Articles

Indicator-Driven Conservation Planning Across Terrestrial, Freshwater Aquatic, and Marine Ecosystems of the South Atlantic, USA

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Abstract

Systematic conservation planning, a widely used approach to identify priority lands and waters, uses efficient, defensible, and transparent methods aimed at conserving biodiversity and ecological systems. Limited financial resources and competing land uses can be major impediments to conservation; therefore, participation of diverse stakeholders in the planning process is advantageous to help address broad-scale threats and challenges of the 21st century. Although a broad extent is needed to identify core areas and corridors for fish and wildlife populations, a fine-scale resolution is needed to manage for multiple, interconnected ecosystems. Here, we developed a conservation plan using a systematic approach to promote landscape-level conservation within the extent of the South Atlantic Landscape Conservation Cooperative. Our objective was to identify the highest-ranked 30% of lands and waters within the South Atlantic deemed necessary to conserve ecological and cultural integrity for the 10 primary ecosystems of the southeastern United States. These environments varied from terrestrial, freshwater aquatic, and marine. The planning process was driven by indicators of ecosystem integrity at a 4-ha resolution. We used the program Zonation and 28 indicators to optimize the identification of lands and waters to meet the stated objective. A novel part of our study was the prioritization of multiple ecosystems, and we discuss the advantages and disadvantages of this approach. The evaluation of indicator representation within prioritizations was a useful method to show where improvements could be made; some indicators dictated hotspots, some had a limited extent and were well represented, and others had a limited effect. Overall, we demonstrate that a broad-scale (408,276 km^2 of terrestrial and 411,239 km^2 of marine environments) conservation plan can be realized at a fine-scale resolution, which will allow implementation of the regional plan at a local level relevant to decision making.

Keywords: conservation planning; core areas; corridors; indicators; landscape conservation; prioritization; Zonation

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Introduction

Conservation efforts around the world are increasingly using a systematic conservation planning approach to conserve biodiversity and ecological systems within a social and political context. Systematic conservation planning is a science that includes the development of an objective, efficient, transparent, and defensible plan with clear conservation targets (Margules and Pressey 2000). Limited financial resources and competing land uses are common constraints to conservation; therefore, the prioritization and coordination of effort among diverse stakeholders, including nonprofit organizations and federal, state, and local agencies, have become valuable components of landscape-scale conservation and management. Stakeholder and practitioner involvement in the formal planning process has even received increased emphasis in scientific studies, as these groups are key to implementation (Knight et al. 2006; Sewall et al. 2011). The concept of large landscape conservation has been recognized as conservation that crosses political and jurisdictional boundaries, encompasses multidisciplinary stakeholders, and seeks to balance competing social and ecological objectives (McKinney et al. 2010). Moreover, as diverse organizations (e.g., wildlife agencies, cultural resource groups, urban planners, emergency management organizations, and the military) join to conduct comprehensive conservation planning, the participation of local groups in broad-scale planning poses a specific challenge: modeling a broad geographic extent while maintaining a fine spatial resolution to allow localities to identify how their individual efforts fit into and benefit the greater landscape.

Ecologically, a broad extent is needed to identify landscape characteristics, such as corridors and core areas for fish and wildlife populations. Concurrently, a fine-scale resolution is needed to account for ecosystems and their complexity, including the interconnectedness among systems in close proximity. Few conservation planning studies incorporate the links among divergent ecological realms like terrestrial, freshwater aquatic, and marine (see Stoms et al. 2005; Beger et al. 2010). Likewise, within these realms, highly heterogeneous systems, such as interspersed isolated wetlands and coastal zone communities, have received little attention in prioritization studies. For coastal zones in particular, additional challenges are presented by the proximity and interconnectedness of beaches and dune, maritime forest, and estuarine marsh ecosystems. Species (e.g., shorebirds), natural processes (e.g., barrier island rollover), and functions (e.g., protection from storms) all interact with the combination of these divergent ecosystems. Furthermore, threats—such as urbanization, climate change, invasive species, fragmentation, water pollution, and water scarcity—cross ecosystem or jurisdictional boundaries, and addressing these broad-scale threats requires conservation at an appropriate extent and resolution.

To address broad-scale, multidisciplinary conservation challenges in North America, landscape conservation cooperatives (LCCs) were organized to bring together stakeholders and conservation practitioners. The LCCs are self-directed partnerships among federal, state, nonprofit, and other organizations to address broad and long-term challenges of natural and cultural resource conservation. The South Atlantic LCC, located in the southeastern United States, encompasses a diverse range of environments, including coastal systems, freshwater aquatic, fire-dependent longleaf pine savanna, upland hardwood, marine, isolated wetlands, and globally rare peatland pocosin wetlands. Closely interspersed ecosystems commonly occur; examples include estuarine marsh interwoven among maritime forest, freshwater marsh interwoven among forested wetlands, beaches adjacent to estuarine marsh, and freshwater aquatic systems among terrestrial lands. Additionally, cultural landscapes are increasingly recognized as valuable components of landscape planning (Antrop 2005). To more efficiently prioritize their conservation activities, major international organizations originally focusing on either natural or cultural resources are now integrating both into their respective ranking criteria (UNESCO World Heritage Center 2003).

In 2014, the South Atlantic LCC began development of version 2.0 of its conservation plan (hereby, Conservation Blueprint; Groves 2003) to sustain natural and cultural resources for current and future generations. The South Atlantic LCC, composed of federal, state, and nonprofit organizations, decided to use a systematic conservation planning approach to achieve an efficient, defensible, and transparent plan. Ecosystem-specific indicators were sought to characterize the ecological integrity of 10 ecosystems encompassing terrestrial, freshwater, and marine environments. Here, we define ecological integrity as stated by Karr and Dudley (1981) and interpreted by Parrish et al. (2003) as, "the ability of an ecological system to support and maintain a community of organisms that has species composition, diversity, and functional organization comparable to those of natural habitats in the region." As not all characteristics of ecological integrity can be measured, indicators were used as measurable surrogates to represent ecological integrity and cultural landscapes.

Our objective was to use the South Atlantic LCC indicators to develop a conservation blueprint by optimizing indicator representation to identify the highest-ranked 30% of the area within the South Atlantic region, including the identification of highly ranked corridors. Simultaneously, we sought to maintain a fine-scale spatial resolution (4-ha). Although Svancara et al. (2005) found that local and regional policies often target 10–12% of lands for protection, they also show that a mean target of 30% is identified on the basis of conservation needs of species. Similarly, Gaines et al. (2010) recommend a marine protected network composed of a minimum of one-third of the marine environment. Importantly, the 30% goal for the South Atlantic includes targets for land and water protection as well as areas for private land incentives and management.

