When, Where, and How Nature Matters for Ecosystem Services: Challenges for the Next Generation of Ecosystem Service Models

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Many decision-makers are looking to science to clarify how nature supports human well-being. Scientists' responses have typically focused on empirical models of the provision of ecosystem services (ES) and resulting decision-support tools. Although such tools have captured some of the complexities of ES, they can be difficult to adapt to new situations. Globally useful tools that predict the provision of multiple ES under different decision scenarios have proven challenging to develop. Questions from decision-makers and limitations of existing decision-support tools indicate three crucial research frontiers for incorporating cutting-edge ES science into decision-support tools: (1) understanding the complex dynamics of ES in space and time, (2) linking ES provision to human well-being, and (3) determining the potential for technology to substitute for or enhance ES. We explore these frontiers in-depth, explaining why each is important and how existing knowledge at their cutting edges can be incorporated to improve ES decision-making tools.

Keywords: ecosystem services, decision-support tools, decision-making, modeling, natural capital

A crucial window of opportunity is now opening to deliver scientific understanding of the coupled dynamics of people and the biosphere to decision-makers who will influence the future of our planet (Armsworth et al. 2007). Many leaders have awakened to warnings—and increasingly to actual experience—that the degradation of nature is elevating socioeconomic risks and costs and undermining human well-being, as well as to unique opportunities afforded by protection of natural processes (Guswa et al. 2014, Steffen et al. 2015, Ouyang et al. 2016). Deforestation, for example, can decrease water quality and flow regularity, increase the risk of downstream flooding, and lower the efficiency of hydropower production (Li et al. 2015). In contrast, healthy upstream watersheds can effectively, sustainably, and economically provide clean water for those who need it, and watershed protection programs are being implemented to secure clean drinking water in cities worldwide (Guerry et al. 2015). However, investing in nature for the provision of benefits may have implications for how quickly or efficiently these benefits can be delivered and for the long-term resilience of service provision. Increasing interest from decision-makers is prompting deeper examination of the case for investing in nature for the provision of vital ecosystem services (ES) across a wide range of decision contexts (box 1).

Several decision-support tools for spatially explicit ES assessment have been developed (e.g., ARIES, Villa et al. 2014; Co$tingNature and its related tool Water World, Mulligan 2012; InVEST, Sharp et al. 2014; and LUCI, Jackson et al. 2013) that promise to provide easily accessible, quantitative assessments of ES provision across a range of scenarios (Bagstad et al. 2013). These tools assess provision of multiple ES, ideally allowing a decision-maker to understand the impact of a decision on multiple ES and the trade-offs among them. However, although promising in their generality, accessibility, and multiobjective capabilities, most ES decision-support tools are missing crucial components of the complexity needed to fully answer the question of when,

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MONTÉRÉGIE
Regional Government

The Montérégie region of Quebec, Canada, contains both the province's most productive agricultural land and its areas of highest biodiversity. A new regional development plan aims to enhance biodiversity and ES by conserving 17% of the region as green space and developing a greenbelt around the city of Montreal (CMM 2011). Regional municipalities have been tasked with identifying which land is most critical to preserve, and how to manage it to reach these goals, especially in the face of regional development and global climate change. To do this well, the municipalities must understand when and where nature matters most, especially in comparison to technological solutions, for providing the services that people need.

Questions: *Which land should be conserved to maintain long-term ES provision in a region facing both regional and global change? How will changing habitat connectivity affect ES beyond the direct effects of conserving land? How can the mandated green space be best selected to complement the region's need for sustainable and resilient food production?*

PEOPLE'S REPUBLIC OF CHINA
National Government

Following massive drought and flooding in the late 1990s, the People's Republic of China has launched major initiatives to restore natural capital. It is in the process of zoning nearly half (49%) of the country's land area into Ecosystem Function Conservation Areas (EFCAs), where 200 million residents are paid for restoration and conservation activities to protect ES (water supply, flood mitigation, soil retention, erosion control) and biodiversity, and alleviate poverty (Van Den Hoek et al. 2015). To support all of these efforts and for each particular conservation activity, Chinese officials and scientists must understand how much nature matters to improving human well-being.

Questions: *Which areas are of the highest conservation or restoration priority, based on both the potential of different places to supply services and the human need for those services? What investments in natural or other capital can enable and promote more sustainable livelihood options for rural populations? What are distributional effects of these policies; who wins and loses as land development options are limited by the EFCAs?*

INTER-AMERICAN DEVELOPMENT BANK
International Investor

The Inter-American Development Bank's (IDB) Biodiversity and Ecosystem Services (BIO) Program is piloting innovative biodiversity and ES initiatives to support sustainable development in several Caribbean and Latin American countries, focusing on infrastructure development to support growing and urbanizing populations (IDB 2016). The IDB must understand how much nature matters for each infrastructure project in order to know when to invest in biodiversity and ecosystems, when engineering or other solutions will be more effective, and when investment should be split between the two.

Questions: *How will a development project (e.g. a new road) impact the well-being of people locally, nationally, and globally, both now and in the future, both directly (e.g. increased access to markets) and indirectly (e.g. increased landslide risk)? Can projects take advantage of natural capital to protect infrastructure investments? What are the benefits of investing in natural capital versus engineered solutions, and what are the consequences of investing in the wrong type of capital?*

COCA-COLA
International Corporation

The Coca-Cola Company, a major purchaser of corn globally, has set goals to source the natural resources it uses in an environmentally and socially responsible way (Coca-Cola 2015). Coca-Cola is working with local and national partners in Iowa's Cedar River Valley to identify risks to clean water supplies and to develop collaborative plans for protection and restoration, including cost-effective changes to agricultural best management practices. To achieve its sustainability goals, Coca-Cola needs to understand where and when investments in nature matter most to preserving water quality standards, while controlling business costs and maintaining a reliable corn supply.

