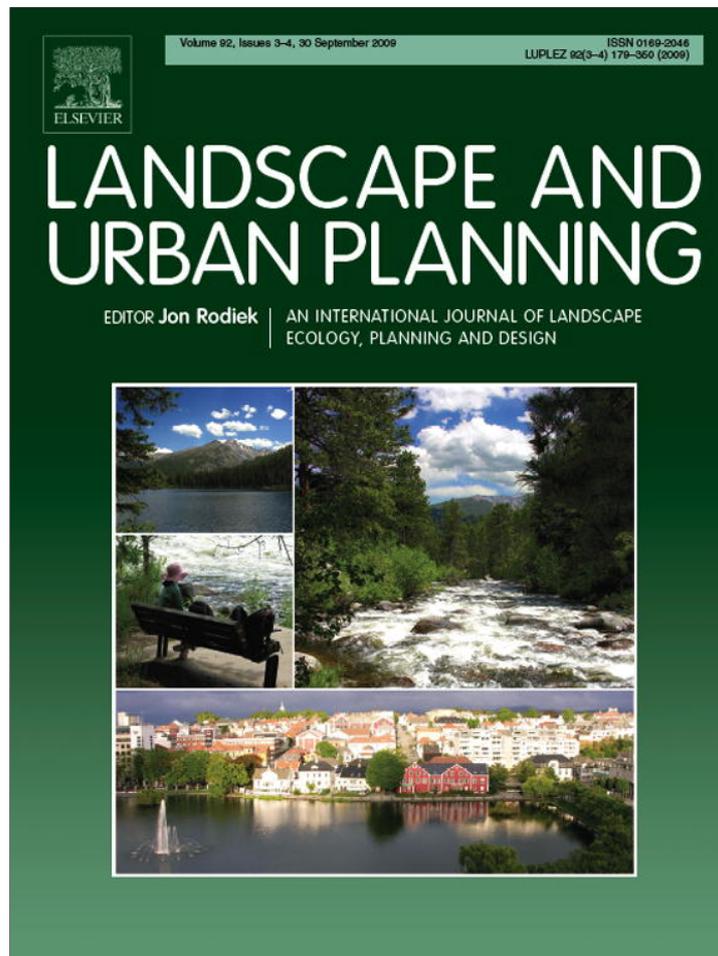


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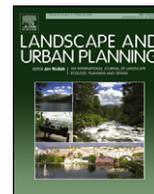
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Exurban development influences woodland bird composition

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ABSTRACT

One of the fastest growing types of land-use change is exurban development—low-density housing outside urban service boundaries. However, how individual species are responding to exurban development remains uncertain. We monitored birds for 5 years across three housing density levels in northern California oak woodlands. We compared community and species responses to exurban development (4–16 ha parcels) with suburban and undeveloped natural areas. We found that individual species and groups of species exhibited variable responses to exurban development. Some species and guilds were impacted by exurban development to the same extent as suburban development while others were less sensitive to this type of land use. For example, the proportion of the bird community composed of tree-and-shrub feeders was similar between exurban and natural areas, whereas proportions of temperate migrants showed significant reductions at both suburban and exurban sites. Similarly, Northern Flicker, Hutton's Vireo, and Orange-crowned Warbler were equally rare in exurban and suburban sites, making large, undeveloped parcels essential for their conservation. By explicitly measuring ecological changes associated with parcel size and density this research provides valuable information to land-use planners on the consequences of zoning for biodiversity conservation.

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1. Introduction

Habitat loss through land-use change represents one of the most serious threats to terrestrial biodiversity (Sala et al., 2000), and although most land-use decisions are made at the local level (Theobald et al., 2000), the results are of global importance (Foley et al., 2005). In fact, spatial analysis demonstrates that land use may be the strongest factor affecting endangered species densities in developed regions (Kerr and Cihlar, 2004). Recent estimates show that 60% of the world's population is projected to live in urban and suburban densities by the year 2030 (United Nations, 2005). These land-use types currently cover only 1.9% of the land area in the United States (Burchfield et al., 2006). In contrast exurban development occupied 15 times the land area of higher-density development in the United States in 2000 (Brown et al., 2005). Exurban development primarily results from minor subdivision of large, rural land parcels into smaller “ranchettes” that rely on private septic systems and groundwater wells. Across the United States nearly 80% of new housing construction between 1994 and 1997 occurred

on lots larger than 1 acre (0.4 ha), and 57% were built on lots 10 acres (4 ha) or larger (Heimlick and Anderson, 2001). California has the greatest recorded number of housing units in the wildland–urban interface (Radeloff et al., 2005), and oak woodlands are particularly susceptible to continued subdivision, because more than 80% of this ecosystem type is in private ownership in California (Pavlik et al., 1991).

Despite calls for more research on the impacts of human settlement (Miller and Hobbs, 2002), particularly beyond the urban fringe (Theobald, 2005; Fraterrigo and Wiens, 2005), attempts to quantify the impacts of exurban development on biodiversity in the field have only just begun. By its very nature, low-density residential development is difficult to map and monitor using existing land-cover databases because natural vegetation cover often remains dense in areas surrounding homes (Sutton et al., 2006). Hence, the consequences of exurban development for biodiversity cannot be easily predicted from landcover analysis of remotely sensed imagery.

Conversion of privately owned ranches and wildlands to exurban developments results in increased anthropogenic disturbances such as the introduction of domestic animals and non-native plant, and the construction and increased use of rural roads. Additionally, the extent and intensity of land use on exurban lots is highly variable, ranging from infrequently occupied second homes to grazing, small-scale agriculture, or wetland creation—activities that result in

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different levels of habitat modification and produce heterogeneous landscapes (Bock et al., 2006a).

