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Developing population models: A systematic approach for pesticide risk assessment using herbaceous plants as an example

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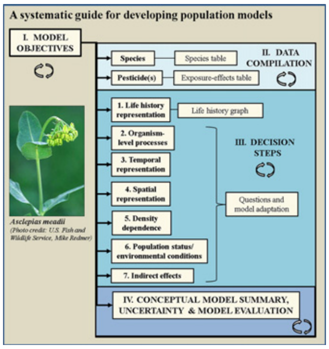
HIGHLIGHTS

- Guidance for systematic development of population models is provided.
- Example for development of herbaceous plant models in pesticide risk assessment presented.
- Step-by-step adaptation of models is based on species' life history.
- The resulting conceptual model reflects model objectives and data availability.
- Guidance increases transparency and efficiency of model development.

GRAPHICAL ABSTRACT



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ABSTRACT

Population models are used as tools in species management and conservation and are increasingly recognized as important tools in pesticide risk assessments. A wide variety of population model applications and resources on modeling techniques, evaluation and documentation can be found in the literature. In this paper, we add to these resources by introducing a systematic, transparent approach to developing population models. The decision guide that we propose is intended to help model developers systematically address data availability for their purpose and the steps that need to be taken in any model development. The resulting conceptual model includes the necessary complexity to address the model purpose on the basis of current understanding and available data.

We provide specific guidance for the development of population models for herbaceous plant species in pesticide risk assessment and demonstrate the approach with an example of a conceptual model developed following the decision guide for herbicide risk assessment of Mead's milkweed (*Asclepias meadii*), a species listed as threatened under the US Endangered Species Act. The decision guide specific to herbaceous plants demonstrates the details, but the general approach can be adapted for other species groups and management objectives.

Population models provide a tool to link population-level dynamics, species and habitat characteristics as well as information about stressors in a single approach. Developing such models in a systematic, transparent way will increase their applicability and credibility, reduce development efforts, and result in models that are readily available for use in species management and risk assessments.

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1. Introduction

Population models are commonly used tools in species management and conservation to estimate population dynamics over extended time periods, and under varying scenarios of stressors or management activities encountered by the population. Data from field surveys and experimental data can be combined to assess how populations might be fairing under conditions they are currently facing, and how conditions may be altered to improve the outlook for rare or declining species (e.g., Crone et al., 2009).

Population models can represent effects of stressors as measured on organisms (rather than populations) affecting survival, growth and reproduction, and set them in the context of species' life-history characteristics, population structure and other factors acting on the species over extended time periods (Schmolke et al., 2010a). Ecologically relevant measures including population abundance, population growth rate, and other characteristics can be estimated (Pastorok et al., 2002; Barnthouse et al., 2008). In this context, population models are receiving increasing attention as tools in ecological risk assessment of chemicals (Schmolke et al., 2010a, Galic et al., 2010, Hommen et al., 2010, EFSA, 2014, Forbes et al., 2010, Thorbek et al., 2010, Grimm and Thorbek, 2014; Galic and Forbes, 2014). Risks of pesticides to non-target species are often based on exposure estimates and toxicity tests conducted with a few species and are most often based on organism-level responses. Thresholds of toxicological response including the ANOVA-based no observed effect concentrations (NOECs) or regression-derived effects concentrations (EC_x; concentration resulting in x% effect) are obtained from these experiments and used as benchmarks for comparison with estimated exposure concentrations (EECs) in order to inform potential risks to species of concern. This approach has low ecological relevance because it ignores the role of life history in translating organism-level responses to population-level dynamics and does not account for feedbacks or nonlinearities in the relationships between organismal and population responses (Forbes et al., 2008). Population modeling provides an opportunity to combine species life histories with standard laboratory toxicity assessments and exposure estimates, and characterize risk in terms directly relevant to environmental protection goals which are frequently aimed at the population scale (Forbes et al., 2009; Grimm et al., 2009; National Research Council, 2013). For these reasons, population models have recently been identified as "necessary to quantify the effects of pesticides on populations of […] species" listed as threatened or endangered under the US Endangered Species Act (ESA) (National Research Council, 2013, p. 104).

In order to be used in support of environmental decisions, including regulatory assessments, population modeling must achieve an appropriate level of transparency (documentation, reproducibility, uncertainty characterization, validation) in line with the concept of "Good Modeling Practice" (Schmolke et al., 2010b; Augusiak et al., 2014; EFSA, 2014). Specific guidance for the documentation of models has been proposed to make it possible to reproduce model approaches, and to evaluate the model concept, data sources and underlying assumptions (Grimm et al., 2006, 2010; Schmolke et al., 2010b; Grimm et al., 2014). However, detailed guidance for the process of model development for specific purposes (e.g., to achieve a particular management goal) is not available. When developing a model for a specific purpose, many considerations are involved in arriving at a conceptual model, and these tend to be subjective and implicit. The properties of a model developed for a specific purpose depend on multiple factors including the questions to be answered with the model, the species modeled, and data availability. Nevertheless, the development of any population model requires addressing a fundamental set of questions and systematic decision steps. Defining and outlining this process provides a guideline for good modeling practice in the development phase of a model. Model development should follow a consistent and transparent set of decisions, and this can be facilitated if each step is laid out and used consistently for every new model.

In this paper, we provide a standard decision guide for developing a conceptual population model to assess the risks of pesticides to herbaceous plants. The specific application makes it possible to provide a comprehensive description of the steps necessary in the development of a conceptual model, i.e. the questions arising during the development of a model are laid out systematically and do not have to be compiled for each new modeling project. The presented decision guide is adaptable to a variety of model applications as its structure is not specific to pesticide risk assessment of herbaceous plants. Development of a conceptual model is divided into four phases: the definition of the specific model purpose and pre-defined model requirements, the systematic compilation of available data for the species of interest and the factors to be investigated (in this case pesticides), decision steps during which the model design is developed, and the summary of the conceptual model. Following the decision guide step by step aides model developers to compile a 'minimal conceptual model' that represents the appropriate level of complexity necessary for the model to fulfill its purpose. This conceptual model can either be used to assess whether existing models can be applied or adapted to meet the model objectives, or it can serve as the basis for a new model. The decision guide aims to build the model around its purpose, rather than develop a model around a particular technical methodology. However, the conceptual models produced following the decision guide can help inform the selection of an appropriate technical methodology for model implementation depending on the questions to be addressed, the properties of the population to be modeled, and data availability.

