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# Effectiveness of biodiversity indicators varies with extent, grain, and region

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## ABSTRACT

The use of indicator taxa for conservation planning is common, despite inconsistent evidence regarding their effectiveness. These inconsistencies may be the result of differences among species and taxonomic groups studied, geographic location, or scale of analysis. The scale of analysis can be defined by grain and extent, which are often confounded. Grain is the size of each observational unit and extent is the size of the entire study area. Using species occurrence records compiled by NatureServe from survey data, range maps, and expert opinion, we examined correlations in species richness between each of seven taxa (amphibians, birds, butterflies, freshwater fish, mammals, freshwater mussels, and reptiles) and total richness of the remaining six taxa at varying grains and extents in two regions of the US (Mid-Atlantic and Pacific Northwest). We examined four different spatial units of interest: hexagon (~649 km<sup>2</sup>), subcoregion (3800–34,000 km<sup>2</sup>), ecoregion (8300–79,000 km<sup>2</sup>), and geographic region (315,000–426,000 km<sup>2</sup>). We analyzed the correlations with varying extent of analysis (grain held constant at the hexagon) and varying grain (extent held constant at the region). The strength of correlation among taxa was context dependent, varying widely with grain, extent, region, and taxon. This suggests that (1) taxon, grain, extent, and study location explain, in part, inconsistent results of previous studies; (2) planning based on indicator relationships developed at other grains or extents should be undertaken cautiously; and (3) planning based on indicator relationships developed in other geographic locations is risky, even if planning occurs at an equivalent grain and extent.

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## 1. Introduction

By some estimates, modern extinction rates are between 100 and 1000 times greater than in the past (Pimm et al., 1995) and

these rates are perhaps even larger in “biodiversity hotspots” (Pimm and Raven, 2000) where many of our most imperiled species are found (Myers et al., 2000). In response to this crisis, preservation of biodiversity is considered by many to be

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one of the most important challenges facing the conservation community today (Balmford et al., 2005). Despite its importance, biodiversity conservation is often hindered by lack of data and resources to collect more data. One popular solution to these problems is the use of surrogate species or taxa, a practice that assumes protection of the surrogate will also protect other species, taxa, or overall biodiversity (Margules and Pressey, 2000).

Surrogates can be subdivided into three broad categories: flagship, indicator, and umbrella (Simberloff, 1998; Caro and O'Doherty, 1999; Andelman and Fagan, 2000). Flagships typically are large, charismatic species with substantial public appeal, whose conservation will indirectly conserve other species that share its habitat. Indicators are species or taxonomic groups whose presence or diversity are associated with overall levels of biodiversity (Landres et al., 1988). Umbrella species are those that utilize such large areas of habitat that protecting them will, by default, protect many other species.

We examined the spatial congruence between species richness of seven indicator taxa and overall levels of species richness at multiple scales. Indicators have been used to focus data collection, conservation planning, and land management on a small number of species or taxa (Simberloff, 1998; Ferrier, 2002). There is empirical evidence that the richness of certain taxonomic groups are indicators of overall species richness in the same geographic unit of analysis (Ricketts et al., 1999; Reyers et al., 2000; Kati et al., 2004; Sauberer et al., 2004; Warman et al., 2004; Lamoreux et al., 2006; Maes et al., 2005; Tognelli, 2005). There is also evidence to the contrary (Prendergast et al., 1993; Howard et al., 1998; Juutinen and Monkkonen, 2004; Heino et al., 2005) and studies with mixed results (Dobson et al., 1997; Ricketts et al., 1999; Moritz et al., 2001; Negi and Gadgil, 2002; Larsen and Rahbek, 2003; Lawler et al., 2003; Meijaard and Nijman, 2003; Moore et al., 2003; Thomas, 2005). Other researchers have used indicator groups successfully in combination with complementarity-based approaches, in which sites are selected to include all or most species in an indicator group (Prendergast et al., 1993; Pressey et al., 1993; Howard et al., 1998; Lawler et al., 2003). On balance, the evidence suggests that the effectiveness of indicators for identifying biodiversity hotspots is context dependent.

Variation in findings is likely the result of differences among species and taxonomic groups studied, geographic location, or scale of analysis (Wiens, 1989; Levin, 1992; Margules and Pressey, 2000; Ferrier, 2002). The scale of a study can be defined in two ways, which are often confounded: grain and extent. Grain is the size of each observational unit and extent is the size of the entire study area (Wiens, 1989). Researchers working at coarse grains or across large extents, such as those at continental or ecoregional scales, have found high, positive correlations between the richness of various taxa and overall species richness (Olson and Dinerstein, 1998; Ricketts et al., 1999; Myers et al., 2000; Lamoreux et al., 2006). However, conservation planning often occurs at finer grains or smaller extents (Cooper, 1998; Reid, 1998; Ferrier, 2002).

