Spatial interactions among ecosystem services in an urbanizing agricultural watershed

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Understanding spatial distributions, synergies, and tradeoffs of multiple ecosystem services (benefits people derive from ecosystems) remains challenging. We analyzed the supply of 10 ecosystem services for 2006 across a large urbanizing agricultural watershed in the Upper Midwest of the United States, and asked the following: (i) Where are areas of high and low supply of individual ecosystem services, and are these areas spatially concordant across services? (ii) Where on the landscape are the strongest tradeoffs and synergies among ecosystem services located? (iii) For ecosystem service pairs that experience tradeoffs, what distinguishes locations that are “win–win” exceptions from other locations? Spatial patterns of high supply for multiple ecosystem services often were not coincident; locations where six or more services were produced at high levels (upper 20th percentile) occupied only 3.3% of the landscape. Most relationships among ecosystem services were synergies, but tradeoffs occurred between crop production and water quality. Ecosystem services related to water quality and quantity separated into three different groups, indicating that management to sustain freshwater services along with other ecosystem services will not be simple. Despite overall tradeoffs between crop production and water quality, some locations were positive for both, suggesting that tradeoffs are not inevitable everywhere and might be ameliorated in some locations. Overall, we found that different areas of the landscape supplied different suites of ecosystem services, and their lack of spatial concordance suggests the importance of managing over large areas to sustain multiple ecosystem services.

Spatial interactions among ecosystem services

Research on ecosystem services—the benefits people obtain from nature—has grown rapidly (1–3), yet understanding of the interactions among multiple ecosystem services across heterogeneous landscapes remains limited (3–5). Ecosystem services may interact in complex ways (6, 7). Synergies arise when multiple services are enhanced simultaneously (4), and tradeoffs occur when the provision of one service is reduced as a consequence of increased use of another (7). Managing spatial relationships among diverse ecosystem services may help to strengthen landscape resilience, but interactions among services and their spatial patterns are not well understood (4). Ecosystem service supply has been mapped at various scales (8–12), and spatial concordance among services has been examined to identify “win–win” opportunities for ecosystem service conservation (13–19). However, few studies have dealt simultaneously with tradeoffs and synergies among a suite of ecosystem services (20–22), and none have done so using spatially explicit analyses. Thus, little is known about where tradeoffs and synergies among ecosystem services are most pronounced. Such information could identify areas of disproportionate importance in a landscape, such as locations where synergies are strong or conflicts among competing services are likely, and spatially target management actions designed to conserve ecosystem services (23).

Ecosystem services related to freshwater (e.g., water supply, surface and groundwater quality, and flood regulation) are of particular concern in agricultural and urban landscapes. These hydrologic services are strongly influenced by the terrestrial landscape (24), and degradation of water resources is often associated with agricultural and urban land use (25–27). Surprisingly few studies have quantified the distribution of key biophysical components of hydrologic services and assessed their relationships with other ecosystem services in regional watersheds, and these studies have focused on a limited set of freshwater services and/or pairwise correlations with other services (19, 24). Research is needed to quantify a range of freshwater services at regional scales and to understand their interactions with other ecosystem services.

Interest in achieving win–win outcomes (in which two or more services are enhanced) through management of ecosystem services is growing (28, 29). Several recent studies have suggested that it is possible to alleviate conflicts among competing services and produce win–win situations through proper interventions or conservation efforts (15, 18, 30, 31). However, these studies considered a limited range of ecosystem services (32), and none has examined win–win exceptions for services that were inversely correlated. Overall, win–wins appear to be uncommon and challenging to attain, and enthusiasm for such outcomes may be outpacing evidence of what is possible and how to achieve them (29). More effort is required to detect win–win outcomes and to evaluate their potential for mitigating tradeoffs and conserving multiple ecosystem services.

We studied the production, spatial distribution, and interactions among multiple provisioning, regulating, and cultural ecosystem services in the Yahara Watershed, Wisconsin (Fig. S1). This largely agricultural watershed drains 1,336 km² and includes five major lakes. Presettlement vegetation was a mix of prairie and savanna vegetation (33) that was converted to agriculture during the mid-1800s. Farms are currently dominated by corn, soybeans, and dairy, but the watershed also includes a densely populated urban area (Madison, WI) and remnant native vegetation. The Yahara Watershed typifies many agricultural landscapes in the Midwest, making it an ideal microcosm of the larger region (34). We used empirical estimates and spatially explicit models to quantify and map indicators of supply of 10 ecosystem services (Table 1) at 30-m spatial resolution for 2006, the most recent year for which data were available for all services. We asked three questions: (i) Where are areas of high and low supply of individual ecosystem services, and are these areas spatially concordant across services? (ii) Where on the landscape are the strongest tradeoffs and synergies among ecosystem services located? (iii) For ecosystem service pairs that experience tradeoffs, what distinguishes locations that are win–win exceptions from other locations? We assessed the degree of spatial congruence of the upper and lowest 20th percentile (by area) of each service to identify “hotspots” and “coldspots” of...
multiple service delivery. Hotspots were defined as locations containing six or more services in the upper 20th percentile and coldspots as locations with six or more services in the lowest 20th percentile. No area on the landscape can have high or low supply of all 10 services, and some services are mutually exclusive based on land-cover class; six services represented a majority that allowed all land-cover types to provide multiple services (SI Text). We used factor analysis to identify tradeoffs and synergies among the 10 services based on a random sample of 1,000 points. Factor scores were mapped to identify locales with the most pronounced synergies and tradeoffs across the landscape. We identified win–win exceptions from ecosystem service tradeoffs by multicriteria analysis and used backward logistic regression model to explore biophysical and social factors that distinguish these win–win areas. Please see Materials and Methods and SI Text for further details.

**Results**

Production of individual ecosystem services varied substantially across the landscape (Table 1, Fig. 1) and showed distinct

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**Table 1. Ecosystem services, biophysical indicators, median, and range for 10 ecosystem services quantified and mapped for the Yahara Watershed, Wisconsin, for the year 2006**

<table>
<thead>
<tr>
<th>Ecosystem service</th>
<th>Biophysical indicator</th>
<th>Estimated values for 2006</th>
</tr>
</thead>
<tbody>
<tr>
<td>Provisioning services</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crop production</td>
<td>Expected annual crop yield</td>
<td>0 (0–57.6 bushel/y)</td>
</tr>
<tr>
<td>Pasture production</td>
<td>Expected annual forage yield</td>
<td>0 (0–2.2 animal unit mo/y)</td>
</tr>
<tr>
<td>Freshwater supply</td>
<td>Annual groundwater recharge</td>
<td>41.7 (0–126.0 cm/y)</td>
</tr>
<tr>
<td>Regulating services</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carbon storage</td>
<td>Amount of carbon stored</td>
<td>70.9 (0–192.3 Mg/ha)</td>
</tr>
<tr>
<td>Groundwater quality</td>
<td>Probability of groundwater nitrate concentration &gt;3.0 mg/L</td>
<td>0.5 (0–1.0; unitless)</td>
</tr>
<tr>
<td>Surface water quality</td>
<td>Annual phosphorus loading</td>
<td>0.1 (0–0.6 kg/ha)</td>
</tr>
<tr>
<td>Soil retention</td>
<td>Annual sediment yield</td>
<td>0.01 (0–1.0 t/ha)</td>
</tr>
<tr>
<td>Flood regulation</td>
<td>Flood regulation capacity</td>
<td>67.9 (0–100; unitless)</td>
</tr>
<tr>
<td>Cultural services</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest recreation</td>
<td>Recreation score</td>
<td>0 (0–100; unitless)</td>
</tr>
<tr>
<td>Hunting recreation</td>
<td>Recreation score</td>
<td>0 (0–100; unitless)</td>
</tr>
</tbody>
</table>

See SI Text and Fig. S2 for details and validation of estimates.

