A Multicriteria Assessment of the Irreplaceability and Vulnerability of Sites in the Greater Yellowstone Ecosystem

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Abstract: *We conducted a systematic conservation assessment of the 10.8-million-ha Greater Yellowstone Ecosystem (GYE), integrating three basic approaches to conservation planning: protecting special elements, representing environmental variation, and securing habitat for focal species (grizzly bear [*Ursus arctos*], wolf [*Canis lupus*], and wolverine [*Gulo gulo*]). Existing protected areas encompass 27% of the GYE but fail to capture many biological hotspots of the region or to represent all natural communities. Using a simulated annealing site-selection algorithm, combined with biological and environmental data based on a geographic information system and static (habitat suitability) and dynamic (population viability) modeling of focal species, we identified unprotected sites within the GYE that are biologically irreplaceable and vulnerable to degradation. Irreplaceability scores were assigned to 43 megasites (aggregations of planning units) on the basis of nine criteria corresponding to quantitative conservation goals. Expert opinion supplemented quantitative data in determining vulnerability scores. If all megasites were protected, the reserved area of the GYE would expand by 43% (to 70%) and increase protection of known occurrences of highly imperiled species by 71% (to 100%) and of all special elements by 62% (to 92%). These new reserves would also significantly increase representation of environmental variation and capture critical areas for focal species. The greatest gains would be achieved by protecting megasites scoring highest in irreplaceability and vulnerability. Protection of 15 high-priority megasites would expand reserved area by 22% and increase the overall achievement of goals by 30%. Protection of highly imperiled species and representation of geoclimatic classes would increase by 46% and 49%, respectively. Although conservation action must be somewhat opportunistic, our method aids decision-making by identifying areas that will contribute the most to explicit conservation goals.*

Evaluación de Criterios Múltiples de la Irremplazabilidad y Vulnerabilidad de Sitios en el Ecosistema Mayor de Yellowstone

Resumen: *Realizamos una evaluación sistemática de conservación de las 10.8 millones de Ha del Ecosistema Mayor de Yellowstone (GYE), empleando las tres rutas de protección de los elementos especiales, la representación de la variación ambiental y asegurando hábitat para especies focales (el oso grizzli [*Ursus arctos*], el lobo [*Canis lupus*], y el carcayú glotón [*Gulo gulo*]). Las áreas protegidas abarcan 27% del GYE pero no logran capturar muchas áreas prioritarias para la conservación de la región ni representar a todas las comunidades naturales. Usando un algoritmo simulado de selección de sitio, combinado con datos biológicos y ambientales basados en GIS y empleando el modelado estático (aptitud del hábitat) y dinámico (viabilidad poblacional) de especies focales, identificamos sitios desprotegidos dentro del GYE que son biológicamente irreemplazabilidad y vulnerables a la degradación. Se asignaron puntajes de irreemplazabilidad a 43 megasitios (agregaciones de unidades de planeación) en base a nueve criterios correspondientes a las metas cuantitativas de conservación. Si todos los megasitios fueran protegidos, el área reserva del GYE se expandiría en un 43% (a 70%) e incrementaría la protección de ocurrencias conocidas de especies altamente en peligro en un 62% (a 92%). Estas nuevas reservas también incrementarían significativamente la representación de la*

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variación ambiental y capturarían áreas críticas para especies focales. Las mayores ganancias se obtendrían mediante la protección de megasitios con los puntajes más altos de irreemplazabilidad y vulnerabilidad. La protección de 15 megasitios altamente prioritarios expandiría el área de reserva en un 22% e incrementaría el éxito general de las metas en un 30%. La protección de especies altamente en peligro y la representación de clases geoclimáticas podría incrementar en un 46% y un 49% respectivamente. A pesar de que la acción de conservación debe ser de alguna manera oportunista, nuestro método ayuda a la toma de decisiones al identificar áreas que contribuirán más a explicar las metas de conservación.

Introduction

Systematic planning on a regional scale has become the standard approach of conservation organizations and agencies worldwide (Noss 1983; Pressey 1994; Dinerstein et al. 1995; Noss et al. 1997; Groves et al. 2000; Pressey & Taffs 2001). Systematic conservation planning is superior in many ways to opportunistic or politically biased approaches, which have resulted in a skewed distribution of protected areas (Pressey et al. 1993; Scott et al. 2001). Among the key attributes of systematic conservation planning are explicit goals, quantitative targets, explicit methods for locating new reserves to complement existing ones, and rigorous criteria for implementing conservation action (Margules & Pressey 2000).

The Greater Yellowstone Ecosystem (GYE) was first defined as the area necessary to sustain the Yellowstone population of grizzly bears (*Ursus arctos*; Craighead 1979). Today, the GYE is the southernmost area in North America that still contains a full suite of native carnivores, along with other wilderness qualities (Clark et al. 1999). Although the GYE is not a biological hotspot on a global or continental scale (Ricketts et al. 1999; Myers et al. 2000), it presents an opportunity that most hotspots do not—to conserve a reasonably intact temperate ecosystem. Nevertheless, biodiversity in the region is threatened. The GYE's scenic qualities have attracted a burgeoning human population, the impacts of which now rival the traditional threats of resource extraction. Population-growth rates for the 20 counties within the GYE averaged 14% between 1990 and 1999 and ranged up to 66% (Greater Yellowstone Coalition, unpublished data). The GYE is unique in that large core refugia lie in close proximity to a rapidly growing human population.

We conducted a conservation assessment of the GYE to serve four well-accepted goals of conservation (Noss & Cooperrider 1994): (1) to represent ecosystems across their natural range of variation; (2) to maintain viable populations of native species; (3) to sustain ecological and evolutionary processes; and (4) to build a conservation network that is resilient to environmental change. In pursuit of these goals we integrated three basic approaches to conservation planning: (1) protection of special elements, including imperiled species and communities; (2) representation of a broad spectrum of environmental variation, including that of vegetation, geoclimatic, and aquatic classes; and (3) protection of critical habitats of focal species (Lambeck 1997; Miller et al. 1998–1999), whose needs help planners address issues of habitat area, configuration, and quality. Together, these three approaches constitute a comprehensive approach to conservation planning (Noss et al. 1999).

Using a simulated annealing site-selection algorithm applied to several classes of conservation targets, we identified sites within the GYE that have the most to lose if not protected. To identify priority sites, we relied on two key concepts: irreplaceability and vulnerability (Pressey et al. 1994; Margules & Pressey 2000; Pressey & Cowling 2001). Irreplaceability provides a quantitative measure of the relative contribution made by different areas to reaching conservation goals, thus helping planners choose among alternative sites. We assessed vulnerability on the basis of expert opinion and consensus about the threats faced by each site, taking into account available quantitative data. Our findings provide a template for determining conservation priorities and making land-allocation decisions with awareness of the trade-offs involved.

