of presence, and predictions of absence by Alabama Gap Analysis Program's maps of breeding bird distributions within an urban landscape in Auburn, AL and a rural landscape in Tuskegee National Forest, AL.

	Site	Correct	Incorrect	% Correct	*p*
All	Urban	57	16	78	0.04
	Rural	67	6	92	
Presence	Urban	55	12	82	0.03
	Rural	66	4	94	
Absence	Urban	2	4	33	1.00
	Rural	1	2	33	

is important to clearly show the problems inherent in using GAP at fine scales. Overall, our assessment supports GAP's recommendation that it is best used at larger spatial extents (Csuti & Crist, 1998; Scott et al., 1993), in efforts such as identifying large areas for preserves or when predicting responses to changes in land use or climate over broad spatial extents.

Although, on average, ALGAP performed poorly at the point count level, some species were still predicted relatively well. Important inference into the usefulness of the methodology used by GAP can be made if errors are associated with certain suites of species whose ecology may not be adequately explained by GAP's models. Accuracy of ALGAP at the level of individual point counts was highest for species associated with interior forest conditions (Fig. 1). The size of forest-tracts is an important feature of the habitat associations of forest interior species (e.g., Freemark & Merriam, 1986; Howe, 1984; van Dorp & Opdam, 1987). Increased accuracy for forest interior species may therefore result because ALGAP incorporates patch-size—which is relatively easy to calculate from a map of landcover—into their models of bird distributions. Maps of distributions of forest interior birds also had significantly lower errors of commission than maps for other species, suggesting that the metrics of forest area that ALGAP incorporates into its models increase its ability to predict the presence of forest bird species.

Other patterns of errors committed by ALGAP at the scale of individual bird surveys provide further inference. Errors of commission were significantly higher for cavity-nesting species. Cavity-nesting birds necessarily choose nesting sites based, at least in part, on the presence of nesting cavities or substrates in which to create them (Brawn & Balda, 1988; Raphael & White, 1984). The poor performance by ALGAP in predicting presence of cavity nesters may be because the presence of snags and cavities cannot be determined by the 30-m pixels used by ALGAP. Also, distributions of secondary cavity nesters—species that do not create their own cavities—are partly dependent on the distribution of the primary cavity nesters that create cavities (e.g., Blanc & Walters, 2008; Martin, Aitken, & Wiebe, 2004; Martin & Eadie, 1999). Such biotic interactions may be important in determining the presence of cavity nesting birds but are not considered in GAP analysis. Further, errors of omission by ALGAP were significantly lower for species that nest in cavities, but the effect was far greater for errors of commission, corroborating the assertion by Lawler and Edwards (2002) that when models do not include fine-scale aspects of habitat they will likely over predict occupancy of cavity nesting species.

At the extent of the landscape, accuracy was significantly higher in the rural area and commission errors were higher in the urban area, supporting the hypothesis that maps of land cover used by GAP do not describe urban areas as well as rural areas (Cadenasso et al., 2007). For instance, the classification of "developed open space" (class 21 in Homer et al., 2004) represents a variety of urban green spaces including residential yards, parks, and vegetation planted for erosion control. Although species may perceive these urban green spaces differently, GAP cannot differentiate between them. Further, fine-scale heterogeneity renders some areas as unsuitable habitat for certain species (Wiens, 2000). Fine-scale heterogeneity is a prevalent feature of urbanized landscapes, but it is not quantified by the maps of landcover used by GAP (Cadenasso et al., 2007). Therefore, unsuitable areas within the urbanized landscape may be more likely to be falsely classified as suitable habitat because they are not adequately quantified using satellite imagery.

An unexpected result was that the accuracy of the model at the landscape level was positively correlated with the number of habitats that a species can occupy. Contrary to other models (e.g., McPherson & Jetz, 2007; Mitchell et al., 2001; Segurado & Araújo, 2004) ALGAP was more likely to predict the presence or absence of species, within a landscape, that were generalists in their habitat preferences. Our results may differ from some other studies because of the nature of the models tested. Empirical models may have difficulty predicting distributions of habitat generalists because there is little variation in their occupancy across a study site, making it difficult to statistically discern habitat preferences (Brotons, Thuiller, Araújo, & Hirzel, 2004). However, Kilgo et al. (2002) and Dettmers, Buehler, & Franzreb (2002) both tested a cover-type model built using expert opinion (Hamel, 1992) and found that it performed better when predicting habitat specialists over generalists. The differences between the Kilgo et al. (2002) and Dettmers et al. (2002) studies and our study are again likely attributable to spatial extent. Kilgo et al. (2002) and Dettmers et al. (2002) were testing predictions at the individual stand level, whereas we tested predictions at a larger scale of 28.26 km^2 study-sites. Generalists may move around a landscape to the extent that their occupancy of any given patch is hard to predict. In contrast, it may be much more reliable to predict that they will occur somewhere within a large area simply because a larger areas should contain more potential habitat (Csuti & Crist, 1998), and that is essentially what we found in this study.

