



Spatial and temporal variability of future ecosystem services in an agricultural landscape

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Abstract

Context Sustaining ecosystem services requires enhanced understanding of their spatial–temporal dynamics and responses to drivers. To date, the majority of research has focused on snapshots of ecosystem services, and their spatial–temporal variability has seldom been studied.

Objectives We aimed to address: (i) How is variability in ecosystem services partitioned among ‘space’ and ‘time’ components? (ii) Which ecosystem services are spatially/temporally coherent, and which are space–time incoherent? (iii) Are there consistent patterns in ecosystem service variability between urban- and rural-dominated landscapes?

Methods Biophysical modeling was used to quantify food, water, and biogeochemical-related services from 2011 to 2070 under future scenarios. Linear mixed-effects models and variance partitioning were used to analyze spatial and temporal variability.

Results Food production, water quality and flood regulation services were overall more variable than climate regulation and freshwater supply. ‘Space’ contributed to a majority of variations across most services, highlighting dominant importance of location-specific factors for service supply. Significant space–time interactions existed for water quality and soil carbon storage, indicating interactive effects between location- and time-specific factors. Variation in the relative controls of ‘space’ vs. ‘time’ factors between urban- and rural-dominated subwatersheds suggests that targeting different key drivers is needed

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for successful management of ecosystem services in urban vs. rural landscapes.

Conclusions Our research reveals relative importance of underlying ‘space’ and ‘time’ controls for diverse ecosystem services. Our study presents a framework to investigate spatial–temporal variability of ecosystem services, and provides theoretical and practical implications for anticipating and managing the dynamics of future ecosystem services at the watershed scale.

Keywords Spatial–temporal dynamics · Scale · Variance partitioning · Landscape sustainability · Biophysical modeling · Agricultural landscape

Introduction

Ecosystem goods and services, broadly defined as benefits people derive from nature (Daily 1997) such as food and fiber products, clean water, flood mitigation, climate and disease regulation, are essential for supporting human wellbeing and prosperity of human civilizations. The notion that nature performs fundamental life-supporting services does not rise de novo (Mooney and Ehrlich 1997), and can be traced as far back as *Man and Nature* (Marsh 1864) on finite natural resources, the pioneering concept of natural capitals (Vogt 1948), and Leopold’s elegant descriptions on nature’s benefits to human society (Leopold 1949). Yet the past two decades have witnessed a rapid proliferation and diversification of ecosystem service research (Chaudhary et al. 2015; Bennett 2017; Qiu 2019). Two milestones—*Nature’s Services* by Daily (1997) and the Millennium Ecosystem Assessment (MEA 2005)—have spurred a vast amount of research and policy interests, and established a framework to mainstream ecosystem service to help guide environmental policy and decision-making (Guerry et al. 2015; Posner et al. 2016).

Previous research on ecosystem service has been instrumental for (i) examining supply and interactions among multiple ecosystem services across large spatial domains (Raudsepp-Hearne et al. 2010; Maes et al. 2012; Qiu and Turner 2013) and over long timescales (Jiang et al. 2013; Renard et al. 2015; Rau et al. 2018); (ii) exploring future trajectories and resilience of ecosystem services, and transition

pathways towards sustainability (Bateman et al. 2013; Oteros-Rozas et al. 2015; Qiu et al. 2018b); and (iii) addressing effectiveness of management, planning and policy interventions for conserving ecosystem services (Wong et al. 2015; Li et al. 2015; Schultz et al. 2015; Qiu et al. 2017). However, most research thus far has focused on the supply of ecosystem services for single or just a few snapshots. A growing number of studies has urged to disentangle effects of multiple drivers acting in concert to understand the dynamics, potential nonlinearities and feedbacks, either retrospectively or prospectively (Stürck et al. 2015; Renard et al. 2015; Qiu et al. 2018a; Rau et al. 2019). Despite such progress, the variability of ecosystem services (e.g., spatial and temporal variability) has seldom been an object of study. In other words, few studies have explicitly investigated the extent to which space- or time-specific factors contributed to ecosystem service variability. Yet the direct analyses of variability could yield key insights into the relative importance of different factors or processes that drive service supply.

The concept of variability in biological and ecological systems has long intrigued scientists, and has been studied through initiatives such as Long-term Ecological Research (LTER) platform (Kratz et al. 2003; Müller et al. 2010) and other research coordination networks. A growing number of empirical, theoretical and practical research has focused on patterns and processes operating at multiple spatial and temporal scales to understand the dynamics of complex and interconnected ecological systems, as well as drivers of their spatial and temporal variability (Loreau et al. 2003; Borcard et al. 2004; Gouhier et al. 2010; Gouhier and Guichard 2014). Rather than perceiving variability as an impediment, prior studies have increasingly analyzed the spatial and temporal variability of ecological parameters (e.g., plant, animal and edaphic measurements) to reveal the forces that structure terrestrial and aquatic ecosystems (Kratz et al. 1987, 1995; Riera et al. 1998). These studies further indicated that the ecological variability in space and time were fundamental yet often neglected properties that determine the “health” of ecosystems, and can be used for large-scale comparisons (e.g., across sites, systems and taxa) and generalizations (Kratz et al. 1995). Moreover, analyses of variability also have management implications. As a matter of fact, the concept of natural variability has been used by

natural resource managers since the early 1960s to provide a baseline from which to determine whether or not a system has changed significantly (Landres et al. 1999).

Similar to biological or ecological processes, ecosystem services are also scale-dependent and variable in both space and time (Cumming et al. 2006; Andersson et al. 2015; Raudsepp-Hearne and Peterson 2016; Lindborg et al. 2017; Qiu et al. 2018a). However, quantitative analyses on the variability of ecosystem services are still rare. It remains unclear whether there are consistent patterns in the spatial and temporal variability of different ecosystem services, and whether there are any interactions of spatial and temporal variability that altogether affect ecosystem service supply. Such empirical evidence is needed to understand the underlying factors of, and also to better predict and manage variability of ecosystem services. It could also inform management and policy efforts that aim to sustain future supply of ecosystem services.

In this study, we quantified indicators of a portfolio of food, water, and biogeochemical-related ecosystem services (Table 1) at 220-m \times 220-m spatial resolution from 2011 to 2070 to investigate their spatial and temporal variability. Our research is focused on the Yahara Watershed (Wisconsin, USA) (Fig. S1)—a microcosm for urbanizing agricultural landscapes in the Upper Midwest and similar regions globally. Detailed descriptions of our study region can be found in the online Supplementary Materials (SM). Indicators of ecosystem services were quantified using biophysical model simulations under four plausible future scenarios (i.e., social–ecological pathways towards the future) that vary drastically in their social–environmental drivers (Carpenter et al. 2015; Booth et al. 2016). These scenarios were developed based on: (1) eliciting archetypal drivers from the global scenario literature; and (2) eliciting perspectives on the future of the watershed through interviews and workshops with stakeholders, which were then condensed into a small number of storylines. Details of the scenario development process can be found in Carpenter et al. (2015), Booth et al. (2016), and Wardropper et al. (2016). Here our use of scenarios allowed us to capture the potential range of spatial and temporal changes in ecosystem service indicators under a wide array of future social–environmental conditions.

