METHODS

Identifying the demographic processes relevant for species conservation in human-impacted areas: does the model matter?

Edgar J. González · Mark Rees · Carlos Martorell

Abstract The identification of the demographic processes responsible for the decline in population growth rate (λ) in disturbed areas would allow conservation efforts to be efficiently directed. Integral projection models (IPMs) are used for this purpose, but it is unclear whether the conclusions drawn from their analysis are sensitive to how functional structures (the functions that describe how survival, growth and fecundity vary with individual size) are selected. We constructed 12 IPMs that differed in their functional structure by combining two reproduction models and three functional expressions (generalized linear, cubic and additive models), each with and without simplification. Models were parameterized with data from two populations of two endangered cacti subject to different disturbance intensities. For each model, we identified the demographic processes that most affected λ in the presence of disturbance. Simulations were performed on artificial data and analyzed as above to assess the generality of the results. In both empirical and simulated data, the same processes were identified as making the largest contribution to changes in λ regardless of the functional structure. The major differences in the results were due to misspecification of the fecundity functions, whilst functional expression and model simplification had lesser effects. Therefore, as long as the demographic attributes of the species are well known and incorporated into the model, IPMs will robustly identify the processes that most affect the growth of populations subject to disturbance, making them a reliable tool for developing conservation strategies.

Keywords Human disturbance · Integral projection models · LTRE · Model selection · Population dynamics

E. J. González · C. Martorell (✉)
Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Circuito Exterior s/n, Ciudad Universitaria, 04510 Mexico, D.F., Mexico
e-mail: martorell@ciencias.unam.mx

E. J. González
e-mail: edgarjgonzalez@ciencias.unam.mx

M. Rees
Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
e-mail: m.rees@sheffield.ac.uk

Introduction

In the increasingly anthropic environment of our planet, understanding how human activities affect species is critical in terms of conservation and sustainable management (Soulé and Kohm 1989; Vitousek et al. 1997; Redford and Richter 1999; Chapin et al. 2000; Goudie 2006). The accomplishment of this goal depends on understanding how humans influence population dynamics and the mechanisms by which this occurs, say through changes in different demographic processes (i.e., survival, growth and reproduction). Identifying which of these modified demographic processes is responsible for the greatest changes in population dynamics would help to direct conservation efforts efficiently, by targeting key human influences (Caswell 2000; Heywood and Iriondo 2003).

Demographic studies provide information on the performance of individuals, and this is usually translated into predicted changes in population characteristics using

mathematical models. Among these, matrix projection models (MPMs; Caswell 2001) and, recently, integral projection models (IPMs; Easterling et al. 2000; Ellner and Rees 2006; Rees and Ellner 2009) have been applied to a wide range of plant species because they allow individual size and other relevant attributes, such as age, to be included as factors that influence an individual's fate (Rees and Rose 2002; Childs et al. 2003; Dahlgren and Ehrlén 2009; Metcalf et al. 2009; Hegland et al. 2010; Zuidema et al. 2010; Dahlgren and Ehrlén 2011; Dahlgren et al. 2011; Jongejans et al. 2011).

Compared with MPMs, IPMs have several advantages when dealing with plant populations. First, the demographic behavior of individual plants usually depends on their size, which is typically a continuous measure, whereas MPMs assume discrete life-cycle stages, and so an artificial partitioning of size into categories is required. Such arbitrary divisions may lead to different results and difficulties in interpretation (Enright et al. 1995; Easterling et al. 2000; Caswell 2001). In contrast, IPMs avoid this problem by incorporating size as a continuous variable. Second, because IPMs are parameterized using regression models, the incorporation of additional individual attributes influencing fate is straightforward; for example, Childs et al. (2003) built an age and size structured IPM with the estimation of only a single extra parameter—describing the effect of age on the probability of flowering. Furthermore, IPMs perform better than MPMs when only small datasets are available, as is the case for species threatened by human impacts that usually have small population sizes (Ramula et al. 2009). Finally, by separately modeling the demographic processes before incorporating them into a population dynamics model, IPMs perform better than MPMs whose matrix elements are usually independently estimated, potentially leading to overparameterization (Gross et al. 2006).

One potential drawback of IPMs is that the functional structure that describes the different demographic processes must be selected from a universe of alternatives. Functional structure comprises both the selection of which demographic attributes need to be included in the model through individual functions, and the mathematical expression of those functions. In contrast, MPMs do not require any assumption on functional structure or probability distributions. Function selection may affect parameters critical for conservation, such as the population growth rate (λ; Dahlgren et al. 2011). This may compromise our understanding of how a species responds to anthropogenic change. We therefore need to know if IPMs can reliably identify (1) whether anthropogenic disturbance has positive or negative effects on λ, and (2) which demographic processes have the largest impacts on population growth, even if we are unsure about the most appropriate functions to

use. Function selection becomes more difficult when dealing with small sample sizes, as in these cases it may be hard to differentiate between competing functions.

Here, we explore a variety of IPMs and assess whether, regardless of the functional structure of the model, we can reliably identify the human-induced changes in λ and the demographic processes that make the largest contributions to these changes. We use data from two endangered endemic cacti species subject to chronic anthropogenic disturbance (CAD), but differing in their response to it (Ureta and Martorell 2009). CAD results from a long-term series of frequent, low-intensity, human disturbance events (Singh 1998), such as extensive grazing, and branch collection for use as firewood (Carpenter et al. 1998; Singh 1998; Shahabuddin and Kumar 2006; Martorell and Peters 2005, 2009). CAD has a not immediately noticeable effect and thus is usually not acknowledged until populations have changed in an irreversible way (Singh 1998). To assess the generality of the robustness of IPMs to changes in their functional structure, we performed simulations using artificial data from virtual populations that showed a wide range of behaviors.

