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Multi-site interactions: Understanding the offsite impacts of land use change on the use and supply of ecosystem services



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ABSTRACT

Managing the impacts of land use change on ecosystem services is essential to secure human wellbeing; but is a task often complicated by landscape-scale spatial dynamics. In this study, we focus on one type of spatial dynamic: multi-site interactions (MSI), which we define to occur when a change in the supply or use of an ecosystem service at one site affects that service at a second site. In search of empirical evidence of MSI, we reviewed 150 papers on one ecosystem service—nature-based recreation. We found many studies assessed impacts of land use change on this ecosystem service, but only 2% of studies quantified changes in its supply or use across multiple sites. Given this limited evidence in the literature, we propose a novel framework to describe the pathways through which MSI emerge and their likely consequences for ecosystem services across multiple sites. We illustrate the utility of this framework for understanding impacts on three other services: crop pollination, fuel wood production and flood mitigation. Obtaining empirical evidence of MSI is an important next step in ecosystem service science, which will help identify when interactions among sites emerge and how they can be best managed.

1. Introduction

Land use change has significant, widespread and long-lasting impacts on ecosystem services—the ecological attributes and functions that contribute to human wellbeing (Millennium Ecosystem Assessment, 2005). For example, tropical deforestation negatively impacts climate regulation (Foley et al., 2007), crop pollination (Kremen et al., 2002), and nature-based recreation (Naidoo and Adamowicz, 2005). Securing ecosystem services for long-term human wellbeing is therefore dependent on effective land management (Crossman et al., 2013; Lawler et al., 2014). This task requires knowledge of the pathways through which land use change impacts the supply of ecosystem services (Kremen, 2005) and their use by human beneficiaries (Arkema et al., 2013; Balmford et al., 2002; Ellis et al., 2015).

Land use change impacts ecosystem services through three basic pathways. (1) Land use change can modify the ecological structure and functions underpinning their ecological supply. For example, converting forests to cropland decreases carbon sequestration and storage (Fearnside and Laurance, 2004; Galford et al., 2015; Rudel et al., 2005). (2) Land use change can influence human demand for ecosystem services. Urbanization has been shown to reduce demand for local food production while increasing demand for environmental quality and cultural experiences (Yahdjian et al., 2015). (3) Land use change affects the non-natural capital (e.g. infrastructure) providing human access to, and thus use of, ecosystem services. Building a new road through a forest increases the use of its harvestable wood resources (Chomitz and Gray, 1996; Soares-Filho et al., 2004). This understanding of how land use change impacts ecosystem services is often used to inform land management decisions; however, these basic pathways do not explicitly capture landscape-scale spatial dynamics.

Impacts of land use change on ecosystem services are spatially dynamic and dependent on environmental and socio-economic landscape context (Bagstad et al., 2013; Crossman et al., 2013). In this study, we focus on one type of spatial dynamic—multi-site interactions (MSI)—which emerge when a change in the supply and/or use of an ecosystem service at one site affects its supply and/or use at a second site. Compared to other spatial dynamics, MSI have received considerably less attention in the ecosystem services literature. Previous work has described their outcomes as "offsite effects" and acknowledged

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their potential significance for achieving land management goals (Seppelt et al., 2011), but have not provided insight into the pathways through which MSI emerge or their impacts on ecosystem services across multiple sites. Without this causal understanding, managing MSI is, at best, reactive.

In other literatures, conceptually similar interactions have been well studied. For example, concepts of 'intensive land use' (Sonter et al., 2015) and 'urban teleconnections' (Seto et al., 2012) suggest that small-scale changes in land use in one location initiate extensive transitions in land use elsewhere. Further, 'tele-coupling' concepts suggest these interactions occur over very long distances (Liu et al., 2013) and indeed have implications for ecosystem services in both locations (Liu et al., 2016). Failing to understand these spatial dynamics can result in offsite impacts on natural resources (Eugenio et al., 2011) or result in unharnessed opportunities to achieve efficient regional-scale management (Sonter et al., 2013). An equivalent understanding of MSI in ecosystem services science is urgently needed. This requires understanding the pathways through which MSI emerge, identifying the conditions leading to their establishment, and quantifying the extent of resultant impacts on ecosystem services across multiple interacting sites. Such insight will aid land managers in deciding when additional resources should be allocated to manage MSI effects.

