

# Threatened and Endangered Species Geography

## *Characteristics of hot spots in the conterminous United States*

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An estimated global extinction rate that appears to be unprecedented in geological time (May 1990) has heightened concern for the increasing number of rare species. Moreover, this elevated extinction rate is being attributed to the activities of humans rather than to some calamitous natural disaster (Pimm et al. 1995). Conservation efforts to slow biodiversity loss have traditionally focused on species with few remaining individuals, based on the assumption that they are the most vulnerable to extinction (Sisk et al. 1994). Consequently, rarity has been used as an important criterion for identifying which species should be the focus of conservation efforts.

The Endangered Species Act of 1973 (ESA) has epitomized this species-by-species conservation strategy (Doremus 1991). The ESA and its subsequent amendments codified broad-ranging protection for all species, plant or animal, that are in immediate danger of extinction or that may be threatened with extinction in the foreseeable future. Although the benefits of ESA are diffi-

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### Hot spot-targeted recovery efforts have the potential to be a more efficient strategy for biodiversity conservation

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cult to quantify, there is general agreement that fewer species have become extinct under ESA than would have without it (Committee on Scientific Issues in the Endangered Species Act 1995).

Despite this success, the ESA has spawned much criticism, which can be traced largely to its single-species orientation (Hutto et al. 1987, Rohlf 1991). Not only is the single-species approach to endangered species conservation unwieldy and slow, but it ignores the dynamics of ecological systems as a whole. This criticism is not directed at the ESA per se but rather at the way in which it has been implemented. Language in the ESA specifically states that it is "...to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved..." (Section 2b). In practice, however, the potential for protecting species collectively through the preservation of critical ecosystems has never been fully realized (Doremus 1991).

Several recommendations to improve the ESA have recently been

suggested, including increased authorization of funds and personnel (O'Connell 1992), more reliance on mathematical modeling (Hyman and Wernstedt 1991), greater emphasis on recovery planning (Cheever 1996), and incorporation of socioeconomic considerations (Heinen 1995). These potential improvements, however, continue to emphasize the single-species approach to conservation and recovery. Far more significant are proposals that reorient US endangered species policy completely, to emphasize the management of representative ecosystems as whole units (Hutto et al. 1987, Scott et al. 1988, Rohlf 1991). Such a system-level perspective, however, is not without difficulties. Most fundamental is the lack of a generally accepted classification of ecosystems that can be used to define those systems that should serve as biodiversity conservation units (Losos 1993, Orians 1993).

A potential solution to this classification shortcoming is to define ecosystems that warrant conservation focus based on geographic and environmental attributes shared by species that are currently listed as threatened or endangered. Distributional information and environmental associations have accumulated for enough species so that geographic patterns of species endangerment can be discerned (Flather et al. 1994, Dobson et al. 1997). In this article, we use this information to delineate regions in which listed species are concentrated. For each of these regions, we further describe the taxonomic composition, prevalence of

## Endangerment factors

Factors that are or have been a threat to species populations of the 631 threatened and endangered species that occur in the conterminous United States (Brown et al. 1984). These factors were compiled from *Federal Register* final listings, US Fish and Wildlife Service *Endangered Species Technical Bulletins*, species recovery plans, federal agency reports, and miscellaneous publications on species life history. A complete list of documents used to assign biological attributes to endangered species is available from the authors.

Adverse weather	Grazing	Recreational areas
Agricultural development	Groundwater drawdown	Reservoir development
Artillery/explosions	Harassment/vandalism/ indiscriminate killing	Residential/industrial development
Bank modification	Heavy equipment (e.g., construction, logging, military)	Rock climbing
Boating	Herbicides	Salinity alteration
Channel modification	Highways/railroads	Shoreline modification
Climate alteration	Hiking/camping	Siltation
Collecting	Hybridization	Spelunking
Commercial exploitation	Incidental killing	Sport hunting/fishing
Competition	Inherent reproductive characteristics	Subsistence hunting/fishing
Disease	Introduction of exotic species	Surface drainage
Dissolved oxygen reduction	Low gene pool	Surface mines
Environmental contaminants	Off-road vehicles	Transmission lines/towers
Erosion	Oil Spills	Underground mines
Fertilizers	Parasites	Vegetation composition changes
Fire suppression	Passage barriers (e.g., dams, locks, gates)	Vertebrate animal damage control
Fire	Pesticides	Water diversion
Flooding	Poaching	Water level fluctuations
Food supply reduction	Predation	Water level stabilization
Forest alteration		Water temperature alteration
Forest clearing		Wetland filling
Gas/oil development		
Geothermal development		

endemism, landcover associations, and factors that have contributed to species endangerment. We also assess whether the distributions of the species that have received the majority of federal funding coincide with regions of high species endangerment. This comparison allowed us to test whether conservation of high-expenditure species has the potential to confer incidental benefits to other listed species that inhabit areas that are rich in endangered species. This descriptive geography, which is a basic prerequisite to defining characteristics of species or environments that are susceptible to endangerment (Slobodkin 1986), can focus conser-

vation efforts in those areas where many endangered species occur.

### Identifying hot spots

Because much is known about species endangerment in island systems (Olson 1989), we examined 631 species that occur within the conterminous United States. This data set represented species listed as of November 1994. County-level distributions of threatened and endangered species were compiled primarily from *Federal Register* final listings, US Fish and Wildlife Service (FWS) *Endangered Species Technical Bulletins*, species recovery plans, environ-

