Wetlands in disturbed landscapes support higher avian biodiversity

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Abstract

Avian demographic and community responses to land development have been closely studied. However most of this work has focused on forest dwelling species. The responses of wetland-dependent birds to landscape alteration are less known. Based on prior work in forested environments, I predicted that wetland dependent bird abundance and richness would be lower in agricultural and urban/suburban environments compared with environments dominated by native forest. Contrary to expectations, I found that avian richness and abundance was higher in developed versus undeveloped landscapes. In particular, I observed greater richness and abundance of birds in wetlands within agricultural landscapes. These results suggest that developed landscapes may offer opportunities to meet conservation objectives for wetland birds.

Introduction

Avian responses to fragmented forest habitats are well described. Many studies report the effects of clearcut logging and agriculture on forest songbirds, particularly in the context of edge and isolation effects (Donovan et al. 1997; Major et al. 2001; Schmiegelow & Monkkonen 2002; Turner 1996). Their findings indicate that forest-dependent birds are generally influenced negatively by altered landscapes. Because similar responses have been documented across a wide variety of taxa and systems (Hansen et al. 2005), conservation frameworks often incorporate assumptions that landscape alteration negatively impacts biotic communities (e.g. Temple & Terry 2007). In contrast to this convention, recent investigations suggest that disturbed landscapes may provide important habitat for species of conservation concern (e.g. Rosenzweig 2003; Balcome et al. 2005; White & Main 2005; Hodgkison et al. 2007; Kareiva et al. 2007; Milne & Bennett 2007; Winfree et al. 2007). These alternative perspectives suggest that avian responses to habitat alteration may vary by species and habitat type. In light of these conflicting views, developing further understanding of the effect of landscape development on biotic communities remains a critical challenge for conservation scientists and practitioners.

Freshwater wetlands have undergone considerable anthropogenic losses and alterations (Dahl 1990, 2000). However, few studies have estimated the community response of wetland-dependent birds occupying wetlands situated in fragmented—as compared with undeveloped—landscapes (Cox et al. 2000; but see DeLuca et al. 2004; Guadagnin et al. 2005; Guadagnin & Maltchik 2007). Based on the patterns prevailing among forest dwelling birds, we might expect congruent responses by wetland-dependent birds. That is, that conversion of landscapes adjacent to intact wetlands should have negative effects on abundance and richness of wetland dependent species. However, this prediction remains largely untested.

Here, I evaluate the distribution and abundance of wetland-dependent birds across land cover types, ranging from forested to highly developed. I hypothesized that wetland-dependent bird communities varied across these land cover types. Specifically, I predicted that richness and abundance was lowest in wetlands situated within developed landscapes. Contrary to this prediction, I observed higher wetland-dependent bird richness and abundance in developed rather than undeveloped landscapes.

Methods

Natural history and study sites

I conducted surveys of wetland-dependent bird richness and abundance at 16 permanent, open-canopy wetlands located in the state of Connecticut between latitudes 41^{o} 28’ 37” N – 42^{o}1’50” N and longitudes 72^{o} 6’ 32” W – 73^{o} 5’ 5” W. Wetlands included for observation were selected from a pool of candidate wetlands classified by land cover in a prior study (Skelly et al 2006; D. K. Skelly unpublished data). From among this compliment, I surveyed those wetlands in which private landowners granted access. To achieve sufficient replication across treatments, I included for survey two additional wetlands (S.P.B., unpublished data). Wetlands ranged in size from 245 m^2 – 47,124 m^2. For a subset of wetlands, size was determined optically using a coincidence rangefinder (Skelly et al. 2006). For the remaining wetlands, size was determined digitally from the U.S. Fish & Wildlife Service National Wetland Inventory (NWI) using ArcView GIS v. 9.1.

Prior to conducting avian surveys, I groundtruthed all wetlands to verify accuracy of previous land cover classifications. Land cover type encompassing wetlands varied, and included native forest, commercial agriculture, and urban/suburban development. Forest wetlands were characterized by a matrix of relatively contiguous deciduous and coniferous forest. Agriculture wetlands were characterized by row crops (berries, corn, and shade-grown tobacco) cultivated at commercially active farms. Impervious surface and turf characterized the areas surrounding urban/suburban wetlands. These wetlands were either situated within residential yards or business park complexes, or located adjacent to community housing developments.

