

A Conceptual Framework for Selecting and Analyzing Stressor Data to Study Species Richness at Large Spatial Scales

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ABSTRACT / In this paper we develop a conceptual framework for selecting stressor data and analyzing their relationship to geographic patterns of species richness at large spatial scales. Aspects of climate and topography, which are not stressors per se, have been most strongly linked with geographic patterns of species richness at large spatial scales (e.g., continental to global scales). The adverse impact of stressors (e.g., habitat loss, pollution) on species has been demonstrated primarily on much smaller spatial scales. To date, there has been a lack of conceptual development on how to use stressor data to study geographic patterns of species richness at large spatial scales.

The framework we developed includes four components: (1) clarification of the terms stress and stressor and categorization of factors affecting species richness into three groups—anthropogenic stressors, natural stressors, and natural covariates; (2) synthesis of the existing hypotheses for explaining geographic patterns of species richness to identify the scales over which stressors and natural covariates influence species richness and to provide supporting evidence for these relationships through review of previous studies; (3) identification of three criteria for selection of stressor and covariate data sets: (a) inclusion of data sets from each of the three categories identified in item 1, (b) inclusion of data sets representing different aspects of each category, and (c) to the extent possible, analysis of data quality; and (4) identification of two approaches for examining scale-dependent relationships among stressors, covariates, and patterns of species richness—scaling-up and regression-tree analyses.

Based on this framework, we propose 10 data sets as a minimum data base for examining the effects of stressors and covariates on species richness at large spatial scales. These data sets include land cover, roads, wetlands (numbers and loss), exotic species, livestock grazing, surface water pH, pesticide application, climate (and weather), topography, and streams.

In recent years concern has grown over the loss of species due to human activities (Wilson 1988, Soulé and Kohm 1989, Finch 1992, Dobkin 1992). Loss of species is generally recognized as a global phenomenon, yet the adverse impact of human activities on species has been demonstrated primarily on much smaller spatial scales (Wickham and others 1995a). Moreover, studies at large spatial scales (e.g., continents) have generally shown

that species richness is most strongly correlated with natural environmental factors, such as climate and topography (Schall and Pianka 1978, Wright 1983, Currie 1991). There has been a lack of conceptual development to date on how to use stressor data in studies of geographic patterns of species richness at large spatial scales.

The purpose of this paper is to develop a comprehensive framework for the selection and use of data sets representing natural and anthropogenic factors that may influence geographic patterns of species richness at large spatial scales (e.g., conterminous United States). In developing the framework, we: (1) clarify the terms

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Table 1. Definitions of stress

Author	Definition
Larcher (1980)	The exposure to extraordinarily unfavorable conditions; they need not necessarily represent a threat to life, but they do trigger an "alarm" response (e.g., defensive and adaptive reactions) in the organism if it is not in a dormant state.
Odum and others (1979)	Deviation from nominal; unfavorable deflections.
Barrett (1981) ^a	A perturbation that is applied to a system by a stressor which is foreign to that system or which may be natural to it but, in the instance concerned, is applied at an excessive level.
Rykiel (1985)	An effect; a physiological or functional effect; the physiological response of an individual, or the functional response of a system caused by disturbance or other ecological process; relative to a reference condition; characterized by direction, magnitude, and persistence; a type of perturbation.

^aAlthough Barrett did not define perturbation, he uses the term as an effect of disturbance [see Odum and others (1979) and Rykiel (1985)].

stress and stressor and distinguish among anthropogenic stressors, natural stressors, and natural covariates; (2) synthesize existing hypotheses on geographic patterns of species richness to identify the scales at which stressors and covariates appear to operate and provide supporting evidence for these relationships through review of previous studies; (3) develop criteria for selecting data sets that can be used to predict and explain geographic patterns of species richness; and (4) recommend scaling-up and regression-tree analyses as approaches for examining the scale-dependent effects of stressors and covariates on patterns of species richness.