Questions: *Where can implementing agricultural management practices most cost-effectively minimize trade-offs between corn production and water quality? How much benefit can be expected through improving agricultural practices, compared to technological solutions for water treatment? How resilient will natural vs. engineered solutions be over time, especially with respect to extreme events?*

Box 1. Examples of ecosystem service (ES) use by decision-makers. These real-world examples span the scales of decision-making from local to national to global, with actors on the leading edge of using ES information in major decisions. The range of contexts demonstrates the diversity of the types of questions and needs that decision-makers have. (Photographs: Jesse T. Rieb, Jillian Treadwell)

where, and how much nature matters to the resilient provision of ES and to human well-being (Akçakaya et al. 2016, Bennett and Chaplin-Kramer 2016).

In some cases, this knowledge exists in more sophisticated, typically discipline-specific models for a limited number of ecosystem functions or services, such as SWAT, LPG, CENTURY, or EPIC. However, although these models can represent more complex processes, they often were developed for a specific realm (e.g., a catchment-scale agroecosystem for SWAT). Within this realm, some trade-off analysis of ES is possible (e.g., Lautenbach et al. 2014), but these tools typically focus on biophysical systems, with limited ability to deeply address the ultimate benefits to people provided by these biophysical systems. Such models also typically require at least several months of work with disciplinary expertise and on-the-ground monitoring for calibration, demanding time and expense that many decision-makers cannot afford. In addition to single-discipline, process-based models, a wide array of more interdisciplinary, empirical models have emerged from detailed field research in specific locations. These place-based models can capture much of the complexity of how ecosystems respond to human activity and the resulting changes in the provision of ES to people (Qiu and Turner 2013, Dawson and Martin 2015, Renard et al. 2015). Although these empirical models have proven valuable for advancing the scientific understanding of ES, they may be less directly useful to decision-makers because of the costs and time involved in developing them. However, some aspects of the complexity found in these models are needed to fully answer the question of when, where, and how much nature matters to the provision of ES and human well-being. The challenge here is to refine the knowledge gained from discipline- or location-specific models into general principles that can be incorporated into decision-ready tools to inform decision-making across multiple services in a wide variety of contexts.

There are also still questions for which the scientific community's understanding of when, where, and how much nature matters for securing human well-being over time is in such an early phase that no models adequately address them. We do not fully understand, for example, what types and levels of ecosystem, functional, or species diversity are needed to provide and sustain vital ES in agricultural landscapes or where possible leverage or tipping points of service provision lie (Bennett 2016). We also do not know when, where, or to what extent nonnatural capitals can substitute for biodiversity, such as pesticides for natural pest control, fertilizer for healthy soils, or gray infrastructure such as dams for functioning floodplains, without causing dangerous—and possibly irreversible—declines in future ES provision (Bennett et al. 2015). For the next generation of ES tools to more effectively meet decision-makers' needs, further research must explore how these factors play a role in ES provision now and in the future and how to model them in ways that can be incorporated into decision-support tools.

Here, we investigate emerging knowledge and promising theory that may help improve ES decision-support tools. Acknowledging that all models face trade-offs between realism, precision, and generality (Levins 1966), we argue that key elements of complexity can be added to current decision-support tools to better represent reality without sacrificing too much of the generality that makes them practical. This is not intended as a critique of the state of all ES modeling but rather as an investigation of off-the-shelf ES decision-support tools. We point to three critical frontiers essential to understanding the relationship between changes in nature and well-being where current tools fall short of meeting the needs of decision-makers: (1) the complex dynamics of ES in space and time; (2) the links between biophysical ES provision and human well-being; and (3) the potential for technology to substitute for or enhance ES. These frontiers are broad categories, each encompassing many more specific issues; together, they represent the most fundamental gaps in current ES decision-support tools. Within each frontier, we identify several specific issues with potential for progress and identify concrete steps that can be implemented to improve models. Together, these frontiers set priorities for improving ES decision tools by integrating recent advances in ES research and point to new avenues of research needed to answer decision-makers' most pressing questions about ES.

Frontier 1: Space–time dynamics

Landscapes can be complex mosaics of different habitats and competing human uses, ever changing in response to human and physical drivers. Attempts to quantify how much natural processes matter to the provision of ES must therefore consider spatial and temporal variation in ES, as well as ES interactions, time lags, and community needs, from a spatially and temporally dynamic perspective. Because managers typically consider both current and future needs in natural-resource decision-making, they require models that can dynamically represent ES. Although ES maps are commonplace, they rarely describe either the spatial and temporal processes that produced the patterns of ES observed today or their ongoing dynamics (Seppelt et al. 2011, Renard et al. 2015). Although one could theoretically adjust maps and model outcomes to understand how changes might affect ES provision, this approach is one-directional (from land use to ES) and fails to capture crucial feedbacks. The lack of sensitivity of many existing models to drivers and mechanisms limits our ability to project future supply and sustainability of ES in the face of environmental change or management interventions.

For example, a corporation seeking to protect its business from reputational and regulatory risk may proactively engage producers in its supply chain to improve water quality through agricultural best-management practices, as Coca-Cola has done in the Cedar River Valley of Iowa (Coca-Cola 2015). Spatially targeting these changes can minimize costs and make interventions more feasible and scalable. However, without understanding how space and time interact in ES models, the targeting can only address immediate impacts. Tools that ignore space and time may mask saturating or cumulative effects and may therefore fail to identify practices that lead to the best long-term outcomes. For instance, an agricultural field yielding high current returns because of drainage and fertilizer input may experience soil degradation and decreasing yields in the future; these risks are typically not identified in static maps. A short-term or static representation of ES provision is especially problematic for managers who must decide where to invest in particular types of land-use changes (e.g., Bonn et al. 2014) when the drivers of ES provisions are themselves changing. We propose the following advances to create spatially explicit and temporally dynamic ES tools.

