The poor management of natural resources has led in many cases to population decline and extirpation. Recent advances in fisheries science have the potential to revolutionize management of harvested stocks by evaluating management scenarios in a virtual world, by including stakeholders, and by assessing its robustness to uncertainty. These advances have been synthesized into a framework, Management Strategy Evaluation (MSE), which has hitherto not been used in terrestrial conservation. We review the potential of MSE to transform terrestrial conservation, emphasizing that the behavior of individual harvesters must be included since harvester compliance with management rules has been a major challenge in conservation. Incorporating resource user decision-making required to make MSEs relevant to terrestrial conservation will also advance fisheries science.
system dynamics and uncertainty and so are prone to failure [1, 2]. The realization of the
importance of learning about the dynamics of the system led to adaptive management [1], in
which monitoring of the system allows updating of managers’ models of system dynamics,
which then produces alterations in the harvest in an iterative process. Adaptive harvest
management (AHM) has been successfully applied to ducks, mule deer and sandhill cranes in
the USA [3-6].

Despite the advances made by AHM, harvest management models still do not explicitly
incorporate the social processes underlying harvester behavior, and are based on the use of a
“best” management solution to achieve a single objective given the current best knowledge.
Where the system is relatively simple and harvesters abide by rules, such as in some
recreational hunts in the developed world, this may not be problematic. However, in complex
systems, with multiple stakeholders and severe uncertainties, it is generally difficult to
provide a single best harvest policy [7]. Instead, there is a need to find robust approaches that
meet management objectives under a range of potential states of the world [8]. One approach
that aims to do this has gained considerable ground within fisheries science, Management
strategy evaluation (MSE), uses simulation models within an adaptive framework that
enables the comparison of alternative strategies in a virtual world under multiple and often
conflicting objectives [9]. In this paper we argue that MSE is a potentially valuable tool for
terrestrial conservation if the framework is expanded to include individual harvester decision
making.

MSE, in common with adaptive management more generally, has four major advantages over
standard approaches to providing management advice: (i) It allows experimentation with a
range of possible management procedures under a range of circumstances. Real world
experimentation is highly desirable in order to disentangle the drivers of a system, but is
difficult to pursue for the majority of natural resources because of the dependence of
individuals and firms on resources for their livelihoods and the spatial extent of the systems.
In conservation, real world experimentation poses ethical dilemmas: local people often
depend on ecosystem services for subsistence, while endangered species may face extinction.

(ii) Stakeholders can be directly involved in the development of the management scenarios
and the evaluation of the metrics by which the performance of different management options
is assessed. A key feature of the MSE approach is that an optimal strategy or solution is not
pursued, but instead policies are sought that are feasible, robust to uncertainty and provide
adequate management performance with respect to multiple criteria [9, 10]. This allows for
more transparency in the management process and promotes stakeholder acceptance and
support. (iii) MSE enables researchers and managers to examine the implications of various
forms of uncertainty, including process, measurement and structural uncertainty, on the
performance of different management options. (iv) MSE carries out prospective rather than
retrospective evaluations of the performance of different management procedures under a
range of circumstances. By comparing the performance of a range of alternative strategies
under plausible scenarios upfront, the response of the system can be compared to the desired
goals and evaluated in advance of implementation (Box 1) [11].

In this paper we start with an explanation how MSE works (Figure 1). We pay special
attention to the improvements in management of a real fishery system that MSE has enabled,
illustrated with a case study (Box 1). We then outline the role of individual harvester
decision-making and socio-economic drivers on management effectiveness, and argue that
there is a need to explicitly include this in order to develop the MSE approach further, both
for fisheries and for terrestrial conservation. We show how MSE can be applied to terrestrial
conservation using two case studies, brown bear *Ursus arctos* hunting in Slovenia and Croatia and bushmeat hunting in the Serengeti (Box 2). Finally, we conclude that explicitly including harvester decision-making in the MSE approach increases its realism and opens new horizons to improve the sustainability of harvesting for exploited species.

**How management strategy evaluation works**

The MSE approach is based upon a set of models of the “true” population dynamics of the species (called “operating model”; Figure 1, Glossary). The operating model aims at capturing the key processes in the dynamics of the fish population given the best ecological knowledge available and can be thought of as a minimum realistic model [12].

