

## CHAPTER

# Modeling Bird Responses to Predicted Changes in Land Cover in an Urbanizing Region

# 23

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Humanity has transformed nearly half of Earth's land areas (Meyer and Turner 1992, Houghton 1994, Lambin et al. 2001). Most of this change has occurred in the last several thousand years as we developed into an agrarian, and then increasingly mechanized, society. A transformed Earth has provided material goods required by modern society and enabled spectacular growth of the human population, but at the cost of long-term provisioning of ecosystem services (Foley et al. 2005). Land transformation is also a major threat to biological diversity now, and increasingly so for temperate regions in the future (Sala et al. 2000).

Urbanization is a growing driver of worldwide change in land cover (Vitousek et al. 1997, Grimm et al. 2000, Alberti et al. 2003). In 1900, only 10% of humans lived in cities, but by 2000, nearly 50% did; by 2030 that number is expected to rise to 60% (Sadik 1999). Depending on economics, social preferences, and land-use policies, the growth of urban populations causes cities, and even more profoundly their suburbs, to spread across large expanses of former agricultural and natural lands (Matlack 1993, Ewing 1994). The worldwide extent of sprawling settlement is visible in the nighttime images of Earth from space (Elvidge et al. 1997). These images reveal that substantial portions of the north temperate zone are heavily settled, most ice-free coastlines are settled, our most fertile lands are quickly being developed, and overall about 3% of Earth's land area is urban (Lawrence et al. 2002, Imhoff et al. 2004).

The influence of rapid urbanization is particularly evident in the western United States (Hansen et al. 2005). People seeking to improve their quality of life are attracted to the west's scenic beauty and its strong service and light industrial job base. As a result of increased urban population growth and immigration, agricultural lands and undeveloped lands that hold great stores of biodiversity are being converted into developed land uses (Mörtberg et al. 2007).

Changed land cover, altered biogeochemical cycles and climate, pollutants, introduced invasive species, and other consequences of human activities directly and indirectly change the selective forces acting upon plants and animals causing some to go extinct and enabling others to thrive and expand (Marzluff 2001, Pickett et al. 2001, McKinney 2002, Kaye et al. 2006). The local difference in extinction and colonization determines standing diversity (Marzluff 2005).

While we are beginning to understand how local urbanization processes influence biodiversity, we know much less about how these altered processes of extinction and colonization will play out through time. To understand how biodiversity responds to land-cover changes requires large-scale modeling. Examples of land-cover and land-use change models abound and are diverse in their theoretical traditions, application, and geographic scope (e.g., Riitters et al. 1997, Pearson et al. 1999, Parker et al. 2003, Turner et al. 2003, Tang et al. 2005). Examples of linking models of land-cover or land-use change to changes in biodiversity are less numerous (Sala et al. 2000, Schumaker et al. 2004, Prato 2005, Mörberg et al. 2007). While there is no generally accepted single method for predicting how biodiversity will change with landscape change (Doak and Mills 1994, Ruckelshaus et al. 1997), there is a rich literature of how species respond to changes (i.e., loss and fragmentation) of their habitat (e.g., Fahrig and Merriam 1994, McGarigal and McComb 1995, Villard et al. 1999).

Linking predictions from landscape change models to ecological models is generally accomplished by developing spatially explicit habitat models, either at coarse scales with coarse input and output such as habitat-association models (e.g., Scott et al. 1993) for a large number of species (White et al. 1997, Schumaker et al. 2004) or individually based finer resolution models for a single (or few) species (Dunning et al. 1995, Schumaker et al. 2004). In this chapter, we build on such approaches by using sophisticated models of urban development and land-cover change to model the influence of urbanization on biodiversity. We show how models of urban development can be translated into changes in land cover and how these changes can be projected to affect the abundance and diversity of birds in the rapidly urbanizing Central Puget Sound region of western Washington, United States. This area has experienced dramatic urban growth, especially during the past 30 years (Hansen et al. 2005, Robinson et al. 2005) and is projected to grow by 31% (an additional 1 million people from 2000) by 2025 (Office of Financial Management, State of Washington: <http://www.ofm.wa.gov/pop/gma/projections.asp>). Currently, remnant forests exist in a variety of sizes and settings, from small urban parks or undeveloped parcels to large blocks of contiguous forests (Donnelly and Marzluff 2004b, 2006). Songbird diversity peaks in landscapes with 50–60% forest cover, because such areas gain more synanthropic and early successional species than the native forest species they lose (Marzluff 2005). This dynamic response of birds to changing land cover allows us to demonstrate how one component of biological diversity might respond to urbanization. While birds have high

public appeal that makes them attractive to policy makers and advocacy groups, their vagility also buffers them from extreme changes (Robinson et al. 1995, Tittler et al. 2006), which may lead us to underestimate the response of birds to local changes in land cover, especially in settings like Seattle, where nearby lands protected from conversion (national parks and forests) may act as source pools for urban populations with high turnover (Alberti and Marzluff 2004).

The objective of this chapter is to provide an example of how to link the output of spatially explicit land-use and land-cover change models to ecological process models. Our ecological response model is a two-scale approach to modeling avian diversity–species richness and relative abundance, but such an approach could have been used to link any spatially explicit ecological process model.

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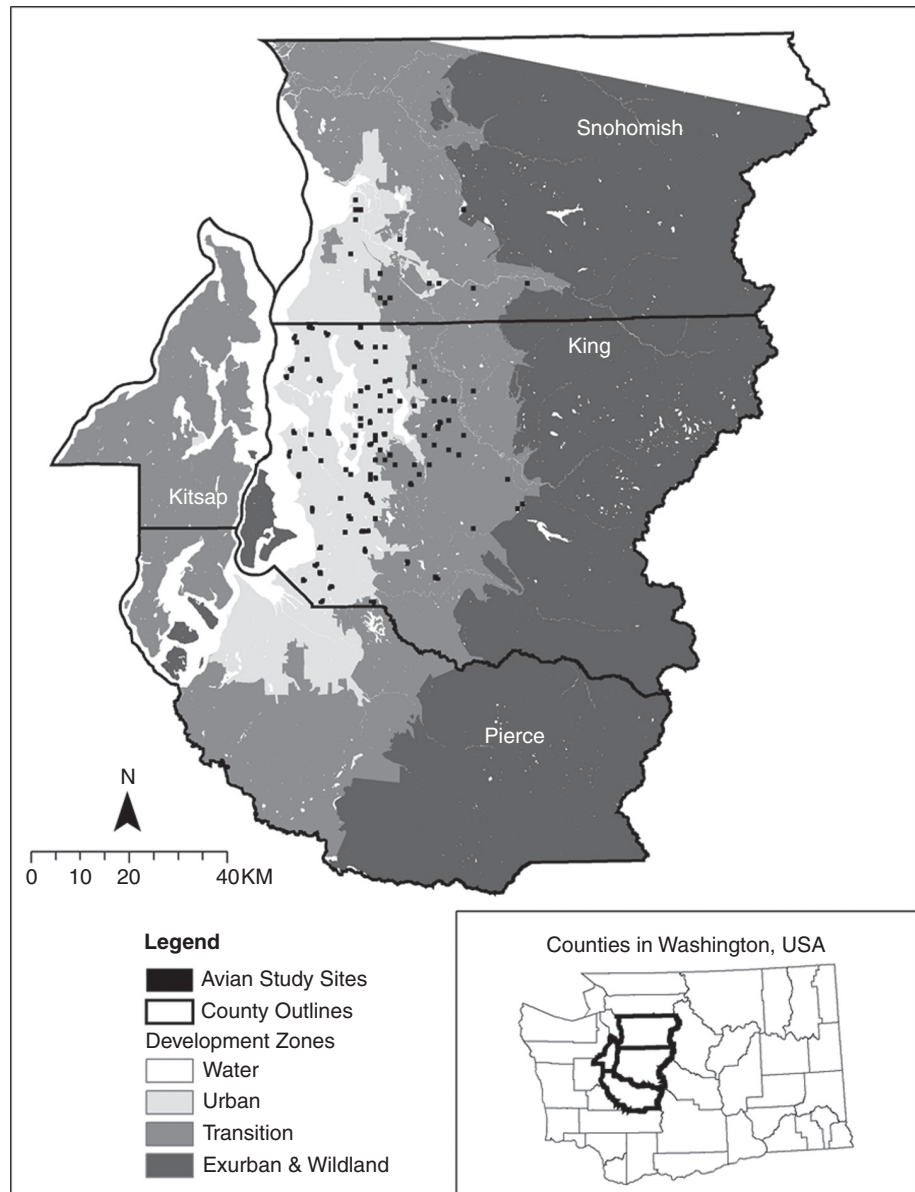
## METHODS

### Study Area

Our study area is the 3,200 km<sup>2</sup> area of temperate, moist forest around Seattle, Washington (Fig. 23-1). Forests were mostly coniferous, including western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*), with a few red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*), and Oregon ash (*Fraxinus latifolia*) occurring near riparian and disturbed areas (Franklin and Dyrness 1988). Elevation varied from sea level to near 300 m on the lower slopes of the Cascade Range. Areas above 300 m, while predicted by our land-cover change model, were not considered in our avian biodiversity models, as these areas were not sampled by our field studies.