The few field studies that have been conducted reveal variable responses of wildlife to exurban development among different species, taxonomic groups and ecosystem types. For example, in southeast Arizona, lizards were scarce in exurban areas likely due to their vulnerability to domestic predators (Audsley et al., 2006), while no effect of exurbia was detected in rodent community composition or species abundance (Bock et al., 2006b). Butterflies and grasshoppers also responded to the conversion of large ranches to exurban ranchettes, with the latter increasing in abundance (Bock et al., 2006a, 2007). Two of the most comprehensive field studies completed to date demonstrate significant effects of subdividing private ranches on bird, carnivore, and plant communities in Colorado (Odell and Knight, 2001; Maestas et al., 2001). On the other hand, differences in the presence of native ant species were not detected in southern Florida, despite marked increases in exotic ants found at exurban sites (Forys and Allen, 2005). The same was true for ants and small mammals in the Sierra Nevada, California (Manley et al., 2006), although the lack of detectable effect could represent an extinction debt that will lead to the loss of native species over time (Tilman et al., 2002). Disturbances associated with exurban development are likely to correspond to a more gradual change to the environment than more intense land uses, and the impacts to wildlife may need to be monitored over a longer time period.

The studies referenced above demonstrate that certain species tolerate human residential landscapes and their associated disturbances ('urban adapters') while other species are rare or not detected ('urban avoiders'). Here, we directly examine how bird communities respond to exurban developments (1 unit per 10–40 acres (4–16 ha) Theobald, 2001), as compared to suburban and undeveloped areas. We collected data on bird community composition and abundance over 5 years in sites located within suburban (0.2–1.0 ha home lots), exurban (4–16 ha lots) and undeveloped (>122 ha lots) land uses. Our specific objectives were to: (1) examine how guilds and species respond differently to the three land-use types, and (2) identify which species respond to exurban development similarly to suburban developments and may require protection from all types of residential development. To account for variability within the land-use treatments, we also measured a range of other site- and landscape-level characteristics that could influence the bird community. Unlike previous work, this study takes into account seasonal and year to year variability in species abundances, which can be especially high in Mediterranean-climate regions.

By sampling multiple sites within three different land-use types (suburban, exurban, and undeveloped) distinguished by parcel size classes, and that fall into residential zoning categories commonly found across rural areas, the results of our research are more easily transferable to land-use planners who seek measured environmental thresholds to guide decisions about development density (Environmental Law Institute, 2003). Fraterrigo and Wiens (2005) aptly point out that most of the insights about bird community response to land use is from urban and suburban areas. Little is known about the impacts of exurban development and how this compares with what we know from urban/suburban studies. Consequently, we focus on the particular impacts of exurban development on the bird community, compared to suburban development and undeveloped woodlands. For example, our research reveals that in exurban areas, the abundance of some species or representation of some guilds changes to a similar degree as in suburban areas, despite the lower development density associated with exurban areas. We refer to this as a "suburban" response as compared to an "intermediate" response where the detection rates fell between what we observed in suburban and wildland areas. Additionally,

we use the term 'undeveloped response' when we did not detect a difference in the abundance of a species or representation of a guild between exurban development and undeveloped woodlands. This information can be used to inform planning decisions and justify the need for policies designed to curtail the continued sprawl of low-density development into privately owned wildlands.

2. Materials and methods

2.1. Study area: Sonoma County, California

Counties surrounding the San Francisco Bay Area in northern California are experiencing extensive exurban growth. For example, more than half of Sonoma County's 1 million acres (404 ha) is an intermix of low-density housing, vineyards, and undeveloped forests and woodlands, resulting in a growing interface between human-dominated landscapes and wildlands. The Mediterranean climate and complex geology of the Coast Ranges that run through Sonoma County have produced a rich flora and a diverse mix of vegetation types and plant communities, including mixed conifer forest, mixed conifer–hardwood forest, oak woodland, mixed hardwood forest, grasslands, and a variety of riparian and other wetland habitats (Barbour et al., 1993). Due to the mild climate and exceptionally high diversity of oak and other hardwood species, the mixed oak woodlands in the study area support a diverse assemblage of birds and other wildlife (Stebbins and Hrusa, 1995).

2.2. Site selection

We used a geographic information system (GIS) database to identify suburban, exurban, and undeveloped sites with similar habitat characteristics in the foothills of the Mayacmas Mountains. Our database included: (1) digital elevation models for the study area (USGS, 30 m resolution); (2) a vegetation map based on classification of Thematic Mapper satellite imagery taken in 1990 (Pacific Meridian Resources, 1994); and (3) parcel lot lines (Sonoma County Information Systems Department). Because plant community composition varies considerably within areas referred to as mixed oak woodland (Sawyer and Keeler-Wolf, 1995), we restricted our study to low-elevation, gently sloped areas to reduce the amount of variation in vegetation characteristics among potential sites. Using ARC/INFO software (Environmental Systems Research Institute, Inc., Redlands, CA USA), we identified areas with hardwood tree cover that had slope values between 5° and 15° and elevation between 100 and 200 m.

Next, we used the county lot line data to identify potential sites that fell within three different land-use type treatments: (1) suburban developments, consisting of 0.20–1.0 ha home lots; (2) exurban developments, with parcels ranging from 4 to 16 ha in size; and (3) undeveloped private land parcels with areas greater than 122 ha. Each suburban site was comprised of a neighborhood consisting of multiple single-family residences. Every exurban site encompassed an area approximately 16 ha in size, comprised of contiguous properties that were each between 4 and 16 ha in size. Each undeveloped site was located on a property >122 ha under single ownership and adjacent to large expanses of public and privately owned wildlands.

After we identified potential sites using GIS, we made field visits to these sites in order to assess site characteristics that are difficult to assess from satellite imagery, such as dominant oak species and extent of shrub cover. This process resulted in the selection of 12 oak (*Quercus*) dominated study sites, 4 within each of the 3 treatments—suburban, exurban, and undeveloped (Fig. 1).

