

EPA Public Access

Author manuscript

Integr Environ Assess Manag. Author manuscript; available in PMC 2018 August 13.

About author manuscripts

Submit a manuscript

Published in final edited form as:

Integr Environ Assess Manag. 2017 January ; 13(1): 52-61. doi:10.1002/ieam.1842.

Using Ecological Product Functions to Link Ecological Processes to Ecosystem Services

Randall JF Bruins, Timothy J Canfield, Clifford Duke, Larry Kapustka, Amanda M Nahlik, and Ralf B Schäfer

¹US Environmental Protection Agency, National Exposure Research Laboratory, Ecological Exposure Research Division Cincinnati, Ohio

²US Environmental Protection Agency, National Risk Management Research Laboratory, Ground Water and Ecosystems Restoration Division Ada, Oklahoma

³Ecological Society of America Washington, DC, USA

⁴LK Consultancy Turner Valley, Alberta, Canada

⁵Kenyon College, Department of Biology Gambier, Ohio, USA, on detail with cooperative status at US Environmental Protection Agency, Western Ecology Division Corvallis, Oregon

⁶Quantitative Landscape Ecology, Institute for Environmental Sciences, University Koblenz-Landau Landau, Germany

Abstract

Ecological production functions (EPFs) link ecosystems, stressors, and management actions to ecosystem services (ES) production. Although EPFs are acknowledged as being essential to improve environmental management, their use in ecological risk assessment has received relatively little attention. Ecological production functions may be defined as usable expressions (i.e., models) of the processes by which ecosystems produce ES, often including external influences on those processes. We identify key attributes of EPFs and discuss both actual and idealized examples of their use to inform decision making. Whenever possible, EPFs should estimate final, rather than intermediate, ES. Although various types of EPFs have been developed, we suggest that EPFs are more useful for decision making if they quantify ES outcomes, respond to ecosystem condition, respond to stressor levels or management scenarios, reflect ecological complexity, rely on data with broad coverage, have performed well previously, are practical to use, and are open and transparent. In an example using pesticides, we illustrate how EPFs with these attributes could enable the inclusion of ES in ecological risk assessment. The biggest challenges to ES inclusion are limited data sets that are easily adapted for use in modeling EPFs and generally poor

Disclaimer

The views expressed in this article are those of the authors and do not necessarily reflect the views or policies of the US Environmental Protection Agency. Mention of trade names or commercial products does not constitute USEPA endorsement or recommendation for use. The peer review for this article was managed by the Editorial Board without the involvement of R Bruins and L Kapustka.

This is 1 of 4 papers generated from the SETAC Pellston Workshop "Ecosystem Services, Environmental Stressors and Decision-Making," organized in 2014 by the Society of Environmental Toxicology and Chemistry and the Ecological Society of America. The main workshop objective was to develop consensus about, and practical guidance for, the application of the ecosystem services concept to environmental decision making as part of a movement towards environmental sustainability.

understanding of linkages among ecological components and the processes that ultimately deliver the ES. We conclude by advocating for the incorporation into EPFs of added ecological complexity and greater ability to represent the trade-offs among ES.

Keywords

Ecological model; Decision making; Stressors; Final ecosystem services; Pesticides

INTRODUCTION

Ecosystem services (ES) have been defined as "benefits people obtain from ecosystems" (MA 2005). The term "ecological production function" (EPF) describes the operational step used to estimate ES production by ecosystems (NRC 2004; Tallis and Polasky 2009). Development of EPFs requires blending of systems ecology and other environmental sciences with social sciences. More attention is needed to the changes in ecological modeling that ES estimation requires.

Although the term is relatively new, EPFs themselves are not. Mathematical models have long been used to enhance the management of ES, although those modeling efforts often had relatively narrow objectives (e.g., maximizing a timber or fishery harvest). With more recent recognition of ES as fundamental to myriad dimensions of human well-being (Daily 1997; MA 2005), the challenge for EPF development lies in the variety of services needing to be managed (e.g., from purified air and water to ecological places of aesthetic and spiritual value) and the ubiquity of the ecological assets that can provide them, for example, agricultural hedgerows (Morandin et al. 2014) and urban trees (USFS 2015).

In this context, EPFs become a tool for framing current knowledge and fostering new research by highlighting knowledge gaps. They link ecosystem structure and processes to ecosystem goods and services (NRC 2004; Daily and Matson 2008; Tallis and Polasky 2009). Wainger and Mazzotta (2011) state that "... EPFs translate ecological changes into outcomes that people use or value." Munns et al. (2015) define an EPF as "a description of the type, quantity, and interactions of natural features required to generate measurable ecological outputs" having "clear…relevance to human well-being." Thus, EPFs integrate ecological modeling and ES.

We define EPFs more operationally as usable expressions (i.e., models) of the processes by which ecosystems produce ES, often including external influences on those processes. We construe "usable expressions" to encompass cardinal (fully quantitative), ordinal (rating, ranking), and qualitative (yes–no, plus–minus) expressions. Even simple ordinal and qualitative models ("conceptual models" in McKenzie et al. 2014) can guide understanding of ES production. However, for rational decision making on technical grounds, quantitative models ("instrumental models" in McKenzie et al. 2014; models with "biophysical realism" in Seppelt et al. 2011) are preferable, and these may range from empirical to mechanistic (with most EPFs combining aspects of both), simple to complex, and static to dynamic. Our definition, based on the assumption that EPFs should be useful for decision making, also

recognizes the inclusion of external influences such as management actions on ecological processes as a common feature of EPFs.

Although the use of EPFs has grown, careful examination of their characteristics is needed, especially in relationship to the challenges of environmental management. Some well-known efforts to quantify biophysical production of ES at global scales (Costanza et al. 1997, 2014; de Groot et al. 2012) have used EPFs to produce snapshots of aggregate ES production, based on estimates of ecosystem extent at points in time. Extent-based models can be used to assess the impacts of ecosystem loss (Costanza et al. 2014), and conversely the benefits of loss prevention, but not the more nuanced impacts of contaminant reduction, ecological engineering (Mitsch and Jørgensen 2003), or enhanced land or wildlife management. Efforts to map ecological resources and the services they produce (Egoh et al. 2012; Maes et al. 2012) often have the same limitations. Reviews of computational tools for ES assessment often focus on the broader analytic context, for example, the bundling of multiple EPFs to create decision-support systems (DSSs) (Bagstad et al. 2013; Peh et al. 2013), the direct linkage of DSSs to data sources, and the integration of ecological and socioeconomic dynamics for policy assessment (Turner et al. 2016). Although critically important, such reviews do not necessarily speak to the characteristics of EPFs not yet included in these systems, or to the potential for application of EPFs to such problems as the risk assessment of chemicals, which are still outside the typical scope of ES assessment (Maltby 2013; Munns et al. this issue).