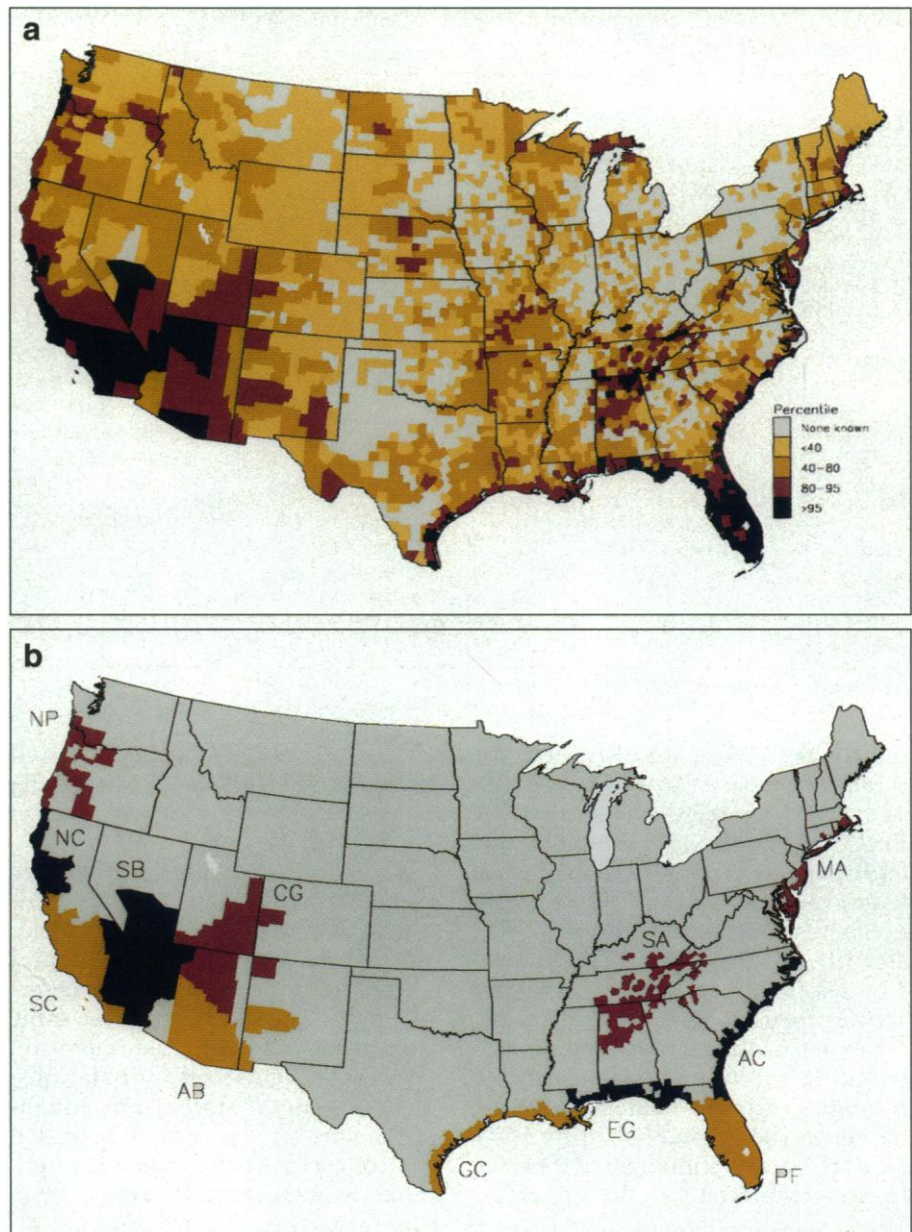
mental impact statements, federal and state agency reports, Heritage Program information, and consultation with FWS regional and field biologists.

We identified geographic areas with a large number of endangered species, also called "hot spots," using the criteria specified by Prendergast et al. (1993)—namely, an arbitrarily defined upper percentile of sample units ranked by species counts. To account for the disparity in county area across the United States, we partitioned counties into "large-area" and "small-area" sets at a threshold of 368,000 hectares. This threshold resulted in 45% of

**Figure 1.** The geographic distribution of threatened and endangered species in the United States. (a) Counties shown in percentile classes according to the number of threatened and endangered species they contain. To account for differential county area, large-area and small-area counties were ranked separately. (b) Species endangerment hot spots were defined by identifying the 5% of large- and small-area counties with the most endangered species (i.e., those above the 95th percentile in map category) as well as the 20% of large- and small-area counties with the most endangered species that were located in proximity to the counties in the top 5%. This set of counties was organized into regions based on the Soil Conservation Service land resource classification system (SCS 1981). AB, Arizona Basin and Range; AC, Atlantic Coast Flatwoods; CG, Colorado and Green River Plateaus; EG, Eastern Gulf Coast Flatwoods; GC, Gulf Coast Marsh and Prairie; MA, Mid-Atlantic and Northern Coastal Plain; NC, Northern California Mountains and Valleys; NP, Northern Pacific Coast Range and Valleys; PF, Peninsular Florida; SA, Southern Appalachians; SB, Sonoran Basin and Range; SC, Southern California Mountains and Valleys.

the conterminous United States being categorized as large-area counties. (We chose this approach because the alternative, a simple conversion to county density, produced an eastern bias and concealed known concentrations of endangered species in the arid Southwest; Hallock 1991.) We then ranked the counties within these large- and small-area sets according to the number of threatened and endangered species that occurred within their boundaries.

Endangerment hot spots were initially located by mapping the top 5% of large- and small-area counties (i.e., those counties in which the greatest number of listed species were found). The areal extent of hot spots was then defined by the top 20% of counties that were also contiguous to, or formed distinct clusters with, those counties in the top 5%. A land resource classification system developed by the USDA Soil Conservation Service (SCS 1981) was used to group those counties that supported many endangered species into regions that have similar climate, physiography, soil, vegetation, and land use, which we call hot spots. The use of a land classification system to define hot



spots was an attempt to identify endangerment regions based on an ecological, rather than a political, template (*sensu* Knopf 1992). However, county-level distribution data are fundamentally political and constrain identification of endangerment regions on purely ecological criteria.

This analysis showed that endangered species are not homogeneously distributed across the conterminous United States. Instead, threatened and endangered species are concentrated in distinct geographic regions (Figure 1a). Based on comparisons with the land-base classification system, we identified a total of 12 hot spots of high species endangerment (Figure 1b). It is important to note

that our county-level occurrence of listed species was based on the species' current distributions. Those portions of the historical range from which a listed species have already been extirpated were not included in our delineations of hot spots because our intent was to focus on areas that have retained some suitable habitat.

