Ecological Applications, 17(4), 2007, pp. 1004–1018

BIODIVERSITY CONSEQUENCES OF ALTERNATIVE FUTURE LAND USE SCENARIOS IN GREATER YELLOWSTONE

Patricia H. Gude,[1] Andrew J. Hansen, and Danielle A. Jones

Ecology Department, Montana State University, P.O. Box 173460, Bozeman, Montana 59717 USA

Abstract. Land use is rapidly expanding in the Greater Yellowstone Ecosystem, primarily from growth in the number of rural homes. There is a need to project possible future land use and assess impacts on nature reserves as a guide to future management. We assessed the potential biodiversity impacts of alternative future land use scenarios in the Greater Yellowstone Ecosystem. An existing regression-based simulation model was used to project three alternative scenarios of future rural home development. The spatial patterns of forecasted development were then compared to several biodiversity response variables that included cover types, species habitats, and biodiversity indices. We identified the four biodiversity responses most at risk of exurban development, designed growth management policies to protect these areas, and tested their effectiveness in two alternative future scenarios. We found that the measured biodiversity responses, including riparian habitat, elk winter range, migration corridors, and eight other land cover, habitat, and biodiversity indices, are likely to undergo substantial conversion (between 5% and 40%) to exurban development by 2020. Future habitat conversion to exurban development outside the region's nature reserves is likely to impact wildlife populations within the reserves. Existing growth management policies will provide minimal protection to biodiversity in this region. We identified specific growth management policies, including incentives to cluster future growth near towns, that can protect "at risk" habitat types without limiting overall growth in housing.

Key words: biodiversity; exurban; Greater Yellowstone Ecosystem; growth management; landscape planning; land use change; nature reserves; residential development; rural development; urban fringe.

Introduction

Yellowstone National Park (USA) is one of many reserves around the world where rapid land use change is occurring in unprotected lands surrounding nature reserves (DeFries et al. 2005). The rapidly changing unprotected lands sometimes form critical parts of the ecosystems containing nature reserves, referred to here as greater ecosystems (Keiter and Boyce 1991, Hansen et al. 2002). Greater-ecosystem-wide management approaches can help scientists and decision makers understand this change and design effective conservation strategies for reserves (D. A. Jones et al., *unpublished manuscript*). Key steps in this process include quantifying biodiversity consequences of past and present conditions and simulating future scenarios that incorporate alternative management strategies (Theobald and Hobbs 2002, Baker et al. 2004). The results of this process will help managers to visualize the region in the future under different management scenarios, and to select policies that are most likely to balance land use and conservation objectives.

The Greater Yellowstone Ecosystem (GYE) provides an excellent case study for this approach. Although 68% of the GYE is publicly owned, critical resources and habitats are underrepresented within the protected lands. This is because the public lands in the GYE are relatively high in elevation, harsh in climate, and low in primary productivity (Rodman et al. 1996), whereas the private lands are primarily in valley bottoms and floodplains with longer growing seasons and higher plant productivity (Hansen et al. 2000). Consequently, hot spots for biodiversity are largely on private lands and many large mammals migrate to low-elevation habitats for parts of the year (Hansen et al. 2002). Within the 32% of the GYE that is privately owned, land use is rapidly intensifying. Developed land is increasing faster than the rate of population growth, largely due to low-density "exurban" development (Hernandez et al. 2004), defined as one home per 0.4–16.2 ha (Brown et al. 2005). From 1970 to 1999, the GYE experienced an increase in population of 58% and an increase in the area of rural lands supporting exurban development of 350% (Gude et al. 2006).

Exurban development is increasingly recognized as an important driver of ecological processes and biodiversity

Manuscript received 3 August 2005; revised 24 March 2006; accepted 9 May 2006. Corresponding Editor: M. Friedl. For reprints of this Invited Feature, see footnote 1, p. 972.

[1] Present address: Headwaters Economics, 566 Highland St., Helena, Montana 59601 USA.
E-mail: patty@headwaterseconomics.org

(McKinney 2002, Miller and Hobbs 2002). During the period 1950 to 2000, exurban development was the fastest increasing land use type in the United States and now covers >25% of the area of the 48 contiguous states (Brown et al. 2005). A recent review (Hansen et al. 2005) found that exurban development can impact biodiversity by: constraining options for allowing beneficial natural disturbances such as wildfires and floods; fragmenting natural habitats and reducing vegetation structure; favoring exotic species and native mesopredators that negatively effect reproduction and survival of native species; and increasing negative human interactions with wildlife including road kill and displacement by pets. Some of these negative impacts can be avoided or mitigated by appropriate placement and design of rural subdivisions (Dale et al. 2005). Hence, in more progressive regions, innovative approaches for land use planning, analysis, and implementation are increasingly practiced (Theobald et al. 2005).

Although land use may affect biodiversity across political boundaries within the GYE, land use planning is generally unrestrictive and is done largely in isolation within each of the 20 counties that make up the ecosystem (Hernandez et al. 2004). Despite high rates of development and population growth, four GYE counties have no full-time planners on staff and 15 of the 20 GYE counties have no county-wide zoning. This land use planning, implemented on a county-by-county basis, results in a patchwork of policies that may not effectively preserve biodiversity.

Many entities in the GYE, including federal, state, and local government agencies, nonprofits, and groups of citizens, are interested in sustaining both the greater ecosystem and the local human communities. These groups desire objective information on which non-protected lands are most valuable for preserving biodiversity, which nonprotected lands are most at risk of future development, and which combination of regional growth management policies will best preserve biodiversity without limiting future economic growth (Theobald et al. 2000, Theobald and Hobbs 2002).

In this paper, we assess the potential biodiversity impacts of alternative future land use scenarios in the GYE. We draw on several previous GYE research efforts, including a simulation model of rural residential development (Hernandez et al. 2004), a model identifying avian biodiversity hotspots (A. J. Hansen, *unpublished report*), a composite of grizzly bear locations (1990–2000) showing current range (Schwartz et al. 2002), a model of potential mammal migration corridors (Walker and Craighead 1997), and a model of irreplaceable areas based on terrestrial and aquatic habitat and wildlife populations (Noss et al. 2002). We estimate past and present impacts of exurban development on various elements of biodiversity to set the context for evaluating five future development scenarios: low growth, status quo, boom, moderate growth management, and aggressive growth management. This type of evaluation of potential habitat, biodiversity, and natural resource responses to future land use change scenarios is becoming more utilized (Verburg et al. 1999*b*, Swenson and Franklin 2000, Farrow and Winograd 2001, Hawkins and Selman 2002, Schumaker et al. 2004, Van Sickle et al. 2004) as land use change is increasingly recognized as a key driver of changes in biodiversity in terrestrial ecosystems (Sala et al. 2000, McKinney 2002, Miller and Hobbs 2002).

The simulation model used in this study to generate alternative scenarios is based on regression and forecasts development, with a measured degree of confidence, based on rates of development during the 1990s and regional covariates including transportation infrastructure, natural amenities, and existing development (Hernandez et al. 2004). This simulation method was chosen over other approaches because of its statistical nature, comprehensive accuracy assessment, and ability to generate scenarios based on alternative land use policies. The method models the path of growth over time and is calibrated to and validated against historical development patterns. This approach differs from "build-out" models that assign the maximum number of building units per parcel as determined by zoning regulations (Theobald and Hobbs 2002). Build-out models may be less suited for landscapes such as the GYE, where the majority of private lands are not zoned.

We quantify the impacts on biodiversity and implications for human land use under alternative future scenarios. The low-growth, status quo, and boom scenarios forecast growth under existing land use policies. The moderate and aggressive growth management scenarios implement hypothetical growth management policies designed to direct growth away from the biodiversity elements that we found to be most at risk of development pressure under the status quo future growth scenario. We evaluate the effect of specific growth management policies on the protection of "at risk" habitat types. By comparing the extent of future habitat loss with the extent of currently protected habitat, we estimate the effects of exurban development outside reserves on biodiversity within the protected lands of Yellowstone.

Our approach is similar to gap analysis, in the identification of biodiversity elements outside of areas currently managed for biodiversity protection (Scott et al. 1993). We take this approach a step further by simulating land use to identify "at risk" elements of biodiversity. Other studies have incorporated land use models into biodiversity assessments (White et al. 1997, Theobald et al. 2000, Noss et al. 2002, Theobald and Hobbs 2002, Schumaker et al. 2004). Some have extrapolated beyond habitats and estimated potential effects on wildlife populations (White et al. 1997, Schumaker et al. 2004). Our approach shows how these methods can be applied to an adaptive-management framework for identifying appropriate policies for protecting biodiversity in greater ecosystems.