Table 1. Ecosystem-specific indicators used for conservation planning in the South Atlantic region of the United States. The score depicts the range of possible values for each indicator. Further information on mapping of indicators, data sources, and scientific literature supporting the indicators are available in Text S1, *Supplemental Material*.

Ecosystem	Indicator	Score	Reasoning for indicator
Landscapes (all terrestrial ecosystems)	Areas of low road density	0 or 1	Good for wildlife populations, water flow, less human disturbance
	Resilient biodiversity hotspots	0 or 1	Climate change adaptation, heterogeneity, connectedness
	Low-urban historic sites	0 or 1	Cultural sites related to rural areas
Beach and dune	Index of beach birds	0–4	Related to wide beaches, washover events, low predators
	Unaltered beach	0–2	Barrier island rollover, less human stabilization of islands
Maritime forest	Hectares of maritime forest	0 or 1	Strongly threatened by human development
Estuarine marsh	Index of coastal condition	1–5	Water, sediment, and benthic habitat quality
	Open-water–vegetation-edge index	0–4	Habitat for fish, shrimp, crabs, marsh birds
	Wetland patch size	0–4	Wave attenuation, wetland loss indicator, habitat component
Forested wetlands	Index of forested wetland birds (potential birds)	0–3	Patch size, flooding, natural disturbance processes
	Amphibian index	0 or 1	Carolina bays, pocosin, and other isolated wetlands
Freshwater marsh	Index of fresh marsh birds (potential birds)	0–2	Related to patch size; flooding regime of wetlands
Upland hardwoods	Index of upland hardwood birds (potential birds)	0–4	Patch size
	Index of urban open space	0–6	Greater property value near green space in urban areas
Pine woodland, prairie, and savanna	Index of pine birds	0–3	Area restricted and fire-dependent species; bobwhite are popular for hunting and management
	Hectares of regularly burned open canopy habitat	0 or 1	Burning is essential to restore and sustain pine savanna structure
	Amphibian index	0 or 1	Wetland species diversity and ephemeral pond habitat component of ecosystem
Freshwater aquatics	Riparian assessment	1–5	Linked to aquatic biodiversity, low erosion, low runoff
	Permeable surface	0–2	Linked to aquatic biodiversity, flood-prone areas
Marine	Index of sea turtles and marine mammals	0–2	Distinct assemblage of species
	Index of potential hard bottom condition	0–3	Fish habitat component
	Index of primary productivity	1–2	Core component of marine food web

Study site

The South Atlantic LCC's geographic region encompasses spans 408,276 km^2 of terrestrial and 411,239 km^2 of marine environments of the southeastern United States and includes the Apalachicola–Chattahoochee–Flint River basin (Alabama, Georgia, and Florida) and part of the St. John River watershed in Florida, which are special integration zones shared with adjacent LCCs. Characterized as a temperate climate, mean precipitation and temperature range from 112 cm and 15°C in Danville, Virginia to 147 cm and 20°C in Tallahassee, Florida (National Oceanic and Atmospheric Administration 2015). To encompass the South Atlantic region, we modeled the following ecosystems: 1) beach and dune; 2) maritime forest; 3) estuarine marsh; 4) estuarine open water; 5) freshwater marsh; 6) pine and prairie; 7) forested wetland; 8) freshwater aquatic; 9) upland hardwood; and 10) marine.

Methods

Step 1. Indicator selection and geographic information system (GIS) processing of indicators

As part of a participatory approach, the South Atlantic LCC selected indicators (Table 1) with involvement from 235 experts from various organizations in marine, freshwater, and terrestrial resources. This input included online comments, phone interviews, input from regional partnerships, and final recommendations from a selection team that represented South Atlantic LCC partner organizations. Indicators included landscape metrics, species' distributions, ecological features, and ecological processes (Table 1, Text S1, *Supplemental Material*, and Data A1, *Archived Material* for details). Indicators were specific to each of the 10 identified ecosystem types, as well as indicators of the whole terrestrial and aquatic landscapes. We compiled indicators, assessed indicators with secondary data sources (Drew et al. 2015), and then revised them with coordination among external review teams.

We conducted all spatial analyses with ArcGIS (ESRI, Redlands, CA) and the Spatial Analyst extension unless otherwise noted. To be consistent, all indicators were initially computed, or in the case of existing data, were resampled to a 1-ha spatial resolution using the nearest neighbor method. For computational reasons, we then used the aggregate function to rescale the resolution to 4-ha raster cells. This method maintains features of 1-ha in size because the maximum value of each cell is used in the conversion (e.g., a 1- ha patch of maritime forest was converted to a 4-ha patch).

Step 2. Defining ecosystem extent for indicators

Landscape indicators (low road density, resilient biodiversity hotspots, and low-urban historic landscapes) were applied across all terrestrial ecosystems. However, the resilient biodiversity hotspots data were not relevant to areas with low elevation (see Text S1, *Supplemental Material*), and therefore were not included in the beach and dune or estuarine marsh ecosystems. All other indicators were specific to a particular ecosystem(s) and were applied only to that ecosystem. Therefore, we first defined ecosystem extents (see *Archived Material* for maps). The beach and dune ecosystem was defined by the 2011 National Land Cover Database (NLCD; Jin et al. 2013) classification of barren land cover if it was within 300 m of the ocean shoreline as depicted by Himmelstoss et al. (2010). The 300-m buffer included beaches, but excluded other unconsolidated sediments. An additional 100-m shoreline buffer defined narrow beaches, which were not otherwise classified. Maritime forest was defined by state-level mapping data (Text S1, *Supplemental Material*). We defined estuarine marsh as the NLCD emergent herbaceous wetlands land cover within the boundaries of estuarine and marine wetland classifications by the National Wetlands Inventory (NWI; U.S. Fish and Wildlife Service 2014). For the Florida Gulf Coast, we used NWI directly, and for the Atlantic Coast we used an update of NWI by The Nature Conservancy (2015). Their classifications of salt marsh, salt marsh impoundments, and tidal flats were used to represent estuarine marsh. Vector data from NWI were converted to 10-m resolution and then aggregated to 4-ha. The NWI classification of estuarine and marine deepwater defined the estuarine open-water ecosystem. We defined forested wetland with the 2011 NLCD classification of woody wetlands and freshwater marsh was defined by the emergent herbaceous wetlands classification excluding the estuarine ecosystem. Upland hardwood was defined as the entire Piedmont area northwest of the historic longleaf pine (*Pinus palustris*) range; we excluded forested wetland and freshwater marsh ecosystems. We defined pine and prairie as uplands within the historic range of longleaf pine as depicted by Little's range (climate change atlas: Landscape Change Research Group 2014). Little's tree range boundaries were originally published in the 1970s, and data were based on field surveys, herbarium records, and expert knowledge. We expanded this range map with historical accounts of longleaf pine in Virginia (Frost 1993). Because of NLCD misclassifications between woody wetlands and mesic longleaf pine communities, we further defined pine and prairie with state-level land cover data and with red-cockaded woodpecker (*Picoides borealis*) locations in known pine and prairie habitats (Text S2, *Supplemental Material*). We used an "other" ecosystem category for areas not represented within one of the major ecosystems identified here. This included coastal plain forests east of the pine and prairie ecosystem, but not classified as maritime forest or forested wetland; unconsolidated sediments outside of the beach and dune ecosystem; agricultural lands in northeast North Carolina east of the longleaf pine range; and a southwestern area between the Piedmont upland hardwood and pine and prairie ecosystems. These areas could not be classified because of human modifications and unknown pre-European settlement vegetation communities.

