

CRITERION 1: CONSERVATION OF BIOLOGICAL DIVERSITY

Indicator 6: The Number of Forest-Dependent Species

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ABSTRACT

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This indicator monitors the number of native species that are associated with forest habitats. Because one of the more general sign of ecosystem stress is a reduction in the variety of organisms inhabiting a given locale, species counts are often used in assessing ecosystem wellbeing. Data on the distribution of 689 tree and 1,486 terrestrial animal species associated with forest habitats (including 227 mammals, 417 birds, 176 amphibians, 191 reptiles, and 475 butterflies) were analyzed. Species richness (number of species) is highest in the Southeast and in the arid ecoregions of the Southwest. Since the mid-1970s, trends in forest bird richness have been mixed. Ecoregions where forest bird richness has increased the greatest are found in the West and include the Great Basin, northern Rocky Mountains, northern mixed grasslands, and southwestern deserts. Declining forest bird richness has primarily occurred in the East, with notable areas of decline in the Mississippi lowland forests, the southeastern coastal plain, northern New England, southern and eastern Great Lake forests, and central tallgrass prairie. Because monitoring species richness over large geographic areas is logistically difficult, we lack systematic inventories that permit the estimation of species richness over time for most taxonomic groups.

Keywords: species richness, bird richness trends, richness hotspots, sustainability indicators, sustainable forest management.

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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 consider ecosystem diversity (five indicators), species diversity (two indicators), and genetic diversity (two indicators). This report focuses on one of the species diversity indicators – namely, the number of forest-dependent species.¹ Our purpose is to provide the rationale underlying the use of species richness as an indicator of biological diversity, review the data available to document the spatial distribution and trend in species richness, and present the findings from these data at national and regional scales. 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 species richness as an indicator of biological diversity.

RATIONALE

The number of species is the most frequently used and easily understood measure of biological diversity (Gaston 1996; Purvis and Hector 2000; Montréal Process Working Group 2000). Because a general sign of ecosystem stress is a reduction in the variety of organisms inhabiting a given locale (Rapport and others 1985; Loreau and others 2001), species counts already have a long history of use in assessing ecosystem well-being (Magurran 1988; Reid and others 1993). Furthermore, species number has been linked conceptually to notions of system

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.

stability, redundancy, resistance, and recovery (Solbrig 1991; Walker 1995; Tilman and Downing 1996) and therefore has relevance to assessments of environmental sustainability (Goodland 1995).

The count of forest-dependent species can change under two conditions. Native species can become extinct (locally or globally) and new species can colonize and become established in the species pool. Both of these outcomes have the potential to alter ecological processes such as productivity, nutrient cycling, or trophic relationships, leading to possible changes in the way humans derive goods and services from ecosystems. Economically or functionally valuable species may be lost, or aesthetic values potentially diminished, as the pool of species is changed or reduced.

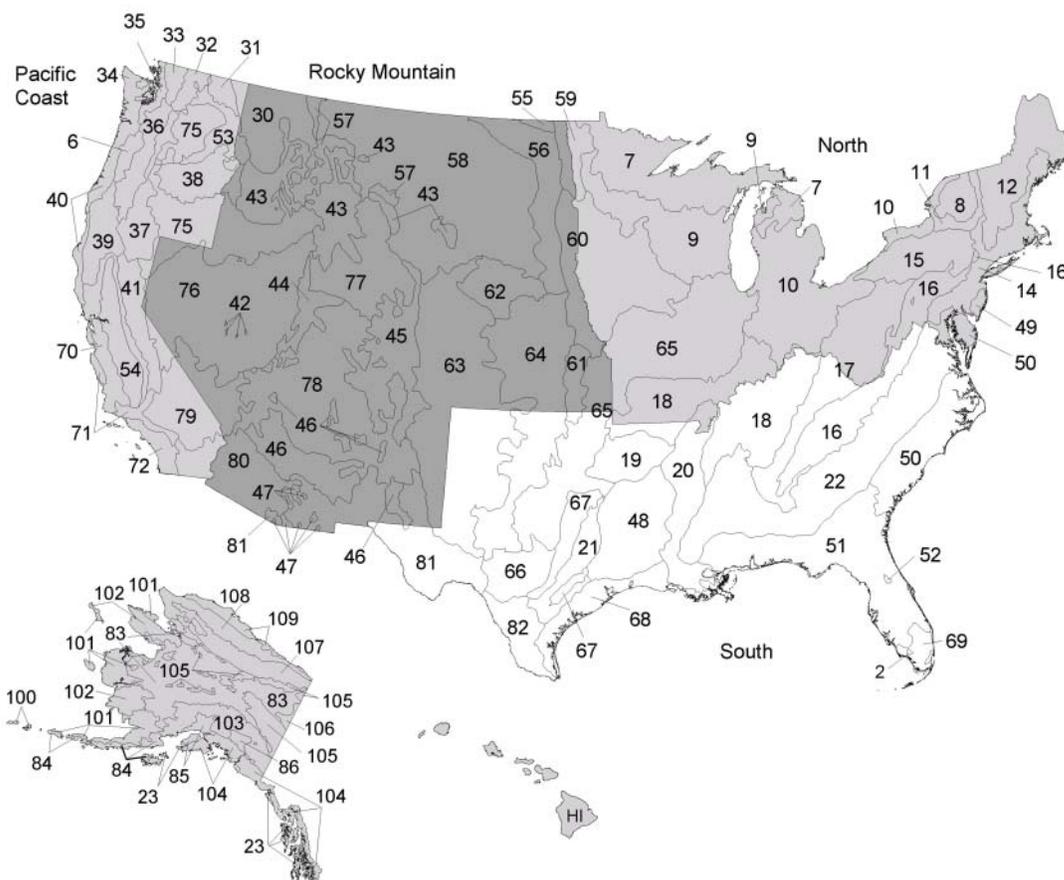
We caution, however, that a focus on species counts may lead to a preoccupation with those ecosystems that have high numbers of species. This is a fallacious interpretation of this indicator for several reasons. First, sustainability is concerned with maintaining the integrity of floral and faunal communities (Lélé and Norgaard 1996; Lindenmayer and others 2000; Pimentel and others 2000) regardless of the underlying size of the species pool. Second, ecosystems with naturally low species counts may be more threatened and less resilient to disturbances (Chapin and others 1998; Loreau and others 2001) – whether these disturbances are natural (for example, extreme weather events or fire) or human caused (for example, land use conversions or timber harvesting) – and therefore warrant greater management attention than more speciose systems. Finally, areas of high richness may in fact be inflated due to the presence of exotic species (see Stohlgren and others 2003) leading some to consider exotics as beneficial to biodiversity conservation despite the substantial literature documenting their detrimental effects (Vitousek 1990).

DATA SOURCES AND ANALYSIS APPROACH

A strict interpretation of this indicator implies that a single estimate of the species count can be used to assess the status of biological diversity. However, the total species richness within an area is extremely difficult to interpret (Huston 1994), if only for the reason that speciose taxa will dominate the pattern of species counts across the country (Ricketts and others 1999a). A simple tally of species counts masks the fundamental ecological differences that exist among the various kinds of species and can therefore make it difficult to identify the underlying mechanisms causing the change in species richness. We therefore report species richness estimates for forest-dependent species for a variety of taxonomic groups.

We summarize our results at a number of geographic scales. At the broadest scale, we report counts of species by taxonomic group at the national level. We also display how species richness varies geographically using the ecoregional classification of Ricketts and others (1999b). Finally, we also present summary statistics organized by U.S. Forest Service regional planning boundaries to support the Forest Service's national resource assessment mandate (USDA, Forest Service 2001). The ecoregional stratification and Forest Service regional planning boundaries are defined in figure 1.

Figure 1. Ecoregions (Ricketts and others 1999b) and U.S. Forest Service planning regions (USDA, Forest Service 2001). Note that Alaska and Hawaii are part of the Pacific Coast planning region.



