UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
ECOLOGÍA

MODELACIÓN Y ANÁLISIS DEL EFECTO DEL DISTURBIO ANTROPOGÉNICO CRÓNICO SOBRE LA DINÁMICA DEMOGRÁFICA A PARTIR DE UNA CRONOSECUENCIA DE ESTRUCTURAS POBLACIONALES

TESIS

QUE PARA OPTAR POR EL GRADO DE:
DOCTOR EN CIENCIAS

PRESENTA:
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MÉXICO, D.F. Abril 2014

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ASUNTO: Oficio de Jurado

Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **27 de enero de 2014**, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del (la) alumno (a) **GONZÁLEZ LICEAGA EDGAR JAVIER** con número de cuenta **99573791** con la tesis titulada: **"Modelación y análisis del efecto del disturbio antropogénico crónico sobre la dinámica demográfica a partir de una cronosecuencia de estructuras poblacionales"**, realizada bajo la dirección del (la) **DR. CARLOS MARTORELL DELGADO:**

Presidente:	DR. JOSÉ JAIME ZÚÑIGA VEGA
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Suplente	DR. IGNACIO MÉNDEZ RAMÍREZ

Sin otro particular, me es grato enviarle un cordial saludo.

Atentamente
"POR MI RAZA HABLARA EL ESPÍRITU"
Cd. Universitaria, D.F. a 25 de marzo de 2014.

M del Coro

Dra. María del Coro Arizmendi Arriaga
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Resumen

Las poblaciones de una gran diversidad de especies están siendo afectadas por procesos ambientales direccionales y a largo plazo, como lo son el cambio climático, la sucesión y el disturbio humano. Estos efectos se reflejan en la dinámica demográfica de dichas especies y varían de una especie a otra, pudiendo beneficiarla, perjudicarla o no afectarla. Sin embargo, los métodos demográficos tradicionales que se usan para estudiar cambios poblacionales no son apropiados para analizar dichos efectos pues requieren del seguimiento de la población durante el periodo de tiempo que este proceso ocurre, lo cual no suele ser factible. Por ello, este trabajo plantea un problema inverso: utilizar un modelo tradicional (modelo integral de proyección; MIP) que toma datos de dinámica poblacional y arroja la estructura y tamaño poblacionales e intentar reconstruir la dinámica partiendo de datos de estructura y tamaño. Para ello, en el capítulo 1 se investiga si la estructura funcional del MIP (*i.e.*, las funciones matemáticas que lo integran) afecta los resultados derivados de él. Para los fines del método, me importaba saber si se veían afectados: 1) el cambio en la tasa de crecimiento poblacional (λ) cuando un proceso ambiental impacta a la población, y 2) la identidad de la tasa vital responsable de este cambio. En este capítulo se demuestra que la estructura funcional no afecta en gran medida ninguno de los dos aspectos anteriores. Esto garantizó que los resultados arrojados por el método a desarrollar no se verían afectados fuertemente por el MIP particular usado.

En el capítulo 2 se presenta propiamente el método desarrollado y se valida tanto con datos generados artificialmente, como con datos de una cronosecuencia de poblaciones de una cactácea globosa, *Mammillaria dixanthocentron,* sujetas a diferentes intensidad de disturbio antropogénico crónico (DAC). Al producir resultados alternativos, la implementación del método requiere descartar aquellos que, con base en el conocimiento básico de la especie, no sean biológicamente realistas. En el caso de los datos artificiales, se muestra que el método logra reconstruir las tasas vitales y su cambio en el tiempo con un 90 % de éxito. En el caso de *M. dixanthocentron*, el modelo logra de igual modo reconstruir dichas tasas y su cambio a lo largo del gradiente de CAD. Sin embargo, se encuentran algunas diferencias cuantitativas cuando se comparan las tasas con aquellas conocidas para dos poblaciones de la cronosecuencia.

Finalmente, en el capítulo 3 se aplica el método a seis especies adicionales de cactáceas globosas. Las tasas vitales reconstruidas muestran que el DAC modifica principalmente la sobrevivencia de los individuos más pequeños y la fecundidad de los más grandes. A partir de dichas tasas se reconstruye el cambio en la tasa anual de crecimiento poblacional (λ_t) y se encuentra que este cambio es particular a la especie: de las siete estudiadas, cuatro se benefician del DAC, dos se benefician solo de intensidades bajas de disturbio y una es vulnerable a cualquier forma de DAC. En la mayoría de los casos, es el efecto del DAC sobre la supervivencia el responsable de estos patrones. Sin embargo, el método no logra reconstruir con precisión los valores de λ_t, pues difieren de los observados para estos cactos.

Se concluye entonces que la estructura y el tamaño poblacionales contienen la información necesaria para reconstruir correctamente las tasas vitales a nivel cualitativo; sin embargo, al ser limitada, dicha información no es suficiente para estimar las tasas con precisión. No obstante, desde un punto de vista de la conservación es más importante tener una idea rápida, aunque cualitativa, del impacto de un proceso direccional sobre una población, que certidumbre sobre el valor exacto de dicho impacto, el cual se obtiene solo tras estudiar a una población por largo tiempo.

Abstract

Directional, long-term environmental processes, such as climate change, succession and human disturbance, impact the populations of a large diversity of species. These impacts can modify the demographic dynamics of such species and vary idiosyncratically, having beneficial, detrimental or null effects on them. However, the application of traditional demographic methods to the study of the effect of these processes is unsuitable, as they require the survey of a population over the time span over which the process takes place, which is usually unfeasible. Thus, I present here an inverse problem: to use a traditional model (integral projection model; IPM) which takes demographic-dynamics data and produces population sizes and structures, and attempt to reconstruct the dynamics from population-size and -structure data. To do this, on Chapter 1 I assess whether the functional structure of an IPM (i.e., the mathematical functions that it involves) influence the results derived from it. Particularly, I was interested in the effect of this structure on: 1) the change in the population growth rate (λ) as the environmental process unfolds, and 2) the identity of the vital rate responsible for such change. I show that the functional structure does not affect substantially any of the aforementioned aspects. This guaranteed that the results given by the method would not be strongly affected by the particular IPM used.

On Chapter 2, I present the method and validate it with artificially generated data, as well as with data from a chronosequence of populations of a globose cactus, *Mammillaria dixanthocentron*, which face different intensities of chronic anthropogenic disturbance (CAD). The implementation of the method produces alternative results, and thus requires discarding those that, based on basic knowledge on the species, are biologically unrealistic. In the case of the artificial data, the method reconstructs correctly the vital rates and their change over time with a 90 % success rate. In the case of *M. dixanthocentron*, the method successfully reconstructs the shape of these rates along the CAD gradient; however, some quantitative differences are found when comparing these rates with those previously known ones for two of the populations in the chronosequence.

Finally, on Chapter 3 I apply the method to six additional globose cactus species. The reconstructed vital rates show that in most species CAD modifies mainly the survival of the smallest individuals and the fecundity of the largest ones. From these rates, the reconstructed change in the annual growth rate (λ_t) shows a species-specific behaviour: from the seven species under study, four beneficiate from CAD, two beneficiate only from low CAD intensities and one is vulnerable to any form of CAD. In most of the cases, the effect of CAD on survival is the one responsible for such behaviours. However, the method does not manage to reconstruct the exact values of λ_t, as they differ from the observed ones for these species.

Therefore, I conclude that the population structure and size contain the necessary information to correctly reconstruct the vital rates at a qualitative level; however, this information is not enough to precisely estimate such rates. Nevertheless, from a conservation point of view, it is more important to have a quick, though qualitative, idea of the impact of a directional process over a population, than to know the precise value of such impact, which in turn can only be obtained after a long-term study of the population.

Introducción general

> *A quick answer that is good enough may be more influential*
> *on policy than a better answer supplied years later.*
> *Benton, 2007*

El estudio del impacto del ambiente sobre las poblaciones de organismos es y ha sido un tema primordial en la ecología de poblaciones (Heller & Zavaleta, 2009; Pereira *et al.,* 2010; Crone *et al.,* 2011). En este contexto, la variedad de factores ambientales investigados incluye procesos periódicos, estocásticos y direccionales, tanto a corto como a largo plazo (Tuljapurkar, 1989; Boyce *et al.*, 2006; Mertens *et al.*, 2006; Chirakkal y Gerber, 2010; Crone *et al.,* 2011). De entre estos, el estudio del impacto de los procesos direccionales a largo plazo sobre las poblaciones siempre ha sido difícil de abordar, pues requiere de gran cantidad de recursos humanos y económicos que no suelen estar disponibles. No obstante, es importante estudiar los procesos de este tipo, pues suelen estar asociados a la acción del ser humano y tener un impacto que trastoca las poblaciones de los organismos afectados (With & Crist, 1995; Singh, 1998).

Al estar el ser humano presente en la totalidad de los ecosistemas terrestres (Vitousek *et al.* 1997; Sala *et al.* 2000), la cantidad y variedad de especies tanto animales como vegetales que está viéndose afectada es enorme. Sin embargo, la falta de conocimiento sobre cómo los procesos direccionales alteran la dinámica poblacional de estas especies, imposibilita tomar decisiones de manejo y conservación adecuadas. Ante la velocidad a la cual el ser humano aumenta la intensidad su impacto y la extensión del mismo, se requiere de alternativas metodológicas que permitan tener, de una manera rápida, una idea del cambio demográfico a lo largo del tiempo. La ecología de poblaciones reconoce que individuos en diferentes estadios de desarrollo responden de manera diferenciada al ambiente (Mandujano *et al.* 2001; Pfister y Stevens, 2003; Benton *et al.*, 2006), y que diferentes procesos demográficos (*e.g.,* la supervivencia, el crecimiento y la fecundidad de los individuos) se verán influidos de diferente manera por este (van Tienderen, 1995; Tuljapurkar *et al.* 2003; Coulson *et* al., 2005; Boyce *et al.* 2006). Por lo tanto, el método a desarrollar requeriría identificar dichas respuestas diferenciadas. Contar con un método de este tipo permitiría desarrollar planes de manejo y conservación para las especies afectadas que incidieran explícitamente sobre los individuos y los procesos demográficos impactados en mayor medida por el proceso ambiental bajo estudio. Es como respuesta a esta necesidad que surge la presente investigación de doctorado: el método que desarrollo en este proyecto intenta, partiendo de información fácil y rápidamente obtenible, proporcionar una idea aproximada, pero útil para efecto de políticas de conservación, de la dinámica poblacional de una especie y su cambio a lo largo de un gradiente direccional.

En lo que resta del capítulo presentaré los diferentes conceptos en los que se sustenta esta tesis y que requieren de una descripción previa: el enfoque tradicional de la modelación de la dinámica poblacional; el problema inverso de modelación de la dinámica poblacional que justifica la tesis; y el disturbio antropogénico crónico, las cronosecuencias y las cactáceas, conceptos que sirven para ejemplificar el método desarrollado en la tesis. Finalizo con el objetivo de la tesis y la relación de los capítulos que la estructuran.

La modelación de la dinámica poblacional

El estudio de la dinámica poblacional se ha basado históricamente en el desarrollo de modelos matemáticos que intentan describir los distintos procesos que, observados a nivel individual, tienen su correlato poblacional. De entre estos, los modelos estructurados toman en cuenta el hecho de que los individuos de una población difieren entre sí en ciertos atributos (*e.g.*, en su edad, tamaño o estadio de desarrollo) y esto se refleja en diferencias en sus tasas vitales (supervivencia, crecimiento y fecundidad). Los modelos matriciales de proyección (MMPs; Caswell, 2001) son un ejemplo de modelos estructurados que han sido ampliamente utilizados durante las últimas décadas (*e.g.*, Silvertown *et al.*, 1993; Godínez-Álvarez *et al.,* 2003; Crone *et al.*, 2011). En los MMPs, los individuos de una población difieren en uno o más atributos categóricos. Sin embargo, ciertos atributos, como el tamaño, varían entre individuos de manera continua y no categórica, por lo que categorizar este tipo de atributos resulta artificial. Los modelos integrales de proyección (MIPs; Easterling *et al.*, 2000; Merow *et al.*, 2014) han sido una respuesta metodológica a este problema, pues permiten la incorporación tanto de atributos continuos como categóricos a la modelación de la dinámica poblacional.

La información necesaria para la construcción de un MMP o MIP involucra seleccionar una muestra de individuos de una población y seguir la supervivencia, crecimiento y fecundidad de estos durante el tiempo que les toma completar su ciclo de vida (Crone *et al.*, 2011; Merow *et al.*, 2014). Con esta información se puede proyectar el cambio en las estructuras y densidades poblacionales a lo largo del tiempo. Sin embargo, para especies longevas, como es el caso de ,muchas cactáceas, este seguimiento suele requerir una gran inversión de tiempo y, por lo tanto, de recursos económicos y humanos.

Un problema inverso de modelación de la dinámica poblacional

En contraposición a lo arriba expuesto, la presente investigación intenta resolver un problema inverso: partiendo de las estructuras y las densidades observadas a lo largo del tiempo, inferir la dinámica que las produciría. A no requerirse de un seguimiento de los individuos se reduce en gran medida el tiempo y los recursos humanos necesarios para conocer la dinámica poblacional de una especie (Fig. 1).

Una versión similar de este problema inverso fue inicialmente planteado en el área de pesquerías utilizando MMPs. Partiendo de series de tiempo de datos de capturas de peces, Fournier *et al.* (1998) lograron estimar tasas de crecimiento, mortalidad y reclutamiento en un contexto metapoblacional, *i.e.*, buscaron reconstruir los movimientos migratorios entre poblaciones y no el cambio de la dinámica poblacional en el tiempo. Diversas aplicaciones y versiones de este modelo se han utilizado para estimar tasas vitales en especies de peces tanto comerciales como no comerciales (Hampton y Fournier, 2001; Kleiber *et al.*, 2003, 2009; Maunder y Watters, 2003; Kristensen *et al.*, 2006). Otro enfoque ha sido modelar la dinámica poblacional como funciones en las que, a diferencia de los MMPs/MIPs, el tiempo es una variable continua (Bertignac *et al.*, 1998; Maury *et al.*, 2005). Más recientemente, Ghosh *et al.* (2012) plantean el problema inverso utilizando un MIP. Sin embargo, a diferencia del enfoque tradicional de modelación de la dinámica poblacional descrito en la sección anterior, ellos modelan la dinámica a nivel poblacional y no individual, lo que les permite simplificar la estructura tradicional de un MIP. Adicionalmente, agregan supuestos como una fecundidad decreciente en el tiempo, lo cual no es algo que, en general, se pueda suponer *a priori*.

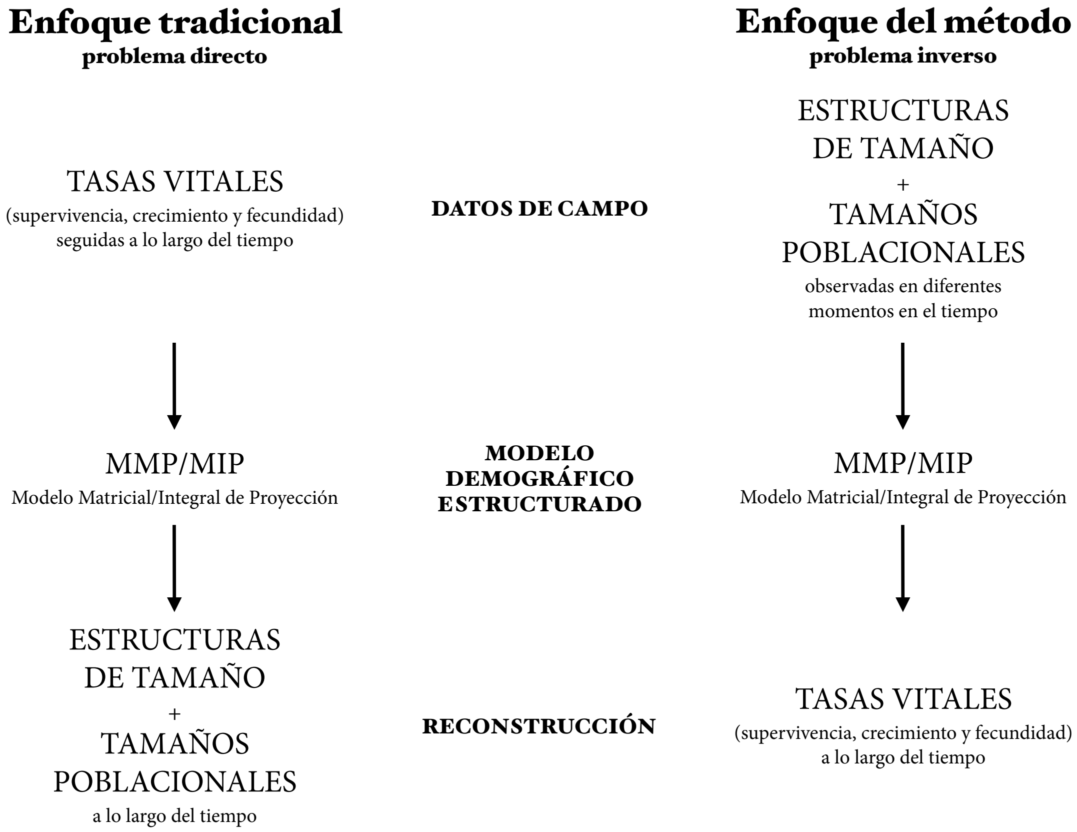

Figura 1. Diagrama comparativo de los enfoques de modelación demográfica. Izquierda: enfoque tradicional, derecha: enfoque seguido por el método presentado en esta tesis.

El problema inverso que esta tesis busca atacar fue inicialmente planteado, sin tomar en cuenta las densidades poblacionales, en mi tesis de maestría (González, 2008). En ella, se buscó desarrollar un modelo que permitiera reconstruir la dinámica poblacional de un cacto, *Mammillaria dixanthocentron*, a partir de una cronosecuencia de estructuras de tamaño de poblaciones sujetas a diferentes intensidades de disturbio antropogénico crónico. Sin embargo, al aplicarse el modelo a datos de una sola especie, no se podía evaluar la capacidad de este para dar buenos resultados para otra especie, *i.e.*, no se había garantía de que el modelo fuera generalizable. La presente tesis intenta, entre otros aspectos, evaluar esto.

El disturbio antropogénico crónico

El disturbio antropogénico crónico (DAC) es un claro ejemplo del tipo de factor direccional a largo plazo cuyo impacto, sobre las poblaciones necesita ser comprendido a profundidad. El disturbio, en su sentido más general, se define como “un factor externo asociado con la destrucción parcial o total de la biomasa vegetal y surge por la actividad de los herbívoros, patógenos, el ser humano, y por fenómenos como el daño por viento, las heladas, la desecación, la erosión del suelo y el fuego" (Grime, 1977). Los disturbio presentan variación a nivel temporal y espacial, así como en su frecuencia e intensidad (Turner *et al.*, 1998; Laska, 2001). Estos dos últimos atributos suelen estar relacionados de manera inversa (White y Jentsch, 2001), lo que permite caracterizar al disturbio como crónico o agudo, siendo el primero un fenómeno con eventos frecuentes pero de pequeña magnitud, mientras que el segundo ocurre de manera rara pero con una mayor intensidad.

Por su parte, el disturbio antropogénico es el causado de manera directa o indirecta por el ser humano. Al ser un agente externo al sistema, este tipo de disturbio es novedoso para él (White y Jentsch, 2001) y altera el régimen natural de disturbios (caracterizado por la "distribución natural de los tamaños, frecuencias, intensidades y tiempos en los que ocurren los disturbios": Hobbs y Huenneke, 1992), tanto en su frecuencia como en la intensidad. Así, a diferencia del disturbio natural que suele ocurrir de manera relativamente predecible y al cual las especies suelen estar adaptadas (Bazzaz, 1983; Sousa, 1984; Puigdefábregas y Pugnaire, 1999), el disturbio humano suele tener efectos negativos sobre estas, causando en muchos casos la reducción o extinción de sus poblaciones o incluso de las especies mismas (Diamond, 1989; Davies *et al.*, 2001; Vega y Peters, 2003). Sin embargo, esto no es cierto para todas las especies, ya que algunas, al ser ruderales (Grime, 1977), se beneficiarán de la presencia de este disturbio (Martorell y Peters, 2009). Esto puede suceder como resultado de la eliminación de competidores y/o de la liberación de recursos (Wilson y Keddy, 1986).

De esta manera, el DAC resulta de procesos humanos que tienen un bajo impacto sobre el sistema, pero que ocurren de manera frecuente. En México, por ejemplo, la extracción de leña y otros productos no maderables, así como la ganadería extensiva, son las fuentes principales de DAC (Vega y Peters, 2003). A diferencia del disturbio agudo, que una vez ocurrido permite la recuperación de las poblaciones vegetales, el DAC la obstaculiza (Singh, 1998), por lo que su efecto se va acumulando a lo largo del tiempo. Esta acumulación puede tardar en hacerse evidente, pero una vez que esta ocurre, los efectos sobre las poblaciones pueden ser irreversibles.

En muchos países en desarrollo, las poblaciones humanas enfrentan pobreza y están en constante crecimiento. Es en ellos donde el DAC suele ser un fenómeno ampliamente presente (Singh, 1998; Walker y Willig, 1999). Además, muchos de estos países cuentan con una gran biodiversidad, por lo que la identificación del impacto que tiene el DAC sobre su biota se hace imperativo.

A nivel poblacional, se sabe que el disturbio afecta diferentes atributos demográficos. Así, de acuerdo con Bazzaz (1983), el disturbio tiene un impacto sobre la densidad, la tasa de crecimiento y la estructura de edades. Sin embargo, las especies, al diferir en su grado de tolerancia frente al disturbio, deberán diferir en su respuesta al mismo (Hobbs y Huenneke, 1992; White y Jentsch, 2001). Esto nos habla de una respuesta ante el disturbio y, en particular ante el DAC (Martorell y

Peters, 2009), particular a cada especie.

Las cronosecuencias

La cronosecuencia ha sido utilizada para el estudio de procesos ecológicos a largo plazo (*e. g.*, Dickson y Crocker, 1953; Twigg *et al.*, 1989; Aide *et al.*, 2000). Esta herramienta metodológica busca inferir una tendencia temporal a partir del estudio de sitios con diferentes edades, *i.e.*, busca sustituir espacio por tiempo (Pickett, 1989). La gran ventaja que presenta la cronosecuencia es que permite analizar de manera relativamente rápida dichos procesos; sin embargo, el supuesto más fuerte que subyace a este método es que los sitios estudiados están, y han estado, sujetos a las mismas condiciones bióticas y abióticas a lo largo del tiempo durante el cual ha ocurrido el proceso de nuestro interés (Twigg *et al.*, 1989; Johnson y Miyanishi, 2008). La violación de este supuesto limita las conclusiones que se pueden obtener a partir de este método (Pickett, 1989; Bakker *et al.*, 1996; Johnson y Miyanishi, 2008). Históricamente, las parcelas permanentes han sido la alternativa metodológica a las cronosecuencias; pero, al requerir de grandes escalas de tiempo y recursos humanos mucho mayores, su uso ha sido limitado. Además, estudios comparativos entre cronosecuencias y parcelas permanentes sugieren que estos métodos pueden complementarse (Bakker *et al.*, 1996; Foster y Tilman, 2000; Myster y Malahy, 2008).

Dado nuestro interés en describir de manera rápida cómo el DAC afecta a la dinámica poblacional, la cronosecuencia resulta una herramienta idónea para nuestro estudio. Al contar con un conjunto de sitios que difieren en el grado de DAC que presentan (Peters y Martorell, 2000) y dado que, como se estableció arriba y se ha observado en el campo (Martorell y Peters, 2009), el DAC observado en un sitio es el resultado de la acumulación a lo largo del tiempo de los eventos discretos de disturbio humano, podemos considerar a las poblaciones que habitan dichos sitios como puntos a lo largo de una cronosecuencia de poblaciones que han experimentado el DAC durante diferentes intervalos de tiempo.

Las cactáceas

México posee la mayor parte de las especies de cactáceas existentes en el mundo: 78% de las poco más de 2000 especies descritas hasta la fecha (Arias-Montes, 1993; Hernández y Godínez, 1994). Aún cuando muchas cactáceas están enlistadas como especies amenazadas por una variedad de organizaciones (*e.g.*, NOM-0591-2010; CITES, 2013), en muchos casos no está claro el estado de conservación de las mismas (*v.g.*, Mandujano *et al.*, 2007). Esta falta de conocimiento tiene consecuencias cuando nos enfrentamos al problema de establecer el nivel de vulnerabilidad de las especies y las medidas para su conservación. Clave para lograr esto es el estudio de su demografía (Godínez-Álvarez *et al.*, 2003).

A nivel demográfico, las cactáceas suelen presentar tasas de crecimiento poblacional lentas, bajas tasas de reclutamiento y ciclos de vida largos. Diversos estudios demográficos utilizando MMPs muestran que, en general, las poblaciones de cactáceas mantienen sus tamaños poblacionales a lo largo del tiempo gracias a la supervivencia y persistencia de los individuos, particularmente de los adultos, en la categoría de tamaño a la que pertenecen (Rosas-Barrera y Mandujano-Sánchez, 2002; Godínez-Álvarez *et al.*, 2003; Godínez-Álvarez y Valiente-Banuet, 2004; Méndez *et al.,* 2004; Valverde *et al.*, 2004; Jiménez-Sierra *et al.*, 2007; Flores Martínez *et al.*, 2010; Rojas-Sandoval y Meléndez-Ackerman, 2013). La mayor mortalidad se da generalmente a nivel de las semillas y las plántulas, siendo sus causas la depredación y la desecación, respectivamente (Valiente-Banuet y Godínez-Álvarez, 2002; Méndez *et al.,* 2004; Martínez-Berdeja y Valverde, 2008; Zepeda-Martínez y Mandujano, 2013).

En cuanto al DAC, se ha observado que la respuesta de las cactáceas ante este agente es particular a la especie, pues para algunas especies el disturbio de cualquier intensidad las afecta negativamente, mientras que para otras una intensidad media de disturbio las beneficia (Martorell y Peters, 2005, 2009; Santini, 2007; Ureta y Martorell, 2009). Asimismo, el DAC puede afectar negativamente a un proceso demográfico y beneficiar a otro (Portilla-Alonso, 2011; Montañana-Palacios, 2009). Lo anterior hace evidente la complejidad con la que el DAC puede afectar a la dinámica poblacional y la imposibilidad de hacer generalizaciones sobre el comportamiento de estas especies ante el DAC (Grubb, 1985).

Objetivo de la tesis

Esta tesis busca resolver un problema inverso: reconstruir el cambio de las tasas vitales de una población a medida que esta experimenta el efecto de un proceso direccional a largo plazo (*e.g.* el DAC), partiendo de datos de estructuras y tamaños poblacionales en diferentes momentos de dicho proceso. Este es un problema inverso en el sentido de que la mayoría de los modelos demográficos estructurados parten de tasas vitales observadas en el campo para modelar el cambio en la estructura y el tamaño poblacionales a medida que pasa el tiempo (Fig. 1; Caswell, 2001; Easterling *et al.*, 2000; sin embargo, *cf.* Doak y Morris, 1999; Ghosh *et al.*, 2012).

Estructura de la tesis

La tesis consiste de tres manuscritos y una discusión general. Estos se relacionan entre sí de la siguiente manera:

- **Capítulo 1**
  Identifying the demographic processes relevant for species conservation in human-impacted areas: does the model matter?
  E. J. González, M. Rees & C. Martorell. 2013. Oecologia 171: 347-356

  Este capítulo demuestra que, sin importar la estructura funcional del MIP utilizado para analizar el impacto del DAC sobre los procesos demográficos, la magnitud y sentido del cambio en la tasa de crecimiento poblacional será correctamente identificado por un MIP. Asimismo, es posible identificar el proceso demográfico cuyo cambio debido al DAC tendrá mayor impacto sobre el crecimiento de la población. Esto era importante de determinar pues, si la estructura del MIP incidiera en gran medida sobre los resultados, el método a desarrollar en el capítulo 2 sería altamente dependiente de la estructura particular del MIP empleado.

- **Capítulo 2**
  Reconstructing shifts in vital rates driven by long-term environmental change: a new demographic method based on readily available data.
  E. J. González & C. Martorell. 2013. Ecology and Evolution 3: 2273-2284

  Aquí se presenta el método desarrollado en la tesis y se valida tanto con datos generados artificialmente, como con datos de una cactácea globosa, *M. dixanthocentron*, cuyas poblaciones están sujetas a diferentes intensidades de DAC. Al no incidir en gran medida la estructura del MIP (capítulo 1), se elige utilizar la que requiere de la estimación del menor número de parámetros. Para ello se recurre a una estimación por máxima verosimilitud. Una vez que se cuenta con valores estimados de dichos parámetros, se tiene un modelo del cambio de las tasas vitales (supervivencia, crecimiento y fecundidad) tanto en el tiempo, como para las diferentes etapas del ciclo de vida. Al producir diferentes valores estimados de los parámetros, la implementación del método requiere descartar aquellos que, con base en conocimiento previo, no son biológicamente realistas. En el caso de los datos artificiales, se muestra que el método logra reconstruir el cambio de las tasas vitales con un 90 % de éxito. Para el caso empírico con *M. dixanthocentron*, el modelo logra de igual modo reconstruir exitosamente las tasas vitales.

- **Capítulo 3**
  The impact of chronic anthropogenic disturbance on cacti: reconstructing the change in their vital rates through chronosequences of static data.
  E. J. González & C. Martorell. En preparación.

  Una vez que se ha presentado el método (capítulo 2), este capítulo presenta su aplicación a siete especies de cactáceas globosas. Las tasas vitales reconstruidas muestran que el DAC modifica particularmente la supervivencia de los individuos más pequeños y la fecundidad de los más grandes. A partir de dichas tasas se reconstruye el cambio en la tasa anual de crecimiento poblacional (λ_t) y se encuentra que esta presenta un comportamiento particular a la especie afectada. De esta manera se identifica que, de las siete especies, cuatro se benefician del DAC, dos se benefician solo de intensidades bajas de disturbio y una es vulnerable a cualquier forma de DAC. Sin embargo, el método no logra reconstruir una caída en λ_t a altas intensidades de DAC, un patrón que se esperaría encontrar en todas las especies.

- **Discusión general y Conclusiones**

  A partir de los resultados obtenidos en los tres capítulos, se concluye que las estructuras y densidades poblacionales contienen la información necesaria para obtener una reconstrucción correcta de la dinámica poblacional y su cambio en el tiempo. Sin embargo, la información no es suficiente para producir una reconstrucción única, por lo que se requiere que el usuario discrimine, de entre un conjunto de soluciones, aquella que, a nivel biológico, tenga más sentido. Se plantean mejoras al modelo que podrían permitir la obtención de resultados más cercanos al comportamiento demográfico esperado de una especie, así como evaluar la sensibilidad y la robustez del mismo.

Literatura citada

Aide, T. M., J. K. Zimmerman, J. B. Pascarella, L. Rivera, y H. Marcano-Vega. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restoration Ecology 8: 328–338.

Arias-Montes, S. 1993. Cactáceas: conservación y diversidad en México. Revista de la Sociedad Mexicana de Historia Natural XLIV: 109-115.

Bakker, J. P., H. Olff, J. H. Willems y M. Zobel. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? Journal of Vegetation Science 7: 147-156.

Bazzaz, F. A. 1983. Characteristics of population in relation to disturbances in natural and man-modified ecosystems. En: H. A. Mooney y M. Godron, eds. Disturbance and Ecosystems. Springer-Verlag: Berlin. Pp. 259-275.

Benton, T. G. 2007. Managing farming's footprint on biodiversity. Science 315: 341-342.

Benton, T. G., S. J. Plaistow, y T. N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society B: Biological Sciences 273: 1173–1181.

Bertignac, M., P. Lehodey y J. Hampton. 1998. A spatial population dynamics simulation model of tropical tunas using a habitat index based on environmental parameters. Fisheries Oceanography 7: 326–334.

Boyce, M. S., C. V. Haridas, C. T. Lee y the NCEAS Stochastic Demography Working Group. 2006. Demography in an increasingly variable world. Trends in Ecology and Evolution 21: 141-148.

Caswell, H. 2001. Matrix population models. Construction, analysis, and interpretation. 2nd edition. Sinauer: Sunderland, Massachusetts. 722 p.

Chirakkal, H. y L. R. Gerber. 2010. Short- and long-term population response to changes in vital rates: implications for population viability analysis. Ecological Applications 20: 783-788.

CITES. 2013. Convention on International Trade in Endangered Species of Wild Fauna and Flora. Appendices I,II and III. Obtenido de: http://www.cites.org/eng/app/appendices.php.

Coulson, T., J.-M. Gaillard, and M. Festa-Bianchet. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology 74: 789–801.

Crone, E. E., E. S. Menges, M. M. Ellis, T. Bell, P. Bierzychudek, J. Ehrlén, T. N. Kaye, T. M. Knight, P. Lesica, W. F. Morris, G. Oostermeijer, P. F. Quintana-Ascencio, A. Stanley, T. Ticktin, T. Valverde, y J. L. Williams. 2011. How do plant ecologists use matrix population models? Ecology Letters 14: 1–8.

Davies, K. F., C. Gascon y C. R. Margules. 2001. Habitat fragmentation: consequences, management, and future research priorities. En: M. E. Soulé y G. H. Orians. Conservation biology: research priorities for the next decade. Island Press: Washington, D. C. Pp. 81-97.

Diamond, J. M. 1989. The present, past and future of human-caused extinctions. Philosophical Transactions of the Royal Society of London B 325: 469-4777.

Dickson, B. A. y R. L. Crocker. 1953. A chronosequence of soils and vegetation near Mt. Shasta, California. I. Definition of the ecosystem investigated and features of the plant succession. European Journal of Soil Science 4: 123-141.

Doak, D. F. y W. Morris. 1999. Detecting population-level consequences of ongoing environmental change without long-term monitoring. Ecology 80: 1537-1551.

Easterling, M. R., S. P. Ellner y P. M. Dixon. 2000. Size-specific sensitivity: applying a new structured population model. Ecology 81: 694-708.

Flores Martínez, A., G. I. Manzanero Medina, J. Golubov, C. Montaña y M. C. Mandujano. 2010. Demography of an endangered endemic rupicolous cactus. Plant Ecology 210: 53–66.

Foster, B. L. y D. Tilman. 2000. Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. Plant Ecology 146: 1-10.

Fournier, D. A., J. Hampton y J. R. Sibert. 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. Canadian Journal of Fisheries and Aquatic Sciences 55: 2105–2116.

Ghosh, S., A. E. Gelfand y J. S. Clark. 2012. Inference for size demography from point pattern data using integral projection models. Journal of Agricultural, Biological, and Environmental Statistics 17: 641-677.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111: 1169-1194.

Godínez-Álvarez, H., T. Valverde y P. Ortega-Baes. 2003. Demographic trends in the Cactaceae. The Botanical Review 69: 173-203.

Godínez-Álvarez, H. y A. Valiente-Banuet. 2004. Demography of the columnar cactus *Neobuxbaumia macrocephala*: a comparative approach using population projection matrices. Plant Ecology 174: 109–118.

González, E. J. 2008. Modelación de la dinámica poblacional de cactáceas endémicas del Valle de Tehuacán a lo largo de un gradiente de disturbio antropogénico crónico. Tesis de Maestría. Facultad de Ciencias, UNAM: México, D. F. 101 pp.

Grubb, P. J. 1985. Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. En: J. White, ed. The Population Structure of Vegetation. Dr W. Junk Publishers: The Hague. Pp. 595-621.

Hampton, J. y D. A. Fournier. 2001. A spatially disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. Marine and Freshwater Research 52: 937–963.

Heller, N. E., y E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142: 14–32.

Hernández, H. M. y H. Godínez A. 1994. Contribución al conocimiento de las cactáceas mexicanas amenazadas. Acta Botánica Mexicana 26: 33-52.

Hobbs, R. J. y L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6: 324-337.

Jiménez-Sierra, C., M. Mandujano y L. Eguiarte. 2007. Are populations of the candy barrel cactus (*Echinocactus platyacanthus*) in the desert of Tehuacán, Mexico at risk? Population projection matrix and life table response analysis. Biological Conservation 135 :278–292.

Johnson, E. A. y K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11: 419-431.

Kleiber, P., M. G. Hinton y Y. Uozumi. 2003. Stock assessment of blue marlin (*Makaira nigricans*) in the Pacific using MULTIFAN-CL. Marine and Freshwater Research 54: 349–360.

Kleiber, P., S. Clarke, K. Bigelow, H. Nakano, M. K. McAllister, and Y. Takeuchi. 2009. North Pacific Blue Shark Stock Assessment. Pages 1–74. U.S, Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC-17. Kleiber, P., S. Clarke, K. Bigelow, H. Nakano, M. K. McAllister, and Y. Takeuchi. 2009. North Pacific Blue Shark Stock Assessment. Pages 1–74. U.S, Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC-17.

Kristensen, K., P. Lewy y J. E. Beyer. 2006. How to validate a length-based model of single-species fish stock dynamics. Canadian Journal of Fisheries and Aquatic Sciences 63: 2531-2542.

Laska, G. 2001. The disturbance and vegetation dynamics: a review and an alternative framework. Plant Ecology 157: 77-99.

Mandujano, M. C., C. Montaña, M. Franco, J. Golubov, y A. Flores-Martínez. 2001. Integration of demographic annual variability in a clonal desert cactus. Ecology 82: 344–359.

Mandujano, M., J. Verhulst, I. Carrillo-Angeles y J. Golubov. 2007. Population dynamics of *Ariocarpus scaphirostris* Bödeker (Cactaceae): Evaluating the status of a threatened species. International Journal of Plant Sciences 168: 1035–1044.

Martínez-Berdeja, A. y T. Valverde. 2008. Growth response of three globose cacti to radiation and soil moisture: An experimental test of the mechanism behind the nurse effect. Journal of Arid Environments 72: 1766-1774.

Martorell, C. y E. M. Peters. 2005. The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. Biological Conservation 124: 199-207.

Martorell, C. y E. M. Peters. 2009. Disturbance-response analysis: a method for rapid assessment of the threat to species in disturbed areas. Conservation Biology 23: 377-387.

Maunder, M. N., and G. M. Watters. 2003. A-scala: an age-structured statistical catch-at-length analysis for assessing tuna stocks in the Eastern Pacific Ocean. Inter-American Tropical Tuna Commission Bulletin 22: 435–582.

Maury, O., B. Faugeras y V. Restrepo. 2005. FASST: A fully age-size and space-time structured statistical model for the assessment of tuna populations. Collective Volume of Scientific Papers ICCAT 57: 206–217.

Mendez, M., R. Duran, I. Olmsted y K. Oyama. 2004. Population dynamics of *Pterocereus gaumeri*, a rare and endemic columnar cactus of Mexico. Biotropica 36: 492–504.