Advance beyond landscape composition as an ES proxy. Early work assessed ES on a per-area basis, assigning one value, in biophysical units or dollars, to each type of habitat everywhere it occurred (e.g., Costanza et al. 1997). Such land-cover proxy information has been mainstreamed by ES practitioners because it can be easily applied anywhere at multiple scales (van der Ploeg and de Groot 2010), although this approach has known limitations and poorly explains the majority of variance in provision for many ES (Eigenbrod et al. 2010). Instead, ES provision is controlled by organisms, ecological properties and processes, and human impacts that interact spatially with the environment in different ways (Syrbe and Walz 2012, van Oudenhoven et al. 2012, Remme et al. 2014). Much is known about these drivers (Kremen 2005), but the links between drivers and ES provision are still missing from many mainstream ES tools. By linking with recent progress in understanding how particular species traits and functional groups underlie ES provision, predictive species-distribution models could be used to forecast changes in ES (Lavorel et al. 2011, Civantos et al. 2012).

Advances in remote sensing products can help push general ES tools beyond the use of land use or land cover (LULC) as a proxy or even as a categorical input. Remotely sensed indicators of habitat quality such as biomass (Baccini et al. 2012) or species composition (Baldeck et al. 2015) are becoming available at increasingly fine resolutions and broad extents, and ES tools should be adapted to better use this information. Cutting-edge approaches to derive ecosystem structure and function from continuous variables could be mainstreamed into ES tools to replace or augment inputs currently represented by categorical land-use information (Cord et al. in press). For example, the normalized difference vegetation index can be linked to bare ground and then to the C-factor (otherwise user-defined by land-use class) in the Universal Soil Loss Equation for sediment retention and water purification (Le et al. 2012). The recent availability of hyperspectral data (e.g., EO-Hyperion) also allows inputs to move beyond categorical land cover to species-specific mapping of key ES providers such as nontimber forest products (Christian and Krishnayya 2009). Nagendra and colleagues (2013) identified many avenues for remote sensing to monitor biodiversity through very high spatial resolution data (e.g., IKONOS, QuickBird, GeoEye, and WorldView-2), hyperspectral data (e.g., ASTER, HyMap, AVIS-2, and AHS-160), or 3-D active remote sensing data (e.g., LIDAR and SAR), which has promising applications for differentiating between higher- and lower-quality habitats of the same type and therefore provide more accurate estimates of the ES provided by these habitats. As the imaging complexity and spatiotemporal resolution of satellite data sets continue to improve, the global coverage of these data sets can provide information currently available only in scattered locations with ground-based or aerial monitoring. As these opportunities expand, the ES community should work together with the remote sensing community to integrate these advances into decision tools.

Where land-use proxies must be used because of data constraints or remaining gaps in the science, models that include both landscape configuration and composition represent these processes better than those that include composition alone (Grêt-Regamey et al. 2014). For example, connectivity of forest patches can affect insect herbivory regulation and soil decomposition rates in surrounding agricultural fields, and more connected forest patches may promote higher agricultural yields (Mitchell et al. 2014). Similarly, the value of forest parcels to pollination in Costa Rica depends on the landscape configuration around those forests (Ricketts and Lonsdorf 2013). Recent evidence suggests that landscape configuration could even affect nonmobile services such as carbon storage across the tropics (Chaplin-Kramer et al. 2015a). Incorporating some of this knowledge into ES tools could facilitate more accurate estimates of ES provision than landscape composition alone.

Include multiple time steps. No current ES assessment tools explicitly incorporate feedbacks to model ES changes through time; instead, users must predict changes in key drivers over time and run models repeatedly with different inputs for each time step. Some studies have projected future changes in ES on the basis of land-use change (Bateman et al. 2013, Lawler et al. 2014), and others have tracked past ES changes using spatially explicit historical ES data sets (Renard et al. 2015, Ouyang et al. 2016). Both kinds of studies demonstrate the importance of temporally explicit ES models and may serve as a useful template for building this capacity into decision-support tools. However, they all still required substantial time and expertise for modeling or compiling location-specific historical data.

Most ES tools are designed to estimate changes in service provision resulting from land-use change, but the practice of comparing only a "current" and even a few different "future" scenarios in ES assessment is poorly suited to answering key questions decision-makers have about how ES provision may change in the future (Goldstein et al. 2012, Bhagabati et al. 2014). For example, to improve water quality in their supply chains, a company may need temporally explicit modeling tools that can account for cumulative effects of agriculture practices or time lags between when a solution's implementation and its results. Although technically possible to conduct such an assessment through iterative runs of current ES tools, in practice, this is often ignored because it is not easily automated, and guidance is lacking on how to convert changes in management or policy into changes in the variables that feed into the ES tool. Scenario tools that translate decisions or policies into spatially explicit inputs are needed, ideally integrated with the decision-support tool, so multiple time steps can be run in a single analysis.

Automating links between spatial and temporal dynamics in ES tools is a crucial first step toward facilitating their integration into decisions, but a major obstacle remains in the synthesis and interpretation of multidimensional spatiotemporal outputs (Stillman et al. 2016). One possible approach to improve the presentation of this complex information would be to adopt a risk framework, similar to that used by decision-makers in many branches of government, that weighs the probability of an event occurring and the severity of the result (DHS 2011, Maron et al. 2017). Such a decision framework would require tools that could quantify the probability of ES falling below a certain level within a certain spatial extent and time frame, representing the minimum desired ES provision set by the decision-maker (figure 1). Applications of this type of approach could include the percentage of land area above a target level of service provision, the number of days for which this level of service provision is maintained, or the number or extent of hot spots of service provision or high-threat areas (Qiu and Turner 2013, Schröter and Remme 2016). Targets could also be set at the minimum level needed to prevent catastrophic future declines in ES or at a level at which other capital investments would be needed to maintain a

