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Hannah E. Birgé University of Nebraska-Lincoln, hbirge@gmail.com

Craig R. Allen University of Nebraska-Lincoln, callen3@unl.edu

Ahjond S. Garmestani United States Environmental Protection Agency, garmestani.ahjond@epa.gov

Kevin L. Pope USGS Nebraska Cooperative Fish and Wildlife Research Unit, kpope2@unl.edu

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Research article

Adaptive management for ecosystem services

Hannah E. Birgé ^{a, *}, Craig R. Allen ^b, Ahjond S. Garmestani ^c, Kevin L. Pope ^b

^a Nebraska Cooperative Fish and Wildlife Research Unit, and School of Natural Resources, University of Nebraska, Lincoln, NE 68583, USA
 ^b U.S. Geological Survey—Nebraska Cooperative Fish and Wildlife Research Unit, and School of Natural Resources, University of Nebraska, Lincoln, NE 68583, USA
 68583, USA

^c U.S. Environmental Protection Agency, National Risk Management Research Laboratory, Cincinnati, OH 45268, USA

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ABSTRACT

Management of natural resources for the production of ecosystem services, which are vital for human well-being, is necessary even when there is uncertainty regarding system response to management action. This uncertainty is the result of incomplete controllability, complex internal feedbacks, and nonlinearity that often interferes with desired management outcomes, and insufficient understanding of nature and people. Adaptive management was developed to reduce such uncertainty. We present a framework for the application of adaptive management for ecosystem services that explicitly accounts for cross-scale tradeoffs in the production of ecosystem services. Our framework focuses on identifying key spatiotemporal scales (plot, patch, ecosystem, landscape, and region) that encompass dominant structures and processes in the system, and includes within- and cross-scale dynamics, ecosystem service tradeoffs, and management controllability within and across scales. Resilience theory recognizes that a limited set of ecological processes in a given system regulate ecosystem services, yet our understanding of these processes is poorly understood. If management actions erode or remove these processes, the system may shift into an alternative state unlikely to support the production of desired services. Adaptive management provides a process to assess the underlying within and cross-scale tradeoffs associated with production of ecosystem services while proceeding with management designed to meet the demands of a growing human population.

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1. Introduction

Management of natural resources is necessary even when there is high uncertainty surrounding the system's response to management actions (Westgate et al., 2013). This uncertainty is the result of incomplete controllability and insufficient understanding of nature and people. One way to reduce this uncertainty is through a cross-scale examination of ecosystem services. When controllability and uncertainty are both high (Fig. 1), adaptive management offers such an approach. Through a structured adaptive approach, managers can design management to test for otherwise-hidden tradeoffs among competing ecosystem services that occur at different scales in social-ecological systems. The application of adaptive management (Fig. 2) in a cross-scale ecosystem services

* Corresponding author.

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This document is a U.S. government work and is not subject to copyright in the United States. context is often poorly articulated; we attempt to eliminate that shortcoming.

1.1. Adaptive management

Holling (1978; further developed by Walters, 1986) introduced adaptive management as part of a growing recognition that ecosystems do not predictably return to an equilibrium state following disturbance (Allen and Gunderson, 2011). Holling and others acknowledged the need for a management approach that addressed — rather than suppressed — the complex internal feedbacks and non-linearities that often interfere with desired management outcomes (Holling and Meffe, 1996). Traditional trial-and-error management can accomplish learning by scrutinizing the error and "adapting" to avoid a similar error. This approach is not suitable in ecological systems for two reasons. First, slow feedbacks may mask long-term undesirable management responses. Second, ecosystems do not recalibrate to some predictable, stable state following failure. Instead, management mistakes can be persistent and costly (Holling, 1978). Ecosystems





E-mail addresses: hannah.birge@huskers.unl.edu (H.E. Birgé), allencr@unl.edu (C.R. Allen), garmestani.ahjond@epa.gov (A.S. Garmestani), kpope2@unl.edu (K.L. Pope).

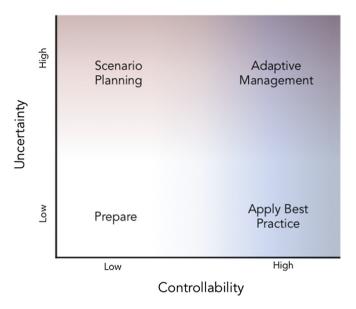


Fig. 1. Adaptive management should be invoked when controllability and uncertainty are both high (modified from Peterson et al. (2003)).

are capable of occupying alternative "states," each associated with different self-reinforcing structures and functions. Adaptive management was designed to identify essential structures and functions and their response to external stressors to avoid critical thresholds (Holling, 1978; Williams, 2011; McFadden et al., 2011). Management that optimizes the production of a single or few ecosystem services may eventually erode the very structures and functions that maintain the state needed to produce the services of interest, eventually leading to an abrupt and persistent loss of those ecosystem services (Scheffer et al., 2001; Gunderson et al., this issue).