Framework for Selecting and Analyzing Stressor Data

Definitions of Stress and Stressor

Larcher (1980) defined stress as a prevailing condition to which an organism or ecosystem responds, whereas others have defined it as a response of an organism or ecosystem to prevailing environmental conditions (Odum and others 1979, Barrett 1981, Rykiel 1985) (Table 1). In the latter context, stress is an effect not a prevailing condition. For example, stress is

Table 2. Examples of factors by category

Categories	Examples
Anthropogenic stressors	habitat fragmentation; pollution; introduction of exotic species
Natural stressors	extreme weather events: prolonged drought; above average precipitation
Natural covariates	prevailing climate; topography; streams; wetlands
Combination of above (depending on circumstances)	fire; pest outbreaks

the effect of a disturbance (e.g., pollution, fragmentation) on a biological entity or process, not the disturbance itself. Thus, for studying geographic patterns of species richness, stressors may be considered as quantitative measures of disturbance, such as amount of habitat lost or amount of a pollutant released into the environment.

Barrett's (1981) definition of stress permits distinction among (1) anthropogenic stressors, (2) natural stressors, and (3) natural covariates. Habitat loss, pollution, and introduction of exotic species are examples of human-induced stressors. Extreme weather events, such as abnormally cold temperatures, are natural stressors. In contrast, prevailing climate, topography, and the occurrence or density of streams and wetlands would be natural covariates that are not stressors, but nevertheless play a role in the geographic patterns of species richness.

We use the term natural covariates for factors that are prevailing conditions because it is consistent with the use of the term covariate in analysis of covariance (ANCOVA), where the effect of one variable (the covariate) confounds the relationship between two others (Wildt and Ahtola 1978).

Table 2 provides examples of anthropogenic stressors, natural stressors, and natural covariates. Some examples do not fit neatly into these three categories (e.g., fire, pest outbreaks). For example, spruce budworm infestations in northern conifer forests are part of the natural regime, but recent outbreaks were more severe than previous occurrences and the greater severity may have been due to silvicultural practices (Blais 1985).

The definition of stress as a response implies that the effect of stressors on species richness can be detected only in relation to a reference condition (Rykiel 1985). That is, the effect of stressors can only be measured if species richness is known without the stressors' influence. An example of using a reference condition is that species and stressor data are measured over time so that

changes can be used to determine the effect of stressors on species richness. Although this method is valid, it requires time series data. An alternative approach is to use natural spatial patterns of species richness that are found in relatively undisturbed environments or patterns predicted by validated theories as reference conditions. When appreciable differences in richness patterns in similar environments and spatial scales are detected, stressor data may be used to evaluate the effect of disturbances on diversity patterns. This is essentially a space-for-time approach, which is common in ecological studies (see Pickett 1989).

Synthesis of Patterns and Hypotheses of Species Richness and Evidence Supporting These Relationships

The literature on patterns of species richness in time and space and associated hypotheses (Table 3) provides a starting point for developing a framework for selecting stressor data sets because many of the hypotheses proposed to explain these patterns can also help explain relationships between stressors and species richness (e.g., Loucks 1970, Brown and Gibson 1983, Begon and others 1986, Currie 1991, Wu and Vankat 1991, 1995, Hall and others 1992, Ricklefs and Schluter 1993, Rosenzweig 1995). For example, habitat fragmentation has been defined as the “transformation of a large expanse of habitat into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitat unlike the original” (Wilcove and others 1986). Both moderate disturbance and habitat heterogeneity hypotheses could be used to explain the effect of habitat fragmentation on species richness.

The influence of scale on the patterns and hypotheses in Table 3 is evident. Connell's (1978) well-known moderate disturbance hypothesis was developed based on local-scale observations of tropical forests and coral reefs, and it was admitted early on in the paper that large-scale variation (e.g., tropical to temperate gradients) would not be considered. Likewise, the habitat heterogeneity hypothesis, which grew out of observations that more diverse islands had more species (MacArthur and Wilson 1967), was developed based on local-scale observations (see Auerbach and Shmida 1987). In contrast, the numerous continental- to global-scale studies of species richness seem to converge on aspects of climate (i.e., available energy) as the driving mechanism (Simpson 1964, Kiester 1971, Schall and Pianka 1978, Wright 1983, Currie 1991) (Figure 1). Brown (1981) captures the importance of scale in his “capacity” and “allocation” rules. The maximum or potential species richness is constrained by energetics at large scales (capacity), while the number of species at

smaller scales is primarily determined by energy partitioning (allocation).

