

CRITERION 1: CONSERVATION OF BIOLOGICAL DIVERSITY

Indicator 8: The Number of Forest-Dependent Species That Occupy a Small Portion of Their Former Range

Curtis H. Flather
Carolyn Hull Sieg
Michael S. Knowles
Jason McNeese

United States Department of Agriculture
Forest Service

ABSTRACT

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This indicator measures the portion of a species' historical distribution that is currently occupied as a surrogate measure of genetic diversity. Based on data for 1,642 terrestrial animals associated with forests, most species (88 percent) were found to fully occupy their historic range – at least as measured by coarse state-level occurrence patterns. Of the 193 species that have been extirpated from at least one state, 72 percent still occupy ≥ 90 percent of their former range. The number of species that now occupy ≤ 80 percent of their former range varies by taxonomic group. Range contraction of this magnitude is most commonly observed among mammals (5.7 percent), followed by amphibians (2.3 percent), and birds (1.4 percent). Geographically, states that have lost the greatest number of animal species are concentrated in the northeastern United States. More refined estimates of geographic range size contraction were obtained for 275 threatened or endangered species. Among this subset of species, animals have undergone a greater degree of range contraction (nearly 50 percent of the species are restricted to less than 25 percent of their historic range) than plants (30 percent of species occupy less than 25 percent of their historic range). For most species, data from which to quantify changes in range occupancy are lacking. Because a species' range is dynamic, a statistically designed inventory that permits an objective and temporally systematic assessment of range occupancy is needed.

Keywords: genetic diversity, sustainability indicators, geographic range contraction, sustainable forest management.

Authors

Curtis H. Flather is a research wildlife biologist with the Rocky Mountain Research Station, USDA Forest Service, Fort Collins, CO 80526.

Carolyn Hull Sieg is a research plant ecologist with the Rocky Mountain Research Station, USDA Forest Service, Flagstaff, AZ 86001.

Michael S. Knowles is an information systems analyst with Materials, Communication & Computers, Inc., Fort Collins, CO 80526.

Jason McNees is a database project specialist with NatureServe, Arlington, VA 22209.

INTRODUCTION

Biological diversity has been defined as “... the variety of life and its processes” that encompasses “... the variety of living organisms, the genetic differences among them, and the communities and ecosystems in which they occur” (Keystone Center 1991:6). Over the last half-century, scientists and natural resource managers have learned much about how biodiversity contributes to human society, the economic significance of which can be considerable (Pimentel and others 1997). Most obviously, many of the goods that are harvested and traded in the human economy are a direct product of the biological diversity within ecosystems (Daily 1997). Biological diversity also provides indirect benefits to humans through its impact on important ecosystem functions (Risser 1995; Huston and others 1999; Naeem and others 1999), and less tangible, but equally important, benefits in the form of recreational opportunity, as well as spiritual and intellectual fulfillment (Postel and Carpenter 1997). Because intensive use of natural resources can stress ecosystems to a point where their ability to provide these benefits is compromised (Rapport and others 1985; Loreau and others 2001), it has been argued that the human enterprise may be jeopardizing the health and continued existence of some ecosystems (Vitousek and others 1997). This argument is the motivation behind a worldwide paradigm shift in natural resource management that is now focusing on long-term sustainability of ecosystems as the measure of responsible resource stewardship (Noble and Dirzo 1997). One of the fundamental goals emerging from the sustainable management paradigm is to use resources in ways that conserve biological diversity (that is, the variety of ecosystems, species, and genes) undiminished for future generations (Lubchenco and others 1991; Lélé and Norgaard 1996).

The nine indicators accepted by the Montréal Process countries for monitoring biological diversity trends consider ecosystem diversity (five indicators), species diversity (two indicators), and genetic diversity (two indicators). This chapter focuses on one of the genetic diversity indicators – namely, the number of forest-dependent species¹ that occupy a small portion of their former range. Our purpose is to provide the rationale underlying the use of geographic range size (also called range occupancy in this report) as an indicator of genetic diversity, review the data available to examine the size of species’ geographic ranges, and present the findings from these data at the national scale. Finally, we will conclude with an evaluation of indicator adequacy and data limitations, which in turn forms the basis for proposing a set of research topics directed at improving the use of range occupancy as an indicator of biological diversity.