Materials and methods

Study system

The study was made in Concepción Buenavista, Oaxaca, Mexico. This region has seen human presence since pre-Columbian times and has suffered from CAD in the form of soil erosion, due to unsustainable agriculture and livestock rearing techniques, and firewood and other non-timber product extraction from the, now sparsely distributed, *Quercus* forests (McAuliffe et al. 2001; Pérez-Negrón and Casas 2007).

Two threatened cactus species were studied. *Mammillaria dixanthocentron* Backeb. is a long-lived globose cactus that grows in *Quercus* forests of the Mexican states of Puebla and Oaxaca. Flowering occurs year round, reaching its peak in February (Arias-Montes et al. 1997). *Mammillaria hernandezii* Glass et Foster is a long-lived globose cactus that lives in *Bouteloua* short-grass prairies within a very restricted distribution area (17.1 km^2). This species buries its stem into the ground and only part of its top protrudes from the soil. Flowering occurs from October through December (Arias-Montes et al. 1997).

For each species, data were collected from two sites differing in their CAD intensity. Three 50×4 m transects at each *M. dixanthocentron* site and two 50×1 m transects at each *M. hernandezii* site were randomly laid and the individuals within them were followed from 2001 to 2006. No less than 100 individuals were studied at each

site. As a proxy for size, a cylinder was calculated based on the diameter (mm) and height (mm) of the *M. dixanthocentron* individuals. For *M. hernandezii* individuals, only the diameter was measured. These data were collected between July and August, when plant stems are turgescent. Flower production was recorded in July and February for *M. dixanthocentron* and in October for *M. hernandezii*.

Integral projection model

Easterling et al. ([2000](#)) developed the IPM, an iterative model that describes the change of a population size structure in discrete time (e.g., yearly time steps). This change is determined by the kernel, a function describing the different ways in which individuals can move from one size to another. Mathematically, an IPM is described by the equation:

$$n_{t+1}(y) = \int_X k(y,x)n_t(x)\,\mathrm{d}x, \tag{1}$$

where x is size at year t, y is size at year $t+1$, and X is the range of possible sizes. n is the distribution of individuals across sizes and k the kernel, which is usually decomposed into three functions describing survival, $s(x)$, growth, $g(y, x)$ and fecundity $f(y, x)$:

$$k(y,x) = s(x)g(y,x) + f(y,x). \tag{2}$$

Building IPMs with different functional structures

In order to assess the effect of the functional structure of an IPM on population properties, such as growth rate and size structure, we combined two reproduction models with three approaches to selecting the functional expressions (i.e., the precise mathematical relation between the variables in a given function) used for constructing the kernel.

Reproduction models

The fecundity function $f(y, x)$ in Eq. [2](#) can be further decomposed into different functions describing the number of flowers produced by a plant with size x larger that a minimum value, $n_{fX}(x)$, the probability of flowering, $p_f(x)$, the number of flowers produced by a plant given that it reproduces, $n_{fR}(x)$, a factor that converts flowers to seedlings, c, and the probability density a seedling has of reaching size y at time $t+1$, $f_s(y)$. In our case, we explored two different reproduction models:

$$f(y,x) = n_{fX}(x)cf_s(y), \tag{3}$$

$$f(y,x) = p_f(x)n_{fR}(x)cf_s(y). \tag{4}$$

In Eq. [3](#), we model flower production as a function restricted to individuals larger than a minimum size, while in Eq. [4](#), we model reproduction as a two-stage process, separating the probability of reproduction from the flower production of those individuals that do reproduce. We refer to the first as the restricted reproduction model and the latter as the conditional reproduction model.

Functional expressions

In order to parameterize the model, we need to determine the specific functional expressions that define the model (i.e., the equations for $n_{fX}(x)$, $p_f(x)$, etc.). Three different functional expressions were used: (1) generalized additive models (GAMs), (2) first order generalized linear models (GLM1s), and (3) third order (cubic) generalized linear models (GLM3s). GAMs allow a very flexible function (thin plate regression spline) to be fitted to the data, guaranteeing a good fit (Dahlgren et al. [2011](#)) and not requiring the modeler to define an a priori function (Wood [2003](#)). The *mgcv* package in R (Wood [2006](#); R Development Core Team [2010](#)) was used to fit the GAMs, as this allows the degree of model complexity to be automatically selected during the fitting process. GLM1s have a simple linear predictor ($\mu = \beta_0 + \beta_1 x$); this structure has little flexibility and thus may sometimes provide poor descriptions of the data. GLM3s have a polynomial predictor ($\mu = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 x^3$), allowing for more complex patterns of dependence of fate on size. In each case, we performed model simplification using analysis of deviance, retaining only the significant terms (Online Resource 1).

Thus, we obtained different IPMs from the two reproduction models (restricted and conditional) combined with the three functional expressions (GAM, GLM1, and GLM3), before and after model simplification, giving a total of 12 IPMs with different functional structures per species per site.

For these models, we obtained λ and compared the observed and stable size distributions by means of the Bhattacharyya coefficient, ρ, which is a goodness-of-fit measure related to the Pearson's χ^2 and bounded between zero and one (where one is a perfect fit; Bhattacharyya [1946](#)).

