Ecological neighborhoods as a framework for umbrella species selection

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ABSTRACT

Umbrella species are typically chosen because they are expected to confer protection for other species assumed to have similar ecological requirements. Despite its popularity and substantial history, the value of the umbrella species concept has come into question because umbrella species chosen using heuristic methods, such as body or home range size, are not acting as adequate proxies for the metrics of interest: species richness or population abundance in a multi-species community for which protection is sought. How species associate with habitat across ecological scales has important implications for understanding population size and species richness, and therefore may be a better proxy for choosing an umbrella species. We determined the spatial scales of ecological neighborhoods important for predicting abundance of 8 potential umbrella species breeding in Nebraska using Bayesian latent indicator scale selection in N-mixture models accounting for imperfect detection. We compare the conservation value measured as collective avian abundance under different umbrella species selected following commonly used criteria and selected based on identifying spatial land cover characteristics within ecological neighborhoods that maximize collective abundance. Using traditional criteria to select an umbrella species resulted in sub-maximal expected collective abundance in 86% of cases compared to selecting an umbrella species based on land cover characteristics that maximized collective abundance directly. We conclude that directly assessing the expected quantitative outcomes, rather than ecological proxies, is likely the most efficient method to maximize the potential for conservation success under the umbrella species concept.

1. Introduction

Faced with limited resources and increasingly larger challenges, conservation scientists developed the umbrella species concept as a heuristic to simplify complex conservation problems. In theory, by using one or a few species to represent larger communities of concern, feasible conservation planning becomes an attainable goal (Chase and Geupel, 2005). Despite the importance of the umbrella species concept in theory and application, there is no consensus definition of the characteristics defining a good umbrella species (Roberge and Angelstam, 2004), which may contribute to its equivocal success (Berger, 1997; Caro et al., 2004; Thorne et al., 2006; Rubinoff, 2001; Ozaki et al., 2006; Breckheimer et al., 2014; Fourcade et al., 2017). Umbrella species are often designated if they fill a certain criterion or multiple criteria, usually with limited validation or assessment. Selection schemes for umbrella species are therefore largely ad hoc (Andelman and Fagan, 2000). Recurring criteria include ease of sampling, sympatry, specialization, home range size, and body size (Roberge and Angelstam, 2004; Caro, 2010; Andelman and Fagan,

2000), but there is limited evidence that such criteria predict conservation success (Branton and Richardson, 2011). Because the outcomes of conservation actions based on the use of umbrella species are equivocal, the underlying assumptions and utility of the umbrella species concept have come into question (Andelman and Fagan, 2000; Branton and Richardson, 2011; Caro, 2010; Roberge and Angelstam, 2004; Landres et al., 1988). The conceptual simplicity of the umbrella species concept may preclude the development of a selection rule-set that works across diverse conservation applications. Many common metrics for selecting umbrella species are assumed to indicate species that will confer protection on additional species. Typically, a formal relationship between protection measures and conservation objectives, such as increased or maximal abundance of additional species of interest, are not tested.

Furthermore, the general assumption that protecting the area occupied by an umbrella species automatically confers protection on species occupying a smaller area disregards ecological hierarchy theory (Johnson, 1980), which postulates that ecological processes operate simultaneously across spatial scales to shape the distribution and

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Table 1
Metrics commonly assumed to represent characteristics of successful umbrella species.

Common name	Scientific name	Species code	Umbrella selection metric[*]	Predicted collective abundance (SD)
Dickcissel	*Spiza Americana*	DICK	4,11	17.73 (2.68)
Eastern Meadowlark	*Sturnella magna*	EAME	1,11	20.64 (15.19)
Field Sparrow	*Spizella pusilla*	FISP	1,3,11	20.79 (10.29)
Grasshopper Sparrow	*Ammodramus savannarum*	GRSP	6,8,11	23.65 (3.20)
Lark Sparrow	*Chondestes grammacus*	LASP	7,11	18.06 (7.76)
Northern Bobwhite Quail	*Colinus virginianus*	NOBO	2,9	17.94 (2.62)
Ring-necked Pheasant	*Phasianus colchicus*	RNEP	2,5,9,10,12	18.77 (2.05)
Western Meadowlark	*Sturnella neglecta*	WEME	2,6,11	23.93 (1.99)

[*] **1**: biodiversity indicator/#co-occurring species; **2**: charismatic; **3**: habitat specialist/resource limited; **4**: minimum area requirement; **5**: large body size; **6**: large geographic range; **7**: low population density; **8**: relatively abundant; **9**: game species; **10**: large home range; **11**: migratory; **12**: dispersal-limited; based on Lambeck (1997); Caro and O'Doherty (1999); and Fleishman et al. (2000).