Study Area

We defined the study area (Fig. 1) in consultation with the Greater Yellowstone Coalition, with consideration of mountain ranges, watersheds, wildlife migration routes, and other features. The core of this 10.8-million-ha region is the 890,000-ha Yellowstone National Park (YNP), the 134,000-ha Teton National Park and John D. Rockefeller Memorial Parkway, and an additional 1.6 million ha of federally designated wilderness. Altogether, 36% of the GYE is private land and 64% is public land. Protected areas recognized by the U.S. Geological Survey (USGS) Gap Analysis Program (GAP) (Scott et al. 1993, 1996) constitute 2.9 million ha, 27% of the GYE.

Lower elevations of the GYE are generally treeless except along streams and are dominated by grass-shrub communities. Coniferous forests dominate middle to upper elevations. Douglas-fir (*Pseudotsuga menziesii*) is the dominant low-elevation tree, whereas Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*P. contorta*) compose mid-elevation forests. Spruce-fir forest would dominate more

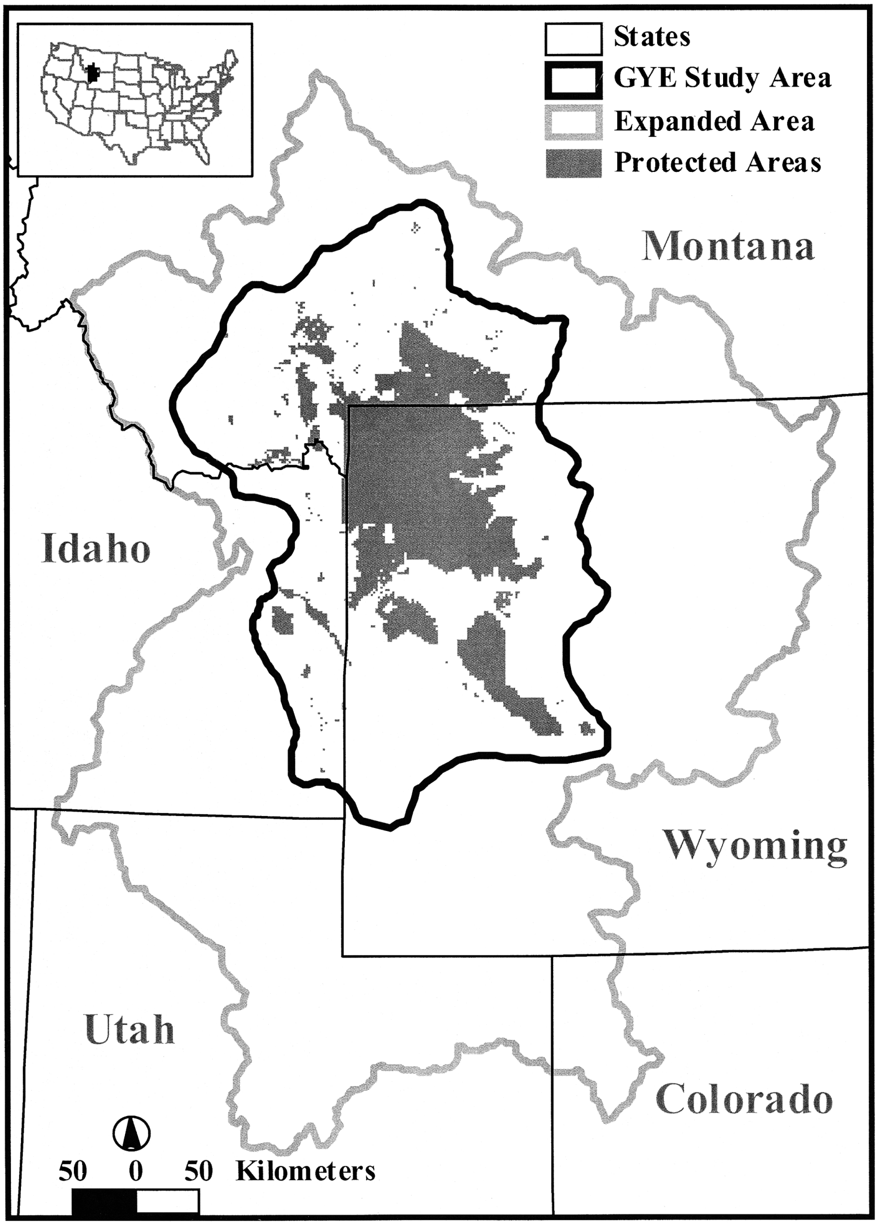

Figure 1. The Greater Yellowstone Ecosystem, showing protected areas and the expanded study area for focal species.

of the area were it not for stand-replacement fires that favor lodgepole pine. Limber pine (*P. flexilis*) occurs throughout on dry, windy sites, and aspen (*Populus tremuloides*) and willow (*Salix* spp.) occur in wetter areas. At high elevations, whitebark pine (*P. albicaulis*) is common. Extensive tracts of alpine tundra occur above timberline (Knight 1994).

Methods

Planning Units

The building blocks of a conservation plan are the sites that are compared to one another. We used sixth-level catchments (hydrologic units; USGS 2001) as planning units because they are ecologically relevant and at a convenient scale for regional planning. Nevertheless, sixth-level catchments had not been delineated for most of the GYE. We used the BASINS function in ArcInfo GRID geographic information system (GIS) software, which is based on a 90-m digital-elevation model to create pseudo (modeled) sixth-level catchments. To better conform the resulting polygons to recognized catchments, we merged them with USGS fifth-level catchments. We eliminated polygons smaller than 2000 ha and divided large polygons to avoid potential species-area effects.

To distinguish existing protected areas, we merged the catchment polygons with USGS GAP polygons of management status 1 (strictly protected) and 2 (moderately protected). This procedure resulted in 1908 planning units (range: 13–43,564 ha; $\bar{x}$ = 5,692 ha). (Smaller units were catchments located partly within existing protected areas. Only portions of the catchments that fell outside protected areas were considered planning units.) After applying a site-selection algorithm (see below), we aggregated selected units into "megasites" for priority setting. These larger sites are likely to be more effective conservation units than sixth-level watersheds. Boundaries of fourth-level watersheds and other natural features were used to define megasite boundaries.

