Drechsler, Martin; Grimma, Volker; Myšiak, Jaroslav; Wätzold, Frank

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Differences and similarities between ecological and economic models for biodiversity conservation

Martin Drechsler[a], Volker Grimm[a],
Jaroslav Myšiak[b], Frank Wätzold[a]

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[a] UFZ Centre for Environmental Research Leipzig-Halle GmbH,
Permoserstr. 15, 04318 Leipzig, Germany

[b] Fondazione Eni Enrico Mattei,
Palazzo Querini Stampalia, Campo S.Maria Formosa, Castello 5252,
30122 Venezia FEEM, Italy

Email of corresponding author: Martin.Drechsler@ufz.de

Abstract:

In this paper we investigate an important obstacle which substantially complicates co-operation between ecologists and economists but which has received little attention so far: differences between the modelling approaches in economics and ecology. To understand these differences, 60 models addressing issues relevant to biodiversity conservation have been selected randomly from eight international economic and ecological journals. The models have been compared according to a number of criteria including the level of generality/universality the models aim at; the mathematical technique employed for formulation and solution of the model; the level of complexity and the way time, space and uncertainty are taken into account. The economic models sampled are formulated and analysed analytically, tend to be relatively simple and are generally used to investigate general questions. Furthermore, they often ignore space, dynamics and uncertainty. Although some ecological models have similar properties, there is also a substantial number of another type of ecological models that are relatively complex and analysed by simulation. These models tend to be rather specific and often explicitly consider dynamics, space and uncertainty. The integrated ecological-economic models are observed to lie "in the middle" between ecological and economic models, an unexpected result being that they are not more complex than ecological and economic models (as one could have expected from a simple "merger" of both modelling attitudes), but have an intermediate complexity.

JEL: B40, C60, Q57

Key words: Ecological-economic modelling, modelling, biodiversity, conservation,

1. Introduction

Over the past two decades, models have become an important tool for aiding decisions related to the conservation of biodiversity. Ecological models are frequently used to predict and assess the outcomes of conservation measures and ecosystem management strategies (cf. for example Burgman et al. 1993, Beissinger/Westphal 1998, Jeltsch et al. 1999, Frank/Wissel 2002, Leslie et al. 2003). These efforts have been greatly facilitated by advances in computer technology, allowing models to be developed with structure and complexity necessary to describe the effects of measures and management strategies on the spatiotemporal dynamics of ecosystems. Despite these advancements, however, the practical use of ecological models for evaluating and improving conservation policies has often been limited as they tend to neglect the economic, institutional and political dimensions related to conservation. This is the realm of economic models which are today also quite common in the field of biodiversity conservation (cf. for example Swanson 1994, Skonhoft 1998, Smith and Shogren 2002, Bulte and Horan 2003). However, like the ecological models that ignore or oversimplify the economic, institutional and political dimension of conservation, economic models often use oversimplified assumptions regarding the ecological effects of conservation measures or, as pointed out by Sanchirico/Wilen (1999), assumptions that are outdated from the point of view of ecological theory.

Given that both ecologists and economists use models whose disciplinary perspectives, however, exhibit apparent limitations complementary to each other, it seems reasonable to combine them into integrated ecological-economic models which are able to overcome the respective disciplinary limitations (Perrings 2002). Indeed, over the past few years, the number of ecological-economic models addressing issues relevant for biodiversity conservation has increased considerably (cf. for example, Ando et al. 1998, Richards et al. 1999, Johst et al. 2002, Holden/Shiferaw 2004, Perrings/Walker 2004, Wätzold/Drechsler 2005).

Although its benefits are well recognised, ecological-economic modelling is still far away from being an established approach. A possible reason may be general barriers complicating interdisciplinary environmental research (e.g., that in terms of career prospects disciplinary research is generally more rewarding than interdisciplinary research). Such an explanation is certainly plausible but does not consider an intricacy inherent to ecological-economic modelling which substantially complicates the cooperation between ecologists and economists and has received little attention so far: differences in approaches, attitudes to, and uses of models in economics and ecology.

Since mathematical models are a common tool of research in both disciplines, probably it is often implicitly assumed that they can easily be combined. Such an assumption, however, neglects that different models and modelling approaches exist and that such differences may make a combination difficult or even impossible. Models may differ in various ways including the level of generality they are aiming at, the mathematical technique that is employed for the formulation and solution of the model, and the consideration of real world phenomena such as time, space and uncertainty.

The aim of this paper is to better understand possible differences and similarities between ecological and economic modelling approaches. A better understanding may help to avoid miscommunication that arises if economists and ecologists talk about “models” and believe they mean the same thing but in fact have something different in their mind. It may also facilitate the search of economists and ecologists for common modelling approaches that are suitable for an integrated analysis.

To enhance our understanding of modelling approaches in ecology and economics we carried out a literature survey and compared 60 models that address issues relevant to biodiversity conservation. All models were selected randomly from eight international journals from both disciplines and classified as either “ecological” or economic” or “ecological-economic”. The models were evaluated according to a number of criteria that were chosen to capture essential differences in the model purpose, structure, design and analysis, and, finally, the outcomes for the three different categories were compared.

The paper is structured as follows: Section 2 explains how the models are selected and classified and presents the criteria chosen to evaluate and compare the models. Section 3 presents the results including a comparison of the models of the three categories by the various criteria and an analysis of possible relationships between the criteria to better understand why models in a particular category have particular properties. The paper concludes with a summary and discussion of the results in Section 4.

2. Methods

2.1 The data base

In ecology, the following four leading conservation journals were evaluated: *Biological Conservation, Conservation Biology, Ecological Applications,* and *Journal of Applied Ecology*.[1] From the years 1998-2003, all papers containing the words 'model' or 'model(l)ing' in either the title, abstract or key word list were filtered. From the resulting approximately 800 papers, 30 were selected randomly for detailed evaluation (see Appendix A1). Papers presenting descriptive, statistical models were not selected because similarities in statistical methods might mask differences between ecological and economical models. Of the economic journals, *Environmental and Resource Economics*, *Journal of Environmental Economics and Management*, *Land Economics* and *Ecological Economics*[2] were chosen. From the years 1998-2003, all papers quoting biodiversity, conservation, nature protection or species in the abstract or title and applying a mathematical modelling approach were selected. A total of 162 articles were found. This number is much smaller than the 800 articles from the ecological journals, which however is probably not very surprising, as conservation biology is a – if not the - central theme in the ecological journals considered while this is different in the economic journals. As with the ecological journals, 30 papers were selected at random, again ignoring statistical and econometric models (as well as contingent valuation studies; see Appendix A1). All 60 selected papers were evaluated according to criteria which are explained below.

