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Simple or complex: Relative impact of data availability and model purpose on the choice of model types for population viability analyses

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ABSTRACT

Population viability analysis (PVA) models are used to estimate population extinction risk under different scenarios. Both simple and complex PVA models are developed and have their specific pros and cons; the question therefore arises whether we always use the most appropriate model type. Generally, the specific purpose of a model and the availability of data are listed as determining the choice of model type, but this has not been formally tested yet. We quantified the relative importance of model purpose and nine metrics of data availability and resolution for the choice of a PVA model type, while controlling for effects of the different life histories of the modelled species. We evaluated 37 model pairs: each consisting of a generally simpler, population-based model (PBM) and a more complex, individual-based model (IBM) developed for the same species. The choice of model type was primarily affected by the availability and resolution of demographic, dispersal and spatial data. Low-resolution data resulted in the development of less complex models. Model purpose did not affect the choice of the model type. We confirm the general assumption that poor data availability is the main reason for the wide use of simpler models, which may have limited predictive power for population responses to changing environmental conditions. Conservation biology is a crisis discipline where researchers learned to work with the data at hand. However, for threatened and poorly-known species, there is no short-cut when developing either a PBM or an IBM: investments to collect appropriately detailed data are required to ensure PVA models can assess extinction risk under complex environmental conditions.

1. Introduction

Population viability analysis (PVA) is an important tool used in conservation biology to assess the viability of populations and rank alternative management scenarios (Beissinger and Westphal, 1998; Reed et al., 2002). Population viability analysis is a generic label affixed to a variety of modelling techniques differing in their complexity, approach, and type of data used (Morris and Doak, 2002) including: patch-occupancy models (POMs, Hanski, 1997, 1994), matrix projection models (Caswell, 2002), structured population models (SPMs, Akçakaya and Sjögren-Gulve, 2000; Schtickzelle and Baguette, 2009), and individual-based models (IBMs, DeAngelis and Gross, 1992; Grimm and Railsback, 2005). Individual-based models themselves cover a wide spectrum of models, ranging from simpler IBMs driven by demographic rates (e.g. Grimm et al., 2003) to more complex models driven by the adaptive behaviour of individuals (Stillman et al., 2015). Generally, the type of PVA model used is believed to be determined by three main factors: the life history of the species in consideration, the specific model purpose, and constraints of data availability and resolution (Akçakaya and Sjögren-Gulve, 2000; Boyce, 1992; DeAngelis and Rose, 1992; Grimm and Railsback, 2005).

The choice of a given model type used for a PVA first depends on the life history of the species in consideration (Boyce, 1992;

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Vucetich and Creel, 1999; Wiegand et al., 1998). As an example, population dynamics will not be modelled the same way for an insect species with an r-selected strategy and abundant populations, and for a rare large mammal, characterized by a k-selected strategy and complex social or territorial behaviour. The latter species is believed to benefit more from incorporation of behaviour in the model, leading to the development of more complex models, such as IBMs (Grimm and Railsback, 2005). Second, the specific purpose of the model guides the choice of the model type. For example, models depicting generic phenomena and those predicting species responses to new environmental conditions are likely to strongly differ in model structure (e.g. Grimm and Railsback, 2005). Last but not least, the availability and resolution of data necessary for modelling certain processes can often impose limitations on the model type that can be developed and parameterized (Boyce, 1992; DeAngelis and Rose, 1992; Reed et al., 2002). Even if model aim or species life history suggest the development of a more complex model, the lack of data or their coarse resolution can force the adoption of less complex model types.

Although these three factors are widely recognized to affect model type choice, in particular its structure and complexity (Akçakaya and Sjögren-Gulve, 2000; Boyce, 1992; Grimm and Railsback, 2005), very few studies explicitly justified why they chose a specific model type over others (Pe'er et al., 2013). Thus, there is no clear understanding of how the species' life history, data at hand (availability and resolution), and model aim can affect the choice of a specific model type for PVA in practice. Given that data scarcity is probably a major limitation in assessing population viability, it is striking that no systematic approach has been undertaken to study the constraints posed by data restrictions on model type choice (Brook et al., 2002; Fieberg and Ellner, 2000; Reed et al., 2002; Thomas et al., 2002). Such an understanding would aid to expedite the decision making in the era of the sixth species mass extinction (Barnosky et al., 2011) by providing a more streamlined and efficient procedure of PVA design and implementation (Pe'er et al., 2013).

