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Selecting umbrella species for conservation: A test of habitat models and niche overlap for beach-nesting birds

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ABSTRACT

Umbrella species are rarely selected systematically from a range of candidate species. On sandy beaches, birds that nest on the upper beach or in dunes are threatened globally and hence are prime candidates for conservation intervention and putative umbrella species status. Here we use a maximum-likelihood, multi-species distribution modeling approach to select an appropriate conservation umbrella from a group of candidate species occupying similar habitats. We identify overlap in spatial extent and niche characteristics among four beach-nesting bird species of conservation concern, American oystercatchers (*Haematopus palliatus*), black skimmers (*Rynchops niger*), least terns (*Sterna antillarum*) and piping plovers (*Charadrius melodus*), across their entire breeding range in New Jersey, USA. We quantify the benefit and efficiency of using each species as a candidate umbrella on the remaining group. Piping plover nesting habitat encompassed 86% of the least tern habitat but only 15% and 13% of the black skimmer and American oystercatcher habitat, respectively. However, plovers co-occur with all three species across 66% of their total nesting habitat extent (~649 ha), suggesting their value as an umbrella at the local scale. American oystercatcher nesting habitat covers 100%, 99% and 47% of piping plover, least tern and black skimmer habitat, making this species more appropriate conservation umbrellas at a regional scale. Our results demonstrate that the choice of umbrella species requires explicit consideration of spatial scale and an understanding of the habitat attributes that an umbrella species represents and to which extent it encompasses other species of conservation interest. Notwithstanding the attractiveness of the umbrella species concept, local conservation interventions especially for breeding individuals in small populations may still be needed.

1. Introduction

The use of umbrella species is attractive in conservation because comprehensive data on all (or the majority of) species are rarely available (Caro and O'Doherty, 1999). Commonly, umbrella species are defined as those whose conservation benefits a group of co-occurring ('target') species and the ecosystem they inhabit (Roberge and Angelstam, 2004; Seddon and Leech, 2008). Effective umbrellas should have a wide enough habitat breadth to encompass a substantial amount of each target's habitat within its range (high degree of spatial overlap) and should share similar habitat criteria across the target group (niche overlap) (Favreau et al., 2006; Suter et al., 2002). Theoretically umbrella species can be an effective management tool, especially with respect to implementing strategies that can benefit several species or ecosystems simultaneously.

Despite its potential utility, the approach is not without criticism (e.g., Andelman and Fagan, 2000; Lindenmayer et al., 2002; Murphy et al., 2011). Much of the debate surrounding the effectiveness of conservation umbrellas stems from a lack of consensus on the objectives and outcomes in using them (Hunter et al., 2016). Reasons for the choice of a particular umbrella species are not always well known or articulated and can be based on anecdotal rather than scientific evidence (Pullin et al., 2004; Sutherland et al., 2004). Many purported umbrella species are actually flagship species (e.g., charismatic megafauna; Arponen, 2012), which are not primarily intended to function as an umbrella (although some do), but rather are used as a means of garnering public support and funding, or enacting legislation (Caro and O'Doherty, 1999; Home et al., 2009). Umbrella species also are often chosen from a list of threatened species (Possingham et al., 2002), likely because those species already carry regulatory protection (Fleishman et al., 2000), which greatly facilitates conservation intervention. Indeed, threat status is increasingly used to assign legislative priorities (Arponen et al., 2005; Marsh et al., 2007), and conservation targets are often policy-driven (Svancara et al., 2005). These decisions reflect

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differences in objectives and expectations rather than a failure of a given species itself to represent a broader range of conservation targets.

Conservation organizations and management authorities have differing ideas regarding the role particular species fill in a conservation context (Hunter et al., 2016). A growing body of literature shows that umbrella species can protect target groups or habitats provided they are carefully chosen using quantitative and standardized methods and explicit criteria (Carroll et al., 2001; Favreau et al., 2006). Umbrella species should also be chosen at the appropriate scale, represent ecologically-linked taxa that share similar habitats (Caro, 2003; Caro et al., 2004; Favreau et al., 2006; Fleishman et al., 2000), and in some cases should have similar life history traits or management requirements as the target group (Báldi, 2003; Lovell et al., 2007).

Proper choice of umbrella species, using transparent methods and explicit criteria, is important to meet conservation goals. Even in the absence of adequate datasets for all species in a target group (i.e. the group of species to be conserved; Roberge and Angelstam, 2004), advanced approaches for delineating species' distributions can help to elucidate the degree of distributional concordance among species, as well as identify species with the appropriate characteristics (Caro and O'Doherty, 1999; Seddon and Leech, 2008). In this paper, we use a maximum-likelihood, multi-species distribution modeling approach to select an appropriate conservation umbrella from a group of candidate species occupying similar habitats. We examine which of these species could, theoretically, offer the largest conservation benefit for other species (i.e., be the most effective and efficient candidate for an umbrella species) by quantifying both the degree of spatial co-occurrence, as well as the niche overlap among each potential umbrella and the residual target species group.

Along the U.S. Atlantic Coast, several beach-nesting bird species are in decline due to habitat loss, beach stabilization and nourishment practices, predation and human disturbance (Andres et al., 2012; LeDee, 2008; Thomas et al., 2006). When anthropogenic activities lower reproductive success in breeding birds, overall population viability may be compromised (e.g., Dowding and Murphy, 2001; Gill et al., 2001). Among these species, the Atlantic Coast population of piping plovers (*Charadrius melodus*) has received significant conservation attention since its federal listing as a threatened species in 1986 (Melvin et al., 1991; Sidle et al., 1991). This small, Nearctic territorial bird occurs sparsely across a wide geographic extent (the North American Atlantic Coast) and breeds from Newfoundland, Canada south to North Carolina, USA (Haig et al., 2005), but local populations can be small. For breeding, the species depends on early successional sandy beach habitats characterized by low-lying dunes, sparse vegetation and access to tidally inundated moist substrates for foraging (Loegering and Fraser, 1995; Maslo et al., 2012; Maslo et al., 2011). Because of its broad geographic distribution, reliance on habitats severely threatened by anthropogenic activities, and its charismatic appeal, the piping plover has been labeled both an umbrella species for coastal species and habitats, as well as a flagship species for coastal conservation more broadly (Gratto-Trevor and Abbott, 2011; Hecker, 2008). The United States Fish and Wildlife Service considers the piping plover a ‘representative’ species of coastal conservation across its entire U.S. Atlantic Coast range (USFWS, 2014).

