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Research Article

The spatial distribution of diversity between disparate taxa: Spatial correspondence between mammals and ants across South Florida, USA

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Abstract

Gap Analysis takes a proactive landscape-level approach to conserving native species by identifying nodes of high biological diversity. It uses vertebrate species richness as an index of overall biological diversity. However, it remains unknown whether or not the spatial distribution of vertebrate diversity corresponds with the diversity of other taxa. We tested whether landscape-level diversity patterns corresponded between a vertebrate and an invertebrate taxon, mammals and ants, across the southern half of the Florida peninsula, USA. Composite digital maps with a 30-m spatial resolution were produced for each taxon. Spatial correspondence between the taxa was determined by normalizing and then subtracting the composite maps. There were large areas of spatial correspondence – indicating that richness between mammals and ants was similar over much of southern Florida. However, spatial correspondence occurred where the richness of both taxa was low or moderate, and areas with the highest species richness (highest 20%) for each taxon, the explicit focus of Gap Analyses, corresponded over only 8752 ha. Gap Analysis provides a much needed assessment of landscape-level diversity patterns and proactive reserve design, but it must be explicit that the results are applicable for vertebrate diversity, which does not necessarily correspond with diversity patterns of other taxa. The two taxa investigated differ by orders of magnitude in the scale that they perceive their environment, and it is likely that diversity hotspots vary as the scale of investigation – and the taxa mapped – vary.

Introduction

Most landscapes in North America have been anthropogenically disturbed within the past two centuries by habitat destruction, fragmentation, or the introduction of non-indigenous species (Noss and Copperrider 1994; Wilson 1985). This has resulted in an increase in the number of species and communities that are considered endangered or threatened (Noss and Copperrider 1994; Noss and Peters 1995; Wilson and Peter 1988). Because many species, communities, and ecosystems are presently imperiled, there is a need for

establishing efficient ways to inventory and monitor areas for inclusion in conservation networks. Efforts aimed at the preservation of single species as they become endangered are remedial and not cost effective. Using one or a few species for the identification and development of reserve systems or conservation plans is a narrow approach that may result in the protection of one organism at the expense of another (Kushlan 1979; Hurro et al. 1987; Landres et al. 1988), and may not efficiently identify areas that need to be protected in a timely and cost-effective manner.

To counter the problems of using single species, the use of indicator species, guilds (Severinghaus 1981; Landres 1983; Verner 1984), or umbrella species (Shafer 1990) have been advocated as efficient methods for identifying areas in need of protection. Recently, the U.S. Fish and Wildlife Service (now under the auspices of the U.S. Geological Survey, Biological Resources Division) initiated the Gap Analysis Program to identify areas of high biological diversity that are not protected by existing reserves (Scott et al. 1993). Gap Analysis attempts to take a proactive landscape-level approach to identifying nodes of high biological diversity. This approach uses vertebrate species richness as an index of overall biological diversity (Scott et al. 1987). Similar techniques are being used throughout the world (Miller 1994). Vertebrates have been used in most spatial analyses of biodiversity patterns because they are relatively well known taxonomically, well-represented in museums, and may be large and charismatic. Vertebrate species richness may not reflect species richness of other groups, however (Prendergast et al. 1993; Kerr 1997).

Vertebrates account for less than 4% of presently described animal species in the United States (Eisner et al. 1995) and fewer than 2% worldwide (Gaston 1991). Almost all undescribed species are invertebrate. Few of the estimated 27 000 species going extinct each year are vertebrates (Wilson 1992). Vertebrates utilize relatively large home ranges that are likely to span several vegetation and habitat types. Most vertebrates, even habitat specialists, are habitat generalists when compared to invertebrates. The scale of perception and environmental exploitation of invertebrates may be orders of magnitude smaller than that of vertebrates. The ability of technicians to classify vegetation types exceeds the resolution of habitat utilization by vertebrate species (Maser et al. 1984). For example, the Florida Gap Analysis Project is using a habitat classification scheme that recognizes >100 plant associations. At this level, few, if any, vertebrates are specific to any one association (C. R. Allen, *unpublished data*), and most species span numerous associations. Vertebrates and invertebrates interact with their environment at different scales. Clearly, an examination of biodiversity patterns should consider invertebrate diversity as well as vertebrate diversity.