RATIONALE

Conservation scientists have often targeted species richness as the primary focus for monitoring the state of biodiversity and in the development of conservation strategies to maintain or restore biodiversity (Vane-Wright and others 1991; Hedrick and Miller 1992). However, species often occur as many genetically isolated (or nearly isolated) populations that serve different functional roles in different systems (Meffe and Carroll 1997:68). Consequently, the sustainable flow of benefits that humans derive from ecosystems is contingent upon maintaining

¹ A forest-dependent species is any species that needs forest conditions for all or part of its requirements of food, shelter or reproduction (Report of the technical advisory committee to the working group on criteria and indicators for the conservation and sustainable management of temperate and boreal forests [“The Montréal Process”], Draft Version 3.0, September 25, 1996). We use the terms “forest dependent” and “forest associated” interchangeably throughout this report.

a large number of populations within species because the unique genetic make-up of these populations permits these benefits to be derived from a diverse ecosystem set (Hughes and others 1997). Furthermore, the genetic diversity that results from populations occupying many habitats from across the species' geographic range ensure that adaptive variation is maximized (Moritz 2001). Conserving populations throughout a species' geographic range, including historically isolated lineages, will lead to conservation of geographic variation in the genome, permitting species to better address future environmental change (Hedrick and Miller 1992; Crandall and others 2000; Moritz 2002).

There is evidence in the literature documenting that average fitness among individuals in populations that have recently lost genetic variability is lower when compared to average fitness among individuals in populations that have not (Caughley 1994; Reed and Frankham 2003). However, this pattern is not universally observed (see Savolainen and Hedrick 1995). Such reductions in fitness can be caused by higher rates of inbreeding or outbreeding, and to the chance expression of deleterious genes (Wright 1977; Rieseberg 1991; Lande 1995). Reductions in fitness caused by these factors have been observed in plants (Templeton 1986; Ellstrand and Elam 1993), vertebrates (Ralls and others 1988; Danzmann and others 1988), and invertebrates (Saccheri and others 1998). Ultimately, the loss of genetic diversity can affect the viability of populations and can be an important consideration in evaluating extinction risks to the species as a whole (see Indicator 7 [Flather and others, 2003b]).

Although the empirical evidence linking genetic diversity and fitness is extensive, long-term monitoring data that quantify genetic variation over time would be extremely difficult and expensive to collect for more than a very few species (Smith and Rhodes 1992). Examples do exist where genetic variation was quantified over a broad geographic area for a single species (for example, Millar and Libby 1991; Ji and Leberg 2002; Jørgensen and others 2002; Williams 2002), or was synthesized over a large number of species in a search for broad macroecologic patterns among various taxonomic groups (Nevo and others 1984). However, these examples do not allow one to assess the change in genetic diversity over time (but see Paxinos and others 2002; Westlake and O'Corry-Crowe 2002). Because of the limitations associated with monitoring a species' genetic composition directly, members of the Montréal Process Working Group (2000) proposed that the size of a species' geographic range be used as a surrogate measure of its genetic diversity.

A species' geographic range is not static, but fluctuates in response to changing weather and climate, shifts in the distribution of vegetation, interspecific competition, and predation (MacArthur 1972). Human activity, through land use conversions and resource management, may be accelerating the change in species' ranges through alteration of native habitats, introduction of exotic species, or direct exploitation. These factors, either singly or in concert, can erode the spatial extent of a species' geographic range. Because the number of populations is an increasing function of range size (Hughes and others 1997), genetic diversity is expected to decrease in response to any range contraction (Soulé and Mills 1998).

DATA SOURCES AND ANALYSIS APPROACH

The primary motivation for using geographic range size as a surrogate measure of genetic diversity is one of cost. The techniques for measuring genetic variation are well established (Hedrick and Miller 1992), but it would be prohibitively expensive to directly measure genetic variation periodically over the species' range for even a small, well-selected subset of species.

Because the geographic range of many species has been described or mapped, it would appear that data to quantify changes in range occupancy would be readily available. However, measuring the extent to which a species is now occupying a greater or smaller portion of its former range requires an independent estimate of its historic distributional pattern.² These data do exist for a much larger set of species than direct measures of genetic variation. However, these data have not been consolidated from the diverse set of source materials into a readily accessible database that lends itself to comprehensive analysis (see Kareiva 2001). Databases have been constructed to address specific research questions related to the delineation of historic and current geographic range (for example, Lomolino and Channell 1995; Channell and Lomolino 2000; Ceballos and Ehrlich 2002). Unfortunately, these databases are restricted to a relatively small number of species and therefore do not allow us to infer taxa-wide patterns of range collapse.