Annually, millions of dollars from the budgets of public agencies and non-profit organizations (Hecht and Melvin, 2009) are spent protecting existing piping plover breeding habitat through symbolic fencing, restrictions on recreational activities (i.e. off-road vehicles, dog walking; Melvin et al., 1994; Patterson et al., 1991), nest and brood monitoring (Hecht and Melvin, 2009; MacIvor et al., 1990), and predator management (Maslo and Lockwood, 2009). Coastal habitat restoration projects along the U.S. Atlantic Coast are often conducted explicitly to benefit piping plovers, and the species is often monitored to measure the success or failure of management interventions (McIntyre and Heath, 2011; Smith et al., 2005). These activities are conducted under the assumption that other beach-nesting bird species will benefit as well, implying that piping plovers are an effective and efficient umbrella species (NPS, 2007; USFWS, 2007).

However, several other beach-nesting bird species of conservation concern use habitats that are generally similar to piping plovers and may act as conservation umbrellas. American oystercatchers (*Haematopus palliatus*), black skimmers (*Rynchops niger*) and least terns (*Sterna antillarum*) are all considered representative species of coastal habitat conservation for at least a portion of the north Atlantic coastal region (USFWS, 2014). An evaluation of each species' ‘performance’ as an umbrella may further increase the efficiency of future conservation efforts, particularly in light of the appreciable investment in management of beach-nesting birds and other coastal species. In this paper, we first ask whether a focus on piping plover conservation benefits other coastal birds in terms of encompassing their habitat. We also evaluate the umbrella species concept more broadly in the context of beach-nesting birds and ask which species (American oystercatcher, black skimmer, least tern, or piping plover) is likely to confer the greatest conservation benefit to other species in this guild by having a distribution that would capture the largest fraction of another species' habitat.

2. Materials and methods

Our study region is the coastal zone of central and southern New Jersey, USA, including the counties of Monmouth, Ocean, Atlantic, and Cape May. To encompass all sites potentially available for nesting by our target species, we designated the specific study area as all land and water within 5 km of the New Jersey coastline from Gateway National Recreation Area – Sandy Hook Unit south to Cape May Point (~1040 km^2; Fig. 1). This area included all beaches, dunes, salt marsh, and tidal flats where our target species could breed. The four beach-nesting bird species – American oystercatchers, black skimmers, least terns and piping plovers - are of high conservation concern in New Jersey and along the North American Atlantic Coast and occur over a significant portion of the study area (Table A.1). While these species have similar habitat requirements, there are important distinctions among habitat needs and life history traits. American oystercatchers and piping plovers breed as solitary pairs, while least terns and black skimmers nest in colonies of up to several hundred pairs (Brunton, 1999; Erwin, 1977). Atlantic coast piping plovers and least terns are obligate beach-nesting birds (Beck et al., 1990; Maslo et al., 2011); rooftop nesting by least terns in not known to occur in northeastern USA (Gochfeld, 1983; Krogh and Schweitzer, 1999). In contrast, black skimmers and American oystercatchers nest in several habitat types, including sand/shell beaches, salt marshes and dredge spoil islands (Burger and Gochfeld, 1990; Simons et al., 2012). Finally, foraging behavior varies widely among species, with piping plovers and American oystercatchers feeding on small marine and terrestrial invertebrates along the intertidal zone and in wrack, and black skimmer and least terns preying upon small fish in surf zone or other nearshore marine habitats (Cuthbert et al., 1999; Gordon et al., 2000; Maslo et al., 2012).

2.1. Modeling the occurrence of breeding beach-nesting birds

To create distribution maps for each species, we used nest or colony occurrence data obtained from the New Jersey Endangered and Nongame Species Program (ENSP). Each year, trained ENSP personnel conduct monitoring of beach-nesting birds in New Jersey from March through September. All beaches are visited at least once, and sites where target species are observed are surveyed repeatedly to monitor all reproductive stages (courting, nesting, chick-rearing, etc.). The GPS coordinates of each nest or colony are recorded. We extracted (from the full ENSP dataset) all documented nest and colony occurrences of our target species for the years 2007–2011. To minimize spatial autocorrelation and remove potential bias from variation in sampling effort, we spatially rarified the points, retaining only points that occurred ≥10 m