Based on an evaluation of the EPF literature, the present article puts forward a list of 9 attributes that address EPF utility, with examples of EPFs exhibiting each characteristic. We then discuss the role of EPFs in promoting greater use of ES assessment in decision making, using risk assessment of pesticides as an example. We conclude with some remaining challenges that affect the use and incorporation of ES assessments into decision making.

DESIRED ATTRIBUTES OF ECOLOGICAL PRODUCTION FUNCTIONS

What constitute the desired attributes (DA) of EPFs? Several commenters have offered criteria that, although varying in scope and purpose, bear some relevance to the question of EPF attributes. These include critical questions for reviewing ES assessments studies at the regional scale (Seppelt et al. 2011), a set of criteria for improving the use of ES quantification methods in decision making (Villa et al. 2014), an itemization of challenges and opportunities for ecologists in improving ES management (Birkhofer et al. 2015), and criteria for selection of tools to estimate forest ES gains from restoration (Christin et al. 2016). Even when criteria are not itemized they can sometimes be inferred, as we have done from ES assessment tool reviews by Vigerstol and Aukema (2011) and Turner et al. (2016). Based on analysis of these studies (see Supplemental Data 1) and our own review of EPF literature, we identify 9 DA that determine the utility and relevance of EPFs for decision making (see Text Box 1). In this section we discuss these attributes and illustrate them with examples (also see a new library of EPFs, the EcoService Models Library, described in Supplemental Data 2 and available online (USEPA 2015), which contains further examples).

Text Box 1

Desired attributes (DA) of ecological production functions (EPFs)

DA1 Estimate indicators of final ecosystem services (ES): Understanding of intermediate services is useful, but EPFs that estimate final services (i.e., those directly meaningful to human beneficiaries) are most valuable to decision makers.

DA2 Quantify ES outcomes: EPFs that yield qualitative outcomes are sometimes useful for scoping and mapping, but quantification is needed for the analysis of ES trade-offs.

DA3 Respond to ecosystem condition: Because delivery of ES may vary with ecosystem condition, EPFs should not rely on land-use and land-cover (LULC) classification alone.

DA4 Respond to stressor levels or potential management scenarios: EPFs should include variables necessary for evaluating stressor impacts and predicting the outcome of management scenarios.

DA5 Appropriately reflect ecological complexity: EPFs must reflect critical complexities (e.g., nonlinearities and feedbacks affecting ES provision) while remaining simple enough to be understandable.

DA6 Rely on data with broad coverage: EPFs must be able to perform using "typical" data, that is, those available for most geographic areas.

DA7 Are shown to perform well: Because EPFs are used to evaluate hypothetical scenarios, it is important to consider the similarity of situations in which their performance has been evaluated to those facing the decision maker.

DA8 Are practical to use: EPFs should run on conventional personal computers, produce usable results with modest data input, and be usable by people other than trained modelers.

DA9 Are open and transparent: EPFs should be thoroughly documented and codes should be publicly available, although well-documented proprietary models may be useful in some situations.

Estimate indicators of final ecosystem services

"Final ecosystem services" (final ES) are the biophysical entities (e.g., potable water or a visually diverse natural viewscape) that are directly meaningful to or used by human beneficiaries (Boyd and Banzhaf 2007; Nahlik et al. 2012). By contrast, ecosystem processes, such as contaminant sequestration by aquatic biota or maintenance of ecological diversity (i.e., most of those referred to as "supporting" or "regulating services" in the Millennium Ecosystem Assessment [MA 2005]), are "intermediate services" in our conceptual model of ES and human well-being (Figure 1a). Effective understanding of intermediate services usually is necessary for management. However, because final ES are directly used by beneficiaries, they are most readily connected to human well-being, and therefore best serve the needs of decision makers. The types and qualities of ecological entities that can be considered final services vary widely, being both environment- and

beneficiary-specific (Landers and Nahlik 2013). Examples of estimating final ES include water that meets specific quality levels (as done by many water quality models), populations or distributions of particular species (e.g., using HexSim; Huber et al. 2014), and viewscapes that include desirable features (e.g., using ARIES; Bagstad et al. 2014); a counterexample would be the estimation of pollutant removal rate by wetlands, which may be an intermediate to many kinds of final ES whose delivery would require additional models to estimate.

Quantify ecosystem service outcomes

Qualitative descriptions of ES may suffice for some decisions; they may foster understanding and reflect values and beliefs (McKenzie et al. 2014). For example, the Corporate Ecosystem Services Review process (Hanson et al. 2012) provides a spreadsheet tool that encourages businesses to evaluate each aspect of their corporate value chain against a checklist of ES. The users consider corporate impacts or dependencies upon each service and judge each impact to be positive, negative, or both. The resulting qualitative profile may inform corporate sustainability strategy and identify priorities for quantitative analysis.

Similarly, semiquantitative ES mapping procedures being used in Europe and the United States often develop ad hoc, multimetric indices that combine diverse types of data through simple weighted summation, resulting in ordinal ratings (see Supplemental Data 3 for further discussion of ES mapping in Europe). This limitation applies especially to cultural ES that require both biophysical data and sociometric and psychological constructs to characterize the EPFs. Casado-Arzuaga et al. (2013) combined land-use and land-cover (LULC) and landscape topography with data from protected natural areas and recreational sites (e.g., cycling paths, climbing sites) to construct relative indices of landscape aesthetic quality and recreation provision, respectively, for the Bilbao metropolitan greenbelt in northern Spain. The US Environmental Protection Agency (USEPA 2013) EnviroAtlas, a user-driven geospatial data and tools system, enables the scoring of watershed polygons in the conterminous United States against each of 7 broad categories of ES, relying on a simple arithmetic combination of indexed data layers judged to contribute to each service category.

It is important to emphasize that many applications of ES require quantification, particularly in the context of rational decision making on technical grounds (McKenzie et al. 2014). Incorporating ES into payment or trading schemes, national accounts, resource damage assessments, and decision analyses all depends on reliable, and in some cases verifiable, quantification (e.g., Daily et al. 2009; Scarlett and Boyd 2011).

