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META-X: generic software for metapopulation viability analysis

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Abstract. The major tools used to make population viability analyses (PVA) quantitative are stochastic models of population dynamics. Since a specially tailored model cannot be developed for every threatened population, generic models have been designed which can be parameterised and analysed by non-modellers. These generic models compromise on detail so that they can be used for a wide range of species. However, generic models have been criticised because they can be employed without the user being fully aware of the concepts, methods, potentials, and limitations of PVA. Here, we present the conception of a new generic software package for metapopulation viability analysis, META-X. This conception is based on three elements, which take into account the criticism of earlier generic PVA models: (1) comparative simulation experiments; (2) an occupancy-type model structure which ignores details of local population dynamics (these details are integrated in external submodels); and (3) a unifying currency to quantify persistence and viability, the 'intrinsic mean time to extinction'. The rationale behind these three elements is explained and demonstrated by exemplary applications of META-X in the three fields for which META-X has been designed: teaching, risk assessment in the field, and planning. The conception of META-X is based on the notion that PVA is a tool to deal with rather than to overcome uncertainty. The purpose of PVA is to produce relative, not absolute, assessments of extinction risk which support, but do not supplant, management decisions.

Key words: Decision support, Extinction, Generic model, Incidence function model, Management, Metapopulation viability, Population viability analysis, Risk assessment, Software

Introduction

Population viability analysis (PVA) has been a declared subdiscipline of conservation biology since the mid-1980s (Shaffer 1981; Soulé 1986; Boyce

1992; Burgman et al. 1993; Beissinger and Westphal 1998; Groom and Pascual 1998). The purpose of PVA is a quantitative risk assessment because verbal classifications of populations as being 'too small' or 'highly endangered' are too vague to be useful in environmental decision making. In PVA, risk assessment is made quantitative by using ecological models. However, producing and analysing models requires experience and plenty of time. Obviously, developing a new model for each threatened population would be impossible. Therefore, there are two major alternatives to tailored PVA models: rules of thumb drawn from extinction theory and specific PVAs, and generic models, which can be applied to many specific populations.

Rules of thumb are general guidelines for managing threatened populations. They refer to broad classes of ecological situations. Generally speaking, rules of thumb place ecological situations into a hierarchical framework (Frank and Wissel 1998) to prioritise management actions. For example, in an ensemble of isolated patches, there is no point in making provision for dispersal among the patches unless the subpopulations on the patches have a certain minimum viability (Frank and Wissel 1998). Although the search for rules of thumb for managing threatened populations is promising (Frank and Wissel 1998; Henle et al. 1999; Vos et al. 2001; Frank 2004 (this issue)), it has not yet led to any generally acknowledged results. Therefore, generic PVA models are currently the main alternative to tailored models.

Generic models are designed to encompass as many specific situations as possible. They are usually made available as ready-to-use software packages such that non-modellers and non-programmers can use them (for comparative overviews of generic models for PVA, see Lindenmayer et al. 1995; Brook et al. 2000a, b; Kindvall 2000). The task of the user is to parameterise the generic model and to tailor it to some degree by choosing from alternative modules. Generic models compromise more detailed descriptions for general applicability. However, generic models have been criticised (e.g., Beissinger and Westphal 1998; Groom and Pascual 1998). The most critical point is that generic software packages may be too easy to use, that is, by users who are unaware of the goals, concepts, methods, and limitations of PVA. The purpose of PVA may become superficial if the generic packages are applied uncritically. Therefore, generic PVA models are needed which are designed to minimise the risk of uncritical usage while still serving the purpose of being applicable by non-modellers and non-programmers.

New generic models should also help overcome the misconception of PVA as a tool for 'decision making' (Burgman and Possingham 2000). To be a decision-making tool, PVA would have to deliver absolute, reliable predictions of the extinction risk, which is impossible given the uncertainties in model parameters and structure. PVA is instead a tool for decision support (e.g., Burgman and Possingham 2000): the predictions of extinction risk are by its very nature relative and comparative. The ultimate goal of PVA is to support the ranking of management scenarios and to base decisions on understanding, not on mere numbers. The conception of new generic PVA models and software should reflect this ultimate goal of PVA.

Here, we present the conception of a new generic model and software for metapopulation viability analysis, META-X (Frank et al. 2003). We will not describe the details of the user interface and the META-X software, which are explained in Frank et al. (2003). The conception of META-X is based on three elements, which take into account the criticism of generic PVA models and which distinguish META-X from other software for metapopulation viability analysis, for example, VORTEX (Lacy et al. 1995; Lacy 2000) and RAMAS Metapop (Akçakaya 1995, 1997): (1) comparative simulation experiments; (2) an occupancy-type model structure, which ignores details of local population dynamics (these details are integrated in external submodels); and (3) a unifying currency to quantify persistence and viability. Below, we explain the rationale behind these three elements and present illustrative applications of META-X in the three fields of application for which META-X has been designed: teaching, risk assessment in the field, and conservation planning.

The conception of META-X

Scenarios and experiments

Although the goal of PVA is quantitative risk assessment, this does not mean that PVA should focus on *absolute* risk assessments. This would mean determining with absolute precision the risk of extinction (or the persistence) of a real population, which is virtually impossible in view of the inherent uncertainty of model parameters and structure. Instead, PVA has to focus on *relative* risk assessments, that is, on comparisons of the risk of extinction for scenarios with different sets of model parameters. The rationale behind this approach is that the insights from the comparison of the scenarios, that is, the relative assessment, may still be valid if the relative errors of the risk assessments of the individual scenarios are more or less the same.

