Species richness alone does not predict cultural ecosystem service value

Rose A. Graves[a,1], Scott M. Pearson[b], and Monica G. Turner[a,1]

[a]Department of Zoology, University of Wisconsin–Madison, Madison, WI 53706; and [b]Department of Natural Sciences, Mars Hill University, Mars Hill, NC 28754

Contributed by Monica G. Turner, February 3, 2017 (sent for review November 14, 2016; reviewed by Gretchen C. Daily and Emily Minor)

Many biodiversity-ecosystem services studies omit cultural ecosystem services (CES) or use species richness as a proxy and assume that more species confer greater CES value. We studied wildflower viewing, a key biodiversity-based CES in amenity-based landscapes, in Southern Appalachian Mountain forests and asked (*i*) How do aesthetic preferences for wildflower communities vary with components of biodiversity, including species richness?; (*ii*) How do aesthetic preferences for wildflower communities vary across psychographic groups?; and (*iii*) How well does species richness perform as an indicator of CES value compared with revealed social preferences for wildflower communities? Public forest visitors (n = 293) were surveyed during the summer of 2015 and asked to choose among images of wildflower communities in which flower species richness, flower abundance, species evenness, color diversity, and presence of charismatic species had been digitally manipulated. Aesthetic preferences among images were unrelated to species richness but increased with more abundant flowers, greater species evenness, and greater color diversity. Aesthetic preferences were consistent across psychographic groups and unaffected by knowledge of local flora or value placed on wildflower viewing. When actual wildflower communities (n = 54) were ranked based on empirically measured flower species richness or wildflower viewing utility based on multinomial logit models of revealed preferences, rankings were broadly similar. However, designation of hotspots (CES values above the median) based on species richness alone missed 27% of wildflower viewing utility hotspots. Thus, conservation priorities for sustaining CES should incorporate social preferences and consider multiple dimensions of biodiversity that underpin CES supply.

discrete choice | aesthetics | biodiversity | wildflowers | amenity-based landscape

Sustaining ecosystem services is an emerging priority in sustainability science, and conservation plans increasingly emphasize joint protection or improvement of ecosystem services and biodiversity. Simultaneous concern for biodiversity and ecosystem services led to establishment of the Intergovernmental Platform on Biodiversity and Ecosystem Services as well as multiple national, regional, and local initiatives (1, 2). Despite recognition that the futures of biodiversity and ecosystem services are interconnected (3), understanding the direct links between biodiversity and ecosystem services and determining the best indicators to represent ecosystem services remain crucial challenges (4–7). Biodiversity is defined and measured in a multitude of ways (e.g., species richness, species evenness, genetic diversity, functional diversity, and community distinctness) (8, 9). In biodiversity and ecosystem service research, species richness is the most frequent unit of measure (6) and hypotheses regarding increased biodiversity are often stated in terms of increased species number [e.g., more species confer greater cultural ecosystem services (CES) value] (10, 11).

Studies of biodiversity-based ecosystem services rarely assess alternate metrics of biodiversity and seldom provide empirical links between biodiversity indicators and social preferences for ecosystem services (12). CES—the nonmaterial benefits provided by ecosystems (13)—are among the least-quantified ecosystem services (14–16). Due to their normative nature and often abstract definitions (17), CES can be challenging to study. They represent complex relationships between people and ecosystems, and the definition and valuation of a particular cultural service can vary across stakeholders (18, 19).

For biodiversity-based CES, common practice has been to map species richness as an indicator and use those maps to assess the spatial provision of CES (see, e.g., refs. 17 and 19–22). However, there is little known about whether maps of species richness correspond to actual social preferences for CES. Biodiversity conservation depends on the values that people attach to it (23, 24) and understanding people's preferences for biodiversity can facilitate communication between the public and land managers and help delineate publicly supported conservation goals (18). In particular, if social preferences can be translated to maps of CES indicators (25) a more complete assessment of conservation objectives targeted at maintaining biodiversity and CES is possible (26, 27).

Aesthetic beauty is a commonly cited CES in amenity-based landscapes (13, 28, 29) and is often assumed to be positively correlated with biodiversity (30, 31). Species-rich, flower-rich views improve the aesthetic value of landscapes, roadsides, field margins, and meadows (32–36), and increased flower color diversity may provide higher CES value, especially in rural landscapes (34, 37–40). Lindemann-Matthies et al. (40) demonstrated that aesthetic appreciation increased with perceived species richness. Moreover, aesthetic appreciation and perceived species richness also increased with evenness (i.e., the equitability of species in

Significance

Sustaining biodiversity and ecosystem services are common conservation goals. However, understanding relationships between biodiversity and cultural ecosystem services (CES) and determining the best indicators to represent CES remain crucial challenges. We combined ecological and social data to compare CES value of wildflower communities based on observed species richness versus revealed social preferences. Using a discrete-choice experiment with images of wildflower communities, we analyzed which aspects of biodiversity were associated with the aesthetic preferences of forest visitors. Although commonly used to indicate biodiversity-based CES, species richness did not predict aesthetic preference. This study suggests that successful management of CES requires understanding stakeholders' preferences to determine conservation priorities.

Author contributions: R.A.G., S.M.P., and M.G.T. designed research; R.A.G. analyzed data; and R.A.G., S.M.P., and M.G.T. wrote the paper.

Reviewers: G.C.D., Stanford University; and E.M., University of Illinois at Chicago.

