

DISTINGUISHING STRESSORS ACTING ON LAND BIRD COMMUNITIES IN AN URBANIZING ENVIRONMENT

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Abstract. Urbanization has profound influences on ecological communities, but our understanding of causal mechanisms is limited by a lack of attention to its component stressors. Published research suggests that at landscape scales, habitat loss and fragmentation are the major drivers of community change, whereas at local scales, human activity and vegetation management are the primary stressors. Little research has focused on whether urbanization stressors may supplant natural factors as dominant forces structuring communities. We used model selection to determine the relative importance of urban development, human activity, local and landscape vegetation, topography, and geographical location in explaining land bird species richness, abundance, and dominance. We analyzed the entire community and groups of species based on ecological characteristics, using data collected in remnant forests along a gradient of urban development in the Lake Tahoe basin, California and Nevada, USA. Urbanization stressors were consistently among the principal forces structuring the land bird community. Strikingly, disturbance from human activity was the most important factor for richness in many cases, surpassing even habitat loss from development. Landscape-scale factors were consistently more important than local-scale factors for abundance. In demonstrating considerable changes in land bird community structure, our results suggest that ecosystem function in urban areas may be severely compromised. Such changes compel local- and landscape-scale management, focused research, and long-term monitoring to retain biodiversity in urban areas to the extent possible.

Key words: communities; development; human disturbance; Lake Tahoe, USA; land birds; model selection; urbanization.

INTRODUCTION

Urbanization presents a complex suite of potential stressors for ecological communities, including habitat loss and fragmentation (Donnelly and Marzluff 2006), changes in local vegetation (McKinney 2002, Miller et al. 2003, Donnelly and Marzluff 2006), and disturbance from human activity (Fernández-Juricic 2000, Miller and Hobbs 2000, Miller et al. 2003). While research has repeatedly demonstrated that urbanization dramatically alters communities, few studies have attempted to discern the relative importance of the multiple stressors that can operate along urban gradients (Donnelly and Marzluff 2006). Stressors typically have been investigated individually (but see Fernández-Juricic 2000, Miller et al. 2003, Donnelly and Marzluff 2006), limiting our understanding of the mechanisms at work among factors and their relative importance in shaping com-

munities (McKinney 2002, Donnelly and Marzluff 2006). In this paper, we explore the relative importance of central aspects of urbanization on various components of the land bird community. Throughout, we use the term “stressor” to indicate an anthropogenic force that commonly has negative impacts on land bird community composition and structure, while we use “factor” more generally to describe any environmental force acting on land bird communities.

Urbanization affects land bird communities at two principal spatial scales: local (<300 m radius) and landscape (300–1000 m). Locally the primary stressor is human disturbance, caused by the presence and activity levels of humans and domestic animals. Human presence has been shown to reduce richness and abundance of birds (Fernández-Juricic 2000, Mallord et al. 2007), resulting from direct disturbance or noise. Noise can interfere with bird communication, leading to population declines (Reijnen et al. 1995, Forman et al. 2002) and potential degradation of community structure (Forman and Deblinger 2000). Human presence can be so disruptive as to result in selective extinctions (Fernández-Juricic 2000).

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Manipulation of native vegetation is also a local effect of urbanization and is commonly more intense in close proximity to urbanization. Manipulations typically include pruning for aesthetics and safety, clearing vegetation to reduce fire danger, and harvesting trees and downed logs for firewood. All of these actions serve to simplify the structure of native vegetation communities. Species that rely on habitat elements commonly altered by people are especially susceptible to this aspect of urbanization (e.g., Blewett and Marzluff 2005).

At the landscape scale, urbanization primarily affects land bird communities through habitat loss and fragmentation. Fragmentation compounds the effects of habitat loss (permanent removal of native vegetation) as remnant areas of native vegetation decrease in size and proximity to one another. Loss and fragmentation effects are well studied individually, but the interaction and relative importance of these two stressors have been tested only occasionally (e.g., Fahrig 1997, Donnelly and Marzluff 2006).

Urbanization studies typically examine factor effects through changes in species richness and abundance along urban gradients (e.g., Blair 1996, Marzluff et al. 2001, Hansen et al. 2005). Species richness and abundance are two simple measures of ecological communities that are highly informative, widely used, and straightforward to interpret (Magurran 1988, Fleishman et al. 2006); examined concurrently, they yield a more detailed assessment of community structure than either examined alone. Community dominance, rarely examined along urban gradients, is an ideal complementary measure that helps explain contrasting patterns of richness and abundance and highlight the simplification of ecological communities resulting from urbanization (McKinney 2006). These three measures represent aggregate responses to multiple scales of urbanization. We expected increases in development to result in declines in total species richness, increases in dominance, and no change in total abundance, based on the findings of others (Marzluff et al. 2001, McKinney 2002, Hansen et al. 2005, Chace and Walsh 2006), where shifts in species dominance maintain total abundance despite reductions in species richness.

Community-wide metrics alone, however, lack information on which segments of the community are responsible for observed responses. The identification of ecological characteristics with differential sensitivities has been highlighted as providing important insights into the mechanisms by which urbanization affects land bird communities (Miller et al. 2003, Blair 2004, Lim and Sodhi 2004, Hansen et al. 2005). We identified three ecological characteristics that we expected to reflect different sensitivities to one or more urbanization stressors: nest type and vertical stratification at the local scale and dietary specialization at the landscape scale. We hypothesized that open nesters would be more vulnerable to human disturbance and changes in nest predator populations (Wilcove 1985, Jokimäki et al.

2005) compared to cavity nesters. Conversely, cavity nesters were hypothesized to be more vulnerable to manipulations of local woody vegetation, such as large tree and snag densities, compared to open nesters (Blewett and Marzluff 2005). Human disturbance was expected to be a greater stressor for birds nesting in the understory or on the ground (Blumstein et al. 2005), and manipulation of local vegetation structure, namely tree density and canopy cover, was expected to be a greater stressor for overstory nesters. Finally, we hypothesized that specialists would be negatively affected by habitat loss and fragmentation, whereas omnivores would benefit (Johnston 2001, McKinney 2002).

We tested the relative importance of urban stressors at local and landscape scales in affecting community-wide metrics and the richness and abundance of species groups in native forests embedded in landscapes with differing levels of urbanization. The differential effects of urban stressors acting on bird communities revealed the mechanisms responsible for relationships between stressors and land bird communities and their implications for conserving native bird communities in urbanizing landscapes.