Results may differ when the same data are examined at varying grains and extents. For example, Bohning-Gaese

(1997) calculated avian species richness in the Lake Constance region of central Europe. She found that varying grain resulted in different conclusions and management recommendations. Garson et al. (2002) correlated avian species richness with threatened and endangered species richness in southern Quebec and found that the strength of correlation increased with increasing grain size. Larsen and Rahbek (2003) found that decreasing grain size did not significantly affect various correlations identified at coarser grains in Africa. This variety of results is not surprising given the complex relationship between grain, extent, geographic location, and species richness (Palmer and White, 1994; Rosenzweig, 1995; Rahbek, 2005). Several researchers have cited scale as a confounding factor of indicator analysis (Andelman and Fagan, 2000; Weaver, 1995; Bohning-Gaese, 1997; Flather et al., 1997; Margules and Pressey, 2000; Rahbek and Graves, 2000).

Although the studies above investigated various aspects of scale, we know of no previous studies that have varied grain and extent systematically while controlling for other important factors (e.g., taxa, region, spatial units, data collection methods). Here, we investigated the correlation of the species richness of each of seven taxa (amphibians, birds, butterflies, freshwater fish, mammals, freshwater mussels, and reptiles) with the richness of the remaining six taxa while systematically changing the grain and extent of analysis for two regions in the United States (Mid-Atlantic and Pacific Northwest). We performed the analysis at three grains while holding extent constant, and at three extents while holding grain constant. We discuss the implications of our findings for conservation planning.

## 2. Methods

### 2.1. Spatial units

We examined taxa richness correlations in two regions of the United States using four spatial units: 648.7 km<sup>2</sup> hexagons developed originally for a US Environmental Protection Agency ecological monitoring effort (White et al., 1992), Omernik's level IV subcoregions (Omernik, 1987; Gallant et al., 1989), Omernik's level III ecoregions (Omernik, 1987), and the entire region (Table 1, Fig. 1). The hexagons provide complete, continuous spatial coverage of the regions and are located without reference to political or ecological boundaries (White et al., 1992). We included only hexagons that were >50% within the region boundary. Rather than using equal-area aggregations of hexagons for our larger spatial units, we used ecoregions and subcoregions. Although ecoregions and subcoregions vary in size, they are based on ecologically meaningful boundaries that are more likely than aggregations of hexagons to reflect the mechanisms underlying biodiversity patterns. Further, ecoregions are being used in a number of broad-scale conservation planning efforts (e.g., Ricketts et al., 1999; Groves, 2003; Hoekstra et al., 2005; Lamoreux et al., 2006). Ecoregions are defined by abiotic and biotic characteristics including climate, geology, hydrology, land use, physiography, soils, vegetation, and wildlife (Omernik, 1987, 1995). Subcoregions are nested within ecoregions and reflect finer delineation of the same

**Table 1 – Characteristics of spatial units in the Mid-Atlantic and Pacific Northwest regions**

	Mid-Atlantic	Pacific Northwest
States included	Delaware, Maryland, Pennsylvania, West Virginia, Virginia	Oregon, Washington
Region extent: km <sup>2</sup> (n hexagons)	315,000 (487)	426,000 (660)
<i>Varying grain analysis</i>		
Subcoregions: number	44	97
Extent: km <sup>2</sup> (n hexagons aggregated)		
Minimum	730 (1)	270 (1)
Mean	7100 (15)	4370 (10)
Maximum	18,940 (45)	26,580 (53)
Ecoregions: number	12	12
Extent: km <sup>2</sup> (n hexagons aggregated)		
Minimum	750 (2)	2570 (3)
Mean	26,182 (42)	35,480 (56)
Maximum	74,000 (122)	79,300 (125)
<i>Varying extent analysis</i>		
Subcoregions: number	26	58
Extent: km <sup>2</sup> (n hexagons included)		
Minimum	3140 (8)	1750 (6)
Mean	10,810 (23)	6330 (14)
Maximum	18,940 (45)	26,580 (53)
Ecoregions: number	11	11
Extent: km <sup>2</sup> (n hexagons included)		
Minimum	8030 (13)	14,890 (22)
Mean	28,490 (46)	38,470 (61)
Maximum	74,000 (122)	79,300 (124)
Extents are reported in km <sup>2</sup> and numbers of hexagons contributing species data during aggregation (for varying grain analysis) or number of hexagons included (for varying extent analysis). Numbers and sizes are reported separately for the varying grain and varying extent analyses, because ecoregions and subcoregions overlapping fewer than six hexagons were eliminated from the analyses in which extent varied.		

characteristics based on higher resolution data that reveal more detail.

## 2.2. Species data and richness calculations

We used native species occurrence records for seven taxa prepared by Lawler et al. (2003) using data compiled by NatureServe for a US Environmental Protection Agency initiative to address questions about species co-occurrence and relationships between species diversity and landscape diversity (Master, 1996; Master and Stock, 1998) (Table 2). Species occurrences for two regions in the US – the Mid-Atlantic and the Pacific Northwest – were assembled at the hexagon grain using Natural Heritage data identifying the location of species and ecological communities of conservation concern, literature reviews, survey data, range maps, museum records, and expert opinion (Master, 1996; Master and Stock, 1998). The data were compiled, digitized, and reviewed for quality

through cooperative efforts of The Nature Conservancy and the Natural Heritage Programs in each state. For each hexagon, we included occurrence records only for species classified as “confirmed” ( $\geq 95\%$  probability of presence) or “probable” (80–95% probability of presence).