Merow, C., J. P. Dahlgren, C. J. E. Metcalf, D. Z. Childs, M. E. K. Evans, E. Jongejans, S. Record, M. Rees, R. Salguero-Gómez y S. M. McMahon. 2014. Advancing population ecology with integral projection models: a practical guide. Methods in Ecology and Evolution 5: 99-110.

Mertens, S. K., J. M. Yearsley, F. van den Bosch y Ch. A. Gilligan. 2006. Transient population dynamics in periodic matrix models: methodology and effects of cyclic permutations. Ecology 87: 2338-2348.

Montañana-Palacios, D. M. 2009. Respuesta poblacional de *Coryphantha werdermannii* a diferentes intensidades de disturbio antropogénico en Cuatro Ciénegas, Coahuila. Tesis de Licenciatura. Facultad de Ciencias, UNAM: México, D. F. 53 pp.

Myster, R. W. y M. P. Malahy. 2008. Is there a middle way between permanent plots and chronosequences? Canadian Journal of Forest Research 38: 3133-3138.

Pereira, H. M., P. W. Leadley, V. Proenca, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarres, M. B. Araújo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D. Cooper, E. L. Gilman, S. Guenette, G. C. Hurtt, H. P. Huntington, G. M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila, y M. Walpole. 2010. Scenarios for Global Biodiversity in the 21st Century. Science 330: 1496-1501.

Peters, E. M. y C. Martorell. 2000. Reporte final del proyecto: Conocimiento y conservación de las mamilarias endémicas del Valle de Tehuacán-Cuicatlán. Proyecto R166, CONABIO, 1998-2000. Instituto de Ecología, UNAM. 38 p.

Pfister, C., y F. Stevens. 2003. Individual variation and environmental stochasticity: implications for matrix model predictions. Ecology 84: 496–510.

Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. En: G. E. Likens, ed. Long-term studies in ecology. Wiley: Chichester. Pp. 71-88.

Portilla-Alonso, R. M., y C. Martorell. 2011. Demographic consequences of chronic anthropogenic disturbance on three populations of the endangered globose cactus *Coryphantha werdermannii*. Journal of Arid Environments 75: 509–515.

Puigdefábregas, J. y F. I. Pugnaire. 1999. Plant survival in arid environments. En: F. I. Puignaire y F. Valladares. Eds. Handbook of functional plant ecology. Marcel Dekker: New York. Pp: 381-406.

Rojas-Sandoval, J., y E. Meléndez-Ackerman. 2013. Population dynamics of a threatened cactus species: general assessment and effects of matrix dimensionality. Population Ecology 55: 479–491.

Rosas-Barrera, M. D. y M. C. Mandujano-Sánchez. 2002. La diversidad de historias de vida de cactáceas, aproximación por el triángulo demográfico. Cactáceas y Suculentas Mexicanas 47: 33-41.

Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Below, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker y D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770-1774.

Santini, B. A. 2007. Efecto de la heterogeneidad temporal y el disturbio sobre la dinámica poblacional de dos especies raras del género *Mammillaria* (Cactaceae). Tesis de Licenciatura. Facultad de Ciencias, UNAM: México, D. F. 63 pp.

NOM-059-SEMARNAT-2010. Norma Oficial Mexicana: Protección ambiental-especies nativas de México de flora y fauna silvestres-categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-lista de especies en riesgo. Dario Oficial de la Federación. 30 de diciembre de 2010. Segunda Sección.

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

Singh, S. P. 1998. Chronic disturbance, a principal cause of environmental degradation in developing countries. Environmental Conservation 25: 1-2.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353-391.

Tuljapurkar, S. 1989. An uncertain life: demography in random environments. Theoretical Population Biology 35: 227-294.

Tuljapurkar, S., C. C. Horvitz y J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. The American Naturalist 162: 489–502.

Turner, M. G., W. L. Baker, C. J. Peterson y R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1: 511-523.

Twigg, L. E., B. J. Fox y L. Jia. 1989. The modified primary succession following sand mining: a validation of the use of chronosequence analysis. Australian Journal of Ecology 14: 441-447.

Ureta, C. y C. Martorell. 2009. Identifying the impacts of chronic anthropogenic disturbance on two threatened cacti to provide guidelines for population-dynamics restoration. Biological Conservation 142: 1992-2001.

Valiente-Banuet, A. y H. Godínez-Alvarez. 2002. Chapter 6: Population and community ecology. En: P. S. Nobel, ed. Cacti: biology and uses. University of California Press: Berkeley. Pp. 91-108.

Valverde, T., S. Quijas, M. López-Villavicencio y S. Castillo. 2004. Population dynamics of *Mammillaria magnimamma* Haworth. (Cactaceae) in a lava-field in central Mexico. Plant Ecology 170: 167–184.

van Tienderen, P. H. 1995. Life cycle trade-offs in matrix population models. Ecology 76 :2482–2489.

Vega, E. y E. Peters. 2003. Conceptos generales sobre el disturbio y sus efectos en los ecosistemas. En: O. Sánchez, O. Monroy, E. Vega, E. Peters y C. Donovarros, comps. Conservación de ecosistemas templados de montaña en México. Instituto Nacional de Ecología: México, D. F. Pp. 137-150.

Vitousek, P. H. Mooney, J. Lubchenco y J. Melillo. 1997. Human domination of Earth's ecosystems. Science 277: 494-499.

Walker, L. R. y M. R. Willig. 1999. An introduction to terrestrial disturbances. En: L. R. Walker. Ed. Ecosystems of Disturbed Ground. Amsterdam: Elsevier. Pp. 1-16.

White, P. S. y A. Jentsch. 2001. The search for generality in Studies of disturbance and ecosystem dynamics. Progress in Botany, Vol. 62. Springer-Verlag: Berlin. Pp. 399-450.

Wilson, S. D., y P. A. Keddy. 1986. Species competitive ability and position along a natural stress/disturbance gradient. Ecology:1236–1242.

With, K. A. y T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446-2459.

Zepeda-Martínez, V. y M. C. Mandujano. 2013. What can the demography of *Astrophytum ornatum* tell us of its endangered status? Journal of Arid Environments 88: 244-249.

Capítulo 1

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

E. J. González, M. Rees & C. Martorell. 2013.

Oecologia ***171****: 347-356*

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 structure (the functions that describe how survival, growth and fecundity vary with individual size) are selected. We constructed twelve 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.

Key words

human disturbance, integral projection models, LTRE, model selection, population dynamics

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 III 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; Martorell and Peters 2005; Shahabuddin and Kumar 2006; Martorell and Peters 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.

Material 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:

$$n_{t+1}(y) = \int_X k(y,x) \cdot n_t(x)dx, \qquad (1)$$

where x is individual size at year t, y is individual size at year $t+1$ and X is the range of possible individual 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 $f(y,x)$:

$$k(y,x) = s(x) \cdot g(y,x) + f(y,x). \qquad (2)$$

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 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 than 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:

$$f(y,x) = n_{fX}(x) \cdot c \cdot f_s(y), \tag{3}$$

$$f(y,x) = p_f(x) \cdot n_{fR}(x) \cdot c \cdot f_s(y), \tag{4}$$

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. GML3s 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 c^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 1000 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 expression 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 ± 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,

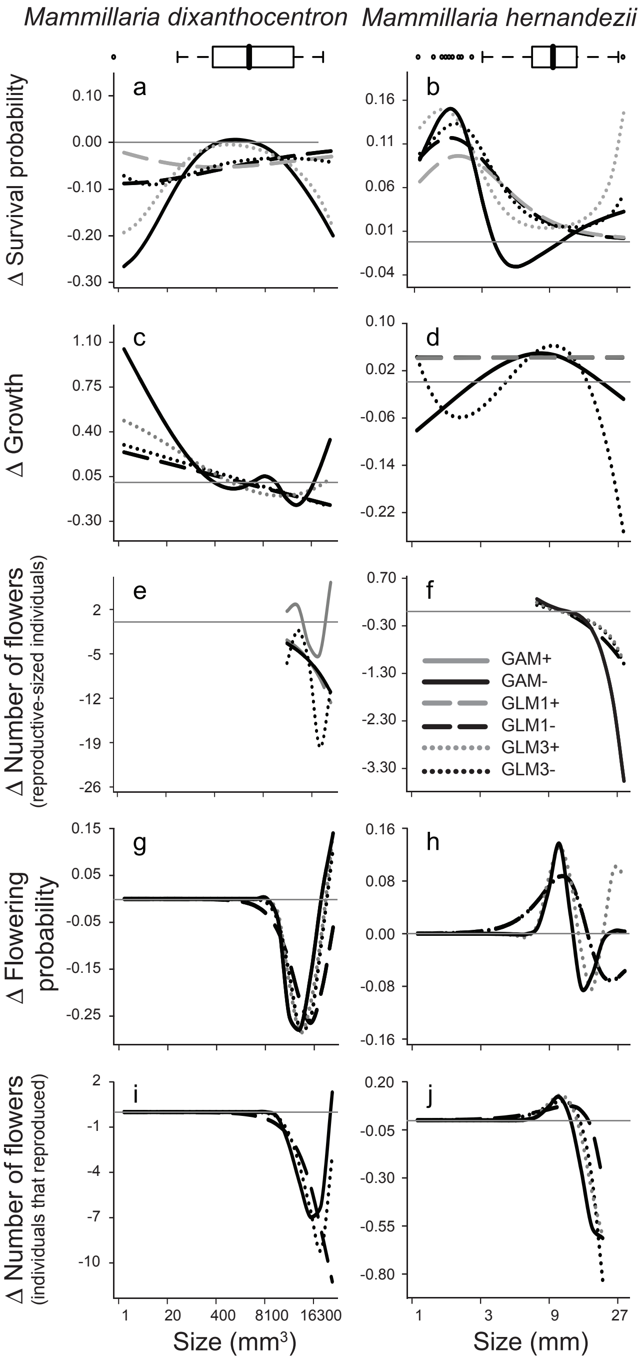

Fig. 1 Changes (Δ) in demographic processes due to chronic anthropogenic disturbance (CAD) on two cactus species, Mammillaria dixanthocentron (left) and M. hernandezii (right), estimated from different models: generalized additive (GAM), linear (GLM1) and cubic (GLM3) models, before (+) and after (-) model simplification. The change in number of flowers was estimated using in e) and f) all individuals larger than a minimum reproductive size, and in i) and j) only those that reproduced in any given year. The axis of zero CAD effect is shown in grey. Only models in which there was a significant effect of CAD are shown. Box plots show the distribution of the plant-size data

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.

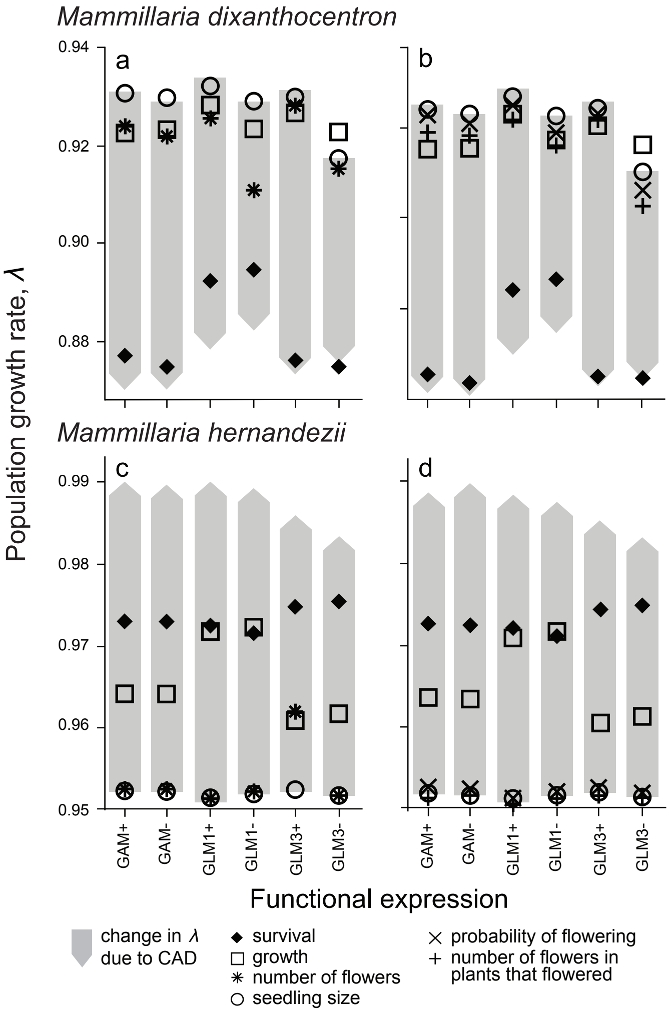

Fig. 2 Population growth rates (λ) of two cactus species obtained from integral projection models differing in functional structure. The flowering process was described through either a) and c) a simple functional description, or b) and d) a more complex one. Demographic processes were modeled using 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

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 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).

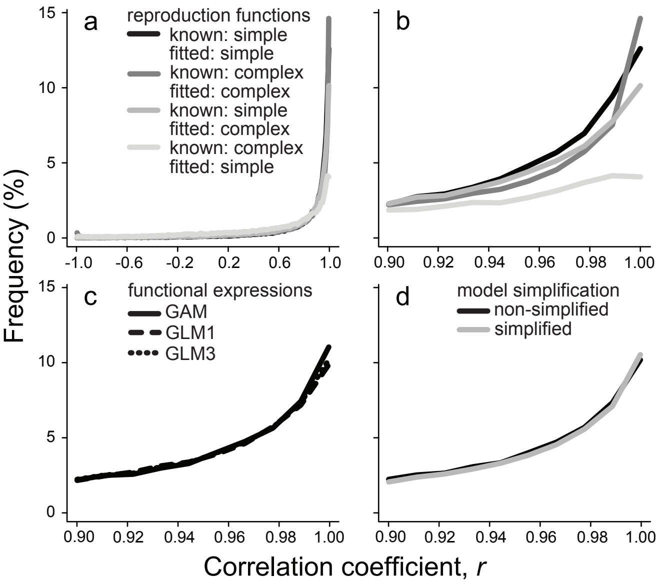

Fig. 3 Frequency of the correlation coefficients between known and estimated contributions of different demographic processes to the differences in population growth rate due to disturbance in simulations employing artificial data. The known contributions were derived from models whose reproduction was 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

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) reconstructed more accurately the population dynamics and its changes with 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.

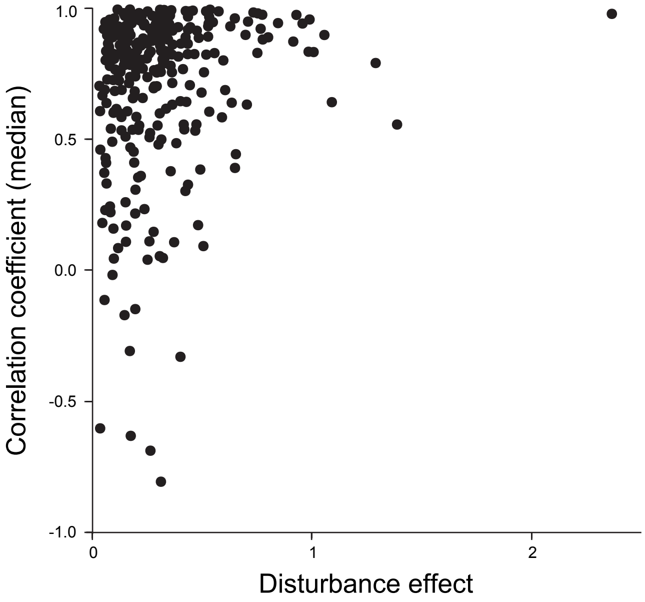

Fig. 4 Influence of the magnitude of disturbance-induced changes in population dynamics on the capability of models to estimate accurately the contributions of different demographic processes to population growth rate. The magnitude of the disturbance effect was calculated as the geometric mean of the 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

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 to be selected.

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 it 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 modelled. 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. In 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 modelling 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; Caswell 2001; de Kroon et al. 2000). Supporting our results, using life table response experiment analysis, 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 life table response experiment analysis, 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 for evaluating 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.

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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, D. F.

Bhattacharyya A (1946) On a measure of divergence between two multinomial populations. Sankhya: The Indian Journal of Statistics 7:401-406

Buhl-Mortensen L (1996) Type-II statistical errors in environmental science and the precautionary principle. Marine Pollution Bulletin 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. Ecological Applications 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, Massachusetts

Chapin III FS, 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. Proceedings of the Royal Society of London Series B-Biological Sciences 270:1829-1838 doi: 10.1098/rsb.2003.2399

Dahlgren JP, Ehrlén J (2009) Linking environmental variation to population dynamics of a forest herb. Journal of Ecology 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. Conservation Biology 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. The American Naturalist 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. Botanical Review 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 Publishing, Malden, Massachusetts

Gray JS (1990) Statistics and the precautionary principle. Marine Pollution Bulletin 21:174-176

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

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

Hanson M (2003) The precautionary principle. In: Page EA, Proops J (eds) Environmental Thought. Current Issues in Ecological Economics. Edward Elgar Publishing, Inc., Northampton, Massachusetts, 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. Biological Conservation 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. Biological Conservation 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. Environmental Health Perspectives 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. Population Ecology 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*. Biological Conservation 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. Conservation Biology 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'. Journal of Arid Environments 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

Miller TEX, Louda SM, Rose KA, Eckberg JO (2009) Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. Ecological Monographs 79:155-172 doi: 10.1890/07-1550.1

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. Journal of Arid Environments 70:356-379 doi: 10.1016/j.jaridenv.2006.12.016

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. Journal of Applied Ecology 46:1048-1053 doi: 10.1111/j.1365-2664.2009.01706.x

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

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

Rees M, Ellner SP (2009) Integral projection models for populations in temporally varying environments. Ecological Monographs 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. Proceedings of the Royal Society of London Series B-Biological Sciences 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. Animal Conservation 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. Journal of Ecology 81:465-476

Singh SP (1998) Chronic disturbance, a principal cause of environmental degradation in developing countries. Environmental Conservation 25:1-2

Soulé ME, Kohm KA (1989) Research Priorities for Conservation Biology. Island Press, Washington, D. C.

Ureta C, Martorell C (2009) Identifying the impacts of chronic anthropogenic disturbance on two threatened cacti to provide guidelines for population-dynamics restoration. Biological Conservation 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. Journal of the Royal Statistical Society Series B-Statistical Methodology 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. Journal of Ecology 98:345-355 doi: 10.1111/j.1365-2745.2009.01626.x

Online Resource 1

Analysis of deviance of the different statistical models examining the effect of size and chronic anthropogenic disturbance on the demographic processes of *Mammillaria dixanthocentron* (Table S1) and *M. hernandezii* (Table S2)

Table S1 Analysis of deviance of the generalized linear (GLM1), cubic (GLM3) and additive (GAM) models to examine the effect of size (x) and chronic anthropogenic disturbance (d) on the demographic processes of *Mammillaria dixanthocentron*. The statistic is a chi-square when error distribution is binomial or Poisson, and Fisher's F when it is normal.

Demographic process	Link function	Error distribution	Model	Term	Parameter value	Statistic	*P*-value
survival: $s(x)$	logit	binomial	GLM1	intercept	-0.059		
				d	-0.067	4.008	0.045
				$\log(x)$	0.245	71.793	< 0.001
				$d \cdot \log(x)$	-0.040	0.527	0.468
			GLM3	intercept	-0.523		
				d	-1.019	4.008	0.045
				$\log(x)$	0.397	71.793	< 0.001
				$[\log(x)]^2$	-0.007	20.135	< 0.001
				$[\log(x)]^3$	0.000	0.277	0.599
				$d \cdot \log(x)$	0.236	0.644	0.422
				$d \cdot [\log(x)]^2$	-0.006	3.356	0.067
				$d \cdot [\log(x)]^3$	-0.001	0.059	0.808
			GAM	d		-2.914	0.110
				spline($\log(x)$)		89.370	< 0.001
growth: $g(x)$	identity	normal	GM1	intercept	0.816		
				d	0.257	0.072	0.789
				$\log(x)$	0.926	13346.706	< 0.001
				$d \cdot \log(x)$	-0.032	4.179	0.041
			GLM3	intercept	2.420		
				d	0.513	0.076	0.783
				$\log(x)$	0.223	14107.410	< 0.001
				$[\log(x)]^2$	0.088	40.629	< 0.001
				$[\log(x)]^3$	-0.003	17.638	< 0.001
				$d \cdot \log(x)$	-0.047	5.034	0.025
				$d \cdot [\log(x)]^2$	-0.008	1.719	0.190
				$d \cdot [\log(x)]^3$	0.001	0.221	0638
			GAM	d		-5.185	0.005
				spline($\log(x)$)		3556.000	< 0.001
number of flowers (whole size range): $n_{fX}(x)$	log	Poisson	GLM1	intercept	-9.476		
				d	-9.231	2986.710	< 0.001
				$\log(x)$	0.942	601.680	< 0.001
				$d \cdot \log(x)$	0.638	85.320	< 0.001
			GLM3	intercept	-47.730		
				d	-1572.000	601.68	< 0.001
				$\log(x)$	6.004	2986.710	< 0.001
				$[\log(x)]^2$	-0.003	178.290	< 0.001
				$[\log(x)]^3$	-31.780	1.710	0.191
				$d \cdot \log(x)$	387.000	11.160	< 0.001
				$d \cdot [\log(x)]^2$	-0.001	1.330	0.249
				$d \cdot [\log(x)]^3$	0.870	35.590	< 0.001
			GAM	d		-627.030	< 0.001
				spline($\log(x)$)		293.500	< 0.001

Table S1 (*continued*). Analysis of deviance of the generalized linear (GLM1), cubic (GLM3) and additive (GAM) models to examine the effect of size (x) and chronic anthropogenic disturbance (d) on the demographic processes of *Mammillaria dixanthocentron*. The statistic is a chi-square when error distribution is binomial or Poisson, and Fisher's F when it is normal.

Demographic process	Link function	Error distribution	Model	Term	Parameter value	Statistic	P-value
flowering probability: $p_f(x)$	logit	binomial	GM1	intercept	-14.268		
				d	-8.719	24.146	< 0.001
				$\log(x)$	1.184	266.411	< 0.001
				$d\cdot\log(x)$	0.627	4.427	0.035
			GLM3	intercept	-419.940		
				d	-203.806	24.146	< 0.001
				$\log(x)$	101.984	266.411	< 0.001
				$[\log(x)]^2$	-8.268	6.889	0.009
				$[\log(x)]^3$	0.224	2.826	0.093
				$d\cdot\log(x)$	47.862	10.020	0.002
				$d\cdot[\log(x)]^2$	-3.841	0.094	0.760
				$d\cdot[\log(x)]^3$	0.105	0.063	0.802
			GAM	d		34.900	< 0.001
				$\text{spline}(\log(x))$		19.29	< 0.001
number of flowers (reproductive size range): $n_{fR}(x)$	log	normal	GLM1	intercept	-3.282		
				d	0.332	7.344	0.008
				$\log(x)$	0.475	11.998	< 0.001
				$d\cdot\log(x)$	-0.095	0.123	0.726
			GLM3	intercept	791.046		
				d	-2095.834	7.860	0.006
				$\log(x)$	-200.261	12.841	< 0.001
				$[\log(x)]^2$	16.847	0.081	0.776
				$[\log(x)]^3$	-0.470	0.469	0.495
				$d\cdot\log(x)$	522.376	0.079	0.779
				$d\cdot[\log(x)]^2$	-43.283	0.036	0.850
				$d\cdot[\log(x)]^3$	1.192	10.138	0.002
			GAM	d		1.454	0.239
				$\log(x)$		2.213	0.074

Table S2 Analysis of deviance of the generalized linear (GLM1), cubic (GLM3) and additive (GAM) models to examine the effect of size (x) and chronic anthropogenic disturbance (d) on the demographic processes of *Mammillaria hernandezii*. The statistic is a chi-square when error distribution is binomial or Poisson, and Fisher's F when it is normal

Demographic process	Link function	Error distribution	Model	Term	Parameter value	Statistic	P-value
survival: $s(x)$	logit	binomial	GLM1	intercept	-1.270		
				d	0.323	0.067	0.796
				$\log(x)$	1.869	268.664	< 0.001
				$d\cdot\log(x)$	0.098	0.135	0.713
			GLM3	intercept	-1.656		
				d	0.716	0.067	0.796
				$\log(x)$	1.473	268.664	< 0.001
				$[\log(x)]^2$	1.154	5.347	0.021
				$[\log(x)]^3$	-0.383	2.999	0.083
				$d\cdot\log(x)$	-0.024	0.008	0.931
				$d\cdot[\log(x)]^2$	-0.407	2.611	0.106
				$d\cdot[\log(x)]^3$	0.160	0.173	0.677
			GAM	d		-1.696	0.245
				spline($\log(x)$)		164.1	< 0.001
growth: $g(x)$	identity	normal	GM1	intercept	0.404		
				d	0.041	0.022	0.883
				$\log(x)$	0.823	6025.368	< 0.001
				$d\cdot\log(x)$	0.000	0.000	0.983
			GLM3	intercept	0.516		
				d	0.076	0.022	0.883
				$\log(x)$	0.756	6087.700	< 0.001
				$[\log(x)]^2$	-0.020	5.329	0.021
				$[\log(x)]^3$	0.011	3.428	0.064
				$d\cdot\log(x)$	-0.389	0.476	0.490
				$d\cdot[\log(x)]^2$	0.335	0.934	0.334
				$d\cdot[\log(x)]^3$	-0.073	7.096	0.008
			GAM	d		-0.059	0.237
				spline($\log(x)$)		2629.000	< 0.001
number of flowers (whole size range): $n_{fX}(x)$	log	Poisson	GLM1	intercept	-10.249		
				d	2.420	0.020	0.880
				$\log(x)$	3.518	476.550	< 0.001
				$d\cdot\log(x)$	-0.857	5.570	0.020
			GLM3	intercept	-15.923		
				d	-74.885	0.020	0.877
				$\log(x)$	5.676	476.550	< 0.001
				$[\log(x)]^2$	0.672	4.620	0.032
				$[\log(x)]^3$	-0.249	0.470	0.492
				$d\cdot\log(x)$	93.481	13.530	< 0.001
				$d\cdot[\log(x)]^2$	-37.658	0.000	0.950
				$d\cdot[\log(x)]^3$	4.922	3.180	0.074
			GAM	d		-16.686	< 0.001
				spline($\log(x)$)		215.3	< 0.001

Table S2 (*continued*). Analysis of deviance of the generalized linear (GLM1), cubic (GLM3) and additive (GAM) models to examine the effect of size (x) and chronic anthropogenic disturbance (d) on the demographic processes of *Mammillaria hernandezii*. The statistic is a chi-square when error distribution is binomial or Poisson, and Fisher's F when it is normal

Demographic process	**Link function**	**Error distribution**	**Model**	**Term**	**Parameter value**	**Statistic**	***P*-value**
flowering probability: $p_f(x)$	logit	binomial	GM1	intercept	-13.267		
				d	4.035	4.580	0.030
				$\log(x)$	4.775	331.670	< 0.001
				$d\cdot\log(x)$	-1.434	5.260	0.020
			GLM3	intercept	-17.065		
				d	-151.903	4.580	0.032
				$\log(x)$	7.077	331.670	< 0.001
				$[\log(x)]^2$	-0.026	1.840	0.175
				$[\log(x)]^3$	-0.112	1.050	0.305
				$d\cdot\log(x)$	185.256	7.240	0.007
				$d\cdot[\log(x)]^2$	-73.808	0.840	0.358
				$d\cdot[\log(x)]^3$	9.637	3.060	0.080
			GAM	d		-17.782	< 0.001
				spline($\log(x)$)		170.7	< 0.001
number of flowers (reproductive size range): $n_{fR}(x)$	log	normal	GLM1	intercept	-2.218		
				d	1.373	20.392	< 0.001
				$\log(x)$	0.934	93.710	< 0.001
				$d\cdot\log(x)$	-0.562	13.117	< 0.001
			GLM3	intercept	4.500		
				d	3.629	22.417	< 0.001
				$\log(x)$	-4.108	103.015	< 0.001
				$[\log(x)]^2$	0.932	41.920	< 0.001
				$[\log(x)]^3$	0.001	0.002	0.041
				$d\cdot\log(x)$	-3.397	4.211	0.784
				$d\cdot[\log(x)]^2$	1.087	0.075	0.968
				$d\cdot[\log(x)]^3$	-0.126	0.013	0.910
			GAM	d		-0.206	0.286
				$\log(x)$		48.840	< 0.001

Online Resource 2

Simulation and analysis of artificial data

Generation of random kernels

The assessment of the robustness of IMPs to variations in functional structure requires testing their performance under several conditions. We developed 14 000 random kernels by generating survival, growth and reproduction functions that were reasonably realistic but encompassed an ample variety of behaviours. In order to model a realistic variety of functional relationships, we started with linear functions of individual size (x) at time t. Because the standard structure of a kernel is

$$k(y,x) = s(x)\cdot g(y,x)+f(y,x), \quad \text{(S1)}$$

and the fecundity was modelled using two alternative functions,

$$f(y,x) = n_{fX}(x)\cdot c\cdot f_s(y), \quad \text{(S2)}$$

and

$$f(y,x) = p_f(x)\cdot n_{fR}(x)\cdot c\cdot f_s(y), \quad \text{(S3)}$$

we needed functions for survival probability, $s(x)$, growth, $g(y,x)$, number of flowers produced by a plant with size x larger that a minimum value, $n_{fX}(x)$, probability of flowering, $p_f(x)$, number of flowers produced by a plant given that it reproduces, $n_{fR}(x)$, and probability density a seedling has of reaching size y at time t+1, $f_s(y)$. Each function had two parameters (intercept and slope), except $f_s(y)$, which was described by a single parameter (mean seedling size) as it does not involve the size of the parent. For $g(y,x)$ and $f_s(y)$ an additional parameter, the standard deviation of the distribution, was included. Therefore, when equation S2 was used to model fecundity, nine parameters determined the dynamics of the population, while eleven parameters described the dynamics when equation S3 was used.

Plant size was assumed to range from 0 to 1. We initially set intervals for the 11 parameters of the kernel so as to produce different demographic behaviours. As in most plants survival, size at time t + 1, and reproduction all increase with size at time t, slopes were restricted to be positive. Because some processes have a ceiling effect (*e.g.*, an already large individual cannot grow much more without exceeding the assumed limit of 1), some dependencies among parameters had to be introduced (Table S3). Parameter values were sampled from a uniform distribution on those intervals. The sampled values were then introduced into the kernel in equation S1, and its λ was computed. Minor changes in the intervals were introduced to warrant a symmetrical distribution of λ values about 1, and to keep most of them in the range 0.8–1.2. A very wide range of demographic behaviours was produced when sampling within these parameter intervals.

Table S3 Intervals for the 13 parameters of the kernel used in the simulation process

Function	**Parameter**	**Lower limit**	**Upper limit**
$s(x)$	Intercept	-3	1
	Slope	3	10
$g(y,x)$	Intercept (g_1)	0.01	0.1
	Slope	$(0.75–g_1)/0.75$	$1–g_1$
	Standard deviation	0.05	0.2
$p_s(x)$	Intercept (p_{s1})	-20	-4
	Slope	$-1.2p_{s1}$	$-1.46p_{s1}$
$n_s(x)$	Intercept (n_{s1})	-2	-1
	Slope	1.5	$2.5–n_{s1}$
$f_s(y)$	Intercept (f_{s1})	0.05	0.2
	Standard deviation	$f_{s1}/2$	$f_{s1}/2$

To assess if IPMs can detect which demographic processes are responsible for the change in λ between two sites (in our case, disturbed and undisturbed sites), we needed a kernel for each one. We first sampled values for all the parameters following the above procedure, and assigned them to the undisturbed population (Figure S1a, solid line). In order to keep the effect of disturbance within a restricted, predictable range (i.e, avoiding extreme, catastrophic effects), a random change ≤ 30 % was introduced to each parameter value. This new set of values was considered to represent the dynamics of the disturbed population (Figure S1a, dashed line).

Because we wanted to apply three functional expressions to the simulated data (generalized additive, first and third order linear models), we needed non-linear functions to describe the demographic processes. If the raw linear functions generated so far were to be used, the best-fitting models would always be straight lines independently of the statistical procedure employed. Thus, we distorted the linear functions produced in the previous steps (*e.g.*, as in Fig S1b) by the following procedure. For each function in the kernel, we divided its image into four intervals delimited by five equidistant points ($y_{\min}$, y_2, y_3, y_4, $y_{\max}$, where $y_{\min}$ and $y_{\max}$ are the image limits). We then chose three random points from a uniform distribution with limits $y_{\min}$ and $y_{\max}$. A cubic spline was interpolated through the coordinates ($y_{\min}$, $y_{\min}$), (y_2,r_1), (y_3,r_2), (y_4,r_3), and ($y_{\max}$,$y_{\max}$) where r_1, r_2 and r_3 are the random points sorted in increasing order (Fig S1c). Sorting was performed to lessen the frequency of, but not to completely discard, very wriggly splines as we would expect demographic processes to vary smoothly with size. The two original linear functions (for the disturbed and undisturbed sites) were then distorted by projecting every point in the

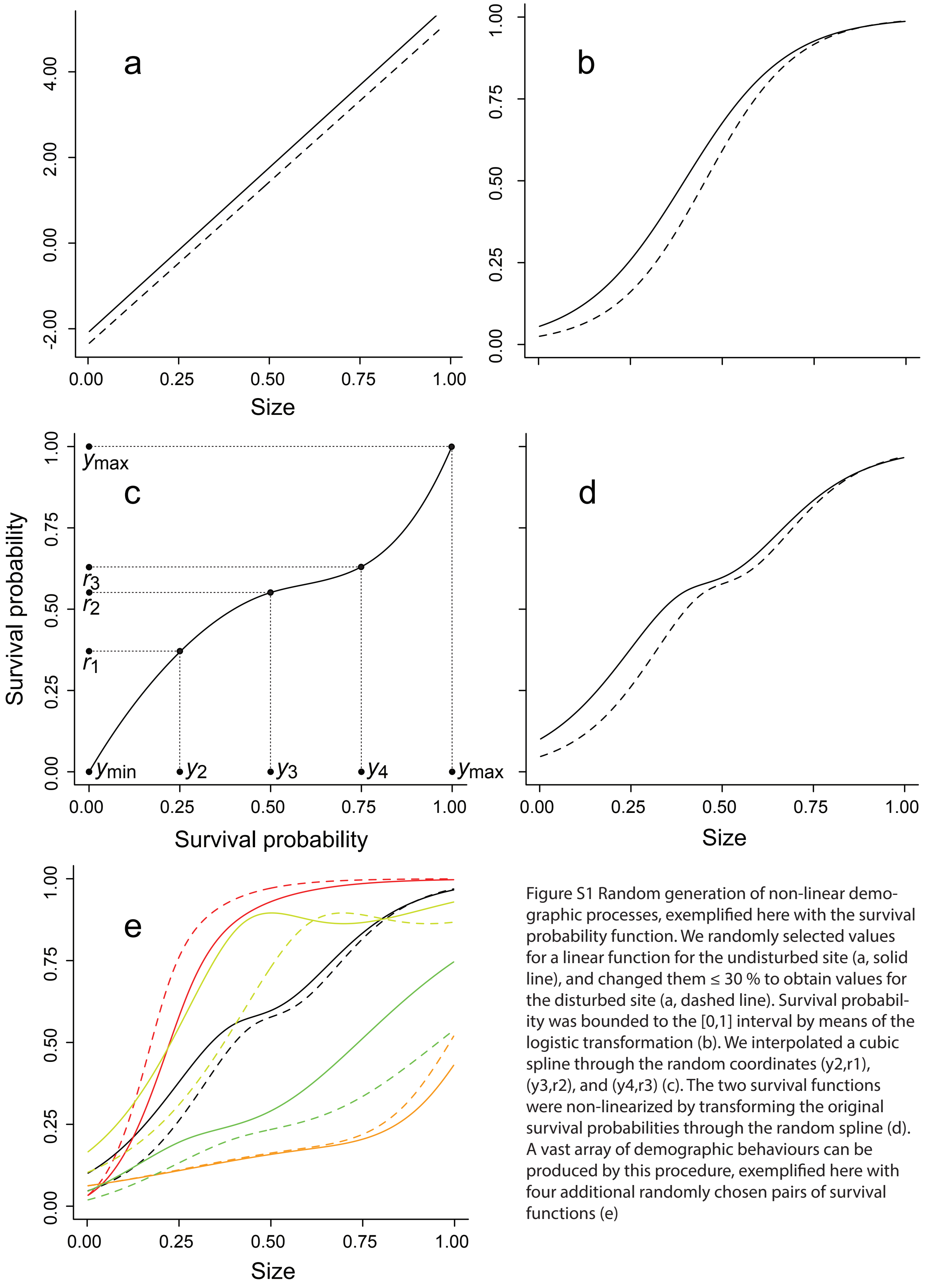


Figure S1 Random generation of non-linear demographic processes, exemplified here with the survival probability function. We randomly selected values for a linear function for the undisturbed site (a, solid line), and changed them ≤ 30 % to obtain values for the disturbed site (a, dashed line). Survival probability was bounded to the [0,1] interval by means of the logistic transformation (b). We interpolated a cubic spline through the random coordinates (y2,r1), (y3,r2), and (y4,r3) (c). The two survival functions were non-linearized by transforming the original survival probabilities through the random spline (d). A vast array of demographic behaviours can be produced by this procedure, exemplified here with four additional randomly chosen pairs of survival functions (e) original image onto the spline's image (Fig S1d). This procedure made it possible to produce a vast array of demographic behaviours, as well as varied degrees of wiggliness (Fig S1e).

The non-linear functions produced for each demographic process were then assembled into a kernel, and its λ value was calculated. Those kernels with $\lambda < 0.8$ or $\lambda > 1.2$ were discarded as these values seemed unrealistic, and a new set of functions was randomly produced. In total, 28 000 pairs of kernels were retained. Each pair of kernels consisted of the models for the disturbed and the undisturbed sites. Half of the pairs were built using equation S2 to model reproduction (type-1 kernels), while the remainder used equation S3 (type-2 kernels).

Generation of artificial data

The hypothetical populations whose dynamics were described by each kernel were sampled to produce the data sets to be used in the statistical model fitting. Samples were generated by randomly evaluating the functions associated to each kernel. We assumed that samples consisted of 1 000 individuals at each site. The initial size of each individual was obtained from a uniform distribution over the whole size range [0,1]. Then, we calculated its expected survival, growth and fecundity values using the equations in the kernel. Finally, the fate of each individual was modelled using the expected values from Bernoulli (survival), normal (growth) and Poisson (reproduction) distributions. The sizes of recruits were sampled from a normal distribution using the respective parameters of the kernel.

