Are Keystone Species Effective Umbrellas for Habitat Conservation?
A Spatially Explicit Approach

Shelly A. Johnson^{a1}, Holly K. Ober^b, and Damian C. Adams^a

^a School of Forest Resources and Conservation, University of Florida, PO Box 110410,
Gainesville, FL 32611, USA.

^b Department of Wildlife Ecology and Conservation, North Florida Research and
Education Center, University of Florida, 155 Research Rd. Quincy, FL 32351, USA.

¹ *Corresponding author present address:* Department of Wildlife Ecology and
Conservation, North Florida Research and Education Center, University of Florida, 155
Research Rd. Quincy, FL 32351, USA. shelly.johnson@ufl.edu, Tel.: +1-928-814-6107

E-mail addresses: shelly.johnson@ufl.edu, holly.ober@ufl.edu, dcadams@ufl.edu

Abstract

As native ecosystems are degraded throughout the world, the importance of
managing, conserving, and restoring wildlife habitat escalates. We must carefully

consider which approach to habitat conservation is optimal, given that resources for habitat conservation are limited. One enticing option involves channeling limited resources to manage for a single umbrella species, assuming that a number of other species within the same ecosystem would also benefit. The danger inherent to this approach is that care must be taken when selecting an umbrella species that maximizes ecosystem-wide benefits. This paper presents a combination of methods to quantitatively evaluate if keystone species, given their integral role in affecting the ecosystem where they reside, can also function as effective umbrellas for habitat management. In a case study, we evaluate two imperiled keystone species, the gopher tortoise (*Gopherus polyphemus*) and the red-cockaded woodpecker (*Leucontopicus borealis*), within a global biodiversity hotspot, the longleaf pine (*Pinus palustris*) ecosystem of North American coastal plain. We 1) develop spatial habitat models in MaxEnt for 10 terrestrial vertebrate wildlife species of conservation interest across an 11 million hectare region, 2) identify the preferred umbrella candidate with spatially-explicit correlation and range overlap analyses using ENMTools, and 3) evaluate the effectiveness of the chosen umbrella species with a test of niche similarity and quantitative habitat suitability comparisons in ArcGIS. Our results suggest the potential for an endemic keystone species to effectively function as an umbrella species. Specifically, we identified the gopher tortoise as the preferred umbrella, given the overlap in suitable habitat for 9 of 10 species evaluated in this ecosystem. These results are significant for habitat management within this region, but most importantly, this application of spatially-explicit modeling to quantitatively measure habitat suitability is an advance in approaches to habitat conservation planning. We encourage others to

use these accessible methods and consider evaluating keystone species as umbrellas to optimize their approach for managing, conserving, and restoring ecosystems.

Keywords

Gopherus polyphemus; habitat management; longleaf pine ecosystem; MaxEnt; niche; spatial habitat modeling

1. Introduction

As the human population expands and alters natural ecosystems and landscapes (e.g., residential and urban development, intensive agricultural use; Van Lear et al. 2005, Matta et al. 2009), wildlife habitats are fragmented, degraded, and ultimately lost (Fahrig 1997, Morrison et al. 2006). ‘Wildlife habitat’ refers to the species-specific conditions that are required for individuals and populations to survive (e.g. food, water, shelter, and space). If wildlife and the ecosystems where they reside are to be sustained, specific resource needs of wildlife must be considered and the natural processes that maintain the resources they require must be actively managed (Wright and Bailey 1982, Grumbine 1994, McPherson 1997). In particular, endemic species that occur exclusively in one area or ecosystem are at high risk of loss if that area or ecosystem becomes incompatible with their resource needs (Myers et al. 2000). Similarly, wildlife species experiencing prolonged population declines (e.g., endangered, threatened, or of conservation concern) often require active management to create conditions that enable their continued survival (Noss and Cooperrider 1994).

Given limited resources available for management of wildlife habitat, it is necessary to carefully consider the best approach (Morrison et al. 2006, Hutchins et al. 2009). Development and implementation of species-specific management strategies is

challenging because of the sheer number of species present in each ecosystem, making it difficult and often infeasible to manage for all species simultaneously (Franklin 1993, Mann and Plummer 1995). In contrast, ecosystem-based approaches often focus on defining and enhancing the natural processes within an ecosystem that benefit wildlife, which can be complicated and unmanageable on a large scale (Orians 1993, Tracy and Brussard 1994, Lambeck 1997).

