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Research

Interactions between human behaviour and ecological systems

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Research on the interactions between human behaviour and ecological systems tends to focus on the direct effects of human activities on ecosystems, such as biodiversity loss. There is also increasing research effort directed towards ecosystem services. However, interventions to control people's use of the environment alter the incentives that natural resource users face, and therefore their decisions about resource use. The indirect effects of conservation interventions on biodiversity, modulated through human decision-making, are poorly studied but are likely to be significant and potentially counterintuitive. This is particularly so where people are dependent on multiple natural resources for their livelihoods, when both poverty and biodiversity loss are acute. An inter-disciplinary approach is required to quantify these interactions, with an understanding of human decision-making at its core; otherwise, predictions about the impacts of conservation policies may be highly misleading.

Keywords: ecosystem services; conservation; social–ecological system; management strategy evaluation; adaptive management; incentives

1. INTRODUCTION

The theme of this issue of the journal is predictive systems ecology. However, in order to be truly predictive in any human-altered environment, the system under consideration must include human users, and this requires the integration of ecology with social science. In this paper, I focus on the potential for closer integration of ecology and social science in order to improve the predictive power of system dynamics models. I draw my examples primarily from conservation science, with an emphasis on guiding the implementation of policies aimed at improving the sustainability of natural resource use.

Traditional ecological studies addressing the effects of human activities on ecosystems include a body of literature on the sustainability of direct resource exploitation, and other major literatures on the effects of by-products of human activity, such as pollution, habitat destruction and climate change. The over-exploitation literature has moved in recent years from a concern with the sustainability of particular levels of harvest mortality, in terms of the population trends of the species being harvested, to a wider concern about ecosystem effects of harvesting, and a more nuanced understanding of the heterogeneity of harvesting effects between species and locations. For example, much work in the 1970s focused on how best to manage fisheries to maintain stocks above a target level [1,2]. Broadening the scope to multi-species fisheries, in the 1990s, authors such as Roberts [3] highlighted the phenomenon of 'fishing down the food chain' such that smaller species at lower trophic levels appeared in the catch as larger predatory fish were depleted. Nowadays, the ecosystem approach to fisheries management is embedded in national legislation (e.g. the USA's Magnuson–Stevens act; [4]) and the challenge is to operationalize this concept [5,6].

At the broader scale, there is increasing attention to predicting the effects of human activities on biodiversity and on particular species groups, difficult because of the likely threshold or nonlinear nature of their response to stressors. For example, climate models predict that the Amazon rainforest is likely to suffer substantial and rapid die-back beyond a climate threshold [7,8], while there is a threshold pH beyond which marine organisms are unable to sequester calcium for their exoskeletons from seawater [9]. Meta-population persistence is also a threshold process depending on the size, quality and configuration of habitat patches [10]. Different processes may lead to different abundance trends for the species concerned, some more linear than others [11].

The ecosystem services research field takes the other side of the equation—how do changes in natural systems feed through to changes in human well-being (as defined by the Millenium Ecosystem Assessment (MEA) [12])? Several steps are required in order to quantify this contribution; firstly, there needs to be an understanding of how changes in human activities impact the dynamics of ecosystems, then how these changes in ecosystem structure, function and diversity affect the range of services that humans use and then