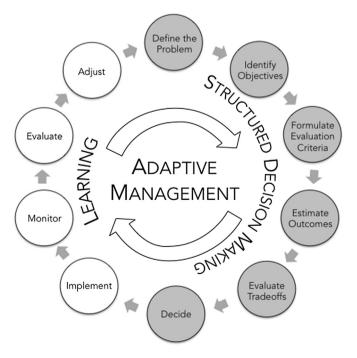


Fig. 2. The adaptive management cycle (from Allen et al. (2011)).

As a result of its promise for tackling management problems while avoiding system thresholds, adaptive management is popular among academics and practitioners. However, there are critical gaps between the theory and practice of adaptive management (Allen and Gunderson, 2011; Westgate et al., 2013). Many trial-anderror approximates of adaptive management result not from proactively uncovering system mechanisms, but rather from adjusting after failure, or, as Ruhl and Fischman (2007) characterize it, "ad hoc contingency planning." Other misapplications of adaptive management occur when too little controllability at large scales prevents robust hypothesis testing, or when a focus at overly small scales provides enough certainty so as not to require hypothesis testing (Fig. 1). Controllability allows managers to experimentally measure the effects of their management by treating management options as alternative hypotheses testable through monitoring data. When controllability is largely absent, scenario planning may be more appropriate (Gregory et al., 2006). Similarly, when there is high certainty surrounding a system component and its cross-scale feedbacks, managers can apply the known best practice.

Despite frequent pathology and failure in its design and application, adaptive management remains at its core a well-formulated approach for learning through doing while safeguarding management decisions from cognitive shortcuts, stakeholders' conflicts, non-linear system responses, and complex social-ecological interactions. When applied in the appropriate contexts, adaptive management's capacity to uncover mechanistic relationships among system components and thus continuously improve management decision-making is unmatched (Johnson and Williams, 1999: Allen and Garmestani, 2015). As Westgate et al. (2013) argue, proponents of adaptive management should be arguing that it is too risky not to use adaptive management. Additionally, there are a growing number of tools at the disposal of natural resources managers to improve the structured decision-making steps of adaptive management. Peterson and Freeman (this issue), for example, describe how Bayesian statistics can be used within an adaptive management framework to assess the probability of alternative candidate models based on results from monitoring data. They illustrate how this approach can be used to weigh alternative hypotheses prior to implementing management for the production of riverine ecosystem services.

By conceptualizing management goals in an ecosystem services context, we present an application of adaptive management that explicitly accounts for cross-scale tradeoffs in the production of ecosystem services. The ecological processes underlying multiple ecosystem services often interrelate in poorly understood ways. Human interventions aimed at maximizing the output of a single ecosystem service is common, but the implication of such actions for other ecosystem services is often complex, and deserves a critical examination (Rodriguez et al., 2006). This includes an assessment of the tradeoffs that occur for ecosystem services at multiple scales, and the mechanistic processes and feedbacks that underpin multiple concurrent suites of ecosystem services. Adaptive management provides an existing framework for revealing causal mechanisms and relationships among multiple ecosystem services.

1.2. Ecosystem services

The ecosystem services concept was first formalized (SCEP, 1970; Holdren and Ehrlich, 1974; Westman, 1977; Ehrlich and Ehrlich, 1981) in part to grant ecosystems greater leverage in policy decisions. The United Nations' Millennium Assessment defines ecosystem services as "benefits people obtain from ecosystems" (MEA, 2003, 2005) and classifies ecosystem services into supporting, provisioning, regulating, and cultural services. Supporting

ecosystem services are foundational to the other three classifications, and together ecosystem services contribute to human wellbeing (Fig. 3). Though this classification scheme is widely used to inform research, ecosystem services valuation, and policy, its shortcomings have inspired alternative approaches (Carpenter et al., 2009). Specifically, other methods have been proposed to improve consistency in ecosystem service valuation (e.g., Fisher and Turner, 2008), establish common indicators for comparison across ecosystems and institutions (Fisher et al., 2009), and explicitly separate end products from their underpinning ecological processes (Boyd and Banzhaf, 2007; Wallace, 2007, 2008). These alternative approaches, experts argue, better reflect the complex realities of social-ecological systems (Haines-Young and Potschin, 2010) (Fig. 4). The Millennium Assessment's tendency to confound ecosystem service end products with their means of production is exemplified by the "supporting services" classification (Boyd and Banzhaf, 2007; Wallace, 2007). Inability to distinguish between a shared underlying process and multiple end products could result in unintentionally imbalanced valuation of services. In management schemes where tradeoffs must be carefully weighed to achieve multiple objectives using finite resources, this is especially problematic (Wallace, 2007).

