



Promoting the Science of Ecology

The Human Footprint in the West: A Large-Scale Analysis of Anthropogenic Impacts

Author(s): Matthias Leu, Steven E. Hanser, Steven T. Knick

Reviewed work(s):

Source: *Ecological Applications*, Vol. 18, No. 5 (Jul., 2008), pp. 1119-1139

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/40062217>

Accessed: 21/03/2012 14:15

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecological Applications*.

<http://www.jstor.org>

THE HUMAN FOOTPRINT IN THE WEST: A LARGE-SCALE ANALYSIS OF ANTHROPOGENIC IMPACTS

MATTHIAS LEU,¹ STEVEN E. HANSER, AND STEVEN T. KNICK

*U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk Street,
Boise Idaho 83706 USA*

Abstract. Anthropogenic features such as urbanization, roads, and power lines, are increasing in western United States landscapes in response to rapidly growing human populations. However, their spatial effects have not been evaluated. Our goal was to model the human footprint across the western United States. We first delineated the actual area occupied by anthropogenic features, the physical effect area. Next, we developed the human footprint model based on the ecological effect area, the zone influenced by features beyond their physical presence, by combining seven input models: three models quantified top-down anthropogenic influences of synanthropic predators (avian predators, domestic dog and cat presence risk), and four models quantified bottom-up anthropogenic influences on habitat (invasion of exotic plants, human-caused fires, energy extraction, and anthropogenic wildland fragmentation). Using independent bird population data, we found bird abundance of four synanthropic species to correlate positively with human footprint intensity and negatively for three of the six species influenced by habitat fragmentation. We then evaluated the extent of the human footprint in relation to terrestrial (ecoregions) and aquatic systems (major rivers and lakes), regional management and conservation status, physical environment, and temporal changes in human actions. The physical effect area of anthropogenic features covered 13% of the western United States with agricultural land (9.8%) being most dominant. High-intensity human footprint areas (class 8–10) overlapped highly productive low-elevation private landholdings and covered 7% of the western United States compared to 48% for low-intensity areas (class 1–3), which were confined to low-productivity high-elevation federal landholdings. Areas within 1 km of rivers were more affected by the human footprint compared to lakes. Percentage human population growth was higher in low-intensity human footprint areas. The disproportional regional effects of the human footprint on landscapes in the western United States create a challenge to management of ecosystems and wildlife populations. Using footprint models, managers can plan land use actions, develop restoration scenarios, and identify areas of high conservation value at local landscapes within a regional context. Moreover, human footprint models serve as a tool to stratify landscapes for studies investigating floral and faunal response to human disturbance intensity gradients.

Key words: *abiotic interaction; anthropogenic disturbance; ecological human footprint; human footprint; human population growth; landscape management; land stewardship; physical human footprint; western United States.*

INTRODUCTION

Landscapes within the western United States have drastically changed over the past century. Historically, the impact by native peoples on these landscapes was minimal and localized (Vale 2002). In contrast, high demands for natural resources by European settlers greatly influenced wildlands (unsettled land containing human habitations widely dispersed across large extents; Marzluff et al. 2001). Fluctuating natural commodity markets and availability of natural resources has defined contemporary human land use patterns both in time and space. Human modifications in the area encompassed by

the states of Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming have steadily expanded over the past three decades (for review see Hansen et al. 2002, Maestas et al. 2003). Today, human land use patterns are characterized by expanding human populations into rural and exurban areas often exceeding human population growth of urban areas (for review see Knight et al. 1995b, Odell et al. 2003, Hansen et al. 2005). As a consequence, western ecosystems are affected by an increasing suite of anthropogenic features, such as roads, power lines, and other infrastructure necessary to maintain these human populations.

The extent of the impacts of human presence and actions are collectively delineated as the “human footprint” (Janzen 1998, Sanderson et al. 2002). The human footprint may influence ecosystems directly by anthropogenic actions that induce land cover change

Manuscript received 20 March 2007; revised 19 September 2007; accepted 18 December 2007; final version received 22 January 2008. Corresponding Editor: D. D. Breshears.

¹ E-mail: mleu@usgs.gov

(Meyer and Turner 1992) or indirectly by actions that degrade ecosystem functions (Noss et al. 1995). Both direct and indirect changes may be facilitated via "top-down processes," "bottom-up processes," or both (Bolger 2001, Sinclair and Krebs 2002). Humans influence top-down processes, for example, via global climate change (Vitousek 1992, Vitousek et al. 1997), or bottom-up processes by disrupting abiotic processes, such as nutrient cycling (Shugart 1998). Considering wildlife population regulation, human induced top-down processes occur directly via the introduction of exotic predators (Alterio et al. 1998, Harding et al. 2001). Indirectly, the addition of anthropogenic resources facilitates the expansion of synanthropic predators (predators benefiting from anthropogenic resources and land actions; Johnston 2001), into habitats where they, in the absence of anthropogenic features, are either found only at low densities or not at all (Restani et al. 2001, Kristan and Boarman 2003, DeLap and Knight 2004). In both scenarios, synanthropic predators disrupt native community processes by increasing rates of "incidental predation" (Schmidt et al. 2001) in which food-subsidized predators prey on animal populations even when prey populations are at very low numbers (Sinclair et al. 1998, Kristan and Boarman 2003). Bottom-up processes may occur directly via wildland loss or conversion, or indirectly by altered disturbance regimes following the introduction of exotic plants. Exotic plant invasions, even in communities still dominated by native plants, potentially initiate synergistic processes. For example, fire regimes can be altered to such a degree that resultant postfire plant communities are dominated by exotic plants (D'Antonio and Vitousek 1992, Vitousek et al. 1996, Mack and D'Antonio 1998). Understanding how bottom-up processes influence habitat loss/change is important because habitat loss (85%) and introduction of nonindigenous species (49%) are the most influential factors affecting species endangerment in the United States (Wilcove et al. 1998).

Recent advances in satellite imagery analysis and geographic information systems allow the evaluation of anthropogenic actions at various scales. This is reflected in an increase in recent human footprint models, which incorporate proxies for human disturbance such as "population density, land transformation, accessibility, and electrical power infrastructure" worldwide (Sanderson et al. 2002), road distance within the conterminous United States (Riitters and Wickham 2003), management status—land use, human population growth, and road effect size within California (Stoms 2000), extent of oil and gas development within Wyoming (Weller et al. 2002), spatial effects of public land use on fish and wildlife species in Montana (Schumacher et al. 2000), and the wildland—urban interface based on housing densities (Radeloff et al. 2005) or population census (Martinuzzi et al. 2007). However, spatial models evaluating the human footprint for the western United

States, to the best of our knowledge, have not been accomplished to date and existing models have not evaluated output predictions.

Our first objective was to model the human footprint across the western United States based on spatial data sets representing the extent of anthropogenic features. In developing the human footprint model, we first delineated the physical effect area of anthropogenic features (the actual area occupied by anthropogenic features) to estimate the extent of each anthropogenic feature as well as their cumulative effect. We then used these physical effect area models in the development of the human footprint model. Our model was a summation of seven standardized input models (Fig. 1) of which three delineated ecological effect areas (the area influenced by anthropogenic features beyond the physical effect area) influenced by top-down processes (avian predators, domestic dog and house cat presence risk), and four by bottom-up processes (invasion of exotic plants, human-caused fires, energy extraction, and fragmentation model). The number of input models included in our human footprint model reflected the availability of regional or continental spatial data sets delineating human actions (Stoms 2000). For example, spatial data sets on grazing allotment stocking rates and CO₂ emissions were not available. Consequently, we could not model livestock grazing (Fleischner 1994, Freilich et al. 2003) or delineate exotic plant invasion based on air pollution (Weiss 1999, Smith et al. 2000).

Our second objective was to evaluate the results of the human footprint model using bird population trends. Using Breeding Bird Survey (BBS) data (Sauer et al. 2005), a long-term survey of avian populations across the United States, we selected four species that differed in their degree of synanthropy: (1) positively regulated by anthropogenic resources ("full synanthrope with humans"), (2) exploiting anthropogenic resources but are not regulated by them ("casual synanthrope with humans"), and (3) sporadically exploiting anthropogenic resources ("tangential synanthrope with humans") (Johnston 2001). For species that respond negatively to human actions, we selected six species that differed in breeding habitat requirements and response to fragmentation.

Our third objective was to apply the human footprint model to land use planning and policy. First, we evaluated the human footprint extent among terrestrial systems, using The Nature Conservancy (TNC) ecoregions (Nature Conservancy 2001), and aquatic systems using the 11 longest rivers and seven largest lakes of the western United States, to provide a regional context within which land managers can develop priorities at the local scale. Second, we assessed management and conservation status across the human footprint intensity gradient, such as land ownership, roadless status (U.S. Forest Service Roadless Area Conservation), and protection status (Gap Analysis Program stewardship status). These types of analyses will enhance the

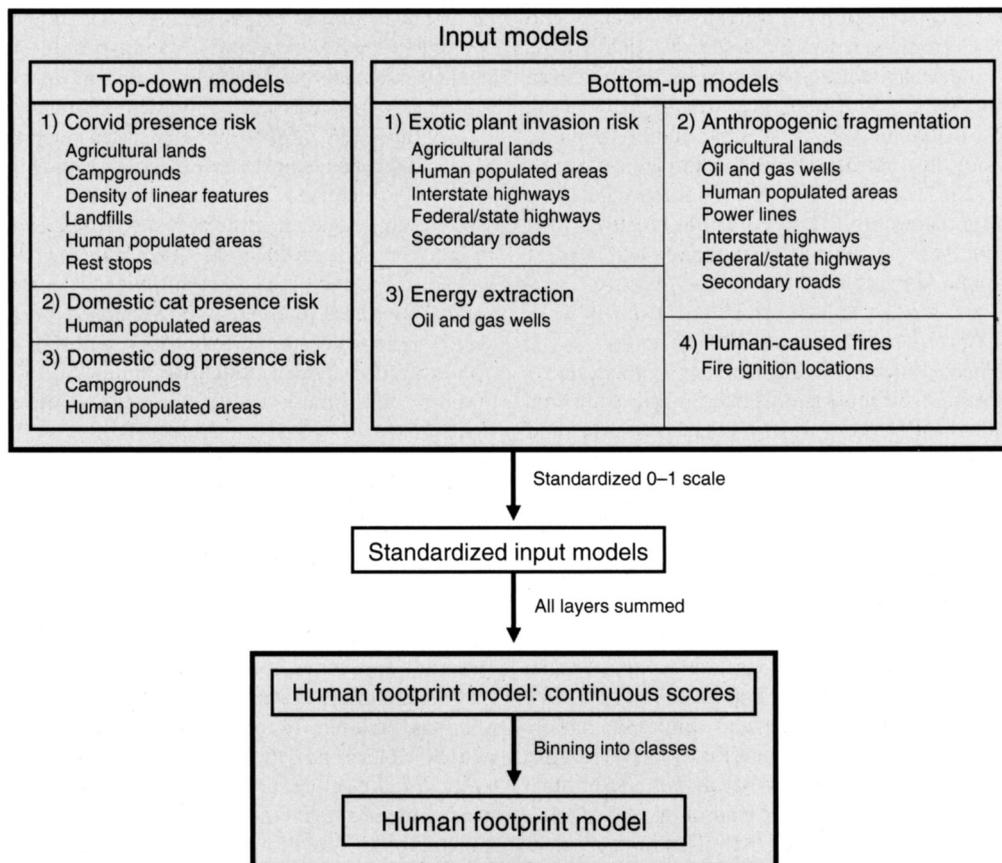


FIG. 1. Schematic representation of the human footprint modeling approach. Shown are spatial data sets used to develop input models (density of linear features = federal and state highways, interstate highways, irrigation canals, power lines, railroads, and secondary roads; see Appendix A) and steps incorporated to standardize input models in the development of the human footprint model.

planning of ecologically and economically feasible strategies for new activities on public lands, such as wind energy development or wildland restoration. Third, because biological productivity relates to biodiversity (Scott et al. 2001, Hansen et al. 2002), we compared the human footprint intensity with physical environment gradients (i.e., topographic accessibility, aboveground productivity, and belowground productivity). Last, to examine spatial trends of human actions, we evaluated human population change between 1990 and 2000, a proxy for anthropogenic action intensity, across the human footprint intensity gradient. Similar analyses at smaller scales will aid planners to evaluate, for example, how adding low-density housing zoning to an area will affect dispersal matrices as well as breeding and wintering habitats for wildlife species. All spatial data sets used in the development of the human footprint are accessible to the public on the SAGEMAP PROJECT web site.²

² (<http://sagemap.wr.usgs.gov>)

METHODS

All spatial analyses presented in this paper were performed in Arc/INFO 8.3 and ArcMap 8.3 (ESRI 1998).