Respond to ecosystem condition

Whereas some EPFs rely on LULC classification and other static, land-surface information (such as soil maps and elevation) as driving variables, others include variables that are more descriptive of ecosystem processes. For example, in a mapping of several different ES for European Union countries, Haines-Young et al. (2012) based EPFs for habitat diversity and recreation on LULC class without regard to any measurement of ecological condition, whereas their EPFs for crop-based production and wildlife-based products incorporated MODerate resolution Imaging Spectroradiometer (MODIS) satellite-observed actual net

primary production. The inclusion of measured condition variables can improve EPF accuracy. Lavorel et al. (2011) demonstrated that empirical models that include measured abiotic factors or vegetation traits predicted ecosystem properties and services better than did land-use–alone models. Inclusion of condition and process measures may be even more important for flexible application because models reflecting LULC alone are not useful for assessing impacts of decisions (such as pesticide registration, management of invasive species, or adaptation to climate change) that could alter ecosystem functioning without affecting LULC classification.

Respond to stressor levels or potential management scenarios

Models to manage ES must contain variables that can reflect the influence of management decisions. Stressor variables should be incorporated, as should variables related to potential management actions that moderate stressor effects on ES. A model is more likely to represent the available suite of management actions if its original development was guided by management-related objectives. In general, EPFs should allow decision makers to predict the outcome of different management actions and scenarios.

Recent enhancements of the terrestrial ecological components of USEPA's Community Multiscale Air Quality Model (CMAQ) enable it to show air-quality response not only to traditional regulatory emission controls but also to changes in vegetation type and spatial pattern, enabling evaluation of ecosystem management approaches for improving air-related ES (Cooter et al. 2013). Terrestrial and aquatic models of contaminant fate, transport, and impact processes satisfy this attribute and can be combined with ecological models having variables that correspond to a final ES. Endpoints modeled in relation to US regulatory decision making have included Hg concentrations in edible tissue of recreationally or commercially important fish associated with emissions from coal-fired power-generating facilities (USEPA 2005; Knightes et al. 2009) and population levels of recreationally or commercially important fish and shellfish in relationship to 1) dissolved O₂levels (USEPA 2003) or 2) larval fish impingement and entrainment by cooling-water intakes for power generation facilities (USEPA 2006, 2014b).

Appropriately reflect ecological complexity

Ecological systems are complex and heterogeneous; the ecological processes that produce ES occur across markedly different scales of space and time having different rates and controlling feedbacks (Kapustka 2008; Gamfeldt et al. 2008; Johnson and Turner 2010). Ecological production functions must simplify this complexity enough to make modeling both tractable for modelers (from the standpoints of data availability and computational efficiency) and understandable to decision makers, without ignoring elements of complexity that alter ES delivery (Bradford et al. 2014). The most useful models incorporate the abovementioned rate functions and feedback loops for suites of linked services and run iteratively, given that linear extrapolation is incapable of capturing ecological complexity (Müller et al. 2011). For example, soil C, soil stability, crop growth, and clean water provision services associated with agricultural conservation practices can be jointly estimated in a dynamic simulation system such as the Soil and Water Assessment Tool with the Agricultural Policy/Environmental eXtender (SWAT/APEX; Gassman et al. 2010).

However, most EPFs focus on individual (or a few similar) services, and those DSSs that do evaluate multiple ES usually do so by linking multiple EPF modules to a common framework, without intermodule interactions.

Even without fully dynamic interaction, the use of multiple linked EPFs can illustrate tradeoff complexity that arises from differential ES responses across management scenarios. System feedback that occurs by way of human response trajectories also can be simulated using the modeling system Evoland 3.5, in which ES levels at time *t* influenced land-use decisions, and therefore all other services at time t + 1 (Guzy et al. 2008). McKane et al. (2014) plan to demonstrate the usefulness of an Evoland successor called ENVISION by linking models of intermediate services (including retention and transformation of nutrients, distribution and abundance of wildlife populations, and waterborne disease regulation) to the provision of final ES (such as clean water for residential beneficiaries, timber for businesses, and fish for recreationalists).

Rely on data with broad coverage

Model dynamism and the inclusion of variables on ecological condition and stressors can render EPFs more useful for decision making. However, EPF realism often competes with spatial extent. Unless decision making occurs in areas that are already data rich, or where new data can be acquired easily, EPFs have to perform using data of less than ideal resolution and quality. Some types of remotely sensed data and derived geospatial data (e.g., LULC, elevation, vegetation indices) have nearly complete global coverage. Others, based on fixed monitoring stations (e.g., meteorology, stream discharge), are spatially discontinuous. Last, those relying on field surveys are more limited in coverage. Often, EPFs developed for broad-scale mapping rely on data with global coverage (see the discussion of Haines-Young et al. 2012 in "DA3, Respond to ecosystem condition"), though the results may be of limited usefulness.

An approach sometimes used to extend the predictive value of broad-scale data begins with application of a complex model within a limited area that has higher quality data. Empirical relationships are next developed between the modeled outputs and the more widely available data, and finally the resulting empirical estimates are applied with complete spatial coverage. For example, USEPA's Coral Reef Ecosystem Services Project (Yee et al. 2011) used St. Croix, US Virgin Islands, as an example location for EPF development and ES estimation. Data with complete coverage for the study area were limited to nearshore bathymetry and maps of benthic habitat. Information on coral ecosystems condition was also available, but only in the form of point survey data. By developing empirical relationships among bathymetry, habitat, and coral condition parameters, the team was able to generate the needed ecological condition values to map relative levels of a number of ES (e.g., divesite favorability; relative density, presence, or value of marketable species or materials; biomass of key commercial fish species) over the entire study area. Similarly, Nedkov and Burkhard (2012) first calibrated a hydrologic model (KINEROS2) in a limited area having gauged hydrology (River Ravna watershed, Bulgaria); next they developed empirical relationships to land cover and soil type, allowing them to estimate hydrologic responses

over a much larger area (Municipality of Etropole, Bulgaria); and finally they mapped relative land-parcel contribution to flood moderation.

A typical drawback of this kind of statistical interpolation approach, however, is the reduction of the model's dynamic character and its ability to model ES interactions or the influences of environmental change. For practical reasons, therefore, EPF developers must make compromises among dynamism, scale optimization, and data requirements (see Villa et al. 2014).

Are shown to perform well

Ecological production functions take a variety of computational forms and use data of different types and qualities obtained from a variety of sources. Therefore, the error associated with model estimates does not behave predictably, and characterization of model performance may be challenging. Model performance evaluation methods generally involve comparisons of model predictions against observational data that either were not used in model development or were partitioned to allow model performance testing (Bennett et al. 2013).

