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Research Paper

What you find depends on where you look: responses to proximate habitat vary with landscape context

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ABSTRACT. There is persistent interest in understanding responses of passerine birds to habitat fragmentation, but research findings have been inconsistent and sometimes contradictory in conclusions about how birds respond to characteristics of sites they occupy, such as habitat patch size or edge density. We examined whether these inconsistencies could result from differences in the amount of habitat in the surrounding landscape, e.g., for woodland birds, the amount of tree cover in the surrounding landscape. We compared responses of 22 woodland bird species to proximate-scale tree cover in open landscapes versus wooded landscapes. Our main expectation was that woodland birds would tolerate less suitable sites (less tree cover at the site scale) in open environments where they had little choice–where little tree cover was available in the surrounding area. We compared responses using logistic regression coefficients and loess plots in open and wooded landscapes in eastern North Dakota, USA. Responses to proximate-scale tree cover were stronger, not weaker, as expected, in open landscapes. In some cases the sign of the response changed from positive to negative in contrasting landscapes. We draw two conclusions: First, observed responses to proximate habitat measures such as habitat extent or edge density cannot be interpreted reliably unless landscape context is specified. Second, birds appear more selective, not less so, where habitat is sparse. Habitat loss and fragmentation at the landscape scale are likely to reduce the usefulness of local habitat conservation, and regional drivers in land-use change can have important effects for site-scale habitat use.

Ce que vous trouvez dépend d'où vous regardez : les réactions aux milieux avoisinants varient selon le contexte paysager

RÉSUMÉ. La compréhension des réactions des passereaux face à la fragmentation d'habitat est un sujet d'intérêt continu au sein de la communauté scientifique, mais les résultats sont variables d'une recherche à l'autre, parfois même contradictoires en ce qui concerne la réaction des oiseaux en fonction des caractéristiques des sites qu'ils occupent, comme la taille du peuplement ou la densité de lisières forestières. Nous avons examiné si ces contradictions pouvaient être attribuables à l'étendue des différents milieux dans le paysage environnant, par exemple, pour les oiseaux forestiers, le couvert d'arbres dans le paysage avoisinant. Nous avons comparé la réaction de 22 espèces forestières relativement au couvert forestier à l'échelle locale dans des paysages ouverts et des paysages forestiers. Nous nous attendions à ce que les oiseaux forestiers tolèreraient des sites moins propices (superficie du couvert d'arbres faible à l'échelle du site) dans des environnements ouverts où ils avaient peu de choix, c'est-à-dire qu'il y avait peu de couverture forestière dans les environs. Nous avons comparé les réactions au moyen de coefficients de régression logistique et de nuages de points loess dans des paysages ouverts ou boisés dans l'est du Dakota du Nord, aux États-Unis. Les réactions au couvert d'arbres à l'échelle locale étaient plus fortes dans les paysages ouverts, et non moins fortes, tel qu'attendu. Dans certains cas, le sens de la réaction est passé de positif à négatif dans des paysages opposés. Nous avons tiré deux conclusions : premièrement, les réactions observées face aux caractéristiques des milieux avoisinants, comme l'étendue du milieu ou la densité de lisières, ne peuvent être correctement interprétées que si le contexte paysager est spécifié. Deuxièmement, les oiseaux semblent plus sélectifs, et non moins sélectifs, là où l'habitat est rare. La perte d'habitat et la fragmentation à l'échelle du paysage concourent vraisemblablement à réduire l'utilité de la conservation d'habitat à l'échelle locale, et les facteurs régionaux jouant dans le changement d'usage des terres peuvent avoir des effets importants dans l'utilisation de l'habitat à l'échelle du site.

Key Words: *area sensitivity; habitat; habitat selection; landscape context; landscape fragmentation; North Dakota; scale; tree cover; woodland birds*

INTRODUCTION

Studies of habitat responses of bird species have sometimes produced inconsistent findings regarding sensitivity to habitat area, edges, and other aspects of habitat composition or fragmentation (Villard 1998, Thompson et al. 2002, Bayard and Elphick 2010, van der Hoek et al. 2013, Vetter et al. 2013). This inconsistency limits our ability to address both basic and applied questions, such as differences in population vulnerability in the face of landscape change, variation among species in habitat area requirements, plasticity in habitat use, and the likely effectiveness of conserving one habitat area versus another.

Multiple factors can help explain differences in findings, such as study design, regional variation in species abundance, or variation

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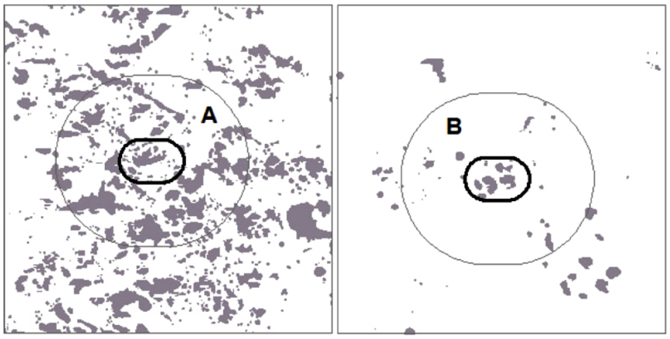
in habitat amount at the landscape scale. We focus here on the third of these. Amount of habitat in the landscape has long been understood to influence species occurrence, with landscape-scale effects operating simultaneously with proximate-scale effects (e.g., Cunningham et al. 2006, Desrochers et al. 2010, Zitske et al. 2011). Landscape-scale habitat amount also can influence local-scale edge effects (Thompson et al. 2002). We examine whether landscape-scale habitat amount influences habitat occupancy at the proximate scale. We also consider how the shape of response to habitat availability at the proximate scale, as visualized using loess plots, may respond to habitat availability at the landscape scale. This visualization can add important nuance to our understanding of species responses to habitat amount. We explore this question in a mixed savanna landscape, which allows us to explore these dynamics in landscapes that vary from largely wooded to largely open.

We proposed that landscape context could influence site-scale responses in one of two directions (Fig. 1). In landscapes where little suitable habitat is available, e.g., little tree cover, for woodland birds, a species could (1) become less selective and broaden its tolerance to occupy less-suitable sites (occupying areas that are lightly wooded at the site scale), or (2) become more selective, i.e., avoiding lightly wooded sites. For woodland birds, we consider mostly-wooded sites to be more suitable and lightly-wooded sites to be less suitable. Stated more generally, we consider the following competing hypotheses:

Fig. 1. Schematic representation of hypotheses regarding interaction of proximate and landscape scales. The two inner ovals each have 50% tree cover, but there is more tree cover surrounding oval A. The no-effect hypothesis (H0) predicts that there is no difference in the probability of a woodland bird occurring in the two inner ovals. The tolerance hypothesis (H1) would suggest that a woodland species is more likely to occupy patches in B than in A, because it has few alternatives. The avoidance hypothesis (H2) would suggest that a woodland species is less likely to occur in B than in A.



H_0: No effect. Responses to site-scale habitat are similar in different landscapes;

H_1: Tolerance hypothesis. When little habitat is available in the landscape, birds are more likely to occupy less-suitable sites; they discriminate little between abundant and sparse habitat at the local scale.

H_2: Avoidance hypothesis. When little habitat is available in the landscape, birds are less likely to occupy less-suitable sites; they discriminate more strongly between abundant and sparse habitat at the local scale.

These alternatives have fundamental implications for conservation strategy. If H_0 is true, then protecting all available habitat areas, including isolated ones, is equally important. If H_1 is true, then conservationists should give special attention to species occupying less-suitable habitat areas: these may provide critical resources when other habitat is unavailable; they may also act as ecological traps. For example, area-sensitive species could be forced to occupy unsuitably edge-rich habitat, presumably with corresponding higher abundance of edge-dwelling predators, where expansive interior habitat is unavailable (see Vetter et al. 2013). In this case, controlling predators or reducing other risk factors would be a conservation priority. If H_2 is true, then reduced habitat availability at the landscape or regional scale could make local habitat remnants less useful for species conservation. This would imply that fragmentation is a positive feedback process, in which habitat loss leads to reduced suitability of remaining fragments. In this case, conservation efforts should focus on strategies to prevent widespread habitat loss, such as attention to the economic and political drivers that influence landscape change.

These conservation implications are not academic questions. Conservation agencies with limited budgets frequently must prioritize spending among different habitat areas. Decisions to maintain or purchase a particular area of habitat sometimes depend on managers' expectations of how well small or isolated areas are likely to support wildlife of concern.

Some studies have investigated the interaction of proximate and landscape scales. Parker et al.'s (2005) meta-analysis of 33 separate studies found a nonsignificant tendency for patch size effects to diminish as the amount of surrounding forest increased. Radford et al. (2005) found that species richness responded differently to amount of tree cover in landscapes with aggregated versus dispersed tree cover. Ribic et al. (2009*a*) found that abundance of some avian species was positively associated with proportion of suitable habitat in the landscape around a site, and in a broader literature review of area sensitivity in grassland birds, Ribic et al. (2009*b*) reported that most studies found weaker evidence for area sensitivity in landscapes comprising a high proportion of grassland. In meta-analyses of edge effects on nest predation, both Batáry and Báldi (2004) and Vetter et al. (2013) found contrasting results among different study areas and concluded that landscape context, in particular forest cover, strongly influences the effect of edge density on nest predation. Our data set allowed us to address the issue directly and with 22 different species.