Within this context, the objectives of this paper are to: (1) describe MSI and how they differ from other spatial dynamics; (2) review the literature on one ecosystem service (nature-based recreation) in search for evidence of MSI; (3) develop a framework that describes the pathways through which MSI emerge and their likely consequences for ecosystem services among sites; and (4) illustrate the utility of this framework for assessing and managing impacts of land use change on three other ecosystem services: crop pollination, fuel wood production and flood mitigation.

2. Spatial dynamics: ecosystem service distribution, flow and MSI

Two types of spatial dynamics are currently considered in the ecosystem services literature: spatial distribution and flow. In this section, we briefly summarize how each dynamic affects the impacts of land use change on ecosystem services. We then propose MSI as a third spatial dynamic, which relates to and is often initiated by spatial distribution or flow, but would not necessarily be detected from analyzing either spatial dynamic alone.

2.1. Spatial distribution of ecosystem services

Ecosystem services are unevenly distributed across landscapes, according to their ecological supply and their consequent use by humans (Chan et al., 2006; Fisher et al., 2009; Villamagna et al., 2013). For example, the distribution of pest control agents varies with altitude, and their contributions to crop yield depend on the distribution of farms along this elevation gradient (Poveda et al., 2012). Ecosystem services are also influenced by landscape-scale spatial patterns. For example, their supply can depend on landscape characteristics, such as habitat fragmentation (Gret-Regamey et al., 2014), while their use by humans can depend on the quantity and distribution of forested landscapes (e.g. Sonter et al., 2016). Therefore, land use change impacts the supply and use of ecosystem services differently in different places (Bateman et al., 2013; Chaplin-Kramer et al., 2013; Polasky et al., 2008) and changes in landscape characteristics can cause non-linear changes in ecosystem services when thresholds are crossed (Mitchell et al., 2015a).

2.2. Flow of ecosystem services

Ecosystem services are also spatially dynamic in their flow across a

landscape. Services can flow from sites of supply to sites of use, and human beneficiaries flow from where they reside to where they use these services (Fisher et al., 2009). For example, native bees that supply crop pollination services flow from natural habitat to farms of pollinator-dependent crops to forage (Kremen et al., 2007), and tourists flow from their homes to national parks to enjoy natural recreation opportunities (Wood et al., 2013). As a result, impacts on a service's supply in one location may affect its use elsewhere: e.g. removing upstream wetlands affects downstream flood mitigation (Mitsch and Gosselink, 2000; Watson et al., 2016). Land use change can also impact these processes of flow directly (Bagstad et al., 2013; Mitchell et al., 2015b). For example, landscape fragmentation can affect access to and use of recreational sites (Kovacs et al., 2013). Therefore, land management requires information on both the flow of ecosystem services, and how land use change impacts these flows over space and time (Mitchell et al., 2015b; Tallis et al., 2008; Villamagna et al., 2013).

2.3. Multi-site interactions

MSI are a related spatial dynamic, which occur when a change in the supply and/or use of an ecosystem service at one site affects its supply and/or use at a second site. The change in ecosystem services at the first site may emerge due to changes in its supply, use or demand (as described in Section 1). Within our definition, the term "site" refers to the location at which the ecosystem service is used or enjoyed by people, i.e., where supply and demand meet. Interactions between these sites are driven by the flow of ecosystem services and people across the landscape, but manifest as relative changes in the flows between sites.

For example, two bird watching sites used for nature-based recreation interact if changes in the supply of bird watching opportunities to one site (e.g. through habitat degradation) cause a change in their supply to a second site (e.g. by increasing its relative quality as bird habitat). These two bird watching sites also interact if changes in the use of one site (e.g. due increased access) cause a change in their use at the second site (e.g. by diminishing its relative appeal). Similarly, increasing the quality of pollinator habitat may increase crop pollination on one nearby farm (e.g. due to increased pollinator visitation), but in turn reduce pollination at another farm (due to pollinators shifting their visitation away from the first farm).

Sites would not be considered to interact if they responded independently to a similar perturbation. For example, the following would not be considered MSI: a loss of bird habitat that simultaneously decreased birds at multiple bird watching sites; increasing surrounding pollinator habitat increased bee abundance and visitation to multiple farms. These examples represent similar changes in flow to multiple sites, rather than interactions among sites.

As these examples suggest, failing to understand MSI could lead to unexpected offsite impacts of land use change on ecosystem services that aggregate across multiple sites. In this study, we limit our discussion to interactions between sites for a single ecosystem service, although acknowledge that multiple services may be affected by MSI, for example, through changes in interactions among bundled services (Bennett et al., 2009).