### Study Sites

We chose 139 1-km<sup>2</sup> study sites within this study area (Fig. 23-1): 119 single-family residential (SFR) sites, 13 mixed use/commercial/industrial sites, and 7 forested (“control”) sites with minimal development. We stratified 54 randomly selected SFR sites study area along three axes of urbanization: (1) percent of urban, forest, or grass in a landscape; (2) average patch size of urban land cover; and (3) the probability that two randomly chosen adjacent pixels belong to the same class (contagion) per km<sup>2</sup> using a 1999 land-cover map derived from Landsat Thematic Mapper imagery (Alberti et al. 2004). We reclassified the original land-cover types into urban (pixels containing >20% impervious area), forest (deciduous and mixed forest and coniferous forest), grass (grass and agriculture), and other (e.g., wetlands, shoreline, snow/rock/ice). These sites represented a gradient of those sites dominated by urban land cover to those dominated by remnant patches of forest (details in Donnelly and Marzluff

**FIG. 23-1**

Four-county study area in western Washington, USA, used to model bird response to changes in land cover and the locations of the 1 km<sup>2</sup> bird study sites ( $n = 139$ ) and the three development zones (urban, transition, and exurban and wildland) defined by distance to urban center, population density, and elevation above sea level.

2004a, Blewett and Marzluff 2005). We selected an additional 65 SFR sites across the following gradients: (1) development age (i.e., housing age 5–15 years [young], 40–50 years [middle-age], and >70 years [old]) derived from 2002 parcel data for each county; (2) percent urban in the 1 km<sup>2</sup> landscape; and (3) settlement canopy composition (percent native versus exotic tree species as determined by vegetation surveys on each site [Donnelly and Marzluff 2004a]). We selected 13 highly developed sites using 2002 land-use maps derived from each county's parcel database (commercial, heavy commercial, industrial, heavy industrial, institutional/office, and multifamily residential) to improve our ability to understand bird communities in the more developed portions of the landscape. We selected our seven control sites in areas of large contiguous patches of forest with minimal (<5%) developed land within the 1 km<sup>2</sup> study site.

## Avian Surveys

Trained observers conducted 6,437 fixed-radius (50 m) point count surveys of breeding birds at 992 locations within 139 study landscapes during the spring and summers of 1998 through 2005. Individual sites were sampled 1–7 years. We visited locations within sites 3–5 times per year (late March–late August). Observers arrived at point count locations between 30 minutes prior to and approximately six hours after sunrise, where all possible identifications by sight or sound were recorded during a 10-minute period at each point (details in Donnelly and Marzluff 2004a, b, 2006). For most sites, eight point counts were conducted in each site: six located in the developed areas and two in the remnant patches of forest. Greater effort was allocated to sampling birds in the developed areas than forests because a previous study of forest reserves in the same region indicated that birds and vegetation were more variable in developed areas (Donnelly and Marzluff 2006). All points were >100 m apart, with the exception of a small number ( $n = 83$ ; mean distance between these points = 76 m) where the separation was maximized within the only forest fragment that existed within the study landscape. Our sampling effort resulted in a total of 2,866 counts at 302 locations in forested portions of sites and 3,571 surveys at 690 locations in the built portions of sites.

We categorized a subset of 57 common species into three development-sensitive guilds (Appendix A). The guild approach centers on different colonization and extinction probabilities of different birds. We grouped species into “native forest” birds, those typically found in intact, mature forest ( $n = 19$ ), “synanthropic birds,” those native or nonnative birds that thrive in human-dominated landscapes, making use of increased resources not available prior to human development ( $n = 9$ ), and “early successional” birds, those that exploit the heterogeneous vegetation of fragmented landscapes following some type of physical disturbance ( $n = 29$ ; Marzluff 2005). We calculated relative abundance for each site as the mean number of individuals detected per point, per survey. This

method was preferable to others, such as maximum abundance per survey, because it prevented young of the year and migrating individuals from inflating abundances.

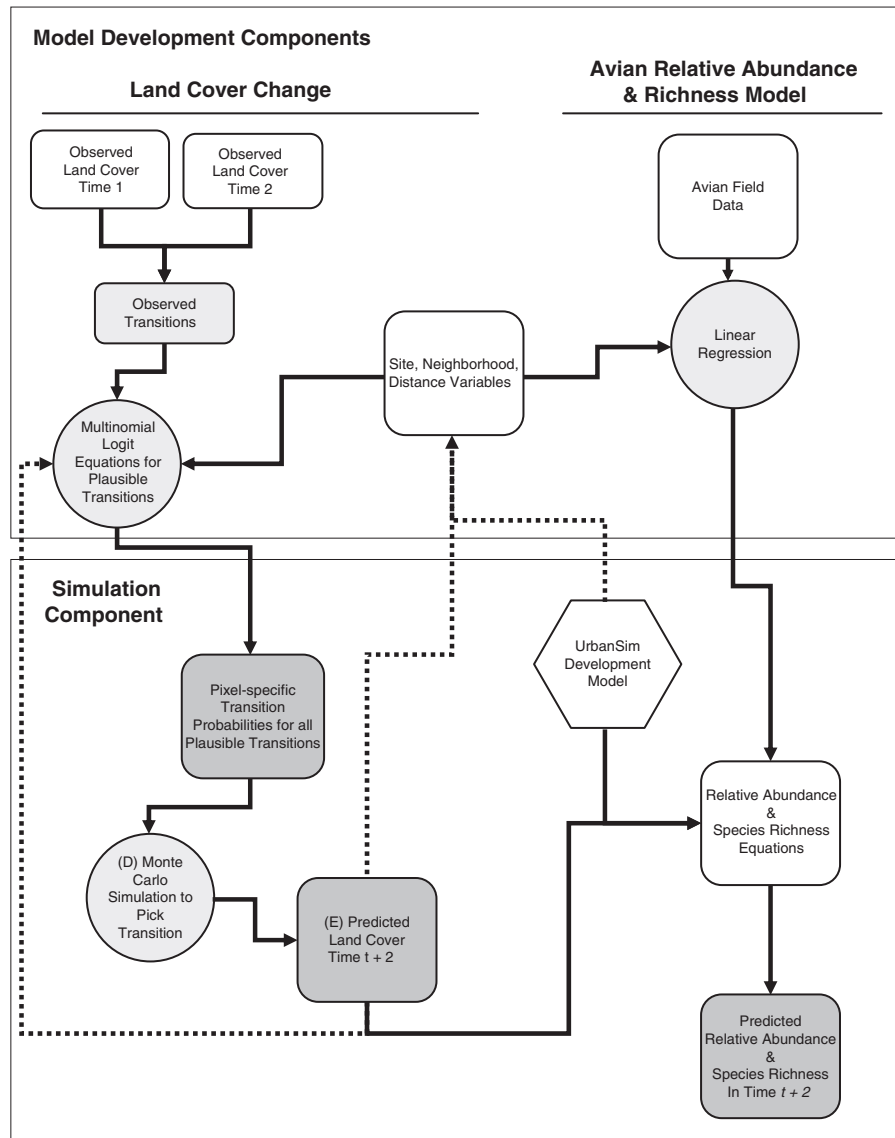
## Land-Cover Change Modeling

The land-cover change model (LCCM) consists of a set of discrete choice equations of site-based land-cover transitions derived from observed land-cover change (Fig. 23-2) that are applied to geographic information system (GIS) layers to predict land-cover change at a 30 m resolution across four counties in western Washington, representing the central Puget Sound Region. A short description of the model follows; a complete description of the theoretical foundations of the model is available in Hepinstall et al. (2008).

The LCCM framework derives from the traditions of modeling landscape change as a dynamic interaction between socioeconomic and biophysical processes (Turner et al. 1996, Wear and Bolstad 1998, Wear et al. 1998). The LCCM is written in Python and is designed as a module within the larger Open Platform for Urban Simulation (OPUS) and UrbanSim modeling platforms (Waddell 2002, Waddell et al. 2003, <[www.urbansim.org](http://www.urbansim.org)>). UrbanSim consists of a series of modules that have been developed to, among other things, model land-use change in response to changes in transportation networks, household and business location, property development and intensity, infrastructure changes, and policy choices. UrbanSim is designed to aid regional land-use planning.

Urban development models such as UrbanSim predict changes in land use (e.g., undeveloped, residential, commercial, mixed use, timberlands) and development intensity (number of residential units or square feet of commercial space), whereas avian communities respond to changes in vegetation type and structure. We must link models predicting change in land use to models of land-cover change, which then can be used to predict the effects of land development on avian communities. Our LCCM predicts future land cover in response to land-use change and biophysical constraints.

For our implementation of the LCCM, we simulated the potential change to one of eight land-cover classes: heavy urban (>80% impervious surfaces), medium urban (20-80% impervious surfaces), low urban (a mixed class with <20% impervious area and the remaining area in vegetation), grass, agriculture, deciduous and mixed forest, coniferous forest, and clearcut. Each land-cover class can transition from a variable number of other classes. We empirically estimated 26 transition equations as a function of observed land-cover and independent variables from two dates (Fig. 23-2; Turner et al. 1996). The focus of the LCCM is to model urban growth, which in the central Puget Sound is limited to the lower elevations that have little commercial forestland. We chose not to model forest regeneration and instead converted any predicted new clearcut into regenerating forest in the subsequent time step and retained all regenerating forest for the duration of the LCCM run (28 years in this application).



**FIG. 23-2**

Flow chart of steps performed as part of the land-cover change model and the avian richness and relative abundance models used to predict bird response to changes in land cover.