In this study, we quantified the relative importance of specific model purpose and data availability and resolution (hereafter abbreviated to "data availability") for the choice of PVA model type. We used 37 pairs of PVA models identified from the literature, each consisting of an individual-based model (IBM) and a population-based model (PBM) developed for the same species. This 'paired' design effectively controls for the effect of species life history and therefore allows us to objectively assess the impact of data availability and model purpose on the choice of model type. We first extracted from each PVA study the information on the model purpose and a series of factors describing data availability about the species and its environment. We then elicited identical information via a questionnaire sent to the authors of the 74 PVA models to verify that the published information indeed reflected what data were available to modellers at the time of model development. We then quantified the importance of data availability and model purpose on the choice of model type.

2. Methods

2.1. Selecting published PVA models in a 'paired' design

We searched the ISI "Web of Knowledge" for papers reporting PVA models constructed for the same animal species but differing in their complexity: IBMs vs. PBMs (including structured population models, projection matrix models and patch occupancy models). Throughout this manuscript we consider IBMs to be generally more complex than PBMs, although we acknowledge that both PBMs and IBMs can range in their complexity. We used the following search keys: (1) for PVA: "(population viability analysis) OR (vulnerability analysis) OR (population dynamics model)"; combined with either (2) for IBMs: "(individual based model) OR (behavioural model) OR (mechanistic model)"; or (3) for PBMs: "(structured population model) OR (matrix model) OR (Leslie model)". The literature search (conducted on 29.07.2014) yielded 542 papers, all classified as either IBM or PBM. From these papers, we identified 37 pairs of PVA models (Table 1), i.e. when at least one IBM and one PBM were developed for the same species. When more than one PVA of a certain type was developed for the same species (17 out of 37 species, 46%), we retained only the model of each type that was published first. Such focus on the earliest studies is believed to better reflect the general lack of data, which is characteristic for species for which a PVA is typically performed (Sitas et al., 2009). However, to assess how this decision to use only the papers published first affected our conclusions, we also ran the analyses with all available PVA studies for the 37 species.

2.2. Assessing data availability

From each PVA model, we extracted a series of nine factors to describe the availability of data covering all main model components that we identify as relevant to PVA model structure (Fig. 1 and Table 2), grouped into factors describing the species and factors describing its environment (Beissinger and Westphal, 1998). We distinguish three factors for species data: *demography* (i.e. vital rates, specifics of sociality or territoriality if relevant), *genetics* (e.g. inbreeding depression, heterozygosity, etc.), and *dispersal* (e.g. immigration, emigration, movement rules); three factors for environment data: *climate* (covering both the short-term weather component, and the longer-term climatic component), *biotic interactions* (e.g. the influence of competition, predation or parasitism on survival and/or reproduction), and *landscape*, further subdivided into *space representation* (i.e. location and configuration of territories/populations) and *habitat heterogeneity* (i.e. habitat quality, here defined as any measure of structural and/or functional habitat heterogeneity that was considered in the study); and two factors about the impact of the environment on species demography: *effect of climate on vital rates* (i.e. quantification of how weather factors affect survival and/or reproduction), and *effect of habitat on vital rates* (i.e. quantification of how habitat affects survival and/or reproduction). These nine factors characterize both the availability and, whenever possible, the resolution of relevant data (see Table 2 for details).

Information about data availability extracted from published studies does not necessarily reflect the true data availability at the time of model development. To obtain a more accurate understanding of what data were available at the time of model development, we contacted the authors of the 74 case studies by e-mail and asked them to fill in a questionnaire (see Supplementary material). Authors were asked to give their assessment about the availability of data for each of the nine factors (listed in Table 2) at the time when the model was developed. Additionally, we asked authors to assess how the choice of the model type they used may have been affected by their expertise and familiarity with a certain type of PVA. We obtained information on data availability for 38 models (a 51% response rate). Because not all of these models represented paired studies, we acquired author-based estimates for data availability and resolution for 12 pairs of published PVA studies.

We then assessed whether we could glean data availability from the published model structure. To that end, we used Kendall's rank correlation (a modified version for data with ties based on normal approximation with continuity correction) between the values for each of the nine factors reflecting data availability as extracted directly from published studies and those obtained from questionnaire responses. We considered Kendall's rank correlation more appropriate than Spearman rank correlation because most of our

Table 1
List of the 37 pairs of PVA models used in this study; a pair consists of a PBM and an IBM developed for the same species.

