Ambio 2019, 48:280–292
https://doi.org/10.1007/s13280-018-1068-1

KUNGL. VETENSKAPS-AKADEMIEN
THE ROYAL SWEDISH ACADEMY OF SCIENCES

RESEARCH ARTICLE

Effects of bird community dynamics on the seasonal distribution of cultural ecosystem services

Rose A. Graves, Scott M. Pearson, Monica G. Turner

Received: 9 March 2018 / Revised: 24 May 2018 / Accepted: 31 May 2018 / Published online: 13 June 2018

Abstract Biodiversity-based cultural ecosystem services (CES), such as birdwatching, are strongly influenced by biotic community dynamics. However, CES models are largely static, relying on single estimates of species richness or land-use/land-cover proxies, and may be inadequate for landscape management of CES supply. Using bird survey data from the Appalachian Mountains (USA), we developed spatial–temporal models of five CES indicators (total bird species richness, and richness of migratory, infrequent, synanthrope, and resident species), reflecting variation in birdwatcher preferences. We analyzed seasonal shifts in birdwatching supply and how those shifts impacted public access to projected birdwatching hotspots. Landscape patterns of CES supply differed substantially among indicators, leading to opposing conclusions about locations of highest birdwatching supply. Total species richness hotspots seldom overlapped with hotspots of migratory or infrequent species. Public access to CES hotspots varied seasonally. Our study suggests that simple, static biodiversity metrics may overlook spatial dynamics important to CES users.

Keywords Avian diversity · Biodiversity · Birdwatching · Ecosystem services · Recreation · Species richness

INTRODUCTION

Sustaining ecosystem services has become a priority in landscape management and environmental policy worldwide (MA 2005). Cultural ecosystem services (CES; i.e., non-tangible benefits from nature) are among the least studied ecosystem services (ES) (Daniel et al. 2012; Hernández-Morcillo et al. 2013) and empirical and biophysical models of CES remain rare (Bagstad et al. 2016). CES, which include mental health benefits, recreational opportunities, and aesthetic enjoyment, can be challenging to quantify because an ecosystem's capacity to deliver CES depends both on biophysical characteristics of the ecosystem as well as the experience of the ES user or beneficiary (Satz et al. 2013).

Many CES depend on biodiversity (e.g., birdwatching, fall foliage, wildlife photography) and the supply of such CES relies on the presence, abundance, diversity, and/or functional traits of biotic communities (Lavorel et al. 2017a). Life history traits of the underlying biota, like phenology or animal behavior, affect CES supply and cause changes over time in landscape patterns of CES supply (Kremen 2005; Graves et al. 2017a). However, most CES studies rely on simple indicators, proxies, and static data sources to map CES supply, ignoring the underlying biotic community dynamics (Martínez-Harms and Balvanera 2012).

Birdwatching, a key biodiversity-based CES, has increased steadily in popularity, especially in the US where approximately one in five Americans participates in birdwatching (Carver 2013). Birdwatching has large economic impacts; in 2011, 47 million birders in the US spent $41 billion on birding-related expenditures (Carver 2013). Furthermore, bird diversity contributes to the amenity value in semi-rural landscapes (Fuller et al. 2012).

Bird communities vary even within a single season (Boulinier et al. 1998; Leveau and Leveau 2012; Zuckerberg et al. 2016), and such dynamics are likely to affect spatial patterns of birdwatching supply. Yet, birdwatching

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13280-018-1068-1) contains supplementary material, which is available to authorized users.

supply has typically been represented by static, coarse measurements of species richness, which accumulate all species possibly present in an area (Bateman et al. 2013; Villamagna et al. 2014; Dallimer et al. 2015). While these estimates demonstrate that bird-based CES have strong spatial trends, they ignore temporal dynamics in bird communities. Thus, static species richness may not represent the number and types of bird species likely to be observed during an average birdwatching visit (Cumming and Maciejewski 2017) and may not equate to actual CES supply.

Furthermore, how bird species richness relates to benefits received by birdwatchers is not well known (Belaire et al. 2015; Cumming and Maciejewski 2017) and may vary with birdwatcher motivation and expertise (Cox and Gaston 2015). While more casual birdwatchers may be motivated by observing "many types of birds" (Cordell and Herbert 2002), avid birders are more likely to plan birding trips around the likelihood of observing particular types species, such as migratory birds, and ascribe more importance to seeing rare birds or birds they have not seen before (McFarlane 1994; Hvenegaard 2002; Booth et al. 2011). By focusing solely on overall avian species richness, CES models may misrepresent the spatial distribution of bird CES and limit managers' ability to manage landscapes for multiple ES and multiple beneficiaries.

Managers need to know not only where CES are produced but also where CES can be accessed and where they are currently used (Burkhard et al. 2012; Villamagna et al. 2014). By comparing the spatial–temporal supply of CES with public access and use of CES, managers can identify opportunities for increasing the availability of CES (Villamagna et al. 2014), educate people about important CES in their own backyard (Cox and Gaston 2015), and incentivize management to maintain CES across the landscape.

In this study, we sampled bird communities across topographic and land-use gradients in the southern Appalachian Mountains and developed spatial–temporal models of five indicators of birdwatching supply (i.e., richness of all bird species, and richness of rare, migratory, synanthropic, and resident species). We asked (1) How do projected patterns of birdwatching supply vary among bird CES indicators and over space and time? (2) How do changing landscape patterns of birdwatching supply affect public access to birdwatching? (3) How well does birdwatching supply align with direct estimates of birdwatching (i.e., eBird locations)?

We hypothesized that bird community dynamics driven by migratory species' arrival and habitat specialization during the nesting season would generate distinct seasonal patterns of CES supply. Specifically, we expected the following:

- Species richness would increase in higher elevations during the late spring as both migratory and resident species moved into these areas.
- Migratory species richness would be greater in areas with low building density and higher forest cover; that pattern was expected to be strongest during late spring after nesting territory establishment.
- Spatial–temporal patterns of birdwatching supply would result in changing public access for birdwatching and birdwatching use would reflect those patterns.

MATERIALS AND METHODS

Study area

This study was conducted in the southern Appalachian Mountains (USA), an ecotourism destination with over \$1330 million in combined visitor expenditures in 2014 (Strom and Kerstein 2015). The region's landscape heterogeneity and long evolutionary history have led to high diversity of flora and fauna (Whittaker 1956). Regional avian species richness (i.e., gamma diversity) is estimated as high as 141 species (Mckerrow et al. 2006) and bird communities within the study area are diverse and influenced by topography, climate, and land-use patterns (Haney et al. 2001; Lumpkin and Pearson 2013).

We sampled bird communities in the French Broad River Basin (FBRB), a 7330 km^2 watershed ranging from 300- to 2100-m elevation in western North Carolina (Fig. 1). The FBRB is dominated by secondary forest (75%), including spruce-fir and northern hardwood forests at high elevation and mixed-deciduous forests at lower elevations (Whittaker 1956). Agricultural use, mostly meadow and pasture, comprises 12% of the landscape. The remainder is composed of urban areas (12%), and shrubland, water, or barren land (all $<$ 1%) (Homer et al. 2012). Between 1976 and 2006, population increased 48% leading to widespread exurban, low-density housing development (Gragson and Bolstad 2006).

