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Authors: Hansen, Andrew J., East, Alyson, Ashford, Zane, Crittenden, Cassidy, Jakabosky, Olivia, et al.

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Integrating Ecological Value and Charismatic Species Habitats to Prioritize Habitats for Conservation: A Case Study from Greater Yellowstone

Andrew J. Hansen,^{1,8} Alyson East,¹ Zane Ashford,² Cassidy Crittenden,¹ Olivia Jakabosky,¹ Daniel Quinby,¹ Laura Gigliotti,³ Frank T. van Manen,⁴ Mark A. Haroldson,⁴ Arthur Middleton,⁵ Nathaniel Robinson,⁶ and David M. Theobald⁷

¹Ecology Department, Montana State University, Bozeman, MT 59717

²Land Resources and Environmental Sciences Department, Montana State University, Bozeman, MT 59717

³U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, Morgantown, WV 26506

⁴U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Bozeman, MT

⁵Department of Environmental Science, Policy, and Management, University of California Berkeley, Berkeley, CA 94720

⁶The Nature Conservancy, Arlington, VA

⁷Conservation Planning Technologies, Fort Collins, CO

⁸Corresponding author: hansen@montana.edu

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ABSTRACT

Expanding human pressure has reduced natural habitats globally and motivated strategies to conserve remaining natural habitats. Decisions about conservation on private lands, however, are typically made by local stakeholders who are motivated by the elements of nature they most highly value. Thus, national prioritization for conservation should be complemented by local analysis of species or habitats that most influence local land-owner decisions. We demonstrate within the Greater Yellowstone Ecosystem how quantitative mapping of wildlife species that are highly valued by local residents can be integrated with indices of ecosystem integrity to prioritize private lands for conservation. We found that natural vegetation cover (NVC) comprised 81% of the private lands. Some watersheds have lost 6% of NVC since 2001 and developed lands now cover >40% of their areas. Locations high in ecological value, elk habitat, and grizzly habitat occurred in different biophysical settings. Consequently, only 2% of the NVC supports high levels of all three biodiversity measures and 26% of this area was within conservation easements. The remaining areas of high biodiversity value that are unprotected are priorities for conservation. We suggest that national-scale conservation planning will be most effective on private lands if additional within-ecoregion analyses are done on the elements of biodiversity that are most valued by local people.

Index terms: biodiversity value; ecoregion-scale analysis; elk; grizzly bear; habitat loss; natural habitat; prioritizing conservation; Yellowstone

INTRODUCTION

A cornerstone in nature conservation is maintaining natural ecosystems (Hunter et al. 2021). Such ecosystems are composed of viable assemblages of native species and human activity has not modified primary ecological functions and species composition (CBD 2022a). They are valued because they maintain biodiversity, provide ecosystem services, and foster resilience under projected climate change (Watson et al. 2018). Maintaining natural ecosystems is increasingly challenging because of human modification—some 51% of global terrestrial lands have moderate to high levels of human modification (Kennedy et al. 2019). Consequently, biodiversity strategies focus on retaining and restoring natural ecosystems. Currently under debate is how much and which natural ecosystems to protect (Wilson 2020). This is particularly relevant to the Greater Yellowstone Ecoregion (GYE), where human development on private lands threatens ecosystem integrity (Hansen and Phillips 2018).

Both the United States and countries participating in the Convention on Biodiversity aspire to protect 30% of land and waters by 2030 (The White House 2021; CBD 2022b). To achieve this goal internationally, scientists have recommended a “no net loss” approach to conservation (Leadley et al. 2022). This involves halting the degradation of natural ecosystems, restoring transformed ecosystems, and rehabilitating degraded ecosystems. Within the United States, the *America the Beautiful Program* mandates reaching the habitat goal largely through voluntary conservation of private lands (The White House 2021). A crucial need for the US conservation plan is to identify lands that are most valuable and efficient in achieving national conservation goals (Belote et al. 2021). This requires consideration of biodiversity values and threats at multiple spatial scales including national, regional, and local (USFWS 2022).

In the United States, both public and private lands are vital to reaching biodiversity conservation goals. The extensive network of federal lands has contributed greatly to conserving

biodiversity (Keiter 2020). However, it is increasingly recognized that private lands play a critical role in achieving conservation goals (Merenlender et al. 2004; Clancy et al. 2020). Private lands are often located at lower elevations with more mesic habitats and fertile soils and thus are often more ecologically productive (Scott et al. 2001). Consequently, richness and abundance of native species are often highest on unaltered private lands (Jenkins et al. 2015; Chapman et al. 2022). Due to the likelihood of land conversion, concern for threatened species is particularly high on private lands (Hilty and Merenlender 2003).

Human pressure on private lands in the western United States has increased in recent decades due to a wave of natural amenity migration that brings people to rural settings (Theobald et al. 2016). This trend has major social and environmental implications (Hjerpe et al. 2022). Regions with high levels of natural amenities have seen land-use intensification, which ultimately threatens the initial attractants of open space, clean air, and intact ecosystems (Hansen et al. 2022). Protected areas, such as national parks, have acted as centerpieces for amenity-based development (Power and Barrett 2001). Thus, protected areas themselves contribute to population growth and urban sprawl, and ultimately challenge conservation success in the surrounding areas.

The important role that private lands play in conservation and the high pressure to develop these lands led to a study by some of us (Hansen et al. 2021, 2022) on natural habitat values and threats in the northwestern United States. The sub-national scale study included ecoregions across the Rocky Mountains to the Pacific Coast in Colorado, Wyoming, Montana, Utah, Idaho, Washington, and Oregon (hereinafter referred to as the Pacific and Inland Northwest U.S. or PINW). That study asked: where are the remaining areas of natural vegetation cover (NVC) on private lands and which ecoregions and communities have had the highest rates of loss during 2000–2010; which remaining NVC on private lands is the highest priority for biodiversity conservation based on ecological value and risk of development; and are conservation easements in NVC placed preferentially in locations of high biodiversity conservation priority?

The study by Hansen et al. (2021, 2022) found that natural habitats were most proportionately abundant in more remote ecoregions such as the Wyoming Basin and Greater Yellowstone. However, biodiversity value and risk of habitat loss were highest in areas with more mesic climate, fertile soils, closer proximity to urban markets, with high suburban and rural development and with high natural amenities. This described ecoregions in western Washington and Oregon, the Uinta Wasatch area of Utah, and the Colorado mountains. The study findings showed that conservation easements did not preferentially target these high-priority areas.

Conservation easements are agreements between landowners and conservation easement holders in which landowners agree to restrictions on land use to achieve conservation purposes in exchange for payment, tax benefits, or development permits (Owley and Rissman 2016). The purposes for easements typically involve maintenance of open space, agricultural lands,

scenic value, water resources, recreation, wildlife habitat, and natural ecosystems (Farr et al. 2018). While it is widely assumed that easements created for open space, agriculture, scenery, recreation, natural habitats, and water resources also contribute to wildlife and natural habitat protection, evidence of this is mixed (Farr et al. 2018; Graves et al. 2019; Bargelt et al. 2020). These studies largely conclude that existing conservation easements underperformed with regard to various biodiversity conservation objectives.

While some researchers have also criticized investments in conservation easements for not targeting the most important habitat for species of concern or areas that are not the most at risk of land-use conversion (see Bennett et al. 2021), this outcome is a product of at least two realities of the conservation easement process. One of these is the fact that land trusts typically operate by working with willing landowners in a voluntary manner, limiting their ability to strategically target based on biodiversity conservation metrics (Merenlender et al. 2004). Each landowner has unique goals, distinct financial needs, and different land and resource endowments. Each land trust also has its own priorities, style of operation, and varying resources for making transactions and stewarding easements. The differences result in the variety of easement types described above. A second reality is that information on which lands are the highest priorities for conservation is often lacking (Merenlender et al. 2004). Some conservation biologists have developed methods for prioritizing protected-area acquisition (Abbitt et al. 2000; Margules et al. 2002; Hansen et al. 2022). In addition, public resource agencies, such as the Natural Resource Conservation Service, have developed methods to rank land parcels based on local resource evaluation and site considerations (see Merenlender et al. 2004). Also, the Land Trust Alliance has partnered with the Cornell Lab of Ornithology to support land trusts in prioritizing bird conservation (<https://landtrustalliance.org/blog/conservation-it-s-for-the-birds>). However, key data on conservation priority continues to be lacking, and there is a particular need for more detailed conservation priority at more local scales such as within ecoregions.