Avian surveys

I defined wetland-dependent birds as waterfowl, waders, and grebes, belonging respectively to the orders *Anseriformes, Ciconiiformes* or *Charadriiformes, and Podicipediformes*. I surveyed intensively wetland-dependent bird richness and abundance by conducting five point count surveys at each of the 16 total wetlands according to standard protocols (Bibby 1992). A 10-min observation period comprised each of the first and second surveys conducted at all wetlands. A 1-min observation period comprised each of the remaining three surveys. These three additional surveys were included in the design because of the advantages associated with increasing counts (Tozer et al. 2006; Verner & Ritter 1986). All five surveys per wetland were conducted between 11 July – 06 August 2006, a time period that coincides with post-breeding and pre-migration. To include potential seasonal variation in richness and abundance associated with the breeding period, I conducted five additional point count surveys (identical in design to those of 2006) between 22 May – 08 July 2007. In total, I conducted 736 person-minutes of observation (two 10-min surveys + three 1-min surveys X 16 wetlands X 2 years = 736) across 160 point count surveys. For all surveys, the order in which wetlands were visited was haphazard. To minimize the risk of temporal induced bias, I conducted surveys in blocks. Within each block, I surveyed all wetlands within a period of several days, the exact period depending on weather conditions. I conducted 10-min point count surveys between one half hour before sunrise and 1030 hr, a period of increased bird activity (Verner & Ritter 1986). I conducted 1-min point count surveys throughout the day because counts during all hours may yield higher richness (Verner & Ritter 1986), and evening counts are known to yield equivalent sampling efficiency for wetland-dependent birds (Krzys et al. 2002). Each survey was conducted from a single location at the wetland edge. Surveys were not conducted during high wind or rain events. Prior to entering each wetland, I observed open water from a vantage point and recorded all birds detected visually and aurally (Naugle et al. 2000). I recorded all birds detected during the approach and egress into and out of each wetland. All adults and juveniles detected within ca. 100 m of the wetland were recorded. Immediately following the 10-min point count, I walked the wetland perimeter to increase the probability of detecting secretive species (Naugle et al. 2000). At two of the largest wetlands (one forested, one urban/suburban), I chose not to walk through a small portion (< 27%) of the perimeter due to a combination of shear size, deep water, and thick vegetation. This likely had little influence on the results as no new individuals were detected during any perimeter walks.

Land cover assessment

I conducted all geographic analyses in ArcView GIS v. 9.1. For each wetland, I delineated a buffer zone based on a distance of 200 m from the wetland perimeter. I chose this distance because visual inspection of the land cover map indicated that larger buffer zones diluted the land adjacency pattern of interest. Wetland perimeters for 14 wetlands were based on NWI maps. For two wetlands that were not identified on the NWI maps, I traced the perimeter of the wetland as depicted in a 2004 aerial photograph (Univ. of CT Center for Land Use Education and Research [UConn CLEAR] 2007). I overlaid buffers onto a land-cover map generated though supervised classification of 30 m spatial resolution Landsat imagery acquired in 2002 (UConn CLEAR 2007). Within the land cover map, I resampled the data to increase the usable resolution such that each 30 x 30 m pixel was subdivided into four identical pixels. The original land-cover dataset contained eleven classes. From these, I extracted and summed the proportion of land-cover classes within each buffer by defining three types of land cover: forest, agriculture, and urban/suburban (King et al. 2005).

I defined urban/suburban land as the sum of *developed*, *turf & grass, and barren* categories, which described respectively high-density commercial, industrial, and residential areas; cultivated lawns; and non-vegetated non-agricultural areas (e.g. mines, quarries). Percentage agriculture was defined by one class, *other grasses & agriculture*, which included agricultural crop and pasture fields. I defined forest as the summation of two classes: *coniferous forest* and *deciduous forest*. Prior to summing proportions, I subtracted from each buffer any pixels belonging to a wetland classification.

I used the summed proportion data to assign each wetland a land cover classification based on the most common land cover type. Urban/suburban wetlands were located within buffers consisting of 51-90 % urban/suburban cover. Agriculture wetlands were located within buffers consisting of 42-86 % agriculture. Forest wetlands were located within buffers containing 78-97 % forest cover. For each wetland, subdominant land-cover types never exceeded 34 %. I could not describe a complete 200 m buffer for one wetland located near the Connecticut-Massachusetts border. While the wetland basin was entirely within Connecticut, approximately one fifth of the buffer area was located in Massachusetts. To avoid problems associated with using an independently created land cover database, I based the buffer classification for this wetland on the Connecticut portion of the buffer. Inspection of aerial photographs suggested there was little distinction in cover distribution between states.

Statistical analyses

Mixed-model approach

I analyzed the effect of land cover classification—forest, agriculture, and urban/suburban—on species richness and abundance using two approaches: (1) I used a categorical predictor approach to analyze the effect of the three land cover classes on richness and abundance and (2) I used a continuous predictor approach to assess the effect of proportional land cover data on richness and abundance. In both categorical and continuous analyses, I used mixed-effects models to analyze repeated observations at the year level, and to account for the combination of fixed effects (specifically, class and proportion land cover) and random effects (specifically, wetland; Thogmartin et al. 2004). This approach avoided problems with limited power associated with traditional approaches relying on random effects modeling of repeated observations (e.g. ANOVA; R. Baayen et al. unpublished data).