The freshwater aquatic ecosystem overlapped all the terrestrial ecosystems excluding beach and dune, maritime forest, and estuarine marsh. In these three ecosystems, the riparian buffer indicator was not available because of the lack of riparian areas. We also excluded data in coastal hydrologic units (HUC12s) if greater than 10% of the area had an elevation of ≤ 0.91 m, as depicted by The Nature Conservancy's Southeastern Terrestrial Resilience project (Anderson et al. 2014a). Less than 1% of HUC12s did not contain riparian buffer indicator data and were also removed. The marine extent included parts of the Atlantic Ocean, but we excluded the Gulf of Mexico. The western marine boundary was delineated as all open water excluding the estuarine open-water ecosystem or terrestrial ecosystems.

Consistent with the indicators, we used 4-ha raster cells as the spatial resolution to define ecosystems. At the 4-ha resolution, several ecosystems overlapped each other where adjacency occurred. To clearly define one ecosystem per 4-ha raster cell, we ordered ecosystems from high (never excluded by another ecosystem) to low (always excluded by another ecosystem) and combined all ecosystems into a single raster layer. To avoid the underrepresentation of relatively small or linear ecosystems, such as maritime forests, we ranked them highly. The ranking proceeded as: 9) maritime forest, 8) beach and dune, 7) estuarine marsh, 6) estuarine open water, 5) state-level data on pine land cover, 4) forested wetland, 3) freshwater marsh, 2) longleaf pine range, 1) upland hardwood.

Step 3. Individual ecosystem spatial optimizations and boundary length penalties

Indicators were ecosystem specific except for landscape indicators, which were those indicators that were applied to all terrestrial ecosystems (Text S1, *Supplemental Material*). We used spatial optimization procedures on indicators to prioritize areas within each ecosystem before developing a comprehensive model of multiple ecosystems. The goal for each spatial optimization was to find the most efficient representation of indicators in any given amount of area.

We used Zonation conservation planning methods and software (Moilanen et al. 2005, 2014; Lehtomäki and Moilanen 2013) to conduct spatial optimizations on the indicators for individual ecosystems. Zonation algorithms use maximum utility functions to produce a hierarchical ranking, and we used Zonation to rank each of our ecosystems as 0–100%. The procedure begins with the assumption that every place has a conservation value. At each subsequent computational step, a raster cell (i.e., 4-ha in our study), or multiple cells if specified, are iteratively removed on the basis of minimizing the marginal loss of total conservation value. The maximum value is retained at each removal step until all cells are removed and ranked. The algorithm uses a complementary approach, normalizing each conservation feature (i.e., indicator) by converting each one into a proportion of its original distribution (Moilanen et al. 2005) and summing conservation value across conservation features. As a conservation feature's cells are removed, the importance of the feature increases in the next iteration. We had one 4-ha cell removed per iteration whenever possible, as specified in Zonation as warp factor = 1. However, because of computational limitations, we had 10 cells removed per iteration (warp factor = 10) for the pine and prairie ecosystem. In Zonation, the edge removal option specifies that cells can only be removed along the edge of the study area extent, or in areas where cells have already been removed in the iterative process. Edge removal can enhance connectivity and make computational times faster. However, the disadvantage is that inconsistent results are possible when there are a sizeable number of ties in the data (e.g., numerous zeros) or if edges are limited. We used edge removal only when computational times were not logistically feasible and only after a preliminary investigation showed that the stated disadvantages were limited. We used edge removal for upland hardwood, forested wetland, and marine ecosystems.

We used the Zonation "core-area algorithm" because each indicator represented distinct ecosystem characteristics. The algorithm retains highly ranked areas of individual indicators as long as possible, regardless of how common they are in the study area (Moilanen et al. 2014). Therefore, the algorithm helped achieve a balance of representation across all indicators rather than being more strongly influenced by hotspots of indicator overlap (i.e., additive benefit function; see Moilanen et al. 2014). All indicators were weighed equally within each ecosystem. Each terrestrial ecosystem included its own indicators in addition to landscape indicators. All ecosystems were optimized at a 4-ha resolution except freshwater aquatics, which had indicators summarized at a coarser resolution (catchments and HUC12), and we used HUC12s as the planning unit in Zonation. For freshwater aquatics, we used the additive benefit function algorithm because the effects of the two indicators, riparian buffers and permeable surface coverage, were thought to be additive because they both relate to water quality on the basis of surrounding lands. To ensure that the freshwater aquatic ecosystem was represented throughout divergent ecoregions, we stratified the results in the freshwater aquatic optimization by including additional conservation features representing the Coastal Plain (0 or 1) and Piedmont (0 or 1) ecoregions. We assigned HUC12s to the Piedmont using all HUC12s that intersected Omernik (1987) level III "Piedmont" ecoregion; all other HUC12s were assigned to the Coastal Plain.

A few coastal lakes were not covered by the freshwater aquatic indicators and did not possess terrestrial indicators. To rank these lakes in the prioritization, we extended the rankings of surrounding terrestrial lands. Given the limited data on these lakes, we used this approach because terrestrial lands can have a substantial impact on lake water quality (e.g., Kronvang et al. 2005). The process included using the ArcGIS expand tool on water bodies to ensure one water-body cell overlaid with a ranked terrestrial area; zonal statistics were used to allocate the mean terrestrial value to each water body. For the marine optimization, we included ecological depth zones (deep circalittoral, deep mesobenthic, infralittoral, shallow circalittoral, shallow mesobenthic, bathybentic) from the South Atlantic Marine Bight Assessment (The Nature Conservancy 2015). Using each depth zone (0 or 1) as a conservation feature ensured that the prioritization included each zone. Only one indicator, the index of coastal condition, covered estuarine open water, and we used areas ranked $\geq$ 4.0 ("good") to define the highest-priority areas.