The central Puget Sound implementation of LCCM has multiple possible input dates of land cover to use for developing transition models including 1986, 1991, 1995, 1999, and 2002; we used equations developed from observed 1995–1999 transitions (Hepinstall et al., in press). We modeled land-cover change using discrete choice (multinomial logit) statistical models. Developing a discrete choice equation for each transition modeled is an iterative, semi-automated process that can be done directly within the LCCM code base, but still takes multiple days to complete. Transition probabilities for each 30 m pixel to change from one discrete land-cover class  $i$  to another cover class  $j$  is potentially influenced by many factors including (1) the predicted type and predicted intensity of a development event; (2) a set of attributes of the pixel; and (3) the land-cover composition and configuration of neighboring pixels (Fig. 23-2; Hepinstall et al., in press). In the Puget Sound implementation of the LCCM, 65 potential explanatory variables are available for specifying discrete choice equations. Land development, or the probability that a pixel will transition from an undeveloped to a developed state, is derived from UrbanSim development module output. UrbanSim output is also used to determine the type (residential, commercial/industrial, mixed use) and intensity (number of residential units or ft<sup>2</sup> commercial/industrial added) of development. The remaining variables were developed from spatial databases obtained from county, state, and federal GIS data repositories and required several months to compile and error check. Site attributes influence the ability to develop land through increasing the cost of development (e.g., steep slopes, unstable soils), limiting or prohibiting development (e.g., critical areas such as steep slopes, landslide hazard, riparian areas, etc.; proximity to endangered species habitat), or encouraging development (e.g., proximity to existing infrastructure). Because development events generally occur in patches that are greater than the size of an individual 30 m pixel (900 m<sup>2</sup>), land-cover transitions in adjacent cells influence the probability of land-cover transitions in a focal cell. The LCCM, therefore, includes distance variables (e.g., distance to central business district) and variables measuring the spatial context of the target pixel, by calculating several measures (e.g., number of residential units added in the previous three years) within 150 m, 450 m, and 750 m moving windows.

The output of the discrete choice equations are probabilities that any given pixel will transition from its current class to one of the possible options for that class including the no-change option. For example, light urban can transition to medium urban, heavy urban, or remain as light urban. Parameter estimates from the discrete choice equations are applied to GIS layers to derive pixel-specific transition probabilities for each pixel to convert to a land-cover class (Fig. 23-2). Because only a small portion of the landscape changes to a new land-cover class over short time intervals (in our case four years), we used Monte Carlo simulations to pick what land-cover type each pixel will be in the next time step (Fig. 23-2). Specifically, transition probabilities for each land-cover class are normalized by the annualized observed transitions and

scaled to sum to 1.0 for each possible transition from the starting class. Then predicted transitions are implemented by comparing the class-specific probabilities for each pixel to a random number chosen from a uniform distribution between 0 and 1. If the scaled transition probability to a new land-cover class matches the random value, the transition takes place; otherwise, the grid cell maintains its current land cover.

The LCCM is implemented in the Python language as a component of UrbanSim and can be downloaded and used as a template to develop a local implementation for any region with spatial data for at least two dates of land cover and drivers of land-cover change (i.e., biophysical and socioeconomic). While UrbanSim requires many socioeconomic data layers to fully implement, LCCM is independent of UrbanSim, is flexible, and can be implemented using output from any land-use change prediction.

## Coupling Land-Cover Change and Avian Richness and Relative Abundance Models

As a proof of concept linking predicted landscape change to potential changes in the avian community, we developed preliminary statistical models to predict bird species richness and relative abundance as a function of land-use and land-cover composition and configuration. We used linear regression to develop separate models of species richness for all species and the three development-sensitive guilds using point count data from the 139 study landscapes. We also developed linear regression models to predict the relative abundance of three representative species, one from each habitat guild. Linear regression models were appropriate, since mean counts and species abundances were generally larger than 10. Poisson regression methods, while generally useful where average counts less than 10, were not further considered at this point.

We defined two *a priori* models based on previous studies (e.g., [Donnelly and Marzluff 2004a, b, 2006](#)), landscape measures relevant to urban planners, and variables available as output from UrbanSim and the LCCM to allow for predictions of future species richness and relative abundance. We used correlations between landscape variables derived from land cover and land use to eliminate highly correlated variables (Pearson correlation coefficient  $> 0.70$ ) prior to developing our models, yielding 10 variables describing land-cover and land-use patterns. Within the 1 km<sup>2</sup> bird study sites, we used land-cover data from 2002 to calculate the percent forest, percent urban, the aggregation index (Fragstats 3.3; [McGarigal et al. 2002](#)) of forest, the number of patches of forest, and the number and mean patch size of urban patches. We used land use derived from 2002 county parcel data to calculate the percent, patch density, and aggregation index of residential parcels, and the mean age of development of parcels within each study site. Our *a priori* simple model (SM) included (1) percentage of forest; (2) aggregation of residential land use; and (3) mean age of development within a 1 km<sup>2</sup> window. Our *a priori* full model (FM) included these

variables and the following: (1) percentage of grass and agriculture; (2) forest aggregation index; (3) the number of unique patches of forest land cover; (4) number of unique patches of urban land cover; (5) the mean patch size of unique patches of urban land cover; (6) the percent of residential land use; and (7) the patch density of patches of residential land use.

We then applied the parameter estimates from the regression models of species richness and relative abundance to the future landscapes generated by UrbanSim and LCCM to calculate total and guild-specific species richness and relative abundance for three representative species (Pacific-slope flycatcher [*Empidonax difficilis*], native forest guild; yellow-rumped warbler [*Dendroica coronata*], early successional guild; and American crow [*Corvus brachyrhynchos*], synanthropic guild). We calculated landscape variables required for our avian models for each 30 m pixel in our four-county study area with ArcGIS (Environmental Systems Research Institute, Redlands, California) and Fragstats 3.3 (for aggregation index) using a 1 km<sup>2</sup> moving window to match the study site design of the avian surveys, where field surveys were designed to characterize the bird community of 1 km<sup>2</sup> landscapes. We converted relative abundance estimates for 1 km<sup>2</sup> windows from predicted mean number of individuals per point per survey into mean number of individuals per 1 km<sup>2</sup>. We smoothed species richness estimates to represent the mean predicted species richness within a 1 km<sup>2</sup> window. To evaluate trends over time in our predictions and because we could not compare each of the 11 million pixels in our study area directly, we randomly selected 100,000 pixels from our predictions of richness and relative abundance for our starting and ending dates (2003 and 2027). We also calculated the range of variability in our predictions using the upper and lower confidence bounds on the parameter estimates and grouped variability into three classes: low, medium, and high.

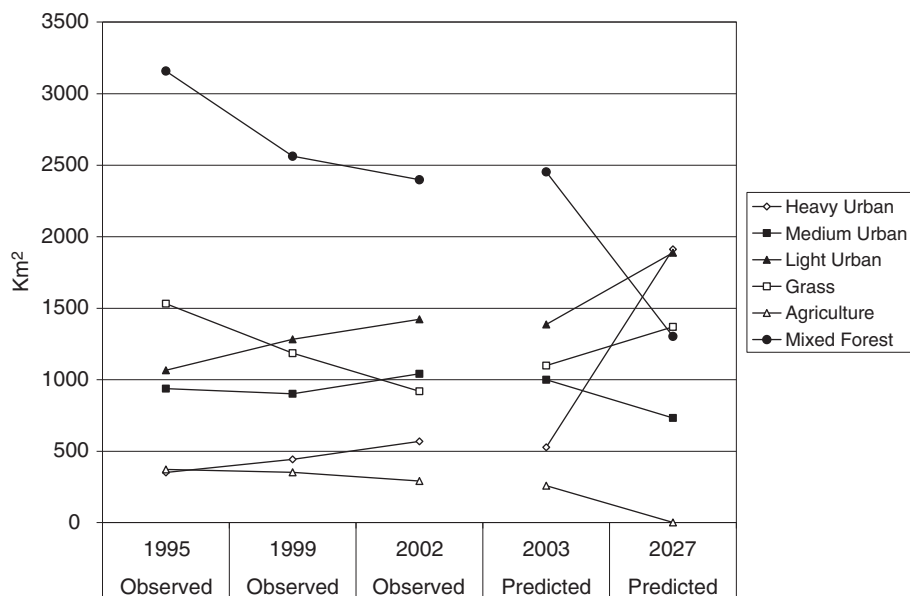
We compared avian model results for two zones of urbanization (urban and transition; [Hepinstall et al., in press](#)), corresponding to the zones where our avian study sites were located, allowing us to examine the changes in avian richness and relative abundance relative to proximity and proportion of development ([Fig. 23-1](#)). The urban zone is dominated by impervious areas (residential, commercial, industrial, institutional, and office) and contains all the major cities of the study area. The transition zone contains a more heterogeneous mix of impervious areas, agricultural lands, and remnant woodlands.

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## RESULTS

### Predictions of Future Land Cover

Between 2003 and 2027 for the full four-county study area, we predict a decrease in mature forest types (deciduous, mixed, and coniferous) from 60% of the area to 38% and an increase in developed land (heavy, medium, and light