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Fig. 1. Spatial distributions of 10 ecosystem services in the Yahara Watershed, Wisconsin, for 2006. Red indicates areas with high supply and green indicates low supply of ecosystem services.
geographic distributions that were spatially aggregated (all Moran’s I > 0.39, P < 0.001). For descriptive statistics and cumulative frequency distributions (CFDs) for each service, please see SI Text, Table S1, and Fig. S3. Areas of high ecosystem service production often were not spatially concordant among different services (Fig. 2). Hotspots occupied only 3.3% of the landscape (Fig. 2B and Fig. S4) and frequently coincided with nature preserves, wildlife areas, parks, and riparian zones. Half of the landscape produced high values of one or no ecosystem service; these locations were primarily croplands or developed lands. Coldspots occupied 24.5% of the landscape (Fig. 2D and Fig. S4) and coincided with croplands, roads, and urban areas. Spatially, hotspots were few in number and small in size (patch density = 3.1 km⁻², area-weighted mean patch size = 12 ha), whereas coldspots were more numerous and larger in size (patch density = 10.2 km⁻², area-weighted mean patch size = 1,594 ha). The cohesion index was also greater for coldspots (98.1%) than for hotspots (84.1%), indicating greater connectivity among coldspots.

For soil retention, surface water quality, and groundwater quality, we also evaluated coldspots by using a complementary approach in which ecological thresholds were used to map areas where levels were undesirable or unacceptable (see SI Text for details). The resulting maps revealed that thresholds were exceeded for soil retention, surface water quality, and ground-water quality in 28.5%, 8.0%, and 20.7% of the watershed, respectively (Fig. S5 A–C). When using these maps of threshold-based estimates along with the lowest 20th percentile maps of the other seven services to identify coldspots among all 10 services, coldspots occupied 23.4% of the landscape, similar to the maps based on the lowest 20th percentiles, and spatial patterns were nearly identical (Fig. S5 D and E).

Three distinct groups of ecosystem services were identified by factor analysis, which revealed synergies and tradeoffs among the 10 services (Table 2). The first factor ("forest and water synergies") identified positive relationships among four services, of which three were regulating services (carbon storage, surface water quality, and soil retention) and one was a cultural service (forest recreation). The second factor ("pasture and water synergies") identified positive relationships among two provisioning services (pasture production and freshwater supply) and a regulating service (flood regulation). The third factor ("crop and water quality tradeoffs") identified tradeoffs between a provisioning service (crop yield) and two regulating services (ground and surface water quality). One service (hunting) remained independent (all factor loadings <0.30). The four hydrologic services (freshwater supply, surface and groundwater quality, flood regulation) were distributed among the three orthogonal factors (Table 2).

The spatial patterns of synergies and tradeoffs among ecosystem services were complex (Fig. 3). The strongest forest and water synergies were patchy, widely scattered (Fig. 3A), and concentrated primarily in forests, woody wetlands, grasslands, and remnant prairies. Some of these areas were adjacent to aquatic ecosystems and likely functioned as buffers for retaining nutrients and sediment. The most pronounced pasture and water synergies were situated on lands dominated by perennial grasses or hay crops, such as alfalfa (Fig. 3B). These areas supplied forage for a large number of animal units while providing groundwater recharge and flood regulation services. The strongest tradeoffs between crop production and water quality were found in the most productive and intensively managed croplands (Fig. 3C), where high crop yield was associated with greater phosphorus and nitrogen supply and thus reduced water quality. Despite tradeoffs between crop production and water quality services, there were areas where both could be high (i.e., win–win exceptions; Fig. 4). These locations were not common, occupying only 2.4% of the landscape, with patch sizes ranging from 0.09 to 9.9 ha. However, these areas could be distinguished from other locations. The occurrence of win–win exceptions was positively associated with the amount of adjacent wetlands, depth to water table, and soil silt content, and negatively associated with slope, soil erodibility, soil permeability, and distance to stream (Table 3; Hosmer and Lemeshow test χ² = 5.6, df = 8, P = 0.69).

Discussion

We identified synergies and tradeoffs among ecosystem services and described complex spatial distributions of these services, their spatial congruence, and their interactions in the Yahara Watershed. Variation in the degree of spatial concordance of different ecosystem services, particularly those related to freshwater, suggests that many services will not be good surrogates for others and underlines the importance of managing spatial relationships among multiple ecosystem services (4). The spatial heterogeneity of ecosystem services and their interactions indicates that sustainability of ecosystem service production will require regional-scale management that accounts for the geographic position and spatial distribution of services (23, 35, 36).

The rareness of hotspots on the landscape indicates that it is difficult to obtain high supply of multiple services from the same area. Nonetheless, at 3.3% of the landscape, hotspots occupied an area greater than 40 km² and may represent conservation priorities; the loss or degradation of these sites could cause multiple services to decline. Hotspots also may be disproportionately important because these areas of high multifunctional supply of services often coincide with higher species and functional diversity, as suggested by Lavorel et al. (11). Coldspots were even more common and often represented areas that maximized the provision of one or few services. Coldspots may be useful in de-marcating areas of concern (e.g., where ecological thresholds are exceeded) for which intervention or restoration may be especially beneficial. The distinct spatial patterns of hotspots and coldspots suggest landscape-scale tradeoffs, as all locations cannot...
be expected to produce all services. Most of the landscape (≤70%) contributed high supply of one, two, or no services, and a low supply of three to five services (Fig. S4). Thus, producing all services will require an area large enough to encompass the spatial heterogeneity in service supply.

We detected both synergies and tradeoffs among ecosystem services. The forest and water synergies were consistent with those reported in other studies (e.g., ref. 21) and suggested suites of services that may be enhanced (or reduced) simultaneously. For example, other studies have found that afforestation, wetland restoration, and practices that increase riparian-zone vegetation have the potential to increase carbon storage, soil retention, surface water quality, and forest recreation simultaneously (e.g., refs. 24, 37). Similarly, conversion of forest or native vegetation to other land-cover classes may reduce this whole group of services. The pasture and water synergies were consistent with known hydrologic benefits of perennial crops (35). Compared with annual crops, deep-rooted perennial forage crops can increase water infiltration, reduce runoff, and attenuate peak flow, thereby enhancing recharge and mitigating flooding (24, 38, 39). If properly managed, perennial bioenergy crops might produce similar synergies with freshwater ecosystem services while supplying energy rather than animal units (40).

Surprisingly, the only tradeoff among the 10 ecosystem services we quantified was between crop production and water quality. This tradeoff is common in agricultural landscapes and exemplifies a recognized conflict between provisioning and regulating services in production landscapes (41, 42). Regulating services underpin the sustained supply of other essential services and are critical to maintain resilience of production systems (7, 20). Hence, this type of tradeoff implies a compromise between current and future needs (43). Environmental externalities that increase food supply at the expense of regulating services such as water purification may undermine the resilience of agricultural landscapes and the ecosystem services they provide.

Concerns about eutrophication, drinking water pollution, and flood regulation are manifest in many agricultural landscapes. Our analyses revealed that freshwater ecosystem services separated among three distinct groups of ecosystem services that were generally supplied at different places in the landscape. These complex spatial relationships indicate that optimizing freshwater supply, ground and surface water quality, and flood regulation in an agricultural landscape will not be simple; there is no “silver bullet” for managing water sustainability. Individual services will require different strategies, and management to sustain the suite of hydrologic services must conserve places on the landscape that supply each service. The pasture and water synergies imply opportunities for enhancing flood regulation and freshwater supply by promoting perennial crops. Enhanced surface water quality should be associated with management practices that reduce soil erosion. Surface and groundwater quality both had positive loadings on the same factor, indicating that they may respond similarly to the same drivers and/or that one may directly influence the other. Our analysis cannot disentangle
cause and effect, but the results suggest that it would be prudent to consider surface and groundwater as an integrated hydrological and biogeochemical continuum for ecosystem service management (44, 45). An enhanced understanding of how ecosystem services interact and an awareness of tradeoffs and opportunities for synergies will improve the ability to sustainably manage landscapes for joint supply of water resources and other ecosystem services.