Avian richness and abundance

ANOVA and mixed model analyses of richness and abundance were conducted using R v. 2.5.0 (R Development Core Team 2007); goodness of fit tests were conducted using S-Plus v. 7.0 (Insightful Corp., Seattle, WA). Prior to analyzing the effect of land cover on richness and abundance, I first used ANOVA to test for an effect of land-cover on wetland size. I log-transformed wetland area values because they were non-normal and thus violated the assumptions of parametric analyses. Wetland size was distributed randomly among classes (ANOVA: $F = 1.44$, df = 2,13, $p = 0.27$), and did not vary significantly with respect to land cover proportion data (Linear Regression of cumulated land cover: df = 1,14, F = 3.24, $p = 0.09$; Multiple Linear Regression of partitioned land cover: df = 2,13, F = 3.23, $p = 0.07$). I therefore did not include wetland size as a covariate in subsequent analyses.

I defined bird richness for each wetland as the total number of wetland-dependent bird species detected across all observations. I defined abundance as the maximum number of individuals detected among each species across all observations (Betts et al. 2005). Within the mixed model, I analyzed the effect of the three land cover classes (i.e. forest, agriculture, and urban/suburban) on richness and abundance. I used Kolmogorov-Smirnov (K-S) tests to assess the goodness of fit (GOF) of the data to multiple distributions. Because the distribution of avian richness data was not significantly different from a Poisson distribution (K-S GOF: $p = 0.11$), I chose a Poisson family to characterize the error term in the mixed model. Poisson distributions often characterize count data (Thogmartin et al. 2004). Because abundance data were over-dispersed, I log transformed the original counts to achieve normality (K-S GOF: $p = 0.75$).

I used a similar mixed model analysis to determine the effect of land cover proportion data on richness and abundance. To address issues of multicollinearity associated with proportion data (King et al. 2005), I removed from analysis the single land cover class—percent forest—present at all sites (Newbold & Eadie 2004). To estimate the influence of anthropogenic landscape development on wetland birds, I performed a mixed model analysis in which the single predictor variable was the cumulative proportion of the landscape containing urban/suburban and agriculture land cover. In cases where either richness or abundance of birds was associated with human development, I performed two subsequent mixed model analyses using the continuous predictor approach. Each of these subsequent models included two explanatory variables: proportion urban/suburban and proportion agriculture. The first of these models lacked an interaction term for the land cover types, while the second model contained the interaction term. In each case, Akaike information criterion (AIC) values indicated that model fit did not improve notably (i.e. AIC values did not decrease by greater than 2) with the addition of the interaction term. I therefore chose to analyze for significance the more parsimonious models lacking the interaction term.

Species composition

To estimate the relationship between species composition and land cover, I used CANOCO software (Version 4.5) to conduct a redundancy analysis (RDA) of species composition against proportion agriculture and proportion urban/suburban. Composition data were based on square root-transformed maximum abundance of all species detected at each site. The RDA was based on the matrix of species correlation coefficients, and was conducted using a split-plot design, such that each wetland site contained two abundance observations—one from each year. The permutation analysis for significance—based on 9999 permutations—was freely interchangeable at the site level and modeled using a time series approach at the observation level (ter Braak & Smilauer 1998). This approach ensured that multiple observations at each site shared an error term, thus yielding a mixed-model. Following a significant result from this test, I reanalyzed the data based on the subset of all species found at multiple sites. This exclusion of singleton species—those species recorded at a single site—enabled inference into the robustness of the model results. Since both analyses were significant, I report here only the former analysis containing all recorded species.

Results

Avian richness and abundance

I detected 15 wetland-dependent bird species during a total of 160 observations. Species detected most commonly (those present across 9-12 % of all observations) include Mallard (*Anas platyrhynchos)*, Green Heron (*Butorides virescens)*, Canada Goose (*Branta canadensis*), and Great Blue Heron (*Ardea herodias*). Species detected less commonly (those present across 6-7 % of all observations) include Wood Duck (*Aix sponsa*) and Killdeer (*Charadrius vociferus*). The species detected least commonly (those present < 3 % of all observations) include American Black Duck (*Anas rubripes*), American Bittern (*Botaurus lentiginosus*), Red-necked Grebe (*Podiceps grisegena*), Spotted Sandpiper (*Actitis macularius*), Solitary Sandpiper (*Tringa solitaria*), Great Egret (*Ardea alba*), Willet (*Tringa semipalmata*), Common Merganser (*Mergus *merganser*), and Hooded Merganser (*Lophodytes cucullatus*). Of these, *B. lentiginosus* and *A. alba* and are considered, respectively, endangered and threatened in the state of CT (CT DEP, 2007). In all, eight species were singletons.

