



# How well do proxy species models inform conservation of surrogate species?

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## Abstract

**Context** Proxy species, which represent suites of organisms with similar habitat requirements, are common in conservation. Landscape Capability (LC) models aim to quantify the spatially-explicit capability of landscapes to support proxy species that represent suites of forest birds.

**Objectives** We evaluated the North Atlantic Landscape Conservation Cooperative (NALCC) proxy models of LC and represented species framework across 13 states in the northeastern United States from Virginia to Maine. We validated a suite of questions related to co-occurrence of proxy and represented species with a compilation of independent datasets.

**Methods** We tested proxy species LC models ability to explain represented species' occurrences, including using multiple proxies together, and benchmarked against empirical data and land cover type classifications. We tested effect of several factors on predictive ability including relative range overlap and ecological and taxonomic dissimilarity between proxy and represented species.

**Results** LC models performed variably, but represented species occurrences were rarely predicted as accurately as proxy species. Models improved predictions over macrohabitat classifications. Using multiple proxies together occasionally improved predictions of represented species. Considerable range overlap was needed for models to be predictive of represented species. Ecological and taxonomic similarity had no effect on predictive ability. LC models worked

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similarly to using empirical observations, suggesting shortcomings were because of imperfect surrogacy.

**Conclusions** Conservation proxies as representatives of species groups that are associated with macrohabitats are useful, but empirical data are necessary to evaluate proxy species' effectiveness. Habitat-based models can provide similar predictive ability as empirical observations of proxies and represent a useful tool in conservation planning.

**Keywords** Appalachians · Bird-habitat modeling · Landscape capability · North Atlantic · Predictive models · Representative species

## Introduction

Mature forest dwelling bird populations have undergone large changes in the northeastern United States following European colonization to the present (Robbins et al. 1989; Schipper et al. 2016). The landscape was largely cleared of ancestral old-growth forest and replaced with agriculture. Reforestation reduced tree diversity, a trend exacerbated by plant pathogens removing keystone American elm [*Ulmus americana*] and chestnut [*Castanea dentata*]. Regenerating and secondary forests dominated much of the late nineteenth and twentieth centuries forests (Thompson et al. 2013). These forests are undergoing another deforestation event as changes in timber harvest practices and urban and exurban growth outpace reforestation and are reducing several forest bird species' populations in northeastern states (Brown et al. 2005; Drummond and Loveland 2010; Pidgeon et al. 2014; Sauer et al. 2017), with potential exacerbation in the form of anthropogenic climate change (Woodall et al. 2009; Sohl 2014; Potter et al. 2017).

Landscape conservation design is inherently dependent on spatial scales and is informed by multiple species (Poiani et al. 2000; Nicholson et al. 2006) and their habitat associations represented in land cover classifications of remotely sensed data. Selecting priority areas for conservation actions, or as reserves, is ideally based on how well those areas serve as representatives for regional biodiversity, and how well a reserve, or targeted management action, will aid in persistence of target species or desired elements of biodiversity (Margules and Pressey 2000). A single

location of conservation interest may support dozens or even hundreds of species, and implementing conservation actions on a species-by-species basis is prohibitively difficult (Hutto 1998; Fleishman and Murphy 2009). Additionally, each species in an area does not occur as an isolated target for conservation. Instead, species are linked via dynamic ecological process and conservation threats (Pressey et al. 2007). It is therefore typically impossible to develop temporally static models for every species in isolation, and thus a common approach to address these correlations among species' occurrences uses proxy species to represent broader suites of represented species with a shared macrohabitat requirement. This "coarse filter approach" (Hunter 1991; Groves et al. 2000) is a widely used practice within the perching birds, related land birds and other diverse taxonomic groups (Hutto 1998; Bonn and Schröder 2001; Caro 2010; Bell et al. 2014). In practice this often means using models of proxy species' habitat quality (or other aggregated diversity metrics within groups; e.g., Fleishman et al. 2000b) as a "stand in" for a broader suite of associated taxa. That is, conservation actions directed toward the proxy species also will benefit the associated or represented taxa. The question naturally arises, however, as to the suitability of transferring models developed for a specific set of ecological considerations (that mediate occurrence for one species) to all represented species of interest. The North American Landscape Conservation Cooperative (<https://lccnetwork.org>) framework uses "representative species" as the particular type of proxy. A representative species, as opposed to an indicator, or umbrella species, explicitly pairs a representative species with those species with which it shares similar habitat requirements (Hutto 1998; Carignan and Villard 2002). A principle rationale for using representative species is that it does not rely on two rarely met assumptions of umbrella and indicator species: (1) species richness of indicator taxa are correlated with richness of lesser known taxa, and (2) richness is in turn correlated with rare or threatened species (Carignan and Villard 2002), a poorly supported assumption (Prendergast et al. 1993). The downside to this approach is that no two competing species can occupy the same niche (Hardin 1960), and there will be some ecological dissimilarity among represented species and proxies. Species representative of the same forest conditions, for example, are not

interchangeable, and may produce different results based on finer-scale ecological requirements (Manton et al. 2005).

Varied responses to microhabitat characteristics, competitive exclusion, imperfect surrogacy, incomplete knowledge of species ecology, and other limitations, all place bounds on the effectiveness of proxy approaches for identifying species' habitat (Wiens et al. 2008). Note that within the literature the use of "surrogate" may differ subtly from proxy although we will use the terms synonymously. Despite abundant literature providing guidelines for the development of proxy species approaches (e.g., Coppolillo et al. 2004; Wiens et al. 2008), the relative effect on predictive accuracy of surrogate-represented species from adherence to or violation of proffered guidelines is rarely directly tested at fine scales (Seddon and Leech 2008). Although proposals for how to select indicators are not new (Noss 1997; Fleishman et al. 2000a; Niemeier and de Groot 2008), rigorous frameworks to validate relationships among surrogates and experimental treatments and desired conservation outcomes have been proposed only recently (Tulloch et al. 2013; Barton et al. 2015), with validation of proxy species prediction accuracy uncommon in practice (Bonn and Schröder 2001; Fleishman et al. 2001; Rowland et al. 2006; Maslo et al. 2016).