In decision-making situations, however, models often are used to address hypothetical scenarios (e.g., projected future change, management alternatives) for which performance cannot be evaluated until after the fact. Therefore, the number of previous situations in which performance has been evaluated and the similarity of these situations to that facing the decision maker could be considered as proxies of performance. Aspects of similarity include modeling objective and ecological context, and because these are multidimensional, expert judgment of model suitability ultimately is required.

In a study of the future vulnerability of Dungeness crab and Pacific oyster harvests in Hood Canal, Washington, USA, Toft et al. (2014) investigated the contribution of watershed ES to marine water quality using the InVEST Water Yield and Scarcity and the InVEST Nutrient Retention models, respectively. Before examining future scenarios of land use and climate change, the modelers used local gauge measurements to calibrate current-state water yield and N loading estimates, and they characterized model sensitivity by varying several inputs over the range of observations. In another example, Busing et al. (2007) used the FORCLIM model to compare simulated and field-measured forest (species and stand) growth response under varying management and climatic regimes in 8 ecoregions in Oregon, USA, before simulating future forest response to climate-change scenarios.

Are practical to use

To ensure decision relevance, the objectives and requirements of the end-user community should be a primary focus during EPF development. Ideally, potential end users and all affected stakeholder groups would be consulted in model development, a process called "Participatory Modeling" (Voinov 2008). Specifically, the model should have a user-friendly interface and accessible user guide and documentation, and all default initial values of variables and parameters that pertain to stakeholder interests should be accessible and modifiable. User-friendliness also requires easy options for input and output of data and information specific to the user's objectives. The system preferably allows the user to select

from multiple levels of complexity. For example, the model should provide a novice user with screening-level information that is based on simple operations and minimal data requirements, but also should allow an advanced user to add complexity and representations of uncertainty. Finally, model development should focus on efficiency to minimize hardware requirements (i.e., models should be run easily on standard notebooks computer).

An example of a relatively user-friendly software is AQUATOX (USEPA 2014a). AQUATOX predicts the fate and effects of pollutants in aquatic ecosystems and includes several endpoints that are relevant to decision making in an ES context (Park et al. 2008). The model is based on EPFs that can be modified and parameterized according to user needs. In addition, it allows adjustment of the desired level of complexity and features data input and output options in commonly used file formats. A limitation is that Aquatox is currently restricted to the Microsoft Windows operating system. Aquatox is relatively easy to learn, and a wide range of documentation, user guides, and teaching materials is freely accessible. Finally, the model has been used in several scientific studies (Rashleigh et al. 2009; McKnight et al. 2012), allowing the user to build on previous experience.

Are open and transparent

A large array of models is needed to accommodate broad differences in ecosystems, spatiotemporal scales, and stakeholders, and to address urgent global needs of decision makers for ES assessment and management (EC 2011). Developing these models de novo is not feasible for most situations. Although existing models largely have been developed for different purposes and may not meet the management requirements listed here, they often contain variables that relate to the ES approach (see Supplemental Data 2). Therefore, we suggest providing the source code of models so they can be adapted to different purposes, scales, and contexts. Doing so requires thorough documentation (e.g., Grimm et al. 2006, 2010) and code commenting. The type of documentation needed to allow for model evaluation has been published by the European Food and Safety Agency Panel on Plant Protection Products and their Residues (EFSA 2014). Although this documentation is targeted on the risk assessment of plant protection products, the approach is applicable to all model development and evaluation.

Importantly, the programming should follow best practices, including code review and adapting code styles (see, e.g., Anonymous 2015a) to make the model and its code readily understandable. Ideally, the modeling approach would be fully reproducible (Stodden 2009; Donoho 2010) to the extent allowed by copyright restrictions. An example of a project with open code and full transparency is the R computing language (Anonymous 2015b), for which contributions have been growing exponentially for years. R has become the de facto standard for data analysis in several disciplines. Regarding ecological modeling, NetLogo is an example of a free, open-source software for agent-based modeling, which has attracted a wide user and developer community (Wilenski 2015). However, more complex models require efficient algorithms written in programming languages such as C or C++.

Though open-code programs have many advantages, commercially available software modeling programs are useful as well, and sometimes provide a more user-friendly interface, but lack automation capabilities for power users. For example, RAMAS (Applied

Biomathematics 2015) provides a number of products ranging from relatively simple singlespecies population models to landscape models that evaluate changes in habitat quality for target species and multiple species assessments. The programs are designed to be user friendly and flexible so they are widely applicable. Importantly, user manuals and documentation provide considerable transparency, offering users the ability to tailor their assessments to the particular features of their project.

AN EXAMPLE APPLICATION OF EPF DESIRED ATTRIBUTES: RISK ASSESSMENT OF PESTICIDES

In the previous subsection, we suggested that the risk assessment of chemicals is still peripheral to the typical scope of ES assessment. Although many studies modeled effects on species that are important for ES provisioning or on intermediate services, quantitative links to final ES are rare (Forbes and Galic 2016). Nevertheless, 2 recent studies (Sabatier et al. 2013; Johnston et al. 2015) used EPFs to assess the effects of pesticides on ES and met several but not all of our desired EPF criteria (see Table S1–3 in Supplemental Data 1). One major limitation of both studies is limited scope: Too few ES were considered to allow for a complete assessment of chemical risks on agroecosystems, though such studies are valuable starting points given the complexity of the matter at hand. Although we agree with Forbes and Galic (2016) that chemical risk assessment could deal with high ecological complexity by limiting its focus to selected species and ES, we describe here a conceptual model that highlights the challenges and aspects to consider when incorporating EPFs into chemical risk assessments. Our conceptual agroecosystem model considers the potential for impacts of a generic pesticide on ES in both the in-crop and off-crop areas (Figure 1b). The diagram is highly simplified; the intended pathways whereby management options improve crop yield are depicted by thick arrows whereas other (often unintended) effects and feedback interactions are represented with brackets and thin arrows.

In-crop effects

Pesticide application aims to reduce the presence of target organisms, allowing the crop to allocate more energy into production and thus increase yield. However, the pesticide can reduce or eradicate one or several nontarget organisms, such as earthworms or microbes, that contribute to the ES of crop production (Power 2010); this impact was addressed in the EPFs employed in the studies of Sabatier et al. (2013) and Johnston et al. (2015), respectively. Other services such as soil formation (Dittbrenner et al. 2010), C cycling (van Wensem et al. 1991), and pollination (Goulson 2014), also required for crop production, can be spatially or temporally decoupled, reducing incentives for socially beneficial management (Power 2010). Indeed, this decoupling is largely not considered in the 2 models just cited. Pesticides also may affect food quality, through the effects of C and nutrient cycling on crop nutritional value (Bara ski et al. 2014) or through the introduction of pesticide residues.