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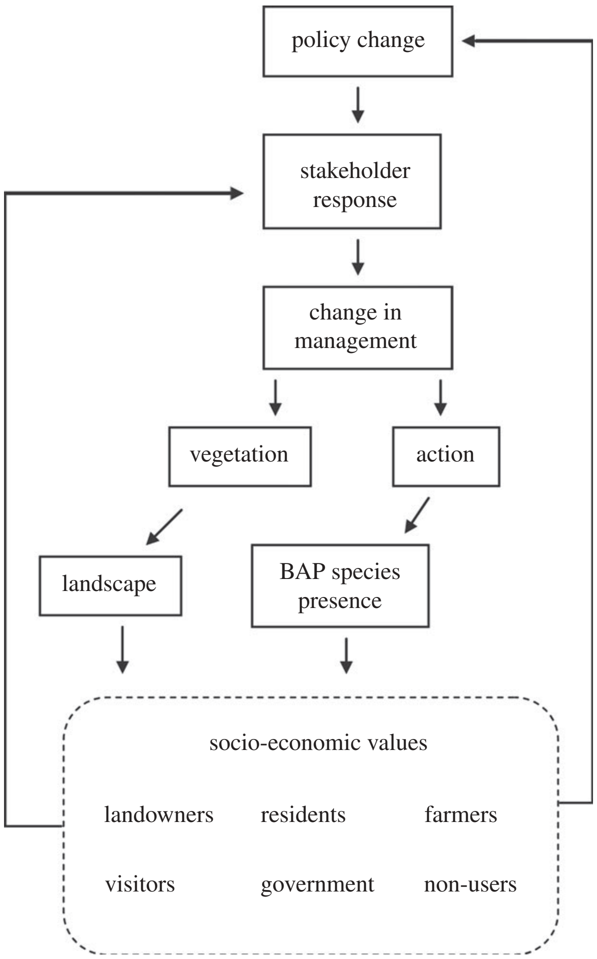

Figure 1. Conceptual model of the links between stakeholder (landowner or farming or grouse shooting tenants) reactions to scenarios of policy or economic change and the conservation value of the UK's North Pennines Area of Outstanding Natural Beauty. 'Landscape' is the proportion of different vegetation types in the area and 'action' refers to stakeholder actions that might affect Biodiversity Action Plan species distributions through means other than changes in the configuration of the vegetation, such as changed grazing regimes altering the level of disturbance. Adapted from Black [15].

how changes in these services feed through into well-being. The metrics at each stage are not straightforward to define and the processes involved are not easy to quantify [13]. This is a very active area of research, following the lead of the MEA [14]. Few people have followed the chain of reasoning right through from changes in management to changes in well-being, with a rare example being Black ([15]; figure 1). She asked land managers in the UK's North Pennines Area of Outstanding Natural Beauty how they would respond to various scenarios of change, including changes in government policy and economic circumstances. For example, in one scenario, consistently low income from shooting grouse (*Lagopus lagopus scoticus*), some land managers suggested that they would turn their moors over to rough grazing. Black then modelled the effects of these changes on the suitability of the habitat for 15 species subject to a UK government Biodiversity Action Plan, and hence on the distribution of these species within the landscape, as modified by land managers in response to the external change. For the grouse income scenario, she was able to link her findings to a study of the relative contributions to visitor well-being of landscape type (grass or heather) and biodiversity presence in the area, measured as willingness to pay for different combinations of biodiversity and landscape composition [16]. This then produced a monetary estimate of the cost of land manager responses to low grouse revenues to a particular stakeholder group—visitors to the North Pennines. Many more studies such as this are required, that take scenarios of policy change right through to monetary estimates of social cost, mediated by land manager decisions and the subsequent changes in habitat and biodiversity.

Research that either quantifies the effect of human activities on biological systems or the effect of biodiversity loss on human well-being is in demand in order to inform current policy initiatives [12]. However, an understanding of the feedback between these two elements is also critical—the process by which changes in people's well-being drive changes in their behaviour towards nature. An understanding of the processes that drive this feedback is required if we are to produce truly predictive models of the effects of interventions or external trends on social–ecological system dynamics, enabling scientists to make management recommendations. There is a substantial field of literature that addresses social–ecological systems (SESs), much of it coming from the Resilience Alliance [17]. This literature has much to say about the dynamics of systems subject to thresholds and nonlinearities, and in some instances includes models of human behaviour as well as ecosystem dynamics [18,19].

The types of approach taken by SES modellers and by ecosystems services and conservation researchers tend to be quite different. Modelling of SESs can be quite abstract and although of heuristic power is not always well grounded in real systems. By contrast, applied scientists working in conservation or on ecosystem services are often too focused on static analyses or on modelling the impacts of one-off stressors, rather than carrying out dynamic analyses that model the underlying processes driving the system and that include the feedbacks between changes in well-being and changes in human behaviour [20]. In this article, I discuss the state of the art in the literatures on quantifying ecosystem services, modelling human decision-making with respect to natural resource use and modelling SES dynamics. I highlight the need for these literatures better to inform the implementation of current conservation approaches that aim to provide incentives for behavioural change. This leads to a discussion of the need to improve the interactions between scientific research and policy implementation. I finish by highlighting the gaps in research effort and understanding which require attention if conservation science is to emerge as a predictive discipline.

