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RESEARCH ARTICLE

How do land-use legacies affect ecosystem services in United States cultural landscapes?

Carly Ziter · Rose A. Graves · Monica G. Turner

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Abstract
Context Landscape-scale studies of ecosystem services (ES) have increased, but few consider land-use history. Historical land use may be especially important in cultural landscapes, producing legacies that influence ecosystem structure, function, and biota that in turn affect ES supply.
Objectives Our goal was to generate a conceptual framework for understanding when land-use legacies matter for ES supply in well-studied agricultural, urban, and exurban US landscapes.
Methods We synthesized illustrative examples from published literature in which landscape legacies were demonstrated or are likely to influence ES.
Results We suggest three related conditions in which land-use legacies are important for understanding current ES supply. (1) Intrinsically slow ecological processes govern ES supply, illustrated for soil-based and hydrologic services impaired by slowly processed pollutants. (2) Time lags between land-use change and ecosystem responses delay effects on ES supply, illustrated for biodiversity-based services that may experience an ES debt. (3) Threshold relationships exist, such that changes in ES are difficult to reverse, and legacy lock-in disconnects contemporary landscapes from ES supply, illustrated by hydrologic services. Mismatches between contemporary landscape patterns and mechanisms underpinning ES supply yield unexpected patterns of ES.
Conclusions Today's land-use decisions will generate tomorrow's legacies, and ES will be affected if processes underpinning ES are affected by land-use legacies. Research priorities include understanding effects of urban abandonment, new contaminants, and interactions of land-use legacies and climate change. Improved understanding of historical effects will improve management of contemporary ES, and aid in decision-making as new challenges to sustaining cultural landscapes arise.

Keywords Land-use change · Urban ecosystems · Exurban ecosystems · Agricultural ecosystems · Historical ecology

C. Ziter (✉) · R. A. Graves · M. G. Turner
Department of Zoology, University of Wisconsin-Madison, Madison, WI 53717, USA
e-mail: ziter@wisc.edu

Introduction

Landscape-scale studies of ecosystem services (ES) have increased in recent years (Maes et al. 2012; Mitchell et al. 2015a), including in the US (Nelson et al. 2009; Qiu and Turner 2013; Carpenter et al. 2015a; Blumstein and Thompson 2015), but relatively little attention has been paid to the role of land-use history. Many studies map ES supply (and ES tradeoffs and synergies) across the landscape (Burkhard et al. 2013; Malinga et al. 2015) as an important

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first step towards incorporating ES into policy (Chan et al. 2006; Naidoo et al. 2008; Raudsepp-Hearne et al. 2010). However, these maps often rely on current land-cover pattern, which is a poor surrogate for ES supply (Eigenbrod et al. 2010; Schulp et al. 2014), but underlying processes are often not well known. Understanding the mechanisms driving landscape patterns of ES is increasingly important as ES become explicitly incorporated in decision-making; for example, the Obama administration issued a 2015 memorandum directing all US federal agencies to incorporate ES into their planning (Donovan et al. 2015). Spatial and temporal drivers of ES supply must be considered to improve mechanistic understanding of ES supply at landscape scales, particularly in human-dominated landscapes. However, most analyses to date have estimated ES supply without addressing the role of land-use legacies—the persistent effects of past events, patterns, or conditions on the contemporary landscape.

Historical land use produces legacies that influence the structure, function, and biota of many ecosystems (Foster et al. 2003; Lunt and Spooner 2005; Bürgi et al. 2017), which in turn affect ES supply. Thus, both contemporary and historical land-use patterns may influence ES supply. In the Southern Appalachian Mountains for example, where land use change is shaped by transition to a nature-based economy, effects of land-use history have been well documented on soil nutrients (Fraterrigo et al. 2005) and the presence and abundance of native (Elliott et al. 2014) and non-native forest understory plant species (Kuhman et al. 2011, 2013). These land-use legacies in soils and vegetation in turn influence opportunities for wildflower viewing, a cultural ecosystem service that attracts tourists, and for which the region is widely known (Graves et al. 2017). In Sheffield, UK, historical land-use patterns were of greater importance than current patterns in explaining variability in several indicators of contemporary ES supply, including aboveground carbon storage, recreational use, and bird species richness (Dallimer et al. 2015). Recent studies also suggest effects of historical land use on ES may change over time (Watson et al. 2014). ES dynamics can differ markedly within the same landscape following recovery from disturbance (Sutherland et al. 2016), and relationships among sets of ES can vary qualitatively over time with land-use history (Renard et al. 2015; Tomscha and Gergel 2016).