As the third in a trilogy of papers, we have developed an analytical framework to assess spatial–temporal variability of ecosystem services, whose spatial–temporal dynamics, tradeoffs and synergies across scales have been investigated previously (Qiu et al. 2018a, b). Specifically, we aimed to address the following research questions: (i) Do indicators of ecosystem services differ systematically in their overall variability? (ii) How is the variability in ecosystem service indicators partitioned among the ‘space’ and ‘time’ components? (iii) To what extent are ecosystem service indicators spatially or temporally coherent, and which ones are space–time incoherent? and (iv) Are there consistent patterns in the spatial and temporal variability of ecosystem service indicators between urban- and rural-dominated landscapes? Here, by ‘*temporally coherent*’, we meant the tendency for different locations within a landscape to behave similarly in different years independent of the average for the locations (i.e., the degree to which differences in time occur independent of location) (Fig. 1a). By ‘*spatially coherent*’, we meant the tendency for locations within a landscape to be consistently different regardless of the time (i.e., the degree to which differences in location occur independent of time) (Fig. 1a). By ‘*space–time incoherent*’, we meant the tendency for different locations within a landscape to behave differently as a function of time, or vice versa (Fig. 1b). Our use of spatial and temporal coherence, and space–time incoherence is consistent with seminal papers by Kratz et al. (1995) and Kratz et al. (1987) that investigated spatial and temporal variability of ecosystem properties.

Materials and methods

Biophysical modeling of ecosystem services

Indicators of nine ecosystem services were quantified using an integrated spatially explicit model—Agro-IBIS (Agroecosystem Integrated Biosphere Simulator) (Foley et al. 1996; Kucharik et al. 2000; Kucharik and Brye 2003). Agro-IBIS is a gridded, physically-based vegetation model that simulates continuous dynamics of terrestrial ecosystem processes, biogeochemistry, water and energy balances. It has been calibrated and validated extensively for performance in both natural and human-dominated systems in the

Table 1 List of ecosystem services in the Yahara Watershed (Wisconsin, USA), quantified at 220-m \times 220-m resolution under four future scenarios from 2011 to 2070, with

corresponding biophysical indicator, unit, and number of years over which there is no temporal autocorrelation

Ecosystem services (ES)	Biophysical indicators	Unit	# year without temporal autocorrelation
Food production ES			
Crop production	Annual total major annual crop yield	bu/ac	8
Perennial grass production	Annual total forage crops and perennial grass yield	kg/ha	8
Water quality ES			
Groundwater quality	Annual total nitrate leached	kg/ha	8
Surface-water quality	Annual total phosphorus yield in runoff	kg/ha	5
Water quantity ES			
Freshwater supply	Annual total drainage of groundwater	mm	5
Flood regulation	Annual number of days with runoff > 10 mm days	days	5
Climate regulating and soil retention ES			
Net ecosystem exchange	Annual net ecosystem exchange (NEE)	Mg C/ha	3
Soil carbon storage	Total soil carbon stored in upper 1-m	Mg C/ha	8
Soil retention	Annual total sediment yield in runoff	t/ha	6

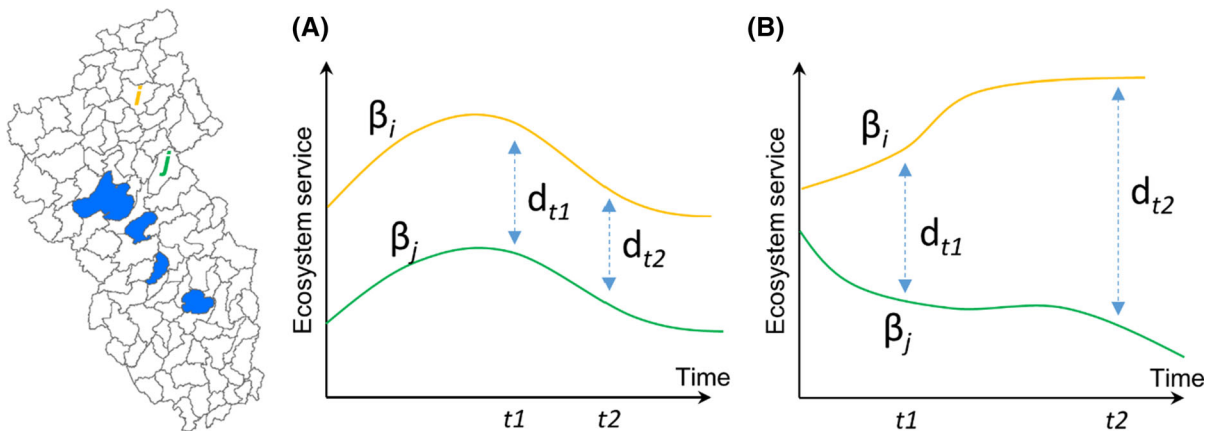


Fig. 1 Conceptual figure illustrating spatial/temporally coherence, and space–time incoherence of ecosystem services. Both panels show changes of ecosystem service indicator over time for two randomly selected subwatersheds i and j , in which parameter β is the rate of change for a given time and parameter d is the difference in the estimates of ecosystem service. In **a**,

when $\beta_i \approx \beta_j$ for any given time, it suggests that this service is temporally coherent; also when both d_{t1} and d_{t2} do not equal to zero, it means that this service is spatially coherent. In **b**, when $\beta_i \neq \beta_j$ and $d_{t1} \neq d_{t2}$ for any given time, it indicates that this service is space–time incoherent

Midwestern United States (Donner & Kucharik 2003; Kucharik and Twine 2007; Motew and Kucharik 2013), including recent applications focusing on surface/subsurface water dynamics and agricultural production in the Yahara Watershed (Soylu et al. 2014; Zipper et al. 2015, 2018). In this study, we used the most recent version that includes the updates of soil physics with those of HYDRUS-1D (Soylu et al.

2014) and the newly developed phosphorus and sediment modules (Motew et al. 2017). Watershed-scale phosphorus, sediment, and streamflow processes were calibrated and evaluated against the historical data with satisfactory model performance (Motew et al. 2017, 2018).

We performed Agro-IBIS model simulations at 220-m \times 220-m spatial resolution from 2011 to 2070

