PATCH AREA CANNOT PREDICT SPECIES RICHNESS OF GRASSLAND BIRDS IN COLORADO'S FRONT RANGE

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ABSTRACT: Birds breeding in grassland have declined steeply over the last 50 years, and green-space systems in Colorado's urbanizing Front Range have not maintained all grassland bird species the area originally supported. Patch area affects the species richness of urban green spaces, and researchers have suggested that protecting or enlarging green spaces should be effective ways to maximize richness and mitigate species loss. In the Front Range, protection of urban green space is expensive, conservation budgets are limited, and tools are needed to guide strategic protection decisions. Front Range planners use patch area as a criterion to prioritize grassland conservation, but the explanatory and predictive powers of patch area have not been comprehensively assessed. Using eBird community science data, I found that log-transformed grassland patch area was positively associated with the species richness of grassland birds and explained a large portion of its variance. However, 95% simultaneous prediction intervals for species richness were wide, and those of the smallest and largest patches examined overlapped. Thus the model cannot precisely predict a number of species, and it should not be used to quantitatively evaluate the expected return on investment from financial allocations to protect or enlarge grassland patches. Nonetheless, the model's explanatory power supports the use of grassland patch area as a general principle guiding conservation of grassland birds. Planners should consider it among a suite of other habitat characteristics and prioritize large, regularly shaped grassland patches situated close to other grassland patches and with limited nearby forest cover and urban development.

As human populations grow and economic development proceeds, urban areas will continue to expand. In one global assessment, Zhou et al. (2019) projected that by 2050 urban cover will exceed 1.68 million km^2, a 40% increase over 2012. Urbanization affects ecosystem composition (e.g., Chace and Walsh 2006, McKinney 2008), structure (e.g., Hahs and McDonnell 2006), and function (e.g., Paul and Meyer 2001), and these effects extend beyond a city's physical boundaries to include a larger regional "footprint" required for resource extraction and waste absorption (Leu et al. 2008, Newman 2006). One ecosystem change associated with increasing urbanization is a reduction in the number of bird species as species that nest on the ground or in the interior of habitat blocks are lost and synanthropic species, be they native or exotic, increase (Chace and Walsh 2006, Marzluff 2001). Urbanization drives changes in bird populations and communities through habitat loss and fragmentation, reduced connectivity, altered vegetation composition and structure, resource competition with invasive species, predation and nest parasitism, human disturbance, and other mechanisms (Marzluff 2001, Marzluff and Ewing 2001). The loss of urban biodiversity reduces human well-being, opportunities for research and education, local biodiversity, and other ecosystem services (Dearborn and Kark 2010). As a result, many cities plan to conserve urban biodiversity (Nilon et al. 2017).

For urban green spaces, area is a primary determinant of bird species

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richness, and researchers have suggested that protecting large green spaces or enlarging already protected spaces should be effective ways to maximize richness or mitigate species loss (e.g., Callaghan et al. 2018, La Sorte et al. 2020). Protecting and enlarging existing green spaces may be particularly important where habitats extend beyond a green space's administrative boundaries, remaining vulnerable to conversion. In urban areas, conservation of green space is challenged by the high cost of land acquisition (Nolte 2020) and limited budgets. Thus resources must be allocated strategically, with the benefits of anticipated species conservation weighed against economic costs. For example, Wilson et al. (2007) modeled the relationship between species richness and area to assess the marginal benefit of conservation measures, including land acquisition, and to strategically allocate investments based on modeled marginal benefits. Such a strategic approach requires models that can reliably predict species richness from area. Existing statistical guidance addresses the evaluation of the explanatory and predictive performance of such models (Boecklen and Gotelli 1984, Power 1993), but, to my knowledge, previous researchers have not applied the full suite of evaluative statistical techniques to the models developed for conservation of urban green space.