Currently, close to 900 flowering plant species are listed under the ESA in the US, and the majority of these are herbaceous species (U.S. Fish and Wildlife Service, 2016). While the decision guide was developed for the purpose of increasing the efficiency and transparency of population model development for these species, its application is not limited to listed species. Guidance for model development addressing organism groups other than herbaceous plants and model purposes beyond pesticide risk assessment can be adapted from this framework with some modification. We hope that the decision guide presented in the current paper may lay out a path to compiling guidance for various other species and contexts.

2. Minimal conceptual model

A practical aim in the development of population models is to achieve the appropriate level of model complexity to address a specific research question. The approach presented in this paper focuses on the process of developing a "minimal" conceptual model that represents the lowest level of complexity necessary to meet a given study objective. Accordingly, "minimal" does not imply the use of simple models, but rather emphasizes that the modeled population is represented at a level of complexity that can be appropriately based on available data and can address the model objectives. The steps in the decision guide (Suppl. Appendix A) aim to systematically and transparently resolve how to best represent each aspect of a plant population. The resulting minimal conceptual model may range from a simple demographic representation of a population to a complex mechanistic model that makes use of data collected specifically to inform the model. In any case, the conceptual model should reflect the minimal complexity necessary to address the model objectives.

The subsequent sections detail the phases of development of a minimal conceptual model for populations of a given herbaceous plant species in the context of pesticide risk assessment (also see Fig. 1). The phases consist of the definition of the model objectives, the systematic compilation of data available about the species and the pesticide to be represented, the decision steps that lead to the conceptual model, and the resulting minimal conceptual model and uncertainties associated with it. The decision steps start with a basic representation of the life history of the species. The following steps encompass sets of questions that can be sequentially addressed by a model developer to build the minimal conceptual model based upon a specific species and study objective. Through this process, it may be determined that a relatively simple model is sufficient for a particular objective, whereas in other instances greater complexity may be needed. In this sense, the approach provides a comprehensive yet practical starting point for model development so that a model can be built in a transparent process during which data gaps, limitations and associated uncertainties are identified and appropriately accounted for when the model is applied. The phases of the model development are laid out in detail in Suppl. Appendix A.

The minimal conceptual model can be used to assess existing models (e.g., from the literature) or as an outline for the implementation of a new model. In the former case, it can be determined if an existing model represents all aspects necessary to achieve the objectives of the model application. For example, if the species life history is represented differently in an existing model compared to the minimal conceptual model, it should be assessed why the differences exist and what their relevance is. Mechanisms or details represented explicitly in an existing model can be assessed for their necessity or applicability for the current model application. If the goal is the implementation of a new model, the minimal conceptual model provides the blueprint. For a more complex model with the aim of representing available information about the species as comprehensively as possible, the minimal conceptual model can be used as a starting point for further model development. In some cases, following the decision guide may reveal that available data are not sufficient to address the model objectives. Essential data necessary for model development can be identified using the minimal conceptual model and model objectives and may inform further data collection priorities.

As previously discussed, the development of the minimal conceptual model is intended to be independent of model type (i.e., technical model structure such as matrix, individual-based, unstructured/scalar, etc.; see model type classifications in Schmolke et al., 2010a and Forbes et al., 2016). However, aspects of a minimal conceptual model may favor one model type over another. For instance, if factors of concern for the population are determined to be spatially explicit, these may be easier to incorporate using individual-based approaches (Forbes et al., 2016). Thus, the model type should be chosen after the minimal conceptual model is completed.

When developing and applying a model, it is important to consider the resources available for the project, i.e. how much time can be spent on model development and analysis. The limitations of the project should be reflected in the model objectives. Once developed, the minimal conceptual model should be reviewed for feasibility of its implementation and analysis. Model objectives may have to be adjusted, and the decision steps reiterated in case the minimal conceptual model suggests that model implementation and analysis may not be feasible within the project limitations.