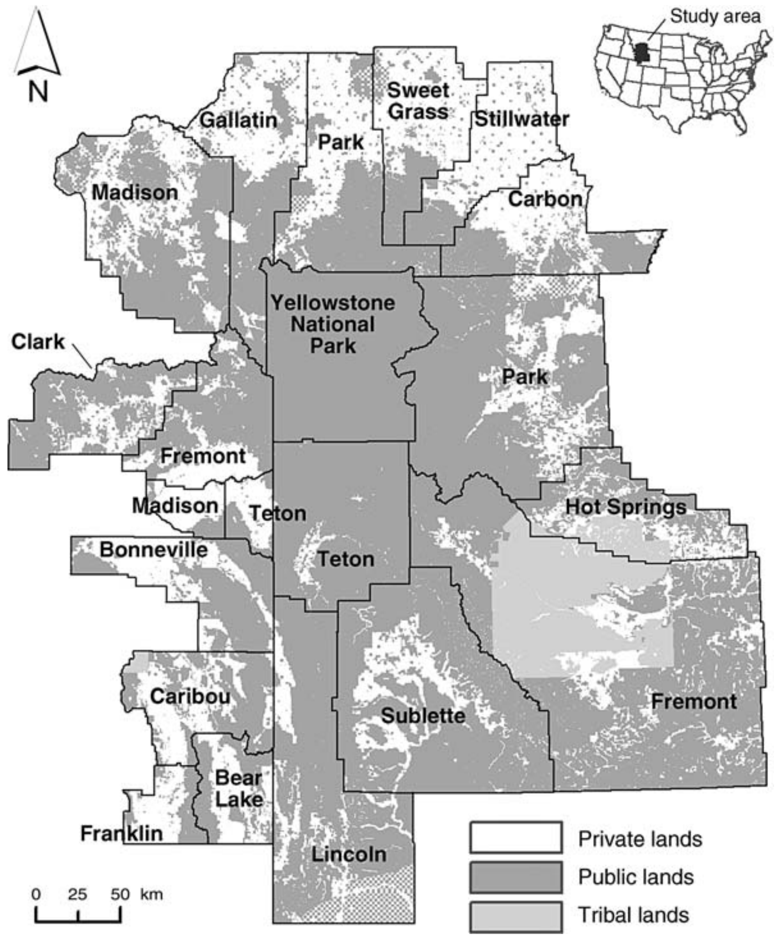

FIG. 1. The study area encompasses those 20 counties of Montana, Wyoming, and Idaho that surround Yellowstone National Park (USA). The public and tribal lands shown comprise 68% of the region.

METHODS

Study area

Centered on the Yellowstone Plateau, the Greater Yellowstone Ecosystem (GYE) was originally defined as the range of *Ursus arctos*, the Yellowstone grizzly bear (Craighead 1991). Subsequently, Rasker (1991) expanded the study area boundary to include the 20 counties within Montana, Wyoming, and Idaho that overlap the GYE, in recognition of the strong ecological and socioeconomic linkages across the public and private lands of this region (Fig. 1). The expanded boundary is appropriate for this study because development regulations and growth management are implemented at the county level.

Of the 145 635 km^2 that make up the 20 counties of the GYE, public and tribal lands comprise 68% (98 386 km^2) of the region. Land ownership is divided among private landowners (32%), the USDA Forest Service (32%), the USDI Bureau of Land Management (19%), Yellowstone and Grand Teton National Parks (7%), Tribal Lands (5%), and state lands, wildlife refuges, and other federal lands (5%). Because of extensive public ownership, it is often assumed that the influence of rural residential development on the ecosystem is limited. However, many species of wildlife in the GYE depend on resources found almost exclusively on the privately owned lowland valleys, where land use is intensifying (Hansen et al. 2002).

The region is unique in the continental United States in that it supports several large carnivores and free-roaming populations of ungulates. Herds of elk (*Cervus elaphus*) and bison (*Bison bison*) inhabit the area, as do bighorn sheep (*Ovis canadensis*), pronghorn antelope (*Antilocapra americana*), moose (*Alces alces*), wolves (*Canis lupus*), and grizzly bears (*Ursus arctos*). The headwaters of seven major rivers originate in and around Yellowstone National Park. These rivers flow mainly through private lands where they form biologically diverse lowland riparian habitats surrounded by the semiarid uplands. The vegetation of the GYE consists of a combination of forest, shrub, and grassland. Coniferous forests occupy much of the Yellowstone Plateau and mountainous terrain, whereas shrub and grassland vegetation is more common in valley bottom and alpine habitats.

Simulation of rural residential development in 2020

Correlates of recent growth were analyzed to calibrate the simulation. The response variable for calibrating the simulation was change in the number of rural homes per U.S. Public Land Survey section (~2.59 km^2) over the time period 1990–1999. The rapid rate of rural home construction in the GYE during this time period is expected to persist according to demographic trends (Cromartie and Wardwell 1999). Therefore, the time period serves as a reasonable model of growth rates within the near future. The response variable was derived from a spatially explicit database of rural residential development per section collected from county tax assessor offices (Hernandez et al. 2004). As defined by county tax assessors, rural residential development includes all homes that are outside of incorporated city and town site boundaries, including subdivisions, and excluding mobile homes, for which location descriptions were not available.

We used 55 potential explanatory variables to analyze the correlates of growth from 1990 to 1999. These variables describe the study area with respect to natural resources, transportation, services, natural amenities, and past home development, and are consistent with the biophysical and socioeconomic factors identified in the growing body of literature investigating the drivers of human settlement patterns (Verburg et al. 1999*a*, Kok and Veldkamp 2001, Schneider and Pontius 2001, Serneels and Lambin 2001, Hansen et al. 2002, Huan et al. 2002, Schnaiberg et al. 2002, Walsh et al. 2003, Gude et al. 2006). Examples include suitability for agriculture, travel time to airports, and travel time to national parks. See Hernandez et al. (2004) for a list of all potential explanatory variables, including their source and scale.

One-quarter of private lands in the study area, a randomly selected 6217 sections, were excluded from the analysis as a "hold-back" data set for use in assessing model accuracy. For the remaining 75% of sections, the potential explanatory variables were fit to the response variable using univariate generalized linear models with the assumption of a negative binomial distribution (Proc GENMOD; SAS Institute 2001). Within each category (natural resources, transportation, services, natural amenities, and past home development), those variables that explained the most variation in growth in rural residential development during the 1990s were identified using Akaike's Information Criteria (AIC) units (Burnham and Anderson 2000). All possible combinations of the selected variables were ranked according to differences in AIC scores, and the best model was identified, tested for spatial autocorrelation and overdispersion, and run for the "hold-back" data set so that predicted growth could be compared to observed growth between 1990 and 1999.

TABLE 1. Coefficient estimates, confidence intervals, and significance levels described for parameters of the best model of growth in rural residential development during the 1990s ($\Delta AIC = 0$).

Model parameters	β	95% CL	*P*
Intercept	9.02	7.39, 10.73	<0.0001
Road density	3.01	2.53, 3.49	<0.0001
Airport travel time	−0.65	−0.98, −0.34	<0.0001
Development indicator	1.75	1.65, 1.86	<0.0001
Homes in one-section radius	3.80	3.12, 4.52	<0.0001
Homes in 20-section radius	0.16	0.03, 0.30	0.0203
Homes in 20-section radius, quadratic term	−0.89	−1.12, −0.66	<0.0001
Construction during previous decade	9.76	8.14, 11.47	<0.0001
Streams/rivers proximity	−1.12	−1.33, −0.92	<0.0001
Forest areas travel time	−3.31	−3.58, −3.03	<0.0001
Dispersion	3.67	3.46, 3.89	

The best regression model of growth during the 1990s (Table 1) incorporated transportation infrastructure and access to services, as well as the effects of natural amenities. The road density variable (1992 TIGER/Line files at 1:100 000) describes kilometers of all roads per square kilometer. The airport travel time variable (1998 National Atlas files at 1:2 000 000) was calculated using cost–distance grid functions incorporating distance and automobile speed limits, following the methods of Nelson (2001). The development indicator (county tax assessor files at 1:100 000) is a binary variable describing whether or not each section contained any homes prior to 1990. Other past-development variables in the best model were also compiled from county tax assessor records and represent the number of rural homes present prior to 1990 within a one-section radius and within a 20-section radius. Proximity to forested areas (1992 National Land Cover Dataset at 1:24 000) was also calculated using travel time. Proximity to rivers and streams (1999 National Hydrography Dataset at 1:100 000) were calculated as Euclidian distance.

