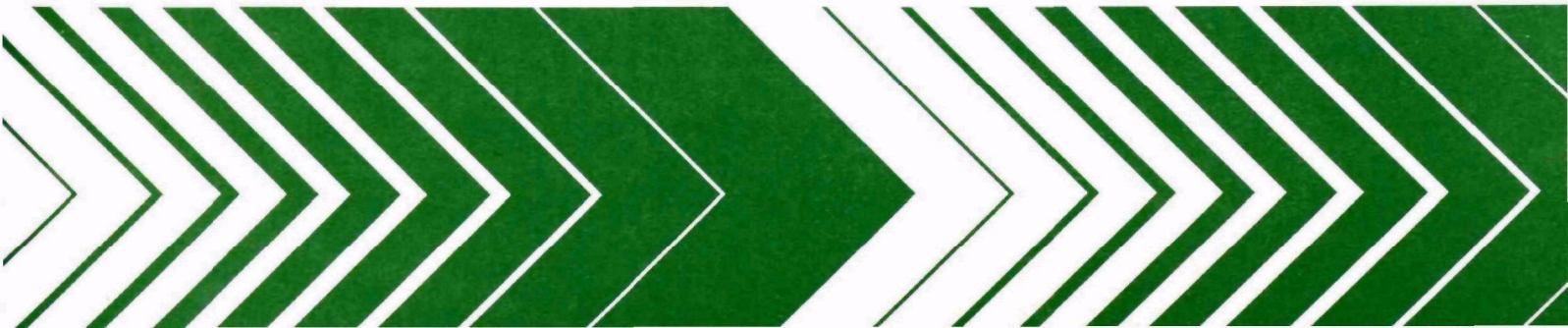




# **Stressor Data Sets for Studying Species Diversity at Large Spatial Scales**



# Stressor Data Sets for Studying Species Diversity at Large Spatial Scales

by

James D. Wickham  
Jianguo Wu  
Desert Research Institute  
Reno, NV

and

David F. Bradford  
Environmental Monitoring Systems Laboratory  
U.S. Environmental Protection Agency  
Las Vegas, NV

Environmental Monitoring Systems Laboratory  
Office of Research and Development  
U.S. Environmental Protection Agency  
Las Vegas, NV 89193-3478



## NOTICE

The U. S. Environmental Protection Agency, through its Office of Research and Development (ORD), funded the extramural research described here under Cooperative Agreement CR-816385-01-0 with the Desert Research Institute. The research undertaken for this report was conducted in collaboration with partners in the Biodiversity Research Consortium, which is comprised of the U.S. EPA, U.S. Forest Service, U.S. Geological Survey, U.S. Fish and Wildlife Service, and The Nature Conservancy. It has been reviewed by the Agency and approved as an EPA publication. Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

## CONTENTS

	Page
NOTICE .....	ii
EXECUTIVE SUMMARY .....	v
ACKNOWLEDGEMENTS .....	vi
1.0 INTRODUCTION .....	1
1.1 Overview of the Biodiversity Research Consortium (BRC) .....	1
1.2 Objectives of the Report .....	3
1.3 Definitions of Stress and Stressors .....	3
2.0 PATTERNS AND HYPOTHESES OF SPECIES RICHNESS .....	5
2.1 Distributional Patterns of Species Richness .....	5
2.2 Hypotheses Explaining Distributional Patterns of Species Richness .....	7
3.0 FRAMEWORK FOR IDENTIFYING AND EVALUATING POTENTIAL STRESSORS ...	12
3.1 Stressor Categories .....	12
3.2 Scales at Which Stressors Operate .....	12
3.3 Criteria for Selecting Stressor Data Sets .....	14
3.4 A Consideration in Studying the Correlation Between Stressors and Species Richness .....	14
4.0 EXISTING DATA FOR IDENTIFYING STRESSORS .....	16
4.1 Habitat Fragmentation Data .....	16
4.1.1 Land Cover .....	16
4.1.2 Digital Line Graphs (Roads) .....	18
4.1.3 Wetland and Riparian Habitat Loss .....	19
4.1.4 Census Data .....	20
4.2 Pollution Data .....	21
4.3 Exotic Species Data .....	21
4.4 Data Sets for Non-Anthropogenic Factors .....	24
4.4.1 Historical Climatology Network (HCN) .....	24
4.4.2 USGS Digital Elevation Model (DEM) .....	25
4.4.3 Federal Insect and Disease Conditions and Wildland Fire Statistics .....	25
5.0 DISCUSSION AND SUMMARY .....	26
5.1 Importance of Scale .....	26
5.2 Proposed Data Sets and Considerations in Examining Stressor-Species Relationships .....	26
6.0 LIST OF ABBREVIATIONS .....	28
7.0 REFERENCES .....	29

## FIGURES

	Page
Figure 1: BRC Hexagonal Sampling Units . . . . .	2
Figure 2: Species Richness Versus Latitude . . . . .	6
Figure 3: Species Richness Versus PET . . . . .	9
Figure 4: Proposed Spatial Scales at which Species Richness Patterns Are Evident (A) and Associated Hypotheses (B) . . . . .	11

## TABLES

	Page
Table 1: Definitions of Stress . . . . .	4
Table 2: Data for Land Use and Habitat Fragmentation . . . . .	17
Table 3: Population Change (1980 to 1990) for Selected High Growth Counties in Pennsylvania and Oregon . . . . .	20
Table 4: Pollution Data Sets . . . . .	22
Table 5: Data Sets for Exotic Species, Including Managed Livestock and Grazing Practices . . . . .	23
Table 6: Data Sets for Non-Anthropogenic Factors . . . . .	25
Table 7: Data Proposed for Examination of Stressors-Species Relationships . . . . .	27

## EXECUTIVE SUMMARY

There is increasing scientific and societal concern over the impact of anthropogenic activities (e.g., habitat destruction, pollution) on biodiversity. The impact of anthropogenic activities on biodiversity is generally recognized as a global phenomenon. At large spatial scales, several studies have shown geographic patterns in species diversity, and these patterns have been most strongly linked to aspects of climate and topography, not anthropogenic activities. What is known about the impact of anthropogenic activities on species diversity (and loss) is mostly from studies at much smaller spatial scales (e.g., up to a few U.S. counties). This gap in knowledge poses a challenge to the study of the influence of stressors on species diversity patterns at large spatial scales (e.g., regions and continents). Based on the literature, stress is defined as the response of a system to a disturbance, and stressor is the disturbance. The purpose of this report is to review what is currently known about factors that influence distributional patterns of species richness, and to identify the appropriate stressor data sets to evaluate the influence of stressors on patterns of species richness at large spatial scales. This research is being done for the interagency Biodiversity Research Consortium (BRC), which has been formed to study species diversity patterns at large spatial scales.

Spatial patterns of species richness are found across a range of spatial scales. These include latitudinal gradients, elevation gradients, aridity gradients, species-area relationships, and more complex microenvironmental patterns. Several hypotheses of mechanisms controlling species richness patterns are summarized here, including (1) time, (2) origination-extinction dynamics, (3) available energy/productivity (4) habitat heterogeneity, (5) disturbance, and (6) niche theory/species interaction. Particular patterns of species diversity usually occur over a range of spatial scales. Therefore, different patterns and mechanisms should be expected on disparate scales. Based on this scale distinction, we have organized the hypotheses according to scales at which they are likely to operate. Time, origination-extinction dynamics, and available energy/productivity are likely to operate over the entire range of spatial scales from local to global. Habitat heterogeneity and disturbance operate predominantly at local to regional scales. Niche theory/species interaction operates primarily at local scales.

Anthropogenic stressors are most relevant to the habitat heterogeneity and disturbance hypotheses. Stressors (both anthropogenic and non-anthropogenic) are likely to predominate at local and regional scales. In addition, it is proposed that stressors can be separated into four basic categories: habitat fragmentation, pollution, exotic species, and non-anthropogenic factors. Inclusion of data representing each of these categories is necessary to gain a more complete understanding of the relationship between stressors and species diversity. For instance, several studies have shown that habitat fragmentation can lead to species extirpation, but none of these studies has included other stressor data (e.g., drought, extreme temperatures, pollution) to determine the relative contribution of each in explaining species diversity patterns. For each category, two data sets are proposed for evaluation of the influence of stressors on species richness for the conterminous U.S. For habitat fragmentation, road density and wetland loss are proposed. Other metrics of habitat fragmentation, such as patch size, are being developed elsewhere within the BRC. For pollution, data on tissue concentration in selected species are proposed, as well as stream and lake pH measurements. For exotic species, data from The Nature Conservancy's (TNC) Heritage Data Base are proposed. Data on livestock grazing intensity are also recommended. For non-anthropogenic factors, climate data are proposed for the development of departures from averages. Use of topographic data are also proposed. Topography does not represent a stressor per se, but information on it is needed to establish baseline conditions.

## **ACKNOWLEDGEMENTS**

Earlier drafts of this report benefitted from the comments of Drs. Dennis Jelinski of University of Nebraska (Lincoln, Nebraska), Orié Loucks of Miami University (Oxford, Ohio), and Raymond O'Connor of University of Maine (Orono, Maine), and discussions with Drs. Ross Kiester, Raymond O'Connor, Eric Preston, and Denis White. Timothy Wade provided GIS support and valuable advice on many technical points.

Linda Piehl provided administrative support.

## 1.0 INTRODUCTION

### 1.1 OVERVIEW OF THE BIODIVERSITY RESEARCH CONSORTIUM (BRC)

The U.S. Environmental Protection Agency's (USEPA) Science Advisory Board (SAB) has identified habitat and species loss as serious ecological problems in the United States (USEPA 1990). In response to the SAB's finding, the USEPA formed the Biodiversity Research Consortium (BRC) in 1993 in cooperation with several federal and non-governmental agencies, including the U.S. Fish and Wildlife Service (USFWS), the U.S. Forest Service (USFS), the U.S. Geological Survey (USGS), and The Nature Conservancy (TNC). BRC has four primary objectives (*sensu* Kiester et al. 1993):

- 1) To analyze biodiversity nationwide;
- 2) To search for correlations between species diversity, environmental diversity, and stressor information;
- 3) To evaluate the comparative risk to biodiversity using species diversity, environmental diversity, and stressor information; and
- 4) To begin developing approaches to managing environmental diversity in order to achieve species diversity goals.

To accomplish these objectives, BRC will compile species occurrence using TNC's heritage data base and other sources, and use USEPA's hexagonal grid, originally developed for the Environmental Monitoring and Assessment Program (EMAP), as the basis for data collection and analysis (Kiester et al. 1993). The EMAP grid is made up of 640 km<sup>2</sup> hexagons that completely cover the conterminous United States (Figure 1). Vertebrate species richness will be used as the measure of biodiversity by the BRC. A generally accepted definition of biodiversity (Noss 1990) is "the variety and variability of life and the ecological complexes in which they occur" (U.S. Congress Office of Technology Assessment (OTA) 1987). Species richness is a measure of the variety of different organisms.

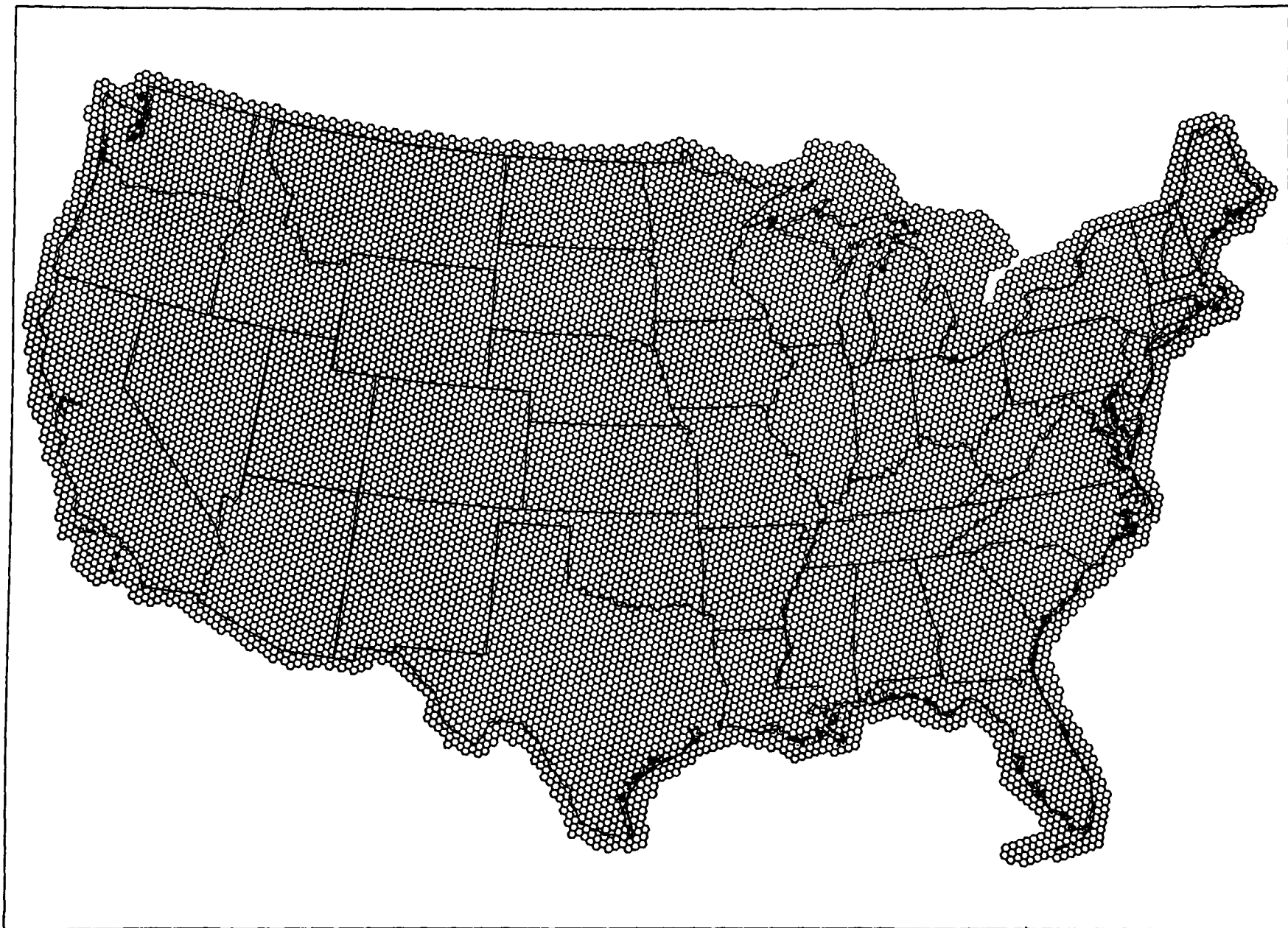
Species diversity includes both the variety and variability of different organisms. Species, environmental, and stressor data will be compiled for each hexagon and analyzed using multivariate statistical techniques to meet objectives 1, 2, and 3. The results of the multivariate analyses will be used to address the fourth objective.