It is essential to test models against independent data to assess their predictive abilities (Fielding & Bell, 1997), but independent survey data are not without their own errors. For instance, we used point-count data collected 2004–2007 to test maps built from habitat data collected in 2001. Because maps of land cover are updated roughly once every ten years, GAP analysis will rarely be completely up-to-date. Therefore, use of point counts conducted concurrent with collection of land-cover data may not present a test of GAP's usefulness in most real-world applications.

Further, heterogeneity in the probability of detection across species and sites can confound model performance (Boone & Krohn, 1999; Schaefer & Krohn, 2002; Schlossberg & King, 2009). Species with lower probabilities of detection are less likely to be recorded and thus may have artificially inflated commission errors (Boone & Krohn, 1999; Schaefer & Krohn, 2002). Our analysis of bird detection rates shows that, among the species analyzed, average detection rates were extremely high at both sites (rural = 1.00, urban = 0.99). Our results also show that detection rates were not correlated with ecological traits or landscape context. Therefore, we believe that it is unlikely that any of our results are artifacts of imperfect detection and that our point-count data provide a valid test of ALGAP's predictive abilities.

When testing a model it is important to remember that utility is not determined by how well it describes the “truth”, but by its usefulness in answering a specific question (Starfield, 1997). Our results highlight the pitfalls of using cover-type models to predict distributions of birds in certain situations. Collecting habitat information that is not captured in the land cover maps used by GAP would likely improve accuracy in some situations. However, GAP vertebrate distribution maps are built to identify areas that contain high biodiversity, at a large spatial extent, thus helping to prioritize areas to set aside for conservation (Jennings, 2000; Scott & Jennings, 1997). At a large extent, ALGAP performed well, achieving GAP’s standard of 80% accuracy. With scarce conservation funding available, cover-type models will likely become more attractive compared to empirical models, or models that incorporate fine-scale attributes of habitat. Therefore it is important, moving forward, to understand where cover-type models are most useful, and not apply them in contexts for which they are inappropriate.

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Appendix A.

Bird species predicted by Alabama Gap Analysis Program to be within the urban (Auburn, AL) and rural (Tuskegee National Forest, AL) landscapes. Accuracy is presented for species detected during surveys of breeding birds conducted 2004–2006.