The SITES Selection Algorithm

We used SITES (version 1.0; Andelman et al. 1999) to assemble and compare alternative portfolios of planning units. SITES can use either of two algorithms—the greedy heuristic or simulated annealing with iterative improvement—to assemble portfolios (Possingham et al. 2000). We used simulated annealing, the more efficient of the two. This algorithm does not guarantee an optimal solution, which is prohibitive in computer time for large, complex data sets. Rather, the algorithm attempts to minimize portfolio "cost" while maximizing attainment of conservation goals: cost = area + species penalty + boundary length, where area encompasses all planning units selected for the portfolio, species penalty is imposed for failing to meet target goals, and boundary length includes the total boundary of the portfolio (Andelman et al. 1999; Possingham et al. 2000). The boundary-length modifier is a notable improvement on early site-selection algorithms, which often neglected the configuration of sites and resulted in fragmented portfolios that are difficult to manage (Briers 2002; McDonnell et al. 2002). SITES minimizes portfolio cost by selecting the smallest overall area needed to meet target goals and by selecting planning units that are clustered or adjacent to existing reserves rather than dispersed.

We had SITES perform 1,000,000 iterative attempts to find the minimum cost solution per simulated annealing run and perform 10 such runs for each of dozens of alternative scenarios. Alternative scenarios were constructed by varying target goals and inputs to the cost function. Often, several different portfolios will meet goals almost equally well, providing flexibility to the planning process (Leslie et al. 2002). Varying goals and inputs, and examining alternative portfolios, allow expert knowledge to be incorporated into an interactive decision-making process. The final set of goals and the final portfolio were ones we and the client (the Greater Yellowstone Coalition) felt comfortable with.

Special Elements

Following guidelines established by The Nature Conservancy (Groves et al. 2000; Stein & Davis 2000), we assembled element-occurrence data for the GYE from natural heritage programs in Montana, Idaho, and Wyoming. After we excluded occurrences of species or communities last observed prior to 1982 or ranked as nonviable or nonbreeding by the heritage programs, 2303 occurrences of 435 species and communities remained (Fig. 2), 203 of them for the 55 species and communities with conservation status ranks of G1 (critically imperiled globally) or G2 (imperiled globally). Considering the disparate area requirements and databases describing the distributions of different taxa, we divided the occurrence data into four groups for separate SITES analysis: local-scale species, vulnerable and declining bird species, coarse- and regional-scale aquatic (fish) species, and plant communities (Groves et al. 2000; Poiani et al. 2000; Noss et al. 2001). We set goals for capturing 100% of the G1 and G2 occurrences in all groups and at least 50% of occurrences of less-threatened elements.

We made 10 runs for each target group, using the SITES "sum runs" option (Andelman et al. 1999). Output from sum runs included the number of times each planning unit was included in the 10 portfolios, and the "best" (lowest-cost) portfolio of the 10. Contiguous or near-contiguous planning units with sum-runs values of >1 were aggregated into megasites. The number of times the planning units in a megasite were selected during the 10 runs was used, in part, to determine irreplaceability (similar to the method of Leslie et al. [2002]).

Representation

We used a combination of vegetation types derived from satellite imagery and mapped by the state GAP programs and a new classification of physical (abiotic, geoclimatic) classes to represent variation in terrestrial ecosystems. A combination of biotic and abiotic surrogates is likely to capture more variation than either class alone (Kirkpatrick & Brown 1994), especially because each GAP vegetation type encompasses considerable internal heterogeneity. Moreover, representing a spectrum of physical substrates and associated vegetation—ideally along intact gradients—may facilitate shifts in species distributions in response to climate change (Noss 2001).

We merged state-level GAP vegetation maps into a single map portraying 39 vegetation types in the GYE. We set goals for capturing at least 25% of the area of each wetland vegetation type—lowland riparian, mountain riparian, water, wetland, wet meadow—and 15% of all others, with the justification that wetlands are considered of higher biological value in the region (Patten 1998). We used the major components of climate variation in the region to classify geoclimatic types in ArcInfo GIS: (1) mean annual precipitation, (2) spring precipitation, (3) mean annual low temperature, (4) mean annual high temperature, and (5) the difference between winter mean low temperature and summer mean high temperature (Daly et al. 1994), in addition to mean annual growing degree days. Edaphic variables, assumed to be of secondary im-