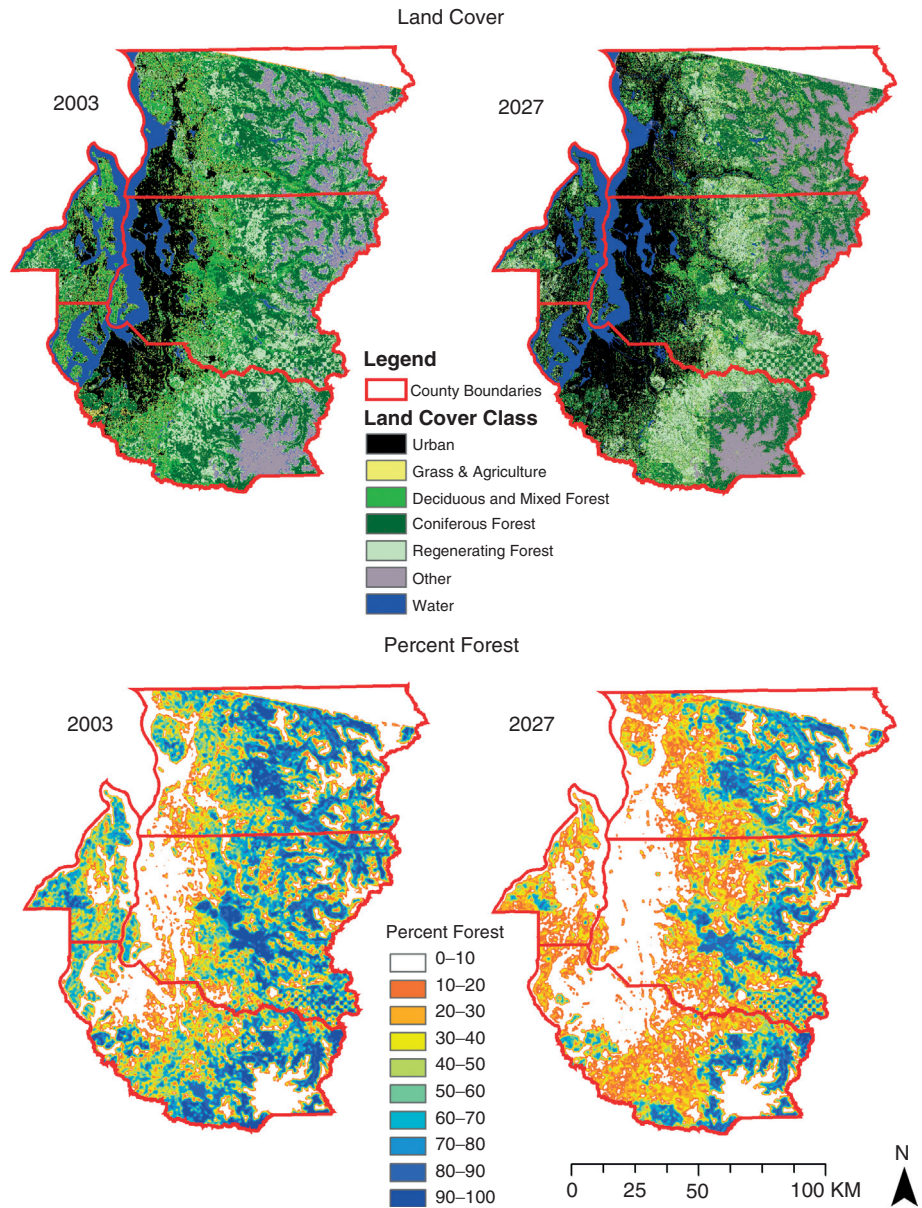
**FIG. 23-3**

Area (km<sup>2</sup>) of observed and predicted land cover for four-county study area in western Washington, USA, within the urban and transition development zones derived from 1995–1999 observed transitions (classes include heavy urban, >80% impervious surfaces; medium urban, 50–80% impervious; light urban, 20–50% impervious; grass; agriculture; deciduous and mixed forest—100–25% deciduous species; coniferous forest – >75% conifers; clearcut—recent forest harvest with no regrowth yet visible on satellite imagery; and early regenerating forest—recent forestland harvest with regrowth visible).

urban classes) from 17% to 34% (Figs. 23-3 and 23-4). We predict a decrease in grass and agriculture from 14% to 10% of the area and an increase in clearcut and regenerating forest from 9% to 18%. We predict a decrease in percentage of forest (per 1 km<sup>2</sup>) and a movement of primarily forested areas up the slopes of the Cascades (Fig. 23-4).

## Avian Surveys

Across the 139 sites, we identified 114 species of birds. Each site contained an average of 31.5 ( $\pm 1.0$  SE) species. Average species composition per site was  $11.2 \pm 0.4$  forest species,  $11.3 \pm 0.4$  early successional species, and  $5.2 \pm 0.2$  synanthropic species. We observed Pacific-slope flycatcher, yellow-rumped warbler, and American crow, on average, on 25.3 (yearly range 14–40, 80 total in 7 years of sampling), 9.5 (yearly range 3–12, 32 total), and 30.5 (yearly range

**FIG. 23-4**

Predicted land cover and percent forest within a 1 km<sup>2</sup> moving window in 2003 and 2027 for the four-county study area in western Washington, USA, based on the 1995–1999 observed land-cover transitions and the Land-Cover Change model.

13–60, 132 total) sites, respectively. We observed, on average,  $7.8 \pm 1.7$  Pacific-slope flycatchers,  $2.0 \pm 0.6$  yellow-rumped warblers, and  $14.0 \pm 8.3$  American crows per site.

## Models of Avian Species Richness and Relative Abundance

Approximately 18–20% of the variation in total species richness was accounted for in our simple and full models (Table 23-1). Richness increased with increasing percentage of forest and aggregation of residential development in the 1 km<sup>2</sup> study site, and decreased with age of residential development. These relationships were all significant in the simple model, but percent forest was not significant in the full model, possibly in response to including somewhat co-varying land-cover classes (percent grass) in that model.

Within habitat guilds, we explained more (44–51%) of the variation in native forest species richness than in the richness of early successional (12–15%) and synanthropic species (23–28%; Table 23-1). Native forest species richness mirrored total species richness and increased with increasing percentage of forest and aggregation of residential development in the 1 km<sup>2</sup> study site, and decreased with age of residential development (Table 23-1). Native forest species richness also was positively correlated with forest aggregation with our full model explaining 51% of the variation in observed native forest species richness. Early successional species richness was only significantly correlated with mean age of development (–) in both models and residential aggregation (+) in the full model, but even with the full model, only 15% of the observed variation in guild richness was explained by our models. Synanthropic species richness was significantly associated with percentage forest (–) and residential aggregation (+) in the simple model and year built (–) and percentage grass (+) in the full model.

In general, our full models of species richness explained little variation beyond that explained by the simple models (Table 23-1). The few variables that significantly contributed to the full models included those in the simple models and additional, biologically relevant variables. Specifically, percentage of grass was an important contributor to explaining variation in richness of those species utilizing developed landscapes, and forest configuration was important to native forest species.

Our *a priori* simple model for predicting relative abundance of three species had significant relationships with percent forest (Pacific-slope flycatcher [+], American crow [–]) and residential aggregation index and mean year built (yellow-rumped warbler [–]; Table 23-2). Percent forest was significant (–) for both yellow-rumped warbler and American crow for the full model. Only two other variables were significant predictors of relative abundance for these three species in the full models: number of patches urban (yellow-rumped warbler)

**Table 23-1** Linear Regression Model Results for Simple Models of Species Richness (Species/point/survey) for Total Species Richness and for Three Guilds (Native Forest, Early Successional, Synanthropic) as a Function of Landscape Metrics for 139 Suburban Landscapes In Puget Sound, Washington, USA, 1998–2005, for (A) Simple and (B) Full Models. Standardized Coefficients (B) Lower 95% Confidence Interval (LCI) and Upper 95% Confidence Interval (UCI) Presented for Each Unstandardized Parameter Estimate. Simple Models had 3 Regression Degrees of Freedom and 135 Residual d.f. Full Models had 10 Regression Degrees of Freedom and 128 Residual d.f.

<b>A) Simple Model</b>							
<b>Species Richness</b>	<b>Adjusted R<sup>2</sup></b>	<b>P</b>	<b>Constant</b>	<b>Percent Forest</b>	<b>Residential Aggregation Index (AI)</b>	<b>Mean Age Development</b>	
Total Species	0.178	0.000	B		0.201	0.165	−0.305
			LCI	18.910	0.014	0.006	−0.365
			UCI	38.534	0.159	0.188	−0.109
Native Forest Species	0.440	0.000	B		0.550	0.222	−0.221
			LCI	3.132	0.071	0.022	−0.111
			UCI	9.585	0.118	0.082	−0.026
Early Successional Species	0.120	0.031	B		0.033	−0.690	0.755
			LCI	7.675	−0.024	−0.003	−0.155
			UCI	15.740	0.035	0.072	−0.050
Synanthropic Species	0.225	0.000	B		−0.458	0.173	−0.095
			LCI	3.451	−0.050	0.003	−0.037
			UCI	7.028	−0.024	0.036	0.010

**B) Full Model**

<b>Species Richness</b>	<b>Adj-R<sup>2</sup></b>	<b>P</b>	<b>Constant</b>	<b>% Forest</b>	<b>Res. Agg. Index</b>	<b>Mean Age Dev.</b>	<b>% Grass</b>	<b>Forest Agg. Index</b>	<b>Number Patches Forest</b>	<b>Number Patches Urban</b>	<b>MPS Urban</b>	<b>% Resid.</b>	<b>Patch Density Resid.</b>	
Total	0.000	0.208	B	0.140	0.252	-0.348	0.185	0.148	0.055	-0.090	0.042	-0.203	0.068	
Species			LCI	9.837	-0.072	0.024	-0.426	0.028	-0.044	-0.298	-0.616	-0.613	-0.194	-0.188
			UCI	35.265	0.192	0.273	-0.114	0.889	0.187	0.533	0.269	0.887	0.011	0.381
Native Forest	0.000	0.508	B		0.347	0.199	-0.167	0.020	0.394	0.141	-0.072	-0.045	-0.049	0.090
			LCI	-2.053	0.018	0.008	-0.101	-0.115	0.040	-0.010	-0.194	-0.293	-0.041	-0.038
			UCI	5.927	0.101	0.086	-0.003	0.155	0.112	0.251	0.084	0.178	0.023	0.140
Early Succ.	0.000	0.151	B		-0.018	0.225	-0.384	0.202	0.139	0.019	-0.076	0.086	-0.193	0.053
			LCI	3.891	-0.057	0.002	-0.183	0.022	-0.021	-0.155	-0.240	-0.198	-0.077	0.619
			UCI	14.345	0.051	0.104	-0.054	0.376	0.074	0.187	0.124	0.419	0.008	0.147
Syn.	0.000	0.281	B		-0.380	0.307	-0.205	0.245	-0.041	-0.159	-0.152	0.112	-0.139	0.026
			LCI	2.668	-0.054	0.012	-0.058	0.037	-0.024	-0.138	-0.134	-0.066	-0.030	-0.044
			UCI	7.214	-0.007	0.056	-0.002	0.191	0.017	0.011	0.024	0.202	0.007	0.058

**Table 23-2** Linear Regression Model Results for Relative Abundance for One Representative Species from Each Habitat Guild as a Function of Landscape Metrics for 139 Survey Sites in Puget Sound, Washington, USA, 1998–2005, for (A) Simple and (B) Full Models. Standardized Coefficients (B) Lower 95% Confidence Interval (LCI) and Upper 95% Confidence Interval (UCI) Presented for Each Unstandardized Parameter Estimate. Simple Models had 3 Regression Degrees of Freedom and 135 Residual d.f. Full Models had 10 Regression Degrees of Freedom and 128 Residual d.f.