Many conservation organizations operate locally to regionally. They are often guided by biodiversity values and threats as perceived by people within the region. Moreover, key scientific data sets are sometimes available within ecoregions and allow more detailed analysis than can be done nationally. Thirdly, the *America the Beautiful Program* relies on conservation implementations by private landowners, who typically are most interested in local and regional conservation issues and needs.

In this study we demonstrate downscaling the methods of the Hansen et al. (2021, 2022) study to an individual ecoregion, the Greater Yellowstone Ecoregion (GYE). The GYE is of high interest for several reasons. It is home to some of the most charismatic megafauna on the continent and is known as one of the largest intact wildland expanses in the contiguous United States (Middleton et al. 2020). The GYE has experienced a transition to a “New West economy,” a multidecadal shift away from agriculture, timber, and mining and toward nonlabor

industries and amenity consumption (Haggerty et al. 2018). Coinciding with this economic transition, the human population within the GYE has doubled and housing density has tripled since 1970, and both are predicted to double again by the year 2050 (Hansen and Phillips 2018). Currently, 31% of the area of GYE is human-modified (Hansen and Phillips 2018). Conservation easements cover 14% of the private lands in the GYE but how well they protect areas of high biodiversity value is not well known until now. The goal of this study was to provide objective information and help facilitate implementation of a “no net loss strategy” on private lands in the GYE.

To achieve this goal within this ecoregion, we modified the sub-national analyses of Hansen et al. (2021, 2022) in three ways. We added to the ecological value themes consideration of habitat of two of the most highly valued wildlife species, elk (*Cervus canadensis*) and grizzly bear (*Ursus arctos*). We scaled the analyses down to the watershed level to reveal spatial variation within the ecoregion. Thirdly, we used a new land-use layer that allowed analyses not only for the period 2000–2010 as in the subcontinental study, but also 2000–2019 to reveal more recent land-use change.

The sub-national study of Hansen et al. (2021, 2022) ranked ecological value of NVC by an index that integrated national data sets on net primary productivity, vertebrate species richness, imperiled species, ecosystem representation in protected areas, and connectivity for forest mammals among protected areas. In the current study, we added consideration of elk and grizzly bear habitat to the analysis. This was done to represent biodiversity value of natural habitats in ways most tangible and meaningful to the people that influence conservation decisions within the ecoregion. We reasoned that the study would more highly motivate conservation concern and action if it included consideration of wildlife species that are highly valued within the region.

Elk are the most abundant large herbivore in the ecoregion and are of high importance in shaping plant communities, providing a major food source for large predators and scavengers, and being a major game species for human hunters (Middleton et al. 2020). We include them in this analysis because of the ecological (Middleton et al. 2020) and economic (Maher et al. 2023) benefits they provide and because of the high interest of diverse stakeholders in maintaining elk habitat in the GYE, including on private lands. Many GYE elk migrate seasonally to access high-quality forage, which enhances their survival and reproduction (Middleton et al. 2018). Elk migration has shown to be reliant on private lands, with some herds moving off public lands for up to 80% of the winter season (Middleton et al. 2020, 2022). Human modification of the landscape can be detrimental to migratory elk herds, disrupting habitat connectivity and preventing elk from accessing viable habitat (Gigliotti et al. 2022).

Bears are excellent flagship species for conservation (Simberloff 1999). By virtue of their low densities and large home ranges that require extensive areas of relatively undisturbed habitat, grizzly bears also serve as an effective umbrella species whose maintenance on the landscape benefits

many other species (Simberloff 1999). Grizzly bears are a high-profile species in the GYE owing to their threatened status under the US Endangered Species Act (van Manen et al. 2017). For these reasons, grizzly bears motivate substantial efforts in the western United States and Canada to protect habitat, enhance landscape connectivity, and reduce human–bear conflicts through conservation easements and purchases of private lands (e.g., Proctor et al. 2018). We also recognize that large carnivores can be controversial and polarizing in the context of private land conservation; however, our experience is that grizzly bears are a major motivating factor for a number of large NGOs and land trusts (e.g., Yellowstone to Yukon, Vital Grounds, The Nature Conservancy) in the region working on land conservation as well as reducing human–bear conflicts (e.g., Defenders of Wildlife).

Conflict with humans is the dominant cause of documented mortality for bears past the age of independence (i.e., ≥ 2 years of age) in this population and is most prominent at the interface between human development and wildlands (Schwartz et al. 2010). These border areas typically represent population sinks (i.e., population growth $[\lambda] < 1$), with core regions as source populations (i.e., $\lambda \geq 1$). Increases in human pressure on private lands may convert grizzly bear source areas to sink areas.

We addressed the following research questions in the GYE: (1) where are the remaining natural habitats on private land and what has been the rate of loss; (2) which of these natural habitats are most valuable ecologically from the perspective of high-profile species of elk and grizzly bear, and for other measures of ecological value (primary productivity, species richness, imperiled species, connectivity); and (3) to what extent have conservation easements targeted natural habitats of highest biodiversity value and how could this be better realized in the future? The purpose of the study was to provide objective scientific information to inform conservation within this particular ecoregion and to demonstrate methods for assessing conservation priorities within individual ecoregions that complement those used across ecoregions for national-scale priorities assessment. The primary outcome of the study is to provide additional information on conservation priorities for those land trusts and land owners that wish to consider conservation priority among their criteria for enabling easements.

METHODS

Study Area

We used the Environmental Protection Agency (EPA) Level III Greater Yellowstone Ecoregion (Omernik 1987) as the extent of the study area (Figure 1). The boundaries of the ecoregion roughly coincide with the various definitions of the GYE that was first defined as the range of Yellowstone grizzly bears (Craighead 1991) and later based on ecological and socioeconomic factors (e.g., Hansen et al. 2002). Approximately 64% of this 97,985 km² ecoregion is in federal ownership and includes three national park units, five national forests, and other federal jurisdictions. Tribal lands occupy 6.2% of the GYE.