We do not focus here on the relative importance of habitat amount and habitat configuration, a question that has been explored extensively elsewhere (Thompson et al. 2002, Fahrig 2013, Villard and Metzger 2014) and that continues to be debated (Fahrig 2015, Hanski 2015). Indeed, Lindenmeyer and Fischer (2007) and Didham et al. (2012) have argued that while this dichotomy has become entrenched in our understanding of habitat change, it has not always been useful for furthering conservation goals (see also Villard and Metzger 2014). We focus on habitat amount as an explanatory variable, and we examine the interaction of its effects on species occurrence at the landscape and proximate scales.

Understanding the influence of landscape context on proximate-scale habitat responses is also useful for comparing population abundance and population trends among regions. Many eastern North American bird species, for example, occur from the Atlantic coast to the Great Plains. Monitoring efforts such as the North American Breeding Bird Survey (BBS) have found contrasting population trends in different parts of those ranges (Sauer et al. 2014). The BBS shows the value of incorporating data from throughout the continent to gain a broader understanding of population trends. Further studies that compare multiple study areas are important for improving our understanding of fundamental species ecology (van der Hoek et al. 2013, Vetter et al. 2013). For example, if one particular landscape factor, such as edge density or habitat area, is important in one region, is its influence similar in others? If not, does this imply plasticity in response to habitat, or are other factors in play? Integrating studies across multiple landscapes and regions would help elucidate general patterns in influences of habitat on population distributions and on population trends.

STUDY AREA AND METHODS

We assessed the consistency of site-scale responses in contrasting landscape contexts by examining responses of woodland birds to the amount of proximate-scale tree cover (within 100 m around sample locations) in open landscapes and in wooded landscapes. We did this comparison in a naturally fragmented oak savanna landscape of grassland and woodland that provided a range of landscape-scale tree cover.

Our study area was the Sheyenne National Grassland in southeastern North Dakota (97.5W, 46.5N), which comprises 28,400 ha of tallgrass prairie, mixed-grass prairie, wetlands, and woodland. Manske (1980) and Seiler and Barker (1985) have described the vegetation of the area. Plant communities include tallgrass and mixed-grass prairie on rolling upland topography, bur oak (*Quercus macrocarpa*) savanna and quaking aspen (*Populus tremuloides*) stands on upland dunes, and sedge meadows and wetlands in low-lying areas. Low (0.5 - 1 m) shrubs, primarily western snowberry (*Symphoricarpos occidentalis*), are scattered throughout the mixed-grass prairie. A riparian deciduous forest dominated by basswood (*Tilia americana*), cottonwood (*Populus deltoides*), and willow (*Salix* spp.) occurs on the northern end of the area. With its diversity of vegetation types, the Sheyenne National Grassland supports a rich variety of birds (Cunningham et al. 2006, Martin and Svingen 2010) and a diversity of landscape types minimally interrupted by human settlements or agriculture.

Bird count data

Indicated breeding pairs were counted (Stewart and Kantrud 1972, Igl and Johnson 1997, Desrochers et al. 2010, Pickens and King 2014) along belt transects 2 - 6 km long. We designated indicated breeding pairs, following Stewart and Kantrud (1972) and Igl and Johnson (1997): If sexes were alike, the number of singing males was counted. If no individuals were singing, then the number of observed individuals was halved and rounded up to derive indicated pairs. Birds flying over the segment were included only if they apparently were using the area for foraging. Transects allowed us to efficiently acquire a relatively large data set remote from roads. There were 24 belt transects. Bird counts were conducted between half an hour before sunrise and four hours after sunrise, between late May and early July from 2002 to 2005. One observer walked these transects slowly (1 km/hour), recording all birds seen or heard within 50 m on either side. The same observer did surveys in all years. We used this conservative distance to reduce variation in detectability: although detection varies among species and habitat types, especially at distances of 100 m or more (Matsuoka et al. 2012), detections do not tend to decline appreciably within 50 m (Simons et al. 2007, Koper et al. 2016), and previous studies have found that a 50 m distance provides reliable data for a broad range of species in wooded as well as open habitats (Matsuoka et al. 2012). Studies of auditory-only detections have shown that detection distances are subject to error (Alldredge et al. 2007), especially in windy or noisy conditions (Koper et al. 2016). To reduce these risks, we sampled only in weather conditions with little wind and no rain; other noise sources were minimal. A 50-m distance also ensured that we were sampling local habitat use, rather than landscape-scale habitat. Field methods are described more fully by Cunningham et al. (2006).

A global positioning system (GPS) unit was used to divide transects into 100-m segments and to record bird counts by these segments, which later were georeferenced to land-cover data. All analysis was done on these 100-m transect segments, for which we calculated amount of tree cover (X) and the presence or absence of a species (Y).

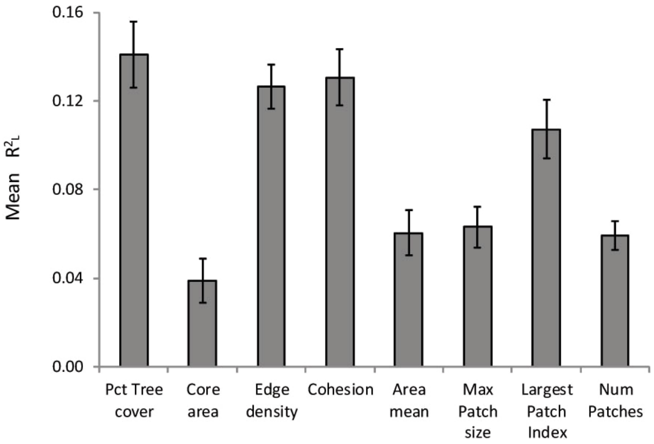
Land cover and landscape metrics

Definitions of “habitat” vary in ecological studies and may include factors as diverse as vegetative density, maturity, species composition, vertical structure, and other features; moreover, for many birds habitat includes multiple types of vegetation, such as edges, shrubs, or grassland, as well as trees. In studies aiming to maximize explanation of site selection in individual species, detailed descriptors of habitat and fragmentation can be essential. For comparisons across a number of species and environments, however, or where exact details of habitat preferences are unclear, a more generalized approach can provide useful insights. Thus many studies of woodland bird responses to landscapes generalize habitat in terms of the extent or amount of tree cover (e.g., Andrén 1994, Freemark and Collins 1992, Parker et al. 2005, Radford et al. 2005, Desrochers et al. 2010). We follow this convention in the present study.

Landscape composition and fragmentation also can be described with many measures, such as patch shape, isolation, core area, or edge density, or other metrics (McGarigal et al. 2002). In preliminary analysis, we used FRAGSTATS (McGarigal et al. 2002) and the FragStatsBatch utility in ArcGIS 9.2 (Mitchell 2007, ESRI 2004) to calculate these different metrics. We calculated these metrics using land cover data that was digitized from 1-m resolution digital air photos and converted to raster format with a cell size of 5 m. We then compared explanatory effects among metrics to evaluate which were most useful for explaining species presence/absence. Habitat amount is widely understood to be more informative than configuration factors (Fahrig 2013, Villard and Metzger 2014). For example, in some studies it has been only at low levels of habitat availability in the landscape that configuration variables (size or proximity of patches) have become important (e.g., Villard and Metzger 2014, Hanski 2015). We compared the explanatory effect of landscape metrics in our study area and found that overall habitat amount provided as good as or better explanation than other fragmentation metrics (Fig. 2). This measure is increasingly recognized as influential for proximate-scale habitat occupation in fragmented landscapes (Dunford and Freemark 2005, Ribic et al. 2009*b*, Desrochers et al. 2010, Cunningham and Johnson 2011, 2012, Vetter et al. 2013).

Habitat extent (amount) and configuration (such as edge density or cohesion) are often considered to be different approaches to evaluating fragmented landscapes. But if we consider fragmentation in terms of the difference between extensive, unbroken habitat and more mixed landscapes (see Andrén 1994, Wiens 1995), then the contrast between 90% and 40% tree cover (within 100 m, for example) does serve to distinguish expansive habitat from mixed habitat (see Fig. 1). Amount of tree cover is also less sensitive to scale than many configuration measures, such as edge density, core area, shape, or cohesion (McGarigal et al. 2002). Therefore we used tree cover measured within a 100-m radius to represent habitat extent at the proximate, or site, scale.

Fig. 2. Average response and standard error (vertical lines) among 22 grassland species to 8 landscape fragmentation metrics, where the response variable was likelihood of occurrence. All transect segments were used in these averages. (Data from Cunningham and Johnson 2011; for metric definitions, see McGarigal et al. 2002.)