2. QUANTIFYING ECOSYSTEM SERVICES

Many of the important questions concerning how best to manage ecosystem services are spatial, involving the trade-offs that occur when managing a single area that provides multiple ecosystem services. For example, Anderson *et al.* [21] mapped three ecosystem services (crops, carbon and recreation) against biodiversity for the UK, and found that the spatial covariance between them was scale- and location-specific, so that in some cases there was a trade-off between the provision of one or the other, while in others there was congruence of provision. Chan *et al.* [22] explored the overlap and trade-offs between ecosystem services and conservation in the Californian coastal region. The Natural Capital project has developed the InVest tool to map and model provision of ecosystem services [23]. These types of analysis are a vital first step towards gaining the information base for making management decisions, but much of the literature is still based on static representations of what is inherently a dynamic situation. Scenarios of future land use can be used to represent alternative futures, ideally based on explicit models of the processes by which these land-use changes come to pass, for example, the LandSHIFT model [24].

Other studies in a similar vein include Naidoo & Adamowicz's [25] mapping of the opportunity costs of proposed protected areas in Paraguay. This involved calculating the potential monetary value of different land uses for the region surrounding a protected area, based on a statistical model of the predictors of production as a function of, for example, remoteness and topography. This type of analysis is valuable when calculating the compensation required under payments for ecosystem services contracts, in which landowners agree to manage their land in particular ways, thus reducing the potential monetary value of the land in order to preserve biodiversity. This spatial approach is also useful in enabling conservation planners to quantify the financial costs involved in different configurations of protected areas. These models are based on current production decisions rather than the feedback between the institutional and economic environment and landowner decisions. As protected areas or conservation contracts are put in place, or as trends occur in external variables such as crop prices, thus changing landowner incentives, the analysis becomes outdated. In other words, statistical models are predictive only to the extent to which current conditions hold; the question then is the extent to which the planned conservation intervention itself would change conditions, hence invalidating the analysis upon which it is predicated.

The conservation planning literature is starting to incorporate dynamics, for example, in modelling the optimal sequence of acquisitions of land under uncertainty [26,27]. Very rarely do these studies consider the effect of changing circumstances on these sequencing decisions, and rarer still are studies that consider the feedback between the conservation actions themselves and external changes. Armsworth *et al.* [28] used a model to demonstrate the potential feedbacks between reserve acquisition and land market prices, and to caution that these feedbacks can even lead to reserve acquisition being counterproductive for conservation if a large proportion of biodiversity is found in unprotected areas. Knight *et al.* [29] highlighted the importance of stakeholder engagement in ensuring that planning is successful. However, an understanding of the mechanisms by which human decision-making (other than the decisions of the planners themselves) has consequences for land use is still lacking in much of conservation planning.

One approach that has been widely used to model possible futures is scenario analysis [30]. For example, Singh & Milner-Gulland [31] examined the effectiveness of current and planned protected areas in covering areas of predicted high probability of the presence of a critically endangered species, the saiga antelope (*Saiga tatarica*) within a landscape in Central Kazakhstan. The scenarios included potential climate change plus conservation success (a large population of the species in substantial herds) or failure (antelopes heavily poached, keeping away from settlements and a low population in fragmented herds). They showed that although the protected areas, concentrated in the northwest of the region, provided good coverage of the current distribution, future scenarios suggested that the southeast would become increasingly important for the species, and would also benefit from protection. However, in this, as in other scenario analyses, the mechanisms by which conservation might fail or succeed, or saigas might stay away from settlements, are assumed rather than modelled.