Given the absence of a comprehensive database from which to quantify range occupancy patterns, we too resort to an ad hoc compilation of data that were available and consistent with the intent of this indicator. We compiled estimates of historic and current geographic range for some taxa from two sources. First we used NatureServe's Central Databases³ to obtain occurrence information on terrestrial vertebrates (mammals, birds, amphibians, and reptiles) and some insects (grasshopper and butterfly taxa only) that are considered to be forest dependent. These data document state-level occurrence and extirpation information for each species. A species' historic range was defined as the sum of state areas where a species occurs and where a species has been (or is thought to have been) extirpated. A species' current range was defined as the sum of state areas where a species now occurs. The percentage of the former range that is now occupied was calculated as: $(\text{area of current range} / \text{area of historic range}) \times 100$. Because aquatic species within the NatureServe databases had not been assigned to broad habitat affinity classes that would permit a focus on forest-associated species, we estimated range occupancy for all species of fish and mollusks. Data on range occupancy for plants were not available from NatureServe. These data were also used to determine if range contraction has been concentrated in a particular geographic area. This was accomplished by mapping the number of species that have been extirpated from each state and identifying those states where the greatest number of state-level extirpations has taken place. Use of NatureServe's data to estimate range occupancy and to identify states with high numbers of extirpations assumes that survey effort has been relatively equitable among states.

Our second source of geographic range data focused on species that are currently listed as threatened and endangered under the U.S. Endangered Species Act of 1973 (ESA). We abstracted information on historic and current range from each species' final listing decision as published in the Federal Register.⁴ Because the ESA offers protection to species, subspecies, and distinct population segments (Committee on Scientific Issues in the Endangered Species Act 1995), these data necessarily include range size estimates for taxonomic units below the species level. Information that would allow us to readily determine which listed species are forest dependent was not available. Therefore, these data capture the pattern of range contraction for all

² Note that geographic range contraction is estimated only for extant species. Consequently, the proportion of the historic range that is occupied is always > 0 .

³ Data available upon request from Jason McNeese, NatureServe, 1101 Wilson Blvd., Arlington, VA 22209 (jason_mcneese@natureserve.org).

⁴ Data available upon request from Curtis H. Flather; USDA Forest Service, Rocky Mountain Research Station, 2150 Centre Ave., Fort Collins, CO 80526 (cflather@fs.fed.us).

formally listed species regardless of their broad habitat affinity. For our purposes we limited our focus to information that directly estimated either the magnitude of the geographic range reduction, or provided area estimates of historic and current range from which we could calculate range reduction (table 1). For some species, the final listing decision did not provide information on range reduction but did provide information on habitat reduction. We recognize that habitat loss does not necessarily translate directly into a measure of range reduction; however, habitat loss is expected to lead to the extinction of local populations which will affect the genetic make-up of the species in the same way as a loss in geographic range. In order to maximize the number of species contributing information that is relevant to this indicator, we also recorded information from the final listing decisions on estimated habitat loss (table 1). Habitat loss estimates were only used as a surrogate measure of range occupancy when data on a species' current and historical geographic range were not provided.

Table 1. Data elements abstracted from final listing decisions for threatened and endangered species as reported in the Federal Register.

Data element	Description
Scientific name	Provides the genus and species name.
Common name	Provides the full common name.
Federal Register reference	Volume, number, and page numbers for the final listing decision.
Status	Designates whether the species was listed as a threatened or endangered species.
Date listed	The effective date of the listing rule.
Historic range data location	Page numbers where historic range data appear in the final listing decision.
Current range data location	Page numbers where current range data appear in the final listing decision.
Historic range area estimate	Estimated area of the historic distribution.
Historic range area units	Units on the area estimate (for example, km ²).
Current range area estimate	Estimated area of the current occupied range.
Current range area units	Units on the area estimate (for example, km ²).
Percent range reduction	Percent reduction in the historic range (1-[current range / historic range]).
Range reduction narrative	Description of how the estimation was made (for example, calculated from area estimates or simply reported in the Federal Register).
Historic habitat area estimate	Estimated area of historic habitat available.
Historic habitat area units	Units on the area estimate (for example, km ²).

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Current habitat area estimate	Estimated area of the current habitat available.
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Percent habitat reduction	Percent reduction in the habitat available (1-[current habitat / historic habitat]).
Habitat reduction narrative	Description of how the estimation was made (for example, calculated from area estimates or simply reported in the Federal Register).

RESULTS: INDICATOR INTERPRETATION

Range Size Reduction Among Forest-Associated Species

Comparing species' historic and current distributions based on state-level occurrence data indicated that range occupancy has not been appreciably reduced among forest-associated species. Of the 1,642 terrestrial animal species that are associated with forest habitats, 1,449 (88 percent) were estimated to fully occupy their former geographic range (table 2). Of the 193 species that have been extirpated from at least one state, 140 (72 percent) still occupy at least 90 percent of their former range. The number of species that now occupy less than 80 percent of their historic range varies by taxonomic group (table 2). Range contraction of this magnitude was most commonly observed among mammals (5.7 percent), followed by amphibians (2.3 percent), birds (1.4 percent), and reptiles (less than 1 percent).