2.2 The disciplinary approach of a model

<u>Criterion:</u>

Disciplinary approach = {ecological or ecological-economic or economic}

In the first step each of the 60 models was assigned into one of the three categories "predominantly ecological", "predominantly economic", and "ecological-economic". Such an assignment is not easy, because it is generally difficult to draw a line between a

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[1] Please note that models in theoretical and applied ecology are different and that we have chosen journals that focus on applied ecology.

[2] *Ecological Economics* is as a transdisciplinary journal rather than a pure economic one. It was nevertheless chosen because it contains a large number of purely economic models related to biodiversity conservation.

‘disciplinary’ model and an ‘ecological-economic’ model. Various papers that were reviewed are clearly dominated by one discipline but also contain elements from the other (e.g. an ecological paper which contains a cost analysis as a sub-component of an otherwise ecological model). However, classifying such a model as ‘ecological-economic’ would be inappropriate as knowledge from the non-dominant discipline is only taken into account to a very limited extent. Instead of a clear distinction between disciplinary and ecological-economic models, there is evidently a continuum and an arbitrary line has to be drawn somewhere. Bearing this in mind, we chose a two step approach to distinguish between the different categories of models. In the first step, we differentiated between purely disciplinary models which do not contain any knowledge from the other discipline and other models. For the second step, we screened the papers containing models of the latter type and categorised those as ecological-economic when the paper included references to journals from both disciplines. The choice for such references as an indicator for ecological-economic models was motivated by the assumption that building ecological-economic models requires in-depth knowledge from both disciplines and that such knowledge is usually acquired through a careful reading of the disciplinary literature. We excluded references to general journals such as *Science* or *Nature*, as well as to journals which are mixed by their very nature such as *Ecological Economics*.

2.3 Purpose of the model

Criteria:

General model = {yes or no}

Specific model (case study) = {yes or no}

Models may have different purposes. We distinguish between models that try to explain general phenomena and models designed for specific situations. We classify the models by the data used in them: general models may be completely hypothetical or use observations and data to exclude unrealistic settings, but the models are not parameterised for specific cases; by contrast, specific models use data related to specific situations. Both of these criteria are evaluated independently, because some papers include both, a general model and an application of it to a specific situation, such that the two criteria are not mutually exclusive.

2.4 Criteria describing model formulation, solution and complexity

<u>Criterion:</u>

Model formulation = {analytical or algorithmic}

Model solution = {analytical or numerical or by simulation}

Number of model parameters

Next to its purpose we characterise a model by the way in which it is formulated and how the model results are obtained. We make the following distinctions: The formulation may be analytical (the model is completely described by equations), or algorithmic (flow charts or if-then rules are needed to describe the model). The results of analytical models are obtained either analytically (e.g. by solving equations for equilibrium solutions), numerically (e.g. by determining eigenvalues in a matrix model), or through simulation (e.g. by simulating the dynamics of a population time step by time step); algorithmic models are always run on a computer, i.e. they are solved through simulation. Numerical methods are distinguished from simulations by the fact that simulations try to mimic a real process whereas numerical methods approximate analytical solutions of analytical models.

Modelling approaches may differ in terms of the model's complexity. An obvious indicator of model complexity is the number of parameters. For the purpose of the present analysis we consider a parameter a number mediating the relationship between state variables. State variables measure or characterise the state of the system modelled, such as the size of a population. A parameter here may be the growth rate of the population that determines how the population size changes from this year to the next. Parameters are constant during the run of a model or for the analysis of a certain model scenario. Sometimes parameters are not known with certainty and to cope with this uncertainty frequency distributions are used. Or, relationships between state variables may be described not by single numbers but graphically by curves. The proper description of the shape of such frequency distributions or curves may require more than one parameter. For simplicity, we generally assume a number of two parameters in these cases (representing, e.g., mean and variance of a frequency distribution, or slope and offset of a straight line).

2.5 Consideration of uncertainty, time and space

Criteria:

Uncertainty is considered = {yes or no}

Model is dynamic = {no, or yes with continuous time, or yes with discrete time}

Model considers space = {no, or yes being spatially differentiated, or yes being spatially explicit, or yes being both spatially differentiated and explicit}

Often, modelling faces the challenge of having to deal with uncertainties of various types. These can be modelled and considered in a number of ways, e.g. through stochastic differential equations, probability density functions, sensitivity analysis, etc (see, e.g., Brown 2004). While a detailed review and comparison of these approaches is beyond the scope of the present paper, we simply record whether uncertainty is taken into account at all.

Besides uncertainty, the consideration of time and space are decisive characteristics of a model. We differentiate between dynamic and static models. In a dynamic model, time is explicitly introduced as a variable, whereas this is not the case in a static model. Models that investigate equilibria are counted as static, as the dynamics of the system are not considered explicitly. In order to classify a model as a dynamic model the state variable(s) has/have to be calculated for different points in time in a single model run. Within the dynamic models we distinguish between models that consider time in a continuous and models that consider time in a discrete manner.

We distinguish between three classes of models that take into account space to varying degrees. For a model to be considered as 'spatially explicit', state variables must exist which explicitly refer to space, i.e. co-ordinates in the landscape. This includes the explicit consideration of topological relations (e.g. neighbourhood), direction, distances and distance-dependent interactions between state variables at different locations. Typical examples are cellular automata with, for example, next neighbour interaction. In a 'spatially differentiated' model, parameters differ between patches of land. However, the location of the patches is not considered. Examples include economic models with two or more regions, whose locations are irrelevant in the analysis, and in particular, whose interactions are not distance-dependent. Models that are both spatially differentiated and spatially explicit form the third class of spatial models. Models which are spatially explicit but not spatially differentiated consider a homogeneous environment so that heterogeneities only can arise due to the interaction of model entities. An example is Conway's famous 'Game of Life' (Gardner 1970).

For each of the three model categories, ecological, economic and ecological-economic, the proportion of models falling into a particular class (e.g., formulated analytically, being spatially explicit, etc.) is recorded. In a few cases models may not be uniquely assigned to a particular criterion. For instance, a model may be solved partly analytically and partly numerically. In this case it is counted both as analytical and numeric. Alternatively, from the description of the model in the paper it may be impossible to decide on a certain characteristic. For instance, it may be unclear whether the model is solved numerically or through simulation. In such a case, the model is counted half as numerical and half as simulation. Based on these counts, differences between the three model categories can be formulated.