We divide spatial scales into local, regional, and continental domains. Putting bounds on these domains is somewhat arbitrary, but nevertheless helps to conceptualize the relative size of each. The upper limit of the local domain is about 10^4 km². Delaware is about 5000 km². The regional scale extends from the upper limit of the local domain to about 3×10^6 km². This is about equivalent to the size of the 11 western states (Washington to New Mexico and Montana to California). The continental (to global) scale would extend upward from the upper limit of the regional domain. The area of the continental United States is slightly less than 8 million km². Below we discuss the scales at which anthropogenic stressors are likely to operate for each example in Table 2 and for natural stressors and covariates as a group.

Habitat fragmentation. Based on previous studies, habitat fragmentation appears to impact species richness at local and regional scales. Lynch and Whigham (1984) examined the effects of forest fragmentation on breeding birds for a 5900-km², six-county area in Maryland. Studies on the effect of habitat fragmentation of chaparral species was restricted to coastal San Diego County (Bolger and others 1991, Soulé and others 1992). Studies of the effect of fragmentation on red squirrel (Verboom and van Apeldoorn 1990) and other small mammals (Bennett 1990) covered 150 km² and 105 km², respectively. Lauga and Joachim's (1992) study of forest fragmentation on breeding birds covered 2327 km². Lyon's (1979, 1983) study of the impact of road density on elk covered about 205 km², and a similar study by Thiel (1985) on the gray wolf covered about 13 counties in northern Wisconsin. Other studies suggest that habitat fragmentation is likely to have a regional impact on larger species (Holling 1992, Riitters and others 1997).

Pollution. Newman and others (1992) suggested that animal species diversity is affected by pollution at local and regional levels. Numerous toxic releases (e.g., oil spills) have caused local impoverishment of species. In contrast, region-wide pollution from acidic deposition has caused region-wide declines in aquatic diversity (Dickson 1986). In addition, pesticide use is region-wide. The contiguous states of Nebraska, Minnesota, Iowa, Illinois, Indiana, and Ohio are in the top ten in application of pesticides (Waddell and others 1988). The region-wide use of pesticides may be contributing to regional declines in the number of species.

Exotic species. Work on modeling the rate of spread of an invading organism provides some insight into scale characteristics of species introductions. Much of the work has been based on diffusion models (see Skellam

