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Source: *Ecological Applications*, Vol. 15, No. 6 (Dec., 2005), pp. 1893-1905
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/4543492
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Ecological Applications, 15(6), 2005, pp. 1893–1905
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EFFECTS OF EXURBAN DEVELOPMENT ON BIODIVERSITY: PATTERNS, MECHANISMS, AND RESEARCH NEEDS

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Abstract. Low-density rural home development is the fastest-growing form of land use in the United States since 1950. This "exurban" development (~6–25 homes/km^2) includes urban fringe development (UFD) on the periphery of cities and rural residential development (RRD) in rural areas attractive in natural amenities. This paper synthesizes current knowledge on the effects of UFD and RRD. We present two case studies and examine the patterns of biodiversity response and the ecological mechanisms that may underlie these responses. We found that many native species have reduced survival and reproduction near homes, and native species richness often drops with increased exurban densities. Exotic species, some human-adapted native species, and species from early successional stages often increase with exurban development. These relationships are sometimes nonlinear, with sharp thresholds in biodiversity response. These effects may be manifest for several decades following exurban development, so that biodiversity is likely still responding to the wave of exurban expansion that has occurred since 1950. The location of exurban development is often nonrandom relative to biodiversity because both are influenced by biophysical factors. Consequently, the effects on biodiversity may be disproportionately large relative to the area of exurban development. RRD is more likely than UFD to occur near public lands; hence it may have a larger influence on nature reserves and wilderness species. The ecological mechanisms that may underlie these responses involve alteration of habitat, ecological processes, biotic interactions, and increased human disturbance. Research on the patterns and mechanisms of biodiversity remains underdeveloped, and comparative and experimental studies are needed. Knowledge resulting from such studies will increase our ability to understand, manage, and mitigate negative impacts on biodiversity.

Key words: biodiversity; biotic interactions; ecological mechanisms; fire; habitat fragmentation; landscape management; land cover; land use; rural residential development; urban fringe development; weeds.

INTRODUCTION

Rural America is undergoing a dramatic transition. For the first time in more than a century, more people are moving to rural areas than from rural lands (Johnson 1998). Fleeing the cities, many retirees, entrepreneurs, and others are seeking the small-town lifestyles and natural amenities of rural landscapes (Rudzitis 1999). This rural in-migration is driving large changes in land use. The typical trajectory of land use change across the United States prior to 1950 was from wild land and resource extraction uses to agriculture and to suburban and urban uses. An entirely new land use has become prevalent in many parts of the United States since 1950. Many people are choosing to live "out of town" on small "ranchettes" and in rural subdivisions. Termed exurban development, low-density housing (~6–25 homes/km^2) within a landscape dominated by native vegetation is now the fastest growing form of land use in the United States (Brown et al. 2005). Land long used for forestry or ranching is now being converted to home sites. The effects of exurban development on native species and ecological communities have only recently been the topic of ecological studies.

Since 1950, there has been a five-fold increase in the area within the conterminous United States that is occupied at exurban densities (Brown et al. 2005). The

Manuscript received 21 July 2003; revised 10 September 2004; accepted 8 November 2004; final version received 10 December 2004. Corresponding Editor: M. G. Turner. For reprints of this Invited Feature, see footnote 1, p. 1849.

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PLATE 1. Rural residential development in the Greater Yellowstone Ecosystem near Red Lodge, Montana, USA. The rural homes are placed near low-elevation riparian forests that are especially important for biodiversity. Photo by A. Hansen.

exurban land use type currently covers nearly 25% of the area of the lower 48 states. The most rapid gains were in the eastern deciduous forest, the southwest, the western seaboard, the Rocky Mountains, and the upper Midwest.

This exurban development is manifest in two forms. Urban fringe development is the expansion of exurban densities on the periphery of cities. This urban fringe development (UFD) is largely driven by urban dwellers seeking more rural lifestyles while still having access to urban jobs and services (Ulmann 1954, Healy and Short 1987, Raish et al. 1997). Exurban development in counties adjacent to metropolitan counties increased six fold since 1950 (Brown et al. 2005). Over time, these exurban developments often transition to suburban and urban land uses.

A second form of exurban development is occurring distant from cities. It is focused on rural areas attractive in scenery, climate, outdoor recreation and other "natural amenities" (Rasker and Hansen 2000). Rural counties not adjacent to metropolitan counties increased fivefold in exurban area since 1950 (Brown et al. 2005). This rural residential development (RRD) is common in the rural counties of the Rocky Mountain West, the Pacific Northwest, the upper Midwest, and the southeastern United States (Gersh 1996). Rather than being randomly distributed, this development is often associated with the borders of national parks and other public lands; rivers, lakes, or coastal areas; areas of moderate climate and good outdoor recreational opportunities; and towns and small cities that offer national airports, high-speed internet access, and cultural amenities (Cromartie and Wardwell 1999, McGranahan 1999, Nelson 1999; see Plate 1).

The effects of both forms of exurban development on wildlife and biodiversity are poorly known. Relative to other types of land use, exurban development is substantially understudied. Miller and Hobbs (2002) found that only 6% of the papers on human landscapes published in *Conservation Biology* dealt with exurban and urban places. The majority of these consider the general gradient from rural to urban in and around cities. While these studies typically do not cleanly separate biodiversity in exurban places relative to suburban and urban places, they do provide a context for assessing general trends in biodiversity under land use intensification. RRD has been examined in only a few recent studies, with most of them being in the Rocky Mountain West.

Understanding the effects of exurban development on biodiversity is important to public policy. With a quarter of the nation's land area in this land use type, policies on exurban development may have a substantial effect on biodiversity nationwide. The general view among conservationists and the public is that exurban development alters ecological processes and biodiversity to a greater extent than forestry and agriculture (Marzluff and Ewing 2001). Hence, many initiatives have emerged to protect "open space" from exurban development through conservation easements and other approaches. There is also the view that the effects of exurban development are proportional to home density. Thus, zoning for lower density housing is often used to protect ecological resources.