The magnitude of range contraction among aquatic species was notably larger than for terrestrial species. Of the 1,069 fish and the 1,860 mollusk species, 88 (8.2 percent) and 114 (6.1 percent) species now occupy less than 80 percent of their historical range, respectively. Recall that aquatic species were not assigned broad habitat affinity classes; therefore, it was not possible to determine whether this degree of range contraction was representative of those species whose aquatic habitats are associated with forest ecosystems.

States that have lost the greatest number of terrestrial animal species that are associated with forest habitats are concentrated in the Northeast (figure 1a) with at least 20 species being lost from Pennsylvania, Ohio, and Illinois. Within these three states, species extirpations were most numerous among mammals (20 species), followed by insects (13 species, grasshopper and butterflies only), birds (nine species), reptiles (three species), and amphibians (two species).

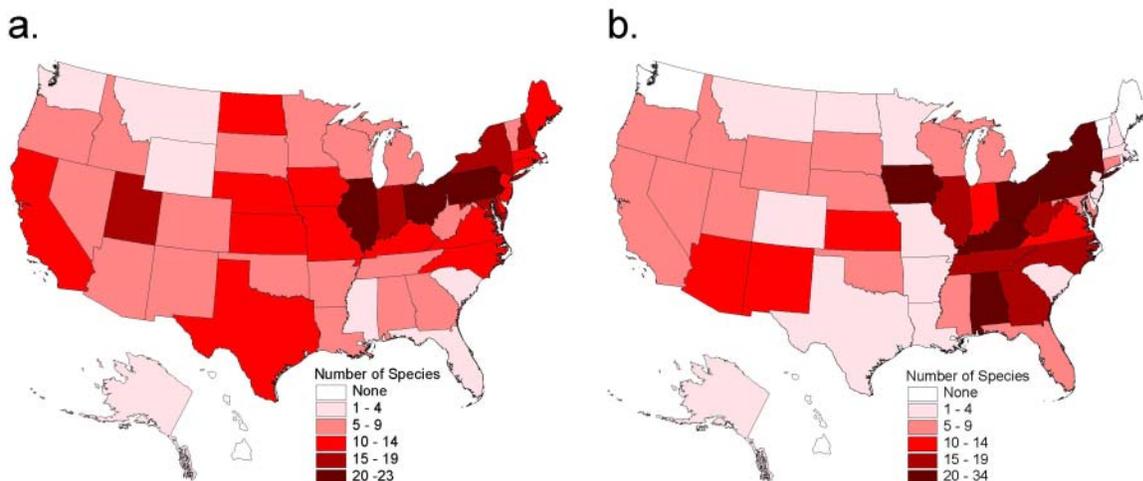
The geographic pattern of state-level extirpations among aquatic species was more broadly distributed across the eastern United States (figure 1b). At least 20 species have been extirpated from Iowa, New York, Ohio, Pennsylvania, Kentucky, and Alabama. Among the aquatic species extirpated from these six states, most were mollusks (68 of 121 species). Although we do not know the broad habitat types used by these species, the concentration of extirpations in the East suggests that many are likely to be associated with forest ecosystems.

Table 2. The count (and percent) of forest-associated species with varying degrees of range occupancy based on occurrence and extirpation at the state-level.

Taxonomic group	Number of forest species	Degree of range occupancy		
		Full occupancy	< 100 percent occupancy	≤ 80 percent occupancy
		----- number (percent) of species -----		
Mammals	227	177 (78.0)	50 (22.0)	13 (5.7)
Birds	417	354 (84.9)	63 (15.1)	6 (1.4)
Amphibians	176	161 (91.5)	15 (8.5)	4 (2.3)
Reptiles	191	174 (91.1)	17 (8.9)	1 (0.5)
Insects	631	583 (92.4)	48 (7.6)	4 (0.6)
Fish	1069 ^a	881 (82.4)	188 (17.6)	88 (8.2)
Mollusks	1860 ^a	1680 (90.3)	180 (9.7)	114 (6.1)

^a Aquatic species (fish and mollusks) were not assigned to broad habitat affinity classes such that forest-associated species could be identified. Therefore, these counts reflect all species.

Figure 1. The number of terrestrial animal species (mammals, birds, amphibians, reptiles, and some insects [grasshopper and butterfly species only]) associated with forest habitats (a) and the number of aquatic species (fish and mollusks) (b) that have been extirpated within each state. Aquatic species were not assigned to broad habitat affinity classes and so the counts within each state reflect species associated with all habitats. Because range occupancy was only estimated for extant species, and because historic and current range size was measured at the state-level, Hawaiian species are not reflected in these data.