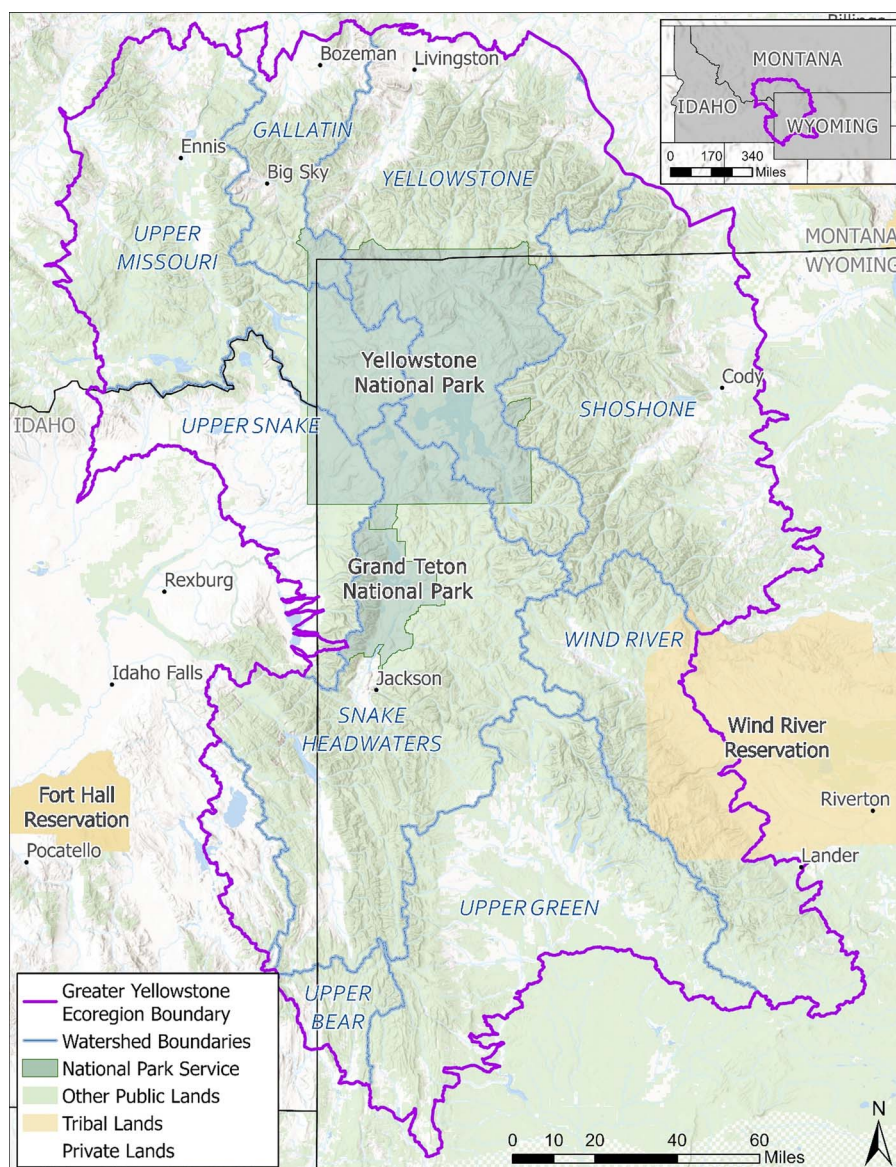


Figure 1.—Map of the Greater Yellowstone Ecoregion study area (Omernik 1987) showing the distribution of public lands, tribal lands, and watershed boundaries used in this study. (See online version of this journal for full-color figures.)

Private lands cover 31% of the ecosystem and include portions of 20 counties across Wyoming, Montana, and Idaho. The federal lands provide a powerful economic engine that has created a diverse regional economy supporting quality of life, agriculture, and outdoor recreation (Quammen 2016). We evaluated land-use patterns on private lands within watersheds (Hydrologic Unit Code 6 and 8 boundaries; Jones et al. 2022; Table 1). Our objective in defining the watershed units was to identify landscape units that fit established watershed boundaries and were relatively homogeneous in rates of population growth and land-use change. Population growth during 2000–2020 for the watersheds was derived from the US Census Bureau 2020 data (<https://www.census.gov/programs-surveys/decennial-census/decade/2020/2020-census-main.html>) by using the proportional overlap of counties within watersheds to scale the values.

Question 1: Natural Vegetation Cover and Loss

We drew on the methods of Hansen et al. (2021) to define land-use classes and rates of loss of natural habitats. We summarize those methods here and describe modifications made for this analysis.

The land-use classes that were mapped included natural vegetation cover (NVC), developed, and agriculture (Table 2). NVC was defined as areas where native vegetation is the dominant land-cover type with no detectable agriculture or impervious surface cover resulting from residential, urban, or human infrastructure. As in Hansen et al. (2021) these classes were mapped based on data from the 30-m raster National Land Cover Database (NLCD) 2000 (Jin et al. 2019), which is well suited to mapping rural residential development. NLCD data for 2000 and 2010 were used in Hansen et al. (2021). In this analysis, NLCD for 2019 had become available and was used in

Table 1.—Watershed delineations at the Hydrological Unit Code (HUC) 8 and HUC 6 level (Jones et al. 2022) for this analysis, based on socioeconomic condition, population growth (2000–2020), and rates of land-use change across the Greater Yellowstone Ecosystem study area.

Watershed	HUC 8	HUC 6	Population growth
Upper Missouri	Madison, Jefferson, Beaverhead, Ruby, Red Rock	Upper Missouri	53.0%
Gallatin	Gallatin	Upper Missouri	73.6%
Yellowstone	Yellowstone Headwaters, Upper Yellowstone, Stillwater, Shields	Upper Yellowstone	16.0%
Shoshone	Clark Fork of the Yellowstone	Upper Yellowstone	13.3%
	North Fork Shoshone, South Fork Shoshone, Shoshone, Dry, Greybull	Big Horn	
Wind River	Upper Wind, Little Wind, Popo Agie	Big Horn	9.9%
	Sweetwater	North Platte	
Upper Green	Upper Green, New Fork, Big Sandy, Blacks Fork	Upper Green	42.2%
Upper Bear	Upper Bear, Bears Lake	Upper Bear	22.1%
Upper Snake	Beaver-Camas, Upper Henrys, Lower Henrys, Teton, Willow, Blackfoot	Upper Snake	33.0%
Snake Headwaters	Snake Headwaters, Gros Ventre, Greys-Hoback, Salt, Palisades	Snake Headwaters	41.8%

this analysis. In addition to NLCD, the National Land Use Data set (NLUD) (Theobald 2014) was used by Hansen et al. (2021). For the current analysis, we updated the Human Modification (HM) data set of Theobald (2013) to 2019. The HM map estimates the intensity of 13 anthropogenic stressors on the landscape at resolution of 90 m, providing a continuous metric of 0–1 of the ecological condition of the land (Theobald 2013). This approach more accurately maps rural residential development, which is prevalent in the GYE, than the NLUD data set. NVC was mapped as areas with low human modification ($HM < 0.15$) and natural vegetation cover classes in NLCD. We defined agriculture based on NLCD classes pasture/hay or cultivated crops.

From the resulting maps of land use, we summarized the proportion of private land comprising each class in 2019 across the study area and within individual watersheds. We also quantified rates and directions of change among the three classes between 2001 and 2019. The change assessment was done for a random sample of 209,769 locations throughout the entire GYE that we generated using a minimum distance criterion of 90 m, reducing spatial autocorrelation and ensuring that no adjacent raster cells were sampled.

Table 2.—Land-use classes mapped across the Greater Yellowstone Ecosystem study area.

Land-use class	Human modification level (Theobald 2013)	National Land Cover Dataset class (Jin et al. 2019)
Natural vegetation cover	< 0.15	12 Perennial ice/snow 31 Barren land 41 Deciduous forest 42 Evergreen forest 43 Mixed forest 52 Shrub/scrub 90 Woody wetlands 95 Emergent herbaceous 71 Grassland/herbaceous
Developed	≥ 0.15	21 Developed, open space 22 Developed, low intensity 23 Developed, medium intensity 24 Developed, high intensity
Agriculture	≥ 0.15	81 Pasture/hay 82 Cultivated crops

Additionally, we quantified the change in mean HM of areas that did not undergo any transition between land use classes between 2001 and 2019 using paired *t*-tests. For this analysis we used the classifications of NVC and agriculture, as described above, and divided the developed lands into four classes based on development intensity as defined by NLCD: open space, low, medium, and high intensity.

Question 2: Habitat Value

To quantify the “biodiversity” value of NVC, we used the Ecological Value Index layer from Hansen et al. (2022), geospatial data of elk winter and migration habitat (Gigliotti et al. 2022), and spatially explicit estimates of female grizzly bear survival (Schwartz et al. 2010). Consistent with the concept of ecological integrity, Hansen et al. (2022) selected ecological metrics for valuation that represented elements of ecological structure, function, and composition. The ecological metrics were connectivity for forest-dwelling large mammals among greater wildland ecosystems, net primary productivity, vertebrate species richness, protection-weighted range-size rarity of imperiled species, and ecosystem representation (see table 1 in Hansen et al. 2022). In the current study, we used upper 10% of the Ecological Value Index to represent locations of high ecological value.