For each of the 12 IPMs, we assessed the contribution of each demographic process to the differences in λ between sites. To do so, we obtained λ for the models of the less and more disturbed sites. These values were then compared to those obtained from a new set of IPMs, each having only one demographic process perturbed by CAD. These IPMs were obtained by taking the IPM of the less disturbed site and setting the parameters associated to the process in question to the values of the more disturbed site. In the case of reproduction, which was modeled by more than one

function (Eqs. 3, 4), we repeated the above procedure changing the parameters of one function at a time.

Generality assessment through simulated data

To assess whether IPMs are robust in general to changes in their functional structure, and not only robust for our particular datasets, we performed a simulation process. This process started with the generation of the kernel of an artificial population in an undisturbed site by assigning random values to its parameters. A random change (<30 % of the original value) was then introduced to these parameters to simulate the kernel of a second population whose dynamics had been modified by disturbance. The functions integrating this pair of kernels were randomly distorted to make them non-linear with respect to size because, if the actual demographic processes were linear, the same linear model would be obtained with all three statistical procedures (GAM, GLM1, and GLM3), resulting in an artificial consensus among models not due to the robustness of the IPMs (see details in Online Resource 2). The pair of kernels generated by this procedure represents the population dynamics of a virtual species studied in an undisturbed and a disturbed site. As we were interested in studying the effects of using different models to describe reproduction, two types of pairs of kernels were generated: type-1 used Eq. 3 and type-2 used Eq. 4.

We generated random samples of 1,000 individuals from each population, and obtained their survival, growth, and reproduction through Monte Carlo simulation using the respective distorted functions. The samples were used as input data for the fitting of the 12 models described in the previous section. We fitted Eqs. 3 and 4 (type-1 and type-2 analyses, respectively) to the samples regardless of the kernel type from which they had been generated. This allowed us to evaluate the effect of using an incorrect reproduction model. The fitted functions for survival, growth and reproduction were assembled into kernels differing in the functional expression used to fit the data.

The contribution of the demographic processes to the differences in λ between sites was assessed for each pair of kernels as described for the empirical data in the previous section. These contributions were then compared with those associated to the initial kernels from which the samples were obtained. Such comparison was made by means of the Pearson's correlation coefficient (r). The procedure was repeated 14,000 times and the distribution of r values was obtained. The simulation was coded in R and its details are described in the Online Resource 2.

Results

In most of the IPMs, CAD had a negative effect on all the demographic processes, with the exception of individual growth in *M. dixanthocentron* and survival in *M. hernandezii* (Fig. 1). The different functional expressions for modeling the demographic processes produced curves that in some cases were very different, though similar within the size range where most individuals were found (Online Resource 3).

Despite these differences, changing the functional structure had little effect on the λ values (Fig. 2, arrowed bars). Thus, the magnitude of the change between sites was relatively constant among models. Also, the observed and predicted stable size structures were similar with high Bhattacharyya coefficients: 0.96 ± 0.01 (mean $\pm$ SD) for *M. dixanthocentron* and 0.98 ± 0.01 for *M. hernandezii*.

In all the models for the more disturbed site, a reduction in λ was projected for *M. dixanthocentron*, while *M. hernandezii* showed the opposite pattern. In general, the same processes were identified as having the largest effect on the population growth regardless of the functional structure. In both species, survival was identified as the process that had the largest effect on λ, only matched by growth in the GLM1 models for *M. hernandezii*. In this species, the second most relevant process was growth, while in *M. dixanthocentron*, no other process made a substantial contribution to λ (Fig. 2).

Most of the r values obtained from the simulation procedure were close to 1, with their distribution sharply decreasing below 0.9 (Fig. 3a). When the known and fitted fecundity models matched, higher r values were obtained (69.70 % of the r values were ≥ 0.80 when a type-1 analysis was used to fit a sample from a type-1 kernel, and 63.79 % for a type-2 analysis of a type-2 kernel sample) compared to those cases when a mismatch occurred (64.05 % when a type-1 analysis was used to fit a sample coming from a type-2 kernel, and 43.19 % for a type-2 analysis fitted to a type-1 kernel sample; Fig. 3b). In comparison, the different functional expressions and model simplification had only a minor impact on the results (Fig. 3c, d). Nevertheless, fitting generalized additive models resulted in a higher frequency of r values close to 1, followed by GLM1 and GLM3 expressions.

Despite the high frequency of near-to-one correlations, the tail of negative values accounted for 8.37 % of the distribution (Fig. 3a). Negative r values may occur when disturbance has no effect on the population dynamics, because in such cases the contributions of the different demographic processes to the change in λ are fully determined by sampling error. To evaluate this for each known model, we measured the effect of disturbance on