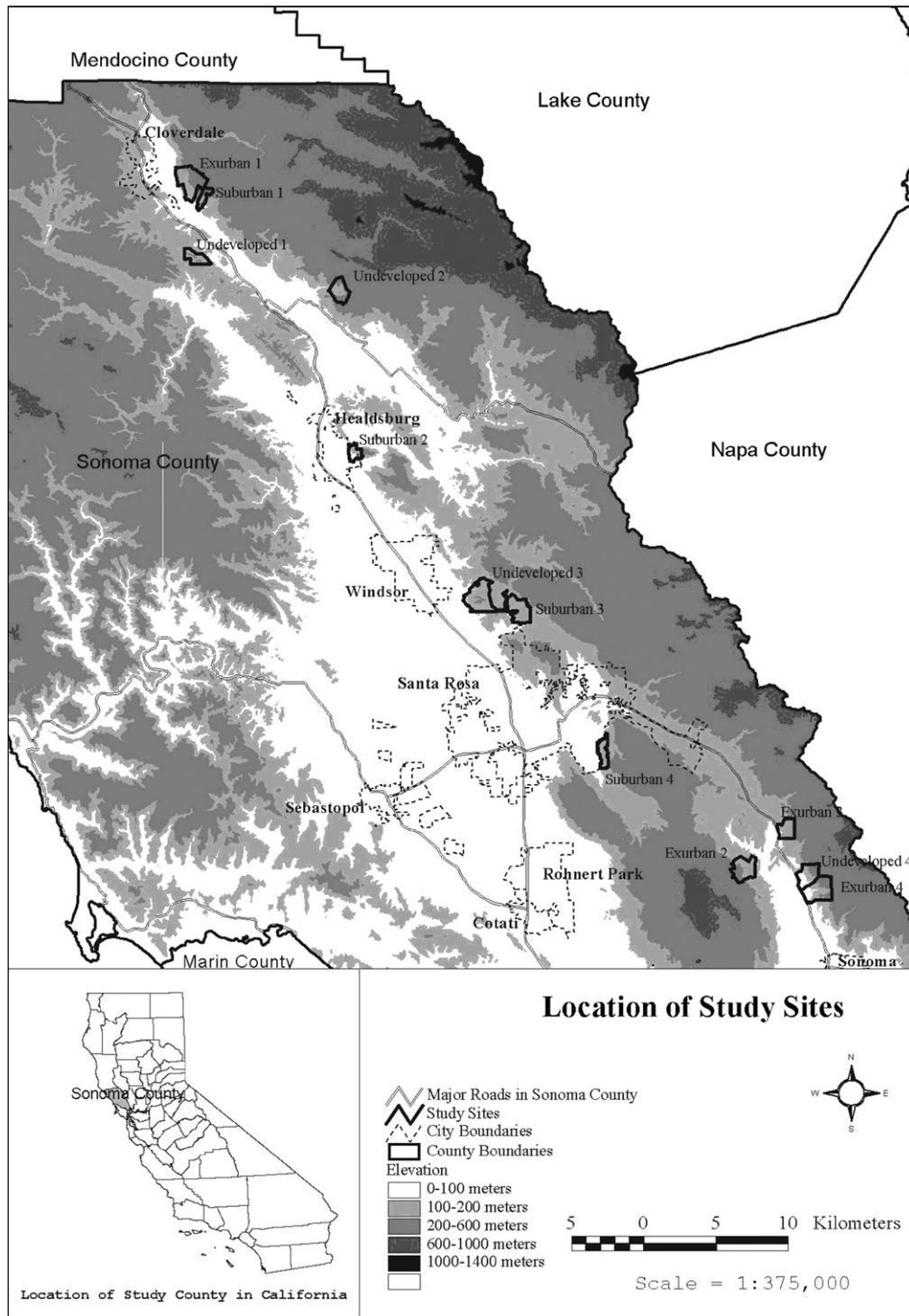


Fig. 1. Location of study sites in Sonoma County.

We included only undeveloped sites that had no livestock grazing for a minimum of 5 years. Two of the exurban sites had horses in a restricted area, which is common for this type of land use, but otherwise no sites had other types of livestock. Permission to conduct our study in the selected sites was obtained from the individual property owners, with the exception of the small lot subdivisions (0.20–1.0 ha lots) where data were collected on public right-of-ways such as sidewalks immediately adjacent to private parcels (for more information on accessing private land for research see Hilty and Merenlender, 2003).

2.3. Field data collection

We established eight sampling points at least 250 m apart from one another in the field at each of the 12 study sites, resulting in a total of 32 sampling points per land-use treatment. For each of the 96 points, we estimated percent cover for all vascular plant species within a 10 m × 10 m macroplot. Tree density at each point was calculated using the point-centered quarter method (Cotton and Curtis, 1956). Based on the data collected in the macroplots, we calculated the following site-level variables for each sampling

Table 1
Landscape variables and their source data.

Variable code	Calculation used	Source data
%F500	% forested within 500 m of bird count points	"Calveg" landcover data, 1994, from CDF-FRAP
Durban	Euclidian distance to urban areas	Urban areas from "Calveg" landcover data, 1994, from CDF-FRAP
%V500	Average % vineyard within 500 m of bird count points	1997 vineyard boundaries, from Sonoma County Grape Growers Association, as digitized by Circuit Rider Productions, Inc.
LOT500	Average lot size within 500 m of bird count points	County parcel layer from the Sonoma County Information Systems Department
DH2024	Euclidean distance to nearest 1:240,000 scale stream or body of water	USGS 1:24,000 scale Digital Line graph data
RoadD	Road density within 500 m of bird count points	US Census Bureau 1998 "TIGER/line" 1:100,000 scale data
DH500	Simple diversity of landcover types within 500 m of bird count points	"Calveg" landcover data, 1994, from CDF-FRAP

point: (1) number of plant species, (2) number of exotic species, (3) percent non-native plant species, (4) percent absolute cover of all vegetation, (5) tree density (# trees/100 m²), and (6) percent shrub cover.

At each survey point, bird species and number of individuals heard or seen were recorded for 10 min within a fixed 50 m radius during the early morning hours (Ralph et al., 1995). Point counts were conducted by one very experienced bird observer at all 96 sampling points once during the spring breeding season (May/June) for 5 years; thereby preventing observer bias.