Model fitting and performance assessment

The samples resulting from each pair of kernels were used as input data for the fitting of the 12 models described in the *Building IPMs with different functional structures* section in the main text. To evaluate the effect of proposing either a right or wrong model to describe fecundity, we performed two analyses on each data set: one fitting equation S2 (type-1 analysis) and the other equation S3 (type-2 analysis). Thus, we had a set of results where the actual and fitted models matched (type-1 kernels with type-1 analysis, and type-2 kernels with type-2 analysis), and another set where they did not. Thus, 48 models were fitted altogether.

As described in the *Building IPMs…* section, for each of the 48 models, we assessed the contribution of the different demographic processes (represented by the individual functions in equations S1–S3) to the differences in λ between the less and more disturbed populations. Each set of λ values obtained from the fitted models (seven values for type-2 kernels analysed with the type-2 analysis, and six for the remainder combinations) was compared with the actual set of values of the original kernels from where the samples were generated. This comparison was made by means of the Pearson's correlation coefficient (*r*).

Online Resource 3

Demographic processes of *Mammillaria dixanthocentron* and *M. hernandezii* populations on two sites differing in the intensity of chronic anthropogenic disturbance, modeled with different statistical models

Fig. S2 Demographic processes of *Mammillaria dixanthocentron* populations on two sites, differing in the intensity of chronic anthropogenic disturbance, modeled through generalized additive (solid), linear (dashed) and cubic (dotted) models. Models are shown before (grey) and after (black) statistical simplification. No line is shown when CAD's effect was discarded

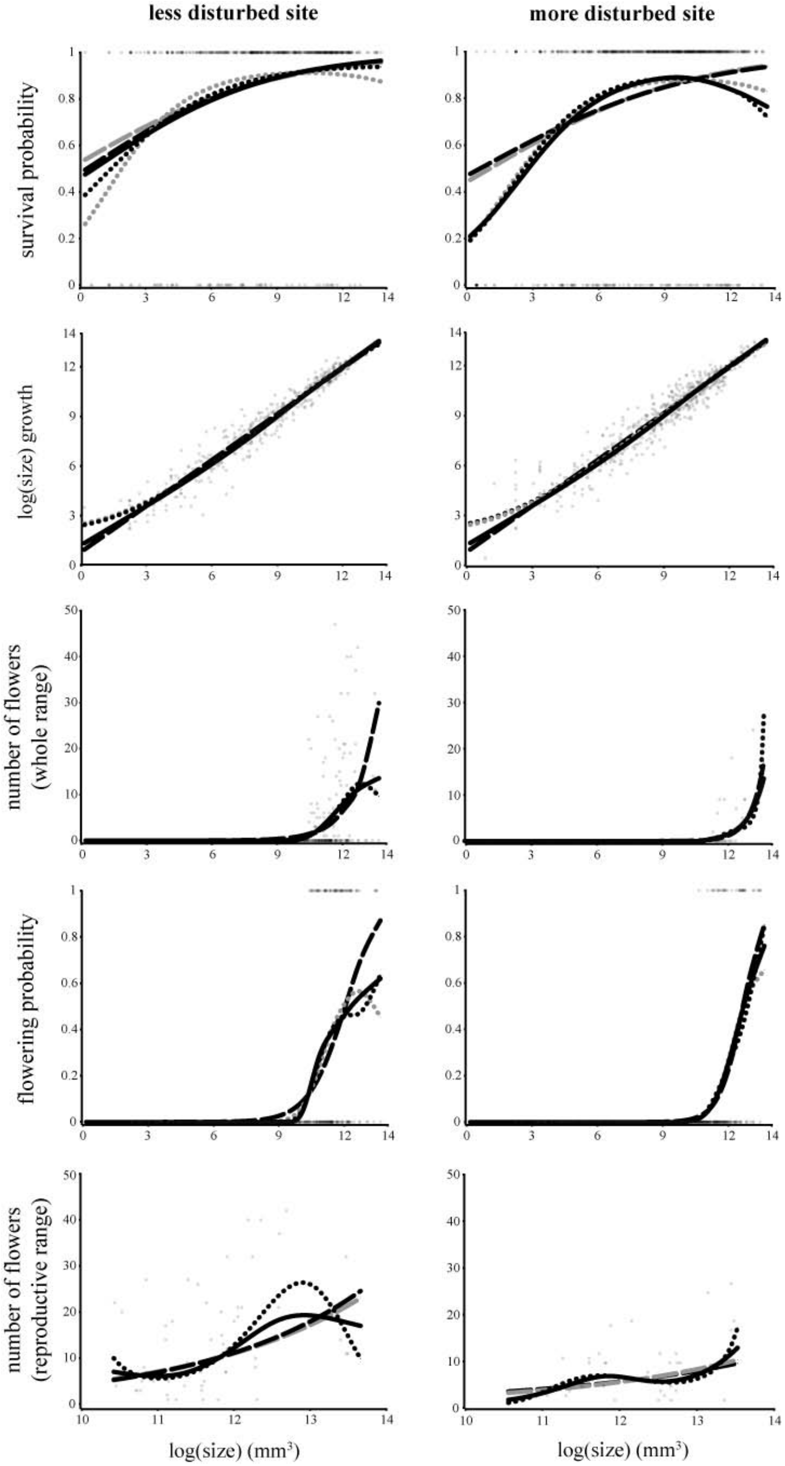
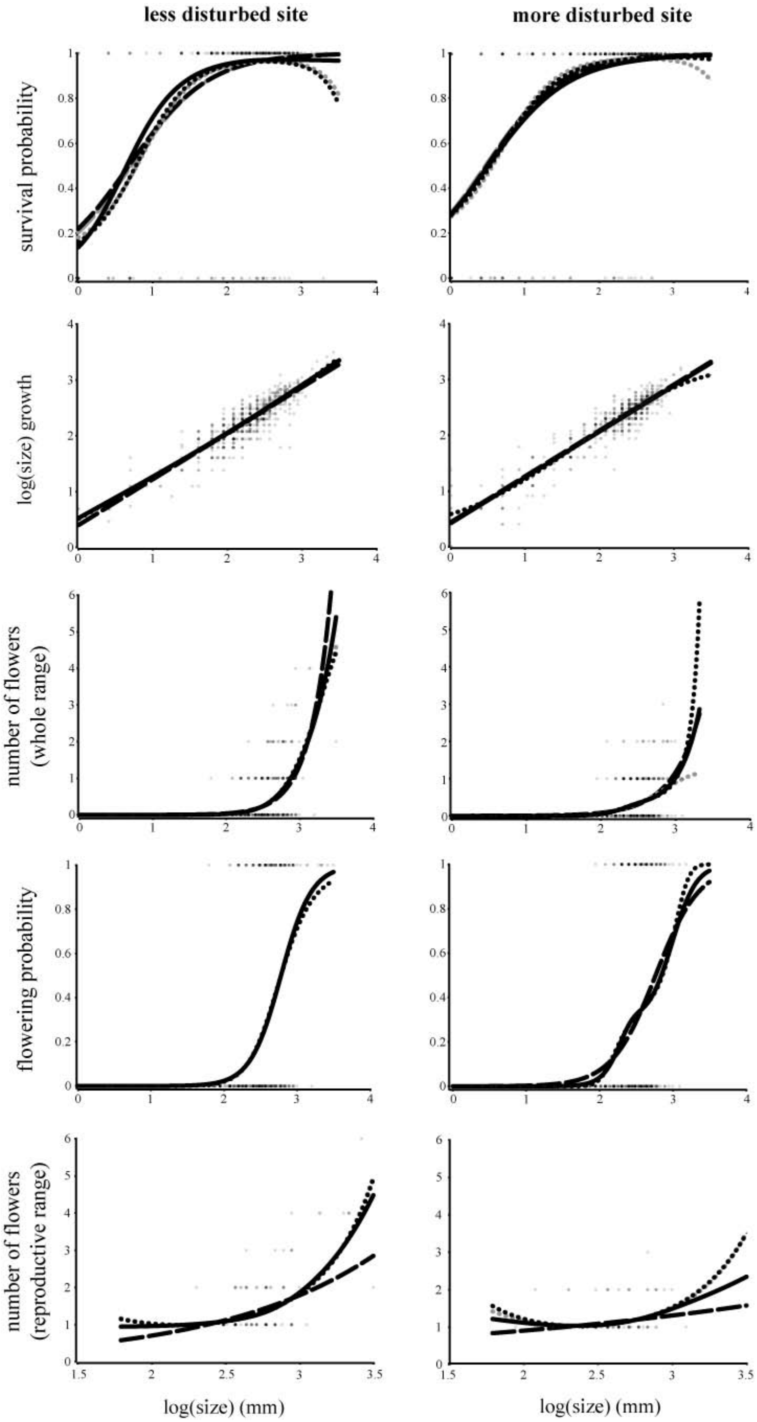


Fig. S3 Demographic processes of *Mammillaria hernandezii* populations on two sites, differing in the intensity of chronic anthropogenic disturbance, modeled through generalized additive (solid), linear (dashed) and cubic (dotted) models. Models are shown before (grey) and after (black) statistical simplification. No line is shown when CAD's effect was discarded.



Capítulo 2

Reconstructing shifts in vital rates driven by long-term environmental change: a new demographic method based on readily available data

E. J. González & C. Martorell. 2013.

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Summary

1. Frequently, vital rates are driven by directional, long-term environmental changes. Many of these are of great importance, such as land degradation, climate change, and succession. Traditional demographic methods assume a constant or stationary environment, and thus are inappropriate to analyze populations subject to these changes. They also require repeat surveys of the individuals as change unfolds. Methods for reconstructing such lengthy processes are needed.

2. We present a model that, based on a time series of population size-structures and densities, reconstructs the impact of directional environmental changes on vital rates. The model uses integral projection models and maximum likelihood to identify the rates that best reconstructs the time series. The procedure was validated with artificial and real data. The former involved simulated species with widely different demographic behaviors. The latter used a chronosequence of populations of an endangered cactus subject to increasing anthropogenic disturbance.
3. In our simulations, the vital rates and their change were always reconstructed accurately. Nevertheless, the model frequently produced alternative results. The use of coarse knowledge of the species' biology (whether vital rates increase or decrease with size or their plausible values) allowed the correct rates to be identified with a 90 % success rate.
4. With real data, the model correctly reconstructed the effects of disturbance on vital rates. These effects were previously known from two populations for which demographic data were available. Our procedure seems robust, as the data violated several of the model's assumptions.
5. Time series of size structures and densities contain the necessary information to reconstruct changing vital-rates. However, additional biological knowledge may be required to provide reliable results. Because time series of size structures and densities are available for many species or can be rapidly generated, our model can contribute to understand populations that face highly pressing environmental problems.

Key-words

Environmental drivers, human impacts, integral projection models, population biology, population structure, time series.

Introduction

Understanding the effects of the environment on populations is central to ecology (Heller & Zavaleta 2009; Pereira *et al.* 2010; Crone *et al.* 2011). However, many environmental drivers of population change, such as land degradation, climate change, pollutant build-up, ocean acidification, and succession, operate on a long-term, directional basis (Singh 1998; Parr *et al.* 2003; Kroeker *et al.* 2010; Wake 2012). The timescales involved make the study of the impact of environmental change on vital rates (survival, growth and reproduction) impracticable. The correct identification of such impact will allow conservation efforts to be directed more appropriately, to better understand the basis of population change, or even to track the evolutionary changes in life-history traits through time. This calls for specific methods that tackle this problem (Doak & Morris 1999; Pereira *et al.* 2010; Crone *et al.* 2011).

Traditional demographic modeling does not provide a solution, as it often assumes that environmental change does not occur in a directional fashion (Caswell 2001; Ellner & Rees 2007). Nevertheless, if the environmental driver we are studying changes directionally, population would never reach stability, which is usually the focus of traditional models. Assuming stability in a changing population leads to biased conclusions (Koons *et al.,* 2005). Furthermore, traditional models use repeat surveys of the individuals as input (Caswell 2001). Doing this for the decades or centuries required for environmental change to unfold is impracticable. A substitute, but also costly, approach would be to survey over a representative time period the individuals of a series of populations at different stages of environmental change (Dahlgren & Ehrlén 2011). However, if we are to accomplish global goals such as the assessment of the conservation status and long-term threats for all plant species by 2020 (COP 10 2010), a faster and cheaper alternative to such traditional demographic methods becomes imperative.

A viable approach would be to use time series of static, population-level data, such as population densities and structures, to reconstruct the species vital rates and their change through time as the environment changes. Such datasets have been recorded over several years for different species in the context of forestry, hunting, fisheries, and long-term ecological research (Waters 1999; Hobbie *et al.* 2003; Parr *et al.* 2003; Clucas 2011). Also, this kind of data can be rapidly collected for several populations that represent different stages of environmental change, and integrated into a chronosequence (Matthews & Whittaker 1987; Mori, Mizumachi & Komiyama 2007). This reconstruction of vital rates from static data has been successfully applied in the context of fisheries stock assessment (e.g., Fournier, Hampton & Sibert 1998; Quinn 2003; Maury, Faugeras & Restrepo 2005; Hilborn 2012). However, the translation of these models into an ecological context is not straightforward, as the amount of information and biological knowledge available in fisheries rarely exists for non-commercial species (Quinn 2003). For instance, the available data for most species will usually be sparsely distributed in time, and not surveyed annually as in fisheries. Also, the demographic behavior of the species that ecologists study can be quite complex, as in many species the vital rates depend on size, rather than on age. In plants, for example, organisms having originally different sizes may end up having the same size after one year, due to growth, shrinkage, or stasis (Caswell 2001), thus complicating the relationship between size structure and vital rates. Therefore, a model is needed that accommodates these complexities as well as a wide variety of life cycles.

As a time series of static, population-level data does not inform on the fate of individuals, more than one combination of vital rates would be expected to lead to the same series. For instance, a high proportion of seedlings in a population may result from a large fecundity, low seedling mortality, or impediments to seedling growth. In a model that uses population-level data, Ghosh, Gelfand & Clark (2012) envisage this problem. However, as their aim is to forecast population structures, they circumvent the problem by making assumptions on the vital rates that simplify their model but that do not reflect their behavior at the individual level (Ellner 2012). However, if we are interested in correctly reconstructing vital rates, we cannot make such assumptions.

In this paper we develop a model that, based on a time series of population size structures and densities, reconstructs the shifts in vital rates caused by a directionally changing environmental driver. The model was validated with artificially generated data and with data from a threatened cactus subject to long-term human disturbance. We show that, although more than one scenario may be obtained, the correct solution is always provided by the model, and that basic information on the biology of the species is frequently enough to discard alternative solutions.

The model

Our model attempts to reconstruct the vital rates (survival, growth and reproduction) and their change over time based on a time series of size structures and densities. If these rates change as the environmental driver shifts, the structure and density of the population would be expected to evolve accordingly. The model explores a variety of vital rates, seeking the ones that produce the size structures and densities that best resemble the observed time series. A succinct description of the model is presented below. Please refer to Appendix 1 for the full details.

The vital rates of the size-structured population were modeled by means of an integral projection model (IPM; Easterling, Ellner & Dixon 2000). An IPM integrates the vital rates into a function k known as the kernel. This function establishes the log-sizes y that individuals of log-size x may reach from time t to t+1, as well as the number and sizes of their descendants. The IPM is expressed through the equation

$$n(y,t+1) = \int k(y,x,t) \cdot n(x,t) dx, \qquad \text{eqn. 1}$$

where n is the size structure of the population. Note that, in our model, k is a function of time because the vital rates are driven by environmental change.

The kernel comprises the functions associated to the survival probability, s, growth, g, number of newborns, f_1, and the sizes of these, f_2, which relate as

$$k(y,x,t) = s(x,t) \cdot g(y,x,t) + f_1(x,t) \cdot f_2(y,t). \qquad \text{eqn. 2}$$

We used the following simple functions to determine these vital rates:

$$\text{logit}(s(x,t)) = \beta_1 + \beta_2 \cdot x + \beta_3 \cdot t + \beta_4 \cdot x \cdot t \qquad \text{eqns. 3}$$

$$g(y,x,t) \sim \text{normal}(\mu = \beta_5 + \beta_6 \cdot x + \beta_7 \cdot t + \beta_8 \cdot x \cdot t, \sigma^2 = \beta_9)$$

$$\log(f_1(x,t)) = \beta_{10} + \beta_{11} \cdot x + \beta_{12} \cdot t + \beta_{13} \cdot x \cdot t$$

$$f_2(y,t) \sim \text{normal}(\mu = \beta_{14} + \beta_{15} \cdot t, \sigma^2 = \beta_{16})$$

As can be seen from these equations, the vital rates and their change through time are determined by 16 parameters.

To assess whether any given set of 16 parameter values is able to reproduce the observed time series, we first calculated the vital rates for every year in the period over which environmental change takes place by substituting the parameter values in equations 3. We then calculated the time series of size structures through the iteration of equation 1. To do so, an initial size structure, $n(x,t_0)$, is required. If no environmental change had occurred before the initial time (i.e., if the environment had remained constant), it would be safe to assume that the population was in its stable state (Caswell 2001). Therefore, in the first iteration of equation 1 we used the stable (asymptotic) size-structure associated with the vital rates at the initial observed time. The time series of densities was obtained by integrating the size structures. Finally, we compared these two time series with the observed ones through the composite log-likelihood:

$$l = l_n + w \cdot l_d, \qquad \text{eqn. 4}$$

where l_n and l_d, are the log-likelihoods associated with the size structures and to the densities, respectively, and w is a weighting factor of the relative importance of the fit of the observed size-structures *vs.* that of the observed population densities. Because at each observed point in time there is only one datum for density, but several for size structure, not using a weighting factor could belittle the contribution of density to l. The right value for w was determined experimentally (see below). The values of the 16 parameters that resulted in the highest l-value determined the kernel that best resembled the observed data.

Material and methods

We performed two validation procedures: one using 10 artificial species for which we simulated time series of size structures and densities, and another using the threatened cactus *Mammillaria dixanthocentron* Backeb. The latter data come from a chronosequence of 11 populations that represent different stages of degradation due to chronic anthropogenic disturbance (CAD). For two of these populations the vital rates were known from repeat surveys (Ureta & Martorell 2009). Both validations were conducted by comparing the vital rates reconstructed by the model with the known ones.

Artificial species

We randomly generated the vital rates of 10 different artificial species by: (1) Establishing intervals for the 16 kernel parameters ample enough to accommodate a wide set of possible demographic behaviors: each vital rate could relate with size and time in a positive or negative way, or even not be affected by any of them. (2) Randomly choosing parameter values within these intervals to obtain the kernel for each artificial species. The resulting species had very different demographic behaviors (see Appendix 2 for details and Appendix 3 for a graphical representation of the behaviors).

We then generated a time series of size structures and densities for each species by (3) iterating the kernel over a time interval of 100 years following the procedure described in the Model section. (4) Randomly choosing 10 points in time in the range 1–100 to simulate the likely scenario in which the population is not systematically sampled, and data are available for a few, sparse years. (5) Generating samples of the population at the selected points in time. We assumed that sampling effort was constant, so that sample size was proportional to density. To introduce sampling error, the number of individuals sampled at each of the 10 points in time was simulated from a lognormal distribution with mean equal to the population density at that time. The size of each individual was obtained through a Monte Carlo simulation using the size structure of the year in question as the probability distribution (see Appendix 2).

We used the simulated time series as input to the model. To maximize the likelihood (equation 4), we used the Automatic Differentiation Model Builder (ADMB; Fournier *et al.* 2012; see Appendix 4 for the model code). As it happens when complex functions are optimized, the program may reach different maxima depending on the starting parameter values (Myung 2003). Therefore, we tried 41 different initial sets of values. These were generated by introducing increasingly larger errors (0, 5, 10, 25 and 50 %) to the parameter values of the known kernel (see Appendix 2). This allowed us to evaluate how close the initial values had to be from the known ones to correctly reconstruct the kernel. Additionally, to experimentally assess the effect of w (equation 4), the 41 sets of initial values were run with w-values of 0, 1, 10, 100, and 1000. To assess whether the vital rates were correctly reconstructed, the Pearson correlation coefficient between the known and obtained survival, growth and fecundity functions (s, g, and f_1 in equation 2) was calculated. These three values, together with the correlation between the reconstructed and observed densities (r_d), were averaged and a mean coefficient (r_m) was calculated and used as an overall measure of fit.

When more than one solution is obtained by an optimization procedure, the researcher needs criteria to discard the incorrect ones. Two different approaches may be used. First, the researcher may resort to goodness-of-fit measures such as the likelihood associated with the size structures (l_n in equation 4), or the correlation between the reconstructed and observed densities (r_d). Second, the decision may be based on biological knowledge of the species: the researcher may discard solutions that do not match the expected relations between size and vital rates, or the values of the latter are unrealistic.

Real species: *Mammillaria dixanthocentron*

Mammillaria dixanthocentron (Fig. 1) is a long-lived globose cactus that grows in tropical and temperate forests in the Mexican states of Puebla and Oaxaca. The region has experienced CAD since pre-Columbian times (McAuliffe *et al.* 2001), resulting in a mosaic of patches at different stages of degradation. Through demographic models, we know that this species responds negatively to CAD (Ureta & Martorell 2009).

Figure 1. *Mammillaria dixanthocentron* Backeb.

CAD is characterized by a long-term series of frequent, low-intensity disturbance events (Singh 1998). It is a multivariate driver typical of traditional management forms such as extensive grazing, branch cutting, and extraction of non-timber forest products, and has a cumulative effect over time (Singh 1998; Martorell & Peters 2009). Thus, it can be assumed that more disturbed populations have been exposed to CAD for a longer time, and that in the past they resembled the less disturbed populations (i.e., chronosequence assumptions hold; Pickett 1989).

Eleven populations that differed in CAD were studied. In each one, the individuals in a variable number of 50 × 4 m random transects were counted, and their diameter and height measured (see Martorell & Peters 2009 for details). Plant size was defined as the volume of a cylinder. We measured CAD intensity using the Martorell & Peters' index (2009). The rate of increase in disturbance was estimated by measuring CAD at 32 sites (eight of which were *M. dixanthocentron*'s study sites) in 1998 and 2010. We found that CAD increases linearly over time, with an annual rate equal to the mean difference in CAD intensity among these 32 sites divided by 12 years. With this figure, we estimated the times since CAD onset for the 11 study sites.

A modification to the kernel was required to achieve biological realism: as in this species survival probability increases with size, the logistic survival function used for artificial species (*s* in equations 3) may estimate zero mortality in the largest individuals. To avoid this, we modified the function by introducing an upper limit different from one that was allowed to change through time. This limit, $s_{max}(t) = [1+\exp(\beta_1 + \beta_2 \cdot t)]^{-1}$, was multiplied by the original function, raising the number of kernel parameters to 18.

We ran the model using the size structures and densities observed at the 11 sites as input. As before, we set wide parameter intervals, allowing ADMB to select from very contrasting demographic behaviors. However, the intervals of the parameters associated with the effect of size over survival and fecundity were restricted to increase with size as it happens in cacti (Godínez-Álvarez *et al.* 2003). Despite this restriction, the interaction between size and time (which could not be restricted without biasing the results) could still modify the relation between size and survival/fecundity as time passes by. One hundred starting points were randomly selected within the parameter intervals, and we used the same *w* values as before. We compared the reconstructed vital rates with the known ones of two *M. dixanthocentron* populations that differ in the intensity of CAD they experience (Ureta & Martorell 2009).

Results

Validation with artificial species

In all the artificial species, a solution with an r_m higher than 0.9 was obtained, indicating that the correct vital rates were reconstructed very accurately (see Appendix 3 for a graphical representation of the solutions). However, incorrect solutions were also produced in nine of these species (Table 1). The goodness-of-fit approach to solution selection was ineffective, as neither l_n nor r_d were consistently higher for the correct one (Table 1). The biological-knowledge-based approach enabled us to distinguish two types of incorrect results. *Type 1:* Solutions that grossly misrepresent the species biology. In these cases, the reconstructed relationship between size and vital rates either had an opposite sign to that known for the species, or strong size-dependence of these rates was reconstructed when none existed. Most incorrect solutions (94 %) were in this category. *Type 2:* Biologically plausible solutions that could not be discarded. For example, all types of solutions were obtained for the problematic species 3. The correct solution accurately reconstructed the actual vital rates (Fig. 2a–b). A type-1 solution was discarded based on its incorrect reconstruction of fecundity: in this case, the number of seedlings was independent of plant size, while a positive relationship could be expected for the species (Fig. 2c). The correct relationship between size and vital rates was found in a type-2 solution, where fecundity was erroneously reconstructed as decreasing with time (Fig. 2d).

When population densities were not considered ($w = 0$), the obtained solutions were often incorrect (Table 1). Low, non-zero w-values frequently produced the best results: after discarding type-1 incorrect results, a single correct solution remained in seven species with $w = 1$ (species 1, 4, 5, 6, 7, 9 and 10; Table 1). However, in species 3 with this w-value, a type-2 result arose which wrongly reconstructed the change through time of the survival probability (solution 3.2 in Appendix 3); although higher w-values produced good results, no criteria could be used to discriminate the wrong reconstructions from the correct ones. For species 2 and 8, no biologically realistic solutions were produced with $w < 1000$ and 100, respectively; with these values, a single realistic solution was obtained. Nevertheless, large w-values increased the chances of observing type-2 results in most species (Table 1).

Increasing the error in the vector of starting parameter values diminished the probability of finding the correct solution (binary regression of the ratio of correct:incorrect solutions on the amount of error: $\chi^2 = 5.51$, $P = 0.018$). However, the model was relatively robust, as the probability of finding a correct solution changed from 0.59 if the initial parameter values have no error, to 0.49 if error is large (Fig. 3, solid line). The ratio of type-2:type-1 incorrect solutions did not depend on the amount of error in the initial guess ($\chi^2 = 3.08$, $P = 0.079$; Fig. 3, dotted line). In some cases,

Table 1. Solutions obtained by the model for the artificial species. ID: species identifier, *w*: factor weighting the fit of the population densities, r_m: mean correlation between the observed and reconstructed vital rates, r_d: correlation between the observed and reconstructed population densities, l_n: log-likelihood of the reconstructed size-structures. Bold: correct solution, roman: biologically unrealistic (type-1) solution, italics: biologically realistic but incorrect (type-2) solution. See Appendix 3 for a graphical representation of these solutions.

ID	*w* = 0			*w* = 1			*w* = 10		
	r_m	r_d	l_n	r_m	r_d	l_n	r_m	r_d	l_n
1	**0.82**	**0.40**	**-51341**	**0.94**	**0.88**	**-51342**	0.79	0.89	-51344
				0.78	0.88	-51342			
2	**0.5089**	**-0.86**	**-76294**	0.84	0.97	-76294	0.84	0.97	-76295
	0.38	-0.86	-76294	0.82	0.97	-76303	0.82	0.97	-76306
3	0.6652	0.7313	-15763	*0.84*	*0.99*	*-15764*	**0.97**	**0.99**	**-15766**
							0.69	0.99	-15779
4	0.60	0.15	-48879	**0.98**	**0.92**	**-48880**	**0.98**	**0.92**	**-48880**
	0.51	**-0.91**	**-48879**	0.33	-0.83	-48888	0.82	0.92	-48881
	0.34	-0.88	-48878						
	0.34	-0.90	-48879						
	0.13	-0.91	-48880						
5	**0.99**	**0.99**	**-935449**	**0.99**	**0.99**	**-935449**	**0.99**	**0.99**	**-935449**
6	**0.90**	**1.00**	**-371092**	**1.00**	**1.00**	**-371094**	**1.00**	**1.00**	**-371097**
				0.54	0.90	-266122			
7	0.93	0.9495	-171629	**0.99**	**0.98**	**-195823**	0.93	0.95	-171629
	0.81	0.9495	-171731				0.81	0.95	-171732
	0.55	1.00	-160253				0.55	1.00	-160255
8	0.78	0.88	-84496	0.84	1.00	-84497	0.87	1.00	-84497
	0.49	-0.40	-84497	0.65	0.88	-84497	0.38	1.00	-84498
	0.40	0.8624	-84497	0.36	1.00	-84498			
	0.11	-0.24	-84877						
9	**0.97**	**0.97**	**-610033**	**0.98**	**0.98**	**-610035**	0.98	0.97	-610033
	0.58	0.72	-610126				0.58	0.72	-610126
10	**1.00**	**1.00**	**-341008**	**1.00**	**0.99**	**-368697**	**1.00**	**0.99**	**-368698**
	0.64	0.9782	-341117	0.63	0.99	-368804			

ADMB was unable to find any solution at all. This occurred more frequently when poor initial values were provided ($\chi^2 = 198.79$, $P < 0.001$; Fig. 3, dashed line), meaning that more computational time is required to find a solution when less biological knowledge is available.

Validation with the real species

The application of the model to *M. dixanthocentron* resulted in a solution that was similar to the vital rates obtained from the two populations (Fig. 4a–c). The 500 ADMB runs (100 starting points with five *w* values) resulted in the identification of 10 solutions: three with *w* = 0, two with *w* = 1, four with *w* = 100, and one with *w* = 1000. A visual inspection of the reconstructed vital rates

Table 1. *(cont.)* Solutions obtained by the model for the artificial species. ID: species identifier, w: factor weighting the fit of the population densities, r_m: mean correlation between the observed and reconstructed vital rates, r_d: correlation between the observed and reconstructed population densities, l_n: log-likelihood of the reconstructed size-structures. Bold: correct solution, roman: biologically unrealistic (type-1) solution, italics: biologically realistic but incorrect (type-2) solution. See Appendix 3 for a graphical representation of these solutions.

ID	w = 100			w = 1000		
	r_m	r_d	l_n	r_m	r_d	l_n
1	0.73	0.90	-51374	0.73	0.99	-53032
2	0.84	0.97	-76296	**0.95**	**0.91**	**-76319**
				0.84	0.97	-76311
				0.49	0.98	-79152
3	**0.96**	**1.00**	**-15828**	**0.99**	**0.99**	**-15861**
	0.85	1.00	-15815	*0.94*	*1.00*	*-17043*
	0.69	0.99	-15797	0.68	0.99	-16113
	0.59	1.00	-15857	0.59	1.00	-17397
				0.44	1.00	-17351
4	**0.93**	**0.91**	**-48952**	*0.93*	*0.92*	*-49082*
	0.93	**0.91**	**-48955**	*0.75*	*0.97*	*-51017*
	0.91	*0.92*	*-48890*	0.60	0.96	-49438
	0.88	0.92	-48883			
	0.67	0.92	-48986			
	0.56	0.92	-48901			
	0.56	0.92	-48900			
5	**0.99**	**0.99**	**-935456**	**0.99**	**0.99**	**-935527**
				0.95	**0.95**	**-953078**
6	**0.99**	**1.00**	**-371100**	**0.99**	**1.00**	**-371123**
7	0.94	0.95	-171765	0.57	1.00	-168163
	0.79	0.95	-171820			
	0.55	0.99	-160562			
8	**0.95**	**1.00**	**-84498**	0.85	1.00	-84519
	0.85	1.00	-84498	0.85	1.00	-84520
	0.39	1.00	-84514.5	0.42	1.00	-84757
9	**0.98**	**0.98**	**-610036**	**0.98**	**0.98**	**-610037**
	0.66	0.97	-611245			
10	0.94	1.00	-341073	0.6396	1.00	-341314
	0.64	1.00	-341073	0.59	1.00	-341145

allowed to discard nine of these solutions as biologically unrealistic (i.e. type-1 solutions; see Appendix 5): eight presented survival probabilities over 80 % for seedlings, which are known to present very low survival probabilities in cacti (Godínez-Álvarez et al. 2003; Ortega-Baes et al. 2010). Another solution was discarded as its fecundity decreased with size, a pattern not expected in plants (Aarssen & Taylor 1992; Weiner et al. 2009). Therefore, only one solution was considered as biologically realistic. This solution reached the limits of seven parameter intervals; however, increasing such intervals did not result in better solutions, but in unrealistic ones such as cacti producing extremely large seedlings (not shown).

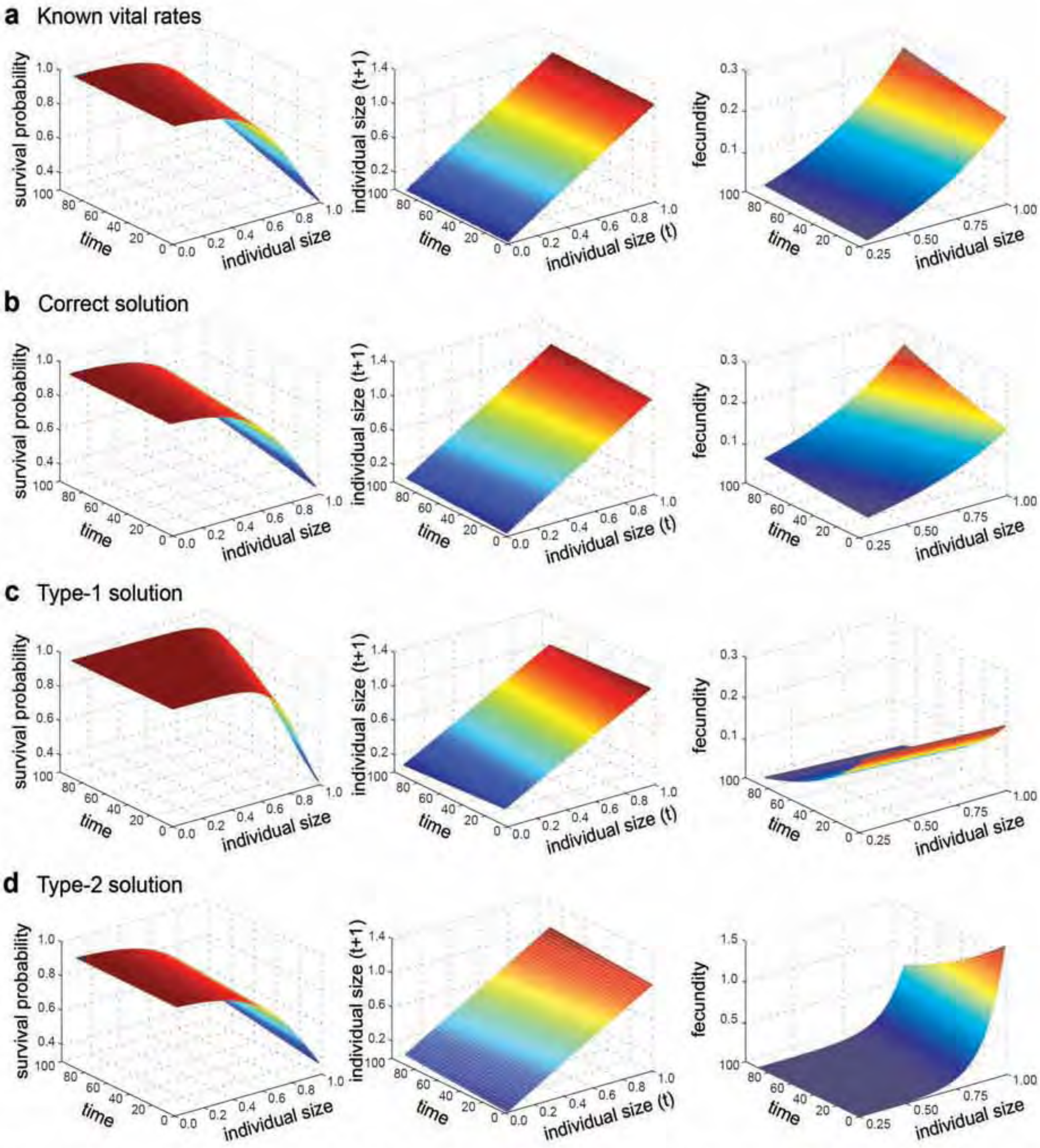

Figure 2. Different kinds of solutions produced by the model. (a) Known vital rates and their change through time for artificial species 3; (b) correct reconstruction; (c) incorrect reconstruction that could be discarded (type-1 solution) because the size-fecundity relation is not expected; (d) erroneous reconstruction that was biologically feasible (type-2 solution) but wrongly estimated that fecundity decreases with time.

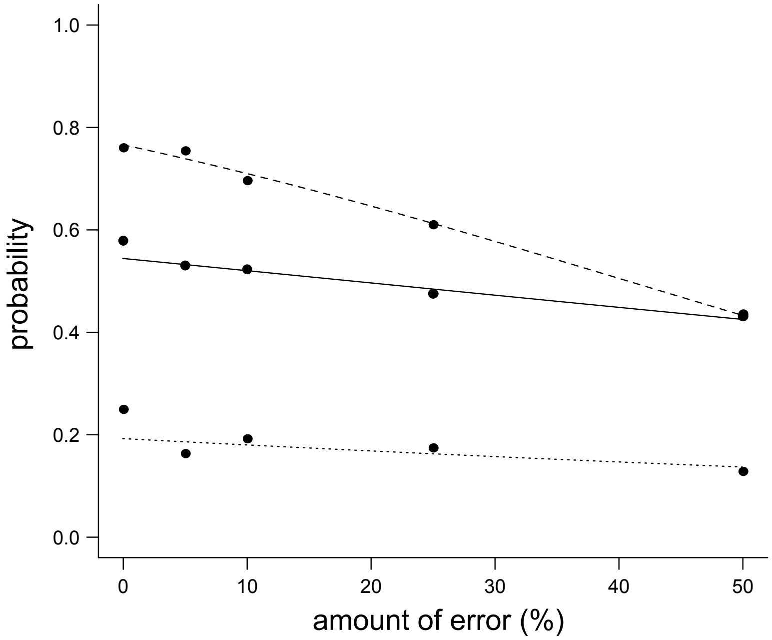

Figure 3. Probabilities of obtaining different results depending on the error in the initial parameters provided to the model. Dashed line: probability of finding vs. not finding a solution. Dotted line: ratio of type-2 to type-1 incorrect solutions (see Results). Solid line: ratio of correct to incorrect solutions.

Discussion

The model we present constitutes a viable alternative to model vital rates when repeat surveys of individuals are too costly, labor-intensive, or simply impossible to conduct. Its major advantage is the data that it uses as input: if we want to understand the demographic response of a species to long-term environmental change, we only require a series of size-structures and densities distributed over time. The model was successful using even very incomplete time series as input. Artificial data showed that the model is able to achieve its goal with a 90 % success rate when its assumptions are met. Moreover, real data showed that our procedure is robust to violations of the assumptions. Nevertheless, a rough knowledge of the species biology is essential to discard biologically implausible (type-1) solutions.

Artificial species: the ideal scenario

The simulation of artificial populations showed that the model successfully reconstructs the sought vital rates under a scenario where all assumptions were fulfilled (see Appendix 1 for a list of model assumptions). The demographic behavior of the artificial species was always correctly reconstructed. Thus, temporally sparse size-structures and densities contain the necessary information to reconstruct the correct species' response to long-term environmental change. However, this information was not sufficient, as additional knowledge is required to discriminate among competing solutions, which were obtained in 60 % of the cases. Nevertheless, even biological knowledge may sometimes not suffice, as type-2 solutions can also occur.