Elk habitat was determined using spatial data from Gigliotti et al. (2022). This study used previously collected GPS (global positioning system) collar data spanning 2000–2020 from 26 of the elk herds within the GYE. Due to the difficulties of trapping animals across such a large spatial extent, the total number of herds in the GYE is not yet documented. However, the data set we used is the most comprehensive available for elk in the GYE. Both migratory and nonmigratory elk were included in the data set. Polygons of seasonal habitats were created for each herd based on 99% isopleths using Brownian bridge movement models. We used data only from winter and migratory ranges and excluded summer habitat, which is mostly on public land. Elk habitat was scored on a binomial scale with a value of 1 signifying the pixel of land as winter habitat, migration range, or both.

Grizzly bear habitat was represented as population source areas as defined by Schwartz et al. (2010). They modeled female

survival using a set of environmental and anthropogenic covariates, and found that road density, level of human development, and land management and hunting regulations within home ranges best explained variation in survival estimates. They mapped population source areas where female survival was predicted to be ≥ 0.91 , the threshold value associated with annual population growth (λ) ≥ 1 , whereas areas with $\lambda < 1$ were considered sink areas. The spatial extent of the grizzly bear source/sink map was a rectangle centered on public lands of the GYE. This extent was smaller than the study area. Although we were able to draw inference on grizzly source habitats only for 69.9% of the GYE study area, this area covered 93.3% of the range occupied by grizzly bears in 2022 (Dellinger et al. 2023). Next, we analyzed the biophysical and land-use setting of high values for each of the three layers using a series of generalized additive models (GAMs). GAMs were used due to their relative ease of interpretation and lack of a priori assumptions about the shape of the response relationship. The candidate predictors were elevation, slope, aspect, landform, vegetation type, and human modification (Appendix Table 1). Model selection was done using AIC. All GAMs relied on a binomial distribution such that 1 represented the occurrence of high values for the response variable and 0 all other values.

We combined the three main metrics of biodiversity value (high ecological value, elk habitat, grizzly source area) to quantify the number of biodiversity layers that occurred for any location in the study area (0, 1, 2, or 3). We do not, of course, claim that these maps are representative of all components of biodiversity. Many studies have demonstrated that spatial patterns often differ among various elements of biodiversity (e.g., Belote et al. 2021). Rather, the maps quantify some elements of ecological integrity and habitats for two species that are likely to influence conservation decisions in this ecoregion, which is appropriate given the goals of this study.

Question 3: Conservation Easements

Similar to Hansen et al. (2022), we evaluated the current distribution of conservation easements among land-use types and numbers of biodiversity layers. The existing conservation easements across the GYE were obtained from the National Conservation Easement Database through 2019, the latest year available (NCED 2020). We overlaid the conservation easement layer onto the land allocation layer and quantified the proportion of each land-use type covered by conservation easement vs. non-easement. We similarly quantified the proportion of locations of 0, 1, 2, and 3 biodiversity layers covered by conservation easements. In these analyses, we did not distinguish conservation easements by type (e.g., environmental vs. other) as was done in Hansen et al. (2022) because this metric in the NCED is not considered accurate by some land trusts in the GYE.

We overlaid the easement and non-easement layers on areas delineated as NVC and estimated the proportion of land in easements in each land-use class. Because land-use types and biodiversity layers differed in spatial extent, we evaluated if the distribution of easements was random and proportional to the

area or showed preference towards land-use types and numbers of biodiversity layers. To do so, we used a stratified random sample to control for differences in extent of easements and to reduce spatial autocorrelation among the data points. We used a series of chi-squared tests to determine if there was a difference between easements vs. non-easements with respect to placement on land-use types or biodiversity score. We used 10,000 samples from easements and 10,000 from non-easements.

RESULTS

Question 1: Natural Vegetation Cover and Loss

Natural vegetation cover comprised 81% of the private lands of the GYE in 2019 (Figure 2). The remaining private lands across the study area were comprised of agricultural (14%) and developed (5%) lands. Land use varied among watersheds (Table 3). The Yellowstone, Upper Missouri, and Wind River watersheds had the highest proportions of NVC (86–92%) and lowest levels of developed and agriculture. The Gallatin Watershed was notable in high levels of developed (15%) and agriculture (27%) with NVC covering only 58% of private lands. The Snake Headwaters Watershed was also relatively high in developed (9%) and agricultural lands (24%).

About 1% of the NVC across the GYE was converted to developed or agriculture classes during 2001–2019. The proportion of NVC lost was highest in the Gallatin (–6.1%) and Snake Headwaters (–5.8%) watersheds. In addition to the change from natural to developed, habitats underwent an increase in human pressure. Human Modification (HM) increased substantially in the NVC class (24.9%, paired *t*-test, $t = -24.8$, $p < 0.001$), moderately in the developed, open space class (3.1%, paired *t*-test, $t = -13.7$, $p < 0.001$), and less in the three higher intensity developed classes (1.50%, 1.05%, and 0.64%; paired *t*-tests, $t = 0.73$, -4.28 , and -0.84 ; $p = 0.466$, $p < 0.001$, and $p = 0.404$), respectively. HM decreased in the agriculture class (–2.9%, paired *t*-test, $t = 22.9$, $p < 0.001$).

Question 2: Habitat Value

Ecological Value Index: The combined Ecological Value metric was relatively high on private lands in the northern and southwest portions of the study area (Figure 3), particularly in the Gallatin (53.8%), Upper Green (70.2%), and Upper Bear Watersheds (66.7%) (Table 4). The individual layers that comprise the Ecological Value Index varied in spatial pattern across private lands of the GYE. Connectivity among greater wildland ecosystems was relatively high in the northwest and southwest portions of the GYE, as influenced by proximity to the Selway Bitterroot and Crown of the Continent ecosystems to the west and north of the GYE, and the Uinta-Wasatch-Cache Ecosystem in Utah. Both net primary productivity and vertebrate species richness were associated with lower-elevation forests, reaching peak levels on private lands in the more forested western portion of the GYE. Poorer representation in protected areas was highest in the lower-elevation grassland, shrubland, and riparian forest habitats. The Ecological Value Index was statistically associated with mid elevations, moderate