Pair ID	Species	Class	IBM	PBM
1	*Aquila adalberti*	Aves	Penteriani et al. (2005)	Ferrer et al. (2009)
2	*Arvicola amphibius*	Mammal	Rushton et al. (2000)	Sutherland et al. (2012)
3	*Boloria eunomia*	Insect	Radchuk et al. (2013)[a]	Schtickzelle and Baguette (2004)
4	*Canis lupus*	Mammal	Vucetich et al. (1997)	Jensen and Miller (2001)
5	*Canis simensis*	Mammal	Haydon et al. (2002)	Mace and Sillero-Zubiri (1997)
6	*Castor fiber*	Mammal	Nolet and Baveco (1996)	South et al. (2000)
7	*Daphnia magna*	Branchiopoda	Vanoverbeke (2008)	Billoir et al. (2007)
8	*Engraulis encrasicolus*	Actinopterygii	Oguz et al. (2008)	Mantzouni et al. (2007)
9	*Folsomia candida*	Entognatha	Meli et al. (2014)	Meli et al. (2014)
10	*Gadus morhua*	Actinopterygii	Scott et al. (2006)	Ginzburg et al. (1990)
11	*Gymnobelideus leadbeateri*	Mammal	Lindenmayer and Lacy (1995a)	Lindenmayer et al. (1993)
12	*Gyps fulvus fulvus*	Aves	Robert et al. (2004)	Sarrazin and Legendre (2000)
13	*Haliaeetus albicilla*	Aves	Green et al. (1996)	Sulawa et al. (2010)
14	*Hypogeomys antimena*	Mammal	Sommer and Hommen (2000)	Sommer et al. (2002)
15	*Icaricia icarioides fenderi*	Insect	McIntire et al. (2007)	Schultz and Crone (2005)
16	*Lagopus muta*	Aves	Suzuki et al. (2013)	Wilson and Martin (2012)
17	*Lepus americanus*	Mammal	King and Schaffer (2001)	Yan et al. (2013)
18	*Lycaon pictus*	Mammal	Vucetich and Creel (1999)	Burrows et al. (1994)
19	*Maculinea arion*	Insect	Griebeler and Seitz (2002)	Griebeler (2011)
20	*Maculinea rebeli*	Insect	Hochberg et al. (1994)	Hochberg et al. (1992)
21	*Marmota marmota*	Mammal	Stephens et al. (2002)[b]	Stephens et al. (2002)[c]
22	*Martes americana*	Mammal	Carroll (2007)	Fryxell et al. (2001)
23	*Morone saxatilis*	Actinopterygii	Rose (2005)	Rose (2005)
24	*Mustela nigripes*	Mammal	Van Kirk (1990)	Groves and Clark (1986)
25	*Oedura reticulata*	Reptilia	Wiegand et al. (2001)	Wiegand et al. (2002)[d]
26	*Oncorhynchus clarki*	Actinopterygii	Harvey and Railsback (2007)	Hilderbrand (2002)
27	*Perca flavescens*	Actinopterygii	Rose (2005)	Sable and Rose (2008)
28	*Peromyscus leucopus*	Mammal	Henein et al. (1998)	Burns and Grear (2008)
29	*Placopecten magellanicus*	Bivalvia	Tian et al. (2009)	Barbeau and Caswell (1999)
30	*Salvelinus leucomaenis*	Actinopterygii	Sato and Harada (2008)	Morita and Yokota (2002)
31	*Strix occidentalis caurina*	Aves	Doak (1989)	Lande (1988a)
32	*Strix occidentalis occidentalis*	Aves	Andersen and Mahato (1995)[e]	Andersen and Mahato (1995)[f]
33	*Sus scrofa*	Mammal	Fernandez et al. (2006)	Howells and Edwards-Jones (1997)
34	*Tetrao urogallus*	Aves	Marschall and Edwards-Jones (1998)	Fernandez-Olalla et al. (2012)
35	*Trichosurus caninus ogilby*	Mammal	Lindenmayer and Lacy (1995b)	Lacy and Lindenmayer (1995)
36	*Ursus arctos*	Mammal	Wiegand et al. (1998)	Saether et al. (1998)
37	*Ursus arctos horribilis*	Mammal	Mills et al. (1996)[g]	Mills et al. (1996)[h]

[a] Among the four alternative IBMs in this paper, we used the model including temperature only, as it was selected to be the most appropriate for the description of population dynamics according to the authors.
[b] As IBM we used “behaviour-based model”, called by the authors “model 4”.
[c] As PBM we used “population-based matrix model”, called by the authors “model 1”.
[d] As PBM we used a model called by the authors “structured no-Allee model”.
[e] As IBM we used the model called by the authors “a simulation model”.
[f] As PBM we used the model called by the authors “a birth-death-catastrophe model”.
[g] As IBM we used the model implemented in VORTEX software.
[h] As PBM we used the model implemented in RAMAS software.

factors had only three categorical levels, and ties were more likely to occur when using Spearman rank correlation.

