

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Valery Forbes Publications

Papers in the Biological Sciences

1-2012

The role of ecological models in linking ecological risk assessment to ecosystem services in agroecosystems

Nika Galic

Wageningen University, The Netherlands, nika.galic@wur.nl

Amelie Schmolke

UFZ, Helmholtz-Zentrum für Umweltforschung, Leipzig, Germany

Valery E. Forbes

University of Nebraska-Lincoln, veforbes@umn.edu

Hans Baveco

Wageningen University and Research Centre, The Netherlands

Paul van den Brink

Wageningen University

Follow this and additional works at: <https://digitalcommons.unl.edu/biosciforbes>



Part of the [Pharmacology, Toxicology and Environmental Health Commons](#)

Galic, Nika; Schmolke, Amelie; Forbes, Valery E.; Baveco, Hans; and van den Brink, Paul, "The role of ecological models in linking ecological risk assessment to ecosystem services in agroecosystems" (2012). *Valery Forbes Publications*. 36.

<https://digitalcommons.unl.edu/biosciforbes/36>

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Valery Forbes Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

The role of ecological models in linking ecological risk assessment to ecosystem services in agroecosystems

Nika Galic,¹ Amelie Schmolke,² Valery Forbes,³ Hans Baveco,⁴ and Paul J. van den Brink^{1, 4}

1. Department of Aquatic Ecology and Water Quality Management, Wageningen University, Wageningen University and Research Centre, P.O. Box 47, 6700 AA Wageningen, The Netherlands
2. UFZ, Helmholtz-Zentrum für Umweltforschung — UFZ, Department Ökologische Systemanalyse, Permoserstr. 15, 04318 Leipzig, Germany
3. School of Biological Sciences, University of Nebraska–Lincoln, 348 Manter Hall, Lincoln, NE 68588-0118, United States
4. Alterra, Wageningen University and Research Centre, P.O. Box 47, 6700 AA Wageningen, The Netherlands

Corresponding author — N. Galic, P.O. Box 47, 6700 AA Wageningen, The Netherlands; tel 31 317 484598, fax 31 317 419000, email nika.galic@wur.nl

Abstract

Agricultural practices are essential for sustaining the human population, but at the same time they can directly disrupt ecosystem functioning. Ecological risk assessment (ERA) aims to estimate possible adverse effects of human activities on ecosystems and their parts. Current ERA practices, however, incorporate very little ecology and base the risk estimates on the results of standard tests with several standard species. The main obstacles for a more ecologically relevant ERA are the lack of clear protection goals and the inherent complexity of ecosystems that is hard to approach empirically. In this paper, we argue that the ecosystem services framework offers an opportunity to define clear and ecologically relevant protection goals. At the same time, ecological models provide the tools to address ecological complexity to the degree needed to link measurement endpoints and ecosystem services, and to quantify service provision and possible adverse effects from human activities. We focus on the ecosystem services relevant for agroecosystem functioning, including pollination, biocontrol and eutrophication effects and present modeling studies relevant for quantification of each of the services. The challenges of the ecosystem services approach are discussed as well as the limitations of ecological models in the context of ERA. A broad, multi-stakeholder dialog is necessary to aid the definition of protection goals in terms of services delivered by ecosystems and their parts. The need to capture spatio-temporal dynamics and possible interactions among service providers pose challenges for ecological models as a basis for decision making. However, we argue that both fields are advancing quickly and can prove very valuable in achieving more ecologically relevant ERA.

Keywords: protection goals, assessment endpoints, extrapolation, pollination, biological control, eutrophication

1. Introduction

The world's ecosystems are increasingly under pressure from various anthropogenic activities. For instance, agriculture is essential for sustaining the human population, but also directly disrupts ecosystem functioning (Power, 2010). Some of the impacts associated with intensive agricultural practices include the conversion of natural habitats into agricultural fields, adverse effects of pesticides on non-target organisms through chemicals and nutrient runoff into adjacent water bodies. Ecological risk assessment (ERA) is a process that estimates potentially adverse effects and risks, to ecosystems or their components, from human activities and multiple human-induced stressors (Munns, 2006). Theoretically, ERA is not limited to any specific activity, yet traditionally it has focused mostly on the assessment of adverse effects caused by toxic chemicals. Pesticides, for instance, are chemicals designed to be highly toxic towards specific organisms and are deliberately and regularly introduced into the environment. As such, they have to go through an extensive risk assessment process, including the provision of large toxicity datasets, to ensure

minimal risks to the ecosystems and their biota (Hommen et al., 2010). Accordingly, this group of chemicals receives a lot of attention and an accompanying body of legislation that regulates its use in the environment. In Europe, current pesticide risk assessment is a tiered approach that, in its first tiers, focuses on measuring adverse effects from specific chemical compounds on a handful of chosen species, thought to represent the most sensitive species in the environment (EU, 2009; SANCO, 2002).

In spite of its name, ecological risk assessment involves very little, if any, ecology because ecological data, such as species' life-history traits, population structure, density-dependent regulation, species composition and interactions, landscape structure etc., are commonly ignored (Forbes et al., 2009; Van den Brink, 2008). Furthermore, the choice of standard test species is usually governed by practicality, i.e., geared towards species that are easily cultured in laboratories, such as *Daphnia* sp. and zebra fish. Neither the relation between the well-being of these species and the targeted ecosystem is well understood, nor do they represent the most vulnerable species in ecosystems. Accordingly, current ecological risk assessment is neither firmly based on scientific knowledge

about ecosystems or their components, nor does it define ecologically relevant protection goals, although both aspects are required by European legislation, and are aspired to by experts in the field. Two main obstacles that prevent more ecologically relevant risk assessments are the lack of definition of concrete protection goals and the complexity of ecosystems that usually lies beyond feasible empirical testing.

Application of the ecosystem services concept as a basis for environmental management has gained momentum in recent years and offers promise as a valuable tool for setting meaningful ecological protection goals. Ecosystem services are the benefits people obtain from ecosystems and can be influenced directly or indirectly by drivers of change (Millennium Ecosystem Assessment, 2005). Examples of indirect drivers are demography and policy while examples of direct drivers are land use and climate change. In this paper we show that models are not only very suitable for describing the mechanistic relationships occurring within ecosystems but also for how these relationships can be influenced by (external) drivers.

Ecological models have the potential to address the other problem that hinders ecologically relevant risk assessment: the inherent complexity of ecosystems. Modeling approaches may help overcome limitations of currently applied approaches to ecological risk assessment (Forbes et al., 2009; Thorbek et al., 2009; Galic et al., 2010) as they allow the inclusion of both intrinsic sensitivity to a toxicant and various relevant ecological factors in a single study. Modeling studies allow investigation of the impacts of various stressors on ecosystem components relevant for ecosystem services, and permit analysis at larger spatial and temporal scales than can be done experimentally. Subsequently, through extensive scenario testing, they can help to identify situations where risks are relatively higher (or lower) and thereby facilitate more efficient use of resources and identification of efficient mitigation measures. Such extended scenarios cannot be approached experimentally in practice, but are essential if larger ecosystem components, rather than individual organisms, are the focus of study.