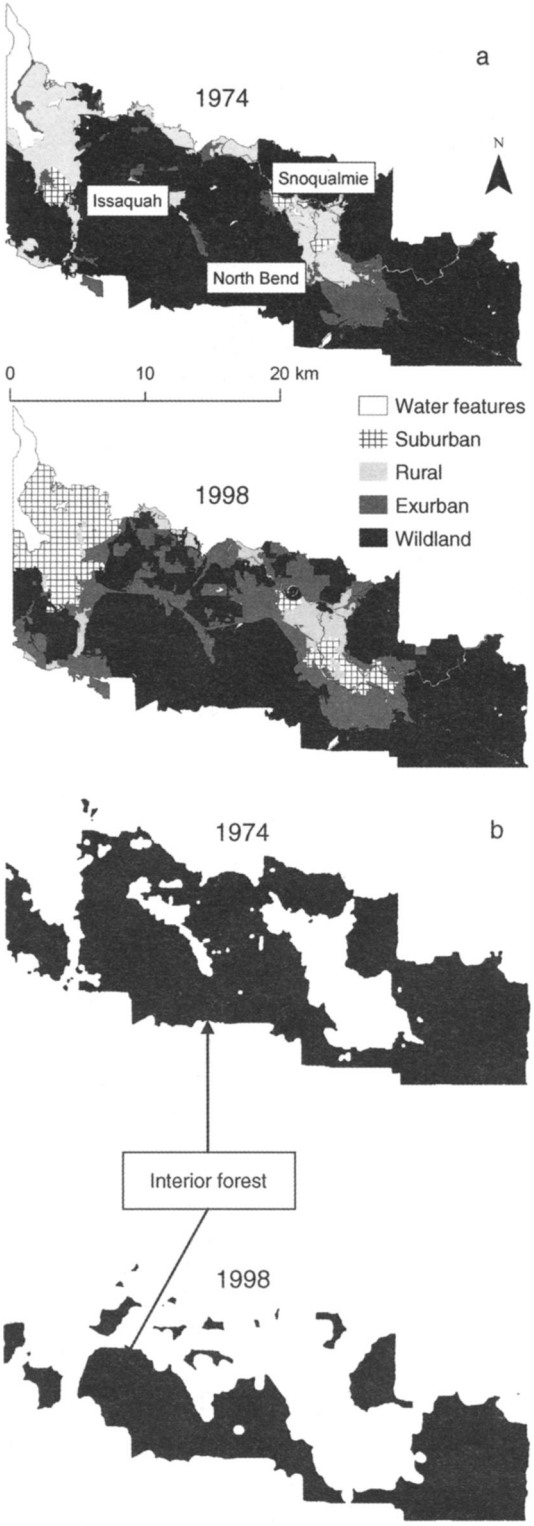

FIG. 1. (a) Change in land use in the urban fringe east of Seattle, Washington, USA. (b) Decline in interior forest resulting from changes in land use. The figure is from Robinson et al. (2005).

Several questions arise. How does exurban development change habitat and landscape patterns from those typical of lower intensity land uses? How do ecosystem, community, and population-level patterns vary as more natural habitats are converted to exurban? Are there thresholds in home density and spatial pattern where biodiversity is disproportionately affected? What ecological mechanisms underlie the response of biodiversity to exurban development? Can exurban development on private lands have consequences on adjacent or distant public lands? How do the effects of UFD and RRD compare?

In this paper, we synthesize current knowledge and attempt to answer these questions. We do so by first examining UFD and RRD and offer a case study of each. We then consider the ecological mechanisms linking both forms of exurban development to biodiversity. Where current research is insufficient to address the questions, we offer hypotheses in an effort to stimulate future research.

URBAN FRINGE DEVELOPMENT AND BIODIVERSITY

Case study: Seattle, Washington

The city of Seattle, in King County, Washington, lies between the Puget Sound and the Cascades Mountains. Like many metropolitan counties on the west coast, King County has been growing rapidly. The population size increased by 44% during 1970–2000 and the number of households grew by 72%. In an attempt to control sprawl around the city, the county instituted an urban growth policy aimed at confining high density development within urban growth boundaries while maintaining low-density housing in the surrounding rural lands. Robinson et al. (2005) quantified change in land use during 1974–1998 in a 474-km^2 study area extending east from Seattle towards the Cascade Mountains. The study area was a matrix of forest lands with dispersed agricultural, suburban, and urban, land uses.

The authors found that the primary trajectories of change were from wildlands to exurban and from exurban and agricultural to suburban. The area of exurban increased by 193%. Exurban and suburban covered 8% of the study area in 1974 and 33% in 1998 (Fig. 1a). The reduction of wildland and agricultural lands represents the conversion of 23% of the study area to development. These changes fragmented once contiguous forest and reduced interior forest area (>200 m from forest edge) by 60% (Fig. 1b). This land use change was largely driven by single-family housing. Despite the effort to concentrate growth within the urban growth boundary, 60% of the land committed to new residential development was outside urban growth boundaries.

This land conversion on Seattle's fringe changed plant, bird, and small mammal diversity. Native forb and tree diversity declined with loss of forest (Fig. 2a). A similar, but nonsignificant trend, was found for