2.6 Relationships between criteria

The comparison of the model characteristics among the three categories also allows to identify relationships between criteria. Ecological models may, e.g., predominantly have a certain structure and consider particular phenomena while economic models may have a different structure and consider different phenomena. In addition to this, models may also vary within each of the three categories which again allows to identify relationships between criteria – this time not among but within model categories. To find these within-relationships we consider the set of all models within each of the three categories of models and determine the correlation between the criteria.

In the present analysis we have a mixture of nominal scaled (e.g., the classification into dynamic or static) and ordinal criteria (the characterisation of models by the number of parameters). In such a case the ordinary correlation coefficient cannot be applied. Instead we perform a contingency analyses (Clauß/Ebner 1978). Due to the presence of an ordinal criterion such a contingency analysis leads to unique results only if all criteria are dichotomic, such that a model either falls into a particular class (e.g., dynamic) or not. Therefore for the contingency analysis we reformulate all above criteria into dichotomic ones (Table 1).

Table 1: List of 17 dichotomic criteria which for each model are either true or false. Note that clearly not all criteria are statistically independent, which however is no problem in the pairwise analysis of contingencies.

No.	Dichotomic criterion
1	Model is formulated analytically
2	Model is formulated algorithmically
3	Model is solved analytically
4	Model is solved numerically
5	Model is solved by simulation
6	Model considers uncertainty
7	Number of parameters is $\leq$ 5
8	Number of parameters is $\leq$ 10
9	Number of parameters is $\leq$ 15
10	Model is general
11	Model is specific
12	Model is dynamic
13	Model is dynamic with discrete time
14	Model is dynamic with continuous time
15	Model considers space
16	Model is spatially differentiated
17	Model is spatially explicit (according to above definition)

Basically, the contingency analysis is a χ^2 test, which measures whether the observed relationship between two criteria is significantly higher than what would be expected if numbers were distributed randomly. To obtain the χ^2 for the relationship between two such classes, e.g., between "the model is general", and "the model is dynamic", it is counted how many models of the set fall into both classes, how many fall only into the former class, how many into the latter, and how many into neither. These counts may be denoted as t_{11}, t_{10}, t_{01}, and t_{00}, respectively. Let $z_0=t_{00}+t_{01}$, $z_1=t_{10}+t_{11}$, $s_0=t_{00}+t_{10}$, and $s_1=t_{01}+t_{11}$, and $s=t_{11}+t_{10}+t_{01}+t_{00}$. With $f_{11}=z_1s_1/s$, $f_{10}=z_1s_0/s$, $f_{01}=z_0s_1/s$ and $f_{00}=z_0s_0/s$ we obtain

$$\chi^2 = \sum_{i,j=0,1} \frac{(t_{ij} - f_{ij})^2}{f_{ij}}$$

which measures the deviation of the t_{ij} from random values. To be statistically significant, the calculated (empirical) value of χ^2 has to exceed χ^2_{crit} which in our case amounts to 3.8 (χ^2 for 1 degree of freedom, α = 5%).

The strength of the correlation is strictly monotonically related to χ^2 and given by $[(\chi^2/(\chi^2+n))]^{1/2}$ where n is the number of elements in the set (Clauß/Ebner 1978). For n=30 (18), the critical χ^2_{crit}=3.8 corresponds to a correlation of 0.34 (0.42) on a scale between zero and one.

The described contingency analysis does not tell whether a contingency is positive or negative, i.e., whether the relationship between two criteria is positive or negative. As our criteria are dichotomic, the sign of the relationship can be identified easily in another analysis: if in the comparison of two criteria the number of models for which both criteria are either true or false is larger than the number of models for which exactly one criterion is true and the other one is false, then the relationship is positive, because then the membership/non-membership of a model in the first class is likely (probability>0.5) to coincide with the membership/non-membership in the other. If it is vice versa, the membership/non-membership in the first class is likely to coincide with the non-membership/membership in the other.

3. Results

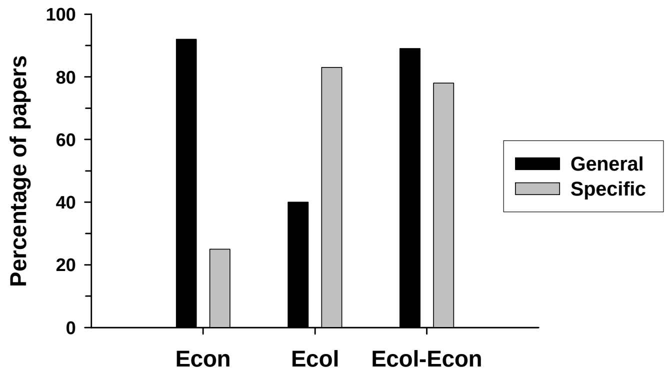
3.1 Disciplinary approach of the model

The assignment of the 60 models in one of the three classes leads to 30 ecological, 12 economic and 18 ecological-economic models. As expected, quite a large number (9) of the ecological-economic models were found in *Ecological Economics*. However, even in the more "disciplinary" economic journals we still found 7 ecological-economic models. In the ecological journals we found only 2. This means that the economic journals (including *Ecological Economics*) contain a higher proportion of ecological-economic models than the ecological ones. In addition, we could not detect a clear trend towards more ecological-economic models in the most recent years of the analysis.

3.2 Model purpose

Nearly all economic models analysed (92%) are of a general nature (Fig. 1). However, approximately one fourth of the models (25%) are also specific. Here, some real world data are usually inserted in the model and the model is used to explain, predict or analyse a certain empirical phenomenon. By contrast, in the ecological models analysed, only 40% are general models, whereas a large majority (83%) have a specific character. On the other hand a large majority of ecological-economic models have both a general (89%) and a specific character (78%). We see that the prevalent model purpose is different in the economic and ecological models of our sample and that the ecological-economic models tend to combine both approaches.