Physical effect area of anthropogenic features

We used three types of anthropogenic features to model the physical human footprint: (1) points (e.g., campgrounds, landfills), (2) linear features (e.g., roads, irrigation canals), and (3) polygons (e.g., agricultural land and urban areas). To estimate the spatial extent of four point features, we multiplied each feature by the average physical effect area estimated from published data (Appendix A) for campgrounds, landfills, and oil-gas wells. We determined the rest stop physical effect area at three locations in Nevada and Idaho using a global positioning system (Garmin Etrex Venture; Garmin, Olathe, Kansas, USA). To calculate the physical effect area for linear features, we multiplied the total length by the average width of each anthropogenic feature. Because data on physical effect area of many linear anthropogenic features were scarce (but see

Ingelfinger and Anderson 2004), we determined the average width (to the nearest 0.1 m) for irrigation canals, interstate highways, power lines, railroads, state and federal highways, and secondary roads at various locations in the states of Idaho and Nevada (Appendix A). Last, for polygon features we used the United States Census Bureau 2000 data (U.S. Census Bureau 2000) to delineate populated areas (≥ 1 person/ha) and various spatial data sources to delineate agricultural areas (Appendix A).

Human footprint model: input models

The human footprint model was a summation of seven input models, three modeling top-down anthropogenic influences of synanthropic predators and four modeling bottom-up anthropogenic influences on habitat (Fig. 1).

Top-down models.—The corvid presence risk model predicted the distribution of synanthropic avian predators (American Crow [*Corvus brachyrhynchos*], Black-billed Magpie [*Pica hudsonia*], and Common Raven [*C. corax*]). Understanding the spatial distribution of these predators is important because common raven populations have increased nationwide between 1966 and 2004 (Sauer et al. 2005) and corvids affect wildlife population regulation negatively, directly via predation (Weidinger 2002, Kristan and Boarman 2003, Manzer and Hannon 2005), or indirectly via habitat avoidance by prey species near corvid nests (Roos and Pärt 2004). The distribution of corvid populations is positively influenced by power lines, which provide nesting platforms (Gilmer and Wiehe 1977, Steenhof et al. 1993), hunting perches (Knight and Kawashima 1993), and roost sites (Engel et al. 1992). Corvids also benefit from linear anthropogenic features that facilitate movements into previously unused regions (Knight et al. 1995a). In addition, rural human developments (Tewksbury et al. 1998), urbanization (Kristan and Boarman 2007), campgrounds (Neatherlin and Marzluff 2004, Marzluff and Neatherlin 2006), landfills (Kristan et al. 2004), and roads (Case 1978, Rolley and Lehman 1992, Knight and Kawashima 1993) provide reliable and often highly abundant food sources. The corvid presence risk model integrated six anthropogenic features (Fig. 1). To delineate the ecological effect area, we buffered anthropogenic resources by a probability function derived from daily movement patterns of common ravens and American crows ($P = 100 - 100 / (1 + \exp(5 - 0.3 \text{distance}))$; Appendix B) and summed probability values across all grid cells.

The domestic mammalian predator presence risk model predicted wildland use of house cats (*Felis silvestris catus*) and domestic dogs (*Canis lupus familiaris*). Domestic cat ownership has increased in the United States over the past decades (for review see Coleman and Stanley 1993, Knight et al. 1995b), and the rate at which domestic predators use wildlands has increased in exurban areas (development at the wildland ecotone; Marzluff et al. 2001), because of accelerated

land conversion (Knight et al. 1995b, Odell and Knight 2001, Maestas et al. 2003). Domesticated predators influence wildlife populations by means of predation (Parmalee 1953, Eberhard 1954, Lowry and McArthur 1978, Scott and Morrison 1990, Alterio et al. 1998) and/or disturbance/harassment (Sime 1999, Miller et al. 2001). To delineate the ecological effect area, we buffered anthropogenic resources ($n_{\text{Cats}} = 1$; $n_{\text{Dogs}} = 2$; Fig. 1) using linear occurrence functions ($P_{\text{Cats}} = 0.216 - (0.96 \text{distance})$, $P_{\text{Dogs}} = 0.548 - (1.4589 \text{distance})$; Appendix B) where intercepts approximated probabilities for a homeowner to possess either a house cat or a domestic dog (Odell and Knight 2001). The final domestic dog model was merged by selecting the maximum probability value in grid cells.

Bottom-up models.—The exotic plant invasion risk model predicted the potential spread of exotic plants according to proximity to anthropogenic features. For example, roads may directly promote exotic plant establishment via vehicle dispersal (Schmidt 1989) or disturbance during road construction and maintenance (Tyser and Worley 1992, Forman and Alexander 1998, Parendes and Jones 2000, Safford and Harrison 2001). In Californian serpentine soil ecosystems several exotic plant species were found up to 1 km from the nearest road (Gelbard and Harrison 2003), and Russian thistle (*Salsola kali*), an exotic forb growing along roads, was wind-dispersed over distances > 4 km (Stallings et al. 1995). Roads may also indirectly promote exotic plant establishment via seeding along road verges or in disturbed areas near roads as a management strategy to control the establishment of less desirable exotic grass species (Evans and Young 1978). Last, human populated areas (Hayden Reichard et al. 2001) and agricultural areas (Vitousek et al. 1996) act as conduits of exotic plant invasion. The exotic plant invasion risk model included five anthropogenic features (Fig. 1) and three exotic plant invasion risk classes: low, medium, and high. For the human populated areas and agricultural land cover we assigned a high-risk value only to those grid cells within the physical effect area because presence of invasive exotic plants varies both spatially and temporally (fallow vs. planted fields). For roads, we modeled the ecological effect area according to differences in exotic plant establishment potential in relation to road type (Parendes and Jones 2000, Gelbard and Belnap 2003), distance from road (Gelbard and Belnap 2003), and ecosystem type (forested vs. non-forested; Parendes and Jones 2000). In forested ecosystems, we modeled exotic plant invasion risk using the road physical effect area and exotic plant invasion risk according to road type: interstate highways, 270 m (high); federal and state highways, 90 m (high); and secondary roads, 90 m (medium). In non-forested ecosystems we modeled exotic plant invasion risk according to the same scheme, but with secondary road exotic plant invasion risk elevated to high and additional ecological effect areas: buffer 90 m (medium), buffer

90–1000 m (low), >1000 m = absent. The final model was merged by selecting the maximum probability value across grid cells.

With the increasing demand on domestic energy (Bay 1989) and favorable oil and gas markets, many areas in the western United States are exposed to accelerated energy extraction (Braun et al. 2002, Knick et al. 2003). This land transformation occurs primarily in wildlands (Weller et al. 2002), increases the human footprint because of infrastructure associated with wells (i.e., well pad, roads, and power lines; Braun et al. 2002), and potentially influences wildlands indirectly via establishment of exotic plants, or directly via loss of wintering and breeding habitat for wildlife (Berger 2003, Lyon and Anderson 2003, Walker et al. 2007) and development of migration barriers for ungulates (Berger 2004). Because associated infrastructures of oil and gas development were poorly mapped and limited to a few disjunct areas, we modeled the spatial extent of active and inactive oil and gas development (Fig. 1) by calculating well-point densities within a circle of 1 km radius.

The anthropogenic wildland fragmentation model delineated percentage wildland (Fig. 1). The addition of roads, railroads, or power lines to wildlands, and the conversion of wildlands to agricultural land and/or urban areas, singly or collectively, transforms wildland-dominated landscapes into regions in which matrices, depending on the degree of anthropogenic disturbance, vary from suitable to unsuitable for wildlife habitat use and from permeable to impermeable to wildlife dispersal. The transformation of wildland-dominated landscapes benefited synanthropic species, ~25% of North American birds species (Johnston 2001), but negatively influenced population regulation and faunal diversity of native species (Bolger et al. 1997a, b, Bakker and Van Vuren 2004). To develop the anthropogenic fragmentation model, we included the physical effect area for human populated areas, agricultural land, and secondary roads. We applied ecological effect areas of 1 km to interstate highways (maximum effect area, 1.5 km; GLOBIO 2002), 0.5 km to state–federal highways (grizzly bears [*Ursos arctos*] avoid habitat within 0.5 km from state highways; Waller and Servheen 2005), railroads (GLOBIO 2002), and power lines (Vistnes and Nellemann 2001). We combined the ecological effect area data sets and performed a moving window analysis to calculate percentage of cells occupied by one of the seven anthropogenic features within a 54.5-km quadrat (analysis window: 303 × 303 cells, area = 2975 km²). The moving window area approximates the home range of far-ranging wildlife susceptible to anthropogenic disturbance: grizzly bear (McLoughlin et al. 2003, Apps et al. 2004, Waller and Servheen 2005), female wolverine (*Gulo gulo*; Banci and Harestad 1990), or the extreme home range of a migratory Greater Sage-Grouse (*Centrocercus urophasianus*; Connelly et al. 2000).

Human-caused fires burned 45% of the total area burned (17 826 km²) within the United States in 2006

(NIFC 2007). Furthermore, fire frequency and size are influenced by housing density, tending to be highest at intermediate levels of human actions (Syphard et al. 2007). Human-caused fires have, in addition to wildfires, the potential to maintain systems dominated by exotic plants and to initiate a positive feedback loop between exotic grass invasion and changes in fire frequency (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998). Resultant plant communities postfire may not support avifauna typically found during prefire conditions (Saab and Powell 2005). Because the spatial extent (i.e., the patch size of each fire) of human-caused fires between 1986 and 2001 was not consistently available among years and across the western United States, we modeled fire ignition density within a circle of 1-km radius.

Human footprint model

Because we did not have a priori knowledge about the relative influence of each anthropogenic resource on ecological processes, we weighted each input model equally during human footprint model development. However, anthropogenic features differed in the frequency in which they were included in the seven input models and thus in their relative weighting in the overall footprint model (Fig. 1). For example, human populated areas were included five times, roads and agricultural lands three times, and all other anthropogenic features were included only once.

To develop the human footprint model, we first resampled six of the seven input models from a 90-m to a 180-m cell size to standardize the resolution to the coarsest layer, the anthropogenic wildland fragmentation model (computing power prevented us from an analysis based on 90-m resolution). We then standardized each model between 0 and 1 by dividing each model by its maximum value (Fig. 1) and summed grid values (Sanderson et al. 2002) of each standardized input model to develop the human footprint model (Fig. 1). Last, we classified our model into 10 classes (range of unclassified values, 0.0009–5.18) ranging from class 1 (human footprint influence negligible) to class 10 (human footprint influence high). We explored various classifying schemes each of which we evaluated against the human footprint gradient around Boise, Idaho. The most parsimonious classification scheme, dividing the continuous human footprint into equal bin sizes, was rejected because of poor performance predicting the extent of the high-intensity human footprint classes. We therefore adopted a hybrid classification system by implementing equal bin ranges for the first nine classes and lumping all values >3 into human footprint class 10 (score 1, 0–0.333; 2, 0.334–0.666; 3, 0.667–1.000; 4, 1.001–1.333; 5, 1.334–1.666; 6, 1.667–2.000; 7, 2.001–2.333; 8, 2.334–2.666; 9, 2.667–3.000; 10, >3.000). Reference locations for each human footprint class are: Class 1, Yellowstone National Park, Death Valley National Park, and the crest of the Sierra Nevada

Mountains; 2, Mount Rainier National Park; 3, Rocky Mountain National Park and the Mount Shasta area in California; 4, Oregon's Columbia River Gorge; 5, foothills west of Boulder, Colorado; 6, Bitterroot Valley south of Missoula, Montana; 7, Salinas Valley, California; 8, agricultural areas in the Snake River Plain, Idaho and Napa Valley, California; 9, agricultural areas near Kennewick, Washington; 10, Los Angeles, California, Boise, Idaho, and agricultural areas south of Fresno, California.

To investigate the spatial patterns of human footprint classes (resampled to 540-m resolution) we used a contagion analysis (Turner 1989, Riitters et al. 1996), a measure of "clumping," which determines probabilistic adjacency of human footprint class cells. We calculated contagion values in FRAGSTATS (McGarigal et al. 2002) for cumulative footprint classes, starting with human footprint classes 1 and 2.