Code	Description	Code	Description
2	South Florida Rocklands	54	California Central Valley Grasslands
6	Willamette Valley Forests	55	Canadian Aspen Forest and Parklands
7	Western Great Lakes Forest	56	Northern Mixed Grasslands
8	Eastern Forest/Boreal Transition	57	Montana Valley and Foothill Grasslands
9	Upper Midwest Forest/Savanna Transition Zone	58	Northwestern Mixed Grasslands
10	Southern Great Lakes Forests	59	Northern Tall Grasslands
11	Eastern Great Lakes Lowland Forests	60	Central Tall Grasslands
12	New England/Acadian Forests	61	Flint Hills Tall Grasslands
14	Northeastern Coastal Forests	62	Nebraska Sand Hills Mixed Grasslands
15	Allegheny Highlands Forests	63	Western Short Grasslands
16	Appalachian/Blue Ridge Forests	64	Central and Southern Mixed Grasslands
17	Appalachian Mixed Mesophytic Forests	65	Central Forest/Grassland Transition Zone
18	Central Hardwood Forests	66	Edwards Plateau Savannas
19	Ozark Mountain Forests	67	Texas Blackland Prairies
20	Mississippi Lowland Forests	68	Western Gulf Coastal Grasslands
21	East Central Texas Forests	69	Everglades
22	Southeastern Mixed Forests	70	California Interior Chaparral and Woodlands
23	Northern Pacific Coastal Forests	71	California Montane Chaparral and Woodlands
30	North Central Rockies Forests	72	California Coastal Sage and Chaparral
31	Okanagan Dry Forests	75	Snake/Columbia Shrub Steppe

Figure 1, cont'd

32	Cascade Mountains Leeward Forests	76	Great Basin Scrub Steppe
33	British Columbia Mainland Coastal Forests	77	Wyoming Basin Shrub Steppe
34	Central Pacific Coastal Forests	78	Colorado Plateau Shrublands
35	Puget Lowland Forests	79	Mojave Desert
36	Central and Southern Cascades Forests	80	Sonoran Desert
37	Eastern Cascades Forests	81	Chichuahuan Desert
38	Blue Mountains Forests	82	Tamaulipan Mezquital
39	Klamath-Siskiyou Forests	83	Interior Alaska/Yukon Lowland Taiga
40	Northern California Coastal Forests	84	Alaska Peninsula Montane Taiga
41	Sierra Nevada Forests	85	Cook Inlet Taiga
42	Great Basin Montane Forests	86	Copper Plateau Taiga
43	South Central Rockies Forests	100	Aleutian Islands Tundra
44	Wasatch and Uinta Montane Forests	101	Beringia Lowland Tundra
45	Colorado Rockies Forests	102	Beringia Upland Tundra
46	Arizona Mountains Forests	103	Alaska/St. Elias Range Tundra
47	Madrean Sky Islands Montane Forests	104	Pacific Coastal Mountain Tundra & Ice Fields
48	Piney Woods Forests	105	Interior Yukon/Alaska Alpine Tundra
49	Atlantic Coastal Pine Barrens	106	Ogilvie/MacKenzie Alpine Tundra
50	Middle Atlantic Coastal Forests	107	Brooks/British Range Tundra
51	Southeastern Conifer Forests	108	Arctic Foothills Tundra
52	Florida Sand Pine Scrub	109	Arctic Coastal Tundra
53	Palouse Grasslands	HI	Hawaii

The estimates of species richness discussed in this report stem from four primary data sources. First, we compiled national estimates of species richness by taxonomic group from the literature (see Appendix A). When possible, we report only species counts for native species that regularly occur within the United States. We made no attempt to compile all of the literature that has reported nation-wide species counts for the United States. Rather, we were interested in sampling the recent literature (since 1990) to gain a sense for how variable national counts of species were by taxonomic group. The sources compiled provided only the total count of species; we did not have access to the complete species lists from which changes in taxonomic nomenclature could be evaluated.

Second, NatureServe's Central Databases (NatureServe 2002a) were used to provide national counts of native, regularly occurring plant and animal species in the United States that were associated with forest habitats.² Designation of species as "forest-associated" had been completed for terrestrial vertebrates (mammals, birds, amphibians, and reptiles) and some invertebrates (grasshopper and butterfly taxa only). Plants, aquatic vertebrates, and most invertebrate species have not, as yet, been assigned to broad habitat affinity classes. Although the subset of plant species that are associated with forest habitats has not been determined, we did partition out trees as a species group primarily associated with forest ecosystems.

Third, a database compiled by the World Wildlife Fund on native species occurrences (Ricketts and others 1999b) was used to provide information on the number of species by taxonomic group that occur within ecoregional strata throughout the United States. For this

² Data on forest-associated species available upon request from Jason McNeese, NatureServe, 1101 Wilson Blvd., Arlington, VA 22209 (jason_mcneese@natureserve.org).

report we focused on the occurrence pattern of forest-associated species as determined by NatureServe (2002a). These data were compiled by collecting published and unpublished distributional maps for native North American species. Presence or absence of a species within ecoregional strata was determined by the intersection of each species' geographic range with each ecoregional boundary (for details see Ricketts and others 1999b: Appendix A). The species list for each ecoregion thus represents the expected or historical species pool for that stratum – it does not mean that all species in that pool have been recently observed. These data represent a one-time depiction of the spatial pattern of species richness across the United States and do not, as yet, incorporate a temporal component that would permit an exploration of trends in species richness.

Fourth, the North American Breeding Bird Survey (BBS) was used to provide trend information on the richness of native forest-breeding bird species at the ecoregional scale. The BBS is a geographically and temporally extensive survey 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 that has been conducted since 1966 (Droege 1990). 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. The BBS is unique among the databases we used in that it permitted an analysis of how avian richness has changed over time. Degraaf and others (1991) was used to determine the set of bird species within the BBS that qualified as forest breeding.

The simplest approach to estimating the trend in species richness using the BBS data is to count the number of species observed between two time periods. However, it is well known that a count of species observed underestimates the number of species actually present. This bias occurs because some unknown proportion of the species pool that is actually present in a given locale goes undetected (Thompson 2002; Thompson and others 1998). Recent research has developed methodologies that account for the differences in detection probabilities among species. These methods permit the estimation of the total number of species present in the pool (detected + undetected), and their associated variances, based on capture-recapture theory (Nichols and others 1998). We used the COMDYN software (see Hines and others 1999) in conjunction with the BBS data to estimate the change in forest bird richness over a 25-year period (1975 to 1999) for each ecoregion defined in figure 1. BBS routes were assigned to an ecoregion based on the location of the starting point of the route. In order to control for differences in sampling effort within ecoregions over time, we identified that subset of routes within each ecoregion that were run in both the starting (1975) and ending (1999) year of our 25-year period. To be included in this set, a route had to meet quality standards based on BBS guidelines including: route was run by a competent observer; route was run under appropriate weather conditions; and route was run during the appropriate time of day and season (see Robbins and others 1986 for a detailed discussion of factors affecting route quality).

Our estimate of species richness for a given year was based on the frequency distribution of species among all routes within each ecoregion (see Nichols and others 1998 and Hines and others 1999 for the details of the estimation). Change in richness was estimated by the quantity λ , which is simply the ratio of estimated richness in the two time periods such that:

$$\lambda = N_{99} / N_{75}$$

where N_{99} and N_{75} are the estimated richness of forest-associated birds in 1999 and 1975, respectively. Values of λ equal to 1 indicate no change in richness over time; λ values greater than 1 indicate that richness is increasing over time; and values less than 1 indicate a decline in

richness. In some ecoregions there was only one quality route that was run in both time periods. Under these circumstances it was not possible to estimate species richness as described above. Therefore, λ was calculated as the ratio of the *observed* species counts in the two time periods. In two ecoregions (Western Great Lakes Forests – 7; Southeastern Mixed Forests – 22) the detection probabilities for the two time periods did not differ statistically from 1.0 and λ were again estimated as the ratio of observed counts of forest-associated bird species in 1999 and 1975.