Off-crop effects

Off-crop effects of pesticide use or other agricultural management practices generally are unintended and can occur in a variety of ecological media, for example, aquatic (Schäfer et al. 2011), terrestrial (Jansch et al. 2006), or atmospheric (Mineau and Whiteside 2013); at a

variety of trophic levels, for example, primary producers such as plants and algae, primary consumers such as invertebrate herbivores, or secondary consumers such as carnivorous invertebrates, fish, and birds, and microbes; and at multiple temporal and spatial scales. The extremely generic rendering of the Off Crop box (Figure 1b) highlights this variety.

Development of EPFs for in-crop and off-crop effects

Development of EPFs for pesticide ecological risk assessment should be informed by the DA outlined above (see Text Box 1). Each agroecosystem landscape is a complex socialecological system in which the ecology influences society and the society influences the ecology (see Biggs et al. 2015). The myriad of potential ES (i.e., each *n* in Figure 1b) must be reduced to a manageable number, based on stakeholder input. Stakeholders will likely identify final (i.e., directly enjoyed) ES, such as impacts on desirable nontarget populations, rather than intermediates such as nutrient cycling (DA1). Quantitative estimates of change (DA2) in these final ES would be needed to fully inform trade-off analysis of pesticide use. The most useful EPFs would be capable of modeling variations in pesticide application scenarios (DA4) and possibly could also account for variations in the specific conditions (such as soil type or the presence of specific nontarget organisms) of surrounding land uses, and not depend on LULC class data alone (D3). Although model simplicity is beneficial (DA8), representation of key ecological interactions (e.g., predator-prey, biomagnification) may be essential (DA5). Although their development may require specialized data sets, when deployed, pesticide EPFs would have to function adequately using widely mapped or remotely sensed data (DA6) for inputs such as meteorology, soils, vegetation, hydrology, and species distributions. Underlying details of model functioning would need to be trusted (DA8) and understood by technical representatives of all stakeholder communities (DA9).

CONCLUSIONS AND RECOMMENDATIONS

Though EPFs are receiving broader attention, relatively few have been applied in an ecological risk assessment context. The National Research Council (NRC 2013) concluded that using ES with respect to the 2010 Deep Water Horizon oil spill in the Gulf of Mexico could expand the spectrum of restoration actions not currently considered under existing assessment procedures. However, they identified as major impediments 1) the paucity of baseline data against which to evaluate ES impacts and 2) the lack of models capable of characterizing the extent of ES change. Others have offered possible reasons for the underuse of EPFs, including a lack of generalizations about ecosystems in terms of relationships among stressors, organisms, and processes on the intermediate scale (Lawton 1999; Galic et al. 2012). Greater attention to our list of DA of EPFs, including scalability, dynamism, and interaction of ES, could do much to increase the use of EPFs.

The perceived complexity of ecosystems and ES seems to be a barrier to wider EPF use by risk assessors. Dedicated efforts to construct agreed conceptual models could help overcome this obstacle by enhancing access to existing ecological knowledge and by focusing research on knowledge gaps regarding basic processes and their relationships to ES. Advancing the use of ES assessment in environmental management requires making existing ecological science more accessible and actionable. We advocate for more sophisticated EPFs than are

sometimes used, avoiding when possible the simplistic summing and scoring of land-cover types. Yet we also support identification of boundaries for the acceptable use of simplified EPFs that are easier to explain to stakeholders and sufficient for decision making, especially at local levels of governance.

Finally, for practical reasons, we suggest that certitudes (those which we are confident we know) along with uncertainties and trade-offs of ES should be better explained to affected stakeholders. Communication may be more effective by using final ES as endpoints. Clearer explanation of trade-offs also requires modeling and communication tools that capture dynamic ecological relationships. And clearer explanation also requires better understanding of the limitations of extrapolating model estimates to different spatial or temporal scales. It is critical that the ES community achieve substantive advances in the emerging transdisciplinary efforts that have been called for in recent years. The ES focus is, after all, much broader than ecology; it extends across all sectors of society and is strongly value driven.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

The authors would like to thank all the participants of the 2014 Pellston Workshop and the anonymous reviewers for their comments and insight on idea development and earlier drafts of this manuscript. The lead author also acknowledges the assistance of M Errend, M Gray, G Lomnicky, and J Wilson with reviews of the EPF literature.

References

- Google styleguide [Internet]. 2015a. [cited 2015 May 10]. Available from: https:// code.google.com/p/google-styleguide/
- 2. What is R? [Internet]. 2015b. [cited 2015 May 10]. Available from: www.r-project.org
- Applied Biomathematics. Ramas1 Software and Services for Risk Analysis [Internet]. 2015. [cited 2015 May 10]. Available from http://www.ramas.com/ramas.htm
- 4. Bagstad KJ, Semmens DJ, Waage S, Winthrop R. A comparative assessment of decision-support tools for ecosystem services quantification and valuation. Ecosyst Serv. 2013; 5:27–39.
- 5. Bagstad KJ, Villa F, Batker D, Harrison-Cox J, Voigt B, Johnson GW. From theoretical to actual ecosystem services: Mapping beneficiaries and spatial flows in ecosystem service assessments. Ecol Soc. 2014; 19:64–77.
- Baranski M, Srednicka-Tober D, Volakakis N, Seal C, Sanderson R, Stewart GB, Benbrook C, Biavati B, Markellou E, Giotis C, et al. Higher antioxidant and lower cadmium concentrations and lower incidence of pesticide residues in organically grown crops: A systematic literature review and meta-analyses. Br J Nutr. 2014; 112:794–811. [PubMed: 24968103]
- Bennett ND, Croke BFW, Guariso G, Guillaume JHA, Hamilton SH, Jakeman AJ, Marsili-Libelli S, Newham LTH, Norton JP, Perrin C, et al. Characterising performance of environmental models. Environ Modell Softw. 2013; 40:1–20.
- 8. Biggs R, Schlüter M, Schoon ML. Principles for building resilience: Sustaining ecosystem services in social-ecological systems. Cambridge (UK): Cambridge Univ Pr; 2015. 290
- Birkhofer K, Diehl E, Andersson J, Ekroos J, Früh-Müller A, Machnikowski F, Mader VL, Nilsson L, Sasaki K, Rundlöf M, et al. Ecosystem services Current challenges and opportunities for ecological research. Front Ecol Evol. 2015; :2.doi: 10.3389/fevo.2014.00087