A combined approach that encourages protection of entire ecosystems without focusing on each individual species, involves using surrogate species as coarse filters (Wilcove 1993) to protect whole communities of species in complex ecosystems (Landres et al. 1988). This umbrella species approach assumes that management for one or a few species will support other co-occurring species (Lambeck 1997, Simberloff 1998, Caro and O'Doherty 1999). In contrast to other types of surrogates, umbrella species do not necessarily need to indicate ecosystem health, population trends, biodiversity levels, or public support (Caro and O'Doherty 1999). The umbrella species approach has been applied widely (see Branton and Richardson 2011), but not without controversy (Landres et al. 1988, Andelman and Fagan 2000, Dale and Beyeler 2001, Fleishman et al. 2001, Roberge and Angelstram 2004). While studies acknowledge there is merit in using umbrella species (Landres et al. 1988, Simberloff 1998), identifying an appropriate umbrella species is essential for implementing this strategy successfully (Branton and Richardson 2011, Lindenmayer et al. 2014).

Numerous methods have been used to select an umbrella species, often with scoring indices based on *a priori* criteria using species traits (e.g. high trophic level, large population size, large home range size, greater longevity, large geographic range;

106 Caro and O'Doherty 1999, Fleishman et al. 2000, Branton and Richardson 2011,
107 Tulloch et al. 2011). Others have relied on co-occurrence within a species range to
108 indicate appropriate umbrellas; which often requires intensive ground surveys to assess
109 (Dunk et al. 2006, Whitman and Sites 2008, Crosby et al. 2015, Weng et al. 2015). In
110 order to account for differences within areas of overlapping range, some have further
111 proposed quantitative examinations of patterns of species co-occurrence that include a
112 measure of habitat suitability (Roberge and Angelstram 2004, Breckheimer et al. 2014,
113 Lindenmayer et al. 2014). Spatial habitat modeling is the process of using
114 mathematical algorithms to predict the distribution of species; it is one promising tool for
115 examining patterns of species co-occurrence because it has the capability to
116 quantitatively measure the probability that an area will be suitable for species (referred
117 to in this paper as "habitat suitability"), even when comprehensive data on species
118 distributions are lacking (Phillips et al. 2006, Rainho and Palmeirim 2013, Nekaris et al.
119 2015).

120 Keystone species (i.e. those whose addition to or loss from an ecosystem lead to
121 large changes in occurrence or abundance of other species; Mills et al. 1993, Paine
122 1995), may be potential candidates for umbrella species (Simberloff 1998, Caro and
123 O'Doherty 1999, Andelman and Fagan 2000). Because a keystone species, by
124 definition, has a positive influence on the structure or function of the ecosystems in
125 which it occurs, enhancement of the species should benefit other species within that
126 ecosystem (Paine 1995, Simberloff 1998). However, to date there is no clear
127 consensus on the reliable use of a keystone species as an umbrella species.

Using the threatened longleaf pine (*Pinus palustris*; “LP”) ecosystem in the North American Coastal Plain (one of 36 world biodiversity hotspots; Noss 2015), as an example case, we evaluate whether a keystone species can serve as an effective umbrella species by comparing habitat suitability among species. We selected the LP ecosystem because it is of high conservation concern due to notably high levels of plant and wildlife biodiversity, with many wildlife species specialized to the ecosystem (Ware et al. 1993, Landers et al. 1995). While presence of the longleaf pine tree is a characteristic of this complex ecosystem, this plant is not a keystone species nor an indicator of habitat suitability for native wildlife or plants, because factors other than the tree are of great importance to the plants and wildlife historically found there (Ligon 1970, Cox et al. 1987, Ashton et al. 2008). The diverse faunal and floral community historically associated with this ecosystem thrived in the relatively open conditions maintained by frequent naturally-occurring fires. Most of the wildlife species now of conservation concern have an affinity for those vegetation conditions maintained by frequent low-intensity fires, such as a low density hardwood midstory and diverse herbaceous groundcover.