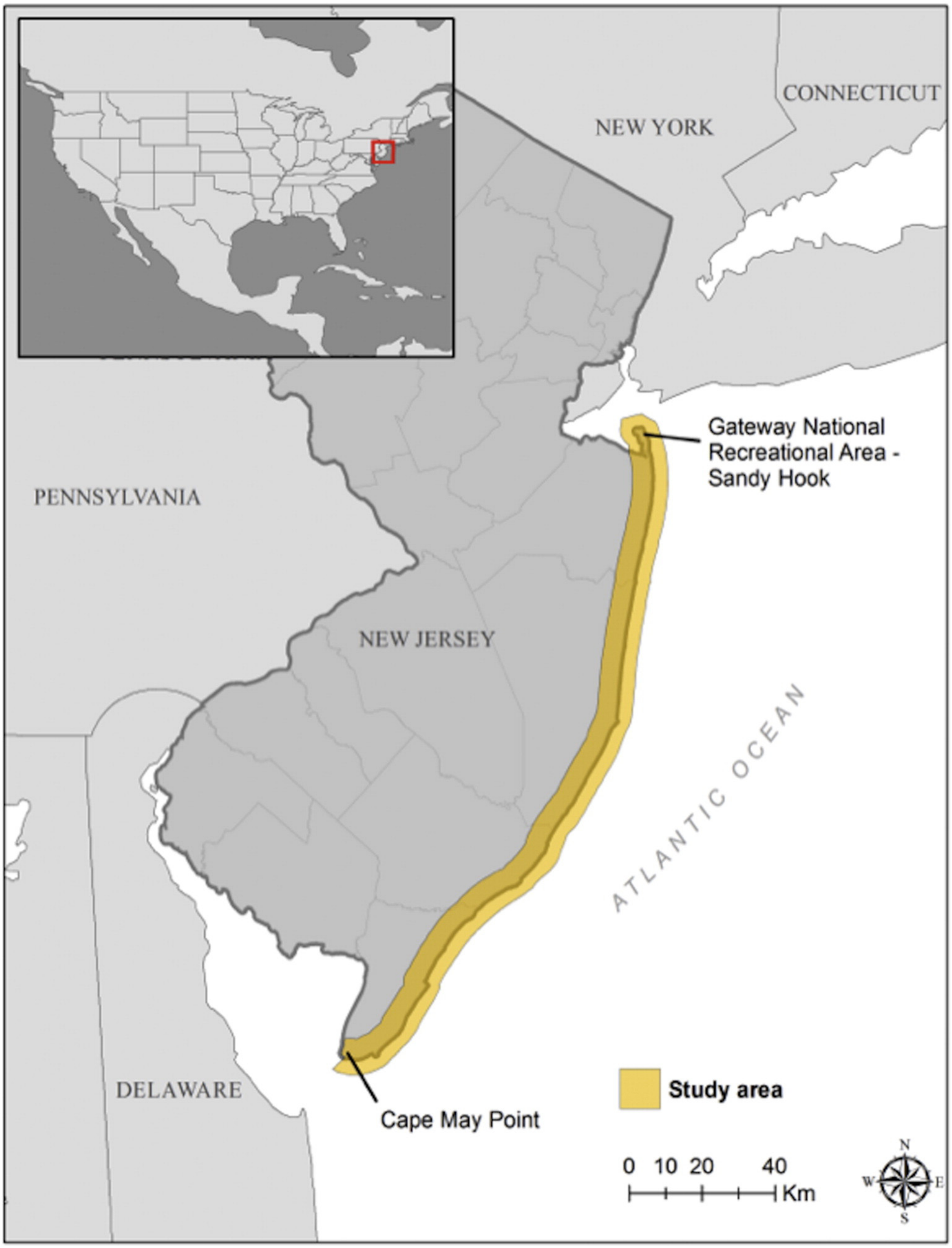

Fig. 1. Map of study area, all land and water within 5 km of the New Jersey coastline from Gateway National Recreation Area – Sandy Hook Unit south to Cape May Point, New Jersey, USA (~ 1040 km^2).

apart (Brown, 2014). Because locations of black skimmer and least tern colonies were recorded as polygons (representing colony location rather than individual nests), we used the centroid of each polygon as the occurrence point for these species (Aguilar et al., 2015). The final dataset included 1288 nest and colony locations (Fig. 1).

We tested eight predictor variables in our models, representing elevation, land use, land cover, beach morphology, and distance to coastal features that are deemed important in nest- or colony-site selection (Table A.2). We examined all data at a 10-m spatial resolution. We acquired digital topographic data from the United States Geological Survey to identify elevation across the study area, and from these data we also calculated the slope as the maximum change in elevation across each 10-m cell within the study area. We compiled detailed information on land use from existing New Jersey Department of Environmental Protection (NJDEP) data (Table A.3). We calculated the Euclidean distance to the high tide line, which we determined either by examining the wet/dry interface of sand depicted on the 2010 United States Department of Agriculture Farm Service Agency aerial imagery (for beaches), or by using the 2012 coastline data generated by NJDEP for marsh and tidal flat habitats (Schupp et al., 2005). To incorporate both the availability of adequate territory size, as well as to examine the influence of the width of nesting habitat (narrow vs. wide shorelines), we calculated the total sandy beach and marsh area (separately) within 100 m using FRAGSTATS v4 (McGarigal et al., 2012). To assess the influence of non-ocean foraging areas in nest- or colony-site selection, we calculated the Euclidean distance to non-ocean tidal waters, which included inlets, bays, and tidal ponds. We processed all geospatial data using ArcMap 10.2.2 (ESRI 2014).

In addition to the landscape features described above, we measured differences among habitats with respect to management status by classifying them as managed or not managed for beach-nesting birds. New Jersey categorizes beaches into four management zones of increasing protection status: 1) unprotected areas; 2) species precautionary areas; 3) species protection areas; and 4) closed areas. In unprotected areas, beaches are routinely maintained for human use either during the summer (late May through early September) or throughout the entire year, and pedestrian and vehicular traffic is permitted from the high tide line to the seaward toe of the primary dune. Precautionary areas have temporary no-rake and no-vehicle designations, but human access is only restricted if nesting birds are present. Species protection areas are open to public use, but there is a high level of proactive protection to birds and habitat during the breeding season; protections include no-rake zones, no-vehicle designations, dog prohibition, symbolic fencing, and human access restrictions in known foraging areas. Closed areas are restricted to the public and all recreational uses except species monitoring by foot during the breeding season. To varying degrees, areas managed for beach-nesting birds are subject to normal beach successional dynamics for all or a part of the year; the upper beach experiences incipient dune formation, shell and pebble deposition and modest vegetative growth, which are all habitat features deemed important in nest-site selection (e.g., Cohen et al., 2008; Maslo et al., 2011).