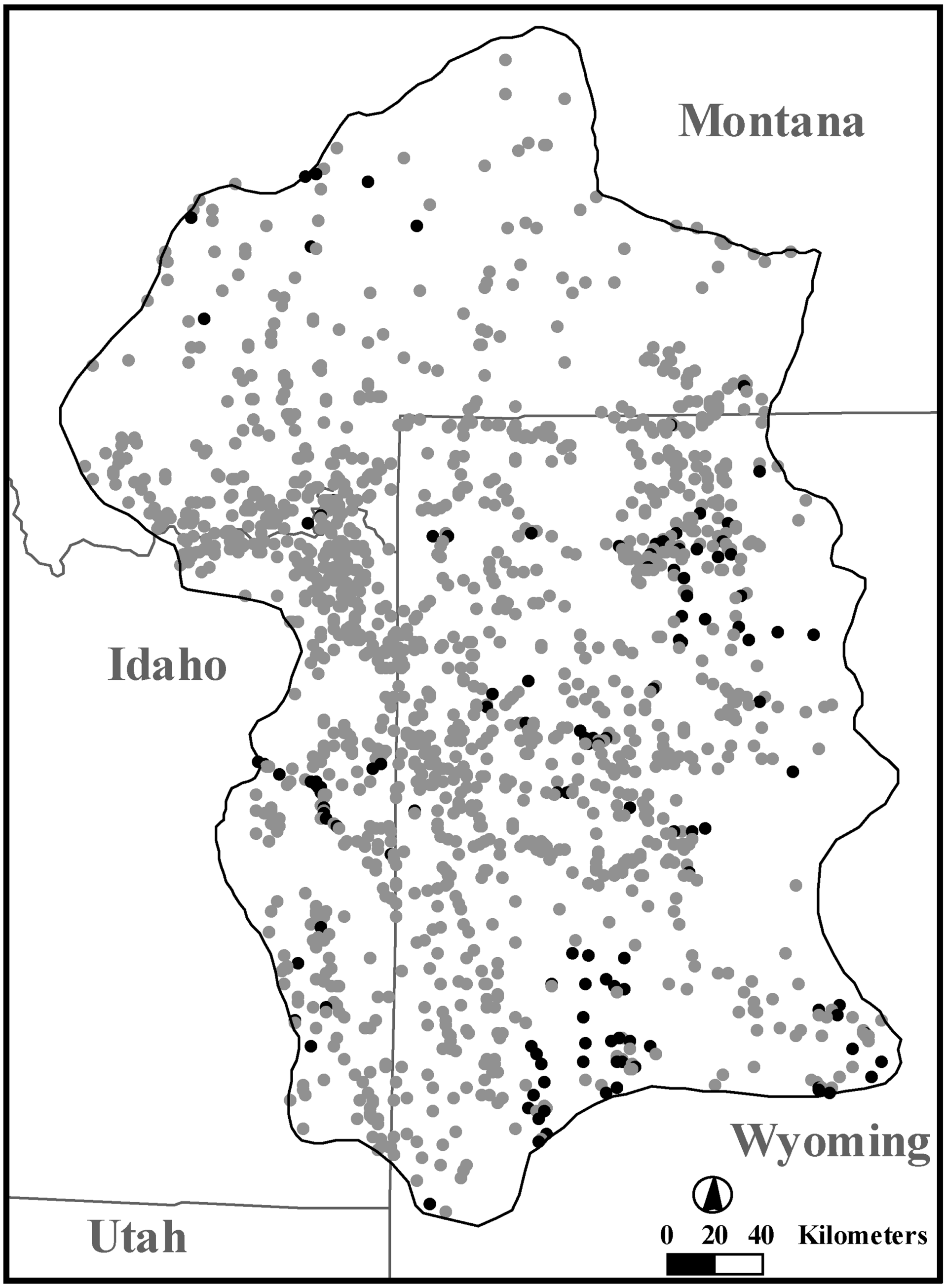

Figure 2. Element occurrences (imperiled species and communities) from state natural heritage programs. Black dots represent occurrences of elements critically imperiled globally (G1) and imperiled globally (G2), and gray dots represent less imperiled elements.

portance in influencing species distributions, were soil depth, water-holding capacity, and organic carbon content, derived from the STATSGO soils database (Soil Survey Staff 1992). A cluster analysis of the nine climate and soil variables recognized 38 geoclimatic classes. We set goals for capturing at least 15% of the area of each type.

For aquatic representation, we used the aquatic classification developed by The Nature Conservancy (M. Lammert, personal communication). We applied two levels of classification: (1) aquatic macrohabitats, identified at the stream-reach level, and (2) aquatic ecological systems, identified at the watershed to basin level. Both classifications utilize four components: stream size (headwater to large river); elevation (low to alpine); stream gradient (low to very steep); and dominant geology (coarse, porous, nonporous). Aquatic macrohabitats were classified by specific portions of the range of each component (e.g., "very steep alpine headwater in coarse geology"). Aquatic ecological systems, being aggregations of macrohabitats, represent a greater range of gradients. We stratified ecological systems by the macrohabitats they contain and set goals for representing at least 20% of each of the 654 strata.

Focal Species

Our study placed greater emphasis on species viability than most previous multicriteria conservation plans. Although a comprehensive set of focal species would encompass taxa sensitive to a range of environmental factors (Lambeck 1997; Miller et al. 1998–1999), we selected four area-limited carnivores and an ungulate: grizzly bear, gray wolf (*Canis lupus*), wolverine (*Gulo gulo*), lynx (*Felis lynx*), and elk (*Cervus elaphus*). Results for the first three of these species, for which the models are most robust, are reported here (for the full analysis see Noss et al. 2001). Because of the large spatial scales over which metapopulation dynamics of these species operate, we analyzed an expanded study region of 31.6 million ha (Fig. 1).

We used GIS data on distribution and habitat characteristics to construct static habitat-suitability models (i.e., resource selection functions; Boyce & McDonald 1999) for each focal species, with methods developed by Carroll et al. (2001). These results were compared with those from dynamic models that considered regional population dynamics within a multiregional context (Noss et al. 2001). Species-distribution data included sightings records of wolverines, radiotelemetry locations of grizzly bears, and the boundaries of wolf-pack territories. Habitat data included vegetation, satellite-imagery metrics, topography, climate, and variables related to human impacts (e.g., road density; Mladenoff et al. 1995; Merrill et al. 1999). We used multiple logistic regression to compare habitat variables at telemetry or sighting locations with those at random points. We used the coefficients from the final model to calculate a resource selection function (RSF) for used (occurrences) and available (random) resources (Manly et al. 1993; Boyce & McDonald 1999).

We performed population viability analyses with the program PATCH (Schumaker 1998). PATCH links the survival and fecundity of individual animals to GIS variables corresponding to mortality risk and habitat productivity, measured within individual or pack territories. The model tracks the population as individuals are born, disperse, and die and allows the landscape to change through time. Hence, the user can predict the consequences of landscape change for population viability and identify probable sources and sinks. Our landscape-change scenarios used estimates of potential change in human-associated impact factors (e.g., roads and human population) during the period 2000–2025, given increased development on either private and public lands or on private lands only.

We set a SITES goal of habitat sufficient to support 75% of the current potential population of each species, as defined by the RSF. We then compared SITES solutions with results from the PATCH model. We scored areas selected by SITES as to their irreplaceability and vulnerability by overlaying megasite boundaries on the PATCH results. Irreplaceability in this context is the value of an area as source habitat, defined by population growth rate (lambda). Vulnerability is the predicted decline in lambda over the next 25 years. Dynamic model results also contributed one of nine criteria determining overall megasite irreplaceability. PATCH irreplaceability in the composite scores was an average of lambda values for the focal species, weighted by the likelihood that a site was occupied by the species. We also ran the PATCH model on potential future landscapes that included increased protection and restoration of megasites.

Expert Assessment

Quantitative data by which to evaluate conservation options are always limited. We supplemented quantitative measures of conservation value with expert opinion, applying a combined approach of one-on-one interviews followed by a workshop. G. Wuerthner interviewed 124 experts on the ecology and conservation issues of the GYE during 1999–2000. Interviews included discussion of habitat conditions, imperiled species, threats, monitoring, survey, and management. After producing our draft report, we participated in a workshop to present our results, evaluate alternative portfolios, and assign vulnerability scores to selected megasites. The workshop was attended by experts on conservation issues across the GYE.

Megasite Ranking

Many potential methods exist for estimating irreplaceability, which cannot be measured directly (Ferrier et al. 2000; Pressey & Taffs 2001; Leslie et al. 2002). Because our assessment considered multiple values of megasites and attempted to achieve a broad set of conservation goals, we assigned irreplaceability values to megasites based on nine criteria assessed as contributions to the following goals (each considered a minimum threshold): (1) protects 50% (or 100% for G1/G2) of viable occurrences of imperiled local-scale species; (2) protects 50% (or 100% for G1/G2) of viable occurrences of vulnerable and declining bird species; (3) protects 50% (or 100% for G1/G2) of viable occurrences of coarse-scale and regional-scale aquatic (fish) species; (4) protects 50% (or 100% for G1/G2) of viable occurrences of plant communities; (5) represents 25% of the area of each wetland vegetation type and 15% of the area of each other vegetation type in the region; (6) represents 15% of the area of each geoclimatic class in the region; (7) represents 20% of the length of each aquatic (stream) habitat type in the region; (8) protects habitat capable of supporting 75% of the population of each focal species that currently could be supported in the region, as identified by RSF models; and (9) maintains viable populations of focal species over time, as determined by PATCH. Each score is an average of the predicted lambda values, weighted by the likelihood that the site was occupied by the species.

