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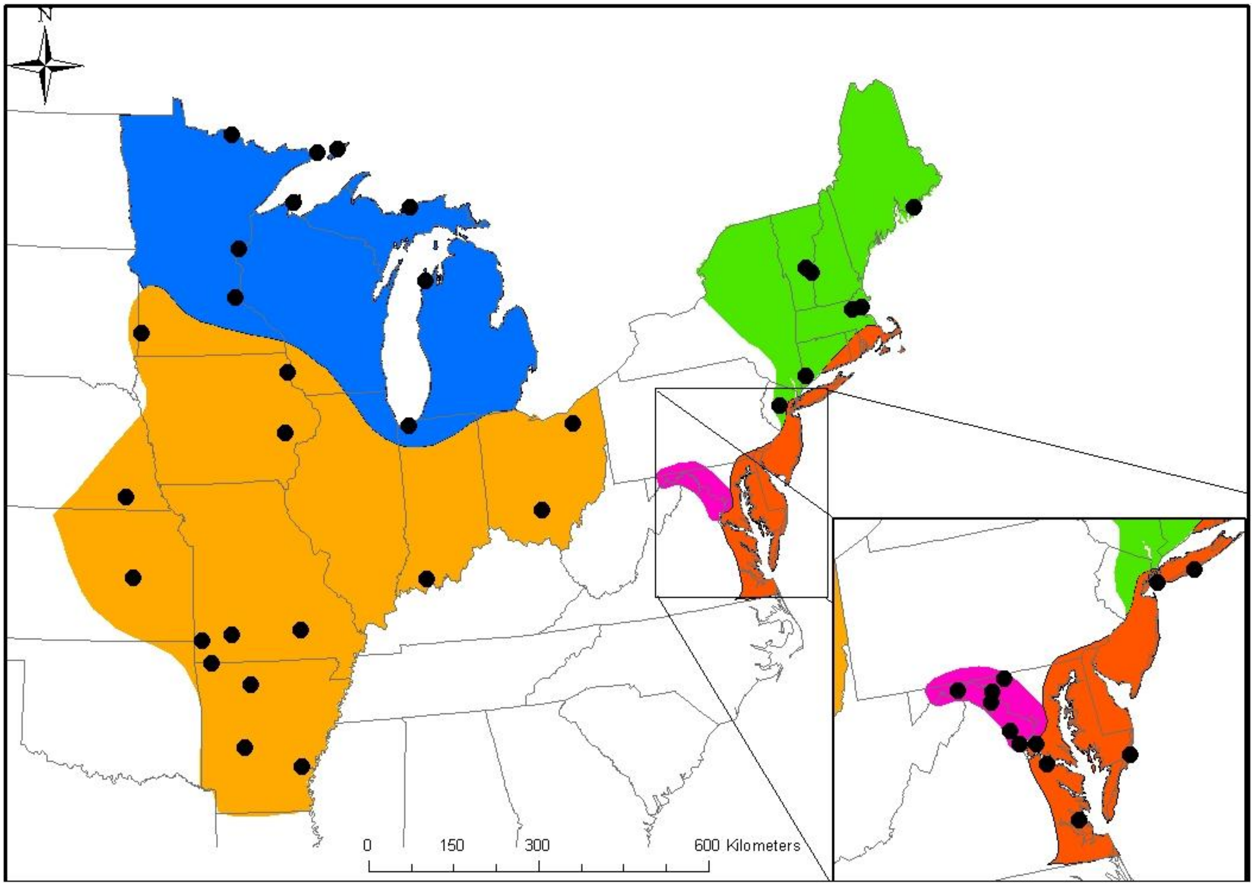
Vascular Plant and Vertebrate Species Richness in National Parks of the Eastern United States

Natural Resource Technical Report NPS/NCR/NCRO/NRTR—2013/002



ON THE COVER
National Park Service (NPS) networks and parks included in this study. See Table 1 for a list of the networks and parks.
Prepared by: Kaci E. Myrick

Vascular Plant and Vertebrate Species Richness in National Parks of the Eastern United States

Natural Resource Technical Report NPS/NCR/NCRO/NRTR—2013/002.

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Abstract

Given the estimates that species diversity is diminishing at 50-100 times the normal rate, it is critical that we be able to evaluate changes in species richness in order to make informed decisions for conserving species diversity. In this study, we examined the potential of vascular plant species richness to be used as a surrogate for vertebrate species richness in the classes of amphibians, reptiles, birds, and mammals. Vascular plants, as primary producers, represent the biotic starting point for ecological community structure and are the logical place to start for understanding vertebrate species associations. We used data collected by the United States (US) National Park Service (NPS) on species presence within parks in the eastern US to estimate simple linear regressions between plant species richness and vertebrate richness. Because environmental factors may also influence species diversity, we performed simple linear regressions of species richness versus natural logarithm of park area, park latitude, mean annual precipitation, mean annual temperature, and human population density surrounding the parks. We then combined plant species richness and environmental variables in multiple regressions to determine the variables that remained as significant predictors of vertebrate species richness. As expected, we detected significant relationships between plant species richness and amphibian, bird, and mammal species richness. In some cases, plant species richness was predicted by park area alone. Species richness of mammals was only related to plant species richness. Reptile species richness, on the other hand, was related to plant species richness, park latitude and annual precipitation, while amphibian species richness was related to park latitude, park area, and plant species richness. Thus, plant species richness predicted species richness of different vertebrate groups to varying degrees and should not be used exclusively as a surrogate for vertebrate species richness. Plant species richness should be included with other variables such as area and climate when considering strategies to manage and conserve species in US National Parks. It is not always appropriate to draw conclusions about analyses of taxonomic surrogates from one area to another. Two patterns evident from the linear regressions were the increase in species richness with the increase of park area and with increase of vascular plant species richness. To test whether there were differences in these patterns among networks, we used analysis of covariance (ANCOVA). Differences among networks were detected only in bird species richness versus plant species richness and for all taxa except mammals for vertebrate species richness versus park area. Some of these results may be due to small sample size among networks, and therefore, low statistical power. Other factors that could have contributed to these results were differences in average park area and habitat heterogeneity among networks, latitudinal gradients, low variation in mean annual precipitation, and different use of vegetation by migratory species. Based on these results we recommend that management of biodiversity be approached from local and site specific criteria rather than applying management directives derived from other regions of the US. It is also recommended that analyses similar to those presented here be conducted for all national parks, once data become available for all networks in the US, to gain a better understanding of how vascular plant species richness, area, and vertebrate species richness are related in the US.

Keywords

Analysis of covariance, linear regression, National Park, species richness, United States

Introduction

Species diversity is thought to be decreasing at 50-100 times the natural rate (ISCBD 1994). The sharp decrease is due primarily to anthropogenic disturbance that seems likely to continue (Kerr and Currie 1995, Loreau et al. 2001). There has also been increasing attention paid to the effects that global warming may have on species distributions and persistence (Parmesan 1996, Hughes 2000, McCarty 2001, Walther et al. 2002).

The United States (US) Congress, in 1998, passed the National Parks Omnibus Management Act, which mandated a program for the National Park Service (NPS) to inventory and monitor natural resources in National Parks (NPS 1999). One resource that the NPS is required to monitor is species diversity. Monitoring species diversity can be challenging. There are often large numbers of species in National Parks (hereafter, “parks”) and many animal species are cryptic, highly mobile and difficult to detect. A monitoring program that requires a list of all species that occur in parks may be unrealistic because of the time and effort required to obtain complete, reliable lists (Noss 1990, Gaston 1996, Balmford and Gaston 1999, Sauberer et al. 2004).

Species are not evenly distributed around the globe (Wallace 1878, Gaston 2000) and the patterns observed in species diversity at different scales, as well as arguments made for the most appropriate scale (e.g., local, regional, and global) at which to analyze species diversity for causal relationships is controversial (Flather et al. 1997, Huston 1999a). Techniques such as hotspot analysis, GAP analysis, and place prioritization algorithms have been developed to identify areas of species diversity (Flather et al. 1997, Kelley et al. 2002, Lamoreux et al. 2006). Yet, these techniques were not explicitly developed for purposes of predicting species diversity. One approach that has been used extensively for predicting a component of species diversity, species richness (i.e., the number of species) is the use of taxonomic surrogates (Kremen 1992, Prendergast et al. 1993, Howard et al. 1998, Hopkinson et al. 2001, Warman et al. 2004b, Hawkins and Pausas 2004). In the context of estimating species richness, research on taxonomic surrogates assesses whether the presence of one well-surveyed group will predict the species richness of other less well-surveyed or not easily surveyed groups (Landres et al. 1988, Caro and O’Doherty 1999).

Taxonomic surrogates offer a coarse measure of the number of species of a variety of taxonomic groups at larger spatial and temporal scales based on the species richness in one taxonomic group, the surrogate (Landres et al. 1988). The usefulness of taxonomic surrogates for estimating species richness appears to be influenced by the taxonomic groups used in the analysis, the spatial scale of the study, and species biogeography (Gaston 1996, Flather et al. 1997, Howard et al. 1998, Warman et al. 2004a). Relationships between groups of higher taxa have generally been weak (Gaston 1996) but plant species richness has been useful for predicting richness of vertebrates, fungi, and insects (Scott et al. 1987, Panzer and Schwartz 1998, Andelman and Fagan 2000, Boone and Krohn 2000, Pharo et al. 2000, Reyers et al. 2000, Lund and Rahbek 2002, Vessby et al. 2002, Hawkins and Pausas 2004, Chiarucci et al. 2005, Zhao et al. 2006, Kissling et al. 2007).

Vascular plants, as primary producers, represent a biotic starting point for understanding ecological relationships and are a logical starting point for evaluating taxonomic surrogates (Loreau et al. 2001). Moreover, because of plant immobility, they are often easier to detect and, hence, monitor than animals. Examining relationships between plant species richness and richness of vertebrate taxa may be useful because surveys to detect these kinds of animals often require specialized sampling techniques and extensive survey effort (Boulinier et al. 1998). The purpose of this study was to assess the extent to which plant species richness could predict the species richness of the major terrestrial vertebrate taxa (i.e., amphibians, birds, mammals, and reptiles) in the northeastern and central US (hereafter, "eastern US"). The assumed mechanism is that a greater diversity of resources should support a greater diversity of consumers (Huston 1979, Hawkins and Porter 2003). Recognizing that plant diversity alone probably does not estimate vertebrate species richness very well, we also included total park area, park latitude, mean annual precipitation, human population density, and mean annual temperature as environmental variables in our analyses. These environmental variables have been shown to be correlated with species diversity and distribution in other studies (Schall and Pianka 1978, Rohde 1992, Qian 1998, Krebs 2001).

Two patterns are evident in previous studies of species richness. One pattern is the positive relationship between the area sampled and species richness (Arrhenius 1921, Cain 1938, Preston 1960, Williams 1964, Rosenzweig 1995). There are several reasons for the positive nonlinear relationship (Preston 1960, Williams 1964, Huston 1994, Rosenzweig 1995). First, as area increases, habitat heterogeneity also increases which provides more resources and niches for species with ecological specializations (Williams 1943). Second, sampling larger areas increases the opportunity to sample species that have restricted ranges (Rosenzweig 1995). Third, above some relatively large area, few additional habitats or species are encountered until another biome or ecoregion is included.

The other pattern in species distributions, already mentioned above, involves the species richness of vascular plants as primary producers (Loreau et al. 2001). Vascular plant species richness can define a community and also show correlations with other taxa (Su et al. 2004). Vascular plants are associated with vertebrates because vertebrates are dependent upon plants for food as well as security from predators and refuge from inhospitable climate (Bolen and Robinson 2003).

The majority of the parks considered in this study were set aside for protection primarily for reasons other than maintaining biological diversity. Better understanding is needed of how they reflect the biological diversity in the regions in which they are located and what differences occur among them (Gorchakovsky and Demchenko 2002). Therefore, this study is also intended to help characterize differences in biological diversity patterns among NPS Inventory and Monitoring (I&M) networks that are at a smaller scale (network areas range from 16,117 km^2 – 988,911 km^2) than the eastern United States (combined area of 1,797,263 km^2). The scales at which species richness patterns are estimated could have management implications for NPS. Species can respond differently to management actions due to differing relationships with the environment and hence, may require site specific management.

There are a number of reasons that the patterns observed at the smaller scale of networks might be different than those observed across the much larger area of the eastern United States. These include variation in environmental heterogeneity among networks. For example, tallgrass prairie ecosystems occur in this region of the eastern United States but they do not occur in all of the networks. Some networks have many kilometers of river while others do not and still other networks occur on the Atlantic coast and have salt marsh areas and maritime forests. The Great Lakes Network (GLKN) is the only network that contains sandy beach habitat along large freshwater lakes.

There are also varying amounts and types of agricultural land among the networks. Nonlinear effects on species richness may occur for park area if one network contains a park of a particular size which possesses a sharp elevation change and another park of the same area runs along a river with little elevation change. If two networks experience the same average annual temperatures but have very different average annual precipitations there is likely a dramatic difference in the species richness. How the network receives the precipitation also can cause differences between the scales of network and the entire eastern United States (e.g., one network receives most of its precipitation in the form of snow rather than rain, or if a network receives large amounts of rain within a few months and then is dry for the rest of the year while the larger region has a homogenous distribution of precipitation throughout the year).

Interactions between environmental factors such as productivity and disturbance can also affect species richness. Natural disturbance regimes that occur on a network basis and do not affect the larger scale of the eastern United States include hurricanes in the networks that occur on the Atlantic coast and tornadoes in the networks that occur in the Great Plains. Some parks use disturbance techniques such as prescribed burns, mowing, livestock grazing, and hunting to create a desired vegetation and vertebrate population structure. The amount of time since a network has experienced major disturbances and how frequently the disturbances occur affects the level of successional stage and productivity.

These relationships all affect the life cycles of species and limit species' ability to successfully compete for resources and reproduce (Huston 1994, Huston 1999a, Huston 2002). Given that these relationships and their causes may differ among networks, it is important for park managers to be aware of the unique local and regional factors that may make their parks respond differently to management versus other parks (Huston et al. 1999).

Thus, in the current study, we investigated the same taxonomic relationships at the smaller scale of the individual I&M networks. Including the networks in our analyses allowed us to examine the variability in species richness over smaller geographical areas, and to test for differences among the park networks in the following relationships: 1) park area and plant species richness, 2) park area and vertebrate species richness, and 3) plant species richness and vertebrate species richness. O'Connell et al. (2004) collected similar data for one network, the Northeast Temperate Network (NETN), and found a positive, linear relationship between the number of park-significant specimens detected in museums and park area (both variables log-transformed). However, they did not report analyses separately for each taxon or comparisons between plant species richness and vertebrate species richness.

Methods

Background of the Data Collection by NPS

In 1998 Congress passed the National Parks Omnibus Management Act which mandated a program to inventory and monitor parks' natural resources. Historically, there has been a serious lack of scientific information, particularly information on species diversity in parks that was easily accessible to park managers. There was little knowledge about the current status of resources or how they were changing over time (NPS 1999a). The Natural Resource Challenge (NRC) is the NPS's "action plan for preserving natural resources" that evolved from this congressional mandate. The NRC has funded the effort of the NPS to document the "vital signs" of parks for significant natural resources such as air and water quality, and to compile a listing of 90% of the vascular plant and vertebrate species found within park boundaries (Paul 1999). The I&M program is the division of NPS in charge of this data collection, the intention of which is to make baseline resource inventories accessible to park managers for future management decisions (Paul 1999).

The I&M program divided the nation into 32 networks that were determined either by geographic location or on a biome basis (NPS 1999b). Originally thirteen networks were scheduled for use in this analysis. Because of delays in data entry and certification of the data by NPS, only five networks from the eastern US have been included for evaluation (Table 1, Figure 1).

The species inventory data used in this study were collected from 43 parks in the five NPS networks (Table 1, Figure 1). These park units ranged from large parks to small historic sites. Vascular plants and vertebrate taxa (mammals, birds, reptiles, amphibians, but not fish) that occurred on NPS-owned land were added to a database (NPSpecies) by staff at each park or by a database manager for the network. Park land that was considered conservation easements or owned by other government agencies was not used in the study. The presence or absence of a species in parks was determined either from direct field identification, voucher specimens, or through published accounts of species occurrences over the history of the park. Only parks that had data for vascular plants and at least one vertebrate taxon were included in our analyses.

NPS Networks

The Northeast Temperate Network (NETN) provided plant and vertebrate data for eight parks that span seven northeastern states. Parks in this network are primarily sites of historical significance, with most occurring on or near the Atlantic coast. The Great Lakes Network (GLKN) contains nine park units that occur around the freshwater ecosystems of the Great Lakes, including parks with island ecosystems, and also parks along the Mississippi and St. Croix Rivers. The largest network in the study is the Heartland Network (HTLN), which covers 10 states and contains features such as the Lower Mississippi River, the Buffalo and Cuyahoga Rivers, prairie landscapes in two of the parks, and hot springs occurring within one of the parks. Most of the National Capital Region Network (NCRN) parks occur on or near the Potomac River and the Chesapeake and Ohio Canal (CHOH). In this area, the five parks range from small national battlefields to larger forested parks but all occur in or near urban areas.

Table 1. Inventory & Monitoring networks and parks of the National Park Service.and corresponding acronyms. Also included are data used as supplemental information on the physical and environmental variables affecting the parks. These variables include park area, mean annual temperature, mean annual precipitation, park latitude, and population density (see text for population density calculation).