2.4. Landscape variables and data analysis

Arc/Info and ArcView 3.2 (ESRI) were used to calculate several landscape variables at a fixed distance from each sampling point. The spatial databases used to develop these variables are listed in Table 1. Rather than using multiple buffer distances (Bolger et al., 1997) which could result in problems with multi-collinearity in the final models, we used a fixed 500 m radius circle to calculate all landscape variables. Preliminary linear regression models indicated that variables calculated at this buffer distance were more strongly correlated with bird community indices than those calculated at 100, 250, and 1000 m, and buffer distances greater than 1000 m would have yielded substantial overlap among areas sampled to calculate variables for different study sites.

Because large, intact woodlands may be important to certain species, "core" habitat was defined and delineated using 1994 TM satellite data of hardwood cover. These core habitat areas were defined as 100 ha or more of contiguous habitat. Individual habitat patches were considered to be not continuous if they were separated by at least 2 pixels. To eliminate edge habitat from consideration, a 1-pixel buffer (25 m) was removed around each identified habitat patch. Core habitat was delineated using a modified version of the "core.aml" habitat analysis program (S. Saving, California's Fire and Resource Assessment Program, pers. comm.).

We limited our analyses to species that comprised at least 0.5% of all observations within a site, to remove non-resident species and occasional sightings. We also omitted feral domesticated birds and waterfowl (Blair, 1996). Thus, a total of 71 species were

retained for statistical analysis. Concerns have been raised that bias in bird detection rates can result from differences in habitat (Thompson, 2002) or in this case land-use types, since all study sites were located in oak woodland habitat. To address these concerns, we examined possible relationships between tree density and the mean number of detections within each land-use treatment through regression analysis. Tree density at each sampling point was measured in the field using the point-centered quarter method (Cotton and Curtis, 1956; see Merenlender et al., 1998 for more details).

The bird species were classified into the following guilds or groups and their respective forms: (1) nest type (cavity, open cup), (2) nest location (cliff/ledge, ground, shrub, tree canopy), (3) feeding location (ground, tree/shrub, aerial, water), (4) migratory status (neotropical, temperate, resident), and (5) origin (native, exotic). This information was determined for each species based on their known behavior in Sonoma County using various references (Ehrlich et al., 1988; Burridge, 1995; Fix and Bezener, 2000; Sibley, 2000; Elphick et al., 2001; USGS Breeding bird survey web site 2003) and local expert knowledge (Emily Heaton, Chuck Vaughn, Robert Keiffer, pers. comm.). Species were classified as 'urban adapters' and 'urban avoiders' based on published results from previous studies conducted in California's oak woodlands (Stralberg and Williams, 2001; Bolger et al., 1997; Blair, 1996). Canonical correspondence analysis (CCA) (McCune and Mefford, 1999) was used to explore how observed variation in the bird community is partitioned relative to housing density and the site and landscape environmental variables. Next, we examined the influence of three different land-use types or treatments (suburban, exurban, and undeveloped) on observed variation in the entire bird community (in terms of species composition and relative abundances of different species). We used permutational multivariate analysis of variance (NPMANOVA), a nonparametric method that compares the variance within and between a distance matrix calculated from distances between each pair of observations. This analysis is similar to using a Fisher's *F*-ratio for a distance matrix generated from the entire bird community data matrix and *P*-values are a result of multiple permutations. (Anderson, 2000; Anderson, 2001). We selected this method because it partitions the variation between our treatments and within sites using a two-way analysis similar to ANOVA and does not require any assumptions about the distribution or correlations among the data (Anderson, 2001). We ran this test for a two-way nested design (level 1 = land-use type, level 2 = site, replicates = sampling points) so that differences in bird communities could be examined relative to both treatment and site differences. To examine whether 'site' contributed to differences in bird communities, permutations of raw data were done randomly across sites but were restricted to occur within the appropriate land-use type. The number of individuals detected for each species over 5 years of sampling was transformed due to the presence of zero detections with a $\ln(x + 1)$ transformation. The chi-square distance measure was used to emphasize compositional differences over differences in abundances. Pair-wise *a posteriori* comparisons were conducted to test for differences in bird communities between different pairs of treatments (e.g., suburban vs. exurban).

The proportion of species detected within each of the guilds listed above, relative to all species detected at each sampling point, provides us with a closer examination of shifts in community composition among the treatment types. Because we were most interested in how land-use type influences bird community composition, we used a three-level nested analysis of variance (ANOVA) with land-use type as the primary factor. Sites were nested within each treatment, sampling points were nested within sites, and the five annual visits were treated as repeated measures. In addition, we used nested ANOVA to explore variation in observed abundance for