Only two animals are considered keystone species in this ecosystem, the gopher tortoise (*Gopherus polyphemus*) and the red-cockaded woodpecker (*Leucontopicus borealis*, previously *Picoides borealis* Vieillot 1809; Dale and Beyeler 2001, Catano and Stout 2015). The endemic gopher tortoise (hereafter “tortoise”) is listed as IUCN Vulnerable (TFTSP (Tortoise & Freshwater Turtle Specialist Group), 1996), and Threatened or Candidate Species throughout its geographic range (USFWS 2013). The tortoise functions as an ecosystem engineer with over 350 commensal species

obtaining food, refuge, and other benefits from the burrows constructed by the tortoise (Cox et al. 1987, Witz et al. 1991, Kent et al. 1997). The endemic red-cockaded woodpecker (hereafter “woodpecker”) also provides essential resources for many species by excavating cavities in longleaf pine trees (e.g., songbirds, other woodpeckers, owls, ducks, flying squirrels, bats, lizards, snakes, skinks, frogs, and invertebrates; Baker 1971, Means 2006). The woodpecker is listed as IUCN Near Threatened (BirdLife International, 2013), and Federally Endangered in the USA (USFWS 2003). Given these species’ keystone role, we hypothesized that each may also serve as umbrella species to promote habitat for other native wildlife species in the LP ecosystem. Furthermore, because current management plans and incentives already channel resources towards management for these two species, identifying how a broader suite of species may simultaneously benefit from their management is prudent in order to support and efficiently allocate resources in the future.

The purpose of this study was to test the prediction that keystone species can function as umbrellas with an application of spatial analyses for identifying umbrellas. In doing so, our objectives were to: 1) assess the viability of using a keystone species as an umbrella species to guide habitat management decisions, 2) demonstrate an application of empirical quantitative methods as an efficient way to identify an umbrella species, and 3) evaluate support for the effectiveness of a keystone as an umbrella species in one region of the declining LP ecosystem of the North American Coastal Plain.

2. Methods

2.1 Wildlife and Environmental Data

The study area boundary for this investigation was the historic extent of the LP ecosystem across the state of Florida, USA (approximately 11 million hectares; see map in Supplemental Materials S1). The vast historic extent of the LP ecosystem in North America (>37 million hectares) covers a diverse range of ecological conditions, with at least 6 different ecoregions, across its expanse (Landers et al. 1995,). Given that the LP ecosystem within Florida is comparatively homogenous and distinct, in particularly poor and declining condition, and the scale at which habitat management decisions occur, it is ecological relevant and pragmatic to investigate at the statewide scale (Wear and Greis 2002, Peet et al. 2006). While we recognize the importance of accessible area in spatial habitat modeling (Barve et al. 2011), the suite of 10 species included in our investigation only co-occur with the 2 keystone species within the state of Florida, thus making the state a reasonable scale for direct comparison among species. All acreage within the historic extent of LP in Florida was included in the analyses (regardless of current land use or land cover) in order to identify potential areas of both high and low suitability for a diversity of wildlife species.

To identify the potential umbrella effects and determine the compatibility of habitat suitability for other species of wildlife relative to the candidate umbrella species, we compiled existing sets of georeferenced occurrence locations for the tortoise, woodpecker, and eight other wildlife species of management concern existing throughout the LP ecosystem within the study region (Table 1). Wildlife species were selected to represent a range of taxa with consideration for conservation status, endemism, a diversity of terrestrial vertebrate classes, specialists and generalists, and

availability of data (Table 1). Species included in the analysis are three mammals, three birds, three reptiles, and one amphibian, all of which provide important ecosystem services (Johnson 2015). Five of these species are of conservation interest (i.e. state or federally endangered, threatened, or listed species of conservation concern). Six are considered LP ecosystem endemics, including the tortoise, woodpecker, eastern indigo snake (*Drymarchon couperi*), Sherman's fox squirrel (*Sciurus niger shermani*), gopher frog (*Rana capito*), and eastern diamondback rattlesnake (*Crotalus adamanteus*) and are adapted to conditions characteristic of the historic LP ecosystem (Engstrom 1993, Guyer and Bailey 1993, Means 2006). The other species are native to the study area, but slightly more diverse in the range of ecosystems they inhabit; the Florida black bear (*Ursus americanus floridanus*), the evening bat (*Nycticeius humeralis*), and the wide-ranging but declining northern bobwhite quail (*Colinus virginianus*), which is a game species highly valued for the revenue, recreation, and food it provides (Burger et al. 1999). Lastly, we include the southern bald eagle (*Haliaeetus leucocephalus*), which is found throughout the region and is not reliant on the LP ecosystem, but is highly valued by the public (Richardson and Loomis 2009, Johnson 2015). Existing records were obtained with cooperation and support from 10 different state and federal governments, non-governmental organizations, and academic institutions (see acknowledgments). To maintain temporal alignment with environmental variables (2005-2012), only records dating from 2000 to 2013 were included in the analyses.