Across sixteen wetlands, land cover classification was associated with avian richness (mixed-model: P = 0.032), but not avian abundance (mixed-model: P = 0.087; Fig. 1). A treatment level contrast revealed that agriculture wetlands had greater richness than forest wetlands (P = 0.007). On average, agriculture wetlands contained 4.5 times the number of species detected in forest wetlands. No other contrasts revealed differences in richness across class. The proportion of a landscape that was developed was positively related to both avian richness (mixed model: P = 0.022, AIC = 43.4) and abundance (mixed-model: P = 0.019, AIC = 45.5; Table 1). The model incorporating the terms for proportion urban/suburban and proportion agriculture was significant for both richness (mixed model: P = 0.023, AIC = 43.1) and abundance (mixed-model: P = 0.036, AIC = 46.4; Table 2).

Species composition

Results from a redundancy analysis (RDA) indicated a relationship between community composition and proportion agriculture (P = 0.027), but not with proportion urban/suburban (P = 0.635). Neither was there evidence for an interaction between agriculture and urban/suburban land covers on community composition (P = 0. 315). The total variance associated with the community data fitted to land cover data was 18.1 %, as indicated by the sum of the canonical eigenvalues. A triplot of the ordination (Fig. 3) shows arrows pointing in the direction of steepest increase of their respective values within the RDA. Species arrow length represents the multiple correlation of each species with the ordination axes (ter Braak & Smilauer 1998). The majority of species associate strongly with agriculture, while a subset associate most strongly with the interaction of agriculture and urban/suburban landscapes. Two species (*L. cucullatus* and *T. solitaria*) show weak or negative correlation with both the ordination axes and the environmental variables.

Discussion

Conservation biologists have typically held that landscape conversion leads to declines in biodiversity (Pimm & Askins 1995; Sala et al. 2000). This pattern is well established for forest dwelling birds. Many studies also report the negative impacts of land development on wetland wildlife (e.g. Findlay & Houlahan 1997; Lehtinen et al. 1999), further supporting the view that anthropogenic impacts erode biodiversity. Based on results from previous forest bird studies, I expected that bird richness and abundance would decrease in wetlands surrounded by natural habitat that had been converted by anthropogenic land use. In contrast to this prediction, I found that wetland-dependent bird richness and abundance increased in the context of landscapes converted for human use.

Both sets of continuous models indicated that wetland-dependent bird richness and abundance increased with the proportion of the landscape that was developed. However, the model containing two terms for land development (proportion urban/suburban and proportion agriculture) was more parsimonious (i.e. lower AIC value) than the model treating development as a single term—comprising the sum of proportion urban/suburban plus proportion agriculture (Tables 1 and 2). Furthermore, in the two-termed model, only agriculture was associated significantly with richness and abundance. RDA results indicated a similar trend, whereby community structure was strongly associated with agriculture. While the majority of species are shown to aggregate along the steepest line of agricultural increase, a small cluster straddles the parameter space representing the interaction of agriculture and urban/suburban landscapes. Strikingly, only two species (*T. solitaria* and *L. cucullatus*) showed weak association with the terms for landscape development.

Taken together, these results suggest that different forms of landscape conversion do not have equivalent influences on wetland-dependent birds. Specifically, while both predominant land type and proportion of land type adjacent to wetlands predicted abundance and richness, agricultural landscapes appear to have the strongest influence on this outcome. In addition to the strong association with agriculture, it is important to note that richness in urban/suburban wetlands did not differ significantly from that of forest wetlands, and that abundance showed a weak positive association with urban/suburban landscapes. Moreover, the two threatened species—*B. lentiginosus* and *A. alba*—were detected only in a suburban/urban and an agriculture wetland respectively.

That species richness and abundance were shown here to increase with increasing anthropogenic development prompts questions concerning the mechanisms by which developed landscapes might positively influence wetland-dependent bird communities. As one possibility, fertilizer runoff in agriculture wetlands might bolster community richness via bottom-up trophic effects. Alternatively, decreased density of wetlands in developed landscapes (Gibbs 2000) may function to concentrate biota in remaining habitat (White & Main 2005).

Insight into these patterns will require further experimental studies. However, partial insight may be gained from previous observational studies that have documented wetland-dependent bird distributions associated with increasing agricultural food resources (Fasola & Ruiz 1996; Czech & Parsons 2002). In particular, Czech & Parsons (2002) note that agricultural areas—especially those dedicated to the cultivation of rice and sorghum—provide important habitat for waterfowl. Similarly, postharvest waste corn remaining on fields is a primary energy source for North American waterfowl, and is believed to augment the success of management programs (Krapu et al. 2004). In practice, the U.S. Fish & Wildlife Service promotes the planting of grain crops adjacent to wetlands as part of a strategy for waterfowl management on agency refuges (Cross & Vohs 1988). The fostering of wetland-dependent wildlife via agricultural land cover typically associated with declines in biodiversity marks an important departure from the views traditionally embraced in conservation science.