When evaluating a set of potential conservation interventions, a counterfactual approach is useful, in which the costs and benefits of the 'business as usual' scenario are contrasted with the situation under the conservation intervention [32]. Although these analyses do not include the feedbacks between social and ecological systems, they are useful as a first cut in quantifying and evaluating the potential costs of conservation inaction. However, the fact that people do adapt and respond to conservation interventions, and that their actions feed through into changes in the conservation situation itself is something that needs to be considered, if only to ascertain the situations in which such feedbacks are likely profoundly to influence outcomes, and those in which it is safe to assume that human adaptation will not affect outcomes. As discussed in §4, the tools exist to incorporate such analyses into predictive conservation models.

3. THE EFFECTS OF INDIVIDUAL DECISIONS ON SYSTEM DYNAMICS

Many of the places where people are most dependent on ecosystem services for their livelihoods and well-being are biodiverse areas in the tropics, where poor people's livelihood strategies include multiple activities. These areas are important both for biodiversity conservation and poverty alleviation, and have been the subject of substantial research and conservation interest. One area of active research is the use of household utility models to understand how individual households decide on their labour allocation to wildlife use (e.g. bushmeat hunting), land clearance and crop production, where 'utility' is a quantitative metric of human welfare or happiness. These approaches have been used particularly to address the effectiveness of integrated conservation and development projects (ICDPs) in the context of protected area management [33,34]. These models are similar to those used in agricultural and development economics, and many of them are quite abstract and aimed at understanding broad patterns of behaviour rather than detailed outcomes of policy or environmental change. One of the pioneering applications of this approach to conservation was that of Barrett & Arcese [35], which models the trade-offs that households in the Serengeti make between farming and wildlife hunting and suggests that investment in improving farming incomes may be a better approach to reduce poaching than directly to address levels of wildlife use through managed wildlife hunting.

Models such as these can highlight the potential for indirect and potentially counterintuitive outcomes of interventions. For example, Damania *et al.* [36] used a model of a household that both hunts for bushmeat and farms to demonstrate the effects of potential conservation interventions on hunting behaviour. One such intervention type is the ‘alternative livelihood’ project, in which people are persuaded to reduce their environmentally damaging behaviour (in this case bushmeat hunting) through improvements in earnings from the alternative livelihood, thus raising the opportunity costs of hunting. However, Damania *et al.*’s model showed that while improved agricultural yields led to an increase in the investment of time in agriculture compared with hunting, people did not stop hunting altogether because hunting still provided utility from consumption of bushmeat, which they were able to satisfy owing to their higher incomes. Instead, hunters invested in the more expensive gun hunting rather than snaring, which had the counterintuitive effect of increasing mortality of the most vulnerable species (primates). This study was just a model, with no empirical validation, as is the case for many of this type of study, so it can only highlight the potential outcomes of interventions. Those working on field studies of alternative livelihoods, however, have highlighted similar dangers, of alternatives either subsidising continued environmentally damaging behaviour, or at the least failing to reduce it [37].

Another area in which the effects of policy change on human behaviour have been modelled is marine fisheries. For example, it is important to predict the effect of potential policy interventions, such as marine protected areas (MPAs), on the distribution and the number of fishers. Will fishers who previously used the MPA exit the fishery, shift location and therefore increase the amount of fishing effort in their new location, continue to exploit the closed area illegally, or shift and also change gear to target different fish? A number of studies have used regression approaches to model the factors affecting the probability of vessel fishing in a given area. For example, Hutton *et al.* [38] showed that the best predictors of beam trawler fishing locations in the North Sea included catch levels in the previous year, while Tidd *et al.* [39] showed that a range of different factors influenced whether a vessel chose to enter or exit the beam trawl fishery, including management measures and congestion within the fishery. The factors were generally related to expected profitability. These types of models can then be used in simulations of the effects of proposed policy changes on overall fishing effort and its location [40]. In this last study, the model considered the effect of fishing effort redistribution on the status of benthic communities. However, there has been very little similar work done on the factors affecting effort levels in time and space in small-scale artisanal fisheries, and then further to the long-term sustainability of fishing as an activity within an SES.