The ecosystem-focused approach to ecosystem services classification attempts to rectify this problem by distinguishing the "final products" that are consumed or used and their underpinning ecological structures and processes (Haines-Young and Potschin, 2010). This approach emphasizes the identification of those ecological components central to the simultaneous production of multiple ecosystem services (multifunctionality), García-Llorente et al. (2011), for example, gathered stakeholder input to assign different levels of value to ecosystem services in order to identify which plant functional traits were the most important for their contribution to different end products. The authors concluded that their ecosystem-based approach revealed otherwise hidden costs and benefits to ecosystem service consumption that would be vastly underestimated using traditional approaches. Birge et al. (this issue) and Hodbod et al. (this issue) discuss the application of such an approach in an adaptive management context for soil and agricultural multifunctionality, respectively. Farley and Voinov (this issue) also discuss the complex, cross-scale interactions underlying ecosystem services production, along with a discussion of economic drivers and social-ecological thresholds, using perspectives from panarchy and Black Swan theories. Adaptive management's structured decision-making stage begins with a conceptual model of the system in order to synthesize competing hypotheses based on assumed system relationships. The ecosystem-focused approach similarly requires a conceptualization of the system, making it well suited to adaptive management.

Regardless of the final ecosystem services classification scheme used, each is susceptible to social-ecological uncertainty and human inconsistencies in valuations, motivations, and expertise. In short, the best ecosystem services classification scheme is likely one consistent with system specifics, user end goals, available resources, and user capabilities. This is perhaps why the most generally used classification scheme remains the Millennium Ecosystem Assessment. However, the ecosystem-focused approach is likely more appropriate for adaptive management.

1.2.1. Ecosystem service suites

When the same ecosystem services repeatedly co-occur, they can be thought of as suites of ecosystem services (de Groot et al., 2010; Raudsepp-Hearne et al., 2010). This concept is helpful because it allows practitioners to identify those ecosystem services that can be simultaneously produced and those that cannot coexist in space and time. For example, lake water with low phosphorus concentration is desirable from a municipal water treatment (Miettinen et al., 1997) and ecological restoration (Schlesinger and Bernhardt, 2013a) perspective, but may be undesirable from a fishery perspective because low phosphorus levels limit fish growth (Boyd, 1976). Much like the processes and structures from which they emerge, two or more ecosystem services may co-occur for a number of reasons. They may derive from the same ecological process (e.g., low phosphorus concentration) or from two different processes that frequently co-occur simultaneously. When describing suites of ecosystem services, a distinction between cooccurrence due to multifunctionality versus high probability of co-occurrence can reduce uncertainty and clarify management. Further, an equilibrium perspective of services moving as fixed groups in space and time fails to capture the cross-scale complexity of the processes that underlie ecosystem services production. Experimentation and synthesis of current information and theory should be used to identify suites of ecosystem services, and how

Provisioning	Regulating	Cultural
 Food Fresh water Fuel Fiber Biochemical products Genetic product Pharmaceuticals 	 Climate Water cycling Water purification Disease mitigation Air purification Nutrient retention Carbon sequestration 	 Spiritual Religious Recreational Aesthetic Cultural Scientific
	Supporting Soil formation Nutrient cycling Primary production 	

Fig. 3. The Millennium Assessment's Framework for Classifying Ecosystem Services (modified from the Millennium Assessment [2005]). The three consumable or usable classes of ecosystem services (provisioning, regulating, and cultural) rely on supporting ecosystem services, which are not directly consumed or used.

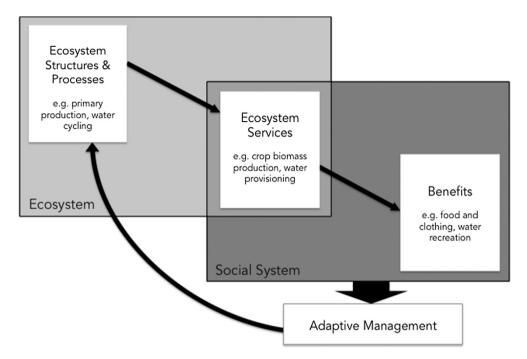


Fig. 4. An ecosystem services classification scheme that distinguishes between means (ecosystem structures and processes) and end products (ecosystem services and benefits), and illustrates how adaptive management may be used to manage the ecosystem to affect the flow of services to the social system (modified in part from Haines-Young and Potschin (2010)).

these suites change through space and time.