In the following paragraphs, we briefly introduce the concept of ecosystem services and identify services relevant to ERA with a special focus on agroecosystems. Ecological modeling has been applied in the context of ERA and several different modeling approaches are available. After providing a short overview of the approaches, we discuss how models can be of particular value if ecosystem services are the protection goals of ERA. We provide three prominent examples of ecosystem services that are commonly affected by agricultural practices. We conclude the paper with a discussion of the challenges and give an outlook on potential future directions for research and legislation.

1.1. Ecosystem services framework

Hommen et al. (2010) reviewed European legislation related to chemical use and showed that environmental protection goals are very broadly and vaguely defined, mostly stating that “no adverse effects on the environment or species” should occur. This has usually been interpreted as protecting exposed populations, rather than individuals. However, in some cases the protection of individuals, such as vertebrates, or of specific ecological properties (e.g., water quality in rice paddy systems), instead of biodiversity parameters, is of interest (Hommen et al., 2010; SANCO, 2002). Recently the European Food Safety Authority (EFSA) suggested a new, more comprehensive approach for setting protection goals against adverse effects of pesticides using the ecosystem service framework (EFSA PPR PoPPatR, 2010).

Ecosystem services (ES) are, in essence, functions of and provisions from ecosystems that are useful for and available to humans. The concept was first elaborated by Daily (1997) and Costanza et al. (1997), and its application in environmental policy was fostered by the Millennium Ecosystem Assessment project (Millennium Ecosystem Assessment, 2005).

In the assessment, four main groups of services are distinguished, namely provisioning services, e.g. food, water, fiber and fuel; regulating services that include regulation of air quality, erosion, disease, pests etc.; cultural services that pertain to non-material benefits such as recreation, cultural and religious values, and cultural heritage; and supporting services that provide a basis for all other services, and involve processes such as photosynthesis and primary production, nutrient and water cycling. Some services can be provided by multiple ecosystems, and the same ecosystem provides multiple services; both of these issues are important since maximizing one service is likely to result in tradeoffs on other services. For a more comprehensive and global analysis of the ecosystem services concept and ecosystems in general see the website of the RUBICODE project (<http://www.rubicode.net>), accessed Jan. 15, 2011).

In agroecosystems, several services are essential for proper functioning of the system, but at the same time they can be negatively affected by standard agricultural practices (Power, 2010). These include pest control, pollination, nutrient cycling, soil structure and fertility, water provision, carbon sequestration and (genetic) biodiversity.

Most services are not typically delivered by an ecosystem as a whole, but rather by its distinct parts. This notion led to the introduction of the concept of service providing units (SPU) (Luck et al., 2003), that represent populations of species that provide the service at a certain temporal or spatial scale. This concept allows a direct link between the service and the part of the ecosystem that provides it to be made (Luck et al., 2003), where changes in the characteristics of a given SPU have consequences for service provision. The exact definition and extent of an SPU varies with the type of service and can be anything from a local population or community of species to a global distribution of a specific species. Kremen (2005) elaborates on this concept by introducing ecosystem service providers (ESP), covering the diversity of functions and traits found in populations, communities, and spatially or temporally disjunct networks that are necessary for service delivery.

In conclusion, the ecosystem services framework offers a different way to formulate protection goals that is especially relevant for ecological risk assessment. Rather than basing all our actions on practicality and several hand picked species, the ES concept facilitates the identification of key services and service providers for a specific system. These key services can therefore be the focus of protection, i.e. protecting the service protects its providers. The spatio-temporal identification of the key services and service providers that will represent the protection goals of ERA will have to be conducted by scientists, regulatory authorities, industry, NGOs and other stakeholders working in collaboration.

Here we argue that well chosen ecological models can be powerful tools to improve the links between what we measure in ERA and what we want to protect, using ecosystem services as specific protection goals.

1.2. Ecological models in ERA

All models, including ecological models, are by definition a simplification of reality, designed to study a given system. Historically, they were used for investigating ecological phenomena and were mainly developed by theoretical ecologists (starting with Malthus, 1798). Their assumptions can be tested in different scenarios, and thus, ecological models can foster mechanistic understanding of ecosystems and their parts.

Ecological models can encompass different levels of biological organization: from individual, population, metapopulation, community to ecosystem, and they can be spatially implicit or explicit. Complexity and amount of detail may be varied depending on the type of question under investigation. As a consequence of increasing computer power, it is becoming more and more feasible to incorporate larger spatial and temporal scales and to include more detail into ecological models. Combination of both biological and spatial dimensions can be necessary for

specific questions, and the level of integrated detail depends on the system and the desired output of the model.

Ecological models of various spatial and biological resolution have been used for ecological applications, e.g., in the fields of conservation biology, wildlife and fisheries management (e.g. Starfield, 1997). In such applied fields of research, ecological models are increasingly used to predict future behavior of tested systems. Some modeling studies are developed for projections beyond available datasets, where the consequences of various scenarios are evaluated in terms of their effects on growth, abundance, structure, or some other population, community or ecosystem, characteristic in the future. Models used for such predictive purposes often require much more mechanistic understanding of the system, i.e. they include knowledge and assumptions about the functioning and underlying processes of the whole system and its parts. In order to confirm the suitability for the specific context, such models typically have to go through multiple comparisons with empirical data to test whether patterns observed in the model output are comparable with patterns observed in the field (Grimm et al., 2005).

In the realms of ERA, the added value of ecological models in obtaining more realistic assessments of risk has been argued (Forbes et al., 2008, 2009; Thorbek et al., 2009; Galic et al., 2010; Schmolke et al., 2010a; Wang and Grimm, 2010). Several different modeling approaches have been applied specifically to questions related to chemical risk assessment (Galic et al., 2010; Schmolke et al., 2010b); their development and use are not, however, restricted to the field of ERA. Differential equation models are typically used in simple assessments of unstructured population growth under different conditions or in more biologically complex systems, such as food web or ecosystem models, where the functional groups are assumed to be biologically unstructured. In matrix models, populations are divided into relevant classes (age, stage, size etc.) with class-specific survival and fecundity schedules. Matrix models are especially popular in chemical risk assessment studies, as they allow extrapolation of toxicity data available for different life stages of an organism to the dynamics of a population and also project population growth into the future, under the assumption that relevant life-history traits remain the same. Relatively straightforward sensitivity analysis, i.e. elasticity analysis, is based on matrix algebra and gives direct insight into the relative contribution of class-specific life-history traits to the overall population growth rate. In cases where more detail on the behavior of individuals is relevant, individual-based models can be used. In typical pesticide risk assessment studies, the level of model complexity will depend on the population-level endpoint that needs to be assessed, whether the model is protective or aims toward more accurate prediction, and also on the extent to which conclusions drawn from the model are intended to be general rather than system specific (Forbes et al., 2008). All of the model types described above can be combined with explicit consideration of space for an assessment of effects of chemicals across spatial scales.

2. Ecological models for the assessment of ecosystem services

Ecological models are valuable tools that can be applied to achieve more ecologically relevant risk assessments, and that seem to be gaining in importance in this field (Grimm et al., 2009). However, models have to be developed around specific questions, in the context of ecological risk assessment, and to address particular protection goals. Current protection goals as specified in relevant legislation are not specific, but phrased in general terms that aim to keep impacts “acceptable” (Hommen et al., 2010). Application of the ecosystem services framework allows the general legislative protection goals to be translated into entities that can be quantified and hence modeled. More details on how this process can be implemented, using mostly pesticides as an example, can be found in other contributions within the Special Issue.

