Human Impacts on Regional Avian Diversity and Abundance

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Abstract: *Patterns of association between humans and biodiversity typically show positive, negative, or negative quadratic relationships and can be described by 3 hypotheses: biologically rich areas that support high human population densities co-occur with areas of high biodiversity (productivity); biodiversity decreases monotonically with increasing human activities (ecosystem stress); and biodiversity peaks at intermediate levels of human influence (intermediate disturbance). To test these hypotheses, we compared anthropogenic land cover and housing units, as indices of human influence, with bird species richness and abundance across the Midwestern United States. We modeled richness of native birds with 12 candidate models of land cover and housing to evaluate the empirical evidence. To assess which species were responsible for observed variation in richness, we repeated our model-selection analysis with relative abundance of each native species as the response and then asked whether natural-history traits were associated with positive, negative, or mixed responses. Native avian richness was highest where anthropogenic land cover was lowest and housing units were intermediate based on model-averaged predictions among a confidence set of candidate models. Eighty-three of 132 species showed some pattern of association with our measures of human influence. Of these species approximately 40% were negatively associated, approximately 6% were positively associated, and approximately 7% showed evidence of an intermediate relationship with human influence measures. Natural-history traits were not closely related to the direction of the relationship between abundance and human influence. Nevertheless, pooling species that exhibited any relationship with human influence and comparing them with unrelated species indicated they were significantly smaller, nested closer to the ground, had shorter incubation and fledging times, and tended to be altricial. Our results support the ecosystem-stress hypothesis for the majority of individual species and for overall species diversity when focusing on anthropogenic land cover. Nevertheless, the great variability in housing units across the land-cover gradient indicates that an intermediate-disturbance relationship is also supported. Our findings suggest preemptive conservation action should be taken, whereby areas with little anthropogenic land cover are given conservation priority. Nevertheless, conservation action should not be limited to pristine landscapes because our results showed that native avian richness and the relative abundance of many species peaked at intermediate housing densities and levels of anthropogenic land cover.*

Keywords: biodiversity, birds, ecosystem stress, habitat loss, human-dominated landscapes, species–energy relationship

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Impactos Humanos sobre la Diversidad y Abundancia Regional de Aves

Resumen: *Los patrones de asociación entre humanos y biodiversidad típicamente muestran relaciones negativas o cuadráticas negativas y pueden ser descritas por 3 hipótesis: áreas biológicamente ricas con densidades humanas altas co-ocurren con áreas de biodiversidad (productividad) alta; la biodiversidad decrece monotónicamente con el incremento de las actividades humanas (estrés del ecosistema); y la biodiversidad alcanza picos en niveles intermedios de influencia humana (perturbación intermedia). Para probar estas hipótesis, comparamos la cobertura de suelo antropogénica y las unidades de vivienda, como índices de la influencia humana, con la riqueza y abundancia de especies de aves en el medio oeste de Estados Unidos. Modelamos la riqueza de aves nativas con 12 modelos de cobertura de suelo y viviendas para evaluar la evidencia empírica. Para evaluar cuales especies eran responsables de la variación observada en la riqueza, repetimos nuestro análisis de selección de modelos con la abundancia relativa de cada especie nativa como la respuesta y luego preguntamos si los atributos de la historia natural estaban asociados con las respuestas positivas, negativas o mixtas. La riqueza de aves nativas fue mayor donde la cobertura de suelo antropogénica fue menor y las unidades de vivienda fueron intermedias con base en predicciones de modelos entre un conjunto de confianza de modelos posibles. Ochenta y tres de 132 especies mostraron algún patrón de asociación con nuestras medidas de influencia humana. De estas especies, approximately 40% se asociaron negativamente, approximately 6% se asociaron positivamente y approximately 7% mostraron evidencias de una relación intermedia con las medidas de influencia humana. Los atributos de historia natural no se relacionaron estrechamente con la dirección de la relación entre la abundancia y la influencia humana. Sin embargo, al combinar especies que mostraron alguna relación con la influencia humana y compararlas con especies no relacionadas encontramos que eran significativamente menores en tamaño, anidaban más cerca del suelo, tenían tiempos de incubación y salida del nido más cortos y tendían a ser altriciales. Nuestros resultados soportan la hipótesis del estrés del ecosistema para la mayoría de las especies individuales y para la diversidad de especies total al considerar la cobertura de suelo antropogénico. Sin embargo, la gran variabilidad en las unidades de vivienda en el gradiente de cobertura de suelo indica que también se soporta una relación de perturbación intermedia. Nuestros resultados sugieren que se deben tomar medidas preventivas de conservación, con lo cual se daría prioridad a áreas con baja cobertura de suelo antropogénica. Sin embargo, las acciones de conservación no se deben limitar a paisajes prístinos porque nuestros resultados mostraron que la riqueza de aves nativas y la abundancia relativa de muchas especies alcanzaron su máximo en densidades intermedias de densidades de viviendas y niveles de cobertura de suelo antropogénica.*

Palabras Clave: biodiversidad, estrés de ecosistema, paisajes dominados por humanos, pérdida de hábitat, relación especies-energía

Introduction

Increased human domination of the Earth's ecosystems (Vitousek et al. 1997) and intensifying human land use (Foley et al. 2005) raise the question of how biodiversity will be affected by these factors. Currently, the observed patterns of association between humans and biodiversity are described by 3 hypotheses (Fig. 1). First, the productivity hypothesis states that more productive systems support more species and more people—a covariation manifesting as a positive correlation between species richness and human population. The positive correlation is thought to be due to productivity gradients caused by varying energy availability (Gaston 2005), with more productive landscapes attracting both humans and other species. Empirical evidence that species richness increases with human population density in Africa, Europe, and North America (Balmford et al. 2001; Hawkins et al. 2003; Gaston & Evans 2004; Luck et al. 2004) appears to support this productivity hypothesis. It remains unclear, however, whether this correlation reflects spatial congruence stemming from selection of high productivity sites by people and wildlife or a causal link, whereby human activities (supplemental feeding, irrigation, plantings) elevate resources and support a more diverse biota (Rapport et al. 1985).