Bird CES supply

Data collection

Bird communities were surveyed at 69 sites located on public and private property. Sites were stratified by elevation and development intensity (e.g., building density). The same sites were used to collect wildflower community data for a concurrent study and detailed site selection methods are published (Graves et al. 2017a). Bird surveys were conducted at least once every three weeks at each site,

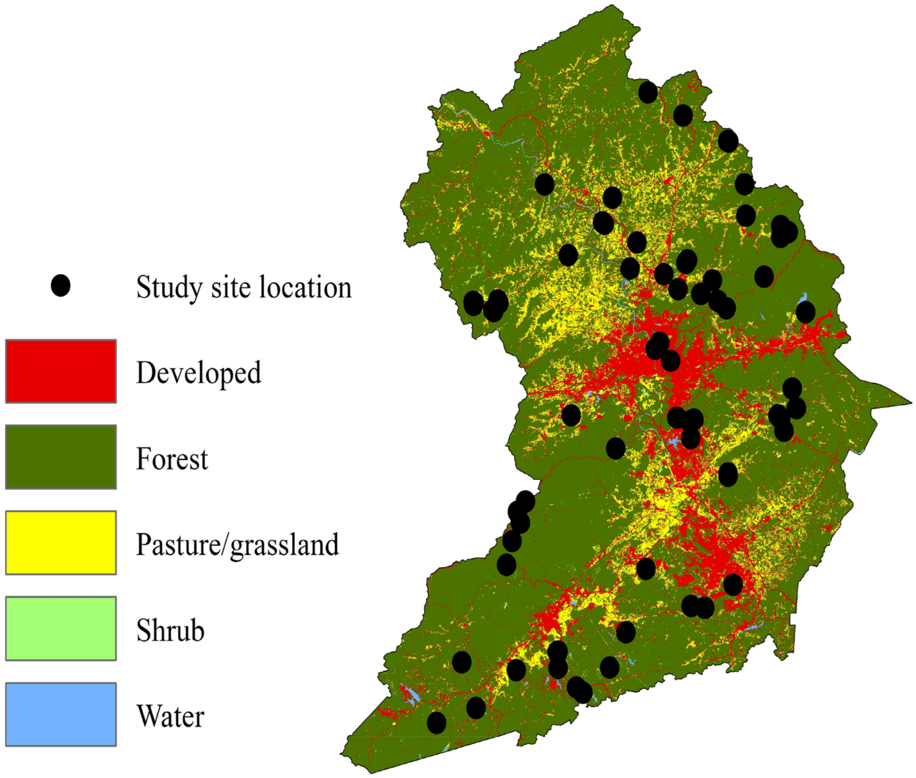

Fig. 1 Study site locations and land use/land cover in the French Broad River Basin, NC

Table 1 Predictor variables used in generalized linear models of bird cultural ecosystem service (CES) indicators in the southern Appalachians, USA

Predictor variable	Analysis scale	Mean (min – max)
Elevation (m a.s.l.)	Study site center	788 (530 – 1475)
Local building density (#/ha)	100-m buffer	0.43 (0 – 2.23)
Landscape building density	1000-m buffer	0.63 (0 – 5.20)
Tree index (proportion of LIDAR returns in canopy)	100-m buffer	0.52 (0.11 – 0.81)
Vegetation structural diversity (Shannon evenness index)	100-m buffer	0.65 (0.41 – 0.87)
Land-cover diversity (Simpson's diversity index; SIDI)	200-m buffer	0.34 (0.00 – 0.65)
Annual vegetation productivity	Study site center	2231 (1885 – 2440)
Season: early spring, late spring, or summer	*na*	Factor: 1, 2, 3

and a subset of sites was visited weekly, from April 1 to August 8, 2014.

Bird surveys consisted of standard 10-min point counts conducted between 05:45 and 10:30. One of 3 trained observers performed each point count and all sites were surveyed by at least 2 different observers throughout the study. Surveys were not conducted on rainy days or days with high wind. Each bird detected by sight or song within 100 m of the point location (i.e., site center) was identified to species and recorded. Birds observed outside the 100-m radius were recorded but not included in the primary analysis.

Remotely sensed and GIS data were used to derive environmental data hypothesized to influence bird community distributions (Table 1). Environmental variables included local and landscape building density, land-cover diversity, tree cover, vegetation structural diversity, estimated annual productivity, and elevation. Annual productivity and elevation were extracted at the center point of each study site. The remaining variables were extracted using buffers of 100, 200, and 1000 m, depending upon the scale at which each variable had the strongest relationship with bird CES indicators (see Appendix S1 for more detail).

Annual vegetation productivity was extracted from a smoothed and gap-filled MODIS Normalized Difference Vegetation Index (NDVI) dataset (Spruce et al. 2016). We calculated the 10-year (2004–2014) median of annual vegetation productivity for each study site. Elevation was extracted from the National Elevational Dataset-Digital Elevation Model (NED-DEM, data available from the U.S. Geological Survey).

Building density (building units per hectare) was quantified by counting the number of buildings located within 100 and 1000 m of the center of each study site to account for local and landscape scale effects of development intensity. Vegetation structure and tree cover were calculated from LIDAR (light detection and ranging) data within 100 m of the site center. Vegetation structural diversity was calculated using the Shannon Evenness index $\left(E_H = \frac{-\sum_{i=1}^{S} p_i \ln p_i}{\ln S}\right)$ using the proportion (p_i) of LIDAR returns in each of four vegetation strata ($S = 4$, i.e., herb, shrub, subcanopy, and canopy layers). Tree cover was recorded as the proportion of LIDAR returns within subcanopy or canopy layers (> 2.0 m above ground) (Graves et al. 2017a).

Land-cover diversity was calculated using Simpson's diversity index $\left(SIDI = 1 - \sum_{i=1}^{m} P_i^2\right)$ with six land-cover categories (grassland/herb, shrubland, cropland, forest, developed, and other/water) within 200 m of each study site. SIDI ranges from 0 to 1.0 and describes the probability of two points chosen at random within a given area being in different land-cover types (McGarigal et al. 2012). We used the 2014 Cropland Data Layer (CDL, USDA-NASS 2014) and calculated SIDI using Fragstats (McGarigal et al. 2012).

Data analysis

Bird species were classified based on (1) migratory status (short- or long-distance migrants vs. resident) and (2) synanthrope status (following Johnston 2001, any species listed as casual, tangential, or full synanthrope) (Table S1). Because uniqueness or rarity of bird species is also important for birdwatcher satisfaction (Booth et al. 2011), we calculated an index of relative species rarity using the observation frequency of each species within the FBRB using the eBird dataset, an online citizen science bird-monitoring project (Sullivan et al. 2014). Species with observation frequencies in the lowest quartile (i.e., the lowest 25% of observations) were considered 'infrequent' and is an indicator of a species' relative rarity within the region, which may be particularly relevant for local birdwatchers. For each site survey, five bird CES indicators were tallied: (1) total number of species, (2) migratory species richness, (3) resident species richness, (4) synanthrope species richness, and (5) 'infrequent' species richness. Instead of modeling total potential bird species richness at a site, we modeled average species richness observed during a survey visit. Average observed species richness, rather than richness estimates corrected for detectability (Nichols et al. 2000), may better represent the experience of a casual birdwatcher and, from a birdwatching perspective, would be equivalent to the average number of species that a birder might expect to observe in a short birding visit ($\sim$ 10 min).

Bird CES indicators were modeled during each of three time periods (i.e., early spring, late spring, and summer) to explore how temporal dynamics in bird communities affected the spatial distribution of birdwatching supply. Early spring (i.e., April 1–May 13) roughly corresponds to the migration/pre-breeding season, late spring (i.e., May 13–June 24) is representative of the breeding season and overlaps with breeding bird surveys in the region, and summer (i.e., June 24–Aug 6) corresponds with post-breeding season (Sauer et al. 2013). Our target was to sample each site at least twice during each period, for a minimum of six surveys across the season. Fifty-six out of 69 sites met this criterion; these were used as the dataset in the subsequent analysis.