Across North America, grassland birds have declined by 53% since the 1970s, the greatest avian decline in any biome (Rosenberg et al. 2019). Within Colorado, between 1966 and 2019, five grassland bird species declined (Sauer et al. 2020). Most of Colorado's Front Range urban corridor, the state's most populous region and commonly referred to as simply the Front Range, lies within the Shortgrass Prairie Bird Conservation Region (U.S. NABCI Committee 2000). A historical analysis revealed that the Front Range's existing green spaces may not sustain all species of shortgrass prairie birds (Jones and Bock 2002). A regional conservation assessment plans to use patch area as a factor to prioritize grasslands and other terrestrial habitats for protection, enhancement, and restoration (C. Hawkins, The Nature Conservancy, Denver, pers. comm.). To support conservation planning in the Front Range, I tested a model relating the species richness of grassland birds to the area of grassland patches, ignoring administrative boundaries of established green spaces. A model demonstrating a significant positive relationship would support protecting large urban green spaces or enlarging existing green spaces beyond current administrative boundaries to encompass the entirety of patches of natural grassland. I further evaluated the model's predictive ability to determine whether it could be used to assess the marginal benefit of actions toward grassland conservation.

METHODS

Study Area

The boundaries of my study area represent the intersection of the Front Range and the Shortgrass Prairie Bird Conservation Region (Figure 1). I defined the Front Range as the Denver–Aurora and Pueblo–Cañon City combined statistical areas plus the adjacent Fort Collins and Colorado Springs metropolitan statistical areas. Combined statistical areas are regions based on social (e.g., weekend recreation) and economic (e.g., commodity distribution) interactions between areas (census.gov). This region contains

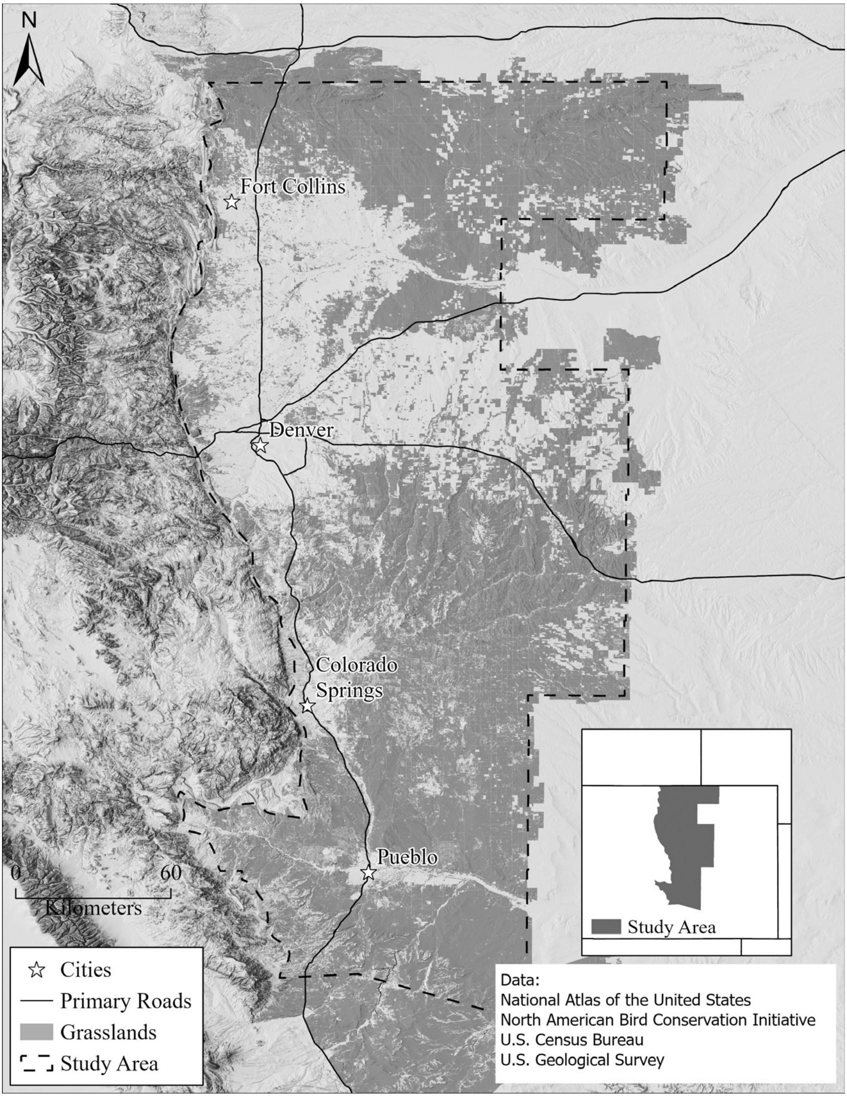

FIGURE 1. Colorado's Front Range (study area) and overlapping grassland patches. The study area represents the intersection between U.S. Census Bureau statistical areas (Colorado Springs, Denver–Aurora, Fort Collins, and Pueblo–Cañon City; census.gov) and the Shortgrass Prairie Bird Conservation Region (U.S. NABCI Committee 2000).