<b>A) Simple Model Parameter Estimates</b>							
<b>Guild/Species</b>	<b>R<sup>2</sup></b>	<b>P</b>	<b>Constant</b>	<b>Percent Forest</b>	<b>Residential Aggregation Index (AI)</b>	<b>Mean Age Dev.</b>	
Native Forest: Pacific-slope flycatcher	0.303	0.000	B	0.529	−0.079	−0.037	
			LCI	−0.316	0.013	−0.011	−0.012
			UCI	1.162	0.024	0.003	0.007
Early Successional: yellow-rumped warbler	0.263	0.000	B	−0.068	−0.513	−0.174	
			LCI	0.438	−0.002	−0.007	−0.005
			UCI	0.784	0.001	−0.004	0.000
Synanthropic American crow	0.327	0.000	B	−0.566	0.048	0.020	
			LCI	1.474	−0.036	−0.006	−0.012
			UCI	3.553	−0.021	0.013	0.015

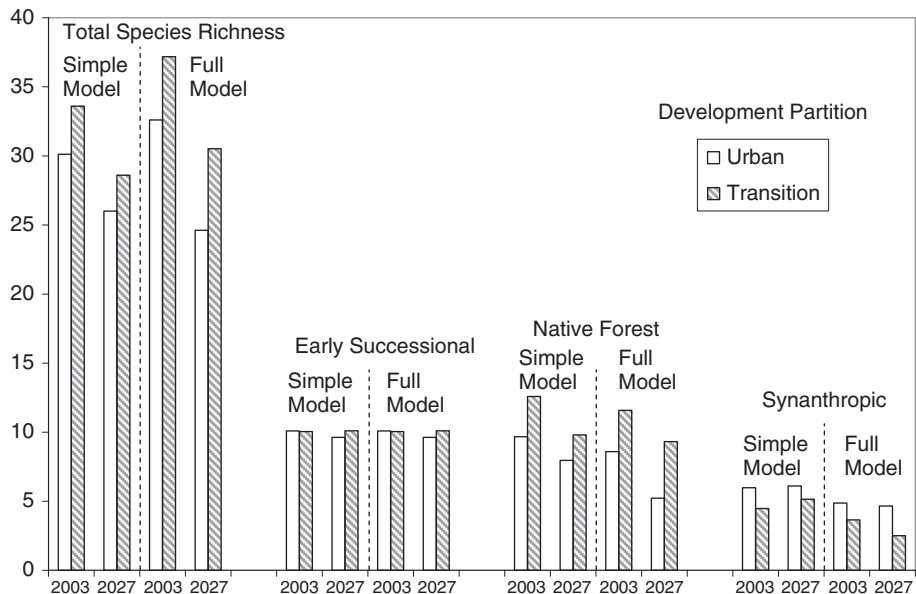
**B) Full Model Parameter Estimates**

<b>R<sup>2</sup></b>	<b>P</b>		<b>Constant</b>	<b>% Forest</b>	<b>Res. AI</b>	<b>Mean Age Dev.</b>	<b>% Grass</b>	<b>Forest AI</b>	<b>NP Forest</b>	<b>NP Urban</b>	<b>LN Urban MPS</b>	<b>% Res.</b>	<b>Res. PD</b>
Native Forest: Pacific-slope flycatcher													
0.345	0.000	B		0.249	0.027	-0.014	-0.111	0.040	0.013	0.040	-0.362	-0.129	0.036
		LCI	0.356	-0.001	-0.008	-0.012	-0.055	-0.007	-0.029	-0.027	-0.151	-0.012	-0.017
		UCI	2.247	0.019	0.011	0.011	0.010	0.010	0.033	0.039	-0.040	0.003	0.025
Early Successional: yellow-rumped warbler													
0.269	0.000	B		-0.303	-0.605	0.101	0.043	0.169	-0.022	0.239	0.081	-0.046	-0.127
		LCI	0.345	-0.005	-0.009	-0.004	-0.010	-0.001	-0.008	0.001	-0.009	-0.002	-0.008
		UCI	0.800	0.000	-0.004	0.001	0.006	0.004	0.007	0.016	0.018	0.001	0.002
Synanthropic: American crow													
0.319	0.000	B		-0.596	0.097	0.080	-0.032	0.083	-0.045	-0.054	0.057	-0.082	-0.120
		LCI	0.703	-0.044	-0.007	-0.010	-0.056	-0.008	-0.056	-0.060	-0.060	-0.015	-0.051
		UCI	3.463	-0.016	0.020	0.024	0.037	0.017	0.034	0.036	0.103	0.007	0.011

and mean patch size urban (Pacific-slope flycatcher). Each of our *a priori* models explained approximately 26–35% of the observed variance in relative abundance for the three selected species.

## Predictions of Future Bird Species Richness and Relative Abundance

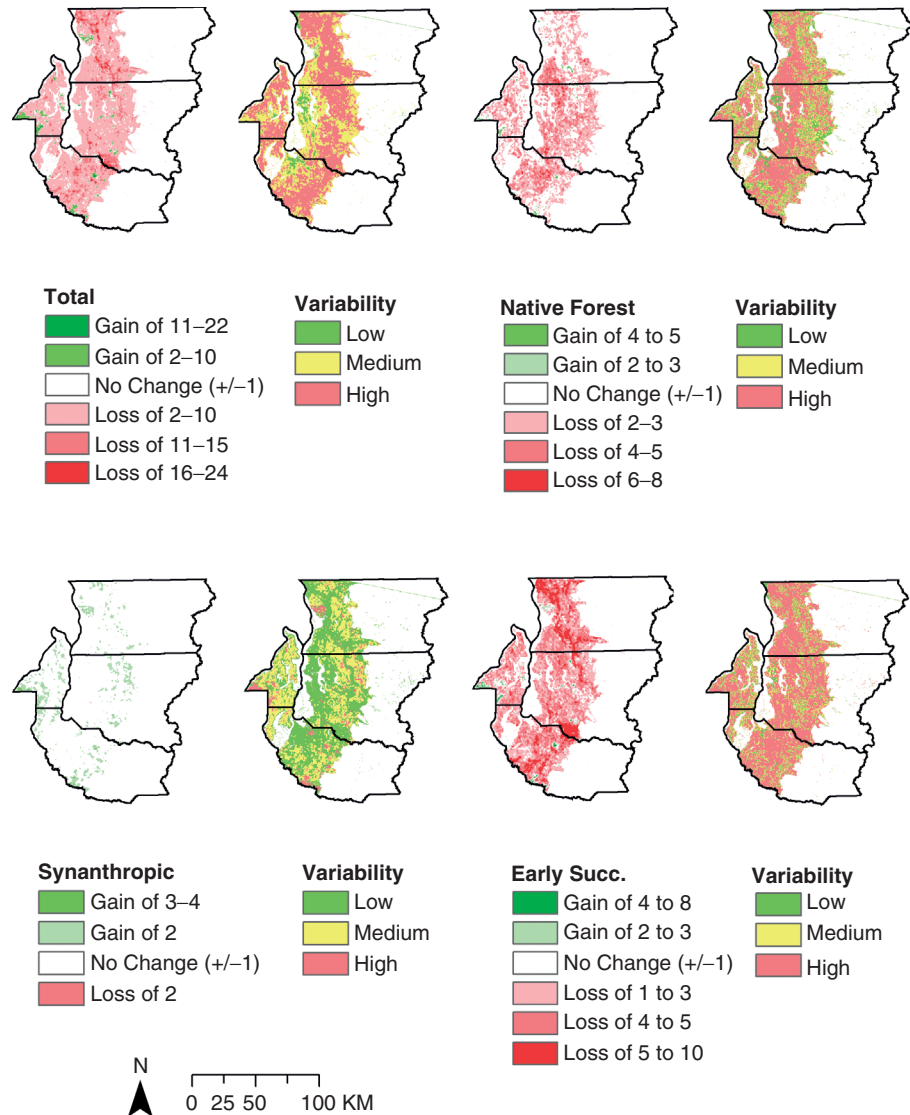
We predicted species richness will decline slightly during the next 25 years as native forest species respond to the loss of forest cover and early successional species respond to the aging of current developments. Both the simple and full models project a decline in total species richness for the four counties from a mean of 34 or 37 in 2003 to 28 or 30 in 2027, respectively, in the transition zone (Fig. 23-5). The guild-specific results indicate that the loss of early successional (~1) and, more significantly, native forest (~2–4) species would be noticeable in both the urban and transition zones. Simple models predict the diversity of the synanthropic guild will increase slightly in the transition zone and remain relatively stable in the urban zone (Fig. 23-5). The full model predicts counterintuitive results for the synanthropic guild—a decrease in species richness in the transition zone (Fig. 23-5). The additional landscape variables in the full models consistently reduce mean predictions of species richness for the three habitat guilds by 1–3 species.



**FIG. 23-5**

Comparison of mean predicted bird species richness for the urban and transition zones (Fig. 23-1.) for simple model and full models in western Washington, USA.