Patch size and configuration affect species' distribution, population viability, and ecosystem processes. Aggregation of conservation lands can also reduce management costs (Moilanen et al. 2014) and ameliorate decision making under uncertainty (Moilanen and Wintle 2006). To induce aggregation of priority areas, we applied a boundary length penalty (BLP). The BLP penalizes reserve networks for having a high edge-to-area ratio (McDonnell et al. 2002) and favors an aggregated network. The BLP parameter does not have a unit and is applied iteratively until the desired

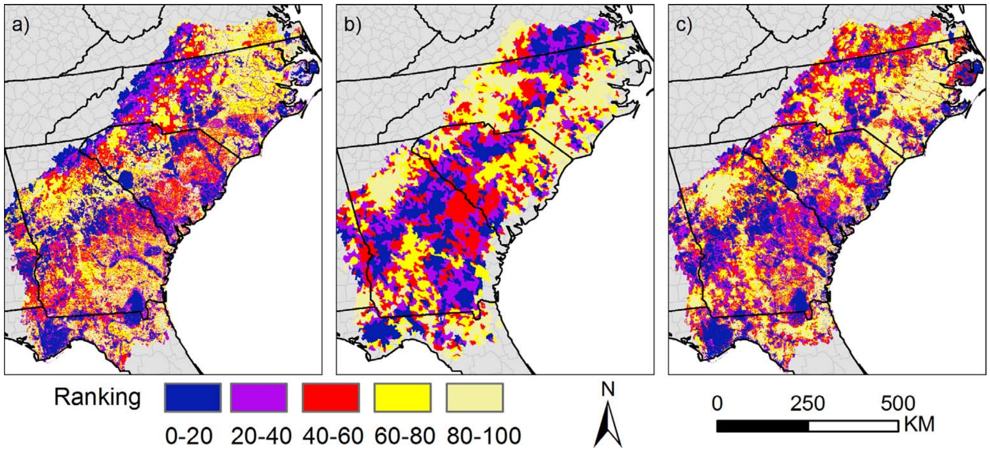

Figure 1. Prioritization results from the spatial optimization of 28 indicators depicting ecological integrity and cultural landscapes of the South Atlantic region of the United States: (**a**) terrestrial ecosystems; (**b**) freshwater aquatic ecosystem; (**c**) mean of all terrestrial ecosystems and the freshwater aquatic ecosystem. Rankings are from the highest- (0–20%) to lowest- (80–100%) priority areas.

condition is met. In our study, the BLP also provided an additional criterion in the optimization, which was helpful when indicator scores were similar in many areas of the ecosystem. For beach and dune (BLP = 0.6) and maritime forest (BLP = 0.8), we first used a BLP of zero and then increased the BLP until there was a 3% loss in the mean of indicators represented within the highest-ranked 20% of the optimization. The 3% threshold was arbitrary, but provided the benefit of favoring larger patches while still primarily optimizing indicator representation. No BLPs were used for estuarine marsh, freshwater marsh, or forested wetland. Estuarine marsh already had a patch size index as an indicator, freshwater marsh and forested wetland naturally occur intermixed with other ecosystems because of disturbances and environmental gradients, and freshwater aquatic data were already depicted at a coarser watershed resolution. For the largest ecosystems, optimizations were not stable without a BLP and the goal was to achieve stability. We defined stability as instances when the mean of indicators represented in the highest-ranked 20% of area changed no more than ±5% over multiple runs; we varied the order of inputs to detect changes across multiple tests. Instability likely resulted from ties in the data, and the BLP assisted by favoring aggregation. For the marine ecosystem, we conducted optimizations until a BLP of 1.0 showed stability. Upland hardwood showed stability at BLP = 0.5 and the pine and prairie ecosystem showed stability at BLP = 0.2.

Step 4. Combining ecosystem optimizations to identify highest-, high-, and medium-priority areas

To identify the highest ranked 25% of the study area (while retaining 5% of area for corridors), we first defined the "highest priority areas" as the highest-ranked 10% of each individual terrestrial ecosystem and the marine ecosystem. For estuarine open water, the highest-priority area classification was defined by one indicator (see Individual Ecosystem Spatial Optimizations), and this covered 70% of its area. Second, we wanted to ensure that we represented a combination of the overlapping freshwater aquatic and terrestrial ecosystems. Thus, we computed the mean rankings of the freshwater aquatic optimization and the seven nonoverlapping terrestrial ecosystem optimizations (Figure 1). We then used this mean, plus the marine optimization itself, to determine the next highest-ranked 10–25%, which was classified as "high priority areas." The mean was also used to define "medium priority areas," as those ranked as the next best 26–50%. The "other" ecosystem category was classified as a medium priority (50th percentile) with recognition that considerable uncertainty exists in these locations.

Step 5. Identifying core areas and high-priority corridors

Core areas and corridors were identified without regard to specific ecosystem types. In our study, corridors were intended to provide a nonhostile environment to allow short-term movements, such as dispersal and gap crossing, but were not generally considered prime habitat. This objective is similar to Nunez et al. (2013), but they focused on connectivity to ensure that species could move to newly suitable habitats because of climate change. Although we did not explicitly direct corridors toward climate gradients, connectivity is widely viewed as beneficial for dealing with potential climate change effects (Heller and Zavaleta 2009). We used Linkage Mapper 1.0 (McRae and Kavanagh 2011) to identify 5% of the study area as high-priority corridors. Linkage Mapper creates corridors among "core areas" by using least-cost path analyses through a defined resistance layer. Least-cost paths are always constructed to connect core areas.

To define core areas for terrestrial ecosystems, we grouped adjacent raster cells within the highest 10% of the rankings using the ArcGIS region group calculation with the four-neighbor rule. Then, we selected areas with aggregations of $\geq$ 2,000 ha to be core areas. This size threshold is consistent with Hoctor et al. (2000) and is used in conservation planning by the Florida Critical Lands and Waters Identification Project (Hoctor et al. 2013; Oetting et al. 2016). The resistance layer for the terrestrial ecosystems was the inverse of the combined freshwater aquatic and terrestrial optimizations (Figure 1c). To include corridors to areas directly outside our study area, we considered areas within 26.1 km of the South Atlantic LCC boundary based on the maximum dispersal distance demonstrated for subadult black bears (*Ursus americanus*) in the Mississippi Alluvial Valley (White et al. 2000); black bear is a species that occurs throughout the study area and is presumed to disperse beyond the study area. To incorporate these areas, we used spatial data depicting local connectedness from The Nature Conservancy's Southeast Resilience and Northeast Resilience projects (Anderson et al. 2014a, 2014b). These data were developed from an index of percent natural areas within 3 km of a cell as well as other land cover data. To identify core areas outside the study area, we used the aggregation of the local connectedness index, which was ranked $>$ 1 SD above the mean, then selected aggregates $\geq$ 2,000 ha. To quantify a resistance layer outside of the study area, we rescaled and inverted the local connectedness index to a scale of 0–100.

