

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application

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Wiegand, T., Jeltsch, F., Hanski, I. and Grimm, V. 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. – *Oikos* 100: 209–222.

We suggest that the conscious use of information that is “hidden” in distinct structures in nature itself and in data extracted from nature (= pattern) during the process of modeling (= pattern-oriented modeling) can substantially improve models in ecological application and conservation. Observed patterns, such as time-series patterns and spatial patterns of presence/absence in habitat patches, contain a great deal of data on scales, site-history, parameters and processes. Use of these data provides criteria for aggregating the biological information in the model, relates the model explicitly to the relevant scales of the system, facilitates the use of helpful techniques of indirect parameter estimation with independent data, and helps detect underlying ecological processes. Additionally, pattern-oriented models produce comparative predictions that can be tested in the field.

We developed a step-by-step protocol for pattern-oriented modeling and illustrate the potential of this protocol by discussing three pattern-oriented population models: (1) a population viability analysis for brown bears (*Ursus arctos*) in northern Spain using time-series data on females with cubs of the year to adjust unknown model parameters; (2) a savanna model for detecting underlying ecological processes from spatial patterns of tree distribution; and (3) the incidence function model of metapopulation dynamics as an example of process integration and model generalization.

We conclude that using the pattern-oriented approach to its full potential will require a major paradigm shift in the strategies of modeling and data collection, and we argue that more emphasis must be placed on observing and documenting relevant patterns in addition to attempts to obtain direct estimates of model parameters.

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Accepted 15 August 2002

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ISSN 0030-1299

Over the past three decades, models have been increasingly used in applied ecology and, in particular, in conservation biology. For example, by the late 1970s results from the island biogeographic theory were widely applied in the design of nature reserves (Meffe and Carroll 1997). During the 1980s population viability analysis became an important tool in assessing the likelihood of a population becoming extinct and PVAs have subsequently been used to aid management decisions about threatened species (Boyce 1992, Beissinger and Westphal 1998, Noon et al. 1999, Beissinger and McCullough 2002). Since the early 1990s, the ideas of metapopulation dynamics have rapidly gained prominence in the literature and now form the conceptual framework for managing populations living in fragmented landscapes (Levins 1970, Gilpin and Hanski 1991, Hanski and Gilpin 1997, Hanski 1999). Since the 1990s grid-based simulation models have increasingly been used to investigate long-term dynamics and management of plant communities and animal populations (Wiegand et al. 1995, in press, Jeltsch et al. 1996, 1998, Jeltsch and Moloney 2002). Most recently, decision theory has been advanced as a tool to aid in reserve design and in assigning relative ranking of management options (Shea et al. 1998, Drechsler 2000, Possingham et al. 2002).

Despite the growing use of models in conservation ecology and the fact that many attempts have been made to compensate for the chronic lack of data by relying heavily upon ecological theory and modeling (Doak and Mills 1994), the use of theory in making actual management decisions about real species and communities has come under increasing attack (Caughley 1994, Doak and Mills 1994, Harcourt 1995, Shea et al. 1998) and early enthusiasm has been tempered by several problems. Besides of unrealistically high expectations for the predictive power of population models (Wiegand et al. 1998, Burgman and Possingham 2000, Possingham et al. 2002), the application of theory is plagued by (1) the inherent lack and uncertainty of data, especially on endangered species, (2) but also by the complexity of realistic simulation models, (3) problems of error propagation, (4) missing criteria for aggregating the biological information, and (5) difficulties in testing model predictions.

The poor quality of data used in most model applications, although quite obvious, is frequently overlooked (Beissinger and Westphal 1998). It is not yet fully accepted that rarity of species itself precludes precise measurement of model parameters, and that in this case there is no hope at all to accurately estimate parameter values through direct measurement in the field. Because traditional measurement of parameter values relies heavily on data obtained from a low hierarchic level of population dynamics, such as mortality rates, model predictions are usually quite sensitive to uncertainty in the data. In principle, spatially-explicit and individual-

based simulation models are able to include many biological details and may contain many parameters (DeAngelis and Mooij, in press). This can be a problem, not only because of error propagation or lacking direct estimates of model parameters, but also because their complexity may prevent an exhaustive model analysis (Beissinger and Westphal 1998). Models that are too complex may result because of missing criteria of how to aggregate biological information in the model (Grimm et al. 1996). On the other hand, models are criticized for being poorly tied to applications (Caughley 1994), mainly due to difficulties in adapting models of sufficient complexity to capture the relevant ecology. Again, we attribute these difficulties largely to missing criteria of how to aggregate biological information in the model (Grimm et al. 1996). As a consequence, the model structure is often poorly adapted to the scales of the system investigated and models are difficult to test. One of our main concerns is that choosing an inadequate model structure, introduced for reasons of tractability rather than biology (Wood 2001) or because of missing criteria for aggregating information in a model, may cause a substantial loss or deformation of the original biological data. Especially under the circumstances typical for conservation biology, where management problems force hasty decisions to be taken in spite of scarce data, we cannot afford such losses.

Mathematical modelers have increasingly used quantitative statistical techniques to make rigorous inference from biological pattern (Wood 1994, Harrison 1995, Hilborn and Mangel 1997, Johst and Brandl 1997, Lewellen and Vessey 1998, Blasius et al. 1999, Casagrandi and Gatto 1999, Doak and Morris 1999, Kendall et al. 1999, Bjørnstad et al. 1999, Briggs et al. 2000, Claessen et al. 2000, Elliot et al. 2000, Turchin et al. 2000, Ellner et al. 2001, Fromentin et al. 2001, Turchin 2003). However, in conservation biology the potentially rich source of data provided by patterns, such as time-series data (Wiegand et al. 1998), that emerge as the high-level outcome of all processes of population dynamics and constraining factors (e.g. landscape structure, climate, management history) has been recognized only sporadically and intuitively. The purpose of this paper is to make this intuition an explicit modeling strategy that could be widely used. By reflecting on what characterizes successful ecological models, Grimm et al. (1996) found that “the most successful models were those that took their orientation from [such] distinct patterns observed in nature”. Such “pattern-oriented models” (Grimm 1994, Grimm et al. 1996) have several features in common: their structure is not arbitrary but is constrained by patterns of the real system, they are explicitly linked to the relevant spatial and temporal scales of the system, and – most importantly – they are testable. Whereas Grimm et al. (1996) focused on model construction and theory, and Wiegand et al. (in press) on uncertainty in spatially

explicit population models, we here focus on application of pattern-oriented models and we generalize the pattern-oriented modeling approach into a systematic framework for exploiting the available biological data at all steps of the modeling process: from the initial model construction to parameter estimation and to detection of deficiencies in the model structure and knowledge.