Given the limitations of a proxy species approach, coupled with the widespread use of medium-fine resolution (e.g.,  $30 \times 30$  m Landsat) remotely sensed data used to represent habitat over broad extents [e.g., Northeast Terrestrial Habitat Classification (Gawler 2008)], we questioned whether coarse filter proxies that rely on multiple species' associations with similar habitats enhance conservation decision making compared with single-species focused models based on macrohabitat. We defined macrohabitat with The Nature Conservancy's macro-group habitat classifications of terrestrial habitat (Anderson et al. 2013). If habitat can be mapped directly at sufficiently fine resolution to predict occupancy at the scale of individual species, then using a proxy species to represent habitat conditions used by other species may result in unreliable models with untenable assumptions. Finer resolution models may capture more of the microhabitat differences that differentiate occurrence/non-occurrence among species (Fleishman and Murphy 2009).

Using an existing proxy-represented species framework (Table 1) and data compiled from diverse sources, we tested the effectiveness of a conservation proxy strategy for forest birds in the northeastern United States. Specifically, we asked: (1) Do proxy species' models explain variation in represented species' occurrences? (2) Does the co-occurrence of proxy species with represented species improve proxy model performance? (3) Does ecological and taxonomic dissimilarity between proxy and represented species affect proxy model performance? (4) Does predictive ability improve when multiple proxy species' models are used to predict a single represented species? (5) Are proxy predictions of represented species' occurrences more accurate than predictions based on macrohabitat classifications? and, (6) How does prediction of represented species' occurrences by proxy species compare with the amount of species range overlap?

To test these questions, we used the representative (i.e., proxy) species framework informing conservation at broad spatial scales devised by the North Atlantic Landscape Conservation Cooperative (NALCC). We sought to understand how models of proxy species' landscape capability (LC; McGarigal et al. 2016; Loman et al. 2017a) could best be used as proxies for represented species. LC models were created to predict the spatially-explicit capability of the landscape to support focal species (McGarigal et al. 2016), and they were designed to be useful at local scales (tens of meters to thousands of hectares; Poiani et al. 2000). LC models incorporate information about land cover, climate, regional prevalence, spatial configuration and extent, habitat relationships, species' space use, and ecological integrity to build fine resolution maps of proxy species that then presumably have some surrogacy value as proxies for preselected habitat types associated with additional species of conservation interest (i.e., the represented species) (McGarigal et al. 2016). The success of the NALCC approach using LC models as proxies has not been previously evaluated with empirical data, although many of the individual models have been evaluated as predictors of occurrence for the respective proxy species (Loman et al. 2017a, b).

**Table 1** Best and worst performing proxy species' models as predictors of occurrence of represented species in Northeastern United States using Landscape capability (LC) models to make predictions

Proxy	Represented Species	% Accuracy (precision)	Macrohabitat	Region
<b>Best performing models</b>				
Northern Waterthrush <sup>a</sup>	Canada Warbler	66.8 (68.3)	Wooded Swamp	N. New England
Blackburnian Warbler	Pine Warbler	63.3 (62.0)	Mixed conifer/hardwood	N. New England
Blackburnian Warbler	Black-throated Blue Warbler	60.7 (63.7)	Mixed conifer/hardwood	N. New England
Wood Thrush	Black-throated Blue Warbler	60.3 (67.8)	Mixed conifer/hardwood	N. New England
Ovenbird	Hooded Warbler	65.3 (61.0)	Mixed conifer/hardwood	S. New England
Ovenbird	American Redstart	61.7 (62.5)	Mixed conifer/hardwood	S. New England
Ovenbird	Black-and-white Warbler	61.6 (56.7)	Mixed conifer/hardwood	S. New England
Wood Thrush	Hooded Warbler	64.9 (59.9)	Mixed conifer/hardwood	S. New England
Wood Thrush	Black-and-white Warbler	61.8 (58.0)	Mixed conifer/hardwood	S. New England
Ovenbird	Black-capped Chickadee	67.5 (66.1)	Dry hardwood	Mid-Atl. and App
Wood Thrush	Black-and-white Warbler	61.6 (58.2)	Mesic hardwood	Mid-Atl. and App
Wood Thrush	Black-throated Blue Warbler	61.3 (58.7)	Mesic hardwood	Mid-Atl. and App
<b>Worst performing models</b>				
Blackpoll Warbler	Purple Finch	47.6 (36.5)	Spruce-fir forest	N. New England
Blackpoll Warbler	Brown Creeper	45.7 (31.0)	Spruce-fir forest	N. New England
Ovenbird	Black-and-white Warbler	47.7 (44.7)	Mixed conifer/hardwood	N. New England
Ovenbird	Pine Warbler	42.9 (40.8)	Mixed conifer/hardwood	N. New England
Wood Thrush	Black-and-white Warbler	47.8 (45.6)	Mixed conifer/hardwood	N. New England
Wood Thrush	Pine Warbler	41.9 (39.2)	Mixed conifer/hardwood	N. New England
Blackburnian Warbler	American Redstart	41.4 (42.2)	Mixed conifer/hardwood	N. New England
Louisiana Waterthrush	Eastern Wood-Pewee	49.1 (46.1)	Hardwood forest	S. New England
Ovenbird	Eastern Wood-Pewee	47.1 (48.2)	Hardwood forest	S. New England
Wood Thrush	Black-billed Cuckoo	44.7 (41.0)	Hardwood forest	Mid-Atl. and App
Wood Thrush	Baltimore Oriole	41.8 (44.0)	Hardwood forest	Mid-Atl. and App
Wood Thrush	Great Crested Flycatcher	40.4 (37.6)	Hardwood forest	Mid-Atl. and App