Using the best regression model of growth during the 1990s (Table 1), the simulation was run for two iterations of one decade each to forecast development patterns for 2010 and 2020 (Fig. 2). The simulation, which consists of interacting Java and ArcInfo programs, was designed to facilitate the manipulation of growth inducing and limiting factors in order to generate maps of alternative future scenarios. Specifically, the simulation was used to implement growth management policies that affected allowable housing densities. Forecasts generated using the best regression model were assumed to reflect the regional demand for rural housing; therefore growth management policies modified the spatial allocation of forecasted homes rather than changing the number of forecasted homes. The remaining growth "capacity" of each section was calculated as the allowable density as specified by land use policies minus the existing density in 1999. In private land sections where no policies applied, the capacity was

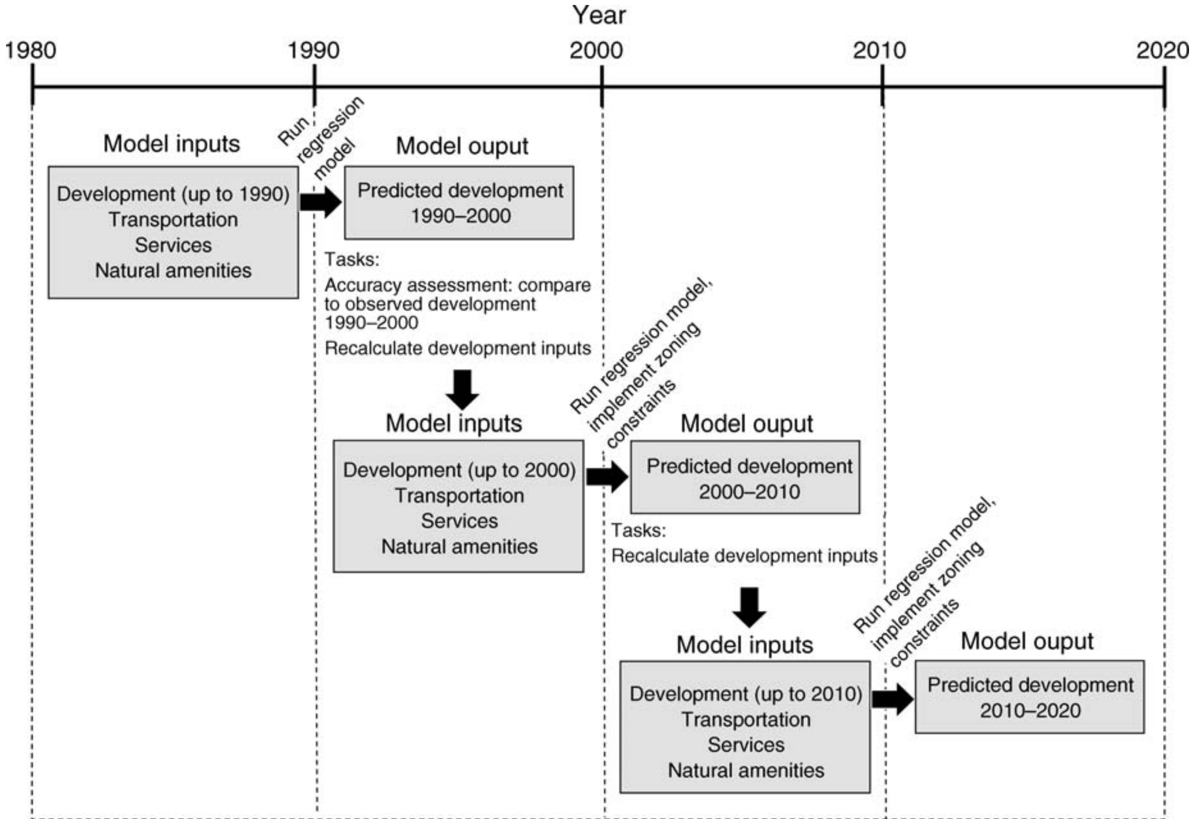

FIG. 2. The best regression model of rural residential development during the 1990s was used iteratively to forecast development for the years 2010 and 2020.

assumed to be unlimited. Therefore the densities forecasted by the regression model were not restricted in these sections. When the forecasted development exceeded the remaining capacity, the simulation displaced the forecasted homes beyond the remaining capacity into similar sections within the same local area. Each section was assigned a "similarity" rating based on the explanatory variables from the best regression model, and the simulation allowed displacement between sections with the same rating. See Hernandez et al. (2004) for further explanation of the simulation of growth management regulations.

We generated five alternative scenarios for the purpose of evaluating impacts of future land use on biodiversity (Table 2). We created the status quo scenario to show potential future rural land use change, given a growth rate consistent with that observed during 1990–1999 and existing growth management policies. For the low-growth scenario, the model parameters were altered to approximate a statistically probable lower

TABLE 2. Future growth scenarios generated by the RDS (rural development simulator), using different assumptions of growth rates, limiting, and driving factors.

	Simulation assumptions		
Scenario	Rate of rural home growth	Limiting factors	Driving factors
Status quo	point estimates of coefficients	existing land use regulations	covariates from best regression model
Low growth	lower coefficient estimates from 95% confidence limit	existing land use regulations	covariates from best regression model
Boom	upper coefficient estimates from 95% confidence limit	existing land use regulations	covariates altered to reflect hypothetical gains in infrastructure and housing
Moderate growth management	point estimates of coefficients	existing and hypothetical land use regulations	covariates from best regression model
Aggressive growth management	point estimates of coefficients	existing and hypothetical land use regulations	covariates from best regression model

TABLE 3. Response variables considered in the assessment of habitat and biodiversity consequences of past and present rural development, and future rural development scenarios.

Response	Description	Source	Scale
Land cover types			
Douglas-fir	as classified by USGS and USFS	USGS/USFS 2002 forest cover types	1:7 500 000
Grassland	as classified by USGS	USGS 1992 National Land Cover	1:24 000
Aspen	on public lands, as classified by USFS; otherwise, deciduous excluding riparian	USGS 1992 National Land Cover; 1990–2001 USFS stand maps	1:24 000
Riparian	major rivers buffered by 256 m and adjacent deciduous habitat	USGS 1992 National Land Cover; USGS/EPA 1999 Hydrography; USFS 1900–2001 stand maps	1:100 000
Species distributions			
Grizzly bear	outer edge of composite polygon of fixed-kernel ranges from all grizzly locations (1990–2000)	Schwartz et al. (2002)	1:24 000
Elk winter range	habitat suitability; expert opinion	Rocky Mountain Elk Foundation (1999)	1:250 000
Pronghorn antelope	habitat suitability; expert opinion	Montana Fish, Wildlife, and Parks (2002); Wyoming Game and Fish	1:250 000
Moose	habitat suitability; expert opinion	Montana Fish, Wildlife, and Parks (1996); Wyoming Game and Fish	1:250 000
Biodiversity indices			
Bird hotspots	areas of >70% of maximum bird diversity and abundance	Hansen et al. (2003)	1:250 000
Migration corridors	landscape corridors based on habitat suitability for grizzly, elk, and cougar	Walker and Craighead (1997)	1:250 000
Irreplaceable areas	multi-criteria assessment based on habitat and population data for terrestrial and aquatic GYE species	Noss et al. (2002)	1:250 000

Note: GIS data set layers are not published, but can be accessed as follows, for the relevant species: USGS/USFS (2002) at ⟨http://svinetfc4.fs.fed.us/rastergateway/forest_type/⟩; USGS (1992) at ⟨http://landcover.usgs.gov/⟩; USGS/EPA (1999) at ⟨http://nhd.usgs.gov/⟩.

estimate of growth. This was done by rerunning the best regression model using the lower coefficient estimates from the 95% confidence interval for each parameter. Similarly, the boom scenario was generated using the upper coefficient estimates from the 95% confidence intervals. The boom scenario also incorporated expert opinion regarding future gains in transportation infrastructure and future subdivisions. Workshops were held in which 15 planners from study area counties identified on hard-copy maps those areas where they anticipated new subdivisions, new roads, and major road improvements within a 10-year time horizon. These features were digitized and used to recalculate transportation and past-development model inputs for 2010, therefore affecting the second iteration of the simulation (2010–2020). Lastly, we generated two growth management scenarios representing future growth under hypothetical growth management policies designed to protect four biodiversity responses found to be most at risk of exurban development in the 2020 status quo scenario.

Biodiversity responses

In order to conduct a regional assessment of biodiversity consequences of the alternative future growth scenarios, we collected three categories of habitat and biodiversity response variables for the GYE: (1) land cover and use data, (2) species and habitat data, and (3) biodiversity indices (Table 3).

Four land cover types were considered in the analyses: Douglas-fir (*Pseudotsuga menziesii*), grasslands, riparian habitat, and aspen (*Populus tremuloides*) stands. The data source for Douglas-fir was the U.S. Geological Survey/U.S. Forest Service Forest Cover Types data set derived from Advanced Very High Resolution Radiometer (AVHRR) composite images. The data source for grasslands was the U.S. Geological Survey's National Land Cover Dataset (NLCD) based on 30-m Landsat thematic mapper (TM) data. Riparian habitats were delineated as major rivers, selected from the U.S. Geological Survey's 1:100 000 scale National Hydrography Dataset, buffered by 256 m into adjacent lands where the slope was less than 3 degrees. These criteria were selected as a conservative approximation of floodplain areas and corresponded well with willow and cottonwood vegetation. Adjacent deciduous forest from the NLCD was also included as riparian habitat. Aspen stands on public lands were classified by individual U.S. Forest Service Districts within the GYE (Brown et al. 2006). Aspen stands on private lands were selected from NLCD deciduous cover, excluding riparian habitat. These data sets were merged, and low-elevation aspen stands, at less than 2200 m altitude, were selected for use in the analyses. Aspen in this lower elevation zone supports higher biodiversity than at higher elevations (Hansen and Rotella 2002).