Interpretation of these data must be made cautiously since the estimates of historical and current geographic range are based on occurrence and extirpation at the state level. We recognize that this is a very coarse measure of range occupancy that likely underestimates the magnitude of range contraction that has occurred for many species. This is particularly true for species whose ranges are restricted to a single state. For example, the range contraction that has occurred among many Hawaiian endemics cannot be captured by a state-level measure of range occupancy. Until finer scale data are available that permit more accurate estimates of range occupancy, coarse state-level depictions of geographic range can, at least, be used to suggest which taxa and which geographic areas could be problematic.

Range Size Reduction Among Federally Listed Species

A total of 1,233 species formally listed as threatened or endangered under ESA were included in the database – 723 plants and 510 animals. The final listing decisions provided sufficient information to either record or calculate the percent of the former range (or habitat) that is now occupied for 275 species (157 plants and 118 animals; see figure 2).

Given that we are focusing on a set of species that are already a viability concern, we expected that species counts would be biased toward the lower range occupancy classes. This was less the case for plants when compared to animals. Only 30 percent of plant species for which we had range size estimates occupy less than 25 percent of their historic range (figure 3a). Furthermore, nearly 45 percent of plants occupy at least 50 percent of their former geographic range. Animals, on the other hand, were more consistent with the expected pattern. Nearly 50 percent of animals currently occupy an area that is less than 25 percent of their historic range (figure 3b). Even among animals, however, there was a relatively high number of species (20 percent) whose current range is still about two-thirds of the land area formerly occupied by the species. We suspect that listed plant and animal species whose ranges have not declined appreciably are largely local endemics that have always had a restricted distribution. Local endemism appears to be a more common attribute among imperiled plants when compared to animals (Falk 1992; Flather and others 1994, 1998).

A number of important caveats concerning the interpretation of these data warrant remark. First, and perhaps most obviously, we only examined the pattern of range contraction among those species that are listed as threatened and endangered. By focusing on this subset of species, we are implicitly assuming that a species whose range occupancy has been significantly reduced would be represented in this list. We know that this is not the case, for there are forest-associated species whose current distribution within the United States is a fraction of its historic range (for example, elk [*Cervus elaphus*] and wolverine [*Gulo gulo*] [Leopold and others 1981; Peek 1982; Pasitschniak-Arts and Larivière 1995]), yet they are not formally listed as threatened or endangered. Second, our dataset abstracted from the Federal Registers included all listed species regardless of broad habitat affinity. Consequently, we cannot, at this time, describe the pattern of range occupancy among forest species currently listed as threatened and endangered. Finally, because historic and current range estimates were not available for most listed species (see figure 2), it is not possible to determine whether range contraction is becoming, over time, a more or less prominent concern among the species considered to be threatened or endangered with extinction.

Figure 2. Number of plant and animal species with range or habitat reduction data relative to the total number of species listed as threatened or endangered. Data were abstracted from species final listing decisions in the Federal Register.

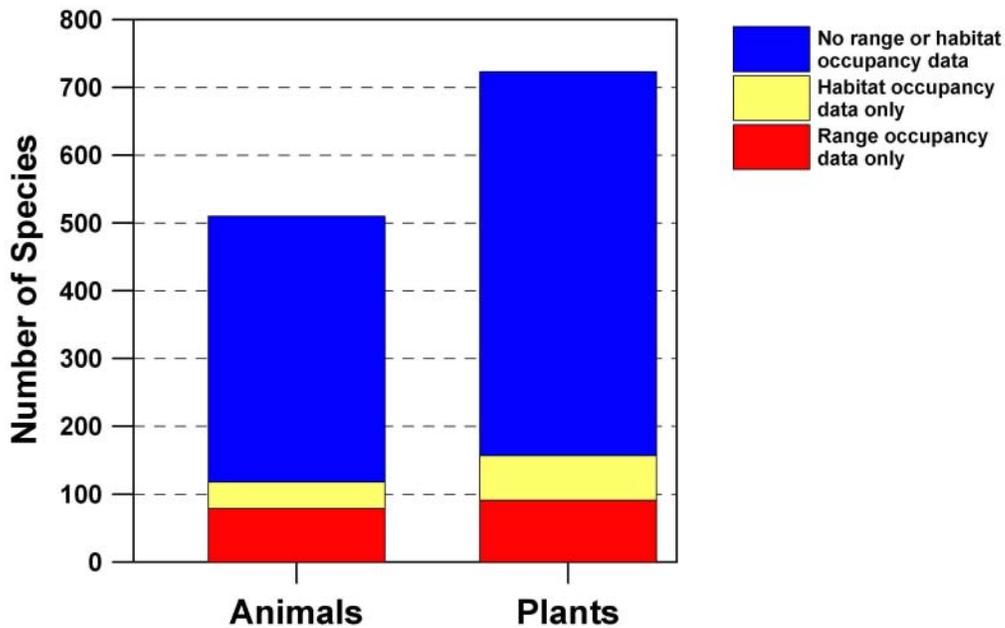
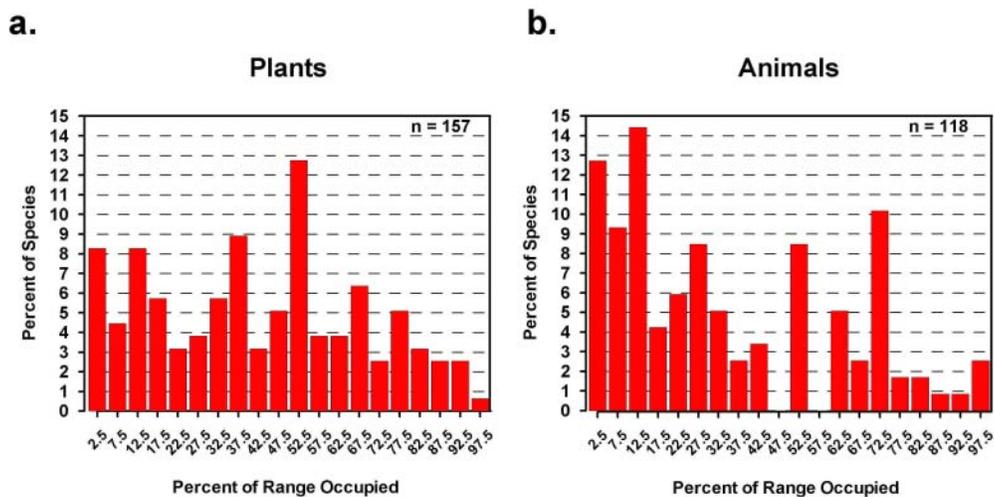