Network	Park Code	Full Name	Park Area (ha)	Average Annual Temperature (°C)	Average Annual Precipitation (cm)	Park Latitude (DD)	Population Density (people/ha)
Great Lakes Network							
GLKN	APIS	Apostle Islands National Lakeshore	17062.42	4.44	82.55	46.95	0.06
GLKN	GRPO	Grand Portage National Monument	287.32	4.44	82.55	48.00	0.01
GLKN	INDU	Indiana Dunes National Lakeshore	4154.08	10.00	95.25	41.64	1.36
GLKN	ISRO	Isle Royale National Park	218247.37	4.44	76.20	48.00	0.02
GLKN	MISS	Mississippi National River and Recreation Area	25.26	7.22	82.55	44.87	3.62
GLKN	PIRO	Pictured Rocks National Lakeshore	14434.66	7.22	82.55	46.56	0.04
GLKN	SACN	Saint Croix National Scenic Riverway	8202.18	4.44	82.55	46.11	0.18
GLKN	SLBE	Sleeping Bear Dunes National Lakeshore	22919.06	7.22	82.55	44.73	0.21
GLKN	VOYA	Voyageurs National Park	53818.09	4.44	69.85	48.50	0.09
Heartland Network							
HTLN	ARPO	Arkansas Post National Memorial	263.02	18.33	139.70	34.02	0.08
HTLN	BUFF	Buffalo National River	35842.04	15.56	107.95	35.96	0.06
HTLN	CUVA	Cuyahoga Valley National Park	7445.14	10.00	95.25	41.24	8.58
HTLN	EFMO	Effigy Mounds National Monument	1022.43	7.22	82.55	42.94	0.09
HTLN	GWCA	George Washington Carver National Monument	84.99	18.33	107.95	36.99	0.32
HTLN	HEHO	Herbert Hoover National Historic Site	73.30	10.00	95.25	41.67	0.12
HTLN	HOCU	Hopewell Culture National Historical Park	383.32	12.78	95.25	39.30	0.41
HTLN	HOME	Homestead National Monument of America	73.30	10.00	82.55	40.29	0.10
HTLN	HOSP	Hot Springs National Park	1996.30	18.33	139.70	34.52	0.50
HTLN	LIBO	Lincoln Boyhood National Memorial	73.17	15.56	107.95	38.12	0.20
HTLN	OZAR	Ozark National Scenic Riverways	21089.62	15.56	107.95	36.92	0.70
HTLN	PERI	Pea Ridge National Military Park	1731.61	15.56	107.95	36.45	0.08
HTLN	PIPE	Pipestone National Monument	114.04	7.22	69.85	44.01	0.04
HTLN	TAPR	Tallgrass Prairie National Preserve	13.06	12.78	82.55	38.44	0.02
HTLN	WICR	Wilson’s Creek National Battlefield	716.28	15.56	107.95	37.10	0.92
Northeast Coastal and Barrier Network							
NCBN	ASIS	Assateague Island National Seashore	3205.82	15.56	107.95	38.08	0.38
NCBN	COLO	Colonial National Historical Park	3257.64	15.56	107.95	37.22	2.06
NCBN	FIIS	Fire Island National Seashore	1250.37	12.78	107.95	40.67	6.01
NCBN	GATE	Gateway National Recreation Area	8160.18	12.78	107.95	40.57	31.28
NCBN	GEWA	George Washington Birthplace National Monument	222.67	15.56	107.95	38.19	0.28
NCBN	THST	Thomas Stone National Historic Site	130.30	15.56	107.95	38.53	1.01
National Capital Region Network							
NCRN	ANTI	Antietam National Battlefield	801.90	12.78	95.25	39.47	1.11
NCRN	CATO	Catoctin Mountain Park	2350.80	12.78	107.95	39.65	1.14
NCRN	HAFE	Harpers Ferry National Historical Park	1203.74	12.78	95.25	39.32	0.78
NCRN	MANA	Manassas National Battlefield Park	1776.56	12.78	95.25	38.82	3.21
NCRN	PRWI	Prince William Forest Park	7241.38	12.78	107.95	38.58	3.21
Northeast Temperate Network							
NETN	ACAD	Acadia National Park	14362.96	4.44	139.70	44.35	0.13
NETN	MABI	Marsh-Billings-Rockefeller Nat'l Historical Park	224.64	10.00	107.95	43.63	0.23
NETN	MIMA	Minute Man National Historical Park	316.98	10.00	107.95	42.45	6.87
NETN	MORR	Morristown National Historical Park	689.91	10.00	107.95	40.77	3.83
NETN	SAGA	Saint-Gaudens National Historic Site	59.96	7.22	95.25	43.50	0.29
NETN	SAIR	Saugus Iron Works National Historic Site	3.44	10.00	107.95	42.47	5.58
NETN	SARA	Saratoga National Historical Park	1167.21	7.22	95.25	42.99	0.95
NETN	WEFA	Weir Farms National Historic Site	27.54	10.00	139.70	41.26	5.45

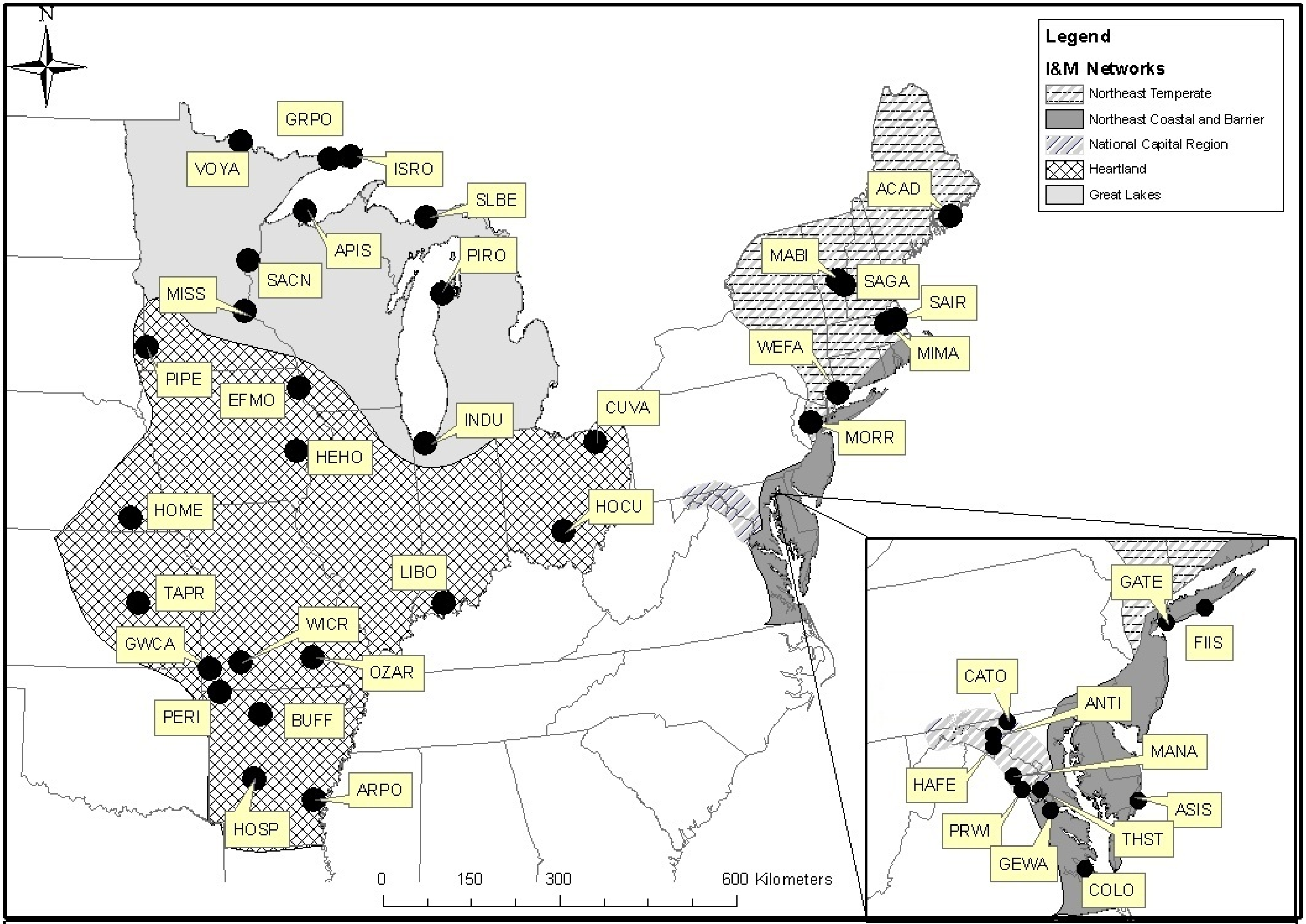

Figure 1. Location of the Inventory and Monitoring Networks and NPS Parks included in the study in Albers equal - area conic projection.

Also located on the Atlantic coast and the Chesapeake Bay is the Northeast Coastal and Barrier Network (NCBN). This network had the fewest lists of species with complete datasets (five that contained plants and at least one vertebrate taxon) of all the networks used in this analysis. Nearly all of the parks in this network had Atlantic Ocean sandy beach areas, sand dunes and salt water marshes.

Corrections to the Datasets

Only data that had been certified for accuracy by NPS were used in this study. Despite the fact that the NPS certification efforts had removed many errors, some still remained (see Myrick 2008, Appendices A-D). Further inspection was required to remove duplicate entries from each park's list (see Myrick 2008, Appendix A) as well as to remove all hybrid species and subspecies (see Myrick 2008, Appendix B). This was done to maintain the analysis at the taxonomic level of species. If a hybrid occurred in a park, it was assumed that the parental species were present.

To locate and correct errors, a list of all species that occur in all the networks was compiled in Microsoft Access and uploaded into the Integrated Taxonomic Information System (ITIS, http://www.itis.gov). The index made it possible to review the submitted species names to identify species that were misspelled (see Myrick 2008, Appendix C) or had synonyms (see Myrick 2008, Appendix D). The resulting master list was compared to each park's list to locate the errors. The corrected species lists (see Myrick 2008, Appendix E) were used in our analyses.

Several parks from NETN and NCRN were excluded from the analysis. The first was Boston Harbor Islands National Recreation Area (BOHA) which does not have any park land that is owned exclusively by NPS. The species occurrences in NPSpecies were documented as occurring only on park land, therefore the data for this park was considered inaccurate. Also excluded from the analysis was the Appalachian National Scenic Trail (APPA) which cuts through the eastern states from Maine to Georgia. This park did not have information on the park area occurring within the individual network sections or the distance off the trail that was considered for species occurrences. CHOH was excluded from NCRN because of the long, narrow, linear characteristics of its park area, a similar reason to excluding APPA from analyses.

Environmental Variables

The five networks covered a total of 25 states in the US and many different ecosystems. To attempt to account for some of the variability between parks, we collected information on environmental factors that might influence species diversity (Table 1). The well known species-area curve shows that species richness and total area display a saturating positive relationship (Arrhenius 1921, Cain 1938, Preston 1960, Williams 1964, Rosenzweig 1995); therefore, data on the total amount of NPS-owned land in each park were collected from NPS. Each park's latitude was determined and recorded in decimal degree (DD) format. Climate data were collected from maps of mean annual precipitation and temperature for 1961-1990, obtained through the National Climatic Data Center (http://www.ncdc.noaa.gov). Total population of the county(s) in which each park occurs was collected from the US Census Bureau for the year of 2000, along with the area in hectares of each county as estimated in 2000. Population density was then calculated for the county. If a park occurred in multiple counties, total populations and areas of the counties were summed and the overall population density of the area was calculated.

Questionnaire

In the summer of 2006 a questionnaire was drafted and sent to the I&M networks requesting more specific information about each park for which data had been received. The information requested from the parks was: verification of NPS acreage; the average number of visitors to the parks each year; linear mileage of features that occur within the park such as roads and trails; the area of different habitat classes such as wetland, agricultural land, open woodland, or closed forest; and the process by which the network "certified" the data. The networks were requested to reply to all questions or provide any relevant resources by November of 2006. Only one network (NCBN) responded to this information request, with data primarily for one park, Assateague Island National Seashore (ASIS). Because of the poor response from NPS, this information was excluded from any further investigation.

Regression Analysis

After all errors and duplications were corrected, species richness was calculated for each taxonomic group in each park. Each vertebrate taxon was compared in a simple linear regression to the species richness of plants with the park as the sampling unit. The r^2 of the simple linear regressions and the adjusted r^2 of multiple regressions were used to determine the strength of the relationship between plant species richness and vertebrate species richness. To test whether there was a statistically significant relationship, P-values of the regression slopes were reported (Hays 1988). Significant P-values were considered to be <0.05.

The species richnesses of plants and the vertebrate groups were plotted in a linear regression against the mean annual temperature, mean annual precipitation, and latitude and park area. The total amounts of NPS-owned park area were transformed using natural logarithms for all analyses. All residuals were checked for deviation from normality and homoscedasticity (see Myrick 2008, Appendix F), and all pairwise correlations of climate and taxonomic variables (see Myrick 2008, Appendix G) were examined for multicollinearity (Sokal and Rolf 1995).

Plant species richness was then estimated by a multiple regression with additional variables (those that exhibited significance with any taxon in the simple linear regressions) included. Similarly, for each vertebrate taxon, vertebrate species richness was predicted with a multiple regression that had the additional variables (that were significant in the simple linear regressions), plus plant species richness. The analyses were based on Type III sums of squares so that the contribution of each variable was independent of the order of entry into the regression (Hays 1988). The adjusted r^2 was reported and significance was again set at $P < 0.05$. All regression analyses were performed with Statistical Analysis System software (SAS 2003).

Analysis of Covariance

The same dataset used in the regressions was used for a type III sums of squares analysis of covariance (ANCOVA, Hays 1988). ANCOVA is a combination of the qualitative treatment of analysis of variance (ANOVA) and the quantitative nature of regression analysis (Hays 1988). In our analyses the categorical variable was the I&M network and the two covariates were vascular plant species richness and natural log of park area, which were determined to be related to species richness across all networks during the regression analyses (see below). These covariates may provide better insight into the cause of the differences among I&M networks than a simple ANOVA, which would only determine if differences existed among networks. As in the regression analyses, the dependent variable in the ANCOVAs was species richness of each taxon.

The ANCOVAs for plants, amphibians, reptiles, and birds were based on all five networks, while the NCBN was excluded from the ANCOVA for mammals since no data were available. Thus, variation in species richness for plants, amphibians, reptiles, birds, and mammals was compared among NPS networks with total park area (natural logarithm transformed) as the covariate. For the vertebrate taxa, plant species richness was also included with area as a covariate. In each ANCOVA the possible interactions between log of park area, plant species richness, and I&M network were also tested to determine whether the slopes of relationships between the covariates and response variable varied among NPS networks. The assumptions of normal distribution and homoscedasticity in the residuals (Sokal and Rolf 1995) from the ANCOVA were assessed as with the regressions. As with the regressions, the ANCOVAs were performed using SAS (2003).

Results

Simple Linear Regressions

Plant species richness accounted for $r^2 = 0.17$, 0.31, and 0.35 of the respective variation in amphibian, bird, and mammal species richness and was statistically significant. Reptiles were the only taxon whose species richness was not significantly related to plant species richness. The three taxa with statistically significant results had positive slopes indicating that as plant species richness increased so did vertebrate taxon richness (Table 2, Figures 2-5).

For the simple linear regressions, the natural log of park area was significantly related to all taxa except reptiles (Table 2, Figures 6-10). The variance explained by park area was highest for plants (0.33) with decreasing values for birds, amphibians, and mammals. The regressions between park latitude and taxon species richness showed the greatest amount of variation explained for reptiles ($r^2 = 0.43$, $P < 0.001$), much less for birds ($r^2 = 0.12$, $P = 0.03$), amphibians ($r^2 = 0.10$, $P = 0.05$), and plants ($r^2 = 0.10$, $P = 0.05$), and it was not statistically significant for mammals. Simple regressions using each park's average annual precipitation also failed to demonstrate any significant relationships except with reptiles ($r^2 = 0.11$, $P = 0.038$) and regressions with average annual temperature were significant only for plant species richness ($r^2 = 0.11$, $P = 0.027$), and reptile species richness ($r^2 = 0.34$, $P < 0.001$). Population density of counties surrounding parks was not significantly related to the richness of any taxon.

Table 2. Simple linear regressions comparing species richness of eastern United States National Parks with vascular plant species richness of each park as well as additional variables that each park experiences. Listed are r^2, P-values, and regression slopes for each regression. Significant relationships (shown in bold) are $P < 0.05$ and n = the number of parks included in the regression.