For each site and time period, means were calculated for each of five bird CES indicators. Then, generalized linear models (GLM) were constructed for each bird CES indicator with the mean as the response variable and all environmental variables as possible predictor variables. Time period and potential interaction effects of time period with tree cover, building density, and elevation were included as predictor variables. Models were fitted first to the full model and variables were progressively eliminated using backward selection. Models were compared based on Akaike's Information Criterion (AICc); top models were defined as having the lowest AICc (Burnham and Anderson 2002). To ensure the most robust models possible, we retained all models within delta-AICc < 2.0. Goodness-of-fit was assessed using AICc values, residual deviance, and McFadden's pseudo-R^2 (McFadden 1974).

The resulting GLMs were used to map projected supply of bird CES in each time period: early spring, late spring, and summer. Maps were produced using the *predict* function in the raster package in R (Hijmans and van Etten 2015) and the best-fitting models identified above. All input layers were standardized to *z*-scores based on the mean and variance of the training dataset ($n = 56$) and referenced to the same projection (Albers Equal Area) and 100-m grid cell. For more detail on input data layers, see Appendix S1. To be conservative in our estimate of bird CES supply, projected bird CES was defined as the predicted value from the GLM minus one standard error. For

Table 2 Observed bird CES indicators at 56 sites compared across time periods using repeated measures ANOVA

Bird CES indicator	Overall mean	Early spring mean (min – max)	Late spring mean (min – max)	Summer mean (min – max)	ANOVA (*F*, *p*)
Total species richness	8.11	8.29 (4.33 – 14.83)	8.23 (4.0 – 17.0)	7.8 (2.5 – 13.5)	$F = 1.34$, $p = 0.265$
Migratory species richness	3.34	3.09 (1.00 – 8.00)^{ab}	3.77 (0.5 – 6.67)^{b}	3.15 (1.0 – 7.0)^{a}	$F = 7.87$, $p < 0.001$
Synanthrope species richness	4.85	4.73 (1.25 – 11.00)	4.78 (1.5 – 9.5)	5.04 (1.5 – 8.6)	$F = 1.39$, $p = 0.26$
Resident species richness	4.77	5.2 (1.00 – 11.67)	4.46 (1.00 – 11.00)	4.66 (1.0 – 9.0)	$F = 0.521$, $p = 0.595$
‘Infrequent’ species richness	2.74	2.91 (1.0 – 7.5)^{a}	3.02 (0.5 – 6.5)^{b}	2.28 (0.5 – 5.0)^{a}	$F = 8.20$, $p < 0.001$

Super-script letters indicate post hoc groupings

response variables with competing top models, we first mapped the projected bird CES (i.e., predicted value minus standard error) from each competing top model. Final maps were created by calculating the weighted-average of top model projections, using the corresponding AICc model weights, rather than using model-averaged coefficients (Grueber et al. 2011; Cade 2015). For maps of standard error of each predicted response, see Fig. S1.

Areas of high birdwatching supply (i.e., hotspots) were identified for each bird CES indicator in each time period as areas where projected bird CES supply exceeded the mean in our training dataset (Table 2). Hotspots of total species richness were compared to hotspots for alternate bird CES indicators by calculating the percent overlap in each season. Hotspots for multiple bird CES were identified by overlaying hotspot maps of each response variable. Hotspots were mapped for each time period and temporal consistency of hotspots was analyzed by overlaying hotspots for each time period and calculating the percent of spatial concordance among time periods.

Bird CES and public access

Maps of projected bird CES supply were compared to maps of two levels of public access to examine how access to bird CES changed over time. ‘Highly accessible’ included locations within 100 m of public-use trails (e.g., hiking trails, greenways), access points (e.g., overlooks, view points), or the Blue Ridge Parkway, a highly traveled scenic byway in the area. ‘Moderately accessible’ included any publicly owned lands (e.g., federal, state, or municipality-owned forests and parks); these areas are considered open to access but off-trail. The remaining landscape was considered private land with limited and/or controlled access. For each time period and bird CES, we calculated the area overlap between hotspots and public access.

Bird CES supply and use

Maps of bird CES supply were compared to demonstrated use of birdwatching CES using data from eBird (Sullivan et al. 2014). Point locations of eBird observations for the years 2009–2014 were mapped using ArcGIS. Observations were limited to those between April 1 and August 31 of each year to represent bird CES use during the time periods for which we sampled bird CES supply. The eBird observations were classified into early spring, late spring, and summer (as with bird CES supply, above). To determine how well bird CES use corresponded with projected bird CES supply, the proportion of eBird points within hotspots of bird CES supply was calculated for each time period.

RESULTS

Over 700 individual bird surveys were conducted from April 1 to August 6 across 69 sites; the training dataset consisted of 656 surveys at 56 sites. A total of 96 bird species were detected and used in the training dataset (Table S1). We observed 65 migratory species, 31 resident species, and 44 synanthropic species. Of the synanthropic species, 21 were migratory species and 23 were resident species. Forty-six species were classified as ‘infrequent’ (38 migratory species, 8 were resident species).

The total species richness observed during a single survey varied from 1 to 21 species (mean = 8.1). Observed migratory species richness varied from zero to 10 (mean = 3.3), and both observed resident species and observed synanthropic species ranged from zero to 15 species (mean = 4.8 and 4.9, respectively). The number of ‘infrequent’ species observed ranged from zero to 9 (mean = 2.7). Migratory species richness was similar in early and late spring, but higher in late spring than summer (Table 2). ‘Infrequent’ species richness was highest in late spring, and similar between early spring and summer (Table 2). Total bird species richness, resident species richness, and synanthrope species richness did not vary among the three time periods (Table 2).

The top models for each bird CES indicator (Table 3) explained between 23 and 48% of the variance in bird CES indicators. Elevation was included in top models for total

Table 3 Model parameter estimates, deltaAIC, AICc weight, and pseudo-R^2 for each top model of bird CES indicators

	ΔAICc	Elev.	Local building density	Neighborhood building density	% tree	Veg. structure	LU/LC diversity	Time period: Late spring (LS)	Time period: Summer (SU)	Time period × %Tree	Time period × local building	AICc wt.	pseudo-R^2
Total species richness	0.00	− 0.41	0.87	− 0.43	− 0.54							0.78	0.23
	2.04	− 0.41	0.87	− 0.43	− 0.54			− 0.06	− 0.48			0.22	0.24
Migratory species richness	0.00		0.26	− 0.69				0.68	0.06		LS: − 0.49 SU: 0.16	0.42	0.27
	0.35		0.29	− 0.64			− 0.14	0.68	0.06		LS: − 0.49 SU: 0.16	0.4	0.28
	1.78		0.29	− 0.63	− 0.07		− 0.19	0.68	0.06		LS: − 0.49 SU: 0.16	0.17	0.28
Resident species richness	0.00	− 0.64	0.64		− 0.36	0.36	0.48	− 0.74	− 0.54			0.61	0.47
	0.86	− 0.64	0.64		− 0.57	0.36	0.48	− 0.74	− 0.54	LS: 0.11 SU: 0.53		0.39	0.48
Synanthrope species richness	0.00	− 0.38	0.76		− 0.65	0.2	0.31	0.05	0.31	LS: 0.30 SU: 0.59		1	0.47
'Infrequent' species richness	0.00		0.26	− 0.57	− 0.14		− 0.29	0.12	− 0.62	LS: 0.41 SU: 0.04	LS: − 0.49 SU: − 0.05	0.45	0.37
	0.67	0.13	0.27	− 0.52	− 0.16		− 0.29	0.12	− 0.62	LS: 0.41 SU: 0.04	LS: − 0.49 SU: − 0.05	0.32	0.37
	1.41	0.16	0.29	− 0.51	− 0.16	− 0.12	− 0.33	0.12	− 0.62	LS: 0.41 SU: 0.04	LS: − 0.49 SU: − 0.05	0.22	0.38