Conflict of interest statement: M.G.T. is a coauthor on a forthcoming paper with Gretchen Daily. This paper is a workshop report and did not involve a research collaboration.

[1]To whom correspondence may be addressed. Email: turnermg@wisc.edu or ragraves@wisc.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1701370114/-/DCSupplemental.

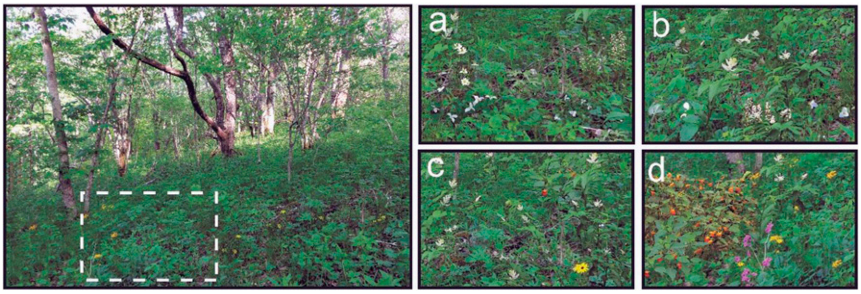

Fig. 1. Examples of digitally manipulated images used in the discrete-choice experiment. A total of 48 images were used. Images all used the same background (see large panel) but varied in the flower species richness, flower abundance, the number of colors, and the evenness of the wildflower community. The cutouts displayed here (*A*–*D*) are illustrative of variation in the images and were selected from images that varied in the number of colors and evenness; species richness and flower abundance were held constant at five species and 90 flowers in these examples. *A* shows one color and low evenness, *B* one color and high evenness, *C* five colors and low evenness, and *D* five colors and high evenness. Based on the results of the discrete-choice experiment, *D* would have the highest predicted wildflower viewing utility. See Fig. S2 for uncropped image examples.

a community), suggesting compositional diversity may also be an important driver of aesthetic preference. Additionally, the presence of species with cultural significance or the presence of rare species can increase satisfaction among wildflower viewers (41) and the aesthetic value of particular species has been used as a reason for conservation (42, 43).

We studied the aesthetic preferences of public forest visitors for trailside wildflower communities to test whether species richness predicted CES value. We conducted the study in the Southern Appalachian Mountains of North Carolina, where wildflower viewing and photographing is one of the fastest-growing outdoor recreational activities (44). Wildflower blooms provide important CES to both residents and tourists (45). The region's high biodiversity, recognized globally, attracts both residents and visitors, many of whom visit public forests to participate in recreation and observe plants and animals (44, 46, 47). We asked three questions about the relationship of biodiversity to CES value: (*i*) How do aesthetic preferences for wildflower communities vary with components of biodiversity, including species richness?; (*ii*) How do aesthetic preferences for wildflower communities vary across psychographic groups? and (*iii*) How well does species richness perform as an indicator of CES value compared with revealed social preferences for wildflower communities?

Public forest visitors were asked to choose among digitally manipulated images of wildflower communities with varied levels of flower species richness, flower abundance, species evenness, color diversity, and presence of charismatic species, as identified from regional tourism websites (*SI Text* and ref. 48) (Fig. 1). Wildflower community preference was analyzed using multinomial logit models that were then used to predict wildflower viewing utility of actual wildflower communities. This analysis is consistent with Lancaster's theory of value (49) and random utility theory (50), which assume that individuals prefer goods or services based on the utility derived from the attributes of those goods or services, and that individuals choose options based on

Table 1. Factor loadings for each forest-based CES and mean factor scores for each psychographic segment

Category	Quiet relaxation	Experiences	Active escape	Collecting
Forest-based CES		Factor loadings		
To find solitude	**0.80**	0.05	0.13	0.16
Spiritual value	**0.74**	0.17	0.14	0.09
To relax	**0.62**	0.18	0.31	0.12
To hear nature sounds	**0.57**	0.50	−0.07	0.07
To see scenic views	0.13	**0.73**	0.16	−0.14
To be with family and friends	−0.25	**0.65**	0.48	0.17
To view wildlife	0.27	**0.65**	−0.04	0.30
To view wildflowers	0.39	**0.64**	−0.10	0.01
To participate in recreation	0.05	0.02	**0.78**	0.06
To be physically active	0.24	−0.03	**0.68**	−0.12
To escape an urban setting	0.42	0.18	**0.43**	−0.02
Educational value	0.29	0.34	**0.40**	0.37
To hunt	0.04	−0.03	0.01	**0.80**
To collect food	0.16	0.09	−0.03	**0.77**
Psychographic segment (*n*)		Mean factor score		
1: Active/experience seekers (77)	−1.27	0.13	0.16	−0.26
2: Quiet seekers (79)	0.48	−0.70	−0.89	−0.38
3: Collectors (36)	0.11	−0.27	−0.02	2.15
4: Generalists (101)	0.55	0.57	0.53	−0.26

Factor loadings along four interpretable dimensions (quiet relaxation, experiences, active escape, and collecting) of respondents' attitudes toward forest-based CES. Factors were extracted from survey response data using principal components solution with varimax rotation. The highest factor loadings for each forest-based CES are bolded. Cluster analysis based on the attitudinal factors identified four psychographic segments of respondents. The segments differed in group size (*n*) and mean scores among the four attitudinal dimensions.

their relative utility. Because individual preferences, beliefs, and expertise may affect aesthetic preferences (51), we tested whether the effect of wildflower diversity on aesthetic preferences varied across psychographic profiles. Finally, using data collected from actual wildflower communities in the study region (48), we compared site prioritization for CES based on empirically measured species richness versus predicted aesthetic preference (i.e., wildflower viewing utility).