- Boyd JW, Banzhaf S. What are ecosystem services? The need for standardized environmental accounting units. Ecol Econ. 2007; 63:616–626.
- 11. Bradford MA, Wood SA, Bardgett RD, Black HIJ, Bonkowski M, Eggers T, Grayston SJ, Kandeler E, Manning P, Setälä H, et al. Discontinuity in the responses of ecosystemprocesses and multifunctionality to altered soil community composition. Proc Natl Acad Sci USA. 2014; 111:14478–14483. [PubMed: 25246582]
- Busing RT, Solomon AM, McKane RB, Burdick CA. Forest dynamics in Oregon landscapes: Evaluation and application of an individual-based model. Ecol Appl. 2007; 17:1967–1981. [PubMed: 17974335]
- Casado-Arzuaga I, Onaindia M, Madariaga I, Verburg PH. Mapping recreation and aesthetic value of ecosystems in the Bilbao Metropolitan Greenbelt (northern Spain) to support landscape planning. Landsc Ecol. 2013; 29:1393–1405.
- 14. Christin ZL, Bagstad KJ, Verdone MA. A decision framework for identifying models to estimate forest ecosystem services gains from restoration. Forest Ecosyst. 2016; 3:1–12.
- 15. Cooter EJ, Rea A, Bruins R, Schwede R, Dennis R. The role of the atmosphere in the provision of ecosystem services. Sci Total Environ. 2013; 448:197–208. [PubMed: 22921509]
- Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, et al. The value of the world's ecosystem services and natural capital. Nature. 1997; 387:253–260.
- Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, Kubiszewski I, Farber S, Turner RK. Changes in the global value of ecosystem services. Global Environ Chang. 2014; 26:152–158.
- Daily GC. Nature's services: Societal dependence on natural ecosystems. Washington (DC): Island Pr; 1997. 412
- Daily GC, Matson PA. Ecosystem services: From theory to implementation. Proc Natl Acad Sci USA. 2008; 105:9455–9456. [PubMed: 18621697]
- Daily GC, Polasky S, Goldstein J, Kareiva PM, Mooney HA, Pejchar L, Ricketts TH, Salzman J, Shallenberger R. Ecosystem services in decision making: Time to deliver. Front Ecol Environ. 2009; 7:21–28.
- 21. de Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M, Crossman N, Ghermandi A, Hein L, et al. Global estimates of the value of ecosystems and their services in monetary units. Ecosyst Serv. 2012; 1:50–61.
- Dittbrenner N, Triebskorn R, Moser I, Capowiez Y. Physiological and behavioural effects of imidacloprid on two ecologically relevant earthworm species (Lumbricus terrestris and Aporrectodea caliginosa). Ecotoxicology. 2010; 19:1567–1573. [PubMed: 20821048]
- Donoho DL. An invitation to reproducible computational research. Biostatistics. 2010; 11:385– 388. [PubMed: 20538873]
- 24. [EC] European Commission. Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions: Our life insurance, our natural capital: An EU biodiversity strategy to 2020. Brussels (BE): EC.Report Nr COM; 2011. 244
- [EFSA] European Food and Safety Agency, Panel on Plant Protection Products and their Residues. Scientific opinion on good modelling practice in the context of mechanistic effect models for risk assessment of plant protection products. EFSA J. 2014; 12:3589–3581.
- 26. Egoh B, Drakou EG, Dunbar MB, Maes J, Willemen L. Indicators for mapping ecosystem services: A review. Luxembourg (LU): European Commission, Joint Research Centre, Institute for Environment and Sustainability; 2012.
- Forbes VE, Galic N. Next-generation ecological risk assessment: Predicting risk from molecular initiation to ecosystem service delivery. Environ Int. 2016; 91:215–219. [PubMed: 26985654]
- Galic N, Schmolke A, Forbes V, Baveco H, van den Brink PJ. The role of ecological models in linking ecological risk assessment to ecosystem services in agroecosystems. Sci Total Environ. 2012; 415:93–100. [PubMed: 21802704]
- 29. Gamfeldt L, Hillebrand H, Jonsson PR. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. Ecology. 2008; 89:1223–1231. [PubMed: 18543617]