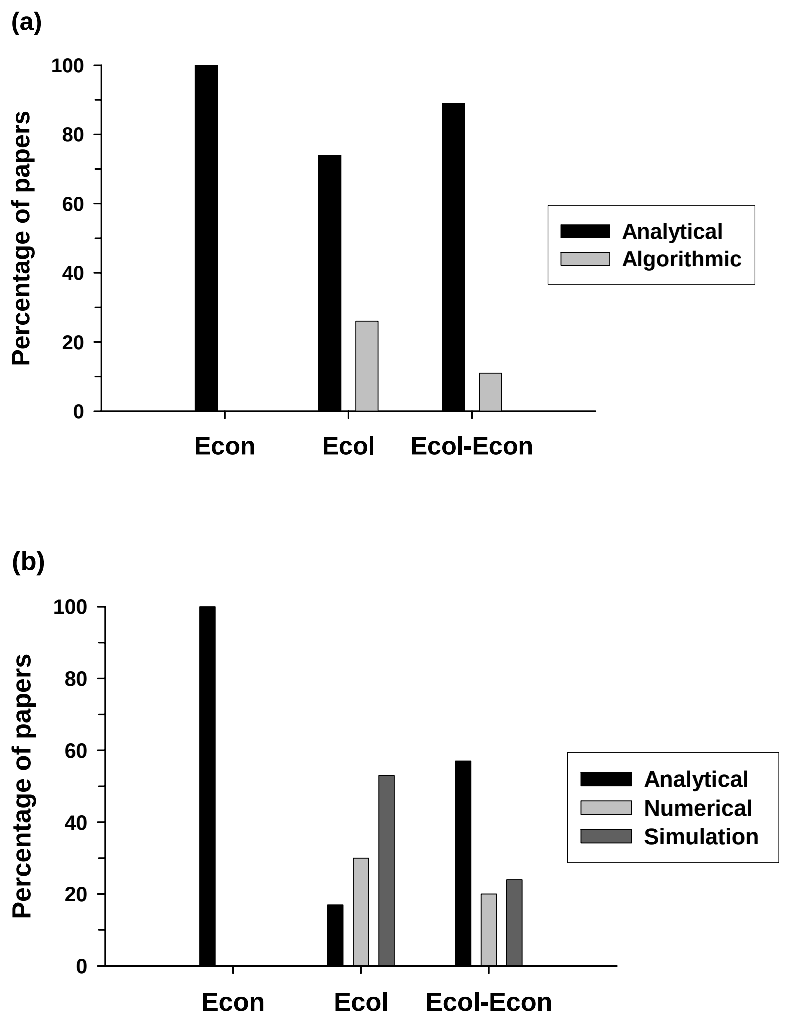
Figure 1: Percentage of reviewed economic, ecological and ecological-economic models that address general or specific problems. Note that a model may address both kinds of problems.



3.3 Criteria describing model formulation, solution and complexity

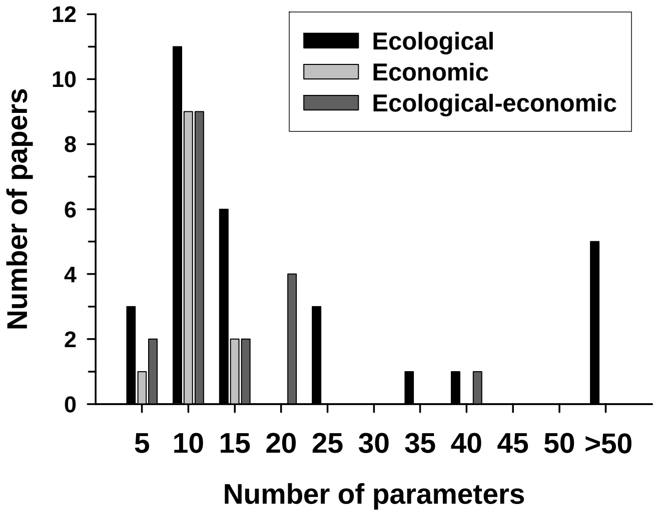
The ways models of the three categories are formulated and solved are shown in Fig. 2. While all economic models of our sample are formulated analytically, a significant proportion (26%) of the ecological models is formulated algorithmically. This means that there is some common ground between ecology and economics in the form of analytical modelling, but that one approach - algorithmic modelling - that is quite common in the ecological models investigated is non-existent in the set of economic models. Even larger differences exist regarding the solution techniques applied in the two disciplines. All economic models reviewed are solved analytically, whereas only a comparatively small fraction of the ecological models (17%) choose this approach. The large majority of the ecological models are solved either numerically (30%) or through simulation (53%). The percentages for the ecological-economic models lie quite well in the middle between those for the ecological and the economic models.

Figure 2: Percentage of reviewed ecological, economic and ecological-economic models that have an analytical or algorithmic formulation (a) and are solved analytically, numerically, or via simulation (b).



Model complexity was measured by the number of model parameters and this was found to be on average higher in ecological (16.5) than in ecological-economic (11.9) and economic (8.8) models (cf. Fig. 3).

Figure 3: Histograms of the numbers of parameters of ecological, economic, and ecological-economic models.



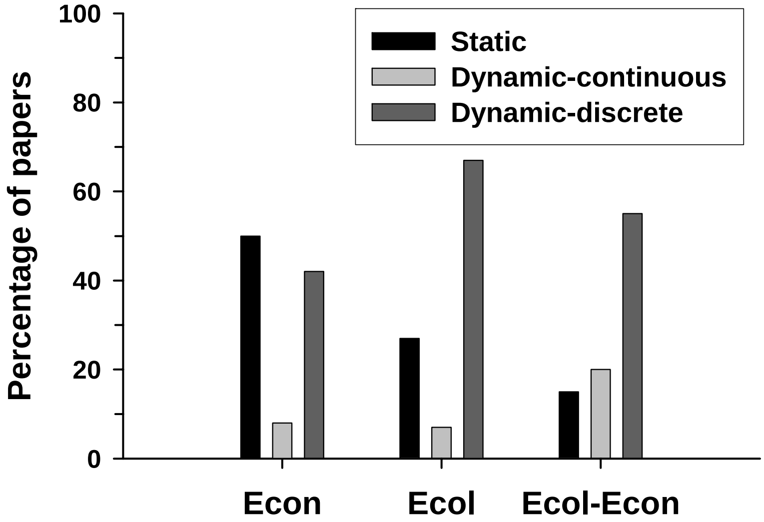
The main reason for the difference between ecological and economic models is that the sample contains some very complex ecological models with a large number of parameters (7 out of the 30 ecological models have more than 30 parameters and 5 more than 50 parameters, whereas none of the economic models has more than 15 parameters). But as a substantial proportion of the ecological models have a relatively small number of parameters (14 ecological models have no more than 10 parameters) it would be wrong to conclude that the complexity of ecological and economic models is different from the outset. Instead, a certain class of complex models with a high number of parameters is used in the ecological models of our sample which does not exist in the economic models investigated.