Table 3. Spatial patterns of species richness and related hypotheses

Description	Generality/evidence	Scale	References
Spatial patterns			
Latitudinal gradient: Species richness tends to decrease with increasing latitude from the equator to the poles, although the relationship is not monotonic for most taxonomic groups of organisms.	General for plants, animals and microbes; well documented	Continental and global scales	Fischer (1960), Simpson (1964), Cook (1969), Kiester (1971), MacArthur (1972), Currie (1991)
Elevation gradient: Species richness decreases with increasing elevation for most taxonomic groups of organisms.	Rather general for different taxonomic groups; fairly well documented	Local to regional scales	Yoda (1967), Glenn-Lewin (1977), Brown (1988), Ricklefs and Schluter (1993)
Aridity gradient: Species richness decreases with increasing aridity across a geographic region or a continent (e.g., from the deciduous forest, to forest steppe, to typical steppe, and to desert in the temperate Eurasian continent).	Relatively general for different taxonomic groups; better documented for plants	Regional to continental scales	Brown (1973), Glenn-Lewin (1977), Brown (1988), Ricklefs and Schluter (1993)
Species-area relationship: Species richness tends to increase monotonically with habitat area (e.g., $S = cA^z$ where S is species richness, A is area, and c and z are positive constants).	General for most taxonomic groups; well documented	Local to regional scales	Preston (1962), MacArthur and Wilson (1967), Auerbach & Shmida (1987), Currie (1991), Rosenzweig (1995)
Microenvironmental pattern: Species richness exhibits gradient-like changes or more complex patterns on local, small scales in response to variations in abiotic and biotic environments. The distribution of species richness is affected by biological processes (e.g., competition, predation) as well as physical environmental conditions (e.g., soil properties, topography) at local scales.	General, but patterns are diverse; well documented for plants in particular	Local scales	Schoener (1974, 1988), Wu (1992), Greig-Smith (1983), Shmida and Wilson (1985), Tilman (1982, 1993), Ricklefs and Schluter (1993), Rosenzweig (1995)
Hypotheses			
Time hypothesis: Species richness increases with time because longer time allows both colonization and speciation to operate which in turn result in more diverse biotas.	Relatively general; little direct evidence on evolutionary time scales, generally acceptable at local scales	Local to continental spatial scales; ecological and evolutionary time scales	Fischer (1960), Ricklefs and Schluter (1993), Rosenzweig (1995)
Origination-extinction dynamics hypothesis: Species richness is a result of the balance between species origination (colonization and speciation) and extinction, and, therefore, the patterns of species richness may be explained by the differences in these processes.	Relatively general; little direct evidence on continental and global scales or on evolutionary and geological time scales	Local to continental spatial scales; ecological and evolutionary time scales	MacArthur and Wilson (1967), Benton (1987), Brown (1988), Ricklefs and Schluter (1993), Rosenzweig (1995)
Available energy/productivity hypothesis: Species richness proliferates with increasing energy availability in the environment. At regional and continental scales, species richness is a function of available energy or primary productivity, whereas at local scales species richness may decrease with increasing productivity.	General; more consistent trends for different taxonomic groups at regional scales, but less evident at local scales	Local to continental scales; mostly ecological time scales	Wright (1983), Currie (1991), Hall and others (1992), Wright and others (1993), Rosenzweig (1995)
Habitat heterogeneity hypothesis: Species richness increases with habitat heterogeneity, which reflects the diversity and variability in the structure, function and dynamics of the environment organisms live in.	General; abundant evidence	Local to regional spatial scales; mostly ecological time scales	Cody (1974), Tilman (1982, 1993), Shmida and Wilson (1985), Ricklefs and Schluter (1993), Rosenzweig (1995)
Moderate disturbance/stress hypothesis: The highest species richness usually occurs where disturbance or stress is intermediate. Disturbance often creates structural and functional heterogeneity in time and space, and promotes the coexistence of species.	General; much empirical evidence from local communities to regional landscapes	Local to regional spatial scales; ecological time scales	Connell (1978), Loucks (1970), Suffling and others (1988), Ricklefs and Schluter (1993), Rosenzweig (1995)
Niche theory/species interaction hypothesis: Species richness in a biotic community is a function of the number of niches; interspecific interactions such as competition, predation, and mutualism, may promote species proliferation through modifying niche relations.	General; abundant empirical and theoretical studies, but relatively little direct evidence	Local spatial scales; ecological and evolutionary time scales	Schoener (1974, 1988), Connell (1978), Krebs (1985), Brown (1988), Ricklefs and Schluter (1993), Rosenzweig (1995)