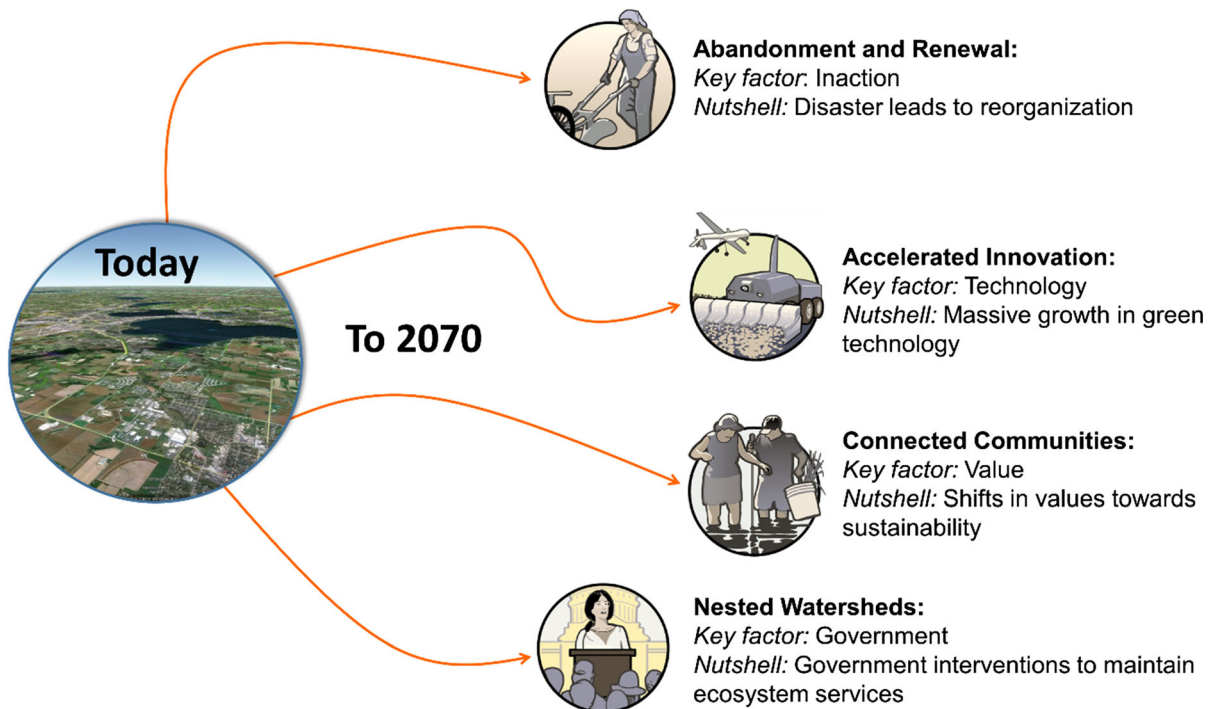


Fig. 2 Illustrations, key factors and nutshells of the four scenarios for the Yahara Watershed that differ fundamentally in their future trajectories

under four stakeholder-driven future scenarios that contrast in social, political, economic and biophysical drivers of change (Fig. 2) (Carpenter et al. 2015; Booth et al. 2016; Wardropper et al. 2016). Scenarios are a series of plausible and often divergent storylines (i.e., ‘narratives’) depicting the future pathways that explicitly incorporate relevant science, societal expectations, and internally consistent assumptions about drivers, relationships, and constraints (Alcamo 2008; Oteros-Rozas et al. 2015; Wiebe et al. 2018). Scenarios were used because: (1) the future of social–ecological systems is highly unpredictable and path-dependent, with enormous uncertainties (Polasky et al. 2011); (2) scenarios can be used for modeling the long-term changes in ecosystem services and their spatial–temporal variability under a wide range of future social–environmental conditions (Thompson et al. 2012; Bateman et al. 2013; Qiu et al. 2018a). A brief synopsis of each scenario for the Yahara Watershed can be found in Fig. 2 and SM Table S1, and complete scenario narratives are available at wsc.limnology.wisc.edu. On the basis of scenario narratives, quantitative drivers (e.g., climate, land use/cover, and nutrients) that are spatially-explicit and

temporally-dynamic were generated (Booth et al. 2016), and then input into the Agro-IBIS to simulate the long-term dynamics of ecosystem service indicators. Distinct from our previous studies (e.g., Qiu et al. 2018b; Zipper et al. 2018; Motew et al. 2019), this research did not focus on nuances in the future trajectories of ecosystem services, but rather used scenarios to provide plausible, and as wide a range as possible to analyze and partition the spatial and temporal variability of ecosystem services.

Rationale for ecosystem service indicators

Based on modeling outputs, we selected indicators capturing key ecological processes underlying the production or condition of each service (Table 1), following Qiu et al. (2018b, 2019). Our selected services range from food production, to water quantity/quality, and climate regulation; these indicators contribute to different aspects of human wellbeing and are socially desirable at local, regional and global scales, based on perceived importance from stakeholders (Wardropper et al. 2020). For instance, annual yield of major crops (including corn, soybean, and

small grains that combined account for 98.5% of the cultivated lands in the watershed) was used as the indicator of crop production. Similarly, annual yield of major forage crops and grasses (including alfalfa, hay and pasture) was used as the indicator of perennial grass production. Drainage replenishes aquifers—main sources of local freshwater in our study region, and was thus used as an indicator for freshwater supply (Qiu and Turner 2013). Phosphorus yield was used as an (inverse) indicator for surface-water quality, because upstream phosphorus runoffs are major contributors to affect regional water quality (Qiu and Turner 2015). Nitrate leaching was used as an (inverse) indicator for groundwater quality, since nitrate is a ubiquitous contaminant of groundwater with detrimental human health impacts through drinking water (McLay et al. 2001). We used the number of days with daily runoff > 10-mm as an (inverse) indicator of flood regulation, which reflects the overall capacity of an ecosystem in mediating effects of extreme weather events, large surface-runoff generation, and thus flooding damages (Nedkov and Burkhard 2012). We also used net ecosystem exchange (NEE) and soil carbon storage as proxies of climate regulation, because they represent the major process and the long-term pool for storing carbon and offsetting greenhouse gas emissions, and are thus relevant for regulating regional and global climate (Smith et al. 2012). Sediment yield was quantified as an (inverse) indicator for soil retention, since this indicator represents the overall capacity of an ecosystem to stabilize soils and regulate the sediment transport across the landscape.

Scales of analysis

Temporal scale

Biophysical indicators from model simulations were first summarized to annual average for all ecosystem services under future scenarios from 2011 to 2070. To determine the period over which there was no temporal autocorrelation, for a given service, we performed autocorrelation function (ACF) and partial autocorrelation function (PACF) analyses, which were done separately for each scenario, and then extracted the maximum lag (at $\alpha = 5\%$) in years across all four scenarios as the time block to calculate temporal averages. For example, our analysis (Table 1) showed

that there was no temporal autocorrelation across all scenarios for crop and perennial production when the lag equaled or exceeded 8 years, whereas such lag threshold changed to 5 years for the indicators of freshwater supply and surface-water quality services. We further calculated mean values of indicators for sequential blocks of duration equal to the time lag for each service (e.g., mean of 2011–2018, 2019–2026...for crop and perennial grass production; mean of 2011–2015, 2016–2020...for freshwater supply, and surface water quality), and the resulting data should thus be uncorrelated in time among blocks. ACF and PACF were performed using ‘*acf*’ and ‘*pacf*’ in R statistical software 3.3.1 (R Core Team 2016).

Spatial scale

Subwatershed is considered as the natural spatial unit of analysis. It is the (1) spatial scale commonly used for conservation planning and ecological assessment, (2) scale at which human activities are likely to exert effects on many ecosystem services, and (3) where ecosystem services are actively managed (Uriarte et al. 2011; Qiu and Turner 2015; Qiu et al. 2017). Based on temporally averaged data, we then calculated subwatershed-means of indicators for each ecosystem service. Second-order subwatersheds ($N = 100$; Fig. S1) were delineated using the 1:24,000 scale stream network, light detection and ranging (LiDAR) elevation, and a field-checked basin map. We delineated the subwatersheds using the ArcHydro module in ArcGIS 10.0; all subwatersheds averaged 12.7 km² (standard deviation = 5.65 km²). All subwatersheds were further categorized into urban-dominated (i.e., if all the developed land cover classes were 50% or more of subwatershed land area) or rural-dominated (Wardropper et al. 2015; Qiu et al. 2017), based on the National Land Cover Database (NLCD) (Homer et al. 2015).

Statistical analyses

To visualize the overall range, variation, and distribution of ecosystem service indicators, we first generated ‘violin’ plots, on the basis of estimates summarized for the subwatersheds and over time blocks with no temporal autocorrelation. Because ecosystem services were quantified using different

indicators with their corresponding units, prior to creating the ‘violin’ plots, we first standardized the data by dividing each value by the grand mean of the indicator of that service. In addition, we also plotted five quantiles (i.e., 10th, 25th, 50th, 75th, and 90th) of subwatershed-level biophysical indicators for each ecosystem service against the chronological order of time blocks from 2011 to 2070.