RESULTS: INDICATOR INTERPRETATION

National Scale

Before reporting on the number of species in the United States, some comments on what constitutes a species and which species should be counted are warranted. Most contemporary definitions of a species are based on the biological species concept – a concept that identifies a species as a population or set of populations that can, or have the potential to, exchange genetic material. The key idea in this definition is that individuals within a species are capable of interbreeding and they are reproductively isolated from other species (Meffe and Carroll 1997). Although this definition of species is regarded as the most useful yet proposed (Wilson 1988), disagreements over its general utility remain (Hey 2001; Cracraft 2002; Faith 2002; Noor 2002). For some plants and animals, hybridization, self-fertilization, and parthenogenesis lead necessarily to arbitrary species designations.

In addition to the debate surrounding the biological species concept itself, there also are systematic uncertainties caused by the incomplete study of some taxonomic groups. Consequently, the number of species described for a particular taxon can expand or contract over time as systematists learn more about the evolutionary relationships among biological entities (McNeill 1993; Wheeler 1995). Given that only about 1.4 million species have been described out of the 10 to 100 million species estimated to occur worldwide (Lovejoy 1997), biologists are left with having to use imprecise estimates of the number of species inhabiting a particular geographic area.

Finally, species that co-occur in an area do not share the same occupancy status. Any species pool is made up of species that regularly occur in the assemblage, those that are vagrants (that is, only found occasionally), and those that are exotics (that is, not native to the system) (Vitousek 1990; Gaston 1996; Magurran and Henderson 2003). The number of species counted for a particular geographic area can vary greatly depending upon which species (that is, what occupancy status) are actually counted. Although we intended to report on native species that regularly occur within the United States, it was not always possible to determine from published counts what species were included in the estimates.

So while a count of species inhabiting the United States appears to be a relatively straightforward task, the ambiguity in the biological species concept, the uncertainties underlying nomenclature, and variation in species occupancy status, make estimating the number of species for a given area difficult and can confound meaningful interpretations of trends. There is certainly a widely held appreciation for these uncertainties among biologists, yet it is still common to see single estimates for the number of species occurring in the United States by various taxonomic categories. This gives the false impression that the species count is known without error, when in fact there can be widely varying estimates among different sources.

In the United States, the variability in species counts differs among taxonomic groups (table 1). For example, the mean number of mammals estimated to occur in the United States was 418 species among the eight sources we examined, with a standard error of 34 (8 percent of the mean). For birds, the mean estimate was 757 with a standard error of 145 (19 percent of the mean). The lower proportionate standard errors associated with invertebrates is likely the result of fewer and closely related sources (see Appendix A) rather than a reflection of lower uncertainty with species count estimates among invertebrate taxa.

Table 1. Mean number and standard error of native species that regularly occur in the United States by taxonomic group as estimated from multiple sources. See Appendix A for a list of the sources and their associated species counts.

Taxonomic group	Mean number of species	Standard error (percent of mean)	Number of sources	Number of forest-associated species
Plants				
Vascular	19,079	2,284 (12.0)	6	689 ^a
Vertebrates				
Mammals	418	34 (8.1)	8	227
Birds	757	145 (19.1)	8	417
Amphibians	243	15 (6.2)	7	176
Reptiles	294	30 (10.2)	8	191
Freshwater fishes	817	25 (3.1)	8	— ^b
Invertebrates				
Freshwater mussels	284	18 (6.3)	3	— ^b
Freshwater snails	650	16 (3)	3	— ^b
Crayfishes	331	8 (2.4)	3	— ^b
Tiger beetles	113	1 (0.9)	3	— ^b
Dragonflies/ damselflies	460	10 (2.2)	3	— ^b
Butterflies/ skippers	612	10 (1.6)	3	475

^a Count of tree species only.

^b Number of forest-associated species had not been determined for this taxonomic group.

The variation in species counts reflected in table 1 highlight a problem with interpreting changes in species richness estimates over time. For example, McDiarmid (1995:117) noted that the number of species comprising the herpetofauna (amphibians and reptiles) of the United States increased by 12 percent (454 species to 507 species) from 1978 to 1995. Much of this increase, however, was the result of applying new molecular techniques to distinguish species in evolutionarily complex groups. Similarly, McKinney (2002) has documented how plant species richness can be inflated by the inclusion of exotics. The increases noted in either example cannot be interpreted as an increase in biodiversity *per se* and call attention to the need to interpret species richness trends using a consistent taxonomic classification over the period of the trend estimate, and being aware of the occupancy status of the species included in the count.

The number of species that are associated with forest habitats varied from 689 trees to 176 amphibians (table 1). Forest-associated amphibians, however, comprise 72 percent of the average count of native amphibian species thought to regularly occur in the United States. Forest habitats in general appear to be important sources of biodiversity – at least among those taxa for which we had broad habitat affinity information. The majority of terrestrial vertebrate and butterfly species use forest habitats to obtain at least some their requirements for food, shelter, or reproduction (table 1).

Regional Scale

Geographic Patterns in Species Richness

A long recognized macroecologic pattern of species richness is the negative relationship between species counts and latitude (Gaston and Blackburn 2000). This pattern is generally borne out by our ecoregional depiction of geographic variation in richness among forest-associated species (figure 2). One reason why a stronger latitudinal gradient was not observed is that our data focused on forest-associated species; a stronger latitudinal gradient was observed when counts of all species were mapped (Flather and others, unpublished data).

For all taxa (trees, mammals, birds, amphibians, reptiles, and butterflies), the highest richness classes are concentrated in the southern half of the contiguous United States in general, and the Southeast in particular (figure 2a). Trees, being the most speciose of the forest-associated taxa, show nearly an identical pattern (figure 2b) to the “All Taxa” map. Conversely, the geographic patterns in richness among forest-associated species vary among the vertebrate and invertebrate taxa examined.

Forest-associated mammals reached their highest richness in the topographically diverse ecoregions of the southern Appalachians, the southern Rocky Mountains, and the Sierra Nevada and Pacific Coast mountains (figure 2c). High forest bird richness was observed in a mixture of ecoregions – occurring in the arid Southwest and extending northeast into New England forests (figure 2d). Forest amphibians and reptiles tended to reach high species counts in the more mesic forested systems of the Southeast, with reptile richness also being high in the more arid southwestern ecoregions (figures 2e, f). Forest butterfly richness patterns were distinctly different from the other taxonomic groups, being conspicuous by the absence of high richness areas in the southeastern United States (figure 2g). Ecoregions supporting the highest richness of forest butterflies include the central hardwood forests, the central forest/grassland transition zone, and a broad band of western ecoregions that include grassland, shrubland, and montane forest habitats. Although there is a general tendency for the richness of forest species to be higher in southern ecoregions, this pattern is not universally observed among taxa. There is also

evidence for strong longitudinal gradients that covary with a number of environmental factors including topographic relief, temperature, and moisture that interact to affect available energy, the occurrence of forest vegetation, and the diversity of forest habitats (Currie 1991).

Figure 2. Geographic variation in the number of forest-associated species occurring within ecoregions (as defined in figure 1) for all taxa (a), trees (b), mammals (c), birds (d), amphibians (e), reptiles (f), and butterflies (g). Richness classes were based on percentiles defined to approximately reflect the upper 90th percentile (dark red), the 80th - <90th percentile, 60th - <80th percentile, 20th - <60th percentile, and < 20th percentile (lightest red). The highest richness class represents the 10 percent of ecoregions with the greatest count of species. Gray boundary lines delineate Forest Service planning regions as defined in figure 1.