Our study attempts to empirically explore win–win exceptions to conflicting services. The existence of win–win exceptions supports prior suggestions that tradeoffs between agricultural production and other services are not inevitable at all locations (38), and our findings suggest where these might be achieved. Crop yield and water quality could both be high in areas with flat topography, less erodible soil, high water-holding capacity, and a deeper water table, conditions that promote plant growth and environmental filtration (e.g., nutrients and contaminants absorption) in soil and root systems (24). Win–win exceptions also had more adjoining wetlands, which trap sediment and remove nutrients from runoff (46, 47), and were closer to streams, where riparian vegetation also filters nutrients (48, 49). Surprisingly, the management factors included in our analysis were not important for distinguishing win–win areas. However, we only considered variables for which continuous spatial data were available in the watershed, and other unmeasured factors or practices (e.g., no-till agriculture, manure digesters) could enhance win–win opportunities. More research is needed to determine the degree to which tradeoffs can be mitigated, and whether the likelihood of win–win outcomes can be increased.

This study has presented an innovative spatially explicit approach for analyzing interactions among multiple ecosystem services and identifying where in the landscape tradeoffs and synergies are most pronounced. We analyzed ecosystem services at fine scales and accounted for landscape heterogeneity in the delivery and relationships among services, contributing to an emerging literature on ecosystem services at landscape scales (11, 18, 23, 50). Relationships observed among services may be a function of the scale at which they are assessed (20), and results could differ if the extent or grain of analysis was changed. The analytic framework could be applied in different regions or other types of landscapes, and it also could be used to explore changes in ecosystem services given alternative future scenarios. Our results also may contribute to improved management of agricultural landscapes for sustainable provision of freshwater and other diverse ecosystem services. Different areas of the landscape supplied different suites of ecosystem services, and their lack of spatial concordance underscores the importance of managing over large areas to sustain multiple ecosystem services.

**Materials and Methods**

Ten ecosystem services that included provisioning, regulating, and cultural services (Table 1) were quantified and mapped at 30-m spatial resolution for the terrestrial landscape of the Yahara Watershed. Ecosystem services were selected based on their importance to this region and the availability of spatial data. Because many services cannot be measured directly and land cover is a poor proxy (51), we used biophysical indicators for each service (Table 1). All services were quantified using data for 2006 or as close as possible to this date. For most ecosystem services, accuracy was assessed by comparing our estimates with field measurements or census data for this region. Full details on data sources, methods, and accuracy assessment for ecosystem service quantification are provided in SI Text, Table S2, and Fig. S2.

All data were imported into ArcGIS 10.0 [Environmental Systems Research Institute (ESRI)] for representation, data manipulation, and analysis. We standardized each service to a scale ranging from zero to one and transformed biophysical indicators as necessary so that higher values corresponded to greater supply of services. We calculated summary statistics (Table S1) and plotted CFDs of the biophysical indicator values for each service on the basis of 30-m grid cells (Fig. S3). The degree of spatial clustering of each service was evaluated using Moran’s I.

Hotspots and coldspots of multiple service supply were identified by overlaying and summing maps of the upper and lowest 20th percentile (by area) of each service (Fig. S3). However, there were two exceptions. First, if >20% (but <80%) of the landscape provided no supply for a given service (e.g., crop production, soil retention; Fig. 1, Fig. S3), we computed the upper 20th percentile directly from the CFD and considered areas of zero service as within the lowest 20th percentile. Second, if <20% of the landscape could potentially provide a certain service (e.g., forest and hunting recreation; Fig. 1, Fig. S3), we considered all areas that produced the service as falling within the upper 20th percentile, and all areas with zero service as within the lowest 20th percentile. Three of the 10 services quantified (soil retention, surface water quality, and groundwater quality) also have ecological or socially accepted thresholds beyond which quality is considered unacceptable (see SI Text for details). Thus, we also mapped areas exceeding ecological thresholds for these services, then recalculated the coldspots map and compared it to the map derived from the lowest 20th percentile data. Spatial patterns of hotspots and coldspots were quantified by computing the proportion of watershed occupied, patch density, area-weighted mean patch size, and patch cohesion index in Fragstats 3.3 (52).

Spatial interactions among multiple ecosystem services were analyzed based on 1,000 randomly sampled points across the watershed. To identify tradeoffs and synergies among services, we used factor analysis, a powerful statistical procedure that determines a smaller number of distinct “factors” that account for the structure of a set of correlated variables (53, 54). The
number of factors was determined by a scree test and the interpretability of derived factors, and we extracted the first three orthogonal factors (with variance explained). Scores for all three factors were calculated for each grid cell based on the loading matrix and mapped to represent the magnitude of tradeoffs and synergies across landscape. All correlation and factor analyses were performed using SAS 9.2 (SAS Institute, Cary, NC).

Multicriteria analysis was used to identify locations of win–win exceptions for crop and water quality tradeoffs (Fig. 56). Specifically, areas with crop production, ground water quality, and surface water quality in the upper 20% of the data set were selected as candidate variables. Three hundred win–win and 300 non–win–win cropland cells were randomly selected and assigned binary values of 1 and 0, respectively. We considered potential explanatory variables at the local (cell) scale (slope, soil physical properties, population density, distance to stream, distance to nearest wetland and forest) and landscape scale (landscape context within a 560-m radius, including the percentage of forest, agricultural, and wetland, as well as percent of areas restricted for nutrient and manure application). The radius for landscape-scale variables was determined as 10 times the size of the largest win–win patch. Please see Table S3 for a full list of candidate variables. All variables were standardized before analysis. Multicollinearity was not a problem among the selected variables, as variance inflation factors ranged from 1.18 to 2.94. We selected the final most parsimonious model and assessed its overall fit using a Hosmer and Lemeshow goodness-of-fit test (55). All logistic regression procedures were performed using R statistical software (56).

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Supporting Information

Qiu and Turner 10.1073/pnas.1310539110

SI Text

Study Area Description

The Yahara Watershed in southern Wisconsin (at 43°6′ N, 89°24′ W), drains 1,336 km² (Fig. S1) and includes five major lakes (Mendota, Monona, Wingra, Waubesa, and Kegonsa). Climate of the region is typically continental (warm humid summers and cold winters) and exhibits strong seasonal and interannual variations. Annual average precipitation is 80 cm, occurring largely from May to September. Topography is generally flat and rolling with gentle hills and shallow depressions often containing wetlands (1). Soils are primarily composed of Mollisols and Alfisols, with some Inceptisol and Entisol (2).

Ecological research in the Yahara Watershed began in the 1880s, and the lakes have been studied intensively within the North Temperate Lakes Long-Term Ecological Research (LTER) Program (3, 4). Originally dominated by prairies, savannas, forests, and wetlands (5), the landscape was cleared for agriculture during the mid-1800s; by about 1870, most of the arable land was used for agriculture (6). Urban expansion into agricultural areas became a prominent land-use change in the mid-1900s. Today, this human-dominated landscape is largely agricultural (65%), but urban areas occupy about 20% of the landscape and are still expanding (7).

Eutrophication of the Yahara lakes has been pronounced since the mid-1800s. Excess nutrient inputs, principally phosphorus, from sewage effluent, urban/agricultural runoff are the main causes of eutrophication (8). Since the 1970s, substantial efforts have been expended to curb these phosphorus inputs, including wastewater diversion, biomanipulation, soil erosion control, storm water management, nutrient management plans, and wetland restoration (7, 9). Although much progress has been made to control phosphorus sources, the legacy of intensive nutrient and manure use still pose a major problem for water quality (7, 8). The economic base of the region is diverse, including agriculture, some light industry, service industries, emerging technologies, state government, and the state’s flagship university (7).