Second, the ecosystem-stress hypothesis states that humans are detrimental to species diversity because they remove habitat and resources of most species and thus predicts a negative relationship between species richness and human influence (Rapport et al. 1985). Evidence that bird and anuran diversity decreases with increases in urbanization (Clergeau et al. 1998; Cam et al. 2000; Genet et al., in Press) supports the ecosystem-stress hypothesis.

Third, the intermediate-disturbance hypothesis (Connell 1978) states that landscapes under moderate levels of human impact have higher habitat and resource diversity compared with pristine or human-dominated landscapes. This higher resource diversity thus leads to higher species diversity and forms a negative quadratic relationship (i.e., a hump-shaped relationship) between species richness and human influence (McDonnell & Pickett 1990). Such patterns have been observed in a number of plant and animal taxa (reviewed in McKinney 2002), typically along rural-to-urban gradients (Blair 1996).

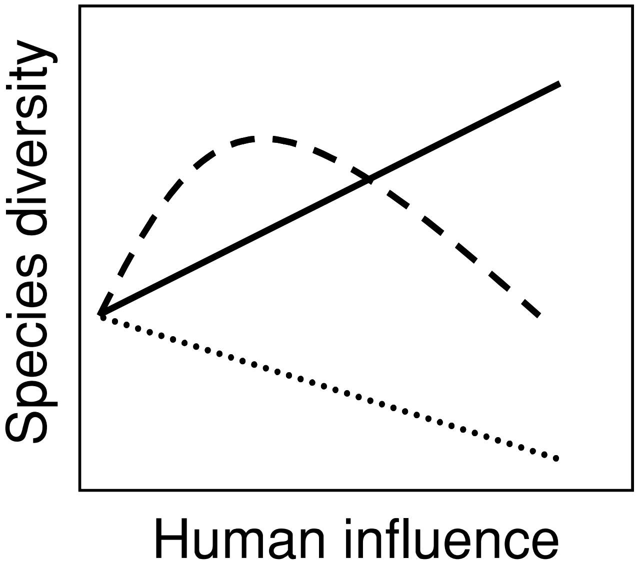

Figure 1. Competing hypotheses that explain the relationships between species diversity and human influence (i.e., population, houses): productivity (solid line), intermediate disturbance (dashed line), and ecosystem stress (dotted line).

Understanding human impacts on species biodiversity is of critical importance for developing appropriate conservation plans and management guidelines (Ricketts & Imhoff 2003). Specifically, the type of relationship that exists between human impacts and species inhabiting the landscape will govern the conservation and management approaches that can be used. For instance, if species diversity and human influence exhibit a positive relationship, conservation conflicts are likely to increase because the increased human demand for resources places species and their habitats at greater risk (Chown et al. 2003). Thus, conservation efforts should focus on areas where human activities are already high so as to offset impending conflicts between biodiversity protection and development (Balmford et al. 2001; Ricketts & Imhoff 2003; Carroll et al. 2004). Conversely, a negative relationship between biodiversity and human activities suggests the focus should be on areas with low anthropogenic disturbance because they harbor greater diversity and may be more cost-effective to protect (Luck et al. 2004).

Sorting out the alternative explanations and support for the 3 hypotheses based on the existing literature is difficult. Previous researchers used disparate methodologies, scales of analysis, and sources of data (Blair 1996; McKinney 2002; Hope et al. 2003; Luck et al. 2004) to examine the relationship. Support for the productivity hypothesis has generally been at regional and continental scales (Balmford et al. 2001; Chown et al. 2003; Ricketts & Imhoff 2003), compared with more local-scale support for ecosystem stress and intermediate disturbance (Beissinger & Osborne 1982; Sinclair et al. 2002; Pautasso 2007). Considering the importance of the relationship between human influence and biodiversity for conservation, it is critical to address which of the 3 hypotheses has the greatest support with methods that control for confounding factors, which was the objective of this study.

Methods

To test the 3 hypotheses, we used 2 complementary measures of human influence (anthropogenic land cover and housing units) and 2 measures of biodiversity response (richness and abundance) across a gradient of 408 landscapes (approximately 1200 km^2 each) of the midwestern United States (an area [1.2×10^6 km^2] twice the size of the Iberian Peninsula; Fig. 2). These landscapes spanned the entire range of human influence, from pristine to human-dominated, and were spatiotemporally congruent with bird data derived from long-term abundance records. They also spanned a gradient that varied from the less-productive grassland and savanna systems in the western portion of the study area to the more-productive temperate forests along the Great Lakes and eastern portion of the study region (Hurlbert & Haskell 2003).

Biodiversity Estimates of Bird Species

Neither richness nor abundance alone can tell the complete story of an area's biodiversity. Richness provides only an estimate of the number of unique species present, whereas abundance provides information on only a single species. Moreover, if biodiversity measures do not distinguish between native and exotic species, relationships may be quite different. To avoid the possible confounding effects of exotic and range-expanding species on the pattern observed, we considered only species native to the study region (see Supplementary Material). We eliminated Ring-necked Pheasants (*Phasianus colchicus*), Rock Pigeons (*Columba livia*), European Starlings (*Sturnus vulgaris*), House Finches (*Carpodacus mexicanus*), and House Sparrows (*Passer domesticus*). Moreover, avian detections that were not identified to species (e.g., unidentified Empidonax) were also dropped from the analysis.