### Biological characteristics of hot spots

We initially compiled biological information on threatened and endangered species from the *Federal Register* final listings. However, because listing decisions lack consistency in the biological criteria reported (Eas-

**Table 1.** Taxonomic composition and levels of endemism within each hot spot. The percentage of species within each hot spot is shown in parentheses.

Taxon	Eastern hot spots						Western hot spots					
	MA <sup>a</sup>	AC	PF	SA	EG	GC	CG	AB	SB	NP	NC	SC
Animals	14 (67)	15 (65)	34 (46)	76 (70)	23 (61)	15 (79)	17 (41)	28 (78)	36 (61)	17 (77)	21 (57)	48 (62)
Vertebrates	10 (48)	15 (65)	31 (42)	29 (27)	22 (58)	15 (79)	16 (39)	25 (69)	33 (56)	16 (73)	15 (40)	39 (50)
Mammals	1 (5)	3 (13)	9 (12)	5 (5)	5 (13)	3 (16)	1 (2)	5 (14)	3 (5)	2 (9)	3 (8)	11 (14)
Birds	4 (19)	6 (26)	10 (14)	3 (3)	6 (16)	7 (37)	5 (12)	8 (22)	7 (12)	7 (32)	8 (22)	14 (18)
Fishes		1 (4)	1 (1)	20 (18)	2 (5)		9 (22)	11 (30)	20 (34)	7 (32)	3 (8)	7 (9)
Reptiles	5 (24)	5 (22)	11 (15)	1 (1)	9 (24)	5 (26)	1 (2)	1 (3)	2 (3)		1 (3)	6 (8)
Amphibians									1 (2)			1 (1)
Invertebrates	4 (19)		3 (4)	47 (44)	1 (3)		1 (2)	3 (8)	3 (5)	1 (4)	6 (16)	9 (12)
Clams	1 (5)			40 (37)	1 (3)							
Snails			1 (1)	4 (4)			1 (2)	2 (6)				
Insects	3 (14)		1 (1)						2 (3)	1 (4)	5 (14)	8 (10)
Crustaceans			1 (1)	3 (3)				1 (3)	1 (2)		1 (3)	1 (1)
Plants	7 (33)	8 (35)	40 (54)	32 (30)	15 (39)	4 (21)	24 (59)	8 (22)	23 (39)	5 (23)	16 (43)	30 (38)
Total	21	23	74	108	38	19	41	36	59	22	37	78
Endemics	2 (9)	2 (9)	58 (78)	33 (31)	14 (37)	1 (5)	17 (41)	19 (53)	33 (56)	3 (14)	16 (43)	48 (62)
Animals	1 (5)	2 (9)	19 (26)	25 (23)	6 (16)		1 (2)	13 (36)	15 (25)		5 (14)	23 (29)
Plants	1 (5)		39 (53)	8 (7)	8 (21)	1 (5)	16 (39)	6 (17)	18 (30)	3 (14)	11 (30)	25 (32)

<sup>a</sup>Hot spot codes are defined in Figure 1.

ter-Pilcher 1996), we also incorporated information from a variety of additional sources, including FWS *Endangered Species Technical Bulletins*, species recovery plans, other federal agency reports, and miscellaneous research publications on species life history. The biological attributes assigned to each endangered species focused on taxonomy, land-cover associations, and factors contributing to species endangerment. Biological attribute categories were based on those established by FWS as part of the Endangered Species Information System (Brown et al. 1984).

We assigned each species to a variety of taxonomic groups, including plants, animals, vertebrates, invertebrates, mammals, birds, fishes, reptiles, amphibians, clams, snails, insects, arachnids, and crustaceans. Landcover associations were based on Anderson et al.'s (1976) land classification system and were used to describe the broad habitat types (i.e., forest land, rangeland, barren land, water, or wetland) in which a species occurs. Factors contributing to species endangerment represented those population threats that are or have been detrimental to the species. A total of 63 endangerment factors have been defined (Brown et al. 1984; see box page 366); those that have had an impact on one or more listed

species were obtained primarily from the "Summary of Factors Affecting the Species" section of the *Federal Register* final listing.

Varying degrees of certainty are associated with assigning these biological characteristics to the species in our database. For example, whereas taxonomy could be determined with high certainty, the same cannot be said for the enumeration of threats to species populations. Because many threatened or endangered species are poorly studied (Wilcove et al. 1993), the set of endangerment factors generated from a literature search does not guarantee a comprehensive list. Therefore, our compilation of population threats should be treated as an initial summary that will require amendments as new information becomes available. Despite the uncertainty in assigning endangerment factors to some species, documenting population threats is an important step toward understanding which threats will have to be addressed by conservation efforts within endangerment hot spots.

**Taxonomic composition.** The taxonomic makeup of endangerment hot spots depicted in Figure 1b is varied (Table 1). Although plants make up the majority of species listed as threatened or endangered, animals domi-

nate in most endangerment hot spots. Only in Peninsular Florida and the Colorado and Green River Plateaus do plant species comprise the majority of listed species.

Birds are a consistently high component of the endangered biota within hot spots, comprising at least 20% of the endangered species in five regions. Among the vertebrate taxa, mammals never comprise more than 16% of the endangered biota within any single hot spot. The greatest number of endangered mammals are found in Peninsular Florida, where small mammals have specialized on dune and marsh habitats (Humphrey 1992), and in the Southern California Mountains and Valleys, where small mammals have specialized on coastal scrub and annual grassland habitats (Grinnell 1922). The distributional pattern of endangered fishes is distinctive because of its concentration in the southwestern United States. Although the Southwest accounts for less than 10% of the continental fish species, many of these species are endemic to the region (Warren and Burr 1994). A second concentration of threatened and endangered fishes is found in the Southern Appalachians region, an area also noted for its high level of endemism (Williams et al. 1989). Reptiles, in particular nesting marine turtles, are relatively numerous

among southern coastal hot spots. Because so few amphibians are listed, this taxon does not make up a notable proportion of the endangered fauna within any of the hot spot regions. Of the many amphibian species of the Southern Appalachians region, an area in which amphibians reach their greatest richness (Currie 1991), none had received formal protection under ESA at the time our database was compiled.