		Predictor Variables					
Species Richness		Plant Species Richness	Natural log of Park Area (ha)	Park Latitude (DD)	Average Annual Precipitation (cm)	Average Annual Temperature (°C)	Population Density (people/ha)
	r^2		**0.33**	**0.10**	0.07	**0.11**	0.01
Plant Species Richness	regression slope		**64.0352**	**23.2309**	-4.0600	**-23.2062**	6.0948
n = 43	P		**<0.001**	**0.0392**	0.0938	**0.0268**	0.4741
	r^2	**0.17**	**0.24**	**0.10**	0.08	0.08	0.01
Amphibian Species Richness	regression slope	**0.0091**	**1.2550**	**-0.4883**	0.0976	0.3902	0.0894
n = 38	P	**0.0113**	**0.0017**	**0.0498**	0.0887	0.0806	0.5735
	r^2	0.06	0.03	**0.43**	**0.11**	**0.34**	0.004
Reptile Species Richness	regression slope	6.6967	0.7475	**-1.5863**	**0.1872**	**1.2645**	-0.1017
n = 38	P	0.1494	0.2677	**<0.001**	**0.0376**	**<0.001**	0.6889
	r^2	**0.31**	**0.32**	**0.12**	0.09	0.09	0.06
Bird Species Richness	regression slope	**0.1646**	**18.4150**	**7.4883**	-1.3722	-5.9077	2.8139
n = 40	P	**<0.001**	**<0.001**	**0.0299**	0.0591	0.0578	0.1053
	r^2	**0.35**	**0.12**	0.07	0.07	0.05	0.005
Mammal Species Richness	regression slope	**0.0262**	**1.6756**	0.7971	-0.1648	-0.6226	0.1342
n = 36	P	**<0.001**	**0.0383**	0.1180	0.1220	0.1827	0.6690

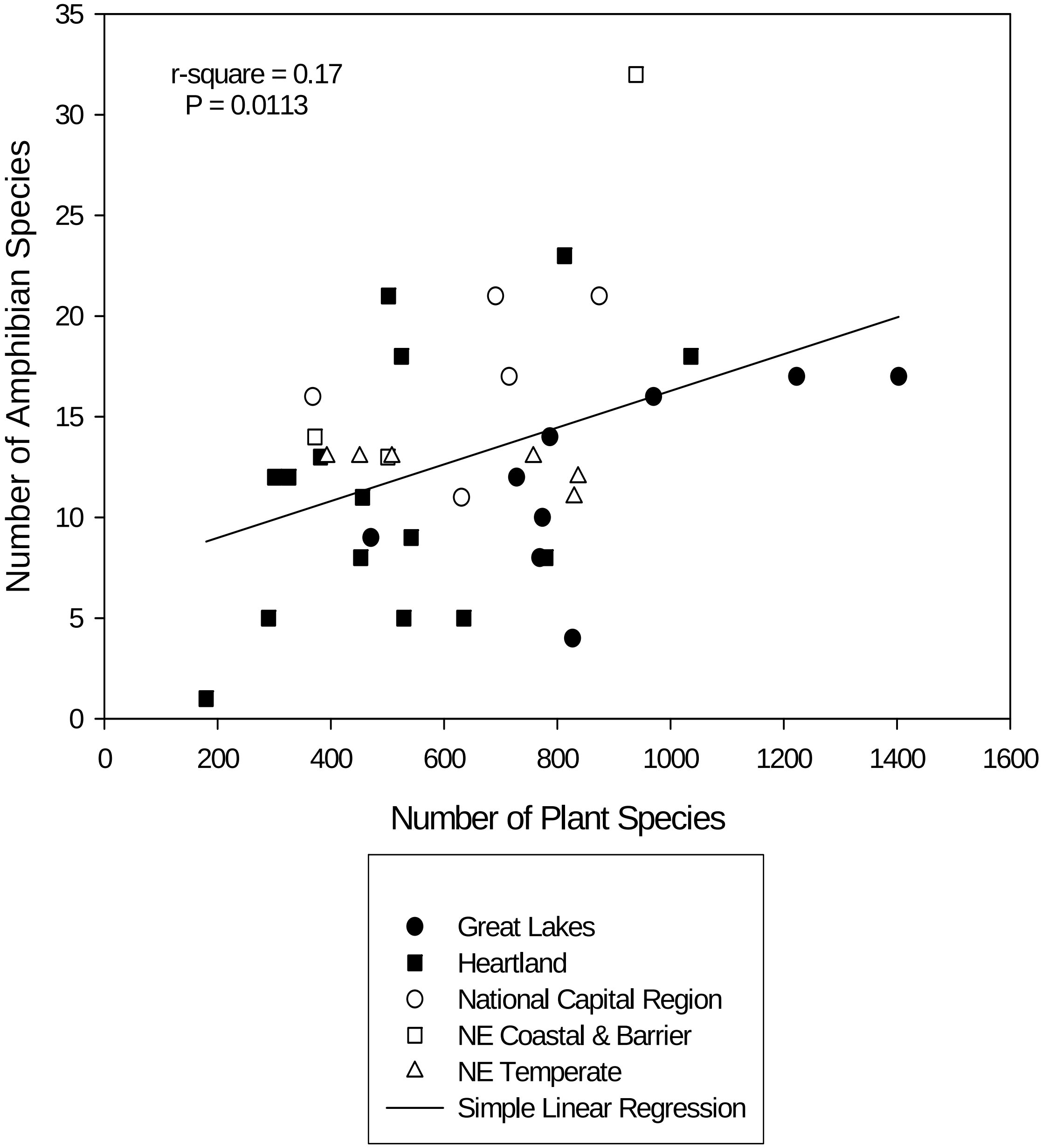

Figure 2. Relationship of vascular plant species richness to amphibian species richness in eastern United States National Parks. A point is the sampling unit of one park. The parks are grouped by Inventory & Monitoring networks of NPS (distinguished in the legend). The r^2 and *P*-value of the regression are labeled on the graph.

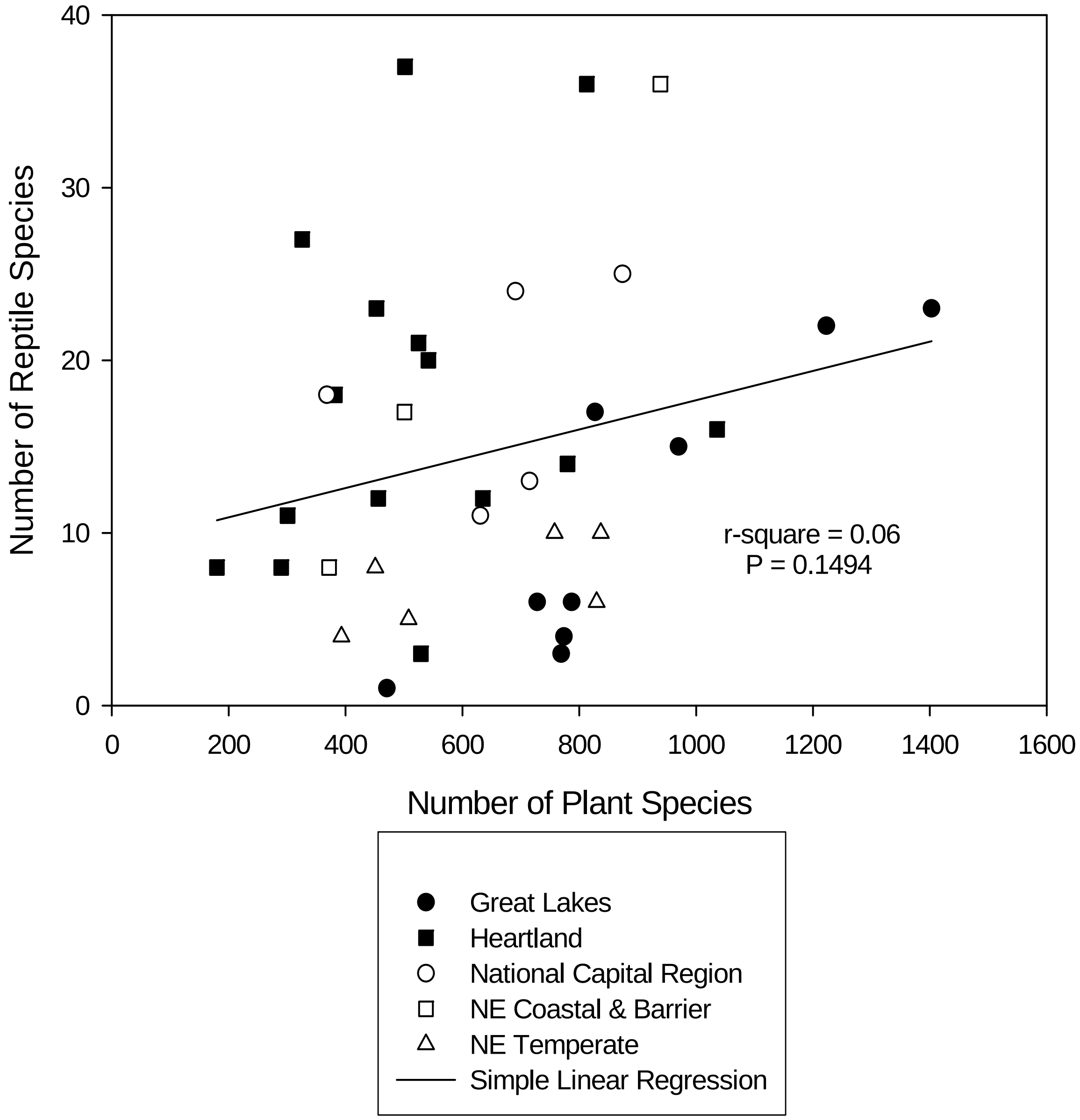

Figure 3. Relationship of vascular plant species richness to reptile species richness in eastern United States National Parks. A point is the sampling unit of one park. The parks are grouped by Inventory & Monitoring networks of NPS (distinguished in the legend). The r^2 and *P*-value of the regression are labeled on the graph.

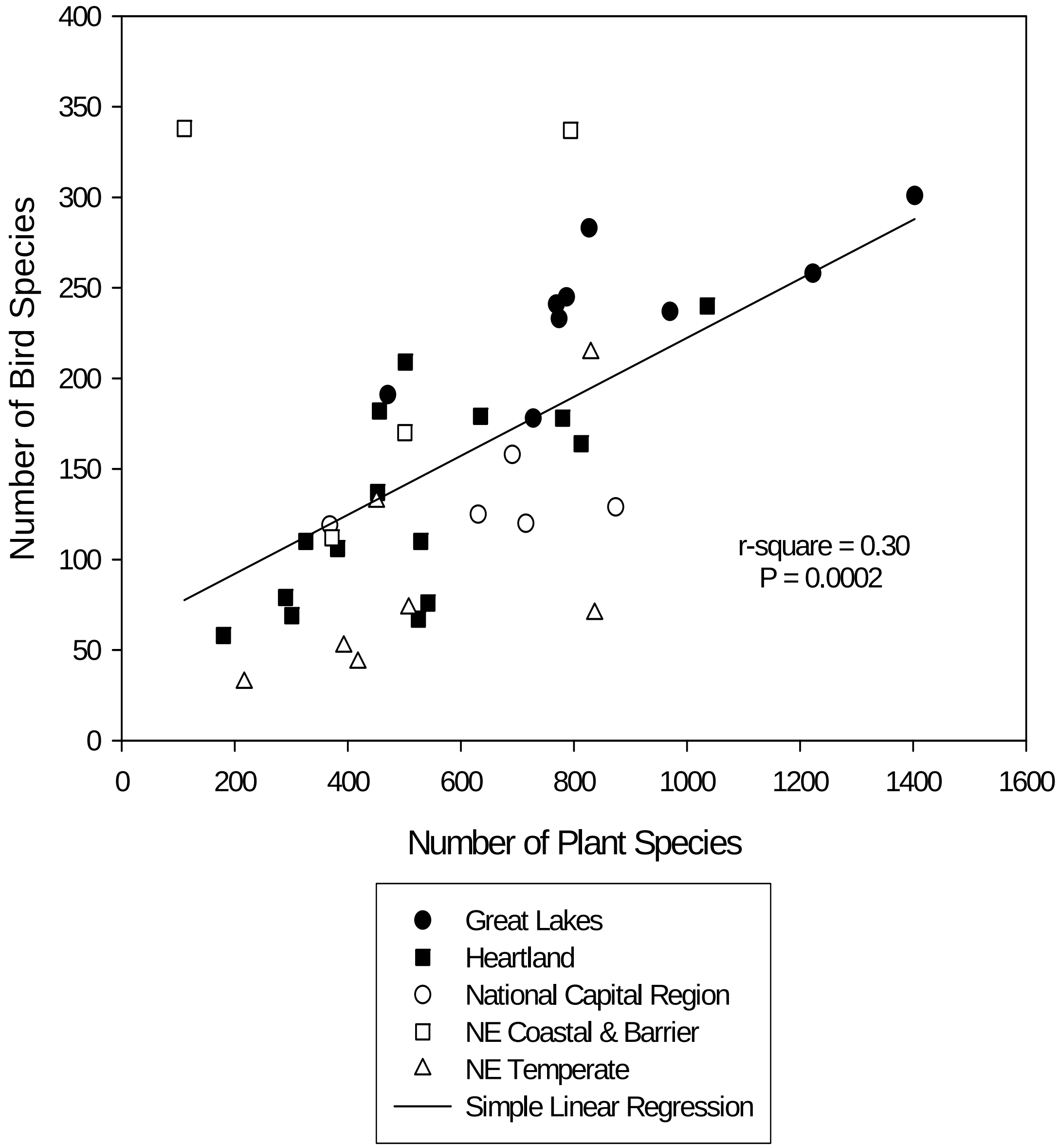

Figure 4. Relationship of vascular plant species richness to bird species richness in eastern United States National Parks. A point is the sampling unit of one park. The parks are grouped by Inventory & Monitoring networks of NPS (distinguished in the legend). The r^2 and *P*-value of the regression are labeled on the graph.

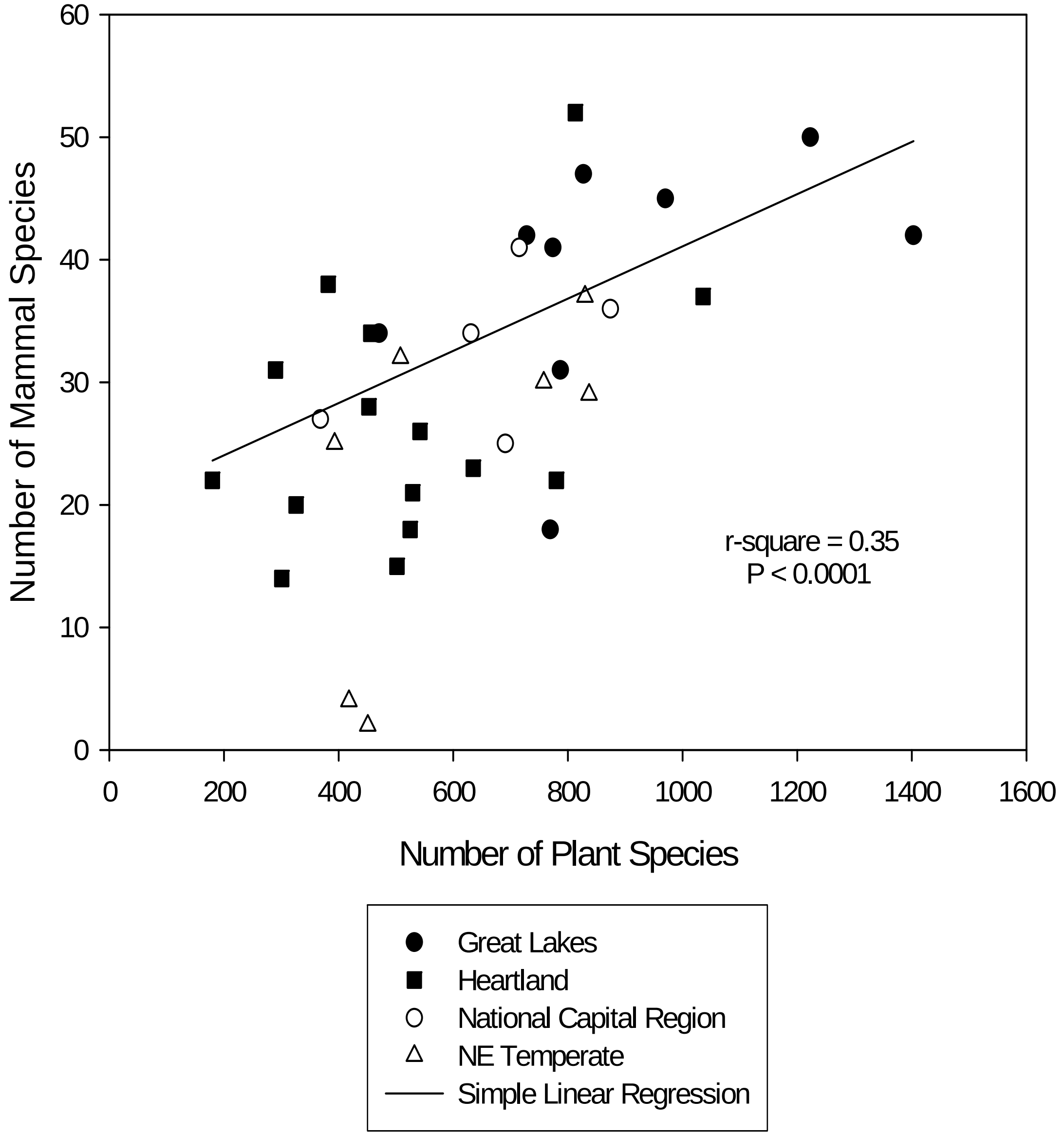

Figure 5. Relationship of vascular plant species richness to mammal species richness in eastern United States National Parks. A point is the sampling unit of one park. The parks are grouped by Inventory & Monitoring networks of NPS (distinguished in the legend). The r^2 and *P*-value of the regression are labeled on the graph.