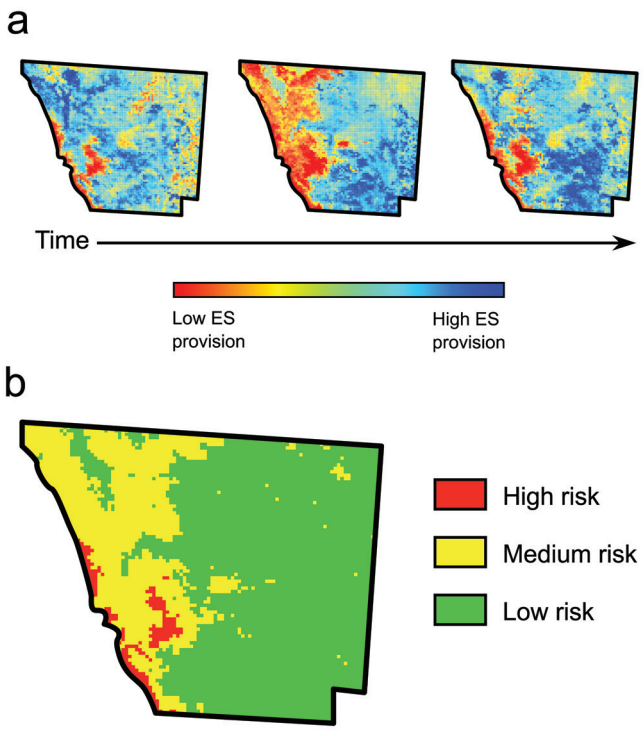

Figure 1. Using risk to better communicate complex spatiotemporal ecosystem service (ES) dynamics. Panel (a) shows the provision of a hypothetical ES across a region at three different points in time. Panel (b) shows the risk of ES provision falling below a set threshold for the same region. Risk is quantified on the basis of the number of time steps ES provision falls below the threshold, with high-risk areas having ES provision below the threshold at all three time steps, medium-risk areas having ES provision below the threshold at one or two time steps, and low-risk areas maintaining ES provision above the threshold at all three time steps.

certain level of human well-being (see Frontier 3). Multiple model runs using Monte Carlo simulation or other statistical probabilistic techniques could estimate the risk of exceeding such thresholds under particular combinations of drivers (White et al. 1997).

Build models that link multiple ES. Many decision-makers' questions involve management of multiple ES at the same time (box 1), but most current ES models disregard potential feedbacks and interactions among ES. Even tools that can model multiple ES, such as InVEST, typically function as suites of single-service models, lacking connections between the models of different ES. Tools that capture interactions among multiple ES through space and time would facilitate more effective management, both by helping prevent ecological surprises, in which the management of one ES has unexpected consequences for the provision of another, or by revealing situations in which one management intervention could positively affect multiple ES. Without modeling the feedbacks and interactions that control spatial and temporal dynamics, it is difficult to fully represent how much nature matters to human well-being in any particular decision context.

Modeling over longer time frames requires understanding ES responses to changing drivers, including identifying whether thresholds in ecosystem dynamics might lead to serious impacts with gradual changes in drivers (Chaplin-Kramer et al. 2015b) or whether time lags in response could lead to greater impacts than initially observed (Carpenter et al. 2009). Building tools that capture feedbacks and interactions would require substantial structural changes from existing tools, which model multiple ES as a suite of single-service models, to tools that integrate multiple ES from the beginning of model construction. This integrated model construction could be guided by efforts to model complex systems in other disciplines, such as biodiversity (Colléter et al. 2015) or climate science (Cox et al. 2000). Linking multiple ES would likely be facilitated by starting with more process-based ES models (see the "Advance beyond landscape composition as an ES proxy" section above), allowing the sharing of biophysical or social drivers among multiple ES when appropriate.

Adding feedbacks and interactions to models rapidly increases their complexity and can result in models with less predictive power than the simpler models they replace. Therefore, decision-makers may also benefit from separate exploratory modeling tools that focus on complex system dynamics. These models, which would focus on predicting general system behavior and directions of change rather than quantitatively accurate ES predictions, could help decision-makers discover important potential feedbacks in their systems, and add them to predictive models when necessary.

Advancing beyond landscape composition as a proxy for ES, modeling multiple time steps, and linking multiple ES in models would all help ES tools better account for spatial and temporal ES dynamics. Although these are complex problems and may require substantial work to fully address, some feasible next steps given current scientific knowledge and capabilities include the following: (a) Use recent advances in remote sensing to move beyond categorical representation of LULC to capture elements of ecosystem structure and function that most matter to ES. (b) Include multiple time steps with integrated feedbacks between services and over time in future scenario models. (c) Improve visualization through approaches such as risk management frameworks to allow easier interpretability of spatiotemporal outputs. (d) Build simple exploratory models that decision-makers could use to learn about potential interactions and feedbacks affecting their systems.

Frontier 2: Connecting to beneficiaries

The unique conceptual power of the ES framework is its ability to illuminate the role of nature in supporting human well-being, the ultimate measure of how much nature matters to

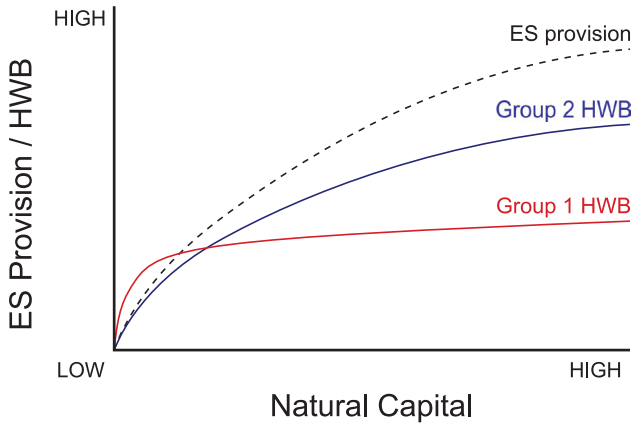

Figure 2. The relationships between provision of an ecosystem service (ES) and human well-being (HWB) can vary among groups of beneficiaries. For example, the provision of freshwater might initially benefit a group of people who live nearby and use it for drinking (group 1). This group's need for freshwater is met relatively quickly, and further increases in service provision do not greatly increase well-being. Other groups of users, such as farmers who use the water to irrigate and who can increase production as more water becomes available (group 2), may continue to benefit from further increases (until other resources become limiting). Depending on the amount of service being provided, environmental changes that affect service provision may disproportionately affect different groups of people.