A similar issue to predicting the effect of an MPA on fishing effort is that of predicting the effect of protecting an area of forest from deforestation on the rate of deforestation in other areas. This issue, termed leakage, is highly topical in the context of reducing emissions from deforestation and forest degradation (REDD) in developing countries, a major component of international actions to curb carbon emissions under the UN Framework Convention on Climate Change. There have been many models of the factors affecting deforestation rates, carried out at a range of scales and using different approaches (reviewed by Angelsen & Kaimowitz [41]). Most are concerned with the drivers of deforestation and the effects of policy interventions on these drivers, but less so with the dynamics of SESs as a whole.

4. MODELLING SOCIAL–ECOLOGICAL SYSTEMS

SES models explicitly include the linkages between ecological and social drivers of system dynamics, often examining the role of uncertainty in driving system dynamics and human behaviour, and often aimed at producing heuristic insights rather than detailed policy recommendations [42]. The social–ecological model of Holdo *et al.* [19] is unusually detailed in exploring the linkages between the complex ecological system of the Serengeti and household decision-making at a landscape scale. It highlights the importance of rainfall in driving the dynamics of both the ecological system and the distribution and the number of households, and contrasts this with the effects of anti-poaching activities, which only affect human use of wildlife. One conclusion of the model is that the configuration of the Serengeti ecosystem means that even if human population density rises dramatically outside the protected area, the wildebeest population is likely to remain high because the remoteness of core areas acts as a refuge from poaching. This is the type of study that needs to be integrated into predictive analyses of conservation interventions, conservation planning and ecosystem service modelling if they are to be truly useful to policymakers. However, Cooke *et al.* [43], in reviewing the field of agro-ecology, found very few integrated social–ecological models, and commented that this meant that the impacts of interactions between social and ecological processes could be missed.

The long tradition of SES modelling, and of modelling human decision-making more generally, means that many tools already exist. One particularly useful technique for representing human decision-making in SES models is agent-based modelling (ABM), in which the decision-making of autonomous agents is explicitly modelled at the individual level, producing emergent behaviour at the population level [44,45]. ABMs are conceptually closely allied to individual-based models in ecology [46]. Within an ABM, each agent uses a decision-rule to choose between a set of strategies based on the available information. ABMs allow great flexibility in the specification of agents' decision rules, in contrast to household utility models, for example, which model rational choices made by households acting to maximize their utility. Evidence suggests that, in many circumstances, humans are only boundedly rational: they may aim to satisfy their basic needs rather than maximize utility, or may make decisions according to simple heuristics or rules of thumb [47]. ABMs also provide a natural route for modelling heterogeneity in individuals' decision-rules, preferences, abilities and resources because these characteristics can be specified agent by agent. Population-level dynamics within an ABM arise through the interaction of agents with one another, and with their natural and institutional environments. Consequently, ABMs have been used in a number of contexts to examine whether the micro-level processes specified in the model lead to emergent patterns corresponding to those observable in the real world (e.g. Ling & Milner-Gulland [48] for hunting and Manson & Evans [49] for deforestation).

ABMs are highly flexible tools for the study of complex SESs, but often they are not linked to a model of ecological dynamics that can be used to examine the long-term effects of interventions on system sustainability. One example where this has been done is van Vliet *et al.* [50], who modelled the combined effect of spatial heterogeneity and hunter movement patterns on duiker population sizes, using a realistic model of duiker biology and data on hunter behaviour from a field study. This model showed that small-scale spatial heterogeneities in duiker habitat preferences and the non-random distribution of hunters and animals led to a higher and more sustainable harvest than if either hunters or duikers had been randomly distributed within the landscape.

5. GUIDING CONSERVATION INTERVENTIONS

It is ironic that the current fashionable approach to conservation interventions is explicitly based on altering the incentives and hence the behaviour of users of ecosystem services, despite the lack of a conceptual foundation for analysing the likely effects of this approach. Conservation interventions based on changing incentives include market-based instruments of various kinds, including payments for ecosystem services (PES) which differs from other approaches to conservation in that payments are made conditionally upon the service provider actually providing the service [51]. A biodiversity PES might involve paying villagers to guard bird nests or to refrain from deforesting their land [52]. Predicting the effectiveness of a PES intervention depends on an understanding of how the intervention will affect the decision-making of the resource user. There have been a number of overviews of the effectiveness of PES, based on empirical data (e.g. a special issue of *Ecological Economics*; [53]). However, the conceptual foundations for understanding the processes behind responses to such interventions are still under-researched. Frameworks such as the theory of planned behaviour [54], the design rules for community-based interventions for common property resource management [55], or approaches from a range of other behavioural sciences (summarized by Gintis [47]) will be useful for building this predictive base.