The next step in the MSE is to simulate the process of monitoring the stock, resulting in simulated measurements such as biomass or number of individuals. Information from monitoring is always imperfect as it is impossible to detect every single individual or cover the entire area of interest. Monitoring is represented by the “observation model”, whereby the statistical features of the collection of relevant data are simulated, including both error and bias.

The observation data are then passed to the “management model”. The management model encompasses the harvest control rule (HCR) but may also contain an implementation error component. The HCR can be either model based, which includes an assessment of resource status, or an empirical algorithm. The HCR may reference biological or socioeconomic reference points to produce management actions in the form of a harvest or effort level, changes in gear or spatial and temporal restrictions. Management actions are rarely implemented without error. This error can come from two main sources: (i) resource users do
not comply with the regulations, and (ii) the individual dynamics of resource users (e.g. when and where harvest is taken) are not accounted for in the HCR. Neither source of implementation error is generally modeled based on human decision-making in standard MSEs, instead implementation is simulated as a probability distribution around the HCR [13, 14]. The full system model therefore contains the operating model (biological “truth”), the observation model, the management model, by which the HCR feeds back into the resource operating model as the model updates to the next time-step (Figure 1).

By evaluating a range of HCRs against a set of plausible operating models, using multiple performance metrics, MSE enables fisheries scientists to give resource managers advice on robust management procedures (see Glossary), and on the trade-offs involved with each procedure. The learning process can be incorporated into (i) the assessment component of the management procedure when new observations become available; or (ii) the decision process based on a review of the performance of the management strategy. Together with modeling tools such as sensitivity analysis, MSEs can evaluate which data and how much of it should be collected and how often monitoring should be carried out to improve management performance. Stakeholders can be involved at various points in the process of proposing and evaluating different HCRs and assessment approaches. There is ample evidence from both terrestrial conservation and fisheries that stakeholder involvement throughout the process of resource management is key to compromise between stakeholders, acceptance of the rules and hence the sustainability of resource use [15, 16].

**Uncertainty in natural resource management**

One of the main strengths of MSE is that it brings uncertainty to the centre-stage in the modeling process. Uncertainty plays a fundamental role in the dynamics of ecological and
economic systems, in our measurement and understanding of these systems, and in the
devising and implementation of rules to control harvesting. Various classifications exist, and
we use that of Milner-Gulland and Rowcliffe [17]: Process uncertainty comes from the
variation in the system itself (e.g. weather affecting demographic rates). Measurement
(observation) uncertainty occurs in any process of collecting field data and might be due to
crude devices or mistakes during measurement. These two forms of uncertainty combine to
form parameter uncertainty. Structural uncertainty, also called model uncertainty, has
received increased attention in modeling natural resources and represents our lack of
understanding of the dynamics of the system [18]. For example, implications of structural
uncertainty on whale stocks was examined extensively by the International Whaling
Commission [19] and whether hunting mortality is additive or compensatory was
incorporated in ducks in the USA [3]. Representing structural uncertainty is generally
difficult because a model representing the real system according to our perceptions is only
one possible way in which the system could function. Implementation uncertainty surrounds
the translation of policy into practice, and has been poorly covered in the natural resource
literature, as its causes lie within social science; one example is institutional inertia, another is
non-compliance with rules. Because MSE models the entire resource management system,
rather than just the resource stock dynamics, it can incorporate all these types of uncertainty
and quantify their relative importance.

Future directions for natural resource management

Including the wider ecosystem

Most applications of the MSE approach to date have focused on harvest strategies for target
species. The indirect effects of harvesting on the ecosystem are still rarely incorporated into
MSEs, but this is changing as fisheries science increasingly takes an ecosystems approach
(e.g. Atlantis model for south-eastern Australia [20, 21]). Multi-species population models and effects on the wider ecosystem have recently been included in an MSE for a prawn fishery in Australia [22, 23]. Similarly, MSEs are now being used to evaluate strategies for limiting bycatch [11] including cetaceans [24].

More realistic economics

Economically-based management has been demonstrated to be better both in terms of the sustainability of the stock and the profitability of fishing [25]. However, many fisheries management plans are still based on outdated concepts of Maximum Sustainable Yield [26]. Although more effort is now being directed towards including economics explicitly into MSEs [27, 28], the development of approaches that allow MSEs to incorporate broader social and economic objectives remains an important and urgent area for future research [8]. One fundamental constraint is the lack of reliable economic data, particularly cost data, as the fishing industry is not always willing to release their financial information. Further institutional effort is required to establish a mechanism to collect reliable cost data, such as through strengthening stakeholder involvement and industry collaboration in developing management objectives.