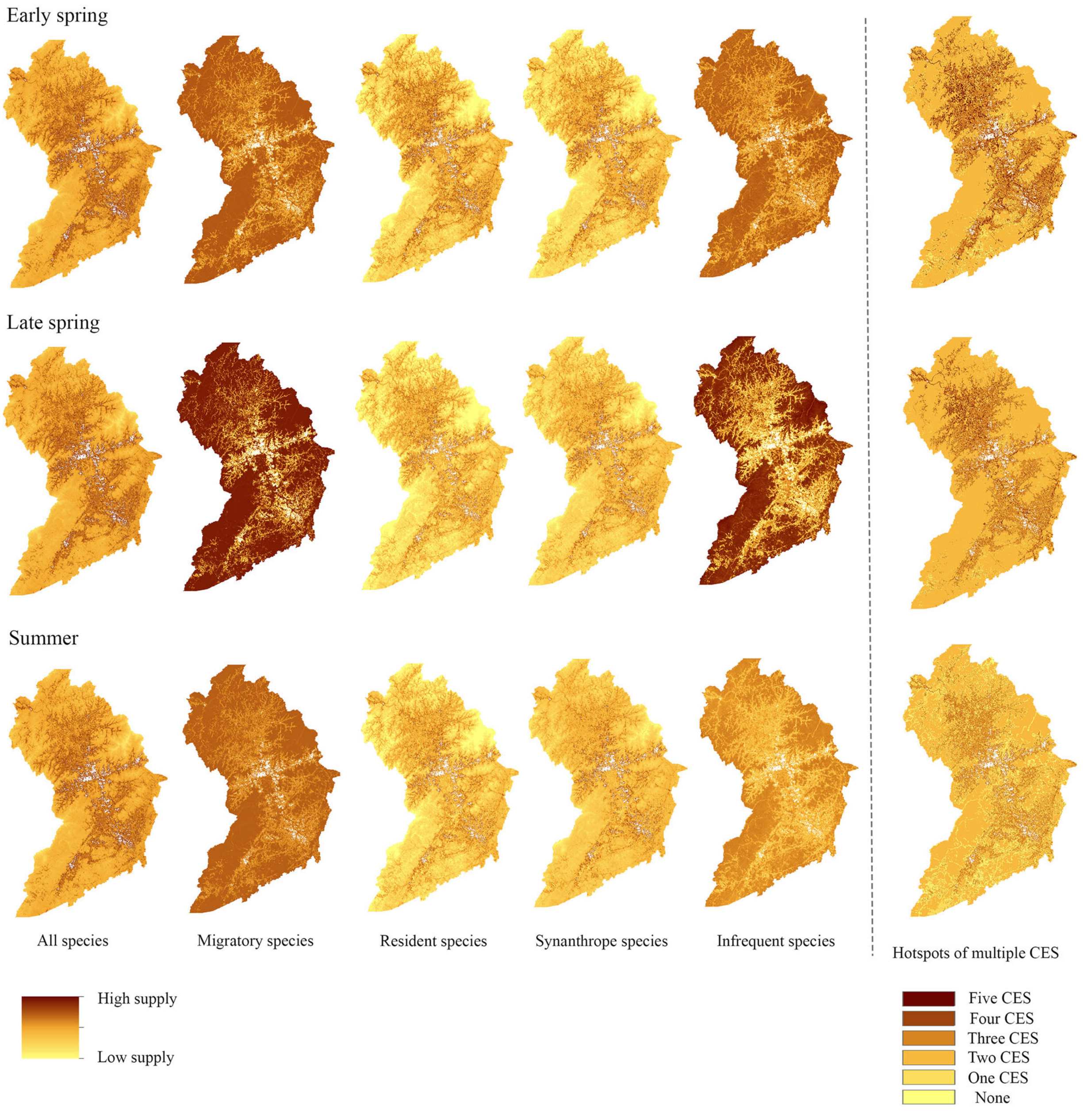

Fig. 2 Maps of projected bird CES supply and hotpots of multiple CES during early spring, late spring, and summer. High/low values differed for each bird CES indicator: all species (range: 2–13 species), migratory species (0–5 species), resident species (0–11 species), synanthrope species (0–11 species), and 'infrequent' species (0–5 species)

Table 4 Summary of bird CES hotspots across time periods

Time Period	Percent of landscape classified as hotspot					
	Total bird species richness (%)	Migratory species richness (%)	Resident species richness (%)	Synanthrope species richness (%)	'Infrequent' species richness (%)	Hotspot of 4 or 5 CES (%)
Early spring	34	66	37	29	71	9
Late spring	34	78	26	26	70	7
Summer	32	64	27	27	45	9

Locations were considered hotspots if the predicted bird CES value was above the mean species richness (negative effect), resident species richness (negative effect), and ‘infrequent’ species richness (positive effect) but not included in models of migratory species richness. Local building density had a positive effect on all bird CES, but neighborhood building density had negative effects on total, migratory, and ‘infrequent’ species richness. Neighborhood building density was not included in models for resident and synanthrope species richness. Tree cover was negatively related to all bird CES, with stronger effects on total, resident, and synanthrope species richness, relatively weak effects on ‘infrequent’ species richness, and only slight effects on migratory species richness. The interaction between time period and tree cover was included in models of resident, synanthrope, and ‘infrequent’ species richness. Vegetation structural diversity was an important predictor in models of resident and synanthrope species richness, with positive effects, and was included in one of the top models for ‘infrequent’ species, with negative effects. Land-cover diversity was not included in the models of total bird species richness; however, migratory species richness and ‘infrequent’ species richness were negatively affected by land-cover diversity, while resident and synanthrope species richness were positively related to land-cover diversity. Effects of time period were included in top models for all bird CES indicators. The interaction effect between time period and building density was included in top models of migratory and ‘infrequent’ species richness.

Bird CES supply

Spatial distribution of bird CES supply varied across time periods and among bird CES indicators (Fig. 2, Table 4). For total bird species richness and synanthrope species richness, the landscape percentage with high birdwatching supply (i.e., hotspots) remained consistent across the time periods (32–34% and 26–29%, respectively). For migratory bird species richness, the majority of the landscape was projected to have high birdwatching supply (> 60%) and projected hotspot area was highest in the late spring (78% of the landscape projected above the observed mean). For high resident bird species richness, the landscape percent declined from early spring (37%) to summer (27%); similarly, ‘infrequent’ bird species richness hotspots declined from early spring (71%) to summer (45%).

Hotspots for total bird species richness were consistent across time periods (Table S2); hotspots shifted on less than 5% of the landscape, while 66% of the landscape was predicted to consistently have low supply. Hotspots of resident and synanthrope species richness were similarly consistent (Fig. 2), with 63–67% of the landscape predicted to have low supply and locations of high supply shifting on only 8% of the landscape. Migratory and ‘infrequent’ bird species richness had the most dynamic patterns of bird CES supply and spatial patterns of these hotspots were different than for total, resident, and synanthrope species richness (Fig. 2). Hotspots of migratory bird species richness consistently comprised 63% of the landscape, and a further 15% of the landscape was projected to have shifting supply of migratory species richness. Similarly, hotspots of ‘infrequent’ bird species richness consistently comprised 45% of the landscape, with an additional 32% of the landscape projected to have high supply of ‘infrequent’ bird species richness during only one or two of the time periods.