Nodes of high biological diversity determined from vertebrate species richness are likely to be in the range of 100s to 1000s of hectares (e.g., Cox et al. 1994). Decisions concerning land use, habitat protection, and purchase, are likely to be an order of

magnitude smaller. In the eastern United States, few, if any, land acquisitions remain to be made that can protect viable populations of medium-sized or larger vertebrates (Allen et al. 2001). However, small areas unable to support a large variety of terrestrial vertebrates or vertebrates with large home ranges may none the less be species rich, containing a high diversity of plant and invertebrate species. Land-use and conservation decisions made using vertebrates as indicators of biodiversity will realistically assess impacts on or protect vertebrates, but may have little usefulness in conserving overall biodiversity.

Our goal was to determine if patterns of vertebrate species richness correspond with invertebrate species richness, using mammals to represent vertebrates and ants to represent invertebrates. We produced high-resolution (30-m) maps of the spatial distribution of species richness of both ants and mammals across south Florida, USA, and compared the spatial distribution of richness between the two taxa. A high degree of spatial correspondence would indicate that the spatial distribution of mammal richness provides an adequate proxy for the spatial distribution of diversity in ants. Alternately, a lack of correspondence would indicate that mammal diversity does not index ant diversity. More broadly, our results may provide an indication of the overall relationship between the distribution of vertebrate and invertebrate diversity at a fine resolution landscape-level.

Methods

Landcover

We used a study area encompassing the southern half of peninsular Florida, USA, which consists of approximately 4 124 421 ha of non-urban and non-agricultural cover types. This complex mosaic of habitat types and land uses is representative of the interspersed land uses and habitats found throughout much of the urbanizing eastern seaboard of the United States. Landcover was mapped from the classification of 1993 and 1994 Landsat Thematic Mapper satellite imagery at a spatial resolution of 30 m. Bands 2, 3, 4, and 5 of the imagery and a Tassel Cap transformation (Crist and Cicone 1984) were used in an iterative unsupervised clustering algorithm. Labeling of the spectral clusters with vegetation associations followed The Nature Conservancy/UNESCO, Southeastern Region classification scheme (The Nature Conservancy 1997). This

hierarchical, ecologically-based classification scheme delineates plant associations in the southeast United States. The UNESCO classification scheme is the basis for the National Vegetation Classification Standard adopted by the Federal Geographic Data Committee. Labeling was assisted with auxiliary information from South Florida Water Management District land use/land cover maps, National Wetlands Inventory maps, county-level soils maps, Everglades National Park (Olmsted 1980; Olmsted et al. 1980a,b, 1980, 1981, 1983) and Big Cypress National Preserve (Gunderson and Loope 1982a–d; Gunderson et al. 1986) vegetation surveys, and photo interpreted points from low altitude aerial videography.

Species richness

Geographic distribution of species (i.e., ants and mammals) was determined at the county-level. For ants, distribution was determined primarily from published sources (Buren and Whitcomb 1977; Carroll 1975; Cole 1982; Creighton 1950; Deyrup 1991; Deyrup and Trager 1986; Deyrup et al. 1988, 1989; Johnson 1986; Klotz et al. 1995; MacKay 1993; Schneirla 1944; Smith 1930, 1933, 1944, 1979; Thompson 1989; Thompson and Johnson 1989; Van Pelt 1947, 1950, 1956, 1958, 1966; Watkins 1985; Wheeler 1932; Wilson 1964), and from the unpublished data of D. P. Wojcik and C. R. Allen.

Most data for the determination of county-level mammal distribution was collected from a national survey of museums holding specimens collected in Florida, but published sources also were used (Blair 1935a, b; Chapman and Feldhamer 1982; Hamilton 1941; Ivey 1959; Layne 1984; Moore 1946; Pearson 1954; Pournelle 1950; Sherman 1952; Starner 1956), especially for endangered species (Humphrey 1992). Additional data on mammal distribution was provided by the Wildlife Observation database of the Florida Game and Fresh Water Fish Commission and by the American Society of Mammalogists series 'Mammalian Species'.

The availability of data varied by county. For several counties largely in private ownership with limited access, few data were available. We interpolated distributions in counties lacking data, based on the presence or absence of species in adjacent counties. These data were then used to produce a county by species matrix for both taxa.

Habitat affinities for both ants and mammals were determined primarily from literature review. Knowl-

edge of the habitat use of individual species allowed us to produce maps that are habitat specific. To date, our Florida species habitat/ecology bibliography includes >1300 sources (which may be accessed online at <http://malthus.wec.ufl.edu/coop/gap/>) which have been used to create descriptors of habitat use by species.