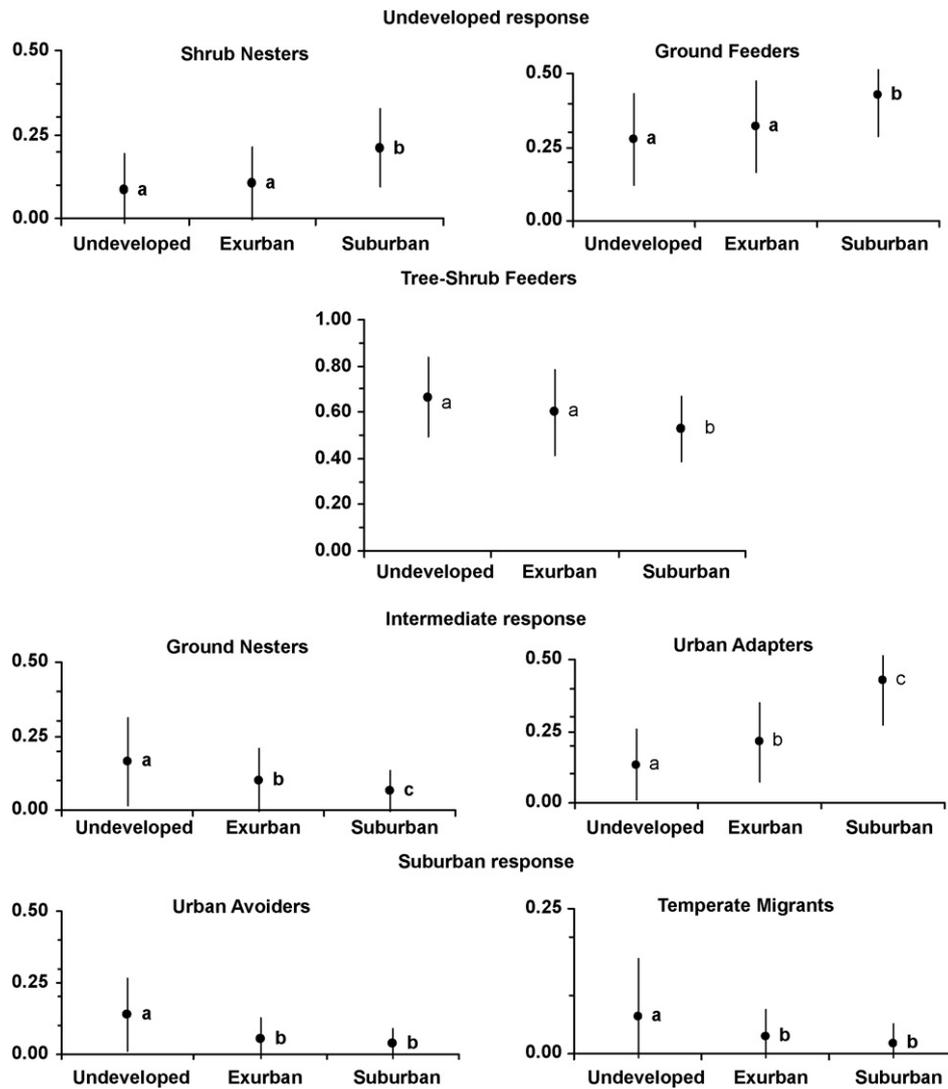


Fig. 3. Guild comparisons among land-use types. The proportions of total detections in each guild are represented on the y-axis; points represent the means and bars the standard deviations. The species assemblages are clustered as whether the proportion of detections in exurban sites was similar to the undeveloped sites (undeveloped response) or intermediate between undeveloped and suburban (intermediate response), or not significantly different from the suburban sites (suburban response); with different letters indicate significant differences between treatments.

4. Discussion

Despite high variability among sites, analysis of our 5-year bird survey effort demonstrated significant differences among the three land-use treatments. The landscape variables offered little explanatory power when trying to partition the variance observed in bird communities (Fig. 2). The larger landscape variables taken from 500 m surrounding each sampling point do result in some spatial autocorrelation that can overestimate the effect of habitat when developing predictive models using regression analysis. However, removing this type of autocorrelation did not influence predictive models for forest birds (Betts et al., 2006).

Our results reveal how groups of species responding to exurban development compare to more developed suburban areas and undeveloped wildlands. For example, the proportion of detections of temperate migrants was two times greater in the undeveloped than the exurban sites and three times greater than the suburban sites, with no significant effect of differences among sites, highlighting the importance of protecting core woodlands from exurban development.

The proportion of detections of tree-and-shrub feeders at exurban sites was similar to that detected in undeveloped sites; while the relative abundance of ground nesters detected fell in between that observed at suburban and undeveloped sites. These ground nesters are likely more susceptible to predation by non-native animals such as cats, dogs, and rats which are more frequently detected near homes (Odell and Knight, 2001; Lenth et al., 2006). Adverse impacts of domestic cats on birds are well-documented (Burbidge and Manly, 2002; Churcher and Lawton, 1987). Shrub nesters and ground feeders, however, such as the California Towhee, comprised a larger part of the bird community at the suburban sites which had higher overall shrub cover than larger, less-developed parcels (Merenlender et al., 1998). The ground feeders may be taking advantage of supplemental feeding by suburban residents.

The proportion of the bird community comprised of urban avoiders was similarly low in both the exurban and suburban sites (Fig. 3), and we expect that the species listed as urban avoiders will be negatively impacted by additional development of low-density housing that has been forecasted for the Mayacamas range (Merenlender et al., 2005). Urban adapter species comprised

Table 2
Mean (s.d.) proportion of bird detections in each guild, by land-use treatment, with results for nested ANOVA analyses for treatment- and site-level effects.

Guild	Undeveloped	Exurban	Suburban	Treatment		Site	
				$F_{2,9}$	P	$F_{9,84}$	P
Nest type							
Cavity	0.338 (0.200)	0.394 (0.169)	0.357 (0.145)	1.55	0.264	4.29	<0.001
Open cup	0.516 (0.185)	0.426 (0.177)	0.498 (0.153)	2.96	0.103	5.25	<0.001
Nest location							
Cliff/ledge	0.053 (0.072)	0.057 (0.095)	0.073 (0.082)	1.17	0.354	4.83	<0.001
Ground	0.164 (0.149)	0.100 (0.105)	0.064 (0.067)	7.26	0.013	2.94	0.004
Shrub	0.083 (0.109)	0.102 (0.109)	0.210 (0.115)	7.34	0.013	7.32	<0.001
Tree canopy	0.729 (0.171)	0.776 (0.150)	0.767 (0.115)	0.73	0.507	4.60	<0.001
Feeding location							
Ground	0.276 (0.155)	0.321 (0.155)	0.427 (0.139)	21.73	<0.001	1.49	0.166
Tree/shrub	0.664 (0.174)	0.598 (0.188)	0.528 (0.140)	26.12	<0.001	0.58	0.809
Aerial	0.063 (0.102)	0.102 (0.126)	0.079 (0.091)	0.12	0.888	59.48	<0.001
Water	0.003 (0.023)	0.002 (0.017)	0	0.50	0.621	2.46	0.015
Migratory status							
Neotropical migrant	0.211 (0.198)	0.231 (0.179)	0.133 (0.107)	0.94	0.425	12.14	<0.001
Temperate migrant	0.063 (0.101)	0.029 (0.047)	0.018 (0.034)	9.48	0.006	1.49	0.164
Resident	0.726 (0.218)	0.740 (0.184)	0.849 (0.114)	2.35	0.151	7.95	0.000
Origin							
Native	0.985 (0.050)	0.975 (0.062)	0.965 (0.065)	1.20	0.346	5.32	<0.001
Exotic	0.015 (0.050)	0.025 (0.062)	0.035 (0.065)	1.20	0.346	5.32	<0.001
Human association							
Urban adapter	0.132 (0.123)	0.212 (0.137)	0.429 (0.156)	40.65	<0.001	3.66	0.001
Urban avoider	0.139 (0.128)	0.055 (0.072)	0.038 (0.052)	12.68	0.002	3.67	0.001