3.4 Consideration of uncertainty, time and space

Uncertainty is considered in 50% of the economic models sampled. It is more frequently taken into account in the ecological-economic models (66%) and in nearly all ecological models (97%).

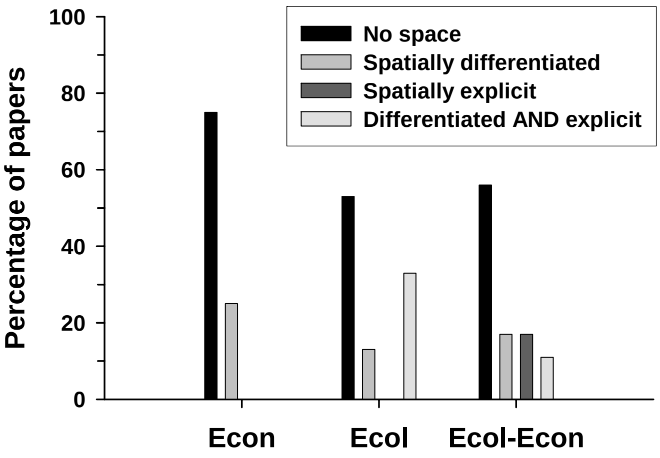
Similarly, a substantial majority of the ecological (74%) and ecological-economic models (85%) are dynamic while this is true for only half of the economic models. In all three categories there are more models discrete in time (time steps, periods) than models with continuous time. The only difference (not shown in Fig. 4) is that time-discrete economic models often use an abstract time (periods) while time-discrete ecological models have a physical time (mostly years, but also hours or decades).

Figure 4: Consideration of time in ecological, economic, and ecological-economic models.



Most of the economic models (75%) sampled do not explicitly consider space (Fig. 5). If space is considered, only spatially differentiated models are applied. By contrast, a significant share of the ecological models (33%) is both spatially explicit and differentiated. A smaller percentage is spatially differentiated (13%) while 53% of the models do not explicitly consider spatial aspects. The fact that none of the ecological models in our sample are spatially explicit but not differentiated means that if space is considered explicitly then also a heterogeneous environment is considered. Similar to the ecological models, about half of the ecological-economic models consider space and they do so more or less equally distributed in a differentiated, explicit, or differentiated and explicit manner. Here, a certain fraction of models (17%) exists which is spatially explicit but does not consider environmental heterogeneity.

Figure 5: Consideration of space in ecological, economic, and ecological-economic models



3.5 Relationships between criteria

The above results indicate that the economic models in our sample form a relatively homogenous group: all of them are formulated and solved analytically, most of them are general and not specific; they have a relatively small number of parameters, do mostly not consider space, and only half of them are dynamic and consider uncertainty. In contrast to this, the ecological models in the sample tend to be more specific, more complex, are to a greater extent formulated algorithmically and solved through simulation and in majority consider time, space and uncertainty. However, they form a much less homogenous group than the economic models. Therefore a closer look at the ecological (and the ecological-economic) models might be worthwhile. We do this in a contingency analysis.

Table A1 in Appendix A2 shows the signs of the significant contingencies ("correlations") between the criteria in the set of 30 ecological models of our sample. Some of them are trivial, because some of the criteria are mutually exclusive. For instance, a model that is formulated analytically cannot be formulated algorithmically at the same time. Or, a dynamic model falls either into the class of time-continuous or time-discrete models. The significant non-trivial contingencies are:

- Models formulated algorithmically (analytically) have more (less) than 15 parameters and are (not) spatially explicit.
- Models solved analytically or numerically have a relatively small number of parameters, are general, not specific and not dynamic.

- Models solved by simulation have a relatively large number of parameters, are specific and not general, are dynamic with discrete time and consider space.
- Models with less than five parameters have continuous time.

Similar to Table A1, Table A2 shows the correlations for the 18 ecological-economic models in our sample. The significant non-trivial correlations are

- Analytical models are general.
- Algorithmic models are solved by simulation, are not general and are spatially explicit.
- Models with less than 5 parameters are solved analytically.
- Simulation models are dynamic with discrete time.
- Uncertainty is not considered in models with continuous time.
- Models with relatively few parameters do not consider space.

From these observations we can classify each of the sets of ecological and ecological-economic models into two classes: the first class, termed "simple models" contains the analytical and general models that have relatively few parameters, are static or continuous in time, often deterministic, and do not consider space; the models in the second class, termed "complex models" have relatively many parameters, are not general but dynamic with discrete time and explicit consideration of space.

This distinction is very similar to that derived from the comparison *between* ecological and economic models. Altogether, we can observe "simple" models in the ecological, ecological-economic and economic models while the "complex models" are found in the ecological and ecological-economic models only. The proportion of complex models is higher among the ecological models than among the ecological-economic models.

4. Discussion

In the present study we have compared 60 ecological, economic and ecological-economic models related to biodiversity conservation employing a range of criteria describing the models' purpose, design, structure and analysis. While some common ground exists significant differences are to be observed in the modelling approaches of the two disciplines economics and ecology. Generally speaking, economic models tend to be general and are formulated and solved analytically whereas ecological models tend to be specific and - while the majority of models is formulated analytically - a significant fraction is formulated algorithmically. In addition, the ecological models that are formulated analytically are mostly solved numerically or through simulation. Another important difference between the two disciplines is that ecological models explicitly take into account time, uncertainty and space to a much larger extent than economic models. Moreover, if they are spatial, economic models are usually spatially differentiated (e.g., two regions with different conditions) while ecological models are often spatially explicit (locations and sizes of regions considered explicitly), an approach which does not exist in the economic models of our sample.

By making the differences between economic and ecological models explicit we hope to have contributed to a better understanding between economists and ecologists and to have helped them in their search for common modelling approaches to analyse and develop conservation strategies and policies. The question that arises from the analysis of this paper is, of course, what are the reasons for the described differences between economic and ecological models? We wish to suggest four possible reasons:

(1) *Different disciplinary traditions*: The two disciplines have evolved historically in a different manner. Being rooted in natural history, detailed observations made by researchers and explorers appear to have shaped the development of ecology quite substantially while theoretical reasoning and mathematics were comparatively more influential in the development of economics.

(2) *Differences in the systems analysed*: Ecological and economic systems may be structured differently. It might be that, e.g., spatial heterogeneity has less influence on the dynamics and the functioning of an economy than on the dynamics and the functioning of an ecosystem.