After a clear protection goal, i.e. service, has been defined, relevant service providers have to be determined, and their role in the service has to be understood and quantified. This will make data collection in the field necessary, but model approaches can greatly help in this venture by making the data collection more focused. The major assets of ecological models are the quantification of the service contribution by a service providing unit and quantification of the effects that various human activities have on these units. For instance, the service of biocontrol is delivered by a number of species belonging to related and unrelated taxonomic groups. Population models describing various bird, insect and spider species have already been developed and used to explore how changes in population dynamics can influence biocontrol and how human activities alter the population dynamics of the modeled species (e.g. Sherratt and Jepson, 1993; Thorbek and Topping, 2005; Topping et al., 2005). If a contribution of one specific species outweighs all the others, we can focus on modeling the population dynamics of that species. In case the contribution of several species to the same service provision is more or less equal, it will be hard to find modeling studies quantifying respective contributions of all service providers. Specific endpoints of a modeling study will depend on the service, service provider and relevant anthropogenic activity that is being assessed, e.g., seasonal abundance dynamics might be of relevance or the spatial distribution of the provider in a given region. Judgments will also have to be made about how detailed our quantification needs to be and the extent to which it is sufficient to have rough estimates of particular responses so that risks can subsequently be assessed. In some situations it might be sufficient to estimate the risk of an effect resulting in 50% mortality of a biocontrol agent that suppresses the pest populations by 20%. In other situations, more detailed and possibly multidimensional risk maps might be needed.

Quantification of service contributions facilitates a dynamic economic appraisal of service providing units. Research on the valuation of ecosystem services had been increasing in the last decade (Fisher et al., 2009). Adding a monetary value to a given service provides a means for trade-off and cost-benefit analyses in the decision-making process, i.e. it makes comparison of alternative scenarios possible (Daily et al., 2009). However, the field of environmental accounting has not realized its full potential mainly due to issues in classification of ecosystem services (Boyd and Banzhaf, 2007; Wallace, 2007), but also because many services are hard to define in monetary terms, such as the value of fresh potable water or some cultural services (Daily et al., 2009; Srinivasan et al., 2008). In spite of the obvious challenges, ecological models are the only tools that can dynamically capture changes in service provision and that can be linked with their economic counterparts for testing alternative scenarios of impacts of human activities.

2.1. Examples of relevant ecosystem services

In the following section, we describe three services delivered by agroecosystems that are potentially affected by human practices, identify the service providers and provide some examples of published modeling studies. These examples demonstrate that model approaches already exist and could be used as a starting point to address the specific needs of risk assessment related to agricultural practices. Table 1 summarizes the key points of the example modeling studies. We finish this section with published examples of models that combine ecological and economic aspects of service trade-offs.

2.1.1. Pollination

According to the Millennium Ecosystem Assessment (2003), pollination is a regulating service, provided by natural pollinator communities in the habitat surrounding crop fields. Pollination receives a lot of attention, partly because it is a service essential for agricultural production, where around 40% of animal pollinated crops depend on wild and

Table 1. Summary of presented case studies (without examples of trade-off analyses). RA: risk assessment, RM: risk management.

Service/protection aim	Service providers	Service beneficiaries	Potential risks	Modeling study	Study aim	Model type	Model output	Supporting empirical data	RA or RM
Pollination	Assemblages of native, wild pollinator species	Local farmers	Land use change, pesticides, competition with domesticated pollinators	Kremen et al., 2007 Rands and Whitney, 2010	Assessing effects of land use change Impact of monocultures on pollinator wild flower preference	Conceptual Unstructured population	/ Pollinator preference	/ No	Both RM
Biological control	Assemblages of natural predator species	Local farmers	Pesticides, habitat fragmentation, agricultural intensification	Bianchi et al., 2010 Visser et al. 2009	Identifying locations for optimal management strategies Role of off-crop habitat for parasitoid persistence	Unstructured population Unstructured population (richer function for the host population)	Pest load Host and parasitoid population size, parasitoid persistence and parasitation rate Ladybeetle population size and energy status in different crops Spider abundance in different landscapes/crops	No No Yes	RM Both RA (retroactive)
Water quality — multiple services	Aquatic communities	Local human population	Multiple — agriculture, flow regulation, pollution	Thorbek and Topping, 2005 Jansse, 1997	Impact of landscape diversity and heterogeneity on the persistence of local spider populations Impact of excessive nutrient load on Dutch lake water quality	Unstructured for the pest, stage-structured for the ladybeetle population Individual based model of spider population Ecosystem (composed of unstructured functional groups)	Nutrient load, total P and N, amount of chlorophyll and submerged vegetation	Yes	Both

domesticated pollinators (Power, 2010). Klein et al. (2007) analyzed crop data from 200 countries and found that 87 major food crops rely on animal pollination. Also, pollination is one of the few ecosystem services that can be relatively easily quantified as its value is easily measured by estimating the change in crop production with changes in service delivery (Losey and Vaughan, 2006). Pollination in agricultural crops is not delivered solely by wild bee populations, but mostly through managed honeybee populations. However, the managed honeybee stocks have been declining worldwide in the last several decades, due to multiple factors, such as disease (Watanabe, 1994), parasites, pesticide use, socio-economic factors (van Engelsdorp and Meixner, 2010), making the contribution of wild pollinators to crop production a research and conservation priority (Winfree et al., 2007). The honeybee issue boosted the development of ecological models relating to more general dynamics of honey bee populations and colonies (Amdam et al., 2006; Becher et al., 2010; DeGrandi-Hoffman et al., 1989; Makela et al., 1993; McLellan and Rowland, 1986; Omholt, 1988; Schmickl and Crailsheim, 2007) as well as those designed to investigate specific causes and dynamics of collapse (Martin, 1998, 2001).

The beneficiaries of pollination are local farmers, and native pollinator species are the providers of the service. Species contributing to pollination consist of around 50 bee species with a global distribution, and around 7 other invertebrate and vertebrate species (Klein et al., 2007). These species can be found in characteristic crops that are grown globally. In order to quantify the given SPU, local bee species have to be identified, their main characteristics determined and population dynamics of different species need to be considered to ensure spatio-temporal coverage of the service. Characteristics such as population size, density in an area, spatial and temporal dynamics, composition, diversity of necessary bee traits (preferred crop species, visiting frequency, foraging time and distance etc.) and diversity of habitats that ensure the presence of this complex all have to be properly investigated and quantified. Moreover, to evaluate the sustainability of a wanted ecosystem service, we have to integrate the sensitivity of various traits and complex characteristics to changes in land use, application of chemicals and/or environmental factors.

Relevant drivers of change and pressures include agricultural intensification, habitat fragmentation and loss due to land-use change favoring agricultural crops rather than natural habitat. Global events such as climate change also need to be taken into account, as well as competition with domesticated bee species.