Understanding when land-use legacies explain variation in contemporary ES is particularly relevant in *cultural landscapes*—landscapes that are shaped by human activities and possess features valued by humans (Schaich et al. 2010; Plieninger et al. 2014). Cultural landscapes have long histories of land-use/land-cover (LULC) change as a result of their deliberate management, and are also areas of high ES demand. While studies have demonstrated lasting effects of land-use legacies in cultural landscapes globally (e.g., Cousins and Eriksson 2002; Bürgi and Gimmi 2007; Plieninger et al. 2010; Dullinger et al. 2013; Dallimer et al. 2015), we focus specifically on land-use legacies and ES in cultural landscapes of the United States. We consider contemporary agricultural, urban and exurban landscapes (Fig. 1) that represent areas most people live and work (Brown et al. 2005; Theobald 2005; Radeloff et al. 2012; Groffman et al. 2014), though we recognize land-use legacies also affect the ecology of other US landscapes (Foster et al. 2003). Sometimes referred to as "vernacular cultural landscapes", these landscapes have evolved unintentionally as a result of everyday human use over time—thus reflecting the physical, biological, and cultural character of everyday lives (Alanen and Melnick 2000; The Cultural Landscape Foundation). Cultural landscapes can also encompass heritage areas shaped by particular religious, racial, or cultural groups ("ethnographic landscapes"), consciously designed landscapes such as parks or campuses ("designed landscapes"), and landscapes associated with historic events ("historic sites") (The Cultural Landscape Foundation, National Park Service); however the types of cultural landscapes we consider here currently make up the majority of cultural landscapes in America (Alanen and Melnick 2000).

Prior to European settlement US landscapes were largely forested, but also contained significant prairie and savanna cover—with landscape and vegetation patterns driven in part by indigenous peoples, particularly through centuries of fire management (Macleish 1994; Delcourt and Delcourt 2004). Land use changed profoundly in the US following European settlement, although the timing and sequence of land-use changes varied among regions (Whitney 1994; Turner et al. 1998). The seventeenth through nineteenth centuries saw widespread forest loss, primarily as a consequence of farming, the burgeoning lumber industry, and widespread fuelwood collection. Occurring in

Fig. 1 Photos illustrating different types of cultural landscape in the United States. **a** An agricultural landscape in the Yahara watershed, southern Wisconsin. Photo credit: University of Wisconsin-Madison Water Sustainability and Climate project. **b** An urban landscape in Madison, Wisconsin. Photo credit: University of Wisconsin-Madison water sustainability and climate project. **c** An exurban landscape in the southern Appalachian Mountains of western North Carolina. Photo credit: US Long-term Ecological Research Network Office

many regions at a pace much faster than analogous forest clearance in Europe, this conversion to cultivated land resulted in fragmentation of North American woodlands (Whitney 1994). Cropland peaked in the US in the 1940s and has since fluctuated around 162 million ha (Turner et al. 1998). Some areas cleared for agriculture have reforested in the past century due to lack of cultivation (e.g., New England, Southeast, and upper Midwest), whereas clearing for agriculture was more permanent in other regions (e.g., lower Midwest) (Whitney 1994). In contemporary cultural landscapes of the US, agricultural areas remain dominated by croplands and pastures (Fig. 1a) while urban landscapes are characterized by high-density commercial, industrial, and residential land use (Fig. 1b). Exurban landscapes are composed of low-density residential development, often in rural areas that offer environmental amenities or on former croplands surrounding mid-sized cities (Fig. 1b). Exurban land use occupies more area than cities in the US and is increasing rapidly (Theobald 2005; Brown et al. 2005). The relatively recent historical context ($\sim$150 years) sets these US landscapes apart from the iconic cultural landscapes of Europe, where land-use patterns have been more stable over much longer periods of time (Keatley et al. 2011).

Cultural landscapes are closely linked to human wellbeing through the services they provide, and like such landscapes elsewhere around the world, they are dynamic (Plieninger et al. 2014). Subject to shifts in land cover and often changing in response to policy or economics, these anthropogenically modified landscapes are defined by transition from a previous LULC type to their current state. Thus, ES provided by these landscapes may be particularly influenced by historical land-use patterns. As landscapes continue to transition towards greater use and dominance by people (Foley et al. 2005; Ellis 2011), understanding how land-use history influences ES supply and how current activities may produce future land-use legacies is necessary for managing cultural landscapes sustainably.

Although some recent research examines effects of historical land use on ES supply, studies that incorporate historical information are rare in the ecosystem services literature. It is often difficult to locate consistent data sources, some of which are qualitative and most of which have not been assembled over whole landscapes. New methods for incorporating historical aspects of ES are emerging (Tomscha et al. 2016), yet the difficulty and cost of assembling the data sources make it unrealistic for every study to consider land-use legacies for each ES in question. Knowing when it is most important to account for history in estimating ES supply is an important step towards understanding patterns of ES provision.