Evaluation of the human footprint model results

We evaluated the human footprint model results (for input model evaluation see Appendix C) with Breeding Bird Survey data (BBS; Sauer et al. 2005), the only large-scale long-term data set available. We tested whether the distribution of 10 songbird species correlated with human footprint intensity. Species included in the analyses were either synanthropic species or species affected by anthropogenic fragmentation. We selected four species with varying degrees of synanthropy (Johnston 2001): (1) "full synanthrope with humans," House Sparrow (*Passer domesticus*); (2) "casual synanthrope with humans," House Finch (*Carpodacus mexicanus*); and (3) "tangential synanthrope with humans," Bullocks' Oriole (*Icterus bullockii*) and Western Kingbird (*Tyrannus verticalis*) (M. Leu, *personal observation*). For these species we predicted positive correlations between abundance indices and human footprint impact classes. We selected six species responding to anthropogenic habitat fragmentation that differed in breeding habitat, forested vs. shrubland, and conservation status, Partners in Flight (PIF) status (Rich et al. 2004). The forest ecosystem species included the Brown Creeper (*Certhia americana*) and Winter Wren (*Troglodytes troglodytes*), both edge-sensitive species (Brand and George 2001), and two wood-warbler species, both included on the PIF watch list (Rich et al. 2004), that differed in their breeding range: the Hermit Warbler (*Dendroica occidentalis*) breeding west of the Cascade Range and Sierra Nevada (Pearson 1997) and the Grace's Warbler (*Dendroica graciae*) breeding in the southwestern United States (Stacier and Guzy 2002). For shrubland ecosystem species, we selected the Sage Sparrow (*Amphispiza belli*), an area-sensitive species (Knick and Rotenberry 1995) and the Brewer's Sparrow (*Spizella breweri*), both included on the PIF list (Rich et al. 2004). For these six species, we predicted negative correlations between abundance indices and human footprint classes.

To derive the mean human footprint class per BBS route, we buffered each route by 400 m (the distance over which birds are sampled on routes; Sauer et al. 1994). Because breeding ranges differ among species, we included only routes on which a species was detected at least once between 1968 and 2003. To overcome biases associated with BBS data (Geissler and Sauer 1990, Sauer et al. 1994, Kendall et al. 1996), we developed a detection index based on the number of years a species was detected between 1994 and 2003 and included only those routes that were sampled at least seven times during this period. We transformed percentage years detected (square-root arcsine; Zar 1984) and used Pearson's correlations to test whether detection indices and mean route-level human footprint scores correlated (we used $P \leq 0.05$ as the level of significance).

Human footprint extent in the western United States

Ecoregions and water resources.—Because historical human settlements often evolved near rivers and lake shores (Marzluff 2001), we evaluated human footprint intensity across (1) terrestrial systems using 31 Nature Conservancy ecoregions (Nature Conservancy 2001; Appendix A), and (2) aquatic systems using the 11 longest rivers and seven largest lakes of the western United States (ESRI Streetmap USA database; ESRI 2006). We derived the total effect area of each human footprint class for each ecoregion and within 1-km buffers surrounding rivers and lake shores.

Management and conservation status.—Within the western United States, management practices and intensities vary among land stewards (Shen 1987, Scott et al. 2001). We evaluated how human footprint intensity, extent, and mean topographic accessibility, expressed as deviation from valley floor (defined in the next subsection) varied among land stewards. To further investigate management practices, we evaluated human footprint intensity in relation to three U.S. Forest Service roadless categories differing in the degree of wilderness designation and road building activities (see Appendix A). Last, because area of unaltered habitat has a profound effect on ecological processes and wildlife population viability (Noss et al. 1995), we created four cumulative maps of the four lowest human footprint impact areas (human footprint class 1–4) and evaluated for each the extent of the National Gap Stewardship protection status (Appendix A) and land ownership.

Physical environment.—Historically, humans settled at low elevations on land readily converted for agricultural uses (Marzluff 2001). We evaluated the human footprint intensity gradient in relation to a topographic accessibility index, a measure of elevation in relation to valley floor corrected for variation in valley floor elevation across the western United States (i.e., valley floor elevation at California's coast is much lower compared to a valley floor in Wyoming). This index was based on 90-m resolution digital elevation

model grids (DEM; National Elevation Dataset, USGS EROS [Earth Resources Observation Systems]),³ and a landform model of the western United States (Manis et al. 2001), which delineates valley flats and near level plateaus or terraces (cell values, 1 or 4). We reclassified the landform model (cell value, 1) and multiplied this layer by the DEM to derive valley floor elevation. Using a moving window analysis (303 × 303 cells; 743.65 km²), we computed mean regional valley floor elevations and subtracted them from the DEM, to derive the difference between the local elevation and regional valley floor elevation. Second, we evaluated the human footprint intensity gradient with aboveground biological productivity. We developed a mean normalized difference vegetation index (NDVI; Rouse et al. 1974) over the interval between 1989 and 2001 using AVHRR (advanced very high resolution radiometer; USGS EROS Data Center) yearly mean NDVI values. NDVI is a greenness index that correlates highly with “aboveground biomass” (Boelman et al. 2003) or annual aboveground primary production (Paruelo et al. 1997). Using annual mean NDVI values circumvents the potential bias introduced by agricultural land that inflates NDVI values in arid ecological systems during periods when noncultivated plants senesce. Third, we compared belowground productivity with the human footprint intensity gradient. Soil depth determines suitability to farming and has been correlated positively with songbird abundance for species breeding in arid shrublands (Vander Haegen 2000). We obtained soils data from the National Resource Conservation Service (NRCS) State Level Soil Geographic (STATSGO) database (STATSGO 2003). The soil depth in the spatial data set was calculated based on the “ROCKDEP” attribute in the STATSGO COMP database, and the final value was the sum of weighted rock depth for all sequential numbers within each map unit identifier (MUID).

To investigate changes in the three physical environments in relation to the human footprint, we randomly selected 64980 cells (0.07% of possible cells) from the human footprint extent to avoid spatial autocorrelations, and determined for each cell the value of the three physical environmental factors. Because large sample sizes result in inflated degrees of freedom, we examined 95% confidence intervals to evaluate differences among human footprint classes.

Temporal changes in human actions.—Because the human footprint model represents a snapshot of anthropogenic actions between 1998 and 2001, we investigated how anthropogenic actions changed both temporally and spatially. Given that a time series of spatial data sets were required to investigate such changes, a time-consuming and costly endeavor, we used a proxy for changes in anthropogenic actions by

evaluating differences in human population size across the human footprint intensity gradient between 1990 and 2000 using United States Census block group data (U.S. Census 2000). We calculated the mean human population density for each human footprint class in each decade. We avoided a pixel-based analysis because census block boundaries changed between 1990 and 2000, and therefore a change in human population at a given pixel could have been the result of changes in census block delineation.

RESULTS

Physical effect area of anthropogenic features

The cumulative physical effect area of 12 anthropogenic features covered 13% (402 000 km²) of the western United States (Fig. 2). The majority of the physical effect area was dominated by agricultural land (9.8%), populated areas (1.9%), and secondary roads (1.1%); interstate rest stops were the least influential (0.003%).

Human footprint model

The majority of the western United States (for results of input models see Appendix C) was dominated by low-intensity human footprint classes 1–3 (48%), followed by the medium-intensity classes 4–7 (45%), and least by the high-intensity classes 8–10 (7%) (Fig. 3). The human footprint intensity varied spatially with high-intensity areas radiating from major urban areas (e.g., Denver, Los Angeles, and Seattle) and areas suitable for agriculture (Central Valley in California, Willamette Valley in Oregon, Columbia Plateau and Puget Trough in Washington, Snake River Plain in Idaho, the Eastern Plains of Colorado and Montana). Low-intensity areas were within National Parks, Wilderness Areas, and Department of Defense installations located in the southwestern United States, but also in the Owyhee region of southeastern Oregon and northwestern Nevada.

Patch configuration of human footprint classes followed a concave distribution (Fig. 4). Aggregated patches (high contagion values) occurred in the low-intensity human footprint class 1 (matrix dominated by wildland) and high-intensity classes 8–10 (matrix dominated by human footprint). Highly fragmented human footprint classes (lowest contagion values) occurred in the most common human footprint classes by area (classes 2–5, land cover ranging from 12.6% to 25.6%; Fig. 3).

Evaluation of the human footprint model results

As predicted, the four synanthropic species showed significant positive correlations between detection indices and mean human footprint class scores (Appendix D: Fig. D1 [panel A]): House Sparrow ($r = 0.54$, $P < 0.0005$, $n = 305$ BBS routes), House Finch ($r = 0.34$, $P < 0.0005$, $n = 416$), Western Kingbird ($r = 0.35$, $P < 0.0005$, $n = 423$), and Bullock's Oriole ($r = 0.23$, $P <$

³ (<http://seamless.usgs.gov/>)

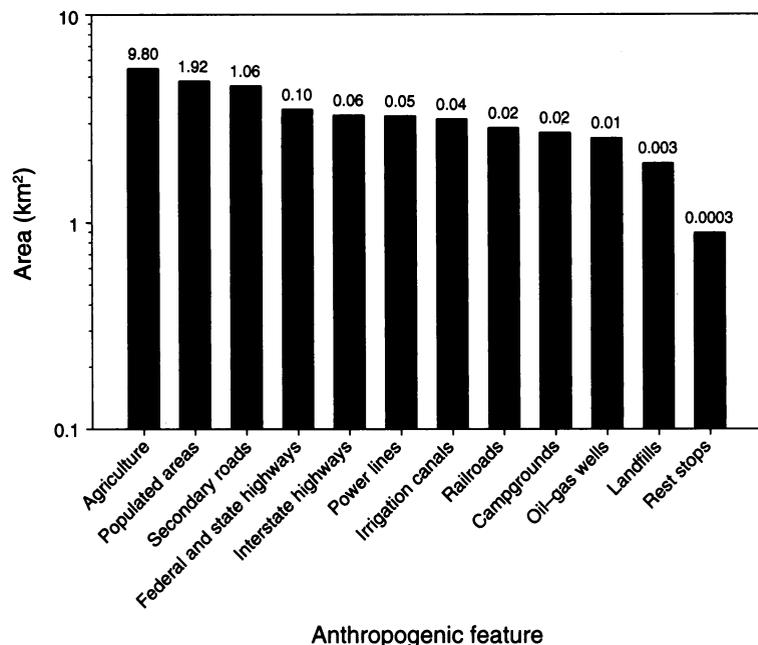


FIG. 2. The physical effect area for 12 anthropogenic features, sorted from highest to least effect area, and physical effect area as a percentage of total area within the western United States (values above bars). Note log scale.

0.0005, $n = 423$). For the six species for which we predicted negative correlations between detection indices and human footprint class (Appendix D: Fig. D1 [panels B and C]), we found a significant negative correlation for the Brown Creeper ($r = -0.17$, $P = 0.02$, $n = 180$ BBS routes), Hermit Warbler ($r = -0.39$, $P = 0.001$, $n = 68$), and Sage Sparrow ($r = -0.18$, $P = 0.02$, $n = 173$), but not for the Brewer's Sparrow ($r = -0.02$, $P = 0.72$, $n = 307$), Grace's Warbler ($r = -0.17$, $P = 0.31$, $n = 33$), or the Winter Wren ($r = 0.04$, $P = 0.71$, $n = 114$).

Human footprint extent in the western United States

Terrestrial systems.—Of the 31 TNC ecoregions, 61.3% had less land (range, 0–3.9%) within the low-intensity human footprint class 1 compared to the human footprint of the western United States (5.5%); of those 19 ecoregions, five (number 1–5, Fig. 5) had no land at all in class 1. Of the 12 ecoregions with more land (range, 5.6–14.6%) in human footprint class 1 compared to the human footprint of the western United States, five (number 27–31, Fig. 5) had >10% of their land cover within class 1. Ecoregions with <1% land in human footprint class 1 were west of the Cascade-Sierra Nevada mountain ranges as well as east of the Rocky Mountains. Ecoregions with >10% land within class 1 were in the Northern Cascades, the Rocky Mountains, and the south-central western United States. Ranking of land within human footprint class 1 did not correspond to land in class 10. Only 19.4% of ecoregions (1, 2, 3, 7, 8, 23; Fig. 5) contained more land (range, 3.7–30.5%) in class 10 compared to the human footprint of the western United States (2.5%).

Aquatic systems.—Compared to ecoregions, rivers were more affected by the human footprint. Of the 11 rivers examined (Fig. 6A), 81.8% contained less land, within a 1-km buffer, in human footprint class 1 (range, 0–2.9%) compared to the human footprint of the western United States (5.5%); only the Colorado (12.5%) and Green River (15.7%) had more land in class 1. Percentage land in human footprint class 10 varied highly among rivers (range, 0.01–44.4%), with 63.6% of rivers having more land in human footprint class 10 compared to the human footprint of the western United States (2.5%). Human footprint intensity did not correspond with river length.

Lakes examined were less affected by the human footprint compared to rivers and ecoregions (Fig. 6B). Only 28.6% contained less land in human footprint class 1 within a 1-km buffer along the shoreline (Salton Sea and Lake Tahoe, 0%) compared to the human footprint of the western United States (5.5%). For the other lakes, land in class 1 ranged between 8.1% and 76.1%; the maximum percentage was about five times higher compared to rivers and ecoregions. Lakes surrounded by agricultural land, such as the Salton Sea, had a low percentage in class 1 as well as in class 10, whereas lakes near urban areas had more land in class 1 but also in class 10. As with river length, lake size was not a predictor of human footprint intensity, neither was human-made vs. natural lakes.