1.3. Biodiversity and ecosystem services

The positive effect of biodiversity on ecosystem services is well supported (Tilman et al., 1996; Hooper and Vitousek, 1997; Worm et al., 2006; Harrison et al., 2014; Nielsen et al., 2015) (Fig. 5). High genotypic, phenotypic, species, and functional diversity of communities can safeguard the production of ecosystem services from shocks and disturbances (Chapin et al., 2000), and specific responses to different perturbations likely mitigates whole system responses to disturbance, buffering major losses of ecosystem services (Chapin et al., 1997; Elmqvist et al., 2003). Adaptive management has been employed to manage biodiversity, with some success (Dallmeier et al., 2002; Keith et al., 2011; van Wilgen and Biggs, 2011). Krueger National Park uses an adaptive management plan with multiple thresholds that trigger specific action when exceeded (van Wilgen and Biggs, 2011). Two of these thresholds are elephant density levels and the presence of a nonnative, invasive plant species. Thresholds are determined through past experimentations and, when crossed, trigger elephant population reduction and nonnative plant eradication efforts, respectively.

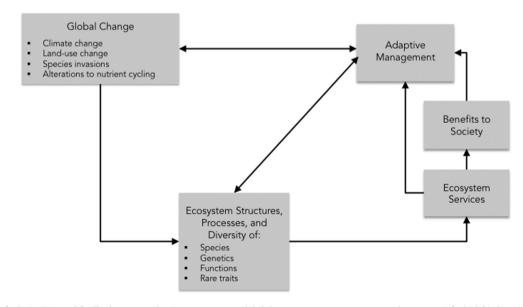


Fig. 5. A framework of relationships and feedbacks among adaptive management, global changes, ecosystem structures and processes (of which biodiversity is a component), and ecosystem services.

Threshold levels, reduction targets, and reduction approaches are adjusted as understanding of the system increases (van Wilgen and Biggs, 2011). Chaffin et al. (this issue a) describe other, underutilized adaptive approaches to better understand, prevent, and minimize the impacts of invasive species on biodiversity. In other management situations, however, loss of biodiversity is the cost of intensive production of a single, narrow suite of services. This includes, for example, the tradeoff between high plant biodiversity (and its associated services) and high agricultural volume from monoculture cover (and its associated services and risks) (Foley et al., 2005; Birge et al., this issue). Similarly, inland recreational fisheries stocked with sportfishes result in greater angler satisfaction often at the cost of native fish biodiversity (Pope et al., 2016, this issue).

2. Adaptive management for ecosystem services

Adaptive management provides a way to clarify otherwise concealed relationships among management actions, ecological processes, and the production of ecosystem services. Here, we provide an adaptive management framework to analyze ecosystem service tradeoffs occurring at multiple spatial and temporal scales. Frameworks identify, organize, and simplify compatible theories and models to aid the investigation of complex phenomena (Pickett et al., 2007; Cumming et al., 2015). By formally merging the concepts of ecosystem services and adaptive management with a unified framework, terms can be clarified, tradeoffs made explicit, and management streamlined to reduce uncertainty and improve decision-making.

2.1. Scale, management, and ecosystem services

Ecological processes have interactions within and across multiple scales (Allen et al., 2014). As the scale of interaction increases, management controllability decreases (Fig. 6) and the possible range of ecosystem services available for production increases. This highlights the need for an explicit consideration of cross-scale tradeoffs between controllability and ecosystem services available for production. Temporal and spatial scales influence the potential tradeoffs in ecosystem services and the extent to which desired ecosystem services are managed (Fig. 7). Managing a single wetland during a single growing season may require a management decision among exclusive suites of ecosystem services. For example, waterfowl hunting and corn production are mutually exclusive ecosystem services from the same patch in space and time. In contrast, managing a complex of patches across a landscape over multiple growing seasons may provide fewer exclusive tradeoffs. Making clear the shifts in tradeoffs that occur at different scales in space and time is essential for reducing uncertainty in adaptive management.

As previously mentioned, ecosystem services often exist in suites of services that tend to co-occur in space and time. Withinscale, top-down (e.g., geomorphology), and bottom-up (e.g., microbial activity) processes constrain the range of services possible in an ecosystem (Fig. 6). However, the realized services are further constrained by management decisions: legal, economic, social, and cultural forces interact with ecological conditions to determine how adaptive management affects the final ecosystem services produced (Ruhl, this issue).