We used maximum entropy modeling software to predict the probability of target species' occurrence across coastal New Jersey. Maxent (Maxent version 3.3.3k; Phillips et al., 2006) is a widely employed species distribution modeling platform that uses a deterministic, maximum-likelihood framework to efficiently analyze presence-only species occurrence data (Elith et al., 2011; Maslo et al., 2015). Using a complex, machine-learning algorithm, Maxent generates the probability of a given species' occurrence (bounded between 0 and 1) across a defined spatial area, giving insight into the spatial and environmental factors that are important to species in the selection of their habitats.

We fit our Maxent models using the linear, product and quadratic model feature classes, which are similar to those used in generalized linear models (e.g., product features model interactions between variables; Phillips et al., 2006). We evaluated model performance with a separate test data file consisting of nest and colony locations from the 2012 breeding season. We determined model fit by examining the area under the curve (AUC) score, which is the area under the receiver operating curve (ROC). We then applied the 10-percentile training presence of the model outputs to determine the minimum probability of occurrence at which we can expect to find the nest of a target species (Phillips and Dudík, 2008; Rödder et al., 2009). We make no assumptions about the quality of the local habitat. To determine the influence of each predictor variable on species' distributions, we examined the permutation importance values generated by the Maxent analyses. These values are calculated as the normalized percentage of the drop in AUC resulting from the random permutation of the values of each predictor variable.

2.2. Evaluation of species' potential as a conservation umbrella

To serve as an effective conservation umbrella, the potential species should have a wide enough habitat breadth to encompass a substantial part of each of the target species' habitat within its range (high degree of spatial overlap) and should share habitat attributes with the target group (niche overlap). We evaluated the spatial overlap criterion of each species by evaluating the conservation benefit of managing each species on the remaining targets. To do this, we overlaid each target species' Maxent output map onto the potential umbrella output map and calculated the percentage of that species' total suitable habitat that was included within the potential umbrella's range (e.g., the percentage of black skimmer [as a target] habitat falling within the boundaries of piping plover habitat [as the umbrella]). Because managers are likely concerned with the efficiency of conservation interventions, we also calculated the percentage of each potential umbrella's distribution that accommodated multiple target species. Umbrellas that co-occur with other target species across most of their distribution are deemed better candidates for selection.

Because species distribution models tend to overestimate the level of niche overlap among species (Broennimann et al., 2012), we used standard ordination techniques to assess similarity in niche requirements among the target species. Tests for normality indicated that some of the response variables were non-normally distributed; we $\log_{10}$-transformed these variables to better conform to constraints of normality (Table A.4). We first performed a Multivariate Analysis of Variance (MANOVA) (SAS 9.4) on 10,000 randomly selected cells from each of the four Maxent output maps (40,000 total cells) to assess overall differences among species with regard to the habitat variables, using univariate ANOVA test results to assess significance for each individual habitat variable. After determining that loss of the categorical variables resulted in diminished predictive performance of the discriminant function, we retained all variables, including categorical variables in the subsequent discriminant function analysis. We then split the data into equal training and test datasets and performed a canonical discriminant function analysis (SAS 9.4), following McGarigal et al. (2013). Species with a poor ability to separate from other groups would likely perform well as a conservation umbrella given their high degree of niche overlap with each member of the target group.

3. Results

3.1. Species' distribution models

The Maxent models performed well (Phillips and Dudík, 2008), returning an AUC ≥0.96 (Table 1). The 10-percentile training presence for the four species ranged from 0.208 for American oystercatchers to 0.474 for piping plovers (Table 1); these occurrence thresholds were typically on narrow beaches or in areas fronting dense coastal development. The maximum probabilities of occurrence for all species ranged from 0.953 for piping plovers to 0.996 for black skimmers (Table 1) and were generally located in undeveloped, wide sandy inlet beaches or spits. Land use was a strong predictor for American oystercatchers, black skimmers, and piping plovers, but did not return a significant permutation importance for least terns. All species used the non-vegetated beach and the dunes for nesting. Black skimmers and American oystercatchers also nested frequently on mud flats and salt marshes; on one occasion, American oystercatchers nested on bare exposed rock (Table A.5).

Distance to non-ocean tidal waters was an important predictor of black skimmer and American oystercatcher nesting (Table 1). In contrast, this variable did not significantly predict least tern or piping plover nest location. Model predictions of nesting probabilities using this variable were only marginally better than random for least terns and piping plovers, and they suggested these species nest within a wide range of several hundred meters from non-ocean tidal waters (Fig. 2). Distance to the high tide line was the most influential predictor for American oystercatchers, returning a permutation importance an order of magnitude greater than all other model covariates. The distance to the high tide line also had a strong influence on nest-site location for black skimmers and piping plovers, with skimmer nests occurring in the closest proximity to the tide line. All species were predicted to nest ≥4 m from the high tide line.

Management zone (e.g., closed, species protection area) was included in the top three ranked predictors for all species. Black skimmers and American oystercatchers responded most positively to species precautionary and protection areas, while piping plovers were predicted to nest at comparable probability in either type of management zone. Similarly, the total sandy beach area within 100 m was a strong predictor of least tern and piping plover occurrence, with probability of occurrence peaking for both species at 2.7 and 2.5 ha, respectively. Although sandy beach area was not as important to American oystercatcher and black skimmer nest-site selection, probability of occurrence increased with increasing sandy beach area. More important to oystercatcher and skimmer occupancy was the total marsh area within 100 m, with

Table 1
Maxent model results for beach-nesting bird species in New Jersey, USA. For each species, area under the curve (AUC) for the test dataset and the permutation importance of each variable are reported.