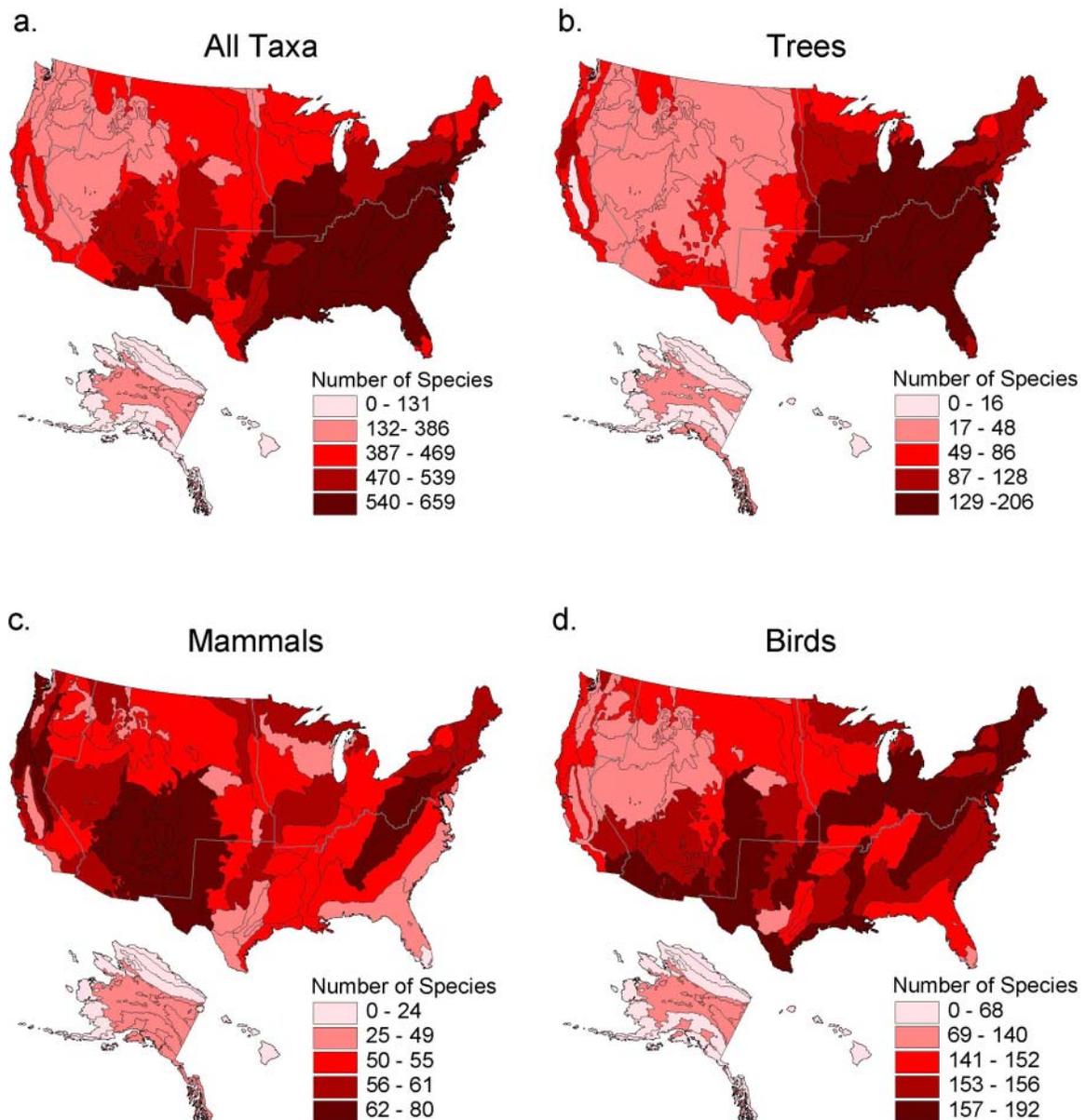
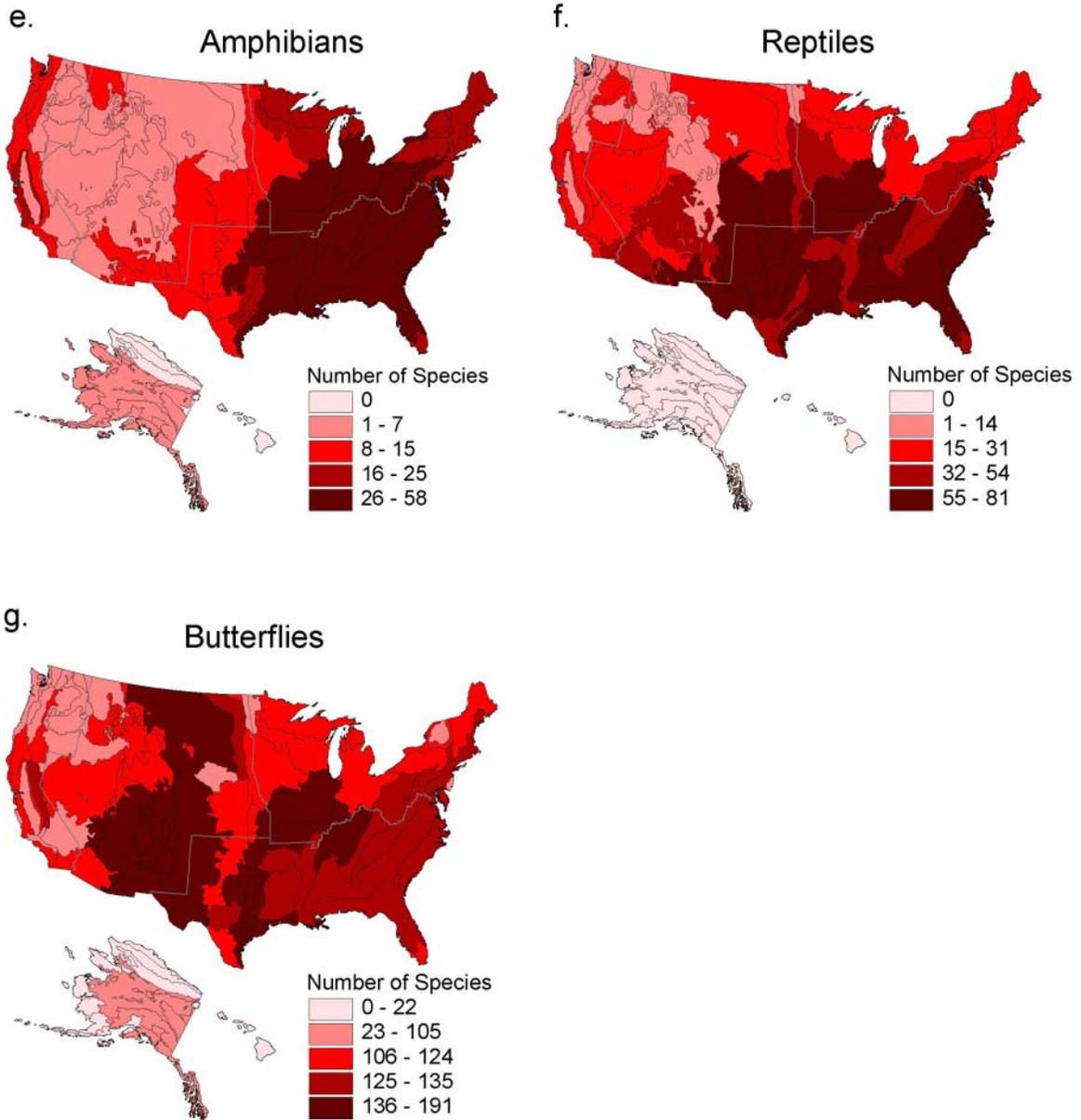


Figure 2, cont'd



Taxonomic variation in the location of high species richness is also apparent when we estimate the area of high-richness ecoregions within each Forest Service planning region (table 2). The South has the majority of high-richness areas for trees, amphibians, and reptiles. High-richness areas for forest birds are prominent in both the South and North. Forest-associated butterflies and mammals have high-richness areas concentrated in the Rocky Mountain Region. The only taxonomic groups with high-richness areas in all four planning regions are mammals and birds.