Endangerment patterns are difficult to interpret for most taxonomic groups of invertebrates because relatively few invertebrate species are listed as threatened or endangered. An exception to this generalization is the freshwater clams, which reach their greatest species richness in large river and drainage lake systems in the eastern United States (Pennak 1978). Indeed, the endangered clams of Appalachian riverine systems make up nearly 40% of all the endangered species found in the Southern Appalachians hot spot. Another notable pattern among endangered invertebrates is the relatively high number of listed insects found in both the Northern and Southern California Mountains and Valleys—regions in which many insect species have recently become extinct (Pyle et al. 1981). No listed arachnids occur within any of our identified hot spots.

**Patterns of endemism.** An endemic species is one whose distribution is restricted to a given geographic region. Because a geographic region can be a continent, a country, an island, or a watershed, endemism patterns are scale dependent (Rapport 1982). For our analysis, we de-

finer species whose current county-defined distribution is contained wholly within a single hot spot as endemic.

Species endemic to hot spots comprise more than 50% of the endangered biota in Peninsular Florida, the Arizona Basin and Range, the Sonoran Basin and Range, and Southern California Mountains and Valleys (Table 1). Because many endangered plants exhibit restricted distributions (Falk 1992), plants make up, on average, 36% of the endemics in these high-endemism hot spots. Other taxonomic groups that make up a large fraction of the endangered endemic biota include mammals in Peninsular Florida and in the Southern California Mountains and Valleys (14% of endemics in both locations), fishes in the Southern Appalachians and in the Sonoran Basin and Range (27% and 24% of endemics, respectively), freshwater clams in the Southern Appalachians (33% of endemics), and insects in the Southern California Mountains and Valleys (12% of endemics).

**Landcover associations.** The two most common landcover classes across the conterminous United States are forest and rangeland. Forest landcover occurs mostly in the eastern one-third of the United States, the Pacific Northwest, and high-altitude regions of the interior West (Powell et al. 1993). Rangeland habitats, which include lands dominated by grasses, grasslike plants, forbs, or shrubs, dominate the central region of the United States, the lower elevations of the intermountain region, and the desert regions of the South-

west (Joyce 1989). Given this distribution of forest and rangeland cover, it is not surprising that endangered species occurring in Eastern and Pacific Coast hot spots are associated with forest ecosystems, whereas species found in the intermountain region and the arid Southwest regions are associated with rangeland ecosystems (Table 2).

More interesting are the species associations with rarer landcover types. Barren land, which includes bare exposed rock, dry salt flats, and dune environments, occurs on only approximately 1% of the land base in the conterminous United States (as estimated from digital landcover data from the US Geological Survey [USGS 1986]). However, an average of 32% of the listed species in hot spots are associated with this landcover class. The largest fraction of endangered species that are associated with barren land habitats are found primarily in coastal areas and secondarily in the arid Southwest.

Wetland habitats are also a rare landcover type, comprising approximately 5% of the land base of the conterminous United States (Brady and Flather 1994). Nevertheless, we found that wetlands represent a particularly important habitat type for endangered species. More than 50% of the endangered species occurring in the Atlantic Coast Flatwoods, Eastern Gulf Coast Flatwoods, and Northern California Mountains and Valleys were associated with wetland habitats. Of particular note is the collection of wetland-associated species in the arid Southwest. Many of these wetland systems represent Pleistocene relics from a period when

**Table 2.** Number of species associated with broad landcover classes within hot spots. The percentage of species within each hot spot is shown in parentheses.

Landcover class	Eastern hot spots						Western hot spots					
	MA <sup>a</sup>	AC	PF	SA	EG	GC	CG	AB	SB	NP	NC	SC
Forest land	7 (33)	10 (43)	54 (73)	93 (86)	27 (71)	5 (26)	10 (24)	13 (36)	8 (14)	16 (73)	12 (32)	11 (14)
Rangeland	5 (24)	6 (26)	21 (28)	5 (5)	9 (24)	10 (53)	34 (83)	30 (83)	51 (86)	12 (54)	15 (40)	51 (65)
Barren land	10 (48)	11 (48)	21 (28)	12 (11)	14 (37)	10 (53)	11 (27)	7 (19)	14 (24)	4 (18)	12 (32)	34 (44)
Water	9 (43)	10 (43)	16 (22)	79 (73)	17 (45)	10 (53)	14 (34)	16 (44)	27 (46)	13 (59)	15 (40)	26 (33)
Wetland	9 (43)	15 (65)	18 (24)	16 (15)	21 (55)	8 (42)	7 (17)	9 (25)	29 (49)	9 (41)	20 (54)	26 (33)
Total number of species in each hot spot <sup>b</sup>	21	23	74	108	38	19	41	36	59	22	37	78

<sup>a</sup>Hot spot codes are defined in Figure 1.

<sup>b</sup>Species counts across landcover categories do not sum to the hot spot total because species can be associated with multiple landcover classes.

**Table 3.** Number of species affected by the five most commonly cited factors contributing to species endangerment within of factors and factor diversity (FD) are based on the total set of endangerment factors cited by all listed species occurring

Factor count and diversity	Eastern hot spots					
	MA <sup>a</sup>	AC	PF	SA	EG	GC
Most commonly cited factors	13 (62) Residential/ industrial development	12 (52) Residential/ industrial development	54 (73) Residential/ industrial development	68 (63) Environmental contaminants	14 (37) Forest alteration	9 (47) Commercial exploitation
	11 (52) Predation	9 (39) Agricultural development	41 (55) Forest clearing	57 (53) Siltation	13 (34) Residential/ industrial development	8 (42) Environmental contaminants
	11 (52) Shoreline modification	8 (35) Commercial exploitation	40 (54) Agricultural development	53 (49) Channel modification	11 (29) Agricultural development	8 (42) Residential/ industrial development
	10 (48) Environmental contaminants	8 (35) Incidental killing	27 (36) Fire suppression	51 (47) Agricultural development	11 (29) Shoreline modification	8 (42) Shoreline modification
	9 (43) Recreational areas	8 (35) Wetland filling	26 (35) Heavy equipment	50 (46) Surface mines	10 (26) Collecting <sup>b</sup>	7 (37) Agricultural development
Number of factors	53	55	57	59	57	54
FD <sup>c</sup> (rank)	3.37 (10)	3.44 (9)	3.45 (7)	3.58 (2)	3.56 (3)	3.36 (11)

<sup>a</sup>Hot spot codes are defined in Figure 1.