We provide a step-by-step protocol for applying the pattern-oriented approach and illustrate it by discussing three pattern-oriented population models from applied ecology: (i) population viability analysis for brown bears (*Ursus arctos*) in northern Spain using time-series data of females with cubs of the year for adjusting unknown demographic model parameters (Wiegand et al. 1998); (ii) a spatially explicit savanna model for detecting underlying ecological processes from the spatial patterns of tree distribution (Jeltsch et al. 1999), and (iii) the incidence function model of metapopulation dynamics as an example for process integration and model generalization (Hanski 1994, 1999). We make no attempt to review the literature on the role of theory in ecological application and conservation, since such reviews exist (Caughley 1994, Doak and Mills 1994, Starfield 1997, Beissinger and Westphal 1998).

Pattern-Oriented Modeling

What is a pattern, and why do we need to consider patterns?

Grimm et al. (1996) defined a “pattern” as a characteristic, clearly identifiable structure in nature itself or in the data extracted from nature. A pattern is anything that goes beyond random variation and thus indicates an underlying process that generates this pattern (Levin 1992, Weiner 1995). Such patterns include time-series data (Wiegand et al. 1998, in press), the distribution of dispersal distances and the spatial pattern of species occurrence in fragmented landscapes (Hanski 1994), wave-like pattern of the spread of rabies (Jeltsch et al. 1997), the spatial pattern of savanna trees (Jeltsch et al. 1999), and size-class distribution of *Acacia* trees (Wiegand et al. 2000).

Such patterns represent high-level manifestations of population dynamic processes and are the outcome of interplay between demographic processes, dispersal characteristics and various constraining factors (e.g. management actions, or a climatic pattern). Therefore, empirically observed patterns contain a great deal of information and memory about the history of the system. Because the patterns describe features of the system at a higher hierarchical level than are addressed by possible model rules (e.g. individual-based rules vs population level data), there are only limited possibilities to include this information directly into the rule set of a

model. Unfortunately, indirect methods of parameter estimation, a standard practice in many areas of science, which would allow the use of the “hidden” information are widely overlooked in conservation (but see Hanski 1994, Lindenmayer et al. 2000, McCarthy et al. 2000, 2001). This is surprising since indirect methods are commonly used in “hard sciences” such as physics, and even increasingly in mathematical biology (Burnham and Anderson 1998, Kendall et al. 1999, Wood 2001, Turchin 2003). In conservation we could learn from this tradition to systematically use observed patterns for revealing information on processes and parameter values. Under circumstances of scarce data, the additional data provided by independent patterns may be especially valuable and could greatly improve the quality of model predictions and the general understanding of the system. We therefore argue that there is an urgent need in ecological application and conservation practice to consciously search for and measure such patterns, and there is an urgent need to develop methods for using these data.

The protocol for pattern-oriented modeling

The basic idea for using the data of observed patterns is to include in the model the constraining factors and the minimal set of processes that are necessary for reproducing the patterns and to systematically compare the observed patterns with patterns produced by different modifications of the model (Fig. 1). In the following we formalize this idea to a four-step protocol of pattern-oriented modeling, which may be repeated in a cyclic manner.

First step: aggregation of biological information and scales. Model construction should not only be guided by the aim of the model and by the available knowledge, but also by patterns that can be detected in the system in question. The reason for this is that patterns are indicating both characteristic structures and processes of the system. By choosing a model structure that in principle allows reproduction of the observed patterns, we achieve a structurally realistic model, i.e. a model that contains key structural elements of the real system. Structural realism is achieved by the formulation of hypotheses on the structures and processes necessary to reproduce the observed patterns. Thereby, hypotheses are automatically defined on the relevant spatial and temporal scales (Grimm et al. 1996). Moreover, the observed patterns define a minimum level of detail that helps decide which processes should be included in the model. Given the aim of the modeling, one has to ask whether or not a particular process is indispensable for the creation of the pattern at the scale of interest. In the context of conservation with limited data, it is important to focus on minimalistic models in which the number of parameters and processes are

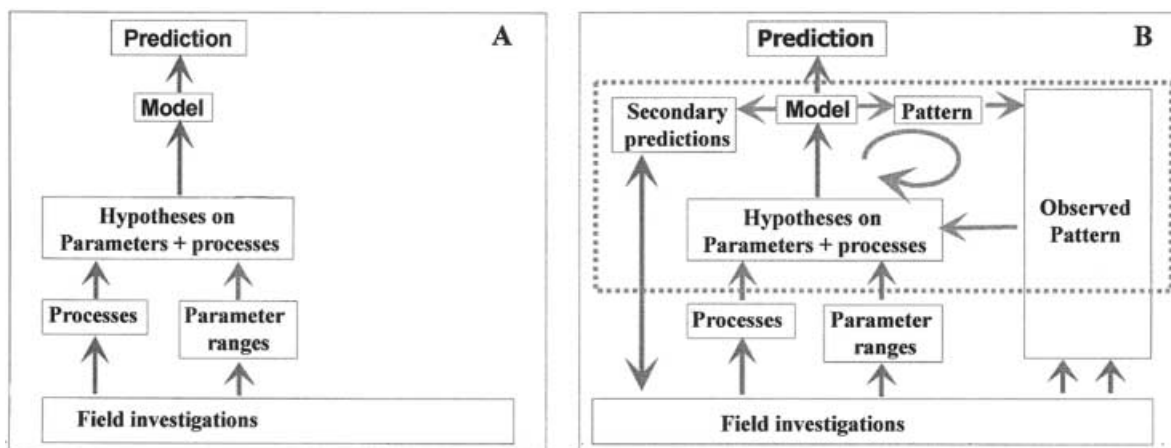


Fig. 1. Error propagation. (A) Non pattern-oriented modeling. Field investigations, additional information from literature, and guesses guide the construction of the model. Because poorly known parameters enter the model at a low hierarchical level, error propagation is unavoidable. (B) Pattern-oriented modeling. The hypotheses on parameters and processes are constrained by the observed patterns, and comparison between the observed patterns and the patterns produced by the model restricts the range of uncertain parameters and can be used for detecting the underlying processes that produce the observed patterns. The observed patterns are compared with patterns produced by several alternative hypotheses on processes and/or a large number of plausible parameter combinations. Because the high-level output of the model (the patterns), which contains relationships between the model parameters, must match the observed pattern, error propagation does not occur. A helpful analysis of the model can be obtained by analyzing internal model relations (secondary predictions), and the model can be validated by comparing secondary predictions with independent field data.

curtailed to what is absolutely necessary information. Otherwise the scarce information will not be sufficient to parameterize the model. However, one should avoid using initially an exceedingly minimalistic model structure, since this may bias model predictions. Formulation of alternative model structures – model variants with nested complexity or model variants with alternative hypotheses about the processes – provides a systematic approach to finding an appropriate minimalistic model. If the simplest model does not reproduce an essential pattern it has to be replaced by a model with a more adequate structure, whereas alternative model structures that do not improve model performance can be rejected (see below “cycles of pattern-oriented modeling”, and step 1 of the savanna tree example).