Management and conservation status.—Overall, 60% of land stewards (all federal agencies) had more land in human footprint class 1 (range, 6.4–32.6%) compared to the human footprint of the western United States (5.5%);

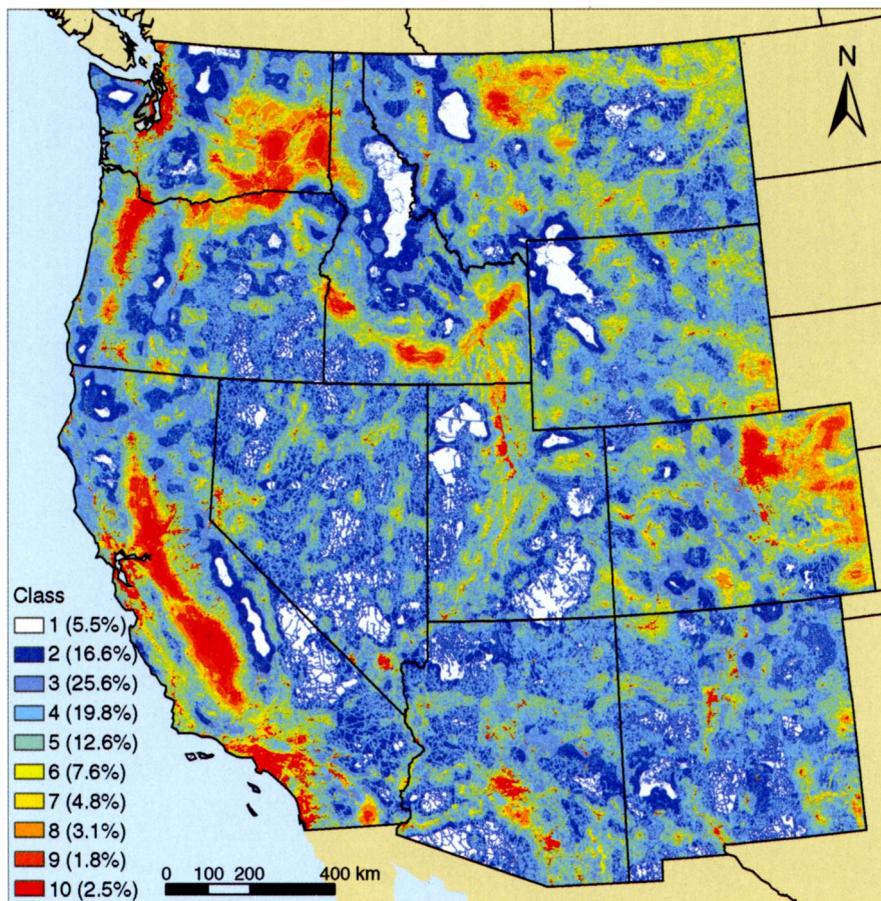


Fig. 3. The human footprint in the western United States in 2001. Human footprint intensity ranges from minimal (class 1, white) to high (class 10, red). The percentage of land covered by each human footprint class within the western United States is provided in parentheses as part of the figure key.

Fig. 7A). Lands administered by state agencies, the Bureau of Reclamation (BOR), the Bureau of Indian Affairs (BIA), or under private ownership, had <3% of their land (range, 0.8–5.4%) in human footprint class 1. Only one land steward, private lands (5.9%), had more land in class 10 compared to the human footprint of the western United States (2.5%). Landholdings that were least affected by the human footprint (United States Fish and Wildlife Service [USFWS], Department of Defense [DOD], and National Park Service [NPS]) covered 5.3% whereas those most affected (BOR, State, Private) covered 46.3% of the western United States (Fig. 7B). Landholdings heavily affected by the human footprint (BOR, State, Private) were at or near valley floors whereas lands least affected by the human footprint (NPS) were situated at high elevations (Fig. 7C).

Roadless areas currently under consideration for designation as wilderness areas (road construction and reconstruction would be prohibited, 1B-1), had more than twice as much land (15.8%) in human footprint class 1 compared to currently established roadless areas (6.5%; 1B) where road construction and reconstruction currently is prohibited (Fig. 8), and three times as much

(4.8%) compared to roadless areas where road construction and reconstruction is allowed (1C; definitions 1B1–1C, see Appendix A). This difference was less apparent in human footprint class 2 (Fig. 8).

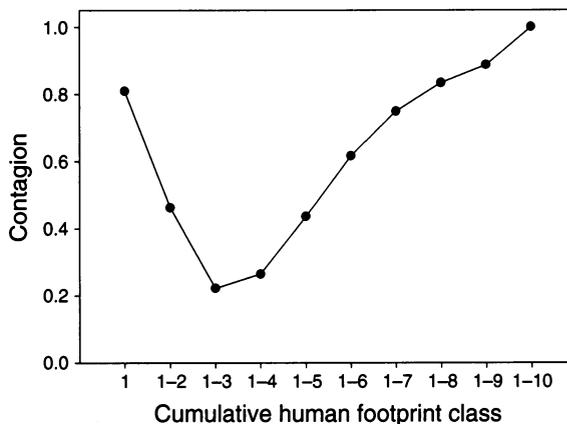


FIG. 4. Contagion indices, degree of patchiness, for cumulative human footprint classes starting with low-intensity human footprint class.

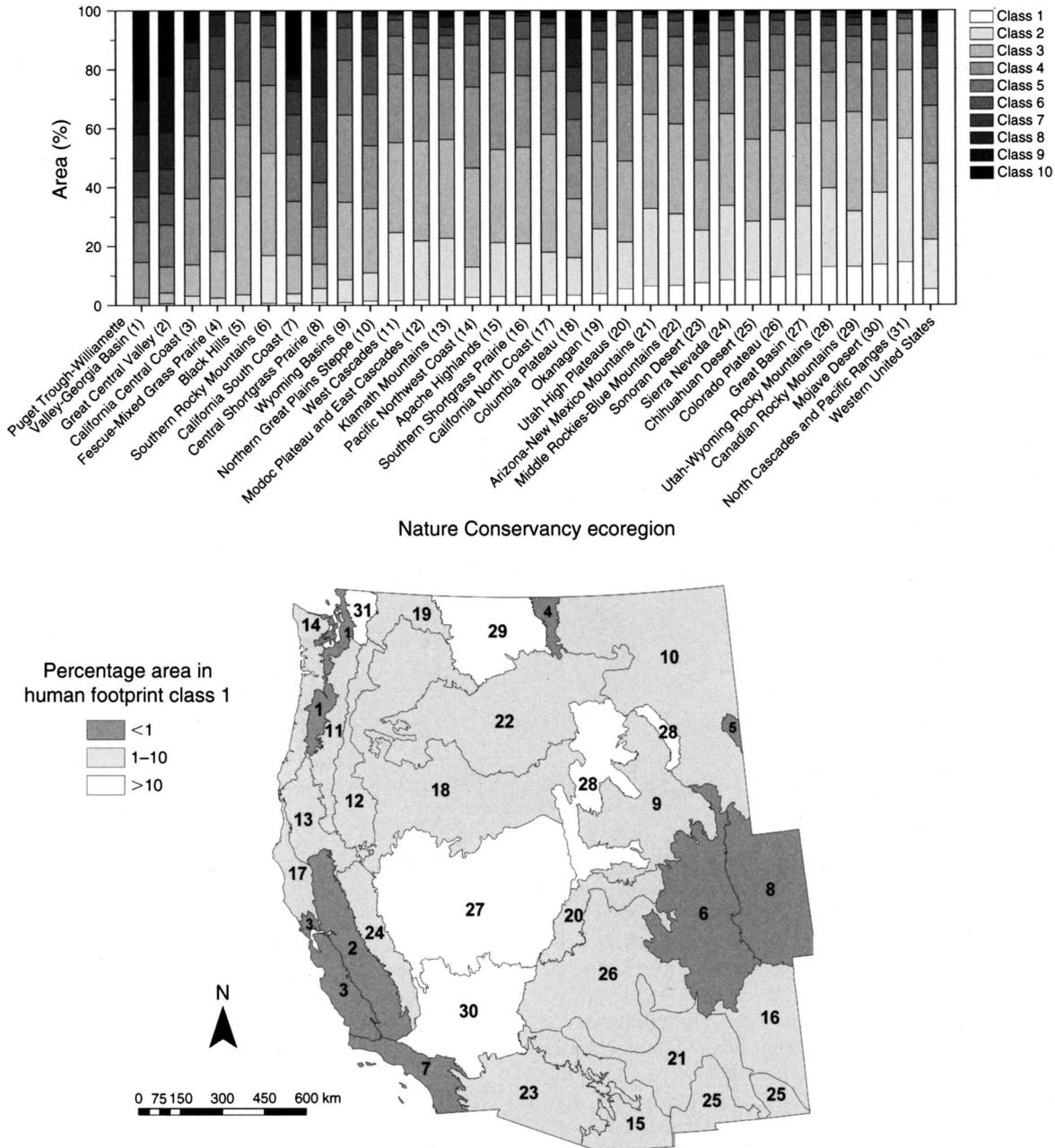


FIG. 5. The upper panel shows the percentage of area within each human footprint class (minimal [1] to high [10] human footprint intensity) for 31 Nature Conservancy ecoregions (Nature Conservancy 2001) and the total human footprint across the western United States, added for reference. Ecoregions are ranked from lowest to highest percentage of total area within human footprint class 1. The map in the lower panel shows the spatial extent of ecoregions classified according to percentage of area within human footprint class 1 (number in each ecoregion refers to ranking of percentage of area within human footprint class 1).

The four minimum human footprint scenarios (human footprint class 1–4; Fig. 3), defined as cumulative low-intensity human footprint areas, covered 6% (human footprint class 1), 22% (human footprint class 1–2), 48% (human footprint class 1–3), and 68% (human footprint class 1–4) of the western United States. Increasing the area of minimum human footprint impact decreased the proportion of area within status 1 (land

kept in a natural state; Appendix A) and status 2 (land kept in a natural state with some anthropogenic disturbance), but increased the proportion of area in the least protected status 4 (private or public lands with intensive anthropogenic disturbance regimes and no management easements or plans to protect ecosystems) (Fig. 9A). Increasing the area of minimum human footprint impact, increased percentage land in private

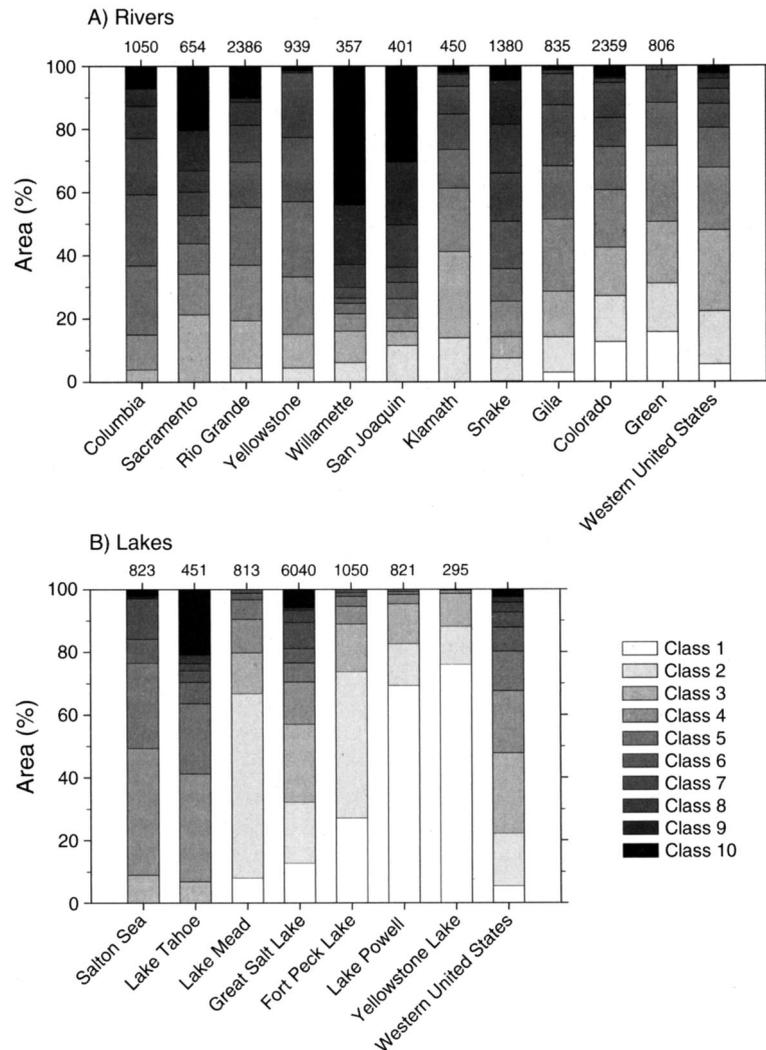


FIG. 6. Percentage of area within each human footprint class (minimal [1] to high [10] human footprint influence) for major (A) rivers ($n = 11$) and (B) lakes ($n = 7$) of the western United States. Total human footprint across the western United States added for reference. Rivers and lakes were ranked from lowest to highest percentage of total area within human footprint classes 1 and 2. In both graphs, the numbers at the top indicate the river length (km) or lake area (km^2). Fort Peck Lake, Lake Mead, Lake Powell, and the Salton Sea are human-made lakes.

stewardship, decreased in land administered by NPS and DOD, and stayed roughly the same for U.S. Forest Service (USFS) and Bureau of Land Management (BLM) landholdings (Fig. 9B)

Physical environment.—Topographic accessibility differed among human footprint classes: low human footprint classes dominated areas high above valley floors whereas high human footprint classes dominated valley floors (Fig. 10A). Mean topographic accessibility values ranged from -8 m (95% CI = 5.0 m) for class 10 to 212 m (95% CI = 6.4 m) for class 2.