We acknowledge that the taxonomic coverage in the databases we used in this analysis is woefully incomplete. One approach for overcoming this data constraint is to assume that the diversity pattern of well-studied taxa reflects the pattern among other taxonomic groups (for review see Reid 1998). Although there is evidence in our data for geographic similarity in the distribution of forest species richness among some taxa, this pattern is certainly not general. This finding is consistent with a growing number of papers that caution conservation planners against using the diversity pattern for a few taxa as a surrogate measure of overall species diversity (Flather and others 1997; Prendergast 1997; Ricketts and others 1999a). For this reason, it is difficult to argue that patterns of high richness for the relatively well-studied species groups used here can be used to indicate the pattern of richness among those species groups that have yet to receive commensurate levels of taxonomic and biogeographic study.

The species richness data displayed in figure 2 simply shows where diversity is relatively high or relatively low based on the geographic range of each species and their intersection with ecoregional boundaries. In this regard, it should be considered a baseline condition or expectation of the number and composition of species within each ecoregion. Long-term monitoring data are required if trends in species richness are to be estimated.

Table 2. Area and percent (shown parenthetically) of high richness areas (the 90th percentile, see figure 2) occurring in Forest Service planning regions. Planning region boundaries are defined in figure 1.

Taxon	Forest Service planning region			
	North	South	Rocky Mountain	Pacific Coast
	----- 1000 km ² (percent) -----			
All taxa ^a	642.9 (27.0)	1,596.6 (67.0)	140.9 (5.9)	–
Trees	777.4 (34.7)	1,429.1 (63.8)	32.4 (1.4)	–
Mammals	162.8 (9.0)	448.5 (24.9)	992.7 (55.0)	199.5 (11.1)
Birds	867.9 (39.3)	808.0 (36.6)	505.4 (22.9)	28.3 (1.3)
Amphibians	777.4 (32.8)	1,559.7 (65.8)	32.4 (1.3)	–
Reptiles	383.0 (14.4)	1,699.4 (63.9)	578.1 (21.7)	–
Butterflies	363.4 (14.0)	739.2 (28.4)	1,498.3 (57.6)	–

^a Includes trees and forest-associated mammals, birds, amphibians, reptiles, and butterflies.

Geographic Trends in Bird Richness

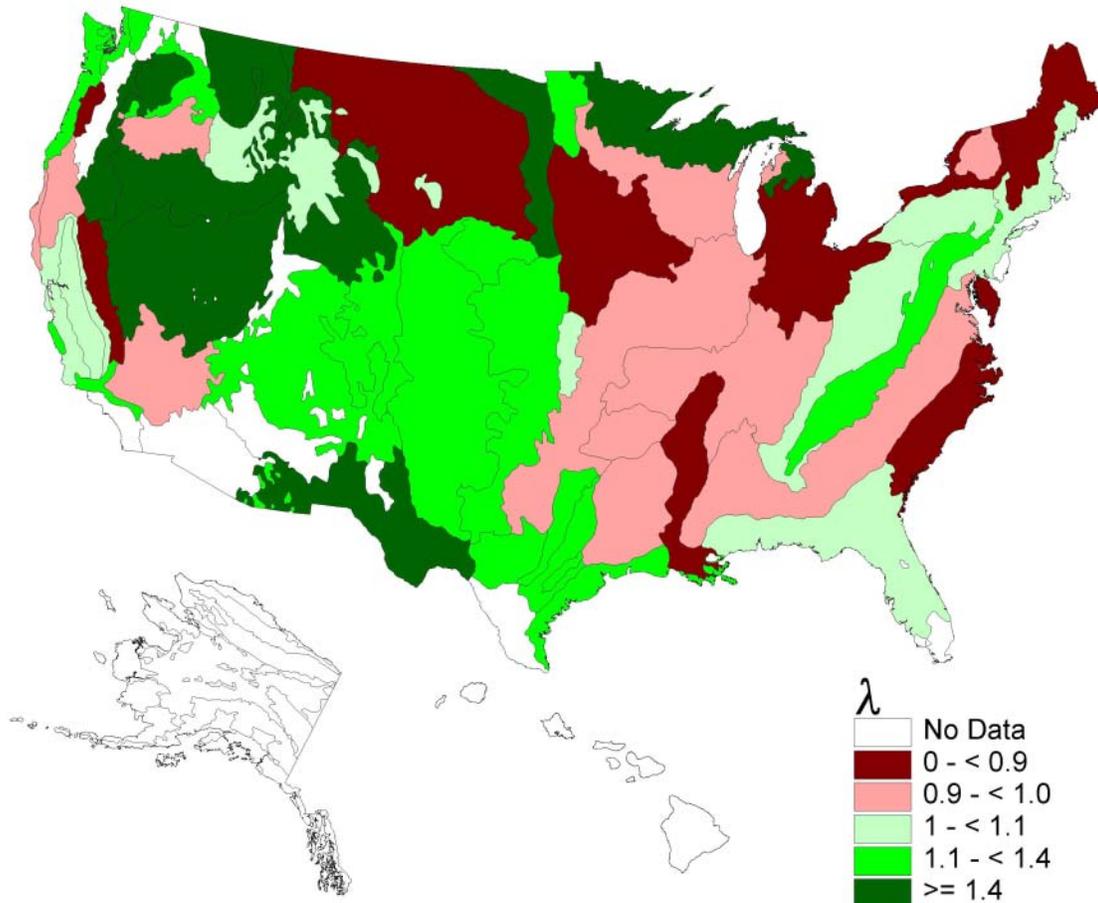
Trends in bird richness from 1975 to 1999 vary by ecoregion (Appendix B). Richness trends for most ecoregions were not statistically different from $\lambda=1$ as indicated by the fact that the 95 percent confidence interval on the estimated λ 's included 1.0. For four ecoregions the trends were significant; richness of forest birds increased in the North Central Rockies Forests (30), the Montana Valley and Foothill Grasslands (57), and the Colorado Plateau Shrublands (78), and richness decreased in the Eastern Great Lakes Lowland Forests (11). In the two ecoregions where the detection probabilities were not statistically distinguishable from 1.0, forest bird richness increased in the Western Great Lakes Forests (7) and declined in the Southeastern Mixed Forests (22).

Although forest bird richness does not appear to have changed appreciably in most ecoregions (at least using statistical criteria), there are some consistencies in the patterns that are suggestive of biologically important changes. When forest bird richness trends are compared among ecoregions that support a similar major habitat type (as assigned by Ricketts and others 1999b), ecosystems that support forest habitats appear to behave differently than ecosystems that support grassland or xeric habitats (table 3). Among the 31 forest ecosystems with richness estimates, slightly more than half of these ecoregions had evidence of declining richness. Conversely, in grassland systems the majority of ecoregions (12 of 15) had evidence for increasing forest bird richness. A similar pattern was observed among xeric systems, with 7 of 8 ecoregions showing evidence of increasing forest bird richness. An examination of λ -values geographically (figure 3) further supports this observation. Ecoregions with evidence of declining forest bird richness tend to be concentrated in the eastern United States, whereas ecoregions with increasing forest bird richness tend to be found in the more arid systems of the Great Plains, Intermountain West, and Southwestern desert and shrublands. Note, however, that the uncertainty in λ -values is high for most ecoregions (see Appendix B). Consequently, we caution that the patterns in λ observed within major habitat type (table 3) and geographically (figure 3) must be interpreted carefully by treating the consistency of increase or decrease in forest bird richness among ecoregions as suggestive of important biological trends requiring further investigation.

Table 3. Number of ecoregions with increasing and decreasing forest bird richness trends from 1975 to 1999 (from Appendix B).

Major habitat type	Increasing trend ($\lambda>1.0$)	Decreasing trends ($\lambda<1.0$)
Forest	15	16
Grassland	12	3
Xeric	7	1
Total	34	20

Figure 3. Trends in forest bird richness by ecoregion (as defined in figure 1) from 1975 to 1999. Change in richness is estimated by λ , which is the ratio of estimated richness in 1999 to the estimated richness in 1975. Values of $\lambda > 1.0$ indicate increasing richness (green shades); values of $\lambda < 1.0$ indicate declining richness (red shades).