Here, we present a framework for considering when land-use legacies matter for ES supply in US cultural landscapes, drawing on illustrative examples from well-studied agricultural, urban, and exurban landscapes. We suggest three related but distinct conditions in which land-use legacies are especially important for understanding current ES supply: (1) intrinsically slow ecological processes govern ES supply; (2) time lags between land-use change and ecosystem responses delay the effects on ES supply; and (3) threshold relationships exist, such that changes in ES may be difficult to reverse. These three conditions are not mutually exclusive, but their influence on ES can be distinct as highlighted by examples presented herein. In all cases, the mismatch between what is suggested by the contemporary landscape and mechanisms underpinning ES supply can yield unexpected patterns of ES. We conclude by considering the influence that current land use may have on future ES supply.

Land-use legacies and contemporary ES supply

Slow processes govern ES supply

Land-use legacies are important for ES when services are underlain by intrinsically slow ecological processes (Fig. 2a) (Walker et al. 2012). Soil-based ES offer useful examples because many ecological processes and soil nutrient stocks are slow to recover from past land use. For example, soil carbon (C) stocks are often used as an indicator of climate regulation services, as well as water retention and general soil fertility, and soil C stocks in urban and exurban landscapes vary with historical land-use and time since development (Golubiewski 2006; Lewis et al. 2006; Raciti et al. 2011). Interestingly, effects of land-use legacies on soil C in cities vary in magnitude and direction among regions. In Baltimore, Maryland (mesic mid-Atlantic coast), residential lots developed on former agricultural land had initially low C stocks compared to those converted from forest, because years of agricultural use depleted soil C (Raciti et al. 2011). Following development, former agricultural lands accumulated soil C over time, whereas former forests did not (Raciti et al. 2011). Contrastingly, in the greater Phoenix area, Arizona (xeric Southwest), residential lots developed on former agricultural lands had substantially higher soil C stocks compared to those converted from native desert. In arid regions, soil C was increased during years of agricultural use, rather than depleted, in response to irrigation and nutrient augmentation (Lewis et al. 2006). Differences in soil

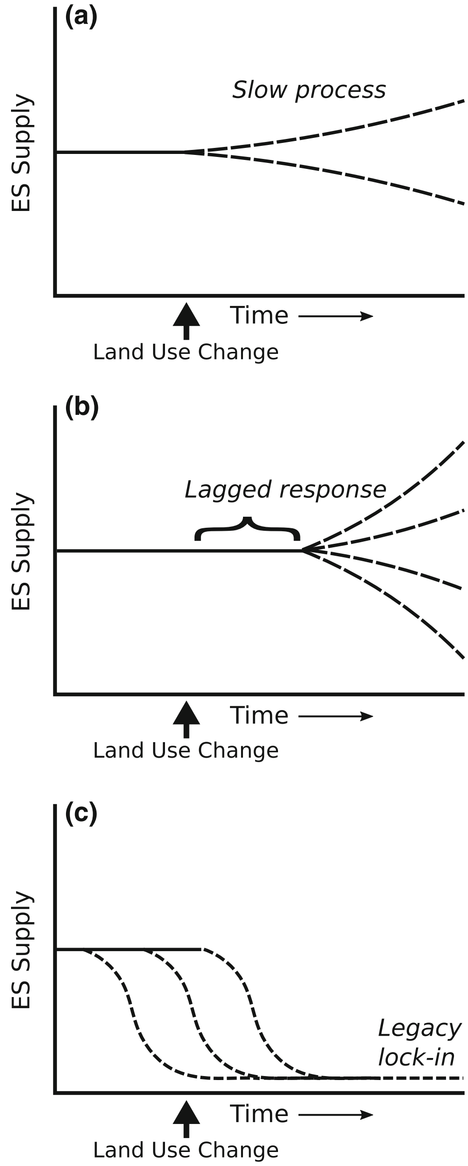

Fig. 2 Three conditions in which land-use legacies are important for understanding current ecosystem service (ES) supply. **a** Intrinsically slow ecological processes govern ES supply. **b** Time lags between land-use change and ecosystem responses delay effects on ES supply. **c** Threshold relationships exist, such that changes in ES are difficult to reverse, and legacy lock-in disconnects contemporary landscapes from ES supply. For each of the three conditions, *dashed lines* represent possible trajectories of ES supply following land-use change

C based on land-use history persisted for decades after residential development because processes that change soil C pools are inherently slow. Although effects of land-use history differed in important ways between regions, variation in present-day soil C stocks could not be explained in the absence of understanding land-use history.