For each hexagon, we calculated species richness for each taxonomic group. When correlating taxon richness to overall richness, we used an index of overall richness that averages the proportional richness of all taxa except the one being correlated against (e.g., when correlating mammal richness to overall richness we excluded mammals from the overall index) (Ricketts et al., 1999). Thus, for each hexagon we calculated seven overall richness indices, each with one taxon excluded:

$$I_t = \frac{1}{6} \sum_{i \neq t} \frac{S_i}{D_i}$$

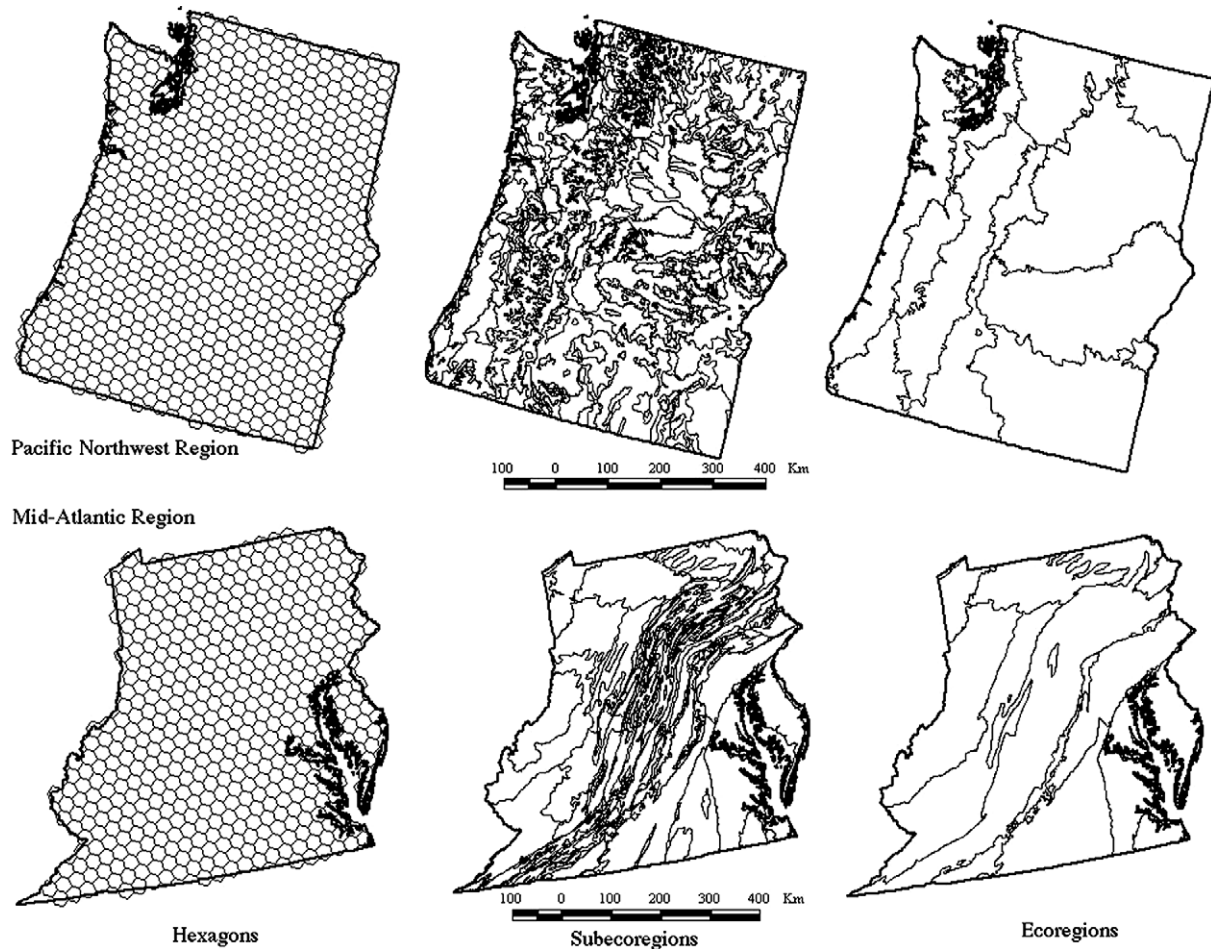
where  $I_t$  is the overall richness index with taxon  $t$  removed,  $S_i$  is the species richness for taxon  $i$  in the hexagon, and  $D_i$  is the number of species in taxon  $i$  in the database for the region (i.e., Mid-Atlantic or Pacific Northwest). This index avoids the dominating effect of more speciose taxa (Ricketts et al., 1999).