<sup>b</sup>Other factors tied for the fifth most common in this hot spot include environmental contaminants, introduction of exotic species, fire suppression, forest clearing, off-road vehicles, predation, and recreational areas.

<sup>c</sup>Other factors tied for the fifth most common in this hot spot include commercial exploitation and introduction of exotic species.

the region was wetter. Because these wetland systems are now embedded in a landscape with drought stress for nearly eight months of the year (Flather et al. 1994), they have been effectively isolated, leading to the development of unique flora and fauna (Hallock 1991).

Associations with aquatic systems are equally prominent in eastern and western endangerment regions. The greatest number of aquatic species was found in the Southern Appalachians region, where nearly 75% of the endangered species were associated with water. Other regions in which over 50% of the listed species were associated with water habitats include the Gulf Coast Marsh and Prairies and the Northern Pacific Coast Range and Valleys.

**Factors contributing to species endangerment.** The set of factors that frequently contribute to species endangerment was different in eastern and western hot spot regions (Table 3). In the East, species endangerment was most often associated with intensive land-use activities. Development associated with residential and industrial land uses and with shoreline modification was cited in all eastern coastal hot spots, a pattern

explained by Culliton et al.'s (1990) finding that over the last 50 years, human population growth in coastal counties was four times the national average. In the Southern Appalachians, contamination and modification of aquatic environments stemming from mining, reservoir construction, and farming affected at least 50% of the listed species inhabiting this region. In Peninsular Florida and the Eastern Gulf Coast Flatwoods, logging and fire suppression were commonly cited threats to listed species. A combination of silvicultural practices and forest clearing for agricultural and urban development appears to have altered the natural disturbance regime under which many of the plant and animal communities evolved—namely, frequent lightning-induced fires (Komarek 1974).

The factor cited most frequently within each western endangerment region tended to be unique to each hot spot (Table 3): off-road vehicles in the Colorado and Green River Plateaus, grazing in the Arizona Basin and Range, introduction of exotic and feral species in the Sonoran Basin and Range, and environmental contamination and pollution in the Northern Pacific Coast Range and Valleys. Residential and indus-

trial development was the most common threat to endangered species in the two California hot spots, again due to development pressures from high population growth in coastal areas.

We also used the information on endangerment factors to predict the difficulty of recovery efforts across the group of species inhabiting each hot spot. We assumed that factor diversity would indicate the complexity of the necessary conservation efforts because it quantifies the number of threats facing species and the relative proportion of species that each factor affects. We measured factor diversity (FD) as:

$$FD = (\ln N! - \sum \ln n_i!)/N!$$

where  $n_i$  is the number of species that each endangerment factor  $i$  affects, and  $N$  is the sum of  $n_i$ . This approach is recommended when estimating diversity from a nonrandom sample or when there is a known collection of objects (in our case, the collection of listed species inhabiting a hot spot; Magurran 1988). Because factor diversity estimates were high in the Southern California Mountains and Valleys, the Southern Appalachians, and the Eastern Gulf Coast Flat-

each hot spot. The percentage of species within each hot spot that is affected by that factor is shown in parentheses. The number in the hot spot. (For a complete list of factors, see box on page 366.)

Western hot spots					
CG	AB	SB	NP	NC	SC
15 (36) Off-road vehicles	18 (50) Grazing	35 (59) Introduction of exotic species	9 (41) Environmental contaminants	22 (59) Residential/industrial development	44 (56) Residential/industrial development
14 (34) Collecting	13 (36) Erosion	32 (54) Water diversion	9 (41) Forest clearing	17 (46) Introduction of exotic species	41 (52) Introduction of exotic species
14 (34) Grazing	13 (36) Introduction of exotic species	25 (42) Agricultural development	8 (36) Predation	16 (43) Agricultural development	35 (45) Agricultural development
14 (34) Surface mines	13 (36) Predation	23 (39) Residential/industrial development	8 (36) Residential/industrial development	16 (43) Off-road vehicles	34 (44) Heavy equipment
13 (32) Gas/oil development	12 (33) Water diversion	22 (37) Surface mines	7 (32) Agricultural development <sup>c</sup>	15 (40) Grazing <sup>d</sup>	28 (36) Grazing
54	59	58	49	55	59
3.44 (8)	3.54 (4)	3.50 (5)	3.26 (12)	3.46 (6)	3.61 (1)

<sup>d</sup>One other factor was tied for the fifth most common in this hot spot: heavy equipment.

<sup>c</sup>Factor diversity was measured using the equation  $FD = (\ln N! - \ln n_i!)/N!$  (Magurran 1988), where  $n_i$  is the number of species that each endangerment factor  $i$  affects and  $N$  is the sum of  $n_i$ . The rank, from the most diverse to the least diverse hot spot, is shown in parentheses.

woods, one would expect that recovery efforts directed at the suite of species inhabiting these hot spots would be more complex than in the Northern Pacific Coast Range and Valleys and the Gulf Coast Marsh and Prairie, where factor diversity was relatively low (Table 3).

**Biological similarity among hot spots.** Our previous discussion of each biological attribute separately makes it difficult to evaluate the biological similarities among hot spots. Knowing the similarities can help managers to determine if conservation efforts could apply to more than one hot spot. We addressed this issue by subjecting our data to principal component analysis so we could graphically depict the similarity among hot spots through simple ordination (Green 1979, Johnson and Wichern 1982). This analysis method is generally used for data exploration rather than hypothesis testing; however, failure to observe patterns of clustering among hot spots in the principal component ordination would indicate that hot spots are unique with respect to the biological attributes we examined.