Results

We collected usable responses from 293 public forest visitors, representing a cross-spectrum of ages, visitation characteristics, and attitudes (Table S1). Respondents tended to be white (90%) and well-educated (73%), which is representative of recreational visitors in this area (44). Respondents were grouped into segments ranging in size and psychographics based on their attitudes toward forest-based CES, measured along four attitudinal dimensions (Table 1). Thirty-four percent of respondents were generalists, characterized by their high valuation of all forest-based CES (e.g., quiet relaxation, experiences, active escape, and collecting things) (Table 1). The remaining respondents were divided among those that placed high value on active escape (26%), quiet relaxation (27%), or collecting (12%). Nearly half (46%) of respondents reported having visited a forest to view wildflowers within the past year (Table S2).

Aesthetic Preferences for Wildflower Communities. People's aesthetic preferences for wildflower communities varied with components of wildflower diversity but not with flower species richness. Flower species richness had no effect on respondents' aesthetic preference for images of wildflower communities (Table 2). The abundance of flowers was the most important predictor of aesthetic preference, followed by number of colors and evenness. Photographs displaying wildflower communities with higher bloom abundance, more colors, and higher evenness were more likely to be preferred.

Aesthetic Preferences Among Psychographic Segments. Results were remarkably consistent across all four psychographic segments of the respondents, indicating no difference in preference patterns among groups (Table 2 and Table S3). Similarly, preference patterns did not differ based on respondents' knowledge of local flora (i.e., novice, intermediate, or expert) or the value they placed on wildflower viewing (i.e., flowers more or less important) (Table S3).

Species Richness Versus Revealed CES Value in Actual Wildflower Communities. Empirically surveyed wildflower communities (n = 54) varied in flower species richness, flower abundance, evenness of species in bloom, number of colors, and whether charismatic species were present and blooming (48). Overall flower species richness ranged from 2 to 34 ($\bar{x}$ = 11 and SD =7.3). Wildflower viewing utility calculated using multinomial models of revealed preferences (Table S3) ranged from −0.11 to 13.29 ($\bar{x} = 2.2$ and SD = 2.5). For surveyed wildflower communities, predicted CES value (i.e., wildflower viewing utility) was correlated with the overall species richness observed at a site (Spearman's *rho* = 0.66, Fig. 2). Species richness was also correlated with aesthetic traits of flower abundance, evenness, color diversity, and number of charismatic species present (Pearson's r 0.48–0.77, all $P < 0.001$). When sites were classified as CES hotspots (CES values above the median) based on either wildflower viewing utility or overall species richness, classification broadly agreed, with 34 hotspots identified by both indicators. However, site classification based on species richness alone missed 27% (seven) of the sites predicted to have high wildflower viewing utility (Fig. 2). Similarly, ranking sites based on wildflower viewing utility alone missed 29% (eight) of sites predicted to have the highest flower species richness.

Discussion

Conservation planning and management increasingly require consideration of both ecosystem services supply and maintenance of biodiversity. However, despite calls for holistic management of a full suite of ecosystem services to achieve landscape sustainability (52–54) CES have been largely absent from biodiversity and

Table 2. Relative importance of wildflower community attributes from multinomial logit models based on respondent preference for digital photos of wildflower displays

	Relative importance of wildflower community attribute				
Model (n)	Species richness	Flower abundance	No. of colors	Evenness	Presence of charismatic species
All respondents (293)	0.02	0.53	0.24	0.12	0.09
	Psychographic segments based on attitudes toward forest CES				
1. Active/experience seekers (77)	0.01	0.50	0.27	0.14	0.09
2. Quiet seekers (79)	0.05	0.56	0.18	0.12	0.09
3. Collectors (36)	0.05	0.50	0.28	0.13	0.05
4. Generalists (101)	0.01	0.49	0.28	0.11	0.11
Wald (=)	0.53	1.05	10.34	0.56	1.32
	Segments based on attitude toward wildflower viewing				
Flowers less important (78)	0.11	0.54	0.11	0.15	0.08
Flowers mores important (210)	0.01	0.50	0.27	0.11	0.10
Wald (=)	2.96	0.02	8.33*	0.34	0.19
	Segments based on knowledge of local flora				
Novice (77)	0.02	0.59	0.18	0.15	0.07
Intermediate (174)	0.02	0.49	0.29	0.12	0.08
Expert (42)	0.03	0.49	0.23	0.08	0.17
Wald (=)	0.23	4.40	5.03	1.30	2.80

The first model is based on all respondents. The remaining models analyzed segments of the respondents based on their attitudes toward forest-based CES, attitudes toward wildflower viewing, and knowledge of local flora. Relative importance values provide a measure of the relative effect of each attribute. See Table S3 for full model results and coefficient estimates. Significant Wald (=) values indicate differences in the estimated coefficient of an attribute between segments.
*$P < 0.05$.