2.3. Assessing specific purpose of the PVA model

We classified each PVA study according to its specific purpose, within the general “viability assessment” aim of a PVA. We distinguished eight purpose categories: (1) reintroduction, (2) harvest management, (3) management of a declining population, (4) understanding population decline, (5) understanding the impact of spatial structure, (6) understanding factors affecting viability, (7) understanding effect of physiology on population viability, and finally (8) finding the appropriate model complexity for depicting the population. Categorization of model purposes is somewhat arbitrary (Holling, 1966; Peck, 2004; Roughgarden et al., 1996). Therefore, we considered two alternative categorizations, which aggregate these eight categories into either five or three categories (Table 3). We used the original categorization with eight categories for the main analyses looking at how model purpose impacted the choice of model type, and performed a sensitivity analysis with the two alternative categorizations to assess how the choice of the categorization affected our results.

2.4. Quantifying the relative importance of specific model purpose and data availability on the choice of model type for PVA

We assessed how the type of the model to be developed (IBM or PBM) was affected by the specific model purpose and data availability, as defined by nine factors, using conditional Random Forest analyses (Hothorn et al., 2006a; Strobl et al., 2008, 2007). Random Forests are a powerful machine-learning algorithm based on ensembles of classification trees that are ideally suited for high-dimensional classification problems (Cutler et al., 2007; Hochachka et al., 2007; Olden et al., 2008). We fit 2500 trees with five variables tried at each split and 35% of data withheld for internal cross-validation. The importance of each variable of interest was estimated by randomly permuting the actual values of each variable of interest and assessing the reduction of model accuracy in internal cross-validation (Grömping, 2009; Oppel et al., 2009; Strobl et al., 2007). Variable importance is inversely related to the reduction in model accuracy after permutation. We conducted this analysis on the dataset consisting of the 37 pairs of PVA studies, and on the complete dataset consisting of all the PVA studies found for each of the 37 species. All analyses were conducted with R software (R, 2013), and we used the functions “cforest” and “varimp” in library

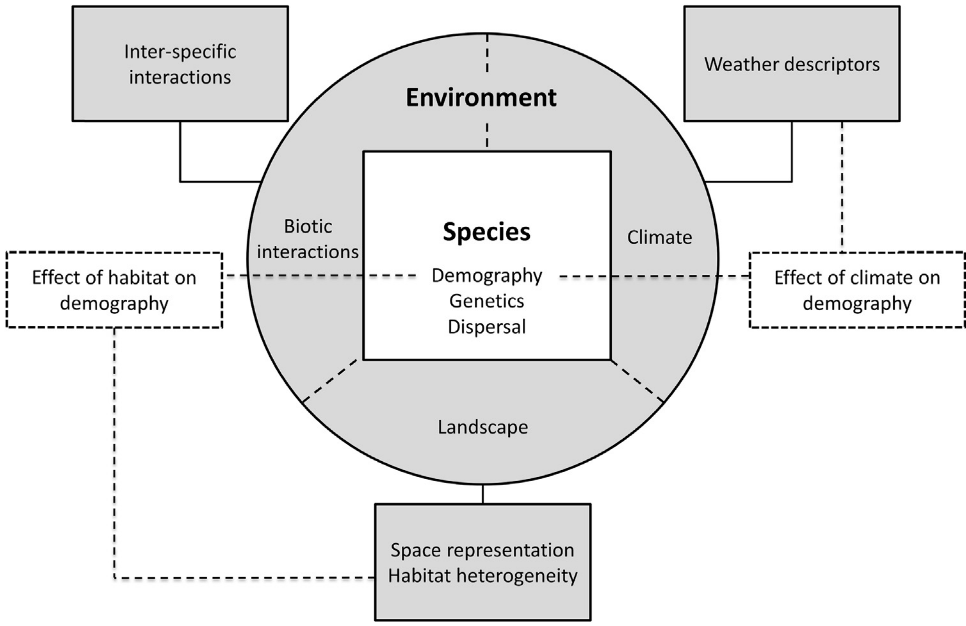

Fig. 1. Data used in PVAs can be grouped into two large categories: data concerning the species and data concerning its environment, and further subdivided into nine factors reflecting data availability. The factors describing species data (shown in a white-background square in the centre) are: *demography*, *genetics*, and *dispersal*. The factors describing environment (squares shown with grey background) inhabited by the species are: *climate* (both short-term weather and longer-term climate); *biotic interactions*, of which we discern interspecific interactions; and *landscape*, which is represented by two further factors: *space representation*; and *habitat heterogeneity*. Two further factors represent the link between the environmental data and species (squares delineated with dashed line): *effect of climate on demography* and *effect of habitat on demography*.