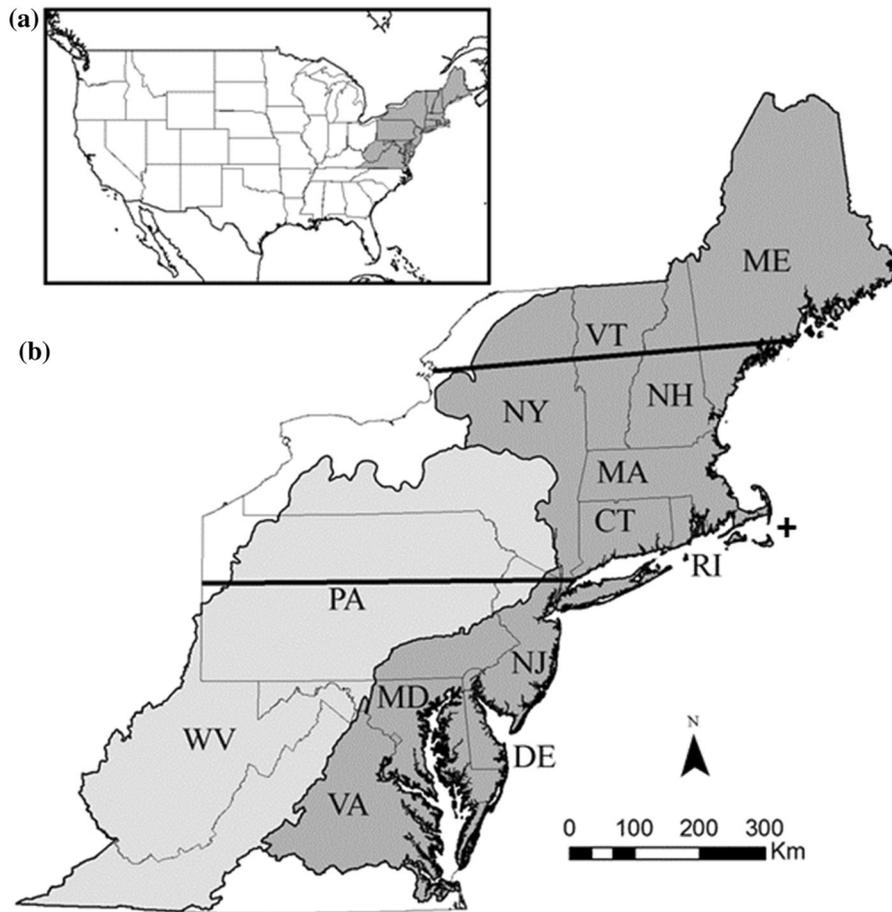
N. New England is northern New England (> 44°N), S. New England is Southern New England (< 44°N and > 41°N) and Mid-Atl. and App. is mid-Atlantic and Appalachians, respectively (< 41°N)

<sup>a</sup>Scientific Names: Northern Waterthrush (*Parkesia noveboracensis*), Louisiana Waterthrush (*P. motacilla*), Wood Thrush (*Hylocichla mustelina*), Ovenbird (*Seiurus aurocapilla*), Canada Warbler (*Cardellina canadensis*), Blackburnian Warbler (*Setophaga fusca*), Pine Warbler (*S. pinus*), Black-throated Blue Warbler (*S. caerulescens*), Hooded Warbler (*S. citrina*), American Redstart (*S. ruticilla*), Black-and-white Warbler (*Mniotilta varia*), Black-capped Chickadee (*Poecile atricapillus*), Purple Finch (*Haemorhous purpureus*), Brown Creeper (*Certhia americana*), Eastern Wood-Pewee (*Contopus virens*), Black-billed Cuckoo (*Coccyzus erythrophthalmus*), Baltimore Oriole (*Icterus galbula*), Great Crested Flycatcher (*Myiarchus crinitus*)

## Methods

We tested six LC models as proxy models span the northeastern United States (Figs. 1 and 2; McGarigal et al. 2016). These models serve as proxies to enhance landscape conservation and planning for a suite of 39 other represented bird species. We evaluated relationships between occurrences of represented species and models for proxy species with point count data

collected over the span 2005–2015 in 34 independent research or inventory projects from across 11 states within this region (See Online Appendix 1). We used a widely distributed sample of 10,122 point locations throughout the region. These data sets were not used to create LC models, thereby serving as an independent assessment dataset. We partitioned data across three sub regions (1) Northern New England, (2) Southern New England, and (3) mid-Atlantic and Northern



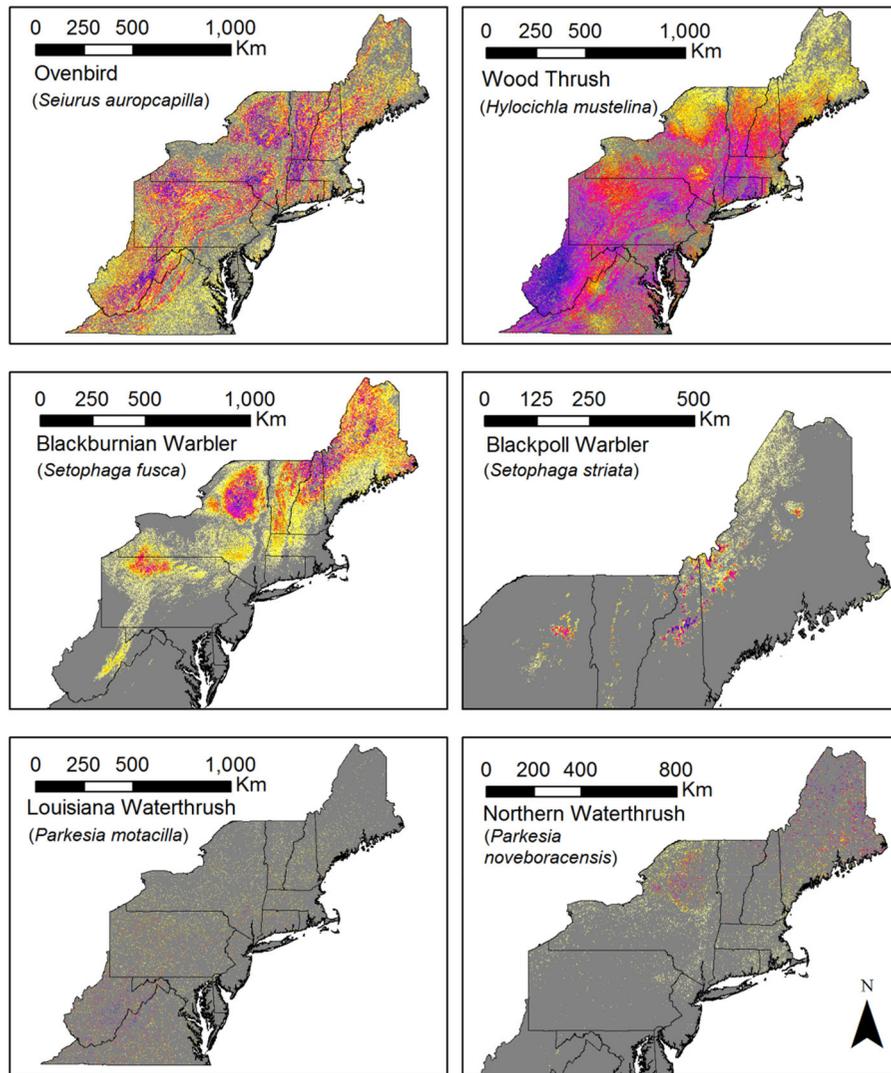
**Fig. 1** **A** Extent of Landscape Capability Models (LC; gray), **B** portion of the Appalachian Landscape Conservation Cooperative within the northeastern United States (light gray), and the North Atlantic Landscape Conservation Cooperative (dark gray). If you put “the + locator is at 69.7950192, 41.7071143. Boundaries between Northern New England, Southern New