To characterize landscape composition, we used amount of tree cover within 400-m radii around bird observations. This is a relatively small area to represent landscape conditions, but our aim was to test for differences, not to characterize landscape effects per se. The choice of scales was therefore arbitrary, and similar analysis could be done at different scales. In preliminary analysis we tested larger "landscapes" of 800 m and 1200 m radius around bird observations, and these produced results similar to those at 400 m. However variation in tree cover at those scales was reduced, because with larger radii we had few areas with a high percentage of tree cover. Thus we had lower confidence in comparisons of open and wooded landscapes at those larger radii than we did with the smaller 400-m radius. Because our purpose was to test whether contrasting landscape conditions had an effect, then, we used a 400-m radius to represent the landscape scale, which ensured that we had a reasonably large sample of "wooded" landscapes for analysis.

Analytical methods

We analyzed data first by comparing strength of response of species' occurrence to 100-m scale tree cover in open landscapes and in wooded landscapes, using logistic regression. In the logistic models we were interested in the relative strength of one model over another, not in the absolute explanatory power of our models, which contained only one explanatory variable (amount of tree cover). We then graphed frequency of occurrence on a gradient of percentage tree cover, again in open landscapes and wooded landscapes, to assess whether patterns of occurrence differed between the two landscape contexts.

Because we were interested in differences between landscape conditions, rather than in examining particular threshold values or landscape scales, we used a threshold of 30% tree cover to distinguish wooded versus open landscapes (within a 400-m radius around bird observations). A higher threshold value was not used because the study area was largely open grassland, and relatively few landscapes had abundant tree cover within a 400-m radius. Thus "wooded" landscapes had at least 30% tree cover within 400 m (N = 562 transect segments, range = 30.1 to 75.4% tree cover, median = 38% tree cover). "Open" landscapes had less than 30% tree cover within 400 m (N = 2699 segments, range = 0 to 29.9% tree cover, median 5% tree cover). In all, 22 species with affinities for woodland habitat occurred at least 20 times in both open and wooded landscape groups (Table 1).

For each species, for each landscape condition, we evaluated the strength of response to 100-m-scale tree cover using logistic regression (Bayard and Elphick 2010, Desrochers et al. 2010), with site-scale percentage tree cover as the explanatory variable and presence/absence as the response variable. Preliminary analysis indicated that quadratic models produced results that were equivalent to or stronger than linear models for all species. Thus for each species we used the following model: Probability of occurrence = $1 - 1/(\exp(\beta_0 + \beta_1 X + \beta_2 X^2))$, where X is percentage tree cover within 100 m of a segment. Results are reported in terms of R^2_L, an analog of the usual multiple correlation coefficient (R^2) appropriate for logistic regression (Menard 2000, Quinn and Keogh 2002). Our data set represented multiple years, so we tested for variation by year on each species' responses to habitat composition. This analysis indicated that year effects and interactions between year and other variables were not significant, so for subsequent analysis we pooled data from the four years (Appendix 1, Methods). This analysis was done using JMP software (SAS Institute 2010). We did this analysis first for the entire data set and then for independent subsets.

Groups of independent observations

Field data were nonindependent, adjacent observations gathered on belt transects, so to reduce dependence among observations we extracted 10 subset groups of transect segments by grouping every 10th segment from the complete data set. All segments in a group were thus separated by at least 900 m. We then analyzed each of the 10 subset groups separately. To assess whether there was a difference between open landscapes and wooded

Table 1. Aggregate logistic regression results for all observations in open landscapes and wooded landscapes. There were 2699 segments in open landscapes and 562 segments in wooded landscapes in this area; T100 = percentage tree cover within 100 m.

		Open				Wooded				R^2_L Ratio
Species	Code	$N^{\dagger}$	R^2_L	T100	$T100^2$	N	R^2_L	T100	$T100^2$	Open/ Wooded
Mourning Dove (*Zenaida macroura*)	MODO	264	0.11**	10.42**	-11.34**	59	0.04**	14.79**	-13.66*	2.5
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	YBSA	79	0.23**	17.71**	-17.81**	82	0.03*	9.96*	-8.61*	7.8
Eastern Wood-Pewee (*Contopus virens*)	EAWP	100	0.35**	16.28**	-11.27**	131	0.09**	15.71**	-11.76**	3.8
Least Flycatcher (*Empidonax minimus*)	LEFL	250	0.27**	12.94**	-9.74**	88	0.19**	4.71	-0.95	1.4
Eastern Kingbird (*Tyrannus tyrannus*)	EAKI	239	0.03**	7.36**	-11.35**	26	0.04	-4.18	1.36	0.7
Yellow-throated Vireo (*Vireo flavifrons*)	YTVI	27	0.28**	16.54**	-11.5*	20	0.02	2.04	-0.22	17.1
Red-eyed Vireo (*Vireo olivaceus*)	REVI	47	0.29**	14.28**	-9.16*	98	0.16**	14.45**	-7.97	1.8
Blue Jay (*Cyanocitta cristata*)	BLJA	35	0.16**	15.52**	-15.95**	40	0.03	10.44	-8.76	5.9
Black-capped Chickadee (*Poecile atricapillus*)	BCCH	29	0.13**	17.74**	-23.59**	33	0.03	13.26	-12.98	4.2
White-breasted Nuthatch (*Sitta carolinensis*)	WBNU	22	0.17**	19.34**	-22.05*	48	0.02	8.71	-6.95	7.1
House Wren (*Troglodytes aedon*)	HOWR	246	0.31**	15.84**	-13.6**	115	0.02*	5.36	-3.56	13.1
Eastern Bluebird (*Sialia sialis*)	EABL	46	0.1**	13.24**	-16.68**	32	0.04	3.95	-7.7	2.5
American Robin (*Turdus migratorius*)	AMRO	94	0.12**	9.83**	-8.69**	36	0.04*	1	-1.47	2.8
Gray Catbird (*Dumetella carolinensis*)	GRCA	102	0.15**	13.68**	-14.96**	59	0.02	1.57	-0.23	7.0
Cedar Waxwing (*Bombycilla cedrorum*)	CEDW	38	0.12**	14.77**	-18.13**	29	0.02	10.46	-9.89	5.3
Yellow Warbler (*Setophaga petechia*)	YWAR	166	0.12**	10.34**	-10.16**	39	0.05**	-0.52	3.01	2.3
Ovenbird (*Seiurus aurocapilla*)	OVEN	20	0.26**	32.31**	-37.07*	98	0.11**	14.07**	-8.94*	2.4
Field Sparrow (*Spizella pusilla*)	FISP	138	0.26**	23.5**	-30.85**	139	0.03**	7.94**	-8.61**	10.0
Lark Sparrow (*Chondestes grammacus*)	LASP	69	0.17**	17.42**	-21.07**	58	0.06**	9.82	-14.38*	2.9
Vesper Sparrow *(Pooecetes gramineus)*	VESP	206	0.11**	10.92**	-12.35**	94	0.02	-2.01	0.31	5.6
American Goldfinch (*Spinus tristis*)	AMGO	204	0.1**	9.96**	-10.64**	71	0.01	3.65	-4.47	11.2
Baltimore Ooriole (*Icterus galbula*)	BAOR	124	0.18**	15.22**	-16.65**	72	0.06**	12.17**	-8.88*	3.3

[†] N = number of observations; $R^2_{L\,=}$ logistic coefficient of determination; estimated regression coefficients (of T100, $T100^2$) are shown.
* $p < 0.01$
** $p < 0.001$

landscapes, we compared the mean responses (R^2_L values) of 10 open-landscape groups and 10 wooded-landscape groups. (Of 440 groups, 86 groups with fewer than 4 observations of a species were excluded from calculation of means).

It is worth noting that independence among samples was not a necessary condition of analysis: Previous studies have demonstrated the usefulness of nonindependent data when conclusions do not rest on estimates of significance in parametric tests, which underestimate variance in nonindependent data and thus overestimate the significance of results in hypothesis testing (Pan 2001, Diniz-Filho et al. 2003). Repeating tests on independent subsamples, however, does increase confidence that we were not repeatedly measuring or evaluating the same observations.