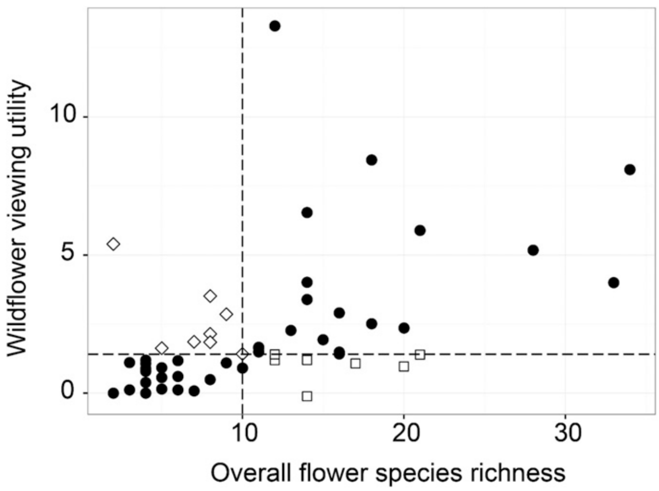

Fig. 2. Predicted wildflower viewing utility correlated with overall flower species richness of 54 wildflower communities in the southern Appalachian Mountains. Dashed lines show the hotspot classification thresholds (median values) for each indicator. Sites were either not hotspots (below the median, bottom left quadrant), agreed-upon hotspots (above the median, top right), or hotspots based on either wildflower viewing utility (top left) or species richness (bottom right) but not the other. Closed circles indicate agreement, and open symbols indicate disagreement in hotspot classification. Wildflower community data were collected over an 18-wk period between April and August 2014 (see ref. 48 for details); discrete-choice data used to predict wildflower viewing utility were collected in 2015.

ecosystem service literature. We linked stakeholders' revealed preferences with empirical measurements of wildflower community diversity and demonstrated that only partial overlap exists between high species richness and high CES supply. Species richness per se was not a significant predictor of aesthetic preference, and site rankings based on empirically measured wildflower communities showed that the use of observed species richness as a CES indicator does not fully encompass sites with high predicted CES value. Thus, management of biodiversity-based CES and conservation of species diversity should be considered complementary, but different, goals when developing landscape conservation targets (55).

People's aesthetic preference for images of trailside wildflower communities was driven primarily by the abundance of flowers and not by species richness of flowers. However, people preferred wildflower communities with more colors, suggesting that although respondents may not distinguish between flower species if they are the same color (Fig. 1 *A* and *B*) they recognize diversity in colors (Fig. 1 *C* and *D*). Our models suggest people respond to a complex combination of these floral traits, which were generally correlated with species richness in our study area, but not perfectly so. Because perceived species richness has been linked to aesthetic value and support for biodiversity conservation (40), misperceptions of the species richness in wildflower communities with lower color diversity could lead to biases in people's attitudes toward these wildflower communities. Our study did not test explicitly whether people judged wildflower communities with more colors to be more species-rich, which limited our ability to judge whether visitors preferred wildflower communities that they perceived as more species-rich. If people's perception and preferences are closely linked (56), and people's perception of species richness does not match actual species richness (57), promoting education that emphasizes knowledge about species diversity could increase appreciation of sites with high flower diversity but low color diversity.

Our study suggests that targeting management at sites with high wildflower viewing utility will yield benefits across a spectrum of visitors. People value nature for many different reasons including intrinsic, economic, emotional, spiritual, or psychological values that are not mutually exclusive (24). Landscape aesthetic preferences can vary based on age (56), gender (58), cultural and social groups (59–61), and recreation patterns (58, 60). However, preferences for wildflower communities in this study were remarkably similar across demographic, attitudinal, and recreational groups and were instead driven by the attributes of the wildflower communities. These results suggest that variation in aesthetic preference is greater among sites than across public forest visitors (61, 62). Because aesthetic appreciation and scenic beauty are desired conditions in recreation and outdoor tourism in amenity-based landscapes (44, 63, 64), understanding how to manage aesthetic CES can have positive impacts for residents and visitors to these areas.

Aesthetic preference varies among persons. Whereas preferences among psychographic groups were similar, the discrete-choice models explained only about 30% of the variation among individual respondents. Cultural preference theories contend that the attitudes of each individual are in constant flux and are shaped by cultural and personal experiences (e.g., ref. 65). Both biophysical and personal–social situational context affects aesthetic experience (30). In our study, we tested both the biological factors (i.e., wildflower community traits) and cultural factors (i.e., age, gender, and botanical knowledge). Unmeasured factors related to a person's attitude and ethnic and cultural background could explain the remaining variation, but this information was beyond the scope of this study and impractical to collect under the field conditions.

In conservation and sustainability science, determining how to best conserve the biosphere while meeting the needs of humans has led to vigorous debate. Although increasing recognition of ecosystem services and the contribution of ecosystems and biodiversity to human well-being has the potential strengthen conservation (1, 28, 66–69), some authors have suggested that increased emphasis on ecosystem services as a conservation goal may lead to unintended losses and inadequate protections for biodiversity (8, 70, 71). In part, this debate stems from lack of clarity about the multiple relationships between biodiversity and ecosystem services (66). Studies have revealed both positive and negative relationships between priority areas for biodiversity and priority areas for the provision of ecosystem services, complicating landscape conservation planning (56–59). To preserve aesthetic beauty and the CES provided by wildflower communities, some maintenance of species diversity, which allows for a diversity of flower forms and colors, is important. However, despite correlations between richness and CES value in wildflower communities, conservation and management priorities based solely on maintaining species richness may not adequately conserve sites that supply biodiversity-based CES. Conservation priorities targeted at achieving sustainability of CES should use suitable indicators, beyond measures of species richness, that incorporate social preferences and recognize the multiple ways that biodiversity may contribute to the provision of ecosystem services.