(3) *Differences in the perception of the system analysed*: Ecological and economic systems might not be dissimilar in structure per se, but they might be perceived differently by the researchers or certain features are given different degrees of relevance. Economists might, e.g., view their systems as being usually in an equilibrium state that only occasionally changes due to some shocks. Ecologists in contrast, might view their systems as constantly changing.

(4) *Varying personal preferences of researchers*: Various ecologists have chosen their discipline, because they love the diversity and complexity of nature, animals and plants and want to understand it. Such a personal background may lead to the desire of including all this richness of ecological systems in a model. In contrast, economists may be rather interested in the general understanding of economic systems. Furthermore, many economists seem to have an affinity to mathematics. They might then prefer those research questions that can be expressed as mathematical problems and solved with mathematical methods.

An in-depth analysis of the various possible reasons is clearly beyond the scope of this paper. It is nevertheless important to understand these reasons, because most likely this will further improve our knowledge about the opportunities but also the limits of ecological-economic modelling. Future research should therefore address this issue in more detail.

Whatever the reason behind the differences between ecological and economic models, presently the answer to ecologist C.A.S. Hall's (1988) question "What constitutes a good model and by who's criteria?" is likely to be different among economists and ecologists: in economics, the majority of modellers prefer simple models which are analytically tractable; specific data, details of space, dynamics and uncertainty are sacrificed to the overall aim of analytical tractability. Thus, most economists probably would rank a simulation model with more than 10 parameters and with reference to specific systems rather low. In contrast, many ecologists would be very sceptical of a simple model addressing real systems; yet, they would accept simple models as a tool to address general problems and concepts.

The general lesson from all this is that economists who start thinking about developing ecological-economic models have to be prepared that they might be involved with complex models which are untypical in economics and even might by ranked lower than simple models by many economists. On the other hand, ecologists starting collaborations with modellers from economics have to be aware that in economics analytical tractability is much higher valued and simple models more dominant than in ecology.

Fortunately, our results indicate that a good compromise between the modelling approaches in economics and ecology is possible. Regarding most criteria that we evaluated, existing ecological-economic models are in between the numbers obtained for the disciplinary economic and ecological models. In particular, the complexity of ecological-economic models is not higher than that of disciplinary models (as one could have expected from a naïve “merger” of models), but also lies in between that of ecological and economic models. This shows that richer models, combining the two disciplines, can be built without excessively increasing model complexity. Instead, ecological and economic modellers seem to seek for a good compromise when co-operating through ecological-economic modelling. Another remarkable observation is that in ecological-economic modelling, simple and complex models coexist to a similar extent as in ecology. This is a promising finding, because most ecologists to date agree that this coexistence of simple and complex models is necessary, useful and productive.

References

Ando, A., Camm, J., Polasky, S., Solow, A. (1998) Species Distributions, Land Values, and Efficient Conservation. Science 279, 2126-2128.

Beissinger S.R., Westphal M.I. (1998) On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62, 821-841.

Brown J.D. (2004) Knowledge, uncertainty and physical geography: towards the development of methodologies for questioning belief. Transactions of the Institute of British Geographers 29, 367-381.

Burgman M.A.S., Ferson S., Akçakaya H.R. (1993) Risk assessment in conservation biology. Chapman and Hall, London, UK.

Clauß, G., Ebner H. (1978): Grundlagen der Statistik. Für Psychologen, Pädagogen und Soziologen. Volk und Wissen Volkseigener Verlag, Berlin, 6th edition.

Frank K., Wissel C. (2002) A formula for the mean lifetime of metapopulations in heterogeneous landscapes. American Naturalist 159, 530-552.

Gardner M. (1970) Mathematical games - the fantastic combinations of John Conway's new solitaire game, Life. Scientific American, Oct. 1970, pp. 120-123.

Hall C. A. S. (1988) What constitutes a good model and by whose criteria ? Ecological Modelling 43, 125-127.

Hanley N., Kirkpatrick H., Simpson I., Oglethorpe D. (1998) Principles for the provision of public goods from agriculture: Modelling moorland conservation in Scotland. Land Economics 74, 102-113.

Holden S., Shiferaw B. (2004) Land degradation, drought and food security in a less-favoured area in the Ethiopian highlands: a bio-economic model with market imperfections. Agricultural Economics 30 (1), 31-49.

Jeltsch F., Wiegand T., Wissel C. (1999) Spatially explicit computer simulation models: tools for understanding vegetation dynamics and supporting rangeland management. In: Dean WRJ, Milton SJ (eds.) The Karoo: ecological patterns and processes. Cambridge University Press, Cambridge, pp. 231-238.

Johst K., Drechsler M., Wätzold F. (2002) An ecological-economic modelling procedure to design effective and efficient compensation payments for the protection of species. Ecological Economics 41, 37-49.

Leslie H., Ruckelshaus R., Ball I. R., Andelman S. and Possingham H.P. (2003) Using siting algorithms in the design of marine reserve networks. Ecological Applications 13, 185-198.

Liu J., Cubbage F.W., Pulliam H.R. (1994) Ecological and economic effects of forest landscape structure and rotation length: simulation studies using ECOLECON. Ecological Economics 10, 249-263.

Perrings C., Walker B. (1997a) Biodiversity, resilience and the control of ecological-economic systems: the case of fire-driven rangelands. Ecological Economics 22, 73-83.

Perrings C., Walker B. (1997b) Introductory remarks: the Beijer biodiversity programme – a postscript. Ecological Economics 22, 63-64.

Perrings C. (2002) Modelling sustainable ecological-economic development. In: Folmer H., Tietenberg T. (eds.): The International Yearbook of Environmental and Resource Economics. Edward Elgar, Cheltenham, Northhampton, 179-201.

Perrings C, Walker B. (2004) Cinservation in the optimal use of rangelands. Ecological Economics 49 (2), 119-128.

Richards S.A., Possingham H.P., Tizard J. (1999) Optimal fire management for maintaining community diversity. Ecological Applications 9, 880-892.

Sanchirico, J.N., Wilen, J.E. (1999): Bioeconomics of spatial exploitation in a patchy environment. Journal of Environmental Economics and Management 37, S. 129-150.

Settle C., Crocker, T.D., Shogren, J.F. (2002) On the joint determination of biological and economic systems. Ecological Economics. 42/1, 301-312.

Skonhoft, A. (1998): Resource utilization, property rights and welfare – Wildlife and the local people. Ecological Economics 26, 67-80.