abundance of populations (Johnson, 1980; Allen and Hoekstra, 2015). Minimum area requirements, which largely reflect a single level in the hierarchy, neglect the importance of land cover composition within home ranges, or neighborhood effects acting on different spatial scales (Dunning et al., 1992). Only recently have studies begun to refer to an 'extended umbrella concept' which aims to define compositional and functional landscape attributes for protection (van Langevelde et al., 2000), and multi-species umbrella plans to cover multiple landscape attributes (Lambeck, 1997) are expected to improve conservation success. Consideration of scale-dependent species-environment associations adds complexity in selecting umbrella species, but if conservation planning using the umbrella species concept fails to systematically achieve desired outcomes, the concept will soon lose scientific credibility and public support. Identifying methods to increase the probability of success is necessary for effective conservation planning within the umbrella species framework.

Conservation efforts typically focus on identifying reserves or priority conservation areas that maintain or maximize target populations. Because species associate with landscape characteristics at multiple spatial scales, the spatial scales at which species respond to characteristics on the landscape should play an important role in informing conservation decisions (Johnson, 1980). We propose that the optimal workflow for developing set-aside areas for multi-species conservation is to first identify multi-scale land cover characteristics that best predict species' abundance for each species in the set of interest. Second, for each species, characterize the land cover attributes within important spatial scales maximizing species abundance. The combined information, scale and attributes within the scale, represents an ideal ecological neighborhood for each species within the community. Finally, to implement conservation actions under the umbrella species concept, we can leverage species-specific information to identify the land cover attributes at spatial scales that maximize collective abundance across all species (e.g., Norvell et al., 2014; Caro, 2001). Identifying the ecological neighborhoods that ensure the greatest conservation potential (e.g., maximizing community-wide abundance) across a community may improve conservation outcomes for multiple species by assessing quantitative conservation objectives, rather than relying on ecological proxies, and avoiding problems associated with scale mismatches in conservation (Keitt et al., 2002; Henebry, 1995; de Knegt et al., 2010; Lennon, 2000).

We present a case study to compare the expected outcomes of designating an umbrella species for a community of birds using two approaches: the first based on commonly used proxies, and the second based on quantitatively identifying land cover characteristics across scales that maximize collective abundance. We identify the ecological neighborhoods that best predict species abundance, and estimate the land cover characteristics within the spatial scale that maximize species abundance. Using information from ideal ecological neighborhoods, we explore the costs and benefits, in terms of species abundance, associated with optimal (e.g., the species maximizing collective abundance) versus sub-optimal (e.g., a species that does not maximize collective abundance) umbrella species selection and their associated conservation areas.

2. Methods

2.1. Point count surveys and field sites

Avian surveys were performed at field sites across southern Nebraska during the breeding seasons of 2010–2012 (Fig. S1; $n = 405$) on sites within Nebraska Game and Parks Commission's (NGPC) Wildlife Management Areas, and private property enrolled in the Open Fields and Waters program, both subsequently referred to as wildlife management areas (WMAs). WMAs had a minimum of 64 ha of contiguous grassland, which is the minimum size assumed necessary to support certain grassland-obligate bird species populations (Clark et al., 1999; Walk and Warner, 1999; Helzer and Jelinski, 1999). We randomly selected 9 survey sites within each WMA, which were sampled three times each breeding season following the 'robust sampling design' to decompose the effect of detection on estimated abundance (Williams et al., 2002). Locations were not sampled during inclement weather, resulting in some survey sites not being sampled all three times per breeding season.

Surveys were performed during maximum vocalization times between 15 min before sunrise and 10 h00 (Luukkonen et al., 1997; Ralph and Sauer, 1995). Trained observers (8 or 9 observers per year, 7 of which were consistent across all years) performed 3-min, unlimited radius surveys, truncated to 500 m for analysis (i.e., focal area), to record detections of eight species (Table 1) identified by sight or sound during April to July (Hutto et al., 1986). During each survey, observers recorded the date and time of the survey, percent cloud cover, wind speed, and temperature, which may influence the probability of detecting a bird present within the survey location.

2.2. Land cover data

The proportion of grassland and woodland land cover were selected as predictors in our analyses of species abundance based on a priori assumptions that they are important predictors of grassland species abundance (Patterson and Best, 1996; Kelsey et al., 2006; Bakker et al., 2002; Van Buskirk and Willi, 2004). Grassland and woodland classifications were derived from the 2011 Rainwater Basin Joint Venture Nebraska Landcover dataset (30 m resolution; Bishop et al., 2011). We used the Circular Focal Statistics Tool in ArcGIS 10.0 (ESRI, Redlands, California) to calculate the proportion of land cover types within seven circular buffers around each focal survey point (500 m, 1000 m, 1500 m, 2000 m, 3000 m, 4000 m, 5000 m radii) as they span from the minimum survey area to beyond the territory sizes of the species considered here. Because surveyed landscapes included other land cover types, the proportion of woodland and grassland were not highly

correlated (rho < 0.26).