The tendency toward increasing forest bird richness among the more semi-arid and arid ecoregions is consistent with a pattern of increasing woody vegetation (caused by an alteration of disturbance regimes including fire and grazing) that has been observed throughout many areas in the United States (Archer 1995). We also note that the bird richness trends reported here parallel those observed for forest bird populations, with declining populations being observed among ecoregions in the eastern United States and increasing populations in the western United States (see Sieg and others 2003).

Although the BBS is a monitoring program that is unique in its geographic and temporal scope, a number of caveats associated with its design and implementation warrant remark in light of these trends in species richness. First, not all bird species are monitored equally well by the BBS. Nocturnal or crepuscular species, cryptic species, some colonial nesting species, and species with restricted geographic ranges are not monitored well by the BBS (O'Connor and others 2000). Second, because the BBS is conducted along secondary roads, bird occurrence patterns may not be representative of the regional bird pool because of biases associated with roadside habitats that may affect species detections (Bart and others 1995; Keller and Scallan

1999). Third, changes in observers over time have the potential to introduce spurious trends since observers can vary in their ability to detect birds; however, analytic methods have been developed to control for this nuisance variable (see Sauer and others 1994). Finally, survey routes can be discontinued (completely or in part) and relocated when urban encroachment results in traffic densities that limit aural detection of species. This relocation of BBS routes could affect how representative BBS-based measures of bird response are to land use and land cover changes that are occurring within an ecoregion. Regional studies that have examined the effects of urbanization on bird communities using the BBS do not appear to have been affected by this potential bias (Cam and others 2000).

INDICATOR EVALUATION

Indicator Adequacy

A count of species is a basic and easily understood measure of biological diversity. Its simplicity and intuitive appeal helps avoid the controversy surrounding the interpretation of more complex diversity indices (Magurran 1988). However, a simple species count is not without its own set of conceptual problems related to its use as an indicator of ecological sustainability. These concerns seem to be focused in two general areas: the sensitivity of richness estimates to changes in biological diversity, and the relationship between species richness and the maintenance of ecosystem function.

Species richness at a national or ecoregional scale can change under two conditions. Species can become locally extinct or species can expand their range. It is important to emphasize that a species does not necessarily need to become globally extinct for richness to be reduced; it simply needs to fail to occur within the geographic boundary of interest whether that be at the national or ecoregional scale. Similarly, establishment of a new species in the species pool is not restricted to exotic taxa, but can simply involve a shift in the geographic range of native species. If local extinctions are balanced by species range expansions then richness will remain unchanged over time despite changes in species composition. There is some empirical evidence that habitat changes across some landscapes do not necessarily lead to changes in the number of species that a given geographic area can support, but rather lead to substantial changes in community composition (Parody and others 2001). Furthermore, species number is not anticipatory (*sensu* Dale and Beyeler 2001) in the sense that an impending change in system sustainability (for example, species loss) cannot be detected prior to the species actually being lost. Consequently, there is a concern that a simple monitoring of species counts will not presage important changes to biological diversity (Flather and Sieg 2000).

The relationship between species richness and ecosystem function is a topic receiving much debate in the recent ecological literature (Huston 1997; Kaiser 2000; Mittelbach and others 2001; Naeem 2002). The focus of the debate is centered on the notion that a loss of species could critically affect ecosystem function (for example, productivity, nutrient cycling, resource capture, resilience to perturbations) and thus the health of the system (Chapin and others 1998; Loreau and others 2001; Cardinale and others 2002). Given the current state of our knowledge, we cannot determine if a diverse species pool is required to maintain ecosystem function or if a few dominant species are sufficient to provide for the functional health of ecosystems (Schwartz and others 2000; Hector and others 2001; Loreau and others 2001). Interpreting trends in species

richness in terms of ecological sustainability will remain difficult until the relationships between species richness and ecosystem function are more clearly understood (Huston and others 1999).

Data Limitations

Monitoring species richness over large geographic areas is a simple idea but logistically very difficult (Lubchenco and others 1991; Lawler 2001). Although it is not surprising that we lack systematic inventories of obscure taxa (for example, non-vascular plants, fungi, bacteria, nematodes, arachnids), it is surprising that we generally lack spatially and temporally extensive data on species distributions for most other taxa as well (Flather and Sieg 2000). Certainly, data that could contribute to macroecologic investigations of species richness patterns exist for a subset of well-studied taxa. However, even these data are not readily available, being widely dispersed among government agencies, museum records, and individual investigator files (Brown and Roughgarden 1990). Furthermore, the primary species location records are often unavailable, having already been analyzed to derive a species' geographic range. Such binary range maps can give a false sense of precision when in fact there is much uncertainty in delineating species distributions. Consequently, species richness estimates derived by overlaying binary range maps may be characterized by substantial errors (see Flather and others 1997), particularly at the periphery of species ranges.

A common strategy for overcoming the paucity of taxonomic inventories has been to estimate species counts based on a mixture of known and hypothesized habitat affinity relationships. Because estimates of species counts based on habitat associations are derived from models, they are characterized by varying levels of bias and imprecision and therefore must be used cautiously. The Gap Analysis Program³ (Scott and others 1993) is an example of an effort in the United States to synthesize existing biodiversity data. Basic point location data from specimen collection sites or observational surveys, and predicted distributions from habitat affinity models, form the basis for analyzing species richness patterns across broad geographic areas. However, because the majority of the species distribution data are derived from habitat association models, interpretation of spatial and temporal patterns in species richness will have to consider the uncertainty associated with habitat-based predictions of species occurrence (Flather and others 1997).

A final data limitation associated with species richness is that even when quantitative data are available they are often based on a convenience, as opposed to a probabilistically based, sample. The result is that formal inference procedures (Anderson 2001) cannot be used to assess species richness changes over time.

Recommendations for Improvement and Research Needs

The species has been regarded as the fundamental unit of biodiversity (Huston 1993). By logical extension, then, a count of species is perhaps the most basic quantification of biodiversity. Although species counts are central to any assessment of biodiversity, important barriers (methodological and conceptual) to its effective use as an indicator of sustainability remain. The shortcomings that we reviewed above imply research needs in four broad areas:

³The Gap Analysis Program is completing its synthesis of biodiversity data on a state-by-state basis. Data from the Gap Analysis Program were not used in this report since national coverage has not yet been attained.

design of broader taxonomic inventories, estimation, testing of alternative indices, and indicator interpretation.

Perhaps the most obvious need for future work concerns the development of monitoring protocols that are economically feasible and ecologically tenable. Part of the difficulty relates to substantial knowledge gaps in the systematics of some taxa, and the fluid nature of taxonomic classifications over time. The emerging discipline of biodiversity informatics (see Bisby 2000), which is focusing on the development of a comprehensive accounting of all species, would help further efforts to monitor richness trends. However, proposed efforts to accomplish a taxonomically comprehensive accounting of species are at least several decades away (Lawler 2001).

Even for taxa with a relatively well-described taxonomy, most have no data from which to draw conclusions concerning trends in species numbers over the geographic and temporal scales that will be necessary to evaluate sustainable resource development. Although recent efforts have extended the BBS-type survey design to amphibians (see the North American Amphibian Monitoring Program, <http://www.im.nbs.gov/amphibs.html>), there is a critical need to develop surveys that can quantify richness patterns for a much broader set of taxa (National Research Council 1992). Designs based on presence-absence detection within a systematic grid laid out over a broad geographic area have the potential to be useful in estimating trends in richness. Such presence-absence surveys are often referred to as atlases and have an advantage over point-based or transect-based surveys in that all habitats within the sampling grid are targeted in an effort to ensure detection of rarer species (Robbins 1990). Although much of the work in developing atlases has focused on birds (see Udvardy 1981), atlas-type inventories are now becoming common for non-avian vertebrates, invertebrates, and plants (Johnson and Sargeant 2002). Atlas data is commonly used to document species geographic ranges and research is needed to evaluate their utility in estimating species richness. Because atlas programs have typically been developed at the state-level within the United States, research is also needed into the feasibility of aggregating state atlas data to derive ecoregional and national trends in species richness.