Realistic representation of implementation

Hunting and fishing are crucial contributors to people’s livelihoods in many parts of the world. Management often works against the short term economic interests of those who depend on resources by decreasing the harvest or closing areas to protect its natural resources. Given the vast areas involved and budgetary constraints, enforcement is generally poor and attempts to control resource use are therefore often ineffectual. The assumption in the vast majority of MSEs that rules are implemented either directly or with simple random
errors is clearly inadequate. Instead, rules affect the resource population indirectly, via the
decisions of resource users. Research into factors affecting compliance with conservation
rules is starting to blossom [29-31].

In commercial fisheries, non-compliance and deviations from set quotas are due to the
economic incentives faced by individual fishers; their knowledge of current and past stock
status and its spatial distribution have recently been included in MSE models [22, 23, 32, 33].
Furthermore, models on the line fishery of the Great Barrier Reef include how individual
fishers select reefs, infringe into marine protected areas, and communicate information
amongst each other [34, 35].

Subsistence or artisanal harvesters operate at the household, rather than the firm level. This
means that rather than maximizing profit, the harvester aims to maximize household utility
(“satisfaction” or “happiness”). Utility is maximized based upon household consumption of a
range of goods, met from production and sale of products derived from livelihood activities
such as agriculture, bushmeat hunting or aboriginal subsistence whaling [36, 37]. Models of
household utility could be incorporated into an MSE as part of the operating model,
representing the “true” state of the harvester component of the system [37-39] (Figure 1). The
harvester operating model mediates the effect of management rules on the resource stock, and
can also be observed, with uncertainty, by the manager.

This enhanced framework allows the inclusion of a wider range of management objectives
and performance metrics than standard MSEs; not just the maximization of biological or
economic yield and minimization of the risk of population reduction below a threshold, but
also maximizing household utility [40]. The welfare of resource users is of key importance in
current conservation thinking, which focuses on the importance of considering human
welfare, securing ecosystem service provision and integrating conservation and development.

Trade-offs in model complexity
With further advancement of knowledge on ecosystems and species interactions and faster
computing power, there is a tendency to increase model complexity. Simple HCRs based on
empirical data and threshold rules make management more transparent, faster and less
technically challenging to implement and should be integrated within model-based
assessments that may more accurately reflect resource stock dynamics [41]. Improving the
apparent realism of the management procedure through more complex model structure may
not necessarily improve performance [42]. The operating models used in the testing process
need to include as much complexity as necessary to adequately capture key dynamics of the
system [43]. Including harvest behavior is a key factor in many natural systems and by
including this explicitly progress may be made more rapid than by increasing the complexity
of the resource operating model. However, performance statistics based on harvester utility
should be simple and transparent to ensure stakeholders engagement and understanding.

Technical challenges to MSE application
If MSEs are to become widely applied outside fisheries, technical capacity building is
required, and theory and models need to become more accessible to less quantitatively
orientated researchers. Collaborative software development projects have started to make
MSE models more widely available [44], but the inclusion of a harvester operating model
would add further difficulty, as these models come from another discipline. Collaboration
between natural scientists, economists and sociologists is required to overcome these
disciplinary barriers. A freely available suite of methods in the R statistical language, FLR
(Fisheries Library in R [44]), already exists. FLR has a wide array of MSE examples across a range of fishery systems and could be adapted to meet the needs of the wider resource management community.

Strengthening links to active adaptive management

Active adaptive management (AAM) is a subset of AHM in which managers set out deliberately to learn from the system through experiments and monitoring in a real-world system [45, 46]. By contrast, in MSE learning is carried out in a virtual world. Since the formulation of the AAM framework, many studies have suggested it could be useful, but seldom have researchers and stakeholders actually implemented the complete framework [47]. Integration of periodic MSEs into the AAM cycle could give added impetus to both, given the great success of the MSE approach in real-life fisheries management [11], and this is already happening in an ad hoc manner in many fisheries.