- 30. Gassman PW, Williams JR, Wang X, Saleh A, Osei E, Hauck LM, Izaurralde RC, Flowers JD. The Agricultural Policy/Environmental eXtender (APEX) model: An emerging tool for landscape and watershed environmental analyses. Trans Am Soc Agric Biol Eng. 2010; 53:711–740.
- Goulson D. An overview of the environmental risks posed by neonicotinoid insecticides. J Appl Ecol. 2014; 50:977–987.
- 32. Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz SK, Huse G. A standard protocol for describing individual-based and agent-based models. Ecol Model. 2006; 198:115–126.
- Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF. The ODD protocol: A review and first update. Ecol Model. 2010; 221:2760–2768.
- Guzy MR, Smith CL, Bolte JP, Hulse DW, Gregory SV. Policy research using agent-based modeling to assess future impacts of urban expansion into farmlands and forests. Ecol Soc. 2008; 13:1–37.
- 35. Haines-Young R, Potschin M, Kienast F. Indicators of ecosystem service potential at European scales: Mapping marginal changes and trade-offs. Ecol Indic. 2012; 21:39–53.
- 36. Hanson C, Ranganathan J, Iceland C, Finisdore J. The corporate ecosystem services review: Guidelines for identifying business risks and opportunities arising from ecosystem change. Version 2.0. Washington (DC): World Resources Institute; 2012. [cited 2016 Sept 16]. http://www.wri.org/ publication/corporate-ecosystem-services-review
- Huber PR, Greco SE, Schumaker NH, Hobbs J. A priori assessment of reintroduction strategies for a native ungulate: Using HexSim to guide release site selection. Landsc Ecol. 2014; 29:689–701.
- Jansch S, Frampton GK, Rombke J, Van den Brink PJ, Scott-Fordsmand JJ. Effects of pesticides on soil invertebrates in model ecosystem and field studies: A review and comparison with laboratory toxicity data. Environ Toxicol Chem. 2006; 25:2490–2501. [PubMed: 16986805]
- Johnson AR, Turner SJ. Relevance of temporal and spatial scales to ecological risk assessment. In: Kapustka LA, Landis WG, editorsEnvironmental risk assessment and management from a landscape perspective. New York (NY): J Wiley; 2010. 55–74.
- Johnston ASA, Sibly RM, Hodson ME, Alvarez T, Thorbek P. Effects of agricultural management practices on earthworm populations and crop yield: Validation and application of a mechanistic modelling approach. J Appl Ecol. 2015; 52:1334–1342.
- Kapustka L. Limitations of the current practices used to perform ecological risk assessment. Integr Environ Assess Manag. 2008; 4:290–298. [PubMed: 18324872]
- Knightes CD, Sunderland E, Barber MC, Johnston JM, Ambrose RB. Application of ecosystemscale fate and bioaccumulation models to predict fish mercury response times to changes in atmospheric deposition. Environ Toxicol Chem. 2009; 28:881–893. [PubMed: 19391686]
- Landers D, Nahlik A. Final ecosystem goods and services classification system (FEGS-CS). Washington (DC): US Environmental Protection Agency; 2013. EPA/600/R-13/ORD-004914
- Lavorel S, Grigulis K, Lamarque P, Colace M-P, Garden D, Girel J, Pellet G, Douzet R. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. J Ecol. 2011; 99:135–147.
- 45. Lawton JH. Are there general laws in ecology? Oikos. 1999; 84:177-192.
- 46. [MA] Millennium Ecosystem Assessment. Ecosystems and human wellbeing. In: Hassan R, Scholes RJ, Ash N, editorsMillennium ecosystem assessment. Vol 1, Current state and trends: Findings of the Condition and Trends Working Group. Washington (DC): Island Pr; 2005. 917
- 47. Maes J, Egoh B, Willemen L, Liquete C, Vihervaara P, Schägner JP, Grizzetti B, Drakou EG, Notte AL, Zulian G, et al. Mapping ecosystem services for policy support and decision making in the European Union. Ecosyst Serv. 2012; 1:31–39.
- Maltby L. Ecosystem services and the protection, restoration, and management of ecosystems exposed to chemical stressors. Environ Toxicol Chem. 2013; 32:974–983. [PubMed: 23589419]
- 49. McKane RB, Brookes A, Djang K, Russell M. A community-based decision support tool for flexible, interactive assessments that quantify tradeoffs in ecosystem goods and services for alternative decision scenarios in the Pacific Northwest. Corvallis (OR): US Environmental Protection Agency Office of Research and Development; 2014. 23

- McKenzie E, Posner S, Tillmann P, Bernhardt JR, Howard K, Rosenthal A. Understanding the use of ecosystem service knowledge in decision making: Lessons from international experiences of spatial planning. Environ Plann C. 2014; 32:320–340. DOI: 10.1068/c12292j
- McKnight US, Rasmussen JJ, Kronvang B, Bjerg PL, Binning PJ. Integrated assessment of the impact of chemical stressors on surface water ecosystems. Sci Total Environ. 2012; 427–428:319– 331.
- Mineau P, Whiteside M. Pesticide acute toxicity is a better correlate of US grassland bird declines than agricultural intensification. PLoS ONE. 2013; 8:e57457.doi: 10.1371/journal.pone.0057457 [PubMed: 23437392]
- 53. Mitsch WJ, Jørgensen SE. Ecological engineering: A field whose time has come. Ecol Eng. 2003; 20:363–377.
- Morandin LA, Long RF, Kremen C. Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. Agric Ecosyst Environ. 2014; 189:164–170.
- 55. Muller F, Breckling B, Jopp F, Reuter H. What are the general conditions under which ecological models can be applied?. In: Jopp F, Reuter H, Breckling B, editorsModelling complex ecological dynamics. Heidelberg (DE): Springer; 2011. 13–28.
- 56. Munns WR, Rae AW, Mazzotta MJ, Wainger LA, Saterson K. Toward a standard lexicon for ecosystem services. Integr Environ Assess Manag. 2015; 11:666–673. DOI: 10.1002/ieam.1631 [PubMed: 25689771]
- Munns WR, Poulsen V, Gala WR, Marshall SJ, Rea AW, Sorensen MT, von Stackelberg K. Ecosystem services in risk assessment and management. Integr Environ Assess Manag. 2017; 13(1):62–73. [PubMed: 27464004]
- Nahlik AM, Kentula ME, Fennessy MS, Landers DH. Where is the consensus? A proposed foundation for moving ecosystem service concepts into practice. Ecol Econ. 2012; 77:27–35.
- 59. Nedkov S, Burkhard B. Flood regulating ecosystem services Mapping supply and demand, in the Etropole municipality, Bulgaria. Ecol Indic. 2012; 21:67–79.
- 60. [NRC] National Research Council. Valuing ecosystem services: Toward better environmental decision–making. Washington (DC): National Academies; 2004.
- 61. [NRC] National Research Council. An ecosystem services approach to assessing the impacts of the Deepwater Horizon oil spill in the Gulf of Mexico. Washington (DC): National Academies; 2013.
- 62. Park RA, Clough JS, Wellman MC. AQUATOX: Modeling environmental fate and ecological effects in aquatic ecosystems. Ecol Model. 2008; 213:1–15.
- 63. Peh KSH, Balmford A, Bradbury RB, Brown C, Butchart SHM, Hughes FMR, Stattersfield A, Thomas DHL, Walpole M, Bayliss J, et al. TESSA: A toolkit for rapid assessment of ecosystem services at sites of biodiversity conservation importance. Ecosyst Serv. 2013; 5:51–57.
- Power AG. Ecosystem services and agriculture: Tradeoffs and synergies. Philos Trans R Soc B-Biol Sci. 2010; 365:2959–2971.
- 65. Rashleigh B, Barber MC, Walters DM. Foodweb modeling for polychlorinated biphenyls (PCBs) in the Twelvemile Creek Arm of Lake Hartwell, South Carolina, USA. Ecol Model. 2009; 220:254–264.
- Sabatier R, Meyer K, Wiegand K, Clough Y. Non-linear effects of pesticide application on biodiversity-driven ecosystem services and disservices in a cacao agroecosystem: A modeling study. Basic Appl Ecol. 2013; 14:115–125.
- 67. Scarlett L, Boyd J. Ecosystem services: Quantification, policy applications, and current federal capabilities. Washington (DC): Resources for the Future; 2011.
- 68. Schafer RB, van den Brink PJ, Liess M. Impacts of pesticides on freshwater ecosystems. In: Sanchez-Bayo F, van den Brink P, Mann RM, editorsEcological impacts of toxic chemicals. Bussum (NL): Bentham; 2011. 111–137.
- 69. Seppelt R, Dormann CF, Eppink FV, Lautenbach S, Schmidt S. A quantitative review of ecosystem service studies: Approaches, shortcomings and the road ahead. J Appl Ecol. 2011; 48:630–636.
- 70. Stodden V. Enabling reproducible research: Open licensing for scientific innovation. Int J Commun Law Policy. 2009:55.
- Tallis H, Polasky S. Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. Ann N Y Acad Sci. 2009; 1162:265–283. [PubMed: 19432652]