5.0 of Colorado's 5.8 million people (86%) (https://www2.census.gov/programs-surveys/decennial/2020/data/, accessed 19 November 2021). Bird Conservation Regions are defined by their bird communities, habitats, and challenges in natural-resource management. Falling in the Rocky Mountains' rain shadow, the Shortgrass Prairie Bird Conservation Region is characterized by vegetation of limited height and diversity and supports some of North America's birds in greatest need of conservation, such as the Mountain Plover (*Charadrius montanus*) and Burrowing Owl (*Athene cunicularia*; U.S. NABCI Committee 2000). For breeding grassland birds, one potential stressor is a shift from a grazing regime characterized by bison and prairie dogs to one characterized by cattle (U.S. NABCI Committee 2000).

Species Richness and Grassland Patch Area

From the 13 Colorado counties—Adams, Arapahoe, Boulder, Broomfield, Denver, Douglas, El Paso, Elbert, Fremont, Jefferson, Larimer, Pueblo, and Weld—overlapping the study area, I selected complete checklists submitted to https://ebird.org by either stationary or traveling observers from 2003 to 2019. Since 2002, eBird participants have reported bird occurrence and abundance through checklists, and for Colorado, as of 3 December 2021, observers had entered 1.3 million complete checklists. I filtered and retained checklists that included bird species for which the North American Bird Conservation Initiative (2016) listed grassland as a major breeding or nonbreeding habitat. I further refined the species list by retaining species only if they were included in a recent breeding bird atlas of Colorado (Colorado Bird Atlas Partnership 2016) or their nonbreeding range overlapped Colorado (Billerman et al. 2022). I processed and filtered eBird data with the R package "auk," version 0.6.0 (Strimas-Mackey et al. 2018). The grassland bird species recorded are listed in Table 1.

I selected pixels identified as grassland (class value 71) in the National Land Cover Database 2011 (Homer et al. 2015), grouping them to define a patch if they shared an edge or corner. I chose to define patches by this criterion rather than the administrative boundaries of urban green spaces because I viewed the extent of actual grassland to be more ecologically meaningful. Furthermore, as administratively defined green spaces do not encompass all remaining grasslands, a relationship between grassland patch area and bird species richness would suggest a conservation benefit to protecting large green spaces or expanding green spaces. I overlaid grassland within the study area on the map from the Protected Areas Database of the United States, version 3.0 (https://www.usgs.gov/gapanalysis/PAD-US/, accessed 12 November 2022), to determine the percentage lying in unprotected areas or in areas lacking mandates, deed restrictions, or easements that should prevent the conversion of natural habitat types. I used ArcGIS Pro version 2.8 (ESRI, Redlands, CA) and QGIS version 3.28.0 (QGIA Assoc., 2022; QGIS.org) for this process.

I totaled the number of grassland bird species reported on complete checklists for eBird hotspots located within grassland patches. Hotspots are user-nominated public birding locations that observers can select when locating and uploading their data. Hotspots are not defined through a sampling design relating bird communities to grassland patch size, so eBird checklists do not currently cover all sizes of grassland patches within the study area. Thus conclusions should be limited to those patch sizes currently represented in eBird (see Results and Discussion). The number of hotspots in a grassland patch ranged from 1 to 7 (median: 1); in quantifying species richness, I

Table 1 Grassland Bird Species Reported on eBird Checklists from Front Range Hotspots between 2003 and 2019