Figure 3. The percent of listed plant (a) and animal (b) species that now occupy varying amounts of their former geographic range. Percentage is based only on those species for which range reduction data were available. Values reported on the x-axis represent the mid-points of a 5 percent interval.



INDICATOR EVALUATION

Indicator Adequacy

The logic for using range occupancy as an indicator of genetic diversity has its ecological basis in the interplay between biogeography and genetics. Species geographic ranges are spatially discontinuous (Brown 1984; Maurer and Nott 1998), which leads to populations that are, to some degree, reproductively isolated. These populations are the source of genetic diversity when measured species wide (Hughes and others 1997). Therefore, a reduction in genetic variation is a likely outcome of a reduction in the size of a species' geographic range (Soulé and Mills 1998) because population extinction is an inevitable consequence of range size contraction. However, we are not aware of any empirical study that has quantified the relationship between change in range size and measures of genetic variation within a species. Part of the difficulty is that the intraspecific relationship between range occupancy and genetic diversity likely changes as a function of life history (for example, dispersal capability), the size of the original geographic range, the degree of habitat heterogeneity within the geographic range, and the spatial pattern of range collapse. A formerly widespread species whose range collapses to some geographically central core area may lead to a much greater degree of genetic homogenization than if range collapse occurs in a dispersed and fragmented fashion (Lacy 1987). Conversely, homogenization of habitats within a species' geographic range caused by human land use intensification could reduce genetic variation in the absence of a detectable change in the geographic range. A test of how well range size predicts genetic diversity awaits research that quantifies how the genome changes with the size and spatial structure of both the historic and occupied range (Flather and Sieg 2000).

A related conceptual issue concerns a tenable definition of what constitutes a "significant" reduction in geographic range (see Maranzana 2002). There has been a long biometric history focused on the quantification of species' geographic ranges (Rapoport 1982; Maurer 1994, 1999; Miller 1994; Gaston and He 2002; Telfer and others 2002), and randomization tests have been developed to infer when a statistically significant change in a species' range has occurred (Rodríguez 2002). Although this research has led to methodological developments for quantifying and assessing change in range structure, it has not addressed the issue of how much of the geographic range can be lost before a significant amount of genetic diversity is lost, or conversely, how much of the geographic range needs to be restored before the species recaptures a certain level of genetic diversity. This issue also begs the question, "What time period should be used as the basis for measuring a species' historic geographic range?" Should we use recent estimates of a species' geographic range as the baseline against which all future measures are judged? Or, should pre-European settlement estimates of geographic range be the standard against which range reduction is quantified? This question defines an important dilemma. The former is technically feasible for some taxonomic groups, but may be biased since it fails to account for the degree of genetic erosion that has already taken place. The latter is potentially less biased, but technically infeasible for many species since good historical descriptions of geographic range do not exist.