2.2. A framework for assessing tradeoffs of ecosystem services with adaptive management

In this framework, different scales (and associated ecosystem services) are connected by a polycentric network of individuals, formal organizations, and informal organizations (Garmestani et al., 2013; Green et al., 2015). Examples of such interactions include the movements of species and nutrients across boundaries and plant-animal interactions. Holling (2001) proposed that the behavior of social-ecological systems derives from the interactions of processes that occur at a minimum of three different spatial and temporal scales. Resilience assessments (RA, 2010) and hierarchy theory (Allen and Starr, 1982) frequently emphasize a focal scale, one scale above, and one scale below. Scale affects the provision of

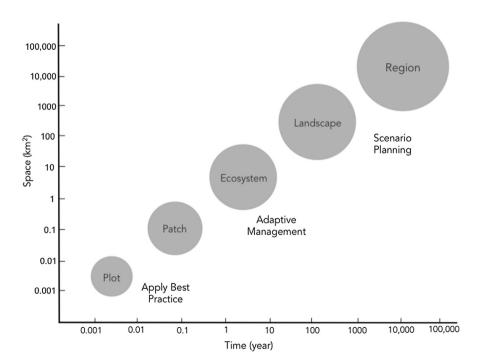


Fig. 6. A framework of thresholds for five spatiotemporal scales, with indications of appropriate management strategies.

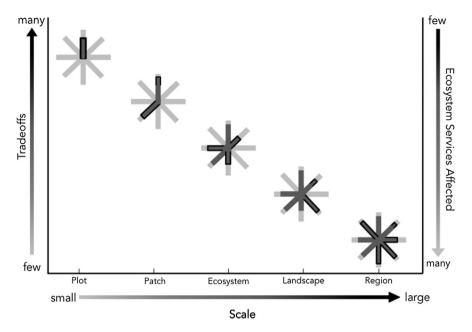


Fig. 7. Model illustrating inherent tradeoffs in ecosystem services from management actions as influenced by scale. Black outlines highlight changes in tradeoffs with increasing scale.

services and the ability of managers to flexibly manage competing suites of services, and should be a critical component of frameworks that focus on tradeoffs among ecosystem services (Pope et al., 2014). In order to use adaptive management for ecosystem services, managers need to account for within- and cross-scale dynamics of ecosystem services (Garmestani and Allen, 2014). For example, cross-scale interactions such as local microbial nitrogen mineralization variability scaling up to affect watershed scale plant productivity requires information sharing to synthesize alternative hypotheses. A viable framework should therefore integrate scalespecific adaptive management that utilizes a suite of policy instruments tailored for the managed (focal), constraining (above), and supporting (below) scales (Green et al., 2014).

We propose a framework that includes a minimum number of scales to encompass key structures and processes in the system. We describe a hypothetical example system with five increasing spatial and temporal scales: plot, patch, ecosystem, landscape, and region. The use of five scales is arbitrary, but useful for giving context to within- and cross-scale dynamics, ecosystem service tradeoffs, and management controllability at different ecological scales (see Angeler et al., [2016] for tools to identify scales of interest in ecological systems). Note that although "ecosystem" is a scale of interest in our discussion, the term "ecosystem services" is applicable to all scales of interest.

The first and smallest scale in our discussion, the plot, is roughly a single square meter over the course of a season. This is also the most frequently used research scale in ecology (Levin, 1992). The plot is constrained to producing ecosystem services associated with a narrow range of land cover and weather, and is thus limited in both type and amount of ecosystem services generated. From a human perspective, the plot scale generates a small suite of ecosystem services at a relatively low rate. Within the plot scale, tradeoffs are explicit and inflexible. Controllability and certainty are both high (Fig. 1), so adaptive management is not applicable here. Cross-scale interactions are largely top-down and feedbacks with higher scales are weak overall, and strongest with the next highest scale (the patch). A synchrony of all plots in space and time could theoretically have significant bottom-up consequences, especially for the patch scale, but the effect of a single plot has little effect on its own. As with all focal scales, larger scales typically constrain from the top-down, and management of the smallest scale is vulnerable to a wide array of disturbances originating at larger scales. At the plot scale, current and past climatic cycles at the regional scale form the template. Characteristics of the surrounding landscape such as land cover heterogeneity define attributes, such as the extant seed bank, local climate, animal movement, and human use of the ecosystem, further narrowing the template for the plot. With each successive filter applied, a manager is limited in the amount and diversity of ecosystem services they can produce. Thus, the plot is constrained by all greater spatiotemporal scales.

The second scale considered in our hierarchy is that of the patch. A patch is generally defined in landscape ecology as a relatively homogeneous area defined by the boundaries of a particular habitat cover type (Forman and Godron, 1986; Turner et al., 2001). The spatiotemporal scale of a patch in this discussion is larger than that of a plot, and it extends temporally over a few seasons but less than a full year. This is the scale where adaptive management is generally applied, because it provides explicit consideration of tradeoffs among ecosystem services generated across multiple seasons (controllability), although services are highly constrained to patch cover type (i.e., row crop agriculture versus wetland ecosystem services). Much like the plot scale, the patch is constrained by larger scales and stochastic events. Because the patch is larger than the plot, bottom-up interactions and feedbacks are now important for explaining patch scale phenomena. The patch is constrained by fewer filters than the plot, and, as a result, contends with fewer ecosystem service tradeoffs. Even so, patches generate a narrow suite of ecosystem services at a low rate vis-à-vis human consumption. Thus, humans still must decide among a handful of often mutually exclusive suites of ecosystem services at this scale.