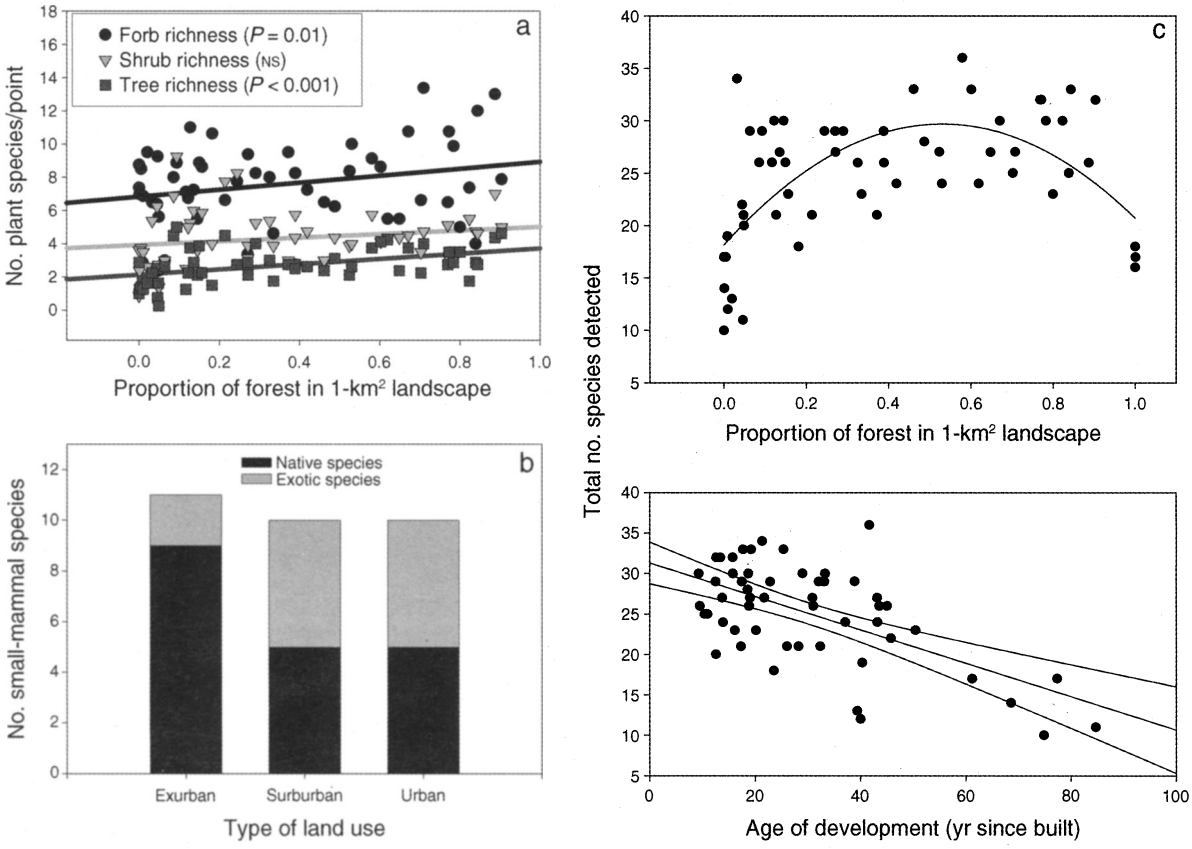

FIG. 2. Changes in biodiversity in response to urban sprawl in the Seattle metropolitan area. (a) Increases in plant species richness with increasing forest land cover. (b) Shifting composition of small mammal communities. (c) Correlation of bird species richness with amount of forest (upper panel) and age of development (lower panel). Bird data are from Donnelly (2002), Donnelly and Marzluff (2004), and Marzluff (*in press*).

shrubs. Alternatively, exotic ground cover increased significantly with development, especially with the interaction between age of development and interspersion of settled and forested remnants. The trends for plants were relatively linear. Small mammal communities changed abruptly from primarily native to mixtures of natives and exotics as landscapes were converted from exurban to suburban or urban (Fig. 2b). Bird species richness in combined samples of forest fragments and settled areas peaked at levels of settlement found in most single-family housing subdivisions (Fig. 2c). It dropped dramatically when development reached a threshold of approximately 80% developed, and when mature, second growth, coniferous forest cover occupied the entire 1-km^2 landscape (i.e., in relatively large forested reserves; Marzluff, *in press*). The peak in landscapes where forest and settlement are both abundant in the landscape occurs primarily because of colonization of early successional and deciduous forest species (Marzluff, *in press*). Native forest birds are predictably and linearly lost with increasing urbanization (Donnelly 2002, Donnelly and Marzluff 2004). Synanthropic birds, those ecologically associated with humans, predictably colonize landscapes as urban land cover increases. Species richness was also related to age of development, with bird species richness continuing to decrease more than 60 years after development. Average bird species richness dropped from about 35 at the time of development to below 15 by 80 years after development. This drop is accentuated by concomitant loss of forest cover with subdivision age in the sample, but additional research of similarly forested, but variously aged subdivisions confirms a general, but less extensive loss of species (Ianni 2004). Species diversity declines as subdivisions age because of losses in native mature forest birds and native birds not typically found in mature forests that colonized the openings, grasslands, ponds, and deciduous forest characteristic of new subdivisions. The loss of bird species was not explained by poor reproductive success. Nest success remained relatively high in developed study plots for all the bird guilds studied, but the numbers of active nests were greatly reduced in densely settled areas (Donnelly and Marzluff 2004). The authors concluded that the reduction in richness was primarily due to the loss of species dependent upon forest habitats,