Methods

Study Area. We collected empirical data on wildflower communities (48) and people's aesthetic preferences in the French Broad River Basin (FBRB) in western North Carolina during the summers of 2014 and 2015. The FBRB, located within the southern Appalachian Mountains, covers an area of 7,330 km^2 (Fig. S1). The region is characterized by complex terrain and is known for its high biodiversity and popular for ecotourism (46) (see *SI Text* for more detail). Approximately 75% of the FBRB is forested, mainly second growth, with spruce-fir (*Picea-Abies*) and northern hardwoods at high elevations, mixed hardwood species at lower elevations, and mixed mesophytic forests on lower slopes and coves (46). The regional economy changed in the last century from resource extraction (e.g., timber) and agricultural production to a nature-based, amenity-driven economy, leading to altered patterns of land use and increased exurban development (72–74). Land-use changes have altered plant communities within the region (73, 75–77) and likewise affect the location and abundance floral resources within the study area (48).

Aesthetic Preferences for Wildflower Communities. We surveyed 295 public forest visitors using a convenience sampling approach at trailheads on national forest and state forest properties. Face-to-face surveys were conducted at trailheads and visitor information points during the summer of 2015. We varied the day of the week and time of day that each trailhead was visited, and individual surveys generally lasted less than 5 min. Once a survey was completed, the next visitor encountered was asked to participate in the study. At remote trailheads with limited use, we posted signs asking people to complete an online version of our survey. Online respondents accounted for 5% of our respondents. This study was approved by the University of Wisconsin–Madison Education and Social/Behavior Science institutional review board (IRB no. 2015-0384). All interviewees gave their informed consent to participate in the study.

The survey (*SI Text*) consisted of three parts: (*i*): respondents' attitudes toward a set of CES provided by public forests, (*ii*) respondents' recreational patterns and social and demographic data, and (*iii*) a discrete-choice experiment to determine preferences for different wildflower communities. Respondents' attitudes toward forest-based CES were measured with the help of 15 statements about forest uses (Table S4). Respondents indicated their personal valuation of each service on a five-point Likert-type scale (1: unimportant, 2: somewhat important, 3: important, 4: very important, and 5: extremely important). Respondents were asked to provide an estimate of the frequency with which they visited public forests in the last year and what activities they participated in while visiting public forests. We also asked them for their gender, age, race, highest level of education, and a self-assessment of their knowledge of plants in the area (1: no knowledge, 2: novice with some knowledge, 3: intermediate knowledge, and 4: expert knowledge).

Preferences for wildflower communities were obtained using a discrete-choice experiment where respondents were shown 8.5- × 11-inch photographs of near-view forest wildflower communities manipulated to contain different levels of diversity (i.e., flower abundance, flower species richness, number of colors, evenness or the distribution of abundance among species in a community, and presence of charismatic species). Respondents were asked to indicate their preferred alternative between pairs of digital images of wildflower communities. Each respondent was shown four pairs of images, or choice sets. The images were created using Adobe Photoshop and choice sets varied according to a D-efficient sampling design (78, 79), which maximizes the amount of information about each parameter through the most efficient number of choice sets. The choice model included 48 images organized in six blocks of four choice sets (Table S5).

We used factor analysis to identify interpretable dimensions of attitudes toward forest-based CES. Factor analysis has been used previously to study psychographics of survey respondents in nature recreation, ecotourism, and ecosystem service research (33, 80). Exploratory factor analysis identified a four-factor structure describing people's attitudes toward forest-based CES and accounted for 60% of the variance in the dataset (Table 1). We performed K-means cluster analysis to identify segments of respondents with different psychographic profiles based on their attitudes toward forest-based CES, represented by their scores along the four factors (80, 81). The effect of biodiversity attributes on aesthetic preference for wildflower communities was modeled using multinomial logit models (*SI Text*). We first analyzed the preferences of all respondents, without regard for psychographics or demographics, including only the wildflower community attributes. We tested whether the inclusion of interactive effects between the wildflower community attributes and respondents' attitudes toward forest-based CES improved the model fit. We then ran multinomial logit models for groups based on people's preference of different CES, knowledge of plants, demographics, and recreational patterns to determine whether the effect of biodiversity attributes varied across segments. See *SI Text* for more details.

Indicators of CES Value in Actual Wildflower Communities. We used wildflower community data recorded in the study region (48) to evaluate differences between the designation of CES hotspots based on empirically measured flower species richness versus wildflower viewing utility predicted by the revealed preference models. Fifty-four forested sites were visited over the course of an 18-wk growing season (April–August 2014) and richness, abundance, and evenness of plants in flower were recorded, as well as the number of flower colors and presence of charismatic species (see *SI Text* for more details). Sites were visited multiple times, either weekly or triweekly. For each site visit we calculated the predicted wildflower viewing utility, based on the discrete-choice multinomial logit models above. The maximum of the predicted wildflower viewing utility for each site was used as an indicator of CES value. We calculated overall flower species richness for each site using species accumulation curves, which allowed us to account for differences in observed species richness due to survey effort (e.g., weekly sampling versus triweekly sampling).

Finally, we identified sites with the highest CES value, or "hotspots." A variety of methods have been used to define ecosystem service hotspots (4, 81–84). We defined hotspots to be sites above the median value for flower species richness or wildflower viewing utility. We evaluated hotspot congruence based on the two CES indicators: overall flower species richness and maximum wildflower viewing utility. We compared site rankings and hotspot classifications based on these alternate indicators using Spearman rank correlation, Cohen's kappa coefficient, and percent agreement.