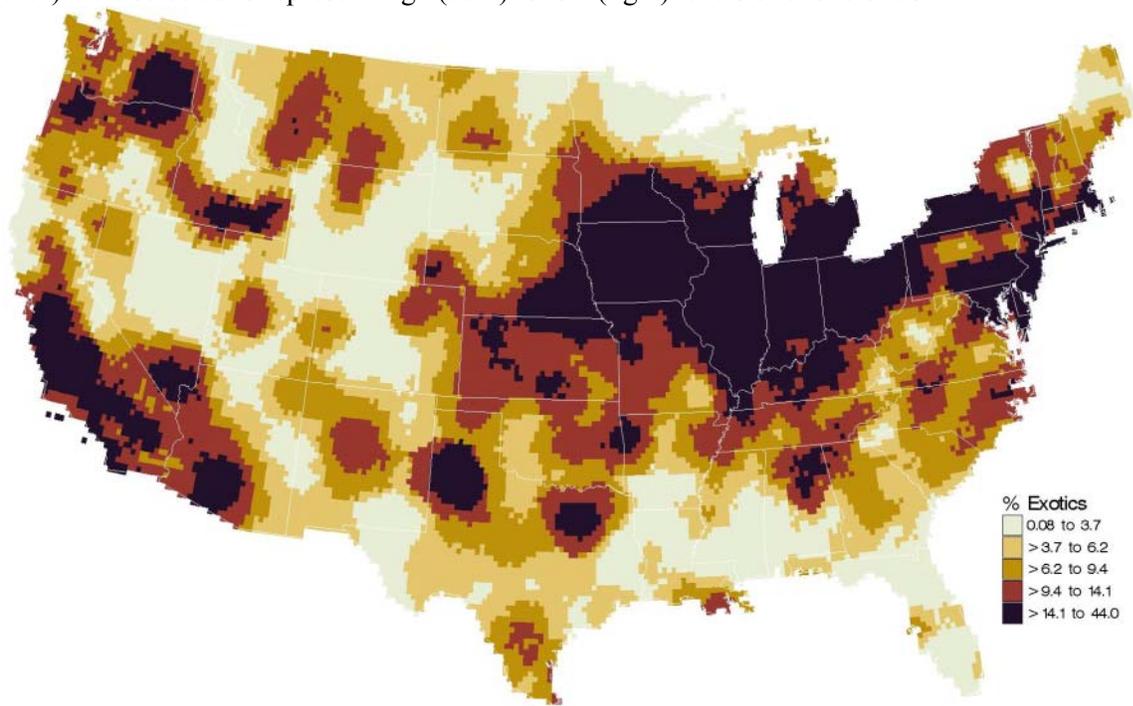
The concept of indicator taxa has been proposed as a potential remedy to the paucity of species count data for some taxa. Under this concept, the richness pattern among well-studied groups is assumed to reflect the pattern among the other taxa. This may be more wishful thinking than ecological reality as there has been little empirical evidence supporting the general applicability of the indicator taxon concept (Prendergast and others 1993; Flather and others 1997; van Jaarsveld and others 1998; Harcourt 2000; Ricketts and others 1999a, 2002). The lack of general support for the indicator taxon concept notwithstanding, there do appear to be circumstances and scales under which some taxa may serve as useful surrogates for the diversity patterns of other taxa (Reid 1998; Allen and others 2001; Moritz and others 2001). The variability in conclusion regarding the utility of indicator taxa argues for a systematic research agenda that will permit the specification of those ecological conditions and scales for which indicator taxa are a tenable conservation concept.

Concurrent with a taxonomic broadening of species inventories, there is a need to address the richness estimation problem. As noted earlier, simple species counts (that is, where the number of species observed is treated as the estimate of richness) are known to underestimate the number species that are actually present. Recent research has used capture-recapture theory to estimate bird species richness locally (Boulinier and others 1998). Such efforts need to be extended to include other taxa and larger geographic areas. Also, there is a need to explore the

behavior of these estimators under known conditions so that the effects of detection rates, spatial clustering in species distributions, and spatial scale can be determined. Although this report applied such a capture-recapture estimator to examine broad geographic trends in bird richness, the approach is applicable to any statistical inventory with sampling replication over time or space. For example, Forest Service inventories of vegetation diversity as conducted within the Forest Inventory and Analysis Program could use these methods to estimate trends in vascular plant richness over time as an indicator of forest health (Stolte and others 2002).

A third area for future research includes the investigation of alternative species richness indicators. We noted above that species richness may be insensitive to important changes in biological diversity caused by, for example, shifts in species composition. In this regard, we suggest two possible alternative indicators focused on detecting changes in the membership of species assemblages. First, a common observation in the ecosystem stress literature is that the intensity of human resource development is positively correlated with the abundance of non-native species (Rapport and others 1985; McKinney 2002). The number of exotic individuals observed compared to the total number of individuals observed has been proposed as a useful indicator to monitor the health of terrestrial and aquatic systems (Committee to Evaluate Indicators for Monitoring Aquatic and Terrestrial Environments 2000) and has been recently used with bird monitoring data as a broad-scale indicator of ecosystem condition (Hof and others 1999; Sieg and others 1999). In these studies, the geographic pattern of exotic bird composition did correlate with land use intensification patterns (figure 4), with large contiguous areas of high proportionate exotic composition being associated with intensive agriculture in the upper mid-west and the California Central Valley, and urban development along the mid-Atlantic seaboard.

Figure 4. Geographic pattern of the occurrence of exotic bird species measured as the proportion of individuals detected that were non-native divided by the total number of individuals observed. Data based on the North American Breeding Bird Survey. Route level estimates were spatially interpolated using kriging (see Cressie 1991). Five equal-area classes (each representing approximately 20 percent of the area) were selected to represent high (dark) to low (light) levels of exotic birds.



A second alternative indicator has its basis in the identification of the expected native species composition in a defined geographic area. Applied species conservation has been dominated, for the most part, by the notion that local conditions and processes determine the mix of species that occur at that location. Explanations for changes in species richness often focus on human-caused modification of habitat conditions, with sites harboring fewer species being interpreted as impoverished. There is increasing evidence, however, that conditions and processes that define the regional context are also important in determining the composition of species at any particular place (Ricklefs 1987). If the regional species pool from which the local community is drawn varies from place to place (or over time), then a community comprised of fewer species may not be impoverished. What is needed is a measure of “relative” species richness, where the metric shifts from a simple estimate of species richness to one that compares the members of the current species assemblage with that expected based on a regionally defined species pool. Species richness is invariant to the loss and replacement of species that can occur with changes to species composition. For example, species richness would not detect the replacement of the passenger pigeon (*Ectopistes migratorius*) and gray wolf (*Canis lupus*) with the European starling (*Sturnus vulgaris*) and Norway rat (*Rattus norvegicus*) as an important change in biological diversity. An estimate of relative species richness, which is sensitive to species compositional shifts, is often referred to as a measure of faunal integrity (Karr 1990) or community completeness (Cam and others 2000). Because it is a relative measure, community completeness varies from 0 to 1.0, with values <1.0 indicating that some subset of the expected species pool is no longer being detected in the current species assemblage.

A final area requiring additional research concerns the interpretation of species richness as an indicator of ecological sustainability. The relationship between indicators of biodiversity and the success of biological conservation is weak (Lindenmayer and others 2000). As we discussed earlier, it is not yet known whether a diverse species pool is required to maintain the ecological functions that characterize any given system. How many species can be lost before ecosystem functions are degraded or lost? Is the degradation proportional to the number of species that are lost from the system, or are there non-linearities that result in critical threshold dynamics? The distinction is important because under the former, loss of species always carries with it some cost to ecosystem function, whereas the latter suggests that ecological systems have some inherent redundancy or resiliency that can buffer, to a point, ecological systems against a degradation in ecosystem function (Muradian 2001; Scheffer and others 2001). In the absence of this research, using species richness to indicate whether a particular ecological system is on a trajectory toward or away from ecological sustainability will be difficult.