To investigate whether ecosystem service indicators differ in the magnitude of variability (**Q1**), we (1) computed spatial coefficient of variation (CV) across subwatersheds (i.e., with time blocks as the replicates), and also (2) computed temporal CV for each subwatershed over time (i.e., with subwatersheds as the replicates). CV was chosen because this metric is distributed independently of the mean values (Sokal and Rohlf 1981). To examine whether spatial and temporal CVs differ across ecosystem services, we performed a linear mixed-effects model, with ‘ecosystem service’ as the main effect and ‘scenario’ as the random effect. Models were fit with restricted maximum likelihood (REML) using the *lmer* function of “*lme4*” package in R statistical software 3.3.1 (R Core Team 2016). We further performed the Tukey’s multiple comparison using *glht* function in the ‘*mult-comp*’ package (Hothorn et al. 2008) to calculate 95% confidence intervals of spatial and temporal CVs and test for significance of differences.

To partition the variance and determine the relative importance of ‘space’ and ‘time’ components (**Q2** and **Q3**), we first regressed ecosystem service indicators against ‘scenario’ using the linear mixed-effects model (with ‘scenario’ as the random factor), and then calculated residuals as the updated response variable so as to remove the ‘scenario’ effects. To further decompose the remaining variance into ‘space’, ‘time’, and their interactions, we used the regression commonality analysis (CA)—a technique that explicitly addresses multicollinearity among predictors and is more robust to issues like type I errors and inflated *F* values (Ray-Mukherjee et al. 2014). Based on the CA results, for a given service, if ‘time’ is a dominant factor and contributes to most of the variation, it indicates that this service is most sensitive to drivers specific to time (e.g., climate), and thus time-specific factors would be the primary drivers or controls; in other words, there is a tendency for different locations within a landscape to behave similarly in different years (i.e., *temporally coherent*).

On the contrary, if ‘space’ is a dominant factor and accounts for the majority of the variation, it implies that spatial location and location-specific factors (e.g., land cover, land management) are the primary drivers or controls; in other words, there is tendency for locations within a landscape to be consistently different regardless of time (i.e., *spatially coherent*). To determine the amount of variation due to ‘scenario’, we further performed the variance component analysis (VCA) using original values of ecosystem service indicators as the response, rather than residues after accounting for the ‘scenario’ effect. Analyses were conducted separately for each ecosystem service indicator. We also performed a complementary analysis (Fig. S2), where ‘scenario’ was treated as the fixed effect, because ‘scenario’ can be either interpreted as a sample of possible futures (i.e., as the random factor) or as an explicitly determined set of trajectories by stakeholders (i.e., as the fixed factor). Our results from both analyses were qualitatively consistent, indicative of robustness of our findings. All analyses were conducted in R statistical software 3.3.1 (R core Team 2016); VCA was performed using *remlVCA* function in the ‘VCA’ package (Schuetzenmeister and Dufey 2017) and CA was performed using *regr* function in the ‘*yhat*’ package (Nimon et al. 2015). Residual plots from all regressions were assessed for assumptions of normality and homogeneity of variance, where no violations of the assumptions were detected in our analyses.

In addition to variance partitioning, we further tested for significance of ‘space’, ‘time’, and their interactions using linear regressions to determine which ecosystem services are space–time incoherent (**Q3**). Specifically, if the ‘space–time’ interaction term is significant, it indicates the tendency for different subwatersheds to change or behave differently over time (i.e., *space–time incoherent*). For ecosystem services that did show significant ‘space–time’ interactions, we further mapped the rate of change using simple linear regressions with the time block as the predictor to illustrate such space–time incoherence. Finally, to determine whether or not there are consistent patterns on space/time coherence for ecosystem services between urban- and rural-dominated landscapes (**Q4**), we performed VCA separately for subwatersheds categorized as urban or rural. We also illustrated the overall flow of data processing and analyses in Fig. S3.

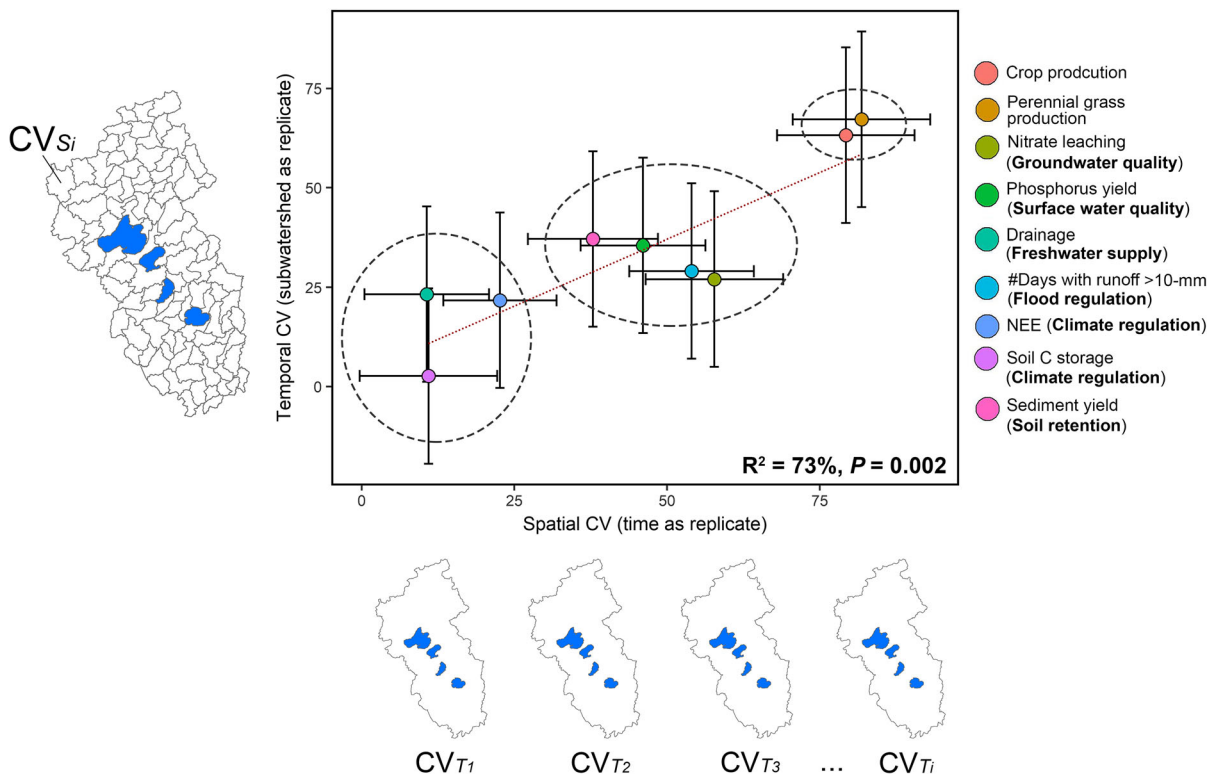


Fig. 3 Spatial and temporal coefficient of variation (CV) for all ecosystem service indicators (with names of ecosystem services shown in parentheses). In this figure, x-axis indicates spatial CV where time blocks serve as the replicates, and y-axis indicates temporal CV where spatial units of subwatershed are the replicates. Error bars are standard errors estimated from the

linear mixed-effects models. Dashed ellipses indicate groups of services that are significantly different from each other based on Tukey's multiple comparisons (see details in SM Table S2). Dashed lines are fitted linear regression with the mean values of spatial and temporal CVs

Results

Ecosystem service indicators demonstrated substantial spatial and temporal variability across scenarios (Figs. 3 and S4), indicating that all these services were overall spatially heterogeneous and temporally dynamic in nature. However, different ecosystem service indicators showed varied levels of variability (Fig. 3 and Table S2): (1) two food production services (i.e., crop and perennial grass production) were most variable, as shown by the highest spatial and temporal CVs among all services; (2) nitrate leaching, phosphorus yield, sediment yield, and number of days with runoff > 10-mm (i.e., inverse indicators for groundwater quality, surface-water quality, soil retention, and flood regulation services, respectively) were the group with intermediate levels of variability; and (3) drainage (i.e., a proxy for potential freshwater supply service), soil carbon storage and

NEE (i.e., proxies for climate regulation services) formed the cluster with the least amount of variability, as demonstrated by the lowest spatial and temporal CV values. In addition, we also found a strong linear correlation (Pearson $r = 0.88$, $P = 0.002$) between spatial and temporal CVs across all ecosystem service indicators (Fig. 3).