Focusing on relative risk assessment means acknowledging that quantitative risk assessment is only the proximate goal of PVA, whereas the ultimate goal is to support management for viable populations. Management decisions usually require ranking different management options. Therefore, generic PVA should assist users as much as possible in adopting the comparative attitude required for relative risk assessments. Consequently, in META-X, individual scenarios, that is, single parameterisations of the model, are no longer the basic unit of simulation and evaluation. Instead, sets of scenarios

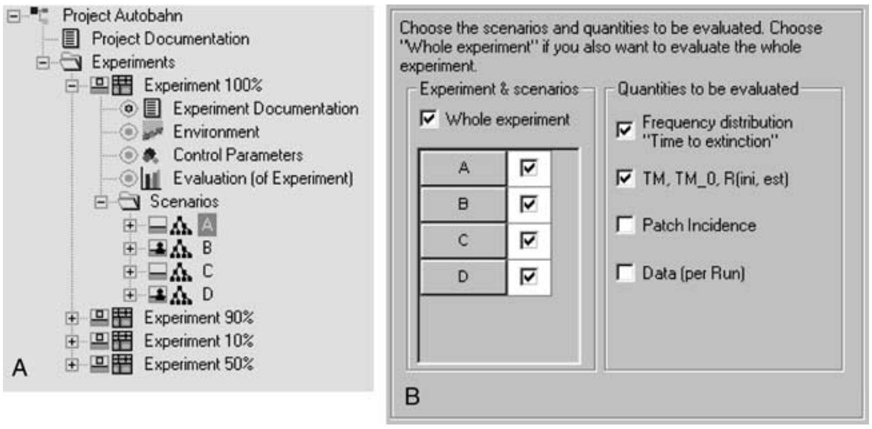

Figure 1. (A) Screenshot of the 'project tree', which shows the hierarchical organisation of META-X projects into experiments and scenarios. (B) Screenshot showing how scenarios of an experiment are chosen for a comparative evaluation of the simulation results.

are grouped together in experiments, and the entire experiment may be simulated and evaluated as a unit (Figure 1). Of course, parameterisation still has to start with a single scenario, but then the user is assisted by various elements of the user interface to assemble an experiment, with new scenarios being defined on the basis of an existing scenario (Figure 2). In this case, the user browses through the input screens up to the screen containing the parameters, which are different in the new scenario. Scenarios can be cut, copied, and pasted within an experiment or between different experiments. Moreover, a special input 'wizard' assists in designing variation experiments for sensitivity analyses: an individual parameter is selected, the range of the parameter value and the number of values within this range are specified, and then the wizard automatically assembles the desired number of scenarios.

Although individual scenarios can be simulated and evaluated, the basic units of META-X are experiments. The user is guided to think in terms of comparative experiments: "What set of scenarios do I need to answer my question?". Once the appropriate scenarios have been specified, the entire experiment is simulated and the comparative evaluation of the experiment displayed.

The three main kinds of problems that have to be tackled with comparative experiments are: (1) determining the ranking order of different management scenarios; (2) analysing the sensitivity of the PVA (e.g., ranking order) to uncertainties in model parameters by varying these parameters; and (3) comparing the sensitivity of different model parameters, which is decisive for identifying key processes determining extinction risk.

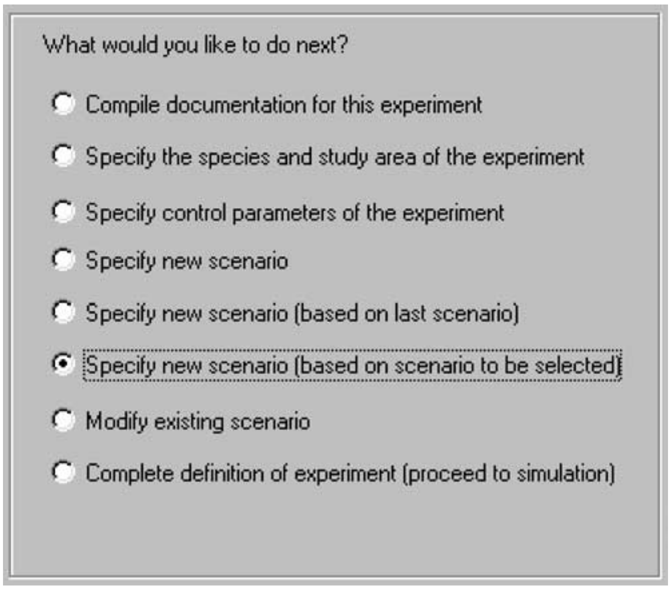

Figure 2. Screenshot of the 'experiment wizard' showing how new scenarios (=parameterisations) may be specified based on existing scenarios.

The generic metapopulation model

Existing generic PVA models have been called 'canned' models because the entire model structure is ready-to-use and the only task required of the user is to parameterise the model. Inexperienced users of 'canned' models may not pay any attention to the model structure and how it determines the results of the model. Moreover, users might be tempted to input specific parameters, which are simply unknown. Some generic PVA programs provide default, or example, values of parameters (VORTEX), and users all too easily use these values. For example, in an application of VORTEX to capercaillie (*Tetrao urogallus*) in Scotland (Marshall and Edwards-Jones 1998), the default value provided by VORTEX for the strength of environmental noise, was used because no empirical information was available about the strength of environmental noise. In this way, PVAs based on generic models might become pseudo-realistic: the high number of parameters suggests a high degree of realism, which may, however, be superficial.

Therefore, a structure should be chosen for generic PVA models, which tries to avoid the pitfalls of 'canned' models. In META-X, this is done by acknowledging the hierarchical organisation of metapopulations: the separation of the local and regional time scales. It can be shown theoretically (Drechsler and Wissel 1997, 1998; see also Verboom et al. 1991; Sjögren-Gulve and

Hanski 2000) that it is not necessary to follow each local population dynamics in detail to describe the dynamics and viability of metapopulations. Only their overall effect on local extinction risk and colonisation is required. Therefore, a 'winking patch' (Verboom et al. 1993) or occupancy-type model structure is sufficient: only the presence or absence of local populations, and the probabilities of local extinction and colonisation are considered, whereas all other details of local population dynamics are ignored (for a detailed description of the META-X model, see Appendix A).