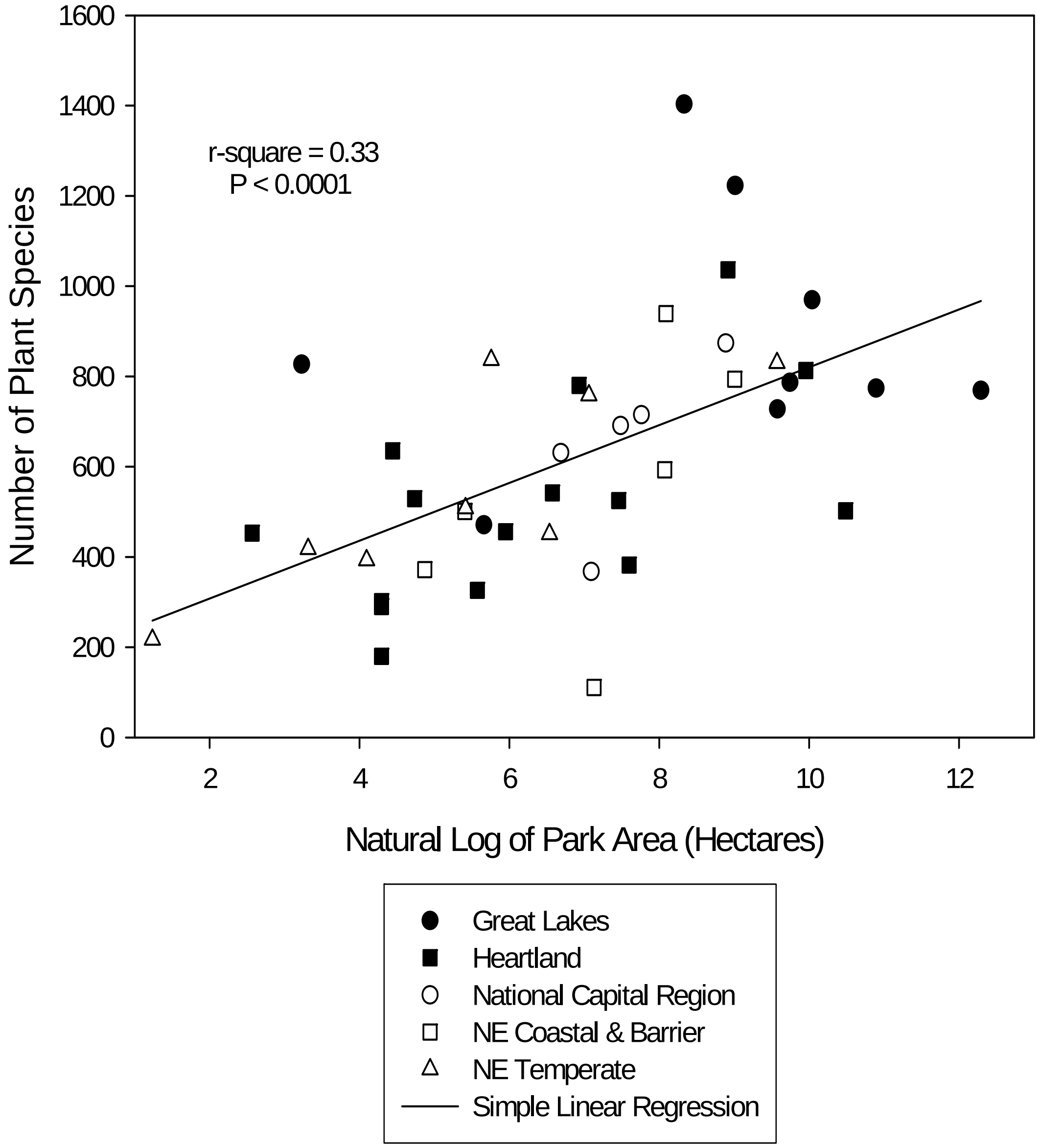

Figure 6. Relationship of vascular plant species richness to natural logarithm of park area in eastern United States National Parks. A point is the sampling unit of one park. The parks are grouped by Inventory & Monitoring networks of NPS (distinguished in the legend). The r^2 and *P*-value of the regression are labeled on the graph.

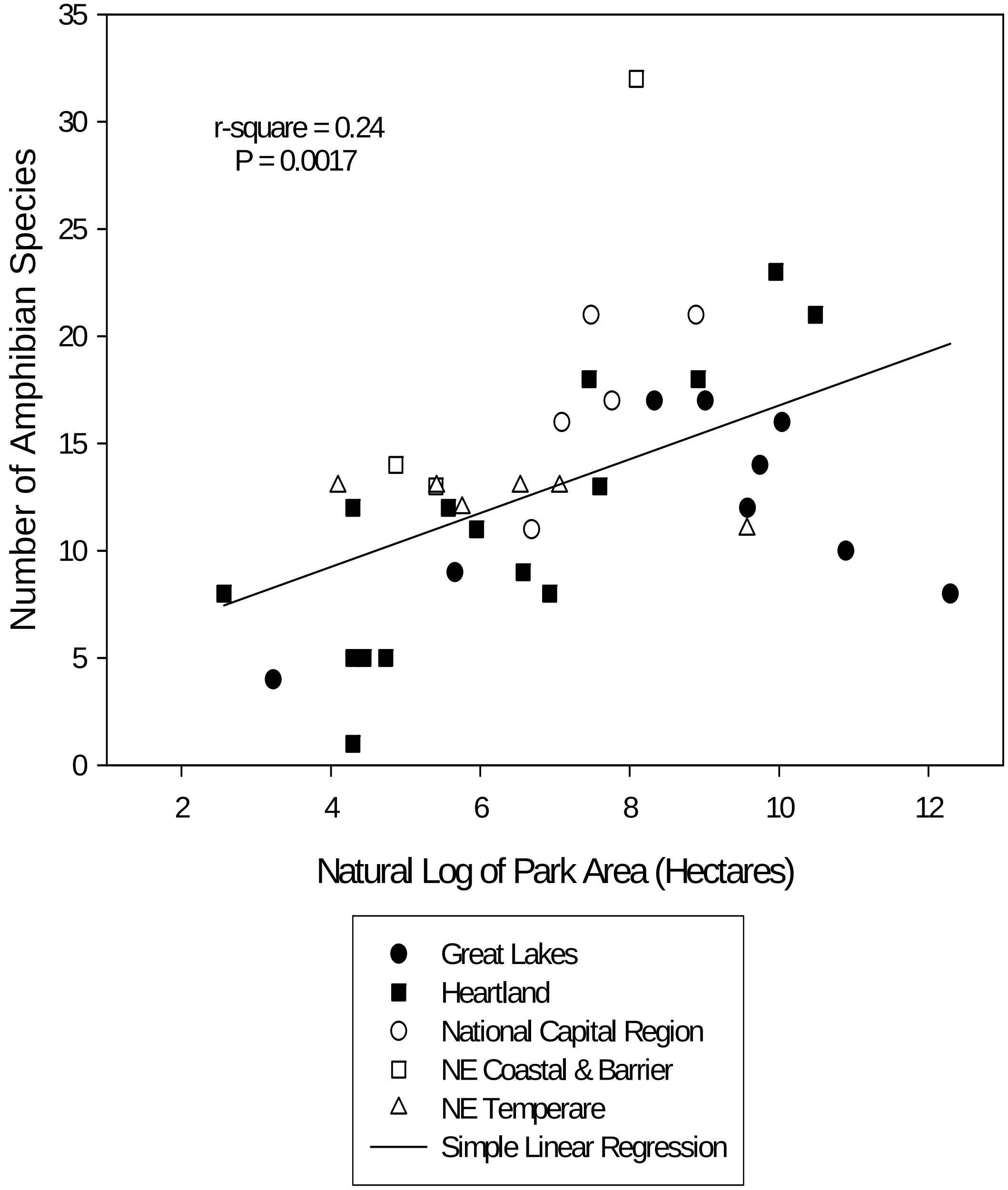

Figure 7. Relationship of amphibian species richness to natural logarithm of park area in eastern United States National Parks. A point is the sampling unit of one park. The parks are grouped by Inventory & Monitoring networks of NPS (distinguished in the legend). The r^2 and *P*-value of the regression are labeled on the graph.

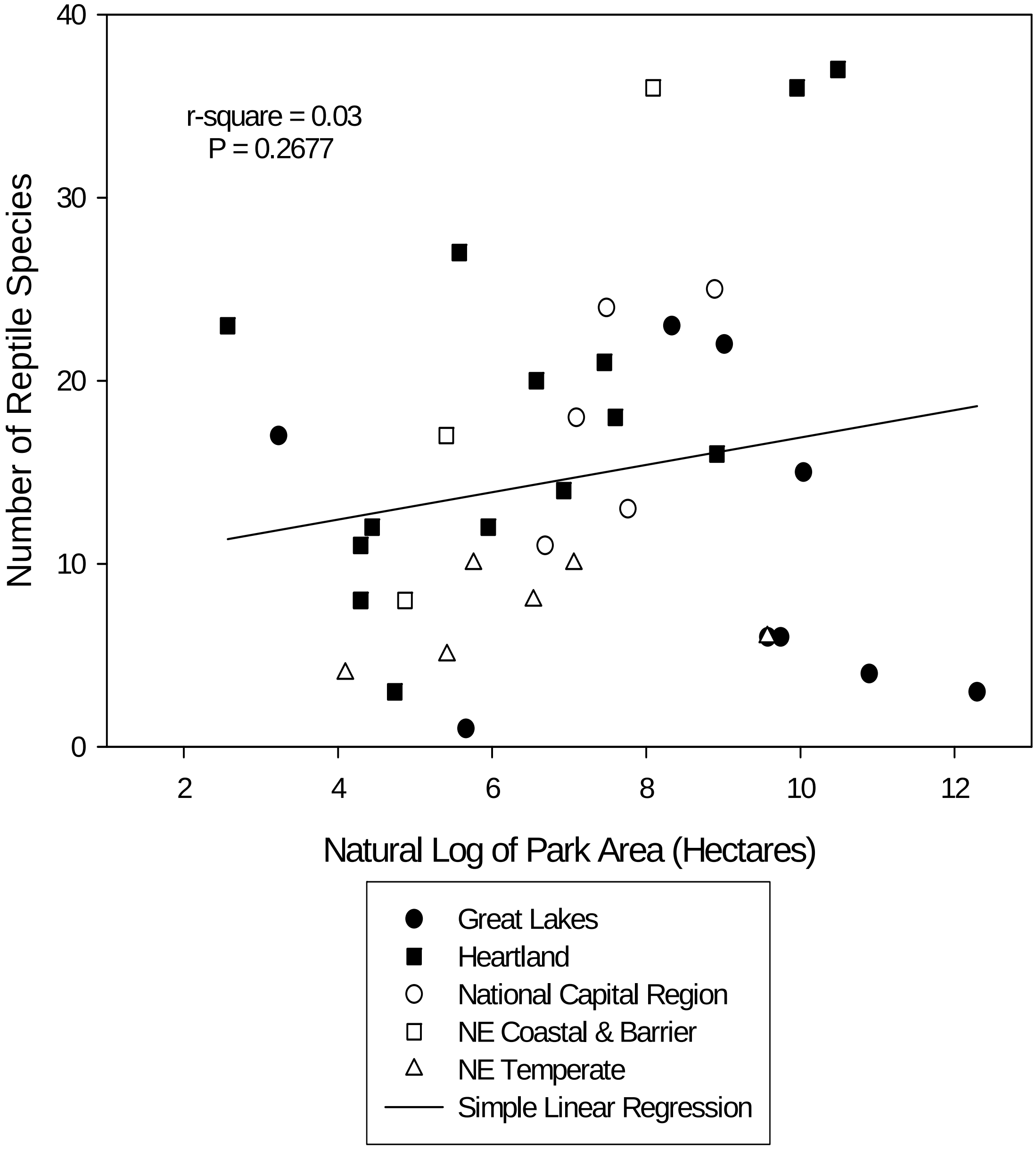

Figure 8. Relationship of reptile species richness to natural logarithm of park area in eastern United States National Parks. A point is the sampling unit of one park. The parks are grouped by Inventory & Monitoring networks of NPS (distinguished in the legend). The r^2 and *P*-value of the regression are labeled on the graph.

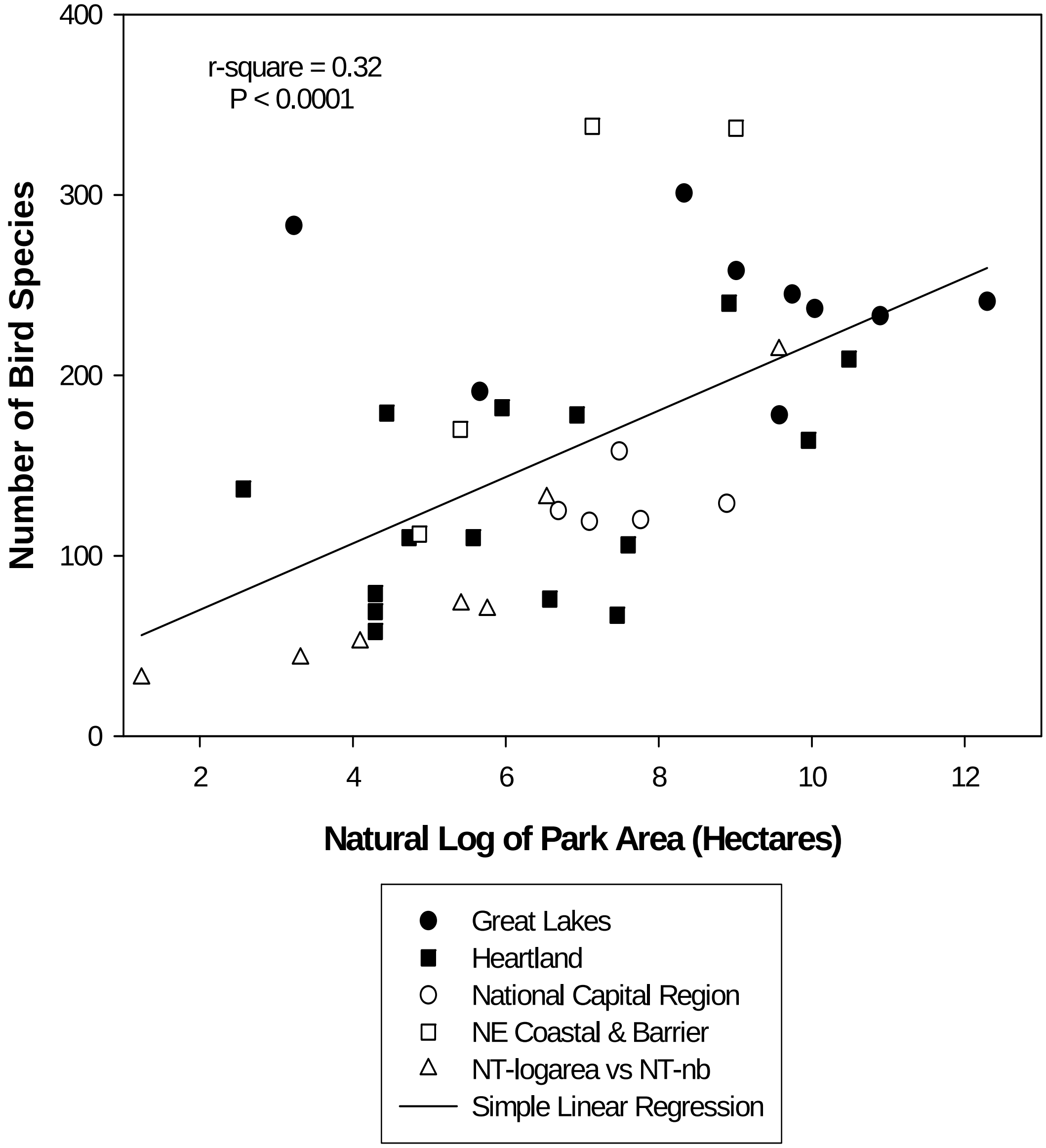

Figure 9. Relationship of bird species richness to natural logarithm of park area in eastern United States National Parks. A point is the sampling unit of one park. The parks are grouped by Inventory & Monitoring networks of NPS (distinguished in the legend). The r^2 and *P*-value of the regression are labeled on the graph.