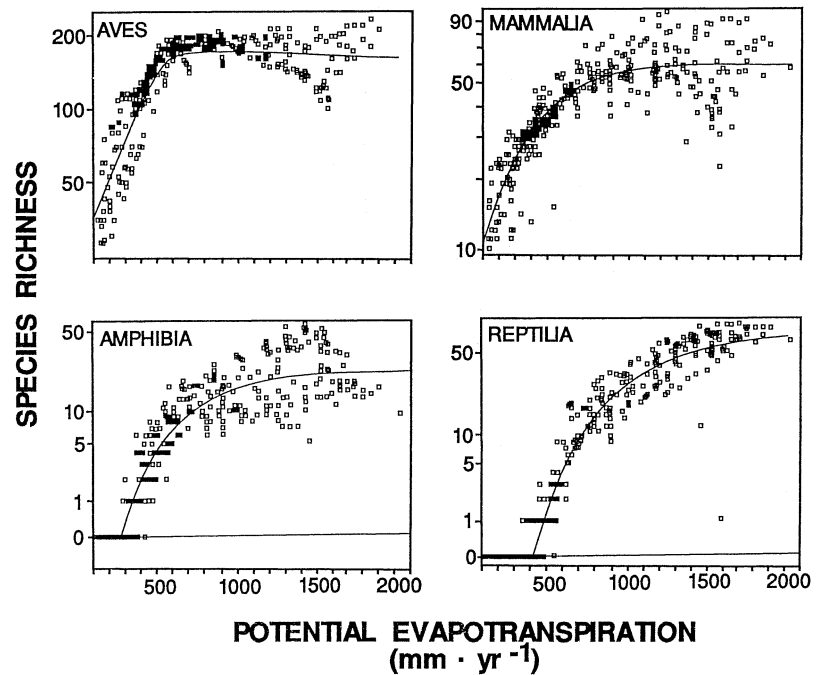


Figure 1. Species richness versus potential evapotranspiration. Model fits range from 0.80 to 0.93. Reproduced with permission from Currie (1991): *American Naturalist* 137(1):27–49, University of Chicago Press.

1951, Roughgarden 1986, Hengeveld 1989, Andow and others 1990). These models predict species spread by assuming biological movement to be similar to random Brownian motion.

The models seem to work well (see Andow and others 1990) when applied to species for which habitat and abiotic requirements do not have to be included (e.g., cabbage butterfly, muskrat). These cases seem to be the exception rather than the rule. Most introduced species do not become established, and several examples show the importance of habitat and the physical environment in restricting the spread of invaders (Hengeveld 1989). Lindroth (1957) observed that only a minority of European insects have invaded North America and few have spread from their liberation point. Mayr (1965) has observed the same pattern for birds. Melaleuca and Brazilian pepper, although widespread in south Florida, are restricted in their northward migration by cold temperature (Ewell 1986). Many of the escaped cage birds in southern US urban environments (e.g., Miami, Los Angeles) have not spread beyond urban boundaries because they require the planted, tropical ornamental trees for food and shelter (Orians 1986). Gray squirrels, introduced into California from the east, are successful only in urban environments where xeric conditions are overridden (Mooney and others 1986). The impact of exotic species on species richness appears to be restricted to local and regional scales, although exceptions do exist (e.g., cattle grazing, see later discussion).

Natural stressors and covariates. Natural stressors and covariates (e.g., aspects of weather, climate, and topog-

raphy) appear to operate from local to continental scales. Several studies have shown the influence of climate and topography on richness measures at continental scales (Schall and Pianka 1978, Wright 1983, Currie 1991, Wickham and others 1995b). Climate has also been shown to be correlated with species richness at regional scales (Pianka 1967, Owen 1990a,b). Glenn-Lewin (1977) cites several examples of changes in species diversity with elevation at local scales.

Criteria for Selection of Stressor Data Sets

Abramovitz and others (1990) published a guide to over 30 environmental data sets that are available through the federal government that could potentially be used to study species–stressor relationships. Time and expense limit their use in testing for correlation with patterns of species richness. Criteria must be established for selecting stressor and covariate data sets.

The first criterion is to select at least one data set from each of the categories identified in Table 3 (anthropogenic stressors, natural stressors, and natural covariates). Most of the studies cited here have examined species richness with regard to only one category (Wickham and others 1995a). To gain a more complete understanding of the relationship among stressors, covariates, and species richness requires data from each category. In addition, data sets within each category should be selected so that as many aspects of that category as possible are represented. For example, both roads and land cover might be needed to study the effect of fragmentation on species richness (see later discussion). Second, to study species–stressor relation-