Table 2
List of the nine factors that describe data availability and resolution and cover all main model components we identified as relevant to PVA model structure. Abbreviation, modalities and coding of factors used in the analyses on data extracted from each PVA study are given.

PVA component	Factor	Data resolution	Description	Coding
Species	Demography	Fine	Variation within stage/age group in vital rates (i.e. survival, fecundity)	1
		Moderate	Average vital rates for stage/age group	2
		Coarse	Yearly population growth rate or patch occupancy	3
	Genetics	Yes	Included	0
		No	Not included	1
	Dispersal	Fine	Mechanistic description of the movement (e.g. trajectories of individual animals)	1
		Moderate	Phenomenological description of the movement (e.g. matrix of transition rates between patches)	2
		No	Not included	3
Environment				
Climate	Climate	Fine	On temporal scale $\ll$ stage/age group	1
		Moderate	On temporal scale around the duration of 1 stage/age group	2
		Coarse	On temporal scale around 1 generation	3
		No	Not included	4
	Effect of climate on vital rates	Yes	Affected	0
		No	Not affected	1
Biotic interactions	Inter-specific interactions	Fine	Mechanistic representation of the other(s) species population dynamics	1
		Moderate	Phenomenological (static) representation of the other species	2
		No	Not included	3
Landscape	Space representation	Fine	The resolution of the spatial data $\leq$ territory size (or a single population) of the species	1
		Moderate	Only the locations of territories (or single populations) included	2
		No	Not included	3
	Habitat heterogeneity	Within-patch	Heterogeneity in habitat quality within a patch	1
		Between-patch	Heterogeneity in habitat quality between habitat patches	2
		Homogeneous	All patches of the same habitat quality/no space included	3
	Effect of habitat on vital rates	Yes	Affected	0
		No	Not affected	1

Table 3
PVA model purpose classified into eight categories, as used in the main analysis, and summarized in coarser categorizations used for sensitivity analysis.

PVA model purpose (fine scale)	PVA model purpose (medium scale)	PVA model purpose (coarse scale)
Reintroduction	Reintroduction	Management
Harvest management	Harvest management	
Management of declining population	Management of declining population	
Understanding population decline		Population diagnosis
Impact of spatial structure (on population viability)	Understanding factors affecting viability	
Understanding factors affecting viability		
Understanding effect of physiology		Academic/methodological
Finding the level of complexity (a search for the appropriate level of model complexity/modelling software)	Finding the level of complexity	

"party" (Hothorn et al., 2006b) for the conditional Random Forest analyses.

3. Results

For eight out of nine factors, the actual data availability reported by authors in questionnaire responses correlated highly with the resulting data inclusion in the model as extracted from published papers (Kendall's tau $\tau > 0.50$, $p < 0.001$, Supplementary material, Fig. A1). Only for genetic data did data availability reported by authors poorly match the information extracted from papers ($\tau = 0.258$, $p = 0.131$). Therefore, the information we extracted from the published studies is a reliable measure of the actual data availability at the time of development of PVA models, and subsequent analyses are based on the information directly extracted from the published studies.

For the dataset consisting of paired PVA studies the conditional Random Forest model successfully distinguished between the two model types (IBM vs PBM), and 76% of the 74 PVA models analyzed were classified accurately in cross-validation. Three data availability factors (space representation, demography, and dispersal) had the highest impact on the choice of the model type (Fig. 2). Having lower resolution of demographic, spatial and dispersal data resulted in an increased probability that the model type used was a PBM (Fig. 2). The conclusions were qualitatively similar when analyses were conducted using all available PVA studies for each species rather than just the pair (i.e. the first published PBM and IBM): the lower resolution of primarily dispersal and spatial data, and less so of demographic data, increased the probability that the model type used was a PBM (Supplementary material, Fig. A2).

Model purpose was the least important variable and had no explanatory power to distinguish model types (Fig. 2; this conclusion also holds for the complete dataset with all PVA papers included, Fig. A2). Aggregating the eight model aims into five or three did not alter the results: specific model purpose remained the least important variable in our sensitivity analysis (Supplementary material, Figs. A3 and A4). Each model type in the paired dataset was similarly often used for each particular model purpose (Fisher's exact test, $p = 0.981$; Fig. 3). This was also generally the case for the complete dataset with all PVA studies per species included (Fisher's exact test, $p = 0.676$, Supplementary material, Fig. A5), except that there was a tendency to more often use IBMs than PBMs for "Management of declining populations".