The human footprint was most prevalent in areas of high biological productivity, as measured by soil depth for belowground productivity (Fig. 10B) and by NDVI for aboveground productivity (Fig. 10C). Mean soil depth decreased with decreasing human footprint

intensity ranging from 143 cm (95% CI = 1.2 cm) in human footprint class 9 to 3 cm (95% CI = 1.8 cm) in class 1. Similarly, mean NDVI values decreased with decreasing human footprint intensity ranging from 0.27 (95% CI = 0.007) in human footprint class 10 to 0.15 (95% CI = 0.007) in class 1.

Temporal changes in human actions.—Between 1990 and 2000, percentage human population increase in the western United States was higher in human footprint classes 1–5 compared to the mean percentage increase for all classes; the highest increase occurred in human footprint class 2 and the lowest in human footprint class 10 (Fig. 11). In contrast, human population density change was higher than the average density change in human footprint classes 6–10. The highest density change occurred in human footprint class 10.

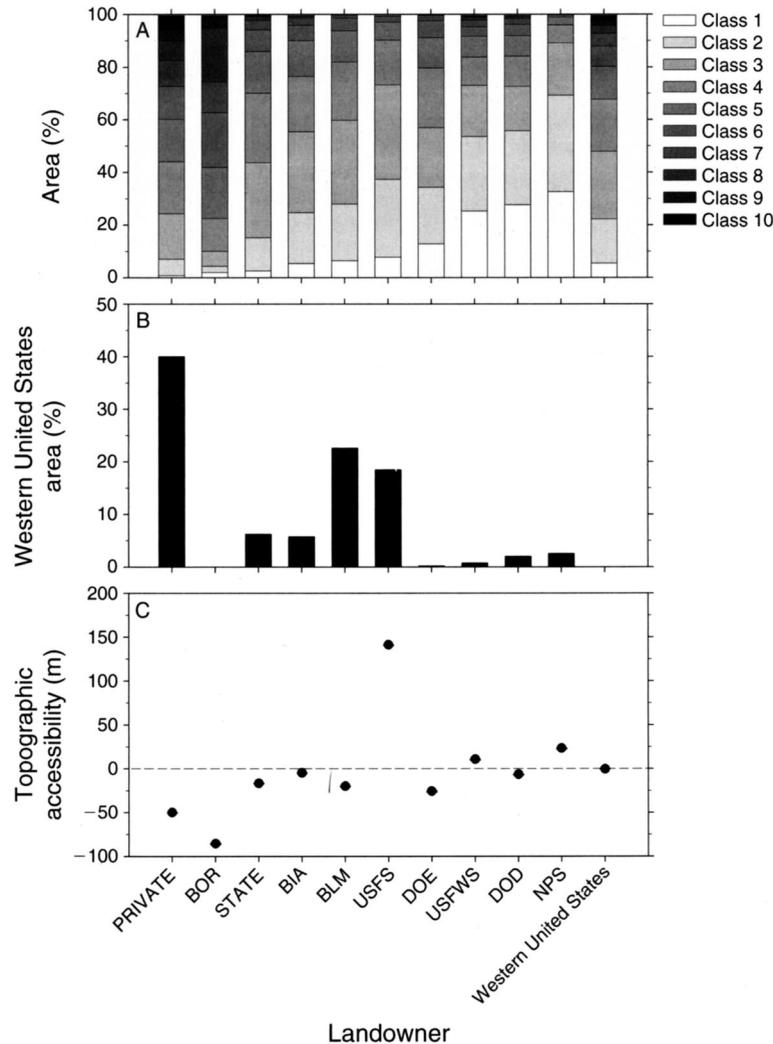


FIG. 7. Land stewardship in the western United States: (A) percentage area within each of human footprint classes 1–10, sorted from lowest to highest percentage of area within low-intensity human footprint class 1; (B) total area; and (C) mean (and 95% CI; note that confidence intervals are too small to be seen due to large sample sizes) topographic accessibility (i.e., deviation from valley floor; see *Methods*). The total human footprint across the western United States is added for reference. The dashed line in the bottom panel represents the average topographic accessibility across the western United States. Land steward abbreviations are: BIA, Bureau of Indian Affairs; BLM, Bureau of Land Management; BOR, Bureau of Reclamation; DOD, Department of Defense; DOE, Department of Energy; NPS, National Park Service; USFS, U.S. Forest Service; and USFWS, U.S. Fish and Wildlife Service.

DISCUSSION

From a global perspective, landscapes in the western United States are considered to be less affected by human actions (Sanderson et al. 2002); nonetheless, we estimated that as of 2003, 13% of this region was covered by anthropogenic features. The dominant feature was agricultural land covering 10% of the western United States. Although agricultural land in the United States is decreasing at the expense of exurban development since its pinnacle of 1950 (Theobald 2001), it ranks in the top three factors affecting species endangerment (Wilcove et al. 1998). The second most common anthropogenic feature was human populated

areas, covering ~2% of the western United States. If current trajectories of human population expansion in the western United States continue, human populated areas will increasingly dominate western landscapes at the expense of ranch and farmland; these landholdings are currently converted to small-lot housing projects at unprecedented rates, and their effects on ecological processes are poorly understood (for reviews see Knight et al. 1995b, Odell and Knight 2001, Theobald 2001). Secondary road networks comprised the third most common anthropogenic feature, summing to 2.7×10^6 km total length. Overall, 46% of the total road network within the conterminous United States (6.3×10^6 km of roads; USDT 2002) was located in the western United

States. This percentage exceeds the expected values in relation to percentage surface area (expected, 33%; U.S. Census Bureau 2003) or human population (expected, 22%; U.S. Census Bureau 2003).

Given the ubiquitous spatial extent of anthropogenic features, particularly secondary roads, it is surprising that very few spatially explicit studies document distance thresholds for anthropogenic effects on ecological processes and/or species distributions. Whereas road effects on ecological processes and species distributions in both terrestrial and aquatic systems have been reported throughout the world (Forman and Alexander 1998, Trombulak and Frissel 1999, Andrews and Gibbons 2005), data on distance thresholds for road effects on species distributions have been limited to invasion of exotic plants (Tyser and Worley 1992, Gelbard and Belnap 2003, Gelbard and Harrison 2003) and songbirds (Ingelfinger and Anderson 2004) in the western United States. Because of the lack of empirical data, anthropogenic feature effect areas are defined by distance thresholds that may not reflect actual effect and may grossly under- or overestimate the true area of effect. Furthermore, the relative influence of anthropogenic features on ecological processes cannot be simply based on their physical effect area because effect area may not be indicative of relative impact on ecological processes. Due to this limitation, we applied effect area thresholds of anthropogenic features conservatively, that is, we applied ecological effect areas more frequently to the less common features (those with total land cover of $\leq 0.1\%$ of the western United States) compared to the three most common features (three of five possible input models only). Moreover, we refrained from assigning weights to input models because weights based on empirical data do not exist. Overall, we suggest that our models are robust given that increasing and decreasing effect areas of the less common anthropogenic features would have minimal influence on the overall results of the human footprint model.

The human footprint may disproportionately affect areas of high biodiversity. Our study suggests that areas located near valley floors (i.e., at low elevation), with higher below- (i.e., soil depth) and aboveground productivity (defined by NDVI) generally overlapped with high-impact human footprint areas. These findings provide a dilemma to ecosystem and wildlife management. First, low-elevation areas are mainly under private ownership and thus may be at greater risk to land conversions (Odell et al. 2003). Second, being more productive, low-elevation ecosystems (Scott et al. 2001, Hansen et al. 2002) and ecosystems with deeper soils (Vander Haegen et al. 2000) often have higher biodiversity. Low-elevation ecosystems may also provide crucial habitat for migratory vertebrate species that breed at high elevations but winter at low elevations, or for species that interrupt fall migration at stopover sites (Skagen et al. 1988, Skagen and Knopf 1993). For example, a small population of pronghorn (*Antilocapra*

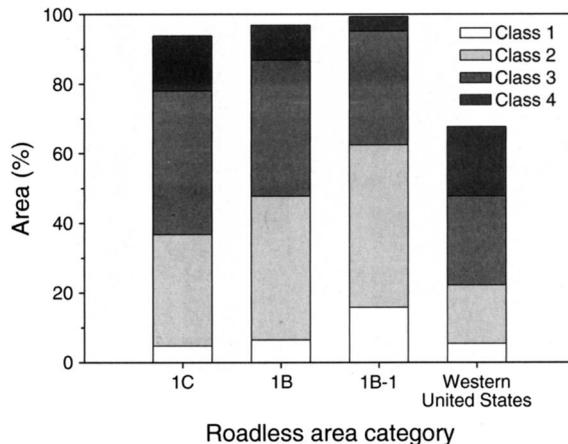


FIG. 8. Percentage of area within each of the four lowest-intensity footprint classes for each of three categories of roadless areas (USFS Roadless Area Conservation): 1B, Inventoried Roadless Areas where road construction and reconstruction is prohibited; 1B-1, Inventoried Roadless Areas that are recommended for wilderness designation in the Northwest Forest Plan and where road construction and reconstruction is prohibited; 1C, Inventoried Roadless Areas where road construction and reconstruction is not prohibited. Total human footprint across the western United States is added for reference.

americana) breeds in the Grand Teton National Park, an area identified in this paper as a low human footprint impact area, migrates through, and winters in the Green River Basin of Wyoming (Berger 2003), an area more intensely affected by the human footprint. Therefore, managing habitat important to wildlife and conserving habitats rich in biodiversity may prove difficult due to ownership issues and necessitates the inclusion of private landowners in management decisions (Imhoff 2003, Sanford 2006). Indeed, private lands harbor at least one population of $\sim 66\%$ of all federally listed species (Groves et al. 2000). One potential approach is to encourage the enrollment of less optimal agricultural land on private property into the Conservation Reserve Program (Imhoff 2003, Wilcove and Lee 2004). However, given that agricultural land is often imbedded in a matrix dominated by high human footprint intensity, restoration efforts need to include monitoring of floral and faunal demography to evaluate effectiveness of habitat restoration (Marzluff and Ewing 2001). Monitoring is important because habitat restoration near high human footprint areas could potentially propagate ecological traps (Misenhelter and Rotenberry 2000).