England, and Mid-Atlantic/Appalachian subregions are indicated with thick black lines. *ME* Maine, *MA* Massachusetts, *VT* Vermont, *NH* New Hampshire, *NY* New York, *RI* Rhode Island, *CT* Connecticut, *PA* Pennsylvania, *NJ* New Jersey, *DE* Delaware, *MD* Maryland, *VA* Virginia, *WV* West Virginia

Appalachian corresponding to subregion latitudinal boundaries identified by the North Atlantic Landscape Conservation Cooperative (<https://lccnetwork.org/map>).

Previous validation of LC models showed they performed moderate to excellent as predictors of occurrence using single species models (range of Cohen’s  $\kappa = 0.32\text{--}0.85$ ), yet they were poor predictors of abundance (Loman et al. 2017a, b). Additionally, LC models were determined to be reliable predictors of occurrence, but not local or regional abundances, for ruffed grouse (*Bonasa umbellus*) and American woodcock (*Scolopax minor*) in that region (Loman et al. 2017b). Thus, we used species’ occurrences as

our metric of interest. We assessed local observed occurrence using point counts that began between 45 min before and 5 h after sunrise (Ralph et al. 1995), and at points spaced  $> 200$  m apart to generate independent survey data. Observers recorded either all birds detected, all birds detected within habitat patches, or only males. We removed females, juveniles, and birds denoted as flyovers from all datasets for consistency, although most detections were auditory detections of males. Observers recorded time of first detection for each individual to within the nearest minute in time bands between 1 and 10 min in duration depending on the study. Point counts were either 5, 10, or 15 min in duration, although most were



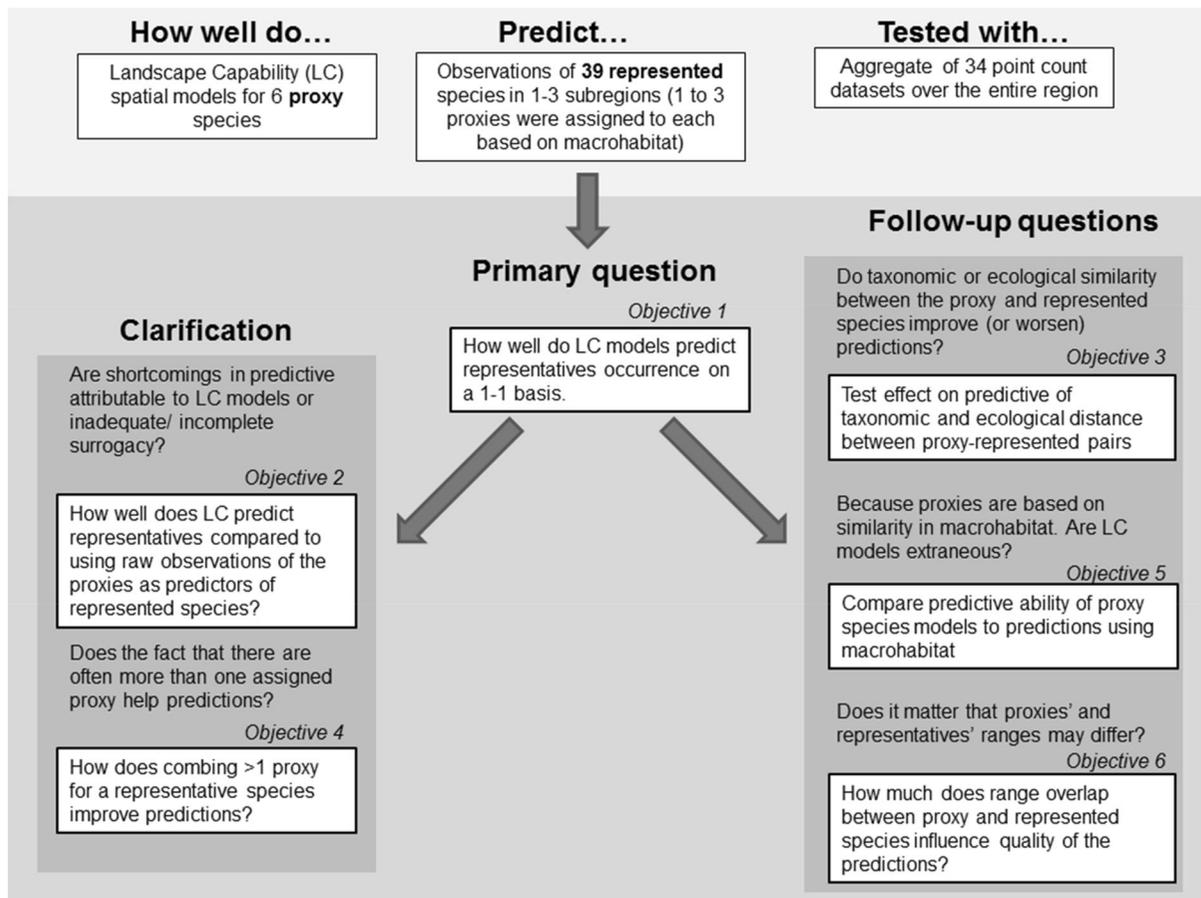
**Fig. 2** Landscape capability models developed by McGarigal et al. (2016) used as proxies for forest birds in the northeastern United States. Relative landscape capability increases in a color

gradient from yellow to orange red and purple, with gray equal to 0 landscape capability

10 min. Observers recorded linear distance in discrete band widths from 10 to 100 m. We excluded detections at distances greater than 100 m when determining point occurrence. We used 30,065 point counts at 10,122 discrete spatially referenced locations that met our criteria (Loman et al. 2017a) to evaluate the following objectives. The first objective is the primary goal, with the subsequent objectives intended to provide additional clarity, or to answer additional questions that arose during analyses (Fig. 3).