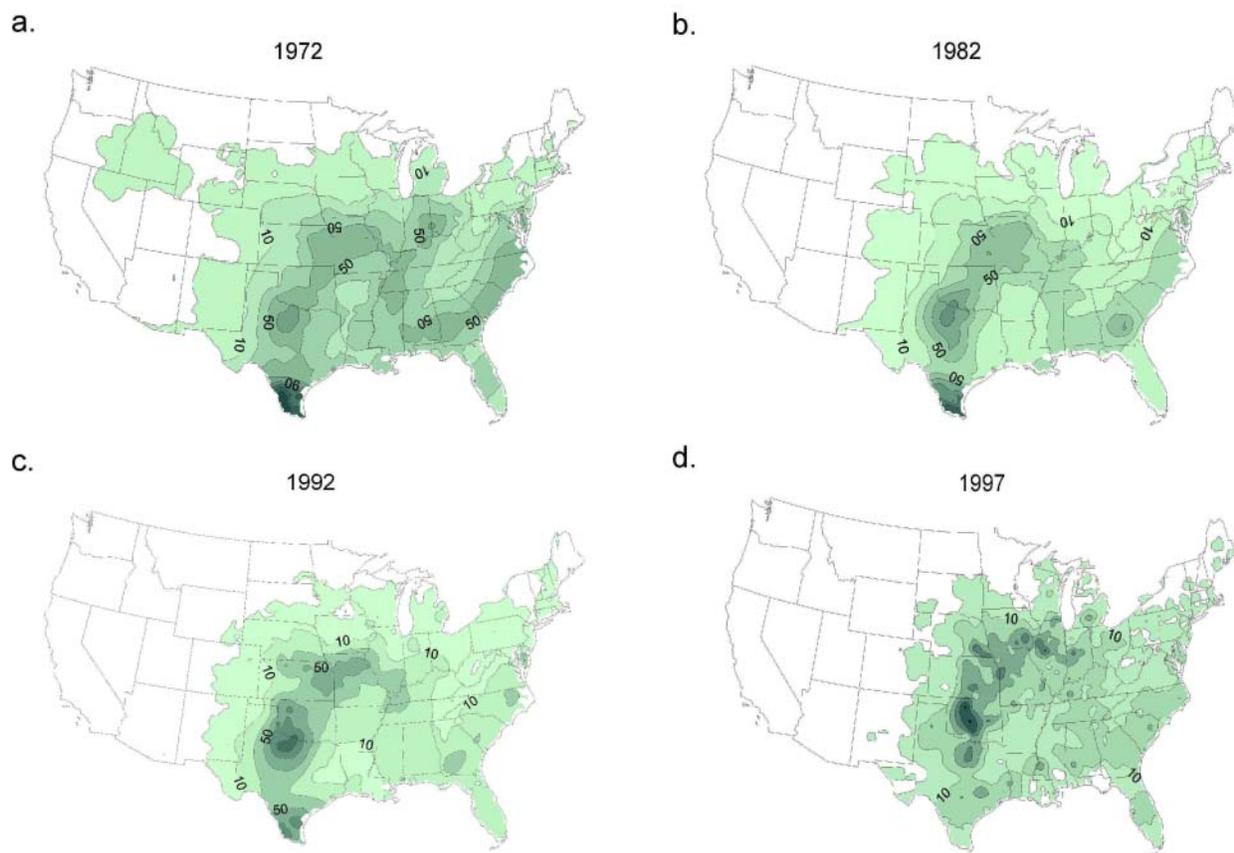
Data Limitations

Geographic range data are routinely used by conservation planners for, among other things, the design of reserve networks that seek to optimally preserve biodiversity (Pressey and others 1997; Camm and others 1996; Polasky and others 2000). As basic as this information is to conservation science, the discipline lacks a consolidated and taxonomically comprehensive set of data from which to quantify changes in range occupancy for most species. This fundamental knowledge gap is now being addressed by various conservation science teams. For example, there has been a recent global effort launched to compile distributional data for all 25,000 terrestrial vertebrate species (Kareiva 2001; <http://www.nceas.ucsb.edu/vertdist>). Similarly, the American Ornithologists' Union, Cornell Lab of Ornithology, and the Academy of Natural Sciences are sponsoring the publication of *The Birds of North America*, which contains detailed species accounts (including geographic range) for all species breeding in North America (<http://www.birdsofna.org/>). Although these data compilation efforts will provide estimates of the current (and in some cases historic) geographic range, they are one-time estimates that reflect the perspectives of species experts.

The geographic range of a species is dynamic; it changes over time in response to short-term weather fluctuations, long-term climate change, shifts in the amount and quality of habitat, and changes in the mix of species (for example, invasive exotics, predators) that inhabit a given locale. Consequently, periodic updating of the current geographic range based on the collective opinions of species experts is more difficult, and perhaps less likely to detect early range shifts, than a statistically designed inventory that permits a more objective and temporally systematic assessment of range occupancy. Extant data of this type are rare and restricted to few relatively well-studied taxonomic groups (see Flather and others 2003a). One taxonomic group where spatially and temporally extensive data exist for estimating range occupancy is birds.