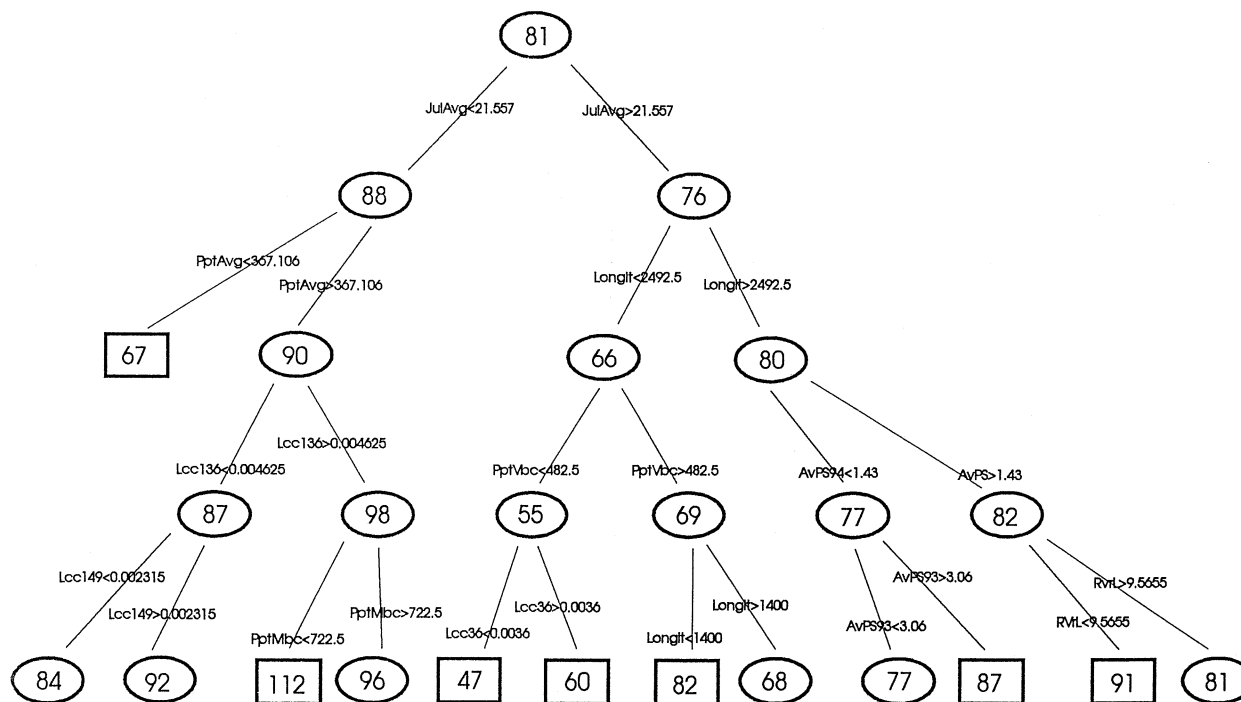


Figure 2. Regression-tree diagram. Squares and circles are groups of birds. Factors responsible for separation of groups (square and circles) are identified on the tree. Natural covariates (aspects of climate) are responsible for upper level splits. Stressors (those beginning with Lcc, AvPS, RvrL) appear in lower tier groups. Lcc is land cover category, RvrL is river length, and AvPS is average patch size. Numbers after AvPS and Lcc are land cover categories. Numbers associated with factors splitting groups are threshold values. (From R. J. O'Connor, University of Maine, unpublished draft.)

ships over an entire continent, the data sets selected should cover that continent or at least the stressor's anticipated region of influence. Third, an assessment of data quality is needed to determine if correlations (or lack thereof) are an artifact of poor data.

Methods for Studying Correlations Among Stressors and Species Richness

Methods are needed to detect the range of scales over which significant correlations exist among stressors, covariates, and species richness. Scaling-up and regression-tree analyses (Efron and Tibshirani 1991) are two possible approaches for determining scale-dependence. By scaling up, correlations between stressors and species richness, as well as among stressors, can be studied progressively. The division of the continental United States into square grids (see Simpson 1964, Kiester 1971, Schall and Pianka 1978, Currie 1991) provides an example for how scaling up might be conducted. A logical subset of grid cells (e.g., those covering southern Florida) would be used to examine species-stressor relationships. Once the relationship for the subset is uncovered, additional grid cells would be added and the analyses conducted again. A pattern of

increasing correlation with increasing geographic extent (more grid cells) followed by a drop in correlation may indicate the scale at which that stressor influences species richness pattern. Wickham and others (1995b) used a modification of this approach to show a scale-dependent correlation between vegetation richness and elevation range for the continental United States. Other techniques are described by O'Neill and others (1991) and Turner and others (1991).