Both 'space' and 'time' were significant factors for indicators of all ecosystem services studied ($P < 0.001$) (Figs. 4, 5 and 6). Such results were robust, regardless of whether 'scenario' was treated as a random or fixed factor in the analyses (Fig. S2). Comparing across different ecosystem services, 'space' explained the majority of variance for most indicators, except for drainage and sediment yield. Specifically, for crop and perennial grass production, 'space' explained 43% and 29% of the variation, respectively, and 'time' explained more variation for crop production (17%) than perennial grass production

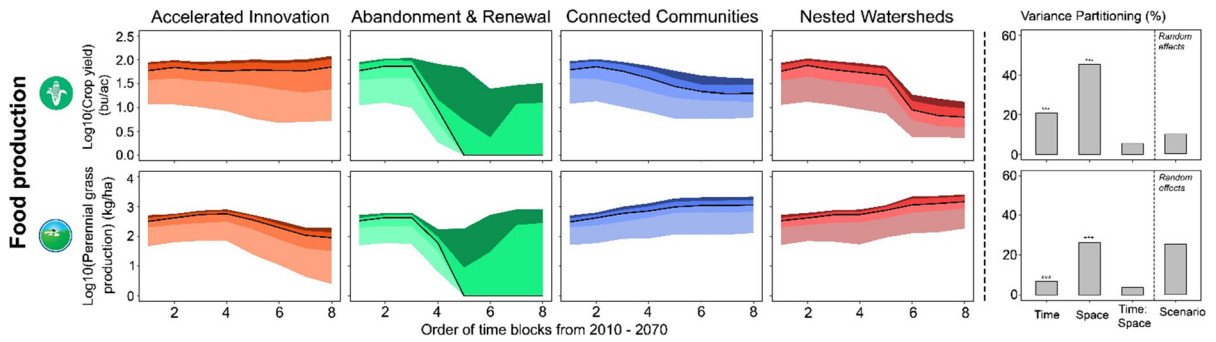


Fig. 4 Spatial–temporal variability and variance partitioning of two food production services. In the figure, each row corresponds one ecosystem service, and the first four columns show the variability of ecosystem service indicators under each scenario. In these panels, five quantiles (i.e., 10th, 25th, 50th,

75th, and 90th) were calculated, and the x-axis shows the order of time blocks beyond which there is no temporal autocorrelation. The last column shows variance partitioning of the ‘space’, ‘time’ and ‘scenario’ components (** $P < 0.01$; * $P < 0.05$;

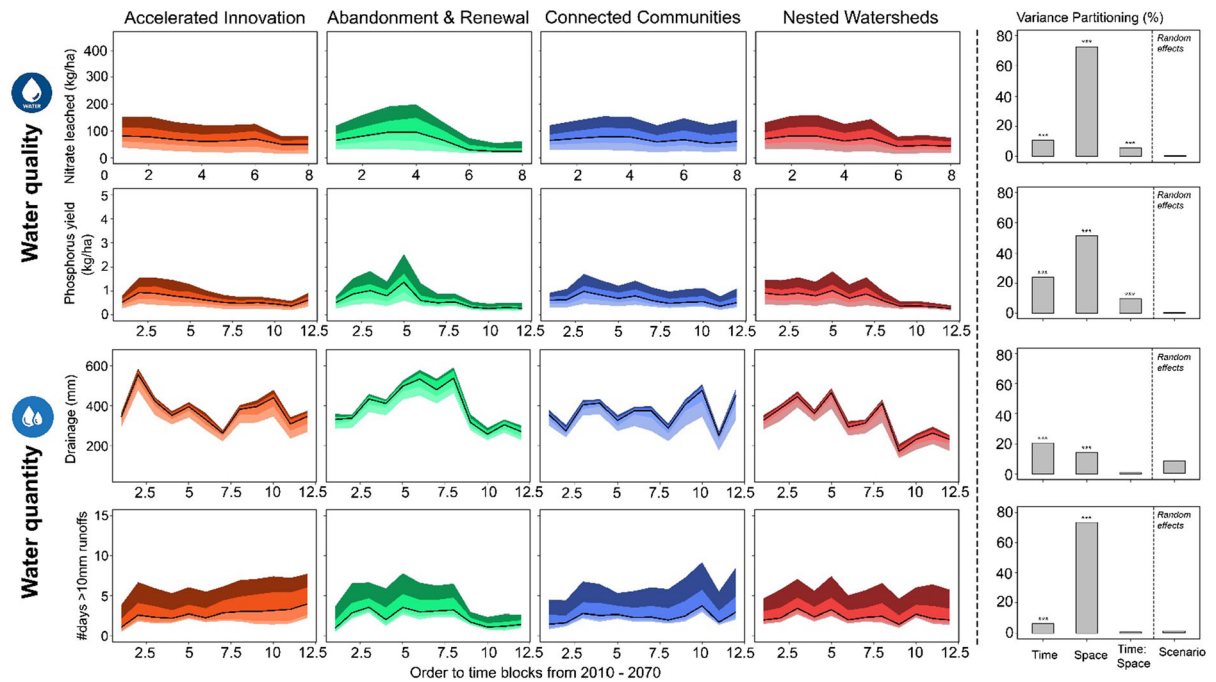


Fig. 5 Spatial–temporal variability and variance partitioning of water quality and quantity services. In the figure, each row corresponds one ecosystem service, and the first four columns show the variability of ecosystem service indicators under each scenario. In these panels, five quantiles (i.e., 10th, 25th, 50th,

75th, and 90th) were calculated, and the x-axis shows the order of time blocks beyond which there is no temporal autocorrelation. The last column shows variance partitioning of the ‘space’, ‘time’ and ‘scenario’ components (** $P < 0.01$; * $P < 0.05$;

(4%) (Fig. 3). For the two water quality services, ‘space’ contributed to 67% and 42% of the variation for indicators of nitrate leaching and phosphorus yield, respectively, whereas the ‘time’ explained 5% and 14% of the variation. With respect to the two water quantity services, for drainage, ‘time’ contributed to a

greater amount of variation than the ‘space’ factor (i.e., 22% vs. 15%), but for the number of days with extreme runoff, ‘space’ again showed as a dominant factor contributing to 73% of variation (vs. 5% by the ‘time’ factor). For climate regulation services, most of variations were attributable to ‘space’ (i.e., 88% for