Using an occupancy-type model as a generic model has three advantages. First, the number of parameters is kept small. This makes it simpler to use the model in teaching and for exploratory analyses. It also helps focus on the essentials of metapopulation dynamics and avoids being drowned in the details of the population dynamics of the individual subpopulations. Second, the winking patch approach allows for a hierarchical parameterisation of the model. Users may either specify metapopulation level parameters (which in META-X are referred to as 'main model parameters', that is, probabilities of local extinction, recolonisation, and correlated extinction), or lower level parameters of built-in submodels describing correlation among patches and recolonisation. Third, META-X provides no built-in submodel for calculating parameters describing the local populations, their risk of extinction, the number of emigrants they produce, or the number of immigrants needed to establish a new subpopulation on an empty patch. Thus, if META-X is to be used to support management decisions, external submodels *have* to be used. META-X is thus not fully 'canned' but requires active users who can decide on additional tools to parameterise META-X. For example, they might run a simple PVA model of the local populations on their own, or might ask PVA experts to develop and run such a model (which is much simpler than developing a model for the entire metapopulation). If presence/absence data are available, all META-X parameters can be determined by fitting the data to the Incidence Function Model of Hanski (1994); see section 'Parameterisation'. Alternatively, users could decide to use another generic PVA model to obtain estimates of local extinction risks.

The basic idea behind this design of META-X is that PVA beginners learn the essentials of PVA, that is, comparative risk assessments, sensitivity analyses, how to quantify persistence and viability, and how to parameterise a stochastic metapopulation model, by using META-X without invoking external submodels. There is no risk of these exploratory analyses being misused in publications or management action plans, because it is evident to the scientific community that PVAs based on META-X but without invoking external submodels can only be crude approximations of reality, which should therefore be regarded as heuristic enterprises. Once beginners have gained some experience of this kind of exploratory PVA, they should have learned enough about the methods, concepts, potentials, and limitations of PVA to become active users of META-X, that is, to try and invoke external submodels.

Quantifiers of persistence and viability

Viability is obviously the fundamental property of populations to be studied and assessed in PVA. Surprisingly, however, a general currency for quantifying viability and persistence seems to be lacking (Beissinger and Westphal 1998). Several different quantifications are used, for example, mean time to extinction, median time to extinction, probability of extinction by time *t*, risk of quasiextinction, risk of decline, ending population size, etc. (e.g., Burgman et al. 1993; Akçakaya 1995; Beissinger and Westphal 1998). All these quantities are useful to some degree, but also have shortcomings. For example, both the mean time to extinction and the risk of extinction by time *t* may be biased by the initial conditions of simulations (Ludwig 1996). How can the effects of initial, or transient, conditions be separated from the intrinsic ability of populations to persist under given circumstances? Is it meaningful to determine mean times to extinction of several thousand years while uncertainties render prediction farther than, say, 20 years virtually impossible (Beissinger and Westphal 1998)? Moreover, what is the relationship between all these measures? Are they all equivalent, or is one of them more fundamental than the others?

The lack of a general currency for quantifying viability and persistence causes confusion and hampers comparative risk assessments within and across specific PVAs. For generic PVA models, this problem might be even more severe, since users of generic models are unlikely to have the theoretical skills to assess the different quantifications of viability. Therefore, a new generic PVA model should be based on a simple, fundamental, and unifying framework for quantifying viability and persistence. META-X is hence based on the calculation of the 'intrinsic mean time to extinction', T_m (Grimm and Wissel, unpublished manuscript; see also Wissel et al. 1994; Stelter et al. 1997).

The calculation and interpretation of T_m is based on the following general relationship for $P_0(t)$ (the probability that the metapopulation goes extinct by time *t*), which can be derived from mathematical models of hypothetical species (Verboom et al. 1991; Wissel and Stöcker 1991; Stephan 1993; Wissel et al. 1994; Grimm and Wissel, unpublished manuscript). After starting at time $t = 0$, this relationship holds after a transient time which usually is very short (i.e., much shorter than the time T_m):

$$P_0(t) = 1 - c_1\, e^{-t/T_m} \qquad (1)$$

For simulation models, $P_0(t)$ is easy to determine with t running over a certain time horizon of, for instance, 1000 years. Then, the prediction of Equation 1 is that a plot of $-\ln(1 - P_0(t))$ versus time t yields a straight line with slope $1/T_m$ and intercept $-\ln(c_1)$ (Verboom et al. 1991). If $c_1 \leq 1$, c_1 can be interpreted as the probability of the population reaching the so-called 'established phase' (Wissel et al. 1994; Grimm and Wissel, unpublished manuscript). The established phase (also referred to as the quasistationary state) is characterised by typical and stationary fluctuations of the models' state variables (in META-X: number of occupied patches). If simulations are started with state variables, which are below the range of typical fluctuations, c_1 gives the probability of the population reaching the range of typical fluctuation. If, for example, the metapopulation is extremely small at $t = 0$, in many simulation runs the population will evidently go extinct before it reaches the established phase. c_1 may be referred to as the probability of establishment, or of recovery, respectively. In some special cases, the transient time until the established phase is reached can be rather long, for example, if the intrinsic mean time to extinction of the subpopulations and of the entire metapopulation are of the same order of magnitude.

Once the population is in the established phase, the risk of extinction per year is constant and equal to $1/T_m$. If T_m is determined with the $\ln(1 - P_0(t))$ plot, it does not depend on the initial condition of the simulation and therefore reflects the intrinsic ability of the population to persist under the given conditions. T_m is therefore referred to as the 'intrinsic mean time to extinction'.

Although T_m may be rather large, for example, 10,000 years, this does not mean we are using PVA models to project 10,000 years into the future. Instead, T_m is the basic currency to quantify persistence and viability. T_m determined by the $\ln(1 - P_0(t))$ plot can be inserted into Equation 1 to specify the risk of extinction for any time horizon t of interest. META-X uses the plot of $\ln(1 - P_0(t))$ to determine T_m and c_1. The user can then decide over what time horizon t to calculate $P_0(t)$. META-X is thus based on a unifying quantification of persistence and viability, which should facilitate comparative assessments of population viability.

Parameterising META-X

The main task when using META-X is parameterisation. First of all, the landscape has to be defined. The coordinates of the patch position correspond to the centre, or centre of gravity, of the patch. The metapopulation is visualised as a network of circles around the patch positions. These circles may represent local patch characteristics, for example, local extinction risk, and do not indicate the spatial extension of the patches. Patch distance is measured from patch centre to patch centre. The matrices describing the correlation and recolonisation probabilities among all pairs of connected patches (see Appendix A) are based on these patch distances. Although in many cases this may be sufficient, for certain species and landscapes it might be necessary for patch shape and distance to be described in a different way. To this end, users can modify or completely overwrite the matrices. This enables specific features of the landscape to be taken into account, that is, features of the patch shape, barriers and corridors inhibiting or facilitating dispersal among patches, or correlation of local extinction risk, which is due to factors other than mere patch distance (e.g., features of habitat quality such as exposure).