Using regression-tree analysis, all stressor and covariate data would be analyzed simultaneously for the entire study area (e.g., continental United States). This technique recursively groups a dependent variable (e.g., species richness) into subsets based on the amount of variance explained by the independent variables. The output is commonly represented as a tree showing the recursive splits of the dependent variable and the independent variables responsible for the categories. Figure 2 shows an example of a regression tree where several data sets were examined to explain the spatial variability of breeding bird richness across the conterminous United States (O'Connor unpublished data). Aspects of climate are responsible for the higher-level splits, whereas stressor data appear further down in the

Table 4. Proposed stressor data base for studying patterns of species richness

Stressor categories	Data sets
Anthropogenic	
Habitat fragmentation	land cover roads (USGS, DLGs) wetland loss (SCS soils, land cover)
Pollution	Census of Agriculture, pesticides National Pesticide Survey (EPA) NASQAN & water reports (USGS)
Exotic species	Heritage data (TNC) Census of Agriculture, grazing HCN (NOAA)
Natural stressors	
Natural covariates	
Topography	DEMs (USGS)
Climate	HCN (NOAA)
Streams	DLGs (USGS)

tree. These results suggest that stressors are operating at finer spatial scales than natural covariates.

Proposed Stressor Data Base for Studying Patterns of Species Richness

Table 4 is a proposed list of data sets that would serve as a minimum data base to study stressor–species richness relationships over large spatial scales. Each is discussed briefly.

Land Cover

Land cover data are the primary source for generating metrics of habitat fragmentation. Landscape ecology (Forman and Godron 1986, O'Neill and others 1994) provides both a conceptual basis and a practical framework for generating these metrics. Land cover data are available from several sources, at several scales, and in several formats.

Roads

Roads are a second data set needed to capture aspects of habitat fragmentation, because land cover data do not typically include roads unless they are of sufficient width (e.g., interstate highways). Several studies have shown that roads have fragmented habitats for larger animals (Storm and others 1967, Lyon 1979, 1983, Thiel 1985). These findings illustrate that for a given species, habitats (e.g., forests) that seem suitable based on interpretation of land cover data alone might actually not be suitable because of the existing road network. Density estimates from US Geological Survey

(USGS) 1:100,00-scale road data appear to be accurate (Wickham and Wade unpublished data).

Wetland and Wetland Loss

Like roads, wetlands are not typically found in land cover data (see Dottavio and Dottavio 1984), and there is increasing recognition that wetland and riparian habitats support greater numbers of species than surrounding uplands (Kauffman and Krueger 1984, Gregory and others 1990, Williams 1991, Finch 1992, Mitsch and Gosselink 1993, Naiman and others 1993). Eighty percent of the United States' breeding bird populations rely on wetlands (Wharton and others 1982). Wetland and riparian habitats also support a disproportionately greater number of the endangered and threatened species in the United States (Mitsch and Gosselink 1993).

To determine wetland/riparian habitat extent and loss requires National Wetlands Inventory (NWI), land cover, streams, and soils data. Present wetland extent can be acquired from NWI data, which has been successfully incorporated into satellite-based land cover maps using geographic information systems (GIS) (Vogelmann personal communication). A combination of land cover, streams, and soils data (in a GIS) can be used to determine where wetlands have possibly been lost by examining where anthropogenic land cover occurs on wetland soils. Soils data are available on a state-by-state basis from the US Department of Agriculture, Soil Conservation Service (USDA 1987).

Pollution

Pesticide application and acidification of surface waters appear to be the most widespread pollution problems that have impacted patterns of species richness. There are approximately 50,000 different chemical compounds that are used as pesticides (Waddell and others 1988) out of approximately 63,000 chemical compounds that are commonly used by industry worldwide (Moriarty 1983). Schindler and others (1989) have modeled the potential loss of taxonomic groups of fish, based on their documented sensitivity to pH values less than 5.0. Fish kills have been reported at pH values of 5.0, apparently because of increased aluminum toxicity (Moriarty 1983).