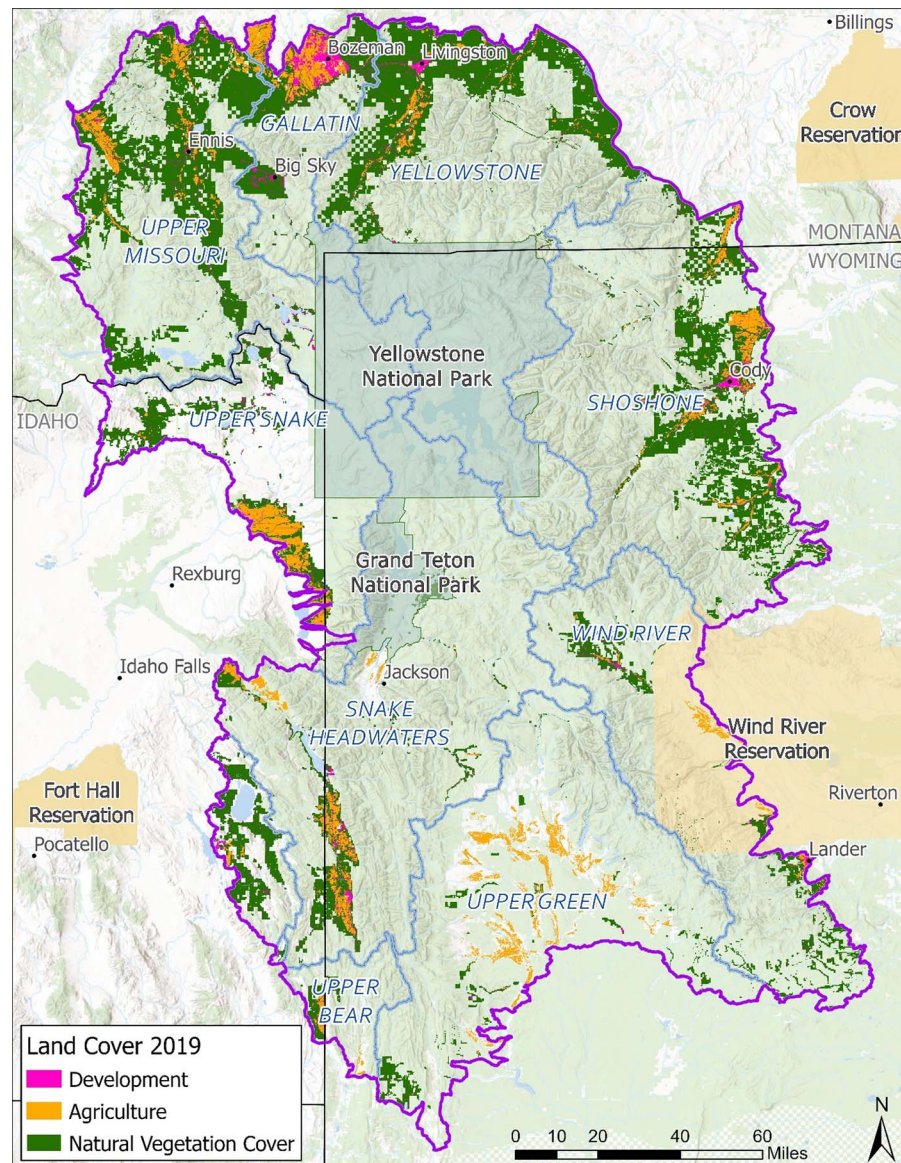


Figure 2.—Distribution of land-use types on private lands across the study area in 2019. The areas within the GYE boundary in white are of uncertain ownership. They are labeled “Undetermined” in the BLM ownership map we used as a base. They may include private as well as land from other jurisdictions. We excluded these areas from the analyses. (See online version of this journal for full-color figures.)

slopes, higher canopy cover, deciduous and evergreen forest cover, and lower human modification ($p < 0.001$, $R^2 = 0.159$).

Elk Habitat: Elk winter and/or migration habitat covered 36.2% of the NVC on private lands in the study area (Figure 3). These habitats were most extensive in the Shoshone (65%), Wind River (38%), and Upper Green (38%) watersheds (Table 4). These habitats were statistically associated with lower elevations, flatter slopes, valley bottom landform, and lower human modification ($p < 0.001$, $R^2 = 0.005$). Although statistically significant, the low R^2 indicates very little variation was explained by the model.

Grizzly Bear Habitat: The extent of grizzly bear mapping did not extend over the full study area (see inset in Figure 3). Watersheds varied from having about 50% of the natural vegetation cover within the bear analysis extent to 100% (Table

4). Within the area mapped, female grizzly survival was above the replacement level of >0.91 (i.e., source areas) on only 16% of the private land NVC. This metric was well below the bear population growth threshold in most areas of NVC, especially in valley bottoms where roads and human structures were more prevalent. Grizzly bear source areas on private lands were best represented in NVC in the Upper Bear (28%), Shoshone (27.5%), and Upper Snake (20.7%) watersheds. Source areas were statistically associated with higher elevations, steeper slopes, peak/ridge landforms, coniferous forest vegetation, and low levels of HM ($p < 0.001$, $R^2 = 0.263$).

Combined Biodiversity Layers: Areas high in Ecological Value Index, grizzly bear population source areas, and elk winter/migration habitats varied across the GYE (Figure 4). Some 46.1% of the NVC on private lands in the study area met

Table 3.—Proportional distribution of three land-use classes (natural vegetation cover [NVC], developed [Dev], agriculture [Ag]) across the Greater Yellowstone Ecosystem study area among each spatial unit in 2001 and 2019.

Spatial unit	Land-use class	2001	2019
Study area	NVC	82	81
	Dev	4	5
	Ag	14	14
Upper Missouri	NVC	89	88
	Dev	2	2
	Ag	8	9
Gallatin	NVC	62	58
	Dev	13	15
	Ag	25	27
Yellowstone	NVC	93	92
	Dev	3	3
	Ag	4	5
Shoshone	NVC	86	85
	Dev	3	3
	Ag	11	11
Wind River	NVC	86	86
	Dev	5	5
	Ag	9	9
Upper Green	NVC	77	79
	Dev	2	3
	Ag	21	18
Upper Bear	NVC	82	80
	Dev	3	3
	Ag	15	17
Upper Snake	NVC	75	74
	Dev	4	4
	Ag	21	22
Snake Headwaters	NVC	71	67
	Dev	8	9
	Ag	20	24

one of these criteria, 16.3% met two of the criteria, and 2.2% met all three. The coverage of all three habitat layers was highest in the Shoshone watershed (5.1%) and lowest in the Upper Bear watershed (0%) (Table 5). Examples of locations where the presence of the three biodiversity layers coincided with loss of NVC to development were around Big Sky, Montana, and Star Valley, Idaho (Figure 5).

Question 3: Conservation Easements

Conservation easements were about 5% more likely to be placed in NVC than expected based on the area of NVC and slightly less likely to be placed in developed and agriculture classes than expected ($\chi^2 = 452.5$, $p < 0.001$). Conservation easements covered 15.7% of NVC, 8.3% of agricultural areas, and 4.8% of developed areas (Table 6). Within the GYE, the Upper Madison, Gallatin, and Yellowstone watersheds stood out with higher proportions of NVC in easements (Appendix Table 2). Conservation easements were slightly more likely to be placed in areas of 2 and 3 biodiversity layers than expected based on the area of the biodiversity zones ($\chi^2 = 407.7$, $p < 0.001$). The area covered by conservation easements was highest where the three biodiversity measures overlapped (26.5% of area) and least (11.7%) in areas of one biodiversity layer (Table 7).

DISCUSSION

The context for achieving “no net loss” of natural habitats varies globally based on human pressure and land-use history. Locke et al. (2019) recognize three conditions that characterize large regions of the world: cities and farms, shared lands, and large wild areas. They recommend broad conservation strategies for each condition. Global- and national-scale studies of biodiversity and human pressure (e.g., Kennedy et al. 2019; Dietz et al. 2020; Belote et al. 2021) provide a basis for identifying the ecoregions that fit into each of these conditions. The sub-national study by Hansen et al. (2021, 2022) provided information that could be used to evaluate which of the 15 ecoregions studied best approximated each of these conditions. The GYE was representative of the “large wild areas” condition where the priority is to maintain existing natural habitats and the natural processes and migrations within them. Achieving conservation objectives under the condition of large wild areas is challenged by the reality that most of the ecologically valuable private lands have few legal mandates to protect biodiversity and that economic pressures to develop these lands are often high, in part due to their high level of natural amenities. The purpose of this study was to scale down from the sub-national study to do finer-scale analyses to inform conservation decision making within an individual ecoregion.

Hansen et al. (2021, 2022) found that the GYE had among the highest proportions of NVC and lowest levels of Developed and Agriculture on private lands among the 15 ecoregions studied. Although the area of NVC lost to development during 2001–2011 was relatively low in GYE, the proportional loss of NVC was intermediate relative to all ecoregions. Some locations within the GYE (e.g., the Bozeman/Big Sky, Montana area) were used as examples of fast developing places. The probability of conversion of NVC to Developed based on 2011 conditions was low in the GYE relative to most other ecoregions. The average Ecological Value Index for NVC in the GYE was relatively low compared to ecoregions in the western and southern portions of the study area. Consequently, a Biodiversity Conservation Priority Index based on ecological value and risk of loss of NVC was lower in GYE than in 11 of the 15 ecoregions. In total, these results indicated that the GYE was a lower priority for conservation than ecoregions in western Washington and Oregon, Utah, and the Colorado mountains.