For analyses at the subcoregion and ecoregion grains, we aggregated species data within larger spatial units. Because hexagon and ecoregion boundaries do not coincide, we developed a rule to specify whether the species occurring in a hexagon were assigned to an ecoregion or subcoregion that contained only a portion of the hexagon: if a hexagon was included in  $n$  regions, any region containing  $1/n$  or more of the hexagon (by land area) was assigned the species from the hexagon (see Section 4). After species data were aggregated to larger grains, taxa richness and indexes of overall taxa richness were calculated using the same approach used at the hexagon grain. For the varying extent analyses, we used the same rule to determine whether a hexagon that overlapped ecoregion boundaries was considered part of a particular ecoregion or subcoregion.

## 2.3. Correlation analyses

We used Spearman's rank correlation coefficients ( $\rho$ ) for all analyses, because the species data were not distributed normally.

When we varied grain, we held the extent constant at the entire region and calculated correlations at three increasingly large grains (decreasing spatial resolution): hexagon, subcoregion, and ecoregion. At the hexagon grain, correlations were between taxon richness and  $I_t$ . The size of ecoregions and subcoregions varies, so that grain size for these spatial units is not constant (Table 1). To account for species–area relationships, we regressed  $\log(S_i/D_i)$  and  $\log(I_t)$  by  $\log(\text{area})$  for these two grains and performed our correlation analyses using the residuals from these regressions. The residuals represent the remaining variation in richness after the portion attributable to area is removed. These analyses generated three correlation coefficients for each taxon within each region. Each coefficient represents the correlation between richness of that taxon and overall species richness at a particular grain (hexagon, subcoregion or ecoregion) within the region.



**Fig. 1** – Four increasingly large spatial units were used for our analyses: hexagon, subcoregion, ecoregion, and region. When varying grain (hexagon, subcoregion, ecoregion) we held extent constant (Mid-Atlantic region shown in bottom row, and Pacific Northwest region shown in top row). When varying extent (subcoregion, ecoregion, region) we held the grain constant (hexagon).

**Table 2** – Number of species in each of the seven taxonomic groups analyzed in Mid-Atlantic and Pacific Northwest regions

Taxon	Mid-Atlantic	Pacific Northwest	Key data sources (see <a href="#">Master and Stock, 1998</a> for details)
Amphibians	78	34	Natural Heritage data; Catalogue of American Reptiles and Amphibians [range maps]
Birds	208	267	Natural Heritage data; Birds of North America species accounts [range maps]; Christmas Bird Counts [survey data]; Winter Population Studies and Breeding Bird Census [survey data]; Breeding Bird Survey [survey data]; state breeding bird atlases [range maps]
Butterflies	150	172	Natural Heritage data; Eastern US Butterfly Atlas; Atlas of Western Butterflies; Fourth of July Butterfly Counts [survey data]; Butterflies East of the Great Plains [range maps]
Freshwater fish	250	79	Natural Heritage data; Atlas of North American Fishes [range maps]; Field Guide to Freshwater Fishes [range maps]
Mammals	73	142	Natural Heritage data; Mammals of North America [range maps]; American Society of Mammalogist species accounts [range maps]
Freshwater mussels	97	6	Natural Heritage data; The Tribe Alasmidontini (Unionidae: Anodontinae) [range maps]
Reptiles	64	29	Natural Heritage data; Catalogue of American Reptiles and Amphibians [range maps]
Total	920	729	

Data sources used to compile species lists are documented in [Master and Stock \(1998\)](#). Expert opinion was used for all taxa.



When we varied extent, we held grain constant at the hexagon and examined correlations among hexagons within increasingly large extents: subecoregion, ecoregion, and the entire region (Table 1, Fig. 1). We eliminated ecoregions or subecoregions that overlapped fewer than six hexagons as having too few observations for correlation analysis. At regional extents, these analyses generated a single correlation coefficient for each taxon, measured across all hexagons within the region. At ecoregion and subecoregion extents, the analyses yielded many correlation coefficients for each taxon, one for every ecoregion or subecoregion within the Pacific Northwest and Mid-Atlantic. At these two smaller extents we also calculated the average correlation for each taxon at that extent.