The question then arises on which solution represents the correct reconstruction. Traditional statistical methods used for this purpose were unsuccessful. From real data, the user can only calculate the correlation coefficient between the observed and estimated densities (r_d) and the likelihood associated with the size structures (l_n). However, these statistics did not always have the highest values associated with the correct solution, and thus should not (nor those statistics derived from likelihood, such as AIC) be used as a selection criterion. This called for a different selection strategy.

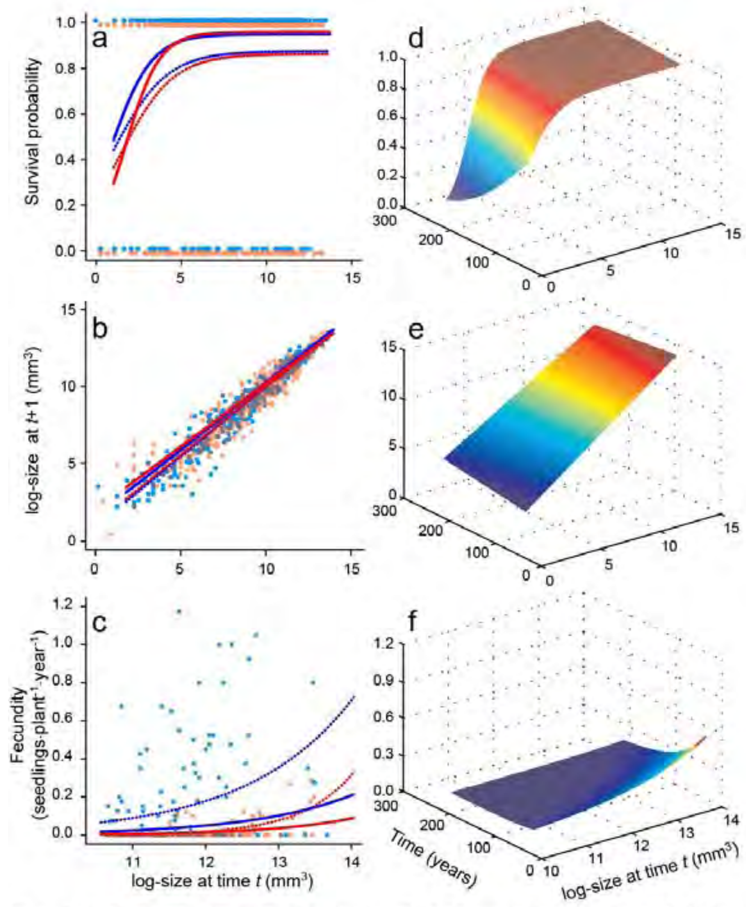

Figure 4. Reconstructed vital rates of *M. dixanthocentron* and their change due to chronic anthropogenic disturbance. Left panels: comparison of the observed (dashed lines) and reconstructed (solid line) rates at the less (blue) and more (red) disturbed sites. Right panels: reconstructed effect of disturbance on the vital rates along the entire time axis.

The successful identification of the correct solution can frequently be achieved through an assessment of the results using minimal biological knowledge. This was the case of the real dataset and in 90 % of the artificial species (Table 1). Most of the incorrect solutions were discarded because the relationship between size and vital rates was opposite to that expected for the species. This is a very general level of knowledge: for instance, it is known that larger plants have higher fecundities (Aarssen & Taylor 1992; Weiner *et al.* 2009), and that survival is lower in seedlings than in established plants (Harper & White 1974). Also, the user would expect parameters to take certain values: e.g., in mammals litter-size ranges are well known (Haysson, van Tienhoven & van Tienhoven 1993). This is indeed a large percentage considering the limited information available to the model and the researcher. The success rate can also be increased if the values used to initiate the likelihood maximization procedure are accurate (Fig. 3). Finally, biological knowledge may be incorporated directly into the analysis through a Bayesian framework, which has been shown to be successful in fisheries models (Punt & Hilborn 1997). However, this requires a much more detailed knowledge of the species life history.

The identification of a correct solution also depends on the factor weighting the fit of the population densities vs. that of the size structures (*w* in equation 4). In 80 % of the cases, the lowest non-zero *w*-value for which a solution was obtained produced the correct reconstruction of the vital rates (Table 1). In the remaining 20 %, increasing the value of *w* until a result is obtained increases the probability that a correct solution is identified without further intrusion of the researcher. Such increase will be expected to be necessary when the size structures are noisy or not sufficiently informative about the effect of the environmental driver. For example, in artificial species 2, a correct solution was found with *w* = 1000 but not with lower values (Table 1), probably because size structures did not change appreciably through time (not shown). However, large *w*-values often produce incorrect results, probably because they lead to overfitted solutions where even sampling errors in density are accounted for by the model. Empirically, it seems that keeping the biologically plausible solution with the lowest *w*-value (excluding zero) will usually be the correct choice. It may be a good idea to explore larger *w*-values; this increases (marginally) the probability of reconstructing the vital rates correctly at the cost of rising substantially the chances of finding erroneous type-2 solutions. This sets a trade-off that the researcher should consider depending on the aims of the research.

Real species: a challenge

Once we showed that the model worked under ideal conditions, we used actual data to evaluate its performance under more realistic circumstances. The model correctly reconstructed the effect of disturbance on the vital rates of the two populations for which demographic data were available. Nevertheless, basic biological knowledge was again required to screen among different solutions.

The reconstructed vital rates were in agreement with what has been previously proposed for cacti sensitive to disturbance: their populations (including *M. dixanthocentron*'s) decline when seedling establishment is reduced by disturbance-driven changes in the environment (Hernández & Godínez-Álvarez 1994; Godínez-Álvarez *et al.* 2003; Ureta & Martorell 2009). In our case, the reconstructed vital rates showed that CAD negatively affects the number seedlings that get established and seedling survival. Thus, the reconstruction correctly indicates that CAD diminishes seedling performance.

The results for *M. dixanthocentron* reveal a possible source for deviations in the reconstructed vital rates from the actual ones. Compared to the known rates, the estimated fecundity was smaller and seedling size was larger. It is possible to envisage several scenarios in which approximately the same population structure will result from the balance between the size and number of seedlings produced: given that small seedlings have a very low survival, producing few large seedlings will have a similar effect on population structure than producing many small ones. These solutions are likely to have similar likelihoods, so it would be difficult to favor one over another. However, it seems that this has no impact on the reconstructed change in vital rates, which is the main motivation for using our model.

Previous biological knowledge becomes more relevant when dealing with species for which poor data are available. Some parameters of the reconstructed vital rates were found at the limits of the parameter intervals. Extending the latter produced absurd results, suggesting that our initial selection was sound. Therefore, when data are scarce or violate model assumptions, special attention should be put when establishing parameter intervals or prior distributions as they may largely influence the results.

The system we studied was in fact a challenge for the model, as the data we used as input violated many of its assumptions (Appendix 1). First, time was measured with error: it was estimated from a disturbance index, an approximation to the actual CAD experienced by the population. Furthermore, the assumption that the CAD-time relationship was linear is not necessarily true (Singh 1998). Second, sites should ideally differ only in CAD, representing the different stages experienced by a population as disturbance increases. However, the actual populations differed in several aspects. To mention but one, altitude ranged from 640 to 2500 m a.s.l. Third, climate fluctuations are important in drylands (Schwinning *et al.* 2004), and thus vital rates are not likely to be deterministic (Fieberg & Ellner 2001; Martorell, Garcillán & Casillas 2012) as assumed by our model. Furthermore, given that we are working with an endangered species, the samples were relatively small (130 ± 97 individuals per site), limiting the amount of information supplied to the model. Despite these complications, the model was able to reconstruct correctly the change in the vital rates due to CAD, an element pointing towards the model's robustness.

Advantages and problems

The use of easy-to-obtain information is the main asset of the model. Size structures and densities require only the count and measurement of the individuals in a population at a single point in time. Comparatively, as demographers have experienced, years and resources are required to repeatedly survey the demographic behavior of even a single population. Yet, we acknowledge that ours is a quick-and-dirty procedure (U.S. EPA 2002; Benton 2007), and that the results derived from it have a lower degree of confidence compared with repeat surveys of individuals.

Another asset is that the reconstructed vital rates are free of short-time environmental noise. Repeat surveys of individuals are highly dependent on the particular environmental conditions experienced by the individuals during the year(s) of study. In contrast, size structures and densities reflect a longer time span (Wiegand *et al.* 2000; Holmes & York 2003), where benign and adverse years have been evened out. In this way, the reconstructed vital rates represent the average behavior of the population as the environment changes.

However, the model will be expected to give poor results in two cases. First, when the species does not respond to environmental change, the model is faced with data that lack the effect of the phenomenon we want to model. If so, only sampling error is fitted, making the reconstruction difficult –if possible at all. In our case, for one artificial species (number 8; Table 1) no single maximum was found probably because its survival probability did not change over time. This situation has also been observed when estimating growth rates of populations that do not respond to environmental change (González, Rees & Martorell 2012).

Second, the reconstruction of the vital rates will be hindered when the functions that describe the behavior of the species are inappropriate. For instance, a simple logistic function for modeling survival in *M. dixanthocentron* caused the largest individuals to become immortal, affecting all the vital rates (not shown). The use of a modified survival function with an asymptote different from one successfully solved the problem, while depicting the biological process more realistically. The specific function employed is probably not so important (González, Rees & Martorell 2012) as long as it captures the key attributes of the vital rate.

Future directions

Several aspects are in need of evaluation to further increase our confidence on the model. Biologically, providing as much information as possible to the model will probably reduce the number of alternative solutions obtained. For instance, the function relating size and fecundity could be easily known by synchronizing data collection with the reproduction period of the species. This information could serve to discard competing solutions or included directly in the model.

Some mathematical aspects of the model also require elaboration. While the case of *M. dixanthocentron* suggests that the procedure is robust, we are yet unaware of how the violation of different assumptions impacts the results. The researcher may be interested in whether some vital rates are significantly affected by environmental change, for which hypothesis testing and model simplification methods are required. However, we advise that the latter should be avoided, as discarding effects related with a relevant environmental driver when they do exist (type-II error) is, from a conservation biology perspective, more costly than keeping them (Haller 2000).

The modeling of vital rates based on time series of population structures has been developed over the last decades by fisheries researchers (Quinn 2003; Angelini & Moloney 2007; Hilborn 2012), and, in this sense, population ecologists are way behind them. The success of fisheries models is encouraging, showing that procedures based on time series have huge potential.

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References

Aarssen, L.W. & Taylor, D.R. (1992) Fecundity allocation in herbaceous plants. *Oikos,* **65,** 225-232.

Angelini, R. & Moloney, C.L. (2007) Fisheries, Ecology and Modelling: an historical perspective. *Pan-American Journal of Aquatic Sciences,* **2,** 75-85.

Benton, T.G. (2007) Managing farming's footprint on biodiversity. *Science(Washington),* **315,** 341-342.

Caswell, H. (2001) *Matrix Population Models*. Sinauer Associates Inc.

Clucas, R. (2011) Long-term population trends of Sooty Shearwater (*Puffinus griseus*) revealed by hunt success. *Ecological Applications,* **21,** 1308-1326.

COP 10 (2010) Decision X/17. Consolidated update of the Global Strategy for Plant Conservation 2011-2020.

Crone, E.E., Menges, E.S., Ellis, M.M., Bell, T., Bierzychudek, P., Ehrlén, J., Kaye, T.N., Knight, T.M., Lesica, P., Morris, W.F., Oostermeijer, G., Quintana-Ascencio, P.F., Stanley, A., Ticktin, T., Valverde, T. & Williams, J.L. (2011) How do plant ecologists use matrix population models? *Ecology Letters,* **14,** 1-8.

Dahlgren, J.P. & Ehrlén, J. (2011) Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. *Oikos,* **120,** 1183-1190.

Doak, D.F. & Morris, W. (1999) Detecting population-level consequences of ongoing environmental change without long-term monitoring. *Ecology,* **80,** 1537-1551.

Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000) Size-specific sensitivity: applying a new structured population model. *Ecology,* **81,** 694-708.

Ellner, S.P. & Rees, M. (2007) Stochastic stable population growth in integral projection models: theory and application. *Journal of Mathematical Biology,* **54,** 227-256.

Fieberg, J. & Ellner, S.P. (2001) Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters,* **4,** 244-266.

Fournier, D.A., Hampton, J. & Sibert, J.R. (1998) MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, Thunnus alalunga. *Canadian Journal of Fisheries and Aquatic Sciences,* **55,** 2105-2116.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A. & Sibert, J. (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods Software,* **27,** 233-249.

Ghosh, S., Gelfand, A.E. & Clark, J.S. (2012) Inference for size demography from point pattern data using integral projection models. *Journal of Agricultural, Biological, and Environmental Statistics,* **17,** 641-677.

Godínez-Álvarez, H., Valverde, T., Ortega-Baes, P., Godínez-Álvarez, H. & H (2003) Demographic Trends in the Cactaceae. *Botanical Review,* **69,** 173-203.

González, E.J., Rees, M. & Martorell, C. (2012) Identifying the demographic processes relevant for species conservation in human-impacted areas: does the model matter? *Oecologia.*

Haller, S. (2000) A prudential argument for precaution under uncertainty and high risk. *Ethics and the Environment,* **5,** 175-189.

Harper, J.L. & White, J. (1974) The demography of plants. *Annual Review of Ecology and Systematics,* **5,** 419-463.

Haysson, V., van Tienhoven, A. & van Tienhoven, A. (1993) Asdell's Patterns of Mammallian Reproduction: A Compendium of Species-specific Data. Ithaca: Cornell University Press. 1030 pp.

Heller, N.E. & Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation,* **142,** 14-32.

Hernández, H.M. & Godínez-Álvarez, H. (1994) Contribución al conocimiento de las cactáceas mexicanas amenazadas. *Acta Botanica Mexicana,* **26,** 33-52.

Hilborn, R.R. (2012) The evolution of quantitative marine fisheries management 1985–2010. *Natural Resource Modeling,* **25,** 122-144.

Hobbie, J.E., Carpenter, S.R., Grimm, N.B., Gosz, J.R. & Seastedt, T.R. (2003) The US Long Term Ecological Research Program. *Bioscience,* **53,** 21-32.

Holmes, E.E. & York, A.E. (2003) Using age structure to detect impacts on threatened populations: a case study with Steller sea lions. *Conservation Biology,* **17,** 1794-1806.

Koons, D.N, Grand, J. B., Zinner, B. & Rockwell, R. F. (2005) Transient population dynamics: Relations to life history and initial population state. *Ecological Modelling* **185,** 283-297.

Kroeker, K.J., Kordas, R.L., Crim, R.N. & Singh, G.G. (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters,* **13,** 1419-1434.

Martorell, C., Garcillán, P.P. & Casillas, F. (2012) Ruderality in extreme-desert cacti? Population effects of chronic anthropogenic disturbance on *Echinocereus lindsayi*. *Population Ecology,* **54,** 335-346.

Martorell, C. & Peters, E.M. (2009) Disturbance-response analysis: a method for rapid assessment of the threat to species in disturbed areas. *Conservation Biology,* **23,** 377-387.

Matthews, J.A. & Whittaker, R.J. (1987) Vegetation succession on the Storbreen glacier foreland, Jotunheimen, Norway: a review. *Arctic and Alpine Research,* **19,** 385-395.

Maury, O., Faugeras, B. & Restrepo, V. (2005) FASST: A fully age-size and space-time structured statistical model for the assessment of tuna populations. *Collective Volume of Scientific Papers ICCAT,* **57,** 206-217.

McAuliffe, J.R., Sundt, P.C., Valiente-Banuet, A., Casas, A. & Viveros, J.L. (2001) Pre-columbian soil erosion, persistent ecological changes, and collapse of a subsistence agricultural economy in the semi-arid Tehuacán Valley, Mexico's 'Cradle of Maize'. *Journal of Arid Environments,* **47,** 47-75.

Mori, A.S., Mizumachi, E. & Komiyama, A. (2007) Roles of disturbance and demographic non-equilibrium in species coexistence, inferred from 25-year dynamics of a late-successional old-growth subalpine forest. *Forest Ecology and Management,* **241,** 74-83.

Myung, I.J. (2003) Tutorial on maximum likelihood estimation. *Journal of Mathematical Psychology,* **47,** 90-100.

Ortega-Baes, P., Sühring, S., Sajama, J., Sotola, E., Alonso-Pedano, M., Bravo, S. & Godínez-Álvarez, H. (2010). Diversity and conservation in the cactus family. In: Ramawat, KG, editor. Desert Plants. Berlin Heidelberg: Springer-Verlag. pp. 157-173.

Parr, T.W., Sier, A.R.J., Battarbee, R.W., Mackay, A. & Burgess, J. (2003) Detecting environmental change: science and society—perspectives on long-term research and monitoring in the 21st century. *Science of The Total Environment,* **310,** 1-8.

Pereira, H.M., Leadley, P.W., Proenca, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarres, J.F., Araujo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guenette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R. & Walpole, M. (2010) Scenarios for Global Biodiversity in the 21st Century. *Science,* **330,** 1496-1501.

Pickett S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. In: Likens GE, editor. Long-term studies in ecology: approaches and alternatives. New York: Springer-Verlag. pp. 110-135.

Punt, A.E. & Hilborn, R.R. (1997) Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries,* **7,** 35-63.

Quinn II, T.J. (2003) Ruminations on the development and future of population dynamics models in fisheries. *Natural Resource Modeling,* **16,** 341-392.

Schwinning, S., Sala, O.E., Loik, M.E. & Ehleringer, J.R. (2004) Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia,* **141,** 191-193.

Singh, S.P. (1998) Chronic disturbance, a principal cause of environmental degradation in developing countries. *Environmental Conservation,* **25,** 1-2.

U.S. EPA (2002) *Methods for evaluating wetland condition: land-use characterization for nutrient and sediment risk assessment.* Office of Water, U.S. Environmental Protection Agency, Washington, D.C.

Ureta, C. & Martorell, C. (2009) Identifying the impacts of chronic anthropogenic disturbance on two threatened cacti to provide guidelines for population-dynamics restoration. *Biological Conservation,* **142,** 1992-2001.

van Tienderen, P.H. (1995) Life cycle trade-offs in matrix population models. *Ecology,* **76,** 2482-2489.

Wake, D.B. (2012) Facing Extinction in Real Time. *Science,* **335,** 1052-1053.

Waters, T.F. (1999) Long-term trout production dynamics in Valley Creek, Minnesota. *Transactions of the American Fisheries Society,* **128,** 1151-1162.

Weiner, J., Campbell, L.G., Pino, J. & Echarte, L. (2009) The allometry of reproduction within plant populations. *Journal of Ecology,* **97,** 1220-1233.

Wiegand, K., Ward, D., Thulke, H.H. & Jeltsch, F. (2000) From snapshot information to long-term population dynamics of Acacias by a simulation model. *Plant Ecology*, **150**, 97-114.

Appendix 1

Full description of the model

The model describes the change of the rates of a size-structured population as time passes by. This was done using an integral projection model (IPM; Easterling, Ellner & Dixon 2000) with a time-variant kernel (Ellner & Rees 2007). An IPM is an iterative model relating the vital rates of a population with its size structure. The mathematical description of the vital rates and their change through time is contained in a function k known as the kernel. This function establishes the sizes y that individuals of size x may reach from time t to t+1, as well as the number and sizes of their descendants. Note that, in our model, k is a time-variant because the vital rates are driven by environmental change.

Therefore, an IPM with a time-variant kernel is expressed through the equation

$$n(y,t+1) = \int_X k(y,x,t) \cdot n(x,t) dx, \qquad \text{eqn. A1}$$

where n is the size structure of the population and is a continuous probability density function, and X is the range of possible individual sizes. Given that we are interested in studying a directional process, $k(y,x,t)$ is not ergodic. As a consequence, an IPM with such kernel does not stabilize and no asymptotic properties can be derived from it (Ellner & Rees 2007). Note that the size-structure at time t+1, $n(y,t+1)$, will not necessarily integrate to one, but in fact will be the growth rate from time t to t+1 (l_t). After each iteration of equation A1, we standardize the size-structure dividing $n(y,t+1)$ by $\int_X n(y,t+1)dx$ to make it a probability density function, which we denote as $\tilde{n}(y,t+1)$.

The kernel comprises the functions of survival, $s(x,t)$, and growth, $g(y,x,t)$, of existing individuals changing from size x to y from time t to t+1, and the functions for the number and sizes of newborns, $f_1(x,t)$ and $f_2(y,x,t)$, respectively, produced by such individuals. The relation between these functions is given by the equation

$$k(y,x,t) = s(x,t) \cdot g(y,x,t) + f_1(x,t) \cdot f_2(y,x,t). \qquad \text{eqn. A2}$$

We assumed that the size of the parent does not influence the size of its newborn, *i.e.* $f_2(y,x,t) = f_2(y,t)$, as this effect is relatively small in the case of many species (Michaels *et al.* 1988). For species with asexual propagation this may not be the case (Méndez & Obeso 1993; Nicholls 2011), but the model can be modified accordingly.

The above functions (s, g, f_1 and f_2) are usually determined via generalized linear or additive models fitted to observed demographic data (Ellner & Rees 2006; Garcia, Dahlgren & Ehrlén 2011). As the identity of such models is not expected to exert great influence over the reconstructed vital rates (González, Rees & Martorell 2012), we used the following simple functions to determine the vital rates with 16 parameters:

Survival: $\text{logit}(s(x,t)) = \beta_1 + \beta_2 \cdot x + \beta_3 \cdot t + \beta_4 \cdot x \cdot t$ eqns. A3

Growth: $g(y,x,t) = \text{normal}(y; \mu = \beta_5 + \beta_6\cdot x + \beta_7\cdot t + \beta_8\cdot x\cdot t, \sigma^2 = \beta_9)$

Fecundity: $\log(f_1(x,t)) = \beta_{10} + \beta_{11}\cdot x + \beta_{12}\cdot t + \beta_{13}\cdot x\cdot t$

Seedling size: $f_2(y,t) = \text{normal}(y; \mu = \beta_{14} + \beta_{15}\cdot t, \sigma^2 = \beta_{16})$

These functions have been previously used when modeling plant demography using IPMs (Easterling, Ellner & Dixon 2000; Metcalf, Rose & Rees 2003).

To assess the capability of any given set of 16 parameter values to reproduce the observed time series we developed a composite likelihood function. Let us first define the notation associated with the observed data that we will use hereafter: M is the number of times the population was sampled, $T_1,T_2,\ldots,T_M$ the times (not necessarily consecutive) at which the populations were sampled, $N_1,N_2,\ldots,N_M$ the number of individuals sampled each time, $X_i = \{X_{i1}, X_{i2}, \ldots, X_{iN_i}\}$ the set of sizes of all the individuals sampled at time i, and D_i the observed population density at time i, $i = 1,\ldots,M$. Note that we are using capital letters to distinguish the observed data from the functions associated with the model.

For a given set of 16 parameter values, we first obtained the vital rates for each point in time (e.g. year) from T_1 to T_M. This was done by substituting the parameter values in equations A3, assembling the kernel (equation A2) and evaluating this function at times $t = T_1,T_1{+}1,\ldots,T_M$. Such evaluations resulted in the vital rates at each point in time. We then calculated the time series of size structures through the iteration of equation A1. To do so, the initial size structure, $n(x,T_1)$, is required. If no environmental change had occurred before the initial observed time (i.e., if the environment had remained constant), it would be safe to assume that the population was in its stable state (Caswell 2001). Therefore, in the first iteration of equation A1 we used the stable size-structure associated with the vital rates kernel at the initial time; i.e. $n(x,T_1)$ is the asymptotic size-structure associated with $k(y,x,T_1)$. In case such assumption would not hold (Yearsley 2004), other functions could be used as the initial size structure, such as the one associated with X_1. Therefore, through the iteration of equation A1, we obtain a series of (reconstructed) size structures spanning from T_1 to T_M: $\tilde{n}(x,T_1),\tilde{n}(x,T_1{+}1),\ldots,\tilde{n}(x,T_M)$. As we were interested in comparing the reconstructed size-structures with the observed data, we retained only those associated with the times of sampling, i.e. we retained $\tilde{n}(x,T_1),\tilde{n}(x,T_2),\ldots,\tilde{n}(x,T_M)$.

The reconstructed population densities resulted from multiplying the growth rates obtained at each iteration by the initial observed density; i.e., for a particular time $t > T_1$, the modeled density

$$d(t) = \Pi_s \lambda_s D_1, \qquad \text{eqn. A4}$$

where $s = T_1,T_1{+}1,\ldots,t$ and $\lambda_s = \int_X n(x,s)dx$.

The composite log-likelihood function we developed combined two log-likelihoods: one comparing the fit of the reconstructed size structures to the observed individual's sizes and one comparing the fit of the reconstructed densities to the observed ones. The first is defined as the natural logarithm of the probability of observing the sizes of the individuals at the different sampling times given the particular values of the parameters. Such probability is calculated using the probability distributions retained above: $\tilde{n}(x,T_1),\tilde{n}(x,T_2),\ldots,\tilde{n}(x,T_M)$. Mathematically, this is defined as:

$$l_n(\beta_1, \beta_2, \ldots, \beta_{16}) = \ln(\Pr(X_1, \ldots, X_M \mid \beta_1, \beta_2, \ldots, \beta_{16})) = \Sigma_i \Sigma_j \ln(\tilde{n}(X_{ij}, T_i)), \qquad \text{eqn. A5}$$

where β_1, β_2, …, β_{16} are the 16 particular values of the parameters, and X_{ij} is the size of the j-th observed individual at the i-th sampling point in time.

For the log-likelihood associated with the population densities we did not have a probability distribution associated with each reconstructed density. Therefore, we assumed that $d(t)$ had a lognormal distribution (denoted lnN). We chose this distribution as density is a positive continuous variable and it would be a reasonable expectation to have $\ln(d(t))$ normally distributed (Engen & Lande 1996). Again, we define the log-likelihood associated to the fit of the reconstructed densities to the observed ones as the natural logarithm of the probability of observing such densities at the different sampling times given the particular values of the parameters. Such probability is calculated using the lognormal distribution. Mathematically, this is defined as:

$$l_d(\beta_1, \beta_2, \ldots, \beta_{16}) = \ln(\Pr(D_1, D_2, \ldots, D_M \mid \beta_1, \beta_2, \ldots, \beta_{16})) = \Sigma_i \ln(\mathrm{lnN}_i(d(T_i))), \qquad \text{eqn. A6}$$

where lnN_i is the lognormal distribution associated with $d(T_i)$.

Finally, we combined the two log-likelihood functions (equations A5 & A6) into the composite function:

$$l(p_1, p_2, \ldots, p_{16}) = l_n(\beta_1, \beta_2, \ldots, \beta_{16}) + w \cdot l_d(\beta_1, \beta_2, \ldots, \beta_{16}), \qquad \text{eqn. A7}$$

where w is a weighting factor of the relative importance on the estimation of the parameters of fitting the observed size-structures *vs.* fitting the observed population densities. This term was introduced because at each point in time (T_i) there is only one datum for density (D_i), but several for size structure ($\{X_{i1}, X_{i2}, \ldots, X_{iN_i}\}$), and not using a weight would make density to have a minor contribution to l. The right value for w can be determined experimentally.

The values of the parameters that maximize equation A7 determine a kernel representing size-structured vital rates and their change through time that best fits the observed size structures and densities.

Model assumptions

The main assumption that the model relies on is that, as size-structured vital rates change directionally through time due to a long-term environmental process affecting them, the size structure and density that derive from them change accordingly.

This general assumption can be decomposed into particular easier-to-verify ones. These assumptions can be mandatory or optional. In this latter case, the work needed to change it is indicated in parenthesis.

1. The species recovery time is larger than the recurrence of the environmental process (mandatory).
2. A continuous variable, in our case size, structures the population (mandatory, but cf. Gross *et al.* 2006).
3. The environmental process is chronic and changes through time, be it in intensity or cumulative effect on the population (mandatory).
4. The form of the relation between time and the environmental process is known (linear in our case, but easy to change).
5. The time elapsed between population's measurements is known without error (mandatory).
6. The form of the relationship between size and each demographic process is known (linear in our case, but easy to change).
7. The form of the relationship between time and each demographic process is known (linear in our case, but easy to change).

Two assumptions relate to the type of data required to use the model:

1. Sample sizes are sufficiently large for the data to contain the information on the effect of the environmental process on the size structure and density (mandatory).
2. Populations are randomly sampled (mandatory).

Another two relate to our decision to use IPMs:

1. Density-independence (easy to change).
2. Deterministic (easy to change will increase complexity and probably reduce confidence on the results, see Ellner & Rees 2007, Ghosh, Gelfand & Clark 2012).

Finally, additional assumptions are particular to the study system used to validate the model with real data:

1. Homogeneity of the environment among sites (violation reduces confidence on the results and other directional factors should be discarded as explanatory variables of the difference between size structures and densities in the different populations).
2. The intensity of the environmental process differs between populations (mandatory).

3. The relationship between chronic anthropogenic disturbance and time is known (linear in our case, but easy to change).
4. Seedling size is parent-size independent (easy to change).
5. Seedling establishment is proportional to flower production (easy to change).
6. The first observed population is in its stable state (easy to change).

References

Caswell, H. (2001) *Matrix Population Models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, MA.

Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000) Size-specific sensitivity: applying a new structured population model. *Ecology,* **81,** 694-708.

Ellner, S.P. & Rees, M. (2006) Integral projection models for species with complex demography. *The American Naturalist,* **167,** 410-428.

Ellner, S.P. & Rees, M. (2007) Stochastic stable population growth in integral projection models: theory and application. *Journal of Mathematical Biology,* **54,** 227-256.

Engen, S. & Lande, R. (1996) Population dynamic models generating the lognormal species abundance distribution. *Mathematical biosciences,* **132,** 169-183.

Garcia, M.B., Dahlgren, J.P. & Ehrlén, J. (2011) No evidence of senescence in a 300-year-old mountain herb. *Journal of Ecology,* **991,** 1424-1430.

Ghosh, S., Gelfand, A.E. & Clark, J.S. (2012) Inference for size demography from point pattern data using integral projection models. *Journal of Agricultural, Biological, and Environmental Statistics,* **17,** 641-677.

González, E.J., Rees, M. & Martorell, C. (2012) Identifying the demographic processes relevant for species conservation in human-impacted areas: does the model matter? *Oecologia*.

Gross, K., Morris, W.F., Wolosin, M.S. & Doak, D.F. (2006) Modeling vital rates improves estimation of population projection matrices. *Population Ecology,* **48,** 79-89.

Méndez, M. & Obeso, J.R. (1993) Size-dependent reproductive and vegetative allocation in *Arum italicum* (Araceae). *Canadian Journal of Botany,* **71,** 309-314.

Metcalf, J.C., Rose, K.E. & Rees, M. (2003) Evolutionary demography of monocarpic perennials. *Trends in Ecology & Evolution,* **18,** 471-480.

Michaels, H.J., Benner, B., Hartgerink, A.P., Lee, T.D., Rice, S., Willson, M.F. & Bertin, R.I. (1988) Seed size variation: magnitude, distribution, and ecological correlates. *Evolutionary Ecology,* **2,** 157-166.

Nicholls, A.M. (2011) Influences of environmental variability, genetics and plant size on variation in sexual and clonal reproduction and allocation of resources in three wetland plant species. PhD, Cleveland State University.

Yearsley, J.M. (2004) Transient population dynamics and short-term sensitivity analysis of matrix population models. *Ecological Modelling,* **177,** 245-258.

Appendix 2

Simulation process description

To generate artificial vital rates representing different species responses to a long-term environmental-change driver, we first had to limit the possible set of rates from where to randomly draw the ones we would use. We did this by setting intervals for the 16 parameters in the model ample enough to incorporate a wide set of possible demographic behaviors. We explored different parameter intervals and chose those that translated into vital rates that were as variable as possible but excluded as many unrealistic ones (see *Parameter Section* of Appendix 4 for these particular intervals). Nonetheless, even the most restricted intervals will contain such rates as certain combinations of values for different parameters can result in unrealistic rates.

We randomly selected parameter values from the intervals and verified if the rates associated with such values were biologically realistic. For a particular set of parameter values, we obtained the associated kernel (k in equation A2), and evaluated this function at times $t = 1,\ldots,100$, a span of years over which environmental change will occur, to obtain the vital rates associated with such points in time. As in Appendix 1, we obtained from this kernel a series of (reconstructed) size structures and densities spanning from time 1 to 100 (i.e. $n(x,1),\ldots,n(x,100)$ and $d(1),\ldots,d(100)$). As explained above, biologically unrealistic rates could be associated with such kernel. Therefore, we verified that the time series fulfilled the following criteria:

1) The population could not increase its density more than a 100 times its original density along the time interval (i.e. $d(t) \leq 100 \cdot d(1)$, for every $t > 1$).
2) Starting with 1000 individuals, the population could not arrive to a density of 50 individuals at any point in time to avoid having underrepresented populations (i.e. $d(t) > 50$, for every $t > 1$).
3) Standardized size structures (made to integrate to one) had to present a minimum value of 0.0001 in order for the size structures to contain information in all their range (i.e. $n(x,t) > 0.0001$, for every $t > 0$).

Also, we verified that the mortality of individuals associated with the kernel was larger than 20 % at some individual size and larger than 0.1 % at the largest size at all times in order to avoid having immortal individuals (i.e. $s(x_1,t) < 0.80$ for some x_1 in $X = [0,1]$, and $s(x_1,t) < 0.999$ for every x in X and every $t > 0$). Using these criteria, we randomly chose 10 biologically realistic kernels, representing the demographic behavior of 10 artificial species. Additionally, we randomly chose 10 points in time in the range 1–100 to simulate the likely scenario in which the population is not systematically sampled, and data are available for a few, sparse years (i.e. $M = 10$ and we chose $T_1,\ldots,T_{10}$).

We then generated samples for each artificial species at the selected points in time. To introduce sampling error, the densities at each of the 10 points in time was simulated from a lognormal distribution with mean equal to the population density at that time, $d(t_i)$, and variance 0.1. We assumed that sampling effort was constant, so that sample size was proportional to density. Therefore, the new densities, D_i, were used to generate samples of individual's sizes in the population. For each point in time T_i, a Monte Carlo simulation was performed to obtain a random sample of size D_i of the size-structure $n(x,T_i)$. The 10 samples obtained in this way, along with densities D_i, represent the type of time series required by the model for the study of a particular species.

For each artificial species, we used its associated time series as input to the model. To maximize the likelihood (equation A7), we used the ADMB. Given that we are dealing with a complex function, the program could reach different maxima depending on the starting parameter values. Therefore, we tried 41 different initial sets of values to explore this function. First, we used as a starting vector the parameter values from which the rates of the species were derived. Then, we obtained additional starting vectors by randomly adding/subtracting to each parameter an error of 5, 10, 25 and 50 % the length of its interval. For each of these percentages, the procedure was repeated 10 times, resulting in 40 random parameter vectors. This allowed us to evaluate how close the initial values had to be from the real ones to correctly reconstruct the kernel.

To assess the effect of the coefficient weighting the relative importance of fitting the population densities vs. that of the size-structures (w in equation A7), we ran ADMB under values of 0, 1, 10, 100, and 1000. As can be seen in equation A7, a zero w-value corresponds to a model where population densities are not considered in the maximization of the likelihood, whilst increasing w-values increase the relevance of fitting the densities in comparison with fitting the size-structures.

After running ADMB with these starting vectors and w values (205 runs per species), we usually did not obtained a single reconstruction, but a set of possible ones, which had to be evaluated. First, we evaluated whether these solutions were in fact a single one. To do this, we calculated the distance between them to detect maxima close enough to represent the same rates. We used the weighted distance $d(\alpha,\beta) = 1/16 \cdot \Sigma_i(\alpha_i - \beta_i)^2(max_i - min_i)^{-2}$, where α and β are two parameter vectors and *max* and *min* are the limits of the parameter intervals. This distance ranges from 0 to 1. Two maxima where considered close to one another when the distance between them was less than 0.05, a value that warranted both maxima to show the same pattern of change of the demographic processes with size and time (not shown).

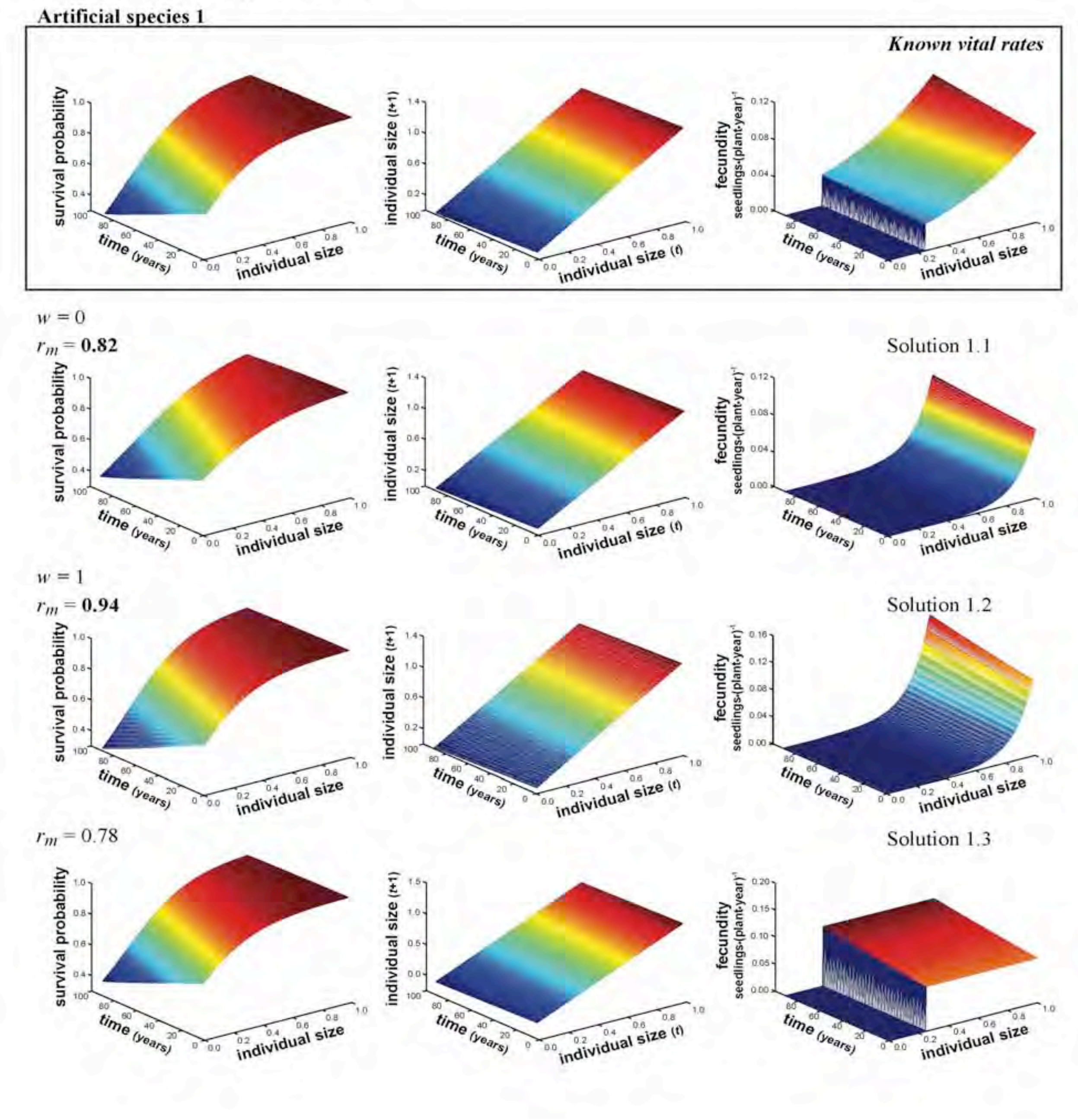
When two or more solutions were in fact different reconstructions of the vital rates, two different approaches could be used to evaluate them in a realistic scenario. First, we could compare the likelihood associated with the size structures (l_n in equation A5) and the Pearson correlation coefficient between the reconstructed and observed densities (r_d) to perform model selection. These two figures would be the only goodness-of-fit measures that a researcher could compute with a time series of size structures and densities as data. Second, evaluation could be based on relatively basic biological knowledge of the species: the expected relations between vital rates and size.