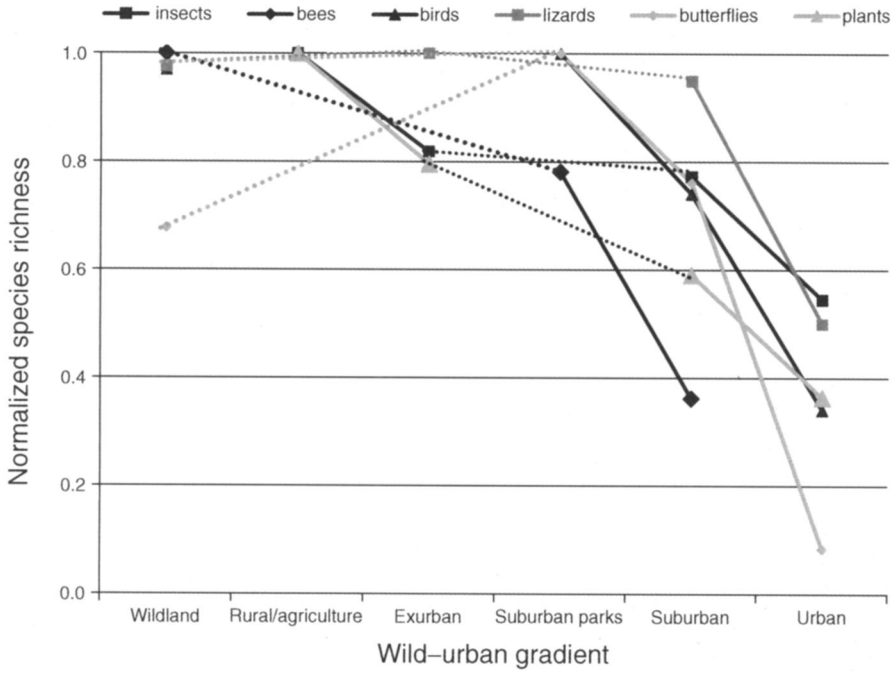

FIG. 3. Distribution of species richness across a gradient in land use for studies of various organisms. Normalized species richness is calculated as a function of the maximum number of recorded species at a point on the development gradient. Dashed lines represent unsampled portions of the gradient. Sources: insects, Denys and Schmidt (1998); bees, McIntyre and Hostetler (2001); birds, Blair (1996); lizards, Germaine et al. (1998); butterflies, Blair (1999); plants, Denys and Schmidt (1998).

rather than to increased predation levels. Reduced survival of adults and newly fledged birds is a potential factor currently being studied.

General biodiversity responses to land use intensification on the urban fringe

The results above are consistent with the growing body of literature finding that the quantity and pattern of urban fringe development strongly influence both native and nonnative flora and fauna. The responses at the community level are a function of species response patterns, which are in turn a function of the demographic responses of individual organisms (Marzluff and Ewing 2001).

Community patterns.—For many plant and animal communities, species richness decreases as housing density increases along the rural–urban gradient. The literature abounds with examples for arthropods (Miyashita 1998), insects (Denys and Schmidt 1998), and amphibians (Lehtinen et al. 1999) (Fig. 3). Along a gradient from wild and undeveloped parks around the outskirts of Phoenix, Arizona, to residential sites in the city, both richness and abundance of pollinator bees (*Hymenoptera: Apoidea*) decreased markedly (McIntyre and Hostetler 2001). Similar results were documented in Tucson, Arizona, for native bird guilds, as housing density best explained the decrease in species richness along the rural–urban gradient (Germaine et al.1998). For native rodents in protected grasslands in Boulder, Colorado, the capture rate exhibited a strong negative relationship with the percentage of surrounding suburbanization (Bock et al. 2002).

While native species often decrease in diversity and abundance along the rural–urban gradient, the opposite is often true for nonnative guilds. In the Tucson study, housing density best explained the increase in species richness for nonnative birds (Germaine et al. 1998). Within plant communities in Ohio, the percentage of nonnative species increased along the rural–urban gradient (Whitney 1985).

Because of these contrasting biodiversity response patterns along the rural–urban gradient, community richness sometimes exhibits a non-linear response in which richness peaks at intermediate levels of development (McKinney 2002). Avian and butterfly richness and diversity were both higher at moderate levels of development than in natural reserves in various sites in California and Ohio (Blair 1996, 1999). Lizard abundance, richness, and evenness all peaked at intermediate levels of development in Tucson, Arizona (Germaine and Wakeling 2001). In shoreline cottage development in central Ontario, moderate levels of development supported the highest levels of small mammal diversity (Racey and Euler 1982).

A recent meta-analysis of avian community response patterns to increasing urbanization (Marzluff 2001)

confirmed the patterns emerging from the individual studies summarized above. He found that richness decreased in 61% and evenness decreased in 56% of the studies (Marzluff 2001). Over 90% of the surveyed studies documented either an increase in exotic species or a decrease in interior habitat nesters with increasing settlement.

An important conclusion from the Seattle case study is that the biodiversity response to urbanization may continue to intensify for several decades after development (Donnelly 2002, Ianni 2004). Thus in the rapidly growing cities of the United States, the full effects of recent development are likely not yet fully manifest and native biodiversity will continue to erode for decades to come.

Species patterns.—The response patterns of individual species to the rural–urban gradient are complex and account for the variety of responses at the community level. Many species decline in abundance with increased intensity of land use. Of 21 species recorded at a nature reserve in Santa Clara County, California, only 14 of these species also occurred at a nearby recreation area, and only three of these species were also found at the most urbanized site (Blair 1996). The species found only in the nature reserves were all natives including Western Wood-pewee (*Contopus sordidulus*), Hutton's Vireo (*Vireo huttoni*), and Ash-throated Flycatcher (*Myiarchus cinerascens*). Other examples of species that are negatively correlated with development levels come from central Ontario where the masked shrew (*Sorex cinereus*), deer mouse (*Peromyscus maniculatus*), red-backed vole (*Clethrionomys gapperi*), and woodland jumping mouse (*Napeozapus insignis*) all decreased in abundance with increasing shoreline cottage development (Racey and Euler 1981).

Other species are able to tolerate and even increase under higher levels of development (Hoffman and Gottschang 1997). Higher densities of nesting Cooper's Hawks (*Accipiter cooperii*) were recorded in urban settings compared to rural settings in and around Tucson, Arizona (Boal and Mannan 1998). Schneider and Wasel (2000) found that the density of moose (*Alces alces*) in northern Alberta, Canada, increased near human settlement. Similarly, Racey and Euler (1982) observed increased capture success with increasing development level for eastern chipmunk (*Tamias striatus*), red squirrel (*Tamiasciurus hudsonicus*), and meadow vole (*Microtus pennsylvanicus*). Several other studies have documented a suite of common bird and mammal species that increase in abundance along the rural to urban gradient. Examples include the House Sparrow (*Passer domesticus*), European Starling (*Sturnus vulgaris*), American Crow (*Corvus brachyrhyncos*), Brown-headed Cowbird (*Molothrus ater*), skunk (*Mephitis mephitus*), raccoon (*Procyon lotor*), and opossum (*Didelphis virginiana*) (Odell and Knight 2001).