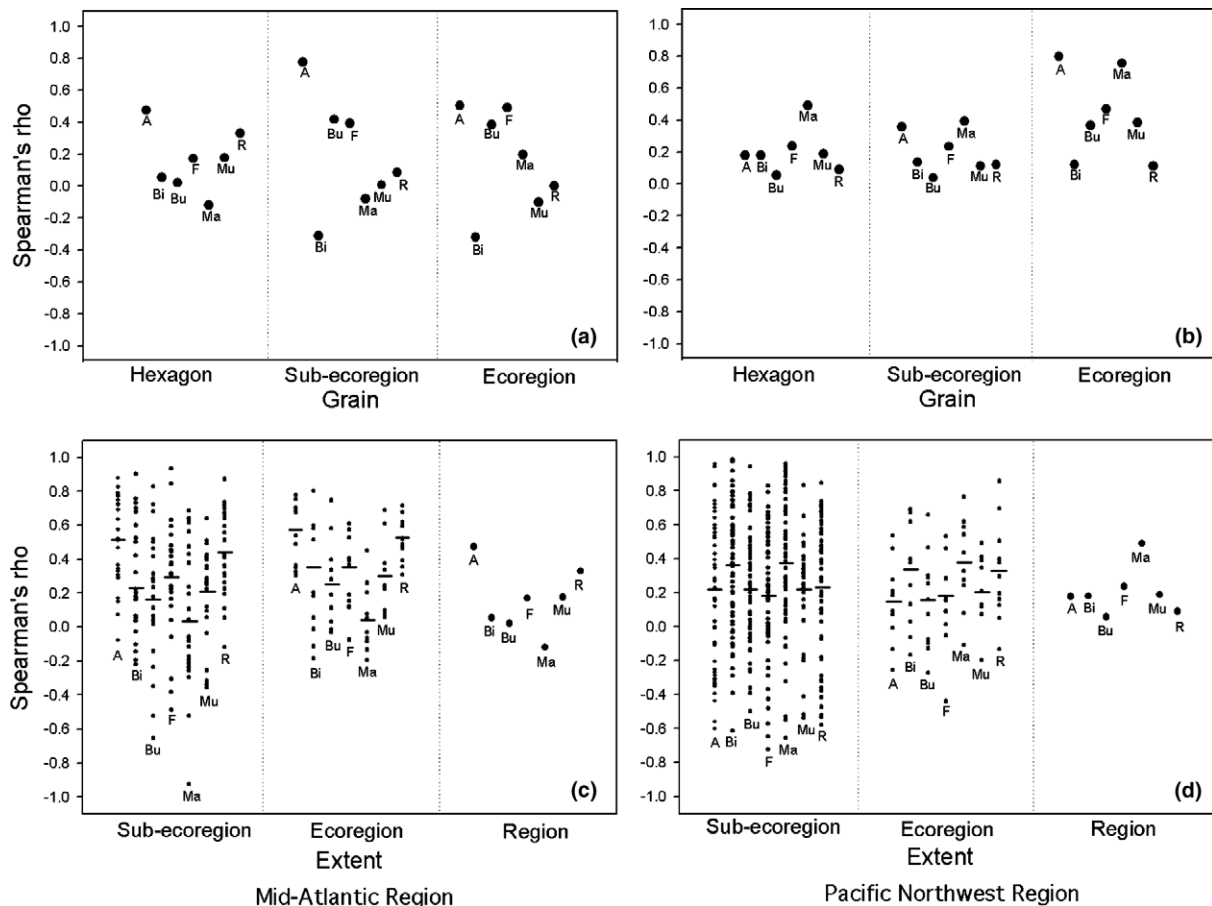
### 3. Results

#### 3.1. Varying grain

In the Mid-Atlantic, there were few discernible general patterns in the strength of the correlations between taxon richness and overall richness (Fig. 2a). Spearman rank

correlation coefficients ranged from  $-0.32$  to  $0.78$  across all grains for all taxa, with negative values mainly among mammals and birds at the subecoregion and ecoregion grains (Table 3). Amphibians had the strongest correlation with overall richness at all grains. Trends in correlation strength for individual taxa varied among taxa as grain size increased. Correlation strength for mammals and fish increased with grain. Correlation strength for mussels and reptiles decreased with grain.

In the Pacific Northwest, the strength of the correlations increased slightly as grain increased from hexagon to ecoregion (Fig. 2b). All correlations were positive, ranging from  $0.04$  to  $0.80$  across all grains for all taxa. The strongest correlation was for amphibians at the ecoregion grain ( $\rho = 0.80$ ). Of all the taxa, mammals were consistently among the most highly correlated at all grains, with amphibians also demonstrating relatively strong relationships to overall biodiversity at the ecoregion grain. Again, trends in correlation strength varied among taxa as grain size increased. Correlation strength for amphibians and fish increased with grain. Correlation strength for other taxa varied unpredictably.



**Fig. 2 – Spearman's rank correlation coefficients ( $\rho$ ) for each taxon for the varying grain (a, b) and varying extent (c, d) analyses for the Mid-Atlantic (a, c) and Pacific Northwest (b, d) regions. Each dot represents a correlation coefficient. In the varying extent analyses (c, d) there is an observation for each taxon in each subecoregion and ecoregion. Bars in the varying extent analyses (c, d) are means of the correlation coefficients for the taxon within the extent. Taxon key: A, amphibian; Bi, birds; Bu, butterflies; F, fish; Ma, mammals; Mu, mussels; R, reptiles.**

**Table 3 – Spearman correlation coefficients for each taxon at each grain for the varying grain analyses (upper half of table) and mean Spearman correlation coefficients (SD) for each taxon at each extent for the varying extent analyses (lower half of table)**