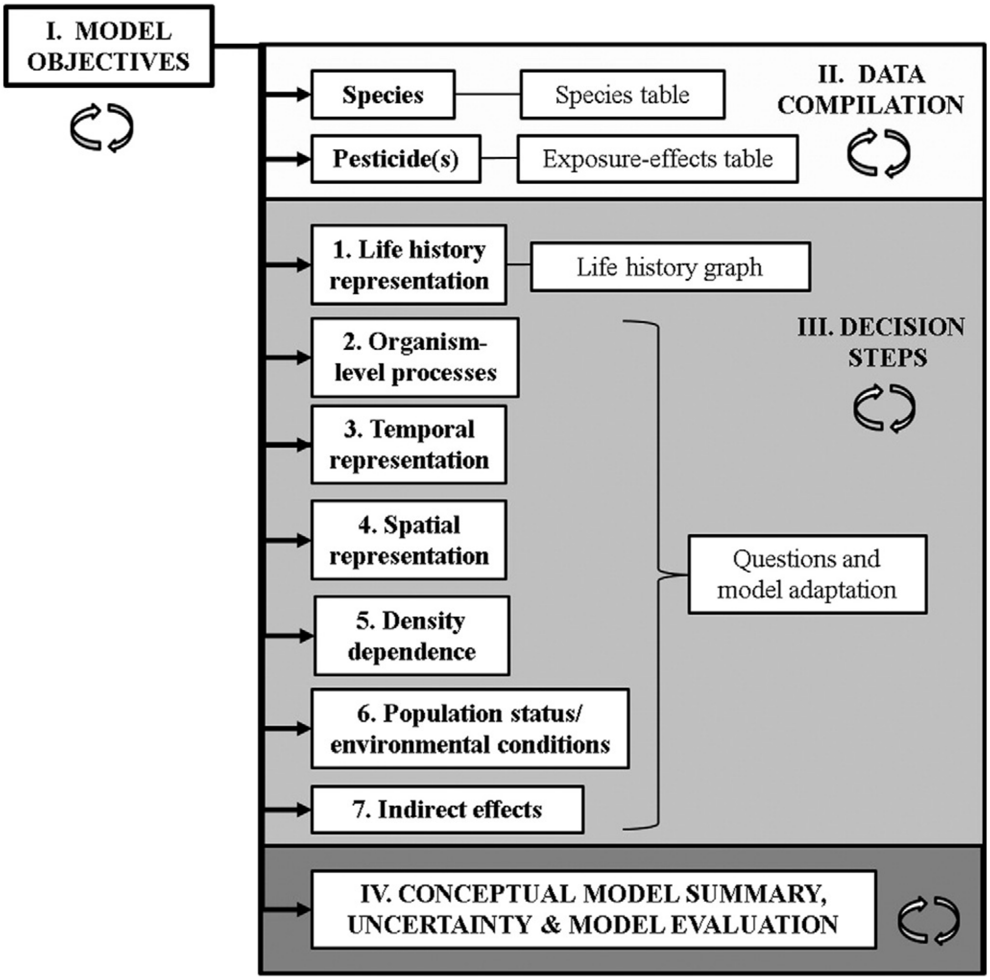


Fig. 1. Graphic overview of the decision guide for minimal conceptual model development, starting with the phase defining model objectives and systematically moving to subsequent phases (all fully detailed in Suppl. Appendix A). The process is conducted iteratively so that previous phases and steps are re-visited as needed throughout the development of the minimal conceptual model.

3. Decision guide for minimal conceptual model

The following sections provide an overview of the decision guide for development of a minimal conceptual model applied for the purpose of assessing the risks of pesticides to herbaceous plant species. In Fig. 1, an overview of the decision process is given. A detailed guidance template that can be used by model developers is provided in Suppl. Appendix A. To provide a practical demonstration of the approach, the process was applied to a threatened herbaceous plant species (Mead's milkweed, *Asclepias meadii*). The decision process and the resulting minimal conceptual model for the species (following the guidance template) are documented in Suppl. Appendix B.

3.1. Phase I: model objectives

The first step in the development of a model is the definition of its objectives, including a summary of the model purpose and an initial specification of model requirements. Depending on the questions we have about the system, we will choose which parts of the system are important to represent and to what level of detail. In this case, the decision guide is designed to aid the systematic development of population models for herbaceous plants in the context of pesticide risk assessment, and this defines the specific model purpose. However, refinements of this general objective are still necessary in order to determine the details that need to be represented in the minimal conceptual model. The following three points guide the specification of the model objectives:

1.) Species: Herbaceous plants are characterized by a wide range of life histories (Salguero-Gómez et al., 2016), habitats and potential for exposures to pesticides. While the current decision guide is geared towards the development of a conceptual model for populations of a single species it can also be used to address multiple (or groups of) species, and to assess whether several species can be represented by the same model.
2.) Exposure-effects: From the exposure and effects perspective, the goals of the model have to be defined on a spectrum of detail. Model objectives may focus on a rather simple extrapolation from individual organism mortalities to impacts on population dynamics over a specified time period. For instance, the model could be used to assess how a population is affected over time after a mortality event caused 50% loss in each life stage at a single time point. Greater detail is required if, for instance, realistic exposure patterns in space and time are to be explored at the population level, for example, to assess how a population is affected if herbicide exposures occur repeatedly and/or affect life stages differently.
3.) Other considerations: Additional considerations may be part of the model objectives. Two important considerations include the time period that the model should represent (weeks, a single year, several years, etc.), and the outputs of interest (e.g., population growth rate, population size, time to recovery, extinction risk, measures of spatial distribution, etc.). In addition, other factors that impact populations may be considered. This could include other stressors (e.g., climate change impacts, habitat loss), management activities (e.g., positive effects due to restoration activities), as well as indirect effects of a pesticide (e.g., reductions in pollinators or competitors). Although the decision guide addresses additional factors that could influence the vulnerability of a species, factors that are mandatory to fulfill the objectives of the model should be clearly stated.

Using the above considerations, the purpose of the model (the research question of interest) and the associated model requirements should be assessed as far as they are defined at the beginning of the development process. The development of a model has been described as an iterative process, the modeling cycle (Grimm and Railsback, 2005; Railsback and Grimm, 2012). The model requirements can be seen as the starting point of the cycle. If a requirement is defined from the outset, it will be considered in the subsequent decision steps, assessed whether it is achievable given the data availability, and refined to inform the conceptual model. An outline of components used to specify the model requirements is provided in the template document (Suppl. Appendix A). A specific example of defined model objectives for *A. meadii* is provided in Suppl. Appendix B.

3.2. Phase II: compilation of available data

As a basis for decisions about an appropriate conceptual model and its complexity, it is necessary to compile the available data and information about the species of concern, pesticide exposure and toxic effects relevant to the species. This information should be systematically inventoried and organized in a tabular format to provide a resource for addressing subsequent decision steps in the model development process. To demonstrate, we describe and present templates for data compilation to support population modeling of herbaceous plant species for pesticide risk assessment.

3.2.1. Species information

Species characteristics that are important for subsequent decisions about a population model are compiled in a "Species Table" (template provided in Suppl. Table S1; see Table 1 for an example for *A. meadii*). The species table may be populated from various data sources. Depending on the objectives of the model, it may make sense to compile the data available from sources such as the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015; http://www.compadre-db.org/), the Global Population Dynamics Database (National Environmental Resource Council, 2010; https://www.imperial.ac.uk/cpb/gpdd2/), NatureServe (2016; http://www.natureserve.org/), the Environmental Conservation Online System (U.S. Fish and Wildlife Service, http://ecos.fws.gov/ecp/). Databases like TRY (https://www.try-db.org/TryWeb/; also see TraitNet for links to multiple databases: http://traitnet.ecoinformatics.org/traits-and-protocols/trait-research-list-of-datasets) provide compilations of plant data by ecophysiological and functional traits. Species with similar traits as the species of interest may be identified, and used for a trait-based approach of representing the species of interest (Adler et al., 2014). Scientific literature and other studies may provide more detailed information for the species of interest or species with similar traits, which is necessary for more complex approaches. If several species will be assessed at the same time, e.g. to compare relative sensitivities due to different life histories, the species data should be compiled separately for each species.