Annual raw counts of breeding birds from 1987 to 1997 were obtained from the North American Breeding Bird Survey (BBS; Sauer et al. 2003). We selected all Midwestern BBS routes that had ≥3 years of acceptable surveys during the 11-year period centered on 1992 (Fig. 2). A survey was deemed acceptable if it was completed by a competent observer during the peak breeding-season window specified for a particular location and was conducted within start time, finish time, and weather standards specified by the survey design (Bystrak 1981; Robbins et al.

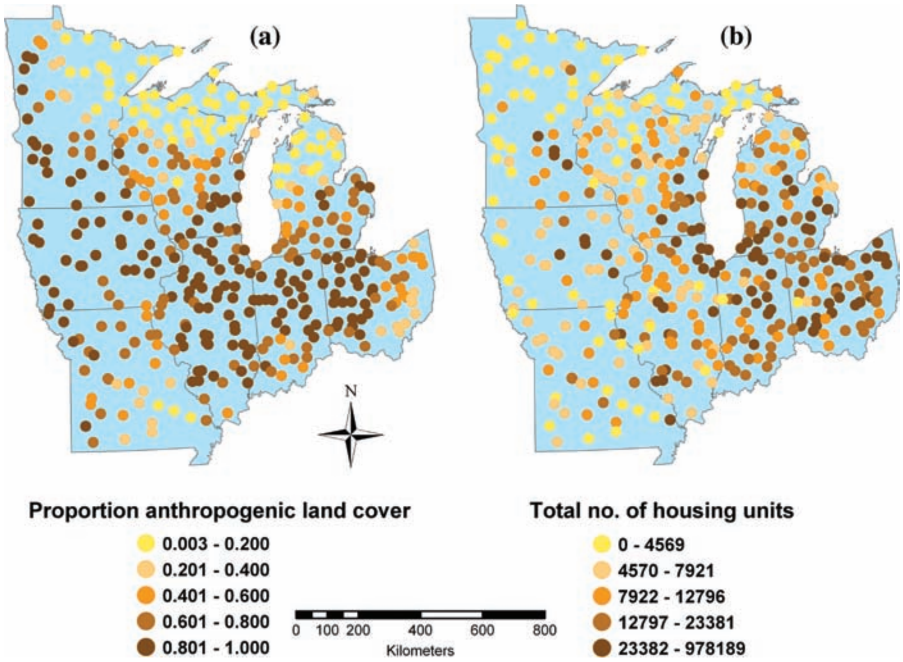

Figure 2. The (a) proportion of anthropogenic land cover and (b) total number of housing units present in each survey landscape in the midwestern United States.

1986). For all analyses, we selected data from the 3 closest years to 1992. A 3-year mean richness and abundance was estimated to control for annual variation in bird counts that was unrelated to our measures of human influence.

Native bird richness was estimated for each year on each route with COMDYN (Hines et al. 1999) software, which probabilistically estimates species richness when not all species are detected. Specifically, COMDYN uses the jackknife estimator of Burnham and Overton (1979) to estimate species richness and accounts for heterogeneity in detectability among species (Boulinier et al. 1998).

For bird abundance calculations we selected all bird species that occurred on at least 30 BBS routes, for a total of 132 species (Supplementary Material). The number of individuals detected, like species, can vary as a function of observer, species, and landscape context (Sauer et al. 1994; Nichols et al. 2000). Nevertheless, the BBS survey methodology does not currently allow these biases to be accounted for analytically at the species level. Consequently, we assumed these biases would not appreciably affect the pattern of spatial covariation between abundance and our measures of human influence.

Measures of Human Influence

We considered anthropogenic land cover and housing units as complementary measures of human influence—anthropogenic land cover provides a measure of land use, whereas housing units provide a measure of human activity. We based anthropogenic land cover on a reclassification of the National Land Cover Data (NLCD; Vogelmann et al. 2001), a 21-class land-cover scheme derived from Landsat Thematic Mapper satellite data (30-m resolution) from 1992 and 1993. We created a binary map of anthropogenic and nonanthropogenic land cover. Anthropogenic land cover was composed of the following NLCD land classes: low-intensity residential; high-intensity residential; commercial/industrial/transportation; quarries/strip mines/gravel pits; orchards/vineyards/other; pasture/hay; row crops, small grains, fallow; and urban/recreational grasses. Similarly, nonanthropogenic (i.e., natural) land cover was composed of the following NLCD land classes: transitional, forest (deciduous, evergreen, mixed), shrubland, grasslands/herbaceous, and wetland (woody, emergent herbaceous). We determined the number of housing units from block-level U.S. Census data. A housing unit is defined as a house, apartment, mobile home, or a room or group of rooms (U.S. Census Bureau 2002*a*, 2002*b*). Together the measures anthropogenic land cover and housing units offered a more complete picture of human influence because anthropogenic land cover included all land covers that had a regular human use associated with them and houses provided additional detail that is often obscured in satellite images of forested ecosystems (Radeloff et al. 2001) and hence is missed in land-cover and -use maps. We did not analyze human population data because housing units and human population were highly correlated ($r > 0.97$ in the study area). Both databases were mapped in Albers conic equal area projection (NAD 83) and analyzed with ArcInfo geographic information systems (GIS) (ESRI, Redlands, California) and Erdas Imagine (Leica Geosystems LLC, Norcross, Georgia).

Circular landscapes of approximately 1200 km^2 centered on each BBS route were clipped from the human-influence databases following protocols in Flather and Sauer (1996) and Donovan and Flather (2002). Under these protocols, some landscapes may overlap if the BBS routes are fairly close to one another. In each landscape we calculated the total amount of anthropogenic land cover and total number of housing units as measures of human influence. Total anthropogenic land cover was described as a proportion of the total amount of terrestrial surface area within each landscape scene, and housing units were $\log_{10}$-transformed to meet assumptions of normality.