3. Statistical analysis

3.1. Species abundance

We modeled the abundance of eight grassland bird species independently using hierarchical Bayesian N-mixture models which combine a Poisson model for the latent ecological process governing the abundance of individuals on the landscape with a conditional binomial model for the observation process regulating how many birds are counted at a given location (Royle, 2004; Royle et al., 2007). Our repeated-measures sampling design enabled us to model species abundance while accounting for imperfect detection of individual birds (Tyre et al., 2003; Royle et al., 2005; Kery and Schmidt, 2008). We assumed a closed population for each survey site (n = 405 sites) within each year (Royle, 2004), and we included year, and linear and quadratic terms for both land cover types (standardized) as fixed effects in the linear predictor for the ecological process. We used WMA and survey site as random effects to account for the repeated-measures sampling design and unmeasured differences between sites and WMAs. The linear predictor for detection probability included seasonal date (days since January 1), the time of the survey and its quadratic effect, cloud cover, wind speed, and temperature all standardized. We included observer identity as a random effect to account for between-individual differences in survey ability (Kendall et al., 1996; Diefenbach et al., 2003).

To determine the spatial scales that land cover variables best predicted species abundance, we used Bayesian latent indicator scale selection (BLISS) estimated with reversible-jump Markov chain Monte Carlo (RJMCMC) sampling (for full details see Stuber et al., 2017), as a modification to the standard N-mixture model. For flexible spatial scale selection, BLISS ties each land cover predictor to a latent scale indicator variable to estimate the posterior probabilities of all candidate spatial scales. For each sampling iteration, BLISS included each land cover variable at a single, independent, spatial scale. This inclusion avoided collinearity with other spatial scales of the same land cover variables. Furthermore, BLISS allows each predictor to be estimated at different spatial scales by using an independent scale indicator for each predictor. The spatial scale with the highest posterior probability was designated as the species-specific spatial scale predicting abundance for grassland and woodland independently. Once spatial scales were selected, we fit the standard N-mixture model with woodland and grassland predictors entered at their designated spatial scales to estimate the coefficients of abundance-land cover relationships using MCMC sampling (i.e., without scale selection).

Analyses were performed using programs JAGS (Just Another Gibbs Sampler; Plummer, 2004) and R (R 3.1.1 package rjags; Plummer et al., 2015). For each species, we estimated the posterior distributions of all parameters based on MCMC simulation of 10,000 iterations after a 5000 sample burn-in period with relatively weak, 0 mean, normally-distributed priors on predictor coefficients, and discrete uniform priors for all candidate scales. We visually inspected trace plots to confirm convergence. If models did not converge under our initial settings, we re-ran the sampling procedure longer until convergence was attained. We extracted the mean and 95% credible intervals (CI) around the mean (Gelman and Hill, 2007) of coefficients of the abundance-land cover relationship, which represent the parameter estimate and its uncertainty. Semi-variograms did not indicate residual spatial autocorrelation left unexplained by our models.

3.2. Umbrella species proxies

All 8 species (Table 1) could have been chosen as potential umbrella species based on satisfying at least two criteria commonly found in the literature (Seddon and Leech, 2008; Lambeck, 1997; Caro, 2010; Fleishman et al., 2000). Of the species considered, RNEP could have been selected a priori as an umbrella species based on the most criteria: charismatic, large body size, game species, large home range, and dispersal-limitation.

3.3. Estimating collective abundance and comparing potential umbrella species

For each species, we calculated the proportions of grassland and woodland within the species-specific selected spatial scales that maximized abundance. The ideal proportion of land cover to maximize abundance was calculated by solving the function (i.e., the estimated model N = $\exp(\beta 0 + \beta 1 \times \text{grassland}_{\text{scale}} + \beta 2 \times \text{grassland}_{\text{scale}}^2 + \beta 3 \times \text{woodland}_{\text{scale}} + \beta 4 \times \text{woodland}_{\text{scale}}^2)$) for land cover values in the observed dataset and selecting the proportion of each grassland and woodland that maximized estimated abundance. $\beta 0$ represents the species-specific intercept, $\beta 1$ and $\beta 2$ represent species-specific estimated coefficients for the linear and quadratic effects of grassland, $\beta 3$ and $\beta 4$ represent species-specific estimated coefficients for the linear and quadratic effects of woodland, and the scale subscript denotes that each land cover type has a species-specific spatial scale at which proportions of grassland and woodland were calculated. By only using land cover values observed in our sample dataset, we guaranteed that the ideal proportion existed in the state of Nebraska; extrapolation of abundance outside of the model-trained land cover range would likely result in unstable estimates. For each species, we randomly selected 1000 locations from the state of Nebraska matching the estimated ideal land cover characteristics (e.g., proportion of grassland and woodland at species-specific spatial scales) of the target species within ± 10% land cover, and calculated collective abundance across species at each location. Collective abundance across species was calculated as the sum over all species' estimated abundance at each random location. The species whose land cover characteristics maximized expected collective abundance across species was selected as the optimal umbrella species (e.g., selection based on estimation). We also calculated the collective abundance using species chosen as umbrella species candidates based on published metrics (Table 1) as a comparison to our estimation-based selection method.