Scientific Name	Common Name
Colinus virginianus	Northern Bobwhite
Callipepla squamata	Scaled Quail
Tympanuchus phasianellus	Sharp-tailed Grouse
Tympanuchus cupido	Greater Prairie-Chicken
Charadrius montanus	Mountain Plover
Bartramia longicauda	Upland Sandpiper
Numenius americanus	Long-billed Curlew
Circus hudsonius	Northern Harrier
Buteo swainsoni	Swainson's Hawk
Buteo lagopus	Rough-legged Hawk
Buteo regalis	Ferruginous Hawk
Athene cunicularia	Burrowing Owl
Asio flammeus	Short-eared Owl
Falco mexicanus	Prairie Falcon
Tyrannus verticalis	Western Kingbird
Tyrannus tyrannus	Eastern Kingbird
Tyrannus forficatus	Scissor-tailed Flycatcher
Lanius ludovicianus	Loggerhead Shrike
Corvus cryptoleucus	Chihuahuan Raven
Eremophila alpestris	Horned Lark
Sialia currucoides	Mountain Bluebird
Anthus rubescens	American Pipit
Calcarius lapponicus	Lapland Longspur
Calcarius ornatus	Chestnut-collared Longspur
Rhynchophanes mccownii	Thick-billed Longspur
Peucaea cassinii	Cassin's Sparrow
Ammodramus savannarum	Grasshopper Sparrow
Chondestes grammacus	Lark Sparrow
Calamospiza melanocorys	Lark Bunting
Zonotrichia querula	Harris's Sparrow
Pooecetes gramineus	Vesper Sparrow
Passerculus sandwichensis	Savannah Sparrow
Dolichonyx oryzivorus	Bobolink
Sturnella neglecta	Western Meadowlark
Sturnella magna	Eastern Meadowlark
Spiza americana	Dickcissel

pooled checklists from all hotspots within a patch. To control for variation in observation effort, I excluded checklists representing observations of <5 min or >240 min, and to decrease the likelihood of spatial mismatches between checklists and patches, I used a checklist only if the distance the observer traveled was less than the perimeter of the grassland patch (Callaghan et al. 2018). As the number of checklists available for the various patches differed, unstandardized richness values—values that did not account for different sample sizes—were unsuitable for comparing the patches' bird communities.

Following steps taken to model species richness for New York City green spaces on the basis of eBird data (La Sorte et al. 2020), I estimated the completeness of survey of each patch and extrapolated its asymptotic species richness with the R package KnowBR, version 2.1 (Lobo et al. 2018). Completeness of survey refers to the percentage of extrapolated asymptotic richness represented by observed species richness. Completeness of survey and extrapolated species richness were based on a smoothed species-accumulation curve in which the accumulated number of species reported in a grassland patch was plotted versus the number of eBird records. The eBird records for a patch encompassed all observations of grassland bird species, including observations of the same species across different checklists. I used the curve fitted by means of the exact estimator of Ugland et al. (2003) and adjusted to the rational function. Following Lobo et al. (2018), I defined a poorly sampled patch as one where (1) the final slope of the species accumulation curve is >0.3, (2) the ratio of number of eBird checklists to number of observed species is <3, and (3) completeness of survey is <50%. I excluded all poorly sampled patches and retained all other patches, using their extrapolated species richness to model its relationship to the area of grassland patches. The extrapolated richness values correspond to the probable number of species when the number of eBird checklists for the patch tends to infinity, thus accounting for the unequal number of checklists across patches.

Statistical Analysis

I randomly split the data into two sets, one for model estimation (based on two-thirds of the patches) and one for prediction (one-third). To make the relationship between extrapolated species richness of grassland birds and extent of grassland patches (ha) linear, I $\log_{10}$-transformed the latter.

Before models relating species richness and patch size serve as a basis for conservation policies, Boecklen and Gotelli (1984) urged they be evaluated statistically. If a model is fit by means of linear regression, researchers should assess (1) the adjusted value of r^2, (2) the influence of patches on estimates of the model's parameter, and (3) the precision of estimated richness (Boecklen and Gotelli 1984). If area is the primary factor guiding conservation, the adjusted r^2 value should be ≥0.70, whereas if area is only a secondary factor, lower values may be acceptable (Boecklen and Gotelli 1984). I calculated Cook's distance values for individual patches to evaluate their influence on the regression slope. To evaluate precision, following Boecklen and Gottelli (1984), I calculated 95% simultaneous prediction intervals. Conservation planners should not base specific conservation recommendations on a model relating species richness and patch size if prediction intervals span orders of magnitude (Boecklen and Gottelli 1984).

Power (1993) detailed an approach to assessing an ecological model's ability to predict new observations that were not used as the basis for estimating the model's parameters. The framework outlined by Power (1993) examines prediction errors to look for evidence of (1) systematic bias, (2) inaccuracies, (3) non-normality, and (4) autocorrelation. Using the model developed in this study, I predicted the species richness of each grassland patch in the prediction data set, and I calculated the prediction error as the difference between richness predicted by the model and richness extrapolated as described in the last paragraph of the preceding section. I evaluated the presence of systematic bias in prediction errors by calculating a standardized bias variable (B) according to equation 3 of Power (1993). To gauge prediction accuracy, I calculated the sum of squared errors of prediction (Q_e) by equation 4 of Power (1993). I determined whether prediction errors were normally distributed through a Shapiro–Wilks test. I used the R package "ape," version 5.6-2 (Paradis and Schliep 2019), to conduct a Moran's *I* test for spatial autocorrelation of prediction errors.