In general, the built-in submodels of META-X describing recolonisation and correlation can be overwritten by external submodels. Users may run these models externally (using spreadsheets, simple programs, or other generic PVA models, including POP-X; Köster et al. (2000), http://www.oesa.ufz.de/pop-x) and store the submodel's results in a specific, simple format that can be imported by META-X. One of the purposes of the META-X homepage on the Internet is to compile links to all kinds of submodels used for different species and landscapes. This should help prevent META-X users continuously reinventing the wheel.

The most difficult and critical part of the META-X model to be parameterised is the local patch characteristics (see Appendix A), that is, local extinction risk, the number of emigrants produced, and the number of immigrants needed to establish, with 50% probability, a new subpopulation on the patch. These parameters will in general require the use of external submodels and, in particular, fieldwork, but the philosophy of META-X is that with PVA users need not wait until the parameters are available. Even an exploratory PVA based on educated guesses of the parameters by experts who know the landscape and species in question well is worthwhile and could support the entire task of supporting management decisions (see examples below).

An alternative and integrated way of parameterising META-X could be based on presence/absence of data, that is, a map of all empty and occupied patches. This kind of data has the advantage of being comparatively easy to obtain. Occupancy maps can be used to parameterise the incidence function model (IFM) of Hanski (1994, 1999), which is one particular stochastic patch occupancy model (SPOM) of metapopulation dynamics (Moilanen 1999). The IFM model is similar in form to the META-X model. The relationship between the parameters of the META-X model (Appendix A) and the IFM submodels is:

$$\nu_i = eA_i^{-x}$$
$$b_{ij} = gA_i{}^b \, \mathrm{e}^{-d_{ij}\alpha}$$
$$c_{ij} = 0$$

The interpretation of these relationships is as follows: Local extinction risk, ν_i, is calculated as a decreasing function of patch area from a simple submodel, which uses patch size A_i and two parameters, e and x. In this submodel, patch area is used as an easily measurable surrogate for population size. In the IFM, the colonisation probability of an empty habitat patch is an increasing function of connectivity. The probability of recolonisation between two patches i and j, b_{ij}, decreases exponentially with patch distance d_{ij}, and depends on the number of emigrants, which is assumed to depend on the area of the source patch, A_i. The parameters b and α are used to scale the IFM connectivity submodel, and parameter g transforms connectivity to colonisation probability. Particularly important is parameter α, which defines the effect of distance on migration. Parameter b, which gives the scaling of emigration as a function of patch area, can be estimated from, for example, mark–release–recapture data, and typical values found for insects are around 0.5 (Hanski et al. 2000). The IFM model typically ignores possible correlations of extinctions on different patches ($c_{ij} = 0$), although correlation in dynamics can be added to the model (see, e.g., Moilanen et al. 1998). Tools exist on the Internet which use presence/absence maps to parameterise the IFM and other SPOMs (Moilanen 1999, 2000, 2002; Moilanen and Nieminen 2002; see www.helsinki.fi/science/metapop for software and more references), and one specific tool directly delivers the parameters of the META-X model (see http://www.oesa.ufz.de/meta-x). Problems with the IFM approach are discussed for example in Ter Braak et al. (1998).

Exemplary applications of META-X

Working successfully with META-X (or with any ecological model) requires adopting the attitude of experimenters (Grimm 1999, 2002). The starting point of a project is always a certain problem or question. The task is hence to design experiments, which help answer the question or solve the problem. To demonstrate how to translate questions into experiments, three examples are presented for illustration below.

The examples are from the three areas for which META-X is designed to be used: teaching general metapopulation theory, analysing specific populations, and decision support in conservation and planning. The purpose of the examples is not to present in-depth analyses of the problems addressed but to demonstrate how META-X can be used in principle to tackle such problems (the META-X project files of the three examples are available on the Internet: http://www.oesa.ufz.de/meta-x).

Teaching

META-X can be used to learn metapopulation theory by doing, that is, by designing experiments, which address theoretical questions. As an example, here we want to understand the role of landscape heterogeneity and spatial relationships. It would, however, be a poor research strategy to introduce several kinds of heterogeneity in an experiment at the same time and to ask unspecifically how heterogeneity affects viability. A better strategy is to perform 'controlled' experiments where only individual factors are changed at a time. After all, controlled experiments are the basis of all predictive, 'hard' natural sciences such as physics, chemistry, or molecular genetics. Therefore, let us consider the theoretical problem of how metapopulation viability changes if the mean number of emigrants produced per year is increased on a certain patch.

For the experiment, we use an arbitrary heterogeneous network of patches (Figure 3) and vary the number of emigrants E on patch 9. An increase in E leads to an increase in the mean time to extinction T_m (Figure 3) up to a

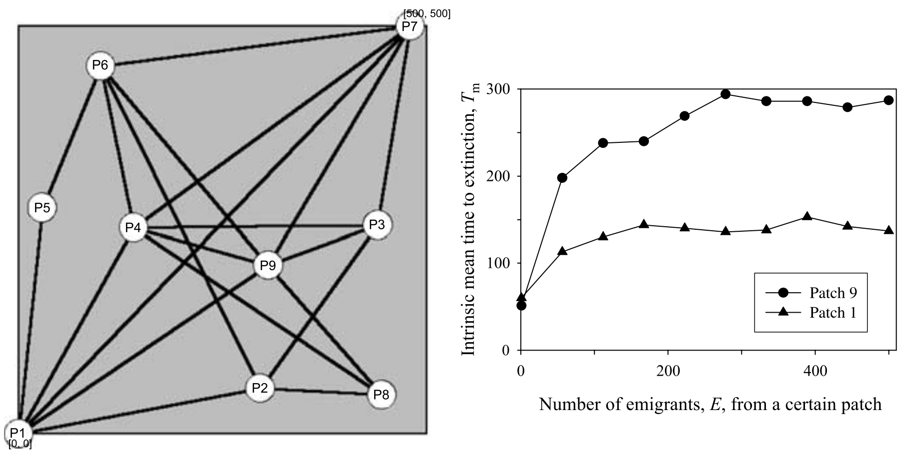

Figure 3. Left: visualisation of the arbitrary network of patches used for the theoretical example (see text). Here, the patch symbols only indicate the position of the patches, not any local patch characteristics. The connections between the patches indicate pairs of patches between which recolonisation is considered. Right: results of the theoretical example showing how the intrinsic mean time to extinction increases if the number of emigrants is increased on patch 1 or patch 9.