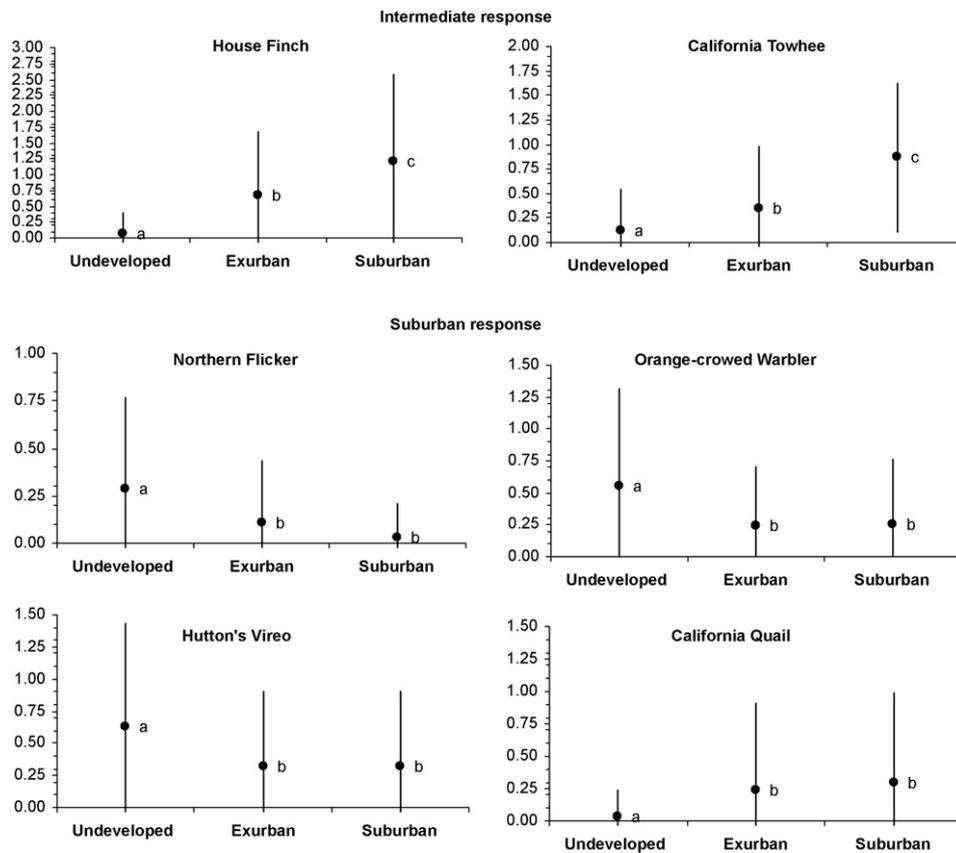


Fig. 4. Comparisons among land-use types for a subset of individual species. Points represent mean numbers of detections (values along the y-axis) by land-use treatment each year, and bars represent the standard deviations around the means. The species are clustered as whether the relative abundance detected in exurban sites was intermediate between undeveloped and suburban (intermediate response) or not significantly different from the suburban sites (suburban response); with different letters indicate significant differences between treatments. The other urban adapters (Oak Titmouse, Western Scrub-Jay, Northern Mockingbird, American Crow, and Turkey Vulture) demonstrated a suburban response (not shown).

approximately 10% of detections in the undeveloped sites, while their proportion was twice as great in the exurban and over four times as great in the suburban sites.

Individual species that respond to development densities in the same manner as the entire assemblage of urban avoiders and urban adapters have the potential to serve as good indicator taxa (Hilty and Merenlender, 2000). Approximately half of the urban adapter species were found at intermediate levels of abundance in exurban sites, leading us to conclude that species such as House Finch and California Towhee appear to be good indicators of intermediate disturbance. However, some urban adapters only reach significantly higher levels of relative abundance in dense housing areas, including Oak Titmouse, Western Scrub-Jay, Turkey Vulture, Northern Mockingbird, and American Crow. The Oak Titmouse is a common resident in oak woodlands, and researchers have noted them as urban adapters in other regions of California (Blair, 1996). Western Scrub-Jay (Blair, 1996; Stralberg and Williams, 2001), California Quail (Blair, 1996), House Finch (Blair, 1996; Bolger et al., 1997; Stralberg and Williams, 2001), Northern Mockingbird (Blair, 1996; Bolger et al., 1997), and California Towhee (Blair, 1996) have also been reported as urban adapters. We were not surprised to find that Western Scrub-Jay and American Crow were species more commonly found in Sonoma County's suburbs. Turkey Vultures were also more commonly found in suburbs, which could be related to increased detectability of this species in the open sky and roads associated with suburban environments. The magnitude of differences in the abundances of urban adapter species among land-use treatments far exceeded the magnitude of any suspected bias in detectability attributable to local woodland structure.