Maps generated from projecting the full and simple models show that changes in species richness are expected to be concentrated in those regions of the study area where land-cover change is most dramatic (Fig. 23-6). This is primarily in the transition development zone surrounding the present heavy



**FIG. 23-6**

Mapped predicted gain or loss and variability of model predictions between 2003 and 2027 for full (total, native forest, early successional) and simple (synanthropic) species models for urban and transition zones within the four-county study area in western Washington, USA.

urban core where forest loss and aging of developments cause the greatest changes in land cover (Figs. 23-1 and 23-2). Total species, native forest species, and early successional species richness show similar patterns of species loss with up to 24 species being predicted to be lost from the total species list at specific locations, and nine each from the native forest and early successional guilds (Fig. 23-6). The full model for the native forest species guild seems to overpredict the number of native forest species in the urban zone in 2003 and then predicted a large loss of species by 2027 (Fig. 23-6), creating a change map that shows a larger loss of species closer to the urban centers than the predicted change from the simple model output (Fig. 23-5). Because full model predictions for the synanthropic guild predicted a slight loss of species over time (Fig. 23-5) in the urban and transition zones, clearly an error in model formulation, we present the predicted distribution of synanthropic species as predicted by the simple model (Fig. 23-6). The majority of change for synanthropic species predicted by the simple model is a gain of 2–4 species in the transition zone (Fig. 23-6). The full model results for synanthropic species indicated that species in the group have a complex relationship (i.e., neither all positive nor all negative) to the variables we included in our *a priori* model. Further exploration of how this group responds to landscape patterns is clearly warranted. Model prediction variability varied by guild and location with total species predictions being most variable in the transition zone (Fig. 23-6).

The spatial pattern of forest loss has additional consequences for future avian communities. Currently, avian diversity is greatest in diverse land-cover characteristic of the transition zone (Fig. 23-5) or equally great in the transition and wildland zones (Fig. 23-5). However, in just a few years and increasingly through 2027, the diversity of the transition zone is expected to drop rapidly (Fig. 23-5). Future bird communities are predicted to increase gradually in richness with distance from development rather than peaking in diversity in the current intermediately settled transition zone. In fact, as the transition zone is transformed into dense development, the region is likely to end up with spatially partitioned bird communities dominated by either adaptable, synanthropic species (in dense developments) or resilient native forest birds (in the wildland zone). This is suggested by the projected distribution of forest cover (Fig. 23-4). Currently, forest cover is very low (<20%; red shades on Fig. 23-4) in the small area proximal to Seattle. Much of the transition zone east of Seattle is a 50:50 mixture of built and forested lands (blue-green in color; Fig. 23-4) with very high avian diversity, but this will not be the case by 2027.

The three species selected as examples of how to apply relative abundance equations to the future landscapes created by the LCCM show clear patterns of response to changes in land-use and land-cover amount and configuration. American crow abundance per km<sup>2</sup> was predicted to increase in both development zones (Fig. 23-7) with the greatest increases predicted in the transition zones by both simple (Figs. 23-7 and 23-8) and full models (Fig. 23-7). Pacific-slope flycatcher predictions from the full model were lower than from the



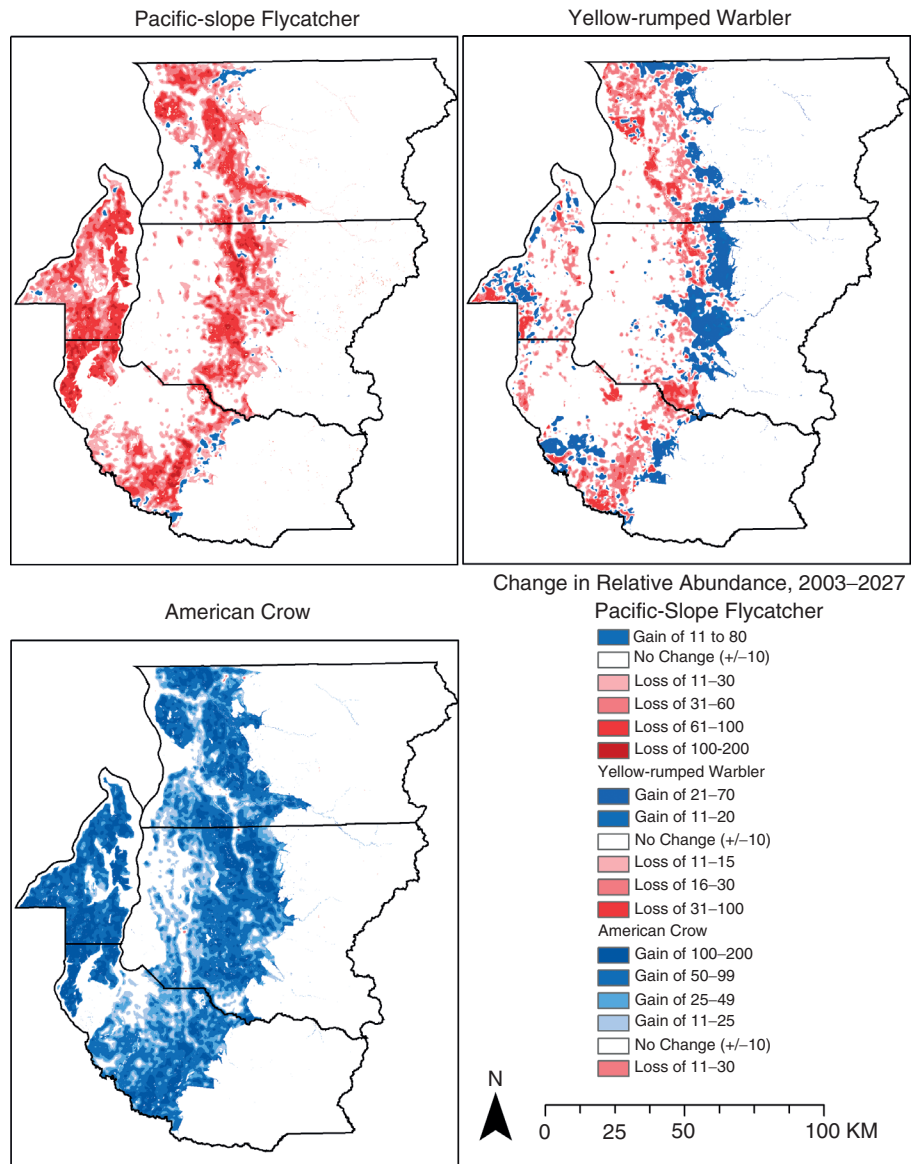
**FIG. 23-7**

Comparison of mean number of individuals per 1 km<sup>2</sup> for the urban and transition development zones (Fig 23-1.) for three individual species (Pacific-slope flycatcher, yellow-rumped warbler, and American crow) in western Washington, USA.

simple model (Fig. 23-7), with a 25% decline in relative abundance over time in the transition zone predicted by the full model. Model predictions for the yellow-rumped warbler were relatively stable over time with slight decreases in numbers for the transition zone using the full model (Fig. 23-7) and a thin strip of lower relative abundance along the zones of greatest new development as land-cover change reduces the amount of forest present in these areas.

## DISCUSSION

We presented a method for combining land-use change models, land-cover change models, and avian biodiversity models as an example of how to couple sophisticated models developed from different modeling traditions. The output from the UrbanSim development model was combined with a discrete choice land-cover change model to predict land-use and land-cover change, which were then used as input to avian richness models to predict changes in avian species richness and individual species relative abundance 28 years into the future. Previous large-scale modeling efforts have used more generalized

**FIG. 23-8**

Mapped differences in predicted relative abundance per km<sup>2</sup> between 2003 and 2027 for American crow (simple model), Pacific-slope flycatcher (full model), and yellow-rumped warbler (full model) within the urban and transition zones in the four-county study area in western Washington, USA.

land-use/land-cover change models such as Markov transition models (e.g., Turner et al. 1996, Wear and Bolstad 1998, Wear et al. 1998, Prato 2005) and/or more general habitat-association models (e.g., Scott et al. 1993, White et al. 1997, Schumaker et al. 2004) to accomplish similar tasks but at lower spatial resolutions and incorporating fewer drivers and constraints of landscape change. What is missing, generally, are links between models that predict how species respond to landscape change and models that predict the future extent and intensity of urban development (Pickett et al. 2001).

Studies that link future landscape changes and the potential effects on biodiversity often use alternative futures analysis (Steinitz 1990, Ahern 1999, Steinitz and McDowell 2001) where scenarios of future growth developed by planning agencies serve as “visions” of the future if different planning principles are followed, rather than explicitly modeling urban growth (e.g., Hulse et al. 2004, Mörtberg et al. 2007). In Oregon’s Willamette River Basin, Hulse et al. (2004) worked with citizen groups to define three value-based future scenarios of development policy, including a continuation of current policies. Schumaker et al. (2004) took these scenarios and evaluated how change in land cover would affect species using simple habitat-association models for 279 vertebrate species and a life history simulator to simulate the potential population effects on a small subset of these species. Mörtberg et al. (2007) used three urbanization scenarios for the Stockholm, Sweden region and logistic regression models for three focal avian species (two requiring large tracts of forest and one requiring smaller patches of forest and potentially able to persist in remnant forests in urban and suburban areas). Their avian models included measures of landscape composition and configuration to predict the probability of species occurrence on the landscape.