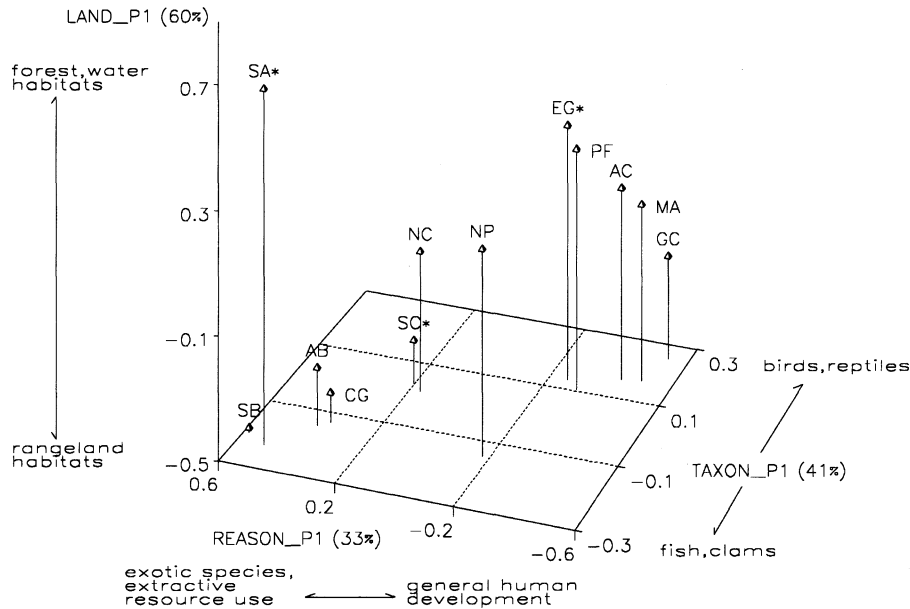
For the principal component analysis, each hot spot represented

an observation, and the variables were the proportions of species in each biological attribute category (i.e., the proportion of species in each taxonomic group and associated with each landcover type and endangerment factor). Each of the three data sets (as depicted in Tables 1–3) was analyzed individually, and the first principal component (i.e., that component explaining the greatest proportion of the variation among hot spots) was extracted from each set.

The first principal component from the taxonomic composition analysis distinguished hot spots according to the observed proportion of birds, fishes, reptiles, and clams. Hot spots supporting a high proportion of birds and reptiles had a relatively high taxonomic principal component score (e.g., Gulf Coast Marsh and Prairie), whereas hot spots supporting a high proportion of fishes and clams had a relative low principal component score (e.g., Southern Appalachians). The first principal component estimated from the landcover association analysis separated hot spots with a large fraction of species associated with forest and water habitats (e.g., Southern Appalachians) from those with a high pro-

portion of rangeland habitats (e.g., Sonoran Basin and Range). For factors contributing to species endangerment, the first principal component was related to a mix of population threats. Hot spots with a high fraction of species affected by introduced exotic species, grazing, surface mines, and water diversion had a high principal component score (e.g., Arizona Basin and Range), whereas hot spots with a high fraction of species affected by rural and residential development, shoreline modification, and commercial exploitation had a low principal component score (e.g., Mid-Atlantic and Northern Coastal Plain). Plotting the three extracted principal components simultaneously resulted in a graphical representation of hot spot proximity in principal component statistical space across all three biological attributes (Figure 2).

The most obvious clustering of hot spots is associated with the upper right quadrante of the taxonomy-factor axes and is composed of the five endangerment regions found in eastern coastal areas. Within this cluster, hot spots tend to be separated along a landcover gradient, with Gulf Coast Marsh and Prairies on one end (due to its relatively high



**Figure 2.** Principal component ordination of endangerment hot spots based on taxonomic composition (TAXON\_P1), land type association (LAND\_P1), and factors contributing to species endangerment (REASON\_P1). Taxonomic groups used in this analysis included plants, mammals, birds, fishes, reptiles, amphibians, clams, snails, insects, and crustaceans. The percentage of total variation explained by the first principal component is shown parenthetically for each biological attribute axis. An asterisk indicates hot spots that have complex species recovery problems as shown in Table 3. Hot spot codes are defined in Figure 1.

proportion of species associated with rangeland) and the Eastern Gulf Coast Flatwoods and Peninsular Florida on the other end (due to the high proportion of species associated with forest habitats). Less pronounced clusters are associated with hot spots in California (i.e., Northern California Mountains and Valleys and Southern California Mountains and Valleys) and in the eastern portion of the desert Southwest (i.e., Arizona Basin and Range and the Colorado and Green River Plateaus).

The remaining three endangerment regions (Northern Pacific Coast Range and Valleys, Southern Appalachians, and Sonoran Basin and Range) appear to be unique with respect to the biological attributes shared by their endangered biota. The Southern Appalachians and the Sonoran Basin and Range have similar taxonomic compositions and endangerment factor sets; however, they have species with very different landcover associations. This difference is explained by the fact that whereas aquatic species are prevalent in both regions, the aquatic habitats are set in different landscape

contexts (mesic forest habitats versus arid grasslands). The uniqueness of the Northern Pacific Coast Range and Valleys appears to be explained by the similarity of its taxonomic composition with regions in the arid Southwest and of its set of endangerment factors and landcover associations with the Eastern Gulf Coast Flatwoods and Peninsular Florida.

Another noteworthy outcome of this principal component ordination concerns the relative proximity of the three endangerment regions with the most diverse set of endangerment factors (from Table 3). If we are correct in assuming that a high diversity of endangerment factors in a hot spot results in complex conservation planning among its species, then lessons learned from multiple-species conservation efforts in one of these complex regions are unlikely to be relevant in the other two.