people (figure 2). A growing number of recent studies highlight the considerations needed to better measure ES contributions to human well-being, such as through psychological benefits (Bratman et al. 2012), cultural services (Daniel et al. 2012), recreational opportunities (Peña et al. 2015), and human health benefits (Myers et al. 2013). Despite these advances in the literature, ES decision-support tools still typically focus on biophysical supply of services (e.g., water purification by wetlands) more than on the resulting benefits to people (e.g., reductions in waterborne disease) (Daw et al. 2016). For example, modeling ES benefits from water purification requires taking account of not only how much water is or can be purified, but also who lives (or will live) downstream, how those people use surface water, what alternative sources of water purification they have access to, and what benefits they gain or lose from a marginal change in water quality. Few ES tools identify the beneficiaries of a given ES in a spatially explicit way, fewer measure specific aspects of well-being for those beneficiaries, and even fewer model the benefit by mapping connections between spatially disaggregated ES demand and spatially explicit supply (Villa et al. 2014, Wolff et al. 2015).

A more explicit focus on beneficiaries in ES tools will help governments, business, and international organizations answer their most important questions (see box 1). China, for example, seeks to target Ecosystem Function Conservation Areas (EFCAs), not necessarily to maximize production of ES, but to optimize benefits to people. Areas that benefit many people are favored over more ecologically productive locations with fewer beneficiaries. The Southwest China EFCA, for example, is valued because many residents depend on wild forest resources for livelihoods, whereas others from the rest of China and beyond derive recreational benefits from these same landscapes. Although the policy of optimizing benefits to populations is innovative in many ways, it can be difficult to apply appropriately without tools that identify beneficiaries and their demand for ES, and that use appropriate metrics to reflect the values different stakeholders place on these services across space and time.

Here, we highlight three areas in which modeling advances are most needed to help incorporate beneficiaries in the valuing of nature.

Identify and locate different beneficiaries. A fundamental first step is to explicitly incorporate information about who the beneficiaries are and where they are located (Fisher et al. 2009). Locating beneficiaries helps identify which ES might matter for different groups and which ES are accessible to different groups, both of which are crucial to understanding the real value of ES. For example, evaluation of a potential road-development project in Peru showed disproportionate losses of water-related ES for local indigenous people relative to nonindigenous populations due to the spatial location of the inhabitants (Mandle et al. 2015). ES tools should disaggregate beneficiaries into meaningful groups whose well-being relates to nature in different ways (e.g., farmers, municipal water users, and local communities). This can help to identify populations that are vulnerable to ES changes, or those for whom ecological changes are likely to represent net benefits or costs (figure 2; Daw et al. 2011, 2015).

Several specific tools and techniques could help identify and model ES beneficiaries. For example, social–ecological inventories catalog individuals and local steward groups who play a role in landscape management. These inventories can be useful for locating individuals and institutions with relevant social–ecological knowledge for identifying and disaggregating beneficiaries (Schultz et al. 2007). New techniques that explicitly summarize demographic and social data by administrative or ownership boundaries allow for more spatially detailed analyses of beneficiaries (Harris et al. 2005, Maantay et al. 2007), which in turn enables ES modeling to better forecast values of hazard mitigation on the basis of the social vulnerabilities of different populations (Arkema et al. 2013). Social media likewise opens up new avenues for data mining to geolocate ES use or beneficiaries (Wood et al. 2013, Sonter et al. 2016). Other recent modeling advances linking ecological production and social benefits, such as for pollination, allow estimates of how much nature matters for each land parcel in the landscape, such as how much a given farmer's production and revenue would change if any given

unit of forest is degraded or restored (Ricketts and Lonsdorf 2013). Such efforts allow decision-makers to identify who relies most on ES provision in different places and who is most vulnerable to disruption in that provision.

ES tools should also be able to disaggregate potential beneficiaries over time, in addition to space, because ecosystem change may affect the timing of who receives flows of benefits, who pays the costs, and when. For short time scales, temporally disaggregating beneficiaries is typically done through a market discount rate in which the present value of benefits received at a point in the future is discounted by some annual percentage (Farber et al. 2002). Over longer time scales, concerns over intergenerational equity must be considered. Discounting can sometimes be used in these cases with a social discount rate, but the choice of a discount rate can be controversial and other metrics for evaluating intergenerational tradeoffs may be more appropriate (Goulder and Williams 2012).

Model changes in human well-being explicitly and in meaningful metrics. To adequately capture beneficiaries and their differences, decision-support tools must explicitly represent the relationships between changes in ES provision and changes in demand. In economic terms, such models would represent the "utility functions" of different groups of beneficiaries—relating changes in ES to changes in some measure of human well-being. Figure 2 depicts a hypothetical example of these utility functions.

In ES assessments, benefits are often considered in monetary terms (Keeler and Polasky 2014), but monetary value is only one metric among many to express changes in human well-being. Others include proxies (e.g., visitor days, Wood et al. 2013, Sonter et al. 2016; number of people at risk, Arkema et al. 2013), metrics for physical and mental health (e.g., cognitive performance scores, Bratman et al. 2012; nutrient deficiency, Ellis et al. 2015), and indicators of cultural value (e.g., sense of place or shared and social values, Chan et al. 2012). Such nonmonetary metrics can capture and communicate benefits that are not easily monetized or that have different monetary values for different stakeholders. Although they can be challenging to define and measure in a meaningful way, there is evidence that they often carry more meaning to beneficiaries and, sometimes, policymakers than do monetary metrics (Martín-López et al. 2014).