According to our questionnaire, the majority of respondents (63%) stated that their model choice was not affected by their modelling skills and they used the best modelling technique appropriate for the purpose. 21% of modellers admitted a moderate influence of their modelling skills on the model type choice (8% PBM-users and 13% IBM-users), 16% a large influence (13% PBM-users and 3% IBM-users).

4. Discussion

Our findings suggest that the availability and resolution of demographic, spatial and dispersal data primarily affect the choice of model complexity, while the specific model purpose appears to be unimportant when authors decide whether to develop a population- or individual-based model. Our paired design, by careful matching of each PBM with an IBM model developed for the same species, appropriately controlled for one key determinant of model complexity, namely the life history of a species (Vucetich and Creel, 1999; Wiegand et al., 1998).

To our knowledge, such an effect of data availability and resolution on the choice of the model type has not been demonstrated empirically before. The practical implications of our findings are important for PVA modelling practice: we identified three main data-limiting factors that define the resulting model type to be developed. Indeed, the chance of developing a complex model (such as IBM) is very low when fine-resolution data on demography, space representation or dispersal are absent. For demography, "fine resolution" implies availability of data on within-stage or individual variation in vital rates; for space representation, it means data are resolved to the level of a single territory or a population; and for dispersal, it means availability of data on mechanistic rules driving the movement of individuals. Thus, authors tend to avoid constructing IBMs whenever the data on one of the above-mentioned components were missing.

We did not find a correlation between the actual genetic data availability and the genetic data used in the resulting PVA model. This finding is not surprising in light of previous PVA practice, where explicit incorporation of genetic information was long considered to be unimportant for the assessment of population viability (Lande, 1988b). In our case, the lack of a correlation was because genetic data available at the time of model development were not used in the resulting models. This phenomenon is likely because of the previously widespread notion that genetics do not have much impact on population viability (Frankham, 2010; Reed, 2010), and no modelling approaches existed that allowed incorporation of genetics in an explicit way. However, the situation has recently changed, with more PVAs explicitly incorporating genetic aspects in models (e.g. Frank and Baret, 2013; Piou and Prévost, 2012; Schiffers et al., 2014).

According to our results, the specific model purpose did not have any effect on the choice of model type. This result is mainly because in our sample both model types were equally likely to be used for each of the distinguished model purposes (Fig. 3), so that the choice of a model type is largely context-dependent and not a simple consequence of a certain model purpose. In addition, the true model purpose may be masked by the scientific publishing process, which can force studies with a straightforward purpose to use an excessively sophisticated modelling approach (e.g. Oppel et al., 2014) to meet the novelty criteria of international journals (Arnqvist, 2013). This lack of impact of model purpose on model type is unlikely to