Increasing rates of land conversion for human settlement and agricultural use have been cited as two of the most important threats to global biodiversity (Ricketts & Imhoff 2003). This is certainly true for a wide diversity of taxa. However, an emerging body of literature reports the positive influence of disturbed landscapes on certain communities of native wildlife species (Balcome et al. 2005; Hodgkison et al. 2007; Winfree et al. 2007), thus underscoring the role of context dependency in describing species responses to landscape conversion. Some conservation goals may be met in disturbed habitats while others are not (Rosenzweig 2003). For instance, many wetland bird species may persist in disturbed wetlands while most wetland amphibian species do not (Gibbs et al. 2005). Parsing contrasting influences of landscape conversion presents a critical challenge for conservation scientists and decisionmakers intent on estimating tradeoffs in ecosystem attributes in "domesticated landscapes" (Kareiva et al. 2007). Estimating the structure of such tradeoffs will require additional studies to address explicitly the nature of community level responses to multiple land cover types across broad spatial and temporal scales (Miller & Hobbs 2002). Insights gained from such an approach may reveal new opportunities for conservation and facilitate a cooperative framework for meeting the frequently conflicting objectives of conservation and land development.

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Table 1. Results of the cumulated mixed-model analyses of avian richness and log-transformed abundance across proportion of the landscape that was developed. Developed is defined as the cumulated proportion of agriculture plus urban/suburban land cover.

Land cover development term	Estimate	Std. Error	df/Chi df	Test Stat.	AIC	*p*
Avian species richness				*Z*		
developed	1.679	0.727	3/1	2.308	43.42	0.022
Avian species abundance				*Chisq.*		
developed	0.771	0.319	3/1	5.518	48.73	0.019

Table 2. Results of the mixed-model analyses of avian richness and log-transformed abundance across proportion of the landscape that was developed. Models contain partitioned land cover terms.

Land cover development term	Estimate	Std. Error	df/Chi df	Test Stat.	AIC	*p*
				Chisq.		
Avian species richness			4/2	9.507	41.17	0.009
				Z		
agriculture	1.796	0.671		3.465		0.001
urban/suburban	0.577	0.682		1.621		0.105
				Chisq.		
Avian species abundance			4/2	8.564	48.18	0.036
				T		
agriculture	1.364	0.380		3.085		0.004
urban/suburban	0.763	0.321		1.775		0.086