Additionally, given that for the artificial species we in fact knew their associated kernels, we calculated the goodness-of-fit between the known and reconstructed vital rates via the Pearson correlation coefficient between the known and obtained survival, growth and fecundity functions (s, g, and f in equations A3). These three values, together with r_d, were averaged and a mean coefficient (r_m) was calculated. We would expect that, if l_n and r_d were useful to discriminate among different solutions, they would be positively correlated with r_m.

Appendix 3

Vital rates reconstructed for the artificial species

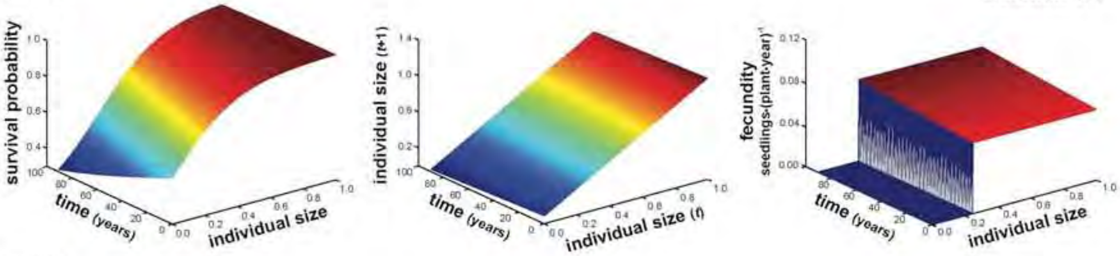
Known survival, growth and fecundity associated to the artificial species (*Known vital rates* rectangle) and solutions obtained by the model with different values of the coefficient weighting the fitting of the population densities vs. that of the size structures (w in equation 4). r_m is the mean Pearson correlation coefficient between the observed and reconstructed demographies. Bold r_m: correct reconstruction, roman r_m: incorrect reconstruction that could be discarded (type-1 solution), italics r_m: erroneous reconstruction that was biologically feasible but wrongly estimated the change over time of the vital rates (type-2 solution).