For all statistical analyses I used R, version 4.2.2 (R Core Team 2022) and set $\alpha = 0.05$.

RESULTS

From 2003 to 2019, 15,664 complete eBird checklists were submitted from 39 grassland patches in my study area (model estimation: 26 patches; model prediction: 13). The median area of these patches was 199.0 ha; the range was 1.1–125,064.2 ha. The median of extrapolated species richness of grassland birds was 16.8, the range 2.4–32.5. The extrapolated species richness of grassland birds was positively related to the $\log_{10}$ of patch area with an adjusted r^2 value of 0.26 (Figure 2). No observations in the estimation data set individually influenced the regression slope ($F_{1,26} \leq 0.30$, $p \geq 0.59$). In the estimation data set, however, the 95% simultaneous prediction intervals for species richness of even the smallest and largest patches overlapped (Figure 2). Predictions of the species richness of grassland birds were not systematically biased ($B = 0.37$, $p = 0.72$), and there was no evidence of predictive

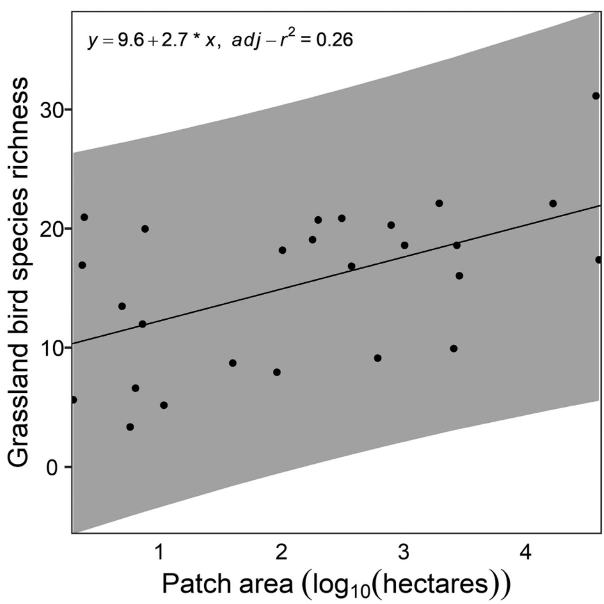

Figure 2. General linear model relating species richness of grassland birds to $\log_{10}$-transformed area of grassland patch in Colorado's Front Range.

inadequacy ($Q_e = 0.57$, $p = 0.85$). Prediction errors were normally distributed ($W = 0.93$, $p = 0.38$) and spatially independent (Moran's $I = -0.03$, $p = 0.69$).

By area, 81.1% of grassland within the study area had no protection from conversion of natural habitat types.

DISCUSSION

For the Front Range, species richness of grassland birds in patches of grassland was positively correlated with the patches' log-transformed area, and four-fifths of the grassland within the study area was unprotected from conversion of natural habitat. Consequently, conservation planners should protect or enlarge existing Front Range green spaces to encompass grassland patches and conserve their bird communities. Limited resources are available for conservation, and predictions of the marginal benefits associated with protection or restoration of grassland could increase the efficiency of conservation. However, the predictive performance of the model relating species richness and patch area fell short of published recommendations, so the model should not be used to make specific predictions about the number of species that would be retained or gained as a result of specific actions toward grassland conservation. Despite its predictive limitations, the model explained a large amount of the variance in species richness, and patch area can be used alongside other characteristics of the patch and landscape to identify areas for conservation of grassland birds in the Front Range.