Species and model variables[a]	N	AUC	Variable permutation importance	10-percentile threshold	Maximum probability of occurrence
American oystercatcher, *Haematopus palliatus*	544	0.971		0.208	0.892
Distance to high tide line			85.2		
Land use			4.3		
Management zone			3.4		
Dist. to non-ocean tidal waters			2.4		
Elevation			2.0		
Marsh area within 100-m radius			1.6		
Beach area within 100-m radius			1.0		
Slope			0.0		
Black skimmer, *Rynchops niger*	27	0.994		0.300	0.996
Dist. to non-ocean tidal waters			59.8		
Distance to high tide line			17.2		
Land use			10.7		
Management zone			9.2		
Elevation			2.1		
Marsh area within 100-m radius			0.6		
Beach area within 100-m radius			0.4		
Slope			0.0		
Least tern, *Sterna antillarum*	111	0.994		0.382	0.988
Management zone			77.9		
Marsh area within 100-m radius			11.5		
Beach area within 100-m radius			6.2		
Distance to high tide line			2.9		
Land use			0.9		
Elevation			0.5		
Dist. to non-ocean tidal waters			0.0		
Slope			0.0		
Piping plover, *Charadrius melodus*	606	0.965		0.474	0.953
Land use			28.6		
Distance to high tide line			26.8		
Management zone			21.3		
Beach area within 100-m radius			17.5		
Dist. to non-ocean tidal waters			3.5		
Elevation			1.9		
Marsh area within 100-m radius			0.3		
Slope			0.0		

[a] For each species, variables are listed in order of importance.

skimmers predicted to nest in areas with ≥1 ha of surrounding marsh and oystercatcher probability of occurrence peaking at ~1.2 ha of surrounding marsh.

3.2. Niche overlap among breeding beach-nesting bird species

The Maxent models identified ~649 ha of piping plover nesting habitat within the study area, which encompassed ~86% of the total nesting habitat of least terns, but only 14.6% of black skimmer and 13.2% of American oystercatcher nesting habitat (Table 2). In contrast, ~4520 ha of suitable American oystercatcher nesting habitat exist across the study area, covering 100% of piping plover, ~99% of least tern, and 47% of black skimmer nesting habitat. In general, piping plover and least tern nesting habitat was restricted to oceanfront sandy beaches. Black skimmer habitat suitability peaked in large, undeveloped sandy spits and also extended into salt marshes in the back bay system (Fig. 3). American oystercatcher nesting habitat was distributed more evenly across both sandy beach and marsh habitats. Oystercatchers co-occurred with at least one other species across 37% (~1838 ha) of their habitat extent (Fig. 4), while least terns co-occurred with all three other species across 72% (~425 ha).

The response curves for least terns and piping plovers followed very similar trends across all predictor variables (Fig. 2). Probability of presence for these species peaked at an elevation of 1.9 m and a slope of 6.5°. Colony and nest locations for plovers and terns were most likely to occur within 87 m and 76 m of the high tide line, respectively. While skimmers were also most likely to occur within this same distance, American oystercatcher nest probability dropped significantly at distances >51 m from the high tide line. Plovers and terns also were predicted to nest at much greater distances from non-ocean tidal waters (589 m and 469 m, respectively) than American oystercatchers and black skimmers (~7 m for both species; Fig. 2). Total marsh area within a 100-m radius was not correlated with either least tern or piping plover presence. American oystercatcher and black skimmer response curves mirrored terns and plovers for total sandy beach area within a 100-m radius. Aside from nesting in close proximity to non-ocean tidal waters, oystercatchers and skimmers differed widely from each other with respect to the remaining predictor variables. Elevation alone was a poor predictor of American oystercatcher occurrence but it appeared influential for skimmers. In contrast, slope alone was a poor predictor of skimmer presence.

Results from the discriminant function analysis supported the Maxent output. Least terns and piping plovers showed similar loadings on the first and second canonical axes (Fig. A1, Table A.4), which explained 99.1% of the total variance. Loadings for black skimmer on these axes discriminated significantly from plovers and terns, particularly along the first axis. American oystercatchers, in contrast, demonstrated considerable overlap with plovers, terns and skimmers, as also indicated by greater misclassification in the other species (Table A.6).

4. Discussion

The current literature describes the ecological attributes of an umbrella species as a habitat specialist with a wide geographic distribution, large home range size, and having moderate sensitivity to human disturbance (Andelman and Fagan, 2000; Caro and O'Doherty, 1999; Fleishman et al., 2000; Seddon and Leech, 2008). Our analyses confirm the narrow habitat preferences and sensitivity to human disturbance