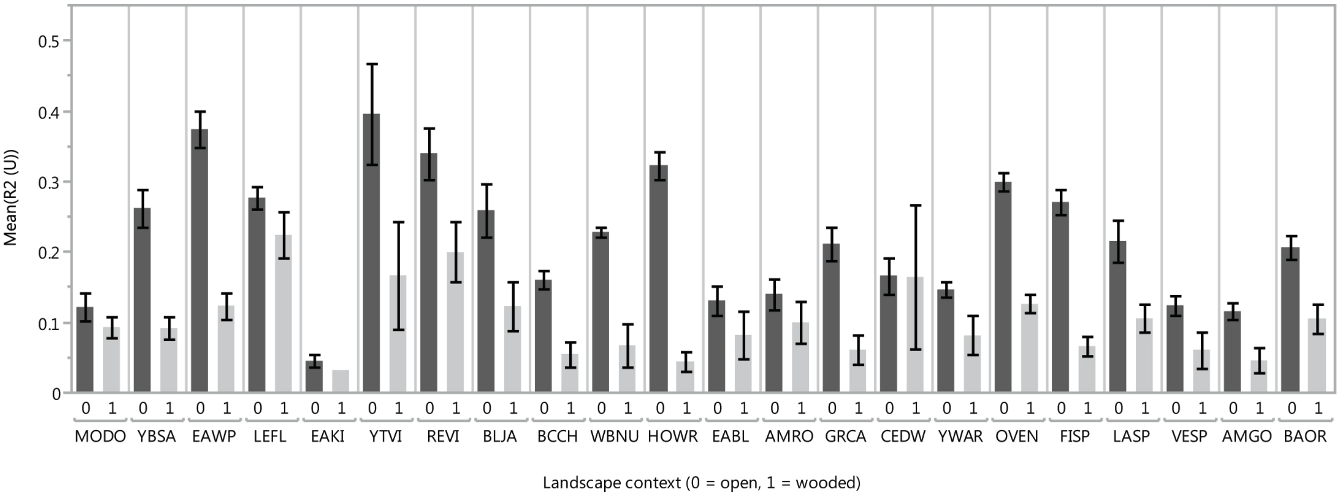
Incidence plots showing patterns of occurrence

In addition to regression results, the shape of a species' response to tree cover is useful in indicating levels of tree cover at which the species is most likely to occur. We used loess (locally weighted estimation and scatterplot smoothing; Cleveland and Devlin 1988, Cohen 1999) to define curves showing changes in the probability of occurrence (incidence) as site-scale tree cover increased. We created scatter plots separately for open landscapes and for wooded landscapes as follows: We sorted all segments by percentage tree cover within 100 m. We then grouped the sorted observations into even-sized groups, and for each group we calculated the observed frequency (probability) of occurrence of a species. Thus, by aggregating the segments, we created continuous data, representing the frequency of occurrence for a group, from binary presence/absence observations. For each group we also calculated the average percentage tree cover. We then plotted frequency of occurrence values against the average percentage tree cover. For the 2699 open-landscape segments, we used 44 groups of 60 observations and one group of 59; for the 562 wooded-landscape segments, we used 20 groups of 27 and one group of 22.

To visualize patterns in the incidence plots, we then used SAS PROC LOESS (SAS Institute 1999), with smoothing parameter of 0.5, which showed patterns while reducing noise. The resulting curves indicated patterns such as thresholds, peaks, and asymptotes in responses to amount of tree cover at the 100-m scale. A flat line would indicate no response to proximate tree cover. A curve rising to the right would indicate selection for abundant proximate tree cover. Peaks would indicate a tendency to occur most frequently at intermediate levels of tree cover at the 100-m scale (Cunningham and Johnson 2012). In plots comparing open and wooded landscapes, we adjusted Y-axes to the data range, to show the relative shape of the patterns.

For loess plots, we used the entire data set to show patterns of response. To test whether results were similar with the entire data set or with subsets (as in logistic regression analysis above), we tested the influence of nonindependence in our study by comparing incidence plots for the entire (nonindependent) data set to plots calculated for five separate subsamples of the data, in which all sites were separated by at least 400 m (see Appendix 1).

Fig. 3. Comparison of regression results in open and wooded landscapes. In all cases, the predictor variable was percentage tree cover within 100 m, and the response variable was likelihood of occurrence for a given species. Bars represent the mean of regression coefficients of determination for 10 groups of observations in open landscapes and 10 in wooded landscapes. Error bars represent 1 standard error from the mean. Open landscapes were defined as having < 30% tree cover within 400 m; wooded landscapes had > 30% tree cover. For species codes, see Table 1.



For all species, subsamples produced similar patterns but, because they were smaller samples, had more variability than did the entire data set. Loess plots with all observations were effectively an average of the different subsamples for a species. Because it is not possible to know which of the subsamples is most "correct" for a species, the most reliable pattern is that of the entire data set. Results are shown for all species in Appendix 1.

RESULTS

Regression models were significant ($p < 0.001$) for all 22 species in open landscapes but for only 9 of the 22 species in wooded landscapes (Table 1). In a comparison of independent subsets of the data, with 10 open-landscape groups and 10 wooded-landscape groups (Fig. 3), small sample sizes led to reduced differences between open and wooded landscapes, but the overall pattern was the same: 16 of 22 species had significantly stronger responses to proximate-scale tree cover in open landscapes, as indicated by nonoverlapping standard error intervals. Several species were strongly different between the two contexts, e.g., Yellow-bellied Sapsucker (*Sphyrapicus varius*), Eastern Wood-Pewee (*Contopus virens*), House Wren (*Troglodytes aedon*). Several edge or generalist species showed little or no difference, e.g., Mourning Dove (*Zenaida macroura*), Eastern Kingbird (*Tyrannus tyrannus*), American Robin (*Turdus migratorius*).

Patterns of responses in incidence plots also differed between open and wooded landscapes for most species (Figs. 4 and 5). For example, the probability of Mourning Dove occurrence increased with tree cover at the 100-m scale in open landscapes, but in wooded landscapes Mourning Doves were more likely to occur in moderately wooded areas and avoided abundant tree cover at the 100-m scale (as shown by the loess curve peaking in the middle range of tree cover). All species except the Eastern Kingbird had generally positive responses to increasing tree cover in open landscapes. In wooded landscapes, in contrast, most species shifted to a weaker or even negative pattern. Some species had a relatively flat response in wooded landscapes, e.g., House Wren, American Robin, Baltimore Oriole (*Icterus galbula*). Other species changed to patterns with an asymptote at intermediate levels of proximate tree cover, e.g., Yellow-bellied Sapsucker, Eastern Wood-Pewee. Still others shifted to declining patterns, e.g., Vesper Sparrow (*Pooecetes gramineus*), Lark Sparrow (*Chondestes grammacus*). A small group of species retained a clearly positive trend even in wooded landscapes; these were species with strongest interior-habitat affinities, Least Flycatcher (*Empidonax minimus*), Red-eyed Vireo (*Vireo olivaceus*), Ovenbird (*Seiurus aurocapilla*).

Only the Ovenbird had a more sharply positive response to proximate tree cover when in wooded landscapes: here the weaker response in open landscapes reflects the small number of observations in open landscapes. This species did not occur at all in sites with less than 20% tree cover at the proximate scale (Figs. 4 and 5). Three species had thresholds of occurrence in open landscapes, Eastern Wood-Pewee, Yellow-throated Vireo (*Vireo flavifrons*), and Red-eyed Vireo. In the wooded landscapes none of these species had thresholds of proximate-scale tree cover, and one (Eastern Wood-Pewee) tended to occupy moderately wooded sites when in a wooded landscape.

DISCUSSION

For the woodland species examined here, the results support our hypothesis 2, that birds show increased selectiveness and use a narrower range of proximate-scale tree cover in landscapes where tree cover is not abundant. In regression analysis, the strength of explanation was stronger in open landscapes than in wooded landscapes for most species; in incidence plots, species that favored abundant tree cover when observed in open landscapes were frequently nonselective or even avoided abundant tree cover when observed in relatively wooded landscapes. Previous work (Parker et al. 2005, Ribic et al. 2009*a*) has indicated similar patterns.

Fig. 4. Comparison of responses (estimated probability of occurrence) to site-scale (100-m radius) tree cover in open landscapes and wooded landscapes. (Open landscapes were defined as < 30% tree cover within a 400-m radius; wooded landscapes had > 30% tree cover.) Lines show loess scatterplot smoothing and 95% confidence intervals for groups of observations (dots; see Methods). An upward linear pattern indicates a strong preference for more tree cover at the 100-m scale. A peaked pattern indicates selection for intermediate amounts of tree cover. For some species, proximate-scale responses in open and wooded landscapes differed, e.g., Mourning Dove (*Zenaida macroura*), weakened, e.g., House Wren (*Troglodytes aedon*), or even reversed, Eastern Kingbird (*Tyrannus tyrannus*). Twelve of the 22 species are shown (see Figure 5 for the remaining 10). For species' scientific names, see Table 1.