The species table includes species' characteristics from four domains: 1. life-history characteristics, 2. population-level and spatial characteristics, 3. external factors, 4. habitat specifications. The habitat specifications may not necessarily be represented in a model, but are useful for, e.g., narrowing down the exposure patterns. For each item in the species table, the quantitative or qualitative characteristic should be listed along with the uncertainty in the stated values or categories. For instance, the range of values measured, sample sizes, estimation method, number of studies, etc., should be listed. It is essential to understand how certain a characteristic can be determined, and what range of values or scenarios should be addressed with the model. The species table also includes a detailed statement of the sources of data or information about the species for each characteristic. An excerpt of the species table (top rows) as compiled for a species-specific adaptation (*A. meadii*) is shown in Table 1, and the full species table for *A. meadii* can be found in Suppl. Appendix B, Table S4.

It is important to mark in the table if no information for a characteristic could be found. Categories in the species table without information represent data gaps. In this case, it may be possible to use information from related species or to predict data on the basis of general theory (e.g., allometric equations or trait-based approaches; Adler et al., 2014). If no reliable source of information can be determined, explicit, simplifying assumptions should be made so that the sensitivity of the

Table 1
Example for the first few items compiled for the species table (Table S1) for Mead's milkweed (*Asclepias meadii*). Along with the information that is available for each characteristic, the uncertainty in the information should be assessed and listed. All sources of information need to be stated. If multiple sources are available for a characteristic, values or descriptions should be identified by source. The full table for Mead's milkweed is found in Suppl. Appendix B, Table S4).

Characteristic	Specification	Uncertainty	Sources
1.1 Life span	[1] Decades; [2] >100 years	Long life span agreed upon; exact number about average/maximum life span not available	[1] Kettle et al. 2000; [2] Bowles et al. 1998
1.2 Reproductive strategy	[1–5] Polycarpic; [2, 4] Not all mature plants reproduce every year	No uncertainty about reproductive strategy	[1] Betz 1989; [2] Kettle et al. 2000; [3] Grman and Alexander 2005; [4] Alexander et al. 2009; [5] Bowles et al. 2015
1.3 Time to maturation (if perennial)	[1] 3 years (in culture, adult stage, not necessarily flowering); [2] 5–7 years (in culture); [3] Up to 15 years (projection from field data); [4] 20–30 years (projection from field data, no maturation within 15 years of study duration observed)	Seedlings grow faster in culture than in the field, i.e. time spans from studies in culture underestimate time to maturation; estimates from field studies uncertain as no plant was followed from seedling to maturity	[1] Bowles et al. 1998; [2] Betz 1989; [3] Alexander et al. 2009; [4] Bowles et al. 2015

model to the characteristic can be determined. The process of working through the decision guide systematically identifies potentially important data gaps with respect to the purpose of the model. If the detailed representation of processes is essential for addressing the model objectives, the possibility to substitute for missing data should be explored. In some cases, the lack of data or limitations of resources for the project may prevent the model objectives from being achieved. The development of the minimal conceptual model can reveal whether the model objectives can be addressed with a population model given resource and/or data constraints. The completion of the species table, and subsequent decisions about model complexity can also be understood as iterative steps in which decisions during development of the conceptual model make it necessary to find available (or collect) data concerning the characteristics of the species.

3.2.2. Exposure-effects table

Information about pesticide exposure and toxicity is collected and compiled in the Exposure-Effects Table (template provided in Suppl. Appendix A, Table S2). The information in the exposure-effects table should be specific for the pesticide (or group of compounds) of interest. In addition, the information should be specific for the populations of concern and the species' range and habitat (as compiled in Table S1, points 4.1–4.5). If a species group is the focus of the model, and species' characteristics may result in different exposures (e.g. due to different habitats), the exposure-effects data should be compiled separately for each species. Specifications should be made according to either the level of detail available, or to the level of detail that exposure and toxic effects should actually be represented in the model as determined by the model objectives. The details to be included on exposure and effects have an important influence on the decisions taken about the model, including temporal and spatial resolution and aspects of the species' life history to be represented. When compiling information for the exposure-effects table, the uncertainties in data, and the data sources should also be listed. An example of an exposure-effects table for *A. meadii* can be found in Suppl. Appendix B, Table S5.

3.3. Phase III: decision steps

In the following steps, the decisions necessary to build a minimal conceptual model are summarized (detailed further in the template provided in Suppl. Appendix A). Decision steps are conducted iteratively, and outcomes may be refined and/or more data may be obtained in order to reach a minimal conceptual model. Following development of an initial life-history graph, the conceptual model development process can be divided into systematic sets of questions representing different model components: organism-level effects, temporal representation, spatial representation, density dependence, population status/ environmental conditions, and indirect effects. In each decision step, the initial model based on the life-history graph is adapted according to the modeled system, the model requirements and data availability. During model development, the modeler summarizes the decision taken in each step ("Model adaptation," see Suppl. Appendix A), including any simplifying assumptions and uncertainties that may influence the model's sensitivity to pesticide effects. Iterations of steps are required if adaptations of the model result from the decisions, and previous steps have to be reiterated in the context of the new specifications. The minimal conceptual model should be based on the minimal number of iterations of the decision process, as the focus should be on the representation that can adequately address the model purpose.

3.3.1. Life history graph

The representation of life history is a fundamental component of a population model. Hence, this decision guide is based on the use of life history as the foundation for the conceptual model for a given species (or species group). The life history for an herbaceous plant species can be represented with an initial general life-history graph (Fig. 2), starting with the assumption of a yearly time step. Using the information compiled in the species table (Table S1), this graph can be modified as needed to apply to the species of interest (see Appendix B, Fig. S9 for an example for *A. meadii*). The life-history graph can then be represented on a time axis (for an example, see Suppl. Appendix B, Fig. S10) which can help to relate life history to exposure occurrences and other processes. As subsequent decision steps are addressed during the conceptual model development process, the life-history graph is further refined to incorporate life-history aspects identified to be important (e.g., representation of growth, pollination, seed dispersal, etc.).