METHODS

Study area and site selection

The Lake Tahoe basin straddles the border of California and Nevada, USA, in the central Sierra Nevada range. The basin's lower-elevation zone ranges from ~1900 to 2100 m, is dominated by Jeffrey pine (*Pinus jeffreyi*) and white fir (*Abies concolor*) (Manley et al. 2000), and is where the majority of urbanization has occurred (P. N. Manley, S. A. Parks, L. A. Campbell, and M. D. Schlesinger, *unpublished manuscript*). Commercial, residential, and recreational development over the past 60 years has populated native forest with urban elements (Manley et al. 2006). Even in locations with greater levels of development, however, native forest elements are retained as undeveloped parcels and yards with native vegetation.

The highly interspersed nature of urban and native-forest elements creates an urbanization gradient that does not lend itself to a patch-matrix characterization of the landscape. In 2003 we modeled development in the study area to facilitate sample site selection along the urban gradient (P. N. Manley, S. A. Parks, L. A. Campbell, and M. D. Schlesinger, *unpublished manuscript*). The study area was divided into 30 × 30 m cells and each cell was assigned a percentage of development value based on land-use type and road density within 300 m, an area commensurate with local effects on community composition and structure. We randomly selected 75 sample points in the lower-elevation zone across a range of development classes and basin orientations to ensure that sample points represented the full spectrum of development values and environmental conditions. All sample points were located in

native forest surrounded by varying amounts of urban development.

Land bird sampling

We conducted point counts (Ralph et al. 1993) at each sample point in either 2003 or 2004, counting all native land birds (all birds detected, excluding waterbirds and raptors) seen or heard within 100 m for 10 min, beginning 15 min after sunrise and ending within 4 h. We conducted counts three times in the breeding season (mid-May to mid-July), with visits separated by at least one week. Five observers conducted the surveys, and we rotated observers such that each site received visits from multiple observers. To assess the validity of sampling a single year for each site, we compared richness values from 2003 and 2004 to a subset of sites in 2005, conducted the relative importance analysis below for total species richness for 2003 and 2004 independently, and performed regressions with year as a covariate (Appendix A).

We calculated species richness of all land birds and species groups at each sample point as the total number of species detected across all three visits. We calculated total abundance and abundance of species groups as the number of individuals detected in the three visits (Nur et al. 1999). Across all abundance metrics, summed abundance across three counts was highly correlated with maximum abundance detected on a single count (0.96 ± 0.004 [mean $\pm$ SE]). We evaluated the potential for differences in detectability along the development gradient using DISTANCE 4.1 (Thomas et al. 2004) for estimates of abundance and CAPTURE (Rexstad and Burnham 1991) for estimates of richness, finding inconsistent patterns of variance in detectability among species and poorly fitting models for many sites, respectively. Therefore, we used unadjusted counts in all analyses. We calculated dominance using the Berger-Parker index (Magurran 1988), which is the ratio of the most abundant species to the total abundance. We determined ecological characteristics of species by consulting Ehrlich et al. (1988; Appendix B).

Urban and environmental factors

We generated explanatory variables representing aspects of urbanization and natural environments, which we grouped into six factors: two urbanization stressors (development and human activity), two environmental factors that can be affected by urbanization (local vegetation structure and landscape vegetation), and two environmental factors unaffected by urbanization (topographic features and geographical location; Appendix C). We reduced collinearity among explanatory variables included in each factor by omitting redundant ($r \geq 0.7$) variables.

We calculated percentage of development at each count station within four radii intended to represent local (150 m) and landscape (300, 500, and 1000 m) scales. We used FRAGSTATS (McGarigal et al. 2002)

to calculate contagion at the same four scales based on a 1-m² GIS grid depicting impervious surfaces. Contagion is a measure of landscape configuration that represents the degree of clumpedness of patch types; landscapes with greater contagion have more adjacent cells of the same patch type (McGarigal et al. 2002).

We measured human activity surrounding each count station as the number of people, dogs, and vehicles detected per hour. Observers walked established transects surrounding each count station. Transects ranged from 50 $\times$ 50 m to 200 $\times$ 200 m depending on the size and shape of the undeveloped forest surrounding each point. Survey time was proportional to the area covered. Observers walked at a fixed pace and stopped at one to five locations along the transect for 3 min noting all people, dogs, and vehicles encountered. At count stations surrounded by <1 ha of undeveloped forest, only the 3-min stationary surveys were conducted. Separate 30-s vehicle counts replaced the 3-min stationary surveys when vehicle traffic was heavy. Surveys were conducted on weekdays, weekends, and holidays from 06:00 to 20:00 and repeated 8–12 times from June to September 2004. No bias was evident in the activity metrics with different survey times; correlations between total survey time and total number of observations were nonsignificant (people, $r = -0.15$; vehicles, $r = -0.02$; dogs, $r = 0.14$; $P > 0.05$ in all cases) and varied in their direction among activity measures. Whereas domestic cats are known to be major predators on birds in many urban areas (Chace and Walsh 2006), we do not believe cats to be a substantial stressor along the urban gradient we studied. Using remote cameras and sooted track plates, a related study detected cats at only 9.1% of 77 sites (as opposed to 63.6% of sites for dogs; L. Campbell, unpublished data).

We assessed local vegetation structure (Appendix C) at each count station using 17.6-m circular plots and line-intercept transects modified from the Forest Inventory and Analysis protocol (USDA 2005, Heckmann et al. 2008). We derived landscape vegetation variables from a GIS vegetation layer based on IKONOS satellite imagery (Tahoe Basin existing vegetation map, version 4.1, available online),⁴ cross-walked to California wild-life-habitat relationships (CWHR) types (CDFG 2002). We calculated the proportion of circles centered on each count station with radii of 150, 300, 500, and 1000 m that were occupied by each of five vegetation types: two conifer forest types, shrub, aspen, and riparian-meadow. We also derived Universal Transverse Mercator (UTM) coordinates, elevation, slope, and distance to water from GIS layers (Appendix C).