Northern Flickers, Orange-crowned Warblers, and Hutton's Vireos were all significantly more abundant in undeveloped sites as compared to exurban sites, and may make good indicators for the entire suite of urban avoiders. Our findings are consistent with prior studies which have identified Hutton's Vireo (Blair, 1996; Stralberg and Williams, 2001) and Orange-crowned Warblers (Stralberg and Williams, 2001) as urban avoiders or woodland associates. If any bias between detection rates among treatments did occur it did not hamper our ability to detect trends for species that were most abundant in the undeveloped sites, where tree density was highest, so we can be confident in the results for the urban avoider species noted above. Species other than those discussed here may be equally or more sensitive to development densities, but because of their low detection rates we were not able to establish a significant relationship between abundance and treatment.

5. Conclusions

We demonstrate that exurban development is differentially impacting certain bird species and assemblages. In some cases the impacts of exurban development can be as significant as that observed in suburban areas but this is not necessarily so for all taxa. The research presented here suggests that parcel size can be applied as a measure of disturbance that has consequences for bird communities, since the land-use types we compared relate back to overall parcel size classes and residential zoning classes.

The subdivision of rural parcels is generally under the jurisdiction of local counties in the United States (Theobald et al., 2000) and it can be difficult to reduce development densities on existing large private parcels through zoning regulations because of the loss in land value that can result and may require compensation (Richardson, 2003). More popular is an incentive-based approach generally implemented through conservation easements (Merenlender et al., 2004). Purchasing development rights before large parcels become fragmented by rural residential development can be an effective way to conserve sensitive species such as Hutton's Vireo, Orange-crowned Warbler, and Northern Flicker.

Unfortunately the drivers that create demand for rural residential development do not disappear when land is purchased for protection against development (Newburn et al., 2005). As a result, this type of development is pushed to other areas not currently protected. Therefore, it is important that we encourage local governments to invoke fees and taxes to pay for enacting nature-friendly policies (Brueckner, 2000) and promote high-density development within city service boundaries to minimize the continued subdivision of large, privately owned wildland parcels. Short of changing zoning regulations, one of the most common ways to prevent further subdivision of large, privately owned land parcels is through trading development rights; this process involves the sale of development rights, usually from designated "sending" areas and allows for more development than is currently zoned for in designated "receiving" areas (Johnston and Madison, 1997). More policy options and incentives are needed to curtail low-density residential expansion throughout the developed world where the demand for exurban development is high and existing land-use policies rarely provide the necessary controls.

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References

- Anderson, M.J., 2000. NPMANOVA: A FORTRAN Computer Program for Non-parametric Multivariate Analysis of Variance (for Any Two-Factor ANOVA Design) Using Permutation Tests. Department of Statistics, University of Auckland, New Zealand.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.* 26, 32–46.
- Audley, B.W., Bock, C.E., Jones, Z.F., Bock, J.H., Smith, H.M., 2006. Lizard abundance in an exurban southwestern savanna, and the possible importance of roadrunner predation. *Am. Midl. Nat.* 155, 395–401.
- Barbour, M., Pavlik, B., Drysdale, F., Lindstrom, S., 1993. California's Changing Landscapes. California Native Plant Society Press, Sacramento, CA, pp. 58–60.
- Betts, M.G., Diamond, A.W., Forbes, G.J., Villard, M.A., Gumnn, J.S., 2006. The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Eco. Model.* 191, 197–224.
- Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. *Ecol. Appl.* 6 (2), 506–519.
- Bock, C.E., Bailowitz, R.A., Danforth, D.W., Jones, Z.F., Bock, J.H., 2007. Butterflies and exurban development in southeastern Arizona. *Landsc. Urban Plann.* 80 (1–2), 34–44.
- Bock, C.E., Jones, Z.F., Bock, J.H., 2006a. Grasshopper abundance in an Arizona range-land undergoing exurban development. *Range Ecol. Manage.* 59 (6), 640–647.
- Bock, C.E., Jones, Z.F., Bock, J.H., 2006b. Rodent communities in an exurbanizing southwestern landscape (USA). *Conserv. Biol.* 20 (4), 1242–1250.
- Bolger, D.T., Scott, T.A., Rotenberry, J.T., 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conserv. Biol.* 11 (2), 406–421.
- Brown, D.G., Johnson, K.M., Loveland, T.R., Theobald, D.M., 2005. Rural land-use trends in the conterminous United States, 1950–2000. *Ecol. Appl.* 15 (6), 1851–1863.
- Brueckner, J.K., 2000. Urban sprawl: diagnosis and remedies international regional. *Sci. Rev.* 2 (2), 160–171.
- Burbidge, A.A., Manly, B.F.J., 2002. Mammal extinctions on Australian islands: causes and conservation implications. *J. Biogeogr.* 29, 465–473.
- Burchfield, M., Overman, H., Puga, M., Runer, M., 2006. Causes of sprawl: a portrait from space. *Q. J. Econ.* 121 (2), 587–633.
- Burridge, B. (Ed.), 1995. Sonoma County Breeding Bird Atlas. Madrone Audubon Society, Inc., Santa Rosa, CA.
- Churcher, J.B., Lawton, J.H., 1987. Predation by domestic cats in an English village. *J. Zool.* 212, 439–456.
- Cottom, G., Curtis, J.T., 1956. The use of distance methods in phytosociological sampling. *Ecology* 37, 451–460.