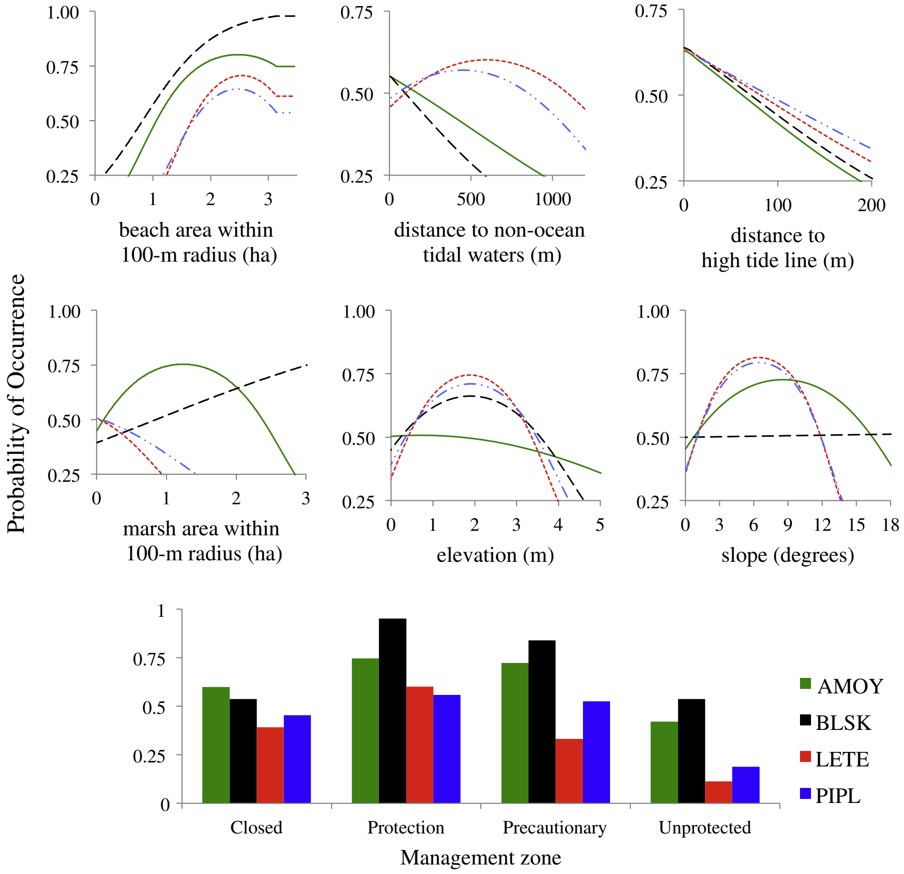

Fig. 2. Maxent response curves indicating each variable's predictive power for species' nest occurrence, as well as the range of conditions correlated with each target species' nesting probability.

of piping plovers relative to other beach-nesting birds in our study (Cairns, 1982; Kisiel, 2009). The plover model returns the highest occurrence threshold (0.474) and reports the lowest maximum suitability score (Table 1), indicating the narrowest range of suitable habitat conditions among the species being assessed. Plovers are widely distributed across the study area, but most nests occur in expansive sandy areas away from coastal development with access to several foraging habitat types. Nests occur almost exclusively on sandy beaches and sparsely vegetated dunes (Table A.5) and are found within a small range of both elevation and slope (Maslo et al., 2011; Fig. 2). Nesting probability increases with increasing sandy beach area (and thus availably breeding territory), demonstrating that plovers require large swaths of protected habitat, which is also an important criterion for the selection of an appropriate umbrella species (Roberge and Angelstam, 2004; Seddon and Leech, 2008).

Protection of piping plover habitat provides appreciable benefit to least terns, likely due to a high degree of niche overlap. Plover and tern habitat preferences are similar across all predictor variables, particularly total sandy beach area, land use, slope and distance to non-ocean tidal waters (Fig. 2). Both species are beach obligates and have historically been documented sharing habitat space (Burger, 1987). The discriminant function analysis revealed almost no distinguishing characteristics between piping plover and least tern nesting habitat (Fig. S1), and the majority of incorrectly identified piping plover nests were misclassified as those of least terns (Table A.6). Protecting all plover nesting habitat in New Jersey would protect 85.6% of the least tern habitat extent; similarly, protecting all least tern habitat would protect 78.0% of all piping plover habitat (Table 2).

Table 2

Total predicted habitat area for each beach-nesting bird species in New Jersey, USA. Percentage values denote the fraction of a species' nesting habitat that is encompassed in the habitat area of another species (e.g., 34.3% of the nesting habitat of American oystercatchers falls within the habitat of black simmers).

	American oystercatcher	Black skimmer	Least tern	Piping plover
	4920.4 ha	3605.6 ha	591.7 ha	649.1 ha
American oystercatcher	100%	46.9%	99.0%	100%
Black skimmer	34.3%	100%	81.0%	81.3%
Least tern	11.9%	13.3%	100%	78.0%
Piping plover	13.2%	14.6%	85.6%	100%

Limited resources for conservation mandates that efficiency of management actions must be maximized (Murphy et al., 2011; Rodrigues and Brooks, 2007). The total extent of piping plover nesting habitat in our study area is just over a tenth of that of American oystercatchers, but two-thirds of it is considered suitable for all three beneficiary species (Fig. 4). The majority of plover-focused management in these areas (i.e. predator control, reduction of human disturbance) would benefit oystercatchers, skimmers and terns. Based upon aforementioned factors, piping plovers appear to satisfy the requirements for classification as an appropriate conservation umbrella.

However, umbrella species are ideally meant to ensure the population viability of beneficiary species (Roberge and Angelstam, 2004; Wilcox, 1984). Piping plovers have a small spatial extent of suitable nesting habitat (~649 ha; Table 2), and it does not overlap extensively with that of American oystercatchers or black skimmers (Fig. S1). Managing only plover habitat would protect < 15% of the total oystercatcher and skimmer habitat in New Jersey, making it highly unlikely plover protections alone would support core populations of American oystercatchers and black skimmers.

In contrast, American oystercatchers have the largest spatial extent of suitable nesting habitat (~4920 ha; Table 2), and the range of habitat