Modeling Biodiversity and Human Influence

We established a framework of 12 candidate models that were suggested by the 3 hypotheses (Table 1). These models considered the effects of anthropogenic land cover and housing units separately and together on native species, from both linear and quadratic perspectives. The models applied a correlative approach similar to Currie's (1991:28) who said, "Even though correlations do not demonstrate causality, they do serve 2 useful functions. When a correlation predicted by a hypothesis is not observed, the hypothesis may be considered false. Furthermore, when a correlation predicted by a hypothesis is weaker than other observed correlations, one may conclude a better hypothesis exits."

We used regression analysis to test the 12 candidate models (Table 1) by modeling 3-year mean species richness and abundances against the proportion of anthropogenic land cover, the $\log_{10}$ of total number of housing units, and their interaction. Abundance models were deemed significant if the adjusted $R^2 \geq 0.1$ and the model F statistic exceeded the $p \leq 0.05$ threshold. If significant, determination of the "best" relationship from among the competing models of the same dependent variable was based on Akaike's information criterion (AIC; Burnham & Anderson 2002). Nevertheless, because AIC can overparameterize models by adding variables that are not significant and do not improve fit (Guthery et al. 2005), we selected the simplest model for each species abundance that was within ΔAIC of 2 of the minimum AIC model and had significant model parameters. For species richness we fit all 12 candidate models and used the AIC model weights to define a confidence set of candidate models (i.e., those models with AIC weights within 10% of the highest weight [Royall 1997]). This confidence model set and their associated weights were used to estimate a model-averaged prediction of the richness of native bird species for each landscape.

Table 1. Models used to test the 3 hypotheses[a] explaining human influence on biodiversity.[b]

Model	*Model description[c]*
1	dependent = land
2	dependent = houses
3	dependent = land + houses
4	dependent = land + houses + (land × houses)
5	dependent = land + land^2
6	dependent = houses + houses^2
7	dependent = land + land^2 + houses
8	dependent = land + land^2 + houses + (land × houses)
9	dependent = land + houses + houses^2
10	dependent = land + houses + houses^2+ (land × houses)
11	dependent = land + land^2 + houses + houses^2
12	dependent = land + land^2 + houses + houses^2 + (land × houses)

[a] *Productivity, ecosystem-stress, and intermediate-disturbance hypotheses.*

[b] *The 12 models were run separately for the dependent variables of native species richness and abundance of each species.*

[c] *Key: land, the proportion of anthropogenic land cover; houses, the $\log_{10}$ of total number of housing units.*

Because of the potential for spatial autocorrelation, we conducted a subsequent analysis of the best models. Specifically, we examined our data for spatial autocorrelation by first modeling the dependent variable (i.e., richness or abundance) against latitude and longitude and saving the residuals. We then modeled the residuals against the human-influence variables that were considered significant in the original model to see whether they remained significant ($p \leq 0.05$) and whether the model's R^2 was still >0.1. For instance, White-eyed Vireo (*Vireo griseus*) abundance was best described initially by anthropogenic land cover alone (model 1; see Results). We then ran a second model of White-eyed Vireo abundance against latitude and longitude and saved the residuals. In turn, we modeled these residuals against anthropogenic land cover, which still yielded a significant fit (adjusted $R^2 = 0.23$, $p = 0.00008$) after the influences of latitude and longitude were removed. Because the richness model and abundance models of a random sample of 20 species all yielded significant fits following this process of testing for spatial autocorrelation, we report only the original model fits. We report both the adjusted R^2 (presented hereafter as adj. R^2) and AIC for all 12 models of species richness, but only the top models and ΔAIC of the second-best model for species abundances.

All best models meeting our selection criteria were visually inspected on the basis of their scatter plots and regression equations to assign which hypothesis (Fig. 1) they supported. Simple linear models were easily assigned to either productivity (+) or ecosystem-stress (−) hypotheses, whereas quadratic models were assigned as either positive (+), negative (−), or intermediate (I), depending on where the apex of the parabola occurred (Fig. 3). Thus, a quadratic model could be essentially positive (supporting the productivity hypothesis) or negative (supporting the ecosystem-stress hypothesis) and not only intermediate. For models in which both anthropogenic land cover and housing units were significant but had opposite or differing influences (e.g., positive for anthropogenic land cover and negative for housing units),

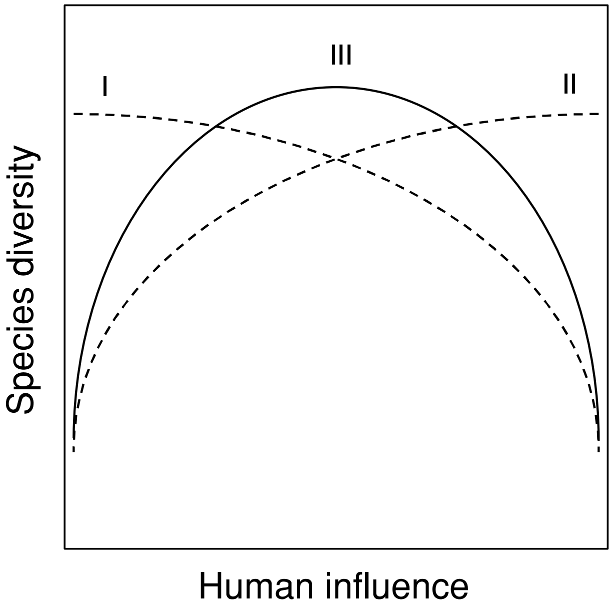

Figure 3. Illustration of how quadratic models relate to the productivity, intermediate-disturbance, and ecosystem-stress hypotheses. If the parabola's apex occurs at the x-axis (I), where human influence is the lowest, the relationship is an ecosystem-stress relationship. If the parabola's apex occurs at or near the greatest level of human influence (II), the relationship is a productivity relationship. If the parabola's apex occurs in the mid ranges of human influence (III), the relationship is an intermediate-disturbance relationship.

conclusive assignment to one of any of the 3 hypotheses could not be made.