### Geographic patterns of species expenditures

As we noted earlier, implementation of ESA has focused on individual species, with approximately 1% of

the listed species receiving half of the funding. It has been argued that expenditures on these high-profile species actually confer protection to other species that occur in the same habitat or that are imperiled by the same threats (Simons et al. 1988, FWS 1995). The ecological merits of this argument remain to be demonstrated (Flather et al. 1997), but if it turns out to be correct, an important question would be whether recent expenditures associated with the conservation of endangered species have been directed toward species whose distributions coincide with regions supporting a high number of endangered species. Such overlap would be necessary if nontarget listed species occurring in a hot spot are to realize incidental recovery benefits.

To address this question, we identified the listed species whose protection has cost the most by examining unpublished data from the *Federal and State Endangered Species Expenditures* annual reports published by FWS from 1989 to 1993. We then compared the location of hot spots defined in Figure 1b with the county-level distribution of the eight species whose total federal expenditures over the period accounted for approximately 50% of the expenditures on all endangered species (Table 4). We estimated overlap in two ways: as the percentage of the hot spot in which the high-expenditure species occurred, and as the percentage of each high-expenditure species' total range that intersected any hot spot. A high percentage value in both of these overlap estimates for a given species would indicate that the expenditures will be concentrated in one or more hot spots and therefore increases the likelihood that this species could serve as an "umbrella" (sensu Murphy 1991) for the other listed species in the hot spot. A high percentage value under the first method but a low percentage value under the second indicates that the conservation benefits of those expenditures have a high chance of occurring outside endangerment hot spots.

Of the high-expenditure species, only the grizzly bear failed to overlap any endangerment region. No high-expenditure species had its entire range wholly contained within



**Table 4.** The percentage of overlap of high-expenditure species with endangerment hot spots.

Species	Eastern hot spots						Western hot spots						Average overlap <sup>b</sup>	Overlap with species range <sup>c</sup>
	MA <sup>a</sup>	AC	PF	SA	EG	GC	CG	AB	SB	NP	NC	SC		
Chinook salmon ( <i>Oncorhynchus tshawytscha</i> )										35	48	3	22	31
Northern spotted owl ( <i>Strix occidentalis caurina</i> )										81	16		54	53
Red-cockaded woodpecker ( <i>Picoides borealis</i> )		77	52	23	56								48	43
Bald eagle ( <i>Haliaeetus leucocephalus</i> )	82	59	85	33	41	68	100	92	100	95	92	86	84	23
Sockeye salmon ( <i>Oncorhynchus nerka</i> )										33			33	38
Grizzly bear ( <i>Ursus arctos</i> )													0	0
Desert tortoise ( <i>Gopherus agassizii</i> )							3		86			25	44	96
Peregrine falcon ( <i>Falco peregrinus</i> )	10					46	92	93	28	24	70	44	56	43
Percentage of hot spot that is the range for one or more of the eight species	82	93	90	52	72	91	100	100	100	100	100	90		
Percentage of hot spot that is the range for one or more of the six species other than bald eagle and peregrine falcon	0	77	52	23	56	0	3	0	86	100	51	28		

<sup>a</sup>Hot spot codes are defined in Figure 1.

<sup>b</sup>An area-weighted average among hot spots in which the species occurs.

<sup>c</sup>The percentage of a species' range that intersects any hot spot.

one or more hot spots. Wide-ranging species such as the bald eagle and peregrine falcon showed the greatest number of hot spot intersections. On average, bald eagle and peregrine falcon distributions accounted for 84% and 56%, respectively, of the total hot spot areas in which they occurred. However, nearly 80% of the bald eagle's range, and nearly 60% of the peregrine falcon's range, lie outside endangerment hot spots, making it unlikely that these species would function well as an umbrella

for other hot-spot species. Consequently, there is a high chance that recent bald eagle and peregrine falcon recovery efforts and their associated costs have actually taken place outside of endangerment hot spots.

When the total range of all high-expenditure species is accounted for within each hot spot, five out of the six western hot spots exhibit complete geographic coverage (Table 4)—that is, the entire hot spot falls in the range of one or more of the eight high-expenditure species. Even

among the eastern regions, at least 90% of three of the hot spots falls in the range of one or more of the high-expenditure species. Much of this overlap, however, is attributable to the bald eagle and peregrine falcon. If we eliminate these widespread species for the reasons noted above, then the proportion of hot spot area accounted for by the joint distribution of the remaining high-expenditure species is reduced significantly. The Mid-Atlantic and Northern Coastal Plain, Gulf Coast Marsh and

Prairie, and Arizona Basin and Range now show no overlap with high-expenditure species. In addition, the Southern California Mountains and Valleys, Southern Appalachians, and Colorado and Green River Plateaus show less than 30% overlap. This pattern, combined with the fact that high-expenditure species have not been generally shown to be good ecological indicators of other endangered species, suggests that hot spot-targeted expenditures would be more efficient than species-targeted expenditures at protecting multiple species.

## Conclusions and cautions

Before April 1995, when a moratorium on species listings under the ESA was implemented, the rate at which threatened and endangered species were being listed had greatly accelerated. The exponential-like cumulative plots of species listings over the past 20 years, together with the inadequate funding to support species recovery, imply that the traditional single-species approach to endangered species protection should be broadened to include multiple-species or ecosystem-level considerations. This recommendation has been made before (Noss 1991), but its implementation has been hindered because ecosystems are difficult to define.

Rather than defining ecosystems explicitly, an alternative way to identify systems that may warrant conservation focus is to examine the distribution of species currently listed as threatened or endangered. By mapping regions in which many endangered species co-occur, ecological systems that are subject to much endangerment stress can be geographically identified. Knowledge of where listed species are concentrated can guide the identification of regions in which habitat protection (Orians 1993) or habitat conservation plans (Pulliam and Babbitt 1997) are likely to affect the greatest number of imperiled species. Location alone, however, says little about why listed species are concentrated where they are or what population threats will have to be addressed by recovery efforts. Geographic patterns of endangered species occurrence, combined with information on the factors that have contributed to species

endangerment, are necessary for developing integrative conservation strategies (Falk 1990).