County-level distribution was used as a course filter of species occurrence for both taxa, and species by landcover type matrices provided specific habitat data. In conjunction, the two matrices were then used to produce habitat-specific spatial distributions of all ant and mammal species present in the southern half of peninsular Florida. Additionally, for mammals, we incorporated home range information to calculate the minimum patch size necessary to support a minimum viable population ($n = 50$) for each species, and modeled species as occurring only in patches that were as large as or larger than that minimum area (Allen et al. 2001). Digital species richness maps (ARC/INFO grid coverages) for both taxa were produced by adding the individual species maps to produce a composite of overall within-taxa richness.

Spatial correspondence between ants and mammals

Spatial correspondence between mammal and ant species richness was determined by subtracting the ant species richness coverage from the mammal species richness coverage. However, overall richness of ants is much higher than the overall richness of mammals. Thus, for those coverages to be comparable, they were first normalized by recalculating richness values so that they ranged between 0 and 100. In both normalized coverages, a value of 100 was equivalent to the highest species richness, regardless of its actual numeric value.

In the coverage of spatial correspondence, values of 0 occur where the relative levels of species richness between mammals and ants are equivalent. High positive values occur where there is higher mammal richness relative to ant richness, and high negative values occur where ant species richness is high relative to mammal species richness. We were specifically interested in (1) examining overall spatial correspondence between the two taxa and (2) determining the correspondence between the nodes of highest richness (top 20%) for each taxon.