The relationship between species abundance and urbanization is often not linear; many species are most abundant at intermediate levels of development, as demonstrated by Blair (1996). Gray foxes (*Urocyon cinereoargenteus*) in several rural communities in New Mexico were found to be tolerant of RRD up to a threshold of 50–125 homes/km^2 (Harrison 1997). A similar nonlinear response was also documented for abundance of mule deer (*Odocoileus* spp.) in an urbanizing valley in southwest Montana (Vogel 1989). Short-tailed shrews (*Blarina brevicauda*) were documented to peak at intermediate lakeshore cottage development levels in central Ontario (Racey and Euler 1982).

The life history attributes of species that avoid or expand with urbanization are not well studied. McKinney (2002) suggested that many human-sensitive species include large mammals with low reproductive rates, birds specializing on natural habitats, and late successional plants. Species most abundant in suburbs may be edge-adapted generalists able to exploit the wider variety of habitat configurations and resources available at intermediate levels of development. Species associated with urban areas may be preadapated to human structures or able to use human-derived food or water supplies (McKinney 2002). However, more study is needed to evaluate these hypotheses.

Demographic patterns.—Patterns of reproduction, survival, and dispersal are drivers for species and community responses to exurban development, yet relatively few studies have quantified population vitality rates across the development gradient. Marzluff (2001) reviewed the literature for results of urbanization on avian breeding success. He found that most studies dealt with species that were most abundant in cities. For these species, breeding success improved with increased settlement. For other species however, research on bird nesting success indicated a negative relationship with increasing development. The abundance of human development was found to be the strongest predictor of brood parasitism by brown-headed cowbirds and reduced nest success of several species such as Yellow Warbler (*Dendroica petchia*) (Tewksbury et al. 1998).

In sum, three general patterns of species abundances emerge along the gradient from rural to urban: decreases, increases, and nonlinear responses (McKinney 2002). Species that decrease in abundance along the development gradient are termed "human sensitive" (Odell and Knight 2001) or "urban avoiders" (McKinney 2002). Species that increase are termed "human adapted" (Odell and Knight 2001) or "urban adapted" and "urban exploiters" (McKinney 2002). "Suburban adaptables" (Blair 1996) reach peak abundance at intermediate levels of development. At the community level, richness for native species generally decreases with increasing development while richness

for nonnative species generally increases with increasing development. As a result, total community diversity often peaks at intermediate levels of development, because both native and nonnative species are present in the community (Marzluff, *in press*). The life history traits of individual species, native and nonnative, likely contribute to the variety of responses at the population and community levels.

Rural Residential Development and Biodiversity

Case study: Colorado

Colorado is representative of much of the new West. Growing at three times the nation's average, it was the sixth-fastest growing state in the United States in the 1990s (Knight 1998). Importantly, this population growth is occurring on rural landscapes as well as within urban areas. Indeed, from 1990 to 1998, population in rural areas grew faster than in urban areas in over 60% of the counties in the Rocky Mountain states (Theobald 2001, Odell et al. 2003).

In much of the Mountain West, there are three principal land uses beyond city limits: protected areas, ranches, and ranchettes. Maestas et al. (2003) examined songbirds, carnivores, and plant communities on these three land uses in Larimer County, Colorado. Importantly, their data came from sites that were similar in elevation, soil type, and plant community type. They found that the density of songbirds and carnivores were more similar between ranches and protected areas (without livestock grazing) than on the ranchettes. The songbirds and carnivores that were most abundant on the ranchettes included dogs, cats, Black-billed Magpies, European Starlings, and other human-adapted species. Songbirds and carnivores that occurred on ranches and protected areas were uncommon or did not occur on land in ranchettes. Importantly, many of these songbirds are of conservation concern, whereas the birds that did best on ranchettes are common and increasing across the West (Maestas et al. 2003).

The plant communities across these three land uses were even more distinct. Native plant species were more prevalent and nonnative species were less prevalent on ranches than in either protected areas or ranchettes (Maestas et al. 2002). The greatest number of nonnative species was found on the ranchettes, with eight of 23 nonnative species being found only on the ranchette developments. In addition, percent cover of nonnative plants was highest on the ranchettes and protected areas and was significantly lower on ranches.

The effects of RRD are often manifest as a function of distance from home site and roads. In Pitkin County, Colorado, the biodiversity responses to ranchettes extended out as far as 330 m into undeveloped areas, although most effects diminished at approximately 100 m from the homes (Odell and Knight 2001). Human-adapted species, such as Brown-headed Cowbirds,

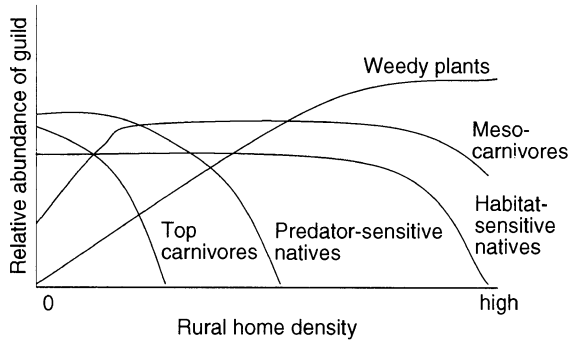

FIG. 4. Hypothesized responses of various guilds of species to rural home density.

Black-billed Magpies (*Pica pica*), and American Robins (*Turdus migratorius*), all occurred at higher densities near homes and at lower densities away from homes. Similarly, domestic dogs (*Canis familiaris*) and house cats (*Felis domesticus*) were more likely to be detected near homes than away from homes, while coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) showed the reverse pattern (Odell and Knight 2001).

Such findings help elucidate the true ecological costs associated with RRD. Rather than simply acknowledging that rural residences perforate the landscape, one can begin to calculate the magnitude of land affected beyond the building site (Theobald et al. 1997). Assuming the depth of the house-edge effect is 100 m, and including a similar depth of road-effect (Forman 2000), Odell and Knight (2001) found that approximately one-fifth of the land area of the subdivided ranches they studied was affected by houses and roads.