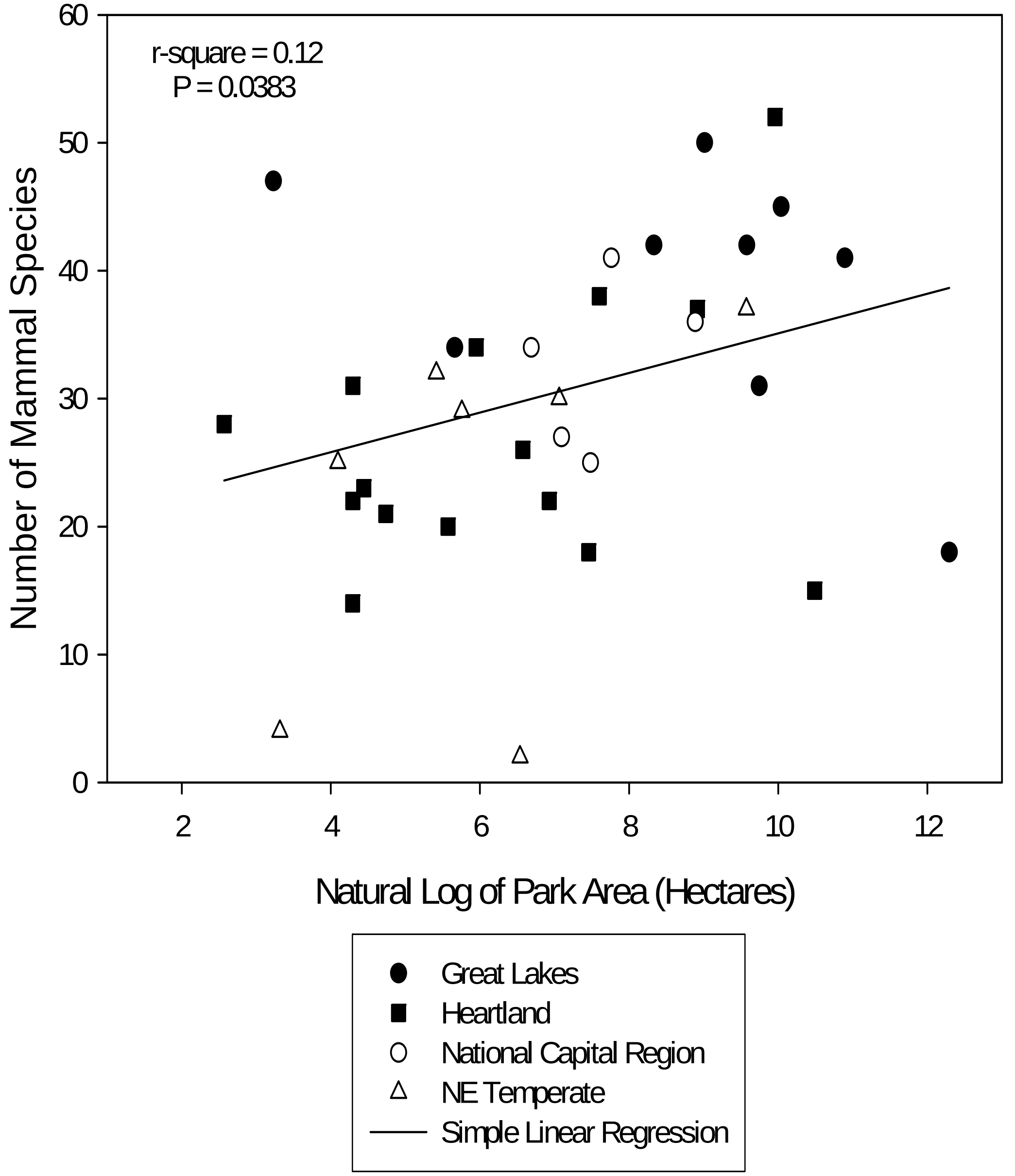

Figure 10. Relationship of mammal species richness to natural logarithm of park area in eastern United States National Parks. A point is the sampling unit of one park. The parks are grouped by Inventory & Monitoring networks of NPS (distinguished in the legend). The r^2 and *P*-value of the regression are labeled on the graph.

Multiple Regressions

Prior to performing the multiple regression analyses, the species richnesses of each taxon and the environmental variables were tested for multicollinearity. Park latitude and average annual temperature were highly correlated ($r = 0.95$, $P < 0.001$; see Myrick 2008, Appendix G). Therefore, latitude was retained in the multiple regression analysis, and average annual temperature was removed to prevent redundancy in the model. Because population density lacked a statistically significant relationship with any taxon’s species richness, it was excluded from the multiple regression analyses.

All multiple regressions predicting species richness for the taxonomic groups were statistically significant ($P < 0.01$, Table 3). The multiple regression for plant species richness ($n = 43$) as the response variable showed an adjusted $r^2 = 0.33$, with only the natural log transformed area of the parks being significant. In the multiple regression for mammals ($n = 36$, adjusted $r^2 = 0.37$) and birds ($n = 40$, adjusted $r^2 = 0.36$), only one predictor variable was significant ($P < 0.05$). In the case of mammals the significant variable was plant species richness and for birds the variable was the natural log of park area. The multiple regression for reptile species richness had the highest adjusted r^2 of 0.71 and all predictor variables except park area were significant. This was the only multiple regression where the effect of mean annual precipitation was significant ($P = 0.048$). The slope of the relationship of mean annual precipitation with reptiles was negative (-0.139). For the comparison with amphibian species richness ($n = 38$), the multiple regression had an adjusted r^2 of 0.49 and a $P < 0.001$. Plant species richness, log transformed park area, and park latitude were all significantly related to amphibian species richness ($P < 0.05$).

Analysis of Covariance

The mean area of the parks in the Great Lakes network (GLKN) was 30,000 hectares more than any other network (Table 4). The network with the lowest mean park area was the Northeast Temperate network (NETN) with 2,107 ha. Mean annual temperature ranged from 6°C in the GLKN to 13°C in the National Capital Region network (NCRN). The lowest average annual precipitation was in the GLKN with 70 cm and the highest average was in the NETN with 113 cm. Park latitude ranged from the lowest in the Heartland network (HTLN) 69.85DD which had mean park latitude of 38.53DD up to the highest park latitude in the GLKN, 48.5DD, and had mean park latitude of 46.15DD. Network mean population density (see Environmental Variables section for how this was calculated) ranged from 0.62 people/ha in the GLKN to 6.84 people/ha in the Northeast Coastal and Barrier Network (NCBN). The network with the greatest mean number of vascular plant species was the GLKN. Amphibian and reptile species richness were the highest in the NCBN. Greatest mean number of mammal species was in the GLKN. There were no data on mammal species richness in the NCBN.

Table 3. Summaries of multiple regressions comparing species richness of plants, amphibians, reptiles, birds, and mammals with environmental variables that each park experiences. Listed are r^2 and P-values of each multiple regression as well as slopes and P-values of each predictor. Significant relationships (shown in bold) have $P < 0.05$.

			Predictor Variables				
Dependent Variables (species richness)	Adjusted r^2	Overall P		Plant Species Richness	Natural log of Park Area (ha)	Park Latitude (DD)	Average Annual Precipitation (cm)
Plant Species Richness	**0.33**	**<0.001**	slope		**59.2692**	10.8656	-1.5270
n = 43			P		**<0.001**	0.3684	0.5471
Amphibian Species Richness	**0.49**	**<0.001**	slope	**0.0082**	**1.1254**	**-0.8714**	-0.0011
n = 38			P	**0.0182**	**0.0045**	**0.0018**	0.9846
Reptile Species Richness	**0.71**	**<0.001**	slope	**0.0158**	0.8212	**-2.5094**	**-0.1388**
n = 38			P	**<0.001**	0.0737	**<0.001**	**0.0475**
Bird Species Richness	**0.36**	**<0.001**	slope	0.0804	**12.1191**	1.9407	-0.5382
n = 40			P	0.1037	**0.0221**	0.5960	0.4707
Mammal Species Richness	**0.37**	**0.006**	slope	**0.0244**	0.1569	-0.1210	-0.0894
n = 36			P	**0.0043**	0.8518	0.8333	0.4384

Table 4. Species richness and physical variable summary statistics for five National Park Service Inventory & Monitoring networks in the eastern United States. Number of parks (*n*) is the sample size in each network for calculating summary statistics. The mean, minimum, maximum, and standard deviation (SD) of each network are listed for the physical variables of park area, average temperature and precipitation, latitude, and population density surrounding the park. (See text of Methods for definition of population density variable.) The mean, minimum, maximum, and standard deviation of each network for the species richness of vascular plants, amphibians, reptiles, birds and mammals are also provided.

			Physical Variables					**Species Richness**				
			Park Area (ha)	**Average Annual Temperature (°C)**	**Average Annual Precipitation (cm)**	**Park Latitude (DD)**	**Population Density (people/ha)**	**Vascular Plant**	**Amphibian**	**Reptile**	**Bird**	**Mammal**
Inventory and Monitoring Networks	**Great Lakes Network**	***n***	9	9	9	9	9	9	9	9	9	9
		Mean	37683.38	5.99	81.84	46.15	0.62	883.56	11.89	10.78	240.89	38.89
		Minimum	25.26	4.44	69.85	41.64	0.01	471	4	1	178	18
		Maximum	218247.37	10.00	95.25	48.50	3.62	1403	17	23	301	50
		SD	69693.39	2.02	6.69	2.15	1.20	279.41	4.51	8.51	39.22	9.83
	Heartland Network	***n***	15	15	15	15	15	15	15	15	15	15
		Mean	4728.11	13.52	102.02	38.53	0.82	516.67	11.27	17.73	130.93	26.73
		Minimum	13.06	7.22	69.85	34.02	0.02	180	1	3	58	14
		Maximum	35842.04	18.33	139.70	44.01	8.58	1036	23	37	240	52
		SD	10206.17	3.85	19.57	2.99	2.17	226.05	6.42	9.89	57.76	10.20
	Northeast Coastal and Barrier Network	***n***	6	6	6	6	6	6	3	3	4	no data
		Mean	2704.50	14.63	107.95	38.88	6.84	551.67	19.67	20.33	239.5	
		Minimum	130.30	12.78	107.95	37.22	0.28	111	13	8	112	
		Maximum	8160.18	15.56	107.95	40.67	31.28	939	32	36	338	
		SD	3007.40	1.44	0.00	1.42	12.16	296.48	10.69	14.29	115.70	
	National Capital Region Network	***n***	5	5	5	5	5	5	5	5	5	5
		Mean	2674.88	12.78	100.33	39.17	1.89	655.8	17.2	18.2	130.2	32.6
		Minimum	801.90	12.78	95.25	38.58	0.78	368	11	11	119	25
		Maximum	7241.38	12.78	107.95	39.65	3.21	874	21	25	158	41
		SD	2619.03	0.00	6.96	0.45	1.21	184.25	4.15	6.30	16.05	6.58
	Northeast Temperate Network	***n***	8	8	8	8	8	8	6	6	7	7
		Mean	2106.58	8.61	112.71	42.68	2.92	551.5	12.5	7.17	88	22.71
		Minimum	3.44	4.44	95.25	40.77	0.13	217	11	4	32	2
		Maximum	14362.96	10.00	139.70	44.35	6.87	837	13	10	214	37
		SD	4968.28	2.10	17.56	1.21	2.82	229.45	0.84	2.56	64.31	13.95

Plant species richness was not significantly different among the networks and park area had a significant influence on plant species richness in all networks (Table 5). The slopes of the relationship of park area and plant species richness were similar among the networks (Figure 11).

Amphibian species richness was similar among the networks and was not influenced by either park area or plant species richness. The slopes of the relationships for park area with amphibian species richness as the dependent variable differed among the networks (Figure 12). The slope of the relationship for the NETN was negative and the slope for the NCBN was steeper than the slopes for the HTLN, GLKN, and NCRN. The slopes of the relationships for plant species richness and amphibian species richness were not statistically different among networks, but the slope for the NETN was negative (Figure 13).

Reptile species richness did not differ among the networks and was not influenced by either plant species richness or by park area. However, the slopes of the relationships among the networks for park area and reptiles species richness were significantly different (Figure 14). The slope of the relationship with park area was negative for GLKN. The slopes of the relationships for plant species richness and reptile species richness were similar among networks (Figure 15).

Bird species richness was significantly different among networks and influenced by park area but not by plant species richness. The slopes of the relationships of park area (Figure 16) and plant species richness (Figure 17) with bird species richness both differed among networks. The slope of the relationship for park area and bird species richness was negative for the GLKN. The slopes of the relationship of bird species richness to plant species richness were similar for the NCBN and NCRN and differed from the slopes of the other three networks.

Mammal species richness was not significantly different among the networks. Park area did not significantly influence mammal species richness nor did plant species richness. The slopes of the relationships between park area and mammal species richness (Figure 18) were statistically similar but the slope of the GLKN was negative, unlike the slopes of the other networks. The relationship between plant species richness and mammal species richness were similar among networks (Figure 19).

Discussion

Variation in sampling effort is a common problem in studies of biological diversity (Noss1990, Gaston 1996). Sampling effort by NPS varied among the park networks, and no adjustments for this variability were possible. In some datasets there was an apparently low priority on certain details, including inconsistency among some parks in the degree of reporting of common species, while other parks had comprehensive lists collected by specialists that were carefully checked for inaccuracies and oversights. Complicating the analyses is the wide range of park types, ranging from historic sites,

Table 5. Analysis of Covariance (ANCOVA) comparisons of five National Park Service networks (Great Lakes, Heartland, Northeast Coast and Barrier, National Capital Region, and Northeast Temperate) for the eastern United States. Response variables are plant, amphibian, reptile, bird, and mammal species richness for each park occurring in the networks. Covariates are the five networks, natural log of the total area of each park and plant species richness is included for the vertebrate ANCOVAs. Degrees of freedom, *F* -values, and *P* -values are reported for each ANCOVA.

Plant Species Richness			
source	Degrees of Freedom	*F* -value	*P* -value
NPS Network	4	1.61	0.1955
Log of Park Area	1	7.11	**0.0118**
Network × Area	4	0.99	0.4241
Residuals	33		
Amphibian Species Richness			
source	Degrees of Freedom	*F* -value	*P* -value
NPS Network	4	2.66	0.0589
Log of Park Area	1	2.19	0.1526
Plant Species Richness	1	0.73	0.4005
Network × Log of Park Area	4	2.97	**0.0408**
Network × Plant Species Richness	4	1.07	0.3920
Residuals	23		
Reptile Species Richness			
source	Degrees of Freedom	*F* -value	*P* -value
NPS Network	4	0.27	0.8940
Log of Park Area	1	0.01	0.9048
Plant Species Richness	1	0.37	0.5470
Network × Log of Park Area	4	3.89	**0.0147**
Network × Plant Species Richness	4	2.63	0.0605
Residuals	23		
Bird Species Richness			
source	Degrees of Freedom	*F* -value	*P* -value
NPS Network	4	3.77	**0.0157**
Log of Park Area	1	6.87	**0.0147**
Plant Species Richness	1	0.06	0.8087
Network × Log of Park Area	4	9.9	**<.0001**
Network × Plant Species Richness	4	4.35	**0.0083**
Residuals	25		
Mammal Species Richness			
source	Degrees of Freedom	*F* -value	*P* -value
NPS Network	3	1.56	0.2240
Log of Park Area	1	0.01	0.9127
Plant Species Richness	1	3.29	0.0824
Network × Log of Park Area	3	0.57	0.6374
Network × Plant Species Richness	3	0.25	0.8572
Residuals	24		

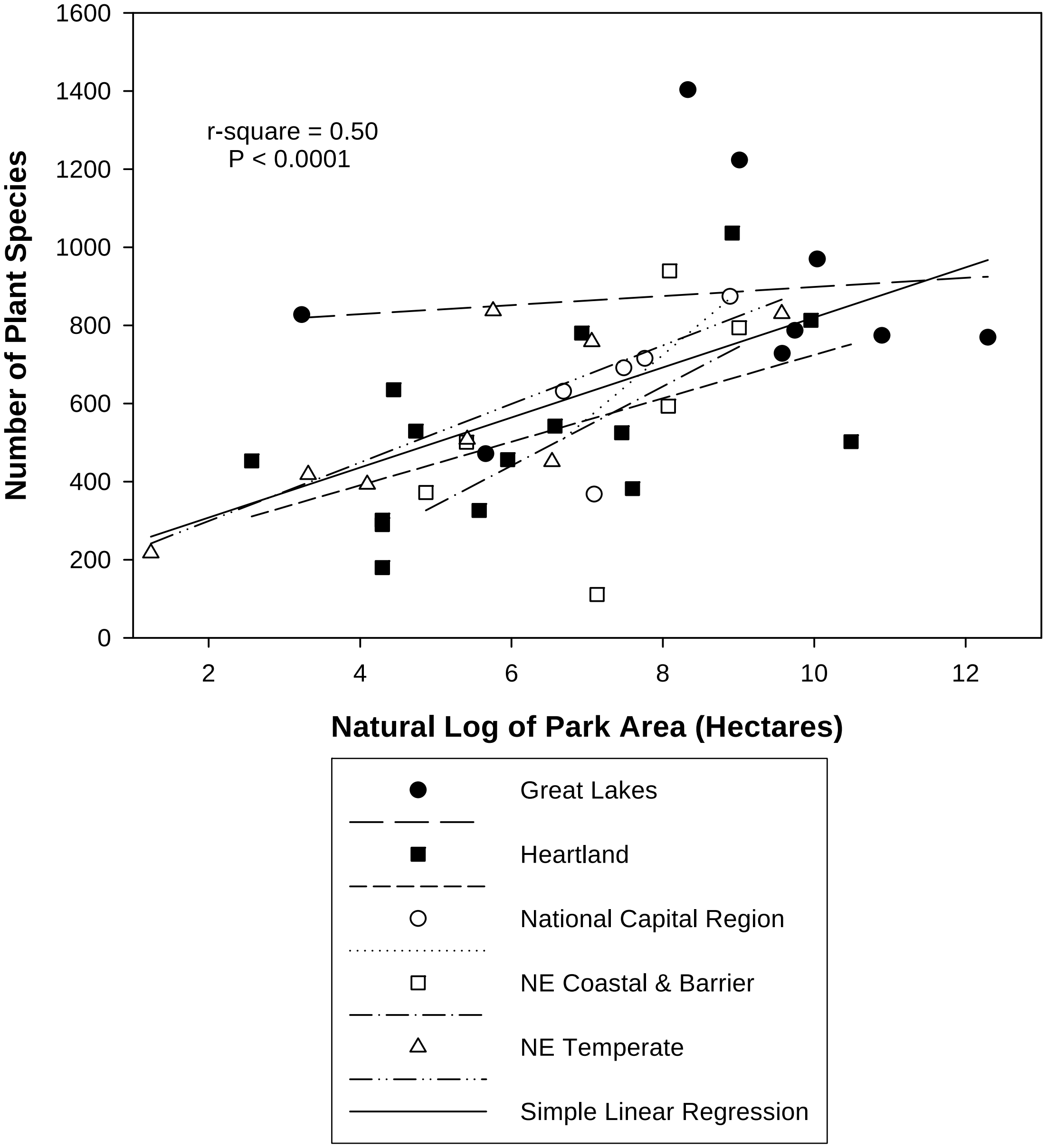

Figure 11. Vascular plant species richness compared to the natural logarithm of park area by NPS networks (distinguished in the legend and with separate regression lines on the graph).