Hotspots of total species richness were not often spatially co-located with hotspots of migratory or infrequent species richness (Fig. 3). However, total species richness hotspots overlapped substantially with resident and synanthrope bird species richness (over 50% overlap, Fig. 3).

Public accessibility of bird CES

Up to 27% of the study area is publicly accessible, with 5% ‘highly accessible’ and 22% ‘moderately accessible’ (Fig. S1). For total, resident, and synanthrope species richness, bird CES hotspots tended to be in privately owned or limited access areas. Only 6–9% of these hotspots were located on publicly accessible land. The percent of hotspots, of all indicators, on accessible lands remained relatively stable across time periods (Table S3). For migratory and ‘infrequent’ species richness, a larger percent (31–41%) of hotspot area was located on publicly accessible land. For ‘infrequent’ bird species richness, the area of hotspots on accessible land increased (8%) from early spring to summer (Table S3). However, the overall landscape percentage of ‘infrequent’ species hotspots declined by 5% from early spring to summer indicating that ‘infrequent’ species richness hotspots contracted to publicly accessible lands from early spring to summer.

Bird CES supply and bird CES use

There were 4347 eBird observations within our study area during the spring/summer (i.e., April–August) of 2009–2014 and were located on both publicly accessible and private land (24% ‘highly accessible,’ 17% ‘moderately accessible,’ and 59% private/limited access). Forty-three percent were recorded within the early spring, 23% within the late spring, and 34% within the summer time periods (Fig. S1). On average across the time periods, more eBird points were located within projected bird CES supply hotspots for resident (62%) and synanthrope (53%) species richness than for migratory (45%), all species (48%), and ‘infrequent’ (33%) species richness. Correspondence between eBird observations and projected migratory and ‘infrequent’ species richness hotspots was higher in early and late spring than summer (Fig. 4). Conversely, eBird

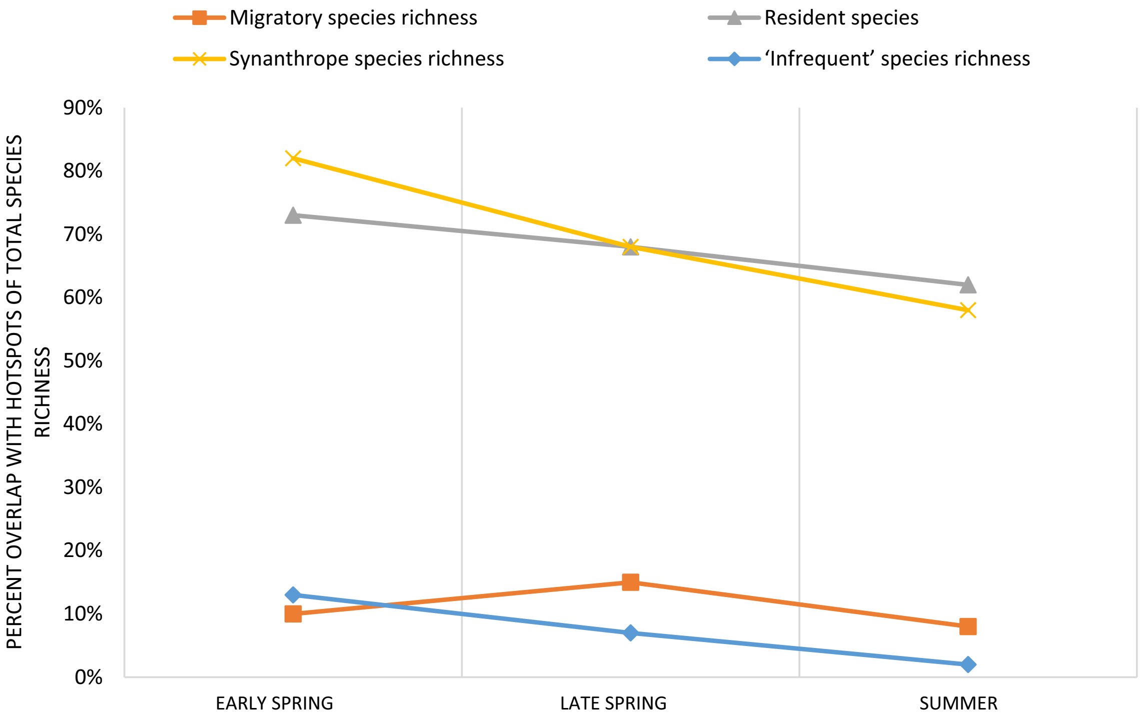

Fig. 3 Percent overlap between hotspots of bird CES indicators (infrequent, migratory, resident, and synanthrope species richness) with hotspots of total species richness during the early spring, late spring, and summer. Percent overlap declined over time and was low for migratory and infrequent bird species

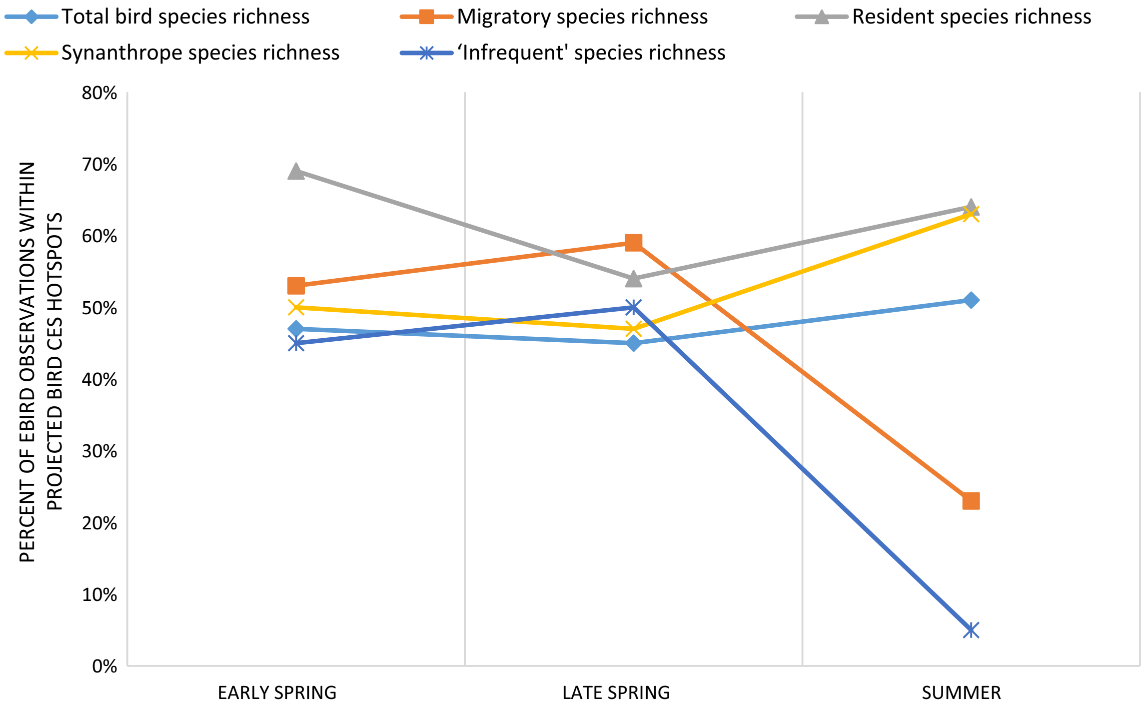

Fig. 4 Percent of eBird observations (n = 4347) from 2009 to 2014 within projected bird CES supply hotspots during early spring, late spring, and summer

observations had the greatest coincidence with hotspots of synanthrope species richness during summer.