Common name	Scientific name	Code	% Predicted		% Observed	
			Urban	Rural	Urban	Rural
Acadian Flycatcher[a]	*Empidonax virescens*	ACFL	10	31	0	36
American Crow	*Corvus brachyrhynchos*	AMCR	100	100	29	51
American Goldfinch	*Carduelis tristis*	AMGO	97	80	3	4
American Redstart[a]	*Setophaga ruticilla*	AMRE	1	29	0	3
American Robin	*Turdus migratorius*	AMRO	54	82	52	2
Bachmans Sparrow	*Aimophila aestivalis*	BASP	0	12	0	1
Baltimore Oriole	*Icterus galbula*	BAOR	0	0	0	0
Barn Swallow	*Hirundo rustica*	BARS	98	64	13	16
Black-and-white Warbler	*Mniotilta varia*	BAWW	7	30	0	2
Blue Grosbeak	*Passerina caerulea*	BLGR	95	83	11	22
Blue Jay[a]	*Cyanocitta cristata*	BLJA	74	100	74	45
Blue-gray Gnatcatcher	*Polioptila caerulea*	BGGN	63	99	44	64
Brown Thrasher	*Toxostoma rufum*	BRTH	49	78	53	8
Brown-headed Cowbird	*Molothrus ater*	BHCO	80	97	20	24
Brown-headed Nuthatch	*Sitta pusilla*	BHNU	55	90	21	8
Carolina Chickadee	*Poecile carolinensis*	CACH	98	99	50	42
Carolina Wren	*Thryothorus ludovicianus*	CARW	85	98	69	93
Chipping Sparrow	*Spizella passerina*	CHSP	98	79	5	1
Cliff Swallow	*Petrochelidon pyrrhonota*	CLSW	98	17	0	0
Common Grackle	*Quiscalus quiscula*	COGR	64	91	63	13
Common Ground Dove	*Columbina passerina*	COGD	79	95	0	1
Common Yellowthroat	*Geothlypis trichas*	COYE	6	46	0	9
Dickcissel	*Spiza americana*	DICK	0	1	0	0
Downy Woodpecker	*Picoides pubescens*	DOWO	98	99	18	23
Eastern Bluebird	*Sialia sialis*	EABL	98	84	23	6
Eastern Kingbird	*Tyrannus tyrannus*	EAKI	64	91	9	9
Eastern Meadowlark	*Sturnella magna*	EAME	20	8	5	1
Eastern Phoebe	*Sayornis phoebe*	EAPH	51	72	9	2
Eastern Towhee	*Pipilo erythrophthalmus*	EATO	61	91	55	60
Eastern Wood-Pewee	*Contopus virens*	EAWP	97	99	2	27
Eurasian Collared-Dove	*Streptopelia decaocto*	EUCD	100	100	7	4
Field Sparrow	*Spizella pusilla*	FISP	36	66	0	8
Fish Crow	*Corvus ossifragus*	FICR	100	100	3	13
Gray Catbird	*Dumetella carolinensis*	GRCA	53	75	20	4
Great Crested Flycatcher	*Myiarchus crinitus*	GCFL	74	98	18	38
Hairy Woodpecker	*Picoides villosus*	HAWO	25	67	17	7
Hooded Warbler[a]	*Wilsonia citrina*	HOWA	13	37	1	46
House Finch	*Carpodacus mexicanus*	HOFI	44	59	55	2
Indigo Bunting	*Passerina cyanea*	INBU	51	75	16	54
Kentucky Warbler[a]	*Oporornis formosus*	KEWA	13	37	0	24
Loggerhead Shrike	*Lanius ludovicianus*	LOSH	15	8	1	0
Louisiana Waterthrush[a]	*Seiurus motacilla*	LOWA	0	28	2	8
Mourning Dove	*Zenaida macroura*	MODO	54	82	70	19
Northern Bobwhite	*Colinus virginianus*	NOBO	25	85	0	10
Northern Cardinal	*Cardinalis cardinalis*	NOCA	54	82	92	98
Northern Flicker	*Colaptes auratus*	YSFL	100	100	7	8
Northern Mockingbird	*Mimus polyglottos*	NOMO	47	81	84	13
Northern Parula[a]	*Parula americana*	NOPA	0	29	6	22
Northern Rough-winged Swallow	*Stelgidoptryx serripennis*	NRWS	98	67	5	2
Orchard Oriole	*Icterus spurius*	OROR	98	74	3	10
Pileated Woodpecker[a]	*Dryocopus pileatus*	PIWO	67	100	6	17
Pine Warbler[a]	*Dendroica pinus*	PIWA	5	69	8	29

Common name	Scientific name	Code	% Predicted		% Observed	
			Urban	Rural	Urban	Rural
Prairie Warbler	*Dendroica discolor*	PRAW	48	75	0	16
Prothonotary Warbler[a]	*Protonotaria citrea*	PROW	0	29	0	3
Purple Martin	*Progne subis*	PUMA	98	67	8	17
Red-bellied Woodpecker	*Melanerpes carolinus*	RBWO	99	100	38	46
Red-cockaded Woodpecker	*Picoides borealis*	RCWO	3	59	3	59
Red-eyed Vireo[a]	*Vireo olivaceus*	REVI	87	78	2	65
Red-headed Woodpecker	*Melanerpes erythrocephalus*	RHWO	95	100	6	2
Red-winged Blackbird	*Agelaius phoeniceus*	RWBL	81	29	8	5
Rock Pigeon	*Columba livia*	RODO	93	41	16	0
Scarlet Tanager[a]	*Piranga olivacea*	SCTA	0	0	0	0
Summer Tanager[a]	*Piranga rubra*	SUTA	86	82	4	49
Swainsons Warbler[a]	*Limnothlypis swainsonii*	SWWA	0	29	0	13
Tufted Titmouse[a]	*Baeolophus bicolor*	TUTI	99	99	41	77
White-breasted Nuthatch	*Sitta carolinensis*	WBNU	16	0	16	0
White-eyed Vireo	*Vireo griseus*	WEVI	42	68	5	78
Wood Thrush[a]	*Hylocichla mustelina*	WOTH	20	64	11	31
Worm-eating Warbler[a]	*Helmitheros vermivorus*	WEWA	7	32	0	0
Yellow-billed Cuckoo[a]	*Coccyzus americanus*	YBCU	11	49	1	42
Yellow-breasted Chat	*Icteria virens*	YBCH	54	82	0	39
Yellow-throated Vireo[a]	*Vireo flavifrons*	YTVI	80	95	0	21
Yellow-throated Warbler[a]	*Dendroica dominica*	YTWA	16	46	0	6