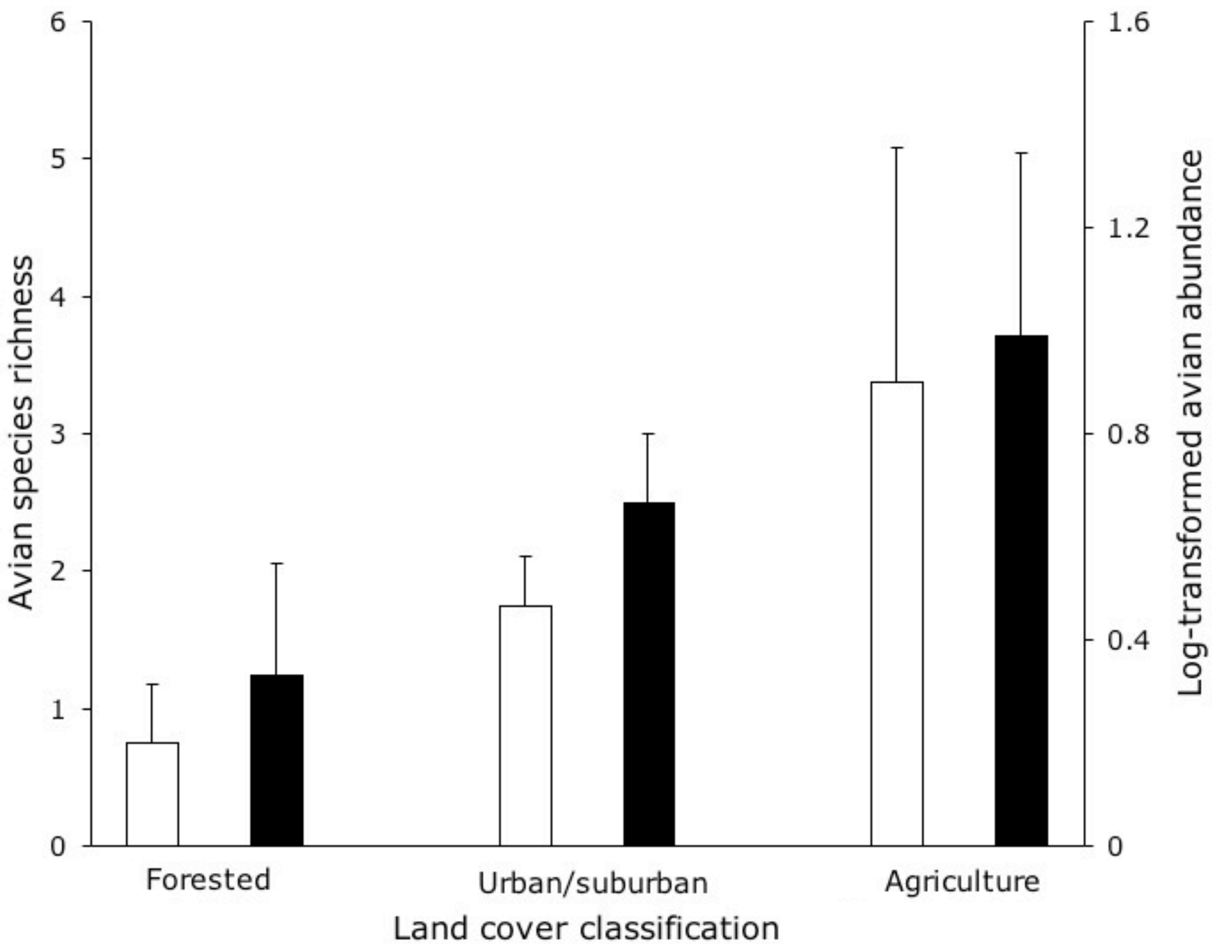
FIGURE LEGENDS

Figure 1. Mean (± 1 SE) avian species richness (open bars) and avian abundance (solid bars) classed by dominant land cover. Mean richness is calculated as the average of the maximum richness recorded in 2006 and 2007. Mean abundance is calculated as the average of the maximum abundances recorded in 2006 and 2007. All abundance values are log-transformed.

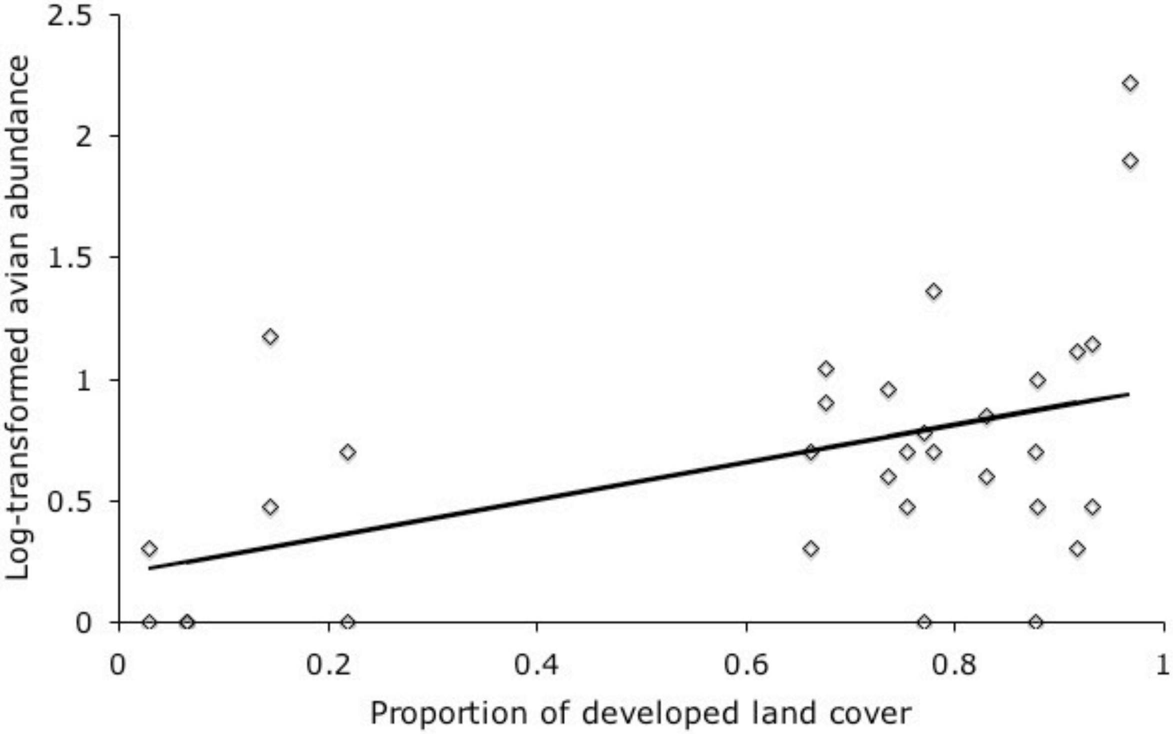
Figure 2. a) Log-transformed avian abundance—and b) log-transformed avian species richness—against the proportion of land that was developed. Richness values plus 0.5 are log-transformed only for graphical presentation. Diamonds indicate log-transformed maximum avian abundance and richness for each set of observations in 2006 and 2007. Land development portrayed here represents the cumulated proportion of agriculture and suburban/urban land cover within a 200 m buffer surrounding each wetland. The solid line indicates the fitted values from the fixed-effect component of the mixed models.