DISCUSSION

Landscape models of birdwatching supply in the Southern Appalachians revealed seasonal variation in birdwatching supply for five CES indicators. Bird CES supply was high across much of the landscape, but only a small percent of the landscape provided high supply for all bird CES indicators. Spatial variation in hotspots of CES supply for different indicators suggested that public accessibility of birdwatching may differ depending on birders' motivations. Shifts in birdwatching supply were accompanied by shifts in use of bird CES; thus, dynamics of both biotic communities and users of CES should be considered in order to fully understand landscape patterns of CES.

Biodiversity-based CES provision may be driven by more than total species richness, and users of CES may be interested in other aspects of biotic communities (Cumming and Maciejewski 2017; Graves et al. 2017b). We developed landscape projections of birdwatching supply that account for different components of the bird community (e.g., where are the *birds* vs. where are the *migratory birds*). Projected birdwatching supply differed among models of different components of the bird communities, leading to sometimes opposing conclusions regarding the places with the highest supply of bird CES. In particular, hotspots of total bird species richness, a commonly used metric for birdwatching supply (Bateman et al. 2013), did not often overlap with high supply of migratory or infrequently sighted species richness. However, total bird species richness was a reasonable surrogate for common (i.e., resident and synanthrope) species richness. Studies that rely only on simple, static metrics of biodiversity may overlook seasonal and spatial dynamics important to users of CES and future studies should consider multiple facets of biotic communities.

Spatial–temporal variation in birdwatching supply was driven by bird community response to land use/land cover and development patterns within the study area. In the Southern Appalachians, abundant forest cover provides habitat for several species of Neotropical migrants and forest specialists (Haney et al. 2001). From a birdwatching perspective, extensive forest cover resulted in high supply of migratory birds over a large percentage of the landscape. However, complex interactions between habitat characteristics and season are evident in the models of birdwatching CES. With tree cover, negative coefficients for main and interaction effects (Table 3) can be explained by increased habitat heterogeneity in this heavily forested landscape. Canopy gaps and forest edge reduce tree cover and create habitat for additional species not found in closed canopy forest. Resident species diversity increased with greater structural diversity in vegetation, and the effects of tree cover varied seasonally. Resident species richness was higher in early spring with less tree cover; however, that negative influence of tree cover decreased in late spring and disappeared by summer (cf. Table 3). Thus, openings and canopy gaps enhanced richness in early spring but that enhancement attenuated by summer.

Birdwatching supply increased with local building density, reflecting community-level versus species-level responses to building density. Exurban development occurs widely within the study area (Gragson and Bolstad 2006) and individual bird species response to local building density varies depending on habitat and migratory guild (Lumpkin and Pearson 2013) and season (this study). For migratory species, effects of local building density varied seasonally at sites with more buildings; richness was lower in late spring and higher in summer (cf. time period × local building density interactions, Table 3).

Increased avian species richness with increased low-level and exurban building density is not uncommon (Luck 2007). In the predominantly forested Southern Appalachians, local increases in building density provide habitat heterogeneity that can enhance avian diversity, consistent with the idea that human settlement acts as an intermediate disturbance on the landscape (McDonnell et al. 1993). However, birdwatching supply of migratory and infrequently sighted species declined with increased neighborhood building density. For these groups of birds, community-level responses to building density are complex and stronger at local scale, suggesting that, for these groups, birdwatching supply may be driven by threshold responses to human settlement at broader landscape scales.

Birdwatchers' expectations may be an important driver of final CES provision and the geographic location that birders choose may be a function of the bird community as well as public access or other landscape features, like mountain views, waterfalls, or wildflowers (Potschin and Haines-Young 2013; Cumming and Maciejewski 2017). We found that only about half of eBird observations were located on publicly accessible land, that birding locations shifted over time, and thus overlap between birding locations and predicted bird CES varied over time. Shifts in birder locations suggest that birdwatchers may choose locations with high migratory bird species richness during the migration and nesting season, and then concentrate birdwatching activity elsewhere throughout the summer. Birdwatchers may be adjusting their expectations based on landscape context (Cumming and Maciejewski 2017), leading to different spatial patterns of social demand for bird CES across time periods. Furthermore, the predominance of birding locations located on private or limited access lands highlights the importance of backyard birdwatching and private land in provision of a key CES.

Given the extensive supply of birdwatching across the landscape, public access may be a limiting factor for provision of bird CES to birdwatchers in the Southern Appalachians. For instance, while over 60% of the landscape was projected to have high supply of migratory and infrequently sighted species, less than 25% of those hotspots were also publicly accessible. For the other bird CES indicators, less than 5% of the landscape provided high birdwatching supply and was also publicly accessible. Since birdwatching can increase connections people feel with nature (Zelenski and Nisbet 2014; Cox and Gaston 2015) and being connected to nature is linked to people's support for conservation issues (Miller 2005; Restall and Conrad 2015), enhancing public accessibility in locations projected to have high birdwatching supply could lead to increased human well-being as well as benefits for biodiversity conservation.

Biodiversity, in many forms, plays a key role in the provision of ecosystem services and local biodiversity may strongly influence ES supply (Balvanera et al. 2006; Mace et al. 2012). Additionally, the scientific community has shown that ES supply varies through time (Holland et al. 2011) in response to changing land-use change (Lavorel et al. 2017b), environmental conditions (Seidl et al. 2016), and societal characteristics (Reyers et al. 2009; Renard et al. 2015). Temporal variance in ES supply can also be attributed to biological community dynamics (Koch et al. 2009; Genung et al. 2017). Yet, the influence of biological community dynamics on the temporal patterns of CES is not well understood and seldom incorporated into landscape ES assessments (Graves et al. 2017a).

A variety of approaches and analytical techniques have been used to conduct landscape assessments of CES (Hernández-Morcillo et al. 2013). We demonstrate an approach to mapping nuances in CES supply resulting from shifts in bird communities. By incorporating species and biological community dynamics into spatial models of CES, geographic locations that play an important role in maintaining the supply and accessibility of CES over time can be identified. As with other CES studies, our study illustrates that mapping CES supply is a complex process (Paracchini et al. 2014; Bagstad et al. 2016; Cumming and Maciejewski 2017) and that the choice of CES indicator is non-trivial and influences conclusions about CES availability (Tratalos et al. 2014; Chan et al. 2016). While our study specifically focused on birdwatching, we expect that analyzing the underlying biological dynamics of additional biodiversity-based CES (e.g., fall foliage viewing, coral reef tourism and tropical fish viewing, flower tourism, wild foraging) would similarly reveal important variation in CES otherwise missed by static, coarse metrics of biodiversity.

DATA AVAILABILITY

Data are available through the National Science Foundation Long-term Ecological Research Program data catalog.

Acknowledgements Thank you to the landowners who provided permission for data collection. G. Lancaster, J. Mackie, and Z. Hane helped compile data. M. Hopey assisted with data collection. E. Damschen, C. Kucharik V. Radeloff, B. Zuckerberg, C. Ziter, and C. Latimer provided helpful comments on early development of these ideas. Thank you to A. Alstad for comments on an earlier draft. This study was funded by the National Science Foundation Long-term Ecological Research Program (Grants DEB-0823293 and DEB-1440485) and by the University of Wisconsin-Madison Vilas Trust.

REFERENCES

Bagstad, K.J., J.M. Reed, D.J. Semmens, B.C. Sherrouse, and A. Troy. 2016. Linking biophysical models and public preferences for ecosystem service assessments: A case study for the Southern Rocky Mountains. *Regional Environmental Change* 16: 2005–2018. https://doi.org/10.1007/s10113-015-0756-7.