General effects of RRD on biodiversity

Compared with the urban fringe, development in rural areas distant from cities generally involves the lower intensity land uses of exurban home development. The Colorado case study suggests that this low-density housing can have effects on biodiversity that are more extreme than traditional rural land uses such as such as protected areas or ranching. The relative impacts of RRD on biodiversity compared to other rural land uses such as logging, grazing, crop agriculture, and backcountry recreation, however, are little studied. We can speculate that each has unique influences on biodiversity that are related to the nature of the land use. The plowing associated with crop agriculture likely alters soil communities to a greater extent than does RRD, but has fewer impacts associated with roads or with human disturbance. Similarly, logging may more greatly change forest structure and composition and disrupt soil layers. There may sometimes also be considerable overlap in impacts among these land use types. A study in south western Montana found that density of cowbirds and parasitism of native bird species were significantly associated with density of homes, area in

crops, and livestock densities within 6 km of riparian habitats (Hansen et al. 1999). Presumably this results because all three of these land use types provide supplemental foods that attract cowbirds. One way that RRD differs from the other rural land uses is its longevity. While logging and recovery typically occur in cycles, and livestock grazing and crop agriculture often have rest rotations, RRD is permanent on the order of decades or longer and its effects may intensify over this time.

The effect of land use is a function not only of land use type but also its intensity. In the case of RRD, home density is likely an important measure of intensity. A common perception is that homes scattered at low densities have little influence on biodiversity, while dense subdivisions have a large effect. Again, however, little research has examined how impacts on biodiversity vary with rural home density and development pattern.

As is the case with development intensity under UFD, we speculate that the relationship with rural home density under RRD varies among the different elements of biodiversity (Fig. 4). Top carnivores may be reduced even at low home densities as the expanding network of roads allows increased human access, hunting, and human disturbance. This may allow for an expansion of native or exotic meso predators and brood parasites. Consequently, native species vulnerable to predation and nest parasitism may undergo reduced survival and reproduction at low to medium densities of homes. Weedy plant diversity may increase at low home densities in association with roads, increase somewhat linearly with home density, then drop at high home densities as most of the land area is converted to lawns and ornamental plants. Suburban adaptables that benefit from human food sources and habitats may increase in proportion to home density. Finally, species richness of native species that require native habitats may decline only at higher home densities as the area of remaining habitat fall below key thresholds. Future research is needed to test these hypotheses and to identify key thresholds.

The effects of rural home density undoubtedly interact with the spatial distribution of homes and the behaviors of home owners. If homes are clustered, total road density is reduced and the ecological effects of each home overlap, allowing a larger proportion of the landscape to be free of these effects. Consequently, local planners often recommend clustered development to reduce ecological impacts and to reduce costs of government services (Daniels 1999). Also, home owners may reduce impacts on biodiversity by controlling weeds along roads, landscaping with native plant species, confining pets, covering compost, and managing livestock, pet foods, trash, and other artificial food sources including bird feeders to prevent access to wildlife.

A unique aspect of RRD compared with UFD is that rural homes are more likely to be placed in landscapes that include public lands with natural habitats and wilderness conditions. Typically, the sites productive for agriculture were claimed for private ownership, while less-productive mountain and desert settings remained under public control (Huston 2005). This has resulted in a high level of interspersion among private and public lands (Theobald 2000). An increasing number of people are now building homes on the edges of public lands for increased access to outdoor recreation, scenery, and solitude (Knight and Clark 1998). Consequently, the aura of impacts radiating from each home may extend hundreds of meters to kilometers within the public land boundary and alter biodiversity within this zone. Homes on the periphery of public lands may also attract wilderness species such as bears from the public lands, leading to increased mortality and declines in population sizes within the public lands (Mace and Waller 2002).

In the Greater Yellowstone Ecosystem, for example, national parks, national forests, and other public lands cover the majority (71.6%) of the land area. The private lands are largely in river valleys. These private lands have a longer growing season, better soils, and higher primary productivity than the public lands (Hansen et al. 2000). These same attributes make these settings attractive for native species. Consequently, the distribution of rural homes overlaps significantly with hotspots for birds (Hansen et al. 2002). The rural homes, livestock, and agriculture near the bird hotspots attract nest parasites and predators and result in reduced nest success of several native species (Hansen and Rotella 2002). P. H. Gude, A. J. Hansen, and D. A. Jones (*unpublished manuscript*) found that 49% of deciduous woodlands (the richest bird habitat in the area) across Greater Yellowstone are within 1 km of a home. Hence, even in this large, wilderness system, which is dominated by public lands, the effects of rural homes may extend over a substantial portion of key habitats.

We conclude that like exurban development on the urban fringe, exurban expansion in rural landscapes may have substantial negative impacts on native biodiversity. Considerable research is needed to better understand the effects of rural home density, spatial distribution, and homeowner behavior on biodiversity impacts. A particular concern about exurban development in rural areas is that it is more likely to be in close proximity to public lands and associated wilderness species.

Mechanisms Linking Exurban Development and Biodiversity

The mechanisms underlying these responses to land use are generally less well studied than the patterns described above. Case studies provide insights for some mechanisms, but adequate comparative study and ex-

perimentation is generally not available to allow for derivation of general predictive principles. Below we describe the suite of factors that have been suggested to explain biodiversity responses to exurban and urban development. These involve changes in habitats, ecological processes, interactions among species, and human-related disturbance of native species. Our goal is to encourage additional research on these mechanisms. Beyond improving scientific understanding, knowledge of these mechanisms may provide the basis for management strategies to reduce the effects of exurban development on biodiversity.

Habitat alteration

As human settlement progresses, conversion of native habitat to roads, yards, and structures tend to fragment the landscape (Soulé et al. 1998, Marzluff and Ewing 2001). Fragmentation influences biodiversity through reduction of habitat area, creation of dispersal barriers (Trombulak and Frissell 2000, Marzluff and Ewing 2001), disruption of nutrient cycling, and increases in predation, parasitism, and competition (Marzluff and Ewing 2001). In the Seattle case study, reduction in the area of forest patches was thought to explain the loss of forest-dwelling bird species. Isolation of small canyons in California by subdivisions lessened the dispersal capabilities of and resulted in decreased species diversity for chaparral-requiring birds (Soulé et al. 1988).