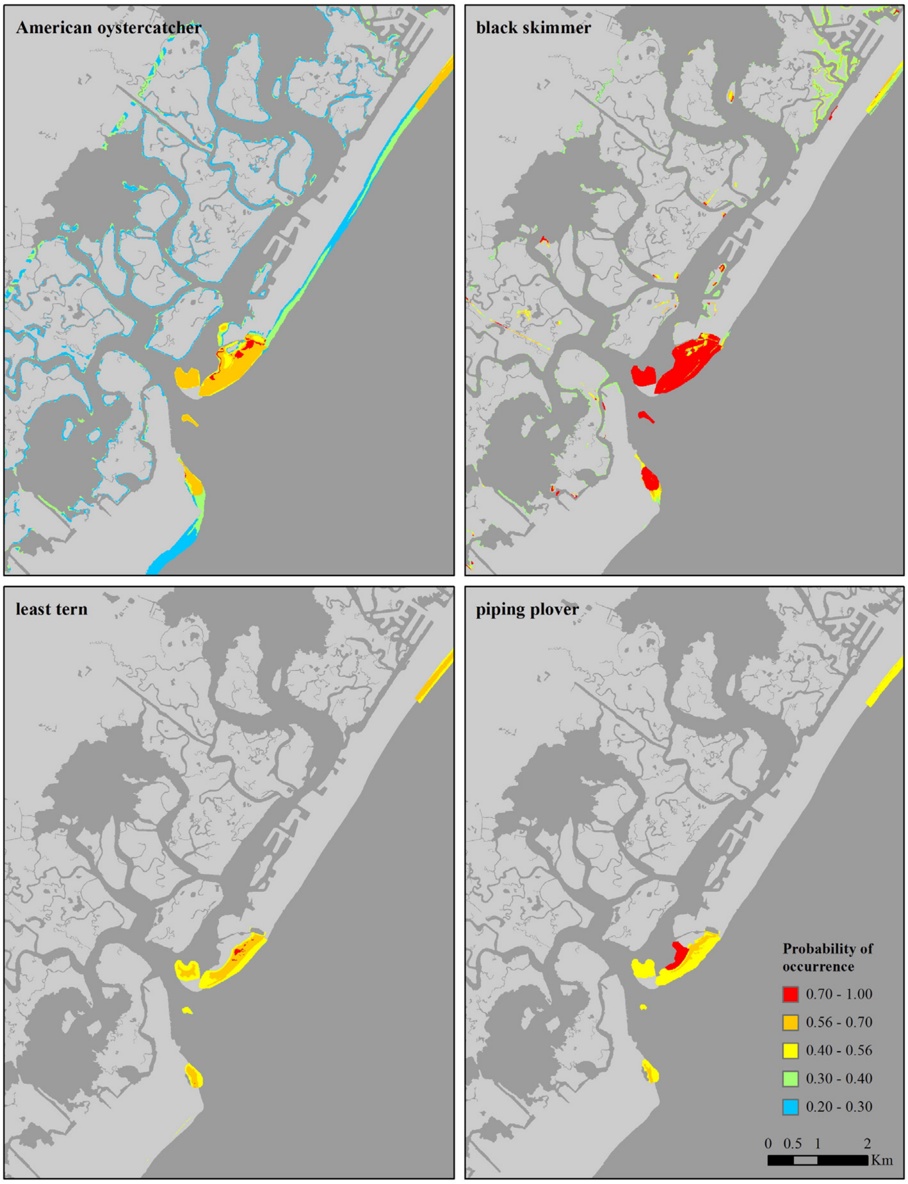

Fig. 3. Example of Maxent model results for American oystercatchers, black skimmers, least terns, and piping plovers for part of the study area. Images represent differences in breadth of suitable habitat across species, with least terns and piping plovers being restricted to sandy, oceanfront beaches. Black skimmer probability of occurrence peaks on large, undeveloped sandy spits but is only marginally above the suitability threshold in some salt marsh areas. American oystercatcher habitat is more widely distributed across both beach and marsh habitats.

conditions suitable for nesting is much broader than the remaining three species examined. Indeed the oystercatcher model returns the lowest occurrence threshold (0.208; Table 1). Oystercatchers use a variety of substrates for nesting including sandy beaches, dunes, saline marshes, and mudflats (Table A.5). They are less sensitive to geomorphological conditions, such as elevation and slope, yet they require significant expanses of sandy beach habitat (Fig. 2). The discriminant function analysis indicates that American oystercatchers associate most with black skimmers, but there also is also considerable overlap of American oystercatcher habitat across least tern and piping plover habitat (Figs. 3, A1). Comprehensively protecting all oystercatcher nesting habitat within the study area would protect 100% and 99% of the piping plover and least tern habitat extent, respectively, and almost half of the skimmer habitat (Table 2). Therefore, it is much more likely that as an umbrella species, American oystercatchers would protect core populations of the other three species.

Birds on ocean beaches and coastal dunes use a broad range of environmental attributes for habitat selection, including the spatial distribution of prey resources (Meager et al., 2012; Schlacher et al., 2014). It is important to note that our analyses focused on nesting habitat and did not explicitly include foraging habitat [although foraging resources for piping plovers and American oystercatchers are indirectly considered through some of the model inputs (i.e. distance to high tide line and non-ocean tidal waters)]. Because piping plovers can move broods to foraging areas outside the boundaries of the original nesting territory (Loegering and Fraser, 1995), their overall breeding habitat extent may in some cases be broader than predicted by our models. Therefore, plovers and oystercatchers may experience greater niche overlap in some locations, particularly in the southern portion of the Atlantic Coast piping plover range (Delaware, Maryland, and North Carolina) where they are more dependent upon ephemeral pools and bayside beaches (A. Hecht, United States Fish and Wildlife Service, pers. comm.).

4.1. Conservation implications

Because managers typically oversee one or more small, protected areas within a given region, piping plovers may serve as an effective umbrella at the local scale. Reproductive success of all beach-nesting

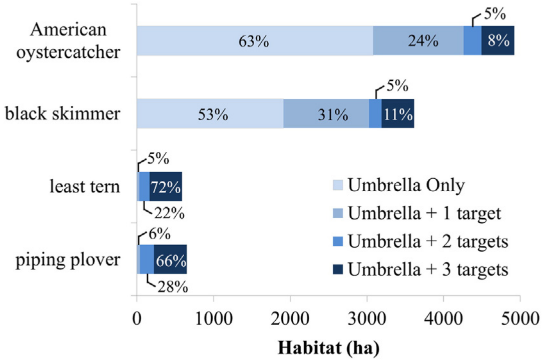

Fig. 4. Distribution of a candidate umbrella species' co-occurrence with 1, 2, and 3 target species, described as both total area and percentage of habitat extent.

birds is lowered both by human disturbance (Dowling and Weston, 1999; Weston et al., 2012; Weston and Elgar, 2007), as well as clutch loss from a suite of egg and chick predators, including foxes (*Vulpes* spp.), corvids (*Corvus* spp.), gulls (*Larus* spp.), and ghost crabs (*Ocypode* spp.) (Dowding and Murphy, 2001; Ekanayake et al., 2015; Watts and Bradshaw, 1995). Reduction of human disturbance through symbolic fencing, vehicle restrictions, and other regulations regarding human recreation will improve reproductive success of all beach-nesting birds within a protected area (e.g., Dinsmore et al., 2014; Lafferty et al., 2006; Melvin et al., 1994). Similarly, predator removal will likely benefit all species present, regardless of the conservation target (Lavers et al., 2010). However, it is important to note that management solely focused on reducing predation of piping plover clutches will only benefit the intended target. As an example, piping plover nests are typically protected with predator exclosures (Cohen et al., 2009; Maslo and Lockwood, 2009), which are wire cages placed around individual nests to prevent access by avian and mammalian predators. These devices do not reduce predation of piping plover chicks or non-target species.