Occurrence and range maps for four species (grizzly bear, elk, pronghorn antelope, and moose) were used in the analyses. For grizzly bears, we used a map of currently occupied habitat, compiled using the outer edge of the composite polygons of fixed-kernel ranges from radiotelemetry locations taken between the years 1990 and 2000 (Schwartz et al. 2002). For elk, pronghorn, and moose habitat, we used maps created by the Rocky Mountain Elk Foundation based upon habitat suitability and expert opinion. The ungulate range maps were unavailable for the Idaho portion of the study area.

Three biodiversity indices were used in the analyses: bird biodiversity hotspots, potential migration corridors, and an index of irreplaceability. Bird hotspots were modeled using topography, climate, and vegetation composition and productivity to predict bird species richness and abundance calculated from USGS Breeding Bird Survey (BBS) data (A. J. Hansen, *unpublished report*). Areas of high bird biodiversity potential were defined as areas with predicted total abundance greater than 70% of maximum and predicted species richness greater than 70% of maximum (A. J. Hansen, *unpublished report*). Potential mammal migration corridors were based upon habitat suitability models for grizzly bears, elk, and cougars, combined with measures of road density to create a spatially explicit "cost of movement" surface (Walker and Craighead 1997). The assessment of the irreplaceability, defined as the likelihood that an area is needed to reach an explicit conservation goal (Pressey and Cowling 2001), was based on criteria including: occurrences of imperiled and vulnerable plant and animal species and communities; habitat suitability models for elk and large carnivores; population models for grizzly bear, wolf, and wolverine; and areas of wetland, geoclimatic, and aquatic habitat types (Noss et al. 2002). The criteria were summed for each location, scaled between 0 and 100, and locations with scores greater than 50 were considered irreplaceable areas (Noss et al. 2002).

The last biodiversity response considered in the analyses was an integrated index combining the four biodiversity measures that were most impacted by future growth under the status quo scenario for the year 2020. The four responses were overlaid and the one-quarter of private lands containing the most "at risk" responses was identified.

Statistical analyses

We conducted a regional assessment of biodiversity consequences of exurban development for each of the alternative future growth scenarios. Incorporated towns (1.88% of sections within the study area) were excluded from the analysis because the model was calibrated to rural residential development and was not run for urbanized areas. Thus, our analyses focused on biodiversity impacts in rural and urban fringe areas.

For each response, we calculated the percentage of area impacted by exurban housing densities in 1980, 1999, and in each of the 2020 alternative scenarios. Areas were considered to be impacted if they overlapped with sections ($\sim$2.59 km^2) containing exurban housing densities. Areas within a one-section buffer of exurban housing were also considered impacted. The assumption that ecological impacts of exurban housing extend into neighboring sections is supported by recent publications reviewing studies and mechanisms by which land use change impacts biodiversity (Hansen et al. 2005, Hansen and DeFries 2007).

We employed use vs. availability analyses to examine the observed distribution of rural homes in 1999 with respect to each biodiversity response. The observed number of rural homes was compared to the "expected" number if homes were distributed randomly within private lands with respect to each response. We calculated expected numbers of homes as the proportion of area occupied by the response (i.e., bird hotspots) multiplied by the total number of rural homes present in 1999. We used a chi-square goodness-of-fit test to evaluate the hypothesis that the observed and expected values were drawn from the same distribution.

Adaptive management approach

We identified the four biodiversity responses most at risk of exurban development according to the 2020 status quo scenario. We then designed growth management policies to protect these areas and tested their effectiveness in two future scenarios: the moderate growth management and aggressive growth management scenarios. Forecasted rural residential development was directed away from "at risk" areas by imposing hypothetical growth management policies, including the purchase of conservation easements and the delineation of zoning districts. Like the status quo scenario, the rate of rural home construction for these alternative scenarios was assumed to be the same as the rate observed during 1990–1999. Thus, the total forecasted increase in rural residential development was the same in the status quo, moderate growth management, and aggressive growth management scenarios. However, the location of forecasted development differed between these scenarios due to the hypothetical growth management policies that were simulated.

The goal of the moderate growth management scenario was to develop growth management policies that would protect the most "at risk" biodiversity responses in one-fourth of the GYE's private lands. In order to accomplish this goal, 4047 km^2 of private land were designated as conservation easements, in which no forecasted development would be allowed. The goal of 4047 km^2 of land in conservation easements was chosen as an optimistic, but not unreachable, target according to members of several land trusts within the GYE (T. Lange, Gallatin Valley Land Trust, *personal communication*). An additional 8094 km^2 of private land

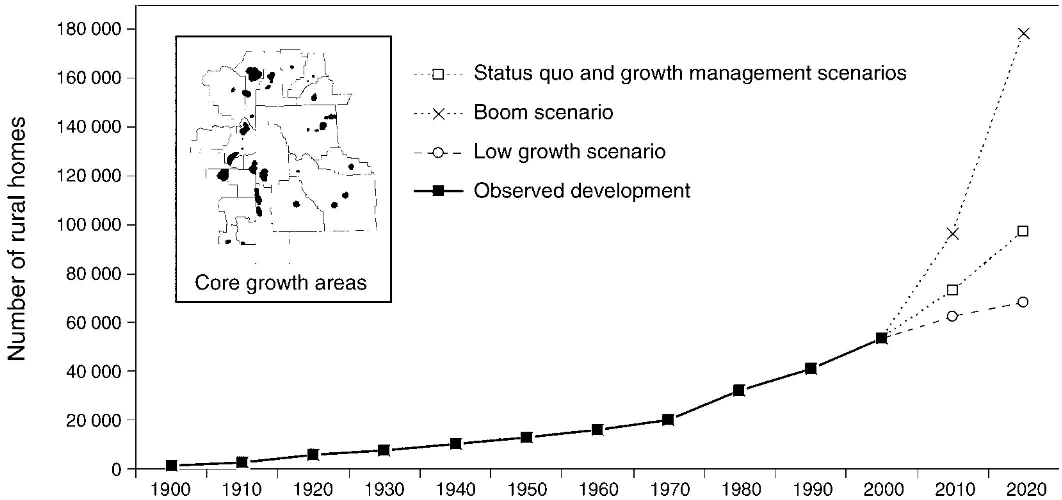

FIG. 3. Observed numbers of rural homes in the Greater Yellowstone Ecosystem are shown from 1900 through 2000. Forecasted numbers for the alternative future scenarios are shown for 2010 and 2020. Areas where growth in housing was greater than one standard deviation above the mean are highlighted on the inset map.

were zoned for agricultural housing densities, and cluster zoning districts were designated in 4310 km^2 of private lands surrounding towns. Sections containing greater than two "at risk" biodiversity responses and with no rural homes were designated as hypothetical conservation easement areas. Sections with less than exurban housing densities that contained greater than one "at risk" biodiversity response were designated as hypothetical agricultural zoning districts. Cluster zoning districts were designated in sections adjacent to towns.

For the aggressive growth management scenario, the same areas were designated as conservation easements, agricultural zoning districts, and cluster zoning districts as in the moderate growth management scenario. In addition, sections with less than exurban housing densities that contained any "at risk" biodiversity responses were designated as hypothetical agricultural zoning districts, an additional 16 188 km^2. The outcome of the policies simulated in the moderate and aggressive growth management scenarios was assessed for each biodiversity response. As was done for 1980, 1999, and the 2020 low-growth, status quo, and boom scenarios, we calculated the percentage of area impacted by exurban housing densities in the 2020 moderate and aggressive growth management scenarios.

RESULTS

Simulation of rural residential development in 2020

The best model of growth in rural residential development during the 1990s (Table 1) was run for a hold-back data set (n = 6217) that consisted of a randomly selected sample of one-fourth of the sections in the study area (Hernandez et al. 2004). For these 6217 sections, predicted growth for the time period 1990–1999 was compared to observed growth to assess model accuracy. The mean difference between predicted and observed growth in the number of rural homes per section was 0.14 homes, with a standard deviation of 3.92. Of the 6217 sections evaluated, the increase in the number of rural homes was correctly predicted for 83% of sections. The increase in the number of rural homes was correctly predicted to plus or minus one home in 94% of sections. In 630 sections, growth was overestimated and in 427 sections growth was underestimated. In sections where growth occurred during the 1990s, the mean percentage deviation was 7.31%. Spatial autocorrelation was not evident in the variation in Pearson residuals of the best model.