Fig. 1 Changes (Δ) in demographic processes due to chronic anthropogenic disturbance (CAD) on two cactus species, *Mammillaria dixanthocentron* (*left*) and *M. hernandezii* (*right*), estimated from different models: generalized additive (*GAM*), linear (*GLM1*), and cubic (*GLM3*) models, before (+) and after (−) model simplification. The change in number of flowers was estimated using in **e, f** all individuals larger than a minimum reproductive size, and in **i, j** only those that reproduced in any given year. The axis of zero CAD effect is shown in *gray*. Only models in which there was a significant effect of CAD are shown. *Box plots* show the distribution of the plant size data
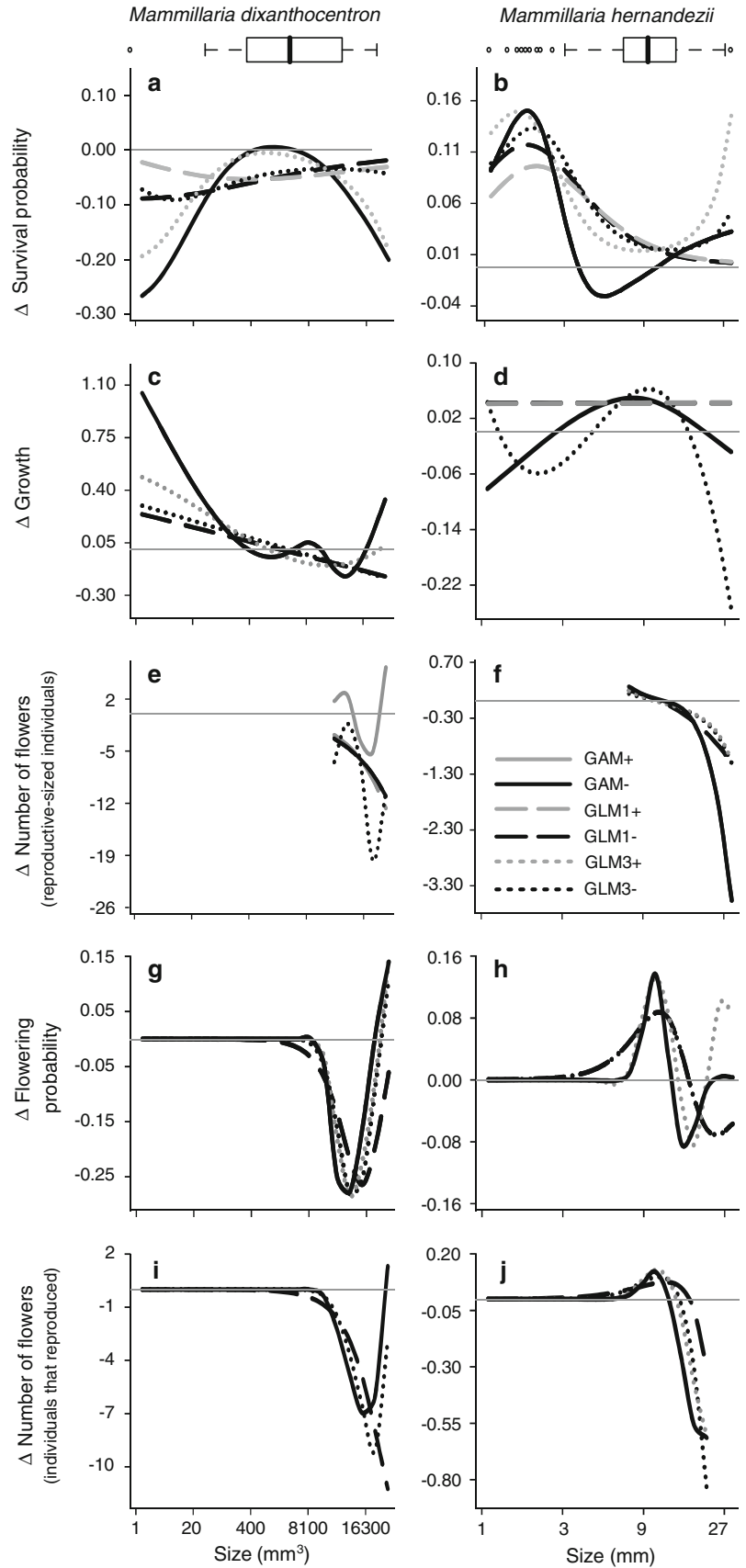
Fig. 2 Population growth rates (λ) of two cactus species obtained from integral projection models differing in functional structure. The flowering process was described through either **a**, **c** a simple functional description, or **b**, **d** a more complex one. Demographic processes were modeled using generalized additive (*GAM*), linear (*GLM1*), and cubic (*GLM3*) models before (+) and after (−) model simplification. The origin of the *shaded arrows* corresponds to the λ observed at a site with low CAD intensity and the tip to the λ at a more disturbed site. The λ value of the population when CAD affects only one demographic process is shown by its respective symbol
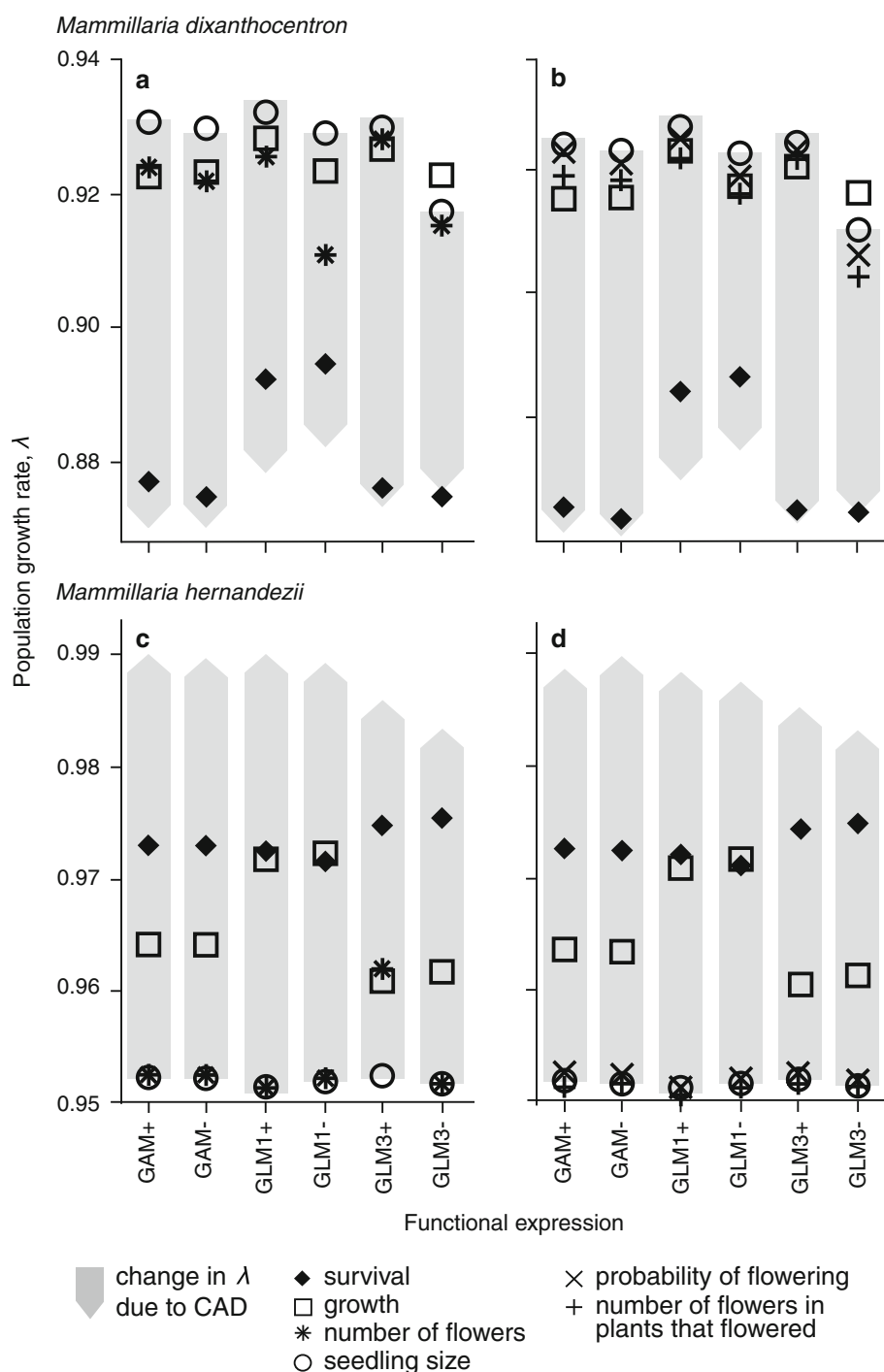
the dynamics as the geometric mean of the integrals of the squared differences between each pair (undisturbed/disturbed) of demographic-process functions. This measure was compared with the median of the 24 *r* values related to a particular pair of kernels. As expected, only when disturbance had no effect, the median had negative values, and tended towards one as the effect increased (Fig. 4).