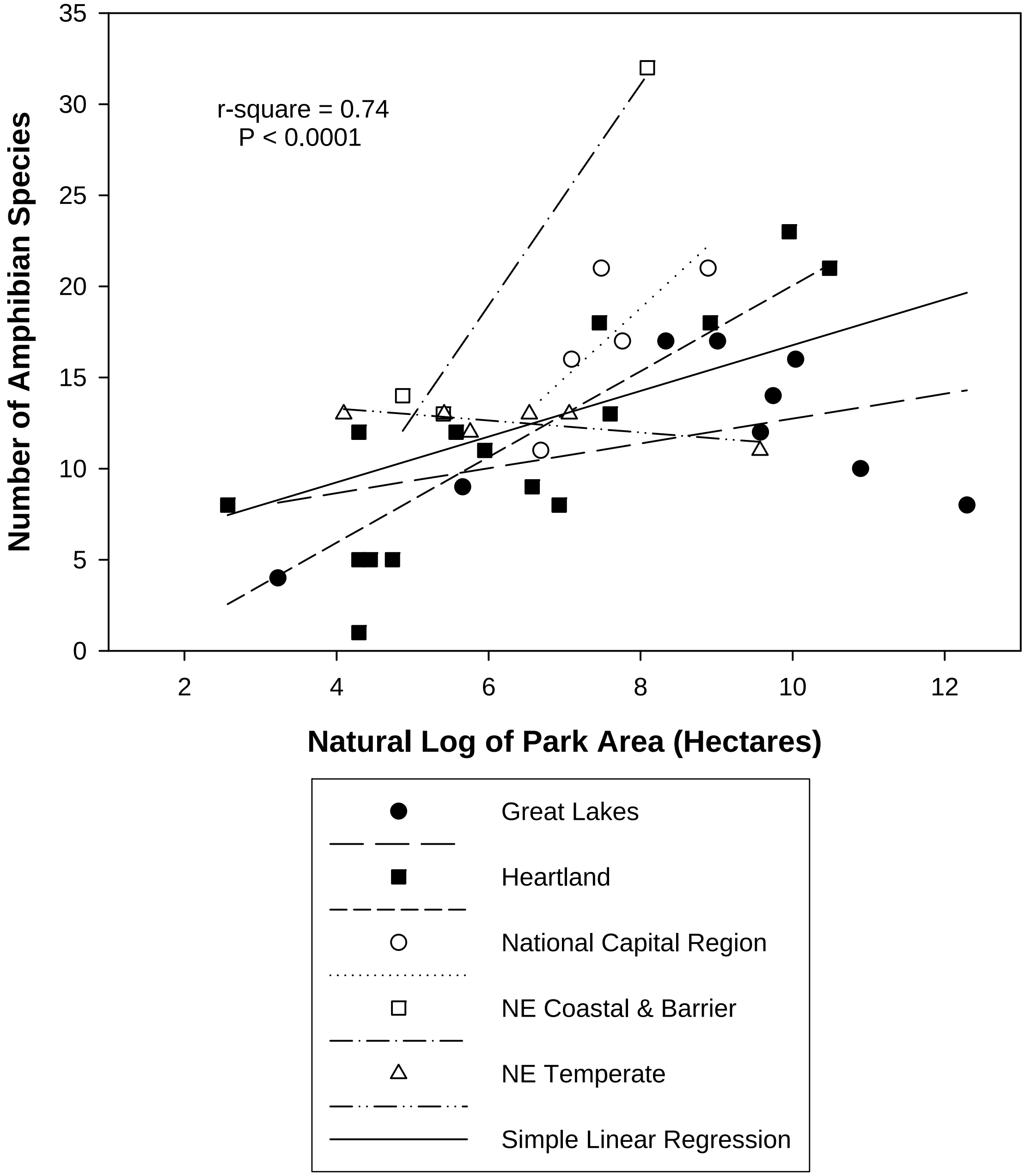

Figure 12. Amphibian species richness compared to the natural logarithm of park area by NPS networks (distinguished in the legend and with separate regression lines on the graph).

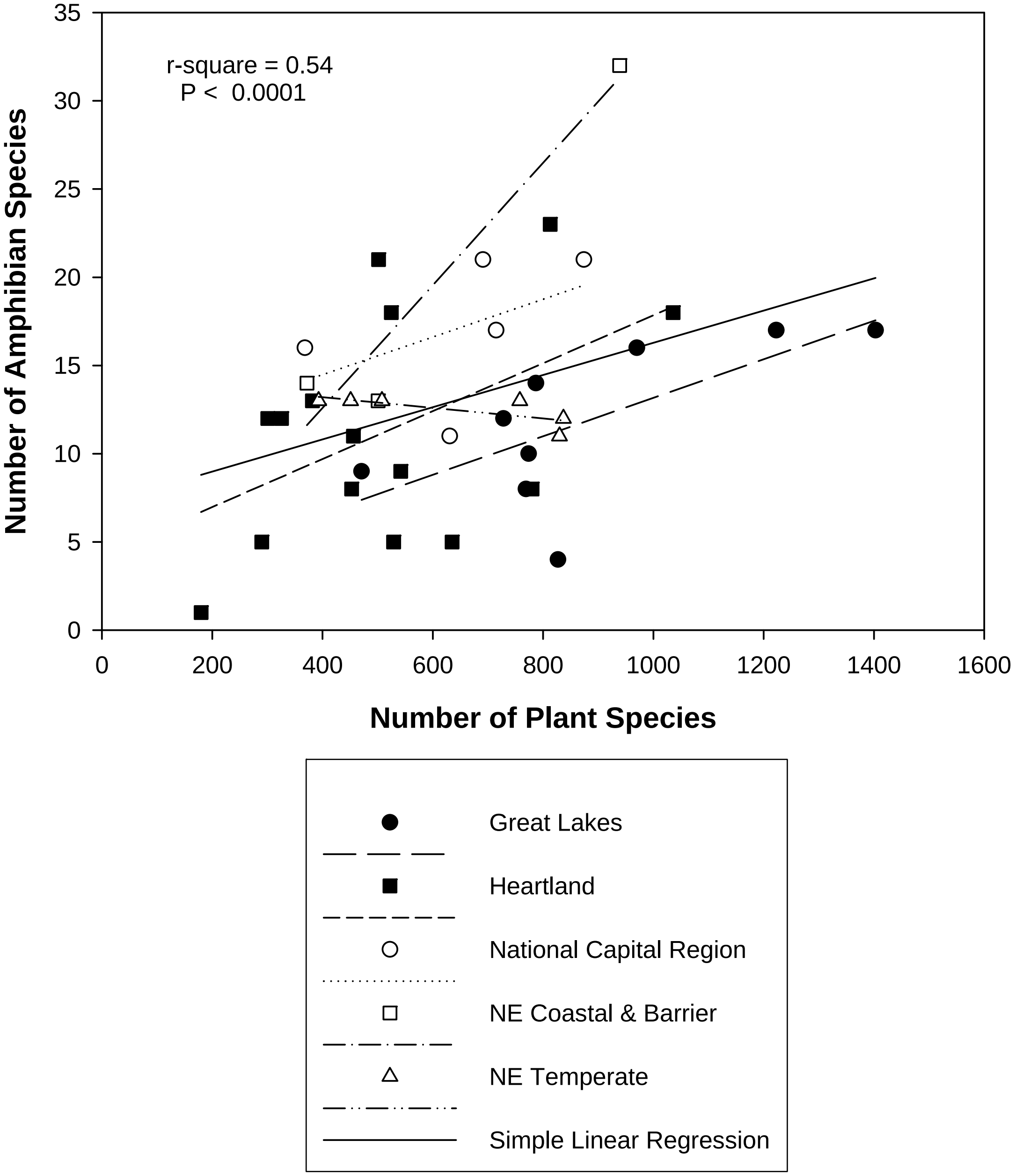

Figure 13. Amphibian species richness compared to vascular plant species richness by NPS networks (distinguished in the legend and with separate lines on the graph).

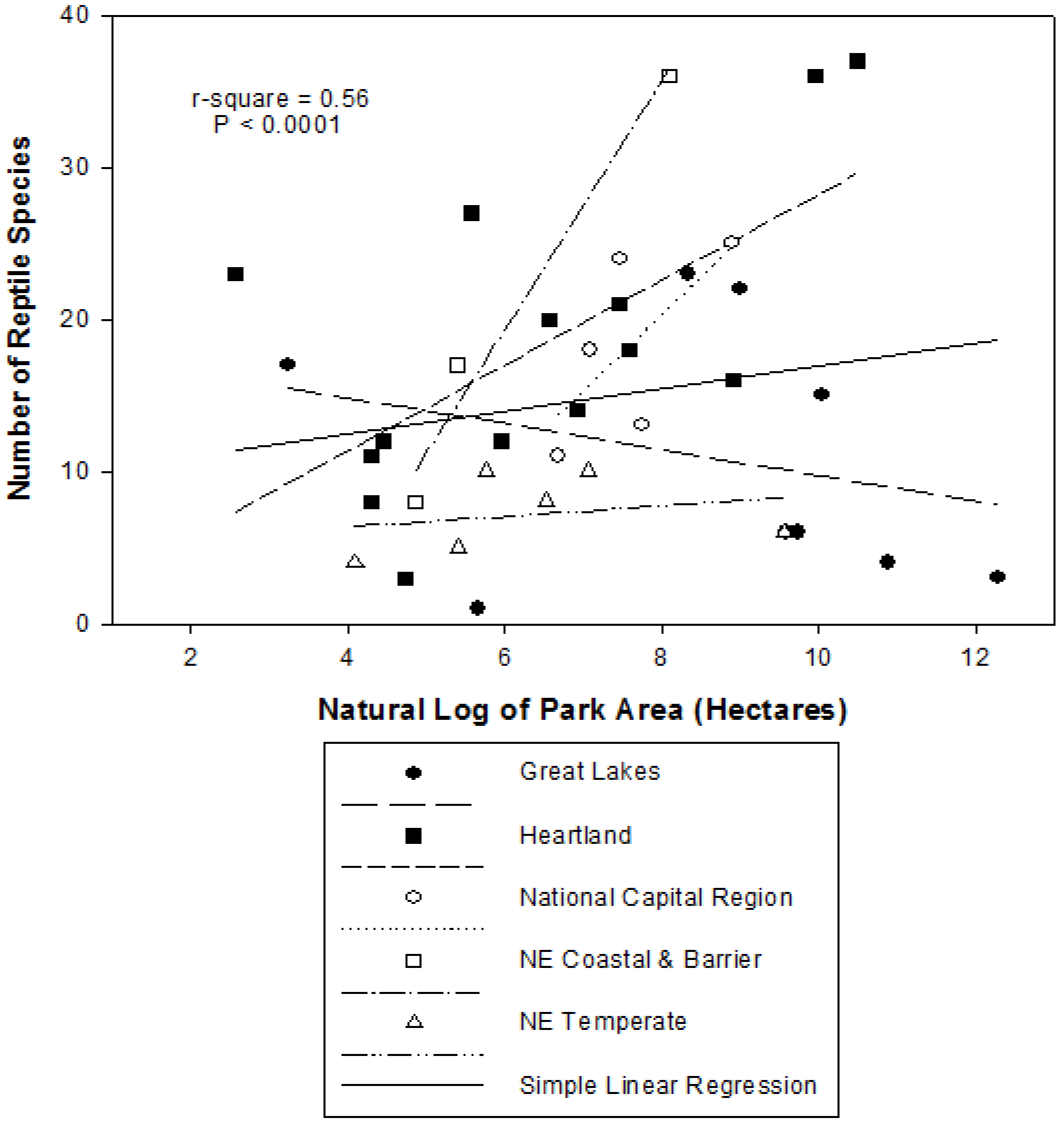

Figure 14. Reptile species richness compared to the natural logarithm of park area by NPS networks (distinguished in the legend and with separate lines on the graph).

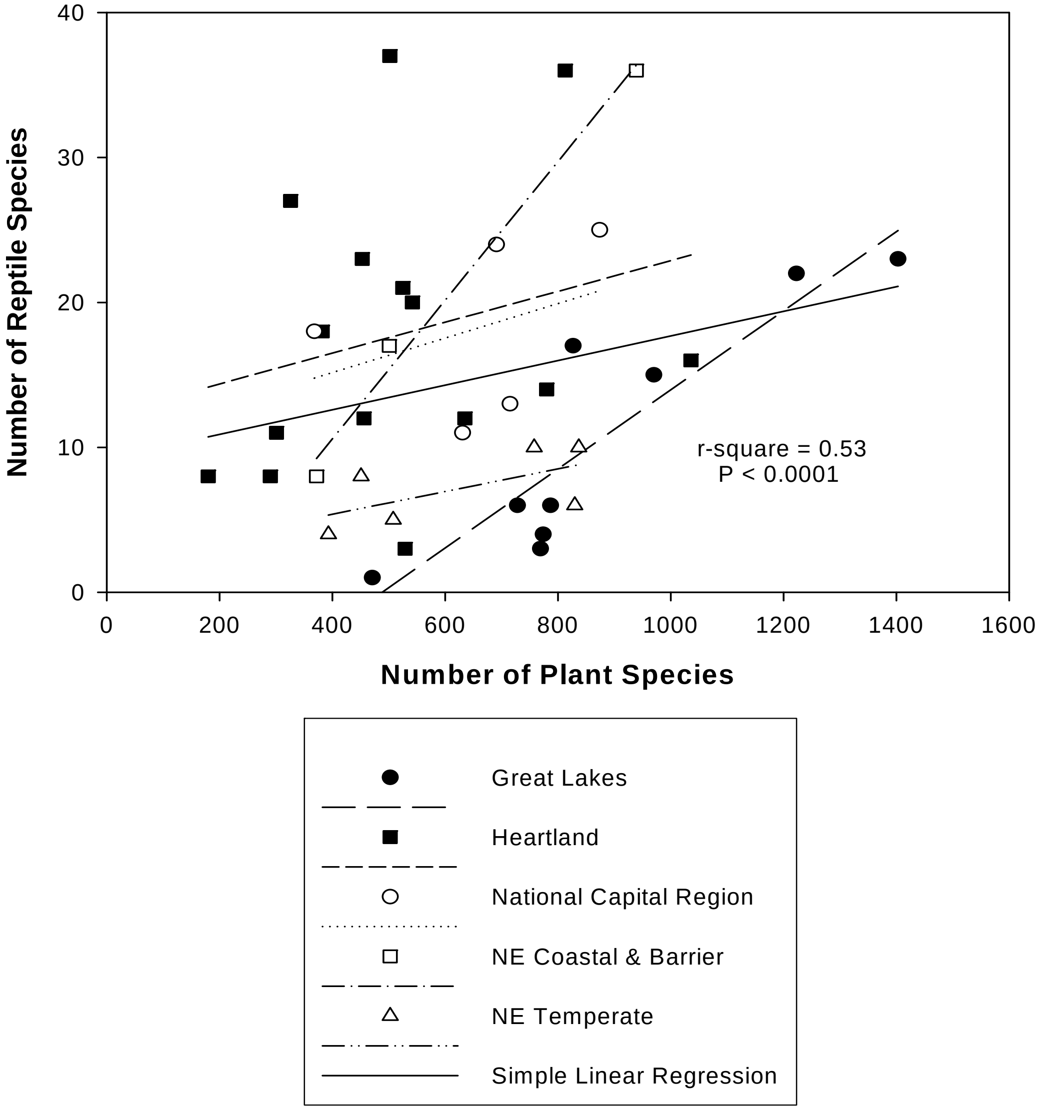

Figure 15. Reptile species richness compared to vascular plant species richness by NPS networks (distinguished in the legend and with separate lines on the graph).