Water quality and associated hydrologic services (Brauman et al. 2007) can be similarly influenced by land-use legacies associated with long-term persistence of nutrients or environmental pollutants long after inputs have ceased. In this case, the rate ecosystems can process or purge a pollutant is intrinsically slow. Consider soil phosphorus (P), a common pollutant associated with eutrophication of inland lakes and widely used indicator of lake water quality and hydrologic services (Carpenter et al. 1998; Lathrop 2007). Fertilizer and manure application increase soil P, often over decades of farming. Because P adheres to soil particles and is not readily soluble, it is transported very slowly from croplands to surface waters via soil erosion and runoff, much of which occurs during high-intensity rain events (Carpenter et al. 2015b). Drawdown of soil P is very slow in agricultural landscapes (Hamilton 2011), and over-fertilized soils remain P enriched for decades (Bennett et al. 1999) even following implementation of conservation strategies and/or land-use change aimed at P reduction (Hamilton 2011; Sharpley et al. 2013). In the Yahara Watershed of southern Wisconsin, a century of agricultural P inputs have resulted in spatially variable but highly elevated soil P levels that continue to act as a hidden driver of water quality (Bennett et al. 2005; Kara et al. 2011). Persistent efforts to control P pollution have produced negligible improvements to water quality (Gillon et al. 2016), and expanding urbanization on former croplands continues to release soil P in urban runoff (Betz et al. 2005). Land-use history is a key driver of soil P that is not necessarily apparent or explained by contemporary LULC patterns.

Environmental pollutants such as mercury and organochlorine pesticides (e.g., DDT, PCBs) also persist in cultural landscapes for decades to centuries as a legacy of industrial, agricultural, and residential use (Wang et al. 2004; Weber et al. 2008). Contaminated water and sediments enter the food web at low trophic levels and bioaccumulate in higher trophic organisms such as fish; the resultant reduction in seafood quality impacts provisioning and cultural ES (Holmlund and Hammer 1999). Loss of these pollutants from water and sediments through degradation or volatilization is a slow process. Consider the densely populated San Francisco Bay watershed in California. Although regional organochlorine pesticide use peaked 30–40 years ago, pesticide residues remain high enough to warrant current sport fish consumption advisories (Connor et al. 2007; Davis et al. 2007; Schoellhamer et al. 2007). Comparable trends are seen in urban and ex-urban landscapes encompassing the Houston Ship Channel system in Texas, where contaminated sediments from historical dioxin use are the primary contributor to seafood consumption advisories for several species (Dean et al. 2009), and in the city of Oak Ridge, Tennessee, where legacy mercury continues to accumulate in freshwater fish as a result of streambank erosion (Southworth et al. 2011). Similarly to P, these legacy pollutants are likely to endure for decades despite substantial reduction in inputs. Model predictions suggest a 10–30 year period for pesticide loads to reach risk-reduction goals under scenarios of zero pesticide loading in San Francisco Bay (Connor et al. 2007), while in Oak Ridge, fish have sustained high concentrations of mercury and PCBs for decades despite discontinued use and multiple remediation efforts (Southworth et al. 2011). Thus, when processes that mitigate land-use legacies associated with an ES are intrinsically slow, land-use history will affect ES supply.

Time lags delay effects of land use on ES supply

Time lags between land-use change and ecological responses can cause delayed effects on ES that are better explained by historical land use than current landscapes (Raudsepp-Hearne et al. 2010). The ultimate change in ES may occur slowly, similarly to the previous examples, or relatively quickly, but a key factor is a notable delay between land-use change and the ES response ("lagged response" in Fig. 2b). Time lags occur when, for a time period following land-use change, ES supply remains consistent with supply prior to land-use change, or when the rate of change in ES supply increases or decreases over time following land-use change, even in absence of further land-use change. Such delayed effects may be especially pronounced for biodiversity-based services (Kremen 2005) because historical habitat loss or fragmentation caused by land-use changes can lead to extinction debts wherein species loss continues beyond the initial event or driver (Tilman et al. 1994; Jackson and Sax 2009; Essl et al. 2015). Extinction debts can be assumed if historical land use, habitat area and connectivity better explain current species distribution than do current land use and landscape variables. From an ES perspective, an extinction debt can substantially delay the effects of land-use change on supply of biodiversity-based ES, such as C storage, pollination, pest control, and nature viewing. Dependent upon the resultant change in species composition and the particular ES, these effects may be negative or beneficial, and may occur as a result of changes in both native and invasive species. Consequences may be particularly large if species affected act as ecosystem service providers (Luck et al. 2009).