Relationship of Natural-History Factors with Human Influence

We also conducted a separate natural-history analysis to discern the factors that may portend the nature of species' responses to human influence and to not limit ourselves to testing an a priori set of expectations. In other words, we grouped species by common response and then looked for patterns in shared natural-history attributes, instead of using a guild approach that assumes members of the guild respond similarly to a stressor (sensu Severinghaus 1981), thereby providing information on what species were responding.

We initially tested for relationships between natural-history classes (body mass, fledging, incubation, nest height, nest type, clutch size, mode of foraging, and mode of development) and human influence with a multivariate approach, whereby we grouped all species that exhibited the same type of relationship (i.e., positive, negative, mixed [+/− or −/+ with the 2 human-influence factors] or negative quadratic). Nevertheless, with the exception of foraging, there were no significant relationships between natural-history classification and direction of the relationship. Because of this lack of difference, we conducted a second analysis, whereby we pooled all species exhibiting a relationship with human influence and compared them with species exhibiting no relationship for each natural-history classification.

To test for the possibility of phylogenetic dependence in the natural-history data of individual species (Harvey & Pagel 1991), we conducted within-family contrasts for each natural-history attribute following the approach of Norris and Harper (2004). For each family we calculated the difference in the mean natural-history attribute between the uncorrelated and correlated species. Hence, a positive value would indicate that the uncorrelated species had a greater value for that natural-history attribute (e.g., greater mass or nest height from ground). We then tested whether the difference score was consistently positive or negative across families with a 1-tailed t test and a null hypothesis of zero (Norris & Harper 2004). Notably, the t test could only be run across 14 of the 38 total families that contained at least one species in both uncorrelated and correlated classes. Because none of the within-family contrasts were significant (i.e., $p > 0.05$), thus indicating no phylogenetic dependence in the analyses, we present only the results based on the initial comparison. Natural-history determinations were from Dunning (1992), Ehrlich et al. (1988), and Poole (2005) (see Supplementary Material). All statistical analyses were performed with Systat 10 (SPSS 2000).

Results

The model with the highest weight of evidence indicated that richness of native birds exhibited a negative relationship with anthropogenic land cover, an intermediate relationship with the number of housing units, and an interaction between anthropogenic land cover and housing (model 12, Table 2). The same model, but without the interaction term (model 11, Table 2), and a land-cover-only model (model 5, Table 2) were close competitors of the best model. These 3 models comprised the confidence set based on Royall's (1997) suggested criterion. Under this criterion, model 7, and all remaining candidate models, were excluded from the confidence set because they were >13 times (based on the ratio of model weights [0.66/0.05]) less likely to be the best explanation for avian diversity when compared with model 12 (Table 2).

The model-averaged prediction among the confidence set (Fig. 4a) indicated that species richness decreased with increasing levels of anthropogenic land cover, but exhibited an intermediate relationship with housing units. At very low levels of housing (<1000 units), species richness quickly declined with increasing levels of anthropogenic land cover (Fig. 4a). On the other hand, as the number of housing units on the landscape increased, the slope of the relationship between richness and anthropogenic land cover decreased and ultimately began to show a slight quadratic relationship when housing numbers reached 1,000,000 units. This quadratic relationship at high housing density illustrates the interaction between housing units and anthropogenic land cover, but the relationship was tenuous as evidenced by only a slight increase in species richness (<4 species) when <50% of the landscape was anthropogenic (Fig. 4b). Nevertheless, there were few landscapes where either very low or very high numbers of housing units (Fig. 4c) existed. Regardless of how many housing units were present on the landscape, the relationship between species richness and the number of housing units always exhibited a negative quadratic relationship (i.e., intermediate; Fig. 4d) that became more pronounced as anthropogenic land cover increased.

Native species abundances were also strongly correlated with the amount of human influence present in the landscape. Overall, 62.9% of all species (83 of 132; see Supplementary Material) were related to either one or both measures of human influence (maximum adj. $R^2 = 0.55$; mean of adj. $R^2 = 0.23$), well above the level expected due to random chance (7 significant correlations would be expected by chance at $p = 0.05$). In 33 of these relationships, abundance decreased with increasing levels of anthropogenic land use and housing density measured either alone or together (Table 3). Only 5 of the species exhibited a positive correlation with a model containing a solitary human-influence measure or both together. Similarly, only 6 species exhibited negative quadratic relationships that fit the characteristics of intermediate disturbance (curve III, Fig. 3) with solitary or combined human-influence models. The remaining 39 species fell into 1 of 6 possible relationships (Table 3), whereby species exhibited either mixed relationships with the 2 human-influence measures (i.e., positive relationship with one measure and negative relationship with the second measure) or an intermediate relationship with 1 human-influence measure and a positive or negative relationship with the second measure.

Among the 83 species that had significant relationships with human influence, there were large differences in terms of which models were selected (Table 3). For instance, model 6 (houses as a quadratic relationship) was never selected, whereas model 7 (quadratic relationship of land cover + houses) was selected 19 times. Among the models that contained only one human-influence measure, land cover (models 1 and 5) was selected 19 times compared with 4 times for houses (models 2 and 6). Model 12 (best model for predicting native bird richness) was selected as the best model predicting bird abundance for only 5 species.