Balvanera, P., A.B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9: 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x.

Bateman, I.J., A.R. Harwood, G.M. Mace, R.T. Watson, D.J. Abson, B. Andrews, A. Binner, A. Crowe, et al. 2013. Bringing ecosystem services into economic decision-making: Land use in the United Kingdom. *Science* 341: 45–50. https://doi.org/10.1126/science.1234379.

Belaire, J.A., L.M. Westphal, C.J. Whelan, and E.S. Minor. 2015. Urban residents' perceptions of birds in the neighborhood: Biodiversity, cultural ecosystem services, and disservices. *Condor* 117: 192–202. https://doi.org/10.1650/CONDOR-14-128.1.

Booth, J.E., K.J. Gaston, K.L. Evans, and P.R. Armsworth. 2011. The value of species rarity in biodiversity recreation: A birdwatching example. *Biological Conservation* 144: 2728–2732. https://doi.org/10.1016/j.biocon.2011.02.018.

Boulinier, T., J.D. Nichols, J.E. Hines, J.R. Sauer, C.R. Flather, and K.H. Pollock. 1998. Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proceedings of the National Academy of Sciences of the USA* 95: 7497–7501.

Burkhard, B., F. Kroll, S. Nedkov, and F. Müller. 2012. Mapping ecosystem service supply, demand and budgets. *Ecological Indicators* 21: 17–29. https://doi.org/10.1016/j.ecolind.2011.06.019.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. In *Ecological Modeling*, 2nd edn. New York: Springer.

Cade, B.S. 2015. Model averaging and muddled multimodel inferences. *Ecology* 96: 2370–2382. https://doi.org/10.1890/14-1639.1.

Carver, E. 2013. *Birding in the United States: An Economic and Demographic Analysis*. Arlington: U.S. Fish and Wildlife Service, Division of Economics.

Chan, K.M.A., P. Balvanera, K. Benessaiah, M. Chapman, S. Díaz, E. Gómez-Baggethun, R. Gould, N. Hannahs, et al. 2016. Why protect nature? Rethinking values and the environment. *Proceedings of the National Academy of Sciences of the USA* 113: 1462–1465. https://doi.org/10.1073/pnas.1525002113.

Cordell, H.K., and N.G. Herbert. 2002. The popularity of birding is still growing. *Birding* 34: 54–61.

Cox, D.T.C., and K.J. Gaston. 2015. Likeability of garden birds: Importance of species knowledge & richness in connecting people to nature. *PLoS ONE* 10: 1–14. https://doi.org/10.1371/journal.pone.0141505.

Cumming, G.S., and K. Maciejewski. 2017. Reconciling community ecology and ecosystem services: Cultural services and benefits from birds in South African National Parks. *Ecosystem Services* 28: 219–227. https://doi.org/10.1016/j.ecoser.2017.02.018.

Dallimer, M., Z.G. Davies, D.F. Diaz-Porras, K.N. Irvine, L. Maltby, P.H. Warren, P.R. Armsworth, and K.J. Gaston. 2015. Historical influences on the current provision of multiple ecosystem services. *Global Environmental Change* 31: 307–317. https://doi.org/10.1016/j.gloenvcha.2015.01.015.

Daniel, T.C., A. Muhar, A. Arnberger, O. Aznar, J.W. Boyd, K.M.A. Chan, R. Costanza, T. Elmqvist, et al. 2012. Contributions of cultural services to the ecosystem services agenda. *Proceedings of the National Academy of Sciences of the USA* 109: 8812–8819. https://doi.org/10.1073/pnas.1114773109.

Fuller, R.A., K.N. Irvine, Z.G. Davies, P.R. Armsworth, and K.J. Gaston. 2012. Interactions between people and birds in urban landscapes. In *Urban bird ecology and conservation*, ed. C.A. Lepczyk and P.S. Warren, 249–266. Berkeley: University of California Press.

Genung, M.A., J. Fox, N.M. Williams, C. Kremen, J. Ascher, J. Gibbs, and R. Winfree. 2017. The relative importance of pollinator abundance and species richness for the temporal variance of pollination services. *Ecology* 98: 1807–1816. https://doi.org/10.1002/ecy.1876.

Gragson, T.L., and P.V. Bolstad. 2006. Land use legacies and the future of Southern Appalachia. *Society & Natural Resources* 19: 175–190. https://doi.org/10.1080/08941920500394857.

Graves, R.A., S.M. Pearson, and M.G. Turner. 2017a. Landscape dynamics of floral resources affect the supply of a biodiversity-dependent cultural ecosystem service. *Landscape Ecology* 32: 415–428. https://doi.org/10.1007/s10980-016-0452-0.

Graves, R.A., S.M. Pearson, and M.G. Turner. 2017b. Species richness alone does not predict cultural ecosystem service value. *Proceedings of the National Academy of Sciences of the USA* 114: 3774–3779. https://doi.org/10.1073/pnas.1701370114.

Grueber, C.E., S. Nakagawa, R.J. Laws, and I.G. Jamieson. 2011. Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology* 24: 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x.

Haney, J.C., D.S. Lee, and M. Wilbert. 2001. A half-century comparison of breeding birds in the Southern Appalachians. *Condor* 103: 268. https://doi.org/10.1650/0010-5422(2001)103[0268:AHCCOB]2.0.CO;2.

Hernández-Morcillo, M., T. Plieninger, and C. Bieling. 2013. An empirical review of cultural ecosystem service indicators. *Ecol. Indic.* 29: 434–444. https://doi.org/10.1016/j.ecolind.2013.01.013.

Hijmans, R., and J. van Etten. 2015. Raster: Geographic analysis and modeling with raster data. R Packag. version 2.4-20.

Holland, R.A., F. Eigenbrod, P.R. Armsworth, B.J. Anderson, C.D. Thomas, and K.J. Gaston. 2011. The influence of temporal variation on relationships between ecosystem services. *Biodiversity and Conservation* 20: 3285–3294. https://doi.org/10.1007/s10531-011-0113-1.

Homer, C., J. Fry and C. Barnes. 2012. The National Land Cover Database. US Geol. Surv. Fact Sheet 1–4.

Hvenegaard, G.T. 2002. Birder specialization differences in conservation involvement, demographics, and motivations. *Human Dimensions of Wildlife* 7: 21–36. https://doi.org/10.1080/108712002753574765.

Johnston, R.F. 2001. Synanthropic birds of North America. In *Avian ecology and conservation in an urbanizing world*, ed. J.M. Marzluff, R. Bowman, and R. Donnelly, 49–67. New York: Springer.

Koch, E.W., E.B. Barbier, B.R. Silliman, D.J. Reed, G.M. Perillo, S.D. Hacker, E.F. Granek, J.H. Primavera, et al. 2009. Non-linearity in ecosystem services: Temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment* 7: 29–37. https://doi.org/10.1890/080126.

Kremen, C. 2005. Managing ecosystem services: What do we need to know about their ecology? *Ecology Letters* 8: 468–479. https://doi.org/10.1111/j.1461-0248.2005.00751.x.

Lavorel, S., A. Bayer, A. Bondeau, S. Lautenbach, A. Ruiz-Frau, N. Schulp, R. Seppelt, P. Verburg, et al. 2017a. Pathways to bridge the biophysical realism gap in ecosystem services mapping approaches. *Ecological Indicators* 74: 241–260. https://doi.org/10.1016/j.ecolind.2016.11.015.

Lavorel, S., K. Grigulis, G. Leitinger, M. Kohler, U. Schirpke, and U. Tappeiner. 2017b. Historical trajectories in land use pattern and grassland ecosystem services in two European alpine landscapes. *Regional Environmental Change* 17: 2251–2264. https://doi.org/10.1007/s10113-017-1207-4.