Figure 3. Ordination diagram based on redundancy analysis of avian species composition against proportion agriculture, proportion urban/suburban, and their interaction. An open circle (O) denotes an urban/suburban wetland (labeled: Urb); A closed circle (•) denotes a forest wetland (labeled: For); An X denotes an agricultural wetland (labeled: Ag). Dotted arrows represent species response, labeled with species common names. Bold arrows represent the two land cover terms in the model (proportion agriculture; proportion urban suburban) along with a term for their interaction (agriculture*urban/suburban). The angle between arrows indicates correlation,

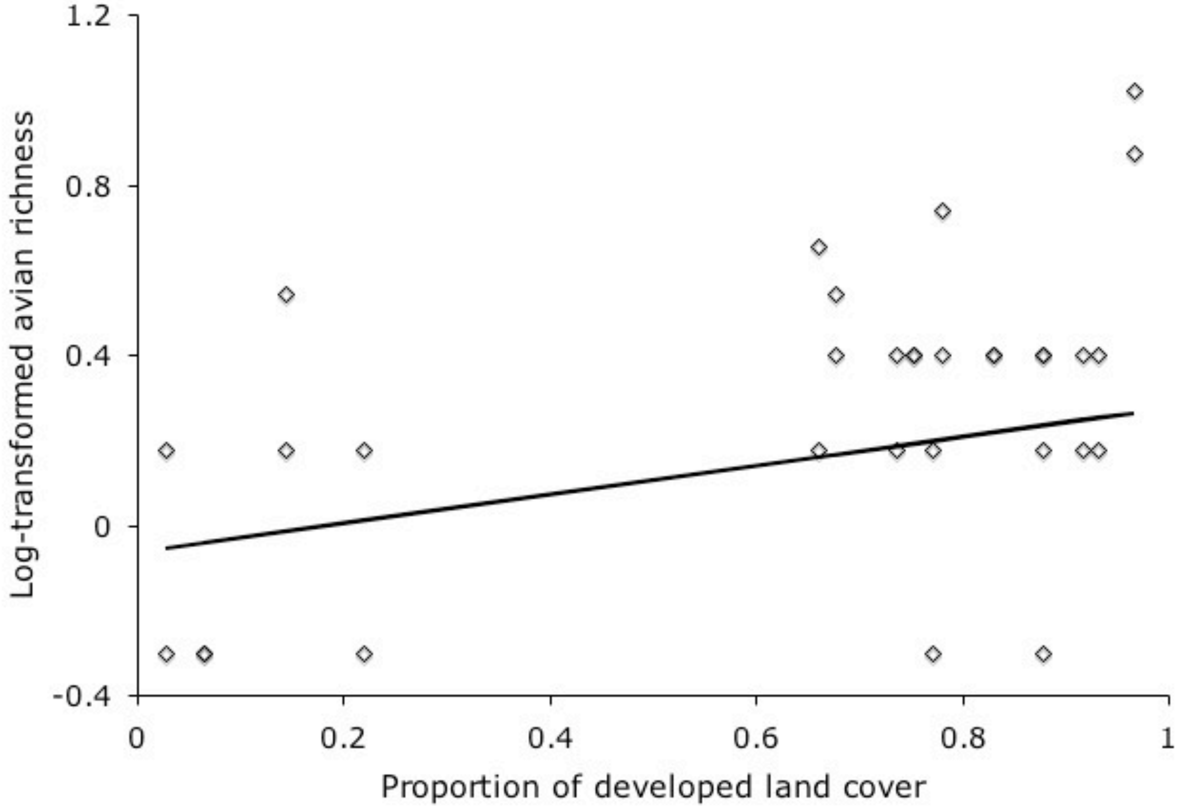
with positive correlations represented by angles less than 90 deg and negative correlations at angles greater than 90 deg.