3.3.2. Organism-level processes

Representation of life history is deemed essential for a species-specific population model of herbaceous plants. In real plant populations, countless processes underlie a plant's life cycle and are influenced by multiple factors from the environment of an individual plant. The goal of a population model is not to represent all processes that govern a plant's life and interactions with its environment, but to develop a simplified representation of a plant population that can capture long-term population dynamics and the effects of pesticides with the required accuracy. In this step, it is assessed whether detailed processes at the organism level need to be represented beyond the representation of the plant's life history.

Pesticides may affect plants in different ways. Individual mortality, as assessed in standard toxicity studies ('lethal effects'), immediately affect population dynamics as plant numbers are reduced within a short interval after pesticide application. Sublethal effects refer to the effects that do not immediately affect plant numbers, but are measures of performance of individual plants in comparison to control individuals that were not exposed to the pesticide. In a field population, sublethal effects may ultimately influence population dynamics over a longer time period, for instance, by decreasing growth rates, reducing reproductive rates or affecting spatial distributions of plants. The relationship between sublethal effects and effects relevant for the population outcome are conveyed by dynamic processes at the level of an organism (for instance, growth of a plant). For the purpose of the current paper, we will refer to these processes as "organism-level" processes. Such processes have to be considered in the minimal conceptual model if sublethal effects of pesticides need to be assessed. In pesticide risk assessments, indirect effects (due to pesticides affecting species on which the modeled species depends in one way or another) are also of interest, and these can often be modeled as organism-level effects on the modeled species. The decision process (set of questions) to determine the inclusion of organism-level effects in the minimal conceptual model is detailed in Suppl. Appendix A (Fig. S2) and an example of this process for *A. meadii* is provided in Suppl. Appendix B (Fig. S11 and S12).

3.3.3. Temporal representation

A crucial decision in any modeling effort is concerned with the representation of temporal resolution and time span. A time step in the model defines the temporal resolution; one time step usually represents a fixed time interval in the "real world." If a time step is chosen to represent a time interval that is too long, the model may miss important processes happening in shorter time periods; if it is too short, a temporal resolution is represented that is too detailed for the corresponding available data. In some cases, varying time spans may be applied to each time step to represent the time in which each life stage is present instead (e.g., Smith et al., 2005). Because we are concerned with herbaceous plants, in which reproduction, other life history transitions, and pesticide exposures generally occur during the course of a year, we will initially assume that the temporal resolution should not be lower than a yearly time step. A diagram illustrating the decision process to determine whether a higher temporal resolution should be represented in the minimal conceptual model is shown in Box 1 (left), along with the process applied specifically for *A. meadii* (Box 1, right). Similar diagrams for the decision processes for other model components are provided in the decision guide template (Suppl. Appendices A and B).

The time horizon of the minimal conceptual model, i.e. the time period over which population dynamics are to be simulated, is initially specified in the model requirements based on the objectives of the study (see Suppl. Appendix A), and can be further evaluated and refined in this decision step. Population models do not restrict the number of time steps that can be conducted with the model, but the relevant time period to be modeled will need to be determined. The time horizon should be represented by an adequate number of time steps, i.e. the time period to be explored with the model should not be covered by a single or very few time steps.

3.3.4. Spatial representation

The simplest approach to modeling spatial relationships between individual plants and their environment is to assume that these relationships do not have a significant impact on population dynamics. The resulting non-spatially explicit model assumes that all individuals in a population experience the same conditions independent of their location and that interactions between plants either do not occur, are not of importance, or can be represented by affecting all plants in a population equally. However, if spatial relationships are deemed to be essential for the population dynamics, they should be represented explicitly. The template document (Suppl. Appendix A, Fig. S4) provides a list of questions to determine whether populations should be represented in a spatially explicit manner, and what the resolution and extent of this representation should be. An example of this step for *A. meadii* is provided in Suppl. Appendix B (Fig. S16).

Space can be represented in different ways. For instance, different levels of pesticide exposure may require that spatial relationships are accounted for in the model. Specific exposure levels can be identified, e.g. by habitat location in relation to agricultural areas or other conditions. In this case, it might be possible to split up the population into subpopulations that are exposed to each pesticide level, and assess effects separately for these subpopulations. Alternatively, exposures and effects can be calculated outside of the population model, and estimated for the population in its current state by making assumptions about the spatial locations, and thus, exposures of individual plants within the population at the time of each exposure. These two solutions would be considered as partially spatially explicit approaches, i.e. one process is spatially explicit, but the other processes in the model are not.

A spatially explicit model assigns each plant in a population a specific location. Locations can be defined by detailed coordinates or by grid cells subdividing the landscape. Such a spatial model allows the inclusion of several different processes happening in space, for instance, competition between neighboring plants (Berger et al., 2008) and dispersal. Spatially explicit representation of competition between plants leads to density controlled populations, i.e. density dependence is represented mechanistically in the model as interactions between individual plants rather than imposed on the population using a specified mathematical function (see section 3.3.5 Density dependence). The resolution of the spatial representation should be guided by the sizes of individual plants (for instance, in a grid-based model, a grid cell should not be smaller than the diameter of a single plant) and the spatial resolution of the processes to be represented. To use the example of exposure once more: if exposure levels differ every 10 m, it might not be