Table 2. Native species richness results for each possible model in Table 1.*

	Coefficients													p				
Model	*intercept*	*land*	*houses*	*interaction*	*land*^{2}	*houses*^{2}	*adj.* R^2	*-2LL*	K	*AIC*	*Δ AIC*	*AICC*	w_i	*land*	*houses*	*interaction*	*land*^{2}	*houses*^{2}
1	95.01	−32.51	.	.	.	.	0.366	3248.6	3	3254.6	12.3	3254.7	0.001	<.0001				
2	104.03	.	−7.24	.	.	.	0.044	3416.3	3	3422.3	180	3422.3	5×10^{-40}		<.0001			
3	92.83	−32.87	0.60	.	.	.	0.365	3248.4	4	3256.4	14.1	3256.5	0.0006	<.0001	0.679			
4	84.66	−19.47	2.81	−3.54	.	.	0.364	3247.8	5	3257.8	15.5	3258	0.0003	0.27	0.386	0.45		
5	90.65	−3.47	.	.	−28.62	.	0.381	3237.8	4	3245.8	3.5	3245.9	0.11	0.70			0.001	
6	107.69	.	−9.05	.	.	0.22	0.042	3416.3	4	3424.3	182	3424.4	2×10^{-40}		0.578			0.91
7	93.46	−1.48	−0.83	.	−30.09	.	0.380	3237.5	5	3247.5	5.2	3247.6	0.05	0.879	0.576		0.001	
8	100.46	−10.40	−2.82	3.01	−32.47	.	0.379	3237.1	6	3249.1	6.8	3249.3	0.02	0.558	0.437	0.55	0.001	
9	23.04	−33.97	35.20	.	.	−4.19	0.374	3241.8	5	3251.8	9.5	3251.9	0.006	<.0001	0.010			0.01
10	15.37	−56.88	42.10	5.96	.	−5.47	0.374	3240.7	6	3252.7	10.4	3252.9	0.004	0.012	0.006	0.31		0.008
11	38.62	−6.00	26.49	.	−26.59	−3.28	0.385	3233.4	6	3245.4	3.1	3245.6	0.14	0.546	0.054		0.004	0.045
12	25.50	−50.84	39.91	13.88	−34.63	−6.00	0.391	3228.3	7	3242.3	0	3242.6	0.66	0.023	0.008	0.025	0.0005	0.003

* *Model number and coefficients are described in Table 1. Key: -2LL, -2log likelihood;* w_i*, AIC weights. The* w_i *was recalculated for only the 3 models in the confidence set, yielding weights of 0.125 (model 5), 0.153 (model 11), and 0.722 (model 12). These values were used to determine the predicted richness in Fig. 4.*

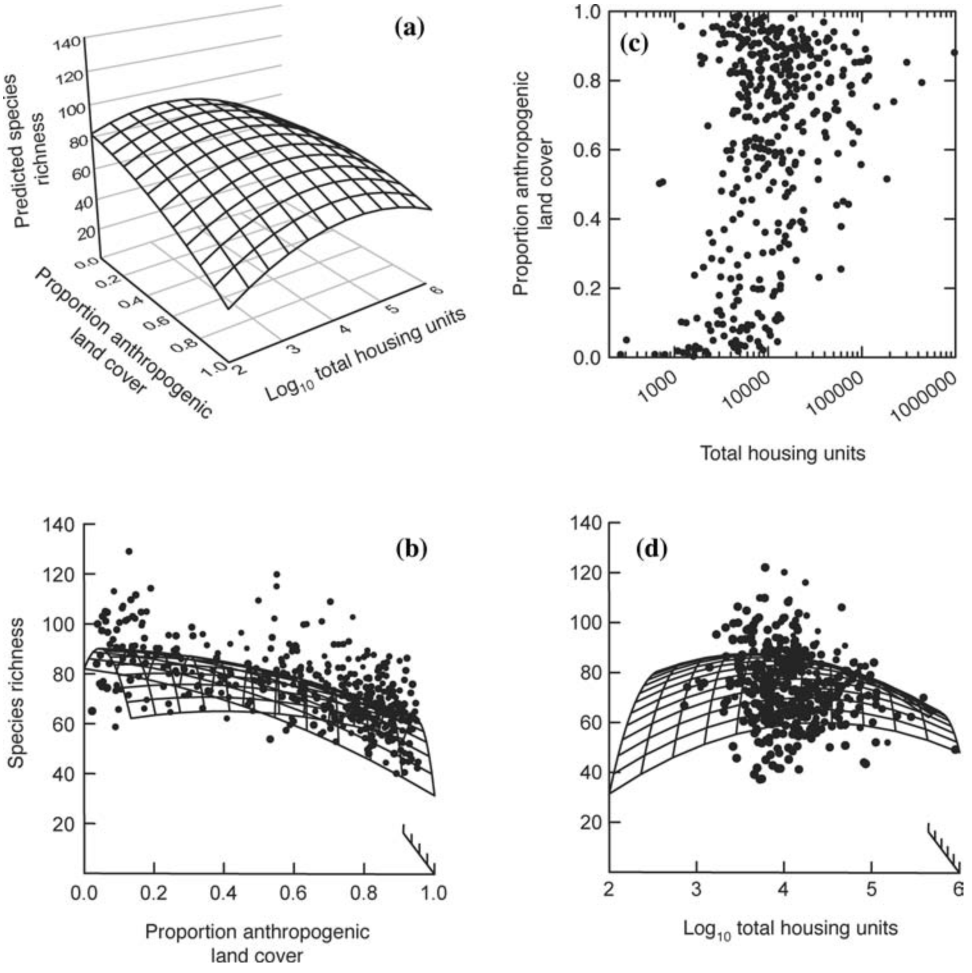

Figure 4. (a) Predicted native species richness in relation to the proportion of anthropogenic land cover and the $\log_{10}$ total number of housing units on the landscape. (b) Predicted (surface) and observed (●; i.e., Comdyn estimates) species richness in relation to anthropogenic land cover. (c) Location of landscapes on the anthropogenic land-cover and housing-unit gradient (log scale). (d) Predicted (surface) and observed (●; i.e., Comdyn estimates) species richness in relation to $\log_{10}$ total housing units.