One powerful conceptual framework for predicting the strategic behaviour of resource users is game theory. This framework is still underused in conservation [56]. Game theory can be used to construct experiments in which predictions about how people will behave under particular circumstances are tested in the field; these tests can be used to better understand how interventions may change people's resource use behaviour. For example, Travers *et al.* [57] used a game involving the extraction of fish from a communal pond to investigate the relative effectiveness of a range of interventions in controlling resource use. The interventions (treatments) included allowing the participants to discuss and agree extraction rates in advance and then telling the group what each person had done after each round of the game (to mimic social pressure to conform to rules), as well as fines for overexploitation or payments for sustainable use, either to individuals or to the community as a whole. In some treatments, the fines or payments were externally imposed, in others, the players were able to decide among themselves who was to receive them. One interesting result was that those treatments that promoted self-organization by the group, rather than individual responses to external pressures (such as the scenario in which the group as a whole had to decide who among them would get the payment) not only substantially reduced extraction rates, but also had a knock-on effect in reducing extraction in subsequent treatments, regardless of which treatments these were. Other field studies have also highlighted the importance of self-organization in promoting cooperation in natural resource use [58,59]. In the context of PES, these types of studies suggest that payments made just to individuals may be much less effective in the long run than the more difficult and longer term approach of improving local governance and fostering institutional structures that promote cooperation [52].

6. LINKING SCIENCE AND MANAGEMENT

Prediction in applied science is most useful if it guides decision-making by policy-makers. While SES models are powerful tools for modelling and predicting system behaviour, they are not explicitly intended as frameworks for evaluating the performance of competing management strategies, or for exploring the effect of different approaches to generating management rules or monitoring strategies (although they could be used in such a way). One framework that has been developed explicitly to do this is management strategy evaluation (MSE), which is used to provide management advice in the presence of uncertainty, and in situations in which the potential for real-world experimentation is limited. It is fast becoming the dominant framework for the development and assessment of management procedures for commercial fisheries [60,61]. The approach uses simulation in a virtual environment to test the robustness of potential management strategies to a range of uncertainties. Unlike traditional approaches, an MSE explicitly models the whole management system; not just the resource stock and its reaction to different harvest rules, but the gathering of data, the conversion of those data into a harvest rule and the implementation of that rule [62]. This allows fisheries scientists to evaluate the effects of a lack of knowledge or understanding on the performance of harvest rules. The management advice that comes from MSEs is non-prescriptive and probabilistic, enabling stakeholders to evaluate the trade-offs inherent in choosing one or other management procedure. Indeed, one of the strengths of MSE is that it can encourage the participation of stakeholders, both in defining the metrics against which the performance of harvest rules can be evaluated, and in the generation of scenarios for testing the robustness of these rules, leading to greater buy-in to the eventual agreed procedure [63].

Although MSEs have been extensively and almost exclusively applied to commercial fisheries to date, the approach has substantial potential in other areas of resource management, wherever large-scale experimentation to resolve uncertainty is impracticable [64]. However, the applicability of current MSE models is limited by their general lack of realism in the modelling of harvester behaviour. Illegal exploitation is a recognized problem for commercial fisheries and is a key reason why the outcome of fisheries management may differ from managers' expectations. Despite this, the majority of past and current research into MSEs is still focused on the uncertainties surrounding the resource population and its observation, rather than on the implementation of harvesting rules [65]. Milner-Gulland [66] incorporated a household utility model into an MSE framework, which dramatically increases the flexibility of the framework, for example, enabling the analysis of the trade-off between monitoring the ecological system to improve estimates of the resource population size and monitoring harvesters to deter them from poaching (figure 2). The addition of a household utility model also opens up the possibility of examining the effectiveness of interventions targeting other livelihood activities such as farming, not just the direct effects of harvest rules.