Each megasite was scored from 0 to 10 for each of the nine criteria. For criteria 1–8, the number of times (out of 10) that individual planning units were selected in SITES sum runs was used to calculate an area-weighted mean score for each megasite. For criterion 9, entire megasites were scored as units. A total irreplaceability score was calculated for each megasite by summing the area-weighted mean scores for the nine criteria. These total scores were then rescaled to range from approximately 1 to 100. We weighted the nine criteria equally in this exercise, although planners could apply different weightings to emphasize particular criteria.

Vulnerability cannot be estimated as objectively as irreplaceability (Pressey et al. 2000). We prepared a site description for each megasite (Noss et al. 2001), which included a discussion of known threats and management issues, as derived from interviews with the 124 experts. We also acquired region-wide data on such threat surrogates as human population and development trends (e.g., Theobald 2001). We then assigned a preliminary vulnerability score from 1 to 100 to each megasite based on multiple criteria, including the proportion of the site in private versus public ownership; presence of active grazing, mining, oil and gas, or timber leases or potential for such in the near future; road density and trends; human population and housing density and trends; disruptive recreational uses and trends, among others. Preliminary vulnerability scores were revised by consensus by participants in the workshop, and those revised scores were rescaled to range approximately from 1 to 100.

Following Margules and Pressey (2000), we plotted megasites on a graph of irreplaceability (y-axis) versus vulnerability (x-axis) and divided the graph into four quadrants. The upper right quadrant, which encompasses megasites with high irreplaceability and high vulnerability, is the highest priority for conservation. This top tier of megasites is followed by the upper left and lower right quadrants (moderate priority), and finally by the lower left quadrant, encompassing megasites that are relatively replaceable and face less severe threats.

Results and Discussion

Our assessment resulted in a portfolio of planning units grouped into 43 megasites, which collectively met or exceeded the stated conservation goals for the three approaches of special elements, representation, and focal species. These megasites constitute areas of public and private land that currently lack formal protection. Megasites range in size from 11,331 to 315,662 ha ($\bar{x}$ = 109,268 ha) and total 4,573,047 ha (42% of the GYE). Private lands constitute 36% of the total portfolio area. If combined with existing protected areas (totaling 2,889,518 ha), our portfolio would bring the total protected area to 7,462,565 ha, nearly 70% of the GYE.

Special Elements

The complete portfolio, together with existing protected areas, captured 100% of the 236 documented occurrences of G1 and G2 species and communities in the GYE, as targeted, compared with 29% in existing protected areas. On average, protection of element occurrences for the four classes of special elements—local-scale species, birds, fish, and plant communities—increased by 62% with this portfolio.

The proposed portfolio captured occurrences of 80 local-scale species that are not recorded in existing protected areas, including five G1 species (for details see Noss et al. 2001). The 318 occurrences of vulnerable bird species in the portfolio, combined with 139 in existing protected areas, encompassed 457 (86%) of the 534 occurrences in the GYE. The 55 occurrences of imperiled fish species or subspecies in the proposed portfolio, when added to 24 occurrences in existing protected areas, encompassed 88% of the 90 known occurrences. Seven fish species or subspecies not recorded in existing protected areas were captured by the proposed portfolio. The 341 plant-community occurrences in the proposed portfolio and 148 in existing protected areas captured 95% of the 515 occurrences in the GYE. Seven G1 plant communities in the proposed portfolio are not known from existing protected areas.

Representation

Of the three approaches, our proposed portfolio most fully met stated goals for representation. Current protected areas met our 15–25% representation goals for over 61% of the 39 GAP vegetation types and our 15% goal for 41% of the 39 physical habitat types. Our proposed portfolio met stated goals for 100% of these classes. Current protected areas met our 20% representation goal for over 44% of the 654 aquatic habitat strata. Our proposed portfolio raised this to 98%.

Focal Species

Habitat-suitability modeling produced resource selection functions for the focal species that predicted association of individual animals with habitat variables on a regional scale (Table 1). Of particular management significance is the negative association of grizzly bear and wolf locations with road and trail density and the positive association of all three species with parks and wilderness areas, especially compared with private lands. These relation-

Table 1. Focal species resource-selection function models for grizzly bears, wolves, and wolverines of the Greater Yellowstone Ecosystem.[a]

Variable	*Grizzly bear*	*Wolf*	*Wolverine*
July brightness	−	−	
July greenness	+	+	
July wetness		−	−
November brightness	+		
November greenness	+		
November wetness	−	−	
Annual precipitation			cx[b]
Annual snowfall		cx	
Elevation			cx
Slope	+	cx	
Elk winter range	+	+	
Road and trail density	−	−	
General public land	+	−	+
Wilderness	+	+	+
Park	+	+	+
Road density × public land	−		
Road/trail density × wilderness	−		
Road/trail density × park	−		
November brightness × wetness	+		

[a] *Selected models are those that explained the most variation in occurrences (locations). Models were highly significant* ($p < 0.001$) *for each species. Variables are shown as positively (+) or negatively (−) associated with occurrences. See Noss et al. (2001) for model coefficients and other details.*
[b] *cx, quadratic, convex up.*

ships reflect the need of these species for security from human persecution and harassment (Noss et al. 1996; Carroll et al. 2001). The wolf model was generally similar to that for the grizzly bear but differed in the strong negative association with slopes above 20 degrees and the lower contrast between parks and wilderness and private lands, reflecting somewhat greater tolerance of wolves for human-modified landscapes. The wolverine model had poorer predictive power than those of the grizzly bear and wolf, consistent with the scarcity of field knowledge of habitat relations for this species.

Our dynamic model (PATCH) showed strong source habitat for grizzly bears in the areas that encompass most of the current distribution, centered on protected areas in the core GYE (Fig. 3a). The model suggests that, given time, bears could expand into adjacent unprotected public lands, especially on the eastern and southern periphery of the core. Expansion is limited, however, by the surrounding sink habitat. Assuming that road-building continues on private and public land over the next 25 years, core areas of the GYE are predicted to remain strong sources but would no longer be able to support the peripheral distribution. Essentially, the ring of sinks that envelops the core GYE becomes increasingly constricted (Fig. 3b). Although we predict a relatively high probability of persistence for the grizzly bear over the short to medium term, future landscape change may greatly reduce the distribution and size of the population.