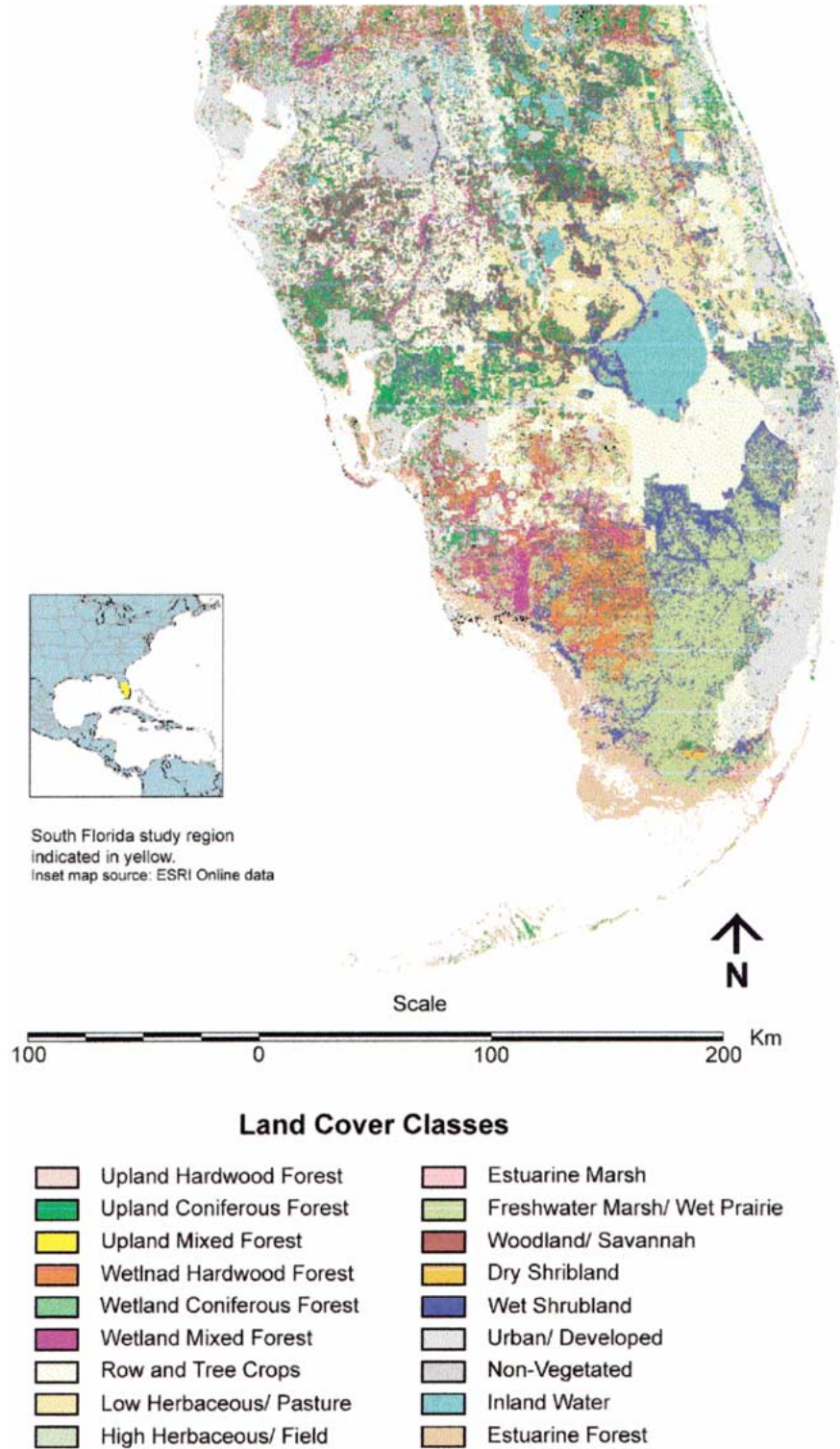


Figure 1. Landcover mosaic of the southern one-half of the Florida peninsula. Landcover was mapped from the classification of 1993 and 1994 Landsat Thematic Mapper satellite imagery at a spatial resolution of 30 m. The 70 landcovers (60 natural and 10 urban or agricultural) we used for modeling have been aggregated to 18 classes for clarity of presentation.

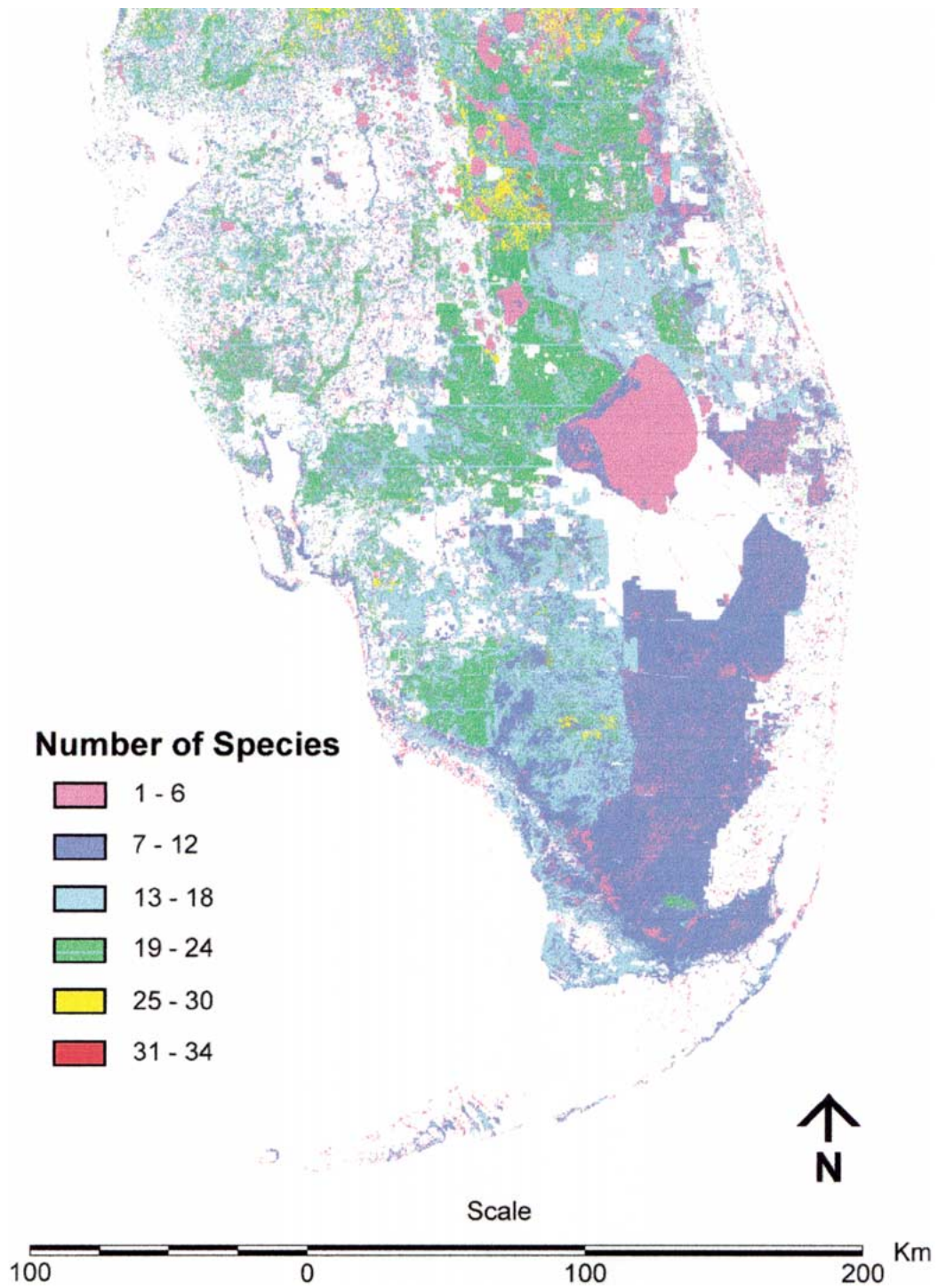


Figure 2. Species richness of mammals in the southern one-half of the Florida peninsula. Values of richness ranged from 1–34.