Ecological models developed for studying any of these aspects are the only tools available to integrate different levels of service provision in one study and to test various trade-off scenarios without massive time, energy and financial costs of field experiments. Kremen et al. (2007) developed a conceptual mobile-agent-based ecosystem service (MABES) model in which they integrated the biology of service providers, policies on land-use and market laws. Landscape structure is of pivotal importance here, as it impacts spatio-temporal dynamics of pollinators through availability of food, nesting, mating and overwintering habitat. Furthermore, they included various abiotic variables, such as increase in pesticide use, and biotic factors influencing the persistence of pollinator communities, such as foraging behavior, internal species traits affecting dynamics (e.g. haplodiploidy and low fecundity, competition, parasitism). In this publication the authors did not present an actual ecological model, but rather developed a framework that clearly identifies areas where ecological models can be used for the quantification of effects of different land-use strategies on the pollinator complex.

Rands and Whitney (2010) developed a simple spatially explicit model to investigate how the pollinator's wild flower foraging preferences are affected by monocultures. In a very simple modeling setting, where space was modeled as a two dimensional grid with discrete cell units, pollinators were allowed to forage within a radius from their nests, which were positioned within the managed field margins. Simulation output showed that the width and geometric design of the margins,

together with wild flower density, will enhance pollinator visits to wild flowers, and increase the service in the monocultures too. These results have yet to be empirically verified, but their findings have direct implications for landscape management: the ecosystem service of pollination will benefit from increased wild flower density and from fewer, but wider field margins, as opposed to more numerous, but smaller margins. Both of these findings can be further tested and implemented in real case studies.

2.1.2. Biological control

Biocontrol is also a regulatory ecosystem service that is often evaluated within the field of ecological risk assessment especially in relation to pesticide use. It is very similar to pollination in that the service beneficiaries are local farmers, the service providers are usually assemblages of natural predator species whose viability, abundance and population density can be affected by pesticides, habitat fragmentation, agricultural intensification etc.

Bianchi et al. (2010) provide a theoretical investigation of how predator dispersal abilities and habitat configuration could govern the identification of locations where management strategies would have highest impact on service delivery. They developed a spatially explicit model in which the pest species populations grow exponentially within habitat cells and do not disperse, whereas the natural predators disperse across habitats, but show no population dynamics. An exponential power distribution is used as the dispersal function that produces a number of distributions by alternating one of the parameters; as a consequence predators become more or less mobile. Moreover, the model assumes that the time the predators stay in a single cell can be dependent (aggregating) or independent (non-aggregating) of pest densities, which, together with dispersal abilities, yields four theoretical species of predators in total for their analysis. They simulated the pest suppression over 1000 landscapes that varied in the arrangement of predator and pest cells and showed that the highly aggregating, mobile predators have highest pest suppression rates. Furthermore, landscapes with shortest distances between predator and prey cells show highest pest suppression. Their findings have implications for integrated pest management strategies that should aim at larger than one-field scales and should define distance of habitats to crops and ecological function of off-crop habitats, e.g. if it is a source of or sink for biocontrol agents. Finally, knowledge on biological traits of pests and natural predators will facilitate predictions about the areas prone to pest attacks and estimates of successful control by regionally present predators.

A more biologically detailed system was modeled by Visser et al. (2009) who developed a spatially explicit simulation model for a pest, the rape pollen beetle, and its parasitoid to investigate the role of off-crop habitat, including the amount, fragmentation and isolation, for parasitoid persistence. Both species can reside in a single habitat cell where the processes of reproduction, mortality and parasitism occur. Pest population dynamics is modeled via the Ricker function, with a yearly time step, and only females are modeled for both species. The distribution of parasitoid eggs is random and limited by individual fecundity. Both species are univoltine and die if they disperse to non-crop habitat or when parasitized. Parasitoid persistence was highest at intermediate isolation levels, but the parasitism rate was negatively correlated with isolation and fragmentation. This has clear landscape management implications for cases where natural habitat is scarce, in that either persistence of parasitoids or parasitism rate can be optimized, but not both simultaneously.

Another example of a simple, unstructured population model in a spatially explicit setting was developed by Bianchi et al. (2007) where the interaction between host plants, aphids as pests and ladybeetles as natural predators was investigated. The authors explored whether the historical changes in land use in the Czech Republic had any effects on decreasing populations of ladybeetles. Modeled landscape consisted of habitat maps

with various crop species in which pests would realize their population dynamics. Aphid population growth was modeled with a logistic growth function, and the only population loss term was mortality that was dependent on the number of ladybeetles in one habitat cell. The ladybeetle population was composed of seven stages, consisting of egg, four larval, pupal and adult stages. Each stage had stage-specific parameters for different processes, such as developmental and mortality rates, search rates and handling times, etc. The foraging activities of ladybeetles were governed by their energetic status, and the predation rate was described by a Holling type 2 functional response. Simulation results suggest that the steep decline in ladybeetle populations can indeed be explained by the decrease in aphid abundance due to agricultural de-intensification and lower fertilizer input. Ladybeetles seem to be following intensively cultured crops that harbor highest aphid densities. Once the aphids become less available, ladybeetles will become more dependent on off-crop habitat to meet their energetic needs, making the conservation of this type of habitat pivotal in sustaining their populations. Even though the service of aphid biocontrol might not always be necessary, ensuring high ladybeetle abundances provides insurance that, when necessary, aphid populations can be controlled.

Natural predator populations can also be modeled in a very detailed way: Thorbek and Topping (2005) developed a spatially explicit, individual-based model of a linyphiid spider, a typical predator in agroecosystems, to investigate the impact of landscape diversity and heterogeneity on the persistence of local populations. In this model, linyphiid spider individuals go through an egg, juvenile and adult phase. In different phases, they experience certain probabilities of development, dying, dispersing and reproducing, where each individual is unique and based on a number of given variables. Landscape was modeled according to a real Danish, intensely cultivated landscape with various crop and off-crop vegetation types. The authors show that the diversity of habitat types, especially presence of refugia from pesticide exposure with higher abundance of prey species, greatly influences the persistence of these predators, but that actual arrangement of these habitat types matters less, due to the species' high dispersal abilities. Implications for management here include ensuring diverse crop rotation or leaving greater parts of the habitat unmanaged.

The modeling studies we described for the services of pollination and biocontrol need to consider spatial relationships, as the organisms that deliver the service depend on off-crop habitats that are spatially segregated from the location where the service is provided (the crop). To ensure delivery of both services, the amount of natural habitat, its geometry, quality and distance to crops are important aspects of management. Spatially explicit models, either more theoretical in nature or more region-specific, allow testing of the impacts of these aspects in various landscape management scenarios and possible trade-offs that may result. The necessary levels of biological detail and resolution will be dependent on the research question or protection goal relevant for the study.

2.1.3. Water quality

Good water quality in natural aquatic ecosystems provides multiple services, from good potable quality for local communities, making it a provisioning service, to ensuring certain levels of biological diversity and community structure that has esthetic and recreational value, e.g. for sport fishing. Also, more indirectly, good water quality supports the functioning and stability of aquatic communities and food webs that can play a role as nursery habitat or gene pool protection, making water and its aquatic communities also a supporting service. The multiple purposes of well-functioning water bodies are utilized by various beneficiaries, from local communities depending on the water source, to sports fishermen and tourists in the area. At the same time, aquatic ecosystems are under intense pressure from human activities and are considered to be among the most globally threatened ecosystems (Dudgeon, 2010).