Time lags between human LULC change and species loss may help explain differences in ES supply that are unexplained by current LULC patterns (Fig. 2b). Ignoring potential extinction debts or colonization patterns may lead to overly optimistic assessments of such ES, or underestimation of ES supply, if species changes influence ES positively. Cultural landscapes in which natural and semi-natural habitats are reduced or fragmented may be especially susceptible to future species extinctions and permanent loss of certain biodiversity-based ES (i.e., biodiversity-based ES debt, Isbell et al. 2014). Despite the potential for biodiversity and ecosystem function lags in response to land-use change (Valiente-Banuet et al. 2014), time lags have been largely absent from ES research (but see Dallimer et al. 2015).

Perennial plant communities often display time lags between habitat loss or degradation and eventual species loss (Helm et al. 2005) which can lead to biodiversity-based ES extinction debts. In the agricultural and exurban landscapes of the Midwestern US, prairie remnants provide multiple services. Consistent with predictions of extinction debt, extinction rates in prairie remnants have accelerated over time, suggesting a lagged response of community diversity to land-use changes; present day extinction and colonization in prairie remnants is strongly related to historical land use (Alstad et al. 2016). Historical land management in prairie remnants explained colonization by non-native species and extinction of native species; loss of native species can impact ES in surrounding agricultural lands by affecting the diversity and identity of beneficial arthropods such as predators, parasitoids, and pollinators. Indeed, experimental work identified distinct assemblages of beneficial arthropods associated with different native prairie plant species (Bennett and Gratton 2013). In addition to extinction debts for ES such as pollination and pest control, lagged species loss or gains in prairie and grassland habitats can lead to unpredicted change in above-ground and below-ground C stocks (Isbell et al. 2011). In the Midwestern US prairie remnants, historical land-use patterns explained shifts from perennial species to annual species in the prairie remnants (Alstad et al. 2016) and eventual reductions in C storage.

Time lags in biodiversity-based ES can exist due to slow processes of re-colonization that depend on historical land use and connectivity (Lindborg and Eriksson 2004; Gonzalez et al. 2009; Aguirre-Gutiérrez et al. 2015). Current land-use patterns and connectivity strongly affect supply and delivery of ES (Kremen et al. 2007; Cardinale et al. 2012; Mitchell et al. 2013, 2015b), but some effects of habitat fragmentation on ES (e.g., C and N retention, productivity, pollination) can be delayed up to a decade (Haddad et al. 2015). Effects of historical habitat fragmentation can persist even after connectivity is re-established. In formerly fragmented longleaf pine (*Pinus palustris*) forests on the southeastern US coastal plain, current understory plant community composition on previously agricultural sites was explained by historical connectivity (Brudvig and Damschen 2010). In addition, historical land use was an important factor in predicting the presence and abundance of the highly invasive fire ant (*Solenopsis invicta*) (Stuhler and Orrock 2016), which can cause acute health issues in human populations as well as major economic and ecological impacts (Kemp et al. 2000).

Similarly, in amenity-based landscapes of the eastern US, time lags in understory herb recovery following agricultural abandonment and eventual forest regeneration can produce lagged responses in associated ES (e.g., nature viewing, wildflower photographing, wild edible or medicinal plants; Graves et al. 2017). In the southern Appalachian Mountains, where ecotourism is economically important, lower richness and abundance of charismatic wildflower species in post-agricultural forests is only partially explained by current forest patch size, suggesting time lags in re-colonization (Pearson et al. 1998; Mitchell et al. 2002). In exurban landscapes in New York, species richness of understory herbs in post-agricultural forests depended on historical isolation and the effect persisted up to

100 years after agricultural abandonment (Flinn and Marks 2004).

Time lags between human-driven land-use change, ecosystem function and resulting ES are not unique to biodiversity-based ecosystem services. Hydrologic services may be particularly affected by time lags in cultural landscapes, in many cases linked to the slow processes discussed above. For example, time lags can range from months to years to decades before changes in landscape pattern improve water quality in non-point source watersheds (Meals et al. 2010). Groundwater in agricultural landscapes can have high pollutant concentrations, and groundwater travel time coupled with biogeochemical processes leads to time lags of decades between changes in agricultural landscapes and corresponding changes in water quality (Meals et al. 2010; Hamilton 2011). In Iowa, despite changes in agricultural practices between the 1970s and 2000, groundwater nitrate–N concentrations measured in the early 2000s remained strongly influenced by 1970s land use (Tomer and Burkart 2003). Actual lag times vary by ES and mechanism, but ES models based solely on current LULC patterns will be inaccurate if ES demonstrated lagged responses and historical land use is not considered.