Feedback loops between beneficiaries and provision of ES. The two points above represent the first simple steps toward better integrating human well-being measures into ES tools. But if different groups depend differently on ES over space and time, ES demand must be dynamically coupled to ES provision. Preferences for and use of different ES, the availability of technical substitutions for those ES (see frontier 3), and the importance and location of service-providing ecosystems all differ among groups of beneficiaries (Wolff et al. 2015), and this must be taken into account to accurately model the delivery of benefits to stakeholders.

Most simply, incorporating utility functions that determine the probability of ES use explicitly based on the social and ecological qualities of the system (e.g., harvesting costs adjusted for quality of the harvest for timber) will help predict changes in preferences, and therefore changes in benefits received through the provision of ES. Without modeling ES demand as well as supply, we cannot predict whether service provision will be adequate to meet current and future needs, making it difficult for a government, development agency, or other decision-maker to assess the true consequences of development for human well-being (García-Nieto et al. 2013).

Furthermore, for large changes or over long periods, links between sectors of the economy and changes in nature become more important. A typical scenario approach to modeling ES might link expected changes in socioeconomic drivers first to changes in landscape patterns, and then to the benefits populations derive from an ES. But communities often respond to changes in the environment through shifts in the workforce, net in- or out-migration, and other dynamic changes. Such transformations in a community may require more sophisticated economic modeling techniques such as general equilibrium modeling, in which different sectors of the economy are linked. This has rarely been considered in ES assessments (but see Pattanayak et al. 2009, Lawler et al. 2014), but integrating such links into ES tools would clearly show how each economic sector feeds back to affect land-use and ecosystem function (Holland et al. 2015, Liu et al. 2015).

Locating beneficiaries, using appropriate valuation metrics, and incorporating feedback loops represent some of the advances required to better model the value of ES to beneficiaries in decision-support tools. Some immediate next steps toward realizing these include the following: (a) Distinguish different groups of potential beneficiaries (e.g., farmers, municipal water users, and out-of-state tourists) for each ES in question, and map them in space. This would facilitate linking already-available demographic and social data with ES models. (b) Devote as much effort to developing rigorous utility functions, which link ES supply to realized benefits, as the ES community has devoted to date on production functions, which link natural capital to ES supply. (c) Create demand-side models that easily interface with readily available supply-side models to allow for dynamic feedback, perhaps through simple iterative updating. (d) At the beginning of an ES assessment, simply ask stakeholders which metrics of value are salient to decisions and those affected by them. Tailor models to report outcomes in these metrics.

Frontier 3: The role of different types of capital in ES provision

Although provision of ES results from the interplay between social and ecological systems (Fisher et al. 2008, Díaz et al. 2015), how the exact combinations of social and ecological contributions affect the resilient and sustainable provision of multiple ES remains unclear (Carpenter et al. 2009).

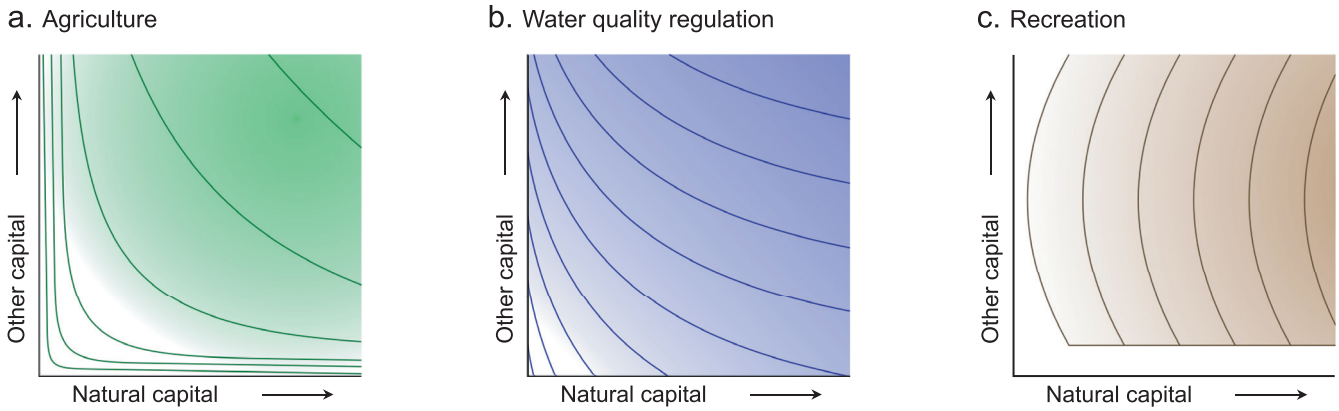

Figure 3. Hypothetical relationships between natural capital and other capital and utility toward the provision of three ecosystem services (ES). The x- and y-axes represent stocks of natural capital and other capitals, respectively. Utility (conceptualized here as ES provision) is shown by the contour lines and shading (darker shading, increased utility). For agriculture (a), both capitals are complementary, and both are necessary for service provision. Growing crops requires a certain amount of human labor and technology (e.g., seeds and tools) but also requires natural capital (e.g., soil and pollinators). Investing in either natural or other capitals can increase utility up to a point, but eventually, a further investment in the other will be necessary for a continued increase in service provision. For water-quality regulation (b), natural and other capitals are substitutes: Water can be cleaned by a natural wetland or by a man-made water-treatment plant, and each can be completely effective without the other. Here, we assume utility increases linearly with other capital, because we assumed demand for water was unlimited and that capacity could readily be added to a water-treatment plant over the range of values shown, whereas we assumed it increases at a decreasing rate with natural capital, because there is a limit to the water-purifying capacity of even the most well-maintained wetland. Therefore, although investments in natural capital might be most effective when demand is relatively low, technology may become a better investment as demand increases. For recreation (c), we assume utility is primarily driven by natural capital, with the scenic quality of the area largely determining the number of visitors and the enjoyment they derive from it. However, there is a minimum amount of other capital (e.g., roads and parking areas) required for people to access the areas and benefit from the service. Once basic access is established, further investments in other capital (e.g., trail improvements and interpretive signs) can increase utility up to a point. However, continued investments in other capital eventually decrease utility, either as the area becomes too crowded or as overdevelopment begins to degrade the natural experience.