BRC's focus on nationwide patterns of biodiversity is based partly on previous work that has shown the existence of continental scale patterns of species richness (Simpson 1964, Kiester 1971, Currie 1991). These studies highlighted patterns that are not observable at smaller spatial scales (Kiester et al. 1993). The national level focus also helps to link the first three analysis-based objectives with the fourth, management-oriented objective.

BRC is organized into four functional groups: species, landscape, stressors, and analysis. The species team is responsible for compiling the species data for each hexagon. The landscape team is responsible for development of environmental diversity measures from remotely sensed data. Many of these metrics will come from studies of landscape pattern and dynamics (O'Neill et al. 1988, Turner et al. 1991). AVHRR satellite data will be used at the outset to derive these measures. The stressors team is responsible for the development of measures, outside those developed by the landscape team, which are likely to influence geographic patterns of species richness. Once completed, the three teams will provide their data to the analysis team, who will conduct the multivariate analyses using species, landscape, and stressor data.

This report reviews what is currently known about the relationships between stressors and species diversity. Information on the relationship between stressors and species diversity patterns is important to achieving BRC's objectives 2 and 3. BRC has initiated pilot studies in Pennsylvania and Oregon to evaluate data quality and test proposed methods. The results of the pilot studies will be used to guide the national effort. Where possible, examples will make reference to Pennsylvania and Oregon.





**Figure 1: BRC Hexagonal Sampling Units**

## 1.2 OBJECTIVES OF THE REPORT

The objectives of this report are four-fold. The first is to review the extensive body of literature on anthropogenic and natural factors that influence geographic patterns of species richness. A review and synthesis of this literature provides a starting point to develop a framework for selecting stressor data sets. The second is to develop a comprehensive framework for the selection of appropriate stressor data sets. The third objective is to survey and select existing stressor data, based on the framework developed. The fourth objective is to examine, to the degree possible, the quality of the data. Since the analyses proposed by BRC are correlative, information on data quality is critically important.

Error propagation is an important component of data quality analysis. Error propagation, in regard to stressor data sets and BRC, is the impact of error in collection and compilation of data on measurements derived from the data and, subsequently, on interpretation of results showing relationships between stressors and species diversity. However, error propagation is an empirical phenomenon that must be investigated on a case by case basis, since the collection methods are different for each data set. The impact of error in any given data set on derived measurements and interpretation of results is more appropriately addressed during data analysis. Discussion of data quality will not extend to error propagation in this report.

## 1.3 DEFINITIONS OF STRESS AND STRESSORS

One of the goals of BRC is to evaluate the comparative risk to biodiversity using species diversity, environmental diversity, and stressor information (*sensu* Kiester et al. 1993). Unfortunately, the term stress has not been used consistently in the ecological literature (Rykiel 1985). For example, stress has been defined as a prevailing, unfavorable condition to which organisms respond (e.g., Larcher 1980), or the response of an organism to prevailing environmental conditions, either favorable or unfavorable (e.g., Odum et al. 1979, Barrett

1981, Rykiel 1985). A list of definitions by different authors is given in Table 1.

The definitions by Odum et al. (1979), Barrett (1981), and Rykiel (1985) are consistent in that each defines stress as an effect, not a prevailing condition (e.g., Larcher 1980). For example, stress is the effect of a disturbance (e.g., pollution, fragmentation) on a biological entity or process, not disturbance itself. The definition of stress as an effect is most appropriate for BRC because of its goal to evaluate comparative risk to biodiversity. USEPA defined risk assessment as the evaluation of the likelihood of adverse ecological effects as a result of exposure to stressors (Norton et al. 1992). In the context of BRC, stress may manifest itself as a change in species richness.

The definition of stress by Barrett (1981) is the most clear and explicitly uses the term stressor. Barrett (1981) defined stressor as the agent (e.g., prolonged drought) which causes a physical or functional effect. Barrett's (1981) definition is also valuable because it (1) distinguishes anthropogenic from natural stressors and (2) identified natural factors as stressors only when applied at excessive levels (e.g., prolonged drought). Rykiel's (1985) definition of disturbance - a physical force, agent, or process, either abiotic or biotic, causing a stress in an ecological component or system - is consistent with Barrett's (1981) definition of stressor. For BRC, stressors are quantitative measures of disturbance which can be used to explain geographic patterns in species richness.

Odum et al. (1979) distinguished stress as having only negative effects and reserves the term "subsidy" to connote positive effects. We do not necessarily recommend making a distinction between stress and subsidy, and stress will be used herein to include both positive and negative effects. The reason is not to introduce additional terminology.

The definitions of stress by Odum et al. (1979), Barrett (1981), and Rykiel (1985) all indicate that stress must be measured against a reference condition. An example of using a reference condition is that species and stressor data are measured over time so that changes in

the species and stressors data can be used to determine the impact of stressors on species richness. Although this method seems valid and feasible, it requires time series data. An alternative (or complimentary) approach is to use natural spatial patterns of species richness that are found in relatively undisturbed environments or predicted by validated theories as reference

conditions. When appreciable differences in species distributional patterns in similar environments and at similar scales are detected, stressor data may be used to evaluate the effect of disturbances on species richness. This is essentially a space-for-time method, which has long been used in ecological studies (see Pickett 1989).

**Table 1: Definitions of Stress**

<b>Author</b>	<b>Definition</b>
Larcher (1980)	Stress: 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 et al. (1979)	Stress: deviation from nominal; unfavorable deflections.
Barrett (1981)	Stress: 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)	Stress: 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.

## 2.0 PATTERNS AND HYPOTHESES OF SPECIES RICHNESS

The study of the distributional patterns of species richness is an important step to understanding the relationship between biological diversity and underlying ecological factors and processes. This relationship is fundamental to conservation biology in general and the identification of stressors in particular. The distributional patterns of species richness found in natural or semi-natural ecological systems on different scales may serve as one kind of baseline condition, against which changes in species richness can be detected in relation to anthropogenic stressors. In this section, we shall discuss several major geographic patterns of species richness and hypotheses of mechanisms, which serves as a conceptual basis for later sections.

### 2.1 DISTRIBUTIONAL PATTERNS OF SPECIES RICHNESS

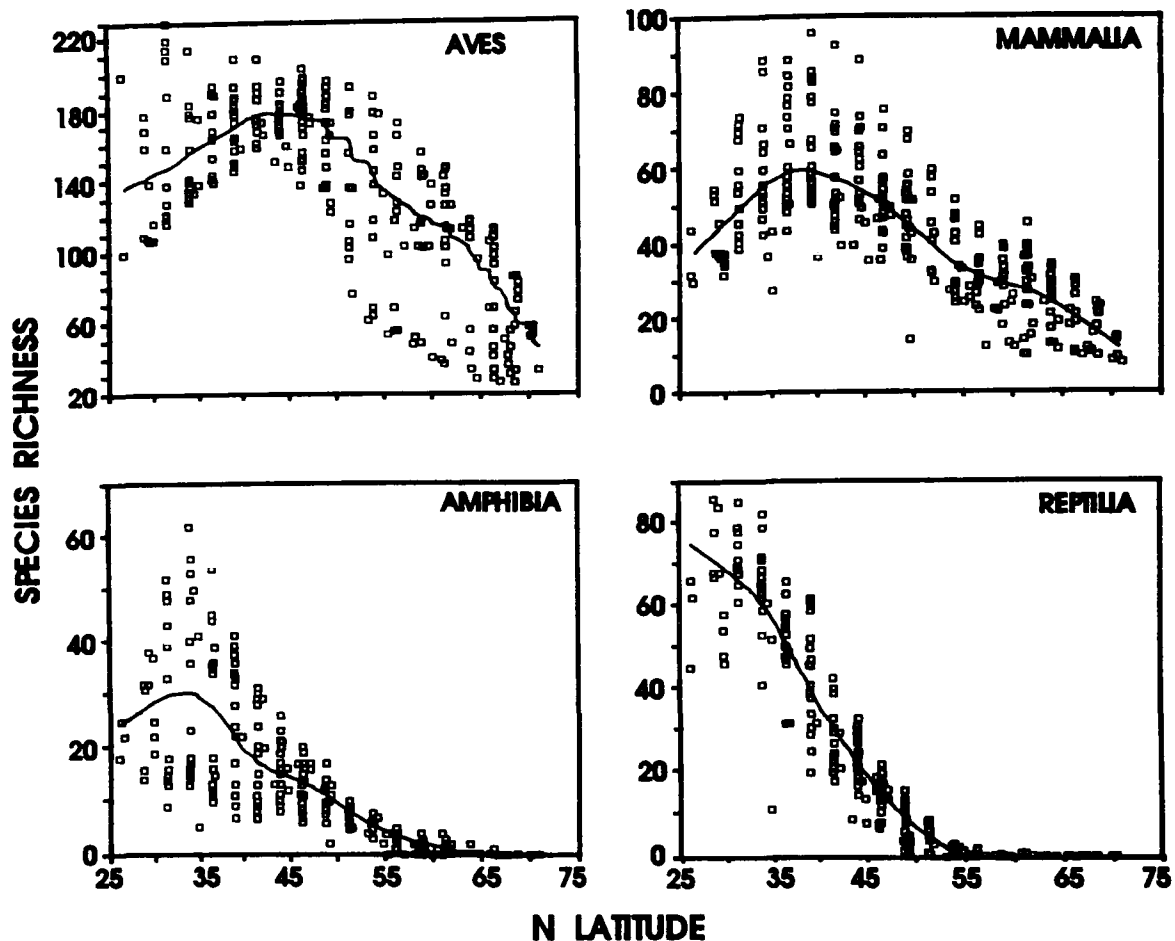
The pattern of species richness distribution in time and space has been a major theme in both ecology and biogeography for several decades (e.g., Pianka 1966, MacArthur 1965, MacArthur and Wilson 1967, Loucks 1970, Brown and Gibson 1983, Begon et al. 1986, Hall et al. 1992, Currie 1991, Wu and Vankat 1991, 1994, Tilman and Pacala 1993). Several geographical patterns have been documented across a range of spatial scales. For terrestrial systems, the patterns include gradual, sometimes monotonic, changes in species richness along physical environmental gradients (e.g., latitude, elevation) on large scales, as well as more complex patterns that are determined by both local physical factors and biotic interactions on smaller scales. There have been several recent reviews of the patterns of species richness for plants, animals, and microbial organisms (e.g., Krebs 1985, Begon et al. 1986, Brown 1988, Ricklefs and Schluter 1993, Orians 1994). Here, we compile a list of the major spatial patterns of species richness with related hypotheses pertinent to explaining the patterns (cf. MacArthur 1965, Pianka 1966, MacArthur and Wilson 1967, Brown and Gibson 1983, Brown 1988, Orians 1994, Wu and Vankat 1994).

**Latitudinal gradient.** Species richness tends to decrease with increasing latitude from the equator to the poles, though the relationship is not monotonic for most taxonomic groups of organisms (Figure 2). This pattern appears equally general for plants, animals, and microbes, and has been well documented in the literature (e.g., Fischer 1960, Simpson 1964, Cook 1969, Kiester 1971, MacArthur 1972, Currie 1991).

**Elevation gradient.** Species richness decreases with increasing elevation for most organisms. The elevation gradient of species richness is also rather general, and has been fairly well documented (Yoda 1967, Glenn-Lewin 1977, Brown 1988).

**Aridity gradient.** Species richness decreases with increasing aridity across a geographic region or a continent. A striking example is in the temperate Eurasian continent where the number of plant species declines dramatically as one moves westward, across the north-south oriented vegetation zones, from the deciduous forest, to forest steppe, to typical steppe, and to desert. An aridity gradient often interacts with other gradients like elevation, which complicates the species richness patterns and their interpretation (Brown 1973, Whittaker and Niering 1965, Glenn-Lewin 1977, Brown 1988).

**Species-Area relationship.** Species richness tends to increase monotonically with habitat area. A widely cited mathematical expression is of the form:  $S = cA^z$ , or,  $\log S = z \log A + \log c$ , where  $S$  is species richness,  $A$  is area, and  $c$  and  $z$  are positive constants.  $c$  usually reflects the effect of geographical variation on species richness, and  $z$  usually varies between 0.18 and 0.35. This relationship has long been found in numerous studies of terrestrial community ecology and island biogeography (e.g., Preston 1962, MacArthur and Wilson 1967, Williamson 1988, Wu 1989). The spatial scales on which this relationship is most likely to hold are from local communities (e.g.,  $10 - 10^5$  unit area) to landscapes ( $10^4 - 10^9$  unit area) (Auerbach and



**Figure 2: Species richness versus latitude.** Reproduced with permission from Currie (1991), *American Naturalist*, 137(1):27-49, University of Chicago Press.

and Shmida 1987). The effect of area on species richness seems to disappear at larger spatial scales, such as continents (see Currie 1991).

**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. Numerous studies have demonstrated the importance of biological processes (e.g., competition, predation, mutualism) on species

richness through mechanisms such as niche differentiation and competitive exclusion (e.g., Schoener 1974, 1988, Shmida and Wilson 1985, Auerbach and Shmida 1987, Tilman 1993). Spatial patterns of species richness correlated with local-scale physical environmental conditions (e.g., soil properties, micrometeorological conditions) have been well documented for plant species (e.g., Goodall 1970, Tilman 1982, Greig-Smith 1983, Wu 1992), but much less for animals and microbes.

## 2.2 Hypotheses Explaining Distributional Patterns of Species Richness

Several hypotheses that invoke various mechanisms have been proposed to explain the observed spatial patterns of species richness on different scales (see Pianka 1966, Loucks 1970, Brown and Gibson 1983, Krebs 1985, Brown 1988, Currie 1991). These include time, origination-extinction dynamics, available energy/productivity, habitat heterogeneity, disturbance, and niche theory/species interaction. In the following sections, we shall summarize these hypotheses by providing a concise description of their essential elements with a few relevant references. Then, a synthesis will be given based on a hierarchical and scale perspective.

**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. This hypothesis has been applied on both ecological ( $10^2$  years) and evolutionary ( $10^6$  years) time scales. Time was first proposed as a hypothesis to explain the decrease in species richness with increasing latitude, in which tropical areas were thought to have more time to diversify because of the absence of the glaciation that took place at temperate latitudes (e.g., Fischer 1960). However, there is little direct evidence available, and it is extremely difficult to test the hypothesis for evolutionary or geological time scales. At local spatio-temporal scales, it seems generally acceptable that the longer the time since last disturbance, the more species are likely to colonize (Pickett and White 1985, Pickett et al. 1987).