Our current study focusing on GYE confirmed that NVC was expansive here, comprising 81% of private lands. As mentioned previously, this coverage by natural habitats is large relative to ecoregions across the PINW where NVC ranges from 40% to 88% of private lands (Hansen et al. 2022). The rate of loss of NVC to development and agriculture across the GYE during 2001–2019 was only 1%, suggesting natural habitats in the ecoregion have not been under substantial risk of loss. However, the loss rates differed substantially among watersheds. The Wind River and Yellowstone watersheds had 86% and 92% NVC coverage and loss rates of only 0.02–0.77% in 2019. In contrast, the Gallatin and Snake Headwaters watersheds had only 62% and 71% NVC coverage, respectively, and NVC loss rates of

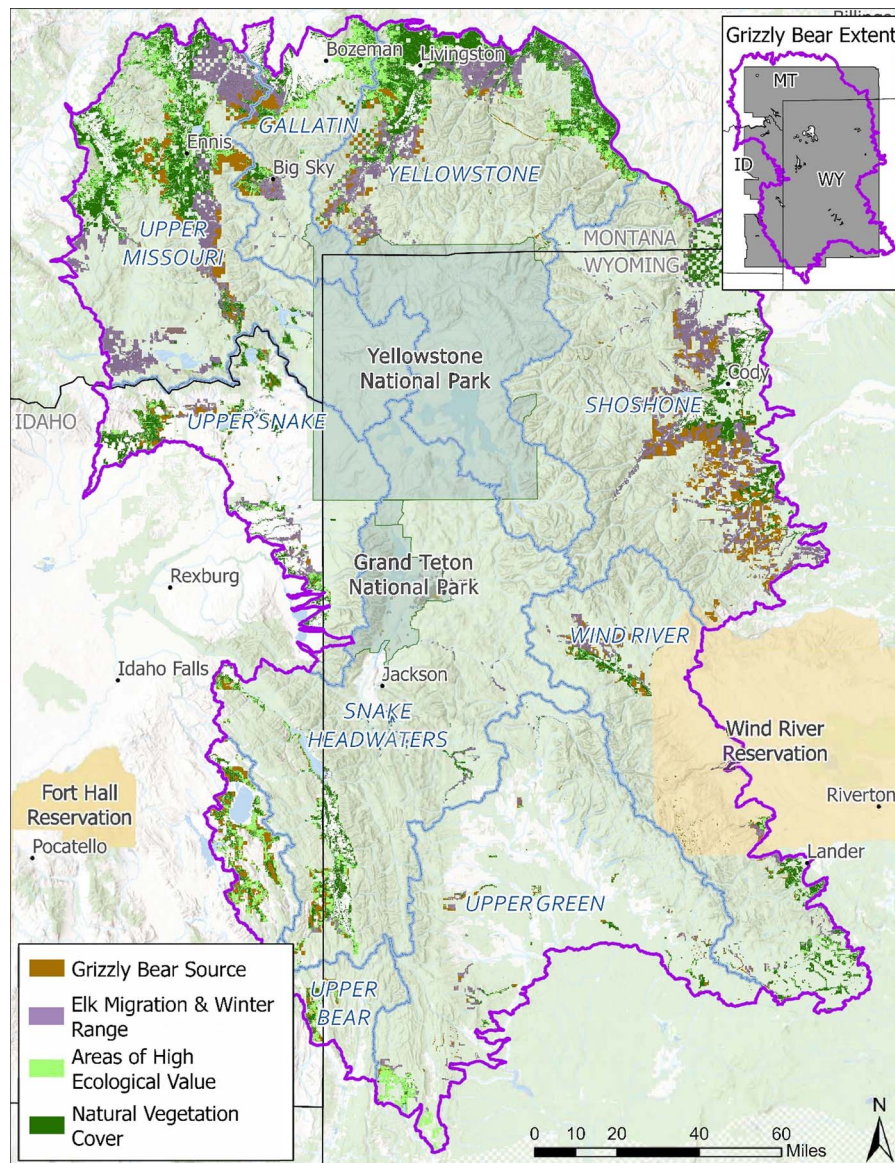


Figure 3.—Biodiversity response layers on private lands in the Greater Yellowstone Ecosystem study area, 2019. The layers are in order of precedent on the map: grizzly bear source area, elk migration and winter range high ecological value, and natural vegetation cover. The inset shows in gray the extent of the area over which the grizzly bear layer was mapped. (See online version of this journal for full-color figures.)

about 6%. The faster-changing watersheds in GYE have lost NVC at rates comparable to the ecoregions with the greatest loss across the PINW (up to 6%; Hansen et al. 2022).

This variation in rates of loss of NVC among the watersheds of the GYE is consistent with spatial patterns of known predictors of land development across the PINW. Loss of NVC to development was associated with proximity to markets, existing development, roads, various natural amenities, and New West demographics (Hansen et al. 2021). The Bozeman/Big Sky area in the Gallatin watershed of Montana typified these conditions. Consequently, the Bozeman area had the fourth-highest percent loss of NVC among 88 cities in the PINW (Hansen et al. 2022). The Jackson and Star Valley, Wyoming, and Swan Valley, Idaho, areas in the Snake Headwaters watershed have similar socioecological attributes and relatively

high rates of NVC loss, as does the Driggs, Idaho, area in the Upper Snake watershed.

In addition to risk of loss, the value of natural habitats for maintaining native species and ecological functioning is often used to prioritize conservation strategies (Watson et al. 2018). Because much of the conservation interest in the GYE focuses on large charismatic wildlife species (Middleton et al. 2020), we added the Ecological Value Index used by Hansen et al. (2022) to consideration of habitat for elk and grizzly bear in our analyses. We found that these three biodiversity layers tended to occur in different settings in the landscape. Elk winter and migration habitats were centered on valley bottoms and grassland/shrubland vegetation. Grizzly bear population source areas were largely on ridges and upper slopes with conifer forests and low levels of human pressure. Areas of high ecological value

Table 4.—Percent of natural vegetation cover in each of three biodiversity classes, Greater Yellowstone Ecoregion study area, 2019.

Watershed	Ecological value	Elk habitat	Grizzly bear source habitat	% of natural vegetation cover in bear extent
Upper Missouri	32.1	36.3	12.1	51.3
Gallatin	53.8	19.6	13.1	52.5
Yellowstone	38.0	30.2	7.8	51.9
Shoshone	14.5	65.0	27.5	97.8
Wind River	18.4	37.8	16.9	67.6
Upper Green	70.2	37.7	15.5	68.9
Upper Bear	66.7	0.0	28.0	99.9
Upper Snake	41.0	14.0	20.7	93.1
Snake Headwaters	40.6	23.5	16.9	100.0
Study area	33.3	36.2	16.0	69.9

were largely between the elk and bear habitats, at lower slopes with conifer and woody deciduous vegetation. Because of the differences in the distributions of these biodiversity metrics, 46% of the NVC was suitable for one of the layers, about 16% was suitable for two of the layers, and only 2% was suitable for all three layers.

The distributions of suitable habitats for elk and grizzly bear reflect differences in tolerance of humans. Elk across the GYE generally either tolerate or benefit from intermediate levels of human land use. Winter habitats are often centered on croplands, hay, and pasture lands because of forage quality and access due to lower snowpack in these low-elevation areas (Vavra et al. 1999). However, recent studies suggest that elk may be negatively influenced by certain types of human infrastructure and activity such as fences, buildings, roads, and rural homes and subdivisions (Polfus and Krausman 2012).