$w = 10$

$r_m = 0.79$

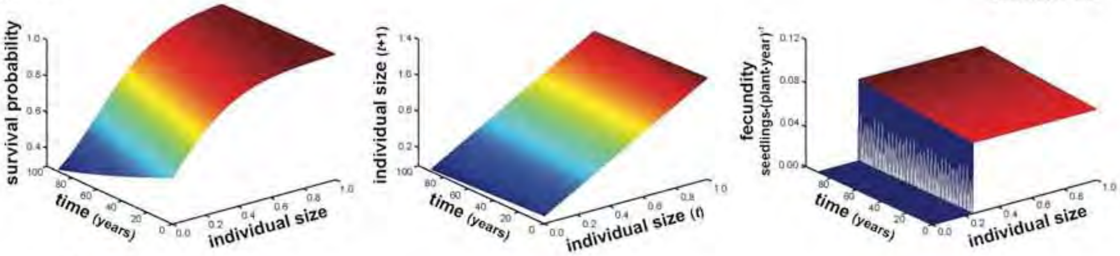
Solution 1.4



$w = 100$

$r_m = 0.73$

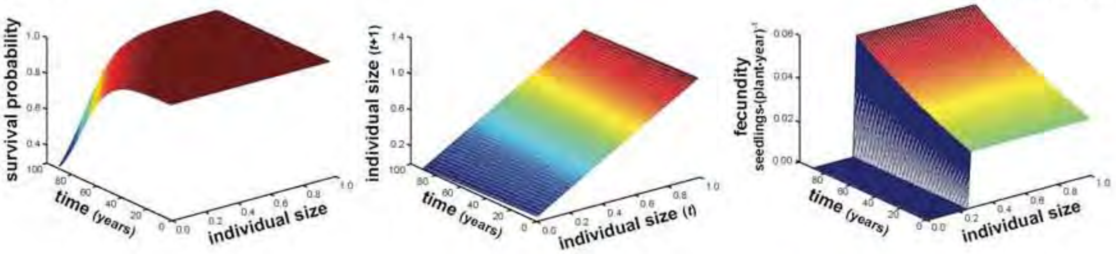
Solution 1.5



$w = 1000$

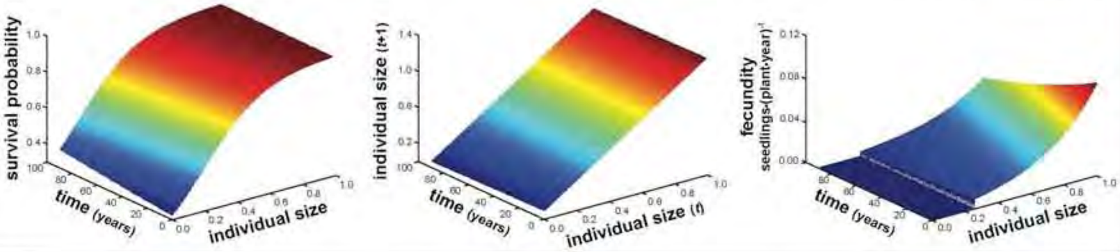
$r_m = 0.73$

Solution 1.6



Artificial species 2

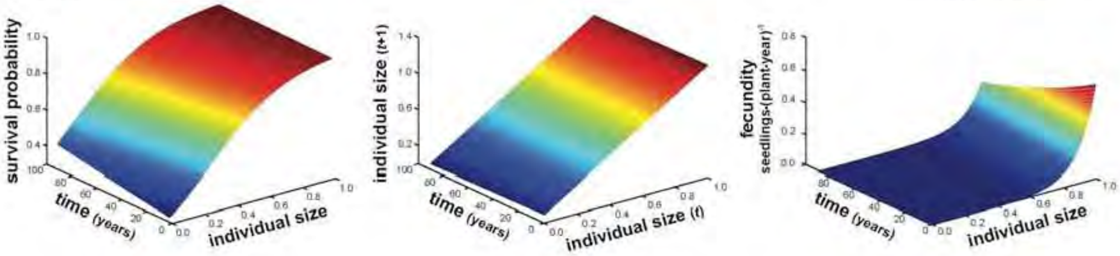
Known vital rates



$w = 0$

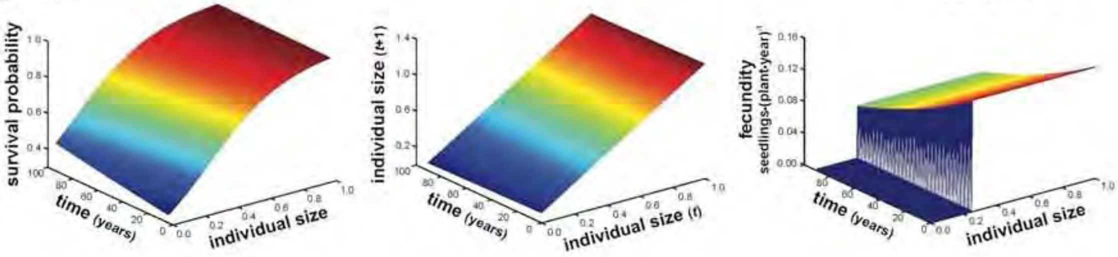
$r_m =$ **0.51**

Solution 2.1



$r_m = 0.38$

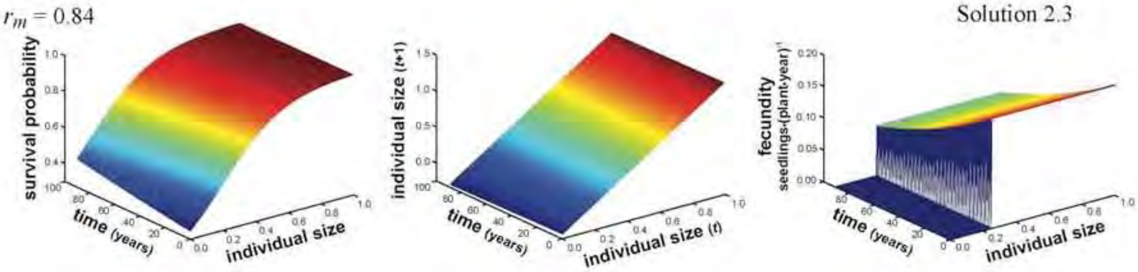
Solution 2.2



$w = 1$

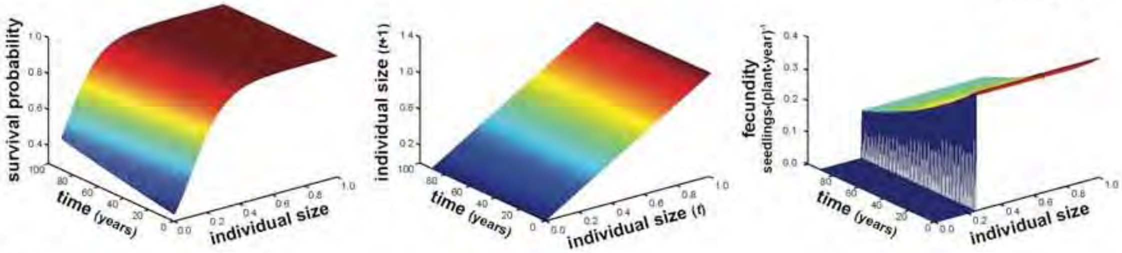
$r_m = 0.84$

Solution 2.3



$r_m = 0.82$

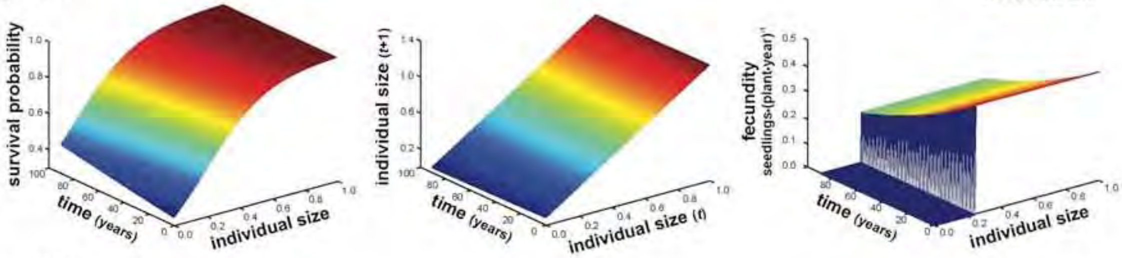
Solution 2.4



$w = 10$

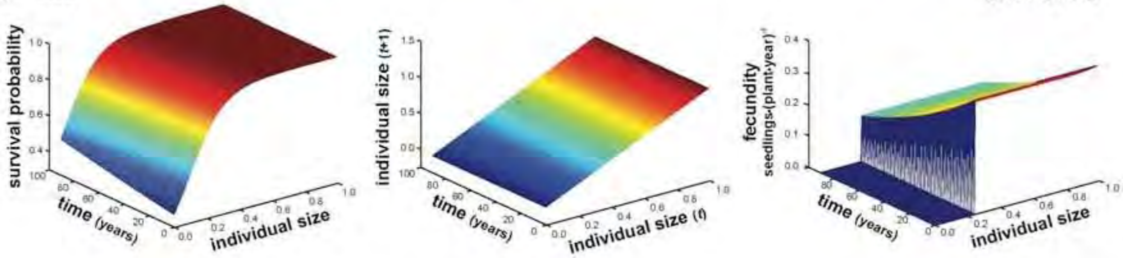
$r_m = 0.84$

Solution 2.5



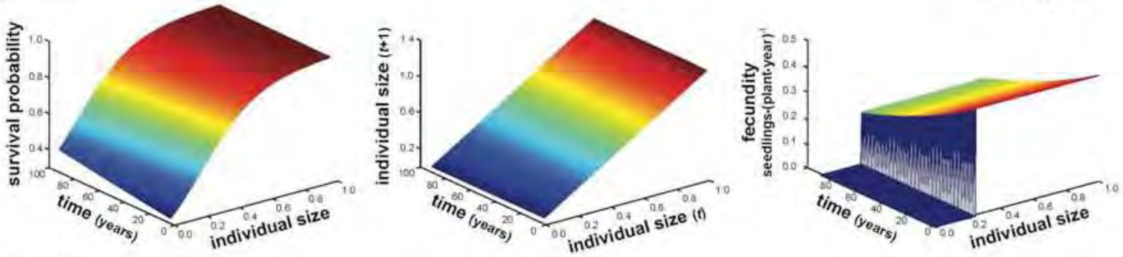
$r_m = 0.82$

Solution 2.6



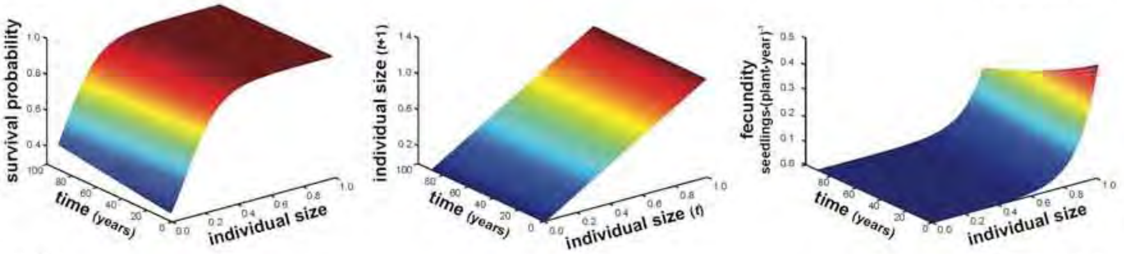
$w = 100$
$r_m = 0.84$

Solution 2.7



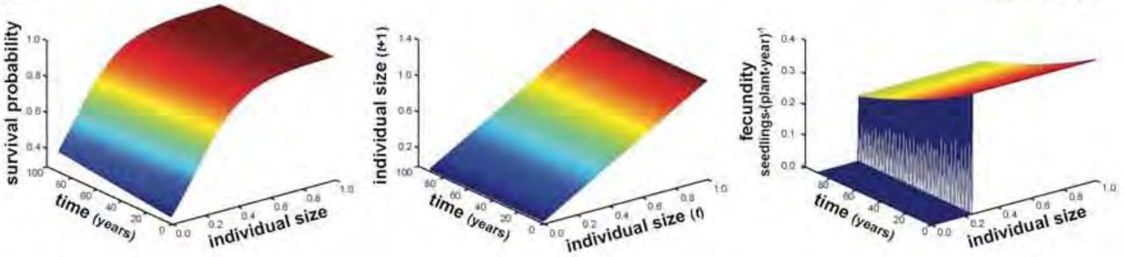
$w = 1000$
$r_m =$ **0.95**

Solution 2.8



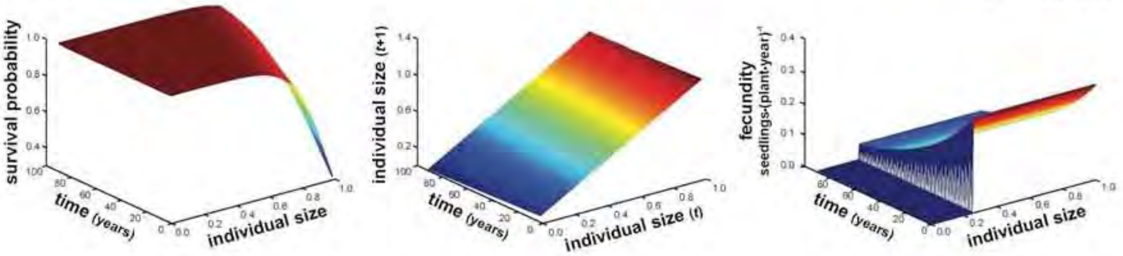
$r_m = 0.84$

Solution 2.9



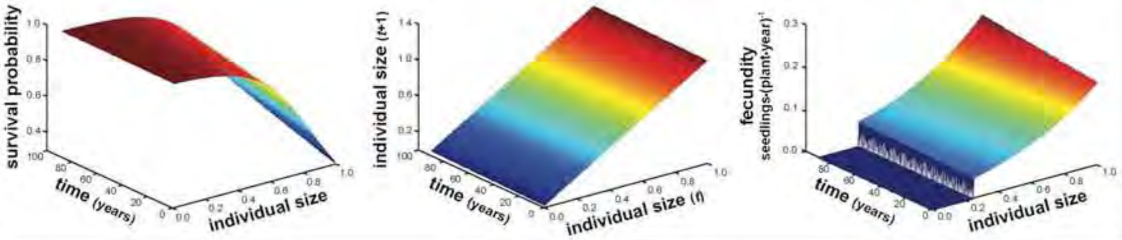
$r_m = 0.49$

Solution 2.10



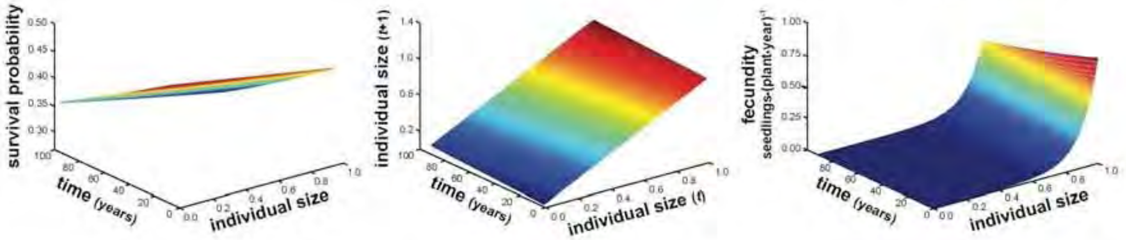
Artificial species 3

Known vital rates



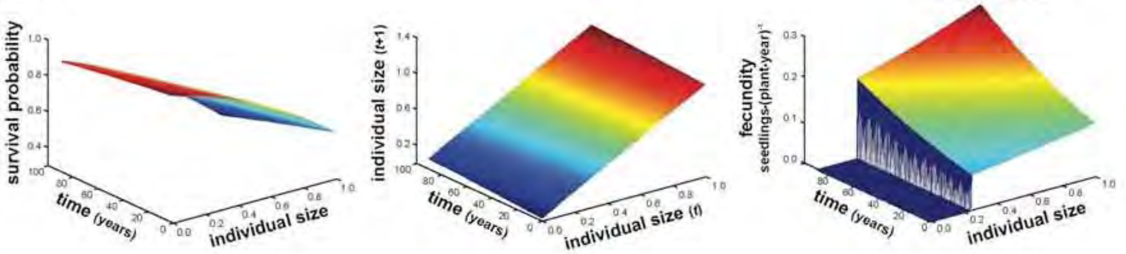
$w = 0$
$r_m = 0.67$

Solution 3.1



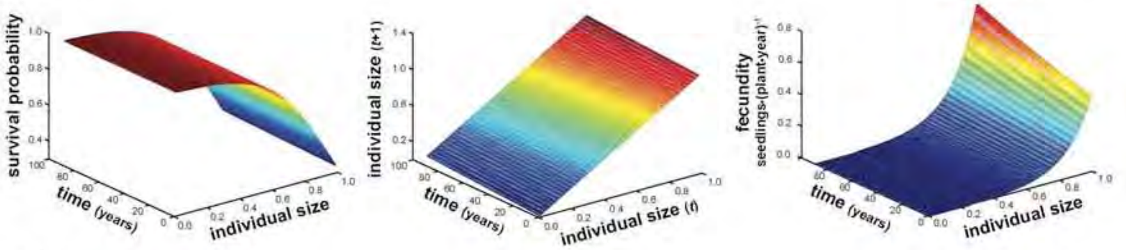
$w = 1$
$r_m = 0.84$

Solution 3.2



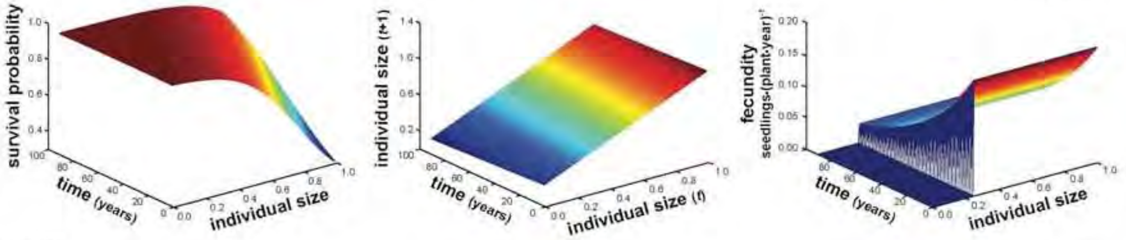
$w = 10$
$r_m =$ **0.97**

Solution 3.3



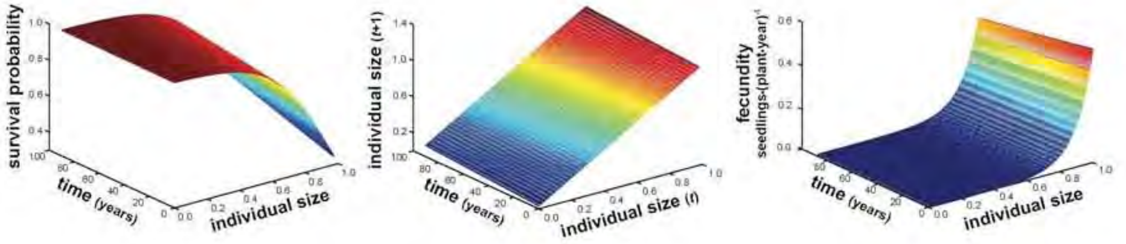
$r_m = 0.69$

Solution 3.4



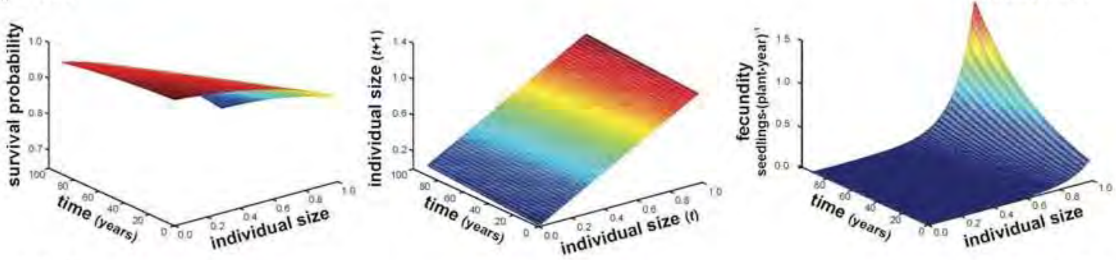
$w = 100$
$r_m =$ **0.96**

Solution 3.5



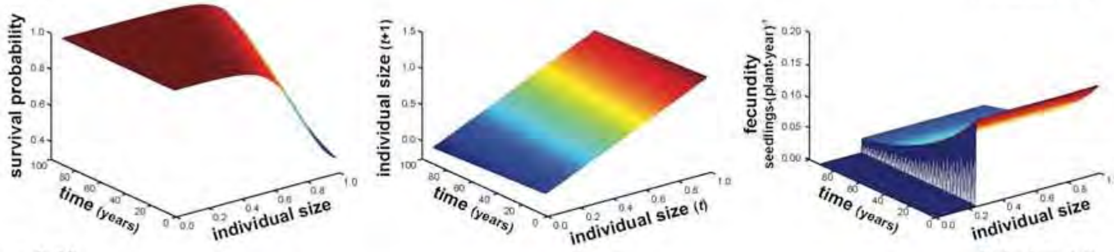
$r_m = 0.85$

Solution 3.6



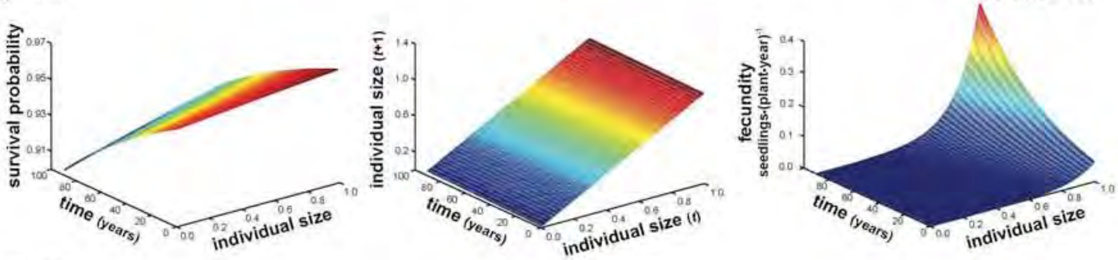
$r_m = 0.69$

Solution 3.7



$r_m = 0.59$

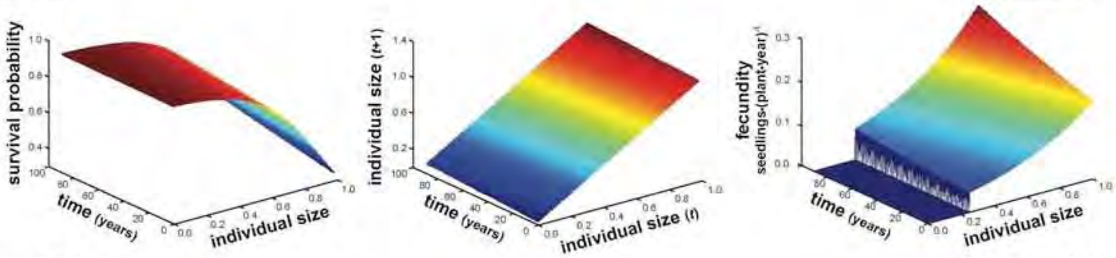
Solution 3.8



$w = 1000$

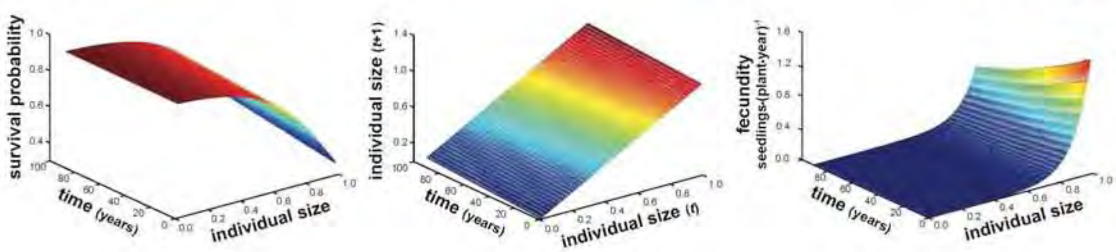
$r_m = \mathbf{0.99}$

Solution 3.9

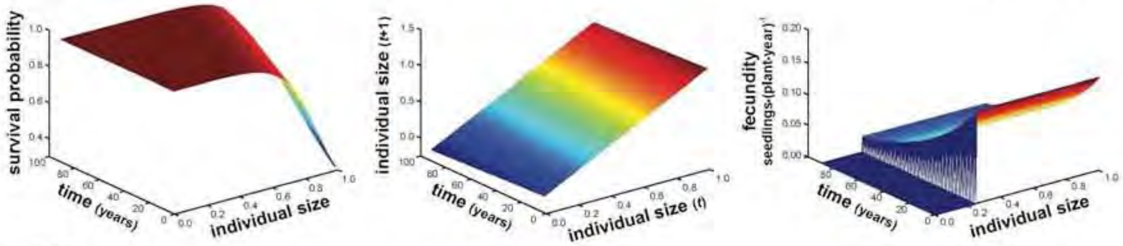


$r_m = 0.94$

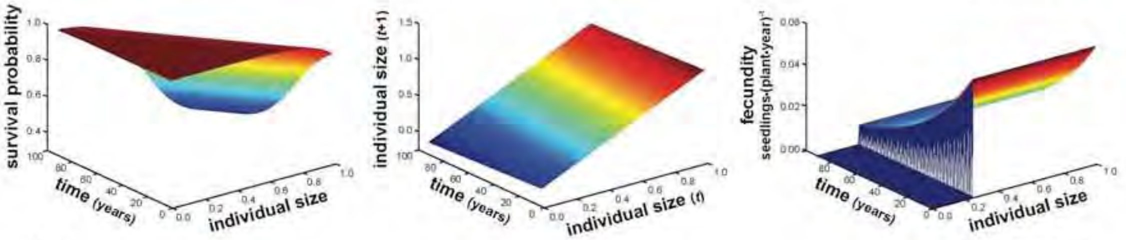
Solution 3.10



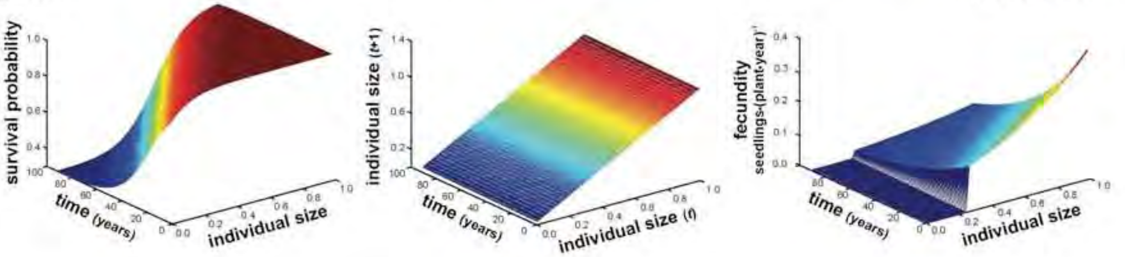
$r_m = 0.68$ Solution 3.11



$r_m = 0.59$ Solution 3.12

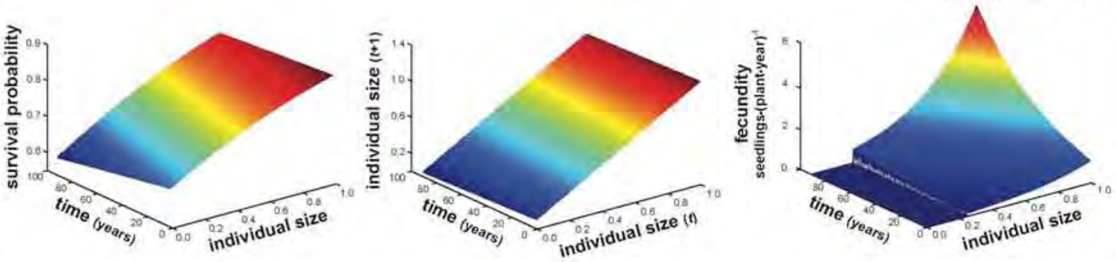


$r_m = 0.44$ Solution 3.13



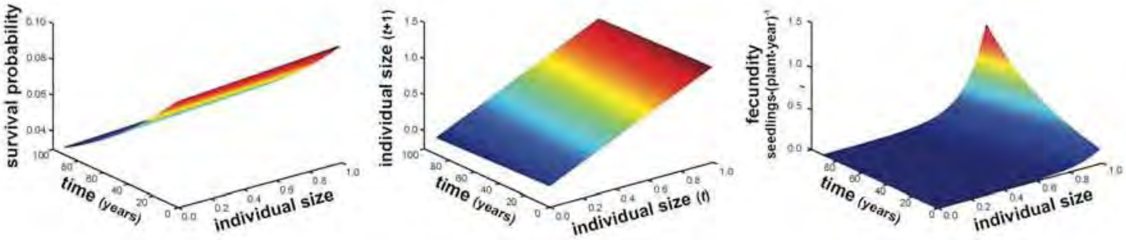
Artificial species 4

Known vital rates



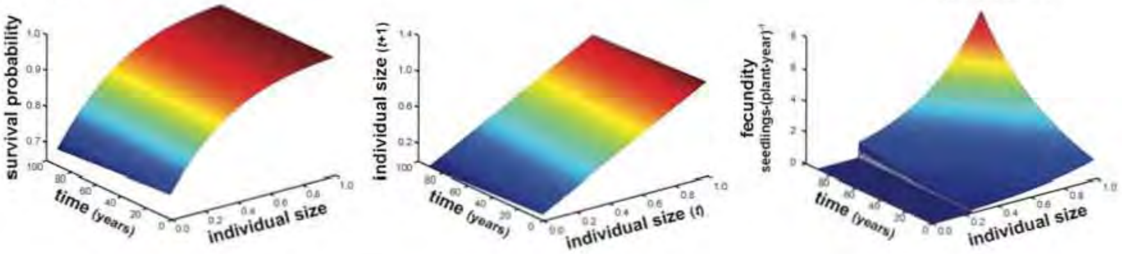
$w = 0$

$r_m = 0.60$ Solution 4.1



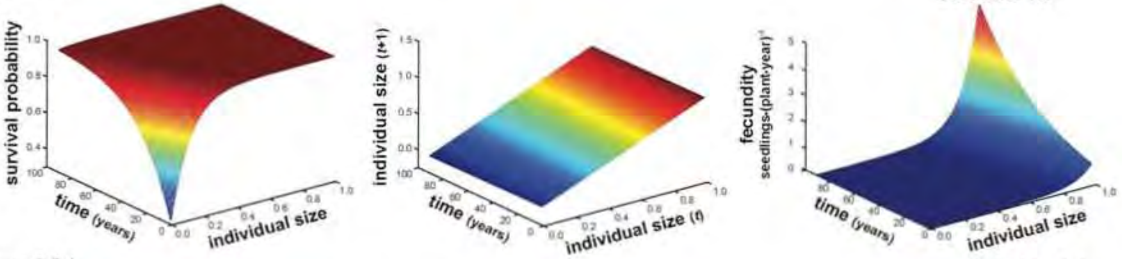
r_m = **0.51**

Solution 4.2



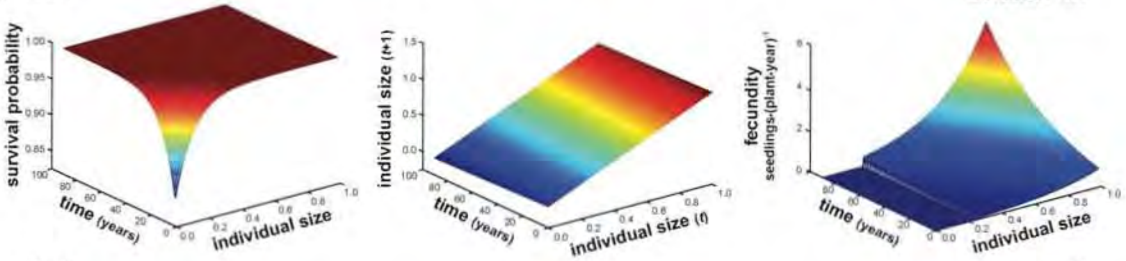
r_m = 0.34

Solution 4.3



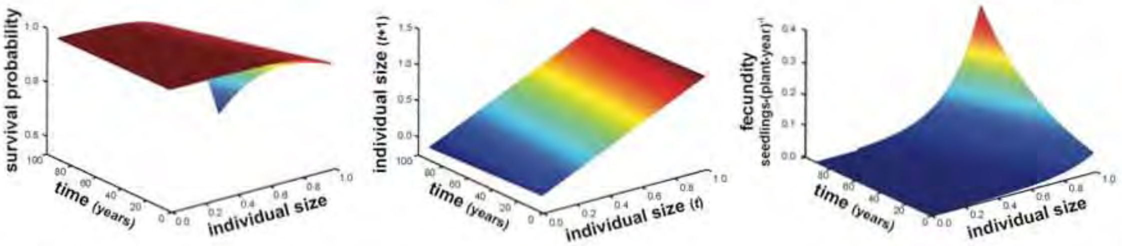
r_m = 0.34

Solution 4.4



r_m = 0.13

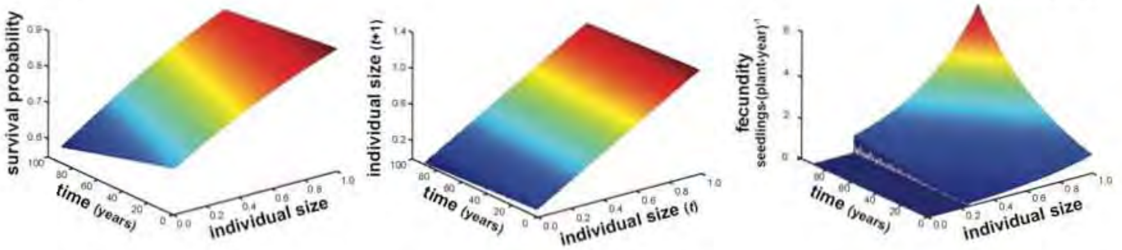
Solution 4.5



w = 1

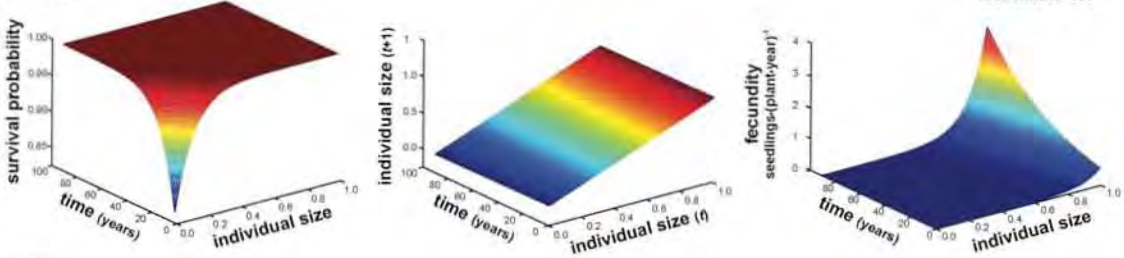
r_m = **0.98**

Solution 4.6



$r_m = 0.32$

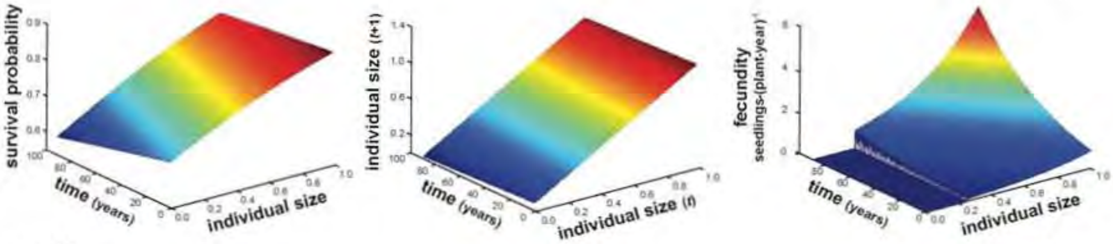
Solution 4.7



$w = 10$

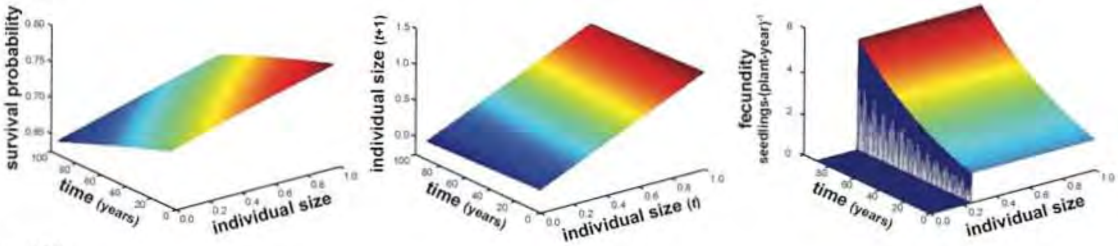
$r_m =$ **0.98**

Solution 4.8



$r_m = 0.82$

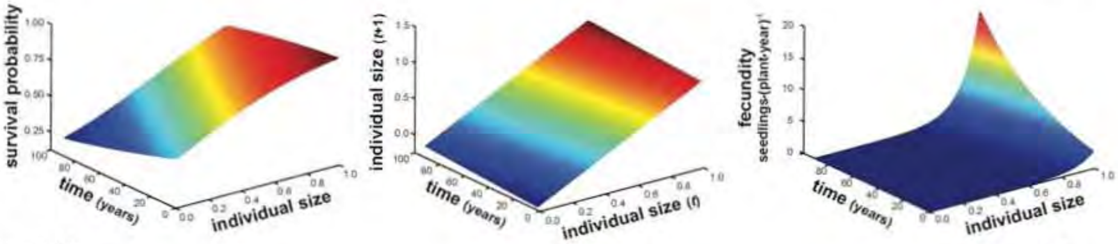
Solution 4.9



$w = 100$

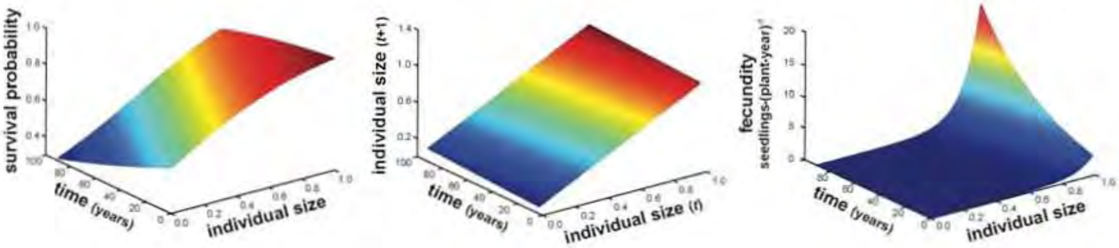
$r_m =$ **0.93**

Solution 4.10

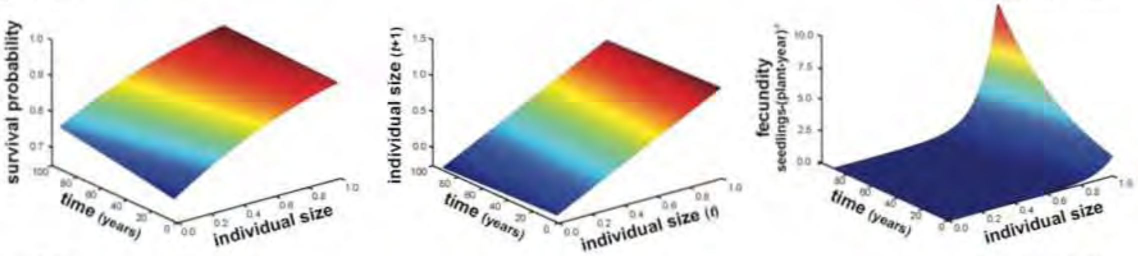


$r_m =$ **0.93**

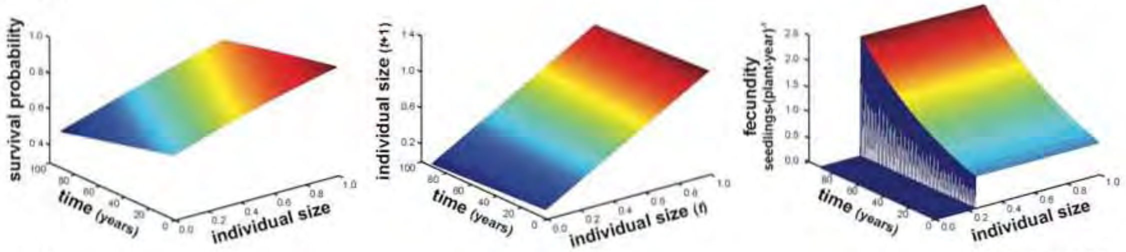
Solution 4.11



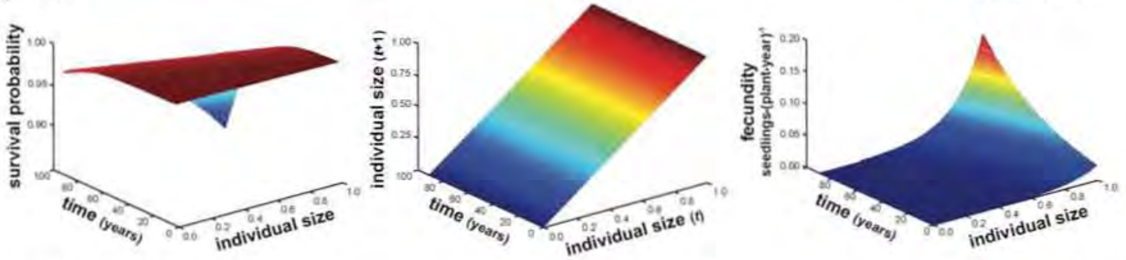
$r_m = 0.91$ Solution 4.12



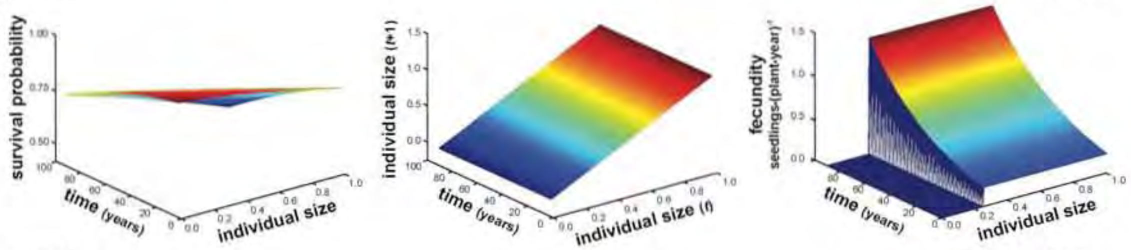
$r_m = 0.88$ Solution 4.13



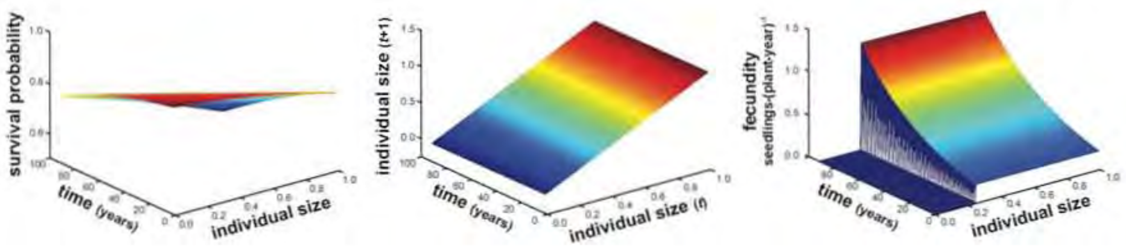
$r_m = 0.67$ Solution 4.14



$r_m = 0.56$ Solution 4.15



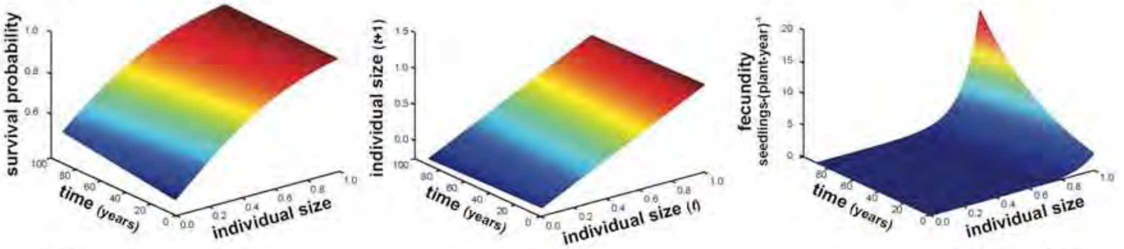
$r_m = 0.56$ Solution 4.16



$w = 1000$

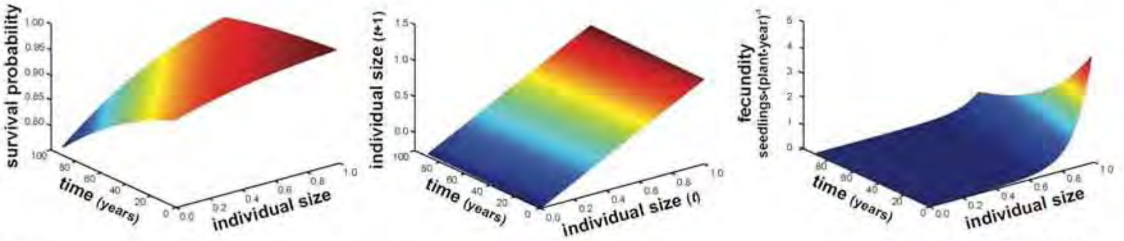
$r_m = 0.93$

Solution 4.17



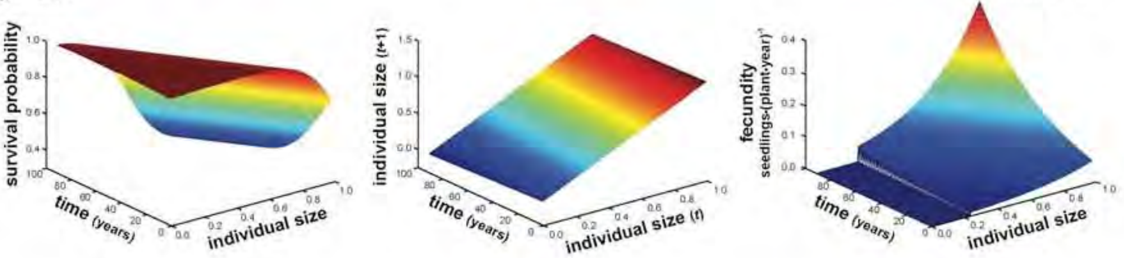
$r_m = 0.75$

Solution 4.18



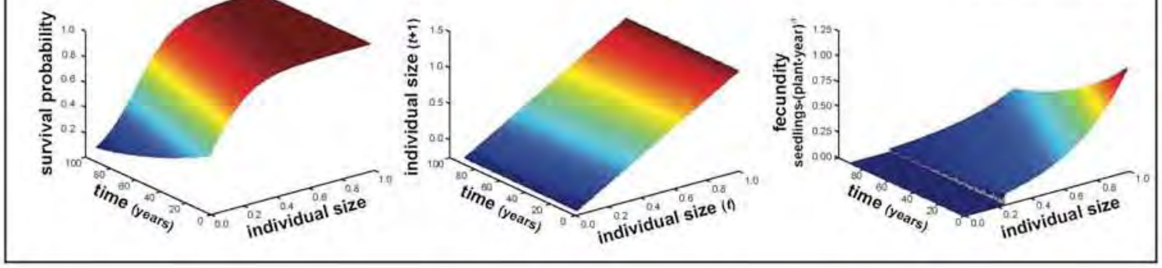
$r_m = 0.60$

Solution 4.19



Artificial species 5

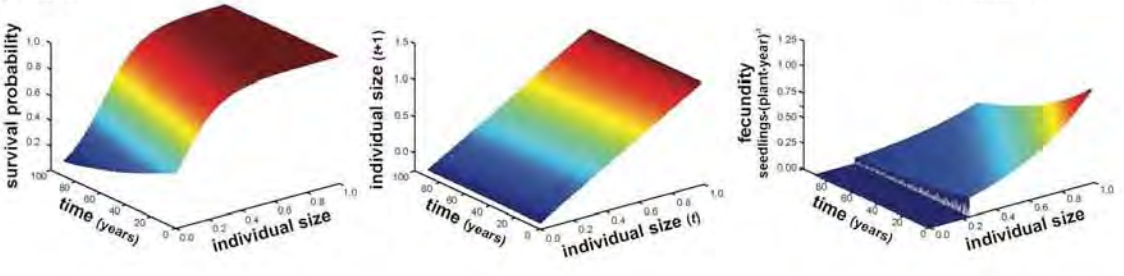
Known vital rates



$w = 0$

$r_m =$ **0.99**

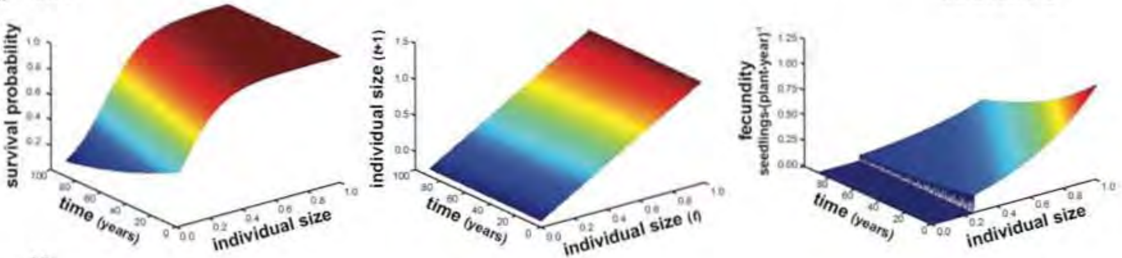
Solution 5.1



$w = 1$

$r_m =$ **0.99**

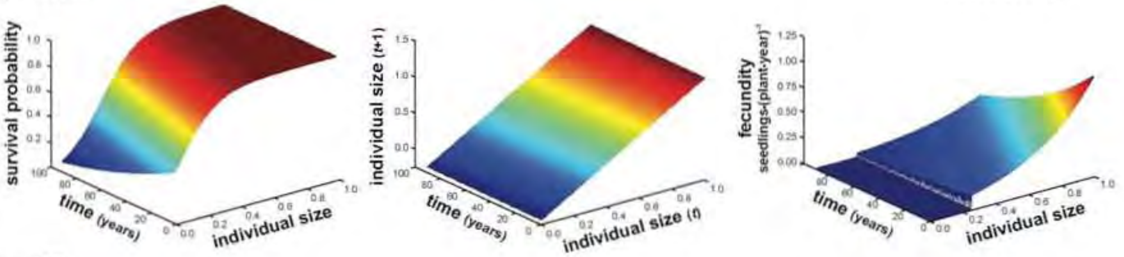
Solution 5.2



$w = 10$

$r_m =$ **1.00**

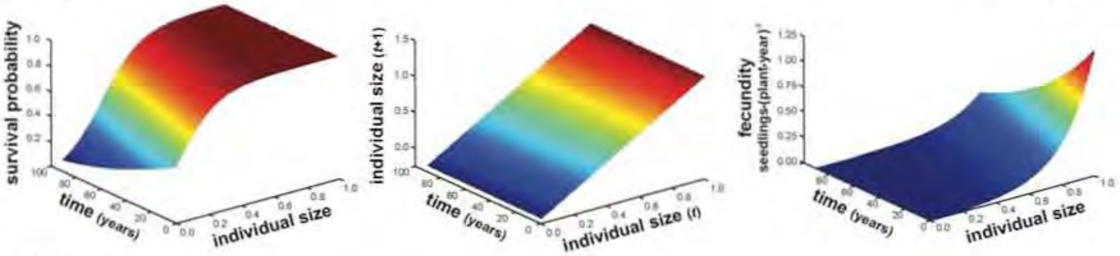
Solution 5.3



$w = 100$

$r_m =$ **0.99**

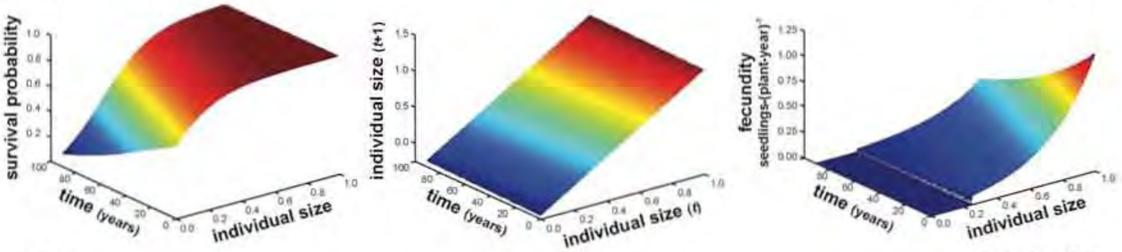
Solution 5.4



$w = 1000$

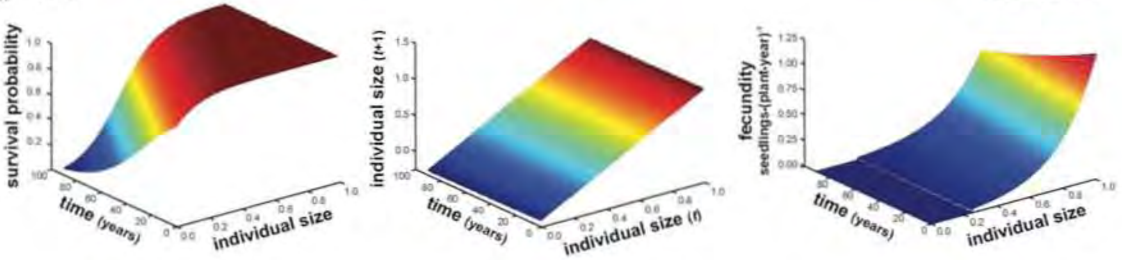
$r_m =$ **0.99**

Solution 5.5

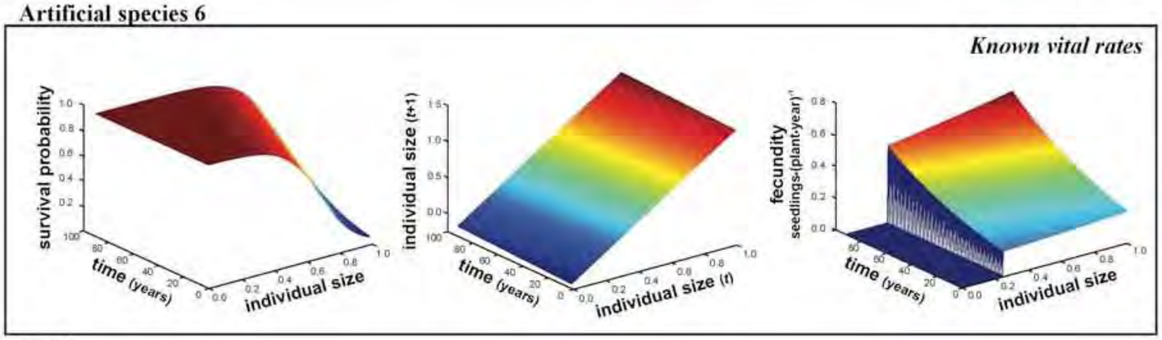


$r_m =$ **0.95**

Solution 5.6



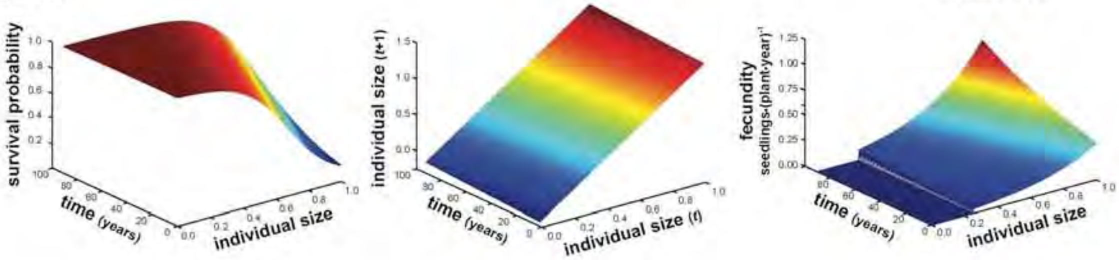
Artificial species 6



$w = 0$

r_m = **0.90**

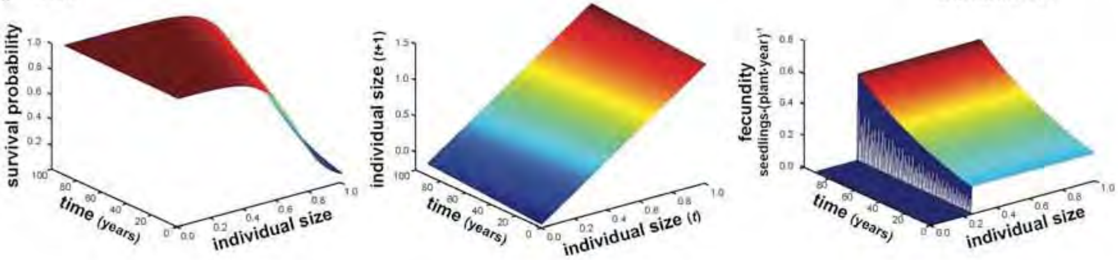
Solution 6.1



$w = 1$

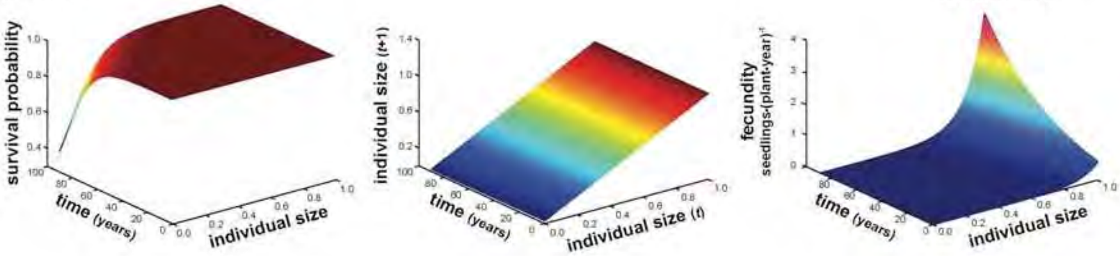
r_m = **1.00**