Discussion

Irrespectively of their functional structure, IPMs managed to identify whether a species benefits from or is hindered by CAD and which processes made the largest contributions to this effect. In general, models with flexible structures (i.e. conditional fecundity, GAMs) more accurately reconstructed the population dynamics and its changes with

Fig. 3 Frequency of the correlation coefficients between known and estimated contributions of different demographic processes to the differences in population growth rate due to disturbance in simulations employing artificial data. The known contributions were derived from models whose reproduction was described by either a simple or a more complex function. The estimated contributions were calculated from models whose demographic-process functions were fitted to samples derived from the known models. Reproduction was analyzed by fitting either the simple of the more complex functions to samples produced by each type of model. **a** Effect of different reproduction functions, **b** same as (**a**) but restricted to the range 0.9–1.0, **c** effect of different functional expressions, and **d** effect of model simplification
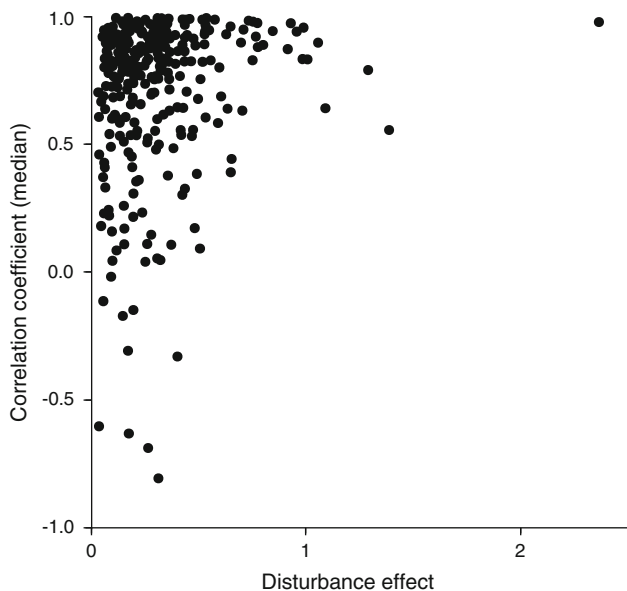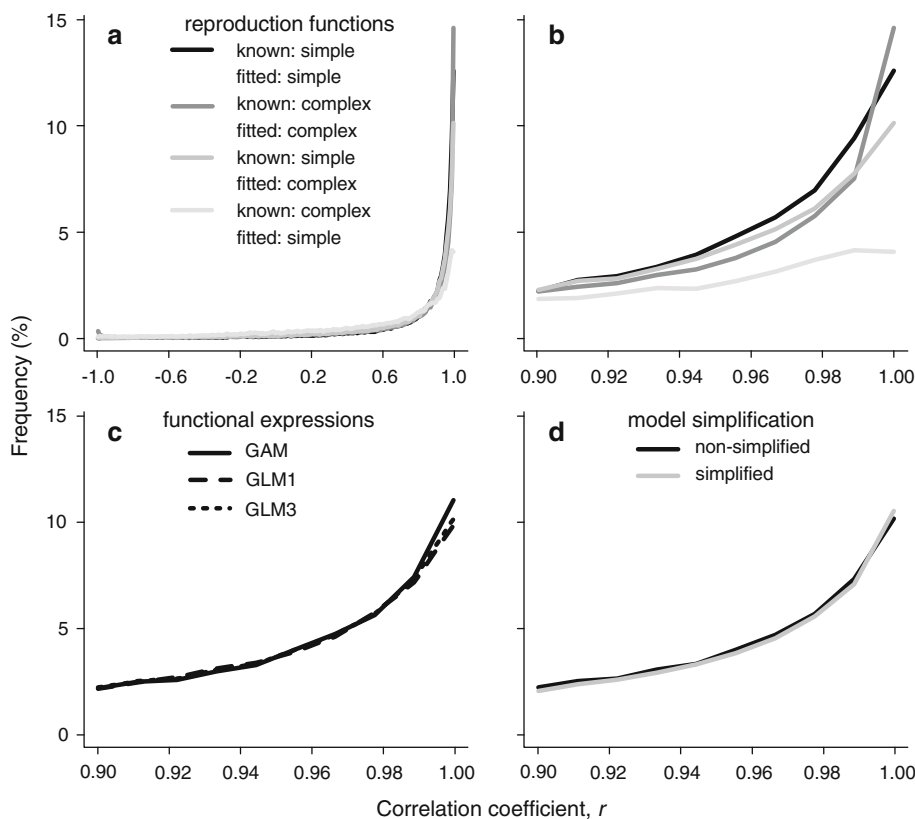