Second step: determination of parameter values. After the hypotheses on the processes have been formulated and the appropriate modeling technique has been identified, the values and the ranges of the model parameters have to be determined. This step does not differ from any conventional parameterization of a population model.

Third step: systematic comparison between the observed patterns and the patterns predicted by the model. In this step the model is applied with a large number of parameterizations and alternative hypotheses about the processes, and the predicted patterns are systematically compared with the observed ones (Fig. 1). The observed patterns acts as “filter” that sorts out implausible parameter combinations and implausible processes. Note that this technique is especially powerful when multiple patterns are used (Kendall et al.

1999, Reynolds and Ford 1999, Ford 2000, Railsback and Harvey 2002, Wiegand et al. in press). While it might be relatively simple to reproduce one feature of a system, the simultaneous fulfillment of several patterns describing different features of the system is by far non-trivial. For a quantitative comparison, statistical methods are needed to decide whether or not a given pattern matches the data (see e.g. Hilborn and Mangel (1997), Burnham and Anderson (1998), Wood (2001) for methods), and under which model the patterns are most probable. In the time-series context, Kendall et al. (1999) and Turchin (2003) refer to such statistical descriptors collectively as “probes”.

The third step necessarily includes a critical assessment of whether or not the pattern is genuine (Grimm et al. 1996). A reproduction (or “explanation”) of a pattern with a model does not guarantee that the model actually identified the processes or mechanisms responsible for the patterns in reality (Levin 1992, Moloney 1993, Jeltsch et al. 1999). To minimize the risk of misinterpretation one has to ensure that predicted patterns that match the observed patterns are neither a singular output of the model nor that they can be reproduced with arbitrary combinations of parameters and/or processes. If the model is able to reproduce multiple patterns, each describing a different feature of the system, the risk that many different processes may have caused this particular combination of observed patterns is lower than when relying only on one pattern (Kendall et al. 1999, Wiegand et al. in press). At this stage, the modeler must adopt the attitude of an experimenter (Grimm 1999, 2002) and systematically investi-

gate the behavior of the model with respect to the patterns. To achieve a comprehensive understanding of the model, the experiments or scenarios included in this step are required to change processes or parameters beyond their realistic ranges. The goal of this step is to identify and understand the processes, or combinations of processes and circumstances that lead to the specific patterns observed in nature.

The third step necessarily includes a critical assessment of the “quality” of the patterns; that is the magnitude of error connected with data collection. Clearly, taking a purported pattern with possible observer bias and misinformed interpretation too seriously may bias the model results. For example, long time series data may be severely flawed if the data originate from counts or otherwise statistically questionable studies. On the other hand, an attempt to adjust the simulated patterns to agree with the observed pattern more closely than stipulated by the measurement error in the observed pattern would be inconsistent and erroneous. However, the assessment of the error of the observed pattern may guide the selection of an adequate criterion for deciding when the simulated pattern matches the observed one.

If the patterns are genuine and contain additional information, the indirect and simultaneous parameter adjustment prevents error propagation, as may happen in conventional models based on point-estimates of parameter values (Fig. 1). The degree to which the initial uncertainty is reduced depends on the amount of information that is carried by the observed patterns, and on how well the model describes the most important processes and the major constraints that generate the observed patterns.

Fourth step: secondary predictions. Several inherent features of pattern-oriented models, such as the linkage to relevant scales and the matching of realistic pattern at a high hierarchical level, make it possible to derive additional relationships (secondary predictions, or ancillary data, Turchin 2003). These relationships, which are not identical with the initial patterns nor model assumptions, but which arise out of the interactions between the simulated processes, offer potentially valuable possibilities for making predictions, for better understanding the model performance, and for model validation. To derive secondary model predictions one may create a “virtual” ecologist or observer (Grimm et al. 1999) that scans the internal model performance, recording for example age structures, mortality rates, dispersal distances, population sizes, patch occupancy, extinction events, distribution of individuals in a landscape, etc. The secondary predictions can be used for model validation if field estimates are available. Alternatively, they may also be used to further improve the determination of parameters and processes in the third step of our protocol (i.e. they are treated as patterns, Wiegand et al., in press). However, in many cases it

may be interesting to check whether or not internal relationships produced by the model, which are not primarily envisaged as model output and are thus usually not recorded, are within biologically realistic ranges. Such tests can greatly improve the confidence in the model and may help prevent unrealistic assumptions from creeping in. These tests may also suggest new patterns.

Cycles of pattern-oriented modeling. Ideally, the four steps of our protocol are repeated in a cyclic manner (Thulke et al. 1999). In the first cycle the biological information is arranged in a logical manner and the data and (preferably simple) hypotheses about the functioning of the system are integrated into a first model. Comparison between the predicted and observed patterns will usually point to sensitive parameters or processes, problems in the formulation of the processes, or missing data. For example, a pattern may only be reproduced if a certain process is included. Such a finding may stimulate new field investigations for closer examination of the process that appeared indispensable for reproducing the pattern. On the other hand, if the model structure is too simple the model will not be able to reproduce one or more patterns. This failure of the model, however, can be valuable in stimulating specific field investigations on the missing processes and for deriving a more adequate model structure. In the second cycle the new information and hypotheses on alternative model structures are included in the model, which is again tested by comparing predicted and observed patterns. Several feedback loops and steps between field investigations, modifying hypotheses, and running the model may be required before an optimal model structure, that is, a minimal model that reproduces all observed patterns, is identified and the mechanisms behind the observed patterns are well understood.

Examples

Parameter estimation: the brown bear population model and the temporal pattern of females with cubs

Wiegand et al. (1998) compiled the knowledge available about the western brown bear population in the Cordillera Cantabrica, Spain, and performed a population viability analysis (PVA) to diagnose the current state of the population and to support management. The PVA required a close determination of demographic model parameters. Model calibration was done using an independent data set with 14-yr data on the number of females with cubs.

The pattern. The pattern used in this example is the observed 14-yr time series of females with cubs of the year (COY index, Fig. 2), which provides data at

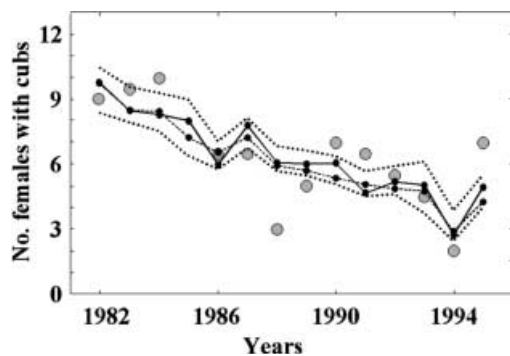


Fig. 2. Observed and simulated patterns: the observed pattern (gray circles) and the two simulated patterns with the smallest error Δ (solid line: $\Delta = 1.42$, dashed line: $\Delta = 1.45$), and range of the simulated patterns for the 90 best parameter combinations (minimal and maximal values; dotted lines).

several levels: the COY index is related to the overall population size, to the overall population trend, and to demographic parameters and environmental variation.