ES research has tended to frame research questions either with respect to human intervention or with respect to ecological processes rather than on the complex interactions between ecological and social components in the provision of ES (Bennett 2016). Because the fragmented knowledge obtained from disciplinary studies cannot simply be combined to better understand a complex system (Norgaard 2008), the interactions between social and ecological processes are not often incorporated in ES assessment tools (figure 3; Raudsepp-Hearne et al. 2010), rendering these tools incomplete and potentially causing predictions of ES provision to be inaccurate.

Ecologists' conceptualization of ES, and therefore models of them, often begin with ecosystems and end with the delivery of services to people (e.g., Haines-Young and Potschin 2010), despite acknowledgement of the role of human intervention in the provision and delivery of services (Norgaard 2010, TEEB 2010). Similarly, in the economic literature, work has focused primarily on understanding the value of ES in an attempt to value natural capital, without deeply addressing ecological factors (Fisher et al. 2008). Recently, there have been calls to address ES from a social–ecological perspective that would more accurately include other forms of capital or social factors such as infrastructure (e.g., pipes for irrigation) or management institutions (e.g., collective use rights around irrigation water) that can be critical to the delivery or accessibility of ES and their benefits (Reyers et al. 2013, Palomo et al. 2016). However, little quantitative work has been done to understand the complex interplay between biophysical and social systems in ES provision (but see Rathwell and Peterson 2012, Mogollón et al. 2016). Instead, much of what we know remains disciplinary, useful for answering the most important questions of a field of study, but perhaps not as useful for building models that can address decision-makers' key questions (box 1), which often relate to the complex interactions of social and ecological systems in ES provision (Braat and de Groot 2012).

A deeper, more subtle understanding of the roles of human and technological complements and substitutes for ES provision could support more effective ES management and policymaking, especially when decision-makers are choosing between providing a service through ecological

processes or through built infrastructure (e.g., Chichilnisky and Heal 1998). For example, farmers in the Montérégie must decide each year how much to rely on native predators to control pests such as soybean aphids and how much to rely on pesticides; the magnitude of the pest outbreak, populations of natural-control organisms, and pesticide costs are factors that might affect these decisions. To make this decision, farmers need tools that incorporate natural and social factors and go beyond simply estimating landscape capacity to provide pest control. Likewise, city planners in the region are deciding where to invest in conservation to meet the regionally mandated target of 17% of land allotted to green space with greatest overall benefit to people (CMM 2011); they therefore need to anticipate service delivery and human use by understanding how infrastructure and human institutions complement and enable access to that space. Although these examples are not simple, they are relatively straightforward to address, because they involve questions about the provision of only one or two services and are strongly linked to a particular place. Situations requiring more generalized tools or models that predict outcomes for multiple services are considerably more complex, and existing tools therefore tend to simplify by focusing on only one component (usually ecosystems) of ES provision.

The role and balance of ecological and social components in ES provision may also lead to contrasting emergent system properties or different effects on sustainable long-term ES provision (Fischer et al. 2015). For example, to evaluate an infrastructure loan, the Inter-American Development Bank (box 1) may need to know the relative economic costs of investing in a dam or wetland restoration to prevent flooding of a road. A cost–benefit analysis will be inaccurate without considering long-term maintenance costs of either solution and the sustainability of multiple services provided. Although it often appears that technology can, in the short term, fully substitute for nature in providing for human well-being, it is unclear how these two strategies compare in the long run in terms of resilience to different perturbations or sustainability under different conditions (Raudsepp-Hearne et al. 2010). Being able to model these dynamics would enable decision-makers to better consider the broad implications of different management options. We propose three necessary scientific advances.

Include institutional and technological factors of ES provision in models. In most ES models and tools, the nonnatural capitals that enhance ES provision are either implicit (e.g., a timber production model that only measures trees and assumes necessary infrastructure and management practices for harvesting them are in place) or ignored (e.g., a pollination model that does not account for pollination provided by managed honeybees). This failure to explicitly include human made infrastructures and capital in ES models and tools means it is impossible to assess their relative importance to service provision. Improved models could show when it makes sense to invest in complementary infrastructure (that takes advantage of services nature provides) versus technological solutions that replace (substitute for) the role ecosystems could play in service provision. For example, provincial law mandates riparian buffers between streams and agricultural fields in the Montérégie to protect water quality, but subsurface drainage systems, which are common in the region, allow runoff to bypass these buffers, reducing their effectiveness (Terrado et al. 2015). Here, investments in water-purification technology or different agricultural drainage practices may be more effective than investments in natural capital (e.g., higher-quality riparian buffers) at regulating water quality.

Define the role of technology and nature in the provision of services at multiple scales. Other capitals can substitute for some ES locally, but may fail to compensate for a widespread, global decline in ES provision (Raudsepp-Hearne et al. 2010). Large-scale interventions may also have secondary consequences that undermine ES resilience. For example, dikes constructed to regulate flooding can create a false sense of security, encouraging development in previously flood-prone areas and leading to greater consequences should a flood occur that is larger than the dikes are designed to handle (Vis et al. 2003). Although other capital can potentially substitute for some provisioning and regulating services, most cultural services depend on a genuine experience, often relating to a feeling of wilderness or existence of areas without human interference, which is impossible for other capitals to replicate (Carpenter et al. 2006). It is also not yet understood to what extent the substitution potential of natural and other capitals is reversible (i.e., how easily one can move along the isoclines in figure 3) or where tipping points might be reached that would affect the long-term provision of ES. Incorporating the effects of technology into ES models could help understand and quantify the possibilities and limits of technological substitution for ES.