Fig. 4 Influence of the magnitude of disturbance-induced changes in population dynamics on the capability of models to estimate accurately the contributions of different demographic processes to population growth rate. The magnitude of the disturbance effect was calculated as the geometric mean of the differences between the functions describing the demographic processes at undisturbed and disturbed sites. The accuracy in the estimation was measured as the correlation between the known and estimated contributions. As each population dynamics has 24 associated models, the median of the coefficients is shown

disturbance. Nevertheless, the selection of a model that correctly depicts the underlying biological processes is likely to produce more reliable results.

Are IPMs robust to changes in functional structure?

Both in real and simulated data, there was large agreement between models on the processes making the largest contributions to λ despite the differences in functional structure. In both *Mammillaria* species, the demographic process that was identified as making the largest contribution to the differences in λ was survival. This is in line with other studies that have found that survival has the largest impact on population status in cacti and other long-lived perennials (Silvertown et al. 1993; Godínez-Álvarez et al. 2003; Franco and Silvertown 2004; Jiménez-Sierra et al. 2007; Ureta and Martorell 2009). IPM robustness is encouraging, as the management conclusions drawn from the models are in general independent of the relatively arbitrary functional structure chosen by the researcher. The fact that IPMs are also robust when faced with small datasets (Ramula et al. 2009) makes them an appropriate choice when designing management strategies of endangered species.

Nevertheless, the relatively high incidence of low or even negative correlations suggests that utterly wrong results can be obtained. Such results seem to be alarming when the conservation of an endangered species is at stake.

However, negative correlations occurred only when population dynamics were unaffected by disturbance. In such cases, it would be unnecessary to mitigate the effects of anthropic activities. Furthermore, it would be expected that the researcher's judgment during model fitting would result in higher r values compared with the automatic procedure performed here by the computer. A concerned conservation biologist would discard irrelevant factors, detect outliers, and screen models more efficiently. Thus, despite the relative robustness of IPMs, careful selection of the functional structure of a model is needed.

IPMs may be especially robust when long-lived perennials, such as cacti, are studied. In those species, changes in reproduction do not have large effects on λ (Silvertown et al. 1993; Godínez-Álvarez et al. 2003; Franco and Silvertown 2004). This would make sensitivity, which is proportional to the reproductive values and the stable size distribution (Easterling et al. 2000), largely dependent on the latter. As can be observed in Fig. 1, the functions obtained from different expressions were similar within the size range where most of the individuals were located, but different elsewhere. This is not an unlikely result, as it is statistically difficult to discern between curves that differ where data are scarce as they have similar likelihoods. In a population close to its stable size distribution, the range where functional expressions disagree would have a low sensitivity, and such disagreements would have minor effects on λ. Seemingly, this was the case in our species, where the populations were near their stable distribution (as shown by the Bhattacharyya coefficient) and there were small differences in λ between models with different functional structure.

Lessons on model selection

Perhaps the most critical issue when selecting the functional structure of an IPM is selecting the demographic attributes to be modeled. While the functional expression was relatively irrelevant, using the incorrect functions to model fecundity significantly reduced the frequency of high correlations. Nevertheless, using a type-2 analysis on a sample from a type-1 kernel produced better results than the opposite combination. This is probably the result of the flexibility of the function used to model the probability of flowering, $p_f(x)$ in Eq. 3. At its limit, $p_f(x)$ becomes a step that mirrors the reproductive threshold characteristic of type-1 kernels.