First step: aggregation of biological information and scales. A model able to reproduce a time-series of the number of females with cubs must necessarily be a demographic model that includes the processes of reproduction, mortality and family break-up. Because the number of females with cubs was small (< 11 in any one year, Fig. 2), the individual-based approach is well suited in this case. Preliminary model runs showed that the COY index is critically influenced by environmentally caused variation in mortality rates, litter size and probability for reproduction (Wiegand et al. 1998: Fig. 4). Therefore, the criterion for including biological information required consideration of environmental variation. Examination of data showed that environmental variation had indeed a significant impact on cub mortality and litter size, and the authors suspected that subadult and adult survival could also be influenced by environmental variation. To examine alternative hypotheses on environmental fluctuations, the same procedure of comparing observed and predicted patterns (step 3) was repeated for alternative scenarios of how environmental variation influenced adult and subadult mortality rates. Besides environmental variation, the COY index may be influenced by the availability of habitat suitable for reproduction. Brown bear habitat is limited and may support no more than 18 breeding females in the same year, which is the sum of the largest number of females with cubs observed in any year in each area. Therefore, density-dependent regulation was considered by limiting the number of females that can breed simultaneously to 18.

Second step: determination of parameter values. Following the data and literature analysis a total of 8 model parameters remained uncertain, and the authors selected for each of them 2, 3 or 5 probable values that entered into the final grid in parameter

space which yields a total of 9000 parameter combinations. Additionally, five alternative hypotheses of environmental variation were considered.

Third step: systematic comparison between the observed pattern and the simulated pattern produced by the model. The mean COY index obtained from a series of 200 replicate simulation runs [$\text{COY}(t)$], and the observed number of females with cubs from 1982–1995 [$d(t)$] were compared through the error measure $\Delta(\text{COY}) = (\sum_{\text{years } t} (\text{COY}(t) - d(t))^2 / N)^{0.5}$, where N is the number of years with data. The error Δ served as a criterion to distinguish between probable (Δ small) and less probable (Δ high) parameter combinations. Only in two years was the confidence range of the pattern greater than ± 1 and the overall maximal measurement error of the pattern yields $\Delta \approx 0.9$. Therefore, Wiegand et al. (1998) did not attempt to adjust simulated pattern below the inherent error of the pattern of $\Delta < 0.9$. Simulations were performed for the 9000 possible parameter combinations and five alternative hypotheses of environmental variation. Not all parameter combinations were able to reproduce the observed pattern of females with cubs (Fig. 3). For parameter combinations that resulted in too high or too low overall rates of increase, differences in $\text{COY}(t)$ and $d(t)$ were marked, and even if the overall population trend was matched, “wrong” parameter combinations could cause clear differences between the shape of the observed and the simulated COY index (e.g. produce wrong minima and maxima in the time series). The scenarios with low (and no) variation in adult mortality had minimal errors of $\Delta \approx 1.4$, but high variation in adult mortality rate always resulted in worse fits, with errors $\Delta > 1.5$ (Wiegand et al. 1998). Thus, the authors rejected the hypothesis of high environmental variation in adult mortality rate, but not the hypothesis of high environmental variation in subadult mortality rate. Individual parameter values varied little among the best parameter combinations (Wiegand et al. 1998: Table 8), thus rejecting the possibility of several “optimal” model parameterizations. Use of a second pattern, the number of known mortalities from 1982–1994, further improved the quality of the fit from $\Delta \approx 1.4$ to $\Delta \approx 1.0$, but did not alter the parameter estimates. The procedure of indirect parameter estimation thus allowed the determination of credible reference parameter set.

Fourth step: secondary predictions. Because the observed pattern restricts the degree of freedom of population dynamics, the values of several unknown variables of population dynamics (e.g. total population sizes and numbers of independent females at different years, growth rates, mortality rates) could be determined with simulation runs produced by parameter combinations that yielded a good match between the observed and simulated patterns (Fig. 3A). Especially the estimate of the current number of independent females (25–26 in 1995) was an important reference

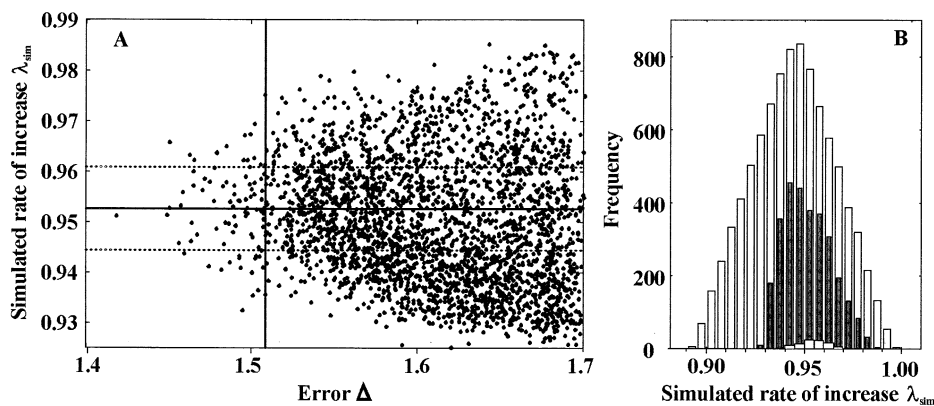


Fig. 3. Secondary prediction for the unknown simulated rate of population increase λ_{sim} during the study period 1982–1995. (A): The simulated rate of increase, λ_{sim} , is plotted for the 31% best parameter combinations, over the resulting error Δ between the observed and the simulated COY index. The results are shown for the scenario with no environmental variation in adult and subadult mortality rates (scenario S1 in Wiegand et al. 1998). The 90 “best” parameter combinations are located left from the vertical line $\Delta < 1.51$. The solid horizontal line gives the mean simulated rate of increase λ_{sim} obtained from the 90 best parameter combinations and the dashed lines indicate the standard deviation ($\lambda_{sim} = 0.953 \pm 0.008$). (B): Distribution of λ_{sim} for all 9000 parameter combinations (white bars), for the 31% best parameter combinations (gray bars), and for the 90 best parameter combinations (white bars).

point for determining minimal viable population sizes and for assessing the risk of extinction for the brown bear population in the Cordillera Cantabrica (Wiegand et al. 1998). Because the COY index is also tied to the overall population trend, it considerably restricts the range of the simulated rate of population increase during the study period 1982–1995 (Fig. 3A).