Data analysis

We transformed richness, abundance, and dominance values as necessary to approximate normality, using log

⁴ <http://casil.ucdavis.edu/projects/tbevm>

and square-root transformations (Sokal and Rohlf 1995). We transformed explanatory variables as necessary to reduce the influence of outliers and account for nonlinear relationships with dependent variables, including adding a quadratic term when relationships were determined to be unimodal based on a priori examination of scatter plots. When transformations were unhelpful, we reduced the influence of outliers by substituting the second-highest value plus the difference between the second- and third-highest values, a version of “winsorizing” (Sokal and Rohlf 1995). Prior to building models, we standardized all explanatory variables by subtracting the mean and dividing by the standard deviation.

We used a multiple regression approach employing model selection to determine the relative importance of factors affecting land bird community metrics. All model selection analyses were performed using PROC GLIMMIX in SAS 9.1.3 (SAS Institute, Cary, North Carolina, USA), with either a normal or Poisson distribution of the response variable assumed. To compare candidate models, we used two second-order variations of Akaike’s Information Criterion, AIC_c and $QAIC_c$, which adjust for small sample sizes and account for overdispersion ($\chi^2/df \gg 1$; Burnham and Anderson 2002), respectively. For convenience, we refer to both metrics as AIC_c .

We used combinations of the six factors (Appendix C) in different models to evaluate the relative explanatory power of urban and environmental factors alone and in combination with one another. Our approach consisted of three steps for each land bird community metric: (1) identifying core variables for each factor to avoid overfitting; (2) building models consisting of all combinations of factors, ranking them based on AIC_c , and determining Akaike weights (Burnham and Anderson 2002) for all models; and (3) determining the relative importance of each factor based on the weights of all models containing that factor (Burnham and Anderson 2002).

We determined core variables for each factor by constructing models of all combinations of explanatory variables within each group and retaining only the variables in the model with the lowest AIC_c . Selection of local vegetation variables was tailored to be relevant to each species group. For both development and landscape vegetation, we used model selection to determine which combination of the four possible spatial scales was best supported. Both variables in the geographical location factor were retained as core. We carried all core variables forward into the model selection analysis. We used model averaging to generate intercepts and model coefficients, weighting parameter estimates for each model by the model’s Akaike weight and summing the weighted estimates (Burnham and Anderson 2002).

We determined the relative importance of each factor by summing the Akaike weights of each model containing that factor (Burnham and Anderson 2002).

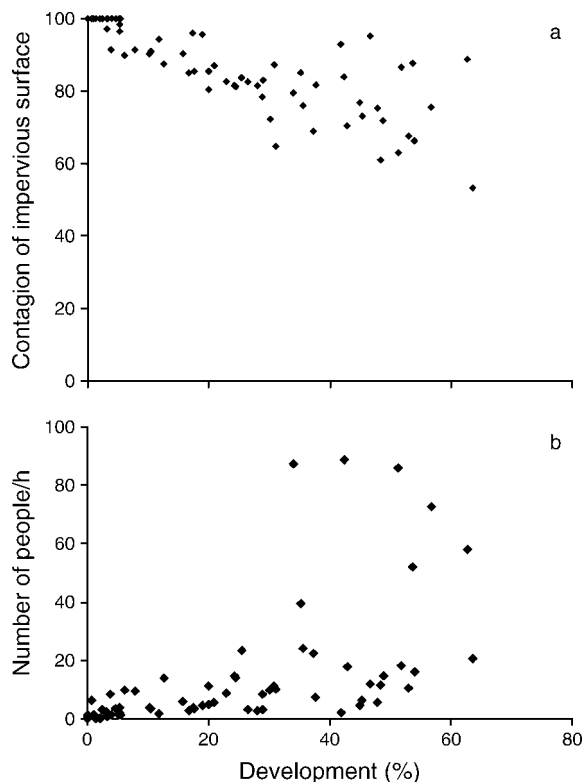


FIG. 1. (a) Contagion of impervious surface and (b) number of people detected per hour as functions of percentage of development within 150 m of 75 sample points in the Lake Tahoe basin, California and Nevada, USA, 2003–2004.

We also examined r^2 of global models (models including all six factors) to assess model fit (Burnham and Anderson 2002) and univariate Pearson’s correlations to identify the direction of each metric’s relationships with development and human activity. Because development and human activity variables were correlated, we complemented this approach post hoc using partial correlations in Statistica 6 (StatSoft 2003) to further distinguish between development and human activity (Appendix D).

Because contagion typically declines with increasing development (Forman 1995), we investigated the relative importance of development vs. contagion in post hoc analyses, when development was among the top three factors in importance. For these analyses, we used only count stations with 150-m development $> 30\%$ ($n = 25$), which was the threshold above which development and contagion diverged (Fig. 1). We compared models with development at the selected scale(s) and contagion at the same scale(s) to determine whether development, contagion, or both factors best explained the land bird community metric.

RESULTS

We detected 4483 individual birds of 58 native land bird species; per species, the proportion of sites occupied

ranged from 0.01 to 1.00 and abundance ranged from 0.03 to 25.47 individuals per point (Appendix B). Recounts at a subset of sites in 2005 showed richness to be similar from year to year (Appendix A).

The number of people detected per hour was somewhat correlated with 150-m development ($r = 0.58$, Fig. 1), but some count stations at the low end of the development gradient had substantial human activity (nearly 20 people/h). As expected, the amount of development and contagion of impervious surface were highly correlated ($r = -0.822$; Fig. 1), particularly at the low end of the development gradient.

All three community-wide metrics were influenced by development and/or human activity (Tables 1 and 2). Global models (all factors included) for total species richness, abundance, and dominance (Table 3; Appendix E) explained $\sim 40\%$ of the variation in each metric ($r^2 = 0.44, 0.38$, and 0.44 , respectively). Species richness was negatively affected by both the amount of development and human activity; human activity was the most important factor, with nearly twice the importance of development, the next most important factor (Fig. 2). Abundance was positively affected by development, but the most important factors in explaining total abundance were landscape vegetation and geographical location. Dominance increased with development, and development and landscape vegetation were the most important factors in explaining dominance. Partial-correlation analyses to further disentangle effects of development and human activity supported or did not refute the results of model selection for 14 of 17 land bird community metrics; the remaining three metrics were not strongly related to development and human activity relative to other environmental variables (Appendix D).

The influence of the pattern of impervious surface on bird richness and dominance (for which development amount was among the top three factors; Fig. 2) was consistently less than the influence of the amount of development. For both bird community metrics, the model including only the amount of development carried nearly three-quarters of the weight of evidence, with the models including contagion of impervious surface having little support (Appendix F).