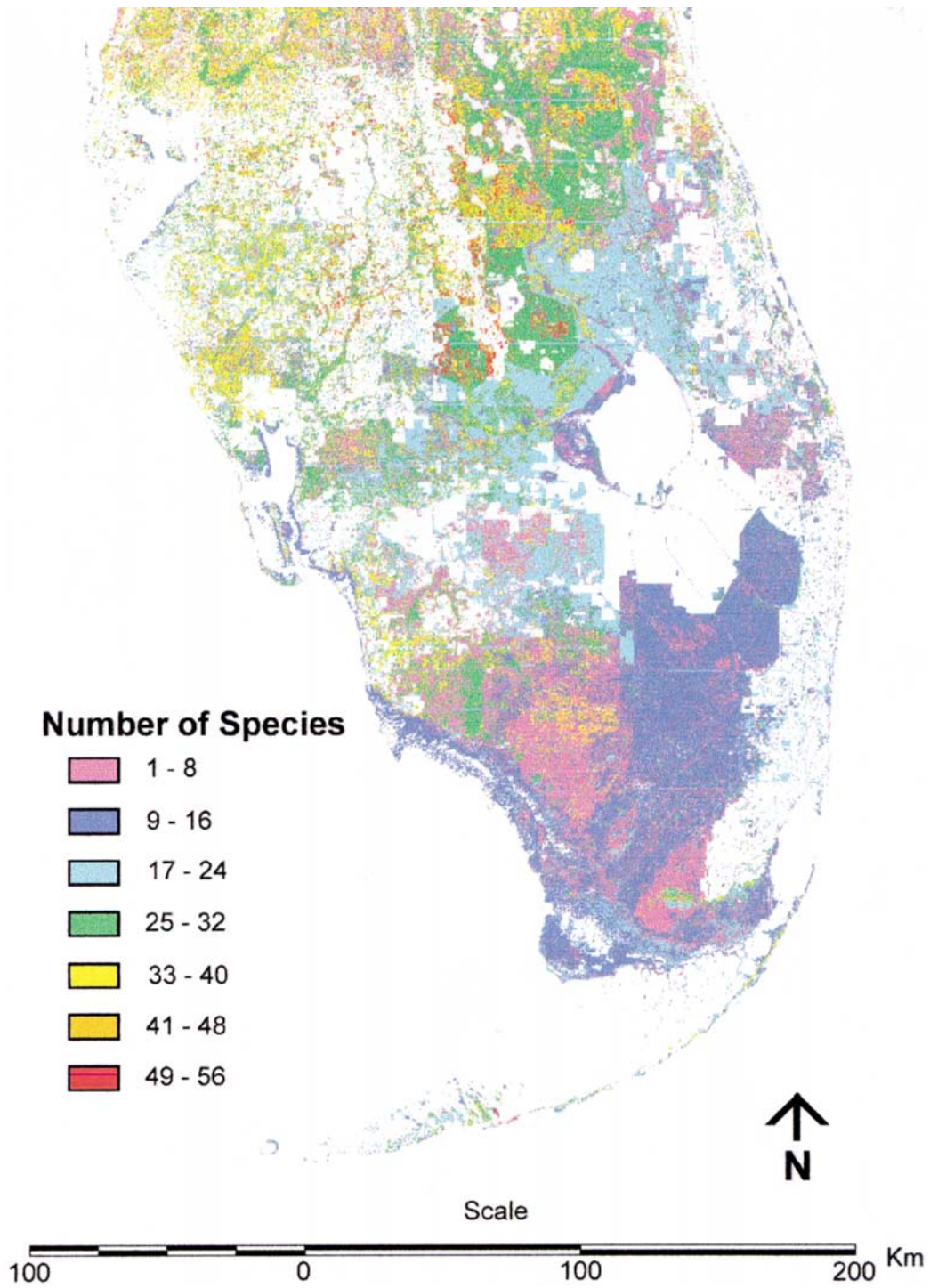


Figure 3. Species richness of ants in the southern one-half of the Florida peninsula. Values ranged from 1–56.