Our implementation of this approach showed clear patterns of concentration within the conterminous United States along coastal areas, in the arid Southwest, and in Southern Appalachia. Regions supporting many listed species showed varying degrees of similarity based on the biological attributes we examined. The broad biological resemblance observed among eastern coastal regions suggests that conservation planning directed at this set of hot spots may be made easier because the ecological issues that will have to be considered by recovery efforts will be similar. By contrast, endangerment hot spots that are likely to involve complex conservation efforts, due to a high diversity of endangerment factors among listed species that occur there, were found to be biologically distinctive. Consequently, multiple-species or system-level conservation measures among these regions will be complicated by their atypical characteristics.

Although we are suggesting that the recovery of endangered species could benefit from hot spot-targeted conservation planning, this approach is not the only one that should be used to conserve biodiversity. Single-species planning, particularly if viable populations of wide-ranging species are to be maintained, remains a valid and important conservation approach. Similarly, predictive models should be used to anticipate where future concentrations of endangered species may surface so that conservation can be implemented before the ESA listing process is triggered. Hot spot-targeted conservation planning should be just one of several approaches that can contribute to a comprehensive biodiversity conservation strategy.

Some conservation planners may argue that recent federal expenditure patterns already target regions with a high concentration of endangered species. We did find high levels of correspondence between endangerment hot spots and the distribution of species that have received the most federal funds in recent years. However, much of the coincidence between the distribution of high-ex-

penditure species and hot spots was attributable to two wide-ranging species (the bald eagle and the peregrine falcon). When we eliminated these species from consideration (because the majority of their geographic range occurs outside of endangerment hot spots), we found that many hot spots showed little opportunity for incidental multiple-species benefits stemming from current expenditure patterns.

Our analysis rests on two assumptions, whose validity could be questioned. First, we have assumed that biases associated with species listings do not translate into geographic biases in locating sites with a high concentration of endangered species. Because plants and invertebrates comprised over 60% of the species we examined, the early focus on warm-blooded vertebrates as candidates for listing under the ESA has probably not affected the geographic patterns observed in our analysis. Second, we have assumed that the delineation of hot spots is robust to errors in the published accounts of species occurrence within counties. County-level distribution data represent information that is continually evolving. Species distributions are not static, and comprehensive surveys have not been conducted to systematically document where threatened and endangered species occur. However, evidence of the validity of our findings comes from the fact that they are similar to those of Dobson et al. (1997), despite differences in data sources and analysis criteria. Dobson et al. (1997) identified hot spots based on a criterion of complementarity—that is, they looked for patterns of geographic overlap among different taxonomic groups in counties that were selected to maximize the number of endangered species that occurred in the minimum area. Although complementarity results in a much more geographically restricted set of hot spots, these workers also identified the Southern Appalachians, eastern coastal counties, and arid Southwest as important for endangered species conservation. The geographical similarity of our findings and those of Dobson et al. (1997) suggests that the areas delineated as endangerment hot spots are affected little by differences in data sources and mapping criteria and are there-

fore not likely an artifact of any particular analysis.

Although this similarity is reassuring, in the absence of comprehensive species surveys uncertainty will remain relatively high, particularly for poorly studied taxa. In addition, definition of hot spots based on distributional patterns of endangered species needs to be paired with an analysis of the ecological processes that are important to the maintenance of endangered species populations and their habitats. Consequently, the geographic patterns revealed by our analysis should be interpreted as the first approximation of hot-spot boundaries—that is, boundaries that have the potential to shift as new information on species distributions becomes available, as new species are listed, and as more is learned about the ecological processes (e.g., natural disturbance regimes, metapopulation dynamics, land use, and resource management activities) that have influenced the endangerment patterns we now observe.

Despite these caveats, our analysis makes clear that the geography of endangered species is characterized by areas in which extinction risk is particularly concentrated. Rather than relying on incidental multiple-species benefits from expenditures that have focused on high-profile species, a more geographically targeted approach to species recovery in those ecological systems in which endangerment is prevalent would seem to offer a more efficient strategy to biodiversity conservation.

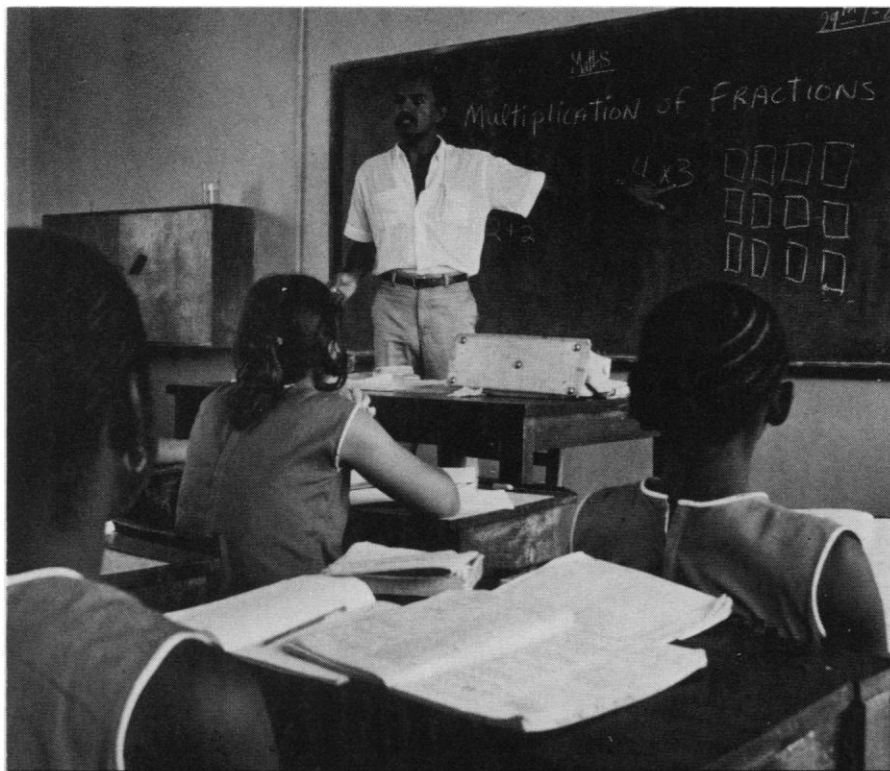
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