ACKNOWLEDGMENTS. We thank B. Beardmore for helpful guidance on study design; G. Daily and E. Minor for constructive suggestions on the manuscript; and A. Mace, E. Damschen, C. Kucharik V. Radeloff, and B. Zuckerberg for helpful comments on early development of these ideas. We also thank the land owners and managers who provided permission for data collection and the many willing survey respondents for their participation. This work was supported by National Science Foundation Long-term Ecological Research Program Grants DEB-0823293 and DEB-1440485 and the University of Wisconsin–Madison Vilas Trust (M.G.T.).

1. TEEB (2009) *The Economics of Ecosystems and Biodiversity (TEEB) for National and International Policy Makers*, ed ten Brink P (Earthscan, London).
2. Díaz S, et al. (2015) The IPBES Conceptual Framework — Connecting nature and people. *Curr Opin Environ Sustain* 14:1–16.
3. Balvanera P, et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* 9(10):1146–1156.
4. Eigenbrod F, et al. (2010) The impact of proxy-based methods on mapping the distribution of ecosystem services. *J Appl Ecol* 47(2):377–385.
5. Anderson BJ, et al. (2009) Spatial covariance between biodiversity and other ecosystem service priorities. *J Appl Ecol* 46(4):888–896.
6. Feld CK, et al. (2009) Indicators of biodiversity and ecosystem services: A synthesis across ecosystems and spatial scales. *Oikos* 118(12):1862–1871.
7. Müller F, Burkhard B (2012) The indicator side of ecosystem services. *Ecosyst Serv* 1(1): 26–30.
8. Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: A multilayered relationship. *Trends Ecol Evol* 27(1):19–26.
9. Cardinale BJ, et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486(7401):59–67.
10. Balvanera P, et al. (2014) Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps. *Bioscience* 64(1):49–57.
11. Fuller RA, Irvine KN, Devine-Wright P, Warren PH, Gaston KJ (2007) Psychological benefits of greenspace increase with biodiversity. *Biol Lett* 3(4):390–394.
12. Plieninger T, Dijks S, Oteros-Rozas E, Bieling C (2013) Assessing, mapping, and quantifying cultural ecosystem services at community level. *Land Use Policy* 33:118–129.
13. Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Multiscale Assessments* (Island, Washington, DC).
14. Cardinale BJ, et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486: 59–67.
15. Daniel TC, et al. (2012) Contributions of cultural services to the ecosystem services agenda. *Proc Natl Acad Sci USA* 109(23):8812–8819.
16. Hernández-Morcillo M, Plieninger T, Bieling C (2013) An empirical review of cultural ecosystem service indicators. *Ecol Indic* 29:434–444.
17. Satz D, et al. (2013) The challenges of incorporating cultural ecosystem services into environmental assessment. *Ambio* 42(6):675–684.
18. Plieninger T, et al. (2013) Exploring futures of ecosystem service in cultural landscapes through participatory scenario development in the Swabian Alb, Germany. *Ecol Soc* 18(3):39.
19. De Vos A, Cumming GS, Moore CA, Maciejewski K, Duckworth G (2016) The relevance of spatial variation in ecotourism attributes for the economic sustainability of protected areas. *Ecosphere* 7(2):e1207.
20. Dallimer M, et al. (2015) Historical influences on the current provision of multiple ecosystem services. *Glob Environ Change* 31:307–317.
21. Villamagna AM, Angermeier PL, Niazi N (2014) Evaluating opportunities to enhance ecosystem services in public use areas. *Ecosyst Serv* 7:167–176.
22. Villamagna AM, Mogollón B, Angermeier PL (2014) A multi-indicator framework for mapping cultural ecosystem services: The case of freshwater recreational fishing. *Ecol Indic* 45:255–265.
23. Saunders CD, Brook AT, Myers OE, Jr (2006) Using psychology to save biodiversity and human well-being. *Conserv Biol* 20(3):702–705.
24. Trombulak SC, et al. (2004) Principles of conservation biology: Recommended guidelines for conservation literacy from the education committee of the Society for Conservation Biology. *Conserv Biol* 18(5):1180–1190.