The third scale in our hierarchy is that of the ecosystem, which encompasses multiple habitat patches. An ecosystem is considered a complex system encompassing living things with similar traits and structures, and the abiotic structures, processes and flows with which they interact (Chapin et al., 2002). Although, like the patch, ecosystem edges are porous and dynamic through space and time, and similarity is relative. For this discussion, the ecosystem scale extends roughly ten to a hundred square kilometers in space and multiple years in time. At this increased spatiotemporal scale, there is greater capacity for stakeholder involvement, a wider range of potential ecosystem services, and higher uncertainty surrounding ecological processes. Data from replicated experiments at this scale provide crucial information during the learning stages of adaptive management (Fig. 2). The effect of stochastic events on this scale from the patch and plot scales may range from background noise to serving as significant drivers. Disturbances can scale up to the ecosystem level if a single change occurs on all patches, such as a synchronized eutrophication in multiple ponds or transformation of all wetlands to a corn-soybean rotation cover type. The ecosystem scale is small enough to be influenced by bottom-up perturbations, and large enough to experience larger scale disturbance events that occur every 3-15 years (such as historical fire regimes of the Great Plains or El Niño cycles in the Pacific Ocean). In addition to disturbance events, ecosystems are constrained by large scale variables like climate and topography that determine the type of services possible for production, whereas the size of the ecosystem and nature of the services determine production rates, and ecosystems can only produce suites of ecosystem services associated with their component patches.

The fourth scale in our hierarchy is that of the landscape, which we define here as comprising multiple ecosystems and covering 100-1000 square kilometers over multiple decades to roughly a century. Landscapes deliver all of the ecosystem services that are produced within their nested ecosystems. Tradeoffs at this scale are largely non-exclusive, and can be made within different ecosystems or replicates of similar ecosystem types distributed in space and time. The landscape is less affected by plot and patch scale disturbance, unless there is a positive "runaway" feedback that creates bottom-up effects. Synchronized stochastic events at the ecosystem scale can affect the landscape but, again, this is dependent on multiple factors. Controllability and consistent monitoring at this scale are extremely difficult to attain, so adaptive management is rarely applied to the landscape scale. Instead, adaptive management programs are implemented within smaller subsets of the landscape (i.e., ecosystems, watersheds) to infer landscape scale relationships. Caution should be taken with this approach, however. Structuring relationships that underlie ecosystem service tradeoffs at one scale may not apply to a larger scale. For a review of such institutional efforts in social-ecological river basins in the USA, see Thom et al. (this issue).

A developing body of theoretical and empirical evidence is rejecting the notion that significant ecological relationships at one scale can be preserved across different scales (Gunderson and Holling, 2002; Allen et al., 2014). Recent advances in fields such as landscape ecology, ecosystem ecology, and paleoecology have revealed the necessity of interdisciplinary "big data" sets encompassing large spatial and temporal scales to reveal the significant relationships among system components at landscape scales (Peters et al., 2015). Factors that cause regime shifts at a patch scale, for instance, may have little or no effect at the landscape scale unless there is synchrony among patches (Allen et al., 2014; Peters et al., 2015). Thus, while adaptive management can be used at this landscape scale to reduce uncertainty surrounding ecosystem service tradeoffs, it should not be done so unless there is sufficient cross-scale data to meaningfully reduce ecological uncertainty.

The fifth, and largest, scale in our hierarchy is that of the region, which consists of multiple landscapes and extends over several thousand years and several thousand square kilometers. All other scales described above are nested within this scale. As a result, within-scale and bottom-up drivers define the region. For bottomup stochastic events to meaningfully affect regional scales, synchronicity must occur among component landscapes (Allen et al., 2014). The region can produce all suites of ecosystem services associated with the landscapes. There are relatively few inherent stakeholder tradeoffs to manage for multiple concurrent management objectives but effectively no experimental controllability at this vast scale, so adaptive management is impossible to implement. Often, this scale is appropriate for scenario planning, in which adaptive management may play a supporting role by reducing key uncertainty surrounding specific hypotheses (Baron et al., 2009).