The Yahara Watershed generates multiple ecosystem services, providing cultivated and wild food, fiber, biofuel, freshwater, carbon storage, recreation opportunities for a growing human population, and regulation of water and nutrient flows. Changing land use has already altered ecosystem services in the watershed, and stresses on ecosystem services typify many agricultural landscapes (10). Soil carbon stocks are high in native prairie vegetation, and soil organic carbon (SOC) storage in the watershed declined by ~50% following conversion of native vegetation to agriculture (11, 12). Freshwaters provide many vital benefits to humans, such as irrigation, domestic consumption, flood control, fishing, etc. However, anthropogenic activities have exerted considerable impacts on freshwater ecosystems in this watershed. Groundwater extraction, loss of wetlands, reduced infiltration, and increased runoff from impervious surfaces have altered hydrology and increased flood frequency (13). Nitrate is contaminating groundwater, and phosphorus loads from nonpoint runoff substantially exceed those that occurred before agriculture (8, 14). High use of pesticides, fertilizers, and manure, along with increased “flashiness” of runoff from heavy rainfall events, have prompted concerns about water quality in area lakes. The dynamics of evapotranspiration, infiltration, and runoff differ within the urban setting versus agricultural regions due to temperature differences in addition to direct effects of the built environment (i.e., increased impervious area and engineered drainage systems). These drivers interact to challenge the sustainability of freshwater resources and other ecosystem services throughout the region.

Representativeness of 2006 Climate Conditions

We quantified and mapped the supply of 10 ecosystem services in the Yahara Watershed for 2006, the most recent year for which data were available for all services. Compared with 30-y normal climate conditions (1971–2000), 2006 was wetter and warmer than average. Annual precipitation in 2006 was 9.6 cm higher than the 30-y mean (83.7 cm, SD = 11.8 cm), and average maximum and minimum temperatures were 1.1 °C and 1.6 °C higher than the 30-y means [13.2 °C, SD = 0.8; and 2 °C, SD = 1.0, respectively; Weather Bureau Army Navy (WBAN) 14837]. Agricultural yields were not high in 2006 (15) and may have been affected by the warmer temperatures. Studies (16) have suggested that increased growing season temperature may lead to decreases in crop yield. Based on gauge data [Upper Yahara River, US Geological Survey (USGS) 05427718, and Pheasant Branch, USGS 05427948], 2006 was also a low runoff year. Warmer temperatures may have offset the moderate increase in annual precipitation by enhancing evapotranspiration, resulting in declining runoff. Groundwater recharge typically increases with precipitation. For Dane County, which includes most of the Yahara Watershed, long-term simulation results showed that annual average recharge in 2006 (38.1 cm) was higher than the 30-y mean (30.2 cm, SD = 8.4 cm) (17).

Quantifying Ecosystem Services: Data Sources, Methods, and Accuracy Assessment

Provisioning Services. Crop production (expected annual crop yield, bushels−1). Crop yield was estimated for the four major crop types (corn, soybean, winter wheat, and oats) that account for 98.5% of the cultivated land in the watershed by overlaying maps of crop types and soil-specific crop yield estimates. The spatial distribution of each crop was obtained from the 2006 Cropland Data Layer (CDL), a 56-m resolution, crop-specific remotely sensed land-cover map available from the National Agricultural Statistics Service (NASS) (18). Soil productivity data for the 42 soil types present in the Yahara Watershed were extracted from Soil Survey Geographic (SSURGO) database (19). The SSURGO productivity layer estimates potential annual yield per unit area for common crops based on data from research plots, field trials, and expert knowledge. Crop and soil data were converted to 30-m resolution and the two maps were overlain to estimate crop yield in each cell. For each crop–soil combination, crop area was multiplied by the estimated yield per unit area. Estimates for each crop type were summed to map estimated crop yield for 2006 (Fig. 1).

Accuracy assessment was done at an aggregated level because spatial projections of crop yield could not be evaluated directly. We compared our estimated crop yield with actual yield for 2006 from the US Department of Agriculture NASS at the county level (15). For this comparison, county-based actual crop yield data were adjusted for the watershed by using an area-weighted method based on cropland area. Our estimate performed well, with estimates within 10.5% for the watershed overall and 9.2% for corn, the dominant crop. For soybean, winter wheat, and oats, our estimates were 18.3%, 22.8%, and 12.6%, respectively, greater than actual yield (Fig. S24). However, these three crops occupy a smaller fraction (12.1%) of the watershed.
Pasture production (expected annual forage yield, animal unit mo−1 yr−1). As for crop production, forage yield was estimated by overlaying the distribution of all forage crops (alfalfa, hay, and pasture/grass) and soil-specific yield estimates. The spatial distribution of each forage crop was also derived from 2006 CDL (18) and rescaled to 30-m grid before calculation. The SSURGO soil productivity layer provided estimates of potential annual yield per unit area for each forage crop (19). However, different forage crops varied in measurement unit; alfalfa and hay were reported in metric tons, whereas pasture/grass was reported in animal unit month (AUM). We converted all forage crops into the consistent unit of AUM, multiplying metric tons by 1.67 (20). Overlay analyses were performed for each forage–soil combination, as done for crops, and summed to obtain the total expected forage yield in the watershed for 2006 (Fig. 1).

Accuracy assessment was again done at an aggregated level using county-level data for 2006 (15) because we could not assess spatial estimates directly. Data were only available for alfalfa and hay, so accuracy was only assessed for these forage crops. Overall, there was 4.0% difference between total estimated and actual harvested alfalfa and hay production for 2006. Our estimates were within 9.2% for actual hay yield and 2.4% for alfalfa yield (Fig. S2B).

Freshwater supply (annual groundwater recharge, cm yr−1). We used groundwater recharge as an indicator for freshwater supply because groundwater recharge is important for replenishing aquifers, which are the sources of drinking water and irrigation in this region (21). Groundwater recharge was quantified and mapped using the modified Thornwaite–Mather Soil–Water–Balance (SWB) model. SWB is a deterministic, physically based, and quasi 3D model that accounts for precipitation, evaporation, interception, surface runoff, soil moisture storage, and snowmelt. Groundwater recharge was calculated on a grid-cell basis at a daily step with the following mass balance equation (21):

\[
\text{Recharge} = \left( \text{precipitation} + \text{snowmelt} + \text{inflow} \right) - \left( \text{interception} + \text{outflow} + \text{evapotranspiration} \right) - \Delta \text{soil moisture.}
\]

Main inputs for this model included 30-m 2006 land use/cover from National Land Cover Data (NLCD) (22), surface flow direction derived from 30-m digital elevation model (DEM) vertical (z) resolution = 2.44 m (23), soil hydrological group and available soil water capacity from SSURGO database (19), and daily observed meteorological data from Madison Dane County Regional Airport weather station (WBAN 14837). We ran the model for 3 yr (2004–2006) at 30-m resolution, with the first two years as “spin up” of antecedent conditions (e.g., soil moisture and snow cover) that influence groundwater recharge for the focal year of 2006 (Fig. 1).

The performance of this model was previously tested in a subbasin of the Yahara Watershed (21). The SWB model yielded recharge estimates comparable to field measurements and estimates from two field-calibrated models, the Integrated Biosphere Simulator (IBIS-2, ref. 24) and the 2D Analytic Element (AE) Ground Flow model (GFLOW, ref. 25) (26). We also compared our estimates with a recent analysis for Dane County that assessed average recharge level from 1998 to 2007 (17). Our estimates matched reasonably well with averaged groundwater recharge at the subbasin levels (Fig. S2C).

Regulating Services. Carbon storage (Mg ha−1). We used carbon storage as an indicator for climate regulation service because of its potential for influencing atmospheric CO₂ concentration and lack of data on factors that regulate climate (such as carbon sequestration or albedo) (27–29). We estimated the amount of carbon stored in each 30-m cell in the Yahara Watershed by summing four major carbon pools: aboveground biomass, belowground biomass, soil carbon, and deadwood/litter (Fig. 1). Our quantification for each pool was based mainly on carbon estimates from the Intergovernmental Panel On Climate Change (IPCC) tier-I approach (30) and other published field studies of carbon density and was estimated by land-use/cover type (Table S2).

For assessing above- and belowground live biomass carbon in forests, we first reclassified forest cover into four broad forest stand types: aspen–birch (Populus–Betula), maple–beech–birch (Acer–Fagus–Betula), oak–hickory (Quercus–Carya), and pine (Pinus) based on the Forest Inventory and Analysis (FIA) database (31) and the Wisconsin Land Cover Data (WISCLAND) (32). We also obtained forest stand-age distributions from FIA and overlaid with forest stand types. Aboveground forest biomass carbon stocks were assigned from look-up tables (33), which provide detailed estimates of forest ecosystem carbon stocks on the basis of forest type, age, and regions. Belowground forest biomass carbon was assumed to be 46% of aboveground carbon (30).