Limitations of MSE

The management of natural resources is plagued by uncertainty and feedbacks between the dynamics of resources and users. Although MSE goes some way towards addressing these difficulties, it has been criticized for: (i) having a longer development time, and thus increased costs, than traditional methods such as reference-based off-take rules; (ii) an upfront MSE can provide an overly rigid framework without room for decision makers to change management in an adaptive way; and (iii) poor data inputs, such as gaps in monitoring or extremely low estimates of uncertainty, impact the performance of MSE, which needs to be recognized and explored within the MSE process [48-50]. These criticisms point to the need for an iterative process of monitoring, learning and adaptation, which is entirely in
keeping with the MSE approach if practitioners are prepared to engage with the issues being
raised.

There are barriers to the implementation of MSE in terrestrial conservation, and it is not
appropriate to every situation. Hockley et al. [51] show that the effort and costs involved in
monitoring crayfish trends are too high for the development of a locally-based monitoring
system to be worthwhile which implies the need for more precautionary and risk averse
management. Monitoring must have the potential to inform interventions aimed at changing
the behavior of resource users (whether these are direct HCRs or other approaches such as
alternative livelihoods). If the links in the chain in Figure 1 are non-existent, then a MSE is
not feasible; for example in some natural resource user systems, monitoring needed for the
observation model or a manager might be missing. In some systems harvesters might abide
by the rules set by managers and then a simpler framework would be more parsimonious.
Even in these cases, however, an MSE approach would be a useful tool for highlighting the
effects of uncertainty on management decision-making.

Conclusions
To date, the only application of a comparable approach to MSE outside fisheries has been by
Chee and Wintle [52], for management of over-abundant species. However, the MSE
approach has enormous potential for exploited resources that face competing objectives and
where harvester decision-making is an important consideration. The MSE approach is no
longer limited to top-down management of a single species by an all-powerful manager.
Work has already started to extend the MSE approach to more complex systems, to include
the ecosystem effects of harvest and to improve the economic realism of the models. Further
expansion of the approach to include explicit models of harvester decisions would
dramatically increase the applicability of the approach outside commercial fisheries.

However modeling complexity, particularly when models from different disciplines are combined, comes at the cost of potential loss of transparency and the link to reality. Joint efforts to develop tools to handle, visualize and communicate the models underlying MSEs are ongoing [44], and need to be extended to encompass this wider agenda if the full potential of MSE to improve management of natural resource use is to be realized.

Box 1

Example of the successful use of MSE in fisheries

The Southern and Eastern Scalefish and Shark Fishery (SESSF) in Australia is a complex multi-species, multi-gear fishery with 34 stock units managed under a quota system as well as restrictions on gear and input controls implemented based on expert judgment. Despite the introduction of a quota system in 1992, a number of quota-managed species remained overfished. In 2005 a comprehensive harvest strategies framework was introduced and implemented into the SESSF. This framework is similar to a management procedure, where the process of monitoring and assessment is included as well as explicit harvest control rules [41], but at that time, the performance of candidate strategies had not yet been formally evaluated through simulation prior to adoption (such as is done in MSE). Instead, the harvest strategy framework was implemented based on expert judgment and prior experiences of MSE and harvest strategies for other fisheries. The framework involves a “tiered” approach, where 4 different harvest control rules are applied for stocks based on the information available about the stocks and the levels of uncertainties involved in their stock assessments. For example, a stock is classified as tier 1 if there is a “robust” quantitative assessment, and tier 2 if it has a less certain or preliminary assessment. From 2006, a full MSE was conducted, including formal evaluation of harvest strategies. In 2008, Smith et al. [11]
evaluated the lessons learnt from this fishery concerning the benefits of a harvest strategy framework compared to conventional fisheries management. Since the introduction of the framework in 2005, there has been an overall net decrease in the total quota level set for the fishery, with concomitant conservation benefits, but also a more favorable response to science-based policy recommendations from both industry and managers due to the well-specified and adopted decision rules. This is testified to by the fact that the time and effort taken to reach agreement on the total allowable catch (TAC) limits each year has significantly reduced, from several weeks to less than two days. The general lessons learnt from this case study include the importance of formally testing management options using MSE prior to implementation, rather than post-hoc, the difficulty in defining rules to deal with bycatch TACs for this multi-species and multi-fleet fishery, and the need for flexible and pragmatic implementation by managers [11].