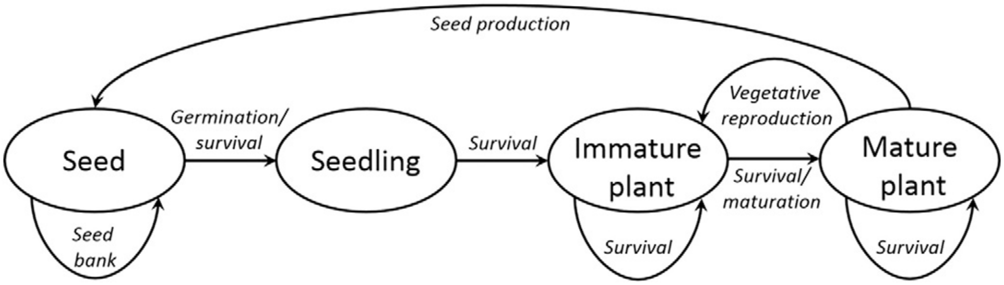
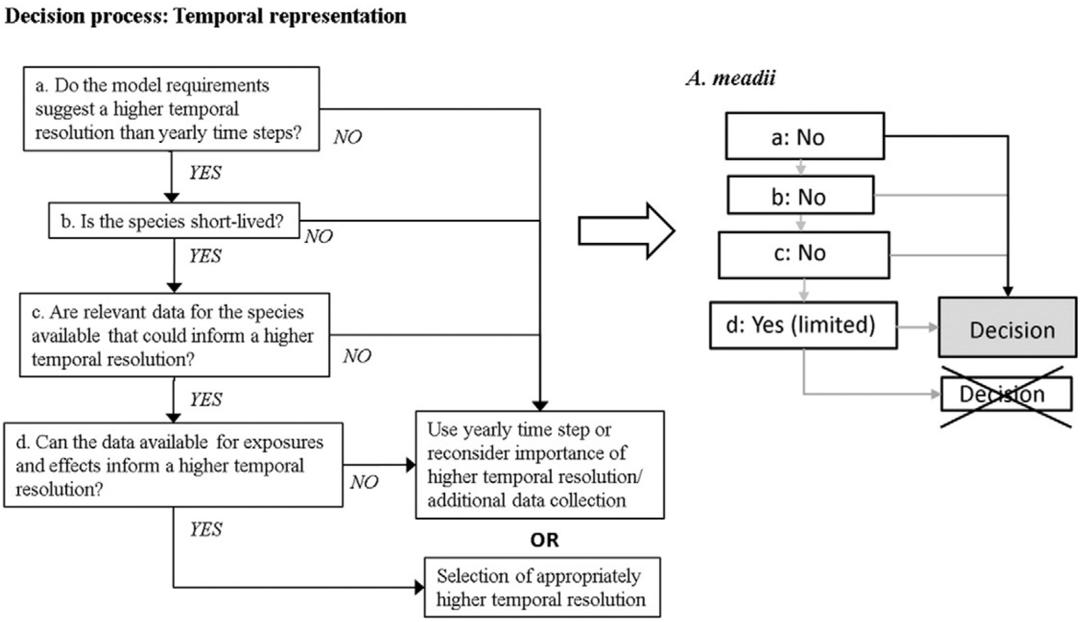


Fig. 2. General life history graph for herbaceous plants, representing the life stages and transitions that occur. For a specific species, the general life-history graph can be used to determine which elements apply.

Box 1

(At left): Decision process diagram for determining temporal representation for a minimal conceptual model, comprised of a set of questions to adapt a model for a given objective and species. (At right): Example of the decision process for temporal resolution for a specific species (*A. meadii*) determining the use of an annual time step for the conceptual model. Suppl. Appendix A provides additional detail and decision process diagrams for other conceptual model components (organism-level effects, spatial representation, density dependence, population status/ environmental conditions, and indirect effects), and Suppl. Appendix B provides corresponding examples for *A. meadii*.

The decision process is designed as a series of questions to which a modeler assigns a “Yes” or “No” answer to ultimately arrive at a decision for whether/how the model should be adapted for a particular component. While a “Yes” or “No” to an initial question may quickly indicate the appropriate decision, it is useful for a modeler to answer all questions to develop a comprehensive justification for a given decision and identify any areas of uncertainty. In some cases, a clear “Yes” or “No” is not apparent (e.g., when data are available but limited). In these instances, uncertainties should be explicitly detailed with the selected “Yes/No” answer, and the decision process should be iteratively re-evaluated as additional information is acquired (as an outcome of the current decision step or other parts of the conceptual model development process). In the example presented here, a yearly time step is determined to be appropriate for a minimal conceptual model for *A. meadii*. This outcome is based on the lack of a need for higher temporal resolution designated by the model requirements, in addition to the long lifespan of *A. meadii* and limitations on adequate available data to model the species at a higher temporal resolution. The yearly time step for *A. meadii* results in the removal of the seed stage from the model representation because seed and seedling stages are not present at the same time (see Fig. 2). If a yearly time step spans from the time of flowering of the plants (matching the time period when field surveys on flowering plants are generally conducted), seeds are not present in the population as it was assumed that the plant does not form a seed bank.



necessary to include a higher resolution in the model than 10 m. The extent of the modeled landscape also needs to be considered in the latter case. The extent should be determined according to the model requirements for spatial representation. For example, it must be determined whether the spatial extent of the model represents the whole range of the species, or if a single habitat should be represented.

3.3.5. Density dependence

Density dependence is an important process controlling abundances of many populations, and has been shown to interact with effects of stressors such as pesticide exposures (Forbes et al., 2016). If a population is density controlled, including density dependence in the model should be considered. Population density becomes an important factor in population dynamics in populations with high densities because intra-specific competition for resources affects survival, growth and/or reproduction of individuals. Even in species classified as threatened or endangered, density-controlled populations are not uncommon as populations might occur in high numbers in some locations or under specific conditions. On the other end of the spectrum, very low densities may result in limitations of sexual reproduction (e.g. due to lack of pollination) and/or potential loss of genetic variability which may result in further decline (Allee effects).

Density dependence may act on all life stages, or just on a subset of life stages. For instance, because density dependence in plants is often related to shading by neighboring plants, it may affect recruitment rate by lowering germination or seedling establishment rate, but not affect mature plants.