Surpassing a threshold leads to legacy lock-in

Land-use legacies will be important for understanding ES supply when threshold relationships exist, and historical land use produced changes in ES supply that are difficult to reverse (Fig. 2c). Crossing thresholds that cannot readily be reversed will effectively disconnect ES supply from the contemporary landscape. However, the potential for threshold dynamics to influence ES supply in cultural landscapes has received relatively little consideration, and to our knowledge, studies have not yet addressed thresholds and reversibility related to land-use legacies. A variety of ecological variables exhibit threshold responses as levels of driver variables change. For example, the likelihood of a species being present in a habitat patch can show a threshold response to patch size (Pereira et al. 2004), and the likelihood of habitat being connected across a landscape increases rapidly once a threshold of habitat abundance is passed (Andren 1994). Supply of some ES may show threshold responses to land-cover abundance in agricultural landscapes, e.g., indicators of water quality vs. percent cropland in sub-watersheds of the Yahara Watershed, Wisconsin (Qiu and Turner 2015) or lake-water clarity and percent of cropland in riparian zones of Wisconsin lakes (Rose et al. 2017). For other services, thresholds associated with socially desirable ES supply, such as health standards for concentrations of pollutants, may be surpassed. Some thresholds are reversible; in others, hysteresis can lead to alternative states that are very difficult to reverse. In such cases, slow processes (Fig. 2a) or time lags (Fig. 2b) are alone insufficient to explain current ES supply. Rather, historical land-use produces a "legacy lock-in" that commits the landscape to consequences for ES that do not readily respond to contemporary intervention. We illustrate several examples where threshold dynamics can cause rapid and surprisingly persistent change in ecosystem services in US cultural landscapes.

Hydrologic ES (Brauman et al. 2007) in cultural landscapes may be especially vulnerable to threshold dynamics associated with past land use and resistant to reversal. In agricultural landscapes, long-term use of nitrogen (N) fertilizers is a ubiquitous cause of groundwater contamination (Di and Cameron 2002), as discussed in the previous section. Groundwater nitrate concentrations may increase gradually over time, and rural wells can exceed threshold concentrations (>3 mg/l) known to result from anthropogenic activities and to be dangerous to human health, e.g., associated with blue baby syndrome (US EPA 1996; LaMotte and Greene 2007; Tesoriero and Voss 1997). Nitrate is the most widespread groundwater contaminant in Wisconsin, and groundwater nitrate concentrations have increased in rural Wisconsin (Saad 2008). In 2015, 20–30% of freshwater wells in south-central Wisconsin could not provide water for human consumption because nitrate concentrations exceeded the maximum contaminant level (Mechenich 2015). There is concern that nitrate concentrations are poised to increase further as nitrate penetrates into deep aquifers and moves farther from original source areas (Kraft et al. 2007). Whether elevated nitrate concentrations produce legacy lock-ins will depend on the balance between groundwater recharge and output. However, groundwater turnover times are typically very slow, making it difficult to reverse water quality degradation.

In similar vein, P enrichment degrades lake water quality and myriad ES associated with lakes across agricultural, urban, and ex-urban cultural landscapes

(Carpenter et al. 1998, 2006; Lathrop 2007; Carpenter and Lathrop 2008) and is associated with slow processes, as discussed above. This bank of soil P guarantees high future loadings to lakes, even if fertilizer application ceases (Carpenter and Lathrop 2008; Kara et al. 2011). However, once a lake becomes eutrophic, additional threshold dynamics may entrain the lake in the turbid state, even if P inputs cease. Specifically, lakes of intermediate depth are least reversible because internal P recycling from sediments cannot be mitigated by aquatic macrophytes, so the lake remains in the undesirable eutrophic state (Genkai-Kato and Carpenter 2005). Thus, land-use legacies associated with slow processes can interact with the abiotic template (e.g., lake morphometry) in ways that make it difficult to improve the hydrologic services associated with high-quality surface water once a threshold has been passed.