The dynamic-model results for the wolf were similar to those for the grizzly bear. Because the wolf can inhabit semideveloped landscapes, it is more affected by simulated future development outside the core GYE (Noss et al. 2001). Currently, potential source areas include most public lands in the central GYE and some adjacent private lands. Connectivity is reasonably good between the GYE and areas to the west and north (e.g., central Idaho, where another reintroduced wolf population exists). Future landscape change threatens to isolate wolves in the GYE from adjacent regions and alienate much of the productive lower-elevation habitat that currently could support wolves. For the wolverine, we predict a pattern of source and sink habitat similar to that of the grizzly bear, with a pronounced ring of sinks surrounding the source habitat of the core GYE (Noss et al. 2001).

Evaluation of SITES Portfolios Based on the PATCH Model

Our irreplaceability and vulnerability scoring based on overlaying megasite boundaries on results of the PATCH models showed broad similarities with the general megasite scoring (Noss et al. 2001). Nevertheless, consistent differences emerged because the PATCH model considered a broader region (Fig. 1) and accounted for the landscape context and source-sink dynamics of sites. For example, sites that emerged as most vulnerable for carnivores were not necessarily those with the highest levels of site-specific threat but rather were those whose continued degradation would pose the greatest risk to the viability of nearby large source areas that sustain regional populations. Hence, improving conditions in strong and worsening sinks is potentially as important to regional population viability as protecting strong sources. Simulations that included megasites within the reserve network showed that sites whose protection would have the greatest effect on the distributions of focal species were those with high demographic irreplaceability and vulnerability. Protection of some smaller megasites would increase occupancy far beyond their immediate boundaries, particularly for the wolf, because of its better ability to inhabit semideveloped landscapes.

Megasite Prioritization

Our procedure for calculating the irreplaceability of megasites necessarily hides information specific to individual planning units. This information is not lost, however, and can be accessed readily by planners engaged in site-level planning and management, a phase beyond the regional scope of this paper. Megasite irreplaceability scores ranged from 0.3 to 99.5 ($\bar{x} = 54.9$) and vulnerability scores from 1.5 to 98.5 ($\bar{x} = 50.3$). Our analysis

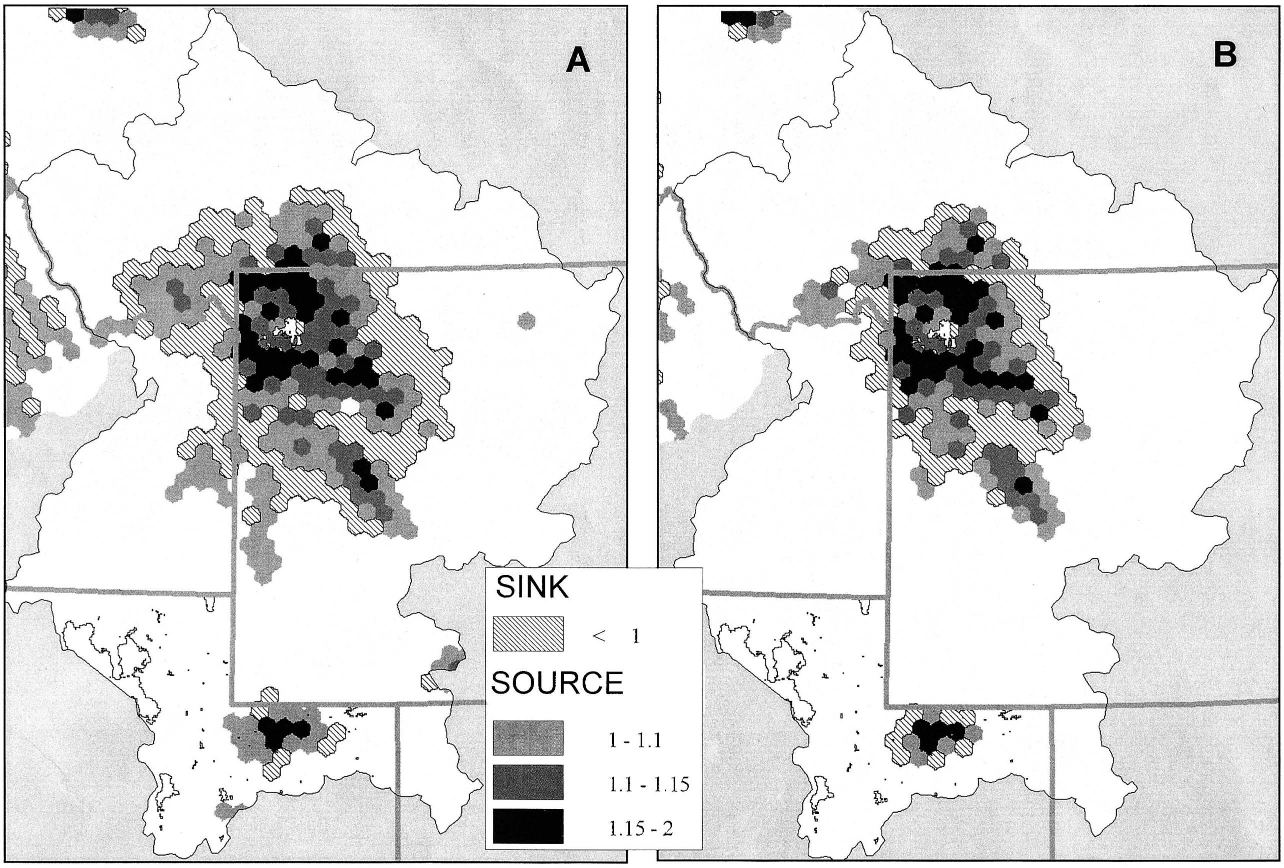

Figure 3. Distribution and demographic potential of grizzly bears in the expanded study region under (a) current and (b) future landscape conditions, assuming road development on both private and public lands. Legend shows population growth rate (lambda) values predicted by the PATCH model simulations. Hexagons represent individual territories.

resulted in 15 megasites totaling 2.4 million ha in the high irreplaceability-high vulnerability quadrant 1, giving them the highest priority for conservation action (Figs. 4 & 5). Ten megasites in high irreplaceability-low vulnerability quadrant 2 cover 1.1 million ha; 5 megasites in low irreplaceability-high vulnerability quadrant 3 cover 0.5 million ha; and 13 megasites in low irreplaceability-low vulnerability quadrant 4 cover 0.8 million ha.

Our grouping of megasites into quadrants (Fig. 4) differs from that of Margules and Pressey (2000) in that we give slightly higher priority to the upper left quadrant (our quadrant 2, their quadrant 3) over the lower right quadrant. We believe that sites of high and irreplaceable biological value merit conservation action even if not highly threatened today. Protecting these sites while they are still reasonably intact is sensible. The private lands in these areas are generally less expensive to protect than those in more threatened sites because they are usually in areas with lower population and development pressure.