Density dependence can be represented in different ways in a model. It can be imposed on the whole population by limiting the abundance of the population. If some life stages may be more affected than others, density dependence can be represented by limiting the numbers in those life stages dependent on the overall population abundance. For this kind of representation, different functions have been applied in population models (Morris and Doak, 2002; Coulson et al., 2008). If a process is already represented through which density dependence may act (e.g., light availability affecting growth), density dependence may be an emergent property of the model rather than an imposed function determining maximum density (Berger et al., 2008). In a (partially) spatially explicit model, local densities may be considered rather than the average density across the whole modeled space. These alternatives and considerations illustrate how decisions about the representation of density dependence are dependent on other model specifications and should be considered in this context. If density dependence is already included as acting on plants through organism-level processes and/or spatial interactions between plants, the conceptual model does not need to be altered in this decision step. See Suppl. Appendix A (Fig. S5) for the detailed decision process for density dependence, and Suppl. Appendix B (Fig. S18) for an example of the process for *A. meadii*.

3.3.6. Population status and environmental factors

Every population is dependent on its habitat and is affected by variation in environmental conditions. Variable conditions faced by populations cannot be ignored in a model because impacts of pesticides may vary considerably, depending on the condition of the plants in the population. In the context of threatened and endangered species, environmental conditions have caused or are currently causing a decline in the species' abundance. Populations in decline or present at low numbers may be more vulnerable to additional stressors, such as impacts from pesticides, than large populations present in stable or increasing abundances (Hanson and Stark, 2012; Salice, 2012; Schmolke et al., 2017). The status of populations (population growth trend and population size) is assessed in the five-year reviews of species listed under the U.S. Endangered Species Act (https://www.fws.gov/endangered/). Beyond U.S. listed species, similar information may be available from sources including the IUCN Red List (http://www.iucnredlist.org/), NatureServe (2016; http://www.natureserve.org/), the Environmental Conservation Online System (U.S. Fish and Wildlife Service, http://ecos.fws.gov/ecp/), etc. as compiled under item 2.2 in the Species Table (see Appendix A, Table S1). In some cases, population sizes may fluctuate considerably between years, and extraordinary environmental conditions may cause occasional high mortalities, reproductive failures or explosive population growth (Morris and Doak, 2002). If such variations in population dynamics and environmental conditions are likely for the species, they should be represented in the model. Environmental factors acting on populations may include floods, fires or extreme weather events, disease outbreaks, fluctuations in pollination services or seed dispersal amongst other factors.

If no clear link (according to available data) can be determined between environmental factors and population dynamics, the representation of generic demographic and environmental stochasticity should be considered. For instance, survival rates of all plants in a population or plant fertility may differ stochastically between years. Such variation may be derived from available survey data across several years. In the absence of data that capture variation in population dynamics, effects can be assessed with the model by sensitivity analysis that covers realistic ranges of variability. Stochastic effects are especially important for small populations (Caswell, 2001; Morris and Doak, 2002; Melbourne and Hastings, 2008; Kendall and Wittmann, 2010).

If specific environmental factors are identified as driving population dynamics of the species, these should be considered in the model (see Suppl. Appendix A, Fig. S6, for the detailed decision process and Suppl. Appendix B, Fig. S19, for an example of the process for *A. meadii*.) In this case, the temporal and spatial patterns of the factors should be assessed and compared with the temporal and spatial representation of the plant species in the model as defined in the previous steps. If the determinations do not match, the previous steps should be revisited in the context of the environmental factors. Environmental factors may be modeled in a generic way, i.e. by how they impact the focal species rather than explicitly. In this sense, the temporal and spatial patterns and the effect size are most important.

3.3.7. Indirect effects

Pesticides may have effects on plants that are mediated by other means than immediate reductions of survival, growth or fecundity due to exposure. A pesticide might affect other plants in the plant community to a different level than the modeled species, which might result in changes in the degree of inter-specific competition. Many plants are dependent on other species, e.g., animal pollinators or seed dispersers. Other essential interactions between different plant species or plants and other organisms exist that might be impacted by pesticides. These impacts affecting other parts of the ecosystem that ultimately reach a plant species are called indirect effects.

Pathways of indirect effects that may influence herbaceous plants are detailed in the decision steps presented in Suppl. Appendix A (Fig. S7; example for *A. meadii* provided in Suppl. Appendix B, Fig. S21). In a minimal conceptual model, the explicit mechanistic representation of the indirect effects pathway should only be considered if detailed data are available for the pathway. In most cases, indirect effects can be accounted for in similar ways as direct effects, i.e. changes in survival rates, growth or fecundity/recruitment of the plants. However, the impact of the pesticide on the indirect effects pathway has to be estimated first. For instance, one might ask by what proportion will pollinator abundance be reduced at the time of flowering due to insecticide application?

3.4. Phase IV: summary of minimal conceptual model and its uncertainties

3.4.1. Summary of the minimal conceptual model

Once all decision steps are completed, the summaries as provided after each decision step ("model adaptation" sections as labeled in the template Suppl. Appendices A and B) can be compiled into a summary of the minimal conceptual model (template provided in Table S3 of Suppl. Appendix A and worked example for *A. meadii* provided in Table S6 of Suppl. Appendix B). In addition to a description of the model, a graphical representation based on the life-history graph can be useful (example for *A. meadii* in Fig. S22 of Suppl. Appendix B). The summary of the minimal conceptual model should also address what output metrics should be collected with the implemented model, e.g. extinction risk, population growth rate, population abundance, etc. Given the iterative nature of the modeling process, the conceptual model will be subject to change throughout the modeling process including implementation, parameterization and calibration, testing and analysis.

The minimal conceptual model can also be seen as a communication tool that can facilitate understanding by any party involved in model development, application, or decision making. For a model to be acceptable as a risk assessment tool (or as any other real-world application), the assumptions and their implications have to be transparent, justified, and comprehensible by all parties involved (Jakeman et al., 2006). Accordingly, the minimal conceptual model should be seen as a description of a population model that can be communicated to and discussed with any party (including non-modelers) rather than a description of a technical implementation.

3.4.2. Uncertainty and model evaluation

When developing a population model, especially for threatened or endangered species, the lack of data about the species is a common problem. A model representation allows the modeler to make explicit assumptions about the system's characteristics that are not well specified by empirical data. With the decision guide, available data for the species modeled are collected systematically, and data gaps and how they are dealt with are made explicit in the model summary (Table S3, Suppl. Appendix A). Data gaps may be bridged using data from closely related species, from relationships observed across multiple species or from general theory. When data gaps are addressed in this way, it is important to clarify the different data sources. Accordingly, we strongly recommend that data should be collected in a species-specific format, i.e., if data from different species will be used, they should be compiled in separate tables. Other sources of data or representation of mechanisms should be clearly stated in the conceptual model.