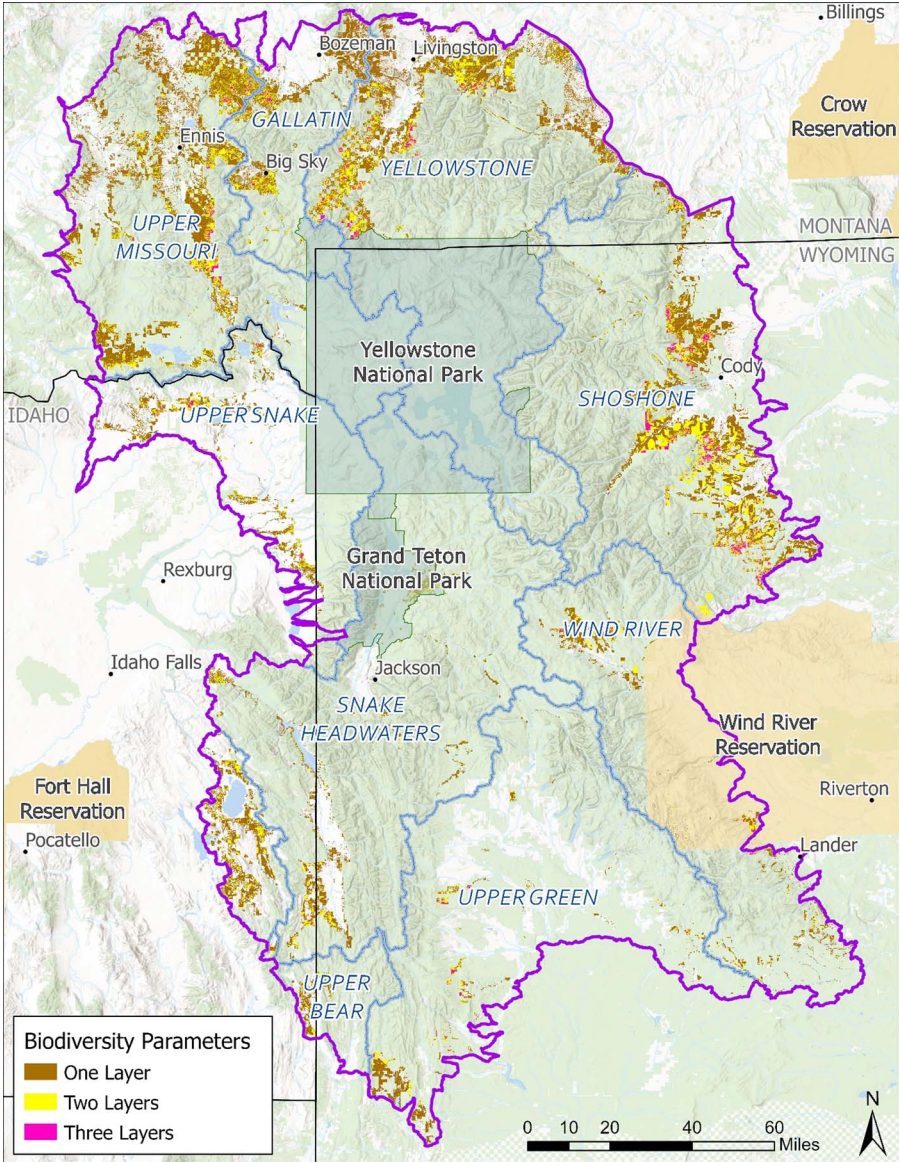


Figure 4.—Areas where one, two, or three of the biodiversity habitat layers (high ecological value, elk migration and winter range, grizzly bear source area) occurred on private lands in the Greater Yellowstone Ecosystem study area, 2019. (See online version of this journal for full-color figures.)

Table 5.—Percentage of natural vegetation cover on private lands in each watershed where one, two, or three of the biodiversity habitat layers (elk, grizzly bear, high ecological value) occurred, Greater Yellowstone Ecosystem study area, 2019.

Watershed	One layer	Two layers	Three layers
Upper Missouri	48.7	14.0	1.3
Gallatin	55.8	13.5	1.2
Yellowstone	42.4	13.8	2.0
Shoshone	42.1	24.8	5.1
Wind River	38.9	14.9	1.5
Upper Green	67.6	21.1	4.5
Upper Bear	59.5	17.5	0.0
Upper Snake	46.2	13.4	0.9
SNAKE HEADWATERS	47.6	15.3	0.9
Study area	46.1	16.3	2.2

Gigliotti et al. (2023) estimated that elk can only tolerate human land use up to a certain threshold: ~3% development (i.e., impervious surfaces) and about 66% agriculture. Thus, whereas elk often benefit from moderate levels of human land use, elk habitat suitability can be degraded by increases in human modification on agricultural lands and conversion of these lands to development.

Grizzly bears, in contrast, were listed in 1975 as a federally threatened species in the Lower 48 states because of their relatively small population size and susceptibility to excessive mortality. Survival of female grizzly bears in the GYE is negatively associated with road density, number of homes, size of developments, and ungulate hunting pressure (Schwartz et al. 2010). Consequently, most private lands in GYE represent sink

Table 6.—Percentage of area of each land use type in conservation easements in 2019.

Land-use type	Non-easement (%)	All easements (%)
Natural vegetation cover	84.3	15.7
Agriculture	91.7	8.3
Developed	95.2	4.8

areas for grizzly bears, such that mortality rates exceed recruitment. Even extremely low-density residential development can create sink habitats for grizzly bears (Schwartz et al. 2012). Increased development in GYE is, thus, likely to convert source areas to sinks. Such conversion would not only have localized demographic impacts on grizzly bears but could also reduce opportunities for future connectivity of this isolated population with nearby populations (e.g., Northern Continental Divide Ecosystem) or to serve as a source population for the Bitterroot Ecosystem (Peck et al. 2017; Sells et al. 2023).

This study demonstrated the benefits of complementing sub-national scale prioritization of biodiversity conservation actions with more detailed analyses within an individual ecoregion. While the GYE was a relatively low priority for conservation among the 15 ecoregions studied by Hansen et al. (2021, 2022), there is high interest in GYE nationally due to it retaining native species of large ungulates and carnivores and large expanse of intact wildlands (Middleton et al. 2022). Moreover, many land trusts are active in the GYE and are expanding lands in conservation easements. Our study revealed high levels of spatial variation in the distribution of NVC, rates of loss of NVC to

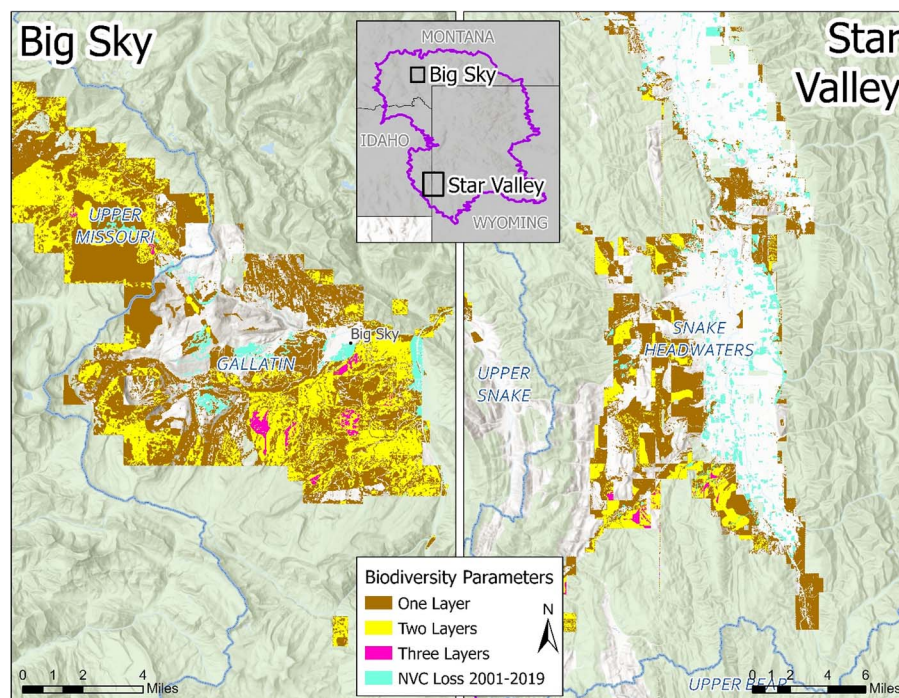


Figure 5.—Examples of locations in the study area where loss of natural vegetation cover coincides with overlap in the three biodiversity layers (high ecological value, elk migration and winter range, grizzly bear source area). Big Sky, Montana (left) and Star Valley, Idaho (right). Private lands that are not within any of the biodiversity layers are in white. (See online version of this journal for full-color figures.)