The mathematical models for all five scenarios were in the form of linear equations; however, forecasted growth was nonlinear (Fig. 3) due to the influence of past development variables. In both the status quo and growth management scenarios, the number of rural homes within the GYE was forecasted to increase by 82.38% (44 011 homes) from 1999 to 2020. In the low-growth scenario, an increase of 27.51% (14 697 homes) was forecasted, and in the boom scenario an increase of 233.63% (124 817) was forecasted. The boom scenario is within the realm of possibility, given that recent tax assessor records show that Gallatin County, which encompasses ~20% of the rural housing in the study area, gained more than 5000 homes between 2000 and 2005. In all scenarios, the distribution of forecasted homes for the year 2020 was skewed toward the northern and western portions of the study area (Fig. 3), near towns and protected areas, defined as national parks, wilderness, roadless areas, and adjacent multiple-use areas (Hernandez et al. 2004).

The growth management scenarios differed from the status quo scenario in the locations of forecasted homes. In the moderate growth management scenario, growth was shifted toward existing towns: north and west of

TABLE 4. The ratio of observed to expected numbers of rural homes.

Response	Observed/expected rural homes	χ^2
Pronghorn range	0.52	16956.28
Elk winter range	0.87	344.78
Grasslands	1.02	181.67
Moose range	1.14	382.29
Douglas-fir	1.26	740.60
Migration corridors	1.36	1316.38
Aspen	1.39	4263.37
Irreplaceable areas	1.53	4340.76
Grizzly range	1.54	1579.59
Bird hotspots	1.73	5021.12
Riparian habitat	2.29	16048.63

Notes: The expected numbers signify a random distribution with respect to each element of biodiversity and were calculated as the proportion of area occupied by the response measure multiplied by the total number of observed rural homes. Each response is significant, by chi-square test, at $P < 0.0001$.

Bozeman, north of Cody, west of Rexburg, surrounding Idaho Falls, and surrounding Victor. Growth was shifted away from nature reserve boundaries: south of Bozeman, in the Big Sky area, west of Cody, and along portions of the Green and New Fork Rivers north and west of Pinedale. In the moderate growth management scenario, exurban development occupied 44.03 km^2 less than in the status quo scenario.

In the aggressive growth management scenario, growth was more concentrated near existing towns and in sections that already supported exurban housing densities in the Gallatin Canyon, Jackson Hole, and Star Valley. Growth was shifted away from nature reserve boundaries and undeveloped areas in the Gallatin Valley, Paradise Valley, West Yellowstone area, Island Park area, Jackson Hole, South Teton Valley, and Shoshone Canyon. There were 551.65 fewer square kilometers of exurban development than in the status quo scenario, and exurban sections tended to have more homes. For example, exurban sections in the status quo scenario had 18.79 homes/km^2, on average, and exurban sections in the aggressive growth management scenario had 21.55 homes/km^2, on average.

Biodiversity consequences

We rejected the hypotheses that rural homes were distributed randomly with respect to each biodiversity response variable (Table 4). Home sites present in 1999 were found to occur disproportionately in grasslands, moose range, Douglas-fir forest, potential migration corridors, low-elevation aspen forest, irreplaceable areas, grizzly habitat, bird hotspots, and riparian areas. Home sites occurred less than expected in pronghorn antelope and elk winter range (Table 4). The discrepancy between observed and expected development pressure was largest in grizzly habitat, bird hotspots, and riparian areas (Fig. 4). In the riparian areas of the GYE, we found more than twice the number of homes one would expect if homes were distributed randomly with respect to this habitat type (Fig. 4).

The percentage of habitat impacted by exurban development in 1980 ranged from 2.0% to 11.8%, for pronghorn habitat and the integrated index, respectively (Table 5). In 1999, the range was from 3.35% to 23.24%. The forecasted percentage of habitat impacted in the 2020 status quo scenario ranged from 5.83% to 29.93%; in the low growth scenario, the range was from 5.05% to 25.84%; and in the 2020 boom scenario, the range was from 7.58% to 40.66%. In the 2020 status quo scenario, five of the 12 biodiversity responses were forecasted to experience degradation in more than 20% of their area due to exurban development. These responses include: bird hotspots, riparian areas, potential migration corridors, and irreplaceable areas. The integrated index, constructed from these four responses, was also impacted in more than 20% of its extent. We considered the distribution of these "at risk" responses (Fig. 5), excluding private lands within one section (1.61 km) of exurban development, in designing the growth management scenarios.

Although both growth management scenarios gained the same number of rural homes as in the status quo scenario, the amount of habitat impacted by exurban development was less in the aggressive growth management scenario than in the low growth scenario for half of the response variables (Table 5). In the moderate growth management scenario, five of the 12 biodiversity responses were forecasted to experience degradation in more than 20% of their area due to exurban development. In the aggressive growth management scenario, four of the 12 biodiversity responses were forecasted to experience degradation in more than 20% of their area

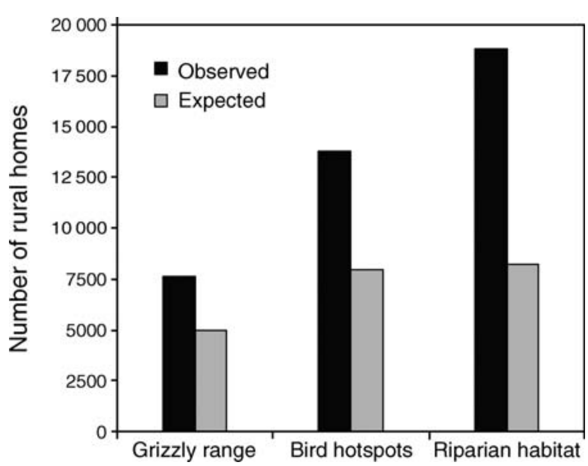

FIG. 4. Observed and expected number of rural homes are shown for the three biodiversity response measures in which the discrepancy between observed and expected development pressure was the largest. The expected numbers of homes reflect a random distribution with respect to the biodiversity response and were calculated as the proportion of area occupied by the response measure multiplied by the total number of homes.

TABLE 5. The percentage of area impacted by exurban development, defined as one home per 0.4–16.2 ha, presented for each element of biodiversity.

	Percentage of habitat impacted by exurban development						
Response	1980	1999	Status quo 2020†	Low growth 2020	Boom 2020	Moderate growth management 2020	Aggressive growth management 2020
Pronghorn range	2.00	3.35	5.83	5.05	7.58	6.06	4.73
Moose range	2.73	5.49	7.96	6.83	11.11	7.24	6.26
Grasslands	2.99	5.57	8.36	7.02	11.97	8.01	6.87
Grizzly range	3.13	5.98	8.52	7.68	10.70	7.74	6.88
Douglas-fir	2.91	6.01	8.85	7.07	13.31	7.82	7.09
Elk winter range	2.36	6.26	9.98	8.61	13.47	9.00	7.23
Aspen	5.55	13.92	19.53	15.58	28.39	18.74	17.60
Bird hotspots	8.42	16.91	23.20	19.23	34.36	21.04	20.23
Riparian habitat	10.22	17.30	23.64	19.43	31.27	22.45	18.77
Corridors	8.89	18.79	24.43	20.83	35.38	22.96	21.80
Irreplaceable areas	11.41	23.15	29.61	25.69	40.08	30.88	26.92
Integrated index	11.80	23.24	29.93	25.84	40.66	29.28	26.43

Notes: Areas were considered to be impacted if they overlapped with sections containing exurban housing densities. Areas within a one-section buffer (1.61 km) of exurban housing were also considered impacted.