4. Results

4.1. Ideal land cover characteristics across scales

During the three breeding seasons, we conducted 643, 1189, and 1105 point count surveys, respectively. Species' selected scales ranged from the minimum to maximum considered (Fig. 1: grassland; Fig. 2: woodland), and ideal amounts of grassland within selected scales ranged from 0.09 to 0.86, and from 0.00 to 0.31 of woodland within selected scales (Table 2). It was difficult to identify neighborhood areas matching even ± 10% of multi-species maximum abundance as points in space never contained all species' ideal land cover characteristics (0% of 10,000 randomly selected points in Nebraska) even when excluding incompatible characteristics. Indeed, some species' ideal land cover excluded others (e.g., ideal proportion woodland of LASP was 0.31 while NOBO was 0.05, both at the 3000 m scale).

4.2. Umbrella species selection based on estimated land cover characteristics

Collective abundance (N_{coll}) was maximized when the ideal land cover characteristics of WEME were used to select 1000 potential conservation areas (N_{coll} = 23.93, sd = 1.99), and represents the estimated optimal umbrella species of this set.
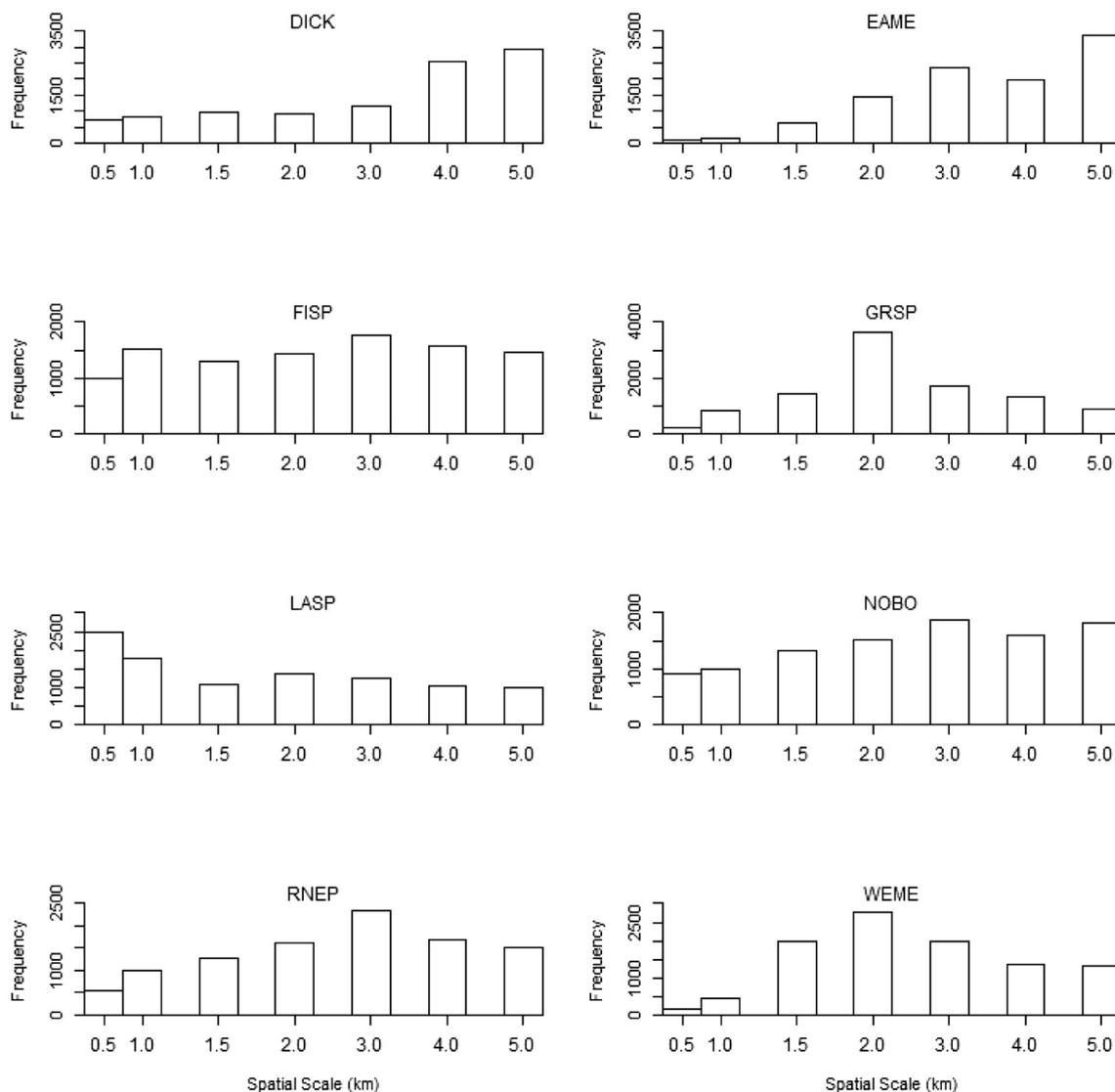
Fig. 1. Posterior frequency distributions (i.e., number of MCMC iterations) from Bayesian latent indicator scale selection for identification of grassland spatial scale (km-radius buffer) for 8 species of birds breeding in Nebraska, USA. DICK: Dickcissel, EAME: Eastern Meadowlark, FISP: Field Sparrow, GRSP: Grasshopper Sparrow, LASP: Lark Sparrow, NOBO: Northern Bobwhite Quail, RNEP: Ring-necked Pheasant, WEME: Western Meadowlark.