Grain	Mid-Atlantic Region			Pacific Northwest Region		
	Hexagon	Subcoregion	Ecoregion	Hexagon	Subcoregion	Ecoregion
n observations	487	44	12	660	97	12
Amphibians	0.47	0.78	0.50	0.18	0.36	0.80
Birds	0.05	−0.31	−0.32	0.18	0.14	0.12
Butterflies	0.02	0.42	0.38	0.05	0.04	0.36
Fish (freshwater)	0.17	0.39	0.49	0.24	0.25	0.47
Mammals	−0.12	−0.08	0.20	0.49	0.39	0.76
Mussels (freshwater)	0.18	0.01	−0.10	0.19	0.11	0.38
Reptiles	0.33	0.08	0	0.09	0.12	0.11
Extent	Subcoregion	Ecoregion	Region	Subcoregion	Ecoregion	Region
n observations	26	11	1	58	11	1
Amphibians	0.50 (0.28)	0.54 (0.18)	0.47	0.22 (0.36)	0.14 (0.23)	0.18
Birds	0.25 (0.33)	0.31 (0.36)	0.05	0.35 (0.37)	0.33 (0.32)	0.18
Butterflies	0.17 (0.36)	0.24 (0.26)	0.02	0.22 (0.36)	0.15 (0.28)	0.05
Fish (freshwater)	0.28 (0.33)	0.31 (0.22)	0.17	0.17 (0.37)	0.17 (0.29)	0.24
Mammals	0.03 (0.39)	0.05 (0.19)	−0.12	0.36 (0.39)	0.38 (0.25)	0.49
Mussels (freshwater)	0.21 (0.27)	0.27 (0.21)	0.18	0.22 (0.32)	0.20 (0.21)	0.19
Reptiles	0.43 (0.25)	0.51 (0.13)	0.32	0.23 (0.40)	0.32 (0.29)	0.09

### 3.2. Varying extent

In the Mid-Atlantic, amphibian richness had the strongest average correlation with overall richness at all extents, most strongly at the ecoregion extent ( $\rho = 0.54$ , Fig. 2c, Table 3). At the ecoregion extent, there was wide variability in correlation strength for all taxa among ecoregions, including some negative correlations. Variability was even larger at the subcoregion extent, including some relatively strong positive and negative correlations. Mean correlations for each taxon were fairly consistent across the ecoregion and subcoregion extents, but were more varied than in the Pacific Northwest (Fig. 2c and d, Table 3).

In the Pacific Northwest, mammal richness was most strongly correlated with overall richness at the regional extent ( $\rho = 0.49$ ), with remaining correlations positive but weaker (Fig. 2d, Table 3). As in the Mid-Atlantic, variability was high at the ecoregion and subcoregion extents. Mean correlations, however, were relatively weak for all taxa at the ecoregion and subcoregion extents (Fig. 2d, Table 3). No taxon showed consistently strong correlation at all extents.

In both regions, the strength of correlation varied among subcoregions within the same ecoregion (Fig. 3). For a given taxon, many adjacent ecoregions and subcoregions showed very different correlation strength. Taxa that showed relatively strong (or weak) correlation with overall richness for a particular ecoregion showed varying levels of correlation within those ecoregions (Fig. 3: amphibians in the Mid-Atlantic; amphibians, butterflies, and reptiles in the Pacific Northwest). We found no relation between the size of the ecoregions or subcoregions (i.e., number of hexagons included) and the strength of the correlation.