3. Literature review: in search of msi evidence

3.1. Methods

We reviewed the literature on one ecosystem service—nature-based recreation—in search of evidence for MSI. Specifically, we addressed three questions: (1) To what extent does land use change impact ecosystem services via MSI? (2) Are there conceptual similarities in how MSI emerge? (3) What are the barriers to studying MSI from the published literature? Our review focused on nature-based recreation

Table 1

Data collected from 150 published papers on nature-based recreation. These attributes allowed us simultaneously gather knowledge of MSI pathways and effects, and to identify barriers to their assessment.

Information collected	
General study information	 Year Title Journal Study location
Measurements: what is measured, where and how?	 What type of land use change was investigated? Which ecosystem service was studied? How was this ecosystem service supplied? How was this ecosystem service used?
Impacts at Site 1 (i.e. where the land use change occurred)	 Did land use change impact the supply and/or use of the ecosystem service at Site 1? What was the response in the ecosystem service (i.e. increase decrease no change)
Impacts at Site 2 (i.e. changes in ecosystem services via MSI)	 Did a change in the supply and/or use of the ecosystem service impact that ecosystem service at Site 2? What was the response in the ecosystem service (i.e. increase, decrease, no change)

because we could reasonably envisage MSI to occur due to changes in both the supply and use of this ecosystem service (e.g. see the bird watching example described in previous section). We obtained review papers from Web of Science in May 2015 using keywords of "ecosystem service*" AND "recreation*" and read the 150 most recent papers, which were published since January 2013. We collected information on MSI pathways and effects when evidence was available (i.e. when studies investigated the impacts of land use change on an ecosystem service across multiple sites) and identified barriers to their assessment when not (Table 1).

3.2. Evidence of MSI

We found 53% (79 of 150) of papers assessed impacts of land use change on the supply and use nature-based recreation opportunities; however, only the following three studies permitted our investigation of MSI. Wiederholt et al. (2015) quantified impacts of land use change on bat roosts and bat viewing recreation in the USA and Mexico. Their results showed that removing bat roosts decreased bat population at Site 1 (i.e. where the land use change occurred), which in turn increased supply of bats at Site 2 via MSI. Their modeling also showed that this change in supply of this ecosystem service to Site 1 decreased its use at this site, but had no effect on use of Site 2. At the broader spatial scale (i.e. across multiple bat viewing sites), bat population remained constant, despite population loss at Site 1, while bat viewing declined because the decreased use of Site 1 did not increase use of Site 2.

In comparison to Wiederholt et al. (2015), Sen et al. (2014) provide evidence of MSI due to change in the use of an ecosystem service. This study found that restoring agricultural land to a natural state at Site 1 increased its use for nature-based recreation, but in doing so decreased use of surrounding alternative recreational sites. In this study, increasing ecosystem services in one site redistributed, rather than increased, the service at the broader spatial scale. Similarly, Kovacs et al. (2013) quantified the ecosystem services provided by establishing new recreation sites in Minnesota. In their model, authors assumed that new sites established in close proximity to existing sites would be used less often than those established at distance. This is due to substitution effects where the use of one park can be substituted for another. Although both Sen et al. (2014) and Kovacs et al. (2013) consider the MSI via relative changes in the use of recreational sites, they did not investigate potential MSI via changes in the supply of this ecosystem service, despite recreational activities (e.g. game hunting, wildlife viewing) being dependent species that move between sites.

3.3. Barriers to investigating MSI

Four barriers limited our investigation of MSI from the reviewed literature on nature-based recreation. The first and second barriers are common issues already identified in ecosystem services science, while the third and fourth are specific to investigating MSI and are thus given more attention here. First, many studies interested in the impacts of land use change on ecosystem services did not quantify changes in their supply or use, but instead established spatial relationships between land use and the ecosystem service and assumed changes in land use would yield corresponding changes in the ecosystem service. Second, 42% (33 of 79) of studies focused on the ecological attributes underpinning the supply of the ecosystem services, rather measuring the ecosystem service. For example, Silva et al. (2014) investigated the impacts of land use change on wild fire frequency in Spain, but did not quantify the service of wild fire prevention in terms of avoided property damage or reduced fire management costs.