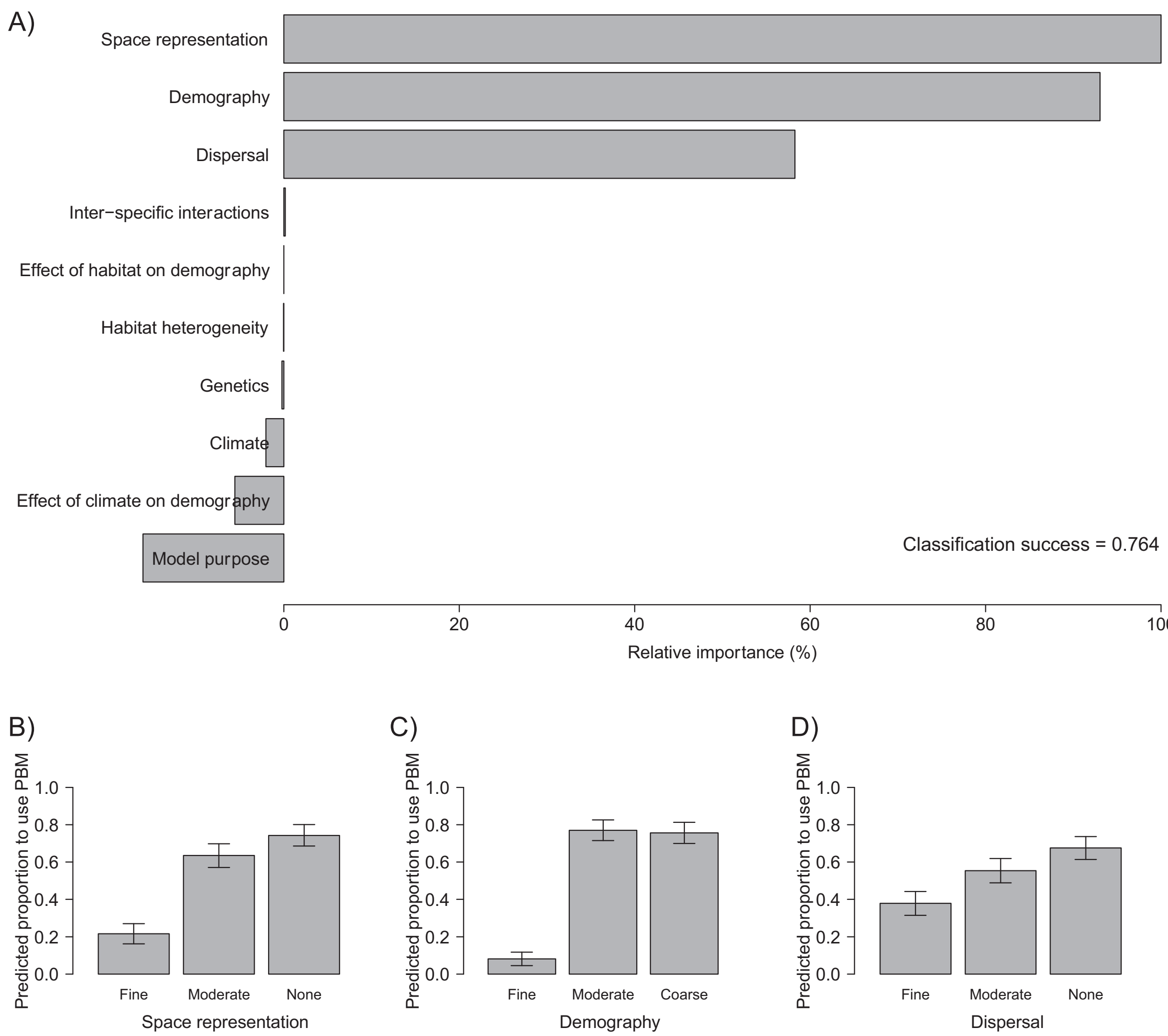

Fig. 2. (A) Relative variable importance of specific model purpose (using eight-level categorization) and nine data availability factors for the choice of model type (IBM vs PBM) assessed with a permutation procedure based on a Random Forest model. Negative variable importance indicates that the variable is not influential in predicting the choice of the model type; negative importance occurs when random permutation of the variable leads to an increase in the predictive accuracy of the model. (B–D) Predicted proportion (mean ± standard error) of studies using PBM as a model type based on the levels in the three most important data availability factors: space representation (B); demography (C) and dispersal (D). Variable levels are as described in Table 1.

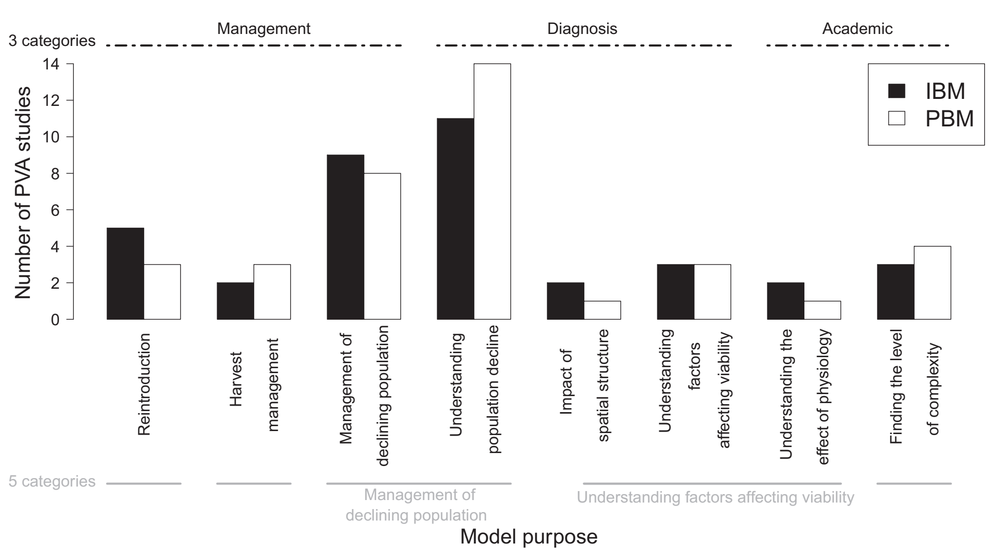

Fig. 3. Number of each model type (IBM – individual-based and PBM – population-based model) used for population viability analysis in 74 studies classified into eight specific model purposes. Light grey lines below the plot and black dot-dashed lines above the plot show groupings of model purpose into five-level and three-level model purpose categorizations, respectively (see Table 3).