Human footprint intensity was not restricted to ecoregions in which urban areas were a large component of the land cover. Ecoregions dominated by urbanized areas (e.g., Puget Trough-Willamette Valley-Georgia Basin, and California Central and South Coast; Fig. 5) ranked as high on the human footprint intensity gradient as did remote ecoregions (e.g., Southern Rocky Mountains). Overall, the degree of human footprint

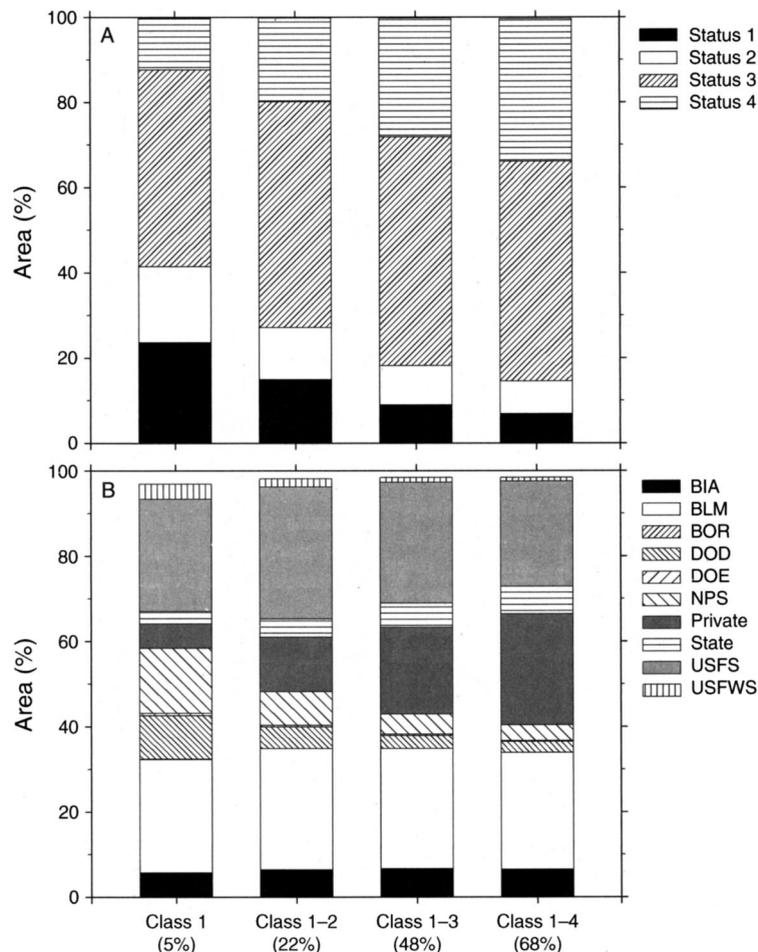


FIG. 9. (A) Percentage of area within the four low-intensity human footprint scenarios (human footprint classes 1–4; Fig. 3) that is in each of four Gap Analysis Program stewardship status classes (status 1, land kept in a natural state; status 2, land kept in a natural state with some anthropogenic disturbance; status 3, land exposed to various anthropogenic disturbance regimes that are in accordance with Federal laws to protect endangered and threatened species; status 4, private or public lands with intensive anthropogenic disturbance regimes and no management easements or plans to protect ecosystems; see Appendix A). (B) The percentage of area in the four low-intensity human footprint scenarios that is in each of ten categories of land stewardship (for key to abbreviations please see Fig. 7). Note that stacked bar graphs do not sum to 100% because water bodies and landholdings spanning multiple federal jurisdictions were not included in the analysis. The numbers in parentheses beneath each of the human footprint class scenarios give the percentage of area in the western United States in that scenario.

intensity within an ecoregion was influenced primarily by the relative spatial extent of the three most common anthropogenic features: urbanized areas, agricultural land, and secondary roads. For example, ecoregions with a large extent of agricultural land ranked as high (e.g., Central Shortgrass Prairie) as did those encompassing urban centers (e.g., California South Coast). Moreover, ecoregions containing elaborate road networks to support extraction of high-commodity natural resources, such as oil, natural gas, and timber, may still contain large extents of high intensity human footprint areas (timber extraction, West Cascades; oil and gas development, Wyoming Basins; Fig. 5). Similarly, Riitters and Wickham (2003), defining the human footprint by roads, identified three of Bailey's ecological provinces (Bailey 1995; Pacific-Lowland-Mixed Forest,

Cascade Mixed Forest-Coniferous Forest-Alpine Meadow, and California Coastal Chaparral Forest and Shrub province) with >60% of land cover within 382 m of a road, which were also identified in our study to have high human footprint influences (Puget Trough-Willamette Valley-Georgia Basin, West Cascades TNC ecoregion, California South Coast TNC ecoregion; Fig. 5).

Rivers of the western United States were more heavily affected by the human footprint compared to lakes. Whether this is an artifact of the rivers and lakes sampled remains to be seen; however, the results are intriguing in that 82% of rivers contained less land in human footprint class 1 compared to the human footprint of the western United States. This percentage was much lower for lakes (29%). The increased human

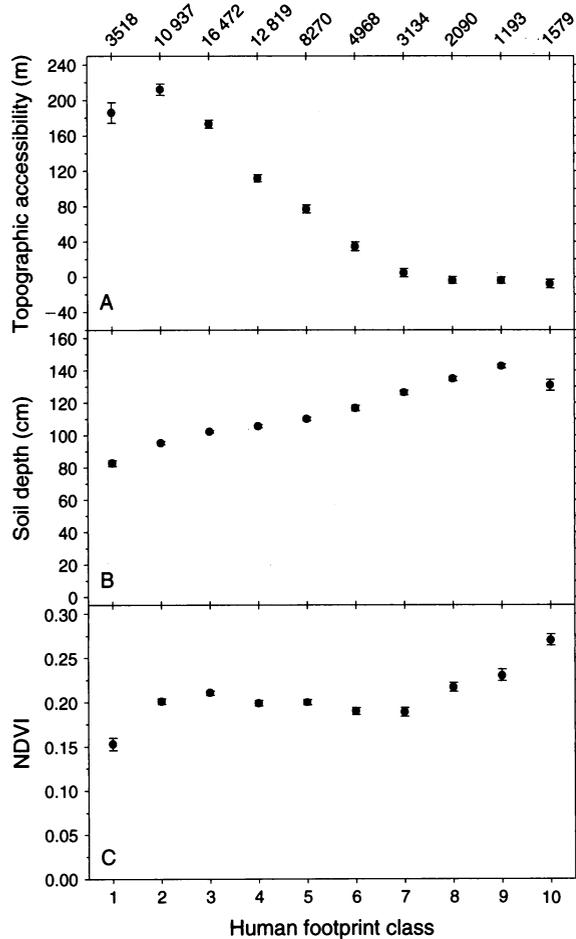


FIG. 10. (A) Mean ($\pm 95\%$ CI) topographical accessibility (deviation from valley floor), (B) soil depth, and (C) above-ground biomass based on NDVI (normalized difference vegetation index for 1989–2001) for each human footprint class (1, minimal influence; 10, high influence). To avoid spatial autocorrelations, means and confidence intervals were generated from 64980 random points. Numbers of random points in each human footprint class are given at the top of the figure.

footprint effects on rivers may be a result of the juxtaposition of rivers to high-intensity agricultural land and urban centers (e.g., Willamette River) or the absence thereof (e.g., Green River). Historical and current settlement patterns of humans revolved around rivers for their commercial value and access to commerce (Marzluff 2001). In contrast, large natural lakes were less economically valuable to historical human settlement because alkaline soils (e.g., Great Salt Lake) and/or high elevation (Lake Tahoe) rendered shorelines not conducive to agriculture. Human-made lakes were often built in areas inhospitable to human use (e.g., Lake Powell). Today, the economic value of lakes has changed with the increasing demand for recreation.

Areas with above-mean percentage human population growth between 1990 and 2000, a proxy for human

actions, occurred within the five lowest human footprint classes or in areas of low biological productivity. For example, urbanization of arid and desert ecological systems in Arizona (Gober 1998, Germaine and Wakeling 2001) and California (Kristan and Boarman 2007) is increasing at a rapid pace. Although more people moved to areas characterized by high-intensity human footprint classes when measured on a density scale, we posit that slight increases in human densities in ecosystems with low biological productivity may have a relatively higher effect on these ecosystems because of their potentially reduced resiliency to anthropogenic disturbance. In other words, the effect may not be linear as one moves from one footprint category to another. Anthropogenic disturbance may modify the slope of habitat-succession trajectories to such a degree that systems post-disturbance are either below, in the case of hydrological dynamics, or above, in the case of exotic plant invasion, a critical threshold from which recovery to any pre-disturbance steady state may no longer occur (Gunderson 2000). For example, in arid ecosystems, air pollution (Smith et al. 2000), roads (Gelbard and Belnap 2003), and grazing (Rickard 1985, Fleischner 1994, Brown and McDonald 1995, Safford and Harrison 2001, Freilich et al. 2003) facilitate the spread of exotic invading plants (e.g., cheatgrass [*Bromus tectorum*]), thereby increasing fine-fuel loadings to such levels that

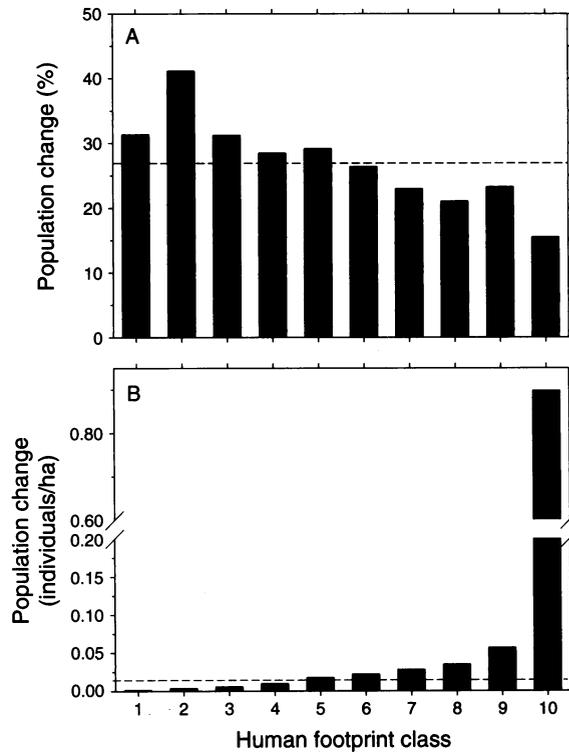


FIG. 11. Human population increase between 1990 and 2000 in (A) percentage and (B) individuals/ha for each human footprint class (minimal to high human footprint influence). The dotted lines represent average increase.

plant communities post-disturbance, depending on the severity and frequency of the disturbance, are dominated by exotic plants (Billings 1990). Arid ecological systems are also less responsive to restoration, which further exacerbated the problem of human disturbance (Whisenant 1999, Bunting et al. 2003). Given the potential intensification of human actions in low-productive ecosystems, we need to understand how trajectories of ecosystem change behave under the combined stresses of increased anthropogenic disturbance and global climate change. In addition, there is a need to understand how anthropogenic actions influence ecosystem resiliency (Scheffer et al. 2001). For example, managing an ecosystem for natural commodities, such as timber harvest, decreases ecosystem resiliency via disrupting functional group interactions at various scales (Peterson et al. 1999). Therefore, an imperative question of ecosystem studies should hinge on how anthropogenic actions affect species and their ecological function (D'Antonio and Vitousek 1992) and how ecological functions interact at various scales (Gundersen 2000).

Results from the human footprint model corroborated with avian responses to human resources and disturbance. Of the four synanthropic songbird species for which we predicted positive responses to the human footprint, all showed positive correlations between human footprint classes and detection indices. However, only three of the six species for which we predicted negative responses showed negative correlations between detection indices and human footprint classes. Of the three species whose response was predicted incorrectly, the Brewer's Sparrow is not considered an area-sensitive species compared to other shrubland bird species (Knick and Rotenberry 1999) and may not respond to landscapes shaped by the human footprint. Similarly, the Winter Wren is considered an edge-sensitive species (Brand and George 2001) but not an area-sensitive species (Donnelly and Marzluff 2004). Last, the Grace's Warbler was found only on 33 BBS routes, a sample size prone to be influenced by outliers (removal of one outlier resulted in a significant correlation). Our findings support those found in a study on how recreational trails influence bird species: specialists were found away from trails whereas generalists were not affected by trails (Miller et al. 1998).

Management implications

Land managers in the western United States increasingly face multifaceted management challenges of natural resources within landscapes exposed to accelerating rates of different types of human land uses. Managers also must deal with the dilemma that human actions taking place outside of their administrative jurisdiction influence ecological processes within their management unit (Hansen et al. 2002). The human footprint model provides a spatial representation of human land uses, thereby allowing land managers to

develop priorities at the local scale with a regional context. In addition, human footprint models serve an important function to: (1) delineate areas in which management actions could lessen the influence of anthropogenic actions on ecological processes; (2) evaluate "what if scenarios" for proposed management actions; (3) delineate areas for habitat restoration based on proximity to areas that decrease restoration potential, such as areas exposed to human disturbances of high frequency and intensity; (4) compare temporal changes in human footprint intensity to project changes in land use; and (5) identify gaps in spatial information. For example, the power line spatial data set used in this study delineated only the major transmission lines but did not include feeder lines; therefore, the physical and ecological effect area for this feature was grossly underestimated, on average by 85% (M. Leu, *unpublished data*). We also could not model all human activities (for example, mining location and extent; all-terrain vehicle use) because spatial data sets in a consistent format were not available across the western United States. Last, human footprint models serve as a building block to which improved and new spatial information on human disturbance can be added. As such, human footprint models are not static, rather they are a work in progress, just as human populations and actions are a dynamic force.