**Box 2**

**The potential for MSE in conservation**

A recent workshop highlighted examples where an MSE approach would shed new light on the issues surrounding the management of harvested terrestrial systems [53]. The first example considers the management of the brown bear (*Ursus arctos*) in Croatia and Slovenia [54] (Figure 1 within Box 2). Traditionally, the brown bear was hunted as a trophy species in both countries but since Slovenia entered the EU in 2004 the species is protected under EU law. Slovenian bears are now culled to control population size. With their neighboring non-EU country Croatia continuing to manage bears as a trophy species, two contrasting systems are currently managing the same population. The MSE approach could contribute to a cooperative approach between the two countries by demonstrating the potential benefits of a joint monitoring and management decision framework. Collaborative monitoring could
potentially reduce uncertainty in the estimated total population size, allowing more informed quota-setting. Furthermore, the incentives of hunters differ between the two countries based on their hunting regimes. Finally, manager decision-making is strongly dependent on social and political conditions in the two countries, and these social issues as well as hunter decision-making need to be incorporated in the development of scenarios for the management of this population.

The second example comes from bushmeat hunting in Tanzania which is in theory state-controlled by licenses and quotas (Figure 2 within Box 2) [55, 56]. However, non-compliance is high and hard to quantify because hunting is dispersed and heterogeneous both spatially and temporally, and in terms of catch compositions. For the sustainable management of such a system it is crucial to understand the incentives of local people who hunt. The current management system faces high uncertainties due to a lack of governance and control, such that the system is effectively open access hunting for an illegal good. There is also no benefit distribution to act as an incentive not to hunt bushmeat. This case study is an excellent example of a linked social-ecological system, where MSE could be used to explore feedbacks between conservation incentives and livelihood decisions (Figure 1). Instead of focusing on testing just the performance of HCRs, the MSE approach can be adapted to investigate the effectiveness of a range of other conservation policies through their effects on hunter’s decision-making (for example providing alternative livelihoods or direct payments for conservation services).

Acknowledgements

NB and EJMG were supported by the European Commission under the HUNT project of the 7th Framework Programme for Research and Technological Development. Neither the
European Commission nor any person acting on behalf of the Commission is responsible for the use made of the information. The views expressed in this publication are the sole responsibility of the authors and do not necessarily reflect the views of the European Commission. EJMG also acknowledges the support of a Royal Society Wolfson Research Merit award, and thanks Franck Courchamp and the Department of Ecology, Systematics and Evolution at the Université Paris Sud for hosting EJMG during working on this paper. We thank Justin Irvine, Emily Nicholson, Ana Nuno and Lynsey McInnes, Charles Edwards, Julia Blanchard, Andre Punt and two anonymous referees for invaluable comments.

**Figure 1:** 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 the perceived stock to create and implement the harvest control rules. In the extended model (dotted line) the harvest control rule is fed into an additional harvester model which allows for individual decision-making by harvesters. In this model, the harvester can also be monitored through the observation model (dotted line).

**Glossary**

**Assessment model:** A mathematical model coupled to a statistical estimation process that integrates data from a variety of sources to provide estimates of reference points and past and present abundance, mortality, and productivity of a resource.

**Harvest control rule (HCR):** A set of well-defined rules used for determining management actions in the form of a total allowable catch (TAC) or allowable effort.

**Harvest strategy:** Intended meaning may be synonymous with MP.
Implementation model: The process of application of the management action, including the uncertainty involved in the process.

Management model: A model of the process of management, which encompasses the harvest control rule (HCR) and may also contain implementation error.

Management procedure (MP): The process of using monitoring data and a formula or model to generate TAC or effort control measure.

Management strategy evaluation (MSE): The process of testing the performance of generic MPs or harvest strategies against predefined metrics such as mean and variance in yield.

Management strategy: Usually synonymous with MP but sometimes used to mean an HCR.

Observation model: The component of the OM that generates simulated monitoring data from observation of the dynamics of the natural resource stock, for input into an MP.

Operating model (OM): A mathematical–statistical model used to describe the true state of the system in terms of (i) the natural resource dynamics and (ii) the harvester behavior.

Total allowable catch (TAC): Catch limit to be taken from a resource within a specified period.

Utility: Measure of relative satisfaction or happiness from consumptive and monetary goods (e.g. amount of harvest) and non-monetary goods (e.g. leisure time, satisfaction from recreational hunting).