Smith, R., Shogren, J. (2002): Voluntary Incentive Design for Endangered Species Protection. Journal of Environmental Economics and Management, 43, 169-187.

Swanson, T. M. (1994) The economics of extinction revisited and revised: a generalised framework for the analysis of endangered species and biodiversity loss, Oxford Economic Papers, 46, 800-821.

Wätzold, F., Drechsler, M. (2005): Spatially uniform versus spatially heterogeneous compensation payments for biodiversity-enhancing land-use measures. Environmental and Resource Economics, forthcoming.

Wu J., Bogess W.G. (1999) The Optimal Allocation of Conservation Funds. Journal of Environmental Economics and Management 38, 302-321.

Appendix A1: Papers reviewed

Papers analysed from ecological journals

Aanes, S., Engen, S., Sæther, B.-E., Willebrand, T., Marcström, V. (2002): Sustainable harvesting strategies of Willow Ptarmigan in a fluctuating environment. Ecological Applications 12(1), 281-290.

Baron, J.S., Hartman, T.G., Kittel, T.G.F., Band, L.E., Ojima, D.S., Lammers, R.B. (Effects of land cover, water redistribution, and temperature on ecosystem processes in the South Platte Basin. Ecological Applications 8(4), 1037-1051.

Baillie, S.R., Sutherland, W.J., Freeman, S.N., Gregory, R.D., Paradis, E. (2000): Consequences of large-scale processes for the conservation of bird populations. Journal of Applied Ecology 37 (Suppl. 1), 88-102).

Cabeza, M., Moilanen, A. (2003): Site-selection algorithms and habitat loss. Conservation Biology 17, 5, 1402-1413.

Carpenter, S.R., Ludwig, D., Brock, W.A. (1999): Management of eutrophication for lakes subject to potentially irreversable change. Ecological Applications 9(3), 751-771.

Clark, M.E., Rose, K.A., Levine, D.A., Hargrove, W.W. (2001): Predicting climate change effects on Appalachian trout: combining GIS and individual-based modelling. Ecological Applications 11(1), 161-178.

Couvet, D. (2002): Deleterious effects of restricted gene flow in fragmented population. Conservation Biology 16, 2, 369-376.

Cuarón, A.D. (1999): Effects of land-cover changes on mammals in a neotropical region: a modelling approach. Conservation Biology 14, 4, 1676-1692.

Drechsler, M., Wissel, C. (1998): Trade-offs between local and regional scale management of metapopulations. Biological Conservation 83, 1, 31-41.

Fenton, A., Gwynn, R.L., Gupta, A, Norman, R., Fairbairn, J.P., Hudson, J. (2002): Optimal application strategies for entomopathogenic nematodes: integrating theoretical and empirical approaches. Journal of Applied Ecology 39, 481-492.

Foley, J.E., Foley, P., Pedersen, N.C. (1999): The persistence of a SIS disease in a metapopulation. Journal of Applied Ecology 36, 555-563.

Harding, E.K. (2002): Modelling the influence of seasonal inter-habitat movements by an ecotone rodent. Biological Conservation 104, 227-237.

Haydon, D.T., Laurenson, M.K., Sillero-Zubiri, C. (2001): Integrating epidemiology into population viability analysis: managing the risk posed by rabies and canine distemper to the Ethiopian wolf. Conservation Biology 16, 5, 1372-1385.

Hebblewhite M., Percy, M., Serrouya, R. (2003): Black bear (*Ursus americanus*) survival and demography in the Bow Valley of Banff National Park, Alberta. Biological Conservation 112, 415-425.

Hokit, D.G., Branch, L.C. (2003): Associations between patch area and vital rates: consequences for local and regional populations. Ecological Applications 13(4), 1060-1068.

Jones, C. (2002): A model for the conservation management of a ’secondary’ prey: sooty shearwater (*Puffinus griseus*) colonies on mainland New Zealand as a case study. Biological Conservation 108, 1-12.

Köhler, P., Reinhard, K., Huth, A. (2002): Simulating anthropogenic impacts to bird communities in tropical rain forests. Biological Conservation 108, 35-47.

Liu, J., Ashton, P.S. (1999): Simulating effects of landscape context and timber harvest on tree species diversity. Ecological Applications 9(1), 186-201.

Liu, J., Ouyang, Z., Taylor, W.W., Groop, R., Tan, Y., Zhang, H. (1999): A framework for evaluating the effects of human factors on wildlife habitat: the case of giant pandas. Conservation Biology 13, 6, 1360-1370.

Lusseau, D. (2002): Effects of tour boats on the behaviour of bottlenose dolphins: using Markov chains to model anthropogenic impacts. Conservation Biology 17, 6, 1785-1793.

Meesters, E.H., Bak, R.P.M., Westmacott, S., Ridgley, M., Dollar, S. (1998): A fuzzy logic model to predict coral reef development under nutrient and sediment stress. Conservation Biology 12, 5, 957-965.

Oli, M.K., Holler, N.R., Wooten, M.C. (2001): Viability analysis of endangered Gulf Coast beach mice (*Peromyscus polionotus*) populations. Biological Conservation 97, 107-118.

Pettifor, R.A., Caldow, R.W.G., Rowcliffe, J.M., Goss-Custard, J.D., Black, J.M., Hodder, K.A., Houston, A.I., Lang, A., Webb, J. (2000): Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. Journal of Applied Ecology 37 (Suppl. 1), 103-135.

Reed, J.M., Elphnick, C.S., Oring, L.W. (1998): Life-history and viability analysis of the endangered Hawaiian stilt. Biological Conservation 84, 35-45.

Shea, K., Possingham, H.P. (2000): Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. Journal of Applied Ecology 37, 77-86.

Sibly, R.M., Newton, I., Walker, C.H. (2000): Effects of dieldrin on population growth rates of sparrowhawks 1963-1986. Journal of Applied Ecology 37, 540-546.

Tyre, A.J., Possinghaam, H.P., Lindenmayer, D.B. (2001): Inferring process from pattern: can territory occupancy provide information about life history parameters? Ecological Applications 11(6), 1722-1737.

Weller, D.E., Jordan, T.E., Correll, D.L. (1998): Heuristic models for material discharge from landscapes with riparian buffers. Ecological Applications 8(4), 1156-1169.

Wilcox, C., Elderd, B. (2003): The effect of density-dependent catastrophes on population persistence time. Journal of Applied Ecology 40, 859-871.