In addition to habitat fragmentation, residential development may change microhabitat features. For example, decreasing abundance of native plant cover with increasing urbanization was correlated with decreasing bee, bird, and lizard species richness in Arizona (Germaine et al. 1998, Germaine and Wakeling 2001, McIntyre and Hostetler 2001). In Illinois, replacement of natural sandy patches with grassy patches in a residential area resulted in decreased snapping turtle (*Chelydra serpentina*) nesting success (Kolbe and Janzen 2002). Reduced course woody debris input (Christensen et al. 1996) tied to exurban development in Wisconsin and Michigan lakes reduced growth rates of bluegill sunfish (*Lepomis macrohirus*) but did not significantly affect largemouth bass (*Micropterus salmoides*) (Schindler et al. 2000).

The nonrandom location of land use relative to biophysical gradients and biodiversity may cause the resulting habitat fragmentation resulting from human settlement to have disproportionately large effects. We described above the concentration of rural residences in productive valley bottoms in mountainous landscapes (Riebsame et al. 1996, Theobald et al. 1996, Soulé et al. 1998, Hansen et al. 2002, Seabloom et al. 2002). Other favored settings for RRD include lakeshores in the upper Midwest (Beale and Johnson 1998), coastal areas (Seabloom et al. 2002), and wetlands in the coastal states (Brady and Flather 1994). Because both humans and native species tend to concentrate in such locations (Hansen et al. 2002, Seabloom et al. 2002), the impacts of exurban development may be focused on the most critical habitats (see also Huston 2005).

Alteration of ecological processes

Less visible than habitat destruction, ecological processes such as disturbance regimes may be altered by exurban development and in turn influence habitats and biotic assemblages. In many parts of the arid west, humans have excluded fires from urbanizing landscapes to protect human property and lives. In Oklahoma, for example, such fire exclusion has led to increased juniper (*Juniperus* spp.) encroachment in suburban and rural habitats since 1950, as human population density increased (Coppedge et al. 2001). Correlated with the increase in juniper, the passerine community has also been altered. American Robin and Eastern Bluebird (*Sialia sialis*) abundance showed a unimodal trend with highest abundance at intermediate levels of juniper encroachment. Three species of potential juniper-feeders, Cedar Waxwing (*Bombycilla cedrorum*), Ruby-crowned Kinglet (*Regulus celendula*), and Yellow-rumped Warbler (*Dendroica coronata*), increased with juniper encroachment levels. Four species, Song Sparrow (*Melospiza melodia*), White-crowned Sparrow (*Zonotricha querula*), House Sparrow, and American Goldfinch (*Carduelis tristis*), declined with increased levels of juniper encroachment. In other urbanizing environments, in contrast, increased human ignitions have accelerated fire frequency and decreased later seral habitats (Keeley 2002).

Flood regimes may also be altered with urbanization with consequences for riparian communities. For example, plains cottonwood (*Populus deltoides*) establishment on the floodplain and terrace of Boulder Creek in Boulder, Colorado declined from 1937 to 1992 as stream diversion, straightening, stabilization, and clearing led to decreased channel movement, decreased peak flow and a decreased flooding frequency in the floodplain. Concurrently, species less tolerant to flooding events—including the exotics crack willow (*Salix rubens*) and Russian-olive (*Elaeagnus angustifolia*)—have encroached upon the floodplain (Auble et al. 1997).

Changes to nutrient cycles are also likely with conversion to exurban land uses. Along an urban–rural gradient in New York, nitrogen and phosphorous levels in oak forest soils increased with increasing urbanization (Pouyet et al. 1995). Increased nitrogen availability tends to simplify biotic communities and favor exotic species (Vitousek et al. 1997). Nutrient effects may be particularly manifest in aquatic systems. Natural-amenity exurban development around four Wisconsin lakes has affected water quality and altered diatom communities (Garrison and Wakeman 2000). As

once-seasonal homes along these lakeshores were converted to year-long use, the amount of impervious surface increased and consequently run-off and sediment load to the lakes also increased. Increased levels of phosphorous, iron, and aluminum were tied to a shift from benthic to mainly planktonic diatoms and an increase in diatom taxa indicative of eutrophic conditions. Water quality in the higher alkalinity lakes showed improvement as construction slowed, but the lower alkalinity lakes appeared to be more sensitive to shoreline development, and water quality did not improve in these lower alkalinity lakes.

Alteration of biotic interactions

As human settlement alters species distributions, interactions among species may be changed with consequences for species viability and ecosystem function (Daszak et al. 2000, Marzluff 2001). Best studied among these changes in biotic interactions are predator–prey relationships. As illustrated by the Colorado case study, both native and nonnative predators may become abundant near human development and inflict heavy prey heavily upon other native species. Similarly, Wilcove (1985) found that suburban woodlots in Maryland experienced significantly higher rates of nest predation than did rural woodlots, likely as a result of higher densities of nest predators such as the Blue Jay (*Cyanocitta cristata*), Common Grackle (*Quiscalus quiscula*), gray squirrel (*Sciurus carolinensis*), and raccoon. Some predators may become abundant near human dwellings due to human subsidized food supplies (Marzluff 2001). This may also result from the loss of large carnivores that are intolerant to urbanizing landscapes, and the consequential release of mesopredators that are tolerant to human influences (Soulé et al. 1988, Crooks and Soulé 1999). Herbivores are also released by the elimination of large predators in developed areas, and the increased herbivory by deer and rabbits can have a major effect on plant diversity, both in urban parks and the surrounding landscapes.

Because predator occurrence and tolerance vary geographically, biodiversity response to urbanization may vary among regions of the United States. As described above, native songbird nest success declined in Montana as cowbird density in creased with rural home density (Tewksbury et al. 1998, Hansen and Rotella 2002). In contrast, the absence of Brown-headed Cowbirds in King County, Washington, may be a factor in the lack of nest parasitism in the Seattle case study (Donnelly and Marzluff 2004).