**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. This hypothesis also involves both ecological and evolutionary time-scales, and has been used to explain species richness patterns from the local community to the continental and global levels

(MacArthur and Wilson 1967, Pielou 1979, Benton 1987, Brown 1988). On ecological time scales, the theory of island biogeography (Munroe 1948, 1953, MacArthur and Wilson 1967) asserts that the number of species in insular habitats is determined primarily by colonization and extinction rates which in turn are affected by habitat area and distance to the colonizing source. While the theory has been criticized on several grounds (Wu and Vankat 1994), there have been many studies of oceanic and terrestrial habitat islands supporting the basic idea of colonization-extinction dynamics (e.g., Pickett and Thompson 1978, Burgess and Sharpe 1981, Harris 1984, Wu 1989). There has been little direct evidence, however, for the applicability of this hypothesis at continental and global scales or on evolutionary and geological times (Benton 1987, Brown 1988).

**Available energy/productivity hypothesis.** Species richness proliferates with increasing energy availability in the environment. At regional ( $10^8$  -  $10^{13}$  m<sup>2</sup> cf. Auerbach and Shmida 1987) and continental scales, it has been shown that species richness is a function of available energy or primary productivity (Wright 1983, Currie 1991, Hall et al. 1992). Based on the species-area relationship and the equilibrium theory of island biogeography, Wright (1983) developed a "species-energy theory." The core of the theory is represented by the mathematical formulation,  $S = kE^z$ , where  $S$  is the species richness,  $E$  is the total production of available energy, and  $k$  and  $z$  are constants. Wright (1983) found that available energy, measured as total actual evapotranspiration (AET) for angiosperms and total net primary production (NPP) for breeding land and freshwater birds, was able to account for 70-80% of the variation in species richness on islands ranging from Greenland and Spitsbergen to New Guinea and Jamaica. Currie (1991) demonstrated that, for the four vertebrate classes in North America he studied (birds, mammals, amphibians, and reptiles), annual potential evapotranspiration (PET) alone accounted for 80-90% of the variability in species richness (Figure 3). At smaller scales, on the other hand, empirical studies (especially in plant community ecology)

have shown that species richness decreases with increasing community productivity (e.g., Whiteside and Harmsworth 1967, Rosenzweig 1968, Tilman 1982, 1993). Therefore, the interpretation of, and mechanisms involved in this hypothesis is scale-dependent.

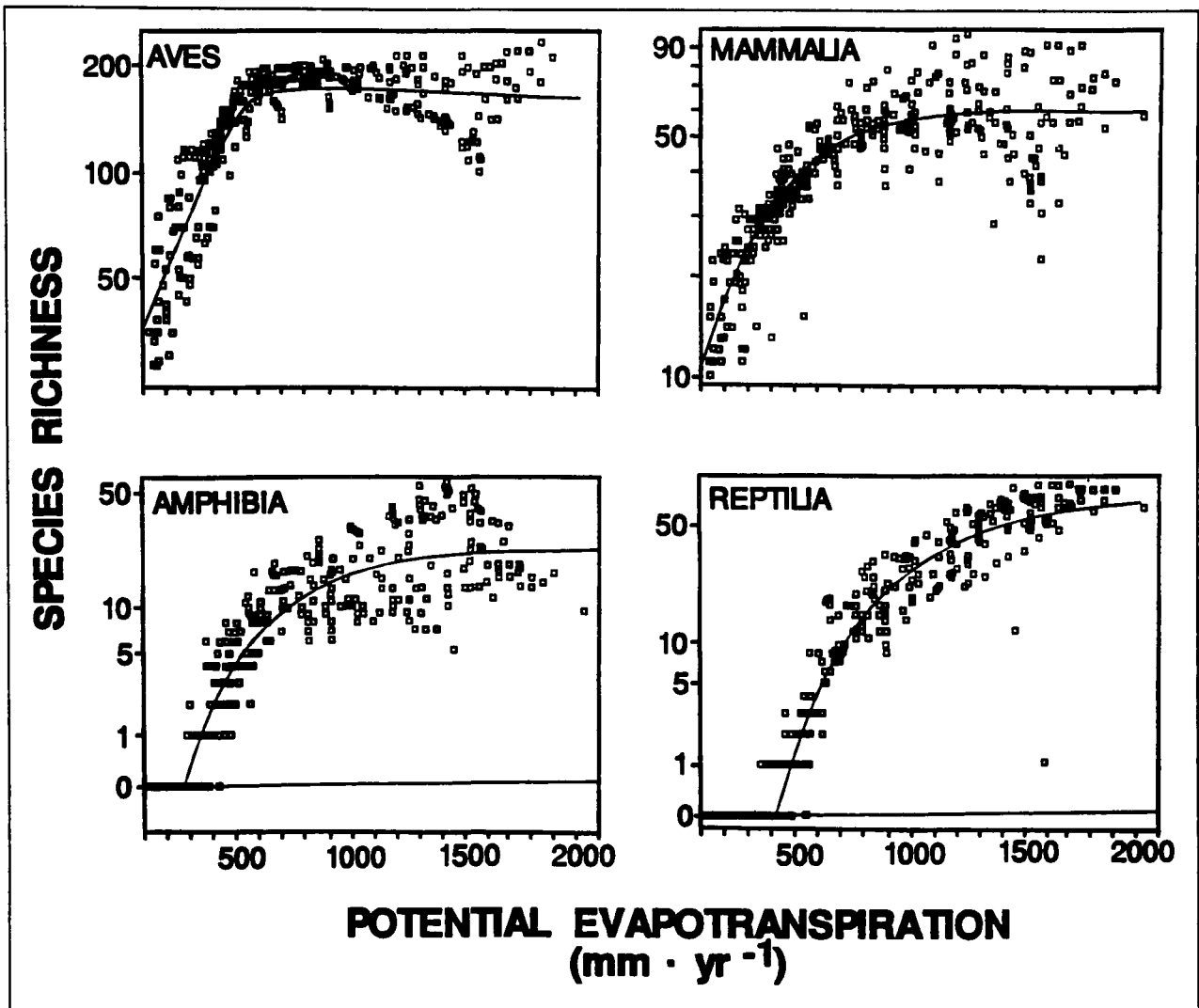
**Habitat heterogeneity hypothesis.** Species richness increases with habitat heterogeneity which reflects the diversity and variability in the structure, function and dynamics of the environment organisms live in. Among the first, Williams (1964) asserted that the species-area relationship results from a positive correlation existing between area and habitat diversity and between habitat diversity and species diversity. High habitat heterogeneity usually supports more species by providing more habitat types and reducing local extinctions caused by adverse biotic interactions such as competition and predation. There has been ample supporting evidence for the habitat heterogeneity-species richness relationship (Cody 1974, Tilman 1982, 1993, Shmida and Wilson 1985, Boecklen 1986). Recent studies of patch dynamics at the local and landscape scales have shown the effects of spatial heterogeneity on species richness by emphasizing the interactions between pattern and process (Pickett and Thompson 1978, Steele 1978, Pickett and White 1985, Auerbach and Shmida 1987, Wu et al. 1992, Levin et al. 1993).

**Moderate disturbance/stress hypothesis.** The highest species richness usually occurs where disturbance or stress is intermediate (Connell 1978). Disturbance often creates structural and functional heterogeneity in time and space, and promotes the coexistence of species by directly suppressing destabilizing biotic interactions (e.g., intense interspecific competition and predation) or by providing regeneration niches. A number of empirical and theoretical studies on scales from local communities to regional landscapes support this notion (Loucks 1970, Grime 1973, Connell 1978, Huston 1979, Suffling et al. 1988). However, the terms "moderate" and "intermediate" seem ambiguous and, therefore, have been used largely in a qualitative sense. The patch dynamics perspective in ecology (Pickett and White 1985, Wu and Loucks 1992) has provided a new and comprehensive

framework for studying the effects of disturbance on species richness at population and community levels.

**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 (Brown 1988, Schoener 1988). The study of interactions between species diversity and niche relations has been a central theme in both theoretical and field community ecology for the past several decades (e.g., Schoener 1974, 1988, Cody and Diamond 1975, Krebs 1985). In particular, it has been suggested that interspecific competition facilitates niche differentiation, while predation reduces competition among prey species which in turn reduces the probability of competitive exclusion (e.g., Paine 1966, Connell 1978, Hubbell 1980, Brown 1988).

The above hypotheses are not mutually exclusive, but are complimentary to each other. Evidence supporting one hypothesis does not imply that others are not valid. Indeed, multiple hypotheses are usually necessary to better account for an observed species distribution pattern. In most cases, each hypothesis represents only one of several explanations (Brown 1988). On the other hand, overlap among some of the hypotheses is evident. For example, time, be it ecological or evolutionary, is critical in the origination-extinction dynamics hypothesis since dispersal and speciation are considered essential. Also, the hypotheses about habitat heterogeneity, disturbance, and niche theory/species interactions are interrelated conceptually and practically. Disturbance is important in both creation and maintenance of habitat heterogeneity, which in turn affects the disturbance regime itself (Pickett and White 1985, Kolasa and Pickett 1991). Both habitat heterogeneity and disturbance interact with species and population dynamics. In concert, these three hypotheses may account for many, if not most, species richness patterns on small scales. The interaction among the three hypotheses is best exemplified by the regeneration niche theory which has been



**Figure 3: Species Richness versus PET.** Reproduced with permission from Currie (1991), *American Naturalist*, 137(1):27-49, University of Chicago Press.

evidenced by numerous studies at the community level (Grubb 1977, Pickett and White 1985, Wu and Levin 1994).

One of the problems in the study of biological diversity has been the lack of a conceptual framework to integrate information obtained from numerous ecological and biogeographical observations on a wide range of scales. Available energy and its allocation across different organizational levels may serve as a basis for developing a general theory of species richness (see Brown 1981, Wright 1983, Currie 1991, Hall et al. 1992). Towards this end, Hall et

al. (1992) has recently developed an integrative framework for the distribution and abundance of organisms using energy cost and gain analysis.

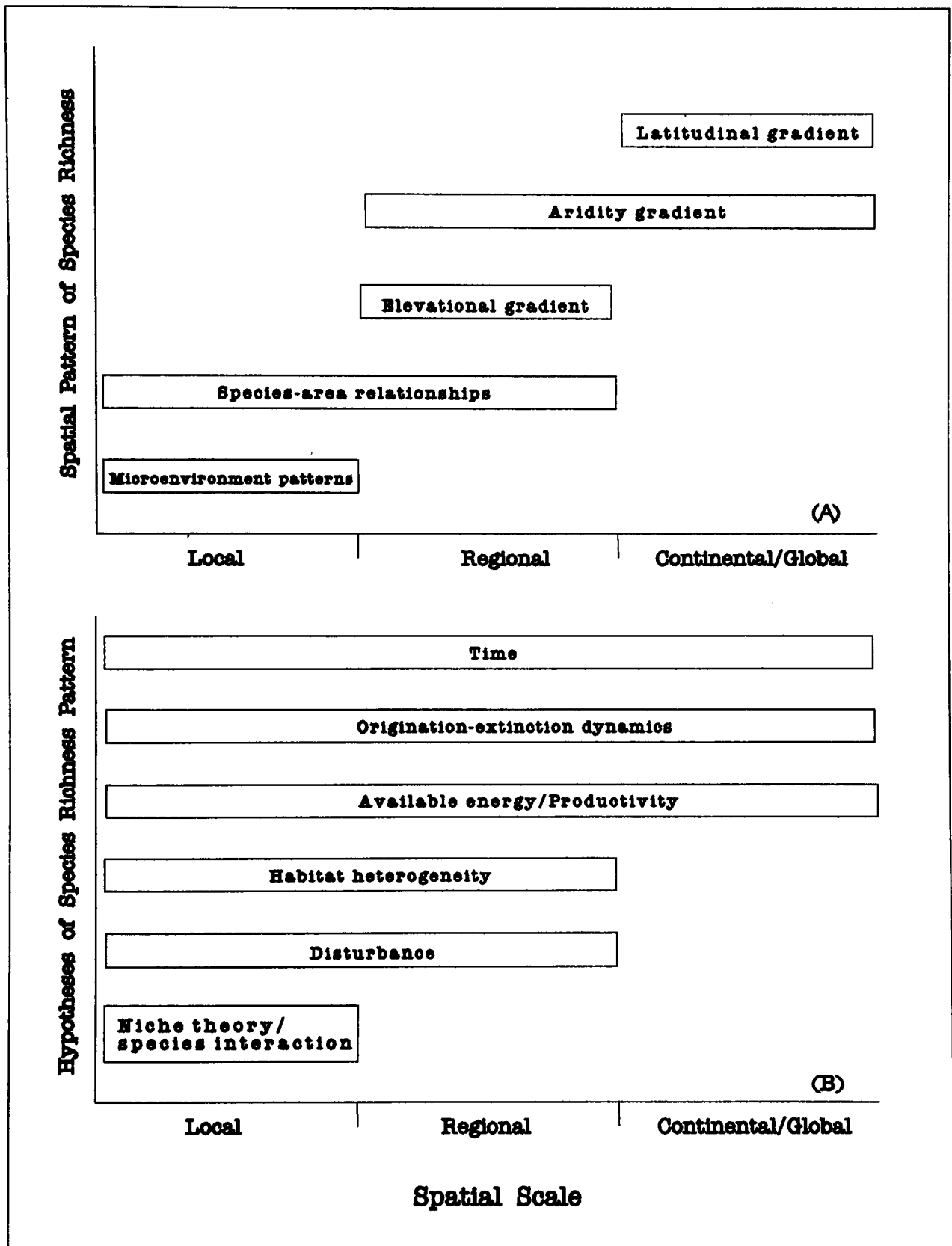
Importantly, any general theory must take a hierarchical and scale perspective that explicitly considers the multiplicity of the various mechanisms that operate on different temporal, spatial and organizational levels. Based on previous studies, we propose a hierarchical structure to relate both the patterns and hypotheses of species richness to spatial scales (Figure 4). We divide spatial scales into continental, regional, and local domains. Based



on the research design adopted by BRC, the continental scale corresponds to all the hexagons that make up the conterminous U.S. (see Figure 1). The regional scale corresponds to some logical subset of the hexagons, such as those of an ecoregion (e.g., Omernik 1987). The local scale denotes a range in spatial dimension from a single hexagon to a small subset, such as those that comprise the Delaware-Maryland-Virginia (DelMarVA) Peninsula.

It is important to notice that a particular pattern of species richness usually occurs over a certain range of spatial scales, and, therefore, different patterns and mechanisms should be expected on disparate scales. In other words, the hypotheses of mechanisms regarding species richness patterns have to be scale-dependent. In particular, at very large (e.g., continental or global) scales, the available energy in the environment seems to be the ultimate determinant of the number of species, although the specific measure of available energy may vary with taxonomic group (see Wright 1983, Currie 1991). That is, the maximum or potential species richness is constrained by energetics on large scales. Brown (1981) conveyed essentially the same idea using the term

"capacity rules." However, to fully explain the large-scale patterns of species richness, other hypotheses such as time and origination-extinction dynamics must be invoked, because processes like colonization and speciation take time and history can be just as important as anything else. The number of species on smaller scales, on the other hand, is primarily determined by energy partitioning and balance. This is consistent with Brown's (1981) concept of "allocation rules." Any factors and processes that affect the energy allocation among species thus may influence the distribution of species richness. On landscape or regional scales, spatial heterogeneity and disturbance are important, whereas on local scales species interactions, disturbances, and microenvironmental factors most likely become the determinants of species richness. Indeed, the pluralism in mechanisms and multiplicity in scale may have been significant sources of controversy and confusion in the study of species richness in particular and biodiversity in general. A hierarchical approach as illustrated here may facilitate the examination of the relationships among different patterns and mechanisms and, therefore, the development of a more comprehensive understanding of species richness.