Above- and belowground biomass carbon stock values for cropland, pastures, natural shrublands, and developed land covers (e.g., open space, low, medium, and high intensity) were obtained from IPCC estimates (30) and Ruesch and Gibbs (34). For grassland and restored prairies (mainly dominated by herbaceous vegetation with extensive root systems), above- and belowground biomass carbon was assigned based on the estimates by Baer et al. (35) and Tilman et al. (36). For wetlands, carbon stock values were estimates from the literature (30, 37, 38) and assumed that belowground biomass was 50% of aboveground biomass.

SOC was partially derived from recent studies in this region that sampled soil in 125 sites from 1999 to 2003 for major nonurban covers, including row crops (corn, soybean, alfalfa, and oats), pasture, forest, and remnant prairies (11, 12). In these studies, soil samples were collected at 0–5, 5–10, and 10–25 cm fixed-depth intervals and standard chemical analyses were done to measure the SOC. We summed SOC for the upper 25 cm for each sample and averaged by cover type to estimate SOC for each land use/cover. For other nonurban cover types lacking field measurement, we calculated SOC using the SSURGO soils data (19) and the following equation (37):

\[
\text{SOC Density} = R \sum_{j=1}^{n} \left( Z_i - Z_0 \right) D_i \rho_j, 
\]

where \( R \) is the carbon content assumed to be 50% of soil organic matter, \( n \) is the number of distinctive soil layers categorized by soil series, \( Z_i \) and \( Z_0 \) are depth below surface (m) of the top and bottom of soil layer \( j \), \( D_i \) is the organic matter faction of soil layer \( j \), and \( \rho_j \) is the moist bulk density (g/cm³) of soil layer \( j \). To be consistent with field measurements, we calculated SOC density from SSURGO to a depth of 25 cm and averaged by cover type. Estimates for developed land SOC were adopted from IPCC (30) and assumed that there was no SOC stored in high-intensity developed areas (such as row houses and commercial and industrial areas with high proportion of impervious surfaces). Considering data availability and relatively low stock of dead organic matter, we evaluated deadwood/litter carbon pool for forests and assumed no deadwood/litter carbon in nonforested areas. Estimates of forest deadwood/litter were derived from Smith et al. (33).

Our approach for quantifying carbon storage was subject to several assumptions and limitations. Our method was land-cover based, and the accuracy of our estimates depends in part on the accuracy of land-use/cover classification. Our method differentiated the carbon storage among cover types but assumed no variation within a cover type. In addition, due to data availability, we assessed SOC to 25-cm depth only, which includes the more active soil carbon pools but underestimates total SOC. However,
our results are still useful as a first approximation of spatial variation in carbon storage across the landscape. As all estimates were drawn from empirical or regional studies, we did not perform accuracy assessment for carbon storage service.

**Groundwater quality (probability of groundwater nitrate concentration >3.0 mg L\(^{-1}\), unitless 0–1).** Nitrate is the most ubiquitous contaminant of groundwater and has detrimental impacts on human health through drinking water (39, 40), and nitrate concentration is a useful indicator of groundwater quality (41). We used the probability of groundwater nitrate concentration >3 mg L\(^{-1}\) as the indicator for assessing groundwater quality service. Nitrate concentration >3 mg L\(^{-1}\) is likely caused by anthropogenic activities, and this level is considered a contamination threshold (42, 43).

Groundwater nitrate data were obtained from Groundwater Retrieve Network (GRN), Wisconsin Department of Natural Resources (DNR). GRN includes groundwater data from public and private drinking water wells, Groundwater and Environmental Monitoring System (GEMS), and System for Wastewater Applications and Monitoring Permits (SWAMP) from the 1970s to present. A total of 528 shallow groundwater well (well depth less than the depth from surface to Eau Claire shale) nitrate samples collected in 2006 were used for our study. We performed kriging analysis (44) to interpolate the spatial distribution of the probability of groundwater nitrate concentration >3 mg L\(^{-1}\). We used probability kriging, rather than other parametric interpolation methods, because it is more robust to nonnormality and less sensitive to outliers (42, 45). An exponential semivariogram with anisotropy provided the best fit to the data (Fig. S2D, r\(^2\) = 0.6) with an estimated range of 6,570 m (i.e., distance over which data are spatially autocorrelated) and proportion of structural variance of 0.85. We mapped the interpolation results at a 30-m spatial resolution using Geostatistical Analyst extension in ArcGIS 10.0 [Environmental Systems Research Institute (ESRI)] (Fig. 1). In this map, areas with lower probability values provided more groundwater quality service, and vice versa.

Cross-validation was performed to determine how well the kriged map predicted nitrate concentration. Two diagnostics, mean prediction error and root-mean-square-standardized prediction error, were used for model evaluation. Ideally, if the model predicts accurately, the mean error should be close to 0 and root-mean-square-standardized error close to 1. Our model performed well; the mean error was −0.0002, and root-mean-square-standardized error 1.05. We also verified the accuracy of interpolation by comparing observed nitrate with predicted nitrate probabilities, and the result showed that overall model reliability was 91.6%.

**Surface water quality (annual phosphorus loading, kg ha\(^{-1}\)).** Eutrophication, caused by excess nutrient inputs, principally phosphorus from nonpoint-source runoff from agricultural or urban landscapes, is one of the most serious and stubborn surface water impairment problems (46–48). In the Yahara Watershed, increasing nonpoint-source phosphorus is the major threat to surface water quality (8, 13, 49). We used the annual phosphorus loading from each 30-m grid cell as the proxy for the surface-water quality service provided across the landscape.

We adapted a spatially explicit, scenario-driven modeling tool, Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) (50–52), to simulate discharge of nonpoint-source phosphorus. This approach estimated the phosphorus contributed to downstream water through the ability of vegetation and soil to avoid nutrient loss and to assimilate nutrients received from upslope areas (53). A grid cell’s phosphorus contribution was quantified as a function of water yield index, land use/cover, export coefficient, and downslope retention ability. Two components in the InVEST model (water yield and water purification) were used. We ran the water-yield module to determine the average annual water yield for each pixel on the landscape. Data inputs for this step included 2006 CDL (18), 30-m DEM (23), 2006 gridded annual PRISM precipitation data (54), average annual reference evapotranspiration (55), maximum root depth (56), and SSURGO soil depth and plant available water content (19).

We then determined the potential phosphorus export from each cell based on cover-type–specific export coefficients. Nutrient export coefficients developed by Reckhow et al. (57) are the annual average pollutant loading derived from field studies that measured export from representative agricultural parcels. We obtained phosphorus export coefficients from published field studies and local estimates (6, 13, 57, 58). Moreover, the adjustment factors for the export coefficients were calculated for each cell based on annual average water yield, allowing us to account for spatial heterogeneity that influences phosphorus exports. The adjustment factors were then combined with the export coefficients to calculate the adjusted loading values for each grid cell. Finally, the actual amount of phosphorus exported from upstream pixel x that eventually reached the downstream water bodies (\(E_{yx}\)) was estimated for each subbasin with the following equation (53):

\[
E_{yx} = ALV_{x} \frac{X}{y=x+1} \left(1 - E_{x} \right),
\]

where \(ALV_{x}\) is the adjusted phosphorus export from pixel x, \(E_{x}\) is the filtration efficiency of each downstream pixel y, and \(X\) represents phosphorus transport route from where it originated to the downstream water bodies. Filtration efficiency was assigned by cover type (53): natural vegetation (such as forest, wetland, or natural grassland) was assigned a high value, seminatural vegetation an intermediate value, and developed or impervious covers were assigned low values. We ran the model for 2006 and mapped estimated phosphorus loading across the watershed (Fig. 1). The ecosystem service of providing high-quality surface water was the inverse of phosphorus loading. Therefore, areas with lower phosphorus loading values delivered more surface water quality, and areas with higher phosphorus loading values supplied less surface water quality.