We combined ideas derived from landscape ecology (i.e., that landscapes change in response to human and natural disturbances, which change the composition and configuration of resources, which then affect species diversity), with sophisticated micro-simulation economic models (Waddell 2002, Waddell et al. 2003) and preliminary avian community models developed from a large and long-term field data set designed to investigate community dynamics in the face of urban development. The central Puget Sound region is experiencing rapid human population growth and concomitant landscape change to accommodate the new individuals and businesses moving into the area. Because the region is bounded by water (e.g., Puget Sound and Lake Washington) and mountain ranges (Cascades and Olympics), development is concentrated in the lower elevations, increasing the pressure in these areas. Our LCCM model has clearly shown the potential impacts of landscape change on land-cover composition and configuration in the future. Development, however, will not occur at the same rate or intensity everywhere. Our method provided a first look at how areas that are likely to develop in the future are spread across the landscape and how these new patterns of land cover and land use may affect the regional avian communities. Spatially explicit predictions of change are important to

inform large-scale conservation planning in urban and urbanizing regions (Mörtberg et al. 2007, Schumaker et al. 2004). The ability to change key assumptions, inputs, constraints, and even statistical approaches through the use of open-source programming modules makes our approach flexible and dynamic (e.g., Waddell 2002, Noth et al. 2003).

## Responses of Birds to Urbanization

The substantial reduction in forest cover and increase in developed land that our models project for the Seattle area in the coming few decades (Fig. 23-1) are expected to challenge the region's avifauna. While the overall diversity of birds is expected only to decline by an average of 3–5 species (Fig. 23-4), the region will be significantly more vulnerable to further loss of forest. Avian diversity in our forested landscape exhibits a slight peak between 40% and 60% forest cover, but is approximately equal at both 40% and 60% forest (Marzluff 2005). Avian diversity declines rapidly and substantially as forest cover is reduced below 40% and bird communities hold fewer and fewer native forest and early successional species (Donnelly and Marzluff 2006). In contrast, avian diversity declines only slightly as forest cover exceeds 60% and bird communities come to be composed of mainly native forest species (Marzluff 2005). Thus, the reduction in overall forest cover from 60% in 2003 to 38% in 2027 that we project is not expected to substantially lower regional avian diversity, but it is expected to threaten the remaining bird communities with rapid and substantial reduction in diversity if loss of forest cover continues beyond 2027.

Forest species increase in landscapes with increasing amounts of forest, recent development, and aggregated (clumped) housing developments because in such landscapes substantial contiguous forests remain. Synanthropic species also increase in landscapes of aggregated development, but where built lands, not forested ones, are extensive. Overall, synanthropic species increase in young developments, but the response of individual species to development age is mixed (e.g., American crow density increases in older developments; Table 23-2).

Farther east, the elevation increases and large patches of contiguous forest likely contain viable populations of native forest birds. By 2027, our projection suggests that the rich 50:50 landscape of the transition zone will be mostly lost and replaced with dense development and low bird diversity. This will then contrast dichotomously with expected diverse bird communities farther east in the forested Cascade Mountain foothills.

In summary, while some of our conclusions may depend on our ability to model native forest and synanthropic species better than early successional species, we expect future bird communities to be slightly less diverse and more vulnerable to future losses than they are at present. We expect native forest birds to become increasingly reliant on higher elevation forests because most low elevation forests will be converted to development too dense to support viable

populations. High elevation bird populations may be less sustainable due to harsher winters and shorter growing seasons that may limit survival and reproduction.

## Policy and Management Implications of Approach

Planning agencies are increasingly challenged by the need to provide evidence of the social and economic benefits of conservation strategies. The assessment of these benefits against societal costs requires the ability to predict future conditions without conservation and under alternative strategies. The coupling of the three models presented here allows policy makers to explore policy options across the landscape and more effectively assess the implications of different policy choices on land development, land cover, and biodiversity. Agencies charged with regional metropolitan planning (Puget Sound Regional Council [PSRC] in the Seattle, Washington metropolitan area) require such integrated modeling systems to develop scenarios, assess alternative strategies, and make effective planning decisions and investment choices. Natural resource and wildlife conservation agencies (e.g., Washington Department of Natural Resources) and nongovernmental organizations (e.g., The Nature Conservancy) also require tools to assist with planning for future landscape changes. Currently, PSRC is using UrbanSim (P. Waddell, personal communication) to inform land use and transportation planning. In addition, we have been working with the Army Corps of Engineers to explore applications of the LCCM model to simulate what will happen to coastal areas if no large-scale projects to restore the nearshore ecosystem are undertaken. In addition, the outputs of the integrated models can potentially be used to inform a variety of new conservation initiatives. For example, they could effectively serve to assess and prioritize conservation strategies as part of the action plan to restore the Puget Sound ecosystem initiated by the new Washington State Puget Sound Partnership Agency.

While urban development is linked to loss of biodiversity, its impacts are by no means homogeneous across the landscape. Thus, the trajectory of urban development that we choose or encourage will influence biodiversity differently. This study clearly indicates that both the landscape composition and configuration resulting from urbanization has variable effects on the region's biodiversity.

Planning agencies will increasingly need spatially explicit models of coupled human-natural systems to realistically assess the effectiveness of conservation strategies. It is critical to better understand and represent mechanisms of interactions among human stressors, land-cover patterns, and ecosystem functioning before we can devise management strategies and target conservation actions. Such models can become extremely complex and data intensive, requiring a balance between simplicity and realism to make models usable. The simplicity of even our full models can be highly useful to urban planners; however, important aspects of biological reality may not be included in our models. For example, we

do not model the response of birds to specific sorts of vegetation, important habitat elements like snags (Blewett and Marzluff 2005), or important aspects of the understory (Donnelly and Marzluff 2006). While these would likely increase realism, and perhaps predictability of avian diversity, they would not necessarily make such models more applicable to city and regional planning. More importantly, by showing how birds generally respond to the amount (% forest, % grass), pattern (housing aggregation), and age of development, we can provide planners with relevant tools to better understand how their decisions concerning zoning, housing density, and designation of conservation areas affect bird communities. Some species and guilds may require measuring more aspects of the landscape than others, but with the increasing ubiquity of spatial data and GIS skills, even local planning offices will increasingly be able to develop such measures.

Avian diversity, while generally less affected by the pattern than the amount of development (Alberti and Marzluff 2004), was sensitive to aspects of both in our current modeling effort (Table 23-1). The importance of residential aggregation to total diversity and the diversity of each guild suggests that a variety of birds in our region will benefit from future development that is aggregated rather than dispersed. Aggregating future residential development may be the only way to provide a variety of forested reserves and variously built areas that together maximize the region's bird diversity (Donnelly and Marzluff 2004a, 2006; Blewett and Marzluff 2005). However, planners should be especially concerned with our projected losses in the transition zone with its diverse land cover and rich bird communities. From an avian perspective, aggregating development in this zone and especially as it extends further east should be done with an eye toward increasing local diversity of land cover rather than simply using this area to accommodate dense development and limit the eastern extent of sprawl. The creation of locally diverse landscapes, while not beneficial to some native forest species and indicative of low density exurban sprawl, is beneficial to many early successional bird species, and therefore regional avian diversity (Marzluff 2005).

Maintaining a diverse bird community in the face of our projected wave of forest conversion will require more than regional and city planning. Individual landowners also need to be engaged in reducing the loss of native forest and early successional species on their properties (Marzluff and Ewing 2001; Donnelly and Marzluff 2004a, 2006; Blewett and Marzluff 2005). Projections of future conditions, such as we have developed, can catalyze the action of multiple stakeholders. Landowners alarmed by our projections can help conserve native birds in developed areas by maintaining native forest conditions (secluded forest tracts with native understories), large snags, and a variety of forest ages and types on their properties. Communities can reduce the loss of native birds by controlling their supplements (e.g., food waste eaten by generalist predators such as opossums and raccoons), keeping pets restrained when in forested areas, and fostering a functional ecosystem. Fostering ecosystem

functionality can be messy and unappealing in urbanizing regions, but it is an important complement to land-use and land-cover planning efforts. This requires less manicured yards with minimal grass, letting trees die and rot, enabling native predators like coyotes to live in our neighborhoods, and seeing the good that comes from natural disturbances like wind (forest openings), floods (soil regeneration), and insect outbreaks (creating snags and feeding opportunities for insectivores). Tending to our lifestyle as well as to land cover will be increasingly important to future bird diversity if we intend to minimize the impacts we expect in the next 25 years.

## Limitations of Approach

Our approach suffers from many potential drawbacks. First, the number of data layers required for each model is large and varied and, in the case of avian models, requires substantial field work. Data development was a large portion of the activities of each modeling team participating in this project. Ideally, input from the community of developers, land owners, and planners to identify those forces driving landscape change will improve both the models' performance and their potential future use. In addition, knowledge of the availability and reliability of spatial data will help determine what variables can easily be incorporated in any modeling exercise.

Because the LCCM does not model forest regrowth into mature forest, predictions of total and native forest species may have underestimated species richness in the commercial forestlands east of Seattle. The LCCM was designed primarily as an urban growth model, and as such does not capture the production forest landscape change as accurately as a model designed specifically for such lands. In addition, our avian field data are derived from the lower elevations, so we cannot be positive how these species will adapt to higher elevation habitat that may already have a full compliment of species occupying the habitat.

We have the greatest confidence in our predictions concerning native forest and synanthropic species. Our models account for substantial proportions of the variation in the diversity (Table 23-1) and abundance (Table 23-2) of these guilds. Their response to the processes of forest conversion is obvious to even the casual observer and captured in our regression equations by considering the amount of forest along with the pattern and age of development. Differences between predictions for the synanthropic guild for simple and full models indicates the importance of including only those landscape variables where we have an understanding of the mechanisms that relate landscape configuration to species responses. Our synanthropic guild predictions using the full model clearly contained errors with species richness predicted to decline in the transition zone where developed land cover was predicted to increase. The full models included more variables that measure landscape configuration to which species may have individualistic responses that are masked by guild-level models

(Taper et al. 1995). In addition, there may be errors in the form of the regression equation with respect to the functional response of the species making up the guild. To address these errors, an exploratory analysis of the exact relationship between landscape metrics and guild responses should be conducted. Poisson regression could be used instead of linear regression to account for the small number of counts for this guild and preclude prediction of negative species richness or relative abundance (e.g., Thogmartin et al. 2007).