The North American Breeding Bird Survey (BBS) consists of more than 4,000 roadside routes that are randomly distributed within a degree block of latitude and longitude, throughout the United States and southern Canada (Droege 1990). The survey has been conducted annually by trained volunteers since 1966. The sampling unit is a 39.4 km route along which 50, 3-minute point counts are conducted at 0.8-km intervals. At each point-count stop, all birds seen or heard are recorded. A study of the range-wide decline of Northern bobwhite (*Colinus virginianus*) serves to illustrate the potential utility of these data in a quantitative analysis of range occupancy change. Brady and others (1998) were interested in exploring the potential contribution of land use activities on long-term population declines in bobwhite. A temporal series of maps that displayed spatial variation in relative abundance was used to document the range-wide declines in this species (figure 4). Although the focus of this study was on population change, such spatially explicit representations of relative abundance can also be used to examine national and subnational shifts in distribution. The BBS represents a potential data source for monitoring range occupancy that should be explored.

Figure 4. Northern bobwhite range occupancy and relative abundance for 1972 (a), 1982 (b), 1992 (c), and 1997 (d). Relative abundance isopleths estimated using kriging of 3-year mean abundance observed on each Breeding Bird Survey route (see Brady and others 1998 for details).



Recommendations for Improvement and Research Needs

The size and structure of geographic ranges are of broad conservation interest because there is accumulating evidence that extinction risk is related to range structure (Brown 1995; Maurer and Nott 1998; Maurer 1999). As such, geographic range contraction can presage change in both species conservation status (Indicator 7; Flather and others 2003b) and species richness (Indicator 6; Flather and others 2003a). If Indicator 8 is to lead to reliable and defensible interpretations of changes in genetic diversity, then a similar foundational set of empirical research findings are needed to quantify the nature of the genetic diversity-range structure relationship. Although there seems little argument among conservation scientists that range contraction will lead to a loss of genetic variation (Soulé and Mills 1998), the numerous factors that can interact to affect the pattern and rate of loss have not been systematically investigated. Until such research is completed, inferences drawn about the status of genetic diversity from trends in range occupancy will remain uncertain.

The merging of spatial statistics and quantitative geographic analysis will form the key methodological basis for a more rigorous examination of range occupancy structure. Referring back to the study of Northern bobwhite (Brady and others 1998), even with this simple depiction of range occupancy and relative abundance (figure 4), there are a number of observations about how geographic range structure can change with declining populations: (1) range occupancy (that is, >1 individual observed on a survey route) appears to collapse on the periphery of the species' distribution; (2) the spatial pattern of occupancy becomes more spatially complex (that is, a convoluted and perforated boundary); and (3) declines in high abundance areas appear more pronounced than the decline in range occupancy. Although it is certainly difficult to draw any general ecological inference from this one example, more comprehensive studies of range collapse patterns among birds do appear to support these observations.

In a study of 242 insectivorous breeding birds, Maurer and Nott (1998) observed that species with smaller geographic ranges had higher degrees of occupancy fragmentation. Although this macroecologic study was comparing range occupancy patterns among species with different range sizes, the results do suggest that if the range of any one species was to decline, it would also become increasingly fragmented. Evidence supporting this deduction was observed by Mehlman (1997) who, in a study of three widely distributed bird species whose ranges had contracted and recovered following an extreme weather event, observed contraction from the periphery to the core accompanied by a roughening of the range margin. In a related study of 27 birds whose populations showed significant long-term (1966-1993) declines, Rodríguez (2002) observed that most species showed a proportionately higher loss of high abundance areas when compared to an overall measure of range occupancy. All three of these studies show patterns that are consistent with that observed for Northern bobwhite (figure 4) and suggest that general patterns of range contraction could be defined. These patterns also suggest that declines in population abundance (see Indicator 9 [Sieg and others 2003]) may presage significant declines in range occupancy.

As is common with most ecological patterns, the literature is not entirely consistent with our described pattern of range contraction. In a study of remnant populations among species whose ranges have severely contracted, Channell and Lomolino (2000) found that current locations of occupied range occurred predominantly at the periphery of the historic range. They also observed this pattern among a variety of taxonomic groups including mammals, birds, reptiles, amphibians, mollusks, arthropods, and plants. These findings tend to suggest that range collapse may not erode from the periphery to some central core of the geographic range. The existence of contradicting patterns only emphasizes the need for additional investigations into the processes affecting range occupancy.

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