Nest type

The richness of open and cavity nesters was negatively associated with development and human activity, and urban stressors were the two most important factors for each (Tables 1 and 2). Global models explained 21–43% of variation in richness and abundance of nest-type groups (Table 3; Appendix E). Development was slightly more influential on open-nester richness than was contagion, although the contagion model also had considerable support (Appendix F). The development-only and contagion-only models were both weak ($R^2 < 0.03$) and indistinguishable in their ability to explain richness of cavity nesters.

In contrast, abundance was best explained by vegetation conditions: open-nester abundance was associated with local vegetation, and cavity-nester abundance was associated with landscape vegetation. Contrary to our predictions, human activity was only weakly associated with the abundance of either nest-type group (Tables 1 and 2).

Vertical stratification

The richness of all three vertical-stratum species groups was negatively related to both the amount of development and human activity. As predicted, urban stressors were more important for richness of ground nesters than for the higher-stratum species groups and, in fact, they were the two most important factors for richness of ground nesters (Tables 1 and 2). Global models explained 21–64% of variation in richness and abundance of vertical-stratification groups (Table 3; Appendix E). Richness of understory and overstory nesters was most influenced by landscape vegetation, but the amount of development was among the top three factors for all three ecological groups. The amount of development was a slightly better predictor of ground-nester richness than contagion of impervious surface, although the contagion model also had substantial support (Appendix F). The development-only and contagion-only models were indistinguishable in their ability to explain richness of overstory nesters, and both models were weak ($R^2 = 0.05$; Appendix F).

Abundance of all three groups was primarily influenced by landscape vegetation, which was always among the three most important factors. The abundance of ground nesters also was influenced by a negative relationship with human activity, while understory and overstory nesters were weakly negatively influenced by urban stressors (Tables 1 and 2).

Dietary specialization

The amount of development was the most important factor influencing both omnivore and specialist richness, but it was more important for specialists (Tables 1 and 2). Global models explained 35–78% of variation in richness and abundance of dietary-specialization groups (Table 3; Appendix E). Landscape vegetation was most important for abundance of both species groups. As predicted, richness and abundance of specialists were negatively related, while abundance of omnivores was positively related to both urban stressors. The amount of development was a considerably better predictor of specialist richness than contagion of impervious surface (Appendix F); however, development and contagion were indistinguishable in their ability to explain richness and abundance of omnivores.

DISCUSSION

We demonstrated that anthropogenic stressors can be the primary forces structuring ecological communities in remnant native forests; that human activity can be more

TABLE 1. The best three models (first through third in succession in each metric; $\Delta\text{AIC}_c \leq 2.00$) for the entire land bird community and species groups based on ecological characteristics, from counts at 75 sites along a development gradient in the Lake Tahoe basin, California and Nevada, USA, 2003–2004.

Land bird community metric	Factor occurrence in models						$K^\dagger$	ΔAIC_c	$w_i^\ddagger$
	Devel- opment	Human activity	Local vegetation	Landscape vegetation	Topographic features	Geographical location			
Entire community									
Richness		X					4	0.00	0.225
	X						5	1.51	0.106
		X			X		6	1.93	0.086
Abundance				X		X	10	0.00	0.263
		X		X		X	11	0.20	0.238
				X	X		11	1.14	0.149
Dominance	X			X			6	0.00	0.505
Nest type									
Open-nester richness	X						5	0.00	0.177
		X					4	1.03	0.106
		X		X			6	1.95	0.067
Open-nester abundance			X	X		X	6	0.00	0.118
			X		X	X	6	0.45	0.094
			X			X	5	0.79	0.079
Cavity-nester richness		X					3	0.00	0.149
	X	X					4	1.66	0.065
	X						3	1.66	0.065
Cavity-nester abundance				X		X	12	0.00	0.113
		X		X		X	13	0.13	0.106
			X	X			11	0.40	0.093
Vertical stratification									
Ground-nester richness		X			X	X	8	0.00	0.125
	X	X			X	X	10	0.74	0.086
	X		X				7	0.90	0.080
Ground-nester abundance				X			7	0.00	0.231
		X		X			9	0.23	0.206
		X		X		X	11	0.74	0.159
Understory-nester richness		X		X			4	0.00	0.092
			X	X			5	0.25	0.081
		X					3	0.39	0.075
Understory-nester abundance				X	X		8	0.00	0.406
Overstory-nester richness				X		X	8	0.00	0.421
Overstory-nester abundance				X		X	6	0.00	0.103
	X			X			5	0.24	0.092
				X			4	1.04	0.061
Dietary specialization									
Omnivore richness	X						4	0.00	0.102
			X				3	0.56	0.077
				X			3	1.32	0.053
Omnivore abundance	X	X		X			18	0.00	0.250
		X		X			14	1.09	0.145
	X	X	X	X			21	1.74	0.104
Specialist richness	X						5	0.00	0.318
	X				X		7	1.94	0.121
Specialist abundance				X	X	X	12	0.00	0.157
				X		X	9	0.47	0.124
		X		X	X	X	13	0.48	0.124

Notes: The occurrence of a factor in a particular model is denoted with an “X.” ΔQAIC_c is provided, rather than ΔAIC_c , for entire-community abundance, cavity nester abundance, and specialist abundance. See Appendix E for variables included in each factor.

† Number of parameters.

‡ Model Akaike weight.

important than habitat loss and fragmentation from development; and that within bird communities a complex diversity of responses can occur. The analysis approach allowed us to untangle a complex suite of factors, consisting of a wide variety of explanatory variables, and facilitated identifying the most important

factors affecting communities in urbanizing areas as well as priority areas for management attention. The use of ecological characteristics as an organizing principle allowed the identification of potential causal mechanisms underlying community change and their implications.

TABLE 2. Relative importance of six factors in explaining (a) richness and (b) abundance of land bird species groups.