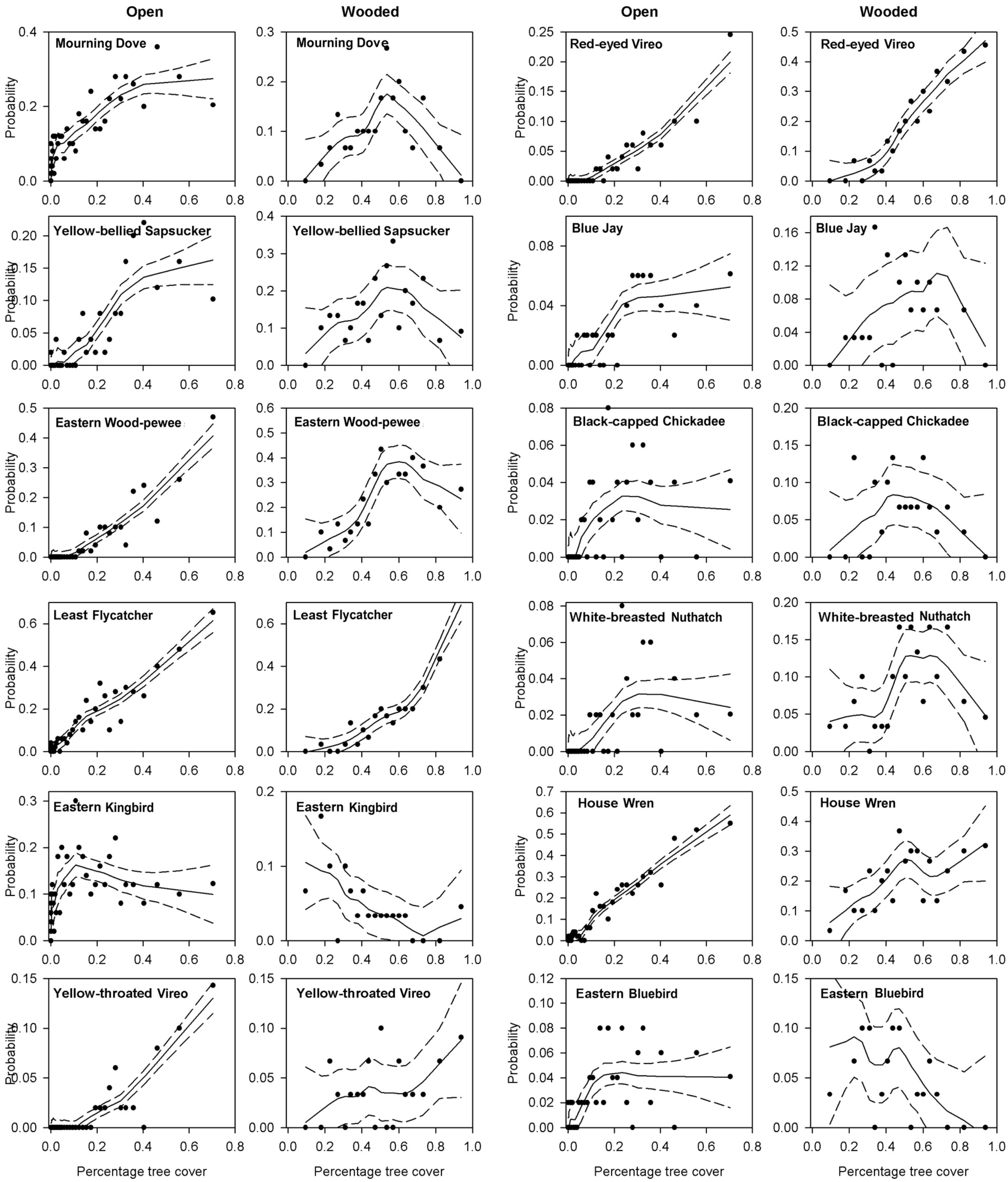
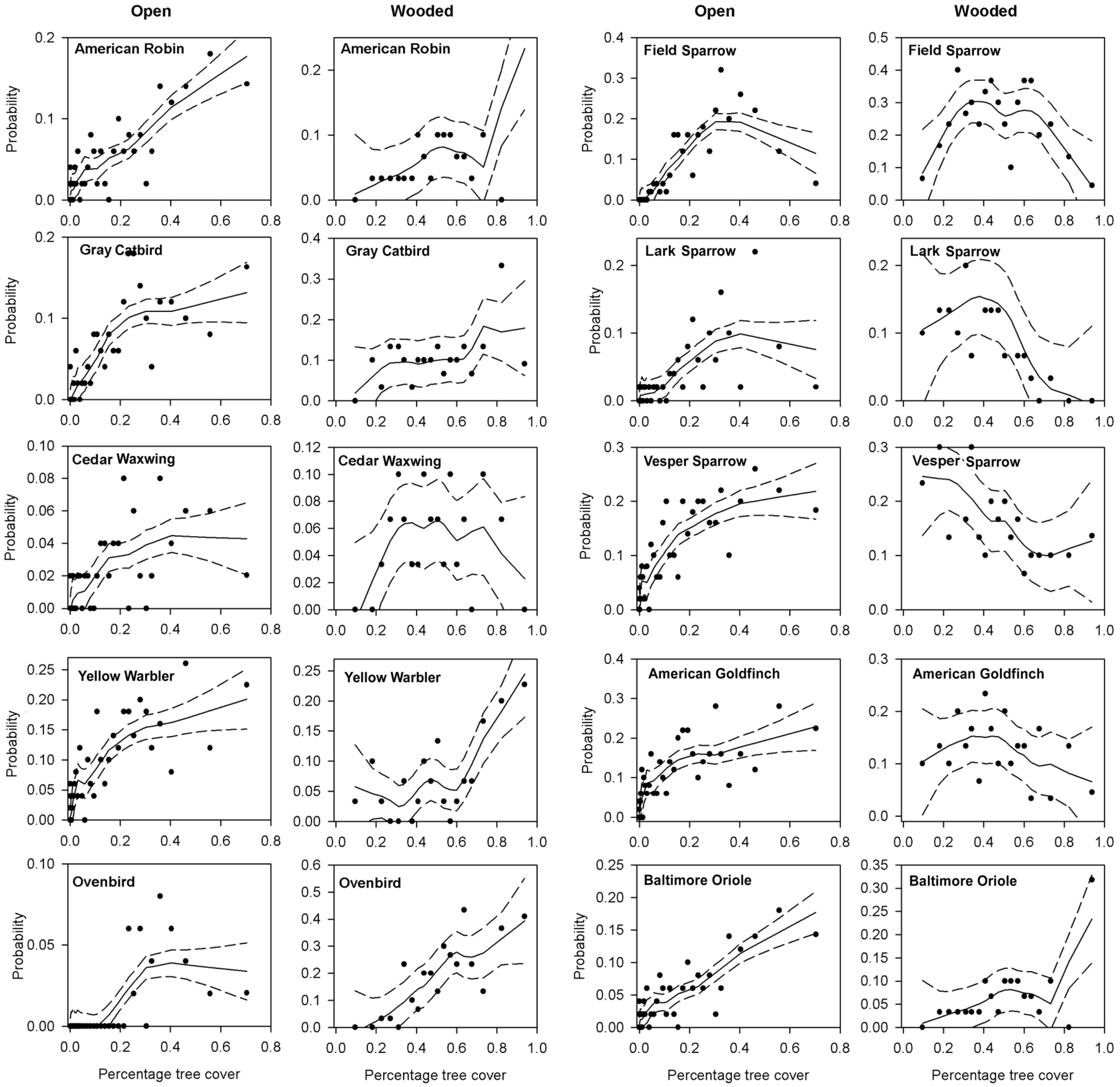


Fig. 5. Comparison of responses (estimated probability of occurrence) to site-scale tree cover in open and wooded landscapes. Ten of 22 species analyzed are shown. For explanation see Figure 4. Some species were mostly absent from open landscapes, e.g., Ovenbird (*Seiurus aurocapilla*) or from heavily wooded landscapes, e.g., Baltimore Oriole (*Icterus galbula*). For species' scientific names, see Table 1.



If a study examined the Eastern Wood-Pewee or White-breasted Nuthatch (*Sitta carolinensis*) only in open landscapes, both species could be described as strongly preferring abundant tree cover. A study examining the same species in a wooded landscape could describe them as indifferent to increasing tree cover or even avoiding heavily wooded habitat at the proximate scale (Fig. 4). Other species that frequent habitat edges, such as the Eastern Kingbird or Eastern Bluebird (*Sialia sialis*), might appear indifferent to increasing proximate tree cover when observed in open landscapes. These same species, studied in a wooded environment, might show an aversion to heavy tree cover. Still sharper contrasts might occur for the Vesper Sparrow and American Goldfinch (*Spinus tristis*), both of which responded positively to increasing tree cover in open landscapes but negatively in wooded landscapes (Fig. 5).

There were species that showed little difference among landscapes: The Ovenbird, for example, showed strong responses to increasing tree cover even in the wooded landscapes. For other species, similar responses in open and wooded landscapes may reflect the particular range of available landscapes in our study area: the Least Flycatcher, for example, is not an interior woodland species in all environments, but in this landscape, at this low range of landscape-scale tree cover, this species strongly preferred greater amounts of proximate tree cover. A comparison with more heavily wooded environments might yield more variation in results. Some edge species or generalist species also may have little difference in their responses in different environments, presumably owing to a wide tolerance of habitat conditions, for example, Cedar Waxwing (*Bombycilla cedrorum*). In addition, it is important to note that we used only tree cover as an explanatory variable, and many species select for shrubs, woodland edges, or other habitat features, e.g. Gray Catbird (*Dumetella carolinensis*), Yellow Warbler (*Setophaga petechia*). A similar approach to modeling other habitat types might produce responses with stronger patterns in loess plots.