Third, 43% (20 of 46) of remaining studies did not analyze ecosystem services at multiple sites. While the definition of "site" varied between studies: from country (Lankia et al., 2014) to region (Johns et al., 2014) to catchment or watershed (Kandulu et al., 2014), many authors focused only on one. Two factors may explain why this occurred. Management interventions are often implemented on a site-by-site basis, which limits research scope to the scale of a single site. Alternatively, analyzing multiple sites increases data, analysis and research costs, and when additional resources were available studies tended to investigate tradeoffs between multiple ecosystem services rather between multiple sites. For example, Schindler et al. (2014) analyzed 798 combinations of land use change impacts on ecosystem services within one floodplain.

Fourth, 80% (21 of 26) of studies that did include multiple sites did not investigate the effects of changes in one site on changes in another site (Boll et al., 2014; Casado-Arzuaga et al., 2014; Gret-Regamey et al., 2014; Lowicki and Piotrowska, 2015; Nahuelhual et al., 2014). For most studies, these interactions between sites were reasonable to envisage. For example, Luisetti et al. (2014) suggested habitat removal decreased bird watching opportunities in salt marshes, but they did not investigate potential impacts of these changes on bird populations in surrounding salt marshes, and Toft et al. (2014) show that land use change decreased crab harvest in multiple coastal sites, but did not investigate potential impacts of these changes on crab harvest rates elsewhere.

Our literature review suggests MSI are likely to occur for the ecosystem service of nature-based recreation, but that evidence of MSI pathways and effects is missing. This lack of evidence may not be true in other related disciplines. For example, studies of population ecology frequently capture MSI that emerge via changes in species underpinning the supply of ecosystem services—such as migratory species across multiple sites (Sutherland, 1998), and economic studies on multi-site decision-making capture changes in the use of services—such as nature based tourism— across the landscape (Naidoo and Adamowicz, 2005; Phaneuf and Smith, 2005). However, the value addition of understanding MSI in ecosystem services science is to integrate both supply and use pathways of MSI. Doing so requires new conceptual frameworks that permit MSI investigation and application of such frameworks to quantify effects on ecosystem services and understand implications for management.

4. Developing and applying an MSI framework

We developed a framework that describes the pathways through which MSI emerge, captures impacts of land use change on an ecosystem service at two interacting sites, and illustrates combinations



Fig. 1. MSI conceptual framework, consisting of 3 MSI pathways (columns) crossed with 3 MSI impacts at Site 2 (rows). Circles represent all ecosystems and their landscape context that supply ecosystem services, squares represent sites where ecosystem services are used, and triangles represent human beneficiaries. Arrow style depicts the impact on ecosystem services at Site 2. Dashed arrows illustrate a decrease in ecosystem services, heavy solid arrows illustrate an increase, and light solid arrows illustrate no change. Colors highlight either supply pathways (pink) or use pathways (blue) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

of pathways and impacts that aggregate to alternative outcomes (Fig. 1). The framework shows that MSI can emerge via either a supply and/or use pathway and that resultant impacts include no interaction effects (a change in the supply or use of an ecosystem service at Site 1 has no effect on that service at Site 2), complementary effects (a change in the ecosystem service occurs in the same direction for Site 1 and Site 2), and substitution effects (a change in the ecosystem service occurs in the ecosystem service occurs in the opposite direction for Site 1 and Site 2). Crossing MSI pathways (Fig. 1, columns) with their effects (Fig. 1, rows) shows nine potential interactions between two sites.

Applying the MSI framework requires quantifying the impacts of land use change on ecosystem services and investigating changes in their flows between sites. Detecting and isolating MSI effects will present methodological challenges. MSI pathways will likely be nonlinear (e.g. nature-based recreation often exhibits diminishing marginal returns, while increasing demand may eventually cross a threshold beyond which dynamics shift; Bateman et al., 2014; Liekens et al., 2013), and MSI impacts will be mediated by other factors, such as changes in beneficiaries' demand for ecosystem services over time (Termansen et al., 2013; Yahdjian et al., 2015). Like other impacts on ecosystem services, consequences of MSI will also likely be unevenly distributed among different groups of human beneficiaries. Overcoming these challenges will benefit from interdisciplinary research. For example, our nature-based recreation example suggests population ecology models can detect MSI supply pathways (Wiederholt et al., 2015), while recreation demand models can capture MSI use pathways (Phaneuf and Smith, 2005). Other useful tools may include multi-scale analysis, multi-agent systems and social-ecological networks. Future research should apply our MSI framework to a diverse set of ecosystem services to obtain insight for their assessment and management.