Species group	Development	Human activity	Local vegetation	Landscape vegetation	Topographic features	Geographical location
a) Richness						
Nest type						
Open nesters	0.481	0.492	0.164	0.292	0.305	0.205
Cavity nesters	0.382	0.636	0.281	0.327	0.293	0.136
Vertical stratification						
Ground nesters	0.675	0.628	0.418	0.285	0.609	0.513
Understory nesters	0.334	0.462	0.384	0.620	0.274	0.122
Overstory nesters	0.452	0.323	0.139	0.729	0.356	0.440
Dietary specialization						
Omnivores	0.464	0.332	0.421	0.401	0.307	0.108
Specialists	0.834	0.328	0.069	0.256	0.281	0.133
b) Abundance						
Nest type						
Open nesters	0.123	0.339	0.776	0.481	0.491	0.645
Cavity nesters	0.258	0.363	0.394	1.000	0.212	0.502
Vertical stratification						
Ground nesters	0.176	0.490	0.136	0.996	0.038	0.352
Understory nesters	0.090	0.333	0.202	0.705	0.999	0.152
Overstory nesters	0.283	0.292	0.074	0.998	0.133	0.997
Dietary specialization						
Omnivores	0.570	0.864	0.402	0.997	0.178	0.214
Specialists	0.300	0.398	0.205	0.940	0.668	0.803

Notes: Values are summed Akaike weights of the 32 models containing each factor. Higher values indicate greater importance. See Appendix E for specific variables included in each factor. Data are from surveys along a development gradient in the Lake Tahoe basin, 2003–2004.

Community-wide responses

Bird species richness was structured more by local factors, while abundance and dominance were structured more by landscape factors. While multiple studies have shown declines in species richness with urbanization (e.g., Blair 1996, Marzluff et al. 2001, Hansen et al. 2005), few have addressed the relative influence of urbanization stressors compared to natural factors (but see Donnelly and Marzluff 2006). Disturbance from human activity was twice as influential on species richness as habitat loss from development, indicating that loss of species in urban areas occurred primarily through behavioral responses to disturbance rather than extirpation from habitat alteration.

Conversely, total abundance was most closely associated with landscape vegetation (i.e., vegetation-type composition and relative amount) and (secondarily) physical features, suggesting that the intrinsic features of an area are the determining factors for abundance. This pattern in total abundance was reflected in the abundance of each species group as well (landscape vegetation was the most important factor explaining the abundance of five of the seven species groups examined), indicating that it was a community-wide response as opposed to abundance being driven by species with particular characteristics. The increase in dominance with development completes the picture of community-wide response, showing at the local scale that as human development and disturbance increase, species are lost

and the site becomes progressively more dominated by fewer species.

Urbanization and habitat fragmentation studies previously have documented the importance of vegetation in the surrounding landscape in determining the land bird community structure of a site (e.g., Donnelly and Marzluff 2004) and species–area relationships for birds in urban areas (Er et al. 2005). Landscape-scale vegetation dictates the potential of sites to support species by providing a source of species and individuals available to populate a site; local conditions then shape the pool of species at the site. However, effects of local vegetation were repeatedly swamped by larger-scale habitat structure and composition, likely because of the varying responses of individual species within the community at the local scale.

Existing local and landscape vegetation conditions in our study area may have resulted from either natural or urbanization-induced disturbances, which our study design did not allow us to distinguish. Local vegetation structure has the potential to be altered by human activity and development. For instance, areas that are frequented by people are likely to have snags, coarse woody debris, and shrubs cleared for firewood, trail maintenance, and reduction of fire risk (USDA 1988). Indeed, other components of this study showed that snags and coarse woody debris were considerably less abundant in urban forests (Manley et al. 2006, Heckmann et al. 2008). Landscape vegetation charac-

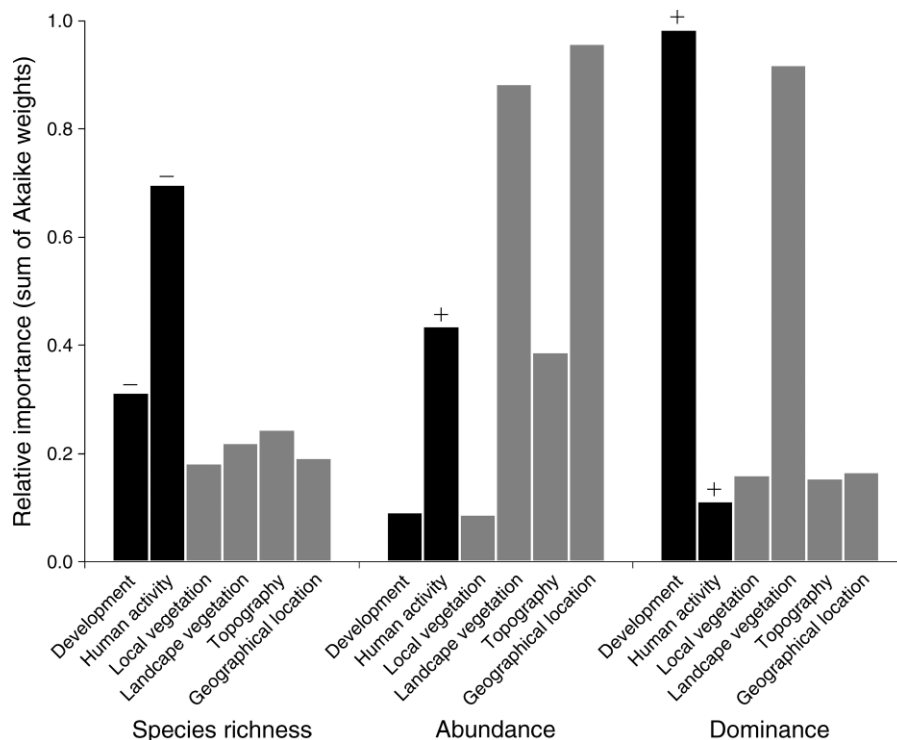


FIG. 2. Relative importance of six factors in explaining total species richness, abundance, and dominance (Berger-Parker index) of land birds at 75 sites along a development gradient in the Lake Tahoe basin, 2003–2004. The importance of each factor was measured by summing the Akaike weights of models containing that factor. Urbanization stressors are shown as black histogram bars; the direction of the relationship is given above these bars for significant ($P < 0.05$) correlations. See Appendix E for the specific variables composing each factor.

teristics reflect development intensity as development by definition involves clearing of native vegetation. Thus, the effects of development may be even further reaching than our results indicate; separating these direct and indirect effects will be important in areas less strongly associated with direct measures of urbanization.