Table 7.—Percentage of the total samples from the biodiversity layer class in conservation easements in the Greater Yellowstone Ecosystem study area in 2019.

Biodiversity layers	Non-easement (%)	All easements (%)
No biodiversity layers	84.1	16.0
One biodiversity layer	88.3	11.7
Two biodiversity layers	82.5	17.5
Three biodiversity layers	73.5	26.5

development, and biodiversity value. The results of this study provide fine-scale (mostly 30 m) scientific information that can be used by land trusts to prioritize lands for conservation easements. For example, we found that some of the 2% of NVC where the three biodiversity measures overlap have relatively high loss of NVC to development. Examples are the Big Sky, Montana area, the west slope of the Teton Mountains in Idaho, and the southern Star Valley in Idaho (Figure 4). Our analyses indicate that biodiversity conservation efforts can be substantially enhanced by prioritizing protection for such areas where NVC has high ecological value, elk winter/migration habitat, serves as a source area for grizzly bears, and are at high risk of development.

Although conservation easements are widely seen as a vehicle for achieving biodiversity objectives, Hansen et al. (2022) found that only 4.5% of private lands with NVC across the PINW were protected by an easement. In contrast, we found in the GYE that 16% of the NVC was protected by easements. Watersheds with the highest levels of NVC loss to agriculture and development also had the highest level of NVC in easements (19% in the Gallatin watershed). In contrast, the three watersheds largely in Idaho with relatively low coverage of NVC had relatively little land in easements (0.5–2.8%). We found that coverage by easements increased with the number of biodiversity layers present, from 12% for one biodiversity layer to 26% for three biodiversity layers. The distribution of easements was not random among land-use types and biodiversity layers. Rather, easements were placed in NVC and in areas with more biodiversity layers than expected. These findings suggest that the organizations facilitating environmental conservation easements have been successful at placing them in areas of natural habitats and higher biodiversity value. The opportunity exists to expand the use of easements further, however, both in areas of NVC, 84% of which is not under easement, and in areas with two or three biodiversity layers, where more than 74% remains unprotected. We appreciate that land trusts differ in their capacity to evaluate, select, and fund properties available for potential easements. For land trusts in the GYE with adequate capacity, we suggest consideration of the results of this study in selection of easement opportunities in the future.

In conclusion, this study demonstrated the benefits of complementing sub-national scale analyses of biodiversity conservation priority with those within an individual ecoregion. The GYE was found to be a relatively low priority for conservation in the sub-national study (Hansen et al. 2021, 2022). Yet, the GYE is of high interest for conservation

nationally. The large expanse of NVC and relatively low rates of loss to development across the ecoregion belie that some watersheds in the ecoregion have had rates of land conversion that are high relative to surrounding ecoregions. Adding consideration of habitats of highly valued wildlife species revealed the specific locations where land trusts could prioritize for conservation easements to favor ecological value, elk habitat, grizzly bear habitat, or combinations of these. Just 5% of the NVC supports all three biodiversity layers and these lands should be high priorities for conservation. The conservation community has protected a relatively large proportion of NVC in the GYE relative to other ecoregions. This suggests the capacity for new conservation in the ecoregion is high and our results can be used to inform the placement of new easements to further protect the three biodiversity layers mapped in this study.

More generally, the study suggests the merits of using multiple scales of analysis to inform conservation to achieve local to regional to national objectives. National-scale (e.g., Dietz et al. 2020; Belote et al. 2021), sub-national scale (e.g., Hansen et al. 2021, 2022), and regional-scale studies (the current study) each reveal unique information about patterns of land-use change and biodiversity that are relevant to effective conservation. Thus, we recommend replicating our analysis in other ecoregions of the United States. Doing so can provide a pathway for identifying, prioritizing, and conserving critical habitats in the context of the *America the Beautiful Program* to better conserve natural habitats on private lands across the United States.

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Andrew Hansen is a professor in the Ecology Department at Montana State University where he studies land use and climate change effects on large landscapes.

Alyson East is a spatial analyst and ORISE Research Fellow at Oak Ridge National Laboratory and the US Forest Service.

Zane Ashford is a Masters of Sciences candidate in the Land Resources and Environmental Sciences Department at Montana State University.

Cassidy Crittenden received a Bachelor of Science degree from the Ecology Department at Montana State University.

Olivia Jakobosky received a Bachelor of Science degree from the Ecology Department at Montana State University. She is currently a Fulbright & Udall Scholar at the University of Exeter for an MSc in Conservation and Biodiversity.

Daniel Quinby received a Bachelor of Science degree from the Ecology Department at Montana State University.

Laura Gigliotti is the Assistant Unit Leader with the USGS WV Cooperative Fish & Wildlife Research Unit at West Virginia University.

Frank van Manen is the Supervisory Research Wildlife Biologist of the US Geological Survey Interagency Grizzly Bear Study Team in Bozeman, Montana.

Mark Haroldson is a scientist with the USGS Northern Rocky Mountain Science Center Interagency Grizzly Bear Study Team in Bozeman, Montana.

Arthur Middleton is an Associate Professor in the Department of Environmental Science, Policy, and Management at the University of California, Berkeley.

Nathaniel Robinson is an ecologist with The Nature Conservancy in Arlington, Virginia.

David Theobald is a spatial ecologist with Conservation Planning Technologies based in Fort Collins, Colorado.

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APPENDIX

Table 1.—Candidate predictors of biophysical and land-use settings used to characterize three biodiversity layers (high ecological value, elk migration and winter range, grizzly bear source area).

Predictor	Description	Spatial resolution	Source
Elevation	Meters above Sea level	30 m	USGS NED ^a
Slope	Percent	30 m	USGS NED - derived
Aspect	Degrees	30 m	USGS NED - derived
Landform	1 - Peak/Ridge/Cliff 2 - Upper slope 3 - Lower slope 41 - Valley 42 - Valley narrow	90 m	Reclassified from Theobald et al. 2015 ^b
Vegetation type	31 - Barren land 41 - Deciduous forest 42 - Evergreen forest 43 - Mixed forest 52 - Shrub/scrub 71 - Grassland/herbaceous 90 - Woody wetlands 95 - Emergent herbaceous wetlands	30 m	Jin et al. 2019 ^c
Human Modification	0 to 1 representing no human modification to total modification	30 m	Theobald et al. 2022 ^d
Canopy Cover	0 to 100%	30 m	Hansen et al. 2013 ^e

^a USGS NED. <https://gdg.sc.egov.usda.gov/Catalog/ProductDescription/NED.html>

^b Theobald, D.M., D. Harrison-Atlas, W.B. Monahan, and C.M. Albano. 2015. Ecologically-relevant maps of landforms and physiographic diversity for climate adaptation planning. *PLOS One* 10:e0143619.

^c Jin, S., C. Homer, L. Yang, P. Danielson, J. Dewitz, C. Li, Z. Zhu, G. Xian, and D. Howard. 2019. Overall methodology design for the United States national land cover database 2016 products. *Remote Sensing* 11:1–23.

^d Theobald, D.M., A.T.H. Keeley, A. Laur, and G. Tabor. 2022. A simple and practical measure of the connectivity of protected area networks: The ProNet metric. *Conservation Science and Practice* 4:e12823.

^e Hansen, M.C., P.V. Potapov, R. Moore, M. Hancher, S.A. Turubanova, A. Tyukavina, D. Thau, S.V. Stehman, D.J. Goetz, T.R. Loveland, et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342:850–853.

Table 2.—Percentage of private land in conservation easements in natural vegetation cover across the watersheds of the study area.

Watershed	Non-easement	All easements
Gallatin	80.8	19.3
Shoshone	95.4	4.6
Snake Headwaters	97.2	2.8
Upper Bear	99.5	0.5
Upper Green	86.0	14.0
Upper Missouri	68.0	32.0
Upper Snake	97.3	2.7
Wind River	90.7	9.3
Yellowstone	85.6	14.4