Natural-history traits poorly predicted whether a bird species was positively or negatively correlated with human influence. The only exception was foraging, in which a greater proportion of terrestrial foragers (i.e., birds feeding on land for one or several food types, such as granivores and frugivores) had a negative response to human influence ($\chi^2 = 17.4$, df $= 9$, $p = 0.048$). Nevertheless, natural-history traits predicted well species that exhibited a relationship with human influence (i.e., species represented in Table 3) compared with those that exhibited no relationship. Birds correlated with human influence were significantly smaller in body mass, weighing only 7.2% as much as species not related to human influence (mean [SE] 45.6 g [7.7] vs. 636.4 g [173.1]; $t_{130} = 4.44, p < 0.0001$), and they fledged in about half the time required by species that were unaffected by human influence (13.8 days [0.7] vs. 27.3 days [2.7]; $t_{128} = 6.03, p < 0.0001$). Incubation times followed the pattern of fledging times in that species correlated with human influences hatched nearly 33% sooner than unaffected species (13.4 days [0.4] vs. 19.6 days [1.1]; $t_{130} = 6.26$, $p < 0.0001$). Nevertheless, clutch sizes were similar for correlated species versus uncorrelated species (4.4 eggs [0.2] vs. 4.6 eggs [0.3]; $\mathrm{t}_{130} = 0.58$, $p = 0.82$). Correlated species more often exhibited altricial development (67.5%), whereas uncorrelated species were more likely (73.3%) to exhibit precocial development ($\chi^2 = 9.51$, df $= 1$, $p = 0.002$). Species responding to human influences had minimum nest heights 42% closer to the ground than species exhibiting no relationship (3.3 m [0.6] vs. 7.8 m [1.4]; $t_{129} = 3.52, p = 0.0006$) and were predominately cavity- or cup-nesting species compared with species unrelated to human influence ($\chi^2 = 9.8$, df $= 2$, $p < 0.007$). Only a single species responding to human influence was an aquatic forager and one other a predator; all other species were generalists or terrestrial foragers ($\chi^2 = 25.4$, df $= 3, p < 0.0001$).

Discussion

Overall, the pattern of declining native species richness with increasing anthropogenic land cover and a preponderance of declining species abundances with both human-influence measures are consistent with the ecosystem-stress hypothesis (Rapport et al. 1985). Although we found no evidence that supported the productivity hypothesis for species richness (Table 2), we

Table 3. Relationships between human influences and bird abundances for native bird species with significant relationships.

		Direction of relationship (land, houses)[a]								
Model	*Times model selected*	+,+	−,−	+,−	−,+	*I*,+	*I*,−	+,*I*	−,*I*	*I*,*I*
1	5		5^b							
2	4		4^b							
3	3		3							
4	9	2	4	1	2					
5	14	2	8							4^b
6	0									
7	19	1	2	6	2	3	5			
8	8		5		2		1			
9	7		1	1	2				3	
10	3		1	1				1		
11	6				1		1		3	1
12	5			1		1	2			1
Total	83	5	33	10	9	4	9	1	6	6

[a] *Direction of relationship indicates whether land cover (land) and housing units (houses) were positively (+), negatively (−), or intermediately (I) related to bird abundance.*

[b] *Only one independent variable included in model results.*

did find support for the intermediate-disturbance relationship. Specifically, richness of native species exhibited a negative quadratic relationship with housing units and the interaction of housing units and anthropogenic land cover (Fig. 4a).

Of the 83 species abundances that exhibited a relationship, the plurality (33) were negative (Table 3, Supplementary Information). Nearly all 33 species that exhibited negative correlations require specific habitat types that are being reduced through human modification (e.g., wetland drainage, simplification of forest structure, loss of shrub, and ground cover), which can also increase nest predation. For instance, 12 of the negatively affected species were warblers, a group of species often restricted to large intact forests. On the other hand, the 5 species that were positively correlated with human influence were those that have cosmopolitan distributions (e.g., American Robin [*Turdus migratorius*]) and tend to be frequent users of human subsidies (e.g., House Wren [*Troglodytes aedon*], Mourning Dove [*Zenaida macroura*]) such as nest boxes and supplemental food (Lepczyk et al. 2004). The 6 species that exhibited purely intermediate-disturbance relationships tended to be either edge or shrub species (e.g., Eastern Towhee [*Pipilo erythrophthalmus*]) or human commensals (e.g., American Crow [*Corvus brachyrhynchos*]; Marzluff 2001). Furthermore, 15 species had a negative relationship with one human-influence measure and an intermediate relationship with the other. Regardless of which factor was negative and which was intermediate, the species exhibiting this combination of relationships were dominated by woodpeckers (e.g., Hairy Woodpecker [*Picoides villosus*]) and grassland/wet-meadow species (e.g., Savannah Sparrow [*Passerculus sandwichensis*], Common Yellowthroat [*Geothlypis trichas*]). Overall, though, the decrease of most native species abundances coupled with very few exclusively positive or negative quadratic relationships provided further support for the ecosystem-stress hypothesis.

Approximately 23% (19/83) of the species exhibited a relationship with human influence that was best explained by anthropogenic land cover alone (i.e., models 1 and 5) rather than by housing units alone (approximately 5% [4/83]) (i.e., models 2 and 6). The second-best models added only one additional species that was best explained by model 1. Interestingly, however, the majority (72%) of species abundances were best explained by a combination of both measures of human influence and their interaction (Table 3; Supplementary Material). Thus, anthropogenic land cover was an important predictor by itself in a large proportion of species, but model performance was enhanced in most instances by including housing unit information. Aside from enhancing model performance, housing units were highly correlated with human population ($r > 0.97$) and thus may serve as a useful surrogate for how human population relates to biodiversity.