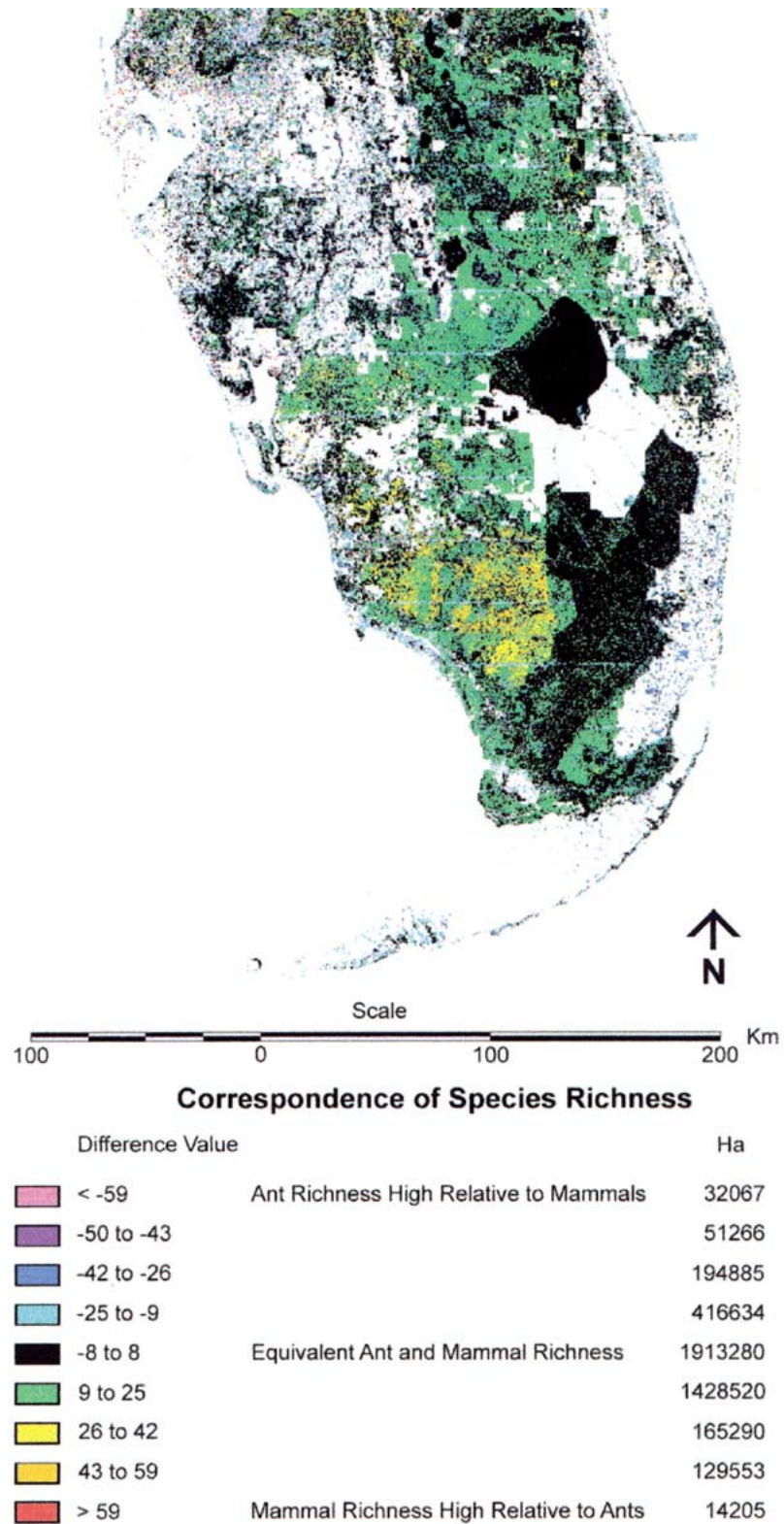


Figure 4. Spatial correspondence of species richness between mammals and ants in the southern one-half of the Florida peninsula. Green, black and turquoise colors represent areas where spatial correspondence is relatively high. Dark blue and purple, ant richness is high relative to mammal richness, and yellow, orange and red, mammal richness is high relative to ant richness.