**Figure 4: Proposed spatial scales at which species richness patterns are evident (A) and associated hypotheses (B).**

### 3.0 FRAMEWORK FOR IDENTIFYING AND EVALUATING POTENTIAL STRESSORS

The previous section summarized major empirical patterns and mechanisms of species richness. However, there has not been a parallel conceptualization of the influence of stressors on species richness patterns. For example, there are no studies known to the authors that simultaneously examined the influence of natural factors (e.g., climate and topography) in conjunction with habitat fragmentation data over a range of spatial scales. In this section we shall propose a conceptual framework for identifying and evaluating stressor data. The framework includes the following elements: categories of stressors, spatial scales at which stressors operate, criteria for selection of stressor data sets, and methodological considerations for studying relationships between stressors and species richness and among stressors.

#### 3.1 STRESSOR CATEGORIES

Based on literature and communication with experts, Finch (1992) compiled a list of threats to 56 bird and mammal species across the five states of Wyoming, Colorado, South Dakota, Nebraska, and Kansas. The threats identified were: (1) agricultural conversion, (2) timber harvesting, (3) livestock industry, overgrazing, (4) fire suppression, (5) accidental pesticide poisoning, (6) pest and predator control, (7) overharvesting (trapping and hunting), (8) human disturbance, (9) mining, energy development, (10) competition (brood parasitism), (11) loss of specialized habitat (wetland/riparian) (12) habitat fragmentation, and (13) causes undetermined. Other researchers have also identified urbanization, desertification, ozone depletion, acid rain, global warming, and introduced species (Hodges 1977, Ehrlich and Ehrlich 1981, Soulé and Kohm 1989, Barker and Tingey 1992). All of these can be broadly categorized as human disturbance.

Stressors affecting species diversity can be grouped into four categories: habitat fragmentation, pollution, introduction of exotic species, and non-anthropogenic disturbances. Agricultural conversion, timber harvesting, and loss of wetlands and riparian habitats, urbanization, and desertification all can be

included in a more general category of habitat fragmentation. Pollution includes the threats posed by pesticide use (herbicides, insecticides and rodenticides), acid rain, ozone depletion, and global warming. Mining and energy development include aspects of both habitat fragmentation and pollution. Livestock grazing can be included in the exotic species category (see Section 4.3).

Overlaid on these human-induced disturbances is a fourth category, non-anthropogenic stressors, that contribute to geographic patterns in species diversity. Using Barrett's (1981) definition of a stressor as a disturbance foreign to the system or natural to the system but applied at unusual levels, examples of non-anthropogenic stress include severe weather or climatic events, man-precipitated or suppressed fires, and some pest outbreaks. In contrast, prevailing climatic and topographic conditions are part of the system where organisms live.

#### 3.2 SCALES AT WHICH STRESSORS OPERATE

Three scales for examination of species-stressors relationships were identified in Section 2.0: the scale of one or just a few hexagons (local), many hexagons covering an entire region (regional); and the entire conterminous United States (continental). The identification of scales on which stressors operate is important to understanding the scope of stressors and their effects on species diversity.

**(1) Habitat Fragmentation.** Habitat fragmentation has been cited by many as posing the most serious threat to biodiversity (NRC 1982, Noss 1983, 1987, Harris 1984, Wilcox and Murphy 1985, Wilcove et al. 1986, Wilcove 1987, Soulé and Kohm 1989, Dobkin 1992). Wilcove et al. (1986) have defined habitat fragmentation as "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." Do measures of habitat fragmentation show correlations with species diversity at continental, regional and local

scales? Many of the empirical studies on the effects of habitat fragmentation have been at what we refer to here as a local scale. The study by Lynch and Whigham (1984) of the effects of forest fragmentation on breeding birds covered roughly a 100x100 km area over six counties in Maryland. The studies by Bolger et al. (1991) and Soulé et al. (1992) on the effect of habitat fragmentation of chaparral species was restricted to coastal San Diego County. Studies of the effect of fragmentation on red squirrel (Verboom and van Apeldoorn 1990) and other small mammals (Bennett 1990) covered 150 km<sup>2</sup> and 105 km<sup>2</sup>, respectively. Lauga and Joachim's (1992) study of forest fragmentation on breeding birds covered 2327 km<sup>2</sup>. Lyon's (1979, 1983) study of the impact on road density on elk covered about 205 km<sup>2</sup>, and a similar study by Thiel (1985) on gray wolf covered about 13 counties in northern Wisconsin. Empirical studies have largely been restricted to local scales. Given that habitat conversion has occurred over larger regions (e.g., agricultural conversion in the American Midwest), it is also logical that there is a relationship between species diversity and fragmentation at a regional scale.

**(2) Pollution.** Newman et al. (1992) have suggested that animal species diversity is affected by pollution at local and regional levels. The range of scales at which pollution is likely to impact species diversity is the result of the combination of the extent of the release of the pollutant, the effect the pollutant has on a particular species, and the geographic range of the species. For example, blindness in big horn sheep populations of the San Bernardino Mountains has been attributed to ozone transport from the Los Angeles Basin (Light 1973). This is an example of a local effect resulting from a more regionally distributed stressor. In contrast, region-wide pollution from acidic deposition has caused region-wide decline in aquatic diversity (Dickson 1986). Pesticides are released over large regions of the United States. The contiguous states of Nebraska, Minnesota, Iowa, Illinois, Indiana, and Ohio are in the top ten in application of pesticides (Waddell et al. 1988). Thus, pesticide use could affect species diversity patterns at regional scales.

**(3) Exotic Species.** The 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 1951, Roughgarden 1986, Hengeveld 1989, Andow et al. 1990). These models predict species spread by assuming biological movement to be similar to random brownian motion. The rate of spread is a function of the species intrinsic growth rate and a diffusion coefficient. The models seem to work well (see Andow et al. 1990) when applied to species for which habitat and abiotic requirements can be relaxed (e.g. cabbage butterfly, muskrat).

The models have not been applied to a suite of species representing a range habitat and abiotic requirements and a range of possible outcomes of introductions (i.e., failure to establish widespread distribution). Most introduced species do not become established. 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; and Mitchell (1978) notes that no European conifers that have been planted as ornamentals in North America have established populations outside their points of introduction. Other examples also show the importance of habitat and the physical environment in restricting the spread of invaders (Hengeveld 1989). Melaleuca and Brazilian pepper, though widespread in south Florida, are restricted in their northward migration by cold temperature (Ewell 1986). Many of the escaped cage birds in southerly U.S. 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 et al. 1986).

Modeling studies highlight that biological invasions can spread over continents when habitat and/or constraints imposed by the physical environment can be ignored. These cases seem to be the exception rather than the

rule. Examples such as European starling, house sparrow, and cattle egret are human commensals. These species have continental (and global) ranges because suitable habitat has been expanded across entire continents.

**(4) Non-anthropogenic Stressors.** Climate is the primary data set for which non-anthropogenic stressors can be developed (see Section 4.4). Characteristic climates (e.g., the Koeppen classification) are regionally distributed. Trewartha (1961), for example, divides North America into six climatic regions, and describes several subtypes within these regions. The severe winter of 1993/1994 in the eastern United States highlights that extreme weather events are also distributed regionally. Record snowfalls were recorded in several locations in the mid-Atlantic States, for example, southeastern Pennsylvania. However, only as far south as Washington, DC, the cold was not as severe and ice storms were the prevailing form of precipitation.

### **3.3 CRITERIA FOR SELECTION OF STRESSOR DATA SETS**

There are several sources of stressor data available. Abramovitz et al. (1990) have published a guide to over 30 environmental data sets that are available through the federal government. It would not be feasible in terms of time or expense to examine each of them. Criteria must be established for selecting data sets to develop stressor measurements.

The first criterion is to select at least one data set from each of the stressor categories identified (habitat fragmentation, pollution, introduced and exotic species, and non-anthropogenic). Hall et al. (1992) noted that at least one example could be found to support a particular hypothesis for explaining species richness diversity, but little work has been done to integrate the numerous hypotheses for explaining species diversity. To gain a more complete understanding of the relationship between stressors and species diversity would seem to require data sets representing stressors from each category. Also data sets within each category should be selected such that as many

aspects of that stressor category as possible are represented. For example, land cover data can be used to develop many stressor metrics of habitat fragmentation. However, land cover data is often deficient in its representation of roads and wetlands. Separate data sets of roads and wetlands might be necessary to develop habitat fragmentation measures that cannot be obtained from land cover data alone. Second, the data sets selected should cover the entire conterminous United States or at least the stressor's region of influence. Third, available reference information (not necessarily part of the data set itself) is needed to assess the quality of the data set. Assessment of data quality is important for the correlative analyses proposed by BRC. Without knowing the quality of the data used, it is impossible to determine whether or not correlations (or lack thereof) are an artifact of poor data quality.

### **3.4 A CONSIDERATION IN STUDYING CORRELATIONS BETWEEN STRESSORS AND SPECIES RICHNESS**

Once the stressor data sets have been selected, the question arises as to how the data sets should be used to determine their effects on species richness. The problem of scale is central to this issue. Many of the continental-scale studies have shown strong correlations with aspects of climate and topography, but there has been little empirical work at similar spatial scales showing strong correlations between species richness and stressors of habitat fragmentation, pollution, or exotic species. The effect of these disturbances appears to be most prominent on local and regional scales (see Section 3.2).

Scaling-up is recommended here. By scaling-up, correlations between stressors and species richness, as well as among stressors, can be studied progressively. The spatial scale can be increased by continually adding more hexagons. A pattern of increasing correlation with increasing geographic extent (more hexagons) followed by a drop in correlation may indicate the scale at which that stressor influences species richness patterns. This approach is conceptually similar to that used by Krummel et al. (1987). The authors examined the change in fractal dimension as a function of

forest patch size. To start, the 200 smallest forest patches were selected and their fractal dimension calculated. This process was repeated, using progressively larger 200-patch subsets. Other examples using a conceptually similar approach can be found in O'Neill et al. (1991) and Turner et al. (1991).

The same approach could be examined in the Pennsylvania and Oregon Pilot Studies by starting with a small subset of hexagons, examining the results of multivariate analyses,

adding additional hexagons to increase the spatial extent, followed by a re-examination of the results of the multivariate analyses. There are several logical starting points in Pennsylvania and Oregon. In Pennsylvania, examples are the Great Valley, Coastal Plain, and Piedmont, all of which would be comprised of only a small number of hexagons. In Oregon, examples include the Willamette Valley and the portion of Malheur County south of the Owyhee River and west of the Owyhee Mountains.

## 4.0 EXISTING DATA FOR IDENTIFYING STRESSORS

### 4.1 HABITAT FRAGMENTATION DATA

Habitat fragmentation alters the physical environment in numerous ways (Wilcove et al. 1986, Wilcove 1987, Saunders et al. 1991). These include loss of habitat area, loss of habitat heterogeneity, isolation, edge creation and changes in edge-to-area ratio, and modification of microclimate in remaining patches. Many biological responses are incumbent with these changes, such as density dependent extinctions (Wilcove et al. 1986, Pimm et al. 1988, Soulé et al. 1988, Bolger et al. 1991), dysfunctional behavior (e.g., inability to avoid nest predation) (Wilcove 1987), and secondary extinctions (Wilcove et al. 1986).

Loss of habitat heterogeneity may be one of the most pervasive but least recognized aspects of fragmentation. Habitat heterogeneity is typically considered a within-stand or community-level phenomenon, such as snags and downed logs in old-growth forests (e.g., Franklin 1993). However, habitat fragmentation may also eliminate juxtaposition of different habitat types (e.g., removal of forest patches near riparian habitat), which can make remnant habitats unusable or less than optimal. Of the 67 bird, mammal, and herptile species studied by Finch (1992), 59 used more than one habitat type. Thomas et al. (1976), in a study of 13 bird species in the Blue Mountains of Oregon, found that all 13 species required at least two habitat types for reproduction and/or feeding. A complex of habitat types has also been demonstrated as a requisite for beaver (*Castor canadensis*) (Genoways 1986) and the desert bighorn sheep (*Ovis canadensis*) (Leslie and Douglas 1979).

Existing data that can be used to measure aspects of habitat fragmentation are listed in Table 2. The data are in four groups: land cover, roads, population, and wetland and riparian habitats.

#### 4.1.1 Land Cover

Land cover data (Table 2) are the primary source for generating metrics of habitat

fragmentation (e.g., shape, size, interspersions, connectivity, and diversity). The developing discipline of landscape ecology (Naveh and Lieberman 1984, Risser et al. 1984, Forman and Godron 1986) provides both a conceptual basis and a practical framework for such studies. Land cover data are available from several sources, at several scales, and in several formats.

The USGS land cover regionalization (Loveland et al. 1991) is a nationwide data base that has 159 classes mapped from the Advanced Very High Resolution Radiometer (AVHRR) satellite at about 1 km<sup>2</sup> resolution. Use of AVHRR-derived land cover data to generate patch-based measures of habitat fragmentation should be undertaken with caution. The AVHRR land cover regionalization data provides a map of the probability of a particular land cover type occurrence (Brown et al. 1993). It is not a traditional land cover map in the sense of providing data with specified geographic and thematic accuracy. Therefore, measures such as patch size, distance between patches of the same type, and patch shape are, too, only probabilities. Also, Gervin et al. (1985) found that thematic accuracy of AVHRR land cover data was poor in heterogeneous areas when compared to those mapped from Landsat MSS.

The USGS Land Use Data Analysis (LUDA) and USFWS GAP land cover have specified thematic and geographic accuracy requirements. These data are more appropriate for developing metrics of habitat fragmentation than AVHRR. USGS LUDA data were compiled from ca. 1975 high altitude aerial photography. The USFWS GAP program (Scott et al. 1993) uses Landsat TM to map land cover. Several state agencies are also mapping land cover using Landsat satellite data (e.g., Florida, Georgia, South Carolina). The Department of Defense (DOD) has published a Digital Chart of the World (DCW), which provides digital, polygon-based data of urban areas for the United States (Loveland, pers. comm.). Urban categories are typically included in land cover maps.