Due to the wide variety of services that aquatic systems provide, it is impossible to cover them all in this paper. Therefore, we focus only on the eutrophication consequences in shallow lakes. Typically, shallow lakes, with a maximum depth of several meters, exist in two alternative stable states, a macrophyte dominated, clear water state, or a phytoplankton dominated turbid state. Excess nutrient loading, both phosphorus and nitrogen, can push the lake from a macrophyte to phytoplankton dominated state (Scheffer et al., 1993). It is considered that a turbid state has a lower value because the macrophyte community with its fish assemblages disappear, hereby decreasing overall biodiversity. The recovery of a lake after such a switch is not straightforward, as just reducing the nutrient loads is not sufficient, and frequently biomanipulation is necessary. This, however, also depends on lake size and climatic region (Jeppesen et al., 2007). The development of the PCLake model (Janse, 1997; Janse et al., 2010) was inspired by agricultural intensification in Dutch lakes and the related effects that excessive nutrient loads had on the quality of lake systems, such as algal blooms. This complex ecosystem model takes into account nutrient and biota dynamics in a shallow lake. Essentially, it is a set of ordinary differential equations in which the biota are modeled as functional groups, a common practice for such complex systems. It was created to estimate the probabilities of shifting into an alternative stable state based on the observed nutrient loads, on the composition of the lake's communities and on management practices, in order to identify feedback mechanisms that hamper or enhance these transitions. The model has been extensively analyzed and parameterized in a number of lakes, and it was implemented for various questions related to water quality management (see Mooij et al., 2010 for examples and references). Mooij et al. (2010) provide a review of the history and current uses of various lake ecosystem models developed for different management purposes.

Consequences of systems shifting to alternative states are far-reaching and long-term and thus deserve to be taken into account when assessing risks to the environment. The alternative stable states have been an interesting topic from a purely theoretical point of view, but with very strong implications for management, corroborated by the suite of lake models calibrated to various climatic conditions. If a lake ecosystem shifts to an undesired state due to agricultural intensification and increased nutrient load, ecological lake models can quantify various restoration activities, such as necessary reduction in nutrient loads or the extent of needed biomanipulation agents in order to recover the system quality. Biomanipulation usually includes drastic reduction of the fish stocks that, through trophic cascades, results in the re-establishment of the macrophyte dominated community. Such biomanipulation experiments have been implemented worldwide with differing success (Mehner et al., 2002) depending on the lake type, depth, complexity of the lake food web and various feedback mechanisms.

2.1.4. Trade-off analysis

Ecosystem service trade-offs take place when one service is valued over another, and when the delivery of one service reduces the delivery of another service. Agricultural activities that deliver provisioning services, such as food and fuel, have historically been favored over services such as biodiversity and water quality, whereas supporting services (such as nutrient cycling or soil formation and quality) have been neglected (Rodríguez et al., 2006). The analysis of land-use change and its impacts on ecosystem services supports the development of various integrative modeling approaches (de Groot et al., 2010). For instance, Nelson et al. (2009) developed a model that takes into account ecosystem services, biodiversity conservation and trade-offs at landscape scales, especially in land use decision making. InVEST (Integrated Valuation of Ecosystem Services and Tools) can be applied to various systems, and the authors offer a case study of the Willamette basin in Oregon, US. They combine an ecological valuation of various services in the area with an economic valuation method. In their study, land use and land cover are the basis for

ecosystem services, biodiversity conservation and commodity production. Biodiversity conservation is based on the species-area relationship (SAR) and marginal biodiversity value (MBV), the latter a more relative metric measuring the value of habitat in the area in relation to the habitat available for all species in the whole landscape.

Nalle et al. (2004) developed a simpler spatially explicit model for finding cost-effective strategies in timber production and endangered species conservation in a forested landscape. The ecological model here is based on the PATCH model (Schumaker et al., 2004) and consists of a matrix model for the great horned owl, *Bubo virginianus*, and the great porcupine, *Erethizon dorsatum* that includes life-history parameters such as survival and reproduction rates. Dispersal of individuals is modeled with maximum dispersal distances in a stochastic search procedure. The habitat preferences include data on the suitability of each land management unit as a function of vegetation cover and other landscape characteristics. The economic model calculates the current market value of timber harvesting, whereas the timber harvest is modeled through another modeling package that takes into account harvesting site quality and lists of trees no younger than 15 years of age. The authors demonstrate how the combined models can be implemented in a case study focusing on a part of the Willamette River Basin in Oregon. The whole study was envisaged as an example of how to link ecology and economics in a natural resources rich area where conflicts between exploitation and conservation could occur.

The choice of presented modeling studies reflects the diversity of applied ecological models related to risk assessment of different ecosystem services potentially affected by agricultural practices. Some of the presented studies are developed for risk management, rather than risk assessment. However, ecological models can be used both ways, to scientifically underpin ecological risk assessment as well as facilitate informed management decisions. For both fields, testing of different scenarios, possibility to ask if-then questions and to explore their consequences can be very informative. It was shown that ecological models can capture population dynamics in a very simple, unstructured way, but also that population models can include a lot of biological detail and span over various spatial scales. Depending on the service, explicit consideration of space can be of lower or higher relevance. For instance, both pollination and biocontrol are delivered by organisms that are dependent on other habitats than the one where the service is provided. Thus, the need to take into account landscape composition and structure is reflected in the choice of models. On the other hand, explicit space might not be as relevant in well mixed systems, such as shallow lakes, where interactions between nutrients and various functional groups are more important in determining the dynamics of and changes in the system.

3. Challenges and outlook

The ecosystem services framework offers a novel way to approach and conduct conservation of our ecosystems. It also provides an effective means for operationalising general legislative protection goals into targets that can be quantitatively assessed. Ecosystem services are, per definition, important for humans and deserve to be protected, or their loss has to be thoroughly weighed against the gain of the human activity that may cause such a loss. If ecosystem services that are affected directly or indirectly by agricultural practices can be identified, their well-being or swift recovery could be a meaningful protection goal for ecological risk assessment. It might not be straightforward to define all relevant aspects of a protection goal, such as temporal and spatial scales for the provision of the given service, but at least the aim of protection should be based on more than just results of toxicity tests performed with species that can be easily cultured in laboratories. There is a big discrepancy between measurement endpoints and protection goals since most ecosystem services are performed by distinct units of ecosystems, i.e. populations or communities, while most tests mandated by the relevant legislation and

supporting documentation, e.g. Technical Guidance Documents, focus on organism-level effects of a few standard species. Ecological models are powerful tools that can link the measurement endpoints with relevant protection goals. With clearly defined goals, ecological models can help to investigate impacts on various ecosystem components, such as service providing units, also incorporating extended temporal and spatial scales if necessary. Their characteristic advantage, over empirical approaches, is their extrapolative power. They are highly useful for extrapolation across levels of biological organization (e.g. from individual-level effects of toxicants, to population level consequences), and across spatial and temporal scales (e.g., for estimating recovery or accounting for spatio-temporal variability in exposure). They are also useful for the analysis of indirect effects and bioaccumulation, both within and across trophic levels (Munns, 2006; Forbes et al., 2008; Galic et al., 2010; Hommen et al., 2010).