We developed a model denoting habitat suitability for each of the 10 selected wildlife species using environmental predictor variables known to be biologically meaningful for wildlife habitat (Franklin 2010) and particularly important for the tortoise

and woodpecker (Baker 1971, Diemer 1986, Ashton and Ashton 2008). The same set of variables were used for all species, in order to evaluate the resulting habitat suitability from the perspective of management for the keystone species. We considered 7 coarse-scale environmental variables that can be impacted by land management (canopy closure, land cover, fuels, landscape integrity, soils, vegetation type, and canopy height; see Supplemental Materials S2) with data available at or convertible from vector geospatial data to a 30m resolution raster on a region-wide scale. We used ArcGIS (v10.3) software to prepare all environmental grids to matching extents within the study region (ESRI 2011). Prior to modeling, we examined pairwise scatterplots of all predictor variables to assess collinearity (Zuur et al. 2010). Due to high correlations ($r > 0.7$), two variables were not included in the final habitat models: dominant vegetation type ($r > 0.7$ with canopy closure, vegetation height, land cover, and soils) and forest canopy height ($r > 0.8$ with canopy closure) (Dormann et al. 2013).

2.2 Spatial Habitat Models

We employed maximum entropy modeling (MaxEnt; Phillips et al. 2006) to link the environmental variables with the occurrence locations of each wildlife species. Maximum entropy is a machine learning technique that uses known locations of a dependent variable (e.g., species occurrence) and predicts the probability of occurrence of habitat at each point on the landscape by comparing each location's environmental characteristics to background points across the landscape. MaxEnt has grown in popularity as a tool to characterize species distributions for the purpose of predictive and exploratory modeling (Baldwin and Bender 2008, Elith et al. 2011, Nekaris et al. 2015). This modeling approach quantifies the distribution of the species on environmental gradients and produces a unique map for each species predicting the

habitat suitability (based on the probability of occurrence of habitat) for each species in geographical space, with each 30m grid cell on the map assigned a habitat suitability score (from 0 to 1)). Comparing the habitat suitability at this resolution across the landscape provides a more detailed comparison than simply comparing the extent of overlap in species' geographic ranges, particularly when geographic ranges are similar. Furthermore, MaxEnt is preferred to other habitat modeling tools because it relies only on occurrence locations and does not require known absence locations, is robust to small sample sizes, and can model both linear and nonlinear relationships (Phillips 2006, Elith et al. 2011).

We used MaxEnt to derive habitat suitability scores for each of the 10 species for each 30m grid cell in the study area following steps suggested by Elith et al. (2011) and Merow et al. (2013). A minimum of 10,000 background points were used in each species' habitat model; maximum iterations were set to 5,000 (although convergence was always reached before 1,000); we used a combination of 3 feature classes (linear, quadratic, product); and we used 3-fold cross-validation involving 2/3 presence data for training and 1/3 presence data for testing the model over 3 replications, calculating the mean for each final model. The default prevalence for model-building of 0.5 was used for all species with the understanding that each species was surveyed with methods specific and appropriate to that species, and thus made the assumption that each had an equal probability of being detected for their given species-specific survey methodologies. We optimized the regularization multiplier (between 0.5-2), based on receiver operating characteristic (ROC) analysis and true skill statistic for each species (Allouche et al. 2006). We evaluated the resulting models using the area under the

ROC curve (AUC; Pearce and Ferrier 2000) as is the standard threshold-independent method and similar to other studies evaluating large scale habitat models developed in MaxEnt (Wisz et al. 2008, Baldwin 2009, Rodriguez-Castaneda et al. 2012, Merow et al. 2013, Reina-Rodriguez 2016, West et al. 2016). While we recognize that partial AUC may be a more robust measure of performance of predictive distribution models (Peterson et al 2008), there is no consensus on the most appropriate model evaluation method to use with MaxEnt, especially when using large raster datasets as input (Mas et al. 2013, Merow et al. 2013). We lastly verified that the habitat model for each species represented a statistically unique habitat with a niche identity test using ENMTools (v1.4.4; Warren et al. 2008, 2010).