2.3. Cross-scale interactions of ecosystem services

Adaptive management is formulated to address a single fundamental and several supporting means objectives (Keeney, 1992), each of which occur at a focal scale. Effective evaluation and subsequent adjustment requires collection of monitoring data at the focal (objective), higher (constraints), and lower (explanatory) scales (Holling, 2001). This approach captures information about system relationships relevant to management outcomes that could otherwise remain hidden. Without this cross-scale approach, managers may lose the capacity to identify potential vulnerabilities, such as synchronizing scaling-up effects or top-down constraints that could ultimately limit management success. Adaptive management does not allow for multiple fundamental objectives to be tested simultaneously at more than one focal scale, so instead when the first iteration of adaptive management strongly indicates that a structuring process is occurring at a scale other than the focal scale, double-loop learning can be employed to examine a set of focal, higher, and lower scales, without a major adjustment to the fundamental management objective. For adaptive management to meaningfully reveal information about the system, it must be targeted at an appropriate scale vis-à-vis the hypotheses in question. As learning drives adjustments, the scale at which management is applied must therefore be similarly adjusted. Unfortunately, scale mismatches often result when management objectives occurring at multiple focal scales are combined. For example, regional scale objectives cannot be met with plot scale temporal monitoring data alone, and a patch cannot be managed with a regional scale data set alone. Though adaptive management at these large scales remains challenging, historical social-ecological catastrophes provide a strong incentive to continue building on the developing big data sets to better understand system drivers and structuring relationships in the social-ecological system (e.g., Twidwell et al., 2014).

2.4. An example

To illustrate our framework, consider an example plot located in an intermittent wetland over a single season. Wetlands fed by runoff tend to have short water residence times, and experience intermittent periods of drying and re-wetting (Schlesinger and Bernhardt, 2013b). As an inundated wetland, this plot generates valuable ecosystem services, including terrestrial carbon storage, waste removal, and habitat for specialized wetland plants (Houghton and Skole, 1990; Lu and Wang, 1995; Hansson et al., 2005; Schlesinger and Bernhardt, 2013b). Intermittent rapid wetting and drying in this plot provide a suite of ecosystem services mutually exclusive to wetland or upland cover types, respectively, through time. Yet this temporal shift between wetland and upland cover has associated tradeoffs: carbon and phosphorus stored in hydric soils may be rapidly mineralized (i.e., no longer stored in the wetland) upon exposure to atmospheric oxygen, ecosystem nitrogen removal dramatically slows, and the high physiological costs of surviving in a wetland often excludes many wetland plants from the intermittently drying wetland plot (Schlesinger and Bernhardt,

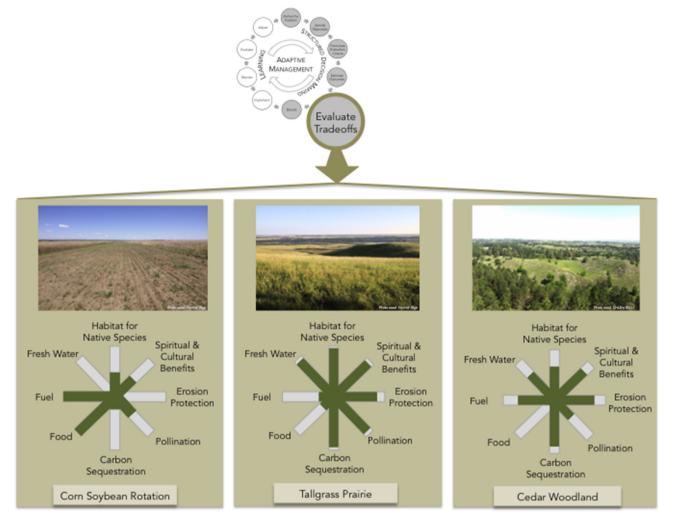


Fig. 8. An example of different potential suites of ecosystem services and the tradeoffs associated with different cover types in a Great Plains landscapes (adapted from Foley et al., (2005)).

2013b). However, due to the small scale of our plot $(1 \text{ m}^2 \text{ over a season})$, management decisions regarding these temporal tradeoffs are limited. Similarly, the influence of a single plot of ecosystem services may be inconsequential relative to the scale at which humans consume and use ecosystem services.

Our patch scale can be considered an entire intermittent wetland or a small network of individual, connected intermittent wetland plots. The suite of ecosystem services possible at this scale is less constrained by temporal and spatial limitations. Hydrological heterogeneity within the patch provides a suite of wetland or upland services that vary over space and time. Hansson et al. (2005) surveyed the nutrient retention and biodiversity of 32 recently constructed (<8 year) wetlands in southern Sweden and found that shallower wetlands with greater shoreline fractal dimension (i.e., complexly shaped) maintained high biodiversity and nitrogen removal rates, likely due to a high edge surface area experiencing rapid drying-rewetting events, whereas deep simply shaped wetlands had lower biodiversity and nitrogen removal rates but much higher phosphorous retention rates. A single wetland patch may consist of enough heterogeneous plots to capture features of both types of wetlands in space and time. In reality, however, managers likely face only moderately flexible tradeoffs at this scale due to other, top-down, social-ecological filters (Ruhl, this issue). Decisions regarding management must be hypothesized and tested through adaptive management, and some wetland ecosystem services will be lost or reduced in lieu of others.