We assumed that urbanized areas presented physical barriers (i.e., hostile) to species' distribution and movement. Thus, we ascribed the highest relative cost to urban land cover as defined by the NLCD: low-, medium-, and high-intensity development classifications. We used Linkage Mapper with its default options, plus the setting to prune corridors if a core area was connected to $>$ 4 of its nearest neighbors. We then manually removed the worst 5% of corridors on the basis of cost-weighted distance of the least-cost path. The worst 5% of corridors tended to be particularly long and moved through a large amount of agriculture and developing regions. To determine corridor width, we used the continuous raster output to select the highest-ranked 20% of corridors around the paths. This provided a minimal width and also added $\sim$5% of area to the Conservation Blueprint. We defined these areas as "high-priority corridors."

We identified corridors between the estuarine open water and marine ecosystems. Connectivity between these ecosystems is important because narrow inlets along the Atlantic Coast allow the migration of anadromous and diadromous species [e.g., summer flounder (*Paralichthys dentatus*; Warlen and Burke 1990), red drum (*Sciaenops ocellatus*; Bacheler et al. 2009), and many other fish species (Joyeux 1998, 1999)]. To define core areas in estuarine open water, we used the region group function (four-neighbor rule) to group adjacent raster cells with an index of coastal condition value of $\geq$ 4.0 ("good" ranking; U.S. Environmental Protection Agency 2012) according to the Environmental Protection Agency) and selected aggregates of $\geq$ 400 ha. Similarly, the marine core area was delineated by grouping the highest-ranked 10% of the marine optimization, and we retained the single largest group. This marine area overlapped two major ecologically important features: the continental shelf break and the Gulf Stream. To define resistance in the marine ecosystem, we rescaled and inverted the marine optimization (0–100 ranking) and defined the estuarine open-water resistance layer by rescaling and inverting the index of coastal condition (0–100 ranking).

Combined ecosystem optimizations and indicator assessment

In summary, we divided the Conservation Blueprint into the following categories (Figure 2): 1) highest-priority areas, 2) high-priority areas, 3) high-priority corridors, and 4) medium-priority areas. An assessment of indicator representation within each ecosystem optimization was conducted to provide insights into the efficiency of the prioritizations as well as to identify advantages and disadvantages of using individual indicators. More specifically, the proportion of indicators represented within ecosystem optimizations is a useful measure of indicator influence, overlap of particular indicators, and the ability of indicators to distinguish specific areas in the prioritization process. We investigated indicator representation within the highest-ranked 25% of area of each ecosystem, as these areas frequently remained high priorities in the conservation plan. As indicators varied in how they were scored (i.e., not simply presence/absence; see Table 1), each indicator was assessed by the proportion of its total score represented in the highest-ranked 25% of the ecosystem's area.

Results

Our assessment of ecosystem optimizations showed that the highest-ranked 25% of each ecosystem area was able to represent 21 of 58 indicators by $>$ 50% of their total possible scores, 11 were represented by 30–50%, 3 were represented by 25–30%, and 3 were represented by $\leq$ 25% of their total scores. The landscape indicators (low road density, resilient biodiversity hotspots, low-urban historic landscapes) comprised the vast majority of indicators represented by $>$ 50% (Figure 3), although the amphibian indices for the forested wetland and pine and prairie ecosystems were also highly represented. Within the highest-ranked 25% of the landscape, the only indicators that were represented by $\leq$ 25% of their total scores were hectares of maritime forest, index of coastal condition, and the open space index (Figure 3). Since the hectares of maritime forest indicator was defined the same as the ecosystem extent, the indicator could only be represented by 25% within the highest-ranked 25% of area. The indicator was selected because of the high level of threat in this forest type. The estuarine marsh index of coastal condition had 71% of its area in the two highest indicator scores, and therefore many highly ranked areas could not be included in the

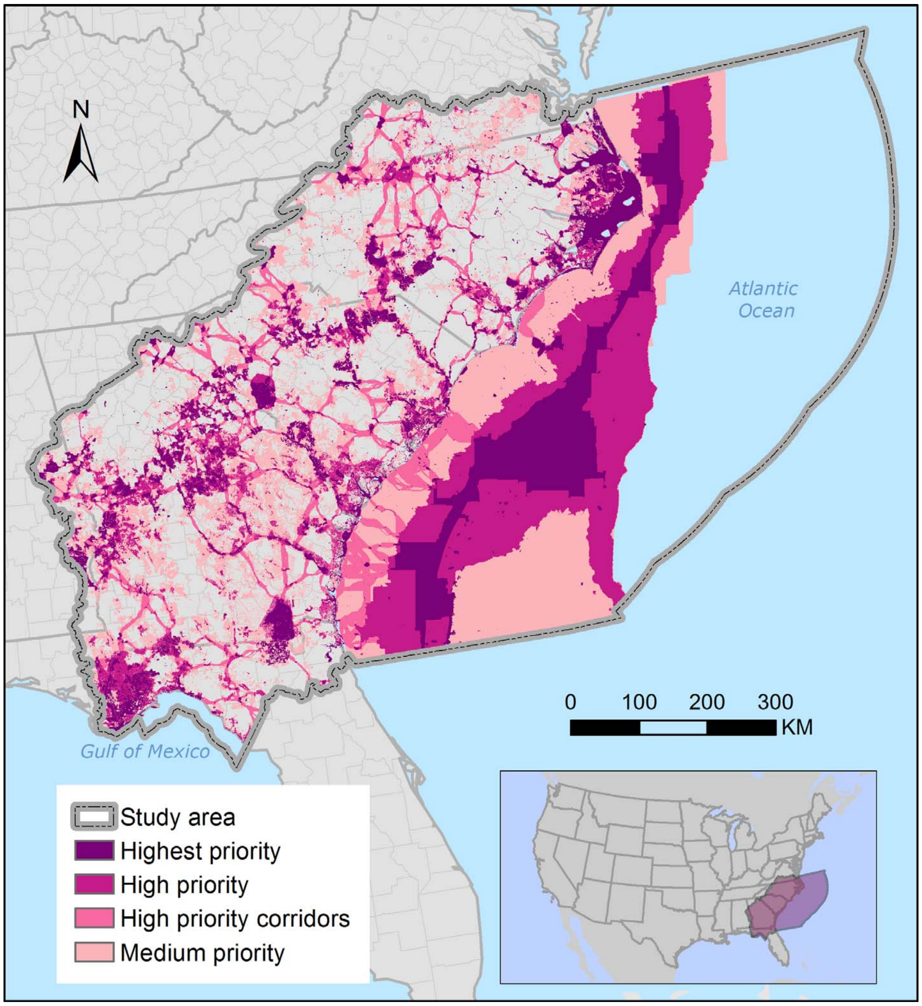

Figure 2. The Conservation Blueprint for the South Atlantic region of the United States. The plan integrates spatial optimizations of 28 indicators of ecological integrity and cultural landscapes across 10 ecosystems and incorporates connectivity across ecosystems. Of the total study area, highest priority represents the highest-ranked 10%, high priority represents the highest 10–25%, high-priority corridors represent the highest-ranked corridors, and medium priorities represent the highest-ranked 30–50%. Interactive depiction of map is available at: blueprint.southatlanticlcc.org and salcc.databasin.org.