saturation value of T_m. Initially, T_m increases because more colonisers boost the chances of recolonisation of empty patches. Once E is large enough to guarantee that virtually all empty patches are recolonised immediately, a further increase in E has no effect on T_m. However, the positive effect of colonisers originating from patch 9 depends on the occupancy of this patch, that is, on how fast this patch itself becomes recolonised. This becomes evident if we perform the same experiment as before, but now vary E on patch 1, which has the same parameters as patch 9, but is located at the periphery instead of the centre of the habitat network. The increase in T_m with E is now less marked and the saturation value of T_m is lower than in the case of patch 9 (Figure 3).

This example demonstrates how subtle the effects of changing patch characteristics may be in a heterogeneous network. Even if management affects only one specific patch, it would be impossible to predict the effect of this management by focusing on just this patch. Instead, the whole network, that is, the specific configuration of patches, their size, and their connectivity, determines the significance of certain patches for the viability of the entire metapopulation. Metapopulation dynamics is largely determined by this reinforcement of negative or positive effects of patch characteristics and configurations. Simple, linear cause–effect reasoning is inappropriate for metapopulation dynamics. The lesson from this example for conservation is that the exclusive management of individual patches may not have the desired effects if the integration of the patch into the network of patches is not appropriately considered. In general, management should, if possible, address the entire network instead of single patches. The example also shows how variation experiments of META-X are designed to obtain such basic but important insights.

PVA of capercaillie in the Bavarian Alps

In this example we demonstrate how META-X can be used for exploratory viability analyses of real metapopulations, and how external submodels may be used for parameterisation. The example looks at capercaillie (*T. urogallus*), a grouse occurring in boreal or mountain forests in Eurasia. Many populations in Central Europe have gone extinct during the past five decades (Storch 2001) and in Germany, only the populations in the Alps and the Black Forest are considered as viable, that is, with an extinction risk of less than 1% in 100 years (Grimm and Storch 2000). The major cause of this decline is the change in forest structure, which is due to changing forest use. In the Bavarian Alps, mountain forests still seem to offer an appropriate habitat for capercaillie. However, most mountain forests are rather small and separated from each other by the farmland and settlements of the valleys. Most populations in a single mountain forest patch consist of 100 or less individuals, which is below the minimum requirement for viability of a capacity of about 500 individuals (Grimm and Storch 2000). The distance between neighbouring mountain forest patches is mostly 5–10 km, a distance over which juvenile capercaillie can disperse (Storch and Segelbacher 2000). It has therefore been hypothesised that the populations of capercaillie in the Bavarian Alps constitute a metapopulation (Storch 1993; Storch and Segelbacher 2000). This metapopulation is linked to an extended distribution range of the species in the Austrian Alps that, albeit spatially structured, can for the purposes of this paper be considered a mainland.

To test whether existing empirical knowledge on the demography and dispersal of capercaillie supports the metapopulation hypothesis, META-X can be used. Parameterisation involves several steps. Each step is only a crude approximation of reality, because the goal is to obtain a rough, initial idea of the hypothetical metapopulation dynamics. The steps are (for the resulting parameters, see Table 1):

1. Delineating the patches. This is roughly achieved by using a GIS to identify those forested areas that are higher than 1000 m above sea level. In the following, only a subset of the patches in the Bavarian Alps is considered (Figure 4A). Patch 86 is actually much larger than assumed here, with the majority of the patch being in the Austrian Alps.
2. The patches are then characterised by the coordinates of their centre of gravity and by their area. The area is converted to a ceiling capacity of the patches by assuming an average capacity of two individuals per square kilometre, although in good habitats the capacity may be higher and in poor habitats much lower.
3. The resulting capacities are used as parameters in a demographic model of capercaillie parameterised for the Bavarian Alps (Grimm and Storch 2000). The model delivers the extinction rates of the subpopulations.
4. The number of emigrants produced by the patches was estimated based on population size, age structure, and patch size. The number of immigrants needed to establish a new population on an empty patch with a probability of 50% was determined with the demographic model and using the linearised plot of Equation 1, where c_1 is the probability of establishment (Grimm and Wissel, unpublished manuscript).
5. The model parameter 'mean dispersal range', d_0, was estimated for female juveniles based on dispersal data of Koivisto (1963), that is, $d_0 = 10\,\text{km}$, although these data were obtained in the contiguous forests of Finland, not in fragmented landscapes. Nevertheless, these are the best data on capercaillie dispersal available. The 'mean correlation length' c_0 was assumed to be zero.

Table 1. Parameterisation of a network of local populations of capercaillie in the Bavarian Alps.[a]

No.	Mountain	X	Y	Area (km^2)	Radius	K	T_m	ν	I	E
39	Steilenberg/Rauhe Nadel	10.00	16.08	9.55	1.743	19	24	0.041	4	5
47	Gurnwandkopf	22.30	17.52	14.93	2.180	29	42	0.023	5	8
48	Hochgern/Hochfelln	18.40	20.37	54.34	4.158	108	230	0.004	12	20
76	Sonntagshorn	31.07	14.02	37.62	3.460	75	121	0.008	10	15
86	Seegatterl/Dürnbachhorn	20.65	10.00	110.94	5.942	221	919	0.001	24	40
57	Rauschberg	29.96	19.47	11.42	1.906	22	30	0.033	5	8
71	Hochstaufen	38.78	22.00	19.39	2.484	38	54	0.018	6	10
70	Teisenberg	35.04	26.96	12.62	2.004	25	34	0.029	5	8

[a] X, Y: patch coordinates (km); K: patch capacity (individuals); T_m: mean time to extinction (years); ν: local extinction risk per year; I: number of immigrants needed for 50% probability of establishment of new population; E: average number of emigrants produced by a patch.