**Table 2: Data for Land Use and Habitat Fragmentation.**

<b>Data</b>	<b>Name</b>	<b>Collection Method</b>	<b>Source</b>	<b>Trends</b>
Land Cover	Land Cover Regionalization	AVHRR	USGS	No
	LUDA	Aerial Photography	USGS	No
	GAP	Landsat TM	USFWS	No
	MLU	Survey	USDA	Yes
	PSU	Landsat TM	USDA	Yes
	NRI	Field Sample	NRI	Yes
	DCW	Satellite	DOD	?
Roads	DLG	Aerial Photography	USGS	No
Population	CENDATA	Survey	Census	Yes
Wetlands & Riparian	NWI	Aerial Photography	USFWS	Yes
	NCSS (soils)	Survey	USDA	No
	DLG (streams)	Aerial Photography	USGS	No

The U.S. Department of Agriculture (USDA) provides at least three sources of land cover data through its various branches. These are Major Land Uses (MLU) from the Economic Research Service (ERS), National Agriculture Statistical Service (NASS) Primary Sampling Units (PSU), and the National Resources Inventory (NRI) of the Soil Conservation Service (SCS). Data from these sources are updated every five years.

MLU provides 5-year trend analysis in 11 land use categories. These data are tabular statistics by state, compiled by correspondence with other federal inventory programs. For

example, forest area is taken from USDA Forest Service estimates. The estimates are adjusted to a total of 100 percent.

NASS collects agricultural and land cover data using a stratified sampling design. Primary Sampling Units (PSU) are the most basic strata. These units vary in size from 40 to 640 acres, and are classified according to the intensity of agricultural land use. An example of a PSU class is an area with greater than 50 percent agriculture. These data are not land cover per se. They are a land cover regionalization based on intensity of agriculture. Over the long term



(20 to 30 years or more), NASS PSU data may have potential for monitoring the trend in agriculture toward fewer but larger farms projected by NRC (1982).

NRI data were first collected in 1982, and repeated in 1987 and 1992. NRI is primarily intended to provide an inventory of status and condition of soil and water resources, but also provides information on land cover. Data are collected using PSUs that are similar in concept to NASS PSUs. These units are about 160 acres in size. Land cover data are collected using 3 sample points within each PSU. Area estimates of land cover are statistically reliable using USGS 8-digit watersheds (cataloguing units) and Major Land Resource Areas (MLRA, an "ecoregion" map based on soils and land use). The 1982 and 1992 data also have information on land cover surrounding each point within 0.25 miles. The point data are available as a GIS data set with attribute coding. A polygon-based land cover data set for the watersheds codes each unit by proportion of land cover classes.

Land cover data mapped from satellites with higher resolution than AVHRR or aerial photography should be used to generate habitat fragmentation metrics. These data are typically compiled with specified thematic and geographic accuracy standards. Use of NRI land cover data should be explored as a substitute when satellite-based land cover is not available. NRI data are compiled from a design that provides statistically reliable estimates of land cover for small watersheds, and can provide change and trend information. Their primary shortcoming is that land cover is represented as points instead of polygons, but habitat measurements (e.g., interspersions) should still be possible. The other land use data generated by USDA is not recommended because measurement of habitat fragmentation would not be possible with them.

#### 4.1.2 Digital Line Graphs (Roads)

Roads are discussed separately from land cover because land cover data do not typically include roads unless they are of sufficient width (e.g., interstate highways). Moreover, metrics such as road density can capture aspects of fragmentation that cannot be measured from land

cover alone. Several studies have shown that roads have fragmented habitats for larger animals. Elk (*Cervus elaphus*) habitat was reduced by 75 percent at a road density of 2 km/km<sup>2</sup> (Lyon 1979, 1983). If the average road width in this study was 20 meters, the area occupied by roads was only 4 percent of a 1 km<sup>2</sup> unit. Thiel (1985), studying gray wolf (*Canis lupus*) in Wisconsin, found that populations failed to survive at road densities greater than 0.93 mi/mi<sup>2</sup>. Storm et al. (1967) found that red fox (*Canis vulpes*) avoided roads. These findings illustrate that for a given species, habitats (e.g., forests) which seem suitable in terms of size, shape, and connectivity with other patches of the same type, might actually not be suitable because of the existing road network. Metrics such as patch size alone would not be able to detect this problem.

Road data are available from various sources, including USGS Digital Line Graphs (DLG), Census TIGER files, EtakMap Corp., Wessex First Street, and Delorme (Street Atlas) Inc. USGS DLG data is probably the most widely recognized source. The other data sets are based on USGS DLGs. For example, Census TIGER files are essentially USGS DLG road data with address geocoding (e.g., zip codes and street addresses). EtakMap Data are updates of the USGS 1:100,000-scale USGS data.

DLG scale options are: 1:24,000, 1:100,000 and 1:2,000,000. These data are attribute-coded, giving information on the types of roads (e.g., interstate highways, limited access/divided highways, other U.S. highways, state secondary highways, improved roads, and unimproved roads). USGS DLG 1:24,000-scale data is not available nationwide. The 1:100,000-scale data is the largest scale data that is available on a nationwide basis. USGS 1:100,000-scale DLGs are created by photomosaicking and then photoreducing the 1:24,000-scale USGS topographic maps. The photoreductions are then scribed and these are scanned to create the digital 1:100,000-scale data (pers. comm., USGS, Reston, VA).

USGS DLG is the most accessible (via INTERNET) road data available, and all other available road data are compiled from DLGs.

Thus, there is no independent data source for comparison. The amount of error in the USGS DLG data is unknown. Three analyses can be performed to assess the quality of DLG road data. First, the spatial pattern in road density can be examined by map sheet. This has been done for Pennsylvania using the 1:100,000-scale DLG data. The highest densities are in the southeastern portion of the state, followed by the southwestern portion. The lowest densities are in the central portion of the state, starting north of Harrisburg and spreading east and west in a "T" along the border with New York. The rank order pattern follows the population distribution in the state. Second, graphs and correlations scores between road and population density can be examined. Since these data should be positively correlated, a finding to the contrary would suggest error in the road data. Third, DLGs can be compared to digital orthophoto quads.

#### **4.1.3 Wetland and Riparian Habitat Loss**

There is increasing recognition that wetland and riparian habitats support greater numbers of species than surrounding uplands (Odum 1979a, 1979b; Thomas et al. 1979; Kauffman and Kreuger 1984; Gregory et al. 1990; Williams 1991; Finch 1992; Mitsch and Gosselink 1993; Naiman et al. 1993). Eighty (80) percent of the United States' breeding bird populations rely on wetlands (Wharton et al. 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). In a survey by Finch (1992), loss of wetland and riparian habitat was the most often cited cause of species decline. Loss of wetland and riparian habitat is likely to be an important measure for explaining geographic patterns of species diversity.

The ability of wetland and riparian habitat to support high numbers of species may be in part due to their greater productivity. In comparing net primary productivity (NPP) for temperate wetlands from Richardson (1979) with NPP estimates of temperate uplands from Leith (1975), Williams (1991) found that temperate wetlands were 2 to 5 times more productive than surrounding upland communities.

There are two reasons why wetland and riparian habitat loss should not be developed from land cover data alone. First, satellite data (even Landsat TM) are not generally capable of detecting wetlands accurately (see Dottavio and Dottavio 1984). A multistage approach (use of several remote platforms simultaneously -- air photos, airborne and satellite spectral data) for accurate detection of wetlands is advocated by Jensen et al. (1986, 1991). Second, much of the wetland loss that has occurred in the lower 48 states predates the advent of satellite remote sensing (Williams 1991). Temporal land cover mapping could not be used to determine wetland loss between the time periods represented by the land cover data.

To determine where wetlands have been lost requires three data sets: land cover, streams, and soils. Soils data are critical. Soils data can be used to determine where wetlands would be supported independent of the present land cover and, since soils change slowly relative to land cover, wetland loss estimates can be generated that reflect a longer history than would be possible by comparison of temporal land cover data.

Soil Conservation Service (SCS) has mapped soils nationwide using the soil series taxonomic unit (USDA 1987). The soils series is "the basic unit of soil classification, ... consisting of soils that are essentially alike in all major profile characteristics except texture of the A horizon" (Steila 1976). There is an extensive list of attribute information that accompanies the data, such as length of flooding. By combining land cover and stream data with soil attributes such as length of flooding, wetland and riparian habitat loss could be measured as the sum (by hexagon) of anthropogenic land use (e.g., agriculture, urban) on wetland soils.

Data for streams is available as part of the USGS DLG series. DLG characteristics previously described for roads also apply to streams (except for classification). Land cover data would be taken from sources previously described. The stream data would be utilized to distinguish riparian wetlands from those that are not.

#### 4.1.4 Census Data

Population growth is the driving force behind the threats to biodiversity. The Bureau of Census provides several data sets covering various aspects of population through its CENDATA system. The County Statistics File 3 contains time-series data for over 1600 items. Population change (1980-1990) for selected high growth counties in Pennsylvania and Oregon are shown in Table 3.

Population growth in both Pennsylvania and Oregon follow urbanization patterns. In Pennsylvania dramatic growth has occurred in the counties that form its eastern and southern borders with New Jersey and Maryland. These include Pike (FIPS 42103) Monroe (42089), Wayne (42127), Adams (42001), York (42133), Lancaster (42071), and Chester (42029) Counties. The improvement of US15 in Pennsylvania is at least partly responsible for increased population growth in Adams County, making Gettysburg, PA a distant but feasible commute into northern Washington, DC and other Interstate 270 markets. Several new residential developments are evident along the Interstate 270/US15 corridor. High growth counties in Oregon are Washington (41067), Clackamas (41005), Marion (41047), Jackson

(41029), Deschutes (41017), and Yamhill (41071). These counties are all in the vicinity of Portland and the Interstate 5 corridor, except for Deschutes which includes the city of Bend.

Use of population data is not recommended because it is an indirect influence. It is not population per se, but the resultant human activities that act as stressors to biodiversity. The danger of using indirect measures such as population in correlative studies was illustrated well by Cole et al. (1993). The authors showed a  $R^2$  of 0.76 between population density and nitrogen concentration in rivers. However, this relationship does not indicate the processes by which human population causes the increase in nitrate concentration. Further investigation showed that sewage discharge, automobile emissions, agriculture, and forest cutting were the true culprits. Use of population density will likely show strong (negative) correlations with species diversity, but finding such a relationship will not provide insight into the activities reducing species diversity. Knowledge of the actual mechanisms that cause a reduction in species diversity is needed to develop management options from analysis of geographic patterns of stressors and species diversity (i.e., linking BRC objectives 1 and 4; Section 1.0).

**Table 3: Population change (1980-1990) for selected high growth counties in Pennsylvania and Oregon (from ArcUSAm ESRI 1992). FIPS is the county identification code.**

<b>Pennsylvania</b>						
FIPS	Population By County			Population Change		
	1980	1986	1990	80 to 86	86 to 90	
42001	68292	71200	78274	4.2	9.9	
42029	316660	339100	376396	7.1	11.0	
42071	362346	393500	422822	8.6	7.5	
42089	69409	82700	95709	19.1	15.7	
42103	18271	22300	27966	22.2	25.4	
42127	35237	38700	39944	9.9	3.2	
42133	312963	326600	339574	4.3	4.0	
<b>Oregon</b>						
41005	241911	256900	278850	6.2	8.5	
41017	62142	68700	74958	10.5	9.1	
41029	132456	140000	146389	5.7	4.6	
41047	204692	215400	228483	5.2	6.1	
41067	245860	271400	311554	10.4	14.8	
41071	55332	57500	65551	3.9	14.0	

## 4.2 POLLUTION DATA

Widespread awareness of the potential impact of pollution on species arose after World War II, following the dramatic increase in pesticide use (Moriarty 1983, Peterle 1993). The field of ecotoxicology began to emerge in the 1970s as a discipline focused on the study of the ecological effects of pollutants (Truhaut 1977). Pesticides use is probably the most serious pollution problem relative to wildlife populations. Land in farms comprises about 50 percent of the conterminous United States (USDA 1989, ESRI 1992), and pesticides are used throughout. There are approximately 50,000 different chemical compounds that are used as pesticides (Waddell et al. 1988) out of approximately 63,000 chemical compounds that are commonly used by industry worldwide (Moriarty 1983).

Another pollution problem that has impacted species diversity is acidification of lakes and streams in the northeastern United States. Schindler et al. (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).

Outside of these two examples much of what is known about the impact of pollution on wildlife is from case studies. Newman et al. (1992) discussed several case studies of impacts of pollutants on wildlife populations. In another recent case study, high concentrations of mercury have been found in the endangered populations of Florida panther (George Taylor, pers. comm.).

Table 4 is a list of available pollution data sets. The data from the USFWS National Contaminant Biomonitoring Program (NCBP) and the USGS National Stream Quality Accounting Network (NASQAN) appear to be the two data sets that are most likely to show a relationship with species diversity patterns at large spatial scales. The others listed in Table 4 provide only ambient concentrations in the environment. Actual concentrations in species are more valuable than concentrations in the environment because of species differential response to the presence of pollutants (Loucks, pers. comm.).

The USFWS NCBP program provides data on tissue concentrations of agricultural pesticides in fish, waterfowl and starlings. There are over 100 fish and starling collection sites; concentrations in waterfowl are collected from hunters. The program was initiated in 1964 with the objective of providing geographic and temporal trends. NCBP data will be stored in the Environmental Contaminant Data Management System (ECDMS). Fish data are already in the EPA STORET system.

Although NASQAN does not provide information on presence of toxics (e.g.,  $Al^{3+}$ ) in aquatic biota, the well documented susceptibility of fish species to pH values less than 5.0 (Dickson 1986, Schindler et al. 1989) suggests that use of pH data for lakes and streams should be a useful stressor metric for correlation with aquatic diversity. Because of the relationship between acid deposition and the buffering capacity of soils (Moriarty 1983), it is probably better to restrict such correlation studies to areas with inherently low Acid Neutralizing Capacity (ANC), such as the northeast United States. It is not likely that the other data listed in Table 4 will provide useful information for correlation with geographic patterns of species diversity. Each provides only information on release of pollutants into or concentration in the environment.