Zonneveld, C., Longcore, T., Mulder, C. (2002): Optimal schemes to detect the presence of insect species. Conservation Biology 17, 2, 476-487.

Papers analysed from economic journals

Alavalapati, J.R.R., Stainback, G.A., Carter, D.R. (2002): Restoration of the longleaf pine ecosystem on private lands in the US South: an ecological economic analysis. Ecological Economics 40 (4), 411-419.

Albers, H, Ando, A. (2003): Could State-Level Variation in the Number of Land trusts Make Economic Sense? Land Economics 79/3, 311-327.

Alexander, R.R. (2000): Modelling species extinction: the case for non-consumptive values. Ecological Economics 35/2, 259-269.

Barbier, E.B. (2001): A note on the economics of biological invasions. Ecological Economics 39/2, 197-202.

Boscolo, M. Vincent, J.R. (2003) Nonconvexities in the production of timber, biodiversity, and carbon sequestration. Journal of Environmental Economics and Management 46/2, 251-268.

Brock, W.A., Xepapadeas, A. (2002): Optimal Ecosystem Management when Species Compete for Limiting Resources. Journal of Environmental Economics and Management 44, 189-220.

Bulte, E.H., van Kooten, G.C. (1999): Economic efficiency, resource conservation and the ivory trade ban. Ecological Economics 28/2, 171-181.

Bulte, E.H., van Kooten, G. C. (2000) Marginal Valuation of Charismatic Species: Implications for Conservation. Environmental and Resource Economics 14, 119-130.

Bulte, E.H, Mason, C.F., Horan, R.D. (2003): Betting on Extinction: Endangered Species and Extinction. Land Economics, 79/4, 460-471.

Cervigni, R. (1999): Incremental Cost in the convention on Biological Diversity. Environmental and Resource Economics 11, 217-241.

Craft, A.B., Simpson, D.R. (2001): The value of Biodiversity in Pharmaceutical Research with Differentiated products. Environmental and Resource Economics, 18, 1-17.

Doherty Jr., P.F., Marschall, E.A., Grubb Jr., T.C. (1999): Balancing conservation and economic gain: a dynamic programming approach. Ecological Economics 29/3, 349-358.

Dyar, J.A., Wagner, J. (2003): Uncertainty and species recovery program design. Journal of Environmental Economics and Management 45/2, 505-522.

Eiswerth, M.E., Johnson, W.S. (2002) Managing Nonindigenous Invasive Species: Insights from Dynamic Analysis. Environmental and Resource Economics 23, 319-342.

Ferraro, P.J. (2002): The local costs of establishing protected areas in low-income nations: Ranomafana National Park, Madagascar. Ecological Economics 43/2, 261-275.

Lichtenstein, M.E., Montgomery C.A. (2003): Biodiversity and Timber in the Coast Range of Oregon: Inside the Production Possibility Frontier. Land Economics, 79/1, 56-73.

Moyle, B. (1998): Species conservation and the principal-agent problem. Ecological

Economics 26/3, 313-320.

Nickerson, D.J. (1999) Trade-offs of mangrove area development in the Philippines. Ecological Economics 28/2, 279-298.

Parkhurst, G.M., Shogren, J.F., Bastian, C., Kivi, P., Donner, J., Smith, R. B. W.(2002): Agglomeration bonus: an incentive mechanism to reunite fragmented habitat for biodiversity conservation. Ecological Economics 41/2, 305-328.

Polasky, S., Doremus, H. (1998): When the Truth Hurts: Endangered Species Policy on Private Land with Imperfect Information. Journal of Environmental Economics and Management 35/1, 22-47.

Prato, T. (2003): Multiple-attribute evaluation of ecosystem management for the Missouri River system. Ecological Economics 45/2, 297-309.

Simianer, H.; Marti, S. B.; Gibson, J.; Hanotte, O., and Rege, J. E. O. (2003): An approach to the optimal allocation of conservation funds to minimize loss of genetic diversity between livestock breeds. Ecological Economics 45/3, 377-392.

Skonhoft, A. (1998): Resource utilization, property rights and welfare-Wildlife and the local people. Ecological Economics. 26/1, 67-80.

Smith, R.B.W., Shogren, J.F. (2002): Voluntary Incentive Design for Endangered Species Protection. Journal of Environmental Economics and Management 43/2, 169-187.

Stranlund, J.K. (1999): Bargaining to preserve a unique ecosystem: the role of anticipatory investments to establish stronger bargaining positions. Ecological Economics 31/3, 425-437.

Sumaila, U.R., Vasconcellos, M. (2000): Simulation of ecological and economic impacts of distant water fleets on Namibian fisheries. Ecological Economics 32/3, 457-464.

Ulph, A., O'Shea, L. (2002): Biodiversity and Optimal Policies Towards R&D and the Growth of Genetically Modified Crops. Environmental and Resource Economics, 22, 505-520.

Wu, J.J., Boggess, W.G. (1999): The Optimal Allocation of Conservation Funds. Journal of Environmental Economics and Management 38/3, 302-321.

Wu, J., Zilbermann, D., Babcock, B.A. (2001): Environmental and Distributional Impacts of Conservation Targeting Strategies. Journal of Environmental Economics and Management, 41, 333-350.

Yang, W., Khanna, M., Farnsworth, R., Onal, H. (2003): Integrating economic, environmental and GIS modeling to target cost effective land retirement in multiple watersheds. Ecological Economics 46/2, 249-267.

Appendix A2: Results of the contingency analysis

Table A1: The signs of the contingencies between the 17 criteria of Table 1 which are significant at the 5% level. Trivial/non-trivial correlations are represented by small/large symbols. The analysis is based on the set of all ecological models. Each row and column represents one criterion.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	-							+								-
2								-								+
3				-		+	+									
4				-			+	+	+	-	-	-				
5							-	-	-	+	+	+		+	+	+
6																
7							+						+			
8								+								
9														-	-	-
10										-						
11											+	+				
12												+				
13													-	+	+	
14																
15															+	+
16																+

Table A2: The signs of the contingencies between the 17 criteria of Table 1 which are significant at the 5% level. Trivial/non-trivial correlations are represented by small/large symbols. The analysis is based on the set of all ecological models. Each row and column represents one criterion.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	-								+							
2				+					-					+		+
3						-										
4																
5									-			+				
6													-			
7																
8								+						-	-	-
9															-	
10																-
11																
12												+				
13													-			
14																
15															+	+
16																

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5/2002	Matthias Bernt	Risiken und Nebenwirkungen des „Stadtumbaus Ost"
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