Results

The southern peninsula of Florida is a complex mosaic of habitat types (Figure 1). Mammal species richness varied from 1 to 34 species, and was especially high in south Florida slash pine, dry prairie, swamp forests, and pine rocklands in southwest Florida and the north-central portion of our study area (Figure 2). Ant species richness varied from 1 to 56, and was highest in pine rocklands, south Florida slash pine, and tropical hardwoods habitats in the northern portion of our study area (Figure 3). In the coverage of spatial correspondence (Figure 4), there are large areas indicating that richness levels between mammals and ants was similar over much of the Florida Everglades. However, in the Big Cypress area of southwest Florida, and in the north-western portion of our study area, there is a lack of correspondence between mammals and ants. This is not necessarily because mammal species richness is especially high in these areas, but because ant richness is low. In the northwest the opposite situation exists: normalized ant species richness is higher than normalized mammal species richness in many pine-dominated habitats.

Areas comprising the top 20% of species richness (Figure 5) for each group did not correspond. Richness levels of ≥ 45 for ants (top 20%) occupied 87 352 ha, and levels of mammals ≥ 27 (top 20%) occupied 34 937 ha. Overlap between these areas of highest richness for each taxa was just 7%, or 8 752 ha, which is 0.2% of the south Florida landscape in natural landcovers.

Discussion

Across most of south Florida, there is spatial correspondence between ants and mammals, that is, ant and mammal diversity levels occur at similar levels. However, the spatial distribution of richness was not normally distributed. Areas of high richness were rare, with the top 20% richness levels for ants and mammals comprising less than 2% and 1%, respectively, of the total natural landscape area. Most habitat patches hold low to moderate levels of diversity, and patches of high diversity are rare. At fine spatial resolutions the landscape-level distribution of nodes of high species richness do not correspond between mammals and ants. Gap Analyses provide a much-needed assessment of landscape-level diversity patterns and proactive reserve design, but must be explicit in that the

results are applicable only for those species mapped, but not necessarily diversity patterns of other taxa. Previous studies also documented a lack of spatial correspondence among different taxa, but the analyses were conducted at very coarse spatial resolutions and were not habitat specific (e.g., Prendergast and Eversham 1997).

The case for the use of arthropods for the inventory of biodiversity has been convincingly made (Kremen et al. 1993). Using some arthropod taxa increases the resolution of biodiversity detection. Prendergast et al. (1993), in an examination of species richness at the resolution of 10 km by 10 km grids in Great Britain, compared the diversity hot spots of birds, mammals, butterflies, and liverworts and found that the species rich areas within each taxa rarely overlapped. Our study is the first conducted at high resolution at a broad scale. Landres et al. (1988) cautioned against the use of vertebrates as an index of biodiversity. A range of well-chosen organisms that will explicitly better represent overall biological diversity is needed to index diversity. Due to the vast number of described invertebrates it would be impossible to include them all. Therefore, invertebrate groups should be carefully chosen to maximize their contribution to determining overall patterns of biodiversity.

Invertebrates contribute more to species richness than do any other taxon. This mandates the inclusion of invertebrates in an index of biodiversity. Among the Arthropoda, the Formicidae are a good family of choice for mapping because data are available or relatively easy to obtain, ants utilize a wide variety and large number of niches, and because some ant species are very habitat and condition specific. Utilizing the Formicidae in biodiversity mapping efforts offers the chance to increase the resolution of nodes of high richness because ants interact with their environment at a very fine scale. Land-use decisions to be made in the future are likely to be at a scale an order of magnitude smaller than can be made by utilizing vertebrates alone. The inclusion of the Formicidae in addition to vertebrate taxa in programs investigating biodiversity assures that land-use decisions will be made using data resolute across a range of scales.

Ants act as keystone species in many instances (Risch and Carroll 1982), and they provide key and irreplaceable ecosystem services such as pollination, nutrient turnover, energy flow, and seed dispersal (Handel et al. 1981). The Formicidae exhibit a wide range of habitat specificities and diversity of lifestyles in Florida (Allen et al. 1998) and elsewhere. Some