As found by Dahlgren et al. (2011), GAMs had an overall better performance than GLM1 and GLM3 functional expressions. This may be especially important in the statistical modeling of a highly relevant process. As an example, in *M. dixanthocentron*, the GLM1 model predicted smaller reductions in λ compared to GAM and GLM3 models. These are closely correlated with the contribution that survival makes on λ (Fig. 2a, b). Additionally, the survival curves obtained with GLM1 differ from the ones obtained through GAM and GLM3 (Fig. 1), a pattern also found by Dahlgren et al. (2011). This suggests that the differences observed in λ are due to the statistical modeling of survival. Also, in *M. hernandezii*, the GLM1 models seemingly failed to gauge the contribution of growth compared to GLM3s and GAMs, although this was not reflected in the change in λ between sites.

Model simplification had a lesser effect on our results. In the simulations, this may be the result of the large samples used for the statistical analyses. In smaller samples, we would expect high order terms in GLM3 models to be dropped (Burnham and Anderson 2002), and wriggly splines in GAMs to be highly penalized (Wood 2003). In both cases, the result would be identical to that obtained from GLM1s. From our simulations, it becomes clear that this would not have a large effect on the accuracy of the model. It would appear then that simplification is the less important element to be considered in the construction of an IPM. However, from a conservation biology perspective, simplification has been disputed. According with the precautionary principle (Haller 2000; Hanson 2003), to discard the effect of CAD when it does exist (type-II error) is more costly than keeping it in the model (Gray 1990; Buhl-Mortensen 1996; Kriebel et al. 2001; McGarvey 2007).

Concluding remarks

The method used here is retrospective in the sense that it decomposes the differences in population growth into contributions made by the different demographic processes (Caswell 2000, 2001; de Kroon et al. 2000). Supporting our results, using life table response experiment analysis (LTRE), Ureta and Martorell (2009) also found that survival was the process that caused the largest changes in λ in disturbed sites in these species. Retrospective methods, such as LTRE, have been used in the context of conservation as a tool to understand how the vital rates have been affected by perturbation events (Ehrlén and van Groenendael 1998; Caswell 2000; Martorell 2007; Ureta and Martorell 2009).

Assessing the reliability of the results provided by this method will be possible by simultaneously fitting different functions to the process that made the largest contributions and checking whether this has an effect on the outcome of the model. When it is difficult to discriminate among different functional structures, the best results may be obtained with the use of more flexible alternatives (conditional reproduction, GAMs, etc.). Finally, assessing whether the population is in its stable size distribution may

be a way to evaluate potential robustness, because more reliable results will be obtained when a population is in this state.

We can conclude that the processes making the largest contributions to the change in λ due to anthropic activities will frequently be identified by IPMs under a variety of biologically reasonably justified functional expressions. In constructing an IPM, getting the species biology right when deciding which demographic attributes need to be modeled will have more impact on the contributions under study than the specific functions used.

References

Arias-Montes S, Guzmán U, Gama S (1997) Cactaceae. Flora del Valle de Tehuacán-Cuicatlán, México, Fascículo 14. Instituto de Biología. Universidad Nacional Autónoma de México, México

Bhattacharyya A (1946) On a measure of divergence between two multinomial populations. Sankhya Indian J Stat 7:401–406

Buhl-Mortensen L (1996) Type-II statistical errors in environmental science and the precautionary principle. Mar Pollut Bull 32:528–531

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Carpenter SR, Caraco NF, Correll DL, Howarth RW, Sharpley AN, Smith VH (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol Appl 8:559–568

Caswell H (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619–627

Caswell H (2001) Matrix population models: construction, analysis, and interpretation. Sinauer, Sunderland

Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Díaz S (2000) Consequences of changing biodiversity. Nature 405:234–242. doi:10.1038/35012241

Childs DZ, Rees M, Rose KE, Grubb PJ, Ellner SP (2003) Evolution of complex flowering strategies: an age- and size-structured integral projection model. Proc R Soc Lond B 270:1829–1838. doi:10.1098/rsb.2003.2399

Dahlgren JP, Ehrlén J (2009) Linking environmental variation to population dynamics of a forest herb. J Ecol 97:666–674. doi:10.1111/j.1365-2745.2009.01504.x

Dahlgren JP, Ehrlén J (2011) Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. Oikos 120:1183–1190. doi:10.1111/j.1600-0706.2010.19063.x

Dahlgren JP, García MB, Ehrlén J (2011) Nonlinear relationships between vital rates and state variables in demographic models. Ecology 92:1181–1187. doi:10.1890/10-1184.1

De Kroon H, van Groenendael J, Ehrlén J (2000) Elasticities: a review of methods and model limitations. Ecology 81:607–618. doi:10.1890/0012-9658(2000)081[0607:EAROMA]2.0.CO;2

Easterling MR, Ellner SP, Dixon PM (2000) Size-specific sensitivity: applying a new structured population model. Ecology 81:694–708. doi:10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2

Ehrlén J, Van Groenendael J (1998) Direct perturbation analysis for better conservation. Conserv Biol 12:470–474. doi:10.1111/j.1523-1739.1998.96420.x

Ellner SP, Rees M (2006) Integral projection models for species with complex demography. Am Nat 167:410–428. doi:10.1086/499438

Enright NJ, Franco M, Silvertown J (1995) Comparing plant life-histories using elasticity analysis: the importance of life-span and the number of life-cycle stages. Oecologia 104:79–84. doi:10.1007/BF00365565

Franco M, Silvertown J (2004) A comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538. doi:10.1890/02-0651

Godínez-Álvarez H, Valverde T, Ortega-Baes P (2003) Demographic trends in the Cactaceae. Bot Rev 69:173–203. doi:10.1663/0006-8101(2003)069[0173:DTITC]2.0.CO;2

Goudie A (2006) The human impact on the natural environment: past, present, and future. Blackwell, Malden