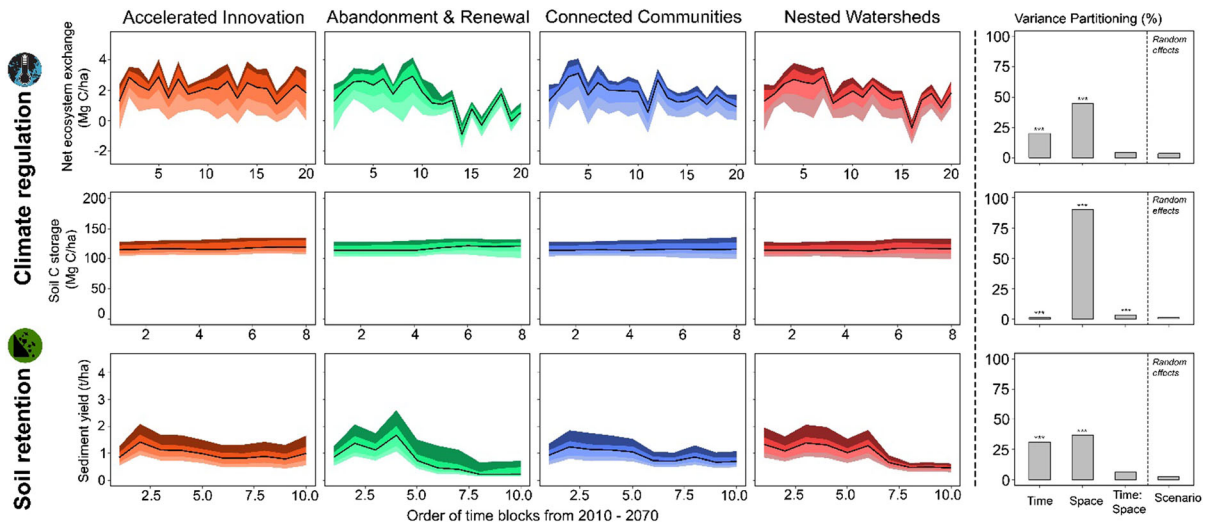


Fig. 6 Spatial-temporal variability and variance partitioning of climate regulation and soil retention services. In the figure, each row corresponds one ecosystem service, and the first four columns show the variability of ecosystem service indicators under each scenario. In these panels, five quantiles (i.e., 10th,

25th, 50th, 75th, and 90th) were calculated, and the x-axis shows the order of time blocks beyond which there is no temporal autocorrelation. The last column shows variance partitioning of the ‘space’, ‘time’ and ‘scenario’ components (** $P < 0.001$; * $P < 0.01$; * $P < 0.05$)

indicator of soil carbon storage, and 42% for NEE), and ‘time’ explained only 1% for soil carbon storage and 16% for NEE. For soil retention, ‘space’ and ‘time’ factors explained comparable amount of variations (31% vs. 25%) in its indicator of sediment yield.

Hence, based on the relative proportion of variations explained, only drainage was categorized as “temporally coherent” (meaning that different subwatersheds behaved similarly in different years), and most of the remaining services were considered as predominantly ‘spatially coherent’ (meaning that subwatersheds consistently differed regardless of time). In addition, significant “space-time” interactions were detected for three ecosystem service indicators (i.e., nitrate leaching, phosphorus yield and soil carbon storage) (all $P < 0.001$; Figs. 5 and 6), suggesting that water quality and climate regulation services were “space-time incoherent”. In other words, for these services, different subwatersheds tended to behave differently as a function of time, or vice versa. Our analyses further demonstrated that there was indeed spatial heterogeneity in the rate of change for the indicators of these three ecosystem services (Fig. 7).

Urban- and rural-dominated subwatersheds showed different patterns in the relative importance of ‘space’ and ‘time’ factors for ecosystem service indicators

(Fig. 8). Specifically, across all services, ‘space’ overall explained more variations for urban-dominated subwatersheds than rural counterparts; however, a greater proportion of the variation was attributable to ‘time’ factor in rural-dominated watersheds. For example, for drainage, phosphorus yield, and extreme runoff days, the ‘space’ factor explained 19%, 46% and 50% of the variation, respectively, in the urban-dominated subwatersheds, as compared to 3%, 34%, and 37% in the rural-dominated subwatersheds. On the other hand, for phosphorus yield and extreme runoff days, the ‘time’ factor explained 14% and 9% of the variation, respectively, in the urban-dominated subwatersheds, as compared to 24% and 21% in the rural-dominated subwatersheds (Fig. 8).

Discussion

Our study uses biophysical model and future scenario to investigate spatial and temporal variability of nine ecosystem service indicators in an urbanizing agricultural watershed. We find that all services are spatially heterogeneous and temporally dynamic, but also differ in their magnitude of variability. Certain ecosystem services such as food production and water quality are more variable than others like climate regulation and

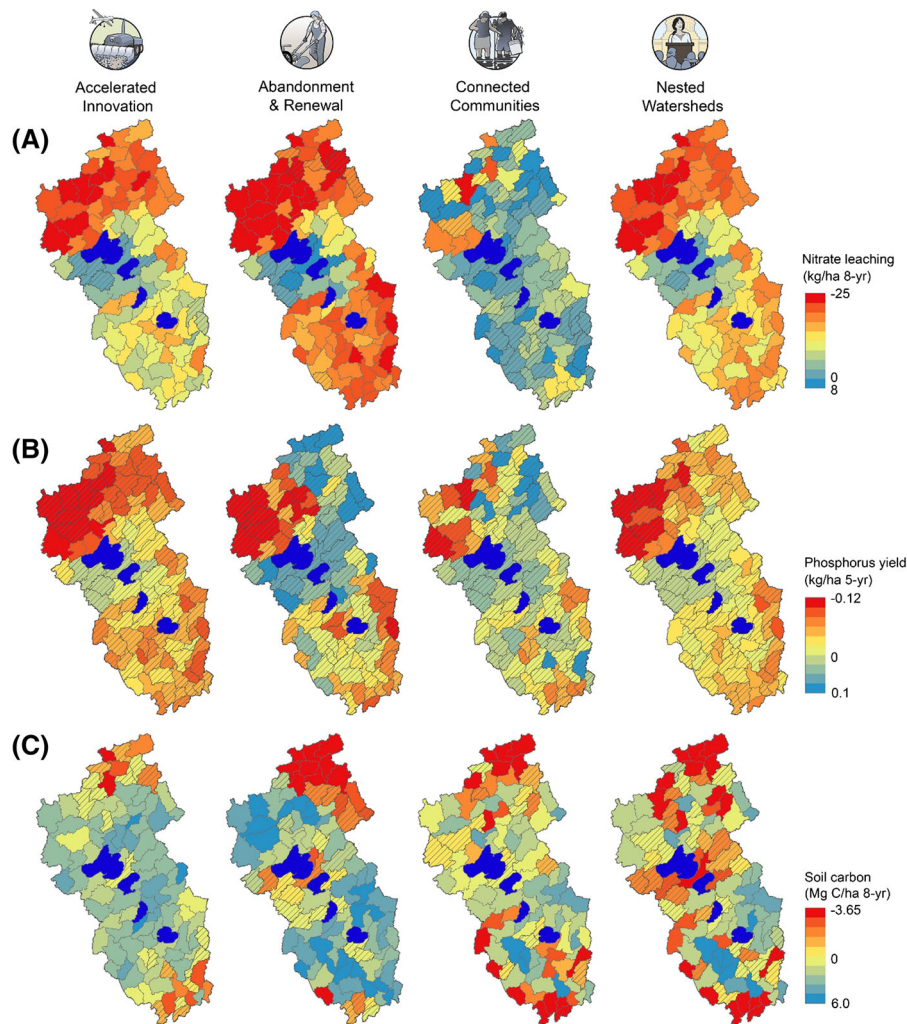


Fig. 7 Rate of change for indicators of three ecosystem services with significant space–time interactions (i.e., space–time incoherence): **a** nitrate leaching; **b** phosphorus yield; **c** soil carbon storage. For a given service, linear regression was