2.3 Choosing an Umbrella Species

The umbrella potential of the two keystone species (tortoise and woodpecker) was assessed with four methods. Correlation and range overlap identified whether the tortoise or woodpecker was the more preferred umbrella given the assemblage of species evaluated. The preferred umbrella was then evaluated with niche similarity and relative suitability analyses to determine its potential effectiveness.

For both the tortoise and woodpecker, correlation analysis was used to examine the strength of associations between each keystone's habitat model and the models of other species. We calculated a Pearson Correlation Coefficient for every pairwise combination of habitat suitability scores in each grid cell between species (Warren et al. 2008). The coefficients were summed to identify whether the tortoise or woodpecker had a higher overall correlation with other endemic species and the entire assemblage.

Next, we conducted range overlap analyses to investigate how much of the most highly suited habitat overlapped between each keystone and the habitat of each

species. We compared areas in which both species had a habitat suitability score >0.50, corresponding with the prevalence of the model-building data (Cramer 2003, Liu et al. 2005, Warren et al. 2008).

2.4 Evaluating the Umbrella Species

Once a candidate umbrella species was selected, we used a niche similarity analysis to measure the overall degree of similarity across the study area between habitat suitability scores for each of the remaining 9 species compared to that of the chosen umbrella species (Aguirre-Gutierrez et al. 2014; Sesink Clee et al. 2015). The habitat models created with MaxEnt were processed with ENMTools to calculate pairwise similarities between the suitability score in each grid cell of each habitat model. We reported the Schoener's *D* metric of niche overlap, which ranges from 0 (no agreement) to 1 (complete agreement; Schoener 1968, Warren et al. 2008).

Lastly, we conducted a relative suitability analysis to determine the value of each species' habitat in areas that provided high, moderate, or low suitability habitat for the chosen umbrella species. Using the Spatial Analyst extraction toolset with three geometric quantiles in ArcGIS (grouping the grid cells of the umbrella's habitat map into three equally-sized groups based on suitability scores: highest 1/3, middle 1/3, lowest 1/3), we quantified the average suitability score across the study area for each species in three scenarios, reflecting conditions that would exist if the only areas that remained in the habitat map of each species were those providing high, moderate, or low suitability scores of the umbrella's habitat. In order to observe the differences between the high and low suitability results, we calculated the percent change in the average suitability scores for each species between the high suitability scenario compared to the low suitability scenario.

3. Results

3.1 Habitat Models

The habitat models that estimated suitability scores for the 10 wildlife species performed moderately to good based on the resulting AUC values, with 9 out of 10 having $AUC > 0.70$ (Table 2). The niche identity test verified that habitat models of each of the species represented a unique habitat and exhibited statistically significant ecological differences from that of each keystone's habitat model. Overall, the explanatory variables that contributed the most to each model differed by species; however land cover type most commonly explained the most variation, followed by fuels, soil type, landscape integrity, and canopy closure, in descending order (Table 2).

3.2 Choosing an Umbrella Species

The correlation analysis recognized similar patterns of association between tortoise and woodpecker habitat models and the models of other species (Table 3). The sum of the correlation coefficients for tortoise and woodpecker were nearly identical for both the endemic species and the entire assemblage, providing limited insight in selecting a preferred umbrella candidate.

However, the range overlap analysis revealed that the amount of overlap between highly suited tortoise habitat and that of the 8 other wildlife species was greater than overlap with the woodpecker, especially for endemic species (Figure 1). In areas with > 0.50 suitability for each species, the most spatial overlap occurred between tortoise and federally-threatened indigo (71%), interpreted to mean that 71% of the area that has at least a 50% chance of providing tortoise habitat also had at least a 50% chance of providing indigo habitat. Woodpecker habitat also overlapped the most with indigo habitat (53%). The other endemic species all had greater overlap with tortoise

(squirrel 29%, frog 18%, and rattlesnake 10%) than with woodpecker (19%, 8%, and 8%, respectively). The bear had slightly more overlap with tortoise than woodpecker (11% vs 10%), while the quail displayed the same amount of overlap with both species (52%). The only two species that had greater overlap with woodpecker than tortoise were the non-endemic bat (19% vs 17%) and eagle (33% vs 4%).