**Objective (1)** Test proxy species' LC models ability to explain observed occurrence of the associated represented species

We tested each LC model's ability to predict forest bird occurrence for the species it was intended to represent within each respective subregion by generating threshold-dependent statistics of the LC models' predictive performances. The subregions roughly correspond to species ranges, or allow different proxies as broad habitat associations shift with latitude. We defined occurrence as a male territorial



**Fig. 3** Logical overview of the linkages between study objectives to answer the effectiveness of the forest bird proxies to predict fine scale occurrence of represented species in the northeastern United States

bird occurring within 100 m of the point count location during any breeding season. For each represented species, we used all occupied sites and randomly sampled unoccupied sites within the appropriate subregion until the number of unoccupied sites matched the number of occupied sites to generate balanced occurrence/non-occurrence data and to ensure validity of predictive measures that are sensitive to skew (Powers 2007). We selected an optimality threshold for assigning points as predicted occupied or predicted unoccupied by using the threshold that provided the maximum sum of specificity and sensitivity jointly (or true skill statistic; Allouche et al. 2006). We repeated the resampling procedure for 100 iterations (for each pair) to generate a bootstrapped estimate of median Cohen's kappa ( $\kappa$ ) for each represented-proxy species pair. We used this median iteration to generate other predictive measures to

assess both positive and negative predictive ability, error rates, accuracy, and precision. We compared LC around the point by averaging the LC model output ( $30 \times 30$  m raster) around the survey point using R (R Core Team 2020) at buffer widths of 50 m, 100 m, 250 m, 500 m, and 1 km representing scales of resolution ranging from  $7853 \text{ m}^2$  to  $3,141,593 \text{ m}^2$ . Although LC models were developed at  $900 \text{ m}^2$  resolution, it is uncertain which scale may most accurately predict occurrence. We averaged all raster cells in which the midpoint of the cell was within each fixed radius buffer. For each proxy LC model-represented species pair, we selected the radius with the best predictive ability as measured by  $\kappa$ .

(2) Characterize observed co-occurrence of proxy species with represented species using empirical data

As a basis for evaluating the predictive ability of LC models relative to direct occurrences for each represented species, we conducted the same bootstrapping procedure above, instead substituting the observed occurrence of the proxy species at each point for the LC model value. If the proxy species was observed, we considered the point prediction for the represented species “occupied”; if the proxy was not observed, we considered the point prediction for the proxy “unoccupied.” We compared the model prediction with the empirical prediction using Mann–Whitney U tests (Sokal and Rohlf 1995).

(3) Evaluate and compare predictions of represented species’ occurrences by proxy species’ models partitioned by ecological and taxonomic rank dissimilarity of proxy and represented species

We assigned each proxy-represented species pair a rank to denote taxonomic dissimilarity. Congeneric pairs were given a score of 1, pairs within the same family were scored 2, pairs in the same order were scored 3, and pairs within the same class (Aves) were given a 4 (Warwick and Clark 1995). Although non-avian proxy species were modeled by the Designing Sustainable Landscapes project, we did not test those as proxy species. We compared taxonomic similarity rankings to predictive accuracy, specificity, and sensitivity using Spearman’s rank correlation ( $\rho$ ; Sokal and Rohlf 1995).

To denote ecological dissimilarity, we generated a trait matrix including each of the proxy and represented species, and calculated Gower’s distance, a measure of ecological dissimilarity in trait space commonly used in functional diversity assessments (Mouchet et al. 2008). We used 26 functional traits to define ecological relationships used in bird functional diversity studies (Petchy and Gaston 2006; Petchy et al. 2007; Meynard et al. 2011). We used four continuous variables: body mass, clutch size, life span, aerodynamic index (body length/wing span), and 22 binary variables: carnivory, insectivory, herbivory, foraging method (aerial pursuit, gleaning, ambush, grazing, digging, scavenging, probing), foraging

substrate (water, mud or sand, ground, vegetation, air), nest location (canopy, mid-story, understory or ground, cavity), migratory habitat, permanent residence, and diurnal activity. We populated the trait matrix with data from the literature as compiled by Birds of North America Online (Rodewald 2016).

We calculated pairwise ecological distance between proxy and represented species and compared this with accuracy, specificity, and sensitivity, again using Spearman’s rank correlation. In the instances when multiple proxies were used to predict a single represented species, we calculated the total dissimilarity measure,  $d_{rt}$  by using reciprocal addition whereby:

$$\frac{1}{d_{rt}} = \frac{1}{d_{r1}} + \frac{1}{d_{r2}} \dots \frac{1}{d_{rn}}$$

for represented species  $r$  with proxy species  $t$ , and the  $d_{r1}, d_{r2}, \dots, d_{rn}$  being the pairwise dissimilarities between represented species  $r$  and each proxy (1 through  $n$ ). It was logical to use this formula to calculate total dissimilarity for three reasons: the total dissimilarity using one proxy is simply equal to the pairwise dissimilarity between the proxy and the represented species, adding proxies decreases the total dissimilarity, and the magnitude decrease in total dissimilarity when adding a proxy is inversely related to the pairwise dissimilarity of the added proxy-represented species pair.

(4) Compare ability to predict occurrence of represented species when using up to three proxy species’ models in combination

We used three nonlinear and two linear ways of combining LC models for multiple proxy species at each point. We tested all combinations of proxies (either two or three proxies) assigned to each represented species. We used each of these combinations as a new predictive measure of represented species’ occurrences, and we tested the relative performance among them using Kruskal–Wallace tests initially, and Dunn’s test for post-hoc comparisons (Sokal and Rohlf 1995). The three nonlinear combinations were: (1) the minimum value of the LC values for all proxy species at a point count location, (2) the maximum, and (3) the harmonic mean of those values. The two linear combinations were a weighted mean and an unweighted mean of the LC values at each point. We

used the maximum likelihood estimates of LC model parameter coefficients from logistic regression across all points (not using bootstrapping samples) to select model weights for each proxy-represented species pair.

(5) Compare proxy species' models ability to predict represented species to that of using remotely-sensed macrohabitat data

Proxy species were originally assigned to represented species based on similarities in macrohabitat use. We tested substituting the respective macrohabitat that each proxy species was supposed to represent for the proxy model, and used this as a predictor of represented species occurrence. We conducted the same bootstrapping procedure as in objectives (1) and (2), instead substituting the habitat classifications for the empirical co-occurrence or prediction from LC models. Habitat classifications were majority habitat type within 100 m of survey locations and were derived from Northeastern Terrestrial Habitat Classification (Gawler 2008). We compared the LC model predictions with the habitat predictions with Mann–Whitney U tests (Sokal and Rohlf 1995).