25. van Berkel DB, Verburg PH (2014) Spatial quantification and valuation of cultural ecosystem services in an agricultural landscape. *Ecol Indic* 37:163–174.
26. Egoh B, et al. (2007) Integrating ecosystem services into conservation assessments: A review. *Ecol Econ* 63(4):714–721.
27. Balvanera P, et al. (2001) Conserving biodiversity and ecosystem services. *Science* 291(5511):2047.
28. Daily GC (2001) Management objectives for the protection of ecosystem services. *Environ Sci Policy* 3(6):333–339.
29. Wallace KJ (2007) Classification of ecosystem services: Problems and solutions. *Biol Conserv* 139(3–4):235–246.
30. Gobster PH, Nassauer JI, Daniel TC, Fry G (2007) The shared landscape: What does aesthetics have to do with ecology? *Landsc Ecol* 22(7):959–972.
31. Quijas S, et al. (2012) Plant diversity and generation of ecosystem services at the landscape scale: Expert knowledge assessment. *J Appl Ecol* 49(4):929–940.
32. Marshall EJP, Moonen AC (2002) Field margins in northern Europe: Their functions and interactions with agriculture. *Agric Ecosyst Environ* 89(1–2):5–21.
33. Junge X, Schüpbach B, Walter T, Schmid B, Lindemann-Matthies P (2015) Aesthetic quality of agricultural landscape elements in different seasonal stages in Switzerland. *Landsc Urban Plan* 133:67–77.
34. Junge X, Jacot KA, Bosshard A, Lindemann-Matthies P (2009) Swiss people's attitudes towards field margins for biodiversity conservation. *J Nat Conserv* 17(3):150–159.
35. Strumse E (1996) Demographic differences in the visual preferences for agrarian landscape in Western Norway. *J Environ Pyschology* 16:17–31.
36. Akbar KF, Hale WHG, Headley AD (2003) Assessment of scenic beauty of the roadside vegetation in northern England. *Landsc Urban Plan* 63(3):139–144.
37. Quétier F, Lavorel S, Thuiller W, Davies I (2007) Plant-trait-based modeling assessment of ecosystem-service sensitivity to land-use change. *Ecol Appl* 17(8):2377–2386.
38. Quétier F, et al. (2009) Social representations of an alpine grassland landscape and socio-political discourses on rural development. *Reg Environ Change* 10(2):119–130.
39. Lindemann-Matthies P, Bose E (2007) Species richness, structural diversity and species composition in meadows created by visitors of a botanical garden in Switzerland. *Landsc Urban Plan* 79(3):298–307.
40. Lindemann-Matthies P, Junge X, Matthies D (2010) The influence of plant diversity on people's perception and aesthetic appreciation of grassland vegetation. *Biol Conserv* 143(1):195–202.
41. Martin SR (1997) Specialization and differences in setting preferences among wildlife viewers. *Hum Dimens Wildl* 2(1):1–18.
42. Hector A, Joshi J, Lawler S, Spehn EM, Wilby A (2001) Conservation implications of the link between biodiversity and ecosystem functioning. *Oecologia* 129(4):624–628.
43. Stokes DL (2007) Things we like: Human preferences among similar organisms and implications for conservation. *Hum Ecol* 35(3):361–369.
44. Cordell HK (2012) Outdoor recreation trends and futures: A technical document supporting the Forest Service 2010 RPA assessment. General Technical Report SRS-150 (US Department of Agriculture Forest Service, Asheville, NC).
45. Watson A, Williams D, Roggenbuck J, Daigle J (1992) Visitor characteristics and preferences for three national forest wildernesses in the SouthResearch Paper INT-455 (US Department of Agriculture Forest Service, Ogden, UT).
46. SAMAB (1996) The Southern Appalachian Assessment. Terrestrial Resources Technical Report 5 (US Department of Agriculture Forest Service, Atlanta, GA).
47. Brown DG, Johnson KM, Loveland TR, Theobald DM (2010) Rural land-use trends in the conterminous United States, 1950-2000. *Ecol Appl* 15:1851–1863.
48. Graves RA, Pearson SM, Turner MG (2016) Landscape dynamics of floral resources affect the supply of a biodiversity-dependent cultural ecosystem service. *Landsc Ecol* 32:415–428.
49. Lancaster KJ (1966) A new approach to consumer theory. *J Polit Econ* 74(2):132–157.
50. McFadden D (1974) The measure of urban travel demand. *J Public Econ* 3:303–328.
51. Gobster PH (1999) An ecological aesthetic for forest landscape management. *Landscape J* 18(1):54–64.
52. Sevenant M, Antrop M (2009) Cognitive attributes and aesthetic preferences in assessment and differentiation of landscapes. *J Environ Manage* 90(9):2889–2899.
53. Lindemann-Matthies P, Keller D, Li X, Schmid B (2013) Attitudes toward forest diversity and forest ecosystem services–A cross-cultural comparison between China and Switzerland. *J Plant Ecol* 7(1):1–9.
54. Nielsen AB, Olsen SB, Lundhede T (2007) An economic valuation of the recreational benefits associated with nature-based forest management practices. *Landsc Urban Plan* 80(1):63–71.
55. Hunter ML, Jr, Redford KH, Lindenmayer DB (2014) The complementary niches of anthropocentric and biocentric conservationists. *Conserv Biol* 28(3):641–645.
56. Kaplan R, Kaplan S (1989) *The Experience of Nature: A Psychological Perspective* (Cambridge Univ Press, Cambridge, UK).
57. Lindemann-Matthies P, Bose E (2008) How many species are there? Public understanding and awareness of biodiversity in Switzerland. *Hum Ecol* 36(5):731–742.
58. Tyrväinen L, Silvennoinen H, Kolehmainen O (2003) Ecological and aesthetic values in urban forest management. *Urban For Urban Green* 1:135–149.
59. Bauer N, Wallner A, Hunziker M (2009) The change of European landscapes: Human-nature relationships, public attitudes towards rewilding, and the implications for landscape management in Switzerland. *J Environ Manage* 90(9):2910–2920.