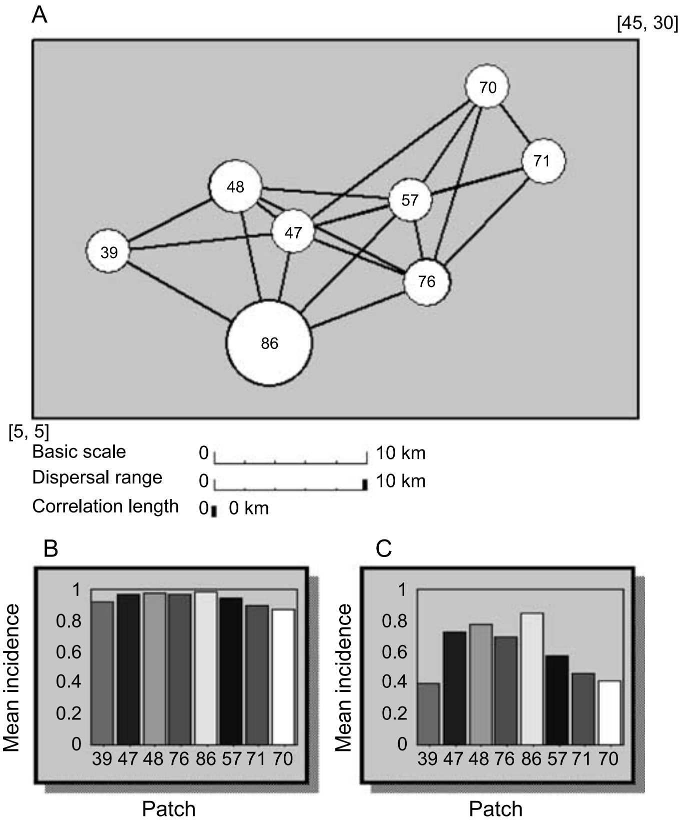

Figure 4. (A) Visualisation of the landscape used in the capercaillie example (see text). Here, patch size indicates the local intrinsic mean time to extinction, ranging from 919 years (patch 86) to 24 years (patch 39; Table 1). 'Basic scale' gives the scale of the map, and 'Dispersal range' the parameter d_0 (see Appendix A). (B) Incidence (=probability of being occupied by a population) of the patches for the base scenario. (C) Incidence for a scenario where $d_0 = 4$ km.

For the network of patches in Figure 4A and the parameters specified above and in Table 1, the metapopulation is viable, that is, it has an extinction risk smaller than 1% over 100 years. The incidence of all patches is close to 1 (Figure 4B). Viability would even be maintained if, for example, patches 39, 47, and 57 did not exist. However, the dispersal range may have been overestimated because dispersing birds might tend to avoid open areas. The metapopulation is still viable for $d_0 = 5$ km, but no longer for $d_0 = 4$ km ($T_m = 4900$ years, which corresponds to an extinction risk of roughly 2% in 100 years). In this scenario, incidence is much smaller, and three patches are only occupied with an incidence of less than 50% (Figure 4C).

These results support the notion that the numerous small populations in the Bavarian Alps are integrated within a viable metapopulation, and that under current conditions, that is, with no further habitat deterioration, no loss of incidence is to be expected – unlike elsewhere in Germany, where most populations seem to be doomed to extinction. However, even this initial exploratory analysis shows that the amount and range of dispersal among patches is critical. Since only anecdotal data are available on the dispersal of capercaillie in fragmented landscapes, other dispersal submodels than the META-X submodel should be tested. Likewise, other elements of the model such as the number of patches considered, local capacities, the number of emigrants and immigrants, dispersal barriers, and the specific pattern of environmental correlation should be tested regarding their significance for viability. Since the existing data on demography and dispersal are not sufficient to parameterise a detailed PVA model, which would produce testable predictions on population time series or structure, the purpose of such analysis can only be to assess the relative importance of processes and structure and, in particular, of the relative importance of the spatial and temporal scales involved.

Planning

The following example of decision support in environmental management is hypothetical, but demonstrates questions often encountered when new roads are planned. Consider a network of patches inhabited by a certain wildlife species (Figure 5A). A highway is going to be constructed through this network (Figure 5B). Because of the heavy traffic to be expected, it can be assumed that all the individuals trying to cross the highway will be killed. The highway will thus threaten the metapopulation by isolating the sub-networks on both sides of the highway and by introducing an additional mortality, which may be rather high. Let us assume that legal regulations stipulate the provision of some kind of mitigation. Two alternatives are discussed by the managers: (1) One 'green bridge', that is, a bridge covered with soil and vegetation, acting as a corridor, plus fences on both sides of the highway (Figure 5C). This scenario thus aims to reduce both isolation and mortality. (2) No fences, but two green bridges (Figure 5D). Here, management focuses on reducing isolation. Besides the issue of how much the two alternative mitigation measures will cost, the question is which of the measures is more effective in reducing the negative effects of the highway on the metapopulation's viability.

The four scenarios of interest in this case are easily implemented in META-X by using the so-called 'Landscape Editor' of META-X, which is an interactive interface visualising the landscape. Individual elements of the