- 72. Toft JE, Burke JL, Carey MP, Kim CK, Marsik M, Sutherland DA, Arkema KK, Guerry AD, Levin PS, Minello TJ, et al. From mountains to sound: Modelling the sensitivity of Dungeness crab and Pacific oyster to land–sea interactions in Hood Canal, WA. ICES J Mar Sci. 2014; 71:725–738.
- 73. Turner KG, Anderson S, Gonzales-Chang M, Costanza R, Courville S, Dalgaard T, Dominati E, Kubiszewski I, Ogilvy S, Porfirio L, et al. A review of methods, data, and models to assess changes in the value of ecosystem services from land degradation and restoration. Ecol Model. 2016; 319:190–207.
- 74. [USEPA] US Environmental Protection Agency. Ambient water quality criteria for dissolved oxygen, water clarity and chlorophyll a for the Chesapeake Bay and its tidal tributaries. Washington (DC): USEPA Region III Chesapeake Bay Program Office; 2003. EPA 903-R-03-002. [cited 2016 Sept 16]. http://www.chesapeakebay.net/content/publications/cbp_13142.pdf
- 75. [USEPA] US Environmental Protection Agency. Regulatory impact analysis for the clean air mercury rule. Vol. Chapter 3. Research Triangle Park (NC): USEPA, Office of Air Quality Planning and Standards; 2005. Ecosystem scale modeling for mercury benefits analysis. EPA-452/ R-05-003.[cited 2016 Sept 16]. http://www.epa.gov/ttnecas1/regdata/RIAs/mercury_ria_final.pdf
- 76. [USEPA] US Environmental Protection Agency. Regional benefits analysis for the final Section 316(b) Phase III existing facilities rule. Washington (DC): USEPA, Office of Water; 2006. EPA-821-R-04-007. [cited 2016 Sept 16]. https://www.epa.gov/sites/production/files/2015-04/ documents/cooling-water_phase-3_regional-benefits_2006.pdf
- 77. [USEPA] US Environmental Protection Agency. EnviroAtlas [Internet]. 2013. [cited 2014 Nov 4]. http://enviroatlas.epa.gov/enviroatlas
- [USEPA] US Environmental Protection Agency. AQUATOX: Linking water quality and aquatic life [Internet]. 2014a. [cited 2015 May 10]. Available from https://www.epa.gov/exposure-assessmentmodels/aquatox
- 79. [USEPA] US Environmental Protection Agency. Benefits analysis for the final Section 316(b) existing facilities rule. Washington (DC): USEPA, Office of Water; 2014b. EPA-821-R-14-005
- [USEPA] US Environmental Protection Agency. EcoService Models Library, beta version [Internet]. 2015. [cited 2016 Aug 01]. Available from https://esml.epa.gov/epf_l/public/signup
- [USFS] US Forest Service. I-Tree: Tools for assessing and managing community forests [Internet]. 2015. [cited 2015 Dec 30]. https://www.itreetools.org/
- Van Wensem J, Akkerhuis G, Vanstraalen NM. Effects of the fungicide triphenyltin hydroxide on soil fauna mediated litter decomposition. Pestic Sci. 1991; 32:307–316.
- 83. Van Wensem J, Calow P, Dollacker A, Maltby L, Olander L, Tuvendal M, Van Houtven G. Identifying and assessing the application of ecosystem services approaches in environmental policies and decision making. Integr Environ Manag Assess. 2017; 13(1):41–51.
- Vigerstol KL, Aukema JE. A comparison of tools for modeling freshwater ecosystem services. J Environ Manage. 2011; 92:2403–2409. [PubMed: 21763063]
- Villa F, Bagstad KJ, Voigt B, Johnson GW, Portela R, Honzák M, Batker D. A methodology for adaptable and robust ecosystem services assessment. PLoS ONE. 2014; 9:e91001. [PubMed: 24625496]
- Voinov AA. Systems science and modeling for ecological economics. Amsterdam (NL): Elsevier; 2008.
- Wainger L, Mazzotta M. Realizing the potential of ecosystem services: A framework for relating ecological changes to economic benefits. Environ Manag. 2011; 48:710–733.
- Wilenski U. NetLogo [Internet]. 2015. [cited 2015 May 10]. Available from https:// ccl.northwestern.edu/netlogo/
- 89. Yee SH, Dittmar JH, Oliver LM. Comparison of methods for quantifying reef ecosystem services: A case study mapping services for St. Croix, USVI. In: Yee SH, Bradley P, Campbell DE, Carriger J, Principe P, Fisher WS, editorsMeasures and methods to quantify production of coral reef ecosystem services. Gulf Breeze (FL): USEPA; 2011. 145EcosystemServices Research Program Long-Term Goal 4, NHEERL, APG 57, APM 111

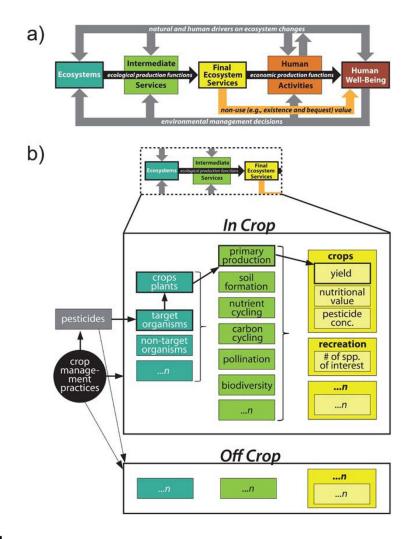


Figure 1.

Respective roles of ecological production and economic benefit functions in the enhancement of human well-being (from Van Wensem et al. this issue) (**a**) and detailed example of an agroecosystem, where the primary ecosystem service of interest is crop production or yield (**b**). The diagram is divided into in-crop and off-crop sections to differentiate between the intended (In Crop) and unintended (Off Crop) actions or effects. Thick arrows demonstrate the intended pathway of pesticide use (i.e., increased crop yield) and crop management, whereas thin lines indicate unintended consequences. For clarity, other connections are subsumed with brackets, and more complex feedback loops are not shown.