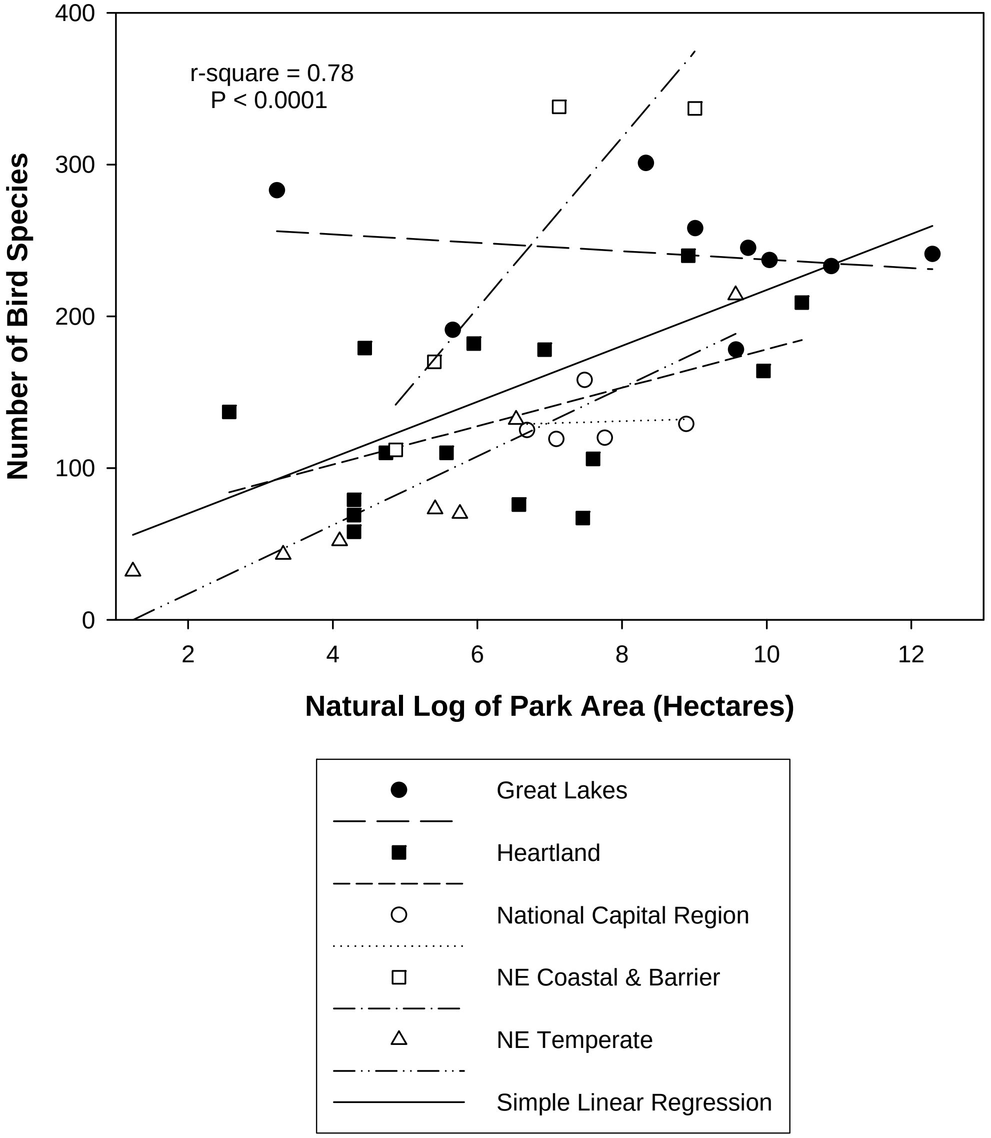

Figure 16. Bird species richness compared to the natural logarithm of park area by NPS networks (distinguished in the legend and with separate lines on the graph).

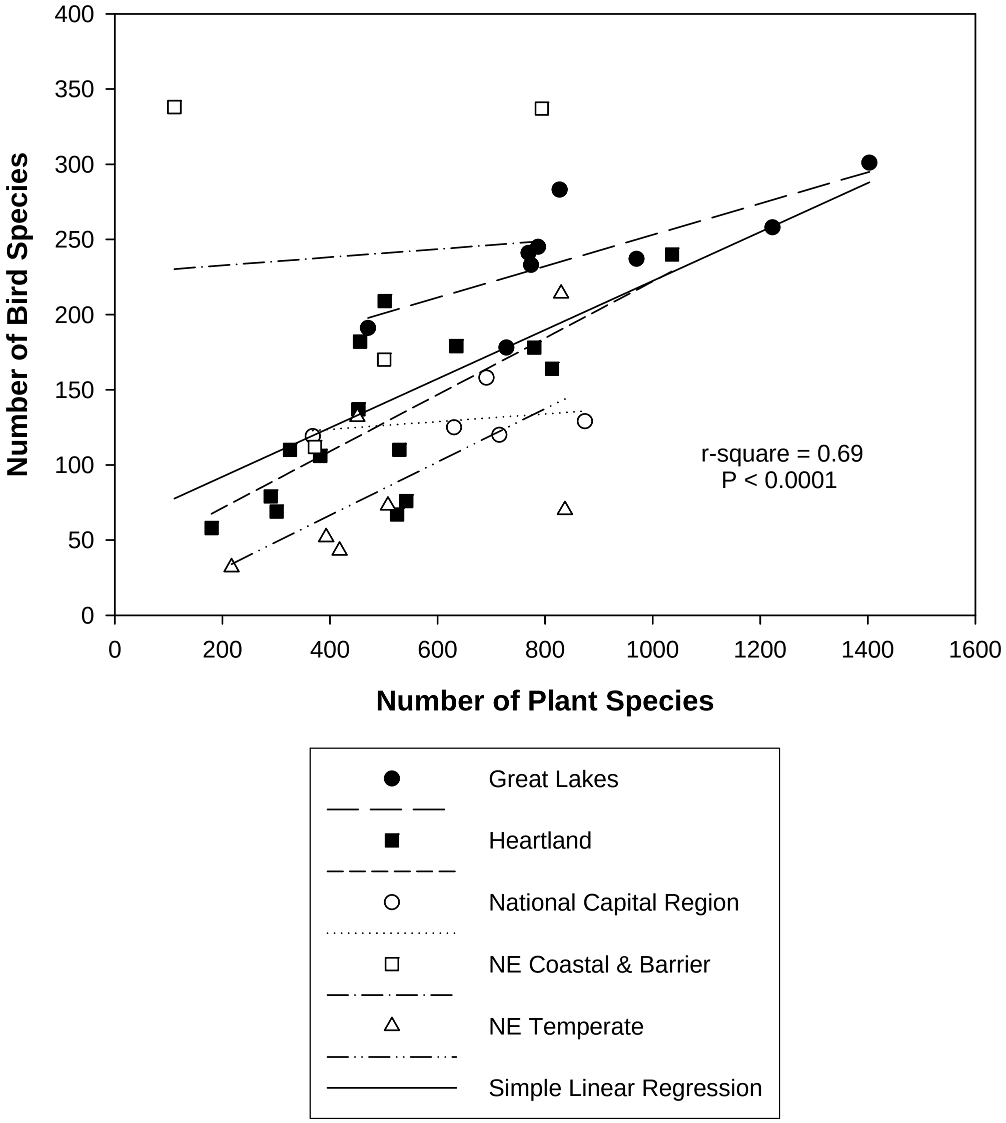

Figure 17. Bird species richness compared to vascular plant species richness by NPS networks (distinguished in the legend and with separate lines on the graph).

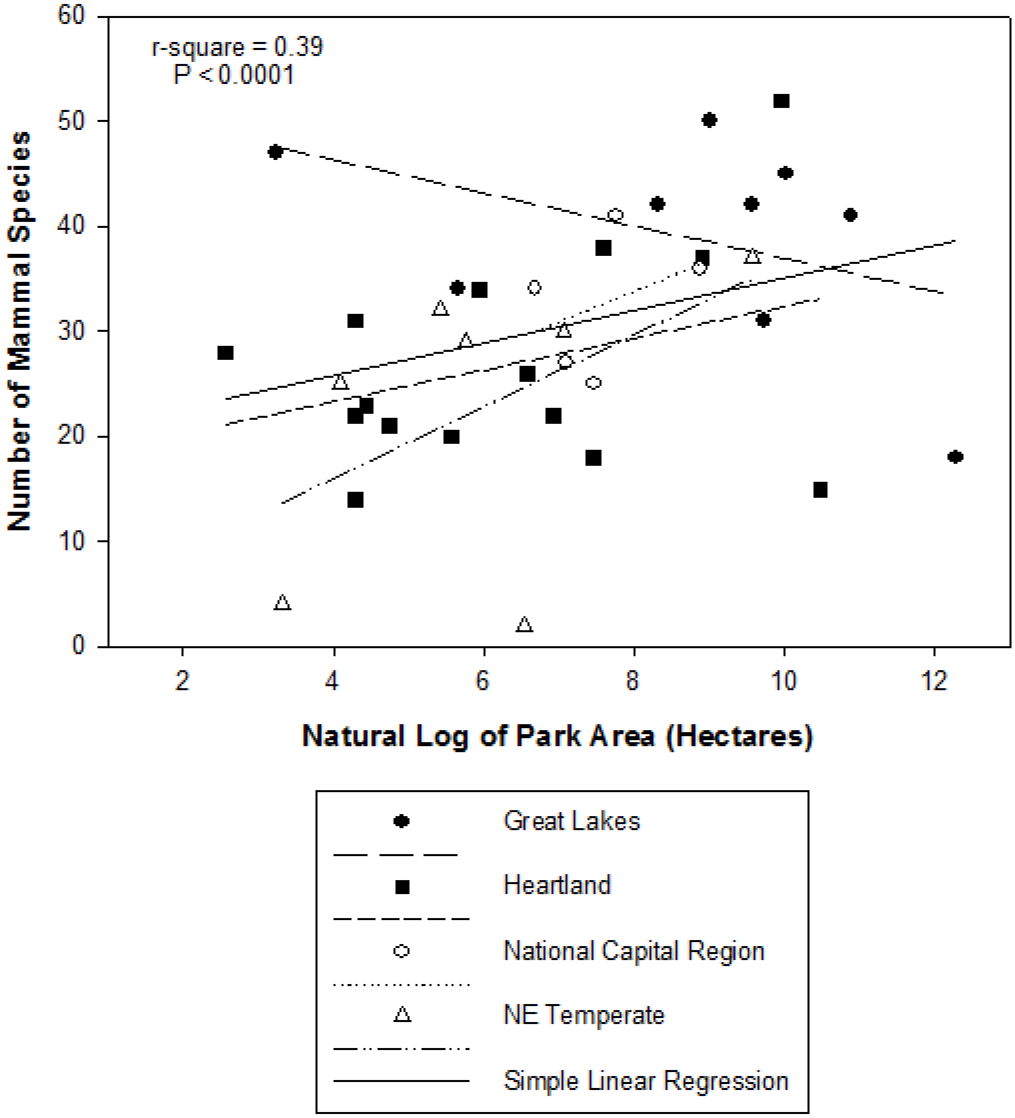

Figure 18. Mammal species richness compared to the natural logarithm of park area by NPS networks (distinguished in the legend and with separate lines on the graph).

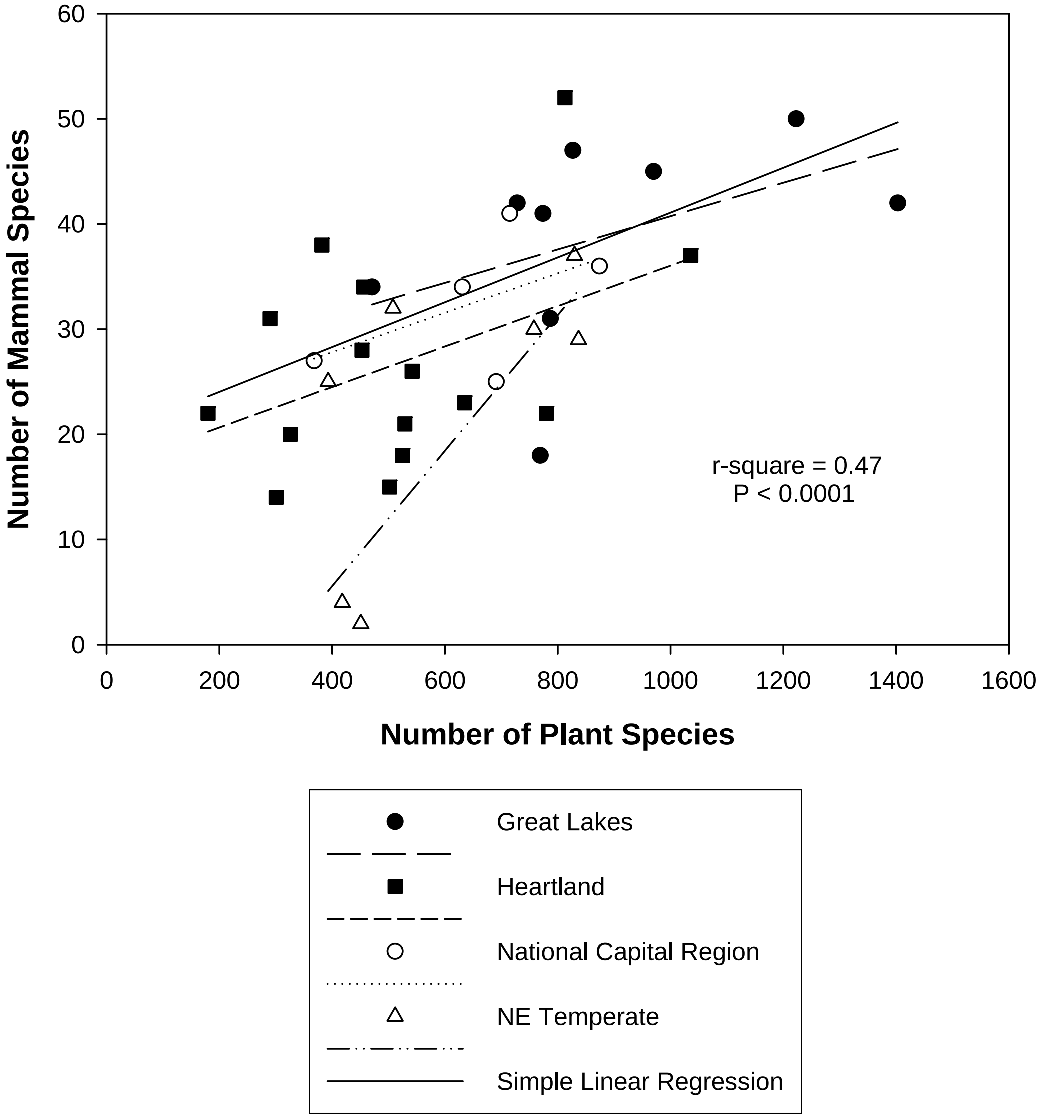

Figure 19. Mammal species richness compared to vascular plant species richness by NPS networks (distinguished in the legend and with separate lines on the graph).

battlefields, national parks, other forested parks, seashore, prairie, and parks in urban areas.

The environmental variables that were compared to vertebrate species richness were general measures that include some of the important environmental, spatial and temporal variation that affects species richness. Due to the coarse resolution of these variables, however, the relationships demonstrated were probably not due to the direct effect of the variable but rather a result of interactions and secondary effects of multiple environmental variables. Factors such as variation in primary productivity, soil, microclimate, habitat heterogeneity, and park management over time all provide or remove resources (e.g., water availability and vegetation structure) that affect the number of species that can exist in a park (Klopfer 1959, Huston 1979, Hawkins et al. 2003). These factors were not explicitly addressed with the environmental variables utilized in our study. Grouping the species at the class taxonomic level also lumps functional attributes of the species (e.g., size, trophic status, specialization, etc.) which may influence species richness relationships (Landres et al. 1988, Huston 1994, Huston 1999a, Hawkins and Porter 2003, Zhao et al. 2006).

There were several parks that had unusually small or large taxon richness in the regression analyses. Fire Island National Seashore (FIIS) in the Northeast Coastal and Barrier Network had the lowest plant species richness of any park in this dataset (111 vascular plant species). This low species richness is believed to be due to the low primary productivity of this harsh environment with high salt spray, resulting in low biodiversity (A.F. O'Connell, Jr., US Geological Survey, personal communication).

For amphibian species richness one park, Colonial National Historical Park (COLO) had substantially more species listed than any other park in the dataset (a total of 32 species). This park has mostly coastal marsh habitat on an island between two rivers (James and York). The park in this dataset that contained the least number of amphibians was Herbert Hoover National Historic Site (HEHO). This park had one intermittent stream occurring within park boundaries and no rivers nearby. In both of these cases, extreme environmental differences seem to explain the contrast in amphibian numbers.

For mammals, there were two parks in the Northeast Temperate Network (NETN) that listed only 2 and 4 species. The park with only two species listed was Morristown National Historical Park (MORR); the two species listed were *Odocoileus virginianus* (white-tailed deer) and *Canis latrans* (coyote). On the park's website (http://www.nps.gov/morr/naturescience/mammals.htm) an additional 11 species of mammals are claimed to be present in the park. Gilbert et al. (2008) lists 17 species that were detected during their surveys there but we did not have access to that publication at the time our analyses were conducted for Myrick (2008). The other park, Weir Farms National Historical Site (WEFA), had four species listed *Marmota monax* (woodchuck), *O. virginianus, Sciurus carolinensis* (gray squirrel), and *Tamias striatus* (eastern chipmunk). Two more species of mammals were found on this park's website (http://www.nps.gov/wefa/naturescience/animals.htm). Gilbert et al. (2008) detected 16 species during their surveys at WEFA, but again, we did not have access to those data when the analyses were conducted for Myrick (2008).

It is unclear why there was a discrepancy between the NPSpecies lists created for scientific review and information provided on park websites to the public. In the Great Lakes Network (GLKN) there was one park, Isle Royale National Park (ISRO) that had an unusually low number of mammals listed. This estimate is likely accurate and the low species richness of mammals is due to the fact that the park is an island 25 km off the Ontario, Canada mainland in Lake Superior (Peterson et al. 1998). The isolation of the park limits the number of mammal species to a total of 18, in comparison to the surrounding mainland where there are over 40 species of mammals (Johnson 1970). In the Heartland Network (HTLN), the Buffalo National River (BUFF) also had unusually low mammal species richness. This park list included 10 species of bats, 2/3 of the total number of mammal species listed for the entire park. This again seems unlikely to represent the true species richness of mammals in a 36,000 ha park and may be due to a result of limited sampling effort at the time our analyses were conducted (Myrick 2008).