Changes in competitive interactions induced by development are well illustrated by invasive plant interactions with native species. English Ivy (*Hedera helix*) was introduced as an ornamental plant and kills native trees through competition for light (Reichard 2000) in much of the continental United States. Similarly, Norway maple (*Acer platanoides*), a shade tree introduced to eastern deciduous forests, out-competes native maples and beeches (Webb et al. 2001).

Many examples of the spread of infectious diseases related to human settlement exist. These can be classified as (1) human facilitated dispersal or translocation of hosts and parasites, (2) supplemental feeding, and (3) disease "spill-over" from domestic to wild populations (Daszak et al. 2000). Supplemental feeding of white-tailed deer at rural home sites was found to be directly related to the maintenance of bovine tuberculosis in Michigan deer populations (Michigan Department of Natural Resources 1999). Similarly, birdfeeders were found to increase the concentration of House Finches (*Carpdacus mexicanus*) and other bird species, enhancing the spread of mycoplasmal conjunctivitis (Fisher et al. 1997, Nolan et al. 1998). Last, many examples of "spill-over" of infectious diseases to wildlife involve domestic dogs. Canine distemper virus, canine parvovirus, and sarcoptic mange (*Sarcoptes scabiei*) are three pathogens known to have spread due to domestic dog–wildlife interactions, and are suspected to have caused population declines in the endangered gray wolf (*Canis lupus*) and black-footed ferret (*Mustela nigripes*) (Daszak et al. 2000).

Human disturbance

Finally, the presence of humans and their pets around home sites can directly influence biodiversity. Human presence in yards or on trails near homes may displace some species of wildlife. Bald Eagles (*Haliaeetus leucocephalus*), for example, may decline in number in areas with increasing human recreation (Brown and Stevens 1997, Stalmaster and Kaiser 1998). Pronghorn antelope (*Antilocapra Americana*) on Antelope Island State Park in Utah retreated further from trails once they were opened for recreational use (Fairbanks and Tullous 2002). Likewise, elk (*Cervus Canadensis*) approached by humans during calving season, were repeatedly displaced resulting in elevated calf mortality (Phillips and Alldredge 2000).

Pets may also displace, injure, or kill wildlife. Pet cats are responsible for the deaths of millions of birds in the United States every year, and in Wisconsin alone, an estimated 39 million birds per year are lost to domestic cats (Coleman and Temple 1996). Pet dogs also act as predators in many ecosystems. In Florida, pet dogs have effected the distribution of the endangered key deer (*O. virginianus clavium*), and are suspected to have eliminated them from several islands in the Florida Keys. In Colorado, the flushing distance of ungulates to human hikers was increased if a pet dog was present (Miller et al. 2001). Because rural pets kill more than their suburban and urban counterparts, adverse effects on native species are potentially greatest in the undisturbed habitat near new rural residential developments (Barratt 1998).

Another direct consequence of suburban and exurban residential growth in the United States has been an increase in vehicle miles traveled per person and per household, escalating the potential for roadkill. Between 1980 and 2000, overall per capita vehicular travel in the United States increased by 48.7%, of which the fastest growing component was "home-based" travel, including shopping, recreation, and driving to school. Although mortality of animals from collision with vehicles is best documented in large mammals, few terrestrial species are immune (Trombulak and Frissell 2000). Roadkill has affected the demographics and migrations of birds, snakes, invertebrates, and amphibians, and is a major cause of mortality for moose, lynx (*Felis pardina*), wolves, and American crocodile (*Crocodilus acutus*) in various regions of the United States (Trombulak and Frissell 2000).

Conclusion

Our major conclusion is that exurban development is a pervasive and fast-growing form of land use that is substantially understudied by ecologists and has large potential to alter biodiversity. Covering about 25% of the land area of the conterminous United States in 2000 (Brown et al. 2005), area in exurban land use increased since 1974 at rates in excess of area in urban or agricultural land uses. Ecologists have traditionally focused research on wild or semi-wild lands (Miller and Hobbs 2002). The relatively few studies on exurban development are mostly done as contrasts to urban land use. Consequently, knowledge of the effects of exurban density, spatial configuration, and homeowner behavior on biodiversity, and specific mechanisms for response is poorly developed.

The relatively few studies on exurban development suggest that its impacts on biodiversity may be substantial, both in the immediate vicinity of homes and even on adjacent or even distant public lands. These impacts are summarized as follows.

1) Many native species incur reduced survival and reproduction near homes and consequently native species richness generally drops with increased exurban densities. At the same time, some exotic species and some human-adapted native species generally increase with intensity of exurban development.

2) The relationship between these elements of biodiversity and intensity of exurban development are sometimes nonlinear, with sharp thresholds were biodiversity changes abruptly with incremental increases in exurban intensity. Knowledge of these thresholds is important for managing exurban development to achieve biodiversity objectives.

3) These affects may be manifest for several decades following exurban development, so that biodiversity is likely still responding to the wave of exurban expansion that has occurred since 1950.

4) The location of exurban development is often nonrandom relative to biodiversity because both are influenced by biophysical factors such that they are concentrated in more equitable landscape settings. Consequently, the effects on biodiversity may be disproportionately large relative to the area of exurban development.

5) The effects of exurban development on biodiversity likely differ among ecosystem types. Additional research is needed to derive generalities on the types of ecosystems that are relatively vulnerable to exurban development.

6) An identifiable set of ecological mechanisms link exurban development and biodiversity. More research is needed on these mechanisms and the resulting knowledge can help with understanding, managing, and mitigating these impacts.

7) In addition to local effects, exurban development may alter ecological processes and biodiversity on adjacent and distant public lands. Consequently, exurban development in rural areas may have even more important impacts than in the urban fringe because of the elevated influence on lands dedicated to conservation and on wilderness species that are rare in human-dominated landscapes.

It is our hope that this review inspires the additional research that is needed to better understand and manage the impacts of this important type of land use.

Acknowledgments

We thank the NASA Land Cover Land Use Program, the EPA Regional Sustainability Programs, and the National Science Foundation (DEB-9875041, BCS-0120024, IGERT-0114351) for financial support. Josh Newell drafted Fig. 1. Michael Huston, two anonymous reviewers, and editor Monica Turner provided helpful comments on the manuscript.

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