4.3. Potential umbrella species based on a priori characteristics

The umbrella species selection rule to choose species with the largest minimum area requirement did not guarantee the selection of ideal land cover for other species. In our set of species, DICK abundance is best predicted by grassland and woodland characteristics at the largest spatial scales (i.e., 5 km radius) and has the largest minimum area requirements, and RNEP had the largest expected home range. Collective abundance under DICK as an umbrella species was 26% less than the estimated optimal umbrella species, WEME (Table 1). Collective abundance under RNEP as an umbrella species, which also could have been chosen because of its relatively large body size and limited dispersal, was 22% less than under the optimal umbrella (Table 1). LASP, selected for its low population density, resulted in a collective abundance 25% less than WEME, whereas GRSP, selected for its intermediate abundance and large geographic range had only 1% lower collective abundance (Table 1). Both game species, NOBO and RNEP, resulted in sub-maximal collective abundance, while EAME and FISP, which co-occur with the greatest number of species led to 14%, and 13%, respectively, lower collective abundance (Table 1). WEME, which satisfied common criteria including charismatic (e.g., the state bird of

NE), large geographic range, and migratory, had the maximum estimated collective abundance (Table 1).

5. Discussion

Our research demonstrated that selecting umbrella species based on commonly used indirect proxies for expected success resulted in choosing a sub-optimal species that did not maximize collective abundance in the majority of cases. Direct, quantitative measures of conservation outcomes can be used to guide umbrella species selection for increased probability of success, and are transferrable to any system of interest where relevant species and environmental data can be collected. Although our framework for guiding umbrella species selection is relatively more data-intensive, it enabled us to quantify the opportunity cost of relying on indirect proxies in terms of lost potential species abundance and can be used to justify conservation decisions by balancing these opportunity costs against monetary cost, public opinion, and feasibility.