Leveau, L.M., and C.M. Leveau. 2012. The role of urbanization and seasonality on the temporal variability of bird communities. *Landscape and Urban Planning* 106: 271–276. https://doi.org/10.1016/j.landurbplan.2012.03.008.

Luck, G.W. 2007. A review of the relationships between human population density and biodiversity. *Biological Reviews* 82: 607–645. https://doi.org/10.1111/j.1469-185X.2007.00028.x.

Lumpkin, H.A., and S.M. Pearson. 2013. Effects of exurban development and temperature on bird species in the southern Appalachians. *Conservation Biology* 27: 1069–1078. https://doi.org/10.1111/cobi.12085.

MA. 2005. *Ecosystems and human well-being: Multiscale assessments*. Washington, DC: Island Press.

Mace, G.M., K. Norris, and A.H. Fitter. 2012. Biodiversity and ecosystem services: A multilayeredrelationship. *Trends in Ecology & Evolution* 27: 19–26. https://doi.org/10.1016/j.tree.2011.08.006.

Martínez-Harms, M.J., and P. Balvanera. 2012. Methods for mapping ecosystem service supply: A review. *International Journal of Biodiversity Science, Ecosystem Services & Management* 8: 17–25. https://doi.org/10.1080/21513732.2012.663792.

McDonnell, M.J., S.T. Pickett, and R.B. Pouyat. 1993. The application of the ecological gradient paradigm to the study of urban effects. In *Humans as Components of Ecosystems*, ed. M.J. McDonnell and S.T.A. Pickett, 175–189. New York: Springer.

McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. In *Frontiers in econometrics*, ed. P. Zarembka, 105–142. Cambridge: Academic Press.

McFarlane, B.L. 1994. Specialization and motivations of birdwatchers. *Wildlife Society Bulletin* 22: 361–370.

McGarigal, K., Cushman, S., Ene, E., 2012. FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps.

Mckerrow, A.J., S.G. Williams, and J.A. Collazo. 2006. The North Carolina gap analysis project: Final report. Raleigh, NC.

Miller, J.R. 2005. Biodiversity conservation and the extinction of experience. *Trends in Ecology & Evolution* 20: 430–434. https://doi.org/10.1016/j.tree.2005.05.013.

Nichols, J.D., J.E. Hines, J.R. Sauer, J.E. Fallon, and P.J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117: 393–408. https://doi.org/10.2307/4089721.

Paracchini, M.L., G. Zulian, L. Kopperoinen, J. Maes, J.P. Schägner, M. Termansen, M. Zandersen, M. Perez-Soba, et al. 2014. Mapping cultural ecosystem services: A framework to assess the potential for outdoor recreation across the EU. *Ecological Indicators* 45: 371–385. https://doi.org/10.1016/j.ecolind.2014.04.018.

Potschin, M., and R. Haines-Young. 2013. Landscapes, sustainability and the place-based analysis of ecosystem services. *Landscape Ecology* 28: 1053–1065. https://doi.org/10.1007/s10980-012-9756-x.

Renard, D., J.M. Rhemtulla, and E.M. Bennett. 2015. Historical dynamics in ecosystem service bundles. *Proceedings of the National Academy of Sciences of the USA* 112: 13411–13416. https://doi.org/10.1073/pnas.1502565112.

Restall, B., and E. Conrad. 2015. A literature review of connectedness to nature and its potential for environmental management. *Journal of Environmental Management* 159: 264–278. https://doi.org/10.1016/j.jenvman.2015.05.022.

Reyers, B., P.J. O'Farrell, R.M. Cowling, B.N. Egoh, D.C.Le Maitre, and J.H.J. Vlok. 2009. *Ecosystem services, land-cover change, and stakeholders: Finding a sustainable foothold for a semiarid biodiversity hotspot*. Ecol: Ecology and Society. https://doi.org/10.2307/26268036.

Satz, D., R.K. Gould, K.M.A. Chan, A. Guerry, B. Norton, T. Satterfield, B.S. Halpern, J. Levine, et al. 2013. The challenges of incorporating cultural ecosystem services into environmental assessment. *Ambio* 42: 675–684.

Sauer, J.R., W.A. Link, J.E. Fallon, K.L. Pardieck, and D.J. Ziolkowski. 2013. The North American breeding bird survey 1966–2011: Summary analysis and species accounts. *North American Fauna* 79: 1–32. https://doi.org/10.3996/nafa.79.0001.

Seidl, R., T.A. Spies, D.L. Peterson, S.L. Stephens, and J.A. Hicke. 2016. Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology* 53: 120–129. https://doi.org/10.1111/1365-2664.12511.

Spruce, J.P., G.E. Gasser, and W.W. Hargrove. 2016. *MODIS NDVI Data, Smoothed and Gapfilled, for the Conterminous US: 2000–2015*. Oak Ridge: ORNL DAAC.

Strom, E., and R. Kerstein. 2015. Mountains and muses: Tourism development in Asheville, North Carolina. *Annals of Tourism Research* 52: 134–147. https://doi.org/10.1016/j.annals.2015.03.006.

Sullivan, B.L., J.L. Aycrigg, J.H. Barry, R.E. Bonney, N. Bruns, C.B. Cooper, T. Damoulas, A.A. Dhondt, et al. 2014. The eBird enterprise: An integrated approach to development and application of citizen science. *Biological Conservation* 169: 31–40. https://doi.org/10.1016/j.biocon.2013.11.003.

Tratalos, J.A., R. Haines-Young, M. Potschin, R. Fish, and A. Church. 2014. Cultural ecosystem services in the UK: Lessons on designing indicators to inform management and policy. *Ecological Indicators* 61: 63–73. https://doi.org/10.1016/j.ecolind.2015.03.040.

USDA National Agricultural Statistics Service Cropland Data Layer, 2014.

Villamagna, A.M., P.L. Angermeier, and N. Niazi. 2014. Evaluating opportunities to enhance ecosystem services in public use areas. *Ecosystem Services* 7: 167–176. https://doi.org/10.1016/j.ecoser.2013.09.002.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1–80.

Zelenski, J.M., and E.K. Nisbet. 2014. Happiness and feeling connected: The distinct role of nature relatedness. *Environment and Behavior* 46: 3–23. https://doi.org/10.1177/0013916512451901.

Zuckerberg, B., D. Fink, F.A. La Sorte, W.M. Hochachka, and S. Kelling. 2016. Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. *Diversity and Distributions*. https://doi.org/10.1111/ddi.12428.

AUTHOR BIOGRAPHIES

Rose A. Graves (✉) is a Postdoctoral Researcher at Boise State University. Her research interests include landscape ecology, ecosystem service science, and landscape sustainability.
Address: Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI 53706, USA.
Address: Human-Environment Systems, Boise State University, 1910 University Drive, Boise, ID 83725-1075, USA.
e-mail: rosegraves@boisestate.edu

Scott M. Pearson is Professor of Biology at Mars Hill University. His research interests include population ecology of native species in forested landscapes of southern Appalachia.
Address: Department of Biology, Mars Hill University, Campus Box 6671, Mars Hill, NC 28754, USA.
e-mail: spearson@mhu.edu

Monica G. Turner is the Eugene P. Odum Professor of Ecology and a Vilas Research Professor in the Department of Integrative Biology, University of Wisconsin-Madison. Her research emphasizes causes and consequences of spatial heterogeneity in ecological systems, focusing primarily on ecosystem and landscape ecology.
Address: Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI 53706, USA.
e-mail: turnermg@wisc.edu