(6) Compare the LC model predictions for represented species with the relative overlap in species' ranges between the proxy and represented species

Proxy and represented species infrequently have exactly the same areal distribution within each subregion, resulting in a potential source of incomplete surrogacy. We compared predictive precision and accuracy for proxy species' models within each of the three subregions with the proportion of range overlap with the represented species as a function of the combined range of both the proxy and the represented species. We used generalized least squares to additionally account for expected heterogeneous variance in the relationship between range overlap and precision or accuracy. We used a quadratic relationship between range overlap and variance in fitted model residuals. Validation points are not guaranteed to be homogeneously dispersed within subregions. In practice, we used the number of validation points within the area of range overlap relative to the total number points in the combined range of both proxy and

represented species rather than the proportion of range overlap. However, both of these metrics were strongly correlated with the same comparison using range area ( $\rho = 0.86$ ,  $t = 11.206$ ,  $df = 43$ ,  $P < 0.001$ ). Range maps were provided as GIS files by Birdlife International and Handbook of Birds of the World (2016).

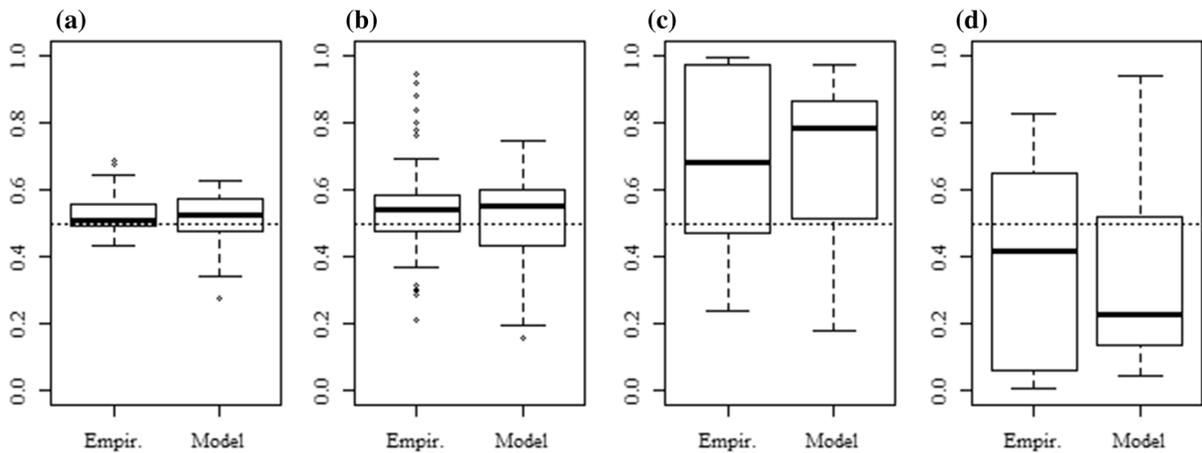
## Results

Objective (1) Test proxy species' LC models ability to explain observed occurrence of associated represented species

Variance among predictive metrics (accuracy or precision) decreased consistently across all model predictions as number of validation points used in model evaluations increased, with variance stabilizing at an upper threshold of 403 sample points within any subregion. Thus, we used 201 point detections and 201 non-detections as the minimum sample size to adequately test a proxy model-represented species pair. In 12 of 45 pairs (26.7%) tested, proxy species' models provided useful predictive information ( $\geq 60\%$  predictive) about surrogates (Table 1). In the remaining 33 pairs, proxy species' models were not useful. In 12 of these 33 remaining pairs, surrogate models were worse than random with  $< 50\%$  accuracy (Table 1).

(2) Characterize observed co-occurrence of proxy species with represented species using empirical data

Using empirical observations of proxy species as a predictor of represented species did not improve or reduce quality of predictions in paired tests with respective model predictions for the same species-pairs (Fig. 4) when evaluated using accuracy (empirical =  $0.512 \pm 0.012$  [ $\bar{x} \pm se$ ], model =  $0.530 \pm 0.009$ ;  $V = 379$ ,  $P = 0.262$ ), precision (empirical =  $0.510 \pm 0.021$ , model =  $0.547 \pm 0.026$ ;  $V = 340$ ,  $P = 0.110$ ), specificity (empirical =  $0.681 \pm 0.037$ , model =  $0.674 \pm 0.042$ ;  $V = 430$ ,  $P = 0.611$ ), and sensitivity (empirical =  $0.342 \pm 0.041$ , model =  $0.384 \pm 0.045$ ;  $V = 443$ ,  $P = 0.920$ ).



**Fig. 4** Comparison of predictive efficacy of using empirical occurrence data (Empir.) compared to landscape capability models (Model) of bird proxies to predict represented species in the northeastern United States using **a** accuracy, **b** precision,

**c** specificity and **d** sensitivity. Median indicated as dark bar, with upper and lower quartiles, minimum and maximum values as whiskers excluding outliers (as points)

(3) Evaluate and compare predictions of represented species' occurrences by proxy species' models based on ecological and taxonomic rank dissimilarity between proxy and represented species

There was no relationship between either accuracy or precision and predictive ability, or with ecological dissimilarity between proxy and represented species (accuracy =  $-0.001 \pm 0.011$ – $0.002 \pm 0.010$  [standardized  $\beta \pm se$ ],  $t = 0.155$  to  $-0.047$ ,  $P = 0.877$ – $0.963$ ; precision =  $0.007 \pm 0.017$ – $0.014 \pm 0.020$ ,  $t = 0.401$ – $0.706$   $P = 0.484$ – $0.691$ ). Similarly, there were no relationships between predictive ability and taxonomic distance between proxy and represented species (accuracy =  $-0.011 \pm 0.012$ – $0.000 \pm 0.010$  [standardized  $\beta \pm se$ ],  $t = 0.049$  to  $-0.892$ ,  $P = 0.377$ – $0.962$ ; precision =  $-0.008 \pm 0.019$ – $0.010 \pm 0.020$ ,  $t = 0.035$ – $0.506$ ,  $P = 0.615$ – $0.972$ ). Further, using proxies in aggregate did not change the qualitative pattern of no relationship between either dissimilarity or taxonomic distance and accuracy (ecological dissimilarity =  $0.005 \pm 0.013$ ,  $df = 31.6$ ,  $t = 0.423$ ,  $P = 0.675$ ; taxonomic distance =  $0.001 \pm 0.009$ ,  $df = 36.1$ ,  $t = 0.078$ ,  $P = 0.939$ ) or precision (ecological dissimilarity =  $0.010 \pm 0.019$ ,  $df = 22.76$ ,  $t = 0.523$ ,  $P = 0.606$ ; taxonomic distance =  $0.001 \pm 0.014$ ,  $df = 37.98$ ,  $t = 0.068$ ,  $P = 0.946$ ).