3.3 *Evaluating the Umbrella Species*

Because the range overlap analysis revealed that tortoise had stronger positive relationships with the other endemic species in comparison to woodpecker, tortoise was selected as the more suitable umbrella species and we evaluated its potential effectiveness with the remaining analyses. Niche similarity analysis found a high degree of similarity between each of the unique species' habitat models and the tortoise habitat model. Schoener's *D* niche similarity scores ranged between 0.59-0.76 (Table 3); they were highest between tortoise and two endemic species: indigo and woodpecker; moderate for bear, frog, quail, rattlesnake, and squirrel; and lowest for two non-endemic species: bat and eagle.

Relative suitability analysis verified that 3 scenarios providing either highest, moderate, or lowest suitability habitat for tortoise altered the amount of habitat available to other species (Figure 2). In the scenario representing highest suitability tortoise habitat, the species that exhibited the highest average suitability scores were indigo (52%), woodpecker (47%), squirrel (40%), and quail (36%), whereas the rattlesnake (30%), bear (30%), eagle (27%), frog (27%), and bat (23%) displayed the lowest average suitability scores. As the suitability of tortoise habitat increased with the lowest (mean suitability score =0.09), moderate (mean suitability score =0.21), and highest (mean suitability score =0.56) scenarios, all species except the eagle also showed an

increase in their average suitability scores. Tortoise had a 530% increase in average suitability in the high scenario when compared to the low scenario. The frog and quail also benefitted greatly, showing a large gain in suitability between the low and high scenarios (470% and 415% respectively). These were followed by woodpecker (240% increase), bat (160%), indigo (130%), and rattlesnake (110%). The bear (85%) and squirrel (60%) benefitted to a limited extent, while all three scenarios provided almost the same habitat suitability for the eagle, which had a 15% difference in average suitability between low and high scenarios.

4. Discussion

4.1 Keystone Species as Habitat Management Umbrellas

This study suggests the potential for a keystone species to function as an umbrella species and promote biodiversity (Simberloff 1998, Caro and O'Doherty 1999, Andelman and Fagan 2000). We verified that increasing the coverage of habitat highly suitable for the tortoise could have positive influences on habitat suitability for an assemblage of other terrestrial vertebrate wildlife in the LP ecosystem. It is worth noting that the results of this analysis are sensitive to the set of species analyzed, therefore care should be taken to acknowledge the limitations therein and choose an umbrella candidate that is an appropriate representative of the system under investigation. In our case, we strived to include a variety of faunal types, including both generalists and specialists. Overall, this study established a strong relationship between tortoise habitat and the other endemic longleaf specialists (woodpecker, eastern indigo snake, squirrel, frog, and rattlesnake). While these species' categorization as endemic suggests they would each generally benefit from a restored LP ecosystem, this study specifically identifies the potential for tortoise habitat management to function as an umbrella

strategy that benefits other endemics and species of conservation concern, while degradation of tortoise habitat would likely be detrimental to these other species' habitats. Further, although the resource needs of the more generalist species (quail, bear, and bat) do not strictly align with those of the tortoise, our analyses conclude that all three would have more habitat if lands were managed to promote quality habitat for tortoise. The eagle, a species known to lack an affinity for the LP ecosystem, was understandably the only species we investigated whose occurrence did not positively correspond with tortoise habitat, as expected.

While the species we identified as an umbrella does not fit all the *a priori* criteria traditionally considered (Caro and O'Doherty 1999), a closer look at the criteria for umbrella species more recently revised by Seddon and Leech (2008) provides a strong basis to conclude that tortoise would be a good candidate. Three of these criteria are inherent within the connotation of a keystone (co-occurrence with other species, habitat management that will benefit other species, and a well-known natural history). The tortoise clearly aligns well given the many commensals it is known to support as a keystone and as exemplified in the results of our analyses with other endemic species of conservation concern. The natural history of any keystone species is also likely to be well understood, since its keystone status necessitates that it has been the subject of in-depth ecological investigation; the tortoise has been intensely studied for decades and correspondingly has a well-understood natural history (Diemer 1986, Cox et al. 1987, Ashton and Ashton 2008). Additional criteria proposed for umbrella candidates include a high probability of population persistence, easy survey methods, moderate sensitivity to human disturbance, and a large home range size (Seddon and Leech 2008). The

keystone species we identified as an umbrella meets three of these four criteria (e.g., tortoise population is declining but widespread, they can be surveyed fairly easily with burrow counts, and they are moderately sensitive to disturbance; Ashton and Ashton 2008). The last criterion, large home range size, becomes less important than a target geographic range that encompasses the population of the umbrella species.