Due to their highly specialized habitat requirements and resulting small extent of suitable habitat, piping plovers may not serve as an effective conservation umbrella at the regional scale. American oystercatchers may instead fill this role, protecting a larger geographic extent as well as a higher diversity of habitats within it. For example, landscape scale conservation of oystercatchers would include restorative or preventative habitat management and protection in marsh areas and would address threats specific to those habitats (e.g., draining, ditching and pollution), threats which are absent or less problematic in piping plover habitat (Roman, 2012). Because umbrella species enable conservation-sensitive planning as well as specific site-based responsive actions, the inclusion of marshes (under the oystercatcher umbrella) would entail areas and issues (e.g., water quality of marsh inflows; Roman, 2012) that would not be identified under the plover umbrella.

Importantly, American oystercatchers are not listed as a threatened or endangered species by the federal government. Securing regulatory protections may pose a substantial challenge, particularly as coastal habitats are commodities that are highly prized for housing and recreation (Defeo et al., 2009; Lockwood and Maslo, 2014). Although the species is classified as ‘special concern’ in New Jersey and there is an active working group focused on its ecology and conservation (www.amoy.org), regional censuses consider the species stable (Morrison et al., 2006); thus, adopting American oystercatchers as a conservation umbrella may require a paradigm shift in the traditional practice of surrogate species selection (Marsh et al., 2007; Possingham et al., 2002). The capacity to formally designate a species as an umbrella taxon under legislation, with umbrella species consequently enjoying legislative protections, would facilitate the systematic selection of the best umbrella species rather than relying upon threatened species which may offer less benefits to target groups of species.

Our results demonstrate that it is improbable that there exists a single strategy that will effectively conserve critical breeding habitat for all species at all scales. As emphasized above, local scale interventions will be important for threatened species where breeding pairs forming part of small populations are located in vulnerable habitats (e.g., the upper beach near the dunes that is heavily used by human and dogs for recreation). This is the case for piping plovers. Such highly targeted actions will, however, need to be complemented by broader strategies that protect habitats for multiple species at the landscape and regional level. This is of critical importance because habitat loss is generally irreversible and, despite the best localized protection measures, spill-over effects from modified habitats can render such efforts ineffectual. In this context, using the American oystercatcher as an umbrella species to identify and map valuable remaining habitat that will have benefits for other species is useful.

This analysis focused on habitat requirements and niche overlap as a metric by which to select an appropriate umbrella species for beach-nesting bird conservation. As for any spatial modeling approach, we assume that the current distribution of each species (which underpinned our models) represents the range of habitats that may be occupied by that species. Where species exhibit different tolerances to anthropogenic change or where the intensity of anthropogenic change varies between habitats, species distribution may be underestimated (Guisan and Thuiller, 2005). For the umbrella concept to be meaningful, it must have contemporary application, so we used recent (and therefore most reliable) nesting data to build our models, and offer an approach that enables conservation in the context of already highly modified and impacted (and managed) habitats in New Jersey.

Our landscape-scale approach did not address habitat quality (which may be manifested, for example, by breeding success) at the site scale. Under specific circumstances, animals can occur in maladaptive habitats such as ecological traps (Schlaepfer et al., 2002), thus an examination of metapopulation dynamics within the umbrella is critical to ensure it, or parts of it, are not functioning as population sinks. We focus here on nesting habitat to illustrate our approach, but we suggest that to ensure effective conservation, full consideration of the geographic extent on which a target species plays out its life history is needed. Breeding success is a critical component of population viability for beach-nesting birds; therefore, selecting an umbrella species that can protect nesting habitat will likely have measureable benefit to populations of target species. However, nesting habitat protections may not effectively conserve a target species if its marine foraging habitat is under threat. Similarly, a conservation umbrella that protects a target species on its breeding grounds does not guarantee population viability if the primary threats occur on the wintering grounds. In terms of habitat heterogeneity and species diversity our model systems of ocean beaches and dunes with four beach-obligate bird species may represent a comparatively low complexity situation for the application the umbrella species in bird conservation. In more diverse and complex settings, the selection of umbrella species may also be more complex, chiefly because more diverse niches are likely to be present and representation has to be extended to a broader suite of species. Selection of an appropriate umbrella species must occur in the context of a broader discourse of what benefits it can or cannot provide and an evaluation of its impact relative to all prominent factors affecting a declining population.

4.2. Conclusions

Because the use of the umbrella species concept is very likely to remain prominent in conservation, it is important to systematically select umbrella species so that they are effective and efficient. Here, we show that substantial investments in piping plover protection are very likely to have benefits for other beach-nesting species at the local scale, chiefly because habitat requirements of plovers are a subset of the niche of other species. At the local scale, protecting plover nesting habitat will encompass potential breeding sites of other beach-nesting birds, supporting the status of piping plovers as umbrella species. In a complementary fashion, at the regional scale the greater breadth of breeding habitat used by American oystercatchers is likely to encompass a larger component of other species' suitable nesting habitats. Complete protection of oystercatchers will also protect species with more restricted breeding site requirements. Large-scale protection is, however, more costly or less politically palatable, and hence may complement local efforts and be used primarily in the wider context of land-use planning.

We suggest that even with systematic selection approaches such as those employed here, there is unlikely to be a single “clearly best” umbrella species candidate identified, particularly in more complex systems with a target species that span several taxonomic groups. The final choice is dependent on the spatial ambit of conservation interventions (local vs. regional), the cost and political feasibility (large vs. small areas), and the conservation status of the species of interest, which dictates the degree of legislative protection offered by the umbrella.

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