highest-ranked 25% of area. The upland hardwood optimization was dominated by indicators directly and indirectly related to large patch sizes (e.g., index of upland hardwood birds, low road density, resilient biodiversity hotspots), and therefore the open space index was not well represented. For the bird indices, individual bird species had a much higher representation in the beach and dune and pine and prairie ecosystems compared with upland hardwood and forested wetland (Table 2).

Substantial variation existed among ecosystems represented in the Conservation Blueprint because of the combination of the overlapping terrestrial and freshwater aquatic ecosystems (Table 3). For example, only 13% of the upland hardwood ecosystem was represented, but estuarine marsh, maritime forest, and beach and dune were represented with a range of 27–29%. Of the total hectares of high-priority corridors, marine accounted for 30%; pine and prairie 27%; upland hardwood 21%; forested wetland 17%; freshwater marsh, estuarine marsh, estuarine open water, and other had 1%; maritime forest and beach and dune had 0%. Of the 528 terrestrial corridors identified, 244 (46%) were $\leq$ 10 km in length, 398 (75%) were $\leq$ 30 km, and the longest had a least-cost path of 145 km (Figure 4). The 145-km corridor weaved through numerous high-priority areas in the Conservation Blueprint.

Discussion

Insights on indicators and patterns of influence

We developed the Conservation Blueprint across terrestrial, freshwater aquatic, and marine environments by using indicators selected through a participatory process. The use of indicators, or surrogate taxa, continues to be the dominant method for systematic conservation planning, as data are typically limited for species, biodiversity, and ecological integrity. Although some studies have shown support for this approach

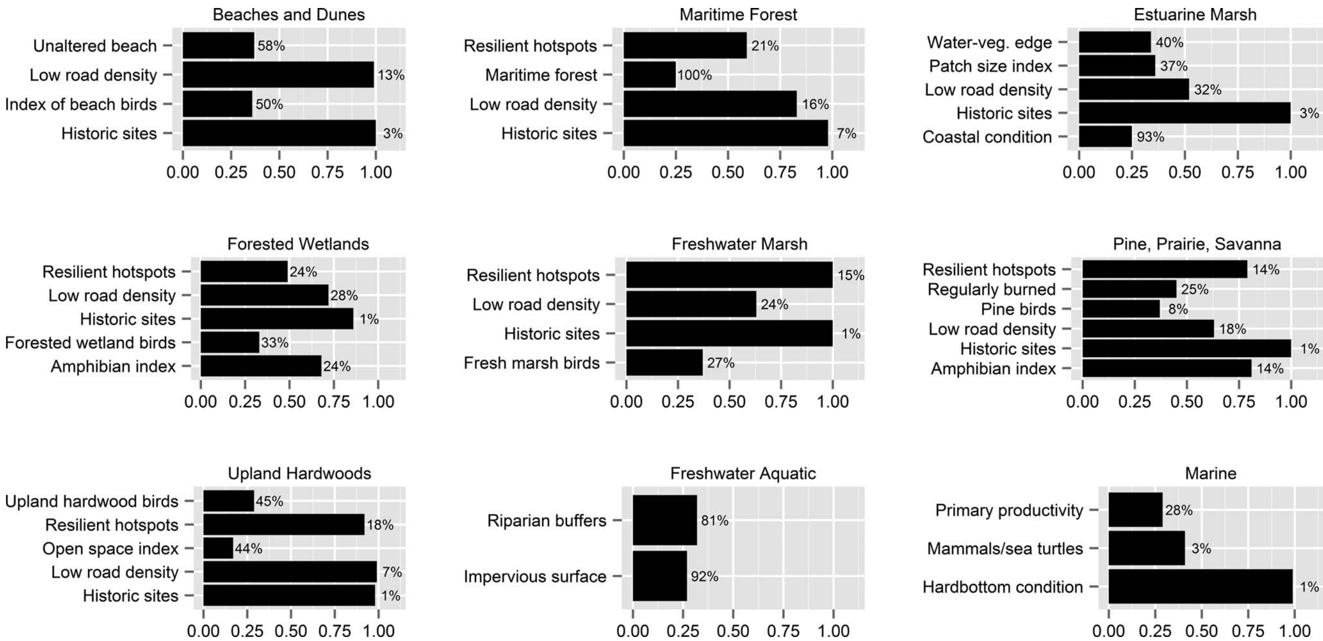

Figure 3. Indicators represented within spatial ecosystem optimizations for 10 ecosystems in the South Atlantic region of the United States. *Y*-axes are indicators. *X*-axes are the proportion of each indicator represented within the highest-ranked 25% of ecosystem area. The percentage stated beside each bar is a measure of the commonness of the indicator within the whole ecosystem. Commonness of the indicator was calculated as either the percentage of ecosystem where indicator was present, or for continuous indicator scores, as the percentage of ecosystem that had an above-average indicator score.

(Fleishman et al. 2005; Banks-Leite et al. 2011), others have cautioned about the use of indicators (Landres et al. 1988; Lambeck 1997), or have shown indicators to be ineffective (Andelman and Fagan 2000). Because of the lack of generalizations regarding indicator effectiveness, careful and systematic evaluation is needed (Favreau et al. 2006). In our study, indicators were not limited to species. The majority of indicators were landscape characteristics and ecological features, which are often more readily modeled compared with species' distributions. For example, the pine and prairie ecosystem has an indicator of regularly burned habitat, which is essential to sustain savanna conditions. For estuarine marsh, indicators of wetland patch size and the water–vegetation index are features directly associated with nekton habitat. Studies regarding the effectiveness of such landscape characteristics are limited, but Banks-Leite et al. (2011) showed that landscape metrics can be more effective than a subset of bird species at representing bird community integrity. Although more science is needed to validate the effectiveness of indicators in the Conservation Blueprint, the results of individual optimizations and how individual indicators fared reveal insightful patterns for indicators in general.