Figure 1 within Box 2

Brown bear (Ursus arctos) management in Slovenia and Croatia as a case study in terrestrial conservation where a Management Strategy Evaluation approach could give new insights.

Photo by Miha Krofel.
Figure 2 within Box 2


References

variable stocks and with conflicting objectives: Experiences in the South African pelagic
fishery. Rev Fish Biol Fisher 8, 177-214
16 Waylen, K.A., et al. (2010) Effect of local cultural context on the success of community-
based conservation interventions. Conserv Biol 24, 1119-1129
Use: A handbook of techniques. Oxford University Press
Fish 8, 315-336
International Whaling Commission
of marine bay ecosystems. Ecol Model 174, 267-307
21 Smith, A.D.M., et al. (2007) Scientific tools to support the practical implementation of
ecosystem-based fisheries management. Ices J Mar Sci 64, 633-639
strategy evaluation: Bringing in economics and the effects of trawling on the benthos. Fish
Res 94, 238-250
fisheries. P Natl Acad Sci USA 107, 16-21
to uncertainty: lessons from the International Whaling Commission. Ices J Mar Sci 64, 603-
612
1601
26 EU (2006) Implementing sustainability in EU fisheries through maximum sustainable
yield In Communication from the Commission to the Council and the European Parliament
COM 360, Commission of the European Communities
management measures for anchovy in the Mediterranean Sea. Ices J Mar Sci 67, 1291-1300
Georgia Patagonian Toothfish Fishery. Mar Resour Econ 25, 265-280
29 Keane, A., et al. (2008) The sleeping policeman: understanding issues of enforcement and
compliance in conservation. Anim Conserv 11, 75-82
conservation. Biol Conserv 143, 1025-1030
Conser Biol 24, 89-100
effort management. Aquat Living Resour 21, 265-273
34 Little, L.R., et al. (2005) Effects of size and fragmentation of marine reserves and fisher
infringement on the catch and biomass of coral trout, Plectropomus leopardus, on the Great
Barrier Reef, Australia. Fisheries Manag Ecol 12, 177-188
fisheries quota. Ecol Model 220, 3404-3412
16, 437-444
development projects: Linking harvest to household demand, agricultural production, and
environmental shocks in the Serengeti. *Land Econ* 74, 449-465
39 Winkler, R. Why do ICDPs fail?: The relationship between agriculture, hunting and
ecotourism in wildlife conservation. *Resource and Energy Economics*
40 Milner-Gulland, E.J. (2011) Integrating fisheries approaches and household utility models
for improved resource management. *P Natl Acad Sci USA* 108, 1741-1746
42 Walters, C.J. (1985) Bias in the estimation of functional relationships from time-series
data. *Can J Fish Aquat Sci* 42, 147-149
44 Kell, L.T., et al. (2007) FLR: an open-source framework for the evaluation and
development of management strategies. *Ices J Mar Sci* 64, 640-646
fishery ecosystem objectives. *Ices J Mar Sci* 57, 731-741
management over a range of time horizons. *J Appl Ecol* 45, 72-81
negatives. *Ices J Mar Sci* 64, 613-617
49 Rochet, M.J. and Rice, J.C. (2009) Simulation-based management strategy evaluation:
problems or misinterpretations? *Ices J Mar Sci* 67, 567-574
51 Hockley, N.J., et al. (2005) When should communities and conservationists monitor
exploited resources? *Biodivers Conserv* 14, 2795-2806
integrated approach to controlling overabundant wildlife. *J Appl Ecol* 47, 1169-1178
through cross-fertilization between fisheries science and terrestrial conservation. *Biol Letters*
6, 719-722
12, 9-20
National Park, Tanzania: the importance of livestock ownership and alternative sources of
protein and income. *Environmental Conservation* 29, 391-398
*Serengeti III: Human Impacts on Ecosystem Dynamics* (Sinclair, A.R.E. and Packer, C., eds),
pp. 7-46, University of Chicago Press
African buffalo in Serengeti. *Biodivers Conserv* 19, 3431-3444
interaction. In *Serengeti II: dynamics, management, and conservation of an ecosystem*
(Sinclair, A.R.E. and Arcese, P., eds), pp. 534-570, Chicago University Press

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