MSE is closely allied to adaptive management (AM). Many authors have highlighted the crucial importance of taking an adaptive approach to conservation, so that science and practice inform one another through ongoing learning about the system [67]. However, it is also widely acknowledged that AM has not percolated into conservation practice, despite its strong appeal to academic researchers [68,69]. This is partly because of the additional costs involved, and the inherent risks of experimentation, but also because there is still a strong divide between practitioners and academics [70]. Knight *et al.* [71] found that two-thirds of conservation assessments in the peer-reviewed scientific literature did not deliver

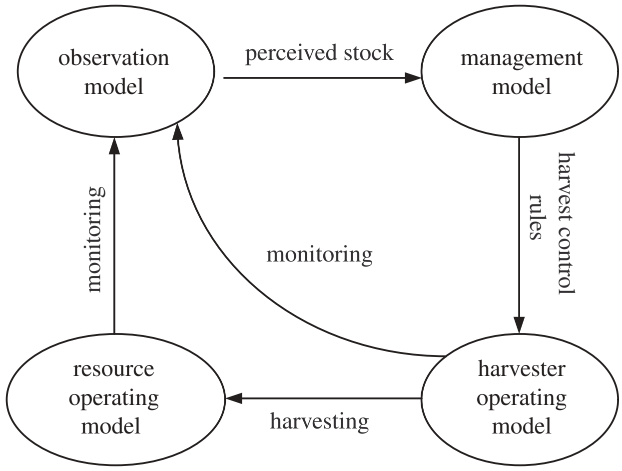

Figure 2. Flow diagram for the management strategy evaluation framework comprising a resource operating model (simulating the 'true' population biology of the species), the observation model to monitor the species (with error) and the management model, using information about the stock to create and implement harvest control rules. In the extended model, the harvest control rule is fed into an additional harvester operating model that allows for individual decision-making by harvesters and monitoring of harvester behaviour.

conservation action, primarily because researchers never planned for implementation of their findings. This is despite the fact that conservation science is an applied discipline founded on the need for intervention to halt the loss of biodiversity.

7. CONCLUSIONS

There is a pressing need for predictive research on the dynamics of linked human and ecological systems in order to inform interventions to conserve biodiversity while sustaining human livelihoods. Research in the field of natural resource management (encompassing conservation, sustainable use and ecosystem services provision) is flourishing, but as yet, the feedbacks between management actions, resource user decisions and ecological sustainability are not receiving the attention they deserve. Instead, there is substantial effort being invested in quantifying the individual directional impacts of humans on nature and nature on humans. This is likely to be a reflection of our lack of knowledge about the processes underlying the relationships between ecosystems and society. However, unless we start to build process-based models and actively test them in an adaptive framework, this situation will not improve [20]. The social sciences have much to offer in terms of existing understanding of human behaviour and analytical frameworks, that could be much better exploited by those concerned with natural resource management [72].

There have been few predictive studies addressing the feedbacks between human behaviour and ecosystem dynamics outside the SES literature. However, there is plenty of empirical evidence for the importance of understanding human incentives in order to intervene effectively to combat biodiversity loss. This is to be found in the litany of conservation failures to date: the criticisms of ICDP as an approach [73], the difficulty of constructing payments schemes that are sustainable into the long term, and the counterproductive effects of alternative livelihoods schemes and buffer zone projects around protected areas [74]. Of course, conservation has successes as well, and researchers are becoming highly sensitized to the need for counterfactuals and controls, so that the impacts of interventions are properly measured and their effectiveness evaluated [75]. There are huge gaps in our knowledge about the dynamics of ecosystems that must be addressed. However, there is also a need for the investment of substantial research effort into understanding the dynamics of human decision-making in a changing world, based on existing bodies of knowledge in social science. In particular, conservation scientists and resource managers need to know how their interventions alter the incentives and thus the behaviour of the people causing biodiversity loss. Unless this research agenda is addressed, robust predictions of the dynamics of human–ecological systems under environmental, social and policy change will remain elusive.

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