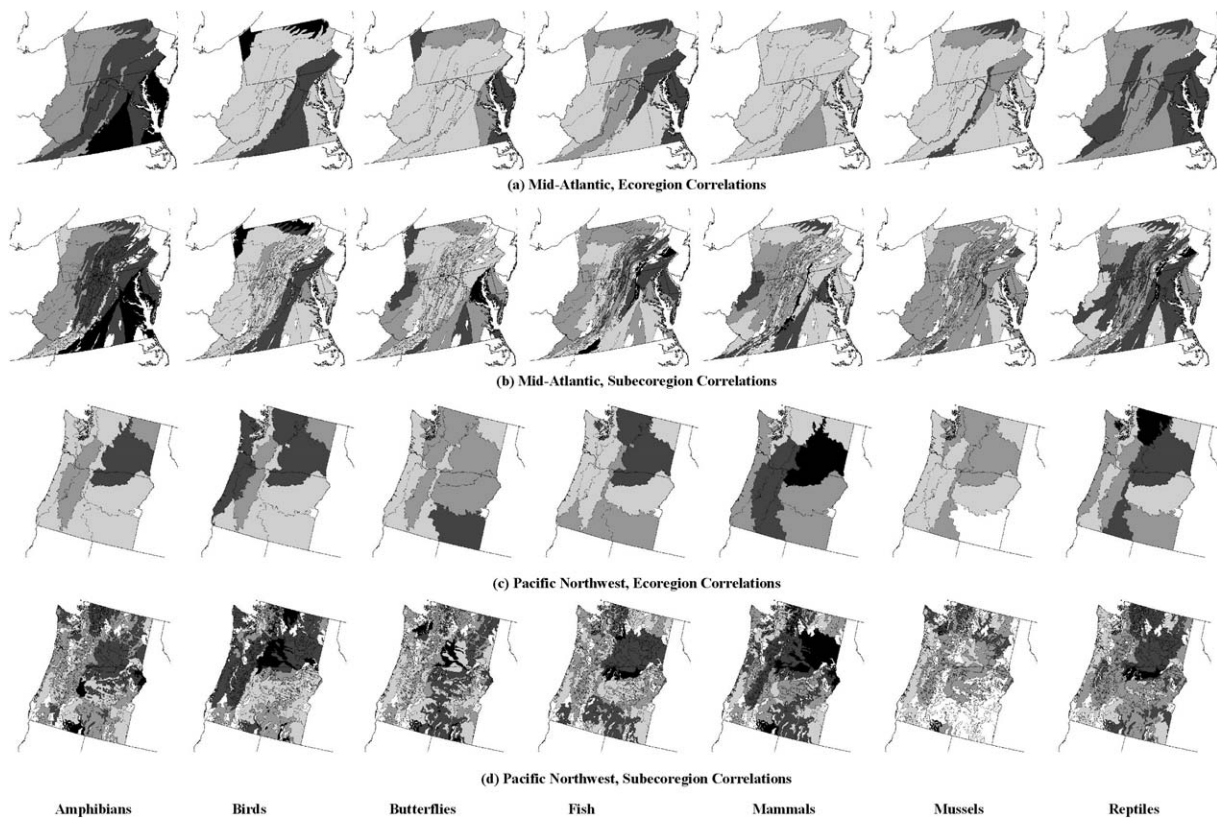
### 3.3. Regional differences

The taxa with the strongest correlation with overall richness varied between the Mid-Atlantic and Pacific Northwest regions. Mammals were among the most highly correlated when we varied grain or extent in the Pacific Northwest; they were among the least correlated in the Mid-Atlantic (Fig. 2). Amphibians had the strongest correlation with overall species richness in both the varying grain and varying extent analyses in the Mid-Atlantic region (Fig. 2a and c). Amphibians also had relatively high correlation when we varied grain in the Pacific Northwest at the subcoregion and ecoregion grains (Fig. 2b), but not when we varied extent (Fig. 2d). Within a particular grain, variation of correlation strength among taxa was greater in the Mid-Atlantic region than in the Pacific Northwest (Fig. 2b and d).

## 4. Discussion

The use of indicator taxa as a conservation tool to identify biodiversity hotspots is viable only if spatial patterns of species richness coincide across taxa. Our results, as well as the work of others (Kerr, 1997; Howard et al., 1998; Whittaker et al., 2005) suggest that these relationships are too context-specific to be reliable, limiting the utility of such an approach as a conservation shortcut. In our study, the performance of the richness of a given taxon as an indicator of total species richness varied widely with the grain, extent, and region of analysis.

Previous studies have yielded inconsistent results regarding the congruence of richness hotspots and the effectiveness of indicator taxa. This seems unsurprising given the range of taxa, grains, extents, geographic locations, and data collection and compilation methodologies covered by the literature.



**Fig. 3 – Absolute value of Spearman's rank correlation coefficient ( $\rho$ ) for ecoregions and subcoregions of the Mid-Atlantic and Pacific Northwest regions from the analyses in which we varied extent; grain is constant at the hexagon size. Correlation strength is shown in quintiles ( $0 \leq |\rho| < 0.2$ ;  $0.2 \leq |\rho| < 0.4$ ;  $0.4 \leq |\rho| < 0.6$ ;  $0.6 \leq |\rho| < 0.8$ ;  $0.8 \leq |\rho| < 1$ ) with darker areas representing stronger correlation; white areas contained fewer than six hexagons and were not analyzed.**

Our results demonstrate that variation in the grain, extent, or location of analysis can lead to such inconsistencies. For example, mammal richness had a relatively strong correlation with overall richness at the ecoregion grain in the Pacific Northwest ( $\rho = 0.76$ , Table 3); in the Mid-Atlantic correlation of mammals was relatively weak at the ecoregion grain ( $\rho = 0.20$ ). At the hexagon grain in the Pacific Northwest, mammals were not very strongly correlated at the regional extent ( $\rho = 0.49$ , Table 3), and the strength of correlation for mammals ranged from  $-0.65$  to  $0.96$  at the subcoregion extent (Fig. 2d). Thus, depending on location, grain, and extent, a researcher might report mammal correlation to overall richness anywhere within the range  $-0.93$  (smallest subcoregion value for the hexagon grain in the Mid-Atlantic) to  $0.96$  (largest subcoregion value for the hexagon grain in the Pacific Northwest).