A contrast in conclusions about the nature and strength of habitat selection in different study areas does not mean we cannot compare study areas or understand habitat responses; it means that comparisons should be explicit about context. General observations regarding habitat requirements should pay explicit attention to extent of suitable habitat in the landscape and region surrounding a study area. Studies of fragmentation and the effects of patch area, isolation, shape, or other metrics should account for, or even control for, landscape context in the study design. This conclusion should not be surprising, as it has long been clear that birds respond to landscapes at a range of scales (Wiens 1995, Lee et al. 2002), and that species occurrence is influenced by the nature of the matrix composition, as well as by a habitat area itself (Ricketts 2001, Haila 2002). Our results further indicate that it is insufficient to describe habitat responses without reference to habitat availability in the larger context.

The variation in shape of our loess plots also indicates that caution should be employed in widely used designations such as “interior” and “edge” species, because context can influence patterns of habitat selection. Several woodland-dependent species selected for abundant tree cover in an open landscape, showing preferences for interior habitat, but selected more edge-rich sites when the surrounding landscape was wooded. Examples include Yellow-bellied Sapsucker, Eastern Wood-Pewee, Blue Jay (*Cyanocitta cristata*), and White-breasted Nuthatch (Fig. 4). Previous studies have suggested that contrasting study areas could account for such variation in observed fragmentation sensitivity (see, for example, Chan and Ranganathan 2005, Vetter et al. 2013). It may seem contradictory that species would prefer trees at the landscape scale but avoid them at the proximate scale, but some of these species may use both edge and interior woodland features: for example, they might benefit from both the better cover of dense woodlands and greater invertebrate prey density at open edges.

This study designated landscape scale at a small radius of 400 m, and it distinguished open and wooded landscapes at a relatively low threshold of 30% tree cover within that 400-m radius. We used these values because our landscape was largely open. It was beyond the scope of this study to identify the scales and percentage tree cover at which contrasts might emerge or diminish for different species, but we do know from this study that responses are not always the same in different landscape contexts. Repeating this analysis in other study areas could help identify further the influence of scale and of thresholds in tree cover on results.

Similarly, there is a possibility that differences in tree species, height, density, and other aspects of tree cover could influence bird species distributions. Clearly bird species respond to many aspects of habitat composition and configuration at a range of scales. In particular, riparian forests were taller and more dense, with more basswood and cottonwood and fewer oaks than in the drier savanna landscapes. These contrasts are difficult to control for in natural environments. However, these contrasts do not diminish the importance of our findings: Suppose, for example, an open landscape that has more oaks and a wooded landscape with more basswood. In general, Red-eyed Vireos, which occupy both basswood and oak forests, were more likely to occur in densely wooded locations within the open landscapes. An Eastern Wood-Pewee, in contrast, which also occupies both types of tree species, was more likely to occur at intermediate levels of tree cover when in the wooded landscape. Is this because Eastern Wood-Pewees prefer oaks to basswood, while Red-eyed Vireos prefer basswood to oaks? Those contrasts were not clearly evident in this study, although detailed analysis of responses to tree species is beyond the scope of this paper. The fact remains that despite variations in habitat composition, the amount of tree cover had an effect, both in strength of explaining species occurrence and in the shape of responses as tree cover in the landscape increased.

For purposes of species conservation, a lesson to be taken from these results is that when suitable habitat is not readily available at the landscape scale, then birds can be increasingly sensitive in habitat requirements. Increased sensitivity to proximate habitat conditions could exacerbate the challenge of species conservation as general habitat availability declines: For species that strongly prefer abundant tree cover, or those with large home ranges, fragmentation in the larger landscape could make species less likely to occupy a local conservation area. Conversely, small conservation areas may become more useful or effective if regional processes and incentives lead to broad-scale habitat regeneration (Renfrew and Ribic 2008). In either case, a piecemeal approach to conservation is likely to be less effective than more regional strategies that address the larger processes of habitat loss.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/865

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Appendix 1

Methods: Variable selection, Independence, and Year Effects

We describe here several aspects of our methods in greater detail than we can do in the paper itself. We first add further details regarding the explanatory effect of tree cover in comparison to other variables. We also discuss the problems of independence in the data set and of year effect in pooling data.

Selecting an explanatory landscape variable

We used percentage tree cover because it was best overall, as discussed in Cunningham and Johnson (2011). Percentage tree cover and edge density were equivalent in their influence on species. Because of the relatively high values for the best-explained species, percentage tree cover had the highest overall average R^2_L values. This finding was consistent at 5 different scales (Table A1.1). Because edge density is scale-dependent, in that it is influenced by scale and grain of analysis (Wu et al. 2002), we used percentage tree cover as our landscape descriptor for subsequent analysis.

Table A1.1. Average R^2 value for each variable for all species at 5 landscape scales, using quadratic models. The strongest measures at each scale are bolded.

	Scale (m)				
Variable	200	400	800	1200	1600
Pct tree cover	**0.14**	**0.12**	**0.10**	**0.08**	**0.08**
Edge density	0.13	0.11	0.09	**0.08**	0.07
Cohesion	0.13	0.10	0.07	0.06	0.05
Largest patch index	0.11	0.08	0.05	0.05	0.05
Core area	0.04	0.02	0.01	0.01	0.01
Mean patch size	0.06	0.06	0.05	0.05	0.05

Amount of tree cover was correlated with other measures of fragmentation. Percentage tree cover was strongly and positively correlated with edge density (Pearson's r = 0.82, using tree cover calculated within 200 m) and largest patch index (r = 0.81). Percentage tree cover was moderately correlated with cohesion (r = 0.58), percentage core area (r = 0.50), and maximum patch size on a segment (r = 0.68). Correlations were also strong between measures of tree cover calculated at different scales: percentage tree cover within 200 m was strongly correlated with that within 400 m (r = 0.93) and within 1200 m (r = 0.72).

Independence

A potential concern in our analysis is that we did not account for possible dependence between variables on adjacent segments of transects. A transect segment will be intrinsically more similar to an adjacent segment than to one some distance away. Moreover, adjacent segments have nearly identical surrounding landscapes, so they are non-independent in that manner, as well. The implication of this for analytical purposes is primarily that Independence allows one to compute the probability of a series of events as the product of the probabilities of the individual events. Reliably computing probability of significant results is especially important in computing probabilities under specified hypotheses.

Where hypothesis testing is not the aim, independence is not always a requisite. Consider an example in which one wishes to estimate the average height of male students in high school classes. Suppose one of the classes includes a set of identical twins. Clearly their heights are not independent. One could eliminate that non-independence by (randomly) choosing one of the two students and excluding his height from the calculation. However, if heights of identical twins differ from non-twins, then elimination of one of the twins results in a biased estimate of average height. Hence the need to ascertain whether or not independence of observations is necessary or even desirable in some applications.

A commonly used approach to deal with non-independence is to use only a fraction of the data set, say every fifth segment in our case, so that segments can more realistically be considered independent. Suppose we did that, using only segments 1, 6, 11, 16, etc. We could estimate the curves and other outputs we show based on this fraction of independent data. Then we could repeat the process, next using segments 2, 7, 12, 17, etc. Ultimately we would obtain five different curves, each of which is based on a set of (more-or-less) independent observations.

We used this approach and compared incidence plots (LOESS curves) from five subsamples of our data to the entire data set. Subsamples were extracted by taking every fifth transect segment, as noted above. Thus subsamples 1 includes segments 1, 6, 11, 16, etc.; subsamples 2 includes segments 2, 7, 12, 17, and so on. The results are plotted below for the five subsamples (in color), each of one-fifth of the data, as well as the LOESS curve based on the entire data set (in black: Fig. A1.2). Which of the five curves should be used? Each has equal credibility. Alternatively, we could somehow average the curves, to obtain a single curve that reflects all of the observations. But this is fundamentally the same as using all of the data initially, which is what we were trying to avoid.

We repeated this process for 16 species with at least 20 observations in each subset (Fig. A1.3). Three conclusions are evident from these plots: 1) the curve based on the entire data set is in fact representative of the overall pattern manifested by the five individual curves; 2) the curve based on the entire data set is, as would be expected, smoother than curves based on partial data sets; and, most importantly, 3) a single curve based on partial data (note curve 5 in the American robin example) may not be representative of the patterns shown by the majority of the curves. To the latter point, curve 5 suggests that the occurrence of American robins peaks at about 10 percent tree cover and is indifferent as tree cover ranges from 25 percent to 70 percent. All other curves show an increasing likelihood of occurrence with increasing tree cover. Using only a fraction of the data would definitely be wasteful of information, resulting in unjustified jaggedness, and could well be misleading, depending on how representative the selection fraction of the data are. It would also be unnecessary, because independence of the observations is not a requirement for such summaries of data.