We developed this conceptual framework to be general, and applicable to multiple ecosystem services occurring under diverse landscape contexts. However, we recognize that framework components (e.g. ecosystems, sites, and people) and MSI outcomes will likely vary among services, landscapes configurations, and actors operating at multiple scales. Therefore, to further investigate MSI for other ecosystem services, and to investigate the general utility of our framework, we applied it to a discussion of crop pollination, fuel wood production and flood mitigation. For each of these ecosystem services, we suggest: (1) MSI emerge via changes in their supply and/or use; (2) failing to capture MSI will have implications for assessing impacts of land use change on ecosystem services across multiple sites, and (3) our proposed framework can help guide these assessments and aid management decisions.

4.1. Crop pollination

Animal-mediated crop pollination depends on mobile organisms (Kremen et al., 2007), whose limited foraging ranges are sensitive to patterns of land use and land cover (Greenleaf et al., 2007; Hadley and Betts, 2012; Winfree et al., 2009). Typically crop pollination consists of spatially separate areas of ecosystem service supply (i.e. natural or semi-natural areas where pollinators, such as bees, nest and forage) and use (i.e. farm of pollinator-dependent crops). Farms near natural areas typically have higher pollinator biodiversity and abundance (Kennedy et al., 2013), and thus benefit from increased crop pollination and higher crop yields (Garibaldi et al., 2013).

There is growing appreciation among ecologists that mobile organisms such as pollinators can link seemingly isolated ecosystems and influence local patterns and dynamics (Lundberg and Moberg). Less is known about pollination services between multiple, interacting farms; however, MSI can be envisioned: altering habitat quality of Farm 1 (e.g. through the addition of hedgerows) could increase or decrease pollination rates at Farm 2, by shifting the abundance and spatial distribution of native bees in the landscape. The resultant response in pollination rates at Farm 2 will be dependent on the distance between farms and surrounding landscape characteristics. Bees may leave Farm 2 for increased forage at Farm 1 if the resources gained in doing so are greater than the costs of traveling between farms. However, interactions between farms could also change over time via system-wide feedbacks. Farms that were once substitutes may become complements if a period of population establishment leads to landscape-level increases in pollinator abundance (Rundlöf et al., 2014; but see Westphal et al. (2009)), which may eventually lead to increased crop yield at multiple sites. If crops are initially pollen-limited, these changes in pollination rates may affect crop yield, and Farms 1 and 2 interact via changes in supply of their ecosystem services (column 1, Fig. 1) either as substitutes or complements.

Failing to consider MSI has implications for pollination management decisions. For example, identifying the conditions under which adjacent sites can facilitate, rather than compete with each other, could increase landscape-level yield for multiple farmers. The MSI framework can clarify effects of shared pollinators via changes in the ecosystem service supply, however outcomes are expected to be a function of spatial and temporal dynamics of the landscape. Future research should employ the MSI framework to ask: 1) How do interactions between farms via shared pollinators affect crop pollination? 2) How do MSI resulting from differential management influence population dynamics of economically important pollinators?

4.2. Fuel wood production

Native forests supply multiple non-timber forest products (NTFPs), such as wild mushrooms, bush meat, fuel wood, medicinal plants and construction materials. NTFP are important for human wellbeing (Schulp et al., 2014), but concerns remain about their long-term sustainability (Ticktin, 2015). An example of a socially important, but potentially unsustainable, use of NTFP is fuel wood collection in Tanzania, where 97.5% of households use fuel wood for heating, but only 13% of that demand is met with purchased wood (Faße and Grote, 2013), suggesting many households rely on self-harvested wood. If collection is limited to dead wood, it may be considered sustainable. However, reports of overharvest raise concerns for forest degradation (Luoga et al., 2000, 2002, 2004) and it appears these impacts may be exacerbated by MSI. For example, changes in forest quality at one location may change foraging behavior, transitioning previously sus-

tainable harvest rates to unsustainable practices. Managing forests for sustainable NFTP collection requires an understanding of interactions between collection sites.

Interactions between fuel wood collection sites in Tanzania emerge primarily via their use as these sites represent substitute (Johnson, 2014). Land use change directly impacts fuel wood supply, and thus collection opportunities, in Site 1. This impact then causes fuel wood gatherers to switch collection activities to a nearby alternative Site 2. The reason for the switch is that Site 1 now offers reduced gathering efficiency (e.g., because collectible wood is now more widely spaced), which increases the comparative advantage of collecting wood at Site 2. Such behavioral shifts can cause large and sudden changes in discrete decisions on where to collect NTFP in the landscape. Further, MSI likely extend beyond two sites considered here. A change in Site 2 may have implications for other beneficiaries, causing them to also switch to other alternative sites—initiating a complex ripple of changes across the landscape (Ahrends et al., 2010).