Our predictions concerning early successional species diversity may be problematic. Understanding this group is vital to understanding the overall response of birds to urbanization in our region (Marzluff 2005) because half of the total bird diversity is included in this group (Appendix A). We may improve these models by relating diversity directly to light urban development (rather than grouping all urban classes) or by better accounting for the dynamics of regenerating forests in our land-cover change models. However, it is likely that the diversity of bird species in this guild will continue to defy unified modeling efforts. Rather, we should look for common responses to land-cover change by subsets of the early successional guild as models of individual species appear more robust (Table 23-2) than models of the full guild (Table 23-1). Improving our ability to model early successional species is an important future direction.

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## FUTURE DIRECTIONS

We have presented here a first step in linking landscape models of urban development, landscape change, and ecological responses. Work continues on increasing the accuracy, flexibility, and applicability of each model. For instance, the LCC accuracy for wildland areas can be increased by using readily available forest growth models and modeling systems (e.g., McCarter et al. 1998, Marzluff et al. 2002). Extrapolation of the avian biodiversity models to these higher elevations would require substantial additional field data to understand how species in these areas respond to changes in the landscape. Also, coupling the land-cover change model with biophysical process models (e.g., climate) is critical when aiming at predicting land-cover change and related avian diversity on a longer time scale.

Modeling total species richness as a single response to changing landscape conditions masks individual species' responses. Ideally, the summary of predictions for individual species abundance would equal the predicted total species richness; however, this is rarely the case due to confounding factors such as differential species detectability (Dorazio et al. 2006). In general, our models of single species relative abundance are better at capturing the diversity of observed responses than guild predictions of species richness (Table 23-1 versus Table 23-2). More realistic estimates of total and guild species richness could be obtained through developing mechanistic relationships of relative abundance for each species and using individual species predictions to build community-level responses to landscape change. Combined individual species predictions

could then be compared against single guild or total species richness predictions to evaluate the validity of each approach. Avian models of relative abundance in their current form have not been corrected for the effects of species detectability, which is something that would be necessary to develop valid summed predictions of individual species richness to predict changes in community richness (A. Royle, personal communication). Additional exploration into and inclusion of the mechanisms (e.g., dispersal, territory size, source-sink dynamics) behind observed bird population responses to landscape change would improve individual and community predictions. In addition, validating avian models has not yet occurred. Data from two additional field seasons will soon be available to use as comparisons with our current and future model's predictions.

Such complex modeling steps we have done for our avian model would benefit from the development of an automated modeling system, such as UrbanSim and LCCM, where the entire process of equation development to prediction of future landscapes and community richness would be present in a single model development environment. Continued development of an open-source software development environment to allow seamless simulation of urban development, land-cover change, and ecological responses will increase the applicability of such integrated models. Research is needed to understand how these different systems influence each other and how to incorporate such feedback into a spatially explicit modeling system. Moreover, individual- or agent-based models will be critical to realistically represent human-nature feedbacks. Furthermore, due to the inherent limitations in predicting the behavior of coupled human-natural systems, future research will need to effectively link predictive models with scenario planning ([Millennium Ecosystem Assessment 2003](#), [Shearer 2005](#)). The more flexible, adaptable, and transparent the model systems, the more likely they will be useful to planners and policy makers.

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## SUMMARY

We presented a unified modeling approach to predict urban development, land-cover change, and ecosystem response to landscape change. We focused on predicting the effects of future landscape change on avian communities as a case example of models that produce results useful to conservation planning across large landscapes. The Central Puget Sound of western Washington State, USA, is a 3,200 km<sup>2</sup> area undergoing significant urban development and resulting landscape change. We used a microeconomic development model of human behavior, UrbanSim, to predict land-use change. The land-cover change model incorporates output from UrbanSim, existing land cover, and biophysical attributes to predict land-cover change every four years, 28 years into the future. Land-cover and land-use predictions are input into models of avian species richness and relative abundance developed from five years of field studies across an

urban to wildland gradient. We found that avian diversity was sensitive to both the amount and pattern of land cover. The amount of forest was a key determinant of species richness and abundance of native forest birds. Additionally, aggregation of residential development was important for total species diversity and the diversity of three habitat guilds modeled, suggesting that a variety of birds in our region will benefit from aggregating future development. The richness of future bird communities will increase gradually with distance from development. As the transition zone between landscapes dominated by human development and wildland areas is transformed into dense development, the region is likely to be composed of spatially partitioned bird communities dominated by either adaptable, synanthropic species (in dense developments) or resilient native forest birds (in the wildland zone). We expect native forest birds to become increasingly reliant on higher elevation forests because most low elevation forests will be converted to development too dense to support viable populations. With increased development, the location of new development in regards to existing and proposed conservation networks will need to be considered. Conservation and planning agencies can use our models to evaluate proposed policies and conservation strategies.

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## ACKNOWLEDGMENTS

We thank Roarke Donnelly, Tina Blewett, Cara Ianni, Kara Whittaker, Jack DeLap, Stan Rullman, Thomas Unfried, and Dave Oleyar for their help collecting data. We thank Stefan Coe for development of the land-cover maps used in the LCC and the staff at the Center for Urban Simulation and Policy Analysis at The University of Washington. Many private landowners graciously gave us their permission to conduct research on their property. This research was supported by the University of Washington (Tools for Transformation Fund), the National Science Foundation (DEB-9875041, BCS 0120024, IGERT-0114351), and the University of Washington's College of Forest Resources, particularly its Rachel Wood's Endowed Graduate Program and the Denman Sustainable Resource Sciences Professorship.

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**Appendix A** List of Common Bird Species by Guild Membership, as Detected in Point Count Surveys of 139 Study Sites in Puget Sound, Washington, 1998–2005

<b>Common name</b>	<b>Genus species</b>	<b>Common name</b>	<b>Genus species</b>
Native Forest		Early Successional	
American robin	<i>Turdus migratorius</i>	American goldfinch	<i>Carduelis tristis</i>
Black-throated gray warbler	<i>Dendroica nigrescens</i>	Band-tailed pigeon	<i>Columba fasciata</i>
Brown creeper	<i>Certhia americana</i>	Bewick's wren	<i>Thryomanes bewickii</i>
Chestnut-backed chickadee	<i>Poecile rufescens</i>	Black-capped chickadee	<i>Poecile atricapillus</i>
Dark-eyed junco	<i>Junco hyemalis</i>	Black-headed grosbeak	<i>Pheucticus melanocephalus</i>
Downy woodpecker	<i>Picoides pubescens</i>	Bushtit	<i>Psaltriparus minimus</i>
Golden-crowned kinglet	<i>Regulus satrapa</i>	Cassin's vireo	<i>Vireo cassinii</i>
Hairy woodpecker	<i>Picoides villosus</i>	Cedar waxwing	<i>Bombycilla cedrorum</i>
Hammond's flycatcher	<i>Empidonax hammondii</i>	Common yellowthroat	<i>Geothlypis trichas</i>
Hermit thrush	<i>Catharus guttatus</i>	Killdeer	<i>Charadrius vociferus</i>
Hutton's vireo	<i>Vireo huttoni</i>	MacGillivray's warbler	<i>Oporornis tolmiei</i>
Pacific-slope flycatcher	<i>Empidonax difficilis</i>	Northern flicker	<i>Colaptes auratus</i>
Red-breasted nuthatch	<i>Sitta canadensis</i>	Northern Rough-winged swallow	<i>Stelgidopteryx serripennis</i>
Spotted towhee	<i>Pipilo maculatus</i>	Olive-sided flycatcher	<i>Contopus cooperi</i>
Steller's jay	<i>Cyanocitta stelleri</i>	Orange-crowned warbler	<i>Vermivora celata</i>
Swainson's thrush	<i>Catharus ustulatus</i>	Pine siskin	<i>Carduelis pinus</i>

continues

**Appendix A** List of Common Bird Species by Guild Membership, as Detected in Point Count Surveys of 139 Study Sites in Puget Sound, Washington, 1998–2005 *cont...*

<b>Common name</b>	<b>Genus species</b>	<b>Common name</b>	<b>Genus species</b>
Western tanager	<i>Piranga ludoviciana</i>	Purple finch	<i>Carpodacus purpureus</i>
Wilson's warbler	<i>Wilsonia pusilla</i>	Red crossbill	<i>Loxia curvirostra</i>
Winter wren	<i>Troglodytes troglodytes</i>	Red-winged blackbird	<i>Agelaius phoeniceus</i>
Synanthropic		Rufous hummingbird	<i>Selasphorus rufus</i>
American crow	<i>Corvus brachyrhynchos</i>	Savannah sparrow	<i>Passerculus sandwichensis</i>
Anna's hummingbird	<i>Calypte anna</i>	Song sparrow	<i>Melospiza melodia</i>
Barn swallow	<i>Hirundo rustica</i>	Tree swallow	<i>Tachycineta bicolor</i>
Brewer's blackbird	<i>Euphagus cyanocephalus</i>	Violet-green swallow	<i>Tachycineta thalassina</i>
Brown-headed cowbird	<i>Molothrus ater</i>	Warbling vireo	<i>Vireo gilvus</i>
European starling	<i>Sturnus vulgaris</i>	Western wood pewee	<i>Contopus sordidulus</i>
House finch	<i>Carpodacus mexicanus</i>	White-crowned sparrow	<i>Zonotrichia leucophrys</i>
House sparrow	<i>Passer domesticus</i>	Willow flycatcher	<i>Empidonax traillii</i>
Rock pigeon	<i>Columba livia</i>	Yellow-rumped warbler	<i>Dendroica coronata</i>