Solution 6.2



r_m = 0.54

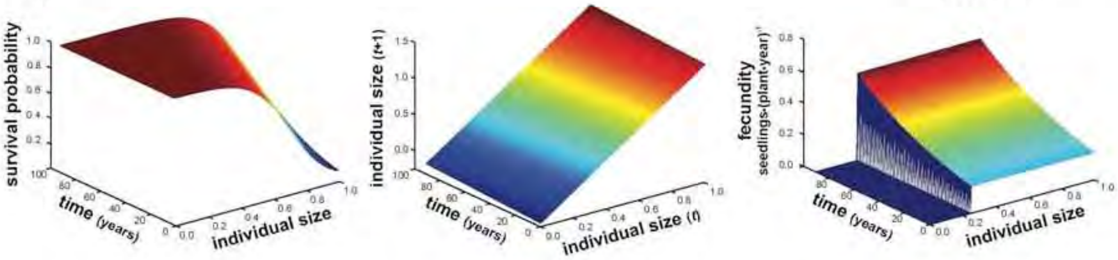
Solution 6.3



$w = 10$

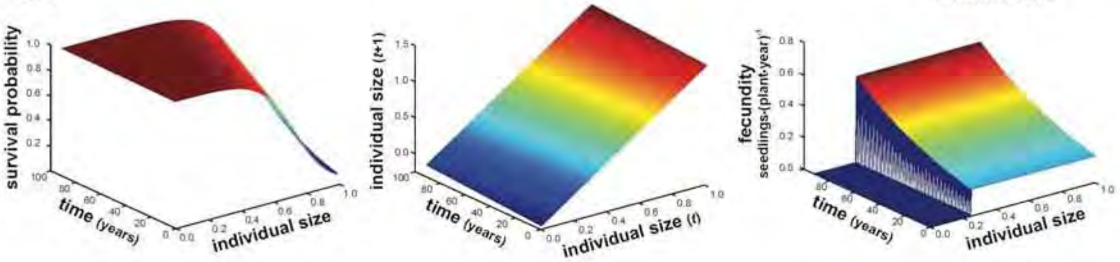
r_m = **1.00**

Solution 6.4



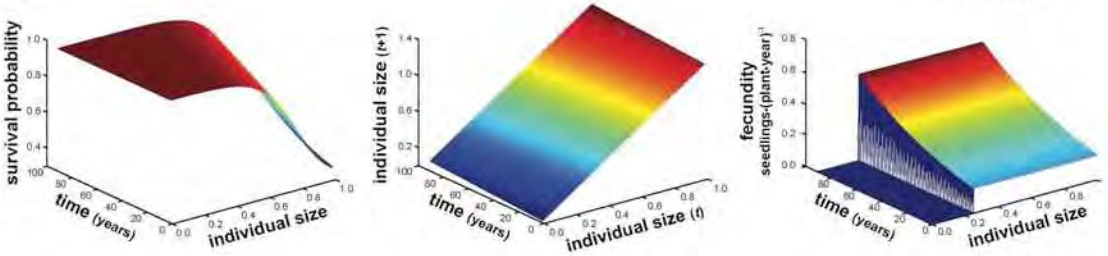
$w = 100$
$r_m = \mathbf{0.99}$

Solution 6.5



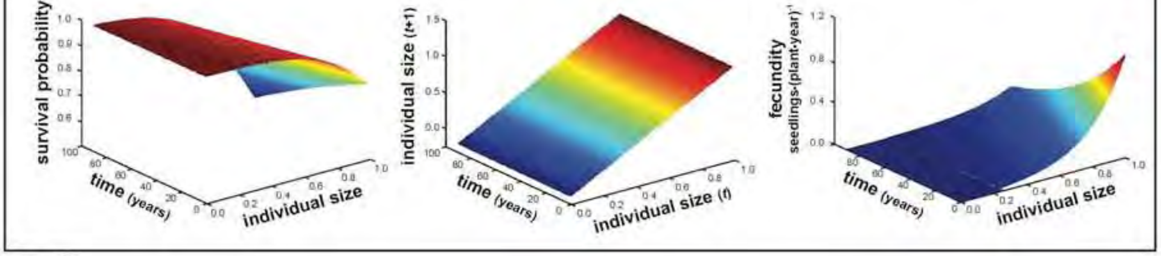
$w = 1000$
$r_m = \mathbf{0.99}$

Solution 6.6



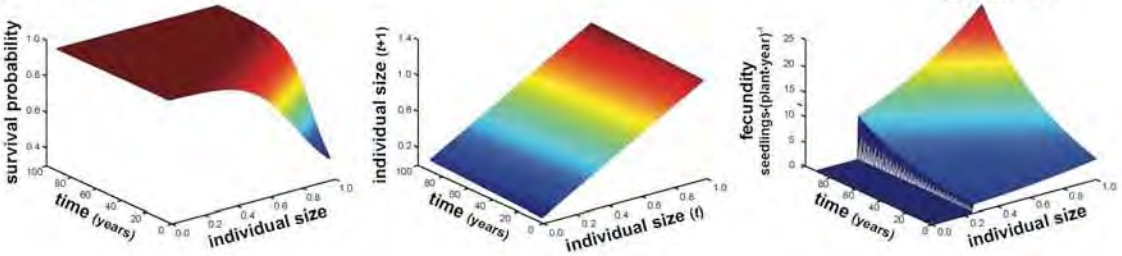
Artificial species 7

Known vital rates



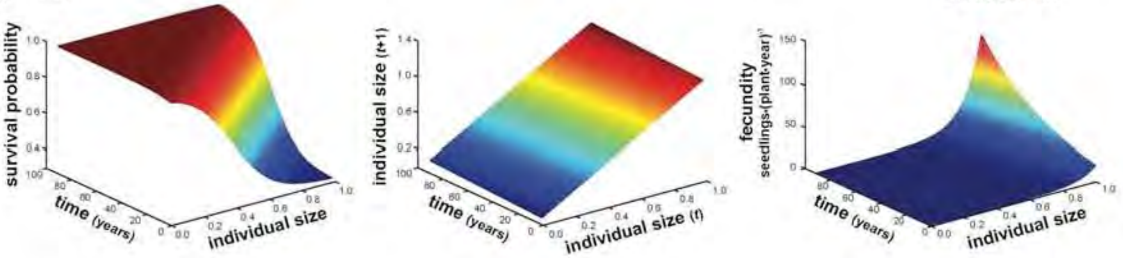
$w = 0$
$r_m = 0.93$

Solution 7.1



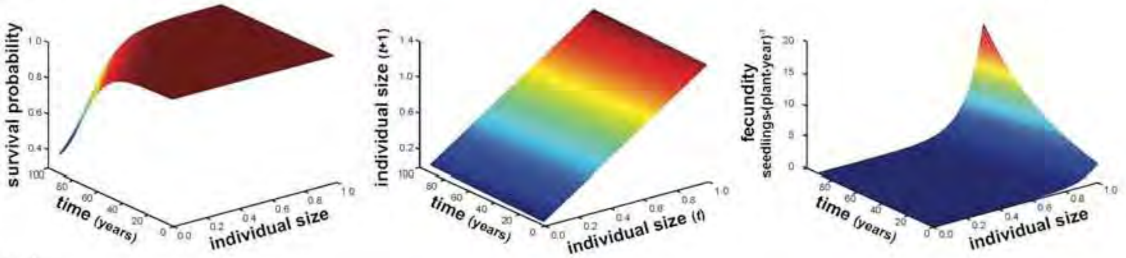
$r_m = 0.81$

Solution 7.2



r_m = 0.55

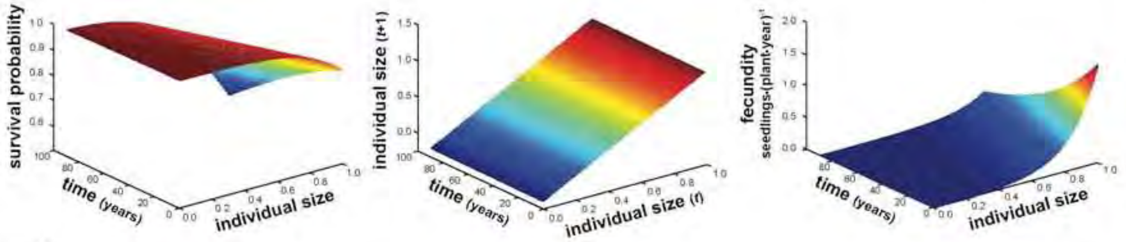
Solution 7.3



$w = 1$

r_m = **0.99**

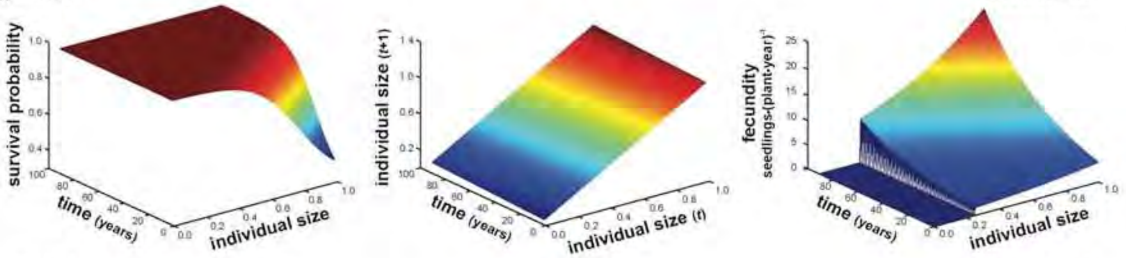
Solution 7.4



$w = 10$

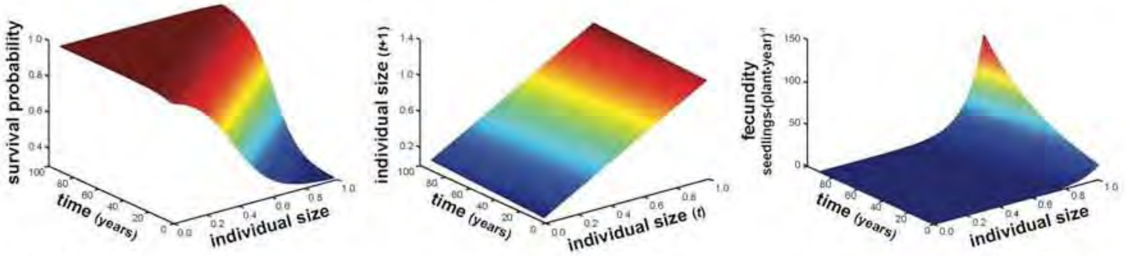
r_m = 0.93

Solution 7.5



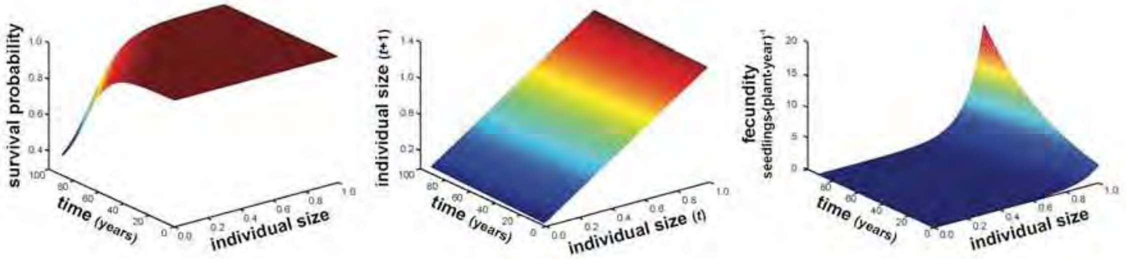
r_m = 0.81

Solution 7.6



r_m = 0.55

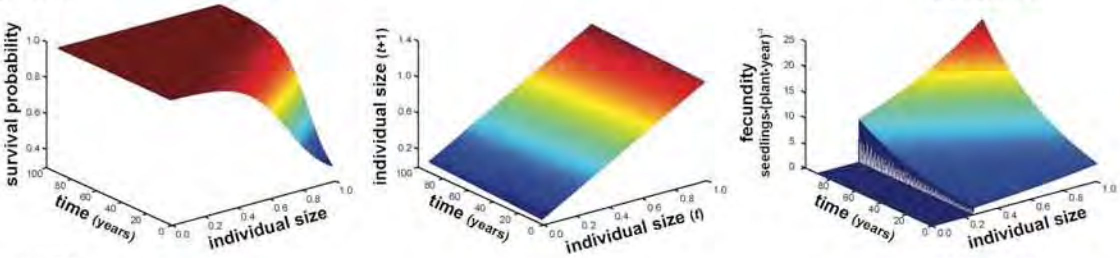
Solution 7.7



$w = 100$

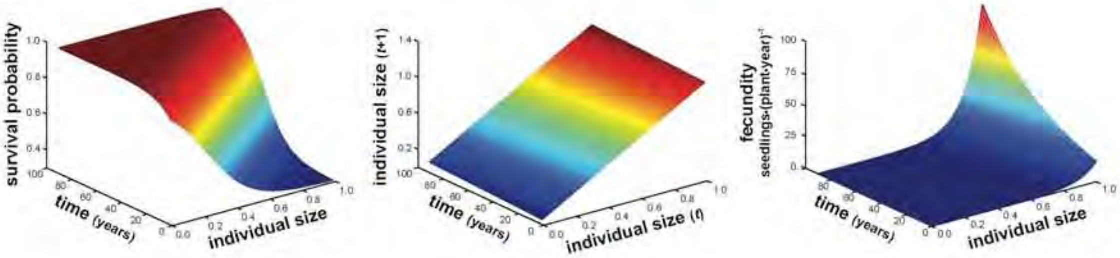
$r_m = 0.94$

Solution 7.8



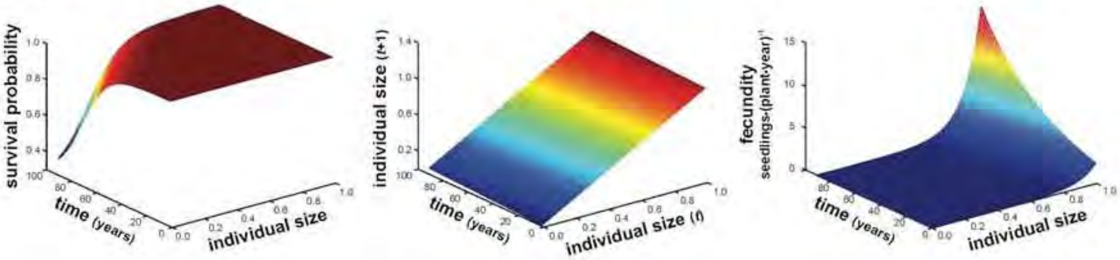
$r_m = 0.79$

Solution 7.9



$r_m = 0.55$

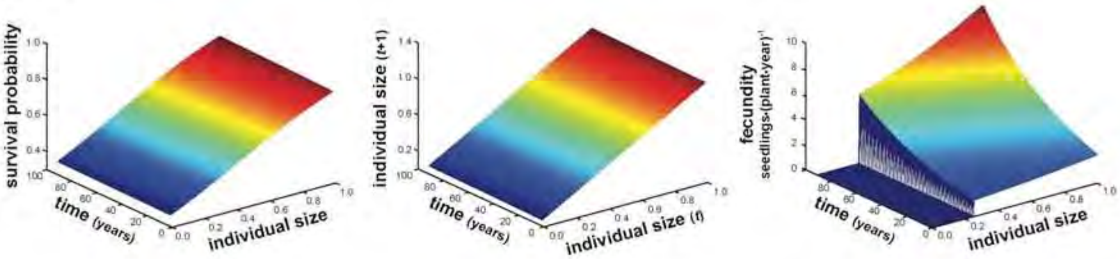
Solution 7.10



$w = 1000$

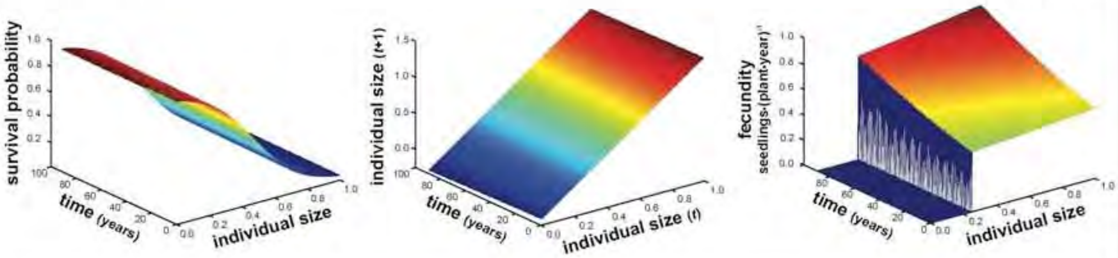
$r_m = 0.57$

Solution 7.11



Artificial species 8

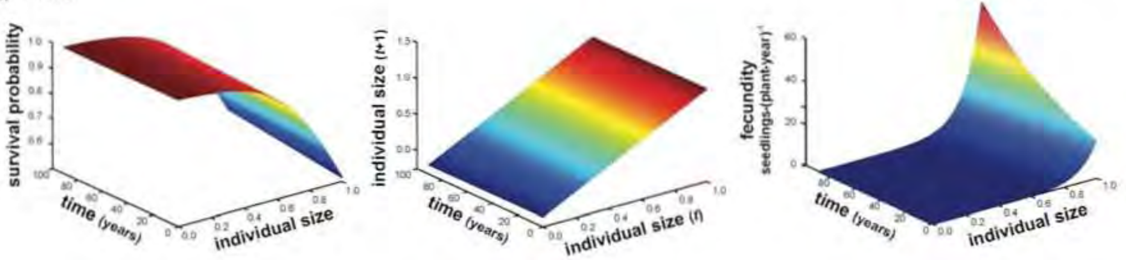
Known vital rates



$w = 0$

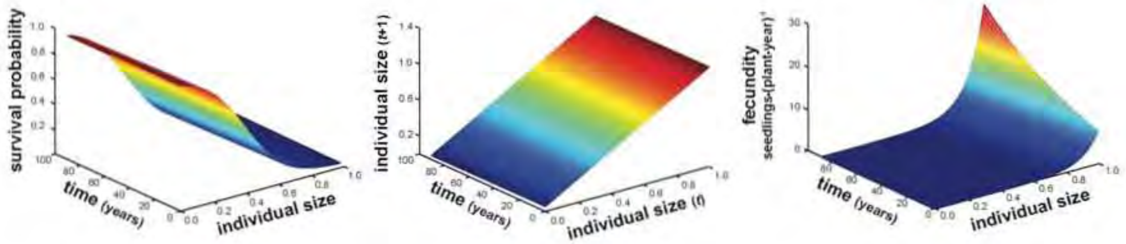
$r_m = 0.78$

Solution 8.1



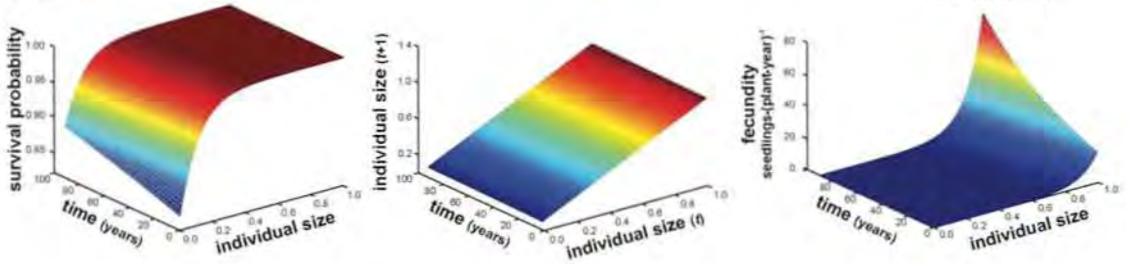
$r_m = 0.49$

Solution 8.2



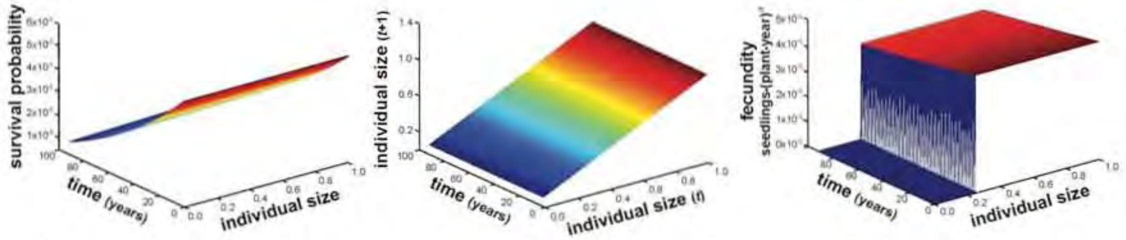
$r_m = 0.40$

Solution 8.3



$r_m = 0.11$

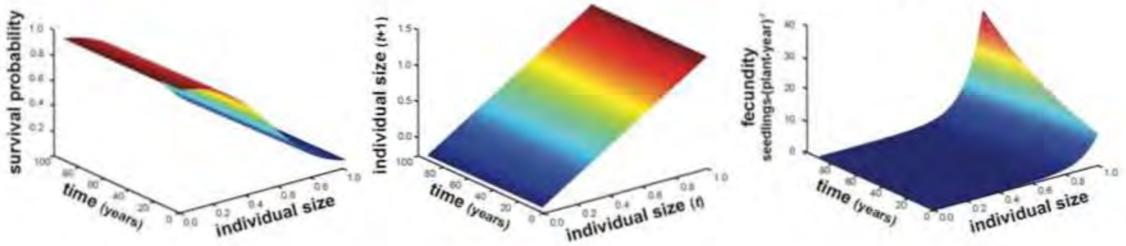
Solution 8.4



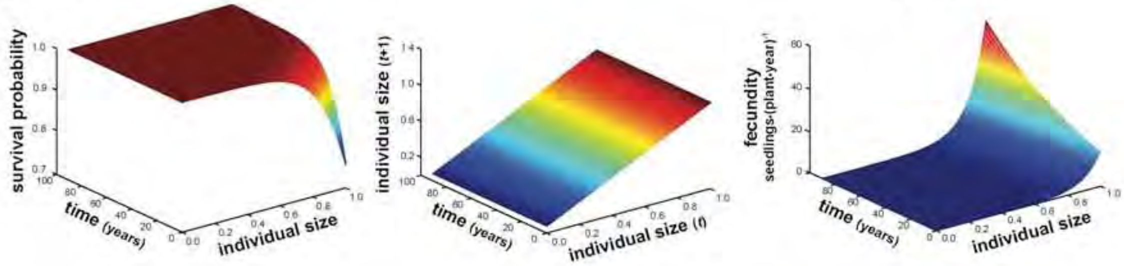
$w = 1$

$r_m = 0.84$

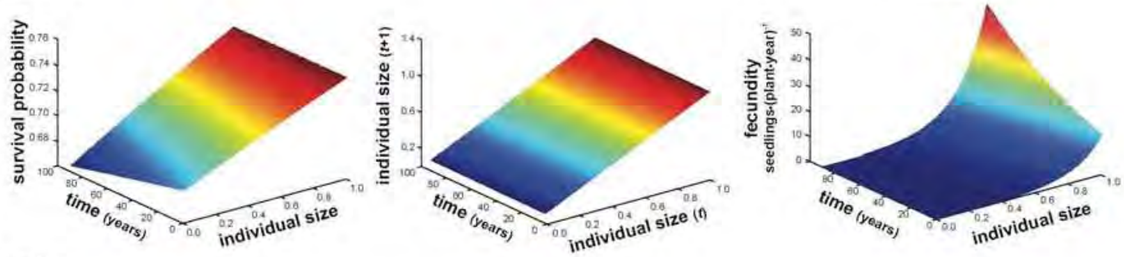
Solution 8.5



$r_m = 0.65$ Solution 8.6

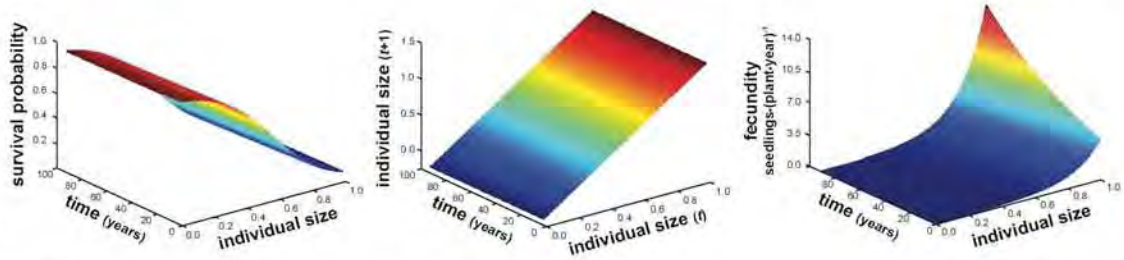


$r_m = 0.36$ Solution 8.7

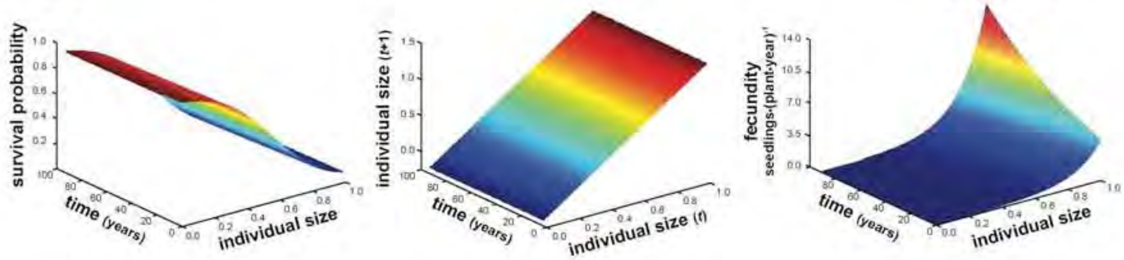


$w = 10$

$r_m = 0.87$ Solution 8.8

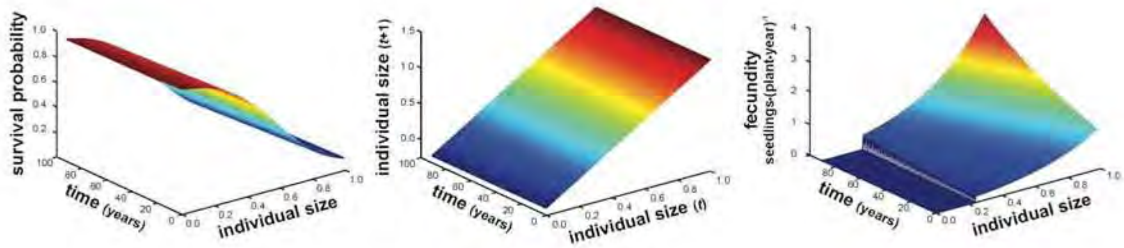


$r_m = 0.38$ Solution 8.9



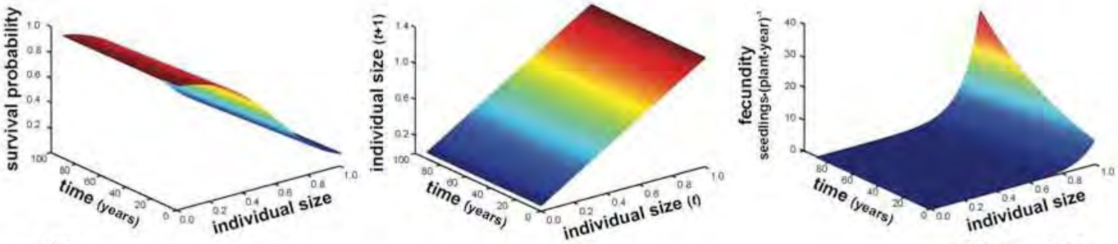
$w = 100$

$r_m =$ **0.95** Solution 8.10



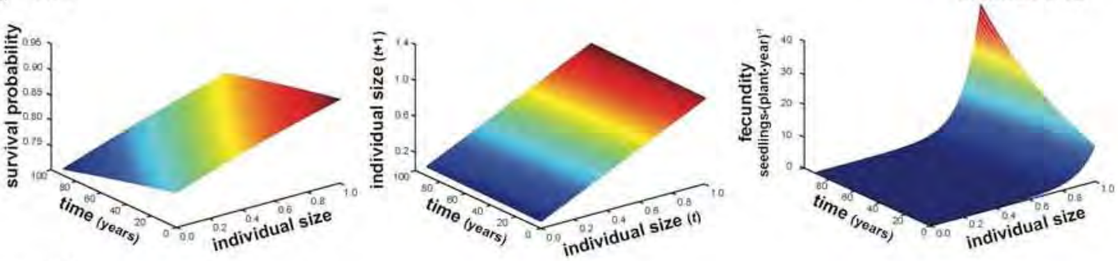
$r_m = 0.85$

Solution 8.11



$r_m = 0.39$

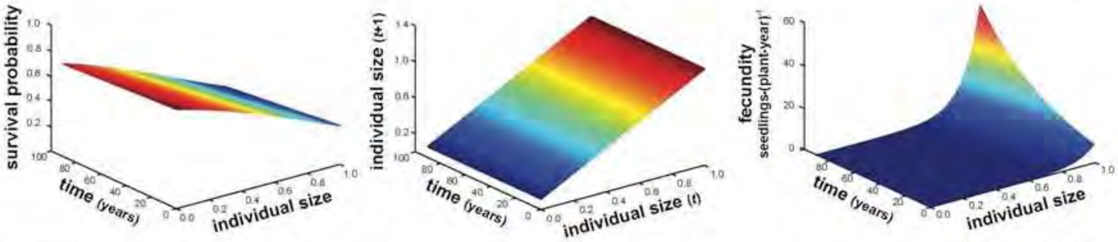
Solution 8.12



$w = 1000$

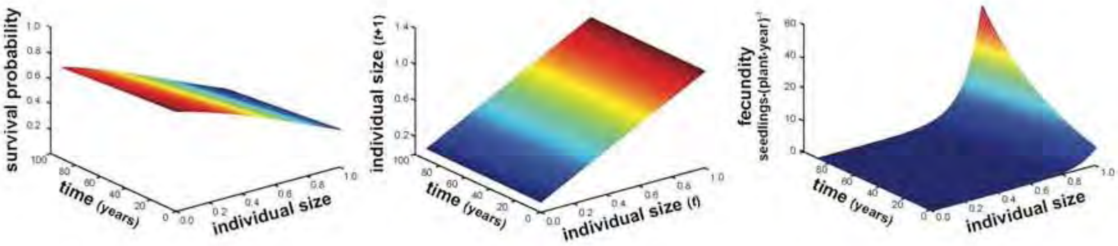
$r_m = 0.85$

Solution 8.13



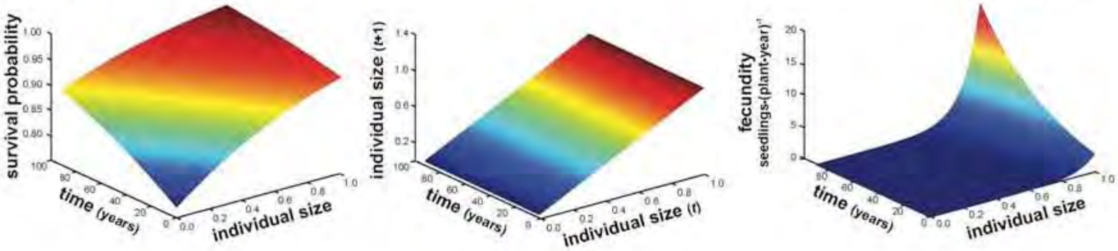
$r_m = 0.85$

Solution 8.14

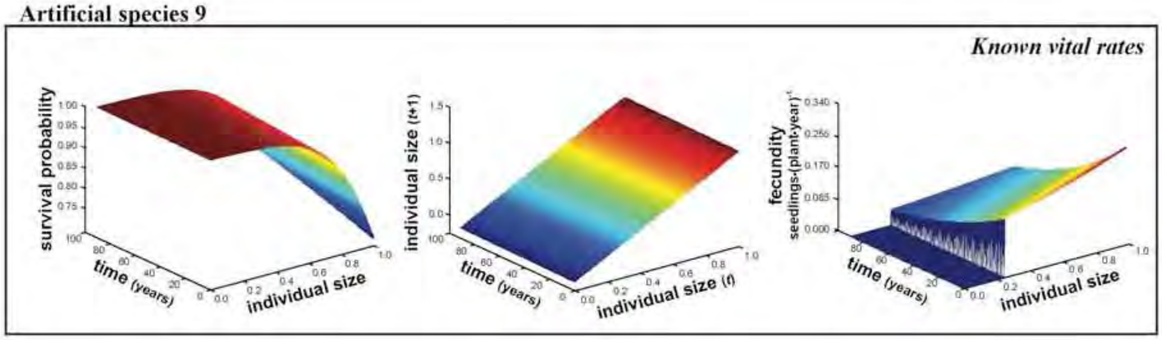


$r_m = 0.42$

Solution 8.15



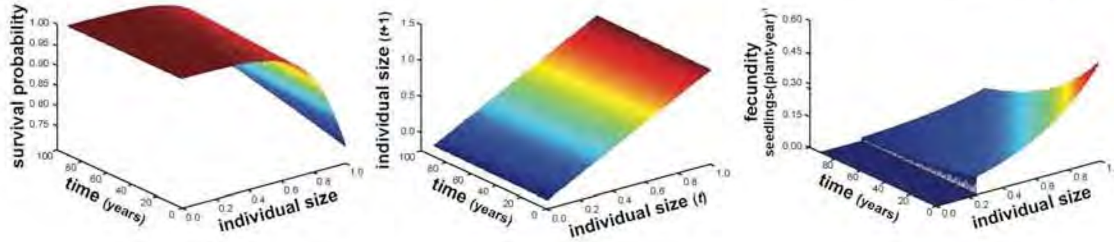
Artificial species 9



$w = 0$

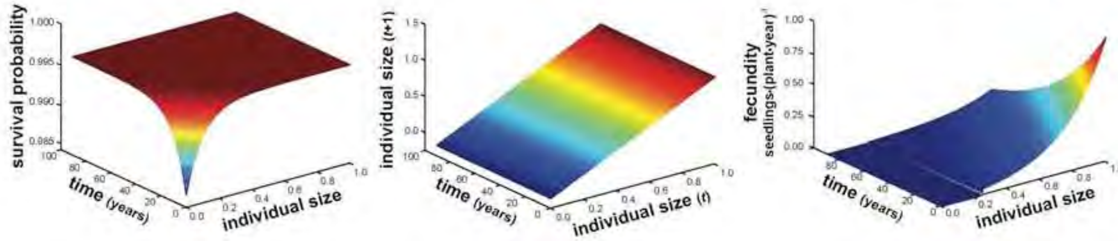
$r_m =$ **0.96**

Solution 9.1



$r_m = 0.58$

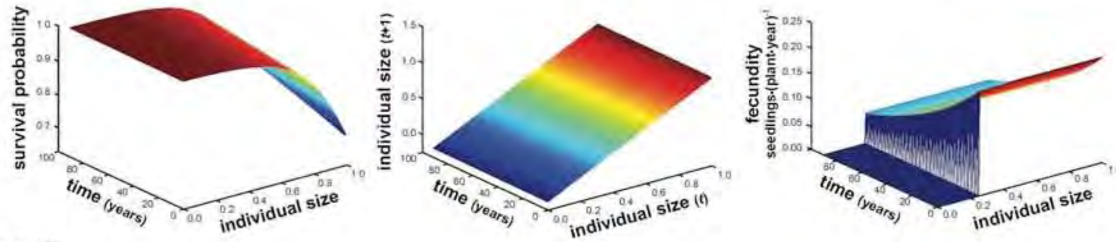
Solution 9.2



$w = 1$

$r_m =$ **0.98**

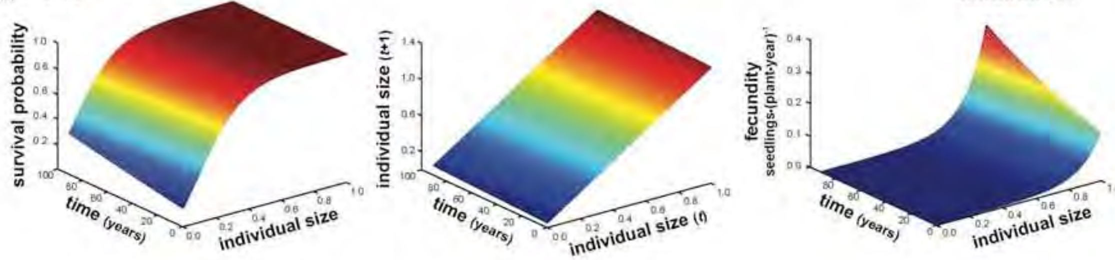
Solution 9.3



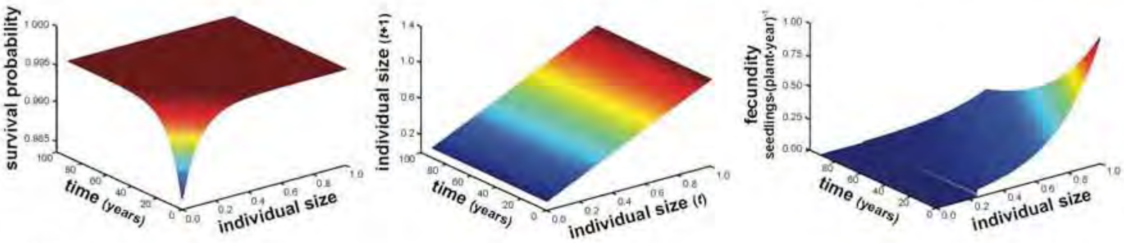
$w = 10$

$r_m = 0.98$

Solution 9.4

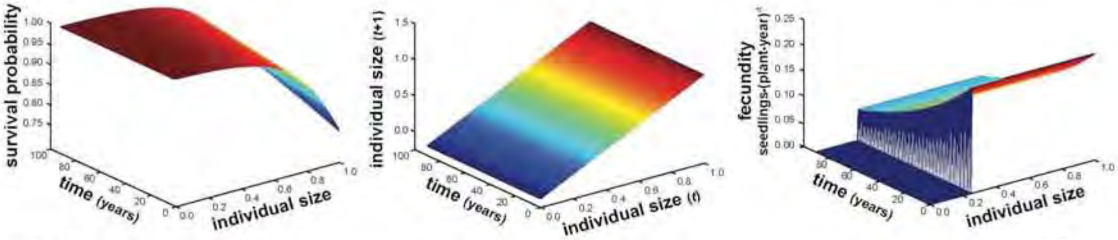


$r_m = 0.58$ Solution 9.5

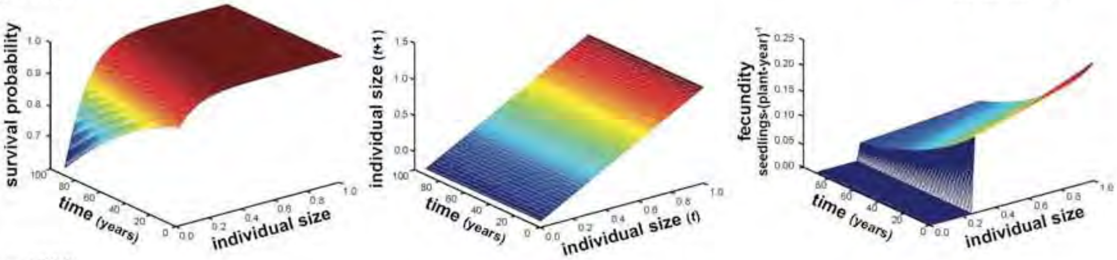


$w = 100$

$r_m = \mathbf{0.98}$ Solution 9.6

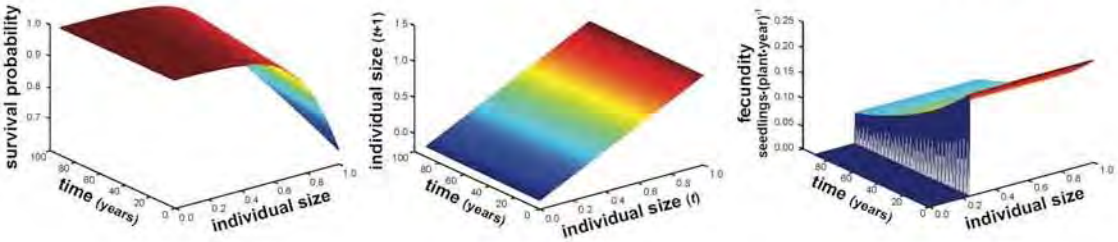


$r_m = 0.66$ Solution 9.7

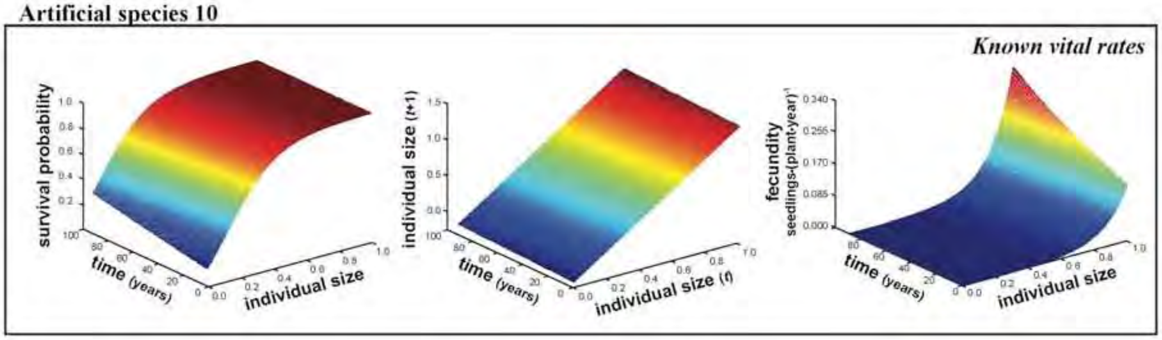


$w = 1000$

$r_m = \mathbf{0.98}$ Solution 9.8



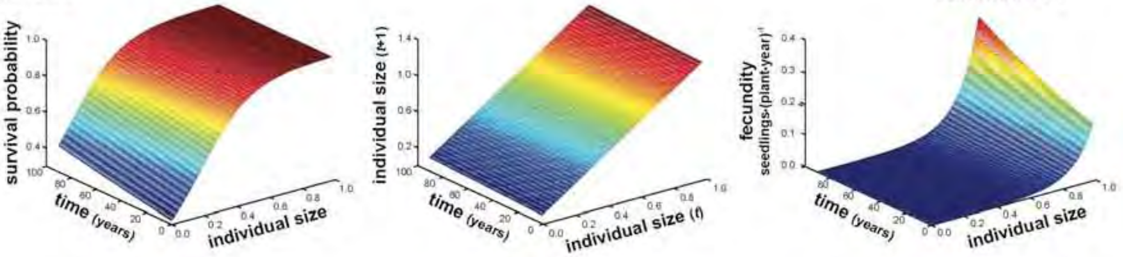
Artificial species 10


Known vital rates

$w = 0$

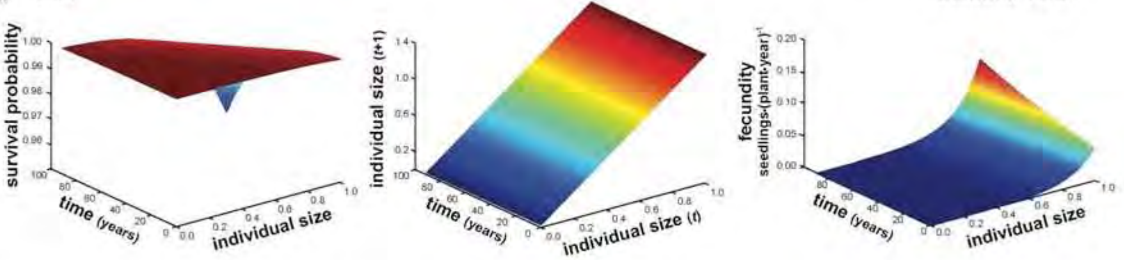
$r_m =$ **1.00**

Solution 10.1



$r_m = 0.64$

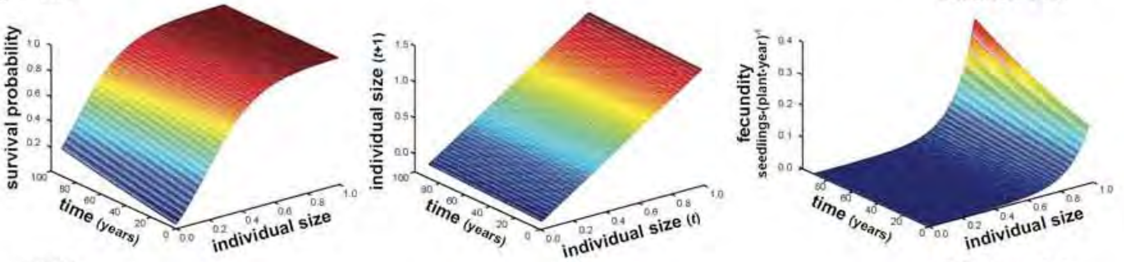
Solution 10.2



$w = 1$

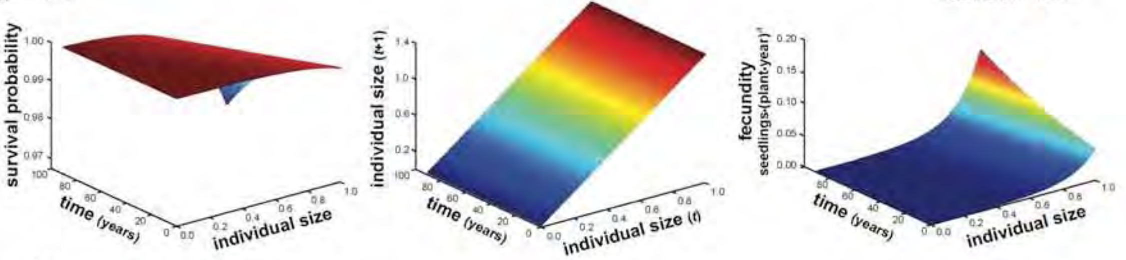
$r_m =$ **1.00**

Solution 10.3



$r_m = 0.63$

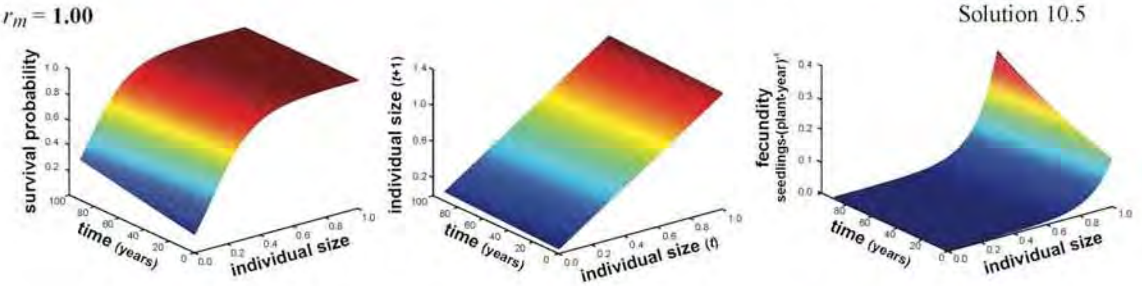
Solution 10.4



$w = 10$

$r_m =$ **1.00**

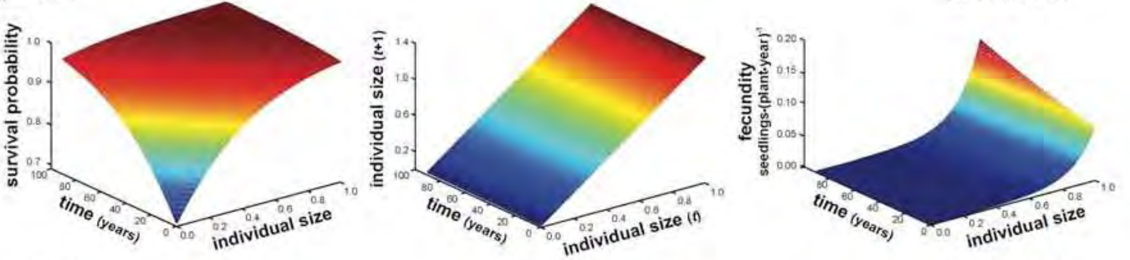
Solution 10.5



$w = 100$

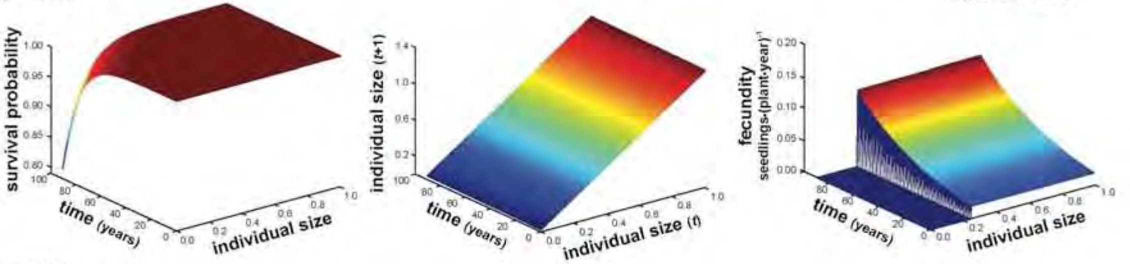
$r_m = 0.94$

Solution 10.6



$r_m = 0.64$

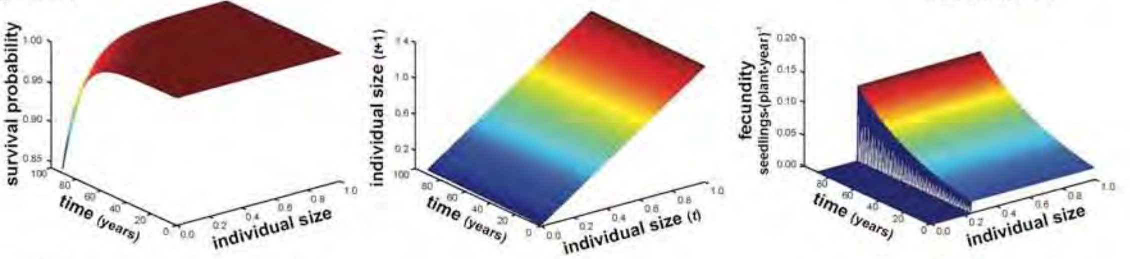
Solution 10.7



$w = 1000$

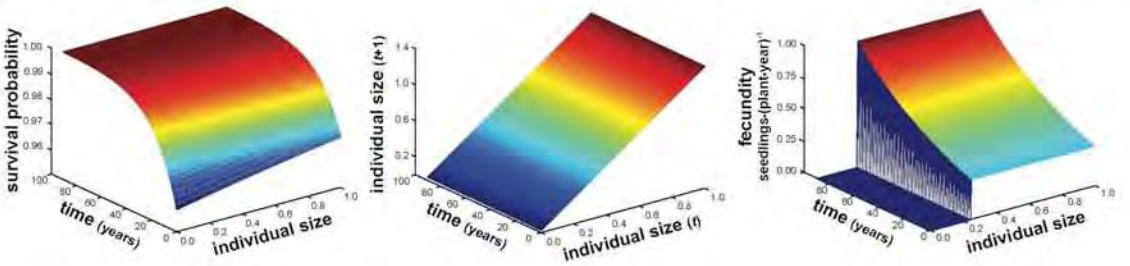
$r_m = 0.64$

Solution 10.8



$r_m = 0.59$

Solution 10.9



Appendix 4

The AD Model Builder (ADMB) software requires three input files: a .tpl file containing the model code (see below), a .dat file containing the dataset (see `DATA_SECTION` for the information to be included in such file), and a .pin file containing the starting point for the exploration of the likelihood surface (a 16-parameter vector). ADMB produces an output of 16 files. For our purposes, we focus on the .rep file, which contains the resulting parameter vector associated with the maximum likelihood (see `REPORT_SECTION`).