Responses by ecological group

The richness of more-vulnerable species groups responded to urbanization stressors at both local and landscape scales; for the most sensitive groups, even the abundance of the species remaining was affected. Dietary specialization showed the strongest differential response to urbanization stressors. The loss of specialists with increasing development and human activity that we observed has been documented in urban areas in other locations (McKinney 2006). Specialists are a key segment of the biological diversity of native forests. The loss of specialists has disproportionately greater impact on biological diversity because it reduces not only species richness, but also the ecological niche diversity represented. Thus, species losses even at low levels of development represent a consequential erosion of biological diversity through simplification of the ecological community.

The concomitant increase in omnivore richness and abundance with development and human activity also may play a role in the reduction of specialists. Omnivores are archetypal synanthropic, or human-associated, species (Johnston 2001) whose dietary flexibility enables their success in environments with altered food resources (Chace and Walsh 2006). Additional features of urban areas, such as the heat-island effect (McKinney 2006), likely benefit only species that are able to adapt to altered food resources and nesting substrates. These increases in generalists result in further degradation of the community by putting additional competitive pressure on specialist species in environments where specialists are already stressed by diminished habitat quality (Shochat et al. 2006).

Vertical stratification showed the second strongest separation along the development gradient, with the primary responses being the richness and abundance of ground nesters. As expected, we observed a decreasing influence of human disturbance from the ground to understory to overstory, given that most human activity occurs at the ground level. Other studies have shown strong effects of anthropogenic stressors on ground nesters (e.g., Miller et al. 2003, Clergeau et al. 2006), which appear to be a species group at great risk of loss of diversity in urban areas. It is most likely that

TABLE 3. Regression equations with model-averaged intercepts and coefficients for 17 land bird community metrics, based on counts at 75 sites along a development gradient in the Lake Tahoe basin, 2003–2004.

Land bird community metric	Mean $\pm$ SE	Equation with model-averaged intercept and parameter estimates	R^2 of global model
Entire community			
Total species richness	16.5 $\pm$ 0.45	2.795 – 0.036 $\times$ Dev150 + 0.048 $\times$ Dev500 – 0.044 $\times$ Dev1000 – 0.051 $\times$ People – 0.037 $\times$ Vehicles + 0.003 $\times$ NDVI – 0.008 $\times$ Trees + 0.013 $\times$ Aspen500 – 0.024 $\times$ LoCon150 + 0.057 $\times$ LoCon300 – 0.030 $\times$ LoCon500 + 0.046 $\times$ Slope – 0.044 $\times$ Slope ² – 0.005 $\times$ UTM E – 0.007 $\times$ UTM N	0.44
Total abundance	59.8 $\pm$ 1.82	4.078 + 0.008 $\times$ Dev1000 – 0.010 $\times$ Dev1000 ² + 0.028 $\times$ Dogs – 0.001 $\times$ Herbs – 0.004 $\times$ NDVI – 0.040 $\times$ Aspen150 – 0.061 $\times$ HiCon500 + 0.538 $\times$ LoCon1000 – 0.636 $\times$ LoCon1000 ² – 0.059 $\times$ Shrubs1000 + 0.144 $\times$ Shrubs1000 ² – 0.015 $\times$ Elev – 0.079 $\times$ UTM E – 0.092 $\times$ UTM N	0.38
Dominance	0.21 $\pm$ 0.009	–1.611 + 0.133 $\times$ Dev150 – 0.005 $\times$ Vehicles + 0.004 $\times$ CanCov – 0.009 $\times$ NDVI + 0.071 $\times$ Aspen150 – 0.085 $\times$ Aspen500 – 0.066 $\times$ LoCon300 + 0.006 $\times$ Elev + 0.004 $\times$ UTM E + 0.006 $\times$ UTM N	0.44
Nest type			
Open-nester richness	10.3 $\pm$ 0.33	2.325 – 0.075 $\times$ Dev150 + 0.104 $\times$ Dev500 – 0.094 $\times$ Dev1000 – 0.029 $\times$ People – 0.037 $\times$ Vehicles + 0.006 $\times$ NDVI – 0.007 $\times$ Trees + 0.019 $\times$ Aspen500 + 0.006 $\times$ LoCon300 + 0.081 $\times$ Slope – 0.079 $\times$ Slope ² – 0.005 $\times$ UTM E – 0.011 $\times$ UTM N	0.43
Open-nester abundance	36.9 $\pm$ 1.31	6.007 + 0.037 $\times$ Dev300 – 0.011 $\times$ Dev1000 – 0.024 $\times$ Dev1000 ² + 0.037 $\times$ Dogs – 0.199 $\times$ SnagVol – 0.076 $\times$ LoCon1000 – 0.084 $\times$ Elev – 0.139 $\times$ UTM E – 0.109 $\times$ UTM N	0.23
Cavity-nester richness	5.2 $\pm$ 0.17	1.642 – 0.025 $\times$ Dev150 – 0.076 $\times$ People + 0.007 $\times$ SnagVol + 0.016 $\times$ LoCon300 + 0.009 $\times$ Slope – 0.006 $\times$ UTM E – 0.003 $\times$ UTM N	0.21
Cavity-nester abundance	18.3 $\pm$ 0.65	2.868 – 0.002 $\times$ Dev150 – 0.046 $\times$ People + 0.027 $\times$ SnagVol + 0.051 $\times$ HiCon150 – 0.107 $\times$ HiCon1000 + 0.371 $\times$ LoCon300 – 0.275 $\times$ LoCon500 – 0.038 $\times$ Shrubs300 + 0.441 $\times$ Shrubs1000 – 0.556 $\times$ Shrubs1000 ² + 0.002 $\times$ DistWtr – 0.061 $\times$ UTM E – 0.092 $\times$ UTM N	0.41
Vertical stratification			
Ground-nester richness	2.2 $\pm$ 0.15	2.24 – 0.022 $\times$ Dev150 – 0.271 $\times$ Dev1000 – 0.191 $\times$ People – 0.122 $\times$ Vehicles – 0.084 $\times$ CanCov + 0.149 $\times$ NDVI – 0.092 $\times$ Trees + 0.067 $\times$ HiCon1000 + 0.042 $\times$ LoCon300 + 0.040 $\times$ Elev + 0.205 $\times$ Slope – 0.154 $\times$ UTM E – 0.018 $\times$ UTM N	0.58
Ground-nester abundance	6.5 $\pm$ 0.55	2.009 – 0.002 $\times$ Dev150 – 0.020 $\times$ Dev1000 – 0.087 $\times$ People + 0.015 $\times$ Vehicles – 0.009 $\times$ CanCov + 0.014 $\times$ NDVI – 0.014 $\times$ Trees + 0.731 $\times$ HiCon150 – 4.572 $\times$ HiCon150 ² – 0.304 $\times$ HiCon500 + 0.536 $\times$ HiCon500 ² + 0.432 $\times$ LoCon300 + 0.012 $\times$ DistWtr – 0.010 $\times$ DistWtr ² + 0.002 $\times$ Elev + 0.003 $\times$ Slope – 0.046 $\times$ UTM E – 0.017 $\times$ UTM N	0.64
Understory-nester richness	9.7 $\pm$ 0.28	2.269 – 0.012 $\times$ Dev150 – 0.027 $\times$ People + 0.008 $\times$ NDVI – 0.029 $\times$ Trees + 0.040 $\times$ Aspen500 – 0.001 $\times$ UTM E – 0.003 $\times$ UTM N	0.21
Understory-nester abundance	38.6 $\pm$ 1.46	6.133 + 0.013 $\times$ Dev300 – 0.008 $\times$ Dev300 ² + 0.173 $\times$ People – 0.212 $\times$ People ² + 0.001 $\times$ Herbs – 0.038 $\times$ NDVI + 0.026 $\times$ HiCon1000 + 0.762 $\times$ LoCon300 – 0.810 $\times$ LoCon300 ² + 0.348 $\times$ Shrubs1000 – 0.524 $\times$ Shrubs1000 ² – 0.531 $\times$ Elev – 0.016 $\times$ UTM E – 0.011 $\times$ UTM N	0.56
Overstory-nester richness	3.7 $\pm$ 0.19	1.277 – 0.056 $\times$ Dev1000 – 0.009 $\times$ Herbs + 0.107 $\times$ LoCon300 – 0.091 $\times$ Rip150 + 0.170 $\times$ Slope – 0.174 $\times$ Slope ² + 0.007 $\times$ SnagVol – 0.037 $\times$ UTM E – 0.053 $\times$ UTM N – 0.022 $\times$ Vehicles	0.43
Overstory-nester abundance	10.3 $\pm$ 0.84	2.18 – 0.024 $\times$ Dev1000 + 0.027 $\times$ Vehicles – 0.010 $\times$ Herbs – 0.002 $\times$ NDVI – 0.005 $\times$ Shrubs + 0.367 $\times$ HiCon150 – 0.276 $\times$ HiCon300 + 0.389 $\times$ LoCon300 – 0.098 $\times$ Rip150 + 0.034 $\times$ Slope – 0.040 $\times$ Slope ² – 0.204 $\times$ UTM E – 0.263 $\times$ UTM N	0.55