## 4.3 EXOTIC SPECIES DATA

The data available for introduced and exotic species are listed in Table 5. The primary source of data is TNC's Heritage Data Base, which is being used to develop the species richness data for each hexagon (see Figure 1). The vertebrate species data set being developed for each hexagon will classify each species according to its probability of occurrence (1: >95%; 2: 80-95%; 3: 10-80%; 4: <10%) and its origin (1: native; 2: introduced; 3: reintroduced; 4: unknown). The quality of these data, relative to whether a species is native or introduced, is probably high, given that distinction between native and introduced is easier in countries that have been explored and settled by Europeans only in the last three hundred or so years (Usher 1988). These data are being developed by the Species Team. Development of specific metrics will likely

**Table 4: Pollution Data Sets (from Abramovitz et al. 1990).**

---

---

Agency	Data	Trends	Description
DOI, USFWS	NCBP	Yes	National Contaminant Biomonitoring Program (NCBP). Tissue examination of fish, waterfowl, and starlings.
EPA	NPS	?	National Pesticide Survey (NPS). Data on 126 pesticides in water supply wells.
Commerce, Census	Census of Ag.	Yes	Census of Agriculture. Data on chemical applications by county.
DOI, USGS	NASQAN	Yes	National Stream Quality Accounting Network (NASQAN). Data on H <sub>2</sub> O quality and quantity. Monitoring was established in 1972.
DOI, USGS	NADP/NTN	Yes	National Atmospheric Deposition Program/National Trends Network (NADP/NTN). Data on precipitation chemistry for ~200 sites nationwide.
Commerce, NOAA	NCDPI	No	National Coastal Pollutant Discharge Inventory (NCDPI). Inventory of 9 categories of pollutants for coastal areas.
DOE	MSCET	Yes	Month & State Current Emission Trends (MSCET). NO <sub>x</sub> , SO <sub>x</sub> , and VOC emissions by state.
EPA	AIRS	Yes	Aerometric Information Retrieval System (AIRS). Data on air quality and pollution collected from state and local agencies.
EPA	CERCLIS	Yes	Comprehensive Environmental Response, Compensation and Liability Information System (CERCLIS). Data on the location of ~30,000 hazardous waste sites.
EPA	TRI	Yes	Toxic Release Inventory (TRI). Toxic release inventory of over 17,000 manufacturing sites.
DOE, ORNL	CDIAC	Yes	Carbon Dioxide Information Analysis Center (CDIAC). Data on CO <sub>2</sub> parameters.

---

---

**Table 5: Data Sets for Exotic Species, Including Managed Livestock and Grazing Practices.**

Agency	Data	Trends	Description
The Nature Conservancy	Species occurrence	?	Species occurrence by hexagon. Species include mammals, reptiles, amphibians, and fish.
USFS, FS	FSRAMIS	Yes	Forest Service Range Management Information Service (FSRAMIS). Data on grazing use in national forests and grasslands.
DOI, BLM	PLS & ESI	?	Public Land Statistics (PLS) and Range (Ecological) Site Inventory (ESI). Provides data on grazing use and ecological condition, respectively.
DOC, Census	Census of Agriculture	Yes	Data on livestock numbers by county.

be a collaborative effort among the Species, Analysis, and Stressors Team.

Data for grazing is presented here under the category of exotic species, instead of creating a separate category. This is because herbivory by large ungulates in the intermountain west was not an ecosystem component prior to their introduction by man (Mack and Thompson 1982). Livestock grazing is the most extensive land use in the interior Pacific Northwest (Kauffman and Kreuger 1984). Demand for rangeland is projected to increase 38 percent by 2030 in the Pacific Northwest (NRC 1982). Data on grazing use seems necessary to help explain species diversity patterns because of the extent and projected increases in grazing use throughout the western United States (NRC 1982), and also because of the potential for domestic livestock grazing to alter competitive relationships with other organisms, transmit disease, accelerate erosion, change plant community composition, and alter riparian habitat (Cooperrider 1990, Kauffman and Kreuger 1984).

Grazing data is available from three federal sources: BLM, the U.S. Forest Service, and the Department of Census (Census of Agriculture). BLM's Public Land Statistics (PLS) provides grazing use data, and the Ecological (Range) Site Index data have been used to determine past grazing use. These data are not stored digitally, but instead are kept as paper records in each BLM state office. Moreover, these data are in Animal Unit Months (AUM), which is the amount of forage necessary to sustain one cow and calf for one month. Since, the amount of forage concept of an AUM is based on the vegetation present, an AUM is unitless in terms of area. It might take only forty acres to make up one AUM in one allotment versus 60 acres per AUM in another. The use of AUM makes it difficult to determine grazing use in terms of number of livestock per unit area. BLM's ESI data classifies allotments into low, mid-, and high seral, and potential natural community (PNC), based on vegetation composition. Some have suggested that each stage reflects past grazing use (L. Walker, pers. comm.). For example, low seral would reflect past heavy grazing pressure. However, there is not complete agreement on the

relationship between grazing use and BLM seral stages. The Forest Service Range Management Information Service (FSRAMIS) stores grazing use in a computerized format. Information collected includes size, state, and county of allotment, and grazing use. Geographic coordinates are optional. The data base is not proprietary. Also, the Census of Agriculture, conducted every five years by the Department of Commerce, provides livestock inventories by county.

The FSRAMIS data base appears to have the most appropriate data (allotment characteristics and actual grazing use in a computerized format with geographic coordinates), but the data only cover Forest Service lands. It is disappointing that BLM does not appear to have this type of data available to the public. At present, the Census of Agriculture data on livestock inventory by county seems to be the only nationwide data.

A per hexagon livestock density data set with known data quality can be developed through boolean modeling using the Census of Agriculture livestock estimates followed by comparison to livestock data from FSRAMIS (for counties of co-occurrence). Livestock distribution is not spatially uniform (Senft et al. 1985, Smith 1988). Studies have shown that cattle avoid steep slopes and exposed aspects (Roath and Kreuger 1982) and tend to congregate near water (Roath and Kreuger 1982, Senft et al. 1983, 1985). These factors combined with land cover data (e.g., presence of urban development) and land ownership permit boolean modeling of the presence of cattle in individual hexagons.

The boolean model would be county based. The model would query each hexagon to establish the proportions of the hexagons with steep slopes, exposed aspects, cropland and urban land use, and land ownership that excluded grazing (e.g., National Park). The result of these queries would eliminate some portion of the area of some or all hexagons in the county from grazing use. For example, assume that livestock density for a county is 100,000 animals, and a hexagon comprises 5 percent of the area of that county. If the modeling eliminated 50 percent of the area of that

hexagon, then 2.5 percent of 100,000 (2,500 animals) would be the density of livestock in that hexagon. For hexagons straddling one or more county boundaries, the starting proportion for the hexagon would be the area in the county being modeled. FSRAMIS data could be used to validate and refine the model, because it contains information on size, state, and county of allotment, grazing use, and geographical coordinates for Forest Service lands.

#### **4.4 DATA SETS FOR NON-ANTHROPOGENIC FACTORS**

Data on climate are the primary source to develop stressor metrics of non-anthropogenic stress - a disturbance which is part of the system but occurs at an excessive level at a particular point in time (Barrett 1981). There are also data on fire and pest outbreaks. The data sets are listed in Table 6.

##### **4.4.1 Historical Climatology Network (HCN)**

Climatic data have been widely used to study geographic patterns in species richness (e.g., Wright 1983; Owen 1990a, 1990b; Currie 1991). Climate is noted to have a particular influence on the distribution of bird species (Temple and Wiens 1989). The National Oceanic and Atmospheric Administration's (NOAA) Historical Climatology Network (HCN) contains 1219 stations of serially complete monthly temperature (mean, minimum, and maximum) and total precipitation throughout the United States. The data represent the best available out of more than 5000 cooperative weather stations, and "probably represents the best monthly temperature and precipitation data set available for the contiguous United States" (Karl et al. 1990).

There are about 22 stations in Oregon; 19 of these stations are along Interstates 5 and 84 corridors. There are three stations east and south of Bend. One is near Oregon's border with California and Nevada, another in the northeastern corner of Malheur County, and a third near Bend. There are approximately 12 stations in Pennsylvania. These stations are

more evenly distributed. Neilson et al. (1992) noted that stations tend to be at low elevations.

Notwithstanding the apparent elevational bias, the data completeness (both within and across years) and quality control to remove urban effects and station changes (see Quinlan et al. 1987) indicate that HCN data would be able to provide relatively error free measurements of both seasonal, annual, and longer term (e.g., five years) departures from average conditions. Averages can be calculated from 65 or more years of data.

#### 4.4.2 USGS Digital Elevation Model (DEM)

Topography has been a primary source of data to test the hypotheses of spatial heterogeneity, elevation, and even aridity as mechanisms influencing spatial patterns (e.g., Whittaker and Niering 1965, Glenn-Lewin 1977, Owen 1990a, 1990b). Although topography is not a stressor as we have defined the term here, such data are essential in establishing a baseline (see Section 2.0). Therefore, we have included topography in the category of non-anthropogenic data sets.

#### 4.4.3 Federal Insect and Disease Conditions (FIDC) and Wildland Fire Statistics (WFS)

Fire and pest infestations are natural components of many ecosystems that in part

determine the dynamics of species occurrence (see Loucks 1970, Hengeveld 1989, Romme annight 1982). Like topographic data, fire and pest outbreaks could be useful in distinguishing between natural fluctuations in species occurrence and the impact of stressors. Also, these data could be useful as stressors, to the extent that fire and pest outbreaks can be determined to be man-precipitated (see Blais 1985, regarding pest outbreaks). Use of these data as stressors, though, would assume that man's hand in causing a fire or pest infestation was out of phase with the normal cycle for that ecosystem, which may be difficult to establish.

The Forest Service publishes annual reports on forest pest conditions (FIDC) and wildland fires on federal and non-federal lands (WFS). FIDC data are compiled from Forest Service regional and district offices. The information in the annual reports is typically in the form of summary statistics. Detailed information would need to be acquired from regional and local offices. The Fire and Aviation Management Staff of the Forest Service collects annual statistics on wildland fires on federal and non-federal land. Statistics include total area burned, source of fire (on Forest Service land only), and year-to-date and annual statistics.

No digital, geographically referenced data exists for either FIDC or WFS. Also, to our knowledge, these data have only been used for reporting. There is no information on the quality of the data.

**Table 6: Data Sets for Non-Anthropogenic Factors (from Abramovitz et al. 1990).**

Agency	Data	Trends	Description
NOAA	HCN	Yes	Historical Climatology Network (HCN). U.S. temperature and precipitation for ≈1200 stations.
DOI, USGS	DEM	No	Digital Elevation Model (DEM). Elevation, slope, and aspect at 1:24K, 1:250K, and 1:2M scales.
USDA, FS	FIDC	Yes	Forest Insect & Disease Conditions (FIDC) across all forest and ownership classes.
USDA, FS	WFS	Yes	Wildland Fire Statistics (WFS). Wildland fires on public and private land. Origin on public land only.



## 5.0 DISCUSSION

### 5.1 IMPORTANCE OF SCALE

The relationship between geographic patterns of species richness and environmental factors are scale-dependent (see Section 2.0). At continental and global scales, available energy, as measured from climatic data, and species richness are strongly correlated (see Currie 1991). Early studies, such as Simpson (1964) and Kiester (1971), showed that species richness patterns were correlated with latitude and longitude. Available energy has also been shown to be the best predictor of decomposition (Meentemeyer 1984) and productivity (Rosenzweig 1968, Leith and Box 1972) at continental and global scales. Little evidence can be found to support hypotheses of time, origination-extinction dynamics, habitat heterogeneity, disturbance, and niche theory to explain species richness patterns at continental and global scales (Rhode 1992).

At regional and smaller spatial scales, the influence of climate on species richness is less universal. While Owen (1990a), studying species richness patterns in Texas, found a strong correlation between aspects of temperature and precipitation, variance in elevation was also significant. Glenn-Lewin (1977) and Whittaker and Niering (1965) also found a relationship between species richness and elevation. Pianka (1967) found that the variety of vegetation life forms was the best predictor of the number of herptile species along a gradient from the Sonoran through Great Basin Deserts.

Based on the review of the literature on the factors influencing patterns of species richness, there seems to be a lack of integration of natural and anthropogenic factors. None of the studies discussed in Section 2.0 included anthropogenic factors. We have proposed that anthropogenic and non-anthropogenic stressors operate primarily at local and regional scales, and, therefore, stronger correlations between species richness and stressors should be more likely found on these scales.

### 5.2 PROPOSED DATA SETS AND CONSIDERATIONS IN EXAMINING STRESSOR-SPECIES RELATIONSHIPS

The data sets proposed for study are listed in Table 7. For habitat fragmentation, these include road density and wetland/riparian habitat loss. Road density would be measured directly using existing digital data. Wetland and riparian habitat loss would be measured by combining land cover, streams, and soils data in a GIS. Other measures of habitat fragmentation, such as patch size and isolation are being developed by the Landscape Team, and therefore are not discussed here. For pollution, use of the USFWS NCBP data and USGS NASQAN water quality data (pH and Acid Neutralizing Capacity (ANC)) are proposed. The USFWS NCBP provides data on pesticide pollutant loading for fish, waterfowl and starling. Samples are collected across the conterminous United States. Decreased pH (below 5.0) in lakes has been shown to result in a decrease in aquatic biota (Schindler et. al. 1989). USGS, NASQAN data can be used to derive pH and ANC measures. Data on exotic species are part of the TNC Heritage data, which is being used to create the hexagon species list for BRC. Livestock density by hexagon, included under the category of exotic species because herbivory by large, congregating ungulates was not an ecosystem component in the intermountain west prior to European introduction (Mack and Thompson 1982), can be modeled using Census of Agriculture livestock density estimates, topography, land cover, and land ownership data. For non-anthropogenic factors, climate and topography data are proposed. The NOAA, HCN data can be used to measure departures from long-term normals (both temperature and precipitation). Topographic data, though not a stressor, should be included because of its importance in establishing baseline conditions.

In examining the relationships between these stressors and species diversity, consideration of scale-dependence and data quality are important. Because the majority of evidence shows that stressors influence species diversity at local and regional scales, and that climate appears to have

**Table 7: Data Proposed for Examination of Stressors-Species Relationships**

<b>Stressor Category</b>	<b>Data</b>
Fragmentation	Wetland loss: Land cover, streams, soils Road density
Pollution	Loading: National Contaminant Biomonitoring Program data Water quality (pH, ANC) in streams and lakes
Exotic Species	Heritage (species occurrence) Data Livestock grazing
Non-Anthropogenic Factors	Climate (departures from normals) Topography

an overriding influence at the continental scale, we have suggested a hierarchical approach to the study of the relationship between stressors and species richness. Also, an assessment of quality of the stressor data must be made prior to analyzing species stressor relationships. Poor data quality can lead to failure to identify a relationship when one exists or identification of a relationship when none exists. A description of data quality analysis procedures have been presented for many but not all of the data sets proposed. This is because data quality

evaluation for some of the data sets proposed is problematic. For example, there is no independent information that can be used to assess the quality of the USGS stream data. One possible approach to evaluation of the quality of such data is to compare the sum of squares (or logical counterpart) using the entire data set with a subset with which one is most confident. If the two sums of squares are not very different it would be fair to conclude that either data quality is good overall or the error in the data is not affecting the statistical results.