Still, challenges remain for the ecosystem service concept itself and for model development. Firstly, the valuation of ecosystem services is not yet fully developed nor globally accepted (Armsworth and Roughgarden, 2003; Boyd, 2007; Boyd and Banzhaf, 2007; Wallace, 2007, 2008). Furthermore, some services may not have been identified yet, and multiple interactions, feedbacks and outcomes in various service combinations have not received much attention (Bennett et al., 2009). Norgaard (2010) argues that a more comprehensive restructuring of relevant governing and economic institutions is necessary to accomplish the full potential of the proposed framework; otherwise we will not move fast enough in the right direction of sustainability.

Secondly, knowledge on the structure and functioning of agroecosystems is still limited, despite the wealth of published information. A lot of the observations and experiments published in the literature are very context specific, and not many have dared to make generalizations on ecosystem structure and functioning. The structure and functioning of ecosystems, and effects of various drivers on them, may very well be context specific to a certain extent and therefore difficult to capture in general ecological models. This is especially true when “real” ecosystems are modeled to evaluate the effects of certain drivers in specific ecosystem case studies. From a review of the literature, Daam and Van den Brink (2010) concluded that the sensitivity of tropical aquatic ecosystems does not seem to be very different from temperate ones, but that recovery patterns and indirect effects can be expected to be very different between climate regions. This means that it should be very clear from the start which specific service in which ecosystem is being captured by the model. Model outputs cannot be easily transferred between contexts, but rather a thorough reconsideration of model assumptions, structure, and parameterization is necessary if a model is applied in a context outside of its intended purpose (e.g., for a different climatic region, for the assessment of new protection goals, etc.).

Thirdly, the required level of complexity of ecological models remains an issue. Decisions on what exactly to quantify and with how much biological detail can be hard to make when a specific service is delivered by many providing units. To perform an ecologically relevant risk assessment, a lot of ecological detail is necessary. However, simulating the natural world is neither realistic nor desired. Finding the right balance between model complexity and ecological realism/relevance remains a crucial challenge and requires precise definition of protection goals which is achievable only through broad stakeholder dialogue combined with collaboration between ecologist and economists. Furthermore, modeling service provision adds another dimension of extrapolation and complexity, especially when a given service is provided by multiple providers. While in ERA extrapolation of effects from the individual to the level of a population could be sufficiently informative, focusing on service provision means that the spatio-temporal dynamics of service providers has to be taken into account as well as possible interactions with populations of other species. Moreover, the general definitions of ecosystem services make quantification very difficult. It might be necessary to

break down general services into more manageable units, for instance, instead of the service of biocontrol we might look into suppression of aphids in cereals in a given climatic region. For many services, including biocontrol and pollination, explicit consideration of space is essential and is expected to result in the increased development of spatially realistic population models. Again, the right balance between the amount of spatial and biological detail will have to be found.

Finally, the execution and implementation of some applied modeling studies has not always been successful (Pilkey and Pilkey-Jarvis, 2007), possibly due to too much reliance on the predictive power of models (Hall, 1988), lack of transparency and bad judgment in model assumptions or parameter choice (Comiskey et al., 2004; Gross, 2005; Patterson and Murray, 2008). Accordingly, there is a need for much more transparency, especially in ecological models used for decision making. In the field of pesticide risk assessment, steps are currently being taken to standardize approaches and reduce skepticism around the development, use and results obtained from modeling studies developed for the purpose of pesticide registration (Schmolke et al., 2010a, 2010b). Consequently, acceptance of ecological models for ERA and decision making is expected to grow in regulatory spheres. For example, pesticide risk assessment is currently taking significant steps toward developing and promoting the use of ecological models for the purposes of product registration (Forbes et al., 2009; Grimm et al., 2009; Thorbek et al., 2009).

In spite of many challenges, the link between measurement endpoints and services as protection goals is feasible only with the help of ecological models. We do not propose abandonment of empirical approaches, indeed, the two are complementary. Necessary parameters can only be extracted from field or experimental data, and the outputs of ecological models, especially those used in decision making, need to be tested against independent datasets to show that they are indeed recreating a part of the system of interest. Only then can they be fully trusted and used for comparing alternative management scenarios.

Acknowledgment — The authors would like to thank two anonymous reviewers for valuable comments on an earlier version of the manuscript. The work of Nika Galic is supported by Syngenta and Bayer CropScience.

References

- Amdam et al., 2006 • G. V. Amdam, O. Rueppell, and P. M. Conn, Models of aging in honeybee workers. *Handbook of models for human aging* Academic Press, Burlington (2006), pp. 267–276.
- Armsworth and Roughgarden, 2003 • P. R. Armsworth and J. E. Roughgarden, The economic value of ecological stability. *PNAS*, **100** (2003), pp. 7147–7151.
- Becher et al., 2010 • M. A. Becher, H. Hildenbrandt, C. K. Hemelrijk, and R. F. A. Moritz, Brood temperature, task division and colony survival in honeybees: A model. *Ecol Modell*, **221** (2010), pp. 769–776.
- Bennett et al., 2009 • E. M. Bennett, G. D. Peterson, and L. J. Gordon, Understanding relationships among multiple ecosystem services. *Ecol Lett*, **12** (2009), pp. 1394–1404.
- Bianchi et al., 2007 • F. Bianchi, A. Honkaniemi, and W. van der Werf, Changes in agricultural land use can explain population decline in a ladybeetle species in the Czech Republic: Evidence from a process-based spatially explicit model. *Landscape Ecol*, **22** (2007), pp. 1541–1554.
- Bianchi et al., 2010 • F. J. A. Bianchi, N. A. Schellhorn, Y. M. Buckley, and H. P. Possingham, Spatial variability in ecosystem services: Simple rules for predator-mediated pest suppression. *Ecol Appl*, **20** (2010), pp. 2322–2333.
- Boyd, 2007 • J. Boyd, Nonmarket benefits of nature: What should be counted in green GDP?. *Ecol Econ*, **61** (2007), pp. 716–723.
- Boyd and Banzhaf, 2007 • J. Boyd and S. Banzhaf, What are ecosystem services? The need for standardized environmental accounting units. *Ecol Econ*, **63** (2007), pp. 616–626.
- Comiskey et al., 2004 • E. J. Comiskey, A. C. Eller, and D. W. Perkins, Evaluating impacts to Florida panther habitat: How porous is the umbrella?. *Southeast Nat*, **3** (2004), pp. 51–74.