A keystone species is one understood to be an integral part of its ecosystem (Mills 1993, Paine 1995, Simberloff 1998), and thus selecting a keystone species as an umbrella encourages protection of the entire ecosystem of which it is a part. In Florida, the native range of tortoise nearly coincides with the original extent of the LP ecosystem (USFWS 1990), and a large portion of the North American Coastal Plain, which is now considered one of 36 world biodiversity hotspots (Noss et al. 2015). Recommended habitat management for tortoise is synonymous with restoration of the native LP ecosystem (FWC 2012). Thus incentives to restore, conserve, or improve the LP ecosystem will benefit the tortoise and vice versa. Indeed, as suggested by our study, tortoise is an excellent umbrella species candidate because habitat management for tortoise can provide standards for the composition, structure, and processes within the LP ecosystem that benefit many other wildlife species, including other endemics and species of conservation concern.

Due to their importance in the ecosystem, keystone species typically have existing management guidelines and conservation support. The tortoise is already recognized as an important conservation and management target in the LP ecosystem, and given limited resources, identifying an umbrella species that already has established management guidelines which would benefit other species is an efficient

use of resources. With the emphasis on tortoise habitat management in the LP ecosystem, it is fortuitous that the other endemics and species of conservation concern would also benefit from improvements to and conservation of tortoise habitat. Additionally, it may be easier to build public and political support to implement management plans for a keystone species, because it's ecological role (e.g. builds burrows that >350 other animals use for food and refuge) may be more clearly understood by a general audience (Johnson 2015). Other umbrella criteria (e.g., population persistence, sensitivity, home range size) are more abstract and may build less public support for finite management resources.

4.2 Using Spatial habitat models to Identify Umbrellas

This study demonstrated a novel approach to model and evaluate potential umbrella species. Rather than using species' ecological traits as selection criteria or assuming the simple overlap in species' geographic range equates to umbrella protections, our study quantitatively compared habitat suitability within the landscape. This approach is particularly useful when evaluating a suite of species with similar habitat extents or unknown geographic ranges. This type of quantitative evaluation is often lacking in identification of umbrella species (Roberge and Angelstram 2004). Relying on range maps to identify habitat management umbrellas does not account for differences in habitat suitability within the range of a species. By modeling habitats spatially and evaluating habitat suitability, we were able to evaluate the potential effectiveness of the umbrella candidate across the entire study area and account for areas within the study area that would be poor or unsuitable habitat.

We believe that investigating our data with multiple methods strengthens the validity of our conclusions and is a justified examination given the complexity of

comparing wildlife habitat for multiple species over a large geographic area. The congruence among results of all 4 of the methods we applied reinforces the results of each method and our conclusions in this case study, supporting the tortoise as an effective umbrella species. We acknowledge there is some redundancy in these methods, and future investigations may reveal reliable results can be obtained using fewer methods. In this case, we used both correlation and range overlap to choose the preferred umbrella candidate. The results of the correlation analysis were consistent yet inconclusive in distinguishing between the best umbrellas, while the range overlap analysis was able to demonstrate greater differences between the two umbrella candidates. The niche similarity and relative suitability comparisons both evaluated the effectiveness of the umbrella species, although the niche similarity only offered a relative scale amongst species, whereas the relative suitability comparison enabled us to quantify 3 hypothetical scenarios of umbrella species management, potentially making it one of the most useful analyses.

We see benefit in using this approach to empirically test the potential effectiveness of an umbrella prior to implementing the umbrella species approach in habitat management plans. We found this method to be relatively efficient because it relies on known presence-only patterns of co-occurrence, does not require absence locations, and is robust to small sample sizes. With the convenience of software such as ArcGIS (ESRI 2011), MaxEnt (Phillips et al. 2006), and ENMTools (Warren et al. 2010), the accessibility of point location data for wildlife species, and the increasing availability of spatial datasets containing environmental variables that affect wildlife and

can be impacted by land management, this method of identifying potential umbrella species should be achievable in a wide variety of study systems.