performed for each subwatershed with binned time blocks as the predictor variable. Parameter estimates were then mapped as the rate of change. Subwatersheds with hatch-lines indicate non-significant temporal trend (at $\alpha = 0.10$)

freshwater supply. Consistent across most services, the ‘space’ factor (relative to ‘time’) contributes to a dominant proportion of the variation, highlighting importance of location-specific factors and landscape management for future supply of ecosystem services. Significant space–time interactions exist for surface- and ground-water quality and soil carbon storage, suggesting that location- and time-specific factors could have interactive effects on these services. Differences in relative controls of ‘space’ vs. ‘time’ factors for urban- and rural-dominated subwatersheds indicate that managing ecosystem services in these landscapes would require strategies that target their

different key drivers. Our study reveals factors or processes that are primary controls for multiple ecosystem services, and has theoretical and practical implications for ecosystem service management. In particular, the knowledge on services that are slow-changing and space–time incoherent is vital for integrating into policy and management to enhance the sustainability of future ecosystem services.

Overall ecosystem service variability

Ecosystem services differ in their spatial–temporal variability, reflecting inherent nature (i.e., slow vs.

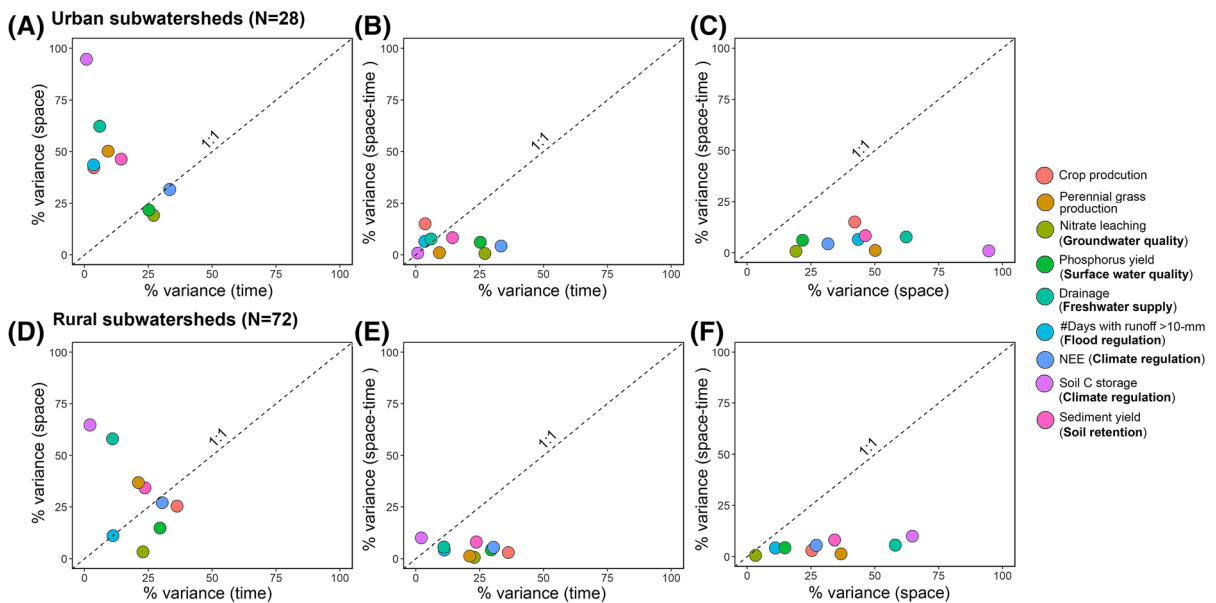


Fig. 8 Variance partitioning results for the urban- and rural-dominated subwatersheds

fast, and spatially heterogeneous vs. homogeneous) of ecological processes and biophysical conditions that underpin the supply of each service (Carpenter and Turner 2000; Lovett et al. 2005; Walker et al. 2012). Provisioning services such as food production are more variable than regulating services, likely because (1) production of crops has large interannual variations subject to climatic variability and extremes (Ray et al. 2015; Zipper et al. 2016), as well as large spatial variations driven by factors including land cover, soil, and management that are spatially heterogeneous (Donner and Kucharik 2003); and (2) regulating services are usually controlled by slowly-changing variables (e.g., soil organic matter) (Bennett et al. 2009; Biggs et al. 2012), which determine whether shifting to alternative state occurs and thus change more slowly than services of more direct concerns to people (e.g., food supply). For example, among our selected indicators, phosphorus yield (a proxy for surface water quality) and soil carbon storage (a proxy for climate regulation) are controlled by processes with very low turnover rate (i.e., from decades to century) (Reed-Andersen et al. 2000; Ingram and Fernandes 2001); these are also the key indicators that denote critical transitioning of systems (e.g., eutrophication, vegetation patchiness) (Gordon et al. 2008). It is important to note that due to the relationship between ‘slow’ and ‘fast’ variables that underlie

ecosystem services (Walker et al. 2012), the dynamics of fast-changing provisioning services and their responses to external factors could likely be shaped by slow-changing regulating services, which can be tested in future research.

Our analyses also highlight which scales (i.e., space and time) would be relevant to study and manage the dynamics of ecosystem services. For example, for a given scale of investigation, a long-term perspective might be relevant for slow-changing services (e.g., climate regulation), whereas a dynamic and spatially-explicit approach would be required for fast-changing, transient, and highly spatially heterogeneous services (e.g., food production). Our study may also help set aside context-specific temporal expectations for policy and management efforts; e.g., for managing a suite of services in a watershed, the amount of efforts and time needed to detect changes may follow: climate regulation > water quality and flood regulation > food production.

There is a strong positive, linear relationship between spatial and temporal variability of ecosystem service indicators (Fig. 3), indicating that the spatial and temporal scales over which patterns and processes of different services are manifested are tightly linked. Such results are consistent with the “Stommel diagram” (Stommel 1963; Delcourt et al. 1982) that demonstrates strong positive correlations between

spatial and temporal scales of ecological and biophysical processes (e.g., disturbance regime and vegetation pattern) over a range of terrestrial and aquatic systems. Recent studies, however, posited that such space–time coupling of ecological processes may not hold under contemporary or unprecedented anthropogenic environmental changes (i.e., spatial–temporal anthropogenic rescaling hypothesis) (Rose et al. 2017). Hence, future research will be needed to address when, how and what anthropogenic changes could decouple the inherent space–time linkages of ecosystem services across social–ecological systems.

Relative importance of ‘space’ vs. ‘time’ factors

Our research reveals that while both ‘space’ and ‘time’ factors matter for all studied ecosystem services, they also vary in their relative importance (Figs. 4, 5 and 6). As compared to ‘time’ factor, the ‘space’ component explains an overwhelming amount of the variation for most services (except for freshwater supply and soil retention), suggesting that spatial location and location-specific factors (e.g., land cover, land management) are the primary controls for most services. Hence, our results highlight the opportunities of proactive landscape management in improving the supply of many terrestrial ecosystem services, and in combating against future environmental changes such as climate (Qiu et al. 2018b).