The content of the .tpl file is as follows (comments are preceded by `//`):

```
DATA_SECTION      // Data included in the .dat file
  init_int nt     // Number of populations studied, M
  init_int ni     // Size of the partition of the size range X in equation A1; in our case 200
  init_int nm     // Largest sample size, i.e., max{N_1,…, N_M}
  init_int minf   // Minimum reproductive size
  init_number xmin      // Smallest size of an individual (observed or biological)
  init_number xmax      // Largest size of an individual (observed or biological)
  init_number factor    // Value of w in equation A6
  init_vector t(1,nt)   // Observed times {T_1, …, T_M}
  init_vector x(1,ni)   // Partition of the size range X
  init_vector z(1,ni+1) // Class marks of the partition
  init_vector dobs(1,nt)      // Observed population densities, i.e. {D_1, …, D_M}
  init_vector tm(1,nt)  // Sample sizes of the populations studied, i.e. {N_1, …, N_M}
  init_matrix data(1,nm,1,nt) // Data matrix, i.e. a matrix with columns X_1, …, X_M
PARAMETER_SECTION
   init_bounded_number S1(-10,10)     // The 16 parameters of the model with their
   init_bounded_number S2(-0.1,0.1)   // associated intervals in parenthesis
  init_bounded_number S3(-10,10)
  init_bounded_number S4(-0.001,0.001)
  init_bounded_number GS(0.001,0.1)
  init_bounded_number G1(0,0.1)
  init_bounded_number G2(-0.001,0.001)
  init_bounded_number G3(0.5,1.5)
  init_bounded_number G4(-0.00001,0.00001)
  init_bounded_number NS1(-10,0)
  init_bounded_number NS2(-0.02,0.02)
  init_bounded_number NS3(0,10)
  init_bounded_number NS4(-0.0002,0.0002)
  init_bounded_number SSS(0.0001,0.1)
  init_bounded_number SS1(0,0.01)
  init_bounded_number SS2(-0.0001,0.0001)
  objective_function_value v
  number eval
  number lambda
  number ssmu
  number sumg
  number sumss
  number temp
  number da
  number dsigma
  number dtemp
  number vd
  number ve
  number ssd
  number ssdmu
  number corrd
  vector colfxy(1,ni)
```

```
  vector colgxy(1,ni)
  vector colpxy(1,ni)
  vector ex1(1,ni)
  vector gmu(1,ni)
  vector inex(1,ni)
  vector nsx(1,ni)
  vector ssy(1,ni)
  vector sumcol(1,nt)
  vector sx(1,ni)
  vector de(1,nt)
  vector dmu(1,nt)
  vector dsubst(1,nt)
  vector zg(1,ni+1)
  vector zss(1,ni+1)
  vector zd(1,nt)
  vector p(1,16)
  vector doscaled(1,nt-1)
  vector descaled(1,nt-1)
  matrix structures(1,ni,1,nt)
  matrix frequencies(1,ni,1,nt)
  matrix nxy(1,ni,1,ni)
  matrix sxtg(1,ni,1,nt)
  matrix sxtp(1,ni,1,nt)
  matrix gmg(1,ni,1,nt)
  matrix gmp(1,ni,1,nt)
  matrix nsxg(1,ni-minf+1,1,nt)
  matrix nsxp(1,ni-minf+1,1,nt)
 LOCAL_CALCS
  int i,j,k;
  eval = 0;
  for(i = 1; i <= nt; i++)
  for(j = 1; j <= tm[i]; j++)
      {
      if(data[j][i] < xmin)
      data[j][i] = xmin;
      if(data[j][i] > xmax)
      data[j][i] = xmax;
      }
  for(i = 1; i <= nt; i++)
      for(k = 1; k <= ni; k++)
            frequencies[k][i] = 0;
      for(i = 1; i <= nt; i++)
            for(j = 1; j <= tm[i]; j++)
                  {
                  if(data[j][i] >= z[1] && data[j][i] <= z[2])
                        frequencies[1][i] = frequencies[1][i]+1;
                  for(k = 2; k <= ni; k++)
                        if(data[j][i] > z[k] && data[j][i] <= z[k+1])
                              frequencies[k][i] = frequencies[k][i]+1;
                  }
END_CALCS
PROCEDURE_SECTION
  int i,j,k,l,ti,tj;
  eval = eval+1;
  de[1] = 1;
  dtemp = de[1];
  for(i = 1; i < minf; i++)
      nsx[i] = 0;
  for(i = 1; i <= ni; i++)
      ex1[i] = 1;
  j = (int)t[1];
  sx = elem_div(exp(S1+S2*j+S3*x+S4*j*x),1+exp(S1+S2*j+S3*x+S4*j*x));
  for(k = minf; k <= ni; k++)
```

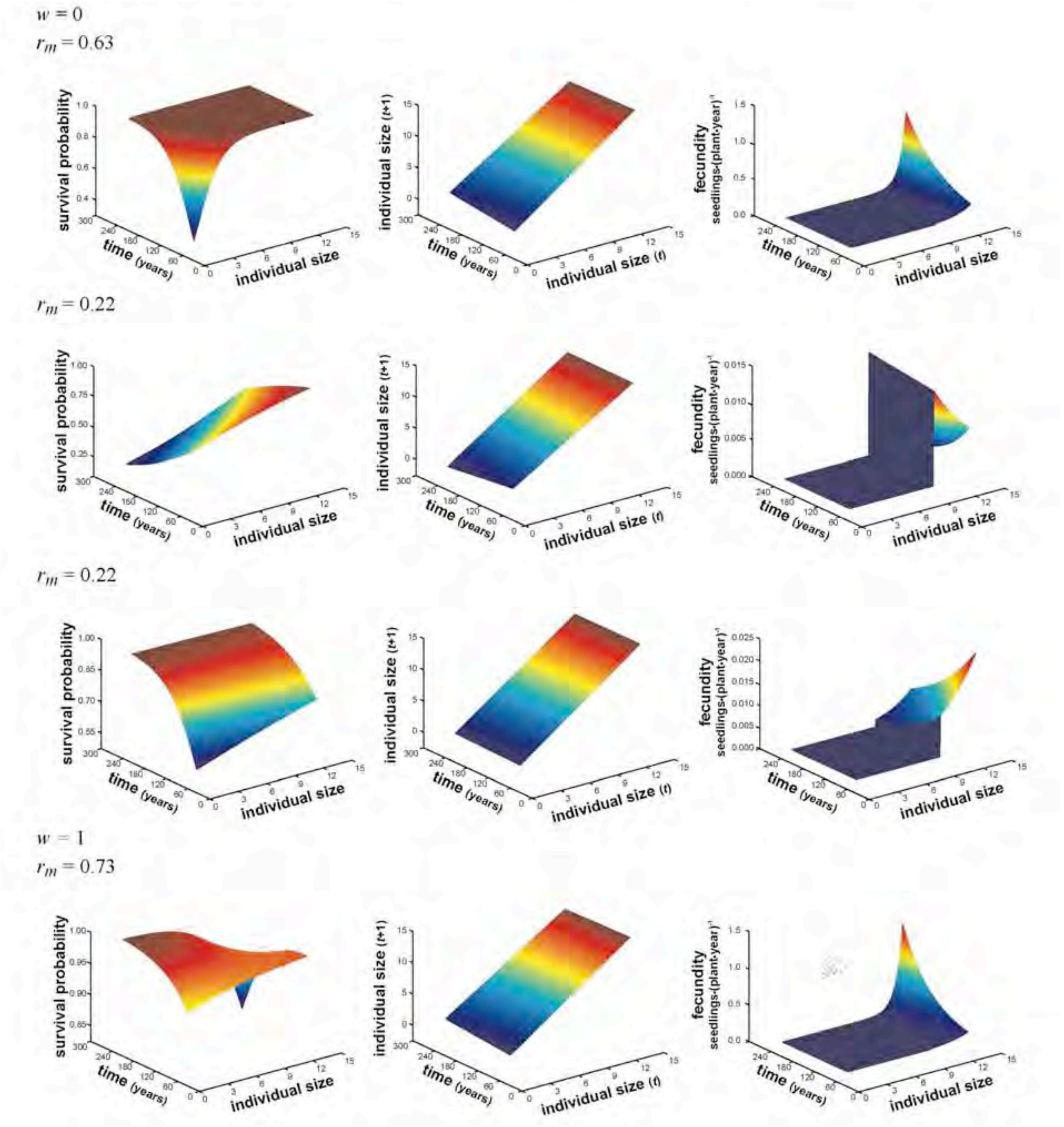
```
      nsx[k] = exp(NS1+NS2*j+NS3*x[k]+NS4*j*x[k]);
  ssmu = SS1+SS2*j;
  zss = (z-ssmu)/SSS;
  for(k = 1; k <= ni; k++)
      ssy[k] = cumd_norm(zss[k+1])-cumd_norm(zss[k]);
  sumss = sum(ssy);
  ssy = ssy/sumss;
  for(k = 1; k <= ni; k++)
      {
      gmu[k] = G1+G2*j+G3*x[k]+G4*j*x[k];
      zg = (z-gmu[k])/GS;
      for(l = 1; l <= ni; l++)
            colgxy[l] = cumd_norm(zg[l+1])-cumd_norm(zg[l]);
      sumg = sum(colgxy);
      colgxy = colgxy/sumg;
      colpxy = sx[k]*colgxy;
      colfxy = nsx[k]*ssy;
      nxy.colfill(k,colpxy+colfxy);
      }
  for(i = 1; i <= 8; i++)
      nxy = nxy*nxy;
  ex1 = nxy*ex1;
  for(j = 1; j <= ni; j++)
      if(ex1[j] <= 0)
            ex1[j] = 1e-323;
  ex1 = ex1/sum(ex1);
  inex = ex1;
  structures.colfill(1,inex);
  for(i = 1; i <= nt-1; i++)
      {
      ti = (int)t[i];
      tj = (int)t[i+1];
      for(j = ti; j < tj; j++)
            {
            sx =
elem_div(exp(S1+S2*j+S3*x+S4*j*x),1+exp(S1+S2*j+S3*x+S4*j*x));
            for(k = minf; k <= ni; k++)
                  nsx[k] = exp(NS1+NS2*j+NS3*x[k]+NS4*j*x[k]);
            ssmu = SS1+SS2*j;
            zss = (z-ssmu)/SSS;
            for(k = 1; k <= ni; k++)
                  ssy[k] = cumd_norm(zss[k+1])-cumd_norm(zss[k]);
            sumss = sum(ssy);
            ssy = ssy/sumss;
            for(k = 1; k <= ni; k++)
                  {
                  gmu[k] = G1+G2*j+G3*x[k]+G4*j*x[k];
                  zg = (z-gmu[k])/GS;
                  for(l = 1; l <= ni; l++)
                        colgxy[l] = cumd_norm(zg[l+1])-
cumd_norm(zg[l]);
                  sumg = sum(colgxy);
                  colgxy = colgxy/sumg;
                  colpxy = sx[k]*colgxy;
                  colfxy = nsx[k]*ssy;
                  nxy.colfill(k,colpxy+colfxy);
                  }
            inex = nxy*inex;
            lambda = sum(inex);
            dtemp = lambda*dtemp;
            inex = inex/lambda;
            }
      for(j = 1; j <= ni; j++)
```

```
            if(inex[j] <= 0)
                  inex[j] = 1e-323;
      de[i+1] = dtemp;
      if(de[i+1] <= 0)
            de[i+1] = 1e-323;
      structures.colfill(i+1,inex);
      }
  da = sum(log(dobs)-log(de))/nt;
  dmu = da+log(de);
  dsubst = log(dobs)-dmu;
  dsigma = sqrt(sum(elem_prod(dsubst,dsubst))/(nt-1));
  zd = (dsubst)/dsigma;
  vd = 0;
  for(i = 1; i <= nt; i++)
      vd = vd+log(500/dsigma*(cumd_norm(zd[i]+0.001)-cumd_norm(zd[i]-
0.001)));
  ve = sum(colsum(elem_prod(frequencies,log(structures))));
  v = -ve-factor*vd;
REPORT_SECTION    // variables preceded by "report <<" are included in the output file .rep
  int i;
  report << S1 << endl; // parameter vector that maximizes the likelihood of the data
  report << S2 << endl;
  report << S3 << endl;
  report << S4 << endl;
  report << GS << endl;
  report << G1 << endl;
  report << G2 << endl;
  report << G3 << endl;
  report << G4 << endl;
  report << NS1 << endl;
  report << NS2 << endl;
  report << NS3 << endl;
  report << NS4 << endl;
  report << SSS << endl;
  report << SS1 << endl;
  report << SS2 << endl;
  report << endl;
  for(i = 1; i <= nt; i++)
      report << de[i] << endl; // densities obtained by the model
  report << endl;
  report << ve << endl; // maximum likelihood of the observed size-structures (eqn. A4)
  report << vd << endl; // maximum likelihood of the observed densities (eqn. A5)
  report << -v << endl; // composite maximum likelihood (eqn. A6)
  report << endl;
  ssd = 0;
  for(i = 2; i <= nt; i++)
      {
      doscaled[i-1] = dobs[i]/dobs[1];
      descaled[i-1] = de[i];
      }
  ssd = norm2(doscaled-descaled);
  report << ssd << endl; // sum of squares between the observed and modelled densities
  report << endl;
  corrd = 0;
  for(i = 1; i <= nt-1; i++)
      corrd = corrd+(doscaled[i]-mean(doscaled))*(descaled[i]-
mean(descaled));
  corrd = corrd/sqrt(norm2(doscaled-mean(doscaled))*norm2(descaled-
mean(descaled)));
  report << corrd << endl; // correlation between the observed and modelled densities
FINAL_SECTION
```

Appendix 5

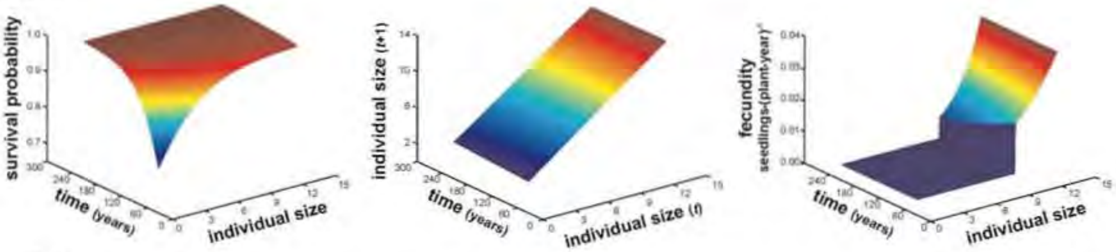
Vital rates reconstructed for *Mammillaria dixanthocentron*

Solutions obtained by the model with different values of the coefficient weighting the fitting of the population densities vs. that of the size structures (w in equation 4). r_d is the Pearson correlation coefficient between the observed and reconstructed population densities. Bold r_d: correct reconstruction, roman r_d: incorrect solution that could be discarded (type-1 solution).



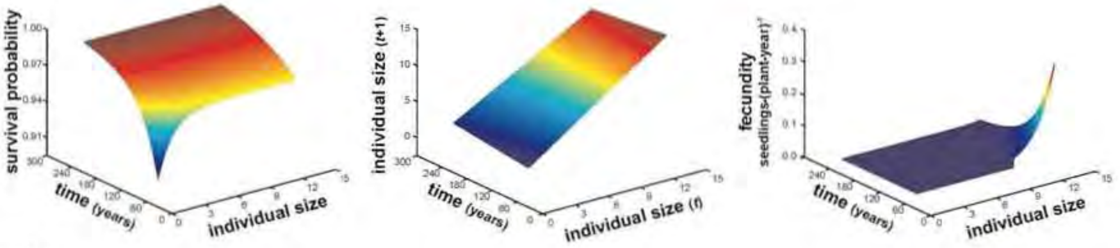
$w = 1$

$r_d = 0.61$

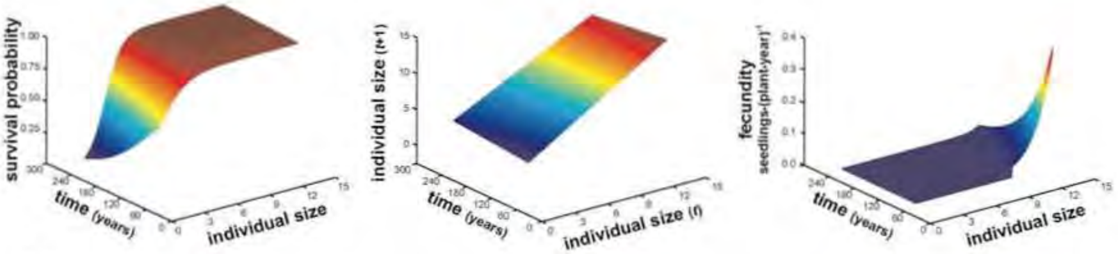


$w = 100$

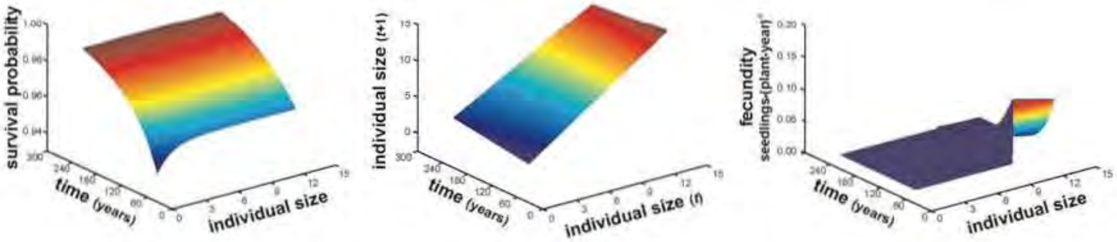
$r_d = 0.81$



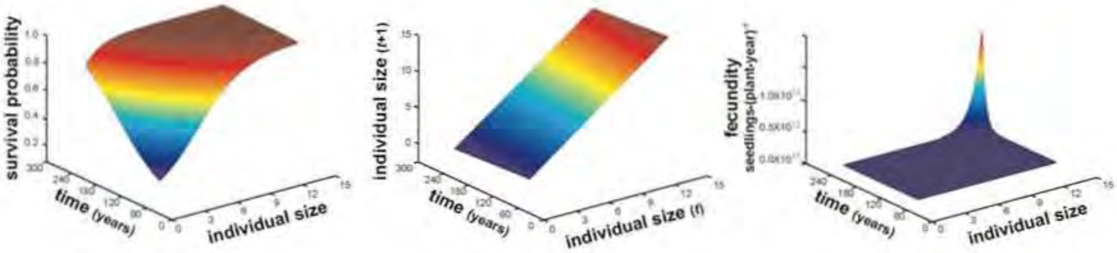
$r_d = \mathbf{0.81}$

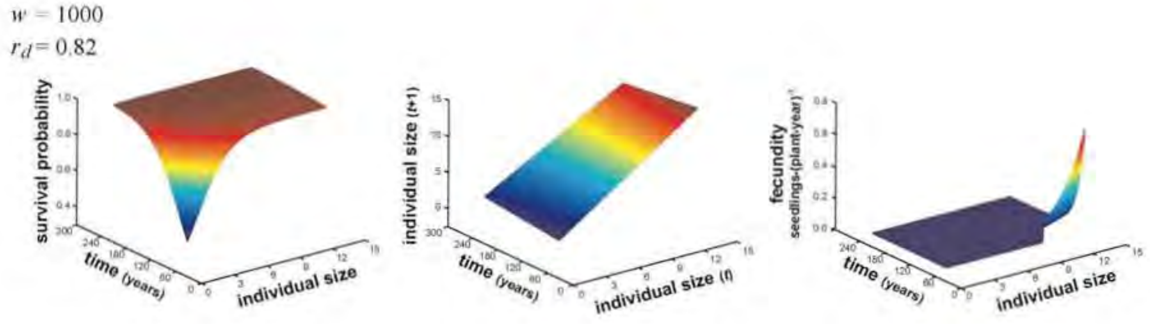


$r_d = 0.80$



$r_d = -0.62$




$w = 1000$
$r_d = 0.82$
survival probability
1.0
0.8
0.6
0.4
300
240
180
120
60
0
time (years)
0
3
6
9
12
15
individual size
individual size (t+1)
15
10
5
0
300
240
180
120
60
0
time (years)
0
3
6
9
12
15
individual size (t)
fecundity
seedlings·(plant·year)$^{-1}$
0.8
0.6
0.4
0.2
0.0
240
180
120
60
0
time (years)
0
3
6
9
12
15
individual size

Capítulo 3

The impact of chronic anthropogenic disturbance on cacti: reconstructing the change in their vital rates through chronosequences of static data

E. J. González & C. Martorell

Introduction

Anthropogenic disturbance is a pervasive presence in all the ecosystems in the planet (Vitousek *et al.,* 1997; Singh, 1998; Sala *et al.,* 2000), and has been associated to the transformation of habitats, the reduction of ecosystem productivity and the loss of biodiversity (Hannah *et al.*, 1995; Millennium Ecosystem Assessment, 2005; Pereira, 2010). Such disturbance can be classified as acute or chronic depending on the frequency and intensity of its occurrence. Acute anthropogenic disturbance occurs infrequently but with high intensity, while chronic anthropogenic disturbance (CAD), the focus of this paper, consists of frequent but mild events. Compared with acute disturbance, the main problem associated with CAD is that it accumulates through time (Singh, 1998). This prevents the populations of many disturbance-sensitive species from completely recovering from a disturbance event before another one takes place (Murali *et al.*, 1996; Singh, 1998). Therefore, even if CAD may appear to be of low relevance at a short time-scale, its long-term effects on ecosystems are as negative as those of acute anthropogenic disturbance, or even worse (Singh, 1998). Nonetheless, CAD will not affect all species negatively: some ruderal species benefit from it, thriving under intermediate CAD intensities (Martorell & Peters, 2009; Martorell, 2013).

Drylands, the largest terrestrial ecosystem, face CAD in the form of extensive livestock raising and the ceaseless extraction of small amounts of resources, reducing vegetational cover and favouring land degradation and desertification (Martorell & Peters, 2005; Reynolds *et al.*, 2007; Villagra *et al.*, 2009). Due to the gradual nature of CAD, degradation gradients are observed at the landscape scale, going from pristine to largely denuded areas (Karanth *et al.*, 2006; Bhat *et al.*, 2012). The transformation of these areas may occur over the period of centuries (Binford & Leyden, 1987; Rundel, 1999; González & Martorell, 2013).

Many dryland plants, such as cacti, have low growth rates and infrequent recruitment, and thus are expected to slowly recover from disturbance events (Hernández & Godínez, 1994; Esparza-Olguín *et al.*, 2002; Godínez-Alvarez *et al.*, 2003; Guo, 2004). These attributes would therefore make them susceptible to CAD (Esparza-Olguín *et al.*, 2002). Accordingly, cacti have been classified as an endangered group in both regional and international red lists (SEMARNAT, 2002; CITES, 2013). However, many small globose cacti tolerate a certain degree of CAD, and even thrive at intermediate CAD intensities (Martorell & Peters, 2005, 2009; Montañana, 2009; Martorell *et al.*, 2012; Martorell *et al.*, unpublished). Under such intensities, livestock may be removing neighbour plants with higher competitive abilities. Given that cacti are known to be poor competitors, such removal would benefit them (Jiménez-Sierra *et al.*, 2007). This would also explain why, when no disturbance is present, cacti are found in low densities (Martorell & Peters, 2009). Conversely, livestock may damage vegetative and reproductive structures, and thus affect cacti populations (Zavala-Hurtado & Valverde, 2003; Ureta & Martorell, 2009; Portilla-Alonso & Martorell, 2011). CAD would also favour recruitment through soil erosion, a process that exposes rocks and gravel. These elements serve as abiotic nurses to several globose cacti, which, contrary to most other cacti, do not require plant nurses (Godínez-Álvarez *et al.*, 2003; Peters *et al.*, 2008). By increasing the availability of such elements, CAD would increase the establishment of seedlings (Santini, 2007; Portilla-Alonso & Martorell, 2011; Martorell *et al.*, 2012; Martorell *et al.*, unpublished). Finally, at high CAD intensities, land degradation affects all demographic processes due to the loss of soil, which hinders the persistence of individuals and the establishment of new plants (Martorell & Peters, 2005, 2009; Santini, 2007; Portilla-Alonso & Martorell, 2011).

Due to the large number of threatened cactus species and their species-specific response to CAD, successful conservation efforts require a detailed understanding of how cactus demography is affected by disturbance. However, obtaining such knowledge requires research that is difficult to perform because it involves the study of both a long-term environmental process and long-lived organisms. The existing knowledge of how cacti respond to CAD at the level of their vital rates has been gathered through the survey over several years of pairs of populations subject to different intensities of CAD. By comparing these populations, conclusions have been made on the effect of CAD on such rates (Valverde *et al.*, 2004; Flores Martínez *et al.*, 2010; Portilla-Alonso & Martorell, 2011; González *et al.,* 2013). Additionally, several years are required to capture the mean demographic behaviour of long-lived plants. Moreover, a pair of populations seems insufficient to describe the changes in demographic behaviour over the whole degradation gradient. Therefore, this methodology is costly and time consuming, making it unviable for the study of the species affected by CAD. Methods that allow the easy identification of how particular species respond demographically to CAD are thus required.

Here, we apply a recently developed demographic method that allows the reconstruction of the shifts in vital rates driven by directional, long-term environmental change. This method has the advantage of not requiring the survey of populations over long time-periods allowing us to study several species at once. The data used as input is a set of population structures and densities of populations subject to different intensities of the environmental factor, in our case, CAD. With this method we aim at understanding how CAD modifies the vital rates of seven species of endangered globose cacti. We also analyse how changes on the vital rates of these species impact their annual population growth rate over time. This information is crucial for the development of successful conservation plans in a planet dominated by human-related processes.

Material and methods

Model

We used the model originally presented in González & Martorell (2013). This model reconstructs the vital rates (survival, growth and reproduction) and their change through time based on a time series of population structures and densities. The model explores a variety of vital rates, seeking the ones that produce the structures and densities that best resemble the observed time series.

The vital rates of the structured population are modeled through an integral projection model (IPM; Easterling *et al.*, 2000). An IPM integrates the vital rates into a function k known as the kernel. This function establishes the log-sizes y that plants of log-size x may reach from year t to t+1, as well as the number and sizes of their seedlings. The IPM is expressed through the equation

$$n(y,t+1) = \int k(y,x,t) \cdot n(x,t)dx, \qquad \text{eqn. 1}$$

where n is the size structure of the population. Note that in our model, k is a function of time because the vital rates are driven by CAD, which in turn increases with time.

The kernel comprises the functions associated to the vital rates: survival probability, s, growth, g, number of seedlings, f_1, and the sizes of these, f_2, which relate as

$$k(y,x,t) = s(x,t)\cdot g(y,x,t) + f_1(x,t)\cdot f_2(y,t). \qquad \text{eqn. 2}$$

We used the following functions to determine these vital rates:

$$s(x,t) = [1+\exp(\beta_1 + \beta_2\cdot t)]^{-1}\cdot[1+ \exp(\beta_3 + \beta_4\cdot x + \beta_5\cdot t + \beta_6\cdot x\cdot t)]^{-1} \qquad \text{eqns. 3}$$

$$g(y,x,t) \sim \text{normal}(\mu = \beta_7 + \beta_8\cdot x + \beta_9\cdot t + \beta_{10}\cdot x\cdot t, \sigma^2 = \beta_{11})$$

$$f_1(x,t) = \exp(\beta_{12} + \beta_{13}\cdot x + \beta_{14}\cdot t + \beta_{15}\cdot x\cdot t)$$

$$f_2(y,t) \sim \text{normal}(\mu = \mu_c, \sigma^2 = \sigma^2_c)$$

As can be seen from equations 3, the vital rates and their change through time are determined by 15 parameters. As in González & Martorell (2013), we used a survival probability function (s) that limits the maximum survival of adults to less than one; this avoids the possibility of immortal adults occurring in the population. However, in this paper we fixed the mean (μ_c) and variance (σ^2_c) of seedling size, assuming that they are largely constrained by seed size, which itself is fairly constant in the species we studied (Martorell & Peters, 2009).

For one of the species studied (*Mammillaria supertexta*), flower production was known. Thus, we included this information in the model in the following manner. As $f_1(x,t)$ models seedling production, we re-expressed this function as the number of flowers produced, $f_1'(x,t)$, multiplied by a flower-to-seedling conversion factor that may change over time, $c(t)$. This factor was modeled as a logistic function of time. Therefore, $f_1(x,t) = c(t)\cdot f_1'(x,t)$, where $c(t) = [1+\exp(\beta_1 + \beta_2\cdot t)]^{-1}$, $f_1'(x,t) = \exp(\beta_{12} + \beta_{13}\cdot \mathrm{x} + \beta_{14}\cdot t + \beta_{15}\cdot x\cdot t)$, β_1 and β_2 are unknown parameters, and β_{12}, β_{13}, β_{14}, and β_{15} are known parameters estimated from the recorded flower production. Thus, in the particular case of *M. supertexta*, the model is determined by 13 parameters.

To assess whether any given set of parameter values is able to reproduce the observed time series, we first calculated the vital rates for every year in the period over which DAC takes place by substituting the parameter values in equations 3. We then calculated the time series of size structures through the iteration of equation 1. To do so, an initial size structure, $n(x,0)$, is required. Assuming that before time zero DAC had not occurred (*i.e.*, the environment had remained constant before the onset of DAC), it would be safe to assume that at such time the population was in its stable state (Caswell, 2001). Therefore, in the first iteration of equation 1 we used the stable (asymptotic) size-structure associated with the vital rates at time zero. This also implies that we are assuming that the population existed in a given area when DAC was not present, a condition not necessarily true for ruderal species.

After calculating the time series of size structures, we calculated the series of densities by integrating these structures over size. These two time series were compared with the observed ones through the composite log-likelihood:

$$l = l_n + w \cdot l_d, \qquad \text{eqn. 4}$$

where l_n and l_d are the log-likelihoods associated with the size structures and to the densities, respectively, and w is a weighting factor of the relative importance of the fit of the observed size-structures vs. that of the observed population densities. Because at each observed point in time there is only one datum for density, but several for size structure, not using a weighting factor could belittle the contribution of density to l. Therefore, for a particular w-value, the values of the 15 parameters that resulted in the highest l-value determined the kernel that best resembled the observed data.

Parameter values were restricted to be within certain intervals. These were established to include a wide set of possible demographic behaviors: each vital rate could relate with size (x) and time (t) in a positive or negative way, or even not be affected by any of them. However, the intervals of the parameters associated with the effect of size over survival and fecundity were restricted to increase with size as it is know to happen in the cactus species we studied. Given that the model may reach different maxima depending on the starting parameter values, 25 sets of values were randomly selected within the parameter intervals. When more than one maximum was obtained with these sets, 75 more random sets were used to guarantee the identification of all local maxima.

From previous experience (González & Martorell, 2013), we know that the model may produce three types of maxima: 1) correct reconstructions of the change over size and time of the vital rates, 2) incorrect reconstructions of the relation between size and the vital rates (opposite sign to that known for the species or strong size dependence of the rates when none is expected), and 3) correct reconstructions of the size-vital rates relationships, but incorrect reconstructions of the change of the vital rates over time. These last reconstructions cannot be discarded on any biological basis, and thus, together with the type-1 reconstructions, we refer to any of them as a biologically plausible reconstruction. We also know that, for a given dataset, the correct (type-1) reconstruction most probably will not be the one with the highest l-value (i.e., will be a local, rather than a global maximum) and that most incorrect reconstructions will be of the second type. Thus, in a scenario where more than one local maximum is obtained it is highly probable that all incorrect reconstructions will be discarded. For the particular cacti species we studied, we considered as biologically plausible the following size-vital rate relations: survival higher for the large individuals rather than the small ones, seedlings cannot have a survival probability larger than 60 %, and fecundity increases with plant size.

The model was run using the Automatic Differentiation Model Builder (ADMB; Fournier *et al.*, 2012). For each species, the model was thus run with up to 100 starting parameter values and w-values of 1, 10, 100 and 1000 to explore different relative contributions of the size-structures vs. that of the population densities. As in González & Martorell (2013), the model was run initially with $w = 1$, and was increased in value only if the previous value did not produce any biologically plausible reconstruction.

Given such a reconstruction, we assessed the change through time of the annual population growth rate [$\lambda_t = \int n(x,t)dx / \int n(x,t\text{-}1)dx$] and the contribution of each of the three demographic processes affected by CAD (s, g, and f_1) to the change in λ_t over time. For each process, its contribution was calculated by obtaining a new kernel where only the process in question changed through time. This was done by setting to zero the parameters associated to time of the other processes. For this new kernel the corresponding time series of λ_t's was calculated. The asymptotic population growth rate of the kernel at time zero, λ_0, was used as a reference value of the state of the population when disturbance was not present. For *M. dixanthocentron*, the plausible kernel had already been identified in González & Martorell (2013) and thus we performed the above assessments on this kernel.

Study system

The seven *Mammillaria* species we studied are threatened globose cacti: *M. dixanthocentron* Backeb., *M. hernandezii* Glass & R.C. Foster, *M. kraehenbuehlii* (Krainz) Krainz, *M. napina* J.A. Purpus, *M. pectinifera* F.A.C Weber, *M. solisioides* Backeb., and *M. supertexta* Mart. Ex Pfeiff (SEMARNAT, 2002; CITES, 2013). These species are endemic to the Tehuacán-Cuicatlán Valley, a region located in the states of Puebla and Oaxaca, Mexico (Martorell & Peters, 2009). This region presents a heterogeneous vegetational mosaic: grassland, pine-oak forest, tropical dry forest and xeric scrub. It has experienced human presence since pre-Columbian times (MacNeish, 1967), 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 forests (Casas *et al.*, 2001; McAuliffe *et al.*, 2001; Pérez-Negrón & Casas, 2007).

For each species, five to 11 sites were sampled depending on the availability of populations, totalling 67 sites. At each site, we delimited the population through a polygon joining the farthest plants in a site. Two to three transects were laid in each polygon and the cacti in each transect were counted and measured (details on the field method are described in Martorell & Peters, 2009). For *M. kraehenbuehlii*, which is a clonal species, a clump of stems was recorded as a single individual and its diameter was used as size. For *M. dixanthoncetron*, size was defined as the volume of a cylinder based on measured diameter and height. For the remaining species only diameter was recorded. For *M. supertexta*, fecundity was recorded as the number of flowers present on each individual. For the remaining species, fecundity was only partially recorded, and therefore was not incorporated in the model, but just used to set the minimum fecundity size. For *M. hernandezii*, the demographic dynamics of two of its populations was followed over six years (2001–2006). Two 50 × 1 m transects were randomly laid and the individuals within them were measured. Sampling was performed over the period of two years (1998–1999) and no less than 100 individuals were studied at each site.

Disturbance was measured at each site through the index developed by Martorell & Peters (2009) in 1998. This index accounts for the main disturbance agents in the region: livestock raising, human activities, and land degradation. The mean annual rate of change in CAD intensity was estimated by remeasuring disturbance in 2010 at 32 sites.

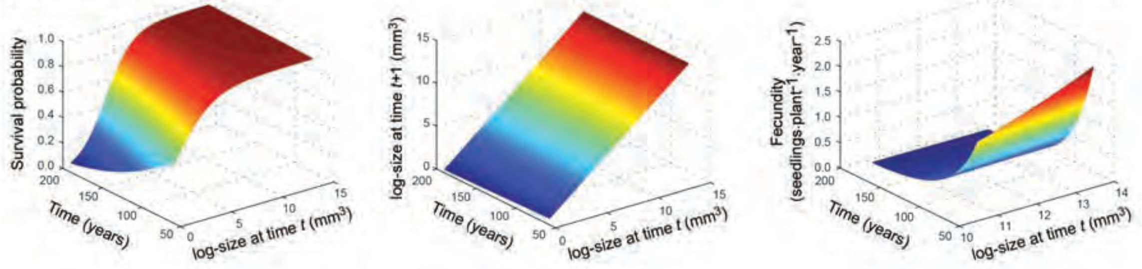
Results

In all the species studied, a biologically plausible reconstruction of the change of its vital rates through time was obtained. These reconstructions show that species have particular responses to CAD over time at the level of their vital rates (Fig. 1). The changes in the vital rates entail changes on the population dynamics: in five species (*Mammillaria hernandezii, M. kraehenbuehlii, M. pectinifera, M. solisioides* and *M. supertexta*) the annual population growth rate (λ_t) increases over time, in one species (*M. dixanthocentron*) it decreases, while in another (*M. napina*) λ_t increases initially, but decreases as CAD becomes too intense (Fig. 2, solid lines).

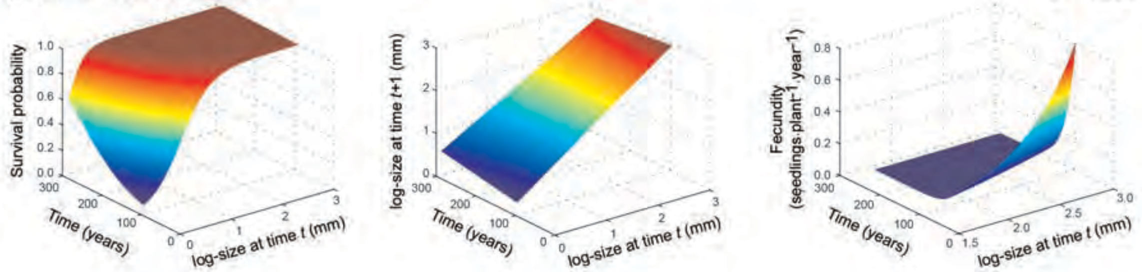
As suggested by González & Martorell (2013), we explored increasingly larger values of the factor weighting the fit of the population densities versus that of the size structures (w in equation 4) until a biologically plausible reconstruction was obtained. Thus, in *M. pectinifera* and *M. supertexta* it was enough to evaluate the model with $w = 1$ to obtain this type of reconstruction, while in *M. hernandezii* and *M. napina* such reconstruction was only obtained until $w = 1000$. Lower w-values only resulted in reconstructions, which showed vital rates that grossly misrepresented the species biology (not shown). With the correct w-values, only one biologically plausible reconstruction was obtained (Fig. 1).

The reconstructions obtained by the model show that the species experience different responses to CAD at the level of their vital rates (Fig. 1). In the case of survival, all species show a relatively small increase in adult survival with increasing CAD intensity. However, survival of seedlings and small individuals is species-specific: three species show decreasing survival with increasing CAD intensity, two show the inverse trend and the rest show no change through time. Growth also shows a response to CAD that is species-specific: adults do not increase their sizes over time (except for *M. hernandezii*, whose adults decrease in size, Fig. 1b), while seedlings and small individuals increase their rate of growth in five species and remain mainly in stasis in the remaining two. However, this response is rather small compared to that of survival. Finally, fecundity increases with CAD in three species, decreases in another three and in the remaining one (*M. supertexta*, Fig. 1g) shows a humped behaviour, with the highest fecundity attained at intermediate CAD intensities, mainly due to the incorporation of fecundity information in the modelling of this species (see Methods).

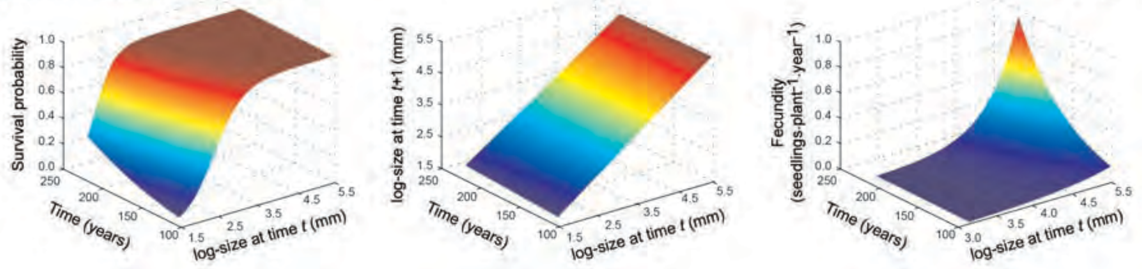
a) *Mammillaria dixanthocentron* $w = 100$



b) *Mammillaria hernandezii* $w = 1000$



c) *Mammillaria kraehenbuehlii* $w = 100$



d) *Mammillaria napina* $w = 1000$

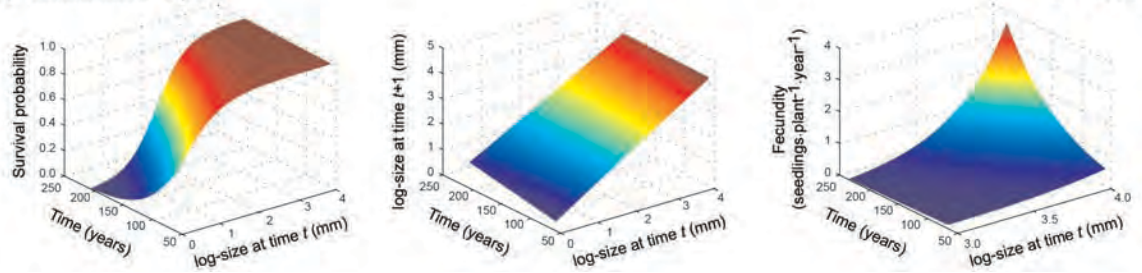


Figure 1. Reconstructed vital rates of seven *Mammillaria* species and their change through time due to chronic anthropogenic disturbance. The value of the parameter w (see equation 4) is the one with which the reconstruction was obtained.