Error propagation. Fig. 3B shows clearly how the data provided by the observed pattern prevents error propagation. Without considering the data contained in the observed pattern, the simulated rate of increase varies due to the initial uncertainty of the model parameters between $\lambda_{sim} = 0.89$ and 1.00 (Fig. 3B), while application of the indirect parameter estimation reduces the probable range of λ_{sim} to 0.953 ± 0.008 (Fig. 3A). Comparison with the results of the sensitivity analysis performed in Wiegand et al. (1998) shows that this uncertainty is of the same magnitude as the uncertainty in λ_{sim} that arose out of the remaining uncertainty for the single most sensitive parameter, the adult mortality rate m_{5-16} : $\Delta\lambda_{sim} = \Delta m_{5-16} \rho(m_{6-16}) = 0.037 \times 0.512 = 0.0189$ (see Wiegand et al. 1998: Table 12). These results are very good news and show explicitly that indirect pattern-oriented parameter estimation can prevent error propagation and reduce the sensitivity of the model output to model parameters.

Detecting processes from pattern: the savanna model and snapshot pattern of tree distribution

In the previous example the data of the observed pattern was used primarily for parameter estimation. In the present example the focus is to show how cyclic repetition of the four step protocol facilitates the iden-

tification of the underlying processes that lead to the formation of the spatial pattern of savanna trees rather than on parameter values of processes that are already known. To investigate whether the tree population of the southern Kalahari Savanna is in a phase of decline, increase, or constancy with respect to tree abundance Jeltsch et al. (1999) applied methods of simulation modeling and point pattern analysis to assess the potential of a spatial pattern, snapshots of observed tree distributions, for identifying relevant pattern-generating processes. They also investigated to what extent the current tree distribution pattern is indicative or even diagnostic of the dynamical status of the tree population.

The pattern. The pattern used in this example consisted of six maps of spatial distributions of trees, each covering an area of 50 ha, and digitized from aerial photographs (Fig. 4A). Tree distribution patterns derived from aerial photographs and from simulation experiments were analyzed and compared using Ripley’s L-function analysis (Bailey and Gatrell 1995), a statistical point pattern analysis (Jeltsch et al. 1999).

First step: aggregation of biological information and scales. Since the pattern in this example is spatially explicit and based on individual trees, a combined spatially-explicit and individual-based modeling approach was chosen. The relevant scales are determined by the spatial scale of the pattern (i.e. at least several hectares) and the temporal scale of several tree generations. Consequently, an area of 50 ha was subdivided into a grid of 20,000 5×5 m cells, an area large enough to accommodate a mature tree canopy, and simulation runs encompassed a timespan of several thousand years. A model capable of reproducing the spatial pattern of savanna trees, assumed to be in a state of

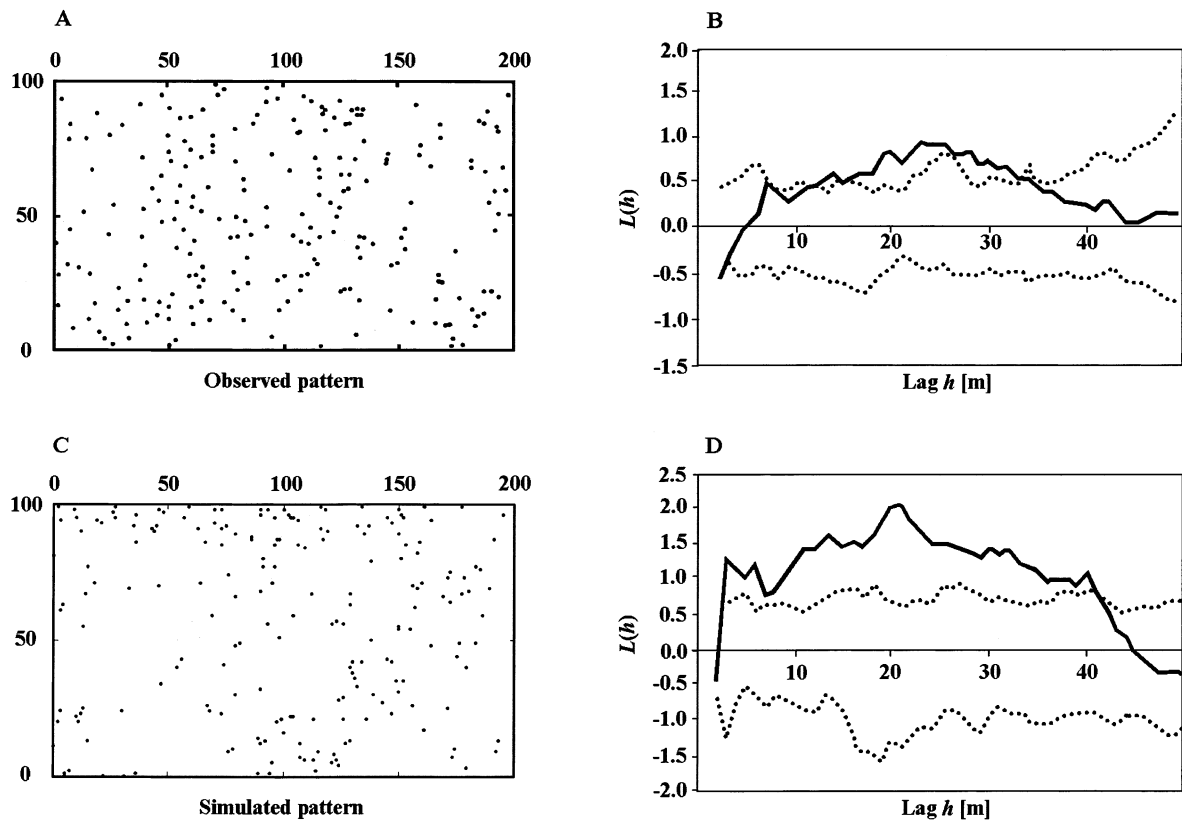


Fig. 4. (A): An example of a snapshot pattern of tree distribution derived from an aerial photograph of a representative 50 ha region in the Kalahari Gemsbok National Park. (B): point-pattern analysis (L -value vs spatial scale given in grid-cell units) of the spatial distribution of trees shown in (A). The L -value (solid line) is given together with the 95% confidence interval (dashed lines). L -values within the range of the confidence interval indicate a random pattern. L -values above (below) the confidence interval indicate a significantly clumped (even spaced) distribution. (C): simulated spatial pattern of adult trees within a 50 ha area. (D): point-pattern analysis of the simulated pattern shown in (C). Modified after Jeltsch et al. (1999).

long-term coexistence with grasses, must contain the classical key processes in savannas, namely competition for moisture, herbivory and grass fires (Walker et al. 1981). However, in a first cycle of pattern-oriented modeling Jeltsch et al. (1996) found that these key processes were not sufficient to explain savanna-like coexistence in their spatially explicit simulation model. Long-term coexistence occurred only with spatially scattered groups of trees, a spatial pattern which is not observed in the southern Kalahari savanna. By introducing hypothetical small-scale heterogeneities and disturbances, which caused differential probabilities of tree establishment and survival, Jeltsch et al. (1998) obtained long-term savanna coexistence with realistic spatial patterns of tree distribution for a broad range of parameter values. This finding gave rise to new field investigations that were aimed at identifying the missing processes. Results of these field investigations and new simulation experiments (the second cycle) showed that seed dispersal in the dung of large herbivores consuming the pods of *Acacia erioloba* was the most important process leading to micro-sites in the land-

scape with improved establishment and survival chances for trees.