† Responses are ranked by the proportion impacted in the status quo 2020 scenario.

due to exurban development. Bird hotspots, riparian habitat, migration corridors, and irreplaceable areas were the most impacted responses across all scenarios. However, in the aggressive growth management scenario, 284.19 fewer square kilometers of bird hotspots were impacted by exurban development than in the status quo scenario. The other "at risk" responses were also less impacted in the aggressive growth management scenario than in the status quo scenario: 482.67 fewer square kilometers of riparian habitat were impacted, 269.87

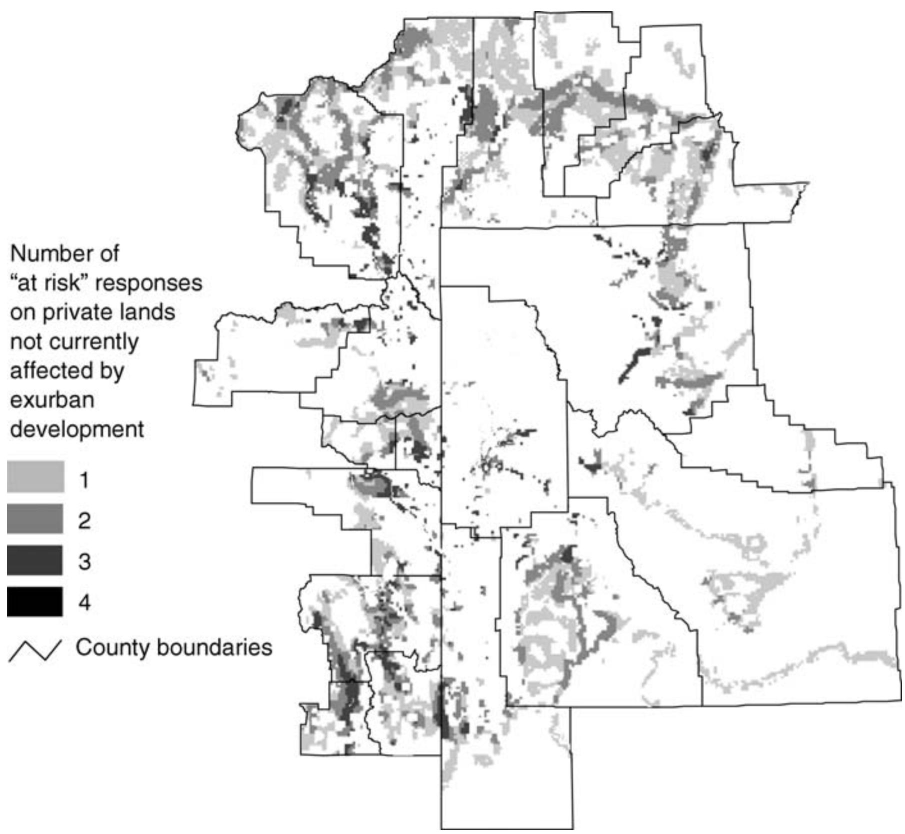

FIG. 5. The distribution and extent of overlap of "at risk" biodiversity responses (bird hotspots, riparian areas, potential migration corridors, and irreplaceable areas). In the key, 1 means that any one of the four "at risk" responses occurs in locations with that shading; 2 indicates any two of the four; 3 indicates any three of the four; and 4 indicates that all four occur in those locations.

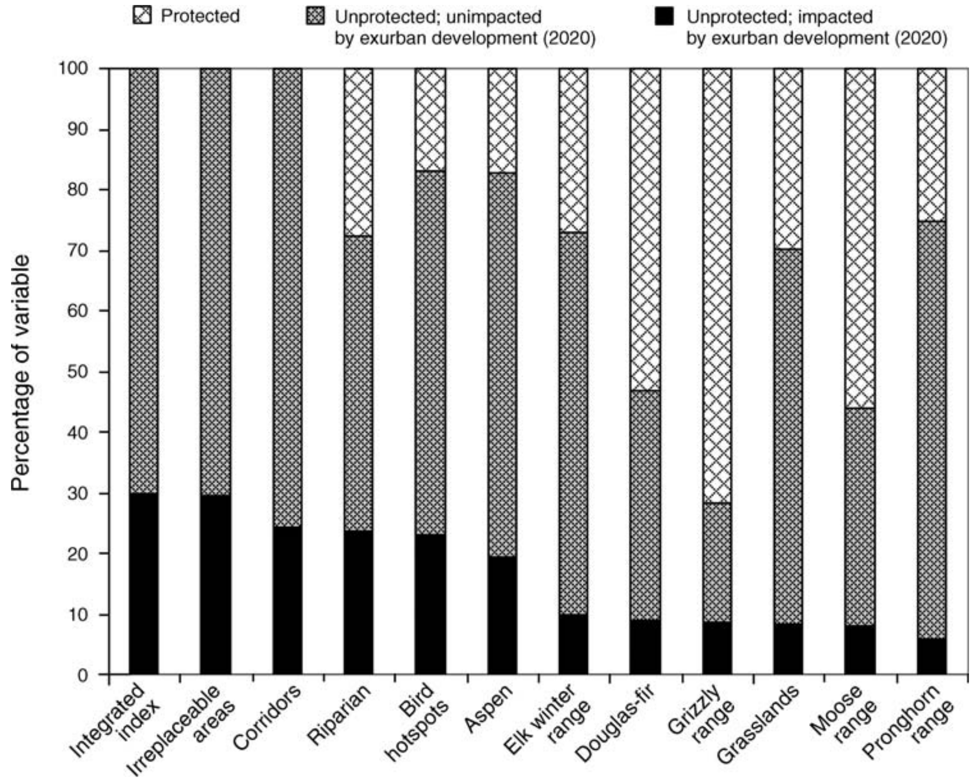

FIG. 6. Each biodiversity response variable is described by the percentage that is protected from exurban development, the percentage that is unprotected and impacted, and the percentage that is unprotected and unimpacted. Biodiversity responses within one section of exurban housing were considered impacted. The integrated index combined the four biodiversity measures that were most impacted by future growth under the status quo scenario for the year 2020: bird hotspots, riparian habitat, migration corridors, and irreplaceable areas.

fewer square kilometers of migration corridors were impacted, and 391.73 fewer square kilometers of irreplaceable areas were impacted.

The percentage of each biodiversity response protected from future exurban development ranged from 0% to 71.56% (Fig. 6). Responses were considered protected from exurban development if they occurred within a nature reserve, farther than 1.61 km from the private land boundary. Corridors, irreplaceable areas, and the integrated index were designated to occur only on private lands, and therefore did not overlap with protected areas. Less than 20% of bird hotspots and low-elevation aspen were protected, and less than 50% of pronghorn range, elk winter range, riparian areas, and grasslands were protected. At 71.56%, currently occupied grizzly habitat overlapped the most with areas protected from exurban development.

TABLE 6. Percentage of the highest ranked 25% of private lands in the Greater Yellowstone Ecosystem (GYE) forecasted to experience two types of land use intensification.

	Forecasted land use change in highest ranked 25% of GYE (%)	
Scenario	Agriculture to exurban	Undeveloped to developed
Aggressive growth management	2.67	1.74
Moderate growth management	4.67	1.63
Low growth	4.70	4.58
Status quo	14.56	7.66
Boom	36.37	24.29

The extent and types of forecasted land use changes in the highest ranked 25% of private lands (according to the integrated index) varied between the scenarios (Table 6). In the status quo scenario, 14.56% of these private lands were forecasted to be converted from agricultural to exurban housing densities. In the boom scenario, 36.37% of the area was forecasted to experience agricultural to exurban conversion, and in the aggressive growth management scenario, 2.67% was forecasted to experience agricultural to exurban conversion. In the status quo scenario, 7.66% of the area was undeveloped in 1999 and forecasted to be developed by 2020. In the boom scenario, 24.29% of the area was forecasted to change from being undeveloped in 1999 to developed in 2020, and in the aggressive growth management scenario, 1.74% of the area was forecasted to change from being undeveloped in 1999 to developed in 2020. Although there were more forecasted homes within the GYE in both the moderate and aggressive growth management scenarios than in the low-growth scenario, there was less extensive exurban development within the highest ranked 25% of private lands.

Discussion

This study utilized an existing simulation of rural residential development to identify habitat types most "at risk" of future exurban development. We estimated probable losses in biodiversity elements due to exurban development, and assessed potential biodiversity impacts of alternative land use policies for managing future growth. We found that: (1) exurban development has occurred disproportionately in currently occupied grizzly habitat, bird biodiversity hotspots, and riparian areas; (2) most habitats are likely to undergo substantial conversion (between 10% and 40%) to exurban development by 2020; (3) habitat conversion to exurban development is likely to impact biodiversity within GYE nature reserves; (4) moderate growth management efforts may result in development shifting to unprotected "at risk" habitats; and (5) aggressive growth management efforts can protect "at risk" habitats types without limiting overall growth in housing.

The regression model used to simulate future rural residential development was strongly influenced by factors correlated with growth during the 1990s, including past development, transportation and services, and natural amenities (Hernandez et al. 2004, Gude et al. 2006). The accuracy of the regression model was high, with the change in rural homes during the 1990s correctly predicted to plus or minus one home in 94% of the study area. This level of accuracy resulted from the spatial and temporal scale of analysis. Large-scale explanatory variables were used to accurately describe the location and density of rural residential development at the scale of 2.59 km^2 and over a period of 10 years within the GYE (Hernandez et al. 2004).

All simulated scenarios forecasted major changes in rural areas of the GYE by 2020. The percentage increase in rural homes ranged from 28% in the low-growth scenario, to 82% in the status quo scenario, to 234% in the boom scenario. The rate of increase varied substantially by county, with the highest forecasted rates occurring in counties typified as tourism and recreation destinations, as evidenced by high percentages of seasonal housing (greater than 10%; U.S. Census Bureau 2000). The distribution of forecasted homes was skewed toward towns and toward the periphery of protected areas, defined as national parks, wilderness, roadless areas, and adjacent multiple-use areas (Hernandez et al. 2004).