Human footprint models also serve as an important tool to delineate areas of conservation potential. At the worldwide scale, Soulé and Sanjayan (1998) suggested minimum areas necessary to protect biodiversity and ecosystem integrity to range anywhere from 33% to 75%. In their review of conservation targets, Svancara et al. (2005) found that the average "research-based threshold" below which habitat fragmentation affected wildlife population regulation negatively was 41.6%. The cumulative area of human footprint class 1–3 covered 48% of the western United States, approximating the minimum protected area suggested previously. However, this area percentage provide a biased conservation potential because low-intensity cumulative human footprint areas are at high elevation, in less productive areas, and in highly fragmented landscapes, except human footprint class 1, as indicated by their low contagion values. In fact, human footprint class 2 and 3 represent landscapes in which linear features increasingly fragment the wildland-dominated landscape indicative of class 1. Therefore, land currently least affected by the human footprint may not adequately conserve biodiversity in low-elevation ecosystems and indeed represent areas of "rock and ice" (Scott et al. 2001). However, we identified that several federal land stewards could have great potential to conserve low-elevation ecological systems. For example, Department of Defense lands have the second largest amount of land in human footprint class 1, rank fourth in percentage of land within the highest conservation status level, and have, on average, a low topographic accessibility score. Indeed, among federal

agencies, Department of Defense lands harbor the highest percentage of federally listed species (Groves et al. 2000). Second, Bureau of Land Management lands, although generally more heavily influenced by the human footprint compared to Department of Defense lands, rank highest in percentage of land within the highest conservation status level and are located, on average, at low elevations. However, these federal lands could be exposed to other anthropogenic disturbances not modeled in this paper, such as pollution or grazing.

Our analysis suggested that roadless areas currently under consideration for designation as wilderness areas had more than twice as much land (15.8%) in human footprint class 1 (least affected) compared to currently established roadless areas and three times as much compared to roadless areas where road construction and reconstruction are allowed. Therefore, there is a need to evaluate the importance of planned roadless areas to ecological systems, particularly those at mid-elevations, given that roadless areas at high elevations already are protected in many regions (Scott et al. 2001). Moreover, evaluation of roadless areas is particularly necessary given the current trend to designate potential roadless areas to areas of multiple use instead (Turner 2006). Our study showed that the human footprint class 1 covers <6% of the western United States, and therefore the addition of anthropogenic features to landscapes in this human footprint class needs to be carefully evaluated when managing, for example, for grizzly bears who avoided high-elevation landscapes fragmented by roads (Apps et al. 2004, Waller and Servheen 2005).

Human footprint models also serve an important function in designing wildlife-habitat studies. Typically, such studies are conducted in the "natural" and very recently also in urban settings (Marzluff et al. 2001), that is, studies are accomplished at the extremes along a disturbance gradient. However, how wildlife population dynamics change along an anthropogenic disturbance gradient is understudied. Therefore, human footprint models serve as a first step in defining a disturbance gradient which then can be overlaid with a habitat gradient, or any other ecological spatial data set, to produce a matrix of n habitat-disturbance combinations. Using this matrix, researchers can then randomly select replicates within each cell of the disturbance-habitat matrix and measure demography of species of interest to identify sink-source relationships (Pulliam 1988, Pulliam and Danielson 1991) and/or ecological traps (Schlaepfer et al. 2002). Moreover, human footprint models aid in the design to study ecological thresholds at which anthropogenic features cease to influence, for example, ecological processes or wildlife-habitat relationships.

ACKNOWLEDGMENTS

We thank John Lowry and Gerald Manis, Utah State University, for the landform model AML, which enabled us to develop a topographic accessibility model for the western United States. We thank the following institutions for

providing vegetation data to test the exotic plant input model: Regional USFS Ecodata Plots, Oregon Natural Heritage Program Data, and Washington Natural Heritage Program Data. We thank Janet Erickson, Erica Fleishman, Kurt Fesenmeyer, Aaron Haines, Cheryl Leu, Cindy Salo, and two anonymous reviewers for comments on a previous version of this paper; their comments have greatly improved the paper. Funding was provided by USGS Joint Venture Capital and by the Bureau of Land Management. This research was performed while M. Leu held a National Research Council Research Associateship Award at U.S. Geological Survey, Snake River Field Station, Idaho.

LITERATURE CITED

- Alterio, N., H. Moller, and H. Ratz. 1998. Movements and habitat use of feral house cats *Felis catus*, stoats *Mustela erminea* and ferrets *Mustela furo* in grasslands surrounding yellow-eyed penguin *Megadyptes antipodes* breeding areas in spring. *Biological Conservation* 83:187–194.
- Andrews, K. M., and J. W. Gibbons. 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia* 2005:772–782.
- Apps, C. D., B. N. McLellan, J. G. Woods, and M. F. Proctor. 2004. Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management* 68:138–152.
- Bailey, R. G. 1995. Descriptions of the ecoregions of the United States. Miscellaneous Publication Number 1391. U.S. Department of Agriculture, Washington, D.C., USA.
- Bakker, V. J., and D. H. Van Vuren. 2004. Gap-crossing decisions by red squirrel, a forest-dependent small mammal. *Conservation Biology* 18:689–697.
- Banci, V., and A. S. Harestad. 1990. Home range and habitat use of wolverines *Gulo gulo* in Yukon, Canada. *Ecography* 13:195–200.
- Bay, K. G. 1989. Writing rules of progress: a look at oil and gas development in the Midwest. *Proceedings Midwest Fish and Wildlife Conference* 43:1–8.
- Berger, J. 2003. Is it acceptable to let a species go extinct in a National Park? *Conservation Biology* 17:1451–1454.
- Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* 18:320–331.
- Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. Pages 301–322 in G. M. Woodwell, editor. *The earth in transition. Patterns and processes of biotic impoverishment*. Cambridge University Press, Cambridge, UK.
- Boelman, N. T., M. Stieglitz, H. M. Rueth, M. Sommerkorn, K. L. Griffin, G. R. Shaver, and J. A. Gamon. 2003. Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia* 135:414–421.
- Bolger, D. T. 2001. Urban birds: population, community, and landscape approaches. Pages 155–177 in J. M. Marzluff, R. Bowmann, and R. Donnelly, editors. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic, Norwell, Massachusetts, USA.
- Bolger, D. T., A. C. Alberts, R. M. Sauvajot, P. Potenza, C. McCalvin, D. Tran, S. Mazzoni, and M. E. Soulé. 1997a. Response of rodents to habitat fragmentation in coastal southern California. *Ecological Applications* 7:552–563.
- Bolger, D. T., T. A. Scott, and J. T. Rotenberry. 1997b. Breeding abundance in an urbanizing landscape in coastal southern California. *Conservation Biology* 11:406–421.
- Brand, L. A., and T. L. George. 2001. Response of passerine birds to forest edge in coast redwood forest fragments. *Auk* 118:678–686.
- Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage-

- grouse. Transactions of the North American Wildlife and Natural Resource Conference 67:337–349.
- Brown, J. R., and W. McDonald. 1995. Livestock grazing and conservation on southwestern rangelands. *Conservation Biology* 9:1644–1647.
- Bunting, S. C., J. L. Kingery, and M. A. Schroeder. 2003. Assessing the restoration potential of altered rangeland ecosystems in the interior Columbia Basin. *Ecological Restoration* 21:77–86.
- Case, R. M. 1978. Interstate highway road-killed animals: a data source for biologists. *Wilson Bulletin* 6:8–13.
- Coleman, J. S., and T. R. Stanley. 1993. Rural residents' free-ranging domestic cats: a survey. *Wildlife Society Bulletin* 21: 381–390.
- Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* 28:967–985.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.
- DeLap, J. H., and R. L. Knight. 2004. Wildlife response to anthropogenic food. *Natural Areas Journal* 24:112–118.
- Donnelly, R., and J. M. Marzluff. 2004. Importance of reserve size and landscape context to urban bird conservation. *Conservation Biology* 18:733–745.
- Eberhard, T. 1954. Food habits of Pennsylvania house cats. *Journal of Wildlife Management* 18:284–286.
- Engel, K. A., L. S. Young, K. Steenhof, J. A. Roppe, and M. N. Kochert. 1992. Communal roosting of common ravens in southwestern Idaho. *Wilson Bulletin* 104:105–121.
- ESRI. 1998. ARC/INFO version 7.1. Environmental Systems Research Institute, Redlands, California, USA.
- ESRI. 2006. Major lakes, major rivers (layers). Environmental Systems Research Institute, Redlands, California, USA.
- Evans, R. A., and J. A. Young. 1978. Effectiveness of rehabilitation practices following wildfire in a degraded big sagebrush downy brome community. *Journal of Range Management* 31:185–188.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8:629–644.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207–231.
- Freilich, J. E., J. M. Emlen, J. J. Duda, D. C. Freeman, and P. J. Cafaro. 2003. Ecological effects of ranching: a six-point critique. *BioScience* 53:759–765.
- Geissler, P. H., and J. R. Sauer. 1990. Topics in route-regression analysis. Pages 54–57 in J. R. Sauer and S. Droege, editors. *Survey designs and spatial methods for the estimation of avian population trends. Biological Report 90(1)*. U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17:420–432.
- Gelbard, J. L., and S. Harrison. 2003. Roadless habitats as refuges for native grasslands: interactions with soil, aspect and grazing. *Ecological Applications* 13:404–415.
- Germaine, S. S., and B. F. Wakeling. 2001. Lizard species distributions in habitat occupation along an urban gradient in Tucson, Arizona, USA. *Biological Conservation* 97: 229–237.
- Gilmer, D. S., and J. M. Wiehe. 1977. Nesting by ferruginous hawks and other raptors on high voltage power line towers. *Prairie Naturalist* 9:1–10.
- GLOBIO. 2002. The GEO-3 scenarios 2002–2032: variables provided by GLOBIO. (<http://www.globio.info/>)
- Gober, P. 1998. The demographics of urban growth in Phoenix. Pages 30–36 in R. Melnick, editor. *Growth in Arizona: the machine in the garden*. Morrison Institute for Public Policy, Tempe, Arizona, USA.
- Groves, C. R., L. S. Kutner, D. M. Stoms, M. P. Murray, J. M. Scott, M. Schafale, A. S. Weakley, and R. L. Pressey. 2000. Owing up to our responsibilities: who owns land important for biodiversity? Pages 275–300 in B. A. Stein, L. S. Kutner, and J. S. Adams, editors. *Precious heritage: the status of biodiversity in the United States*. Oxford University Press, Oxford, UK.
- Gunderson, L. H. 2000. Ecological resilience—in theory and application. *Annual Review of Ecology and Systematics* 31: 425–439.
- Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecological Applications* 15:1893–1905.
- Hansen, A. J., R. Rasker, B. Maxwell, J. J. Rotella, J. D. Johnson, A. Wright Parmenter, U. Langner, W. B. Cohen, R. L. Lawrence, and M. P. V. Kraska. 2002. Ecological causes and consequences of demographic change in the new West. *BioScience* 52:151–162.
- Harding, E. K., D. F. Doak, and J. D. Albertson. 2001. Evaluating the effectiveness of predator control: the non-native red fox as a case study. *Conservation Biology* 15: 1114–1122.
- Hayden Reichard, S., L. Chalker-Scott, and S. Buchanan. 2001. Interactions among non-native plants and birds. Pages 179–223 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic, Boston, Massachusetts, USA.
- Imhoff, D. 2003. Farming with the wild: enhancing biodiversity on farms and ranches. Sierra Club Books, San Francisco, California, USA.
- Ingelfinger, F. M., and S. Anderson. 2004. Passerine response to roads associated with natural gas extraction in sagebrush steppe habitat. *Western North American Naturalist* 64: 385–395.
- Janzen, D. 1998. Gardenification of wildland nature and the human footprint. *Science* 279:1312–1313.
- Johnston, R. F. 2001. Synanthropic birds of North America. Pages 49–67 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic, Boston, Massachusetts, USA.
- Kendall, W. L., B. C. Peterjohn, and J. R. Sauer. 1996. First-time observer effects in the North American Breeding Bird Survey. *Auk* 113:823–829.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611–634.
- Knick, S. T., and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. *Conservation Biology* 9:1059–1071.
- Knick, S. T., and J. T. Rotenberry. 1999. Spatial distribution of breeding passerine bird habitats in a shrubsteppe region of southwestern Idaho. *Studies in Avian Biology* 19:104–111.
- Knight, R. L., and J. Y. Kawashima. 1993. Responses of ravens and red-tailed hawk populations to linear right-of-ways. *Journal of Wildlife Management* 57:266–271.
- Knight, R. L., H. A. L. Knight, and R. J. Camp. 1995a. Common ravens and number and type of linear rights-of-way. *Biological Conservation* 74:65–67.
- Knight, R. L., G. N. Wallace, and W. E. Riebsame. 1995b. Ranching the view: subdivisions versus agriculture. *Conservation Biology* 9:459–461.
- Kristan, W. B., III, and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. *Ecology* 84:2432–2443.