Patterns of indicator representation and influence included those that dictated hotspots by virtue of overlap, those of limited extent that were represented well, and those that could not be efficiently represented in the optimization, and therefore had a limited effect (Figure 3). In extreme cases, indicators simply could not discriminate highly ranked areas within an ecosystem. The indicators least represented in the optimizations were the open space index, index of coastal condition, permeable surface, maritime forest extent, marine primary productivity, and riparian buffers, respectively (Figure 3). These indicators had little effect on optimizations because each ranked a vast majority of their ecosystem as being high integrity. For example, the indicator of coastal condition placed 71% of estuarine marsh in its highest rankings and permeable surface had 92% of the area in its highest rankings. Because any configuration of priority areas would omit many highly ranked areas of these indicators, these optimizations tended to be driven by other, more limited, indicators. At the other extreme, low-urban historic landscapes and marine potential hardbottom condition were extremely limited in their extent, and subsequently, were represented at high rates. In other cases, representation depended on overlap with other indicators and the ranking system of indicators. Discrete, zero or one, indicators tended to have a higher proportion of representation compared with continuous indicators (e.g., estuarine wetland patch size index), as the latter generally had copious amounts of moderately ranked areas that could not be represented in the highest-ranked 25% of area. Therefore, caution should be used when comparing representation of different indicator types.

Landscape indicators of low-urban historic landscapes, low road density areas, and resilient biodiversity hotspots often overlapped with other ecosystem-specific indicators (e.g., regularly burned pine habitat, bird

Table 2. Ecosystem-specific indicators characterized with bird species and used for conservation planning in the South Atlantic region of the United States. If applicable, the indicator score depicts the ranked value given to particular species for ecosystem spatial prioritizations. Indicators with an indicator score depicted assume species with higher rankings are inclusive of species with lower rankings. The results of ecosystem-specific spatial prioritizations are presented as the proportion of an individual species' distribution represented within the highest-ranked 25% of each prioritization. na, not applicable.

Indicator	Common name	Scientific name	Indicator score	Proportion in highest-ranked 25% of area
Pine and prairie birds	Red-cockaded woodpecker	*Picoides borealis*	na	0.76
	Bachman's sparrow	*Aimophila aestivalis*	na	0.63
	Northern bobwhite	*Colinus virginianus*	na	0.24
Beach birds	Piping plover	*Charadrius melodus*	na	0.54
	Wilson's plover	*Charadrius wilsonia*	na	0.46
	American oystercatcher	*Haematopus palliates*	na	0.46
	Least tern	*Sternula antillarum*	na	0.66
Forested wetland birds	Northern parula, black-throated green warbler, red-headed woodpecker, or Chuck-will's widow	*Setophaga americana, Setophaga virens, Melanerpes erythrocephalus, Antrostomus carolinensis*	1	0.17
	Prothonotary warbler	*Protonotaria citrea*	2	0.18
	Swainson's warbler	*Limnothlypis swainsonii*	3	0.22
Upland hardwood birds	Wood thrush or whippoorwill	*Hylocichla mustelina, Antrostomus vociferous*	1	0.11
	Hooded warbler or American woodcock	*Setophaga citrina, Scolopax minor*	2	0.11
	Acadian flycatcher or Kentucky warbler	*Empidonax virescens, Geothlypis formosa*	3	0.13
	Swainson's warbler	*Limnothlypis swainsonii*	4	0.23
Freshwater marsh birds	Least bittern, northern pintail, northern shoveler	*Ixobrychus exilis, Anas acuta, Anas clypeata*	1	0.14
	King rail	*Rallus elegans*	2	0.15

indices, amphibian indices) to create hotspots in the optimizations. Interestingly, these places would not have been highlighted by landscape or ecosystem-specific indicators alone; many were already protected lands thought to be of high quality. As an example, some red-cockaded woodpeckers are present in fragmented or degraded habitats. These areas typically did not have other indicators, such as resilient biodiversity hotspots (related to large patches and connectivity) or hectares of regularly burned open canopy habitat. Conversely, large, connected patches without species indicators were ranked low. For further studies, we recommend a close examination of individual indicators to ensure they can discriminate priority areas from other areas. Our study

Table 3. Area of major ecosystems in the South Atlantic region of the United States and the proportion of ecosystem area included in the conservation plan as highest and high priority (highest-ranked 25% of area), and high-priority corridors (highest-ranked 5% of identified corridors).

Ecosystem	Total hectares	Proportion as highest and high priority	Proportion as corridors	Cumulative proportion
Beach and dune	42,200	0.26	0.01	0.27
Maritime forest	235,256	0.29	0.07	0.37
Freshwater aquatic	36,910,248	0.16	0.07	0.23
Other	477,380	0.00	0.05	0.05
Freshwater marsh	483,976	0.21	0.08	0.28
Estuarine marsh	533,184	0.28	0.05	0.32
Estuarine open- water	1,359,764	0.73	0.04	0.76
Forested wetland	8,999,940	0.21	0.08	0.29
Upland hardwood	11,509,212	0.13	0.08	0.20
Pine and prairie	18,546,496	0.19	0.06	0.25
Marine	41,123,904	0.30	0.03	0.33

shows the value of combining indicators on the basis of landscape metrics, species distributions, and ecological features. However, planners should be aware that divergent data types may result in optimizations that weigh some indicators more than others on the basis of their inherent traits such as ranking system, discriminatory ability, and rarity.

Advantages and disadvantages of a multiple-ecosystem prioritization

We developed the Conservation Blueprint at a relatively fine scale (4 ha), which allowed multiple, intermingled ecosystems to be prioritized. The resolution of other conservation plans has ranged from 500 m (Mikusiński et al. 2007), 1 km^2 (Reyers et al. 2012), and even 10 km^2 for a wide-ranging study (Pearce et al. 2008). In our diverse region, even the 500-m resolution would have meant failing to discriminate among common upland and wetland systems, including those in the coastal zone. A major benefit of Zonation is its ability to use fine-scale data, and our 4-ha raster cells allowed closely intermingled ecosystems to have their own indicators. The prioritization of multiple ecosystems and the identification of connectivity among ecosystems (e.g., marine fish migration to and from estuaries) is a novel part of our study; the specificity of ecosystem-specific indicators is also expected to facilitate the use of indicators with stakeholders focused on individual ecosystems. Nevertheless, we encountered additional

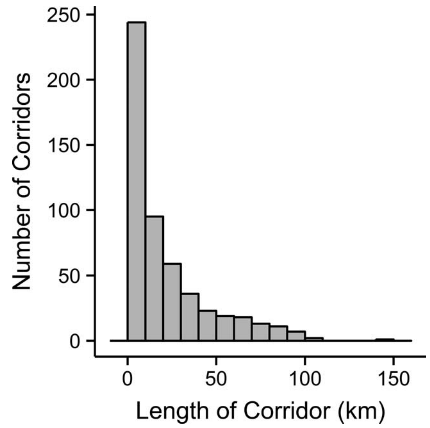

Figure 4. Frequency distribution of corridor lengths identified in the Conservation Blueprint for the South Atlantic region of the United States. Least-cost corridor lengths are reported in 10-km bins.

challenges. First, corridors were established across all ecosystems without regard to ecosystem type or climate; therefore, the benefit to individual species is complex and is currently unknown. Second, boundary length penalties enlarged patch sizes within ecosystems, but such aggregation was not conducted among ecosystems. Consequently, two or more prioritization categories may commingle in relatively small areas. For example, high-priority forested wetlands commingle with pine and prairie ranked as medium or no priority. Future studies of multiple ecosystems and heterogeneous environments such as coastal zones or isolated wetlands should consider addressing connectivity of adjacent ecosystems and determine feasible conservation outcomes.