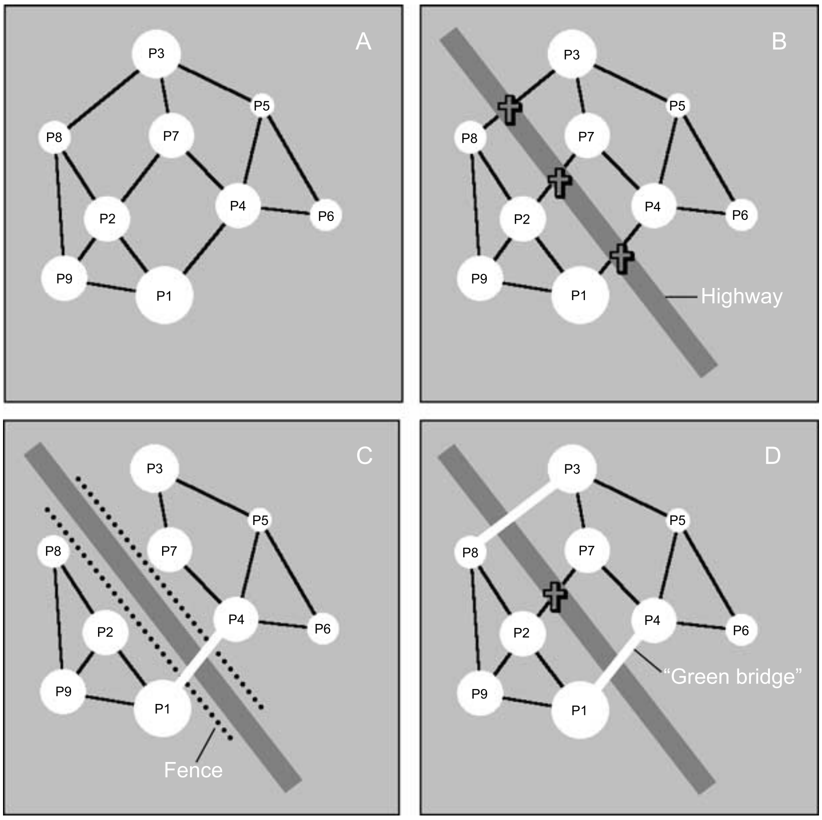

Figure 5. Visualisation of the four scenarios considered in the highway example (see text). The symbol of the cross indicates 100% mortality, i.e., all individuals trying to reach a patch on the other side of the highway are killed.

landscape can be selected by a mouse-click and then their parameter values changed. The results of the simulation show that one green bridge combined with a fence is more effective than two green bridges without a fence (Figure 6). Hence, the loss of individuals due to traffic mortality is more critical than the number of corridors between the two sub-networks. However, it could be argued that this ranking of management options may critically depend on certain parameter values, which are unknown. How sensitive, for example, is the ranking regarding the effectiveness of the green bridges? In the original experiment, an effectiveness of 100% was assumed, that is, the green bridge was as effective in linking the patches as the original landscape corridor undisturbed by the highway. To study the effect of 90, 50 and 10% effectiveness, the original experiment is copied and pasted, and then the recolonisation probabilities among the patches linked by the green bridges are

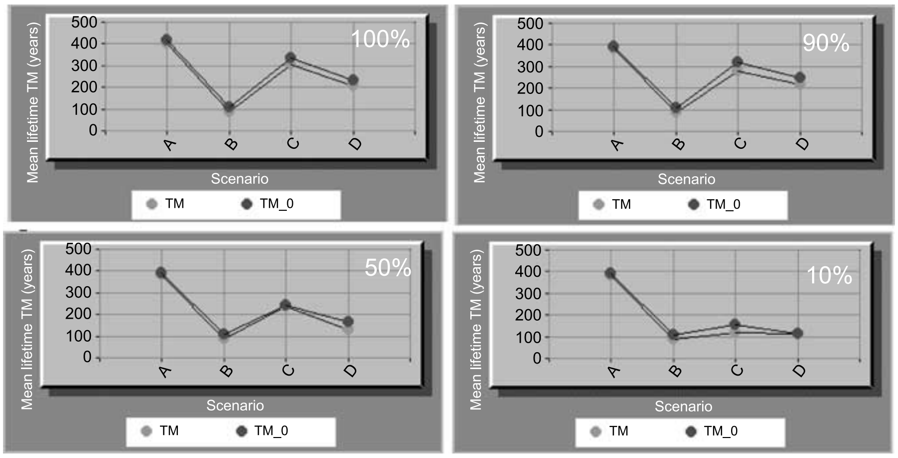

Figure 6. Intrinsic mean time to extinction of the four scenarios A–D of the highway example (Figure 5) for four different assumptions about the effectiveness of the green bridge (100–10%).

modified accordingly. The results show that the ranking of the two management options is insensitive to the effectiveness of the green bridge, although of course the overall effectiveness of management sharply decreases. Note that in this example even the undisturbed, original network has a very low persistence of only about 400 years, which corresponds to a risk of extinction of about 25% in 100 years.

This example demonstrates the main objective of META-X of being a tool for decision support. Many, if not most, management decisions are made without an explicit comparison of the different management options. One reason for this is that, besides financial, legislative, and political constraints, usually the demographic data required for a tailored or generic PVA model are not available. Certainly, a PVA has to be based on demographic data, but previously there was no tool which filled the gap between a fully parameterised PVA and no PVA at all, that is, no quantitative, comparative risk assessment. META-X tries to fill this gap: the consequences of virtual decisions, which are based on more or less justified assumptions about local extinction, recolonisation, and correlation, are made explicit and are thereby open to criticism. Some assumptions may turn out, by performing sensitivity analyses, to be critical for ranking the management options. META-X might thus even at very early stages of the planning process (planning for highways usually takes 10 years or more) direct empirical research to those data, which are most critical.

Discussion

We presented the conception of a new generic model and software for metapopulation viability analysis, META-X. This conception tries to take into account criticism of earlier generic PVA models. The most important feature of META-X is that comparative experiments are the basic unit to be designed, simulated, and evaluated. META-X thus helps focus on comparative risk assessments. Another important, novel feature of META-X is that it is not fully ‘canned’: to fully parameterise the metapopulation model of META-X, external submodels are required. This avoids the naive notion of PVA which is described by Burgman and Possingham (2000, p. 103) as “a tool that will deliver answers after an afternoon’s playing with the computer”. And finally, META-X uses a unifying currency to quantify persistence and viability, the ‘intrinsic mean time to extinction’, which facilitates the comparative attitude required for PVA.

We do not view META-X as an exclusive alternative to earlier generic PVA models. VORTEX (Lacy 2000), RAMAS (Akçakaya 1995, 1997), ALEX (Possingham and Davies 1995), and the other generic PVA models are powerful tools in the hands of PVA experts, but not necessarily in the hands of unguided PVA beginners. META-X tries to fill this gap: beginners are supposed to learn the concepts, methods, potentials, and limitations of PVA by using META-X. Subsequently, users of META-X are supposed to use all kinds of additional tools, including existing generic PVA models.