Second step: determination of parameter values. The spatially explicit simulation model is based on the ecological dynamics occurring in the South African part of the southern Kalahari represented by the Kalahari Gemsbok National Park (KGNP). Most parameter estimates are based on two decades of field research in this area (see Jeltsch et al. 1996, 1998 for details). However, it was not possible from empirical studies alone to identify the rate with which dung patches are formed. To estimate this unknown parameter Jeltsch et al. (1999) used a pattern-oriented approach. Here the pattern is the observed tree density in the KGNP together with the assumption that, historically, this area is in a state of long-term coexistence of trees and grasses. Too high rates of annual seed patch formation lead to an unrealistic continuous increase in tree densities whereas too low rates caused a rapid tree decline. With the determination of this unknown parameter range it was possible to explore the initial question for the dynamical status of the tree population using the more complex spatial pattern.

Third step: systematic comparison between the observed pattern and the pattern predicted by the model. Simulations showed that the pattern of spatial tree distribution was not constant but changed in the course of time. Especially for long-lived plants, this situation limits the amount of information that can be extracted from the pattern. Although there was variability within and among runs, the patterns produced by the model were in general consistent with the actual patterns observed at KGNP (cf. Fig. 4A and C, and 4B and D). However, more detailed investigations of secondary model predictions facilitated by the pattern-oriented approach were necessary to identify the current dynamical status of the tree population in the southern Kalahari.

Fourth step: secondary predictions. The possibility to observe the relevant ecological factors and processes in the course of time allows for the examination of the functional relationship between the ecological state of the model system and the spatial pattern in tree distribution produced over time. Jeltsch et al. (1999) used a virtual observer that recorded during an individual model run, for 50 consecutive 10 yr windows, several internal model relations (e.g. number of years with maximal topsoil and subsoil moisture, the number of cells dominated by perennial grasses and herbs, the mean number of tree seedlings, saplings, and adults). They showed that periods of tree decline caused by lower rainfall are characterized by reduced clumping and an increase in randomness in the tree distribution pattern, and that both reduced fire frequency and increased self-thinning (caused by low rainfall) reduce the tendency of the tree distribution towards clumping. Thus, a spatial pattern that is characterized by a high degree of clumping at different scales, as currently observed in the southern Kalahari, is not in a dynamic state of major decline nor in risk of extinction caused by reduced rainfall conditions.

General models for specific applications: the incidence function model and spatial pattern of habitat patch occupancy

The Incidence Function Model (IFM, Hanski 1994, 1999) of metapopulation dynamics is perhaps the best known and most widely used pattern-oriented model that explicitly relies on indirect parameter estimation. The aim of the IFM is to construct a minimalistic description of metapopulation dynamics that may nonetheless provide guidance to quantitative questions about particular metapopulations (Hanski 1994).

The pattern. The pattern employed in the IFM is defined by the spatially explicit layout of suitable habitat patches within unsuitable habitat matrix, including patch locations and sizes (or qualities), and one or more snapshots of data on the presence/absence of the

species in these patches at stochastic equilibrium. If the model is parameterized with just one snapshot of spatial data, as originally envisioned by Hanski (1994), all the information on extinction and colonization processes is provided by the spatial pattern data. Specifically, at equilibrium the pattern of patch occupancy reflects the reduced colonization rate of isolated patches and the increased extinction rate of small populations in small habitat patches.

First step: aggregation of biological information and scales. The patch occupancy pattern determines the level of detail in the model. Because only two states of the patches are considered, occupied or empty, the model ignores all details of local dynamics (reproduction and mortality) within single habitat patches. To reproduce the pattern of patch occupancy, the IFM relies on a description of local dynamics that only consists of the patch-specific extinction probability and a patch-specific colonization probability of empty patches. The key task is to make reasonable and practical assumptions about how these two population processes depend on measurable landscape variables and some life-history traits of the species.

The IFM assumes decreasing extinction probability with increasing patch area, and a colonization probability that is dependent on patch connectivity to existing populations. The most difficult task is to define the measure of patch connectivity, which summarizes the information on the spatial layout of habitat patches and on the movement behavior of the species. Although it might be possible to derive a formula based on the actual movement behavior of individuals, Hanski (1994) used a simple phenomenological approach, which is consistent with the level of detail in the rest of the model. Note that the observed pattern (distances among the patches, patch areas, and the patch occupancies) enters the model at this step and ties the IFM explicitly to the relevant spatial scales of the system.

Selection of the appropriate spatial scale has to be made with relevant biological information. The patch area and connectivity effects are likely to occur also in e.g. data on the instantaneous distribution of foraging individuals among a set of resource patches, though this pattern has nothing to do with population processes. Determining the appropriate population scale for a particular organism is generally not that difficult, but it is essential that adequate biological knowledge is used in this step.

Second step: determination of parameter values. Because the IFM does not consider local dynamics, there are only five model parameters (x , y , e , α , and b) that have to be determined (Hanski 1994). The parameters e and x describe the local extinction probability and its scaling with patch area, y is a colonization parameter, $1/\alpha$ is the average migration distance, and b scales the emigration rate by patch area. Two of them (b , α) can often be estimated with independent data,

and the data provided by a single snapshot of patch occupancy are then used to estimate the remaining three parameters (Hanski 1994, 1999, Moilanen and Hanski 1998, Moilanen 1999). Alternatively, one may use occupancy data to estimate all the parameters. In the IFM, the third step (below) is part of actual parameter estimation.

Third step: systematic comparison between the pattern produced by the model and the observed pattern. The original parameter estimation method for the IFM does not require simulations since the model is formulated in a closed mathematical form (Hanski 1994). The parameter values are estimated by regressing the transformed model-predicted incidences against the empirically observed patch occupancies (Hanski 1994, 1999). The logistic regression model that contains the observed pattern represents a very explicit connection between the IFM and the empirical field studies (Hanski 1999).