Our proposed portfolio, if protected in its entirety, would cover 43% more of the region than the current reserve network. For that 43% increment, there is a considerable "bang for the buck" for many elements—for example, a 71% increase (to 100%) in coverage of G1/G2 species, a 62% increase for all special elements combined, and a 50% increase for representation of ecological systems.

Progress toward conservation goals could be achieved most effectively by protecting first the highest-priority megasites (quadrant 1), then the medium-priority megasites (quadrants 2 and 3), and finally the lower-priority megasites (quadrant 4), (Table 2). The greatest gains would be achieved with protection of the 15 highest-priority megasites (quadrant 1), resulting in an overall increase in goal achievement of 30% for the three tracks (from 47% of goals achieved currently to 77%), with an increase in reserved area of 22%. Protection of known locations of the most highly imperiled species and representation of geoclimatic classes would increase by 46% and 49%, respectively. The increment for focal species is much less—only a 10% increase from adding quadrant 1 megasites to the reserve network—because most of the best (e.g., roadless) habitat is already in parks and wilderness areas.

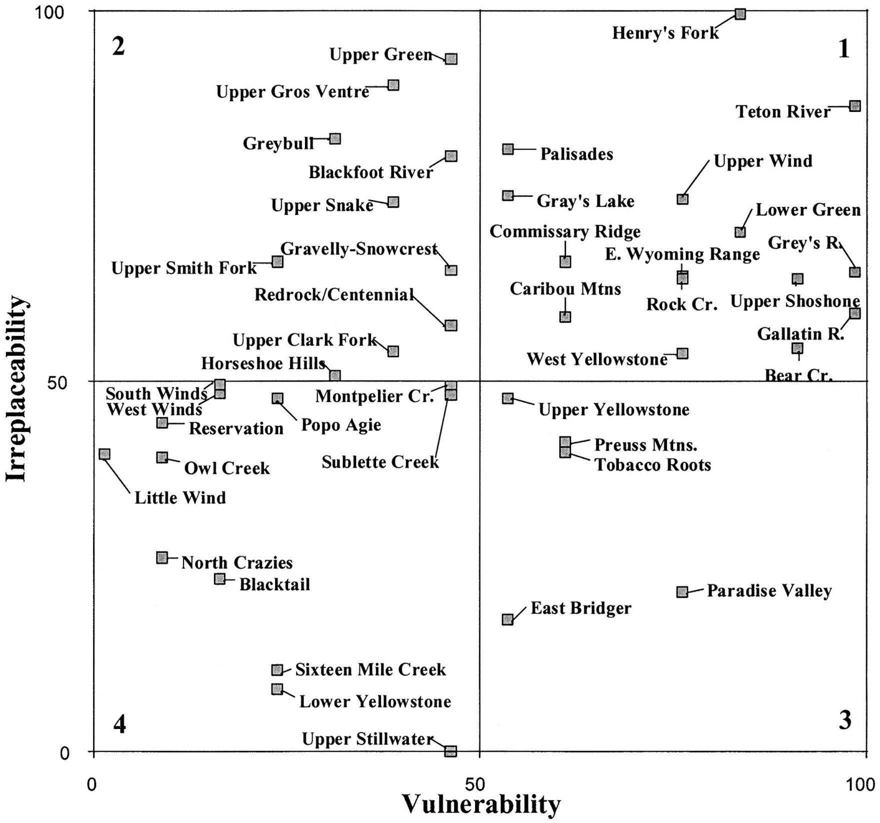

Figure 4. Irreplaceability versus vulnerability of megasites based on nine conservation criteria. Megasites are grouped by priority quadrants 1-4.

Protecting the 10 megasites from quadrant 2 would increase overall achievement of goals from the three approaches another 11% to 88%. Protecting the 5 megasites in quadrant 3 would increase achievement to 91%, and protecting the 13 megasites in quadrant 4 would increase achievement to 94%. Thus, our proposed portfolio would encompass over 94% of special-element occurrences, focal species habitat, and terrestrial and aquatic ecological systems, at targeted levels, within the GYE.

Conclusions

Our methodology is noteworthy in that it combines several approaches and techniques that have previously been applied separately in conservation planning. For example, to our knowledge this is the first case where spatially explicit modeling of population viability has been combined with comprehensive representation analysis. Hence, we were able to address questions concerning the adequacy of alternative reserve networks that are ignored in most reserve designs based on site-selection algorithms (Possingham et al. 2000; Pressey et al. 2000).

Our results provide a reasonably complete assessment of regional-scale conservation opportunities in the Greater Yellowstone Ecosystem, given available information. Like other researchers (e.g., Leslie et al. 2002), we were pleased with the ability of the simulated annealing algorithm to portray multiple conservation scenarios. These scenarios, and the goals upon which they are based, can be evaluated and refined by decision-makers through a flexible, interactive process. Hence, the algorithm is a decision-support tool, not a "black box" that yields a single best solution. Nevertheless, our assessment is a snapshot of the existing conservation scene in the GYE, augmented (for focal species) by a projection of current trends into the future. To be most useful, new assessments of the irreplaceability and vulnerability of sites should be conducted periodically as particular threatening processes increase or diminish and as sites are added to the reserve system or lost to development (Pressey & Taffs 2001). In the real world, conservation priorities change continuously.

We suspect that the three classes of ecological systems—vegetation, geoclimatic types, and aquatic habitats—represented by our portfolio provide a functional coarse filter (Noss 1987), although the coarse-filter hypothesis cannot be tested rigorously without a complete inventory of a region's biota. More uncertainty is associated with special elements. Although the GYE, because of its popularity with naturalists, has been better surveyed than most regions of the American West, biases in heritage-program databases are inevitable. For instance, some portions of the GYE are poorly known biologically, such that the absence of element occurrences