TABLE 3. Continued.

Land bird community metric	Mean $\pm$ SE	Equation with model-averaged intercept and parameter estimates	R^2 of global model
Dietary specialization			
Omnivore richness	5.1 $\pm$ 0.16	$1.629 + 0.165 \times \text{Dev500} - 0.151 \times \text{Dev500}^2 + 0.060 \times \text{People} - 0.083 \times \text{People}^2 - 0.028 \times \text{SnagVol} - 0.025 \times \text{LoCon1000} - 0.011 \times \text{Elev} + 0.002 \times \text{UTM E} - 0.001 \times \text{UTM N}$	0.35
Omnivore abundance	22.8 $\pm$ 1.27	$4.636 + 0.532 \times \text{Dev150} - 0.424 \times \text{Dev150}^2 + 0.374 \times \text{Dev1000} - 0.396 \times \text{Dev1000}^2 + 0.352 \times \text{Dogs} - 0.144 \times \text{Dogs}^2 + 0.851 \times \text{People} - 0.884 \times \text{People}^2 + 0.033 \times \text{Vehicles} - 0.096 \times \text{Vehicles}^2 + 0.058 \times \text{Herbs} - 0.096 \times \text{NDVI} - 0.073 \times \text{SnagVol} + 0.733 \times \text{LoCon150} - 0.722 \times \text{LoCon150}^2 + 0.315 \times \text{LoCon1000} - 0.800 \times \text{LoCon1000}^2 + 0.009 \times \text{Shrubs1000} - 0.306 \times \text{Shrubs1000}^2 - 0.008 \times \text{Elev} - 0.045 \times \text{UTM E} - 0.027 \times \text{UTM N}$	0.78
Specialist richness	11.3 $\pm$ 0.40	$2.404 - 0.171 \times \text{Dev150} + 0.202 \times \text{Dev500} - 0.197 \times \text{Dev1000} - 0.021 \times \text{People} - 0.024 \times \text{Vehicles} + 0.001 \times \text{NDVI} + 0.003 \times \text{SnagVol} - 0.004 \times \text{Trees} + 0.016 \times \text{Aspen500} + 0.012 \times \text{LoCon300} + 0.064 \times \text{Slope} - 0.067 \times \text{Slope}^2 - 0.004 \times \text{UTM E} - 0.005 \times \text{UTM N}$	0.53
Specialist abundance	36.8 $\pm$ 1.36	$3.58 - 0.003 \times \text{Dev1000} - 0.046 \times \text{People} + 0.080 \times \text{LoCon300} - 0.086 \times \text{Shrubs300} - 0.214 \times \text{Shrubs1000} + 0.194 \times \text{Shrubs1000}^2 + 0.028 \times \text{DistWtr} + 0.152 \times \text{Slope} - 0.233 \times \text{Slope}^2 - 0.075 \times \text{UTM E} - 0.085 \times \text{UTM N}$	0.44

Notes: Parameter estimates (regression coefficients) < 0.001 were omitted. Richness is the total number of species detected and abundance is the total number of individuals detected in three visits. Dominance is the Berger-Parker index: the abundance of the most abundant species divided by the abundance of all species. See Appendix C for variable code definitions.

development is affecting the richness of ground nesters by reducing the pool of species available for colonization, whereas human activity is affecting abundance through disturbance.

Open nesters and cavity nesters did not strongly differ in their association with any of the six environmental factors; however, the two trends that were evident were both contrary to our predictions. First, human activity was more important than the amount of development for richness of cavity nesters, but not for richness of open nesters. We expected that human activity would affect open nesters more than cavity nesters due to open nesters' increased exposure to predators (Wilcove 1985, Jokimäki et al. 2005). The finding that a negative relationship with human activity overrode the importance of established key habitat features like snags (Blewett and Marzluff 2005) that were less abundant in urban forests in our study area (Manley et al. 2006, Heckmann et al. 2008) was particularly intriguing. Local vegetation was, however, among the top three factors influencing cavity-nester abundance. This combination of relationships suggests that local habitat conditions affect the abundance of cavity nesters, while human activity has the greatest potential to structure the composition of the cavity-nesting community. Human activity is a heretofore-undocumented stressor for cavity nesters that could have implications for land management.