Using species-specific land cover requirements at the appropriate spatial scales, we were able to identify the species (WEME) whose land cover characteristics maximized the total estimated collective
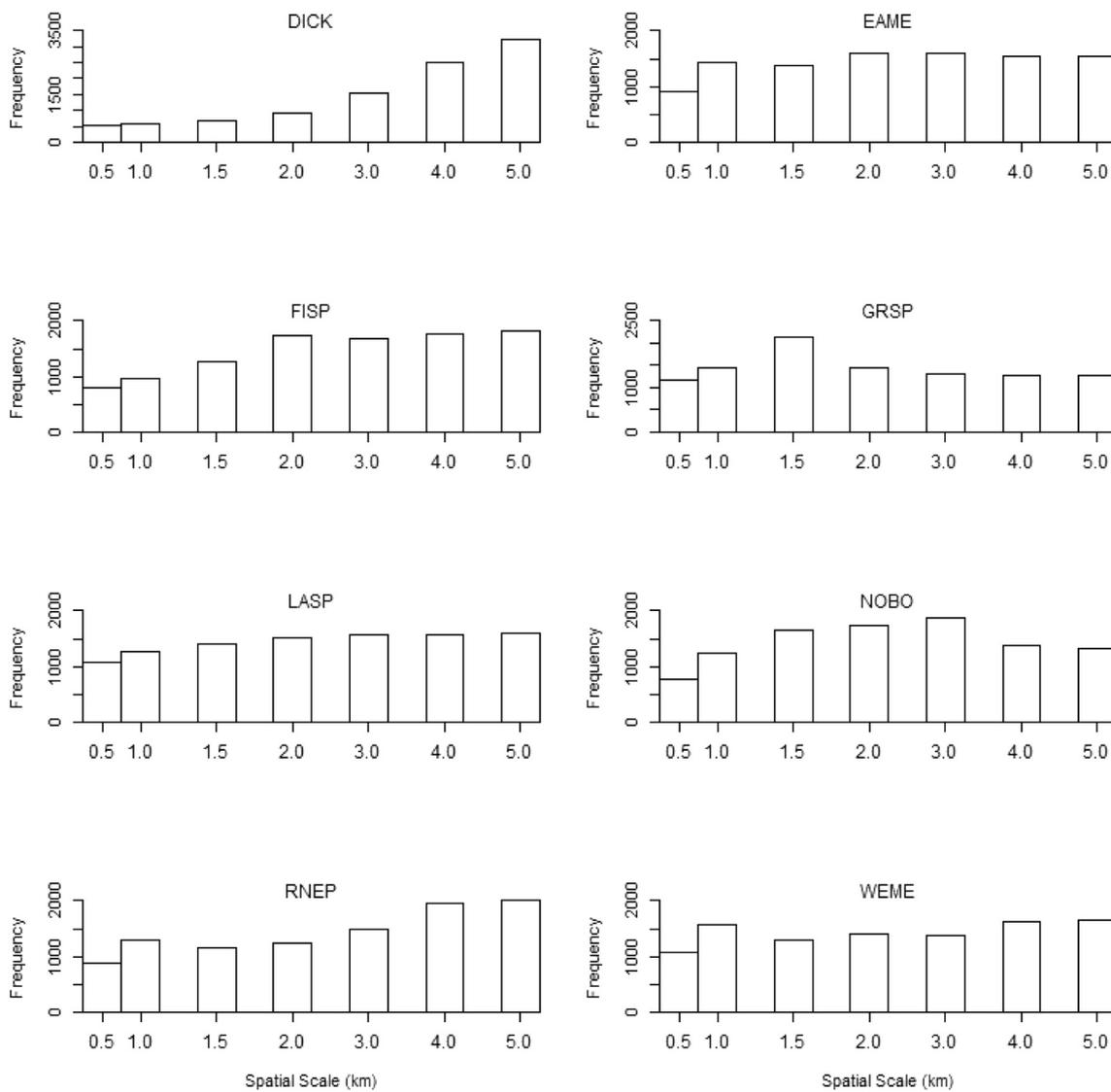
Fig. 2. Posterior frequency distributions (i.e., number of MCMC iterations) from Bayesian latent indicator scale selection for identification of woodland spatial scale (km-radius buffer) for 8 species of birds breeding in Nebraska, USA.

Table 2
BLISS model selection for important spatial scales of grassland and woodland variables predicting species abundance and the expected optimal proportions of grassland and woodland land cover within selected spatial scales where species abundance is maximized based on models estimated with the selected spatial scales. Coefficients of models estimated with the selected spatial scales are presented with 95% credible intervals.

	Intercept	Grassland	Grassland^2	Woodland	Woodland^2	Grassland scale (m)	Proportion grassland	Woodland scale (m)	Proportion woodland	%MAE
DICK	1.92	−0.08	−0.02	0.03	−0.06	5000	0.20	5000	0.05	14
	(1.67, 2.15)	(−0.18,0.03)	(−0.08,0.05)	(−0.08,0.14)	(−0.13,0.00)					
EAME	−0.90	−0.05	−0.43	0.25	0.01	5000	0.53	3000	0.31	7
	(−1.42,−0.39)	(−0.42,0.32)	(−0.71,−0.14)	(−0.09,0.58)	(−0.08,0.10)					
FISP	−0.30	0.14	−0.05	0.42 (0.10,0.72)	0.05	3000	0.53	2000	0.31	8
	(−0.75,0.14)	(−0.13, 0.41)	(−0.27,0.16)		(−0.05,0.15)					
GRSP	0.29	0.56 (0.37,0.75)	−0.07	−0.31	0.13 (0.07,0.19)	2000	0.86	1000	0.0003	15
	(−0.03,0.62)		(−0.22,0.06)	(−0.51,−0.11)						
LASP	−1.11	0.10	0.01	0.07	0.08	500	0.53	3000	0.31	2
	(−1.65,−0.53)	(−0.16,0.34)	(−0.18,0.19)	(−0.23,0.37)	(−0.06,0.22)					
NOBO	0.36	−0.02	0.02	0.05	−0.16	3000	0.20	3000	0.05	9
	(0.02,0.73)	(−0.20,0.16)	(−0.11,0.15)	(−0.17,0.26)	(−0.29,−0.05)					
RNEP	1.33	−0.06	−0.01	−0.69	0.14	3000	0.09	5000	0.003	9
	(1.00,1.65)	(−0.22,0.09)	(−0.11,0.09)	(−0.88,0.50)	(0.01,0.27)					
WEME	0.14	0.37	0.04	−0.72	−0.01	2000	0.86	5000	0.0003	12
	(−0.20,0.47)	(0.21,0.52)	(−0.08,0.16)	(−0.93,−0.50)	(−0.18,0.15)					