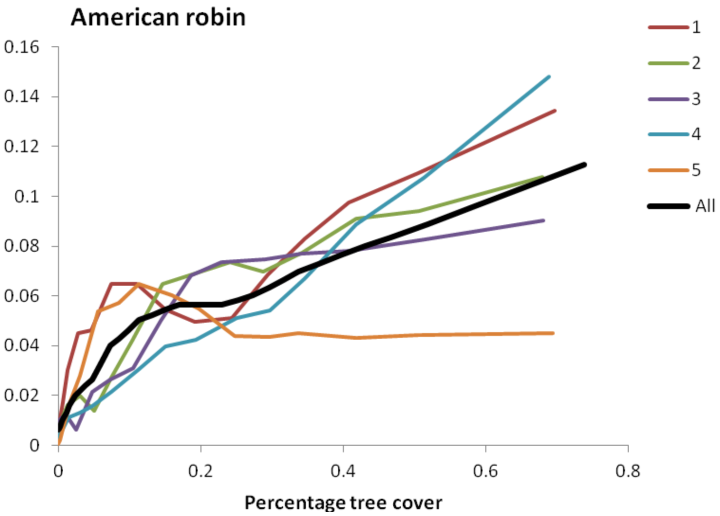

Figure A1.2 Incidence plots calculated using subsamples of the data and all data for American robin.

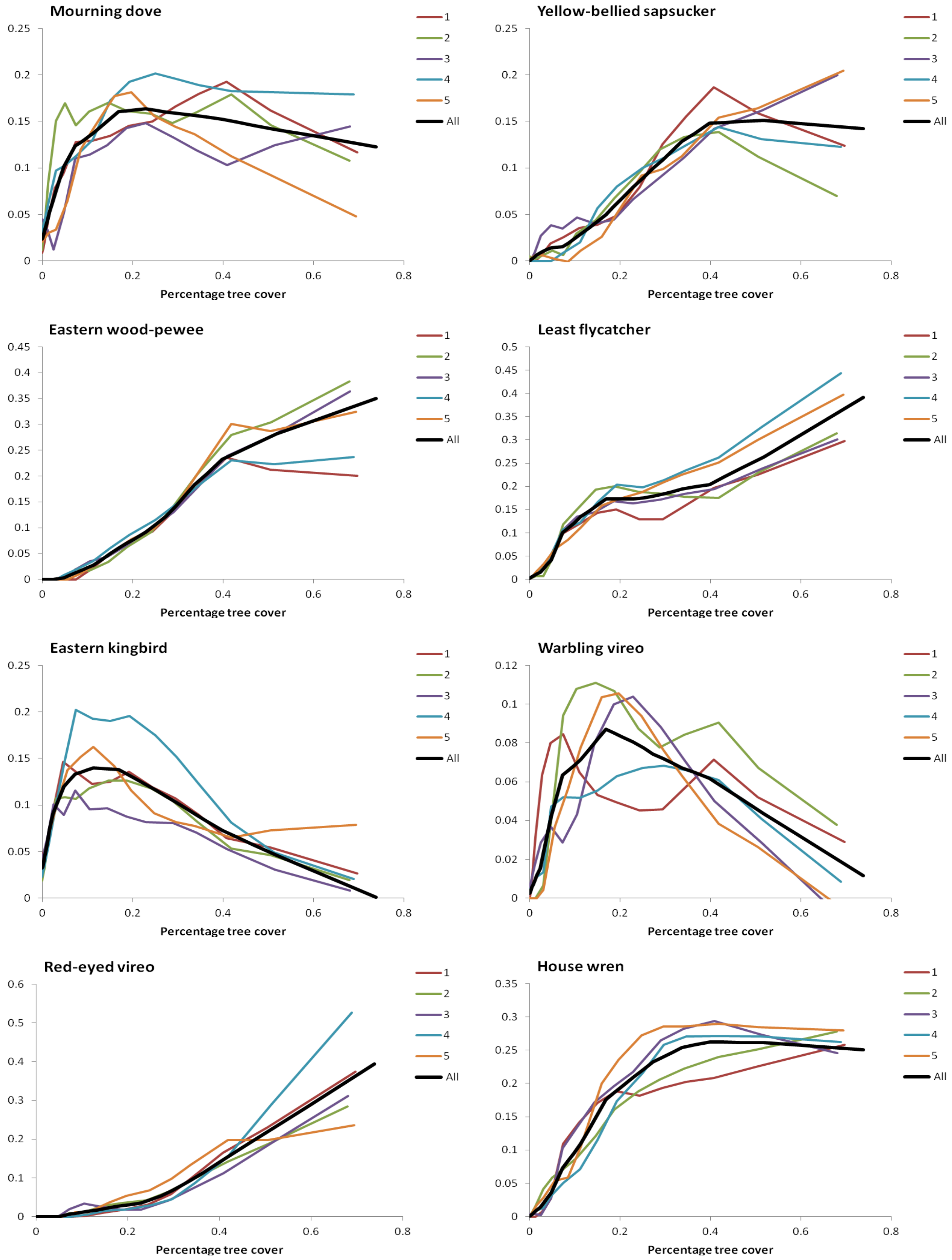

Figure A1.3a Incidence plots calculated using subsamples of the data and all data for 8 of 16 species.

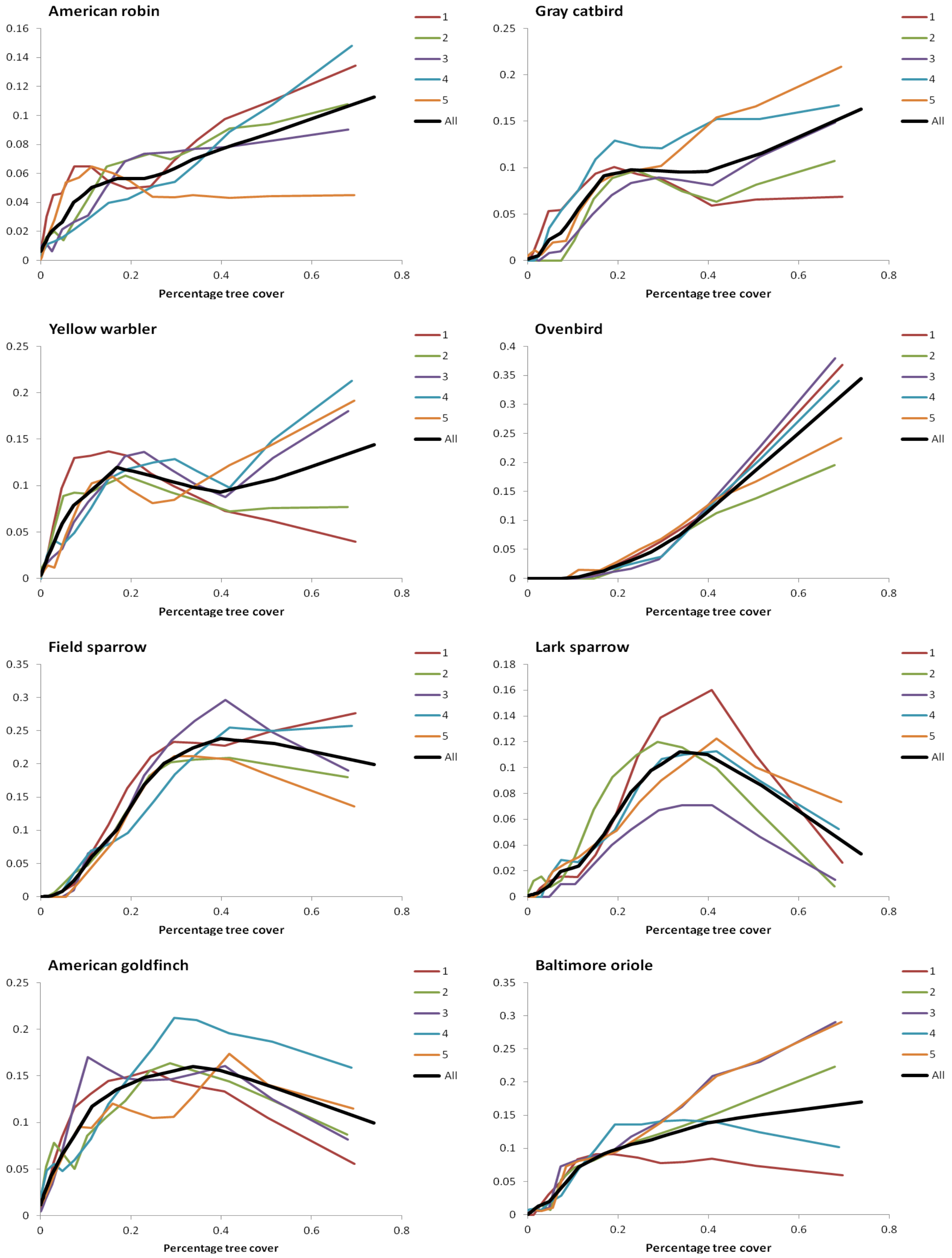

Figure A1.3b Incidence plots calculated using subsamples of the data and all data for 8 of 16 species.

Year effects

Because the abundance and occupancy rates of birds can vary dramatically among years, it is important to consider that variation when estimating preferences for habitat types. As an extreme example, suppose that in one year tree-favoring scarlet tanagers were absent, and if that was the only year that many heavily wooded transects were surveyed, one would obtain mostly zero occupancy values in most of the heavily wooded segments and conclude that the species avoids trees. Numerically, suppose scarlet tanagers were observed on 5 of 500 segments (overall occurrence rate = 0.01) in one year. Next suppose the species was much more common and widely distributed the following year, occurring on 20 of 400 segments (overall occurrence rate = 0.04). We likely would have less-favorable segments occupied than in the previous year, so any preference or selection for certain segments would be less evident.