[a] Requires forest interior conditions.

Appendix B.

Five-minute detection probabilities calculated from removal models (Farnsworth et al., 2002) for breeding bird species observed during point counts within an urban (Auburn, AL) and rural (Tuskegee National Forest, AL).

Species	5-min detection probability	
	Urban	Rural
ACFL	0.72 (0.72)	0.99 (0.01)
AMGO	0.68 (0.39)	0.97 (0.06)
AMRE		0.99 (0.01)
AMRO	0.84 (0.04)	0.76 (0.29)
BACS		0.99 (0.04)
BARS	0.98 (0.01)	0.86 (0.05)
BAWW		0.94 (0.10)
BGGN	0.72 (0.36)	0.99 (0.00)
BHCO	0.69 (0.14)	0.30 (0.30)
BHNU	0.53 (0.21)	0.80 (0.16)
BLGR	0.98 (0.01)	0.98 (0.01)
BLJA	0.92 (0.02)	0.96 (0.02)
BRTH	0.75 (0.07)	0.91 (0.07)
CACH	0.97 (0.01)	0.99 (0.00)
CARW	0.97 (0.01)	0.98 (0.01)
CHSP	0.72 (0.29)	
COGR	0.86 (0.02)	0.89 (0.05)
COYE		0.99 (0.02)
DOWO	0.52 (0.25)	0.90 (0.06)
EABL	0.97 (0.01)	0.96 (0.06)
EAKI	0.95 (0.04)	1.00 (0.00)
EAME	0.99 (0.01)	
EAPH	0.98 (0.02)	0.98 (0.04)
EATO	0.99 (0.00)	0.99 (0.00)
EAWP		0.96 (0.02)
EUCD	0.97 (0.02)	0.79 (0.18)
FISP		1.00 (0.00)
GCFL	0.98 (0.02)	0.94 (0.03)
GRCA	0.04 (0.43)	0.98 (0.04)
HAWO	0.45 (0.43)	0.98 (0.03)
HOFI	0.93 (0.02)	
HOWA	0.86 (0.26)	0.97 (0.01)
INBU	0.99 (0.01)	0.98 (0.01)
KEWA		0.96 (0.02)
LOSH	0.72 (0.72)	
LOWA	1.00 (0.00)	0.72 (0.27)
MODO	0.93 (0.01)	0.91 (0.10)
NOBO		0.51 (0.66)
NOCA	0.99 (0.00)	0.99 (0.00)
NOFL	0.77 (0.30)	0.88 (0.16)
NOMO	0.97 (0.01)	0.98 (0.01)
NOPA		0.99 (0.00)
NRWS		0.88 (0.21)
OROR	0.39 (0.68)	0.99 (0.01)
PIWA	1.00 (0.00)	0.95 (0.02)
PIWO	0.90 (0.11)	0.96 (0.04)
PRAW		0.99 (0.01)
PROW		0.99 (0.01)
PUMA	0.98 (0.01)	0.92 (0.06)
RBWO	0.84 (0.06)	0.90 (0.04)
REVI	0.94 (0.13)	1.00 (0.00)
RODO	0.96 (0.01)	
RWBL	0.99 (0.01)	0.99 (0.01)
SUTA	1.00 (0.01)	0.95 (0.02)
TUTI	0.97 (0.02)	0.99 (0.00)
WEVI	0.90 (0.15)	0.99 (0.00)
WOTH	1.00 (0.00)	0.98 (0.02)
YBCH		0.97 (0.01)
YBCU		0.61 (0.15)
YTVI		1.00 (0.00)
YTWA		0.90 (0.10)

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