MAE: mean absolute error of the residuals.

abundance. We investigated 12 common umbrella selection criteria and identified bird species that fit any of these criteria, producing 22 possible species-criteria combinations. In the scenario investigated, if scientists had selected an umbrella species using typical criteria assumed to reflect likely suitable candidates, 19 out of 22 (86%) possible choices would have resulted in sub-maximal outcomes in terms of collective abundance. Sub-optimal umbrella species were predicted to lead to an opportunity cost, in lost potential collective abundance, ranging from 1% to 26% lost collective abundance compared to the species that maximized abundance. Opportunity cost could be used by conservationists as a quantitative currency to weigh against other costs associated with conservation action, including monetary cost of acquiring land with ideal land cover characteristics, ability to continue monitoring the selected umbrella species, or extent of ideal land in the landscape. Weighing these constraints against expected opportunity costs could lead to informed decisions to designate a sub-optimal species as an umbrella species, if for example monetary costs, or public opinion outweigh the opportunity cost of lost collective abundance. Although selecting a sub-optimal umbrella species does not necessarily equate to conservation failure, it precludes attaining the best possible ecological outcomes, which is increasingly important under limited conservation resources. Our framework would provide conservation teams with quantitative evidence to justify data-driven conservation decisions and justification for stakeholders.

Our analysis of common selection criteria reflects the best-case scenario, as we estimated collective abundance under potential conservation areas that were expected to be ideal for the target umbrella species; such land cover by scale information is often unknown without prior data collection under proper study design (Morrison, 2012). While a substitute to circumvent acquiring land cover data could be to conserve land where the target species is known to occur, occurrence does not guarantee ideal conditions (Brown, 1984), and would represent an opportunity cost in terms of lost potential collective abundance were ideal land cover by scale characteristics to be preserved. However, the accessibility and expansion of freely-accessible remote-sensing data make our framework an increasingly valuable tool for conservation researchers across the globe. Land cover characteristics derived from remote-sensing sources are much less costly to obtain than on-the-ground field data, span a continuous, large spatial extent, are available in temporal and spatial resolutions adequate for a wide range of species, and can represent environmental characteristics general enough to be relevant to suites of species. Species-specific specialized land cover characteristics likely would have improved individual species' models, but would not have contributed much to identifying priority areas that maximize abundance across multiple species. Indeed, thematic resolution, and choices of land cover variables to consider will be study-specific to a degree, but should be general enough to influence the species in the set for which protection is sought. Although we attain acceptable model fit using two coarse land cover classes, it is likely that model fit could be improved by adding additional (e.g., related to configuration or disturbance regimes) or finer-scale (e.g., grassland quality) predictor variables. This creates a trade-off however, between model complexity and feasibility of finding or creating optimal areas to protect, which is further compounded by the size of the species set under consideration.

Even when limiting our land cover search to scale and land cover characteristics that were not mutually-exclusive, no community-ideal land cover existed in the study area (e.g., we expanded our search rule to locate areas within 10% of the community-ideal land cover characteristics). Failure to find the single 'best' location is the norm, where truly optimal land cover does not exist, or cannot be acquired, and conservation reserve designers must locate the best possible locations of those available. Given that land cover predictors are available for the extent of land available to conservation teams for acquisition, our framework enumerates collective abundance for all available land (e.g., not limited to 1000 sites considered here). Such a census allows both

the expected optimal umbrella species to be chosen, and the sites with maximum collective abundance to be identified, rather than relying on statistical averages. For example, in our case study GRSP had only 1.2% lower expected collective abundance on average, but if all possible locations were censused, we could produce exact study-specific interpretations. Nevertheless, while considering land cover composition in addition to minimum area requirements is an improvement on the most simple umbrella species selection criteria, assessing the impacts of model complexity on feasibility of model-based conservation action is necessary for the most efficient use of conservation resources, and will change based on the goals and objectives of the conservation plan. Our framework produces a quantitative ranking of possible umbrella species in terms of ideal land cover by scale characteristics versus the opportunity cost of selecting a sub-optimal umbrella species due to economic, ecological, or practical constraints that preclude similar data collection and analysis that can quantitatively guide decisions.