Flood mitigation is another hydrologic service that can show threshold dynamics and lead to legacy lock-in. In urbanizing landscapes, increase in impervious surfaces (e.g., roads, parking lots, roofs) associated with expanding development reduces the capacity of the landscape to absorb rainfall, which then exacerbates flooding. Short-term increases in runoff volume and rate following rain events (i.e., flashiness; Poff 1996) rise with extent of impervious surface, and early studies suggested a threshold of ~15% impervious surface was associated with undesirable ecosystem responses including flooding (Paul and Meyer 2001). Impervious surface cover increased between 1916 and 2013 in the watersheds of two urban lakes in Wisconsin, reaching 12.6 and 28.9% for Lakes Mendota and Monona, respectively; flashiness also increased, and impervious surface was the strongest driver (Usinowicz et al. 2017). Greater flashiness indicates more potential flooding, which is increasingly observed in these watersheds. If the frequency of high-intensity rainfall increases, even areas of the landscape that did not experience flooding historically may flood in the future (Usinowicz et al. 2017). The negative effect of land-use legacies on flood mitigation may be undetected until the next intense rain event occurs, revealing an ecosystem services debt. Climate change is expected to exacerbate such effects by increasing the frequency and intensity of rain events in Wisconsin (Wisconsin Initiative on Climate Change Impacts 2011), and these land-use legacies may become more pronounced in the future. Historical development patterns may lock-in vulnerability to flooding for a long time because it is difficult to reverse patterns of urban and suburban development. Declines in flood mitigation are theoretically reversible by replacing impervious surfaces with semi-natural land cover, but cities are seldom deconstructed.

The degree to which other kinds of ES may respond to thresholds associated with land-use legacies is not well known (Bürgi et al. 2017). Some threshold responses, such as those related to size or connectivity of semi-natural vegetation in cultural landscapes, may be more amenable to reversal. For example, croplands could be strategically converted to semi-natural vegetation that would support wild pollinators or natural enemies more readily than cities can be deconstructed. Of particular importance, however, is the potential for changing environmental drivers to dampen or amplify effects of land-use history on ecosystem services. As environmental change progresses, thresholds that were not apparent previously may be passed as drivers change—as more land is developed, temperatures warm, or hydrologic variability increases. The interaction of land-use legacies with changing drivers has the potential to alter ecosystem services in cultural landscapes in surprising ways, often over timeframes beyond those seen in the previous conditions.

Discussion

Persistent effects of past land use on ES supply permeate cultural landscapes in the US and many other regions of the world. We have suggested three interconnected conditions whereby land-use legacies are important for interpreting current ES supply, and illustrated these with examples from agricultural, urban, and exurban cultural landscapes in the US. These settings reflect the dominant land-use changes over the past 100–150 years. Identifying mechanisms and consequences of these legacies requires attention to temporal dynamics, including rates of change in ES and time elapsed since land-use change. In some cases, ES dynamics may be driven by system variables that change slowly, leading to lagged responses of ES to land-use change. In other cases, ES may respond rapidly to land-use change but effects persist for long time periods, or changes in ES may exceed a threshold such that recovery to a prior condition is no longer possible.

The three ES/land-use legacy conditions we presented here are also amenable to exploration and testing in regions outside the US. For example, land-use legacies have been shown to influence above-ground carbon storage, recreational services, and bird diversity in urban Sheffield, UK (Dallimer et al. 2015); examples of extinction debts are prevalent throughout European landscapes (Dullinger et al. 2013); and historical grassland management influenced contemporary plant biodiversity in a rural Swedish landscape (Cousins and Eriksson 2002). Application of our framework in other regions is an interesting direction for future study, and may yield new insight into the mechanisms by which historical land-use shapes ES supply. For example, many studies we have highlighted here report legacies from past agricultural use. Studies documenting legacies from alternate land uses (e.g., forest harvest or clearance) are comparatively rare in the cultural landscapes we consider. Whether or not this trend is generalizable outside of the US remains a question amenable to further testing.

What are the implications of land-use legacies for future ES supply? Our examples highlight the influence of past land use on contemporary ES supply, but these examples also suggest that today's land-use decisions will influence future ecosystem services. For example, current agricultural practices continue to enrich soils with P and N. These nutrients will influence water quality and associated ES in tomorrow's cultural landscapes, particularly in the absence of new strategies to mitigate erosion (Heathcote et al. 2013). Similarly, ongoing habitat loss and fragmentation will continue to exert lagged effects on biodiversity-based ES, and current expansion of impervious surfaces risks "locking in" future cultural landscapes to more frequent flooding. As researchers and policymakers increasingly explore possible futures using scenario analyses (Peterson et al. 2003; Polasky et al. 2011), missing the potential for current land-use decisions to exert legacy effects will compromise our ability to project future ES supply. Thus, it is imperative that rates of processes, potential for time lagged effects, and thresholds and reversibility be considered today to manage landscapes sustainably in the decades ahead.