Capturing these dynamics requires spatially explicit data on both fuel wood supply and use, and the socio-economic factors affecting collection decisions. While gathering and analyzing such data can be a difficult, often overwhelming task, failing to capture MSI has implications for sustainable forest management and the wellbeing of human beneficiaries for whom fuel wood represents a large component of household welfare (Rogers, 2014). Unmanaged changes in collection practices may place additional pressure on already threatened forests (Luoga et al., 2004), while tradeoffs between human beneficiaries (e.g. increased use of this ecosystem service for one set of beneficiaries might have negative effects on another) have difficult equity considerations. For example, if Site 2 was previously providing sustainable fuel wood to a second village, but increased gathering by the first village caused harvest to become unsustainable, the second village will be unexpectedly impacted. Understanding MSI is important for land management decisions where NTFP services are present so that changes in, for instance, forest access policies consider the human beneficiaries of ecosystem services beyond those who are directly impacted. The MSI framework proposed in this paper provides a method for understanding these interactions.

4.3. Flood mitigation

Flood mitigation occurs when natural landscapes retain floodwater to avoid flood damages to downstream populations. The basic spatial dynamics of flood mitigation are defined by hydrologic flow of rivers: upstream land use change such as wetland loss and the disconnection of rivers from their floodplains (Bullock and Acreman, 2003; Opperman et al., 2009) decreases flood mitigation downstream. Two spatial dynamics of this ecosystem service are already well understood in the literature: the supply of flood mitigation flows from upstream ecosystems to downstream human beneficiaries, and a change in upstream land use may impact flood mitigation at multiple downstream locations. In terms of MSI, a supply pathway does not exist because water travels in one direction–a change in the supply of flood mitigation at one downstream site does affect its supply to another downstream site.

In comparison, a MSI use pathway is foreseeable, where a change in the use of flood mitigation in one location affects the use of this ecosystem service elsewhere. For example, if land use change increases flooding frequency and thus decreases flooding mitigation for people living at Site 1, these people may relocate to other relatively less flood prone areas. If this shift is localized and humans remain within the same watershed, MSI do not occur. However, if humans move from one floodplain to another (Site 2) the ecosystem services used at Site 2 increases as the indirect result of decreased use at Site 1. In this example, Site 1 and Site 2 are each other's substitutes (right column, bottom row; Fig. 1).

Human responses to changes in flood mitigation are likely to occur

over longer time scales compared to other MSI use pathways considered in this paper (i.e. recreation and fuel wood production). Flooding is an important cause of human migration, displacing those known as environmental refugees (Bates, 2002; Reuveny, 2007); however, long-term human responses to changing flood regimes represent a major knowledge gap within ecosystem services science. The importance of considering where these services reach human beneficiaries is currently understood (Fisher et al., 2009); however, securing ecosystem services for future generations requires information on where demand will grow.

5. Conclusions

Land use change impacts ecosystem services. In this paper, we argue that MSI are a poorly understood, but potentially widespread, pathway through which these impacts can emerge. Through a literature review and by applying our MSI framework, we suggest MSI may emerge for at least four ecosystems services: nature-based recreation, crop pollination, fuel wood production and flood mitigation. MSI are also likely for other provisioning, regulating and cultural services, especially those that humans use directly at spatially explicit sites. The spatial scale at which MSI emerge, and the number of sites required for their analysis, will depend on the ecosystem service and their human beneficiaries. For example, interactions may occur between two watersheds (e.g. flood mitigation), three farms (e.g. crop pollination, pest control) or many forest remnants (e.g. fuel wood production).

Given the knowledge gaps identified in this paper and the significance of MSI for both minimizing negative offsite impacts and enhancing potential management efficiencies, we suggest future research address two general questions: (1) Under what conditions do MSI occur? (2) When are the consequences of MSI sufficiently large that resources be allocated to manage them? Compiling the evidence needed to answer these questions requires a coupled socio-ecological systems approach to studying impacts of land use change on ecosystem services. Specifically, based on the findings of our literature review (Section 3) and application of our framework (Section 4), three requisites for studying MSI can be identified: (1) conduct spatially explicit and temporally dynamic analyses, so as to capture the suite of feedbacks between environmental change and human behavior; (2) measure all three components of ecosystem services: supply, use and demand; (3) be conducted across multiple sites and link changes in ecosystem services in one site to changes in another.

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