Given the structural assumptions of the IFM, a single pattern of patch occupancy provides, in principle, sufficient information to infer the values of the parameters characterizing the metapopulation processes (Hanski 1994). However, including the “rescue effect” into the model leads to a model in which the parameters e and γ occur in a product. In this case, some additional information is needed to separately estimate the values of these parameters. For example, one may estimate the minimum patch area, or one may use information about population turnover rate between two or more time steps (Hanski 1994).

The original parameter estimation method based on logistic regression (Hanski 1994) ignores spatial and temporal correlations in patch occupancy and assumes metapopulation quasi-equilibrium and constant colonization probabilities. Moilanen (1999) has developed a parameter estimation method that is not affected by these problems. Moilanen’s approach however requires data on population turnover, that is, several snapshots of patch occupancy. On the other hand, it is clear that if temporal as well as spatial data are available, one should employ all available information in parameter estimation. A useful feature of Moilanen’s (1999), and Moilanen’s (2000) approach is that one may make a conscious decision as to which kind of information to use in parameter estimation. Moilanen (1999) found that the value of parameter α , which scales distance dependence of migration, was generally estimated well with his Monte Carlo method. This is a good example of how an observed pattern can be used effectively and may replace costly studies for determining single parameter values.

Fourth step: secondary predictions. The use of a virtual observer offers numerous possibilities for testing the model with secondary predictions. For instance, Moilanen et al. (1998) tested the IFM parameterized for the American pica in two different ways using secondary model predictions. First, they constructed a

measure that characterizes the dynamic behavior of the simulated and empirically observed sequences of patch occupancy, and checked whether the measure calculated from the empirically observed sequences of patch occupancy patterns falls within the 95% confidence limits of the predicted distribution. Because the model was parameterized using only spatial data on patch occupancy, a second test was made by comparing the predicted number of turnover events, extinctions and colonizations, with the observed ones.

Because the spatial layout of the patch network is explicitly considered, the IFM can be used as a practical tool for management purposes. The parameter estimates allow numerical simulation of the dynamics of the focal species in any system of habitat patches with known values of patch sizes and patch locations, and starting from any configuration of occupied patches (for an extensive review see Hanski 1999). It should also be noted that, although one has to make the assumption of metapopulation quasi-equilibrium for the purpose of parameter estimation, the model can also be used to make predictions about the transient (non-equilibrium) dynamics. For instance, one may assess the likelihood of colonization of a patch network from one or a few (possibly introduced) local populations (Hanski 1999).

The IFM has been used as a component in a recent individual-based model of the evolution of migration rate (Heino and Hanski 2001). In this model, the long-term dynamics predicted by the individual-based model were constrained to match the predictions of the IFM by comparing patterns of habitat patch occupancy and temporal turnover of local populations. The actual migration of individuals was modeled with another submodel, the “Virtual Migration” (VM) model (Hanski et al. 2000), which can be considered as a pattern-oriented model of mark-release-recapture data (the pattern consisting of the dependence of emigration and immigration rates on habitat patch area and connectivity). A great advantage of this model construction is that most model parameters could be rigorously estimated and the individual-based model was focused on situations that occur in real metapopulations (Heino and Hanski 2001).

Discussion

In this article, we summarize and conceptualize our experience concerning population modeling within a common framework, the pattern-oriented modeling strategy, and we advocate this approach as a possible way out of the problems described in the introduction. Our framework is related to modeling strategies that have been developed to study population cycles and fluctuations using mathematical models (Kendall et al. 1999, Turchin 2003), and to an approach for construc-

tion and analysis of “mechanistically-rich” simulation models (DeAngelis and Mooij, in press). Basically, pattern-oriented modeling is a strategy for optimally exploiting the available biological data in all the steps of the modeling process: from the initial model construction to parameter estimation and detection of deficiencies in the model structure and in our knowledge. However, one may argue that the general features of our protocol are by no means new and that the attempt to explain pattern is the basic program of science. Clearly, scientists have always tried to identify patterns, and by explaining their creation they could reveal essential properties of the system in question. For example, prominent cases in natural sciences where patterns helped to reveal the “essence” of a system include classical mechanics (Kepler’s laws), quantum mechanics (atomic spectra), cosmology (red shift), molecular genetics (Chargaff’s rule), and mass extinctions (Iridium layer at Cretaceous boundary). On the other side of the spectrum, even a simple regression model can be seen as a pattern-oriented model if the underlying hypothesis are consciously derived from the biological information and no data dredging (Burnham and Anderson 1998) was done. Clearly, the challenges and problems for population models in biological conservation are not much different from that in other fields of science where models are used for inference, and our modeling strategy will be similar to that in other fields. Our main objective, however, is to point out to problems related to the application of models in conservation and to provide a practical strategy to overcome them, rather to invent a “new wheel” for science in general. The pattern-oriented modeling strategy provides a framework for consciously deriving hypotheses on processes to be included in a model and for testing them against each other by using (multiple) independent data (i.e. the patterns). Thereby it facilitates the selection of a “best approximation model” regarding a given set of independent pattern data and the detection of deficiencies in the model structure when the model does not match one or more patterns. Thus, the pattern-oriented modeling strategy is in some respects an analogue to statistical approaches of model selection and inference for mathematical models (Hilborn and Mangel 1997, Burnham and Anderson 1998, Wood 2001), which are not necessarily based on mathematical equations but may be based on simulations.

Lessons from the examples

The three examples presented in this article highlight different features of the pattern-oriented modeling strategy. In the first example, a simple non-spatial individual-based model was closely adjusted to the time-series data of the observed number of female brown bears with cubs. While the model itself is quite simple, the proce-

sure of parameter estimation was time-consuming and required non-standard methods. However, as compensation for this effort the additional data provided by the observed pattern helped adjust the formerly unknown model parameters and prevented error propagation. These are important considerations that solved two of the most serious problems in the application of models in conservation biology: the inherent paucity and uncertainty of “conventionally” collected data, and sensitivity of model predictions to parameter values. The major take-home message emerging from this example is that field research should more consciously search and document patterns that can potentially deliver information that is impossible to obtain with traditional methods. Determination of unknown or uncertain demographic parameters (e.g. mortality rates) to a similar precision would be impossible with traditional methods, because that would require extensive telemetric studies and trapping of a high percentage of the entire population, an undertaking that is impossible to perform in practice (J. Naves, pers. comm.). Because data in the pattern can only be used via methods of indirect parameter estimation, a close interaction between field research and modeling is required.