Lessons learned from data synthesis

Our spatial definitions of ecosystems mapped common natural systems across environmental gradients and political boundaries. For our study area, and likely elsewhere, this is a difficult process, as we often relied on separate state-level data sets for the region (e.g., pine and prairie, maritime forest). National data could not provide the detail we required. The extent of presettlement ecosystems also needs further investigation, particularly in heavily human-modified environments. For example, row crops within the pine and prairie geographic range are part of that ecosystem, but these lands might have been drained and were formerly forested wetlands. We noted opportunities to improve data of freshwater aquatic and marine ecosystems as well as species' distributions. The freshwater aquatic indicators of riparian buffers and permeable surface are useful, but do not account for endemism or biodiversity. For the marine ecosystem, data are lacking on the full distribution of hardbottom habitats. The index of primary productivity may be improved by accounting for differences between nearshore areas and deep ocean environments. Species such as sea birds have shown seasonal and annual variability in their distribution (corresponding to chlorophyll *a*; Flanders et al. 2015), and it is unclear how this variability is represented by the mean of productivity. Indices of upland hardwood, forested wetland, and freshwater marsh birds are models of potential habitat as translated from scientific literature, and the models relate to geographic range, coarse land cover, and minimum patch sizes. The models do not predict bird species distribution itself, which is likely further related to the condition within land cover types, including vegetation structure, management, disturbances, patch size gradients, and flooding regimes. These particular avian indices were not well represented in their respective optimizations (Table 2). In comparison, birds in the beach and dune and pine and prairie ecosystems were well represented (Table 2). With the exception of northern bobwhite (*Colinus virginianus*), birds in these latter two ecosystems were depicted by on-the-ground data, or with Bachman's sparrow, a species distribution model based on survey data.

Intended uses and future directions

The Conservation Blueprint is intended to be a filter for locating places to pool organizational resources for conservation. We note that even with a 4-ha resolution, the Conservation Blueprint cannot replace site visits and is not intended for decision making in isolation of local information (e.g., maps of local greenways, land parcel data). For implementation, the limitations of models representing ecological integrity merit consideration. Most notably, we did not consider spatial complexities like the benefits of upstream actions on downstream watersheds; the prioritization represents the current condition of the ecosystems and does not explicitly account for restoration potential of sites or the proximity of sites to protected areas. Additionally, the effect of weighting indicators in the optimizations could be explored.

Here, the Conservation Blueprint has embarked on the first stage of a data-driven, indicator approach. Future iterations of the Conservation Blueprint will incorporate indicator improvements and may include stronger links among ecosystems to help determine how management actions will affect the entire landscape. Additionally, more research is needed to determine the effect of decisions made during the planning process. For example, what is the effect of having 3% of the plan as corridors as opposed to 5%? The Conservation Blueprint focuses on indicators of ecological integrity, but the plan may benefit from explicitly addressing the threats of sea-level rise and urbanization. Workshops conducted with South Atlantic LCC participants suggested that strategies for addressing these threats are specific to organizations, localities, and individuals, but further information on indicator vulnerability, uncertainty, and the effect of collective conservation actions will assist to make appropriate conservation decisions.

Supplemental Material

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Text S1. Conservation Blueprint indicator metadata by ecosystem, including indicator background, reason for selection, input data, GIS mapping steps, and known issues.

Found at DOI: http://dx.doi.org/10.3996/062016-JFWM-044.S1 (149 KB DOCX).

Text S2. Land cover types included in the pine and prairie ecosystem.

Found at DOI: http://dx.doi.org/10.3996/062016-JFWM-044.S2 (16 KB DOCX).

Reference S1. Anderson MG, Barnett A, Clark M, Ferree C, Sheldon AO, Prince J. 2014a. Resilient sites for terrestrial conservation in the southeast region. The Nature Conservancy, Eastern Conservation Science.

Found at DOI: http://dx.doi.org/10.3996/062016-JFWM-044.S3 (38927 KB PDF); also available at http://www.conservationgateway.org/ConservationBy Geography/NorthAmerica/UnitedStates/edc/reportsdata/terrestrial/resilience/se/Pages/default.aspx.

Reference S2. Anderson MG, Clark M, Sheldon AO. 2014b. Resilient sites for terrestrial conservation in the northeast and mid-Atlantic region. The Nature Conservancy, Eastern Conservation Science.

Found at DOI: http://dx.doi.org/10.3996/062016-JFWM-044.S4 (16352 KB PDF); also available at http://static.rcngrants.org/sites/default/files/final_reports/Resilient-Sites-for-Species-Conservation(1).pdf.

Reference S3. Drew CA, White R, Pickens BA, Collazo JA. 2015. Assessment of South Atlantic Landscape Conservation Cooperative terrestrial indicators. North Carolina Cooperative Fish and Wildlife Research Unit prepared for the South Atlantic Landscape Conservation Cooperative, Raleigh, North Carolina.

Found at DOI: http://dx.doi.org/10.3996/062016-JFWM-044.S5 (9540 KB PDF).

Reference S4. Frost CC. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pages 17–43 in Proceedings of the Tall Timbers fire ecology conference. Tall Timbers Research Station, Tallahassee, Florida.

Found at DOI: http://dx.doi.org/10.3996/062016-JFWM-044.S6 (1631 KB PDF); also available at http://americaslongleaf.org/media/2554/historic-landscape-scale-change-in-llp-ecosystems-_nc_.pdf.

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Reference S6. Moilanen A, Pouzols FM, Meller L, Veach V, Arponen A, Leppänen J, Kujala H. 2014. Zonation spatial conservation planning methods and software Version 4, User manual. C-BIG Conservation Biology Informatics Group, Department of Biosciences, University of Helsinki, Finland.

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Data A1. Spatial depiction of indicators in the Conservation Blueprint: http://salcc.databasin.org/galleries/0d47ca17ef30423281718cdbb04c3898#expand=44635

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