Homes built prior to 2000 were found to occur disproportionately in habitats important for biodiversity. Home sites occurred disproportionately in grasslands, moose range, Douglas-fir forest, potential mammal migration corridors, low-elevation aspen forest, irreplaceable areas, grizzly habitat, bird hotspots, and riparian areas. Grasslands, moose range, and riparian areas tend to occur in high-productivity areas with an agricultural history. Many GYE towns were established in areas with an agricultural history, and development continues to occur nearby (Gude et al. 2006). Douglas-fir, low-elevation aspen, grizzly habitat, potential mammal migration corridors, and bird hotspots mainly occur at the public land interface where the number of rural homes is rapidly increasing.

Home sites occurred less frequently than expected in pronghorn antelope and elk winter range. Pronghorn and elk habitats cover extensive areas of dry sagebrush flats. These areas are less productive for agriculture, where early towns were less likely to be established, and as a result, have experienced less development pressure. The flat and windy sagebrush flats may also be less appealing to prospective home buyers seeking natural amenities.

The majority of habitats considered in this study were forecasted to undergo substantial conversion to exurban development. The percentage of each biodiversity response impacted by exurban development in the future scenarios was influenced by the location of forecasted development and the percentage protected in nature reserves. In the status quo scenario, half of the biodiversity responses (low-elevation aspen, bird hotspots, riparian areas, potential mammal migration corridors, irreplaceable areas, and the integrated index) were impacted by exurban development in more than 10% of their extent. These responses tend to occur in areas of high development potential, and a significant portion of their extent is currently unprotected.

We found that future habitat conversion to exurban development outside the region's nature reserves will probably impact wildlife populations within the reserves. Highly productive lands where biodiversity is concentrated, including riparian areas, aspen stands, and bird hotspots, are underrepresented within reserves and highly impacted by exurban development. These habitats are population source areas for some species and their loss would probably increase the risk of extinction within protected areas (Hansen and Rotella 2002). Potential mammal migration corridors are likely to be vital resources for the ungulates and other large mammals that occur within the parks, and were forecasted to be among the most heavily impacted by exurban development (24%). Loss of these corridors would probably reduce gene flow and decrease long-term viability of species isolated within the protected areas of the GYE (Noss 1983, 1987, Noss and Harris 1986).

The biodiversity responses well represented (>50%) within GYE nature reserves include currently occupied grizzly habitat, Douglas-fir dominated forests, and moose range. For these elements of biodiversity, the impact of exurban development may be less severe. However, for wildlife species with large home ranges and low reproductive rates, high mortality rates in a small portion of their habitat can result in population declines

(Woodroffe and Ginsburg 1998). For example, rural development is occurring disproportionately in the parts of currently occupied grizzly habitat that occur on private lands, mainly along the border of reserves. Within these areas, food and garbage may lure bears, and interactions with humans may result in high mortality (Chris Servheen, U.S. Department of the Interior grizzly bear recovery coordinator, *personal communication*). Population-level research on the relationship between grizzlies and rural residential development is needed in order to understand how future land use intensification around nature reserves will impact grizzly populations and the populations of other wide-ranging species.

According to our simulation of rural development, moderate growth management efforts may result in development shifting to unprotected "at risk" habitats. In the moderate growth management scenario, growth management policies were implemented in only 50% of "at risk" habitats (bird hotspots, riparian, and migration corridors). According to the simulation, rural residential development was shifted to the remaining unprotected habitats. As a result, the extent of "at risk" habitats converted to exurban development in the moderate growth management scenario was comparable to the status quo scenario. If we had run the simulation farther into the future, the moderate growth management scenario probably would have outperformed the status quo scenario.

The aggressive growth management scenario presents an alternative in which growth management policies are implemented in all "at risk" habitats, which cover 58% of private lands in the GYE. Although the aggressive growth management scenario has more total forecasted homes than the low-growth scenario, it has less habitat impacted by exurban development for 50% of the response variables. This was achieved, without limiting future growth in housing, by implementing policies that encouraged growth near existing towns and limited growth within strategically located conservation easements and agricultural zoning districts. Agricultural zoning districts were used much more extensively in the aggressive growth management scenario than in the moderate growth management scenario.

Limitations and assumptions

The forecasted rate of future rural home construction was based on historical rates of rural home construction in the 1990s (Hernandez et al. 2004). Substantial changes in federal policies, the economy, or stochastic events such as natural disasters could result in future rates of rural home construction outside of the range forecasted in the alternative scenarios. Also, the effects upon the land markets of macroeconomic and sociopolitical processes, such as economic recession, the influence of baby boomer retirement, and federal agricultural subsidies, were not incorporated into the simulation.

We were unable to directly infer causation regarding the drivers of growth from the regression model of rural home construction in the 1990s. The statistical procedures used allowed us to identify the degree to which biophysical and local socioeconomic variables were correlated with growth in rural residential development; however, we were unable to establish whether the variables caused or resulted from growth.

The accuracy of forecasted development patterns was influenced by assumptions of how specific regulations would influence growth patterns. We assumed that the forecasts generated using the best regression model captured regional demand for rural housing; thus, local land use regulations were assumed to redirect, rather than cap, regional growth. When forecasted development exceeded the allowable home density as specified by a zoning district, the simulation displaced the forecasted homes into similar sections within the same local area, with similarity defined by variables from the best regression model.

In our biodiversity assessment of alternative future scenarios, we did not estimate resulting changes in survival or reproduction of specific wildlife populations. Although other studies have done this (White et al. 1997, Schumaker et al. 2004), we feel that this step should be undertaken only when sufficient data allow for meaningful predictions to be made.

Policy implications

The results from this work support the following policy recommendations: (1) policy makers can promote coordination among neighboring cities, counties, and agencies in setting regional planning goals to advance biodiversity conservation; (2) county-wide zoning and other policies that influence large areas are likely to be most effective in preserving biodiversity; and (3) policy makers can provide incentives to encourage growth near existing towns, such as streamlining subdivision processes in and around urban areas, to further protect biodiversity.

Existing growth management policies will provide minimal protection to biodiversity in the GYE. Forecasted habitat conversion to exurban development under existing conservation easements and zoning districts was as high as 30% in the status quo scenario and 40% in the boom scenario. Even moderate levels of growth management were shown to afford only minimal protection to biodiversity during the next two decades. This resulted from development pressure changing as land availability changed. For example, areas implementing growth management merely displaced rural development to other areas where growth was unmanaged. This work emphasizes the need for regional land use planning at the scale of the entire greater ecosystem. A patchwork of growth management policies may not effectively preserve biodiversity.

We found that regionally coordinated growth management efforts may be necessary to preserve biodiversity within the GYE. Importantly, we learned through simulating the aggressive growth management scenario that preservation of biodiversity can be achieved by redirecting, rather than limiting, future development. We found that incentives to encourage development near existing towns will be instrumental in preserving biodiversity.

Given that extensive amounts of land wihin the GYE are unprotected and threatened by land use intensification, policies such as zoning are needed that can affect large areas. In the aggressive growth management scenario, growth management policies were implemented in all "at risk" habitats, which cover 58% of private lands in the GYE ($\sim$27 000 km^2). Conservation easements afford a high level of protection. However, they are expensive and cannot be purchased at a rate that will guarantee the preservation of biodiversity in the GYE. An effective growth management plan could incorporate incentives to cluster future growth near towns and strategically locate zoning districts and conservation easements.

The GYE is unique in the potential for growth management to preserve biodiversity. Many of the key areas for biodiversity in the GYE remain undeveloped now and through our scenarios for 2020. However, these habitats are vulnerable to long-term future development. Population densities are currently low (7.94 people/km^2 of private land), but population growth is occurring faster than in 78% of counties in the United States (Hansen et al. 2002). In other regions of the world, researchers have documented losses in native habitats approaching 100%, largely due to land conversion (White et al. 1997, Baker et al. 2004, DeFries et al. 2007). In the GYE, several of the biodiversity responses that we measured, although threatened by future land use intensification, are currently largely intact. Counties in the GYE are at various stages of writing comprehensive growth plans, and more progressive policies such as county-wide zoning and incentives to encourage growth near towns are being considered. The opportunity exists to manage long-term future growth to balance conservation of these habitats with human needs.

Acknowledgments

We thank Patrick Hutchinson and Erin Hermanson, who helped to collect the data summarized in this article. The Montana and Wyoming Departments of Revenue, and the tax assessor offices from Clark, Fremont, Madison, Teton, Bonneville, Caribou, Franklin, and Bear Lake Counties in Idaho provided the rural homes data. Biodiversity response variables were provided by Montana Fish Wildlife and Parks, Wyoming Fish and Game, the Rocky Mountain Elk Foundation, the Greater Yellowstone Coalition, American Wildlands, the U.S. Geological Survey, and the U.S. Forest Service. We also thank Ray Rasker of Headwaters Economics, Randy Carpenter and Dennis Glick of the Sonoran Institute, and the graduate students and research associates of Montana State University's Landscape Biodiversity Laboratory for providing thoughtful support and commentary throughout the study. This research was supported by the Futures Research in Socio-Economics Program of the Environmental Protection Agency.