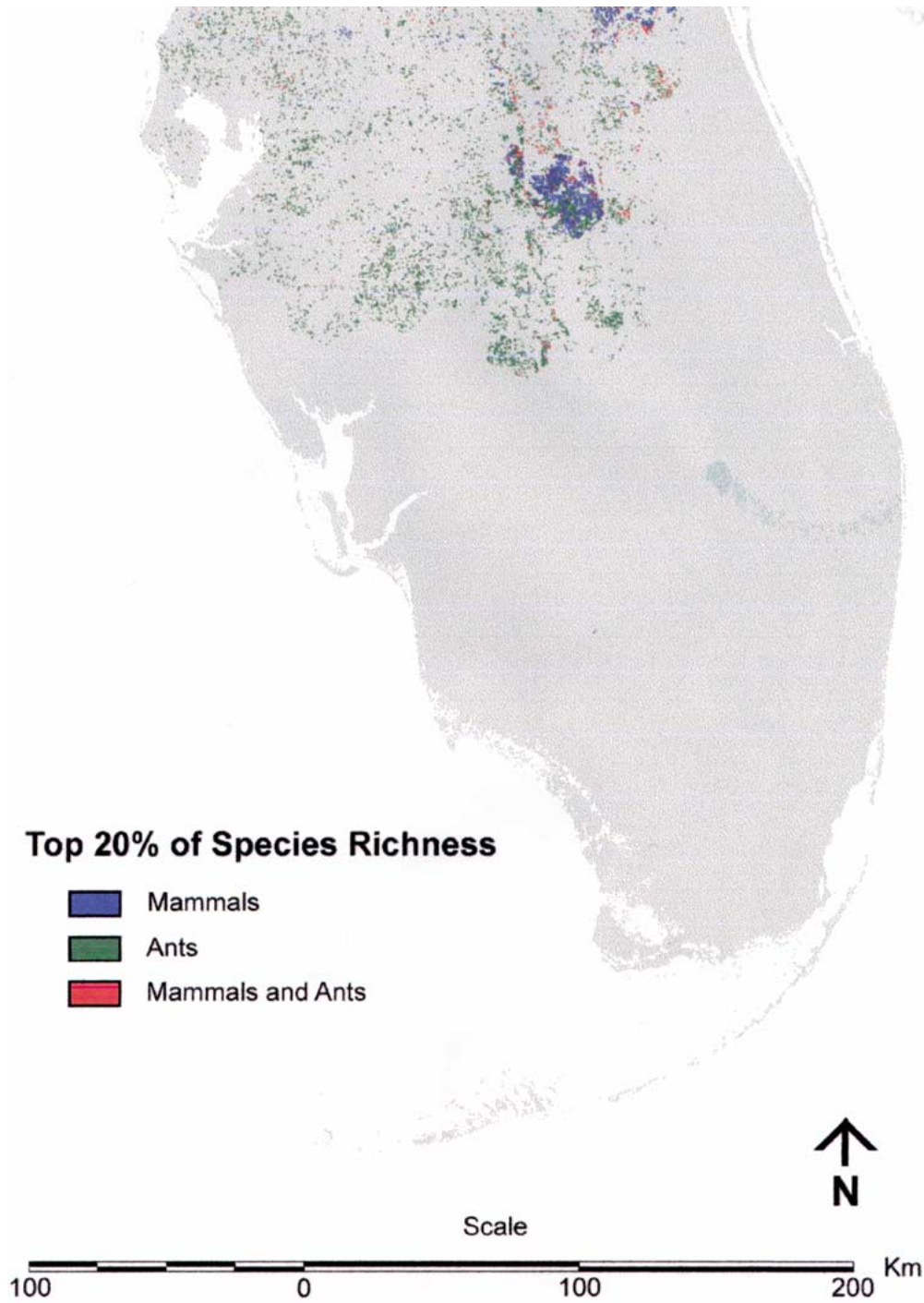


Figure 5. Spatial distribution of the highest (top 20%) levels of species richness for mammals (blue) and ants (green). Spatial correspondence (red) occurs over only 7% of the combined distributions.

species utilize very specialized micro-habitats, and feeding niches are likely to be saturated (Holldobler and Wilson 1990). Because of niche saturation, the Formicidae are excellent indicators of fine scale habitat heterogeneity, which in turn is an excellent indicator of biological diversity. Additionally, niche specialization means that general ant sampling may be used to bioassay ecological trends by monitoring trends of species with specific life-history traits of interest. Short generation time translates to rapid response to environmental change.

For terrestrial vertebrates, the 30 m resolution of the Florida landcover map we used, and the coarser resolution of regional Gap Analyses, may coincide with the scale of perception at which many vertebrates resolve heterogeneity. However, for small-scale species, a single system as defined by humans may well be resolved as highly heterogeneous. Before we can determine how well diversity maps based on a limited number of taxa reflect overall biodiversity patterns, it is necessary to better determine whether different taxa, both within (e.g., different vertebrate taxa) and across (e.g., vertebrates vs. insects) scales, interact with landscape elements similarly or idiosyncratically. If the latter, landscape patterns of biodiversity can only be known by knowing the distribution of everything. If the former, we need to better understand how the scale of ecological perception of species influences species distributions. The two taxa we investigated differ by orders of magnitude in the scale at which they perceive their environment, and it is likely that diversity hotspots vary as the scale of investigation – and the taxa mapped – varies.

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