## 6.0 LIST OF ABBREVIATIONS

### *Federal Agencies*

DOC	Department of Commerce Census NOAA - National Oceanic and Atmospheric Administration
DOD	Department of Defense
DOE	Department of Energy
DOI	Department of Interior BLM - Bureau of Land Management USGS - United States Geological Survey USFWS - United States Fish & Wildlife Service
EPA	Environmental Protection Agency
NOAA	National Oceanic and Atmospheric Administration
USDA	United States Department of Agriculture ERS - Economic Research Service SCS - Soil Conservation Service NASS - National Agricultural Statistics Service FS - Forest Service (USFS)

### *Data*

AVHRR	Advanced Very High Resolution Radiometer (Remotely sensed data acquired from NOAA satellites) (USGS)
LUDA	Land Use Data Analysis (USGS)
DLG	Digital Line Graph (USGS)
NADP/NTN	National Acid Deposition Program/National Trends Network (USGS)
NASQAN	National Stream Quality Accounting Network (USGS)
DEM	Digital Elevation Model (USGS)
MLU	Major Land Uses (USDA, ERS)
NRI	National Resources Inventory (USDA, SCS)
NCSS	National Cartographic Soil Survey (USDA, SCS)
PSU	Primary Sampling Unit (USDA, NASS)
FSRAMIS	Forest Service Range Management Information Service (USFS)
FIDC	Forest Insect and Disease Conditions (USFS)
WFS	Wildland Fire Statistics (USFS)
NWI	National Wetlands Inventory (USFWS)
NCBP	National Contaminant Biomonitoring Program (USFWS)
DCW	Digital Chart of the World (DOD)
CENDATA	Census data (Census)
Census/Ag.	Census of Agriculture (Census)
HCN	Historical Climatology Network (NOAA)
NCDPI	National Coastal Pollutant Discharge Inventory (NOAA)
PLS & ESI	Public Land Statistics & Ecological Site Inventory (BLM)
CDIAC	Carbon Dioxide Information Analysis Center (DOE)
MSCET	Month and State Current Emission Trends (DOE)
NPS	National Pesticide Survey (NPS)
AIRS	Aerometric Information Retrieval System (EPA)
CERCLIS	Comprehensive Environmental Response, Compensation and Liability Information System (EPA)
TRI	Toxic Release Inventory (TRI)

## 7.0 REFERENCES

- Abramovitz, J.N., Baker, D.S., Tunstall, D.B. 1990. Guide to key environmental statistics in the U.S. Government. World Resources Institute, Washington, DC, USA.
- Andow, D.A., Kareiva, P.M., Levin, S.A., and Okubo, A. 1990. Spread of invading organisms. *Landscape Ecology*, 4(2/3):171-188.
- Auerbach, M. and Shmida, A. 1987. Spatial scale and the determinants of plant species richness. *Trends in Ecology and Evolution (TREE)*, 2:238-242.
- Barker, J.R. and Tingey, D.T. (Eds.) 1992. *Air Pollution Effects On Biodiversity*. Van Nostrand Reinhold, New York.
- Barrett, G.W. 1981. Stress ecology: an integrative approach. In: Barrett, G.W. and Rosenberg, R. (Eds.) *Stress Effects on Natural Ecosystems*. John Wiley & Sons Ltd., New York.
- Begon, M., Harper, J.L., and Townsend, C.R. 1986. *Ecology: Individuals, Populations, and Communities*. 2nd. Ed. Blackwell, Boston.
- Bennett, A.F. 1990. Habitat corridors and the conservation of small mammals in a fragmented forest environment. *Landscape Ecology*, 4(2/3):109-122.
- Benton, M.J. 1987. The history of the biosphere: equilibrium and non-equilibrium models of global diversity. *Trends in Ecology and Evolution (TREE)*, 2:153-156.
- Blais, J.R. 1985. The ecology of eastern spruce budworm: a review and discussion. In: Sanders, C.J., Stark, R.W., Mullins, E.J., and Murphy, J. (Eds.) *Recent Advances in Spruce Budworm Research*. pp. 49-59. *Proceedings of the CANUSA Spruce Budworm Research Symposium*, Bangor, ME, September, 16-20, 1984.
- Boecklen, W.J. 1986. Effects of habitat heterogeneity on the species-area relationships of forest birds. *Journal of Biogeography*, 13:59-68.
- Bolger, D.T., Alberts, A.C., and Soulé, M.E. 1991. Occurrence patterns of bird species in habitat fragments: sampling, extinctions and nested species subsets. *American Naturalist*, 137(2):155-166.
- Brown, J.F., Loveland, T.R., Merchant, J.W., Reed, B.C., and Ohlen, D.O. 1993. Using multisource data in global landcover characterization: concepts, requirements, and methods. *Photogrammetric Engineering and Remote Sensing*, 59(6):977-987.
- Brown, J.H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. *Ecology*, 54:775-787.
- Brown, J.H. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. *American Zoologist*, 21:877-888.
- Brown, J.H. 1988. Species diversity. In: Myers, A.A. and Giller, P.S. (Eds.) *Analytical Biogeography*. pp. 57-89. Chapman Hall, London.
- Brown, J.H. and Gibson, A.C. 1983. *Biogeography*. Mosby, St. Louis.
- Burgess, R.L. and Sharpe, D.M. (Eds.) 1981. *Forest Island Dynamics in Man-dominated Landscapes*. Springer-Verlag, New York.
- Cody, M.L. 1974. *Competition and the structure of Bird Communities*. Princeton University Press, Princeton.
- Cody, M.L. and Diamond, J.M. (Eds.) 1975. *Ecology and the Evolution of Communities*. Belknap Press of Harvard University, Cambridge.

- Cole, J.J., Peierls, B.L., Caraco, N.F., and Pace, M.L. 1993. Nitrogen loading of rivers as a human-driven process. In: McDonnell, M.J. and Pickett, S.T.A. (Eds.) *Humans as Components of Ecosystems*. pp. 141-157. Springer-Verlag, New York.
- Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science*, 199:1302-1310.
- Cook, R.E. 1969. Variation in species density of North American birds. *Systematic Zoologists*, 18-81.
- Cooperrider, A.Y. 1990. Conservation of biological diversity on western rangelands. *Transactions of the North American Wildlife and Natural Resources Conference*, 55:451-461.
- Currie, D.J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist*, 137(1):27-49.
- Dickson, W. 1986. Acidification effects in the aquatic environment. In: Schneider, T. (Ed.) *Acidification and Its Policy Implications*. *Studies in Environmental Science* 30. pp. 19-28. Elsevier Science Publishers, Amsterdam, The Netherlands.
- Dobkin, D.S. 1992. Neotropical migrant landbirds in the northern Rockies and Great Plains. USDA, Forest Service, Northern Region, Publication No. R1-93-94, Missoula, MT, USA.
- Dottavio, CL. and Dottavio, F.D. 1984. Potential benefits of new satellite sensors for wetland mapping. *Photogrammetric Engineering and Remote Sensing*, 50(5):599-606.
- Environmental Systems Research Institute (ESRI). 1992. ArcUSA™ 1:2M, Users Guide & Data Reference. Environmental Systems Research Institute, Redlands, CA, USA.
- Ehrlich, P.R., and Ehrlich, A.H. 1981. *Extinction: The Causes and Consequences of the Disappearance of Species*. Random House, New York, NY, USA.
- Ewell J.J. 1986. Invasibility: lessons from south Florida. In: Mooney, H.A. and Drake, J.A. (Eds.) *Ecology of Biological Invasions of North America and Hawaii*. pp. 214-230. Springer-Verlag, New York.
- Finch, D.M. 1992. Threatened, Endangered, and Vulnerable Species of Terrestrial Vertebrates in the Rocky Mountain Region. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-215, Fort Collins, CO, USA.
- Fischer, A.G. 1960. Latitudinal variations in organic diversity. *Evolution*, 14:64-81.
- Forman, R.T.T. and Godron, M. 1986. *Landscape Ecology*. John Wiley & Sons. New York, USA.
- Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications*, 3(2):202-205.
- Gervin, J.C., Kerber, A.G., Witt, R.G., Lu, Y.C., and Sekhon, R. 1985. Comparison of level 1 land cover classification accuracy for MSS and AVHRR data. *International Journal of Remote Sensing*, 6(1):47-57.
- Genoways, H.H. 1986. Causes for large mammals to become endangered or threatened. In: Majumdar, S.K., Brenner, F.J., and Rhoads, A.F. (Eds.) *Endangered and Threatened Species Programs in Pennsylvania and Other States: Causes, Issues, and Management*. pp. 234-251. Pennsylvania Academy of Science, Lafayette College, Easton, PA, USA.
- Glenn-Lewin, D.C. 1977. Species diversity in North American temperate forests. *Vegetatio*
- Goodall, D.W. 1970. Statistical Plant Ecology. *Annual Review of Ecology and Systematics*, 1:99-124.

- Gregory, S.V., Swanson, F.J., McKee, W.A., and Cummins, K.W. 1990. An ecosystem perspective of riparian zones. *Bioscience*, 41(8):540-551.
- Greig-Smith, P. 1983. *Quantitative Plant Ecology*. 3rd. Ed. University of California Press, Berkeley.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature*, 242:344-347.
- Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review*, 52:107-145.
- Hall, C.A.S., Stanford, J.A., and Hauer, F.R. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. *Oikos*, 65:377-390.
- Harris, L.D. 1984. *The Fragmented Forest*. University of Chicago Press. Chicago, IL, USA.
- Hengeveld, R. 1989. *Dynamics of Biological Invasions*. Chapman Hall, New York.
- Hodges, L. 1977. *Environmental Pollution*. Holt, Rinehart and Winston, New York, NY, USA.
- Hubbell, S.P. 1980. Seed predation and the coexistence of tree species in tropical forests. *Oikos*, 35:214-229.
- Huston, M.A. 1979. A general hypothesis of species diversity. *American Naturalist*, 113:81-101.
- Jensen, J.R., Hodgson, M.E., Christensen, E., Mackey, H.E., Jr., Tinney, L.R., and Sharitz, R. 1986. Remote sensing inland wetlands: a multispectral approach. *Photogrammetric Engineering and Remote Sensing*, 52(1):87-100.
- Jensen, J.R., Narumalani, S., Weatherbee, O., and Mackey, H.E., Jr. 1991. Remote sensing offers an alternative approach for mapping wetlands. *Geo Info Systems*, 1(9):46-53.
- Kauffman, J.B. and Krueger, W.C. 1984. Livestock impacts on riparian ecosystems and streamside management implications ... a review. *Journal of Range Management*, 37(5):430-438.
- Karl, T.R., Williams, C.N., and Quinlan, F.T. 1990. United States Historical Climatology Network (HCN) serial temperature and precipitation data. Environmental Sciences Division Publication No. 3404, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA.
- Kiester, R.A. 1971. Species density of North American amphibians and reptiles. *Systematic Zoology*, 20:127-157.
- Kiester, R.A., White, D., Preston, E.M., Master, L.L., Loveland, T.R., Bradford, D.F., Csuti, B.A., O'Connor, R.J., Davis, F.W., and Stoms, D.M. 1993. Research plan for pilot studies of the Biodiversity Research Consortium. U.S. Environmental Protection Agency, Corvallis, OR, USA.
- Kolasa, J. and Pickett, S.T.A. (Eds.) 1991. *Ecological Heterogeneity*. Springer-Verlag, New York.
- Krebs, C.J. 1985. *Ecology: The Experimental Analysis of Distribution and Abundance*, 3rd Ed. Harper & Row, Publishers, Inc., New York.
- Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V., and Coleman, P.R. 1987. Landscape patterns in a disturbed environment. *Oikos*, 48:321-324.
- Larcher, W. 1980. *Physiological Plant Ecology*. Springer-Verlag, New York.

- Lauga, J. and Joachim, J. 1992. Modelling the effects of forest fragmentation on certain species of forest-breeding birds. *Landscape Ecology*, 6(3):183-194.
- Leith, H. 1975. Primary productivity of the major vegetation units of the world. In: Lieth, H. and Whittaker, R.H. (Eds.) pp. 203-216. *Primary Productivity of the Biosphere*. Springer-Verlag, New York, NY, USA
- Leith, H. and Box, E.O. 1972. Evapotranspiration and primary productivity: C.W. Thornthwaite Memorial Model. *Publications in Climatology*, 25(2):37-46. Elmer, New Jersey: C.W. Thornthwaite Associates.
- Leslie, D.M., and Douglas, C.L. 1979. Desert bighorn sheep of the River Mountains, Nevada. *Wildlife Monographs*, 66:5-56.
- Levin, S.A., Powell, T., and Steele, J.H. (Eds.) 1993. *Path Dynamics*. Springer-Verlag, New York.
- Lindroth, C.H. 1957. *The Faunal Connections Between Europe and North America*. Almqvist and Wiksell, Stockholm.
- Light, J.T. 1973. The effects of oxidant air pollution on forest ecosystems of the San Bernardino Mountains, Section B. In: Taylor, O.C. (Ed.) *Oxidant air pollution effects on a western coniferous forest ecosystem: Task B report*. Air Pollution Research Center, University of California, Riverside.
- Loucks, O.L. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist*, 10:17-25.
- Loveland, T.R., Merchant, J.W., Ohlen, D.O., Brown, J.F. 1991. Development of a land-cover characteristics database for the conterminous U.S. *Photogrammetric Engineering and Remote Sensing*, 57(11):1453-1463.
- Lyon, L.J. 1979. Habitat effectiveness for elk as influenced by roads and cover. *Journal of Forestry*, 77:658-660.
- Lyon, L.J. 1983. Road density models describing habitat effectiveness for elk. *Journal of Forestry*, 81:592-595.
- Lynch, J.F. and Whigham, D.F. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation*, 28:287-324.
- MacArthur, R.H. 1965. Patterns of species diversity. *Biological Review*, 40:510-533.
- MacArthur, R.H. 1972. *Geographical Ecology*. Harper and Row, New York.
- MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, USA.
- Mack, R.N. and Thompson, J.H. 1982. Evolution of steppe with few large, hooved animals. *American Naturalist*, 119(6):757-773.
- Mayr, E. 1965. The nature of colonizations in birds. In: Baker, H.G. and Stebbins, G.L. (Eds.) *The Genetics of Colonizing Species*. pp. 29-47. Academic Press, New York.
- Meentemeyer, V. 1984. The geography of organic decomposition rates. *Annals of the Association of American Geographers*, 74:551-560.
- Mitchell, A. 1978. *A Field Guide to the Trees of Britain and Northern Europe*. William Collins and Sons, London.
- Mitsch, W.J. and Gosselink, J.G. 1993. *Wetlands*. 2nd. Ed. Van Nostrand Reinhold, New York.
- Mooney, H.A., Hamburg, S.P., and Drake, J.A. 1986. The invasions of plants and animals into California. In: Mooney, H.A. and Drakes, J.A. (Eds.) *Ecology of Biological Invasions of North America and Hawaii*. pp. 250-272. Springer-Verlag, New York.
- Moriarty, F. 1983. *Ecotoxicology: The Study of Pollutants in Ecosystems*. 2nd. Ed. Academic Press, New York.