Literature Cited

Baker, J. P., D. W. Hulse, S. V. Gregory, D. White, J. V. Sickle, P. A. Berger, D. Dole, and N. H. Schumaker. 2004. Alternative futures for the Willamette River Basin, Oregon. Ecological Applications 14:313–324.

Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950–2000. Ecological Applications 15: 1851–1863.

Brown, K., A. J. Hansen, R. E. Keane, and L. J. Graumlich. 2006. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. Landscape Ecology 21: 933–951.

Burnham, K. P., and D. R. Anderson. 2000. Model selection and inference: a practical information-theoretic approach. SpringerVerlag, New York, New York, USA.

Craighead, J. J. 1991. Yellowstone in transition. Pages 27–40 *in* R. B. Kieter and M. S. Boyce, editors. The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Cromartie, J. B., and J. M. Wardwell. 1999. Migrants settling far and wide in the rural west. Rural Development Perspectives 14:2–8.

Dale, V., S. Archer, M. Chang, and D. Ojima. 2005. Ecological impacts and mitigation strategies for rural land management. Ecological Applications 15:1879–1892.

DeFries, R., A. J. Hansen, A. C. Newton, M. Hansen, and J. Townshend. 2005. Isolation of protected areas in tropical forests over the last twenty years. Ecological Applications 15: 19–26.

DeFries, R., A. Hansen, B. L. Turner, R. Reid, and J. Liu. 2007. Land use change around protected areas: management to balance human needs and ecological function. Ecological Applications 17:1031–1038.

Farrow, A., and M. Winograd. 2001. Land use modelling at the regional scale: an input to rural sustainability indicators for Central America. Agriculture, Ecosystems and Environment 85:249–268.

Gude, P. H., A. J. Hansen, R. Rasker, and B. Maxwell. 2006. Rates and drivers of rural residential development in the Greater Yellowstone. Landscape and Urban Planning 77: 131–151.

Hansen, A. J., and R. DeFries. 2007. Ecological mechanisms linking protected areas to surrounding lands. Ecological Applications 17:974–988.

Hansen, A. J., R. Knight, J. Marzluff, S. Powell, K. Brown, P. Hernandez, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, research needs. Ecological Applications 15:1893–1905.

Hansen, A. J., R. Rasker, B. Maxwell, J. J. Rotella, A. Wright, U. Langner, W. Cohen, R. Lawrence, and J. Johnson. 2002. Ecology and socioeconomics in the new west: a case study from Greater Yellowstone. BioScience 52:151–168.

Hansen, A. J., and J. J. Rotella. 2002. Biophysical factors, land use, and species viability in and around nature reserves. Conservation Biology 16:1–12.

Hansen, A. J., J. J. Rotella, M. L. Kraska, and D. Brown. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. Landscape Ecology 15:505–522.

Hawkins, V., and P. Selman. 2002. Landscape scale planning: exploring alternative land use scenarios. Landscape and Urban Planning 60:211–224.

Hernandez, P. C., A. J. Hansen, R. Rasker, and B. Maxwell. 2004. Rural residential development in the Greater Yellowstone: rates, drivers, and alternative future scenarios. Thesis. Montana State University, Bozeman, Montana, USA.

Huan, T., P. F. Orazem, and D. Wohlgemuth. 2002. Rural population growth, 1950–1990: the roles of human capital, industry structure, and government policy. American Journal of Agricultural Economics 84:615–627.

Keiter, R. B., and M. S. Boyce. 1991. The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Kok, K., and A. Veldkamp. 2001. Evaluating impact of spatial scale on land use pattern analysis in Central America. Agriculture, Ecosytems, and Environment 85:205–221.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. BioScience 52:883–890.

Miller, J. R., and R. J. Hobbs. 2002. Conservation where people live and work. Conservation Biology 16:330–337.

Nelson, A. 2001. Analyzing data across geographic scales in Honduras: detecting levels of organization within systems. Agriculture, Ecosytems, and Environment 85:107–131.

Noss, R. F. 1983. A regional landscape approach to maintain diversity. BioScience 33:700–706.

Noss, R. F. 1987. Protecting natural areas in fragmented landscapes. Natural Areas Journal 7:2–13.

Noss, R. F., C. Carrol, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology 16:895–908.

Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUMs: preserving diversity at all scales. Environmental Management 10:299–309.

Pressey, R. L., and R. M. Cowling. 2001. Reserve selection algorithms and the real world. Conservation Biology 15: 275–277.

Rasker, R. 1991. Dynamic economy versus static policy in the Greater Yellowstone Ecosystem. Pages 201–216 *in* Proceedings to the Conference on the Economic Value of Wilderness, Jackson, Wyoming, USA. USDA Forest Service General Technical Report SE-78.

Rodman, A., H. Shovic, and D. Thomas. 1996. Soils of Yellowstone National Park. Report Number YCR-NRSR-96-2. Yellowstone National Park, Yellowstone Center for Resources, Wyoming, USA.

Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

SAS Institute. 2001. The SAS system for Windows, release 8.02. SAS Institute, Cary, North Carolina, USA.

Schnaiberg, J., J. Riera, M. G. Turner, and P. R. Voss. 2002. Explaining human settlement patterns in a recreational lake district: Vilas County, Wisconsin, USA. Environmental Management 30:24–34.

Schneider, L. C., and R. G. Pontius, Jr. 2001. Modeling land-use change in the Ipswich watershed, Massachusetts, USA. Agriculture, Ecosytems, and Environment 85:83–94.

Schumaker, N., T. Ernst, D. White, J. Baker, and P. Haggerty. 2004. Projecting wildlife responses to alternative future landscapes in Oregon's Willamette Basin. Ecological Applications 14:381–400.

Schwartz, C. C., M. A. Haroldson, K. A. Gunther, and D. Moody. 2002. Distribution of grizzly bears in the Greater Yellowstone Ecosystem, 1990–2000. Ursus 13:203–212.

Scott, J. M., F. Davis, B. Csuti, R. F. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T. C. Edwards, J. Ulliman, Jr., and R. G. Wright. 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123:1–41.

Serneels, S., and E. F. Lambin. 2001. Proximate causes of land-use change in Narok District, Kenya: a spatial statistical model. Agriculture, Ecosytems, and Environment 85:65–81.

Swenson, J. J., and J. Franklin. 2000. The effects of future urban development on habitat fragmentation in the Santa Monica Mountains. Landscape Ecology 15:713–730.

Theobald, D. M., and N. T. Hobbs. 2002. A framework for evaluating land use planning alternatives: protecting biodiversity on private land. Conservation Ecology 6(1):5. ⟨http://www.ecologyandsociety.org/vol6/iss1/art5/⟩

Theobald, D. M., N. T. Hobbs, T. Bearly, J. Zack, T. Shenk, and W. E. Riebsame. 2000. Incorporating biological information into local land-use decision making: designing a system for conservation planning. Landscape Ecology 15: 5–45.

Theobald, D. M., T. Spies, J. Kline, B. Maxwell, N. T. Hobbs, and V. H. Dale. 2005. Ecological support for rural land-use planning. Ecological Applications 15:1906–1914.

U.S. Census Bureau. 2000. Profile of general demographic characteristics: 2000. U.S. Census Bureau, Washington, D.C., USA.

Van Sickle, J., J. Baker, A. Herlihy, P. Bayley, S. Gregory, P. Haggerty, L. Ashkenas, and J. Li. 2004. Projecting the biological condition of streams under alternative scenarios of human land use. Ecological Applications 14:368–380.

Verburg, P. H., G. H. J. Koning, K. Kok, A. Veldkamp, and J. Bouma. 1999*a*. A spatially explicit allocation procedure for modeling the pattern of land use change based on actual land use. Ecological Modelling 116:45–61.

Verburg, P. H., T. A. Veldkamp, and J. Bouma. 1999*b*. Land use change under conditions of high population pressure: the case of Java. Global Environmental Change 9:303–312.

Walker, R., and L. Craighead. 1997. Least-cost-path corridor analysis: analyzing wildlife corridors in Montana using GIS. *In* Proceedings for the 1997 ESRI User's Conference, San Diego, California, USA. ⟨http://gis.esri.com/library/userconf/proc97/proc97/to150/pap116/p116.htm⟩

Walsh, S. E., P. A. Soranno, and D. T. Rutledge. 2003. Lakes, wetlands, and streams as predictors of land use/cover distribution. Environmental Management 31:198–214.

White, D., P. G. Minotti, M. J. Barczak, J. C. Sinfneos, K. E. Freemark, M. V. Santelmann, C. F. Steinitz, A. R. Kiester, and E. M. Preston. 1997. Assessing risk to biodiversity from future landscape change. Conservation Biology 11:349–360.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280: 2126–2128.