4.3 Conclusions

This investigation successfully demonstrates our application of spatial habitat modeling for efficiently identifying umbrellas and provides additional evidence that keystone species can function as habitat conservation umbrellas and promote biodiversity. These results are of value for habitat management within this region, but more importantly, this efficient use of spatial habitat modeling to quantitatively measure habitat suitability is an effective advance in approaches to habitat conservation planning. While no model is completely accurate, we believe these methods yield substantial benefits for habitat conservation planning, which may be applied under limited availability of funding and resources as an approach to optimize the selection of a single umbrella species. We encourage others to use this accessible method and consider evaluating keystone species as umbrellas to optimize their approach for managing, conserving, and restoring ecosystems.

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Figure captions

Figure 1. Percentage of each species' habitat that overlaps with each keystone's habitat, in regions where the suitability scores for each species is greater than 0.50. Asterisk * indicates endemic species.

Figure 2. Average suitability scores of each species' habitat that occurs in scenarios with highest, moderate, or lowest suitability scores for tortoise. Numbers atop bars show the percentage of change observed between the average score in the highest scenario compared to the lowest scenario for each species.

762 **Figures**

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764 Figure 1
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768 Figure 2

Tables

Table 1. Descriptions of the 10 wildlife species included in this study.

Common name	Scientific name	Status ^a	End ^b	Class ^c	Data ^d	Label ^e
Gopher tortoise	<i>Gopherus polyphemus</i>	ST	Y	R	125	Tortoise
Red-cockaded woodpecker	<i>Leucontopicus borealis</i>	FE	Y	B	361	Woodpecker
E. indigo snake	<i>Drymarchon couperi</i>	FT	Y	R	376	Indigo
Sherman's fox squirrel	<i>Sciurus niger shermani</i>	SCC	Y	M	51	Squirrel
Gopher frog	<i>Rana capito</i>	SCC	Y	A	206	Frog
E. diamondback rattlesnake	<i>Crotalus adamanteus</i>	-	Y	R	157	Rattlesnake
Evening bat	<i>Nycticeius humeralis</i>	-	-	M	89	Bat
Florida black bear	<i>Ursus americanus floridanus</i>	-	-	M	777	Bear
N. bobwhite quail	<i>Colinus virginianus</i>	-	-	B	66	Quail
S. bald eagle	<i>Haliaeetus leucocephalus</i>	-	-	B	1376	Eagle

^aStatus: FT=federally threatened, FE=federally endangered, ST=state threatened, SCC = species of conservation concern (FDOS 2012). ^bEnd: Endemic longleaf pine specialist: Y=yes (Engstrom 1993, Guyer and Bailey 1993, Means 2006). ^cClassification (class): M=mammal, B=bird, R=reptile, A=amphibian. ^dNumber of occurrence locations in model. ^eLabel: the abbreviated name used to refer to each species throughout this paper.

Table 2. Test AUCs and percentages of each variable contribution on permuted data to the habitat model.

Species	Test AUC±SD	Land Cover	Fuels	Soil Type	Integrity	Canopy Closure
Tortoise	0.82 ±0.03	61	3	10	9	17
Woodpecker	0.77 ±0.02	72	3	6	16	3
Indigo	0.73 ±0.02	45	15	18	18	4
Squirrel	0.60 ±0.07	47	28	22	1	1
Frog	0.84 ±0.03	53	6	19	15	7
Rattlesnake	0.75 ±0.04	25	52	14	6	3
Bat	0.73 ±0.05	33	42	10	15	0
Bear	0.79 ±0.02	26	62	10	1	2
Quail	0.87 ±0.03	57	31	7	6	2
Eagle	0.73 ±0.01	54	12	21	3	10

781 Table 3. Pearson Correlation Coefficients between each keystone and each species
 782 habitat model. Sum of coefficients shown for endemics (denoted by *) and for
 783 all species. Niche similarity score (Schoener's *D*) compares each species to
 784 tortoise.

Species	<u>Pearson Correlation Coefficients</u>		<u>Niche Similarity</u>
	Tortoise	Woodpecker	<i>D</i> ^a
Tortoise*	1	0.6	---
Woodpecker*	0.6	1	0.76
Indigo*	0.5	0.5	0.76
Squirrel*	0.3	0.3	0.72
Frog*	0.5	0.4	0.70
Rattlesnake*	0.3	0.3	0.69
Bat	0.3	0.3	0.59
Bear	0.3	0.3	0.69
Quail	0.6	0.5	0.69
Eagle	-0.1	0.1	0.62
Coefficient sum: endemics*	3.2	3.1	
Coefficient sum: all species	4.3	4.3	

^aAll *D* similarity scores were significantly different from null models ($p < 0.0001$).

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