Trade and telecoupling. Local demand for ES is sometimes met by ES provided in distant places (Seitzinger et al. 2012, Liu et al. 2016). For example, deforestation in the tropics has been correlated with increases in agricultural exports (DeFries et al. 2010), suggesting that tropical areas were deforested to produce ES benefits to meet demand elsewhere whereas the costs, such as losses in water quality, were experienced locally. Explicitly linking the ES produced in one place to both local costs and distant benefits is a key step toward building tools to better understand the costs of meeting future demand and who will pay those costs. Although some telecouplings are increasingly studied, especially those related to agricultural production and demand (MacDonald et al. 2015) and deforestation (DeFries et al. 2010), models and tools typically do not address the sourcing of distant ES—and the associated nonnatural capital inputs (infrastructure development, finances, and technology) that facilitate this—unless the model is specially built to address questions of telcouplings (Güneralp et al. 2013). The

implications for our ability to understand the true costs of producing ES include an inability to link benefits to cost, and to determine who pays the cost of ES production to meet a particular demand.

Incorporating both ecological and social drivers of ES provision, clearly defining the impact of using technology to substitute for or enhance natural capital in the provision of ES, and considering trade and telecoupling are some of the advances required to better model the role of nature in the resilient provision of ES. Some immediate next steps toward realizing these advances include: (a) Undertake research to quantify the role of nonnatural capital relative to that of natural capital and other ecological factors in the provision of ES. (b) Develop a deeper understanding of system-level feedback loops that influence the resilience of ES provision through joint empirical data collection and modeling. (c) Assess global connections between ES provision and demand to better understand the implications of telecoupling for who benefits from, and who pays for, the provision of ES.

When is the benefit of added complexity worth the cost?

Improving our ability to model ES is critical for improving ecosystem management, but simply adding complexity to existing tools is not always helpful. The addition of complexity can be costly (Schröter et al. 2015), making models harder to test and validate, less certain, more data demanding, harder to explain to end users, and harder to share within the academic community (Voinov et al. 2014). Indiscriminately adding complexity to ES decision-support tools could result in less clear information than simpler approaches if each additional model or parameter brings with it more uncertainty than explanatory power. Here, we have pointed out cases in which adding complexity may be required to make ES tools more useful, reliable, and predictive. The challenge is to identify when understanding space–time dynamics, explicitly linking providers and beneficiaries, and recognizing potential complements and substitutes play an important role in driving ES outcomes in a way that is relevant to decisions, and then incorporating this complexity into decision-support tools in a way that is accessible and clearly communicated.

Some of the advances we have identified—such as moving beyond LULC as a proxy, including multiple time steps, mapping beneficiaries, or expressing different forms of value—are low-hanging fruit that can be incorporated into current tools by changing parameters but not necessarily the model structure. Other advances, such as incorporating beneficiaries into ES decision-support tools, are more complex and may require a different model structure—in this case, one that includes a new feature: beneficiaries of ES provision. Some advances are not yet ready to be incorporated into tools at all; here, we might aim for conceptual rather than instrumental uses of knowledge (McKenzie et al. 2014), building understanding among decision-makers that feedbacks exist or for which components of the system they are most important rather than expecting to precisely predict the quantity of ES provided after perfectly accounting for feedbacks. The final frontier identified here, the interplay between different capitals in the provision of services and its effects on the resilience of service provision to stressors, requires deeper scientific understanding before incorporation into either instrumental decision-support or even into our conceptual understanding of service provision.

There is increasing consensus that to adequately represent social–ecological systems, we must embrace, not ignore, complexity (Topping et al. 2015), and different approaches to modeling may be warranted. Over the last decade, computational modeling of agent-based complex systems has matured (Grimm and Berger 2016), and such approaches have typically succeeded through replicating existing models rather than starting from scratch (Thiele and Grimm 2015).

The question of how useful off-the-shelf or one-size-fits-all tools can really be to decision-makers remains open. Our current challenges demand solutions that can match the pace and scale of environmental change today, but creating useful models or tools requires long-term collaboration by teams that combine different sets of academic expertise with a variety of types of local policy and practical knowledge (Clark et al. 1979, Akçakaya et al. 2016). This does not necessarily mean that models co-produced by scientists and decision-makers cannot successfully transition to more generalized tools. In fact, such a combination of different knowledge, perspectives, and worldviews typically results in better models, more accessible tools, and ultimately, information that is considered more legitimate by decision-makers (Reed et al. 2013, Rosenthal et al. 2015). The co-production of models and tools is not without significant challenges, including balancing differing perspectives on what the important problems are, integrating different types of knowledge and conflicting methodologies, and avoiding relying so much on detailed local knowledge that the model is irrelevant in other contexts (Lang et al. 2012). However, when done well, this process can help scientists and practitioners jointly define socially relevant questions, enhance rather than duplicate work, reduce unintended consequences of research, and accelerate implementation of research results into practice (Davies et al. 2015).

Conclusions

Decision-makers around the world are looking to the ES framework to help make better decisions about the environment. First-generation ES decision-support tools have made substantial progress advancing scientific understanding of when, where, and how nature matters for human well-being but are still unable to fully answer many of the complex questions decision-makers are facing. Although we highlight three different frontiers where we see opportunities to improve current tools, it is important to recognize that these frontiers do not stand alone but are in fact highly interrelated. Advances in one frontier will likely help advance

others, and the most valuable insights gained from ES tools may happen at the intersections of these frontiers. For example, better incorporating other capitals into ES models may also aid in quantifying beneficiaries' demand for ES and where they are produced in space. Working to advance these three frontiers will not only lead to tools that better meet the needs of diverse decision-makers but may also lead to new insights and novel approaches for the management of ES and complex social–ecological systems.

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