- Munroe, E.G. 1948. The Geographical Distribution of Butterflies in the West Indies. Ph.D. Dissertation. Cornell University, Ithaca, New York.
- Munroe, E.G. 1953. The size of island faunas. In: Proceedings of the 7th Pacific Science Congress of the Pacific Science Association, Volume 4, Zoology, Whitcomb and Tombs, Auckland.
- Naiman, R.J., DeCamps, H., and Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications*, 3(2):209-212.
- National Research Council (NRC) 1982. *Impacts of Emerging Agricultural Trends on Fish and Wildlife Habitat*. National Academy Press, Washington, DC, USA.
- Naveh, Z. and Lieberman, A.S. 1984. *Landscape Ecology: Theory and Application*. Springer-Verlag, New York.
- Neilson, R.P., King, G.A., and Koerper, G. 1992. Toward a rule-based biome model. *Landscape Ecology*, 7(1):27-43.
- Newman, J.R., Schreiber, R.K., and Novakova, E. 1992. Air pollution effects on terrestrial and aquatic animals. In: Barker, J.R. and Tingey, D.T. (Eds.) *Air Pollution Effects on Biodiversity*. pp.177-233. Van Nostrand Reinhold, New York.
- Noss, R.F. 1983. A regional landscape approach to maintain diversity. *Bioscience* 33:700-706.
- Noss, R.F. 1987. Protecting natural areas in fragmented landscapes. *Natural Areas Journal*, 7:2-13.
- Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, 4(4):355-364.
- Norton, S.B., Rodier, D.J., Gentile, J.H., van der Schalie, W.H., Wood, W.P., and Slimak, M.W. 1992. A framework for ecological risk assessment at the EPA. *Environmental Toxicology and Chemistry*, 11:1663-1672.
- Odum, E.P. 1979a. Opening address: ecological importance of the riparian zone. In: Johnson, R.R. and McCormick, J.F. (Technical Coords.) *Strategies for Protection and Management of Floodplain Wetlands and Other Riparian Ecosystems*. pp. 2-4. Proceedings of the Symposium, Callaway Gardens, Georgia, December 11-13, 1978, USDA Forest Service, General Technical Report, WO-12, Washington, DC.
- Odum, E.P. 1979b. The value of wetlands: a hierarchical approach. In: Greeson, P.E., Clark, J.R., and Clark, J.E. (Eds.) *Wetland functions and values: the state of our understanding*. pp. 377-388. American Water Resources Technical Application, Minneapolis, MN.
- Odum, E.P., Finn, J.T., Franz, E.H. 1979. Perturbation theory and the subsidy-stress gradient. *Bioscience*, 29(6):349-352.
- Omernik, J.M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers*, 77(1):118-125.
- O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H., and Graham, R.L. 1988. Indices of landscape pattern. *Landscape Ecology*, 1(3):153-162.
- O'Neill, R.V., Turner, S.J., Cullinan, V.I., Coffin, D.P., Cook, T., Conley, W., Brunt, J., Thomas, J.M., Conely, M.R., Gosz, J. 1991. Multiple landscape scales: an intersite comparison. *Landscape Ecology*, 5(3):137-144.



- Orians, G.H. 1986. Site Characteristics Favoring invasions. In. Mooney, H.A. and Drake, J.A. (Eds.) *Ecology of Biological Invasions of North America and Hawaii*. pp. 133-148. Springer-Verlag, New York.
- Orians, G.H. 1994. Global biodiversity I: patterns and processes. In. Meffe, G.K. and Carroll, C.R. (Eds.) *Principles in Conservation Biology*. pp. 78-109. Sinauer Associates, Sunderland.
- Owen, J.G. 1990a. Patterns of mammalian species richness in relation to temperature, productivity, and variance in elevation. *Journal of Mammalogy*, 71(1):1-13.
- Owen, J.G. 1990b. An analysis of the spatial structure of mammalian distribution patterns in Texas. *Ecology*, 71(5):1823-1832.
- Paine, R.T. 1966. Food web complexity and species diversity. *American Naturalist*, 100:65-75.
- Peterle, T.J. 1993. *Wildlife Toxicology*. Van Nostrand Reinhold, New York.
- Pianka, E.R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist*, 100:33-46.
- Pianka, E.R. 1967. On lizard species diversity: North American flatland deserts. *Ecology*, 48(3):333-351.
- Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In. Likens, G.E. (Ed.) *Long-Term Studies in Ecology: Approaches and Alternatives*. pp. 110-135. Springer-Verlag, New York.
- Pickett, S.T.A., Collins, S.J., and Armesto, J.J. 1987. Models, mechanisms, and pathways of succession. *Botanical Review*, 53:335-371.
- Pickett, S.T.A., and Thompson, J.N. 1978. Patch dynamics and the design of nature reserves. *Biological Conservation*, 13:27-37.
- Pickett, S.T.A. and White, P.S. (Eds.) 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Pielou, E.C. 1979. *Biogeography*. John Wiley & Sons, New York.
- Pimm, S.L., Hone, H.L., and Diamond, J.M. 1988. On the risk of extinction. *American Naturalist*, 132:757-785.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology*, 43:185-215, 410-432.
- Quinlan, F.T., Karl, T.R., and Williams, C.N. 1987. United States Historical Climatology Network (HCN) serial temperature and precipitation data. NDP-019, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA.
- Rhode, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 65(3):514-527.
- Richardson, C.J. 1979. Primary productivity values in freshwater wetlands. In. Greeson, P.E., Clark, J.R., and Clark, J.E. (Eds.) *Wetland Functions and Values: The State of Our Understanding*. pp. 131-145.
- Ricklefs, R. and Schluter, D. (Eds.) 1993. *Species Diversity*. University of Chicago Press, Chicago.
- Risser, P.G., Karr, J.R., and Forman, R.T.T. 1984. Landscape ecology: directions and approaches. Special Publication No. 2. Illinois Natural History Survey. Champaign, IL, USA.
- Roath, L.R. and Krueger, W.C. 1982. Cattle grazing influence on a mountain riparian zone. *Journal of Range Management*, 35:100-104.
- Romme, W.H. and Knight, D.K. 1982. Landscape diversity: the concept applied to Yellowstone Park. *Sioscience*, 32(8):664-670.

- Rosenzweig, M.L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. *American Naturalist*, 102:67-74.
- Roughgarden, J. 1986. Predicting invasions and rates of spread. In: Mooney, H.A. and Drake, J.A. (Eds.) *Ecology of Biological Invasions of North America and Hawaii*. pp. 179-188. Springer-Verlag, New York.
- Rykiel, E.J. Jr. 1985. Toward a definition of ecological disturbance. *Australian Journal of Ecology*, 10:361-365.
- Saunders, D.A., Hobb, R.J., and Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, 5:18-27.
- Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'erchia, F., Edwards, T.C., Ulliman, J., and Wright, R.G. 1993. Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs*, 123:1-41.
- Schindler, D.W., Kaslan, S.E.M., and Hesslein, R.H. 1989. Biological impoverishment of lakes in the midwestern and northeastern United States from acid rain. *Environmental Science and Technology*, 23(5):573-589.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science*, 185:27-39.
- Schoener, T.W. 1988. Ecological interactions. In: Myers, A.A. and Giller, P.S. (Eds.) *Analytical Biogeography*. pp. 255-297. Chapman Hall, London.
- Senft, R.L., Rittenhouse, L.R. and Woodmasee, R.G. 1983. The use of regression models to predict spatial patterns of cattle behavior. *Journal of Range Management*, 36:553-557.
- Senft, R.L., Rittenhouse, L.R. and Woodmasee, R.G. 1985. Factors influencing patterns of cattle grazing behavior in a shortgrass steppe. *Journal of Range Management*, 38:82-87.
- Shmida, A. and Wilson, M.V. 1985. Biological determinants of species diversity. *Journal of Biogeography*, 12:1-20.
- Simpson, G.G. 1964. Species density of North American recent mammals. *Systematic Zoology*, 13:57-73.
- Skellam, J.G. 1951. Random dispersal in theoretical populations. *Biometrika*, 38:196-218.
- Smith, M.S. 1988. Modeling: three approaches to predicting how herbivore impact is distributed in rangelands. New Mexico Agricultural Experiment Station Report 628.
- Soulé, M.E., Alberts, A.C., Bolger, D.T. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. *Oikos*, 63:39-47.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Sauvajot, R.S., Wright, J., Soricé, M., and Hill, S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*, 2:75-92.
- Soulé, M.E. and Kohm, K.A. (Eds.) 1989. *Research Priorities for Conservation Biology*. Island Press, Washington, DC, USA.
- Steele, J.H. (Ed.) 1978. *Spatial Patterns in Plankton Communities*. Plenum Press, New York.
- Steila, D. 1976. *The Geography of Soils*. Prentice-Hall, Inc., Englewood Cliffs, NJ, USA.
- Storm, G.L., Andrews, R.L., Phillips, R.L., Bishop, R.A., Sniff, D.B., and Tester, J.R., 1967. Morphology, reproduction, dispersal and mortality of midwestern red fox populations. *Wildlife Monographs*, 49:5-82.

- Suffling, R., Lihou, C., and Morand, Y. 1988. Control of landscape diversity by catastrophic disturbance: a theory and case study of fire in a Canadian boreal forest. *Environmental Management*, 12:73-78.
- Temple, S.A. and Wiens, J.A. 1989. Bird populations and environmental changes: can birds be bio-indicators? *American Birds*, 43(2):260-270.
- Thiel, R.P. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. *American Midland Naturalist*, 113(2):404-407.
- Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology*, 74:2179-2191.
- Tilman, D. and Pacala, S. 1993. The maintenance of species richness in plant communities. In: Ricklefs, R. and Schluter, D. (Eds.) *Species Diversity*. pp. 13-25 University of Chicago Press, Chicago.
- Thomas, J.W., Maser, C., and Rodiek, J.E. 1979. Wildlife habitat in managed rangelands-the Great Basin of Southeastern Oregon. Riparian Zones. USDA Forest Service General Technical Report PNW-80, Portland, OR, USA.
- Thomas, J.W., Miller, R.J. Black, H., Rodiek, J.E., and Maser, C. 1976. Guidelines for maintaining and enhancing wildlife habitat in forest management in the Blue Mountains of Oregon and Washington. Transactions of the North American Wildlife and Natural Resource Conference, 41:452-476.
- Turner, S.J., O'Neill, R.V., Conley, W., Conley, M.R., and Humphries, H.C. 1991. Pattern and scale: statistics for landscape ecology. In: Turner, M.G. and Gardner, R.H. (Eds.) *Quantitative Methods in Landscape Ecology*. pp. 17-41. Springer-Verlag, New York.
- Trewartha, G.T. 1961. *The Earth's Problem Climates*. University of Wisconsin Press, Madison.
- Truhaut, R. 1977. Ecotoxicology: objectives, principles and perspectives. *Ecotoxicology and Environmental Safety*, 1:151-173.
- U.S. Congress, Office of Technology Assessment (OTA) 1987. Technologies to Maintain Biological Diversity, OTA-F-330. U.S. Government Printing Office, March, 1987, Washington, DC, USA.
- USDA, 1987. State Soil Geographic Data Base (STATSGO). United States Department of Agriculture, Soil Conservation Service, Miscellaneous Publication Number 1492, Washington, DC, USA.
- USDA, 1989. 1987 Census of Agriculture. Volume 1, Geographic Area Series, Part 51, United States Summary Data, AC87-A-51. Washington, DC.
- USEPA. 1990. Reducing risk. setting priorities and strategies for environmental protection. Science Advisory Board, Relative Risk Reduction Strategies Committee.
- Usher, M.B. 1988. Biological invasions of nature reserves: a search for generalisations. *Biological Conservation*, 44:119-135.
- Verboom, B. and van Apeldoorn, R. 1990. Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris* L. *Landscape Ecology* 4(2/3):171-176.
- Waddell, T.E., Bower, B.T., and Cox, K. 1988. Managing agricultural chemicals in the environment: the case for a multi-media approach. The Conservation Foundation. Washington, DC, USA.
- Wharton, C.H., Kitchens, W.M., Pendelton, E.C., and Sipe, T.W. 1982. The ecology of bottomland hardwood swamps of the southeast: a community profile. U.S. Fish and Wildlife Service, Biological Services Program FWS/OBS-81/37, Washington, DC.

- Whiteside, M.C. and Harmsworth, R.V. 1967. Species diversity in Chydorid (*Cladocera*) communities. *Ecology*, 48:664-667.
- Whittaker, R.H. and Niering, W.A. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. *Ecology*, 46:429-452
- Wilcove, D.S. 1987. From fragmentation to extinction. *Natural Areas Journal*, 7(1):23-29.
- Wilcove, D.S., McLellan, C.H., and Dobson, A.P. 1986. Habitat fragmentation in the temperate zone. In: Soule, M.E. (Ed.) *Conservation Biology: The Science of Scarcity and Diversity*. pp. 234-256. Sinauer Assoc. Inc., Sunderland, MA, USA.
- Wilcox, B.A. and Murphy, D.D. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist*, 125:879-887.
- Williams, C.E. 1964. *Patterns in the Balance of Nature and Related Problems in Quantitative Ecology*. Academic Press, New York.
- Williams, M. 1991. Understanding wetlands. In: Williams, M. (Ed.) *Wetlands: A Threatened Landscape*. pp. 1-41. Basil Blackwell Ltd., Cambridge, MA, USA.
- Williamson, M. 1988. Relationship of species number to area, distance and other variables. In: Myers, A.A. and Giller, P.S. (Eds.) *Analytical Biogeography*. pp. 91-115. Chapman Hall, London.
- Wright, D.H. 1983. Species-energy theory: an extension of species-area theory. *Oikos*, 41:496-506.
- Wu, J. 1989. The theory of island biogeography: models and applications. *Journal of Ecology (China)*, 8(6):34-39.
- Wu, J. 1992. Detecting spatial patterns: the net-function of interpolation. *Coenoses*, 7(3):137-143.
- Wu, J. and Levin, S.A. 1994. A spatial patch dynamic modeling approach to pattern and process in an annual grassland. *Ecology*, 75:1393-1429.
- Wu, J., Li, B., and Wu, Y. 1992. Patchiness and patch dynamics: I. concepts and mechanisms. *Journal of Ecology (China)*, 11(4):41-45.
- Wu, J. and Loucks, O.L. 1992. The balance-of-nature and modern ecological theory: a shift in ecological thinking. In: Sine-ECO (Ed.) *Advances in Modern Ecology*. pp. 16-29. Science and Technology Press, Beijing.
- Wu, J. and Vankat, J.L. 1991. A system dynamics model in island biogeography. *Bulletin of Mathematical Biology*, 53:911-940.
- Wu, J. and Vankat, J.L. 1994. Island biogeography: theory and applications. In: *Encyclopedia of Environmental Biology*, Academic Press, New York.
- Yoda, K. 1967. A preliminary survey of the forest vegetation of eastern Nepal. II. General description, structure, and floristic composition of the sample plots chosen from different vegetation zones. *Journal of the College of Arts and Science, Chiba University, National Science Service*, 5:99-140.