Researchers working at large grains have found relatively strong correlations between the richness of some taxa or groups of taxa and overall richness (Ricketts et al., 1999; Reyers et al., 2000; Moritz et al., 2001). Although it might be tempting to apply these indicator taxa to local conservation efforts at smaller grains, our research indicates that planning at one grain based on indicator relationships developed at other grains is inadvisable. When we varied grain, the strength of correlation between taxon richness and overall richness differed among taxa at each grain and within each region, as well as between regions. The strength of correlation

varied unpredictably with grain (Fig. 2). Our results correspond to what other researchers have recognized: that the complexity related to species richness and scale implies that planners must exercise caution when applying results from one scale to the solution of problems at other scales (Palmer and White, 1994; Flather et al., 1997; Meijaard and Nijman, 2003).

Planning in one place based on indicator relationships developed in other geographic locations is problematic, even if planning occurs at an equivalent grain and extent. When we varied extent, we found high variability among correlations within an extent for subcoregions and ecoregions (Fig. 2c and d). For example, in the Pacific Northwest correlations between bird richness and overall richness ranged from  $-0.61$  to  $0.99$  among subcoregions (Fig. 2d). Thus, research in one subcoregion might indicate that bird richness is a relatively strong indicator of overall richness, but in another subcoregion the opposite may be true. This variability in correlation strength occurred even among subcoregions nested within the same ecoregion (Fig. 3). Our results were similar to what some other researchers have observed: regional dependence of indicator taxa, with relationships between taxon richness and overall richness fluctuating for different geographic locations (Palmer and White, 1994; Bohning-Gaese, 1997; Rahbek and Graves, 2000). We found differences in the performance of taxa as indicators of overall richness between the Mid-Atlantic and Pacific Northwest in all analyses.

Our analyses were carried out using the best available species data in the United States, a country with numerous organizations and government agencies involved in conservation planning and land-use management. The fact that consistently compiled, rigorously evaluated species data were available for only a single (relatively large) grain for two regions and seven taxa demonstrates how little we still know about biodiversity (Pressey, 2004) and limits our ability to conduct additional tests. Further, there is no quantitative assessment of these data for errors of commission (false presences) and omission (false absences), both of which could affect our analyses. Similar datasets for other parts of the world exist, but are collected for different taxa and at different grains, making comparison difficult (Prendergast et al., 1993; Bonn et al., 2002; Moore et al., 2003; Kati et al., 2004). Nevertheless, further analyses of these other datasets may shed more light on the potential value of indicator taxa.

Hurlbert and White (2005) noted that conclusions drawn from studies like ours depend on whether the species data are derived from surveys or range maps, because range map data portray species locations at a coarser scale than survey data and tend to overestimate the occurrence of species. The data we used were compiled using both range maps and survey data, possibly alleviating the concerns Hurlbert and White (2005) highlight. Nevertheless, more species data and more consistently compiled datasets are needed to uncover patterns in biological diversity that might exist (Margules and Pressey, 2000; Brooks et al., 2004; Thomson et al., 2005; Wilson et al., 2005).

The data we used in our analyses were derived from relatively coarse-grained information (648.7 km<sup>2</sup> hexagons), whereas conservation planning often occurs at finer grains and smaller extents (Cooper, 1998; Reid, 1998; Ferrier, 2002). Indeed, analysis of the 2005 World Database of Protected Areas reveals a median size of 60 ha for the world's protected areas (International Union for Conservation of Nature and Natural Resources Categories 1–4); the hexagons used in our analyses are larger than 97% of protected areas worldwide and 88% of protected areas in the United States (WDPA, 2005). Thus, our conclusions are most applicable to planning efforts to identify priority areas at relatively large scales, rather than efforts to select specific reserves at finer scales.

Our results might be confounded by the manner in which we aggregated species data from hexagons to larger spatial units, because hexagon and ecoregion boundaries do not coincide. Hexagons that overlap ecotonal boundaries might be especially rich in species, containing species from both ecoregions. Thus, the manner in which species from overlapping hexagons are assigned to larger spatial units could affect our results. To explore this possibility, we tried three different aggregation rules:

1. species were assigned to all regions containing a portion of the hexagon;
2. species were assigned only to the region containing the largest portion of the hexagon;
3. if a hexagon was included in  $n$  regions, any region containing  $1/n$  or more of the hexagon (by land area) was assigned the species from the hexagon.

We saw no substantive difference in results among the three rules during preliminary analyses and selected the third rule for the analyses presented here, because it is the moderate choice between the other two more extreme aggregation rules.

## 5. Conclusion

Although testing of additional regions may reveal our results to be the exception rather than the rule, the intra- and inter-regional variability we found suggests serious limitations for conservation planning approaches that use indicator taxa to select biodiversity hotspots. Our interpretation of these results is that (1) choice of taxon, grain, extent, and study location explain, at least in part, the inconsistent results of previous studies examining the congruence of richness hotspots and the potential effectiveness of indicator taxa; (2) planning based on indicator relationships developed at other grains or extents should be done with caution; and (3) planning based on indicator relationships developed in other geographic locations is risky, even if planning is done at an equivalent grain and extent and the locations are close to one another.

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