Specifically, for crop and perennial grass production, land-based factors (e.g., amount of agricultural lands, nutrient management, and land-use intensity) play dominant roles (Fig. 4), consistent with earlier studies (e.g., Lambin et al. 2000; Lawler et al. 2014). The ‘time’ factor, nonetheless, is also non-trivial especially for crop production, indicating that monoculture row crops can be more sensitive to, yet perennial grasses (often more diverse than row crops) may be more resistant and resilient to time-specific factors (e.g., climate) and interannual variations in external environmental conditions (Isbell et al. 2009; Prieto et al. 2015; Tracy et al. 2018).

For surface- and ground-water quality, ‘space’ also shows as a dominant control (Fig. 5), reflecting critical roles of location-specific factors (e.g., land use/cover and management) in these two water quality services. These findings allude to the importance of managing landscape patterns (e.g., composition, configuration, land-use intensity) to sustain regional water

quality (Qiu and Turner 2015; Gallagher and Gergel 2017; Shi et al. 2017; Qiu 2019). In addition, ‘space’ exerts a stronger influence on nitrate leaching (a proxy for groundwater quality) than on phosphorus yield (a proxy for surface water quality), while ‘time’ shows as a more significant factor for phosphorus yield. These results suggest that location-specific controls are stronger for nitrate leaching (than phosphorus yield), because nitrate leaching is primarily a vertical process dominated by factors such as nutrient application and available N in the soil profiles (Donner and Kucharik 2003; DeFries et al. 2004). In contrast, stronger time-specific controls for phosphorus yield (than nitrate leaching) suggest that factors such as interannual climate variability and extremes (e.g., extreme precipitation events) could play a key role in the lateral transfers of phosphorus across the landscape (Carpenter et al. 2018; Motew et al. 2019) and sometimes even have synergistic effects with land- or location-specific factors (Motew et al. 2018).

For two water quantity services (Fig. 5), ‘time’ shows as a strong factor for drainage (a proxy for freshwater supply), indicating that this service is more responsive to time-specific factors like climatic conditions. Such findings are consistent with revelation from prior studies that climate tends to exert the strongest control for recharge and drainage (through the balance of precipitation and reference evapotranspiration), followed by vegetation and soil-related factors (Keese et al. 2005; Kim and Jackson 2012; Zipper et al. 2018). In contrast, dominant location-specific controls are found for extreme runoff days (a proxy for flood regulation). These results concur with earlier modeling and empirical studies (e.g., Qiu and Turner 2015; Usinowicz et al. 2016), where location-specific factors (e.g., amount and spatial configuration of imperviousness and natural vegetation) (e.g., Hamdi et al. 2011; Ogden et al. 2011; Qiu and Turner 2015; Usinowicz et al. 2016) drive the peak flow, extreme runoff, and thus flood regulation service.

For soil carbon storage and NEE, the ‘space’ component exerts a stronger influence relative to ‘time’ (Fig. 6), indicating key roles of location-specific factors (e.g., land conversion, management) in affecting climate regulation service (Lal 2004; Kaplan et al. 2011). Hence, our results highlight the importance of land-based strategies for carbon management, climate mitigation and regulation (Arneeth et al. 2014; Canadell and Schulze 2014). In addition,

the ‘time’ factor explains more variation for NEE than soil carbon storage, suggesting that NEE tends to be more responsive to time-specific drivers. Such differences in the effects of ‘time’ factor likely reflect the short-term (i.e., NEE) vs. long-term (i.e., soil carbon pools) processes related to carbon fluxes and sequestration (Barford et al. 2001). For sediment yield (a proxy for soil retention), the ‘space’ and ‘time’ components explain an equivalent amount of variation, reflecting equal controls of both location- and time-specific factors.

Space–time incoherence in ecosystem services

Our analyses reveal space–time incoherence for three ecosystem service indicators—nitrate leaching, phosphorus yield and soil carbon storage (Figs. 5 and 6). For these services, subwatersheds tend to vary differently over time (e.g., positive or negative depending on the subwatershed) (Fig. 7) and respond in different manners to drivers (i.e., spatial variability in ecosystem service responses to temporal drivers). It also indicates that, for these services, location- and time-specific factors could have interactive effects. Indeed, prior studies have demonstrated synergistic effects of land-based factors (i.e., manure supply) and extreme precipitation on phosphorus loading and surface-water quality (Loecke et al. 2017; Motew et al. 2018). Similarly, previous studies have shown that high concentration of soil nitrogen (from land management such as nutrient applications) could interact positively with high drainage due to climatic and soil conditions to amplify nitrate leaching (Di and Cameron 2016). Significant space–time incoherence also suggests that location-specific changes can be a crucial lever to either exacerbate (e.g., through poor or inadequate management) or, alternatively, improve (e.g., through effective or adaptive management) the resilience of ecosystem services to temporal-specific factors such as undesirable climate changes. Our results further indicate that preserving water quality and soil carbon storage can benefit from spatial–temporal lens that simultaneously addresses spatial fit of management/governance (Qiu et al. 2017), and considers long-term dynamics of management and policy actions (Kratz et al. 2003). Our findings complement previous studies to demonstrate that space–time interactions prevail from community assembly and biodiversity, to ecosystem functions, and the supply of

certain goods and services (Kratz et al. 1987; Legendre et al. 2010; Poisot et al. 2015).

Urban and rural comparisons

Our research reveals that across all services, the ‘space’ factor is a stronger control in urban-dominated subwatersheds, whereas ‘time’ explains more variations in rural counterparts (Fig. 8). These results indicate that ecosystem services in urban landscapes tend to be more sensitive (as compared to rural) to drivers specific to locations, highlighting importance of landscape management (e.g., green infrastructure, low-impact development, and landscape design) for improving urban ecosystem services (Gaston et al. 2013; Lovell and Taylor 2013; Ahern et al. 2014). In contrast, rural landscapes are relatively more homogeneous (as compared to urban) and may respond similarly to time-specific factors. Our results suggest that, while targeting location-specific factors is critical for improving ecosystem services in both urban- and rural-dominated areas, managing time-specific factors can be more effective in rural landscapes. Our study, however, did not explicitly test mechanisms that drive differences between urban vs. rural landscapes. More research will be needed to address how social–ecological factors alter spatial–temporal variability of urban and rural ecosystem services to better inform management.

Methodological considerations

It is important to acknowledge that our study focuses on biophysical indicators that represent production of ecosystem services. Future research is needed to integrate biophysical assessments with social data to study the spatial and temporal variability of ecosystem service consumption and demands, and how they respond to the variability of service supply as well as external drivers (Collins et al. 2011; Angelstam et al. 2019). In addition, it is also worth noting that spatial and temporal variability is likely sensitive to scale of analyses, and our results would be more applicable to the subwatershed scales. Hence, how the variability of ecosystem services and their relative controls change with the scales of analyses also deserves future attention.

Conclusions

Understanding how to sustain land, water, and climate and their life-supporting services in a rapidly changing and unpredictable future is essential for informing policy and management. Our study presents a framework to investigate, interpret and compare the spatial and temporal variability of ecosystem services, and determine the relative importance of ‘space’ and ‘time’ controls for service supply. Our framework is relevant given the increasing awareness of the complex dynamics of ecosystem services, as well as ever-increasing observational, monitoring and analytical capacities (e.g., large-scale long-term research programs such as LTER) of social–ecological processes that underlie ecosystem service supply. Our results provide a baseline to anticipate and manage dynamics and variability of ecosystem services. The knowledge gained in the Yahara Watershed will be relevant for managing Midwestern agricultural landscapes or other similar human-watershed systems elsewhere to sustain diverse ecosystem services.

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