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APPENDIX A. Estimated number of species in the United States, by taxonomic group, according to various sources.

Source	Vascular plants	Vertebrates				Freshwater fish
		Mammals	Birds	Amphibians	Reptiles	
Kartesz (1994)	21,757					
NatureServe (2002a)	16,771	412	710	261	288	867
NatureServe (2002b)		416	773	252	287	791
Page and Burr (1991)						790
Stein and others (2000)	15,990	416	768	231	283	799
World Resources Institute (1994)	19,473	346	650			
World Resources Institute (1998)		428	650	233	280	822
World Resources Institute (2000)	19,473	432	650	263	287	822
World Conservation Monitoring Centre (1994)	21,012	428	768	233	280	822
World Conservation Monitoring Centre (1998)						822
Langner and Flather (1994)		466	1090		368	
McDiarmid (1995)				230	277	
		----- Summary statistics -----				
Mean	19,079	418	757	243	294	817
Standard error	2,284	34	145	15	30	25
Number of sources	6	8	8	7	8	8

Source	Invertebrates					
	Freshwater mussels	Freshwater snails	Crayfishes	Tiger beetles	Dragonflies/ damselflies	Butterflies/ skippers
Kartesz (1994)						
NatureServe (2002a)	263	632	336	114	452	601
NatureServe (2002b)	296	658	335	112	471	661
Page and Burr (1991)						
Stein and others (2000)	292	661	322	114	456	620
World Resources Institute (1994)						
World Resources Institute (1998)						
World Conservation Monitoring Centre (1994)						
World Conservation Monitoring Centre (1998)						
Langner and Flather (1994)						
McDiarmid (1995)						
	----- Summary statistics -----					
Mean	284	650	331	113	460	612
Standard error	18	16	8	1	10	10
Number of sources	3	3	3	3	3	3

APPENDIX B. Estimated change in the richness of forest birds (λ) over a 25-year period (1975 to 1999) by ecoregion, where λ is measured as the ratio of estimated richness in 1999 to estimated richness in 1975. The number of BBS routes used in the estimate is given by n . The “Trend” column indicates whether richness is increasing (+) or decreasing (-) as indicated by $\lambda > 1.0$ or $\lambda < 1.0$, respectively. The “Habitat” column identifies the major vegetation type in each ecoregion. The geographic locations of ecoregions are displayed in figure 1. Only those ecoregions for which an estimate of λ could be calculated are shown here.

Ecoregion	λ	95 percent CI	n	Trend	Habitat
Willamette Valley Forests (6)	0.76 ^a	–	1	-	Forest
Western Great Lakes Forests (7)	1.50 ^b	–	18	+	Forest
Eastern Forests/ Boreal Transition (8)	0.91	0.747-1.051	2	-	Forest
Upper Midwest Forests/ Savanna Transition Zone (9)	0.98	0.642-1.446	27	-	Forest
Southern Great Lakes Forests (10)	0.80	0.498-1.011	14	-	Forest
Eastern Great Lakes Lowland Forests (11)	0.61	0.479-0.838	3	-	Forest
New England/ Acadian Forests (12)	0.89	0.870-1.132	15	-	Forest
Northeastern Coastal Forests (14)	1.04	0.886-1.311	27	+	Forest
Allegheny Highlands Forests (15)	1.06	0.841-1.135	21	+	Forest
Appalachian/ Blue Ridge Forests (16)	1.17	0.838-1.624	15	+	Forest
Appalachian Mixed Mesophytic Forests (17)	1.09	0.990-1.607	22	+	Forest
Central Hardwood Forests (18)	0.99	0.684-1.332	42	-	Forest

Ecoregion	λ	95 percent CI	n	Trend	Habitat
Ozark Mountain Forests (19)	0.97	0.629-1.376	5	-	Forest
Mississippi Lowland Forests (20)	0.74	0.445-1.393	6	-	Forest
East Central Texas Forests (21)	1.31 ^a	–	1	+	Forest
Southeastern Mixed Forests (22)	0.94 ^b	–	30	-	Forest
North Central Rockies Forests (30)	1.41	1.068-1.788	2	+	Forest
British Columbia Mainland Coastal Forests (33)	1.11	0.818-1.406	2	+	Forest
Central Pacific Coastal Forests (34)	1.29 ^a	–	1	+	Forest
Puget Lowland Forests (35)	1.19 ^a	–	1	+	Forest
Eastern Cascades Forests (37)	1.42	1.035-2.026	6	+	Forest
Blue Mountains Forests (38)	0.99	0.707-1.335	2	-	Forest
Klamath-Siskiyou Forests (39)	0.97	0.641-1.301	6	-	Forest
Northern California Coastal Forests (40)	0.93	0.729-1.184	2	-	Forest
Sierra Nevada Forests (41)	0.55	0.383-1.095	5	-	Forest
South Central Rockies Forests (43)	1.07	0.631-1.511	6	+	Forest
Colorado Rockies Forests (45)	1.31 ^a	–	1	+	Forest
Madrean Sky Islands Montane Forests (47)	1.28 ^a	–	1	+	Forest

Ecoregion	λ	95 percent CI	n	Trend	Habitat
Piney Woods Forests (48)	0.97	0.804-1.129	9	-	Forest
Middle Atlantic Coastal Forests (50)	0.75	0.545-1.075	13	-	Forest
Southeastern Conifer Forests (51)	1.05	0.679-1.453	14	+	Forest
Palouse Grasslands (53)	1.35 ^a	–	1	+	Grassland
California Central Valley Grasslands (54)	1.01	0.654-1.532	4	+	Grassland
Northern Mixed Grasslands (56)	1.43 ^a	–	1	+	Grassland
Montana Valley and Foothill Grasslands (57)	1.46	1.084-1.854	2	+	Grassland
Northwestern Mixed Grasslands (58)	0.75	0.530-1.015	8	-	Grassland
Northern Tall Grasslands (59)	1.21	0.978-1.421	2	+	Grassland
Central Tall Grasslands (60)	0.89	0.616-1.234	15	-	Grassland
Flint Hills Tall Grasslands (61)	1.06	0.938-1.161	2	+	Grassland
Nebraska Sand Hills Mixed Grasslands (62)	1.33 ^a	–	1	+	Grassland
Western Short Grasslands (63)	1.30	0.778-1.994	9	+	Grassland
Central and Southern Mixed Grasslands (64)	1.12	0.654-1.789	11	+	Grassland
Central Forest/Grassland Transition Zone (65)	0.99	0.688-1.354	44	-	Grassland
Edwards Plateau Savannas (66)	1.19	0.787-1.701	3	+	Grassland

Ecoregion	λ	95 percent CI	n	Trend	Habitat
Texas Blackland Prairies (67)	1.38	0.904-2.066	3	+	Grassland
Western Gulf Coastal Grasslands (68)	1.11 ^a	–	1	+	Grassland
California Interior Chaparral and Woodlands (70)	1.10	0.656-1.704	5	+	Xeric
California Montane Chaparral and Woodlands (71)	1.13	0.837-1.454	2	+	Xeric
Snake/Columbia Shrub Steppe (75)	1.58	0.815-2.694	6	+	Xeric
Great Basin Shrub Steppe (76)	1.57 ^a	–	1	+	Xeric
Wyoming Basin Shrub Steppe (77)	1.43 ^a	–	1	+	Xeric
Colorado Plateau Shrublands (78)	1.35	1.009-1.678	2	+	Xeric
Mojave Desert (79)	0.93 ^a	–	1	-	Xeric
Chihuahuan Desert (81)	1.50 ^a	–	1	+	Xeric

^a Estimated as the ratio of observed richness in 1999 to observed richness in 1975 since only 1 route was run in each time period.

^b Estimated as the ratio of observed richness in 1999 to observed richness in 1975 since detection probabilities in the two time periods were equal to 1.0.