- Costanza et al., 1997** • R. Costanza, R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, *et al.* The value of the world's ecosystem services and natural capital. *Nature*, **387** (1997), pp. 253–260.
- Daam and Van den Brink, 2010** • M. Daam and P. Van den Brink, Implications of differences between temperate and tropical freshwater ecosystems for the ecological risk assessment of pesticides. *Ecotoxicology*, **19** (2010), pp. 24–37.
- Daily, 1997** • G. C. Daily, *Nature's services: Societal dependence on natural ecosystems*, Island Press, Washington (1997).
- Daily et al., 2009** • G. C. Daily, S. Polasky, J. Goldstein, P. M. Kareiva, H. A. Mooney, L. Pejchar, *et al.* Ecosystem services in decision making: Time to deliver. *Front Ecol Environ*, **7** (2009), pp. 21–28.
- de Groot et al., 2010** • R. S. de Groot, R. Alkemade, L. Braat, L. Hein, and L. Willemen, Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecol Complex*, **7** (2010), pp. 260–272.
- DeGrandi-Hoffman et al., 1989** • G. DeGrandi-Hoffman, S. A. Roth, G. L. Loper, and E. H. Erickson, BEEPOP: A honeybee population dynamics simulation model. *Ecol Modell*, **45** (1989), pp. 133–150.
- Dudgeon, 2010** • D. Dudgeon, Prospects for sustaining freshwater biodiversity in the 21st century: Linking ecosystem structure and function. *Curr Opin Environ Sustainability*, **2** (2010), pp. 422–430.
- EU, 2009** • EU, Regulation (EC) No 1107/2009 of the European parliament and of the council of 21 October 2009 concerning the placing of plant protection products on the market and repealing Council Directives 79/117/EEC and 91/414/EEC. *Off J Eur Commun L*, **309** (2009), pp. 1–50.
- EFSA PPR PoPPatR, 2010** • EFSA PPR PoPPatR, Scientific Opinion on the development of specific protection goal options for environmental risk assessment of pesticides, in particular in relation to the revision of the Guidance Documents on Aquatic and Terrestrial Ecotoxicology (SANCO/3268/2001 and SANCO/10329/2002). *EFSA J*, **8** (2010), pp. 1821–1876.
- Fisher et al., 2009** • B. Fisher, R. K. Turner, and P. Morling, Defining and classifying ecosystem services for decision making. *Ecol Econ*, **68** (2009), pp. 643–653.
- Forbes et al., 2008** • V. E. Forbes, P. Calow, and R. M. Sibly, The extrapolation problem and how population modeling can help. *Environ Toxicol Chem*, (2008), pp. 1987–1994.
- Forbes et al., 2009** • V. E. Forbes, U. Hommen, P. Thorbek, F. Heimbach, P. J. Van den Brink, J. Wogram, H.-H. Thulke, and V. Grimm, Ecological models in support of regulatory risk assessments of pesticides: Developing a strategy for the future. *Integr Environ Assess Manage*, **5** (2009), pp. 167–172.
- Galic et al., 2010** • N. Galic, U. Hommen, J. M. Baveco, and P. J. Van Den Brink, Potential application of population models in the European ecological risk assessment of chemicals II: Review of models and their potential to address environmental protection aims. *Integr Environ Assess Manage*, **6** (2010), pp. 338–360.
- Grimm et al., 2009** • V. Grimm, R. Ashauer, V. Forbes, U. Hommen, T. G. Preuss, A. Schmidt, P. van den Brink, J. Wogram, and P. Thorbek, CREAM: A European project on mechanistic effect models for ecological risk assessment of chemicals. *Environ Sci Pollut Res*, **16** (2009), pp. 614–617.
- Grimm et al., 2005** • V. Grimm, E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H.-H. Thulke, J. Weiner, T. Wiegand, and D. L. DeAngelis, Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science*, **310** (2005), pp. 987–991.
- Gross, 2005** L. Gross, Why not the best? how science failed the Florida Panther. *PLoS Biol*, **3** (2005), p. e333.
- Hall, 1988** • C. A. S. Hall, An assessment of several of the historically most influential theoretical models used in ecology and of the data provided in their support. *Ecol Modell*, **43** (1988), pp. 5–31.
- Hommen et al., 2010** • U. Hommen, J. M. Baveco, N. Galic, and P. J. Van Den Brink, Potential application of ecological models in the European environmental risk assessment of chemicals I: Review of protection goals in EU directives and regulations. *Integr Environ Assess Manage*, **6** (2010), pp. 325–337.
- Janse, 1997** • J. H. Janse, A model of nutrient dynamics in shallow lakes in relation to multiple stable states. *Hydrobiologia*, **342–343** (1997), pp. 1–8.
- Janse et al., 2010** • J. H. Janse, M. Scheffer, L. Lijklema, L. Van Lieere, J. S. Sloat, and W. M. Mooij, Estimating the critical phosphorus loading of shallow lakes with the ecosystem model PCLake: Sensitivity, calibration and uncertainty. *Ecol Modell*, **221** (2010), pp. 654–665.
- Jeppesen et al., 2007** • E. Jeppesen, M. Meerhoff, B. Jacobsen, R. Hansen, M. Sondergaard, J. Jensen, T. Lauridsen, N. Mazzeo, and C. Branco, Restoration of shallow lakes by nutrient control and biomanipulation—The successful strategy varies with lake size and climate. *Hydrobiologia*, **581** (2007), pp. 269–285.
- Klein et al., 2007** • A. -M. Klein, B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Scharntke, Importance of pollinators in changing landscapes for world crops. *Proc R Soc B*, **274** (2007), pp. 303–313.
- Kremen, 2005** • C. Kremen, Managing ecosystem services: What do we need to know about their ecology?. *Ecol Lett*, **8** (2005), pp. 468–479.
- Kremen et al., 2007** • C. Kremen, N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, *et al.* Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecol Lett*, **10** (2007), pp. 299–314.
- Losey and Vaughan, 2006** • J. E. Losey and M. Vaughan, The economic value of ecological services provided by insects. *Bioscience*, **56** (2006), pp. 311–323.
- Luck et al., 2003** • G. W. Luck, G. C. Daily, and P. R. Ehrlich, Population diversity and ecosystem services. *Trends Ecol Evol*, **18** (2003), pp. 331–336.
- Makela et al., 1993** • M. E. Makela, G. A. Rowell, W. J. Sames Iv, and L. T. Wilson, An object-oriented intracolony and population level model of honey bees based on behaviors of European and Africanized subspecies. *Ecol Modell*, **67** (1993), pp. 259–284.
- Malthus, 1798** • T. B. Malthus, First essay on population (an essay on the principle of population as it affects the future improvement of society with remarks on the speculation of Mr. Godwin M. Condorcet and other writers), Macmillan & Company, London, UK (1798).
- Martin, 1998** • S. Martin, A population model for the ectoparasitic mite *Varroa jacobsoni* in honey bee (*Apis mellifera*) colonies. *Ecol Modell*, **109** (1998), pp. 267–281.
- Martin, 2001** • S. J. Martin, The role of *Varroa* and viral pathogens in the collapse of honeybee colonies: A modelling approach. *J Appl Ecol*, **38** (2001), pp. 1082–1093.
- McLellan and Rowland, 1986** • A. R. McLellan and C. M. Rowland, A honeybee colony swarming model. *Ecol Modell*, **33** (1986), pp. 137–148.
- Mehner et al., 2002** • T. Mehner, J. Benndorf, P. Kasprzak, and R. Koschel, Biomanipulation of lake ecosystems: Successful applications and expanding complexity in the underlying science. *Freshw Biol*, **47** (2002), pp. 2453–2465.
- Millennium Ecosystem Assessment, 2003** • Millennium Ecosystem Assessment, Ecosystems and human well-being: A framework for assessment, World Resources Institute, Washington, D. C (2003).
- Millennium Ecosystem Assessment, 2005** • Millennium Ecosystem Assessment, Ecosystems and human well-being: Biodiversity synthesis, World Resources Institute, Washington, D. C (2005).
- Mooij et al., 2010** • W. Mooij, D. Trolle, E. Jeppesen, G. Arhonditsis, P. Belolipetsky, D. Chitamwebwa, *et al.* Challenges and opportunities for integrating lake ecosystem modelling approaches. *Aquat Ecol*, **44** (2010), pp. 633–667.
- Munns, 2006** • W. R. Munns, Assessing risks to wildlife populations from multiple stressors: Overview of the problem and research needs. *Ecol Soc*, **11** (2006), p. 12.
- Nalle et al., 2004** • D. J. Nalle, C. A. Montgomery, J. L. Arthur, S. Polasky, and N. H. Schumaker, Modeling joint production of wildlife and timber. *J Environ Econ Manage*, **48** (2004), pp. 997–1017.
- Nelson et al., 2009** • E. Nelson, G. Mendoza, J. Regetz, S. Polasky, H. Tallis, D. Cameron, *et al.* Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Front Ecol Environ*, **7** (2009), pp. 4–11.
- Norgaard, 2010** • R. B. Norgaard, Ecosystem services: From eye-opening metaphor to complexity blinder. *Ecol Econ*, **69** (2010), pp. 1219–1227.
- Omholt, 1988** • S. W. Omholt, Relationships between worker longevity and the intracolony population dynamics of the honeybee. *J Theor Biol*, **130** (1988), pp. 275–284.
- Patterson and Murray, 2008** • B. R. Patterson and D. L. Murray, Flawed population viability analysis can result in misleading population assessment: A case study for wolves in Algonquin park, Canada. *Biol Conserv*, **141** (2008), pp. 669–680.
- Pilkey and Pilkey-Jarvis, 2007** • O. H. Pilkey and L. Pilkey-Jarvis, Useless arithmetic: Why environmental scientists can't predict the future, Columbia University Press, Chichester, West Sussex (2007).
- Power, 2010** • A. G. Power, Ecosystem services and agriculture: Tradeoffs and synergies. *Philos Trans R Soc Lond B*, **365** (2010), pp. 2959–2971.
- Rands and Whitney, 2010** • S. A. Rands and H. M. Whitney, Effects of pollinator density-dependent preferences on field margin visitations in the midst of agricultural monocultures: A modelling approach. *Ecol Modell*, **221** (2010), pp. 1310–1316.
- Rodriguez et al., 2006** • J. P. Rodriguez, J. T. D. Beard, E. M. Bennett, G. S. Cumming, S. J. Cork, J. Agard, *et al.* Trade-offs across space, time, and ecosystem services. *Ecol Soc*, **11** (2006), p. 28.
- SANCO, 2002** • SANCO, Guidance document on aquatic toxicology in the context