be an artefact of categorization: two alternative categorizations of the model purpose with a higher number of models in each category confirmed that model purpose was irrelevant for the choice of model type (Figs. A3 and A4). Similarly, no effect of model purpose on model type was found when the complete dataset with all PVA studies available per species was used (Supplementary material, Fig. A2), despite some imbalance in the model purpose category "Management of declining populations", for which mostly IBMs were developed. However, the majority of these IBMs were developed for management of *Strix occidentalis caurina* (five models), *Gymnobelideus leadbeateri* (three models) and *Ursus arctos* (three models) and may therefore reflect the higher research interest of certain researchers or agencies and a need dictated by the biological specifics of these species, rather than a broader pattern of model choice based on model purpose in general.

In addition to data availability, other factors that were not the focus of our study may affect the choice of model type. For example, the familiarity of a model developer with a certain modelling technique may bias his/her preferences to apply that particular model type to a problem (Thiele and Grimm, 2015), and the rapid progress in model development may lead to more recent publications using more complex models simply because they are more readily available (LaDeau, 2010). Although the majority of respondents (63%) in our questionnaire stated that their model choice was not affected by their modelling skills, we explored whether our conclusions would have been overturned if we had included a measure of modeller's experience and general progress in our analysis. Because "experience" is a difficult quantity to measure, we used the type of software used for the model development ("ready-to-use software", i.e. packaged software such as RAMAS, ALEX, PATCH, VORTEX, vs "self-made software") as a proxy for modeller's "experience". Re-running our analysis using all available PVA studies with the additional variables for "software" and "publication year", we found that data availability for dispersal and space representation were still the most important variables affecting model choice, followed by "software" and data availability for demographic factors (Supporting material Fig. A6). The small effect of software indicated that PBMs were more likely to be developed with ready-to-use, user-friendly, packaged software, but whether this effect is due to modeller's experience or the fact that most packaged software are designed to fit PBMs is unclear and will require additional analyses with a more expansive dataset. Contrary to our expectation, there was no effect of publication year on model type, indicating that our main analysis using only the first published study of a particular model type did not induce any bias in the conclusions and that our pair-based design was suitable for the question we addressed. Future studies aiming to explore a broader range of factors affecting model choice could benefit from a different dataset that covers a wider variety of species and model type complexities. One example of such a dataset may be a database assembled by Pe'er et al. (2013), which could be used to quantify how model type is affected by the life history, a factor we controlled for in the current study.

PVA models are often constructed in the situation of data scarcity, meaning that the data to estimate all the parameters do not always exist. In such situations, missing parameter values are commonly based on expert judgement or on surrogates from phylogenetically (or ecologically) related species (e.g. Finkelstein et al., 2010; Hernandez-Camacho et al., 2015; Schtickzelle et al., 2005). Several techniques exist to assess the effect of data on the model output, such as sensitivity and uncertainty analysis (Saltelli and Annoni, 2010; Saltelli et al., 2000). Such methods allow estimation of how sensitive the model is to (1) changes in each parameter in turn when the other parameters are kept fixed (local sensitivity analysis); or (2) interactions between parameters and their non-linear behaviour (global sensitivity analysis). While being useful, such techniques and approaches do not replace the data per se, and data collection shall always be encouraged to facilitate the parameter estimation. However, careful consideration what data would provide the most value of information and how they would need to be collected is important to allocate survey resources appropriately (Canessa et al., 2015).

Conservation biology is a crisis discipline, where data are very often scarce, forcing researchers to make the best of a bad job (Soulé, 1985). Our results show that for three main model components (demography, space representation and dispersal), data limitation will impact the choice of the modelling approach, forcing researchers to use simpler PBM models, where the system description is coarser. For threatened and poorly-known species, there is, unfortunately, no shortcut in developing either model type (PBM or IBM) without appropriate data. The structure of the PVA model, however, will affect the possible use of the model: what the model can predict (and at which resolution) and which scenarios it will allow to test (Radchuk et al., 2014; Stephens et al., 2002). Future investigations, possibly with simulated data, are needed to further assess the sensitivity of the predictions and guidelines extracted from PVA models to data availability.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.11.022.

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