- Ehrlich, P.R., Dobkin, D.S., Wheye, D., 1988. *The Birder's Handbook*. Simon and Schuster/Fireside, New York.
- Elphick, C., Dunning Jr., J.B., Sibley, D.A. (Eds.), 2001. *The Sibley Guide to Bird Life and Behavior*. Alfred A. Knopf, New York.
- Environmental Law Institute, 2003. *Conservation Thresholds for Land Use Planners*. p. 55. www.elistore.org.
- Fix, D., Bezener, A., 2000. *Birds of Northern California*. Lone Pine Publishing, Edmonton, Alberta, Canada.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Pataz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* 309, 570–574.
- Forys, E.A., Allen, C.R., 2005. The impacts of sprawl on biodiversity: the ant fauna of the lower Florida Keys. *Ecol. Soc.* 10 (1), 25.
- Fraterigo, J.M., Wiens, J.A., 2005. Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. *Landsc. Urban Plann.* 71 (2–4), 263–275.
- Heimlick, R.E., Anderson, W.D., 2001. Development at the urban fringe and beyond: impacts on agriculture and rural land. *Agricultural Economic Report No. 803*. U.S. Department of Agriculture, Economic Research Service, Washington, DC.
- Hilty, J., Merenlender, A.M., 2000. Faunal indicator taxa selection for monitoring ecosystem health. *Biol. Conserv.* 92, 185–197.
- Hilty, J., Merenlender, A.M., 2003. Studying biodiversity on private lands. *Conserv. Biol.* 17 (1), 132–137.
- Johnston, R.A., Madison, M.E., 1997. From landmarks to landscapes. *J. Am. Plann. Assoc.* 63 (3), 365–379.
- Kerr, J.T., Cihlar, J., 2004. Patterns and causes of species endangerment in Canada. *Ecol. Appl.* 14 (3), 743–753.
- Lenth, B.A., Knight, R.L., Gilgert, W.C., 2006. Conservation value of clustered housing developments. *Conserv. Biol.* 20 (5), 1445–1456.
- Maestas, J.D., Knight, R.L., Gilgert, W.C., 2001. Biodiversity and land-use change in the American mountain west. *Geogr. Rev.* 91 (3), 509–524.
- Manley, P.N., Murphy, D.D., Campbell, L.A., Heckmann, K.E., Merideth, S., Parks, S.A., Sanford, M.P., Schlesinger, M.D., 2006. Biotic diversity interfaces with urbanization in the Lake Tahoe Basin. *Calif. Agric.* 60 (2), 59–64.
- McCune, B., Mefford, M.J., 1999. *PC-ORD. Multivariate Analysis of Ecological Data, Version 4*. MjM Software Design, Gleneden Beach, Oregon.
- Merenlender, A.M., Brooks, C., Shabazian, D., Gao, S., Johnston, R., 2005. Forecasting exurban development to evaluate the influence of land-use policies on wildland and farmland conservation. *J. Conserv. Plann.* 1 (1), 64–88.
- Merenlender, A.M., Heise, K.L., Brooks, C., 1998. Effects of sub-dividing private property on biodiversity in California's north coast oak woodlands. *Trans. Wildl. Soc.* 34, 9–20.
- Merenlender, A.M., Huntsinger, L., Guthey, G., Fairfax, S.K., 2004. Land trusts and conservation easements: who is conserving what for whom? *Conserv. Biol.* 18 (1), 65–75.
- Miller, J.R., Hobbs, R.J., 2002. Conservation where people live and work. *Conserv. Biol.* 16 (2), 330–337.
- Newburn, D., Reed, S., Berck, P., Merenlender, A.M., 2005. Economics and land-use change in prioritizing private land conservation. *Conserv. Biol.* 19 (5), 1411–1420.
- Odell, E.A., Knight, R.L., 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conserv. Biol.* 15 (4), 1143–1150.
- Pacific Meridian Resources, 1994. *California Hardwood Rangeland Monitoring Final Report*. CDF-FRAP, Sacramento, CA.
- Pavlik, B.M., Muick, P.C., Johnson, S., Popper, M., 1991. *Oaks of California*. Cachum Press, Los Olivos, California, p. 184.
- Radeloff, V.C., Hammer, R.B., Stewart, S.I., Fried, J.S., Holcomb, S.S., McKeefry, J.F., 2005. The wildland–urban interface in the United States. *Ecol. Appl.* 15 (3), 799–805.
- Ralph, C.J., Droegge, S., Sauer, J.R. 1995. *Managing and monitoring birds using point counts: standards and application*. USDA Forest Service General Technical Report PSW-GTR-149.
- Richardson Jr., J.J., 2003. Downzoning, fairness, and farmland protection. *J. Land Use* 19 (1), 59–89.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Biodiversity—global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Sawyer, J.O., Keeler-Wolf, T., 1995. *A Manual of California Vegetation*. California Native Plant Society, California.
- Sibley, D.A., 2000. *The Sibley Guide to Birds*. Alfred A. Knopf, New York.
- Stebbins, G.L., Hrusa, G.F., 1995. The north coast biodiversity arena in central California: a new scenario for research and teaching processes of evolution. *Madrono* 42, 269–294.
- Stralberg, D., Williams, B., 2001. Effects of residential development and landscape composition on the breeding birds of Placer County's Foothill Oak Woodlands. *USDA Forest Service General Technical Report PSW-GTR-184*, p. 341.
- Sutton, P.C., Cova, T.J., Elvidge, C., 2006. Mapping exurbia in the conterminous United States using nighttime satellite imagery. *Geocarto Int.* 21 (2), 39–45.
- Theobald, D.M., Hobbs, N.T., Bearly, T., Zack, J.A., Shenk, T., Riebsame, W.E., 2000. Incorporating biological information in local land-use decision making: designing a system for conservation planning. *Landsc. Ecol.* 15, 35–45.
- Theobald, D.M., 2001. Land use dynamics beyond the American fringe. *Geogr. Rev.* 91 (3), 544–564.
- Theobald, D.M., 2005. Landscape patterns of exurban growth in the USA from 1980 to 2020. *Ecol. Soc.* 10 (1), 32.
- Thompson, W.L., 2002. Towards reliable bird surveys: accounting for individuals present but not detected. *The Auk* 119 (1), 18–25.
- Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 2002. Habitat destruction and the extinction debt. *Nature* 371, 65–66.
- United Nations, Department of Economic and Social Affairs, Population Division, 2005. *World urbanization prospects: the 2005 revision*. <http://www.un.org/esa/population/publications/WUP2005/2005wup.htm>.
- USGS, 2003. List of species groupings (breeding bird survey data). <http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>.