The approach using the InVEST model has several assumptions and simplifications (53). It assumes that vegetation plays a key role in mitigating phosphorus export and assumes water travels downslope only along natural flow paths. The model ignores the effects of tile drainage and ditching practices, which occur in the Yahara Watershed (59), and does not consider surface and groundwater interactions. Moreover, other pollutants are not included in this model, and thus our derived phosphorus loading represented a conservative estimate of terrestrial contributions to water quality.

Because accuracy of the spatial projections of phosphorus loading could not be evaluated directly, we assessed our estimates by comparing with USGS gauge-monitored phosphorus loading for two subbasins (Upper Yahara River, USGS 05427718, and Pheasant Branch, USGS 05427948), which had consistent phosphorus-load measurement for the past two decades. For those two watersheds, our estimates were within 13.5% and 15.1% of the gauge-monitored data for the Upper Yahara River and Pheasant Branch, respectively (Fig. S2E).

**Soil retention (annual sediment yield, t ha\(^{-1}\)).** We quantified annual sediment yield as the (inverse) indicator for soil retention by using the Modified Universal Soil Loss Equation (MUSLE, ref. 60). MUSLE is a storm-event–based model that estimates sediment yield as a function of runoff factor, soil erodibility, geomorphology, land use/cover, and land management. Compared with the Universal Soil Loss Equation (USLE) and Revised USLE (RUSLE) that predict soil erosion as a function of rainfall energy, MUSLE improves the sediment-yield prediction by using a runoff factor to account for sediment detachment and transport.
processes (61, 62). Specifically, a grid cell’s contribution of sediment for a given storm event is calculated as:

\[
Sed = 11.8 \left( Q \cdot q_p \right)^{0.56} \cdot K \cdot L \cdot S \cdot C \cdot P,
\]

where Sed represents the amount of sediment that is transported downstream network (1); \( Q \) is the surface runoff volume (m³); \( q_p \) is the peak flow rate (m³/s); \( K \) is soil erodibility, which is based on organic matter content, soil texture, permeability, and profiles; \( L \cdot S \) is combined slope and steepness factor; and \( C \cdot P \) is the product of plant cover and its associated management practice factor.

We used the ArcSWAT interface of the Soil and Water Assessment Tool (SWAT, ref. 61) to perform all of the simulations. SWAT is a physically based model that simulates hydrology, sediment, and nutrient cycling at watershed scales, and in SWAT, sediment yield is estimated on the basis of MUSLE. Major data inputs for this model included 2006 NLCD land use/cover (22), SSURGO soil data (19), 30-m DEM (23), and daily temperature and precipitation data from Madison Dane County Regional Airport weather station (WBAN 14837). We used model parameters for SWAT that were previously calibrated specifically for the Yahara River Basin (63). We ran this model at a daily timestep from 2004 to 2006, with the first 2 y as spin up, then mapped total sediment yield for 2006 across the watershed (Fig. 1). Similar to surface-water quality, the ecosystem service of soil retention was the inverse of sediment yield. In this map, areas with lower sediment yield provided more of this service, and areas with higher sediment yield delivered less.

Accuracy was assessed by comparing our estimates with USGS gauge-monitored sediment loadings for four subbasins (Upper Yahara River, Yahara River, Spring Harbor, and Pheasant Branch). These gauges (USGS 05427718, 05427850, 05427965, and 05427718) provided consistent sediment measurements for past decades. In all cases, our estimates were greater than the measured sediment loadings. Our values overestimated gauge data by 7.1% and 8.0%, for the Upper Yahara River and Yahara River, respectively, but we overestimated gauge data by 30.1% and 61.8% for the Spring Harbor and Pheasant Branch subbasins (Fig. S2F). One possible explanation for this discrepancy involves features that were not captured by the SWAT model. In Pheasant Branch, construction of Confluence Pond (finished in 2001) reduced downstream sediment loading by 45% (64); the Spring Harbor subbasin also includes several retention basins. However, our projections may be biased toward underestimating this ecosystem service.

**Flood regulation (flood regulation capacity, unitless 0–100).** The regulating service of flood includes two aspects. One is the capacity of ecosystems to redirect or absorb incoming water, mainly from precipitation, and consequently reduce surface runoff (so-called “preventative” service); another is the ability of the ecosystem to mitigate a flood when it has already occurred, thereby dampening its destructive impacts (so-called “mitigating” service). We adopted Nedkov and Burkhard’s (65) capacity-assessment approach to quantify the ecosystem service of flood regulation. This approach considers both preventative and mitigating functions of vegetation and soil by using four hydrological parameters: interception, infiltration, surface runoff, and peak flow.

We first applied the Kinematic Runoff and Erosion (KINEROS) model to derive estimates of three parameters (infiltration, surface runoff, and peak flow) for six sampled subbasins in this watershed. KINEROS is an event-oriented, physically based, distribution model that simulates interception, infiltration, surface runoff, and erosion at subbasin scales. Major data inputs for this model included 2006 NLCD land use/cover (22), 30-m DEM (23), SSURGO soil data (19), and a defined stormed event with a 10-y return period and 24-h duration (66). In each simulation, a subbasin was first divided into smaller hydrological units. For the given predefined storm event, the model then calculated the amount of infiltration, surface runoff, and peak flow for each unit. Second, we classified these estimates into 10 discrete capacity classes with range from 0 to 10 (0 indicates no capacity and 10 indicates the highest capacity) and united units with the same capacity values and overlaid with land cover map. Third, we calculated the distribution of all land use/cover classes within every spatial unit (with a particular capacity). We then assigned each land use/cover a capacity parameter based on its dominance (in percentage) within all capacity classes. For instance, forest cover was assigned a capacity value of 10 for infiltration because of its high percentage within capacity class 10. As a result, every land use/cover was assigned a 0–10 capacity value for infiltration, surface runoff, and peak flow. This procedure was repeated for six subbasins, and derived capacity values were averaged by cover type. We applied the same procedure to soil data and derived averaged capacity values for each soil type with the same set of three parameters. In addition, we obtained intercensations from Dripps and Bradbury (21) for each land use/cover and standardized to the same 0–10 range. Finally, the flood regulation capacity (FRC) for each 30-m cell was calculated (Fig. 1) with the equation below:

\[
FRC = \sum_{\text{huc}} \left( \frac{\text{interception} + \text{infiltration} + \text{runoff} + \text{peak flow}}{\text{soil}} \right) + \sum_{\text{huc}} \left( \frac{\text{infiltration} + \text{runoff} + \text{peak flow}}{\text{soil}} \right).
\]

For greater details, please refer to Nedkov and Burkhard (65). To simplify interpretation, we rescaled original FRC values to a range of 0–100, with 0 representing the lowest regulation capacity and 100 the highest.

A novelty of this approach is that it accounts for both preventative and mitigating functions of ecosystems to regulate flooding. However, caveats remain (65). Due to model limitations, this assessment procedure is not applicable to flooding caused by snowmelt. In addition, this approach assumes a linear relationship between the increasing amount of rainfalls and the response of soil-land cover. However, when the saturation point is reached, the flood damage will increase exponentially even with a small amount of increase in rainfall.

To evaluate our estimates, we compared our FRC map with the extent of June 2008 flooding in southern Wisconsin (Fig. S2G), which was one of the most severe and widespread flooding events in the Midwest resulting in substantial damages to life and property (67). The flooding extent map was produced by combined processing of Landsat-5, SPOT-5, and RADARSAT-1 satellite images of Wisconsin during the June 2008 flooding event (68). We overlaid the 2008 flooded areas with FRC map, and calculated the capacity values for these areas. Results showed that the flooded area had an average regulation capacity value of 48.3 and was ranked at the 12th percentile of the regulation capacity value of all grid cells in the watershed (Fig. S2H). This result confirms that our estimate is a good approximation of flood vulnerability and regulation capacity of the landscape; areas with low FRC (in this case, within 12th percentile for the June 2008 flood) are more likely to be flooded during a storm event.