In spite of these short-comings, many significant relationships were detected. Plant species richness was a significant predictor of vertebrate taxa richness, but the strength of the association varied among taxa. In the simple regressions, amphibian species richness showed a statistically significant relationship with plant species richness, but the relationship was weak. However the significant relationship between amphibian species richness and plant species richness was evident in the multiple regression. Reptile species richness did not show a significant relationship with plant species richness in the simple regressions but did so in the multiple regressions. Plant species richness was a strong predictor of bird species richness and mammal species richness in the simple regressions. In the multiple regressions this relationship was not evident for bird species richness but was the only significant predictor of mammal species richness.

The variation in explanatory power of plant species richness for different vertebrate taxa richness is likely due to several different factors. One is the trophic level of the taxon and its dependence on plants (Gaston 1996). Many reptile and amphibian species are carnivores and mostly use plants for cover (Pough et al. 2004). Plant species richness should also have an indirect effect on reptile and amphibian species richness by the association with their food resources (Zhao et al. 2006). The relationship between plant species richness and amphibian species richness is most likely affected by moisture availability that also in turn affects plant diversity (Huston 1994, Hawkins et al. 2003, Zhao and Fang 2006). Birds have a direct and indirect dependence on plants for food (e.g., fruits and seeds) and security (e.g., nest building, camouflage with foliage) (Bolen and Robinson 2003). We suggest this is the reason bird species richness was found to have a significant relationship with vascular plant species richness. Many mammal species are herbivores and omnivores, and therefore have a strong direct dependence on plants for food as well as for cover (Delany 1982); perhaps that is why mammal species richness had the strongest relationship to vascular plant species richness of all the vertebrate groups compared in this study.

Park area had significant relationships with plant, amphibian, and bird species richness in the simple linear regressions. Note that the true relationship between area and species richness is curvilinear, which we linearized by taking the natural logarithm of the area. O'Connell et al. (2004) found a similar relationship between number of park-significant specimens detected in museums and logarithm of park area for parks in the Northeast Temperate Network (NETN). The effect of park area remained in the multiple regression comparisons in our analyses. In the linear regressions, park area was not a significant predictor of reptile species richness and a weak predictor of mammal species richness. In the multiple regressions park area was not a significant predictor for reptile and mammal species richness, despite the general positive correlation almost universally found between species richness and increases in area sampled (Rosenzweig 1995). For the relationship with mammal species richness it is possible that the larger mammal species were dispersing outside of the park boundaries therefore making the park area included in this analysis an inaccurate measurement of the area available for the taxon. A possible explanation for the lack of a significant relationship of park area and reptile species richness is the possibility that the reptile species that occurred in the parks are common species that are found in many habitats outside of the parks, therefore making the size of the park inconsequential.

For amphibians the relationship shown in this analysis is likely due to their dependence on aquatic ecosystems. The five parks that contained greater than 20 species of amphibians were Buffalo National River (BUFF), Manassas National Battlefield Park (MANA), Prince William Forest Park (PRWI), Ozark National Scenic Riverways (OZAR), and, as mentioned previously, Colonial National Historical Park (COLO). A brief look into these parks reveals that they all contain or occur within a few kilometers from rivers or wetland habitat. Upon closer inspection it is likely that the parks with the greatest number of amphibians also contain the greatest variety and area of riparian habitats. The theory of mainland area and habitat heterogeneity (MacArthur 1958, Williams 1964, Pianka 1967, Rosenzweig and Winakur 1969, Anderson 1978) may apply to the specialization of amphibians and their significant relationship with park area, meaning that the larger the park area the greater the number of biological communities occurring within the park, therefore providing more opportunities for amphibians to find resources. Thus, the larger the area sampled, the greater the likelihood of capturing more of the specialized species (Rosenzweig 1995). The same theory can be used to explain the relationship demonstrated by vascular plants and park area in this analysis: the greater the amount of area, the greater the number of resources encountered which provides a greater opportunity for more species (Huston 1999a).

Our results indicated that the strongest relationship of the vertebrate groups with area came from birds. Birds have the highest dispersal ranges compared to mammals, amphibians, and reptiles (Gill 1995). Vascular plants also have great dispersal capability by wind or transport by an organism (Cain et al. 2000) and were shown to have a strong relationship with park area.

Reptile and amphibian species richness demonstrated stronger relationships with the environmental variables than did birds and mammals. This pattern is not surprising given that exothermic organisms require appropriate external environmental temperatures for metabolic regulation (Pough et al. 2004). Park latitude was one of the significant predictors for plant, amphibian, and bird species richness, and was the primary significant predictor for reptile species richness. These patterns are expected since many species of plants and vertebrates demonstrate a latitudinal gradient of species richness (Pianka 1966, Stevens 1989). What was surprising was that park latitude was not a significant predictor of mammal species richness. Mammal species richness has been reported to increase with decreasing latitude (Simpson 1964, Wilson 1974). Sample size may have influenced our findings because the number of parks (*n* = 36) with lists of mammal species was the lowest of all of the taxonomic groups.

Mean annual precipitation of the parks was only significantly related to reptile species richness and this held true in the multiple regressions. Therefore, mean annual precipitation had little explanatory power in our analysis. Almost half of the parks (19 out of 43) had a mean annual precipitation of 107.95 cm and the range of precipitation was 70 cm. A similar study that compared vascular plant richness to the species richnesses of amphibians, reptiles, birds and mammals was conducted by Zhao et al. (2006) using data collected at nature reserves across China. This study also included environmental variables such as mean annual precipitation, mean annual temperature, nature reserve latitude, nature reserve area, and elevation range. Zhao et al. (2006) detected some positive relationships between species richness and mean annual precipitation in these nature reserves, where annual precipitation ranges from 229.51 cm to 5.56 cm. Therefore we hypothesize that the region covered in our study did not have enough variation in mean annual precipitation for this variable to be an effective predictor of species richness. We suggest the inclusion of variables that account for the seasonal differences among these parks such as average summer and winter temperatures and the average distribution of precipitation throughout the year to include the heterogeneity in climate experienced by each taxonomic group. Another possibility would be to look at a larger area than these five networks encompass (e.g., the entire US). Considering climate variables seasonally may reveal a more direct link of the effect of climate on species richness, resulting in stronger statistical relationships.

Surprisingly, the human population density of the counties in which these parks occurred did not show any significant explanatory power for variation in species richness. Many parks are located a fair distance from urban areas and the summed population numbers do not take into account the patchiness of urbanization in a county. It may be more informative to look at the distance of parks from densely populated areas rather than at the overall density of the county.

One feature of the region of the eastern US is that it has some of the lowest species richness in all of North America. The species contour maps produced for mammals by Simpson (1964) and for birds by Cook (1969) show that, for the portion of North America in which these parks occurred, species richness is low in comparison to the rest of the United States. The species richnesses for the eastern US also exhibit less variation than is seen in much of the rest of the United States and Mexico. The greatest number of species for amphibians and reptiles has been described as being located in the southeastern US, western US and Mexico (Kiester 1971, Pough et al. 2004). The relationships between vascular plants and vertebrate taxa richness as well as to the environmental variables would possibly increase in strength if there were more variation recorded in the comparisons (e.g., the entire US).

Inclusion of other variables not included in this study is recommended for future research on plant richness versus vertebrate taxon richness. One candidate variable to be considered is habitat heterogeneity in and near the parks. Most species occur in an area with a specific arrangement of habitats and resources (Rosenzweig 1995). The parks in this study ranged in size from 3.5 ha to over 200,000 ha and many different habitat types are likely to have occurred in the larger parks. Unfortunately, there is only limited documentation by NPS for habitat types within each park. The information available is not at an appropriate resolution for comparison to species richness, which is typically reported for the entire park, not for specific or contrasting habitats. Such documentation should become more readily available as the GIS mapping and land-use documentation efforts of the parks continue.

Our results were similar to previous studies of diversity at the taxonomic level of class (Sillen and Solbreck 1977, Vessby et al. 2002, Wolters et al. 2006, Zhao et al. 2006) and over a broad regional scale. Plant species diversity was consistently related to vertebrate species diversity, particularly when combined with certain other variables, such as latitude and area. Zhao et al. (2006) had very similar results in their comparisons of vascular plant species richness to vertebrate species richness in China. This is interesting because their study was conducted across a much larger area, had a larger sample size, and was conducted at a broad range of latitudes. This indicates that the findings of our study will likely apply under different environmental conditions.

Thus, these analyses demonstrate support for the use of vascular plant species richness as a factor to be considered when planning for the preservation and protection of land for biological diversity. Situations where this information may be beneficial to NPS would be in the purchase of new park land or conservation easements. Having an inventory of the plant species that occur could help prioritize selection of an area using the knowledge of plant species relationships to vertebrate species diversity, but other factors such as number of endemics or endangered species should also be included in this prioritization rather than vascular plant species richness alone. It is important to state that these relationships between plants and vertebrates must be used in conjunction with other variables such as habitat heterogeneity and climate in order to describe more fully relationships of biological species richness (Gaston 2000). It would not be advisable to base park management decisions upon vascular plants alone, as a surrogate for vertebrate species exclusively. Many of the relationships were significant but did not demonstrate enough explanatory power for use as surrogates of biological diversity.

Species area relationships varied among networks for plant species, amphibian, reptile, and bird species richness, while the relationships between plant species and vertebrate taxa richness did not differ among networks, except for birds. One possible explanation could be not including habitat heterogeneity. Habitat heterogeneity can influence species richness (Noss 1990, Huston 1994, Rosenzweig 1995). The inclusion of a variable that accounted for the difference among networks in habitat heterogeneity would likely have been a better predictor of species richness than park area or vascular plant species richness. Habitat heterogeneity is one of the most important explanations for variation in species richness particularly at scales as large as I&M networks (Huston 1999a). It would have been interesting to see if habitat heterogeneity was more related to species richness of some taxa more than other taxa. Increasing or decreasing habitat heterogeneity will affect the resources available to species as well as alter inter- and intra-species interactions for obtaining the resources (Bolen and Robinson 2003). Having knowledge of the habitat heterogeneity of the parks and the relationship of habitat heterogeneity with species richness would be beneficial for park managers when making decisions on altering or disturbing habitat. However, NPS may not have this kind of information available at the present time.

Another reason for the variation among the networks was likely due to small sample size. This study only had five networks and no more than 15 parks for which data were available within a network. These results differed from the results in the regression analyses where all of the parks among the networks were combined. In the regressions, park area was related to plant, amphibian, bird, and mammal species richness. Plant species richness was related to species richness of each vertebrate except reptiles in simple and multiple regressions. Therefore, the primary conclusion here is that the number of parks within each network may be too small to reliably assess differences among networks.

The species diversity in an area is influenced by biotic and abiotic factors (Boone and Krohn 2000). There are three sets of hypotheses about the primary factors influencing species diversity (Zhao and Fang 2006). One set is founded in climatic variables such as temperature and precipitation (Klopfer 1959, Hawkins et al. 2003) and predicts the amount of energy available to vascular plant and vertebrate species thus affecting their distribution. Another set is founded in habitat heterogeneity and topography (Noss 1983, Bohning-Gaese 1997, Jetz and Rahbek 2001) and predicts that species are limited in their distribution based on physical barriers such as water bodies and mountain ranges that limit potential dispersion. A third hypothesis considers the interaction between natural variation in productivity, which is influenced by climate and soils, and variation in natural or anthropogenic disturbances that kill organisms (Huston 1979, 1994). This hypothesis predicts that the effects of disturbances on species diversity can actually reverse between environments that differ sufficiently in productivity. Because many human impacts, including management practices, involve mortality, biodiversity management may actually have opposite results in different parks or different park networks (Huston et al. 1999).

All of these hypotheses are related to one another in various ways and to differing degrees. It is unlikely that species diversity in any region will be determined by only one or even a few of these processes or that one process will have the same effect across multiple regions. Reasons for differences among the networks are likely due to multiple interacting processes.

One factor that differed among the networks was the average park area. The Great Lakes Network (GLKN) had the largest park area on average and the highest average number of plant, bird and mammal species. However this network possessed the lowest average richness of amphibian and reptile species. The lower richness of amphibians and reptiles in this park may be influenced by latitude. Higher latitudes are correlated with colder temperatures. Amphibians and reptiles are exothermic and less capable of exploiting colder environments (Pough et al. 2004). Therefore lower amphibian and reptile species richness at higher latitudes is not surprising.

There was an interaction in the relationships of park area and amphibian, reptile, and bird species richness among networks. The two networks (NETN and GLKN) with parks that occurred at higher latitudes had negative slopes in these relationships. The GLKN slope was also negative in the ANCOVA for mammal species richness although the network and park area interaction was not statistically significant. The lack of a statistically significant interaction is likely due to small sample size, which was the lowest for mammal species richness data ($n = 36$). For amphibian species richness the NETN's negative slope with area is due to the fact that the largest park in the network, Acadia National Park (ACAD), occurs at the highest latitude in that network. For the ANCOVAs for reptile, bird and mammal species richness, the negative slopes with park area in the GLKN was caused by the size and location of two parks. Isle Royale and Voyageurs National Parks both occur at the highest latitudes in the GLKN and have the largest park areas for the entire dataset.

Species richness of most taxa increases as latitude decreases, at least in terrestrial environments (Fischer 1961). Therefore latitude and factors correlated to latitude such as temperature probably influence the differences in species richness seen across the networks for bird species richness. When looking at richness patterns for birds (Simpson 1964) across that region of the United States in which these networks occur, we found a trend of species richness decreasing with increasing latitude.

The longitude of the parks may have also influenced the variation in bird species richness among the networks. Some of the parks occur along one or the other of two major migratory pathways, the Atlantic and the Mississippi, while others do not (Braun 2005). The migratory species will utilize habitat for food and cover rather than for nesting or long term shelter. Migratory species may affect the relationships of plant species richness and bird species richness among the networks because they may be only present a short time and not interact significantly with the heterogeneity of the vegetation (Bolen and Robinson 2003).

Suggestions have been made that one determinant of avian species richness in areas as large as the I&M networks may be available energy (Bohning-Gaese 1997). Mean annual temperature may reflect available energy among the networks. The network with the lowest mean annual temperature (GLKN) surprisingly had the highest average of bird species (240.89). However, this was the network with the greatest average park area and this likely influenced this relationship.

Amphibian, reptile and mammal species richness did not demonstrate strong relationships with park area among the networks. In the linear regressions, a significant relationship was demonstrated between park area and amphibians species richness which was explained by the dependence of amphibians on aquatic habitats. The parks that had the greatest amphibian species richness also had the greatest amount of aquatic habitat. However, these parks were separated into three networks. It is likely that the parks in each individual network did not possess sufficient variation in aquatic habitats to demonstrate the relationship.

For reptiles it is possible that the species that occurred in the parks are ubiquitous throughout the region making the size of the park and environmental differences among the networks inconsequential. For larger mammals in particular, it is possible that the species occurring in these parks disperse outside of park boundaries and therefore the park areas are not representative of the size of the area or the habitats that are required.

Mean annual precipitation varied little among the networks. The range in mean annual precipitation was from 81.84 cm in GLKN to 112.71 cm in the NETN. This similarity among networks of mean annual precipitation may have contributed to the lack of relationships demonstrated among the networks for plant, amphibian, reptile, and mammal species richness. In species richness contour maps for mammals, reptiles, and amphibians in North America (Cook 1969, Kiester 1971), the region in which this study takes place shows little variation. This section of the US has been altered by humans and has been impacted by urbanization longer than the rest of the country (Alig and Healy 1987, Shaw 2004). This could lead to a decline in species diversity and domination of common species in the region (Blair 1996).

Making conclusions about species richness patterns should be done carefully. There are numerous environmental variables that influence species geographic ranges (Hawkins et al. 2003). The response of species to environmental variables in one geographic area may be very different than the response in another area (Landres et al 1988). For biological diversity management in national parks we suggest focusing on species' function in any given ecosystem. Merely conserving biological diversity based on a total number of species overlooks the contribution certain types of species have in specific types of ecosystems. Categorizing the species that occur in a park by their functional attributes and determining the number of species required for a particular function can provide a more specific conservation objective. Monitoring the changes in the number of species in a functional group will help to isolate what is changing in an ecosystem. The reverse could prove true for determining the effect ecosystem change would have on species richness of a functional group (Huston 1999b). Ideally, surveys of species that occur in the parks would be performed on a regular basis by trained professionals in order to determine changes in the species that comprise the functional groups. This information is important when planning for types and rate of human-induced disturbance in relation to overall park management goals, whether it be increased species diversity, improved water quality, or increased access by park visitors.

The amount of variation among the parks is extensive, and includes everything from the goals of the park managers, the ecosystems present in the parks, the functional groups, to the type and number of species that compose the functional groups. This is particularly relevant to park management for biological diversity. Park management should be approached from the local and site specific criteria rather than applying management directives from different regions of the US (Huston et al. 1999, Huston 1999b).

NPS network boundaries are partially designated on a biome basis but also follow bureaucratically designated boundaries (NPS 1999b). Ecoregions were mapped by the Environmental Protection Agency (EPA) and denote areas of similar ecosystems (Omernik 1987). Grouping the parks by eco-regions alone to account for similarities in the underlying causes of the diversity found within different networks may be useful to the long-term management of biological diversity. The groupings would follow the longitudinal pattern of the eco-regions and the park groupings of particular networks (e.g. NCRN and NCBN) would be affected more than others.

As mentioned previously, we also recommend that analyses similar to those presented here be conducted for all National Parks, once species lists become available for all networks in the US, to gain a better understanding of how vascular plant species richness, area, and vertebrate species richness are related in the US.

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