Implications for urban ecology and conservation

We demonstrate that disturbance from human activity can be the predominant factor structuring land bird

communities. Human activity has been shown previously to alter bird communities (Fernández-Juricic 2000), but no ecological research to our knowledge has teased apart development and human activity in an urbanizing landscape. Our results indicate that process-altering stressors, specifically the flow of people, vehicles, and domestic animals through an area, had as great, or greater, an influence on land bird communities in remnant native habitats as vegetation structure- and composition-altering factors, namely habitat loss, habitat fragmentation, and vegetation management. Therefore, urbanization studies that ignore human activity could reach misleading conclusions because population- and community-level effects of human activity often mirror those of development (Boyle and Samson 1985, Fernández-Juricic 2000). As Miller et al. (2003) noted, such strong effects of human activity have profound implications for habitat restoration efforts that recreate suitable vegetation conditions but fail to acknowledge that human activities can prevent target species and species groups from being restored. We acknowledge that the relative influence of development and human activity observed in this study may hold only up to certain thresholds of development, beyond which a lack of habitat will degrade the community to the point at which there is little left for human activity to disturb.

The precise mechanism by which human activity affects species richness in this study system remains uncertain because of the correlative nature of this study. It is likely that human activity directly affects behavior of individual birds (Boyle and Samson 1985, Blumstein et al. 2005) by flushing them from nesting or foraging

sites and reducing time and energy available for other important activities (Newton 1998, Fernández-Juricic 2000). These changes in behavior can lead to the extirpation of sensitive and vulnerable species (Fernández-Juricic 2000), such as the reduction in richness and abundance of ground nesters that we observed. Additionally, noise associated with recreation or vehicle traffic can inhibit communication between individuals, causing reproductive failure or adult mortality and ultimately reductions in species richness (Reijnen et al. 1995).

Development amount was consistently a better predictor than configuration (contagion of impervious surface) along the upper half of the development gradient. This effect matched results of previous work separating habitat quantity from configuration in managed-forest and urban ecosystems (Fahrig 1997, Donnelly and Marzluff 2006) and may be attributable to the mobility of birds (Alberti and Marzluff 2004, Donnelly and Marzluff 2006). However, for several species groups, development amount and configuration were indistinguishable in their relative effects on richness or abundance. Our results suggest that habitat loss is generally a greater factor than fragmentation for land birds in this landscape; this may be a function of the overall high contagion of this landscape resulting from the retention of native vegetation on a large proportion of most private parcels (P. N. Manley, S. A. Parks, L. A. Campbell, and M. D. Schlesinger, *unpublished manuscript*). Maintaining large quantities of contiguous habitat is the most valuable landscape-level management strategy for preserving land birds in urban areas, but maintaining native vegetation wherever possible contributes to landscape connectivity and the maintenance of biological diversity.

The retention of bird community diversity in urbanizing ecosystems requires attention to function, in addition to composition and structure. Recent syntheses of the important ecological functions performed by birds (Sekercioglu et al. 2004, Sekercioglu 2006) highlight the ecological significance of the loss of species we observed in urbanizing ecosystems. For example, the dramatic decrease in richness of dietary specialists, principally insectivores, granivores, and nectarivores, with increasing development may mean that some important ecological functions, control of insect outbreaks, seed dispersal, and pollination, respectively, may be compromised in urban ecosystems. In addition, cavity nesters are important ecosystem engineers (Jones et al. 1994) and their decline, particularly larger-bodied species, could have cascading effects through the reduction of cavities available for many cavity-dependent species. Thus, some ecosystem functions were most sensitive to habitat loss, indicating that landscape-level preservation of habitat is key to their maintenance, whereas others may be most sensitive to human disturbance, stressing the importance of local-scale management to maintain them.

We observed complex responses in the bird community to multiple factors associated with urbanization. Decreases in species richness were accompanied by increases in abundance of synanthropic species, and extirpations of cavity nesters, ground nesters, and dietary specialists were largely compensated for by increases in abundance of omnivores, yielding increased dominance and stable overall abundance. Similarly complex ecological responses have been observed by others along urban gradients (McKinney 2002, Hansen et al. 2005), and they compel two parallel courses of action. First, urban ecology studies need to be designed to enable research to determine which stressors are acting on which components of the community (Shochat et al. 2006). Ideally, various levels of habitat loss and configuration and types and amounts of human activity can be contrasted to determine how and to what degree they shape bird communities in urbanizing ecosystems. Experimentally controlled levels of human activity are likely to be necessary to fully evaluate some combinations of stressors, such as no development and high human activity or high development and no human activity. Alternatively, a wider range of these combinations of stressors, found, for instance, in national parks and heavily industrialized areas, may be found at larger spatial scales.

The second course of action is tracking responses to urban development as it progresses in a landscape. Managers can contribute much to the body of knowledge informing urban planning by investing in monitoring. Effective metrics of community response and biological diversity suggested by this study include species richness, community dominance, richness of specialists, richness of ground nesters, abundance of omnivores, and metrics for functional groups relevant to the urbanizing landscape. Simple but precise measures of these metrics as development progresses, along with measures of landscape change (habitat amount and configuration) and human activity, promise to provide greater insights into the relationships, thresholds, and mechanisms associated with the interface of urban stressors and bird communities.

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APPENDIX A

Sufficiency of a single year of sampling per site (*Ecological Archives* E089-131-A1).

APPENDIX B

List of species detected and membership in three groups based on general ecological characteristics (*Ecological Archives* E089-131-A2).

APPENDIX C

Six groups of explanatory variables used in analyses of land bird community structure in the Lake Tahoe basin, 2003–2004 (*Ecological Archives* E089-131-A3).

APPENDIX D

Partial-correlation analysis (*Ecological Archives* E089-131-A4).

APPENDIX E

Core variable groups for all land bird species and species groups (*Ecological Archives* E089-131-A5).

APPENDIX F

Models of development and contagion for the entire land bird community and species groups (*Ecological Archives* E089-131-A6).