(4) Compare ability to predict occurrence of represented species when using up to three proxy species' models in combination

Hooded Warbler (*Setophaga citrina*) represented by Louisiana Waterthrush (*Parkesia motacilla*) and Ovenbird (*Seiurus aurocapilla*) in Southern New England had accuracy of 62.7% (precision 59.5%) and Black-throated Blue Warbler (*Setophaga caerulescens*) represented by Blackburnian Warbler (*Setophaga fusca*) and Wood Thrush (*Hylocichla mustelina*) had accuracy of 62% (precision 62.9%). These two represented species were the only species for which occurrence was not predicted by single proxy-species LC models, but met our usefulness threshold of > 60% accuracy when proxy species' models were combined rather than used alone. We found the best method for improving predictions when using multiple proxy species was to select the maximum LC value from each of the proxies at each point (accuracy:  $F = 6.52$ ,  $P < 0.001$ ; precision:  $F = 3.75$ ,  $P = 0.003$ ) rather than the other four metrics we calculated from combinations of the LC values.

(5) Compare proxy species models' ability to predict represented species to that of using remote-sensed macrohabitat data

Using the best LC model predicted represented species' occurrences better than using macrohabitat

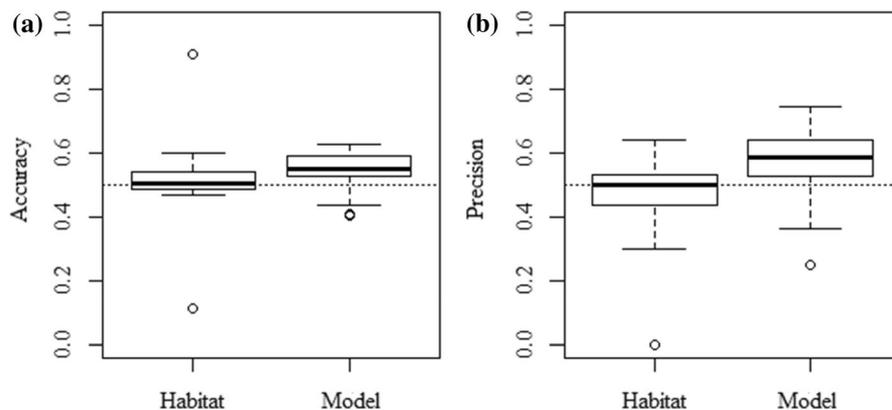
alone (Fig. 5), and increased both mean accuracy (model =  $0.544 \pm 0.013$  [ $\bar{x} \pm se$ ], habitat =  $0.512 \pm 0.022$ ;  $W = 452$ ,  $P = 0.015$ ), and precision (model =  $0.569 \pm 0.024$ , habitat =  $0.445 \pm 0.034$ ;  $W = 487$ ,  $P = 0.002$ ).

(6) Compare the LC model predictions for represented species with the relative overlap in species' ranges between the proxy and represented species

Comparisons of predictive measures as a proportion of range overlap expressed as proportion of validation points within the ranges of both proxy and represented species showed a quadratic relationship (Fig. 6). Pairs with low range overlap had low predictive accuracy and precision. Pairs with intermediate range overlap, however, had increased accuracy and precision. Pairs with almost complete overlap had increased accuracy and precision compared with pairs with low overlap. Pairs with nearly complete range overlap exhibited increased variance in accuracy and precision, however, and included some of the best and worst performing proxy-represented species pairs. A complete list of proxies and prediction statistics is available in the online supporting information (See Online Appendix S2).

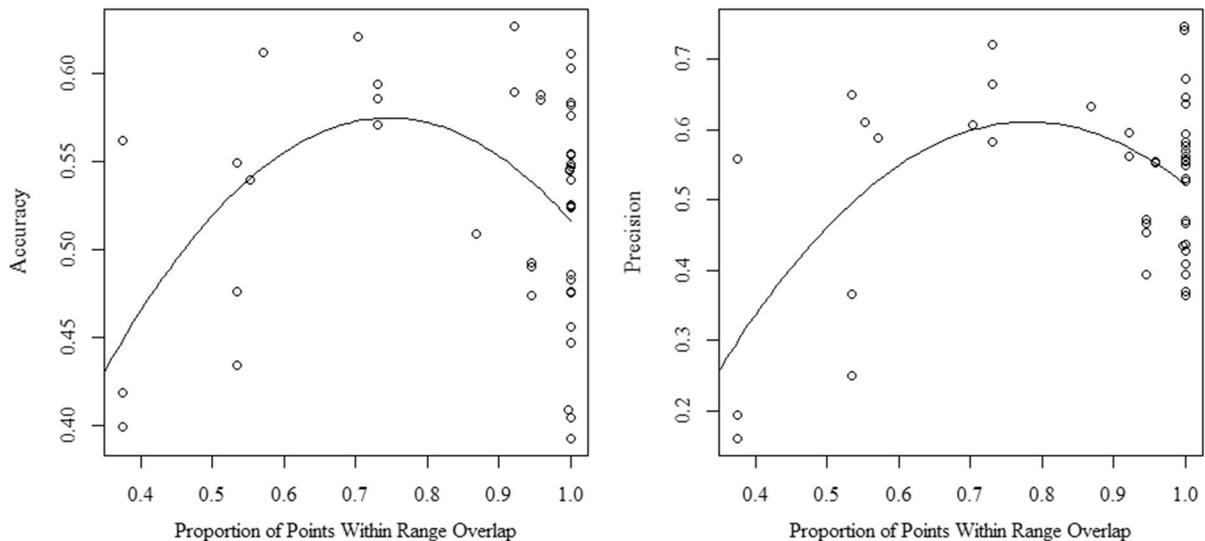
## Discussion

Models of a proxy species can provide the same predictive efficacy as using direct empirical data of occurrence for predicting represented species' occurrences, however, most proxy-represented species pairs did not provide useful prediction. This lends credence to the method employed by the NALCC that uses a set of proxy models to inform conservation planning for a broader list of represented species, but only with the caveat that proxies should be validated to filter out unsuitable proxy-represented species pairs. Not only did LC models perform similarly to empirical data of the proxy species from our validation set when predicting represented species, the best LC models for proxy species outperformed predicting occurrence or absence for represented species based on macrohabitat classifications alone. The idea that a macrohabitat model could substitute for the proxy species, rendering the proxy an extraneous intermediary, was not supported. Likely similarities in area sensitivity, sensitivity to fragmentation and inclusion in LC models of remote sensed information other than land cover, allows proxy models to predict better (when well-selected) than macrohabitat models, which may exclude important information such as habitat connectivity, fragmentation, indirect effects of land cover conversion and patch sizes (Noss 1983; van Dorp and Opdam 1987; Beier and Noss 1998; McGarigal and McComb 1999).