60. Daniel TC (2001) Whither scenic beauty? Visual landscape quality assessment in the 21st century. *Landsc Urban Plan* 54(1–4):267–281.
61. Cañas I, Ayuga E, Ayuga F (2009) A contribution to the assessment of scenic quality of landscapes based on preferences expressed by the public. *Land Use Policy* 26(4): 1173–1181.
62. Needham MD, et al. (2011) Motivations and normative evaluations of summer visitors at an alpine ski area. *J Travel Res* 50(6):669–684.
63. van Riper CJ, Kyle GT, Sutton SG, Barnes M, Sherrouse BC (2012) Mapping outdoor recreationists' perceived social values for ecosystem services at Hinchinbrook Island National Park, Australia. *Appl Geogr* 35(1):164–173.
64. Armsworth PR, et al. (2007) Ecosystem-service science and the way forward for conservation. *Conserv Biol* 21(6):1383–1384.
65. Lothian A (1999) Landscape and the philosophy of aesthetics: Is landscape quality inherent in the landscape or in the eye of the beholder? *Landsc Urban Plan* 44: 177–198.
66. Tallis H, Kareiva P, Marvier M, Chang A (2008) An ecosystem services framework to support both practical conservation and economic development. *Proc Natl Acad Sci USA* 105(28):9457–9464.
67. Ghazoul J (2007) Placing humans at the heart of conservation. *Biotropica* 39(5): 565–566.
68. Kareiva P, Marvier M (2012) What is conservation science? *Bioscience* 62(11):962–969.
69. McShane TO, et al. (2011) Hard choices: Making trade-offs between biodiversity conservation and human well-being. *Biol Conserv* 144(3):966–972.
70. Soulé M (2014) The "new conservation." *Keeping the Wild: Against the Domestication of Earth* (Island, Washington, DC), pp 66–80.
71. Tscharntke T, et al. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol Rev Camb Philos Soc* 87(3):661–685.
72. Wear DN, Bolstad P (1998) Land-use changes in Southern Appalachian landscapes: spatial analysis and forecast evaluation. *Ecosystems (N Y)* 1:575–594.
73. Turner MG, Pearson SM, Bolstad PV, Wear DN (2003) Effects of land-cover change on spatial pattern of forest communities in the Southern Appalachian Mountains (USA). *Landsc Ecol* 18:449–464.
74. Gragson TL, Bolstad PV (2006) Land use legacies and the future of Southern Appalachia. *Soc Nat Resour* 19(2):175–190.
75. Pearson SM, Turner MG, Drake JB (1999) Landscape change and habitat availability in the Southern Appalachian Highlands and the Olympic Peninsula. *Ecol Appl* 9(4): 1288–1304.
76. Fraterrigo JM, Turner MG, Pearson SM (2006) Interactions between past land use, life-history traits and understory spatial heterogeneity. *Landsc Ecol* 21(5):777–790.
77. Kuhman TR, Pearson SM, Turner MG (2011) Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment. *Can J Res* 41:920–929.
78. Lourenco-Gomes L, Costa Pinto LM, Rebelo J (2013) Using choice experiments to value a world cultural heritage site: reflections on the experimental design. *J Appl Econ* 16(2):303–331.
79. Silvestrini RT (2015) Considerations for D-optimal sequential design. *Qual Reliab Eng Int* 31(3):399–410.
80. Galloway G (2002) Psychographic segmentation of park visitor markets: Evidence for the utility of sensation seeking. *Tour Manage* 23(6):581–596.
81. Arnberger A, Haider W (2005) Social effects on crowding preferences of urban forest visitors. *Urban For Urban Green* 3(3):125–136.
82. Egoh B, et al. (2008) Mapping ecosystem services for planning and management. *Agric Ecosyst Environ* 127(1-2):135–140.
83. Qiu J, Turner MG (2013) Spatial interactions among ecosystem services in an urbanizing agricultural watershed. *Proc Natl Acad Sci USA* 110(29):12149–12154.
84. Gimona A, van der Horst D (2007) Mapping hotspots of multiple landscape functions: a case study on farmland afforestation in Scotland. *Landsc Ecol* 22(8):1255–1264.
85. Vogler JB, Shoemaker DA, Dorning M, Meentemeyer RK (2010) Mapping historical development patterns and forecasting urban growth in Western North Carolina: 1976–2030 (Univ of North Carolina at Charlotte, Charlotte, NC).
86. GroWNC (2013) GroWNC regional plan: Final report (GroWNC, Asheville, NC). Available at www.gro-wnc.org/pdf/Regional%20Plan/GroWNC_Regional_Plan_Final_small.pdf.
87. Strom E, Kerstein R (2015) Mountains and muses: Tourism development in Asheville, North Carolina. *Ann Tour Res* 52:134–147.
88. US Travel Association (2016) The economic impact of travel of North Carolina Counties. Available at https://partners.visitnc.com/economic-impact-studies.
89. Visit North Carolina (2015) 2014 North Carolina regional travel summary (Economic Development Partnership of North Carolina, Cary, NC). Available at https://partners.visitnc.com/visitor-profile-studies.
90. Adams K (2004) *North Carolina's Best Wildflower Hikes: The Mountains* (Westcliffe, Boulder, CO).
91. Hair JF, Black WC, Babin BJ, Anderson RE (2009) *Multivariate Data Analysis* (Prentice Hall, Upper Saddle River, NJ), 7th Ed.
92. Costello AB, Osborne JW (2005) Best practices in exploratory factor analysis: Four recommendations for getting the most from your analysis. *Pract Assess Res Evaluation* 10(7):1–9.
93. Oksanen J, et al. (2015) vegan: Community Ecology Package. Available at https://cran.r-project.org/web/packages/vegan/index.html.
94. Revelle W (2016) psych: Procedures for Personality and Psychological Research. Available at https://cran.r-project.org/web/packages/psych/index.html.
95. Vermunt JK, Magidson J (2005) Technical guide for Latent GOLD 4.0: Basic and advanced. Available at https://pdfs.semanticscholar.org/eaaf/8784d711bbc8d67900770ed9dd30e09bcd09.pdf.
96. Smith B, Wilson JB (1996) A consumer's guide to evenness indices. *Oikos* 76(1):70–82.

SUSTAINABILITY SCIENCE