Even though our framework will identify a species as a quality candidate for umbrella species conservation, conservation efforts often face additional constraints that require navigating trade-offs between economic and environmental objectives (DeFries et al., 2004; Kennedy et al., 2016). Acquiring conservation areas with the appropriate neighborhood characteristics of the optimal species may in many cases be intractable, forcing decision-makers to choose a sub-optimal umbrella species because the land cover characteristics of its ecologically important neighborhood are less costly to obtain under limited funds. For example, the second-best umbrella species in our set, with only 1.2% less collective abundance was GRSP, which requires particular land cover characteristics in much smaller spatial scales than WEME, and would represent a substantial monetary savings for a small loss in collective abundance. GRSP would likely be a strong candidate for selection as an umbrella species in our set due to practical versus ecological reasons. Similarly, when it is difficult to identify a single most appropriate spatial scale in predicting animal abundance (e.g., when neighboring scales are equally successful in predicting abundance: EAME, LASP woodland), it would be cost-effective to select the smaller scale to use in conservation decisions. It is worth noting that land cover outside of any reserve is subject to uncertainty in its stability, as the reserve manager is not in control of its use. Even if a small scale area with ideal GRSP land cover characteristics was designated as a conservation area, nearly all other species in the community depend on land cover characteristics at a larger scale, introducing uncertainty to how long maximum collective abundance might be maintained. The most conservative option might be to set-aside an area at least as large as the largest scale needed by a species of interest, but with the land cover characteristics at the scales of the chosen umbrella species.

Our study is a simplification of conservation outcomes, as we optimize collective abundance within a focal area (i.e., a 500 m radius point count survey area; 78.5 ha) based on a subset of particular neighborhood land cover characteristics. When acquiring a conservation area, the neighborhood containing optimal land cover characteristics of the umbrella species would also be obtained as part of the conservation area (e.g., 1257 ha (2 km radius) area with 86% grassland, and a 7854 ha (5 km radius) area with 0.3% woodland for WEME to maximize N_{coll}). If a 7854 ha area were to be purchased, not only would the maximized central 78.5 ha focal area be obtained, but all other 78.5 ha areas within the larger landscape that were not directly maximized. However, if there is spatial autocorrelation in land cover variables, we would expect the conservation area to have greater collective abundance than if another species were selected as an umbrella because the surrounding land would have similar characteristics until spatial autocorrelation decays.

We outline a general framework for using quantitative metrics to justify the designation of a particular umbrella species for a community of interest. While we believe that maximizing abundance, a common state variable in conservation and management, is a useful conservation objective (Bani et al., 2006; Elphick et al., 2001), other quantitative

metrics may be substituted to reflect various conservation objectives. For example, the same workflow could be implemented with collective abundance weighted by species rarity, such that locations containing low-abundance rare species are given a higher score (Williams et al., 1996), or we could constrain total species-specific abundance expectations across locations to be above some minimum value to ensure population viability over a given time period (Traill et al., 2007). Although this and similar weighting rules would be subjective, reflecting specific conservation goals, such rules, including those that reflect trade-offs with economic development and growth, could be added to customize the framework. Alternative conservation objectives could also be substituted for our response variable of interest, collective abundance. For example, the same workflow could be used to maximize species richness instead of collective abundance, if that is a conservation priority. Our framework is broadly applicable to any system where reliable, relevant, species and environmental data can be collected.

Implementation of the umbrella species concept has met with haphazard success (Branton and Richardson, 2011). Our results demonstrate that only limited confidence should be placed in umbrella species selection criteria that are untested proxies of expected community-wide conservation objectives. Our process provides a framework that incorporates species-land cover relationships across scales in assessments of species- and community-response to conservation actions that will provide quantitative justification for selecting umbrella species. Although our framework necessitates high initial species monitoring costs, optimal conservation outcomes should not be expected if not based on a reasonable foundation of understanding. We provide a means to identify umbrella species candidates whose species-specific ideal ecological neighborhood coincides with the community's maximum collective abundance. As our results demonstrate, community-level optima may not always be realistic to attain. In this case, designating the species for which legal protections or conservation plans are already in place (Crosby et al., 2015), or monitoring protocols are most efficient, are practical considerations that may lead to designating a particular species as an umbrella. Although our framework offers a priori, system-specific, data-driven evidence for identifying optimal umbrella species and the spatial scale of conservation priorities, only future work testing the procedure in the field would validate our method. We propose this procedure as a workflow for conservation planners to identify landscapes and management actions that maximize conservation success in terms of quantitative objectives for target communities. Our workflow also provides a method of selecting an umbrella species from the community of interest for continued monitoring. The results generated through the scenarios we have evaluated are not meant to be interpreted as conservation prescriptions; however, they highlight the importance of considering quantitative metrics and ecological constraints in conservation.

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