**Cultural Services. Forest recreation (recreation score, unitless 0–100).** Cultural services are consistently recognized and appreciated, but in most instances they are characterized as being “intangible” or “subjective,” and challenging to quantify in biophysical terms (69). We assessed two cultural services, forest recreation and hunting recreation. We quantified the forest-recreation service as a function of the amount of forest habitat, recreational opportunities provided, proximity to population center, and accessibility of the area (27). Several assumptions were made for this assessment.
approach: larger areas and places with more recreational opportunities would provide more recreational service; areas near large population centers would be visited and used more than remote areas; and proximity to major roads would increase access and thus recreational use of an area.

We first extracted and aggregated all forest cover from the NLCD land use/cover data and calculated the area of each forest patch. In addition, we determined the number of recreational opportunities within major forested areas from Dane County Parks Division (70), which provided detailed information about nature trails, picnic areas, mountain biking opportunities, etc., for major parks and wilderness areas. We classified the number of recreational opportunities into 10 natural breaks using Jenks optimization and rescaled it to a range from 0 to 40. For other small, forested areas that lack information about recreational features, we conservatively assumed that these areas at least could provide basic recreation opportunities, such as hiking or bird watching, and we assigned them a value of 5. To quantify proximity to population centers, we created a population density layer with 500-m spatial resolution based on the US Census tract-level resident population data for 2000, by using a moving window analysis that summed the population density of tracts having their centers within 10 km of each grid cell. We also used Jenks algorithm to classify the population density layer into 10 natural breaks, then weighted these values to the range of 0–40. To quantify access, we obtained road data layer from topologically integrated geographic encoding and referencing (TIGER) of US Census Bureau (71) and performed a buffer analysis based on these road networks. We assumed that larger roads could provide more recreational access to more people for recreation, and we varied buffer distance according to road type: 2,000 m for highways and 500 m for other roads. Road buffers were then weighted to a scale ranging from 0 to 20 based on the square root of distance, with areas closer to roads assigned higher scores. Finally, on the basis of these assumptions and derived data, we quantified forest recreation service for each 30-m grid cells using the equation below:

\[ FRS_i = A_i \sum (Optt_i + Pop_i + Road_i), \]

where \( FRS \) is forest recreation score, \( A \) is the area of forest habitat, \( Optt \) represents the recreation opportunities, \( Pop \) is the proximity to population centers, and \( Road \) stands for the distance to major roads. To simplify interpretation, we rescaled the original hunting recreation service (ranging from 0 to 28,000) to a range of 0–100, with 0 representing no hunting recreation service and 100 representing highest service (Fig. 1). As for forest recreation, we could not perform accuracy assessment for hunting recreation due to lack of available data.

**Statistical Distributions of Ecosystem Service Estimates**

To identify the hotspots and coldspots for each ecosystem service, we examined the cumulative frequency distribution of each ecosystem service that was estimated for 2006 across the Yahara Watershed (Fig. S3). Detailed statistics for each service are summarized in Table S1, and cutoff values for upper and lowest 20th percentile are shown in Fig. S3. Cells on the landscape that were within the upper 20th percentile were considered as hotspots, and those within the lowest 20th percentile were considered as coldspots. See Materials and Methods for further explanation.

We chose to use six (of 10) services that were in the upper 20th or lowest 20th percentile to define hotspots and coldspots of multiple ecosystem services because we wanted a majority of services to indicate the hotspots but faced constraints. It is impossible for any grid cell on the landscape to fall within the upper or lowest 20th percentile for all 10 services. Production of some services is mutually exclusive (e.g., cropland and pasture cover; and eight for forest cover). Based on the cumulative frequency distribution of the number of ecosystem services that were hotspots or coldspots individually on each grid cell (Fig. S4), six was an optimal choice to represent a majority of ecosystem services without precluding any given cover type from contributing to a multiple-services hotspot. Alternative choices of the number of services to include would influence the results.

**Alternative Estimates of Ecosystem Service Coldspots**

Among the suite of ecosystem services quantified in this study, three services (i.e., groundwater quality, surface water quality, and soil retention) have known ecologically meaningful or socially accepted thresholds. Therefore, in addition to estimating coldspots based on the lowest 20th percentile of the data, we also estimated coldspots based on areas that exceeded known thresholds.

For groundwater quality, the US Environmental Protection Agency (EPA) has set a regulation and management standard of 10 mg·L\(^{-1}\) for nitrate concentration in drinking water (72). From the spatial interpolation of groundwater nitrate concentrations, we found that the mean probability of nitrate >3.0 mg·L\(^{-1}\) was 0.76 for all groundwater wells with nitrate concentrations >10.0 mg·L\(^{-1}\), with 95% confidence interval between 0.73 and 0.79. Thus, we used the lower limit (0.73) as the conservative threshold of groundwater quality and considered areas >0.73 as coldspots.

For surface water quality, the Yahara CLEAN Strategic Action Plan set the goal of 50% reduction in the average annual phosphorus loading to the Yahara chain of lakes (73). A recent
study showed this 50% reduction in phosphorus loading would increase the probability of mesotrophy in Lake Mendota (relative to the historic condition, with median concentration of total phosphorus <0.024 mg/L) during July–August from less than 0.2 mg/L to 0.4 mg/L, indicating a considerable improvement in lake water quality (74). Thus, we used the 50% phosphorus reduction goal as the basis for critical loading for surface water quality and calculated this value based on Lake Mendota subbasin as a representative threshold for the entire Yahara watershed. Long-term (1976–2008) monitoring data showed that average phosphorus loading entering to Lake Mendota from direct drainage sources is 29,600 kg·ha⁻¹; with 50% reduction, the derived critical phosphorus loading is 0.25 kg·ha⁻¹.

For soil retention, USEPA and other studies have used all forested watershed condition as a reference for sediment load thresholds, and suggested that 3.6 times, with 80% interval between 3.4 and 4.1, of all forested sediment load be a conservative sediment loading threshold (75, 76). Here, we used this approach and calculated the threshold of 0.16 t·ha⁻¹ for sediment yield in this region.

The resulting maps showed that thresholds were exceeded for groundwater quality, surface water quality, and soil retention in 20.7%, 8.0%, and 28.5% of the watershed, respectively (Fig. S5 A–C). We produced alternative coldspots maps based on these three threshold-based maps along with the lowest 20th maps of other seven services, and compared these with maps of coldspots for all 10 ecosystem services generated from the lower 20th percentile maps. The resulting maps were similar (Fig. S5 D and E).


Fig. S1. Map of the Yahara River Watershed and the land use/land cover pattern (with percent cover) for 2006, derived from NLCD. Delineations of the watershed and major subbasins were based on light detection and ranging (LiDAR) elevation, sewer-sheds from the city of Madison, and a field-checked basin map from Dane County, Wisconsin.
Fig. S2. Accuracy assessment results of ecosystem service quantifications in the Yahara Watershed for 2006: (A) Comparison of estimated yield with actual yield for four major crop types: corn, soybean, winter wheat, and oats; (B) comparison of total estimated and actual harvested alfalfa and hay production; (C) comparison of groundwater recharge estimates from SWB model with average estimates from 1998 to 2007 by Dane County, Wisconsin; (D) semivariogram computed based on nitrate concentration data from 528 shallow groundwater wells, fitted by exponential anisotropy model; (E) comparison of phosphorus loading estimates from InVEST model with USGS gauge-monitored data for Upper Yahara River and Pheasant Branch subbasins; (F) comparison of sediment yield estimates from SWAT model with USGS gauge-monitored data for four subbasins: Upper Yahara River, Yahara River, Spring Harbor, and Pheasant Branch; (G) spatial extent of flooded area in June 2008 Floods; (H) histogram of FRC for all grid cells and mean capacity value of areas flooded in June 2008 floods.
Fig. S3. Cumulative frequency distribution of biophysical indicators for each ecosystem service. Dash lines represent cutoffs of the upper 20th and lowest 20th percentile (by area) for each service.