- of the Directive 91/414/EEC. Working Document of the European Commission Health & Consumer Protection Directorate-General. Brussels, Belgium (2002), 62 pages.
- Scheffer et al., 1993** • M. Scheffer, S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen, Alternative equilibria in shallow lakes. *Trends Ecol Evol*, **8** (1993), pp. 275–279.
- Schmickl and Crailsheim, 2007** • T. Schmickl and K. Crailsheim, HoPoMo: A model of honeybee intracolony population dynamics and resource management. *Ecol Modell*, **204** (2007), pp. 219–245.
- Schmolke et al., 2010a** • A. Schmolke, P. Thorbek, P. Chapman, and V. Grimm, Ecological models and pesticide risk assessment: Current modeling practice. *Environ Toxicol Chem*, **29** (2010), pp. 1006–1012.
- Schmolke et al., 2010b** • A. Schmolke, P. Thorbek, D. L. DeAngelis, and V. Grimm, Ecological models supporting environmental decision making: A strategy for the future. *Trends Ecol Evol*, **25** (2010), pp. 479–486.
- Schumaker et al., 2004** • N. H. Schumaker, T. Ernst, D. White, J. Baker, and P. Haggerty, Projecting wildlife responses to alternative future landscapes in Oregon's Willamette basin. *Ecol Appl*, **14** (2004), pp. 381–400.
- Sherratt and Jepson, 1993** • T. N. Sherratt and P. C. Jepson, A metapopulation approach to modeling the long-term impact of pesticides on invertebrates. *J Appl Ecol*, **30** (1993), pp. 696–705.
- Srinivasan et al., 2008** • U. T. Srinivasan, S. P. Carey, E. Hallstein, P. A. T. Higgins, A. C. Kerr, L. E. Koteen, et al. The debt of nations and the distribution of ecological impacts from human activities. *PNAS*, **105** (2008), pp. 1768–1773.
- Starfield, 1997** • A. M. Starfield, A pragmatic approach to modeling for wildlife management. *J Wildl Manage*, **61** (1997), pp. 261–270.
- Thorbek et al., 2009** • P. Thorbek, V. Forbes, F. Heimbach, U. Hommen, H.-H. Thulke, P. Van Den Brink, et al. Ecological models for regulatory risk assessments of pesticides: Developing a strategy for the future, Society for Environmental Toxicology and Chemistry and CRC Press, Pensacola, Florida, US (2009).
- Thorbek and Topping, 2005** • P. Thorbek and C. J. Topping, The influence of landscape diversity and heterogeneity on spatial dynamics of agrobiont linyphiid spiders: An individual-based model. *BioControl*, **50** (2005), pp. 1–33.
- Topping et al., 2005** • C. J. Topping, R. M. Sibly, H. R. Akcakaya, G. C. Smith, and D. R. Crocker, Risk assessment of UK skylark populations using life-history and individual-based landscape models. *Ecotoxicology*, **14** (2005), pp. 925–936.
- Van den Brink, 2008** • P. J. Van den Brink, Ecological risk assessment: From book-keeping to chemical stress ecology. *Environ Sci Technol*, **42** (2008), pp. 8999–9004.
- van Engelsdorp and Meixner, 2010** • D. van Engelsdorp and M. D. Meixner, A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *J Invertebr Pathol*, **103** (2010), pp. S80–S95.
- Visser et al., 2009** • U. Visser, K. Wiegand, V. Grimm, and K. Johst, Conservation biocontrol in fragmented landscapes: Persistence and parasitism in a host-parasitoid model. *Open Ecol J*, **2** (2009), pp. 52–61.
- Wallace, 2008** • K. Wallace, Ecosystem services: Multiple classifications or confusion?. *Biol Conserv*, **141** (2008), pp. 353–354.
- Wallace, 2007** • K. J. Wallace, Classification of ecosystem services: Problems and solutions. *Biol Conserv*, **139** (2007), pp. 235–246.
- Wang and Grimm, 2010** • M. Wang and V. Grimm, Population models in pesticide risk assessment: Lessons for assessing population-level effects, recovery, and alternative exposure scenarios from modeling a small mammal. *Environ Toxicol Chem*, **29** (2010), pp. 1292–1300.
- Watanabe, 1994** • M. E. Watanabe, Pollination worries rise as honey bees decline. *Science*, **265** (1994), p. 1170–1170.
- Winfree et al., 2007** • R. Winfree, N. M. Williams, J. Dushoff, and C. Kremen, Native bees provide insurance against ongoing honey bee losses. *Ecol Lett*, **10** (2007), pp. 1105–1113.