The striking feature of the savanna model is the close interaction between field investigation and modeling during several cycles of pattern-oriented modeling for specifying initially unknown processes. Early results of the model pointed to critical processes which were necessary to obtain tree distributions typically for the Kalahari savanna. Hypotheses on these processes derived from the initial modeling exercise guided further field investigations that specified the processes. Including the new biological information into the model produced new insight on the status of the savanna that could hardly have been obtained with traditional methods. The possibility to more effectively plan field investigations with the aid of pattern-oriented models is an important advantage, especially in times of scarce resources and pressing environmental problems. However, the savanna model showed not only that the pattern-oriented strategy can be effectively used at different stages of model development, but also that it can serve to improve different parts of the model. While the “big” pattern was the spatial distribution of the savanna trees, data on the mean densities of savanna trees was used as an additional pattern for adjusting the unknown value of the model parameter “rate of annual seed patch formation”. Finally, the savanna model is a good example of how a model can facilitate a deeper understanding of spatial pattern formation in ecological systems, a question that has attracted much interest recently (Levin 1992). A key element in the savanna example was the possibility to scan the internal model performance with a virtual observer. Such an analysis goes beyond the usual approach to sensitivity and error analysis (Grimm et al. 1999).

The incidence function model is an excellent example of how a general minimalistic model can be applied to specific situations; it may represent a signpost of how to reconcile ecological theory with ecological application and conservation. This simple stochastic metapopulation model ignores systematically all biological information (that might to some extent be available) below the scales and the level of detail dictated by the observed pattern. Such conscious sacrifice of detail makes the model general. The model itself is an “empty general structure”, which summarizes very generally how extinction and colonization processes depend on measurable landscape variables and general life-history traits of the species. However, when combined with the spatially explicit information contained in the observed pattern – the locations and areas of suitable habitat patches and the observed incidence of the species in these patches – the model can be closely tied to specific situations.

Advantages and shortcomings of the pattern-oriented modeling strategy

Although the pattern-oriented modeling strategy presented in this article has a number of advantages, we have to discuss also some potential problems of this strategy.

What can one do when no pattern exists? The most obvious shortcoming of our modeling strategy is that a genuine pattern is needed. So what can one do when apparently no pattern exists? The most important point to note is that the pattern does not need to be that distinct and spectacular as e.g. the wave-like spread of rabies (Jeltsch et al. 1997). The pattern can be any characteristic non-random structure in observations or data (Grimm et al. 1996). The term “non-random” implies that there were certain processes or mechanisms that created this pattern, and in turn that the pattern contains information on these processes or mechanisms. While searching for helpful patterns one may ask a number of questions: (1) Are there spatial structures that are related to my question? (2) Are there temporal structures or time-series data that are related to my question? (3) Are there comparable systems that behave differently from my system and are these differences perhaps connected to my question? (4) Are there relevant data or information available on my system that I cannot include directly into the rule-set of my model? (5) Does the system behave markedly differently from my expectations?

Vague and genuine patterns. Different patterns may contain a different amount of information that can be used with the pattern-oriented modeling strategy. “Vague” patterns that contain relatively little information may easily be overlooked, but the use of several vague patterns in combination with the Pareto Optimal

Model Assessment Cycle POMAC (Reynolds and Ford 1999, Ford 2000) may provide just as much information as one strong pattern (Wiegand et al., in press). POMAC uses binary error measures as vector assessment criteria and by revealing which combination of assessment criteria the model can satisfy simultaneously it guides the researcher to locate deficiencies in both the model structure and the assessment criteria.

If the number of parameters to be estimated is large or if the pattern is vague, several parameter combinations might produce equally good results and it might not be possible to determine even with several patterns an optimal model parameterization. In such cases we have to accept that the current knowledge is insufficient; i.e. the model rules and the filter procedure are only stated at a certain level of detail and may contain inevitable errors and subjective interpretations, and the pattern(s) may not carry sufficient information to reduce the degree of freedom of the system. It is important to note that the pattern-oriented modeling strategy is only a strategy that can help to construct a better model rather than a recipe that can solve all problems.

One may argue that one can always find a model that is able to reproduce an observed pattern, provided that one adds enough parameters and processes in the model. Such a critique may hold true for “blind” statistical fits and descriptive regression models that do not rely on information on the underlying biological processes (an example is conventional statistical time series analysis). In contrast, the pattern-oriented approach is a process-oriented approach that uses biological information on patterns and processes rather than arbitrary functions for fitting. Also, the criterion of minimalism prevents arbitrary inclusion of functional relationships into the model, and the critical assessment of whether or not the pattern is genuine (see third step of the protocol for pattern-oriented modeling) ensures that predicted patterns which match the observed patterns are neither a singular output of the model nor can they be reproduced with arbitrary combinations of parameters and/or processes.

Significance for ecological applications and conservation

We argue that a successful application of the pattern-oriented modeling strategy to its full potential may require a major paradigm shift in ecological modeling as well as in data collection.

Paradigm shift in modeling. Modelers should consciously employ observed patterns to construct models useful for practical applications as well as to develop new methods for indirect parameter estimation that rely on observed patterns. A systematic classification of patterns that can be used for pattern-oriented modeling is needed, and modelers should investigate and state

which type of pattern contains most information for determining parameters and processes. Such guidelines would be extremely helpful in conservation practice for enhancing the value of the biological information that has to be collected.

Paradigm shift in data collection. Ecologists need to develop a new consciousness about data by recognizing the potential of observed patterns as a rich source of biological information. Therefore they should look actively for patterns at a high hierarchic level that may provide independent data and document and measure such patterns. In general, some demographic data and some patterns at higher hierarchical levels will be relatively easy to obtain. Both will have some uncertainty, and it is very unlikely that all the demographic parameters needed in a model can easily be obtained with small uncertainties. That is why our approach is important in spatial modeling. On the other hand, it may be hard to say a priori whether information of one particular type or another (patterns versus single demographic parameters) will be more economical to obtain or have less associated uncertainty, and more theoretical and empirical studies are needed to resolve this issue.

Reconciling ecological theory and conservation practice. Pattern-oriented modeling provides means for reconciling theory and practice (Grimm 1994, Grimm et al., unpubl.). At present, most models are either too theoretical and general to be useful for practical applications, or they are too detailed for more general applications to other species and situations. Pattern-oriented models with the “right” scales and the “right” level of detail capture the essence of a system and can therefore often be easily refined for applied questions as well as generalized for a certain class of species or circumstances. A good example of such “intermediate general” models is the incidence function model which captures the essence of population-level spatial dynamics for a wide range of metapopulations. Our hope is that such intermediate general models, which arise out of specific case studies but which are tied to a general modeling strategy, may provide further opportunities for advancing our understanding of more general questions in conservation biology.

Acknowledgements – We thank W. Batista, F. Davis, F. Knauer, B. Kendall, K. Moloney, J. Naves, H. Possingham, K. Wiegand, A. Tyre, S. Schadt, C. Wissel, and especially D. DeAngelis and E. Revilla for assistance during the development of ideas and for comments on drafts of this manuscript.

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