As we consider future legacies in cultural landscapes, wherein lie key uncertainties and research needs? We highlight three areas we expect to be of increasing importance in US cultural landscapes in the years ahead. First, urban landscapes may themselves generate future land-use legacies that will become increasingly prevalent as cites change. In this study, we emphasized effects on ES of transitions *from* natural/semi-natural landscapes or agricultural use *to* urban or exurban lands. However, as urban populations expand in many places and contract in others, legacies of urban land abandonment will become increasingly common (Nassauer and Raskin 2014). Examples are already emerging in US cities with high urban vacancies (Dewar and Thomas 2012), such as "rust belt" cities like Detroit, Michigan that have been changed fundamentally by global shifts in manufacturing. In 2010, Detroit had shrunk to a population of <714,000 from a 1950 peak of 1.8 million (US Census Bureau 2010). The resultant urban vacancies occupy a combined area larger than all parks and open spaces in the city—an area roughly the size of Manhattan, New York (Detroit Future City 2013). Such urban shrinkage provides an opportunity to increase ES provision in and around urban cultural landscapes (Haase et al. 2014). However, sustainable management of ES on abandoned land requires understanding the legacies left behind. Abandoned urban land does not easily "return to nature", as is often construed by urban residents and the popular press (e.g. characterization of abandoned lots as "urban prairie" or "naturescapes"; Ager 2015); altered site hydrology and soil characteristics remain, even following proper demolition of urban structures (Nassauer and Raskin 2014). In the US, such legacies are often compounded by the prevalence of illegal dumping (e.g., of household chemicals, construction debris, and oil and gas products) on vacant land (Beauregard 2012). As urban abandonment and renewal continue, uncertainty surrounding legacy contamination will be a common challenge for management of ecosystem services in cultural landscapes.

Second, the long-term consequences of new contaminants may present unanticipated challenges for future ES supply, creating legacies not yet apparent in today's cultural landscapes. Microplastics, for example, have recently emerged as a threat to marine and freshwater ecosystems (Cole et al. 2011; Eerkes-Medrano et al. 2015). Yet, how, and when, microplastics may affect aquatic ES is not well understood. Similarly, while microplastics are expected to alter physical soil properties and increase concentrations of soil contaminants (Rillig 2012), their impact on terrestrial ES is also unknown. What other materials or practices are being introduced in cultural landscapes today that might have consequences that manifest much later in time?

Third, consequences of land-use legacies on ES supply may change qualitatively as broad-scale drivers continue to change. In particular, shifting climatic drivers may become increasingly important in modulating effects of historical land use on future ES. For example, higher intensity and more frequent storm events predicted due to climate change may mobilize sediment to a greater extent than in the past, exacerbating effects of historical land use on water quality in cultural landscapes (Carpenter et al. 2015a). Climate-driven sea-level rise may also exacerbate legacy effects on ES, most notably in low-lying coastal regions that are home to a significant portion of the US population (NOAA 2014). Combined with a projected increase in storms like Hurricane Sandy, which flooded major sections of the New York Metropolitan area in 2012, sea-level rise is likely to worsen flooding associated with future storm surges in New York (Lin et al. 2016). Some coastal urban areas, such as Broward County in southern Florida, are already considering how to proactively adapt urban infrastructure to reduce future flooding (Broward County Climate Change Action Plan 2015). A long history of industrial land use in many coastal regions also means that sea level rise could mobilize legacy contaminants and threaten water quality and human well being (Duke et al. 2014). Warming sea surface temperatures also may increase mercury concentrations in fish, subsequently increasing human exposure when seafood is consumed (Dijkstra et al. 2013). Thus, future research and landscape planning must consider potential influences of land-use legacies not in isolation, but in conjunction with additional drivers of ES supply.

We have presented three general conditions for when land-use legacies are likely to affect ES supply, yet we recognize characteristics of land-use history not covered here will also be important. For example, the intensity of historical land use, its duration, and the sequence of past land-use transitions can all amplify or dampen the magnitude of effects on ES supply (i.e. modifying the strength of the responses in Fig. 2), but these characteristics were not explicitly addressed in our synthesis. Data availability and quality will influence the ability to detect relationships between historical land use and ES supply, and the scales of historical data and ES estimates must align. Additionally, our examples of particular ES are illustrative, and there are many ES for which the relative role of historical vs. contemporary landscapes is unknown. Lastly, few studies consider effects of land-use legacies on multiple services, or ES bundles (but see Renard et al. 2015; Tomscha and Gergel 2016). With the ES field moving towards understanding interactions between services and management implications (Bennett 2017), future studies should also consider the role of historical land use in shaping ES relationships.

As ES research becomes increasingly mechanistic, further consideration of temporal dynamics and land-use legacies in cultural landscapes is sorely needed. If a function or process underpinning an ES is affected by land-use legacies, the service will be affected as well. Thus, understanding historical land use can be critical for accurately explaining variation in contemporary ES in cultural landscapes and anticipating future ES supply. Improved understanding of the role of history will not only lead to better maps and management of ES supply, but will also aid in decision making as new challenges to sustaining our cultural landscapes arise.

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