Avian species richness
Log-transformed avian abundance
0
1
2
3
4
5
6
0
0.4
0.8
1.2
1.6
Forested
Urban/suburban
Agriculture
Land cover classification

a)

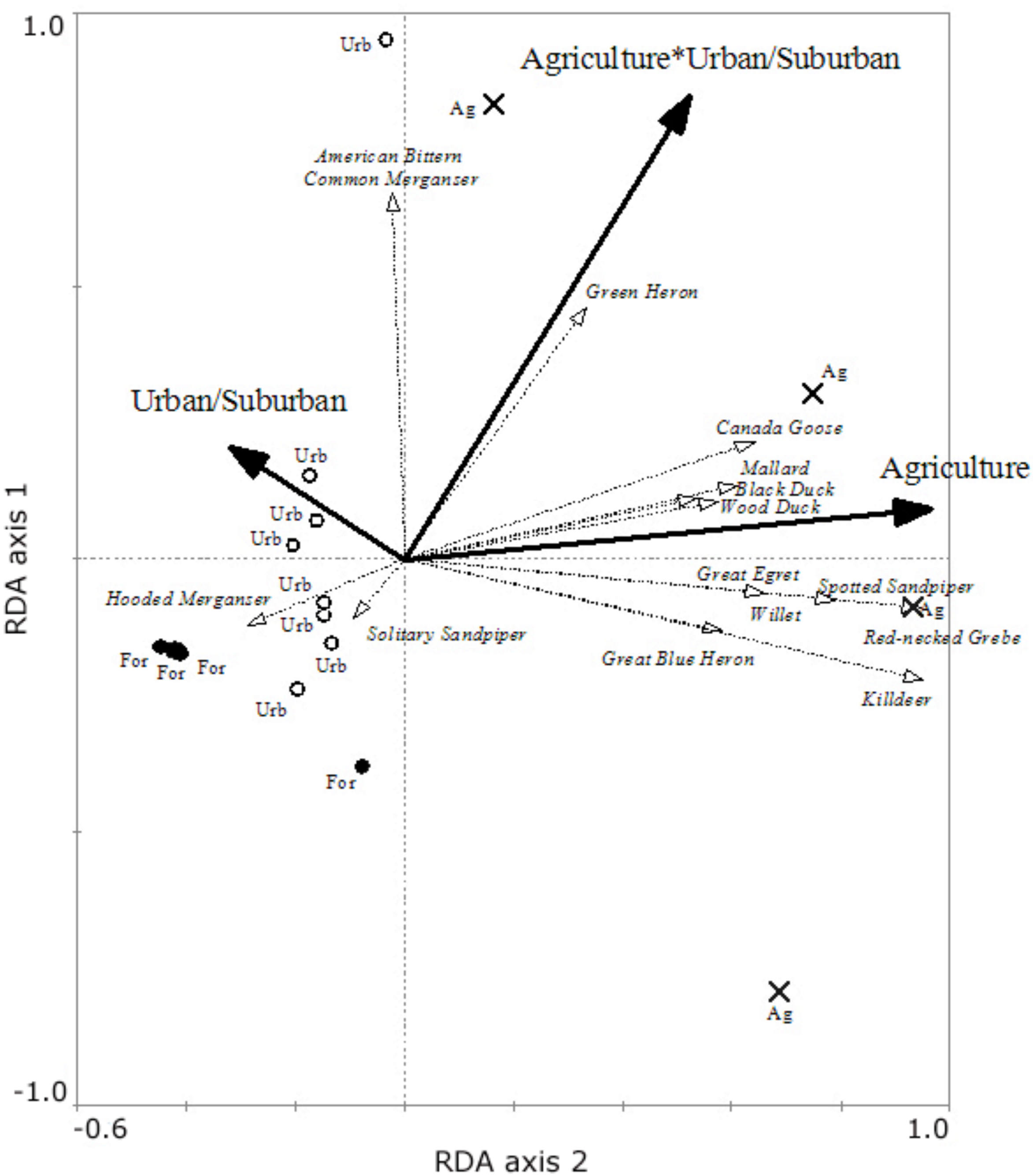

Log-transformed avian abundance
Proportion of developed land cover
2.5
2
1.5
1
0.5
0
0
0.2
0.4
0.6
0.8
1

b)



1.2
0.8
0.4
0
-0.4
Log-transformed avian richness
0
0.2
0.4
0.6
0.8
1
Proportion of developed land cover

549



1.0
-1.0
-0.6
1.0
RDA axis 1
RDA axis 2
Agriculture*Urban/Suburban
Urban/Suburban
Agriculture
American Bittern
Common Merganser
Green Heron
Canada Goose
Mallard
Black Duck
Wood Duck
Great Egret
Spotted Sandpiper
Willet
Red-necked Grebe
Great Blue Heron
Killdeer
Hooded Merganser
Solitary Sandpiper
Urb
Ag
For

550