**Fig. 5** Comparison of predictive ability of using macrohabitat from remote sensed data (Habitat) compared to the best landscape capability model selected to represent the respective macrohabitat type (Model) to predict represented species'

occurrence in the northeastern United States, and evaluated using **a** accuracy, and **b** precision. Median indicated as dark bar, with upper and lower quartiles, minimum and maximum values as whiskers excluding outliers (as points)



**Fig. 6** Accuracy and precision of landscape capability based prediction of proxy species as a function of range overlap between proxy and represented species for birds listed as proxy (or representative) species in the northeastern United States

Although overall mean predictive performance was marginal owing to several poorly performing proxy-representative species pairs, that several pairs worked well suggests the overall strategy using proxies has meaningful potential for conservation planning for a broader suite of represented species. It should be considered that we tested the relationships at the finest scales possible given the survey methods (100 m survey radius) and that covariance in occurrence is scale-dependent with correlations that often are weaker at finer rather than broader scales (Weaver 1995; Prendergast and Eversham 1997). Predictive ability of even the best proxy LC model used to predict a represented species (67% accurate) typically was less than a LC model at predicting its own species' occurrence (i.e., not used as a proxy; range 62–90%; Loman et al. 2017a). Thus, while improving the proxy-represented species pair is likely useful, it is not surprising that development of a larger suite of proxy models and reducing the number of proxy-represented species pairs will provide more accurate and precise predictions. Developing models is a more costly and time-consuming process than selecting proxies, however, and using proxies allows management decisions to be made with fewer variables to consider. There is a tradeoff between proxy realism and model development to be considered on a case-by-case basis.

Selecting a species to act as a proxy for another is a process beset by potential pitfalls (Caro 2010). No

single proxy will completely characterize the ecological space required by a represented species (Carignan and Villard 2002). Nonetheless, research in European forests suggests, that when broken into broad habitat classifications, certain forest birds have potential as proxy species for a broader suite of other forest birds (Roberge and Angelstam 2006). In contrast to our results, where taxonomy had no relationship with prediction accuracy, those authors restricted the proxy-represented species pairs within a fairly circumscribed range of taxa (e.g., all within a single class, and most proxies within the same order). This ensured occurrence and habitat selection occurred on similar scales, and proxies and represented species had similar dispersal abilities and generation times (Sæther et al. 2005), thereby avoiding some common sources of incomplete surrogacy. Perhaps because of these similarities (in dispersal, generation time, etc.), birds selected as indicators can have high within-class correlation with avian diversity, and selecting indicators within high-level taxa is better supported than across these taxa (Sattler et al. 2014). This may be supported by our results that taxonomic distance had no influence on the proxies' ability to predict occurrence of represented species, as within-class taxonomic distinction is less important than across classes (Sattler et al. 2014). It also is perhaps unsurprising that ecological similarity did not correlate with predictive power of proxy species, as co-occurring species often

differ in their habitat requirements or life histories (Carignan and Villard 2002), a logical conclusion stemming from the role of the competitive exclusion principle in structuring biotic communities (Hardin 1960). Even despite similarities in resource use, within-guild responses of forest birds to ecological conditions or disturbances are also by no means necessarily consistent (Mannan et al. 1984; Block et al. 1987).

The use of joint proxies has rarely been tested in practice, although simulations justify potential usefulness of this method (De Cáceres et al. 2012). Our analyses provide an example where multiple proxy models can predict occurrence more accurately than either model singly. In other instances, when the goal is to evaluate avian responses to anthropogenic habitat disturbance, multiple proxy species have been shown to increase capability of cross-taxa prediction, and will likely be a method pursued in future practice (Bachand et al. 2014). Each species used as an indicator represents only the subset of the ecological conditions that mediate its habitat selection or space use, and therefore, using multiple indicators would logically broaden the breadth of those conditions potentially providing a better indicator (Carignan and Villard 2002).

The range overlap comparisons showed what is often stated in guidelines for selecting proxies: that proxies and their represented species have considerable range overlap, and in the absence of these conditions, proxies will universally fail. Range overlap is an insufficient criterion for selecting proxy species even when species are paired based on similar macrohabitat use. When range overlap is extensive we observed an increase in the variance in both the precision and accuracy of the proxies' predictive ability (Fig. 6). It seems likely that dissimilarity in fine-scale resource use is what allows many of these species to co-occur over such a large proportion of each subregion, and means that fine-scale prediction has no guarantee of success owing to these local differences in habitat or resource available that determine presence or absence.

Summarizing the questions we sought to answer at the onset (Fig. 3), we found that proxies can be used for forest birds to represent co-occurrence of species with similar macrohabitat requirements. Using proxy species' landscape capability models provided statistically improved prediction over using macrohabitat

data from remote sensed spatial models alone. Using models of landscape capability for the proxy species provided similar results to using empirical observations of those same proxies as predictors of represented species' occurrence. However, similarity in macrohabitat alone was an insufficient prerequisite for predictive accuracy or precision, as was degree of range overlap, similarity, or dissimilarity, in taxonomy or ecology between the proxy and the represented species. Although proxies were useful in some cases, in most (73%) they were not. Therefore, creating reliable proxies based on perception of similarity in co-occurrence requires validation with independent data. In some instances, using multiple proxies to represent a single represented species is advantageous in comparison to using a single proxy. A tradeoff exists between the practicality of using proxy species for making management decisions and the costlier, more complicated and yet more realistic approach of using species-specific models for each species of interest.

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**Data Accessibility** A list of data sources is provided in Online Appendix 1.

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