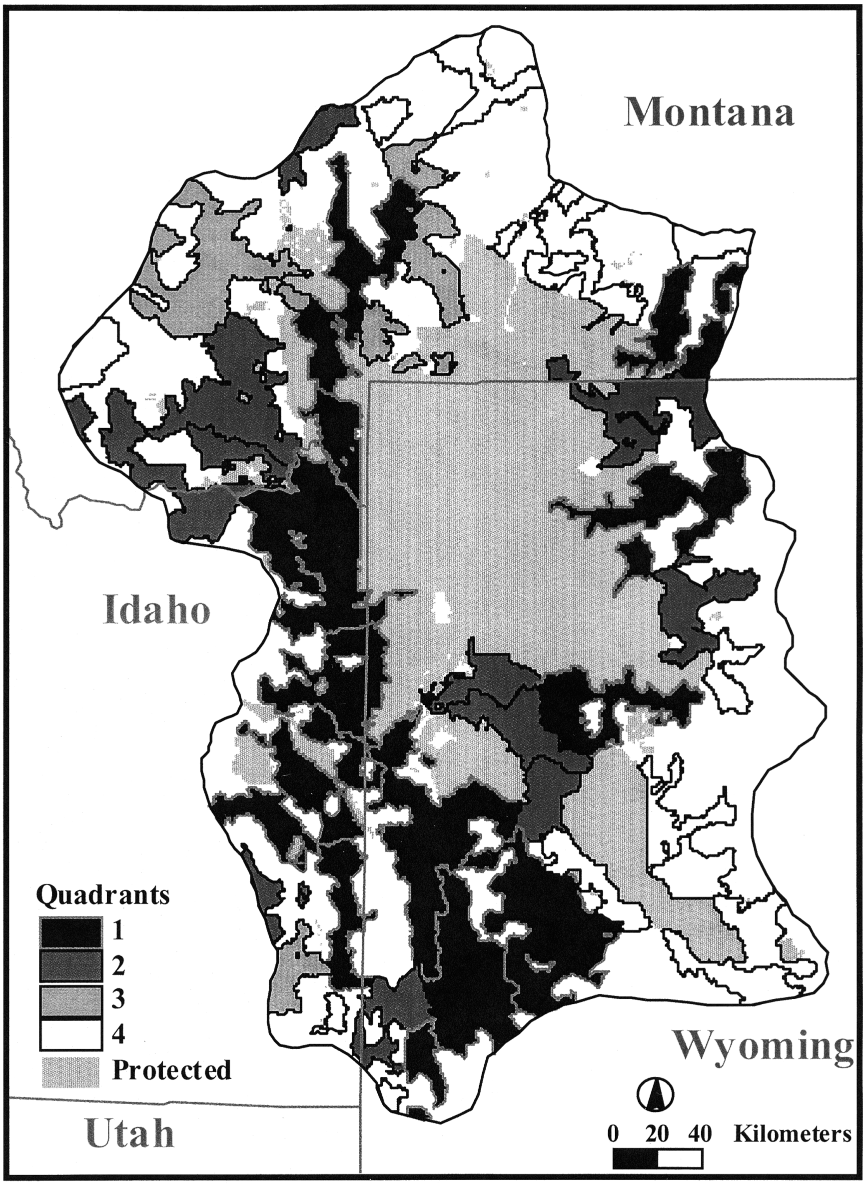

Figure 5. Megasites (by quadrant) and protected areas of the Greater Yellowstone Ecosystem.

from these areas probably reflects an absence of surveys more than an absence of imperiled species and communities. Heritage databases do not allow these two classes of absence to be discriminated. With more complete field surveys, some megasites with low irreplaceability scores might move upward in priority.

Our treatment of focal species differs from conventional approaches in that we use both static and dynamic models to evaluate the relative demographic value of sites. The carnivore populations in the GYE are on the periphery of their ranges due to climatic or historical factors and cannot expect a large demographic rescue effect from surrounding regions. Currently, the core refugia of the national parks and adjacent wilderness areas are strong sources and could support carnivore populations in the extremities of the region. If current trends continue, development will increasingly surround the core GYE with sinks, weakening its ability to sustain populations in outlying areas. It is noteworthy that areas of high value for multiple species combine high biological productivity and security from human impacts (Carroll et al. 2001). Such areas (e.g., undeveloped riparian areas) are scarce in the GYE and tend to be highly threatened by development (Hansen et al. 1999).

Although we have used such terms as "protected areas" and "reserves" to describe the desired fate for megasites, conservation objectives can be met through a variety of means. Protection and management options include direct fee acquisition, conservation easements, management agreements and stewardship assistance to landowners, agency designations of special areas (e.g., research natural areas), congressional wilderness designations, and administrative actions such as national mon-

Table 2. Achievement of conservation goals in the Greater Yellowstone Ecosystem, beginning with the current protected-areas network and continuing with addition of megasites in priority quadrants 1–4.

	Current protected areas (%)	*Current protected areas plus (%)*				*Total change (%)*
		quad 1	*quad 2*	*quad 3*	*quad 4*	
Protected area	26.6	48.4	58.2	62.5	69.8	+43.2
Special elements						
all G1–G2*	28.9	74.9	89.1	93.3	100	+71.1
class 1, local-scale species	40.7	69.2	86.3	89.0	93.2	+52.5
class 2, birds	26.0	67.4	80.3	83.7	85.6	+59.6
class 4, fish	26.7	55.6	82.2	84.4	87.8	+61.1
class 5, plant communities	28.7	81.6	91.7	94.8	95.0	+66.3
Special-elements average	30.2	69.7	85.9	89.0	92.3	+62.1
Focal-species habitat						
grizzly bear	94.4	96.5	98.0	98.3	98.9	+4.5
wolf	77.8	86.0	92.7	94.1	96.3	+18.5
wolverine	41.3	62.7	74.2	76.0	83.1	+41.8
Focal-species average	71.2	81.7	88.3	89.5	92.8	+21.6
Representation (ecological systems)						
≥15% vegetation types	61.5	89.7	92.3	92.3	100	+38.5
≥15% geoclimatic classes	41.0	89.7	92.3	94.9	100	+59.0
≥20% aquatic types	44.3	74.5	90.5	95.9	98.0	+53.7
Representation average	48.9	84.6	91.7	94.4	99.3	+50.4
Total average	46.5	77.1	88.1	90.6	94.4	+47.9

**G1, critically imperiled globally; G2, imperiled globally.*

ument designations. Our simulations of the effects of alternative future scenarios on the viability of focal species showed that the straightforward action of avoiding new road building in existing roadless areas on public lands would have highly positive results (Noss et al. 2001). In keeping with the precautionary principle, the highest-priority (e.g., quadrant 1) megasites generally should receive the highest level of protection, whereas lower-priority megasites could accommodate more human uses.

Protection opportunities in the GYE will not arise in an orderly sequence that corresponds to science-based priorities. For example, megasites in quadrant 3 may become available for protection before megasites in quadrant 1. If not protected quickly, some of these sites may be converted to subdivisions. Yet funds, or political capital, spent protecting these sites may preclude opportunities for protecting biologically more significant sites in the future. What is the optimal course of action under such circumstances?

The irreplaceability-vulnerability approach to recognizing conservation priorities is not perfectly suited to real-world opportunities (Pressey & Taffs 2001). We suggest that conservationists follow an informed opportunism, taking advantage of conservation openings as they arise, but with explicit recognition of the trade-offs involved. Systematic conservation planning allows the effects of single and cumulative decisions to be quantified and considered in a biologically meaningful way (Margules & Pressey 2000). With information made transparent and explicit, decision-makers will be better equipped to take actions that are scientifically defensible and that result in the most biodiversity conserved.

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