Gray JS (1990) Statistics and the precautionary principle. Mar Pollut Bull 21:174–176

Gross K, Morris WF, Wolosin MS, Doak DF (2006) Modeling vital rates improves estimation of population projection matrices. Popul Ecol 48:79–89. doi:10.1007/s10144-005-0238-8

Haller S (2000) A prudential argument for precaution under uncertainty and high risk. Ethics Environ 5:175–189

Hanson M (2003) The precautionary principle. In: Page EA, Proops J (eds) Environmental thought. Current issues in ecological economics. Edward Elgar, Northampton, pp 125–142

Hegland SJ, Jongejans E, Rydgren K (2010) Investigating the interaction between ungulate grazing and resource effects on Vaccinium myrtillus populations with integral projection models. Oecologia 163:695–706. doi:10.1007/s00442-010-1616-2

Heywood VH, Iriondo JM (2003) Plant conservation: old problems, new perspectives. Biol Conserv 113:321–335. doi:10.1016/S0006-3207(03)00121-6

Jiménez-Sierra C, Mandujano MC, Eguiarte LE (2007) Are populations of the candy barrel cactus (Echinocactus platyacanthus) in the desert of Tehuacan, Mexico at risk? Population projection matrix and life table response analysis. Biol Conserv 135:278–292. doi:10.1016/j.biocon.2006.10.038

Jongejans E, Shea K, Skarpaas O, Kelly D, Ellner SP (2011) Importance of individual and environmental variation for invasive species spread: a spatial integral projection model. Ecology 92:86–97. doi:10.1890/09-2226.1

Kriebel D, Tickner J, Epstein P, Lemons J, Levins R, Loechler EL, Quinn M, Rudel R, Schettler T, Stoto M (2001) The precautionary principle in environmental science. Environ Health Perspect 109:871–876

Martorell C (2007) Detecting and managing an overgrazing-drought synergism in the threatened Echeveria longissima (Crassulaceae): the role of retrospective demographic analysis. Popul Ecol 49:115–125. doi:10.1007/s10144-006-0027-z

Martorell C, Peters EM (2005) The measurement of chronic disturbance and its effects on the threatened cactus Mammillaria pectinifera. Biol Conserv 124:199–207. doi:10.1016/j.biocon.2005.01.025

Martorell C, Peters EM (2009) Disturbance-response analysis: a method for rapid assessment of the threat to species in disturbed

areas. Conserv Biol 23:377–387. doi:10.1111/j.1523-1739.2008.01134.x

McAuliffe JR, Sundt PC, Valiente-Banuet A, Casas A, Viveros JL (2001) Pre-columbian soil erosion, persistent ecological changes, and collapse of a subsistence agricultural economy in the semi-arid Tehuacan Valley, Mexico's 'Cradle of Maize'. J Arid Environ 47:47–75. doi:10.1006/jare.2000.0691

McGarvey DJ (2007) Merging precaution with sound science under the endangered species act. Bioscience 57:65–70. doi:10.1641/B570110

Metcalf JE, Horvitz CC, Tuljapurkar S, Clark DA (2009) A time togrow and a time to die: a new way to analyze the dynamics of size, light, age,and death of tropical trees. Ecology 90:2766–2778

Pérez-Negrón E, Casas A (2007) Use, extraction rates and spatial availability of plant resources in the Tehuacan-Cuicatlan Valley, Mexico: the case of Santiago Quiotepec, Oaxaca. J Arid Environ 70:356–379. doi:10.1016/j.jaridenv.2006.12.016

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramula S, Rees M, Buckley YM (2009) Integral projection models perform better for small demographic data sets than matrix population models: a case study of two perennial herbs. J Appl Ecol 46:1048–1053. doi:10.1111/j.1365-2664.2009.01706.x

Redford KH, Richter BD (1999) Conservation of biodiversity in a world of use. Conserv Biol 13:1246–1256

Rees M, Ellner SP (2009) Integral projection models for populations in temporally varying environments. Ecol Monogr 79:575–594. doi:10.1890/08-1474.1

Rees M, Rose KE (2002) Evolution of flowering strategies in Oenothera glazioviana: an integral projection model approach. Proc R Soc Lond B 269:1509–1515. doi:10.1098/rspb.2002.2037

Shahabuddin G, Kumar R (2006) Influence of anthropogenic disturbance on bird communities in a tropical dry forest: role of vegetation structure. Anim Conserv 9:404–413. doi:10.1111/j.1469-1795.2006.00051.x

Silvertown J, Franco M, Pisanty I, Mendoza A (1993) Comparative plant demography: relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. J Ecol 81:465–476

Singh SP (1998) Chronic disturbance, a principal cause of environmental degradation in developing countries. Environ Conserv 25:1–2

Soulé ME, Kohm KA (1989) Research priorities for conservation biology. Island Press, Washington, DC

Ureta C, Martorell C (2009) Identifying the impacts of chronic anthropogenic disturbance on two threatened cacti to provide guidelines for population-dynamics restoration. Biol Conserv 142:1992–2001. doi:10.1016/j.biocon.2008.12.031

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science 277:494–499

Wood SN (2003) Thin plate regression splines. J R Stat Soc B 65:95–114. doi:10.1111/1467-9868.00374

Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton

Zuidema PA, Jongejans E, Chien PD, During HJ, Schieving F (2010) Integral Projection Models for trees: a new parameterization method and a validation of model output. J Ecol 98:345–355. doi:10.1111/j.1365-2745.2009.01626.x