Pesticide application estimates are available through the US Department of Census, Census of Agriculture, reported on a per county basis. Lake and stream pH values can be acquired from the US Geological Survey State Water Reports.

Introduced and Exotic Species

The primary source of information on introduced and exotic species is The Nature Conservancy's (TNC) Heritage Database. These data identify geographic ranges for each species and its origin. Origin is identified as either native, introduced, reintroduced, or unknown.

Data on livestock grazing is also included under introduced and exotic species because herbivory by large ungulates in the Intermountain West (not Great Plains) was not an ecosystem component prior to their introduction by man (Mack and Thompson 1982). Livestock grazing is one of the most extensive land uses in the western United States, and grazing is expected to increase into the next century (NRC 1982). Potential impacts of livestock grazing include changing competitive relationships, disease transmission, accelerated erosion, destruction or alteration of riparian and upland communities, and decreased primary productivity available to native animals (Kauffman and Krueger 1984, Cooperrider 1990). Livestock abundance by county is available from the US Department of Commerce, Census of Agriculture (USDA 1989).

Natural Stressors and Covariates

Data representing natural stressors and covariates include climate, topography, streams, and wetlands. The National Oceanic and Atmospheric Administration's Historical Climatology Network (HCN) contains over 1200 stations of serially complete monthly temperature and precipitation, and "probably represents the best monthly . . . data set for the contiguous United States" (Karl and others 1990). Averages can be calculated from 65 or more years of data. These data could be used to calculate departures from long-term normals, which would represent a natural stressor. Likewise, the long-term normals can be used to represent climatic natural covariates. Topography has been the primary source of data to test the hypotheses of habitat heterogeneity, elevation, and even aridity as mechanisms contributing to spatial patterns of species richness (Glenn-Lewin 1977, Owen 1990a,b, Whittaker 1965). Topographic data (digital elevation model, DEM) are available from the USGS at scales ranging from 1:24,000 to 1:2,000,000. Comparison of spot elevations from these data with their corresponding topographic maps indicates that the data are accurate. Stream distribution would also be a natural covariate, since measures such as the number of streams represent a characteristic of the natural environment. USGS digital stream data at the 1:2,000,000 scale do not appear to be missing streams or include ones that are not there (Wickham and Wade unpublished data), but comparison of stream

densities from 1:100,000-scale data suggests some compilation error (Wickham and Norton 1994). Data on fire and pest infestations, while collected in the United States, is not available in a format that would permit quantification (Wickham and others 1995a).

Summary and Conclusions

A central tenet of hierarchy theory (O'Neill 1995) is that patterns change with scale, which suggests that explanations should also change with scale (Levin 1991, Wu and Loucks 1995). Past studies suggest that continental and global patterns of species richness are most strongly correlated with aspects of climate (Wright 1983, Currie 1991). Anthropogenic and natural stressors most likely invoke the hypotheses of disturbance and habitat heterogeneity as mechanisms for explaining spatial patterns of species richness. These mechanisms appear to operate mostly on local and regional scales.

A framework has been proposed for studying the relationships among stressors, covariates, and patterns of species richness. The framework includes: (1) clarification of the terms stress and stressor and categorization of factors affecting species richness into three groups—anthropogenic stressors, natural stressors, and natural covariates; (2) evidence that anthropogenic and natural stressors most likely operate at local and regional scales, while natural stressors and covariates operate at local, regional, and continental to global scales; (3) criteria for selection of data sets from stressor and covariate categories; and (4) descriptions of scaling-up and regression-tree analyses for examining scale-dependent effects of stressors and covariates on geographic patterns of species richness.

This framework was used to propose ten data sets as a minimum data base for examination of their scale-dependent effects on species richness. These data sets include land cover, roads, wetlands (numbers and loss), exotic species, grazing, surface water pH, pesticide application, climate (and weather), topography, and streams.

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