META-X does not, however, solve the basic problems of PVA *per se*, which are critically reviewed by Beissinger and Westphal (1998) and Groom and Pascual (1998). Burgman and Possingham (2000, p. 97) see the role of population models in conservation biology ‘at a crossroads’. They note a growing “disappointment at the inability of PVA to provide verifiable answers” and a “backlash from early over-enthusiasm and unrealistic expectation that PVA would solve all single-species conservation problems” (pp. 97–98). We fully agree with Burgman and Possingham (2000, p. 104) who “advocate the use of PVA as a decision-support tool, rather than as a decision making tool”.

Earlier generic PVA models focused so much on an all-in-one tool for PVA that uneducated users of these models were not always aware of the subtle but fundamental difference between decision support and decision making. The design of the generic models may unintentionally have been mistaken as a promise that the fully parameterised model and its results would be so reliable that it would allow absolute predictions to be made. META-X goes the other way round: it is based on acknowledgement of the basic uncertainty underlying every PVA. Users are welcome to use META-X first of all as a heuristic and exploratory tool. Beginners thus learn that PVA is a tool to deal with, but not to overcome, uncertainty. Even if META-X is parameterised as soundly as possible for real species and management problems, users of META-X will always be aware that uncertainty is inherent to PVA and that they therefore have to perform comparative simulation experiments. Burgman and Possingham (2000, p. 104) claim that "one of the most important steps in establishing the credibility of a PVA is to communicate the uncertainties embedded in the model and its assumptions". We hope that META-X will contribute to this step because of its coarse model structure and its overall conception.

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Appendix A

The META-X metapopulation model

The metapopulation model of META-X is spatially explicit, that is, the patches have an explicit position in a certain coordinate system and the connectivity (all pairs of patches between which recolonisation is possible) has to be specified explicitly. Conceptually, time proceeds continuously, but since the META-X model is solved numerically on a computer, time proceeds in intervals of length Δt, which is calculated internally. Patches are assumed to have a circular shape. The centre of a circle representing a patch is the position of the patch. Patch distances refer to distances between the centres of the circular patches. The entire metapopulation consists of N patches, each of which is either occupied ($x_i = 1$) or empty ($x_i = 0$). The state of the whole metapopulation is thus given by the vector $x = (x_1, \ldots, x_N)$. A change in such a state can only occur due to local extinction, correlated extinction, or recolonisation. These three processes are described by corresponding short-term transition probabilities, referred to as main model parameters, which are explained in the following.

Local extinction
The short-term extinction probability of patch i is given by the model parameter ν_i, which is the extinction rate per year (rescaled to the interval Δt). The

reciprocal value of ν_i, $T_i = 1/\nu_i$, is the intrinsic mean time to extinction (Grimm and Wissel, unpublished manuscript) of an established population inhabiting patch *i*. No standard submodel is provided for this main parameter.

Correlated extinction

Whenever two patches *i* and *j* are occupied, they have some chance of going extinct simultaneously. If both local extinction processes are completely correlated, then simultaneous extinction will occur with a short-term probability given by the geometric mean, $\sqrt{\nu_i}\sqrt{\nu_j}\,\Delta t$ (Frank and Wissel 1998). In general, if the extinction processes on the two patches are correlated to some degree due to, for example, being exposed to the same weather, the probability of simultaneous extinction is $c_{ij}\sqrt{\nu_i}\sqrt{\nu_j}\,\Delta t$, with c_{ij} being the degree of correlation for patches *i* and *j* ($c_{ij} \in [0, 1]$). When parameterising META-X, the whole matrix of all pairwise correlations of local extinctions has to be specified.

The META-X standard submodel for c_{ij} is

$$c_{ij} = \mathrm{e}^{-d_{ij}/d_0}$$

d_0 is a (sub)model parameter referred to as 'mean correlation length'. For a patch distance d_{ij} equal to the mean correlation length, c_{ij} is e^{-1} or 36% of the maximal value it would have at patch distance $d_{ij} = 0$. This submodel will be appropriate in many cases, but may be overwritten by the user by directly entering c_{ij} obtained from external submodels.

Recolonisation

A certain patch *i* that is empty can be recolonised within a time step by individuals of all patches which are occupied. The overall probability of patch *i* being recolonised is therefore $\sum_{x_j=1} b_{ji}\,\Delta t$ with b_{ji} being the probability that individuals from patch *j* colonise patch *i*. Note that 'colonise' does not only mean that individuals from patch *j* reach patch *i* but that they indeed establish a new population, that is, a population which is characterised by its intrinsic mean time to extinction, $T_i = 1/\nu_i$.

The META-X standard submodel for calculating b_{ij} is

$$b_{ij} = \begin{cases} \dfrac{E_i}{n_i} B_{ij} \dfrac{1}{2I_j} & \text{if patches } i \text{ and } j \text{ are connected,} \\ 0 & \text{otherwise} \end{cases}$$

where E_i is the number of emigrants which on average leave the occupied patch *j* per year, n_i the number of links from patch *i* to other patches, and B_{ij} the probability that an individual which starts to disperse from patch *i* towards patch *j* reaches patch *j*. B_{ij} is referred to in META-X as 'reachability', and I_j the number of immigrants which are needed on patch j to establish a subpopulation with a probability of 50%.

In the submodel for b_{ij} recolonisation is divided into its principal components: dispersal of individuals from an occupied patch, distribution of dispersers on possible target patches, probability of dispersers reaching a target patch, and probability that individuals, which reach a target patch, are successful in establishing a new subpopulation on the target patch. The assumptions underlying the submodel for b_{ij} are: an occupied patch i produces on average E_i dispersers per year. These dispersers are equally divided among all possible links to other patches, n_i (note that in many cases this assumption may not be reasonable!). Next, the reachability B_{ij} determines whether a disperser heading to patch j indeed reaches patch j. B_{ij} is calculated from a further submodel

$$B_{ij} = \mathrm{e}^{-d_{ij}/d_1}$$

The parameter d_1 is, analogous to d_0, referred to as the 'mean dispersal range'.

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