Although natural-history traits did not predict whether or not a species was positively or negatively correlated with human influence, they did predict well species that had a relationship with human influence. That is, natural-history traits predicted the species that covaried with human influence, but not how they covaried. Considering the natural-history factors together, the species that correlated either positively or negatively with human-influence measures tended to be similar to altricial passerine birds.

Bird communities are frequently used as indicators of environmental quality (Mayer & Cameron 2003) and are thought to be a useful proxy for assessing the impact of human influence on biodiversity (Balmford & Long 1995; Garson et al. 2002). We found that species richness and abundances were indeed closely related to the degree of human influence and that for the majority of species neither human land use nor housing development was beneficial. In terms of diversity the overall relationship indicated that species richness was greatest where anthropogenic land cover was lowest and the number of housing units was moderate (Fig. 4a). Similarly, for the majority of species abundances, their relationships with human influence were either negative or negative and intermediate. Thus, the *predominant* patterns displayed by the richness and abundance relationships were consistent with the predicted effects of stressed ecosystems (Rapport et al. 1985) and to a lesser degree with the effects of disturbance regimes on species richness.

Although most of the relationships supported the ecosystem-stress hypothesis, land cover and housing interacted (Fig. 4), resulting in an intermediate disturbance relationship for species richness. Specifically, this dual support for intermediate-disturbance and ecosystem-stress hypotheses varied depending where on the model predicted surface of houses and land cover the landscape was located (Fig. 4a) and may be due to several factors. For instance, because we classified agricultural lands as anthropogenic, our results may be an artifact of the low housing density on predominately anthropogenic landscapes. Although possible, this explanation is unlikely because there were no landscapes that had <1000 housing units and were more than 50% anthropogenic (Fig. 4c). On the other hand, because landowners often manage and subsidize their property for wildlife (Lepczyk et al. 2004), houses may be serving as a proxy for landowner activities that cause elevated species richness in low to moderately populated landscapes. In other words, as the human population increases, there is a concordant increase in the number of houses, which in turn leads to increased habitat manipulation and resource diversity. This increased resource diversity results in increased richness up to a moderate level (1,000–10,000 units) of housing (Fig. 4d). After moderate levels are exceeded, the landscape becomes too disturbed (Fig. 4c), even if manipulation continues, which leads to lower species richness. A case in point is that suburban landowners (i.e., low to intermediate housing density) plant vegetation on their property intentionally for birds in greater proportion than landowners in rural or urban locations (Lepczyk et al. 2004), thereby providing increased resource diversity at intermediate housing levels. Whatever the case may be, the relationships between housing units and land cover suggest that there is an interesting and complex relationship between them.

Our findings suggest that the positive correlation between human population density and biodiversity observed in other studies (Balmford et al. 2001; Gaston & Evans 2004; Luck et al. 2004) is likely related to a pattern of spatial congruence that appears at broad spatial scales. Continental-scale studies with geographically large observation units capture extremes in ecosystem productivity to which biodiversity and human-population density respond similarly. Furthermore, researchers using range maps or data that are not spatiotemporally matched to human population data may find differing relationships compared with spatiotemporally matched data. In contrast, although our study was conducted at a regional scale, it did include a productivity gradient (Hurlbert & Haskell 2003), and we used a finer resolution of analysis that was spatiotemporally matched. Moreover, the direction of relationship between richness and human influence appears to be strongly correlated with the scale of analysis (Pautasso 2007). Thus, our failure to find evidence that supports the productivity hypothesis does not mean birds (richness or abundance) do not positively covary with productivity. It could be that human uses of the land do not covary as predicted by the productivity hypothesis. Because we did not measure productivity directly (e.g., NDVI), but chose to test the productivity hypothesis implicitly using 2 measures of human influence, the direct relationship between productivity and bird communities in this region of the country awaits future research.

Several caveats to our findings need to be considered. First, it is possible that a positive relationship between species richness and human influence occurs when humans first settle an area but that this relationship disappears over time as species become locally extirpated, which results in a negative relationship. Unfortunately, existing data do not allow for examination of changes in the relationship of species richness and human influence over time. Second, some species (e.g., waterfowl, shorebirds) may not have exhibited a relationship to human influence because they were poorly censused by the BBS methodology. Third, even when species can be easily censused, they may be rare, making strong relationships difficult to detect. Fourth, some anthropogenic land cover classes (e.g., pasture/hay) provides suitable breeding habitat and are managed in a way that permits successful reproduction. As a result, some anthropogenic land cover classes would perhaps be more accurately described as seminatural and may actually be more similar to what we had classified as natural land cover.

Our results support a 2-pronged approach to conservation. In areas with little or no human influence, ecosystems should be preserved or managed in ways that discourage human development (e.g., acquisition, conservation easements, economic incentives). Such preemptive conservation is pragmatic and cost-effective in comparison with efforts to save or restore degraded or endangered species and landscapes (Norris & Harper 2004). On the other hand, conservation priorities should not be limited to pristine landscapes because our results suggest that avian richness and the relative abundance were estimated to peak at intermediate housing densities or anthropogenic land cover, depending on overall landscape composition. In human-dominated areas, land managers should consider reestablishment of natural and seminatural habitats (McKinney 2002) when the expected biodiversity gain justifies the greater cost associated with restoration. Such an approach is especially important in relatively pristine locations given that the U.S. population is expected to increase by 65 million people between 1995 and 2025 (Fischer & Heilig 1997). Given the historical trend toward decentralization of human populations, resulting in greater suburban and rural sprawl (Hammer et al. 2004; Radeloff et al. 2005; Lepczyk et al. 2007), our results presage an expanding human influence on avian diversity. As they apply in human-dominated areas, our results highlight the importance of extending conservation efforts to private lands and integrating ecological principles in land-use planning at broad spatial scales.

Supplementary Material

A list of species investigated, a description of the best-fit models, and the natural-history traits of species are available as part of the on-line article from http://www.blackwell-synergy.com/ (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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