We can reduce that potentially biasing effect by dividing the presence or absence value (1 or 0) for each segment by the overall occurrence rate in that year. Hence an occurrence value in the first year would be divided by 0.01, producing values of 100 or 0 for each segment. In the second year occurrence rates would be divided by 0.04, yielding values of 25 or 0. This adjustment scales upward occurrence values in the first year, when the species was less ubiquitous.

Mathematically, suppose the frequency of occurrence of a particular species in year t on segment j is f_{jt} (= 0 or 1). Then the overall occurrence rate of that species in year t is the number of segments on which the species was recorded, divided by the number of segments surveyed in year t: $f_{\cdot t} = \sum_i f_{jt} / N_t$. Then scaled occupancy values $f'_{jt} = f_{jt} / f_{\cdot t}$ will account for annual variation in occupancy when used to develop incidence plots.

We compared incidence plots developed from both standard and scaled occupancy values (f_{jt} and f'_{jt}, respectively) for species with relatively even distributions among years (Fig. A1.4) and for species with uneven distributions among years (Fig. A1.5). Generally the profiles were very similar, regardless of whether standard or scaled occupancy values were used. Thus, for simplicity we present results based on the more familiar 1/0 occupancy values.

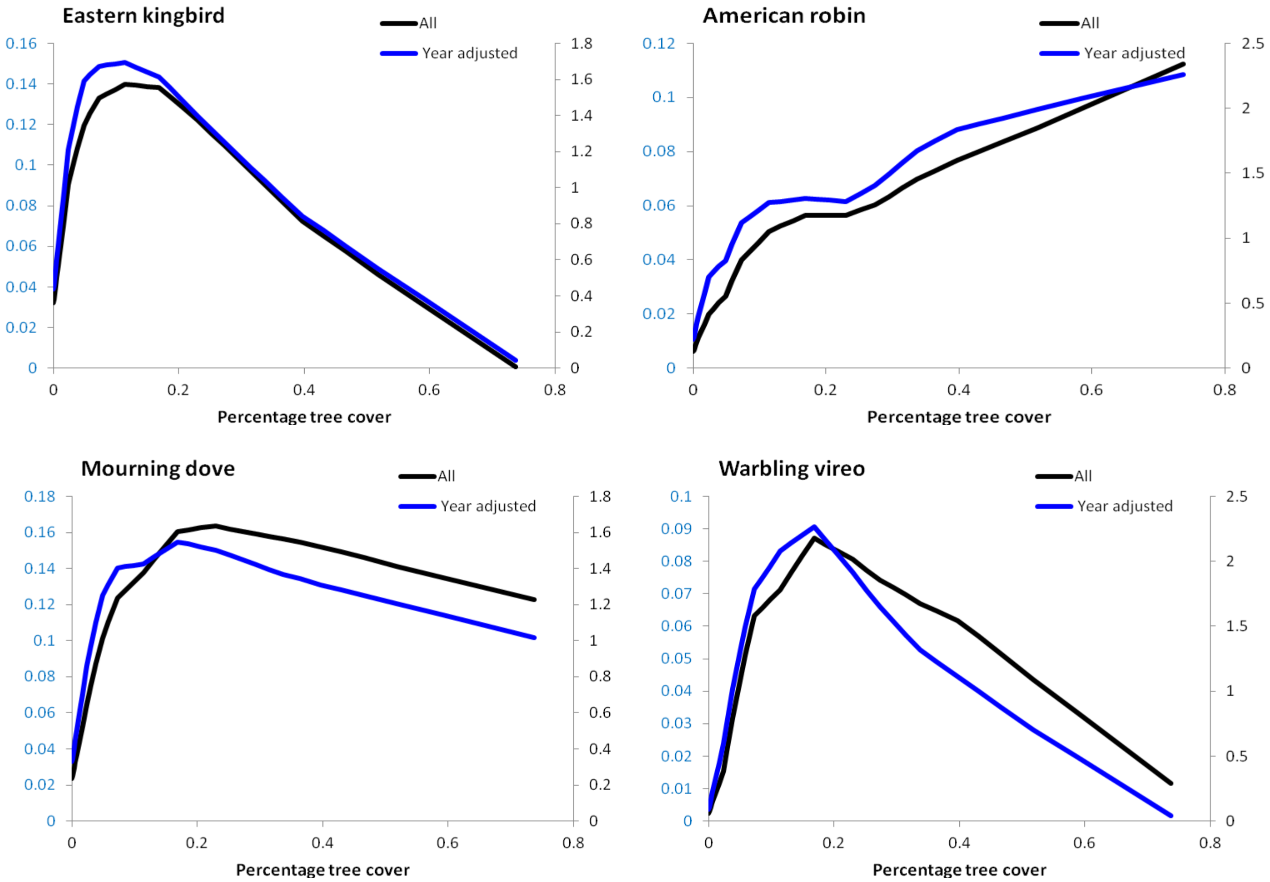

Figure A1.4 Standard (1/0) and year-adjusted results for four species *evenly* distributed among years

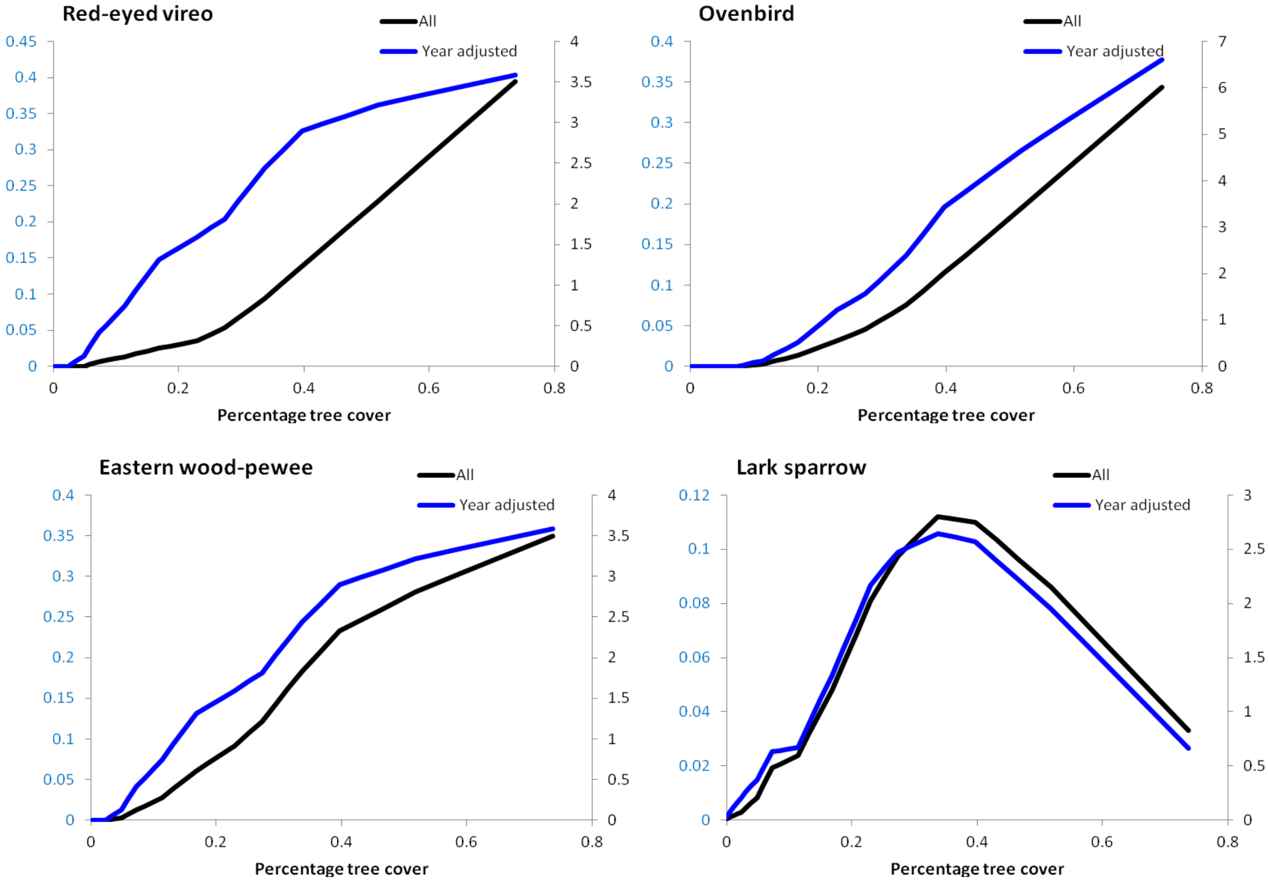

Figure A1.5 Standard (1/0) and year-adjusted results for four species *unevenly* distributed among years.

References

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