The ecosystem in this discussion is the central Sandhills region of Nebraska, USA, where different land management typically leads to wetland, rangeland, woodland, and, to a lesser degree, cropland cover. At this scale, the full suites of wetland ecosystem services are expected through space and time unless there is a synchrony of patch conversion to a different land cover. Uncertainty surrounding the underlying ecological mechanisms of the different wetlands at this scale is high, especially regarding production of ecosystem services in response to climate change over time. However, though tradeoffs are less rigid at this scale, and replication could provide experimentation, lack of coordination among landowners and few public holdings creates a steep decline in controllability in this ecosystem. As a result, adaptive management of the central Sandhills is likely untenable.

Our ecosystem is part of a broader working agricultural landscape of the North Central Great Plains where suites of wetland ecosystem services in the landscape are extensive both in variety and production rate. Under shifting land use in space or time, some individual ecosystem services may be preserved (e.g., erosion control may be generated under both tallgrass prairie and cedar woodland ecosystems), whereas others are unique to only one ecosystem type (e.g., food production from corn-soybean cover). The ecosystem service suites concept underscores that groups of services tend to co-occur in space and time, and are affected similarly by land use change. These suites are not immutable, and the individual services comprising the suite may vary with scale. At this landscape scale, there are fewer inherent spatial and temporal tradeoffs with which stakeholders must contend in order to manage for multiple suites of ecosystem services (available suites differ among cropland, grassland, and woodland cover [see Fig. 8]). Uncertainty and lack of controllability also intensify at this scale. As a result, adaptive management can be applied to reduce uncertainty and learn about specific relationships at the landscape scale, but practitioners may face a lack of controllability, such as governance constraints and a scarcity of cross-scale data sets. At this scale, social uncertainty may begin to emerge, adding another dimension of difficulty to the process (Lee, 1993; Tyre and Michaels, 2011). Adaptive governance provides scientists, policymakers, and natural resources managers a broader context to implement adaptive management, and may be useful at this scale (Allen and Garmestani, 2015). By enabling institutional support for adaptive management, adaptive governance provides organizations a formal way to analyze and adapt from past experiences to better cope with social-ecological complexity (Chaffin et al., this issue b). Sometimes unexpected social-ecological tradeoffs occur when systems are managed for efficiency and predictability; adaptive governance accommodates the use of adaptive management to probe the mechanisms underlying these tradeoffs (Gunderson et al., this issue).

The region in our example is the Great Plains of the USA, which contains the North Central Great Plains, the South Central Great Plains, foothills of the Rocky Mountains, and the Coastal Plains landscapes. Both the landscape and regional scales have fewer spatial and temporal constraints in regard to the inherent tradeoffs in ecosystem services they produce. However, intensifying agriculture in the form of rangeland or row crops across the region is increasingly narrowing the realized tradeoffs available for stakeholders attempting to balance multiple ecosystem services. Adaptive management should make use of monitoring data at this scale to understand mechanistic relationships at smaller nested scales, even though we cannot effectively conduct management at the scale of the Great Plains.

3. Conclusion

Managing for ecosystem services results in trade-offs through space and time, some of which are hidden. The use of adaptive management can reveal these tradeoffs, allowing managers to make explicit decisions and avoid contributing to non-linear system behavior. As such, the concept of ecological resilience (Holling, 1973) is particularly relevant to adaptive management for ecosystem services. Resilience theory recognizes that ecological patterns are regulated by a few central ecological processes (Allen and Holling, 2008; Gunderson and Holling, 2002) operating at discrete temporal and spatial scales (Angeler et al., 2011; Holling, 1992). If management actions erode or remove these processes, the system shifts into an alternative state unlikely to support management objectives. Accounting for the effects of within- and cross-scale tradeoffs associated with these processes is therefore essential for the ongoing provisioning of multiple, simultaneous ecosystem services through space and time.

Increasing human populations are demanding a higher quality of life, leading to conflicts over finite ecosystem services. Here, we combine two concepts, ecosystem services and adaptive management, for understanding how humans shape nature to meet our objectives. By acknowledging the discrete scales within and across which many ecological and anthropogenic phenomena occur, inherent tradeoffs among ecosystem services at different scales of space and time are revealed. This allows managers to learn about system processes affecting production of ecosystem services while conducting management, and elucidate potential spatial and temporal constraints and tradeoffs on production of ecosystem services in their system.

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