The decision guide as presented here is concerned with the development of the conceptual model, and thus, does not address the steps of model implementation and evaluation. For the minimal conceptual model to be used as a tool in risk assessment, it has to be technically implemented and evaluated. The comprehensive evaluation of a model is important for the assessment of its applicability and limitations. This includes several steps, such as the evaluation of uncertainties in data sources used for model development and parameterization, verification of the correct implementation of the conceptual model, elasticity or sensitivity analysis and validation (Oreskes et al., 1994; Rykiel, 1996; Augusiak et al., 2014). Along with the detailed description of the model, these steps should be comprehensively documented (Schmolke et al., 2010b; Grimm et al., 2014).

The development process for the minimal conceptual model provides the basis and first step in the evaluation of the model. Uncertainties in the data used for model development are compiled along with the species and pesticide data in Tables S1 and S2 in Suppl. Appendix A. Assumptions applied in each decision step and the uncertainties arising from these assumptions are systematically inventoried during the process (template table provided in Table S3 in Suppl. Appendix A, and worked example for *A. meadii* provided in Table S6 in Suppl. Appendix B). This exercise results in a transparent and comprehensive summary of potential limitations so that the model can be more effectively implemented and evaluated. The uncertainty gives a measure of the applicability of the model and lays out the necessary analyses that will need to be conducted with the model when implemented. In some cases, a level of uncertainty may be revealed during the development of the minimal conceptual model that does not allow the implementation of a useful model to address the model objectives. How and to what degree uncertainties are addressed will depend upon the study objectives and the required certainty of the risk assessment. The template provides a standard and clear means to communicate and evaluate the decisions made during model development.

With the thorough assessment of uncertainties in the data and the model decisions taken, the path for a comprehensive analysis of the implemented model is laid out during development of the conceptual model. Assumptions can be revisited if the evaluation of the model suggests that high uncertainty is added to the model outcomes due to specific assumptions. In some decision steps, the modeler may not be able to answer every question with a definitive “yes” or “no” and specific assumptions will be made about the system to resolve modeling decisions. If assumptions are not well supported by data, alternative assumptions can be tested during the evaluation of the implemented model to assess their impact on model behavior.

4. Discussion

Population- and other ecological models are increasingly recognized as valuable tools to inform various environmental decision processes (Nienstedt et al., 2012; NRC, 2013). It is essential that such models can be assessed and reviewed by stakeholders, i.e., that a model is transparent in every aspect. Comprehensive standard documentation for models has been introduced that provides a full description of models and their analysis once they are developed (TRACE, Schmolke et al., 2010b, Grimm et al., 2014). However, TRACE does not provide guidance on the decisions involved in model development. Models vary widely depending on the species or system represented, the objectives of the modeling exercise, data availability, technical implementation of the model, and the specific decisions taken by the modeler. Accordingly, the guidance presented here for conceptual model development for pesticide risk assessment of herbaceous plants provides a useful addition to other efforts to ensure Good Modeling Practice (Schmolke et al., 2010b; Augusiak et al., 2014; EFSA, 2014). The decision guide explicitly and comprehensively states the decisions needed during the development of a conceptual model, and thus, has the potential to significantly improve the consistency and transparency of models used to inform management decisions.

Although models may be developed to fulfill a diverse set of objectives within the broad context of environmental management, similar questions need to be asked, and many decisions need to be made during model development. If the systems to be represented (e.g., herbaceous plant populations or species) and the model objectives (e.g., pesticide risk assessment) are limited, this set of questions can be stated comprehensively. The resulting model decision guide that we present in the current paper facilitates model development because the modeler does not have to come up with the questions by herself for every new model. For example, herbaceous plants are a variable group of organisms, but they can be described by a general life history that applies to all species. The model development process as laid out in this decision guide covers the aspects of herbaceous plants that may be of importance in the context of pesticide risk assessment. A similar guidance for other organism groups (e.g., fish, insects, etc.) or other model objectives could be produced by adapting the decision steps accordingly.

In the context of pesticide risk assessment of listed species in the US, the large number of species and population models that would need to be developed to address them all, should be considered. The minimal conceptual model should allow decisions as to whether different species can be represented by the same model, i.e. whether their life histories and habitats are similar enough to be captured by the same model. Simply combining species' traits in a single representation does not lead to a realistic representation of any species, but instead, different parameterizations of a model can be employed to represent different species. If a species can be identified as particularly vulnerable to exposure and effects of pesticides, this species may be used to represent a group of similar species. Population models can also be helpful in identifying the relative vulnerability of species, since they quantify toxicity in a life-history context. For example, models have shown that the same toxic effects at the organism-level can have dramatically different implications for population persistence depending on life history (Forbes et al., 2001; Stark et al., 2004).

Choosing vulnerable species to represent a larger group of species is a conservative approach, since it assumes that the species represented will experience an equal or higher impact of a pesticide at the population level than other similar species. Conservatism of a model is not a function of its structure or complexity, but is determined by the specific assumptions underlying the model, especially about exposure and effects. Whereas model structure should be as realistic as possible, different degrees of conservatism can be applied through the choice of scenarios that explore varying degrees of worst-case assumptions.

The decision guide presented in this paper comprehensively addresses the topics that need to be considered during model development for the specified objectives. This guidance is intended to facilitate the model development process to significantly reduce the effort in developing population models and provide a tool for communication between modelers and other stakeholders. Future developments include automation of aspects of the template provided in Suppl. Appendix A as a user-friendly interface to further improve the accessibility of population modeling to a wider audience. Adaptation of the decision guide to other organism groups will also be explored. This guide, and its future adaptations, is intended to increase the efficiency, consistency and transparency of population models for use in environmental risk assessments.

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Appendix A and B. Supplementary data

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