- Kristan, W. B., III, and W. I. Boarman. 2007. Effects of anthropogenic developments on common raven nesting biology in the west Mojave Desert. *Ecological Applications* 17:1703–1713.
- Kristan, W. B., III, W. I. Boarman, and J. J. Crayon. 2004. Diet composition of common ravens across the urban–wildland interface of the west Mojave Desert. *Wildlife Society Bulletin* 32:244–253.
- Lowry, D. A., and K. L. McArthur. 1978. Domestic dogs as predators on deer. *Wildlife Society Bulletin* 6:38–39.
- Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486–491.
- Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13:195–198.
- Maestas, J. D., R. L. Knight, and W. C. Gilbert. 2003. Biodiversity across a rural land-use gradient. *Conservation Biology* 17:1425–1434.
- Manis, G., J. Lowry, and R. D. Ramsey. 2001. Preclassification: an ecologically predictive landform model. Gap Analysis Program Bulletin Number 10, December. GAP Analysis Program, U.S. Geological Survey, Moscow, Idaho, USA.
- Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. *Journal of Wildlife Management* 69:110–123.
- Martinuzzi, S., W. A. Gould, and O. M. Ramos González. 2007. Land development, land use, and urban sprawl in Puerto Rico integrating remote sensing and population census data. *Landscape and Urban Planning* 79:288–297.
- Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19–47 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic, Boston, Massachusetts, USA.
- Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. A historical perspective on urban bird research: trends, terms, and approaches. Pages 1–17 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic, Boston, Massachusetts, USA.
- Marzluff, J. M., and K. Ewing. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology* 9:280–292.
- Marzluff, J. M., and E. A. Neatherlin. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological Conservation* 130:301–314.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. (www.umass.edu/landeco/research/fragstats/fragstats.html)
- McLoughlin, P. D., H. D. Cluff, R. J. Gau, R. Mulders, R. L. Case, and F. Messier. 2003. Effects of spatial differences in habitat on home ranges of grizzly bears. *Ecoscience* 10:11–16.
- Meyer, W. B., and B. L. Turner II. 1992. Human population growth and global land-use/cover change. *Annual Review of Ecology and Systematics* 23:39–61.
- Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. *Ecological Applications* 8:162–169.
- Miller, S. G., R. L. Knight, and C. K. Miller. 2001. Wildlife responses to pedestrian and dogs. *Wildlife Society Bulletin* 29:124–132.
- Misenhelter, M. D., and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* 81:2892–2901.
- Nature Conservancy. 2001. The Nature Conservancy's ecoregions of the United States. (<http://sagemap.wr.usgs.gov>)
- Neatherlin, E. A., and J. M. Marzluff. 2004. Responses of American crow populations to campgrounds in remote native forest landscapes. *Journal of Wildlife Management* 68:708–718.
- NIFC (National Interagency Fire Center). 2007. Wildland fire statistics 2001–2006. (http://www.nifc.gov/fire_info/lightning_human_fires.html)
- Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. National Biological Service Biological Report 28:1–56.
- Odell, E. A., and R. L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conservation Biology* 15:1143–1150.
- Odell, E. A., D. M. Theobald, and R. L. Knight. 2003. Incorporating ecology into land use planning. *Journal of the American Planning Association* 69:72–82.
- Parendes, J. A., and J. A. Jones. 2000. Role of light availability and dispersal of exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. *Conservation Biology* 14:64–75.
- Parmalee, P. W. 1953. Food habits of the feral house cat in east-central Texas. *Journal of Wildlife Management* 17:375–376.
- Paruelo, J. M., H. E. Epstein, W. K. Lauenroth, and I. C. Burke. 1997. ANPP estimates from NDVI for the central grassland region of the United States. *Ecology* 78:953–958.
- Pearson, S. F. 1997. Hermit warbler (*Dendroica occidentalis*). In A. Poole and F. Gill, editors. *The birds of North America*, Number 303. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and the American Ornithologists' Union, Washington, D.C., USA.
- Peterson, G., C. R. Allen, and C. S. Holling. 1999. Ecological resilience, biodiversity, and scale. *Ecosystem* 1:6–18.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population ecology. *American Naturalist* 137(Supplement):S50–S66.
- Radeloff, V. C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005. The wildland–urban interface in the United States. *Ecological Applications* 15:799–805.
- Restani, M., J. M. Marzluff, and R. E. Yates. 2001. Effects of anthropogenic food sources on movements, survivorship, and sociality of common ravens in the arctic. *Condor* 103:399–404.
- Rich, T. D., et al. 2004. Partners in flight North American landbird conservation plan. Cornell Laboratory of Ornithology, Ithaca, New York, USA.
- Rickard, W. H. 1985. Experimental cattle grazing in a relatively undisturbed shrubsteppe community. *Northwest Science* 59:66–72.
- Riitters, K. H., R. V. O'Neil, J. D. Wickham, and K. Bruce Jones. 1996. A note on contagion indices for landscape analysis. *Landscape Ecology* 11:197–202.
- Riitters, K. H., and J. D. Wickham. 2003. How far to the nearest road? *Frontiers in Ecology and the Environment* 1:125–129.
- Rolley, R. E., and L. E. Lehman. 1992. Relationship among raccoon road-kill surveys, harvests, and traffic. *Wilson Bulletin* 20:313–318.
- Roos, S., and T. Pärt. 2004. Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology* 73:117–127.
- Rouse, J. W., R. H. Haas, J. A. Schell, and D. W. Deering. 1974. Monitoring vegetation systems in the Great Plains with ERTS. Pages 301–317 in *Proceedings of the Third Earth*

- Resources Technology Satellite-1 Symposium. NASA SP-351. Goddard Space Flight Center, Greenbelt, Maryland, USA.
- Saab, V. A., and D. W. Powell. 2005. Fire and avian ecology in North America. *Studies in Avian Biology* 30:1–13.
- Safford, H. D., and S. Harrison. 2001. Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. *Ecological Applications* 11:1112–1122.
- Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last wild. *BioScience* 52:891–904.
- Sanford, M. P. 2006. Extirpating the agriculture versus conservation dichotomy. *Conservation Biology* 20:253–254.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, results and analysis 1966–2004. Version 2005.2. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA.
- Sauer, J. R., B. C. Peterjohn, and W. A. Link. 1994. Observer differences in the North American Breeding Bird Survey. *Auk* 111:50–62.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474–480.
- Schmidt, K. A., J. R. Goheen, and R. Naumann. 2001. Incidental nest predation in songbirds: behavioral indicators detect ecological scales and processes. *Ecology* 82:2937–2947.
- Schmidt, W. 1989. Plant dispersal by motor cars. *Vegetatio* 80:147–152.
- Schumacher, J. V., R. L. Redmond, M. M. Hart, and M. E. Jensen. 2000. Mapping patterns of human use and potential resource conflicts on public lands. *Environmental Monitoring and Assessment* 64:127–137.
- Scott, M. J., F. W. Davis, R. G. McGhie, R. G. Wright, C. Groves, and J. Estes. 2001. Nature reserves: do they capture the full range of America's biological diversity? *Ecological Applications* 11:999–1007.
- Scott, T. A., and M. L. Morrison. 1990. Natural history and management of the San Clemente loggerhead shrike. *Proceedings of the Western Foundation of Vertebrate Zoology* 4:1–57.
- Shen, S. 1987. Biological diversity and public policy. *BioScience* 37:709–712.
- Shugart, H. H. 1998. *Terrestrial ecosystems in changing environments*. Cambridge University Press, Cambridge, UK.
- Sime, C. A. 1999. Domestic dogs in wildlife habitats. Pages 8.1–8.19 in G. Joslin and H. Youmans, editors. *Effects of recreation on Rocky Mountain wildlife: a review for Montana*. Committee on effects of recreation on wildlife, Montana Chapter of The Wildlife Society. (<http://www.montanatws.org/chapters/mt/index.cfm?name=rrmwfull>)
- Sinclair, A. R. E., and J. R. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society B* 357:1221–1231.
- Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology* 12:564–575.
- Skagen, S. K., and F. L. Knopf. 1993. Toward conservation of midcontinental shorebird migrations. *Conservation Biology* 7:533–541.
- Skagen, S. K., C. P. Melcher, W. H. Howe, and F. L. Knopf. 1988. Comparative use of riparian corridors and oases by migrating birds in southeast Arizona. *Conservation Biology* 12:896–909.
- Smith, S. D., T. E. Huxman, S. E. Zitzer, T. N. Charlet, D. C. Housman, J. S. Coleman, L. K. Fenstermaker, J. R. Seemann, and R. S. Novak. 2000. Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature* 408:79–82.
- Soulé, M. E., and M. A. Sanjayan. 1998. Conservation targets: do they help? *Science* 279:2060–2061.
- Stacier, C. A., and M. J. Guzy. 2002. Grace's Warbler (*Dendroica graciae*). In A. Poole and F. Gill, editors. *The birds of North America*, Number 677. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and the American Ornithologists' Union, Washington, D.C., USA.
- Stallings, G. P., D. C. Thill, C. A. Mallory-Smith, and L. W. Lass. 1995. Plant movement and seed dispersal of Russian thistle (*Salsola iberica*). *Weed Science* 43:63–69.
- STATSGO. 2003. U.S. General Soil Map (STATSGO). Soil Survey Staff, Natural Resources Conservation Service, U.S. Department of Agriculture. (<http://soildatamart.nrcs.usda.gov>)
- Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. *Journal of Wildlife Management* 57:271–281.
- Stoms, D. M. 2000. GAP management status and regional indicators of threats to biodiversity. *Landscape Ecology* 15:21–33.
- Svancara, L. K., R. Brannon, J. M. Scott, C. R. Groves, R. F. Noss, and R. L. Pressey. 2005. Policy-driven versus evidence-based conservation: a review of political targets and biological needs. *BioScience* 55:989–995.
- Syphard, A. D., V. C. Radeloff, J. E. Keeley, T. J. Hawbaker, M. K. Clayton, A. C. Stewart, and R. B. Hammer. 2007. Human influence on California fire regimes. *Ecological Applications* 17:1388–1402.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890–2903.
- Theobald, D. M. 2001. Land-use dynamics beyond the American urban fringe. *Geographical Review* 91:544–564.
- Trombulak, S. C., and C. A. Frissel. 1999. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- Turner, M. G. 1989. Landscape ecology: the effect of the pattern on process. *Annual Review of Ecology and Systematics* 20:171–197.
- Turner, J. M. 2006. Conservation science and Forest Service policy for roadless areas. *Conservation Biology* 20:713–722.
- Tyser, R. W., and C. A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). *Conservation Biology* 6:253–262.
- U.S. Census Bureau. 2000. U.S. census 2000: census tract relationship files. (http://www.census.gov/geo/www/relate/rel_tract.html)
- U.S. Census Bureau. 2003. State and County quick facts. (<http://quickfacts.census.gov/qfd/>)
- USDOT (U.S. Department of Transportation). 2002. Highway statistics 2001. Federal Highway Administration, Office of Highway Policy. (<http://www.fhwa.dot.gov/ohim/hs01/>)
- Vale, T. R. 2002. The Pre-European landscape of the United States: pristine or humanized. Pages 1–39 in T. R. Vale, editor. *Fire, native peoples, and the natural landscape*. Island Press, Washington, D.C., USA.
- Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, U.S.A. *Conservation Biology* 14:1145–1160.
- Vistnes, I., and C. Nellemann. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. *Journal of Wildlife Management* 69:915–925.
- Vitousek, P. M. 1992. Global environmental change: an introduction. *Annual Review of Ecology and Systematics* 23:1–14.

- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468–478.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystem. *Science* 277:494–499.
- Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. *Journal of Wildlife Management* 71:2644–2654.
- Waller, J. S., and C. Servheen. 2005. Effects of transportation infrastructure on grizzly bears in northwestern Montana. *Journal of Wildlife Management* 69:985–1000.
- Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of passerine nests. *Journal of Animal Ecology* 71:424–437.
- Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology* 13:1476–1486.
- Weller, C., J. Thompson, P. Morton, and G. Aplet. 2002. *Fragmenting our lands: the ecological footprint from oil and gas development*. The Wilderness Society, Washington, D.C., USA.
- Whisenant, S. G. 1999. *Repairing damaged wildlands. A process-oriented, landscape scale approach*. Cambridge University Press, Cambridge, UK.
- Wilcove, D. S., and J. Lee. 2004. Using economic and regulatory incentives to restore endangered species: lessons learned from three new programs. *Conservation Biology* 18: 639–645.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607–615.
- Zar, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

APPENDIX A

An outline of methods employed to develop spatial data sets of anthropogenic features and to evaluate human footprint model output (*Ecological Archives* A018-039-A1).

APPENDIX B

Additional information on the occurrence functions to buffer anthropogenic features for the corvid and domestic predator presence risk models (*Ecological Archives* A018-039-A2).

APPENDIX C

A description of the results of input models and methods for and results of corvid presence risk and exotic plant invasion risk model evaluation (*Ecological Archives* A018-039-A3).

APPENDIX D

A depiction of detection indices (percentage of years when a species was detected on Breeding Bird Survey routes that were sampled at least seven times during 1994–2003) for 10 songbird species vs. mean human footprint class (minimal to high human footprint influence) (*Ecological Archives* A018-039-A4).