Fig. S4. Cumulative frequency distribution (by area) for the number of ecosystem services in the upper 20th or lowest 20th percentile, as mapped in Fig. 2A and C.
Fig. 55. Spatial distributions of locations that exceed thresholds: (A) groundwater quality (orange areas exceed threshold), (B) surface water quality (purple areas exceed threshold), and (C) soil retention (yellow areas exceed threshold). Maps of coldspots were recomputed using the thresholds for these three services to map: (D) number of services in the lowest 20th percentile or beyond thresholds and (E) coldspots where six or more services were in the lowest 20th or beyond thresholds.
Fig. S6. Scatter plots showing bivariate relationships (Spearman rank correlation) for crop production vs. groundwater quality (Left) and crop production vs. surface water quality (Right), based on a random sample of 1,000 points. Dash lines indicate median values (by area) for ground and surface water quality service, and upper 20th percentile (by area) for crop production service.

**Table S1. Summary of descriptive statistics of biophysical indicators for each ecosystem service**

<table>
<thead>
<tr>
<th>Ecosystem service</th>
<th>Min</th>
<th>25th percentile</th>
<th>Median</th>
<th>Mean</th>
<th>75th percentile</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crop production (bu/y)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>8.9</td>
<td>20.0</td>
<td>57.6</td>
</tr>
<tr>
<td>Pasture production (AUM/y)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.2</td>
<td>0.0</td>
<td>2.2</td>
</tr>
<tr>
<td>Freshwater supply (cm/y)</td>
<td>0.0</td>
<td>40.4</td>
<td>41.7</td>
<td>37.5</td>
<td>43.2</td>
<td>126.0</td>
</tr>
<tr>
<td>Carbon storage (Mg/ha)</td>
<td>0.0</td>
<td>60.5</td>
<td>70.9</td>
<td>77.7</td>
<td>82.3</td>
<td>192.3</td>
</tr>
<tr>
<td>Groundwater quality (probability of NO&lt;sub&gt;3&lt;/sub&gt; &gt; 3.0 mg/L)</td>
<td>0.0</td>
<td>0.4</td>
<td>0.5</td>
<td>0.5</td>
<td>0.7</td>
<td>1.0</td>
</tr>
<tr>
<td>Surface water quality (kg/ha)</td>
<td>0.0</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
<td>0.6</td>
</tr>
<tr>
<td>Soil retention (t/ha)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.1</td>
<td>0.2</td>
<td>1.0</td>
</tr>
<tr>
<td>Flood regulation (unitless 0–100)</td>
<td>0.0</td>
<td>54.9</td>
<td>67.9</td>
<td>65.4</td>
<td>70.6</td>
<td>100.0</td>
</tr>
<tr>
<td>Forest recreation (unitless 0–100)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.5</td>
<td>0.0</td>
<td>100.0</td>
</tr>
<tr>
<td>Hunting recreation (unitless 0–100)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.2</td>
<td>0.0</td>
<td>100.0</td>
</tr>
</tbody>
</table>

**Table S2. Carbon storage estimates for each land use/cover (unit, Mg/ha)**

<table>
<thead>
<tr>
<th>Land-use/cover category</th>
<th>Above- and belowground live biomass carbon</th>
<th>Deadwood/litter carbon</th>
<th>Soil carbon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Developed, open space</td>
<td>23.2</td>
<td>0.0</td>
<td>86.5</td>
</tr>
<tr>
<td>Developed, low intensity</td>
<td>17.4</td>
<td>0.0</td>
<td>64.9</td>
</tr>
<tr>
<td>Developed, medium intensity</td>
<td>11.6</td>
<td>0.0</td>
<td>43.3</td>
</tr>
<tr>
<td>Developed, high intensity</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Aspen–birch (<em>Populus–Betula</em>) forest stands</td>
<td>66.9</td>
<td>20.8</td>
<td>58.4</td>
</tr>
<tr>
<td>Maple–beech–birch (<em>Acer–Fagus–Betula</em>) forest stands</td>
<td>78.7</td>
<td>36.1</td>
<td>57.3</td>
</tr>
<tr>
<td>Oak–hickory (<em>Quercus–Carya</em>) forest stands</td>
<td>85.4</td>
<td>18.2</td>
<td>53.9</td>
</tr>
<tr>
<td>Pine (<em>Pinus</em>) forest stands</td>
<td>107.3</td>
<td>27.8</td>
<td>57.2</td>
</tr>
<tr>
<td>Natural shrub</td>
<td>14.2</td>
<td>0.0</td>
<td>100.3</td>
</tr>
<tr>
<td>Herbaceous grassland/prairie</td>
<td>10.2</td>
<td>0.0</td>
<td>158.4</td>
</tr>
<tr>
<td>Corn</td>
<td>0.0</td>
<td>0.0</td>
<td>70.9</td>
</tr>
<tr>
<td>Soybean</td>
<td>0.0</td>
<td>0.0</td>
<td>60.5</td>
</tr>
<tr>
<td>Other crops</td>
<td>0.0</td>
<td>0.0</td>
<td>60.5</td>
</tr>
<tr>
<td>Alfalfa</td>
<td>5.1</td>
<td>0.0</td>
<td>71.2</td>
</tr>
<tr>
<td>Pasture</td>
<td>5.1</td>
<td>0.0</td>
<td>61.6</td>
</tr>
<tr>
<td>Fallow</td>
<td>5.1</td>
<td>0.0</td>
<td>60.5</td>
</tr>
<tr>
<td>Woody wetland</td>
<td>12.3</td>
<td>0.0</td>
<td>100.3</td>
</tr>
<tr>
<td>Herbaceous wetland</td>
<td>7.6</td>
<td>0.0</td>
<td>115.0</td>
</tr>
</tbody>
</table>
Table S3. List of candidate explanatory variables in backward logistic regression for the occurrence of win–win exceptions

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>Unit</th>
<th>Data source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Local scale</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Topography</td>
<td></td>
<td>DEM (1)</td>
</tr>
<tr>
<td>Slope</td>
<td>Percent</td>
<td></td>
</tr>
<tr>
<td>Soil physical properties</td>
<td></td>
<td>SSURGO (2)</td>
</tr>
<tr>
<td>Soil permeability</td>
<td>m·s$^{-1}$</td>
<td></td>
</tr>
<tr>
<td>Available water content</td>
<td>Volumetric percent</td>
<td></td>
</tr>
<tr>
<td>Depth to water table</td>
<td>mm</td>
<td></td>
</tr>
<tr>
<td>Silt content</td>
<td>Percent</td>
<td></td>
</tr>
<tr>
<td>Soil erodibility (K factor)</td>
<td>(Mg × h)(MJ × mm)$^{-1}$</td>
<td></td>
</tr>
<tr>
<td><strong>Landscape position</strong></td>
<td></td>
<td>Wisconsin Department of Natural Resources; NLCD (3)</td>
</tr>
<tr>
<td>Distance to stream</td>
<td>M</td>
<td></td>
</tr>
<tr>
<td>Distance to nearest wetland</td>
<td>M</td>
<td></td>
</tr>
<tr>
<td>Distance to nearest forest</td>
<td>M</td>
<td></td>
</tr>
<tr>
<td><strong>Demographic</strong></td>
<td></td>
<td>US Census 2000</td>
</tr>
<tr>
<td>Log-transformed population density</td>
<td>Persons × km$^{-2}$</td>
<td></td>
</tr>
<tr>
<td><strong>Landscape scale (buffer radius = 560 m)</strong></td>
<td></td>
<td>Wisconsin Dane County Land and Water Resource Department, Code 590</td>
</tr>
<tr>
<td>Landscape composition</td>
<td></td>
<td>NLCD (3)</td>
</tr>
<tr>
<td>% forest</td>
<td>Percent</td>
<td></td>
</tr>
<tr>
<td>% agriculture</td>
<td>Percent</td>
<td></td>
</tr>
<tr>
<td>% wetland</td>
<td>Percent</td>
<td></td>
</tr>
<tr>
<td>Management practice</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% area restricted for fall nutrient application</td>
<td>Percent</td>
<td>Wisconsin Dane County Land and Water Resource Department, Code 590</td>
</tr>
<tr>
<td>% area restricted for winter manure spreading</td>
<td>Percent</td>
<td>Wisconsin Dane County Land and Water Resource Department, Code 590</td>
</tr>
</tbody>
</table>