Beyond patch area, conserving and maintaining the abundance and diversity of grassland birds with specific habitat requirements will require consideration of grassland configuration, grassland edges, matrix habitat, vegetation composition and structure, and food resources. Within my study area, relationships of grassland birds to their habitat in suburban Boulder have been studied by Bock et al. (1999), Haire et al. (2000), and Jones and Bock (2002). In this area, those grassland birds associated with mixed and tallgrass prairies persist better than do those associated with shortgrass prairie (Jones and Block 2002). Their abundance increases with the extent of their preferred grassland type (Haire et al. 2000). During nesting, their abundance decreases near the patches' edges with suburban development (Bock et al. 1999). In eastern Wyoming, just north of my study area, the number of species of grassland birds along Breeding Bird Survey routes increased with an increasing proportion of herbaceous grassland and increasing species richness of grasshoppers (a food resource) and decreased with increasing distance between grassland patches, increasing density of edges between grassland and non-grassland covers, and the proportion of forests and wooded wetlands (Hamer et al. 2006). Species richness is an aggregate variable reflecting the presence and responses of multiple bird species, and the competing habitat needs of different species must be balanced. For example, breeding Mountain Plovers use heavily grazed sites, whereas breeding Lark Buntings are found in denser vegetation (Vickery et al. 2000). Through spatial analyses, Front Range planners should identify large, regularly shaped grassland patches situated close to other grassland patches and with limited nearby forest cover and urban development. Once patches are identified, additional field-based studies can be used to evaluate vegetation structure and composition, food resources, and other features not readily derived from available land-cover databases.

While patch area alone should not guide grassland conservation planning in the Front Range, my model did explain 26% of the variance (adj-r^2) in species richness of grassland birds. This is a large amount of variance explained given that a single, main factor of interest in ecological and evolutionary meta-analyses explains an average of 2.51–5.42% of the variance (r^2; Møller and Jennions 2002). Patch area affects species richness via three non-exclusive mechanisms: passive sampling, disproportionate response, and heterogeneity (Chase et al. 2019, Connor and McCoy 1979, Helzer and Jelinski 1999). Passive sampling refers to large patches containing a larger sample of individuals and hence greater species richness than small patches. Disproportionate response results from species responding differently to different sizes of patches because of factors such as Allee effects, demographic stochasticity, and edge effects. Limitations to dispersal or habitat heterogeneity can aggregate individuals of the same species to a greater degree in large patches than small ones, leading to a more heterogeneous species composition and greater species richness. Methods are available to assess the relative contributions of these three mechanisms by which species richness depends on patch size (Chase et al. 2019), and these assessments can guide grassland protection and management. For example, if reduced habitat heterogeneity is a strong driver of the effect, management could focus on increasing the structural and compositional diversity of the vegetation in small grassland patches.

Community science data, such as those from eBird, are invaluable because of the extensive geographic and longitudinal coverage of the data, and these data characteristics enable applied analyses to address conservation and management issues at local, regional, and global scales (Sullivan et al. 2017). Meaningful use of these data in applied analyses requires addressing potential errors and bias, including spatial bias in the observations' locations (Johnston et al. 2021). In my study, eBird hotspots evinced spatial bias, as the distribution of sizes of grassland patches they represented (median 199.0 ha; range 1.1–125,064.2 ha) differed from the distribution of all grassland patches intersecting the study area (median 0.6 ha; range 0.1–289,785.5 ha). Thus my conclusions should be applied only to grassland patches falling within the range of patch sizes modeled. Efforts such as the National Audubon Society's Western Rivers Bird Count (www.audubon.org/western-rivers-bird-count) have mobilized community scientists to address spatial gaps in eBird data. A similar effort could be organized to ensure that data on the Front Range's grassland birds represent the full range of sizes of patches of grassland.

Grasslands' bird communities and other biological and physical features can supply ecosystem services such as regulating water flow, storing carbon, mitigating climate change, and providing opportunities for recreation (Bengtsson et al. 2019, Mitchell et al. 2015). Grasslands also have the potential to provide disservices, including acting as a fuel source for wildfires that threaten human communities. In the urbanizing Front Range, the area and configuration of grassland can be expected to influence biodiversity and the balance of such ecological services and disservices (Mitchell et al. 2015). Biodiversity, services, and disservices may relate to patch area differently (e.g., Grafius et al. 2018), so planners must consider tradeoffs when designing landscapes. However, when the number of tradeoffs among biodiversity, services, and disservices becomes large, a decision can be too complex for the application of simple decision-making rules (Hammond et al. 1999). In this context, models, including the demonstrated empirical relationship between grassland birds and patch area, are important tools enabling urban planners to consider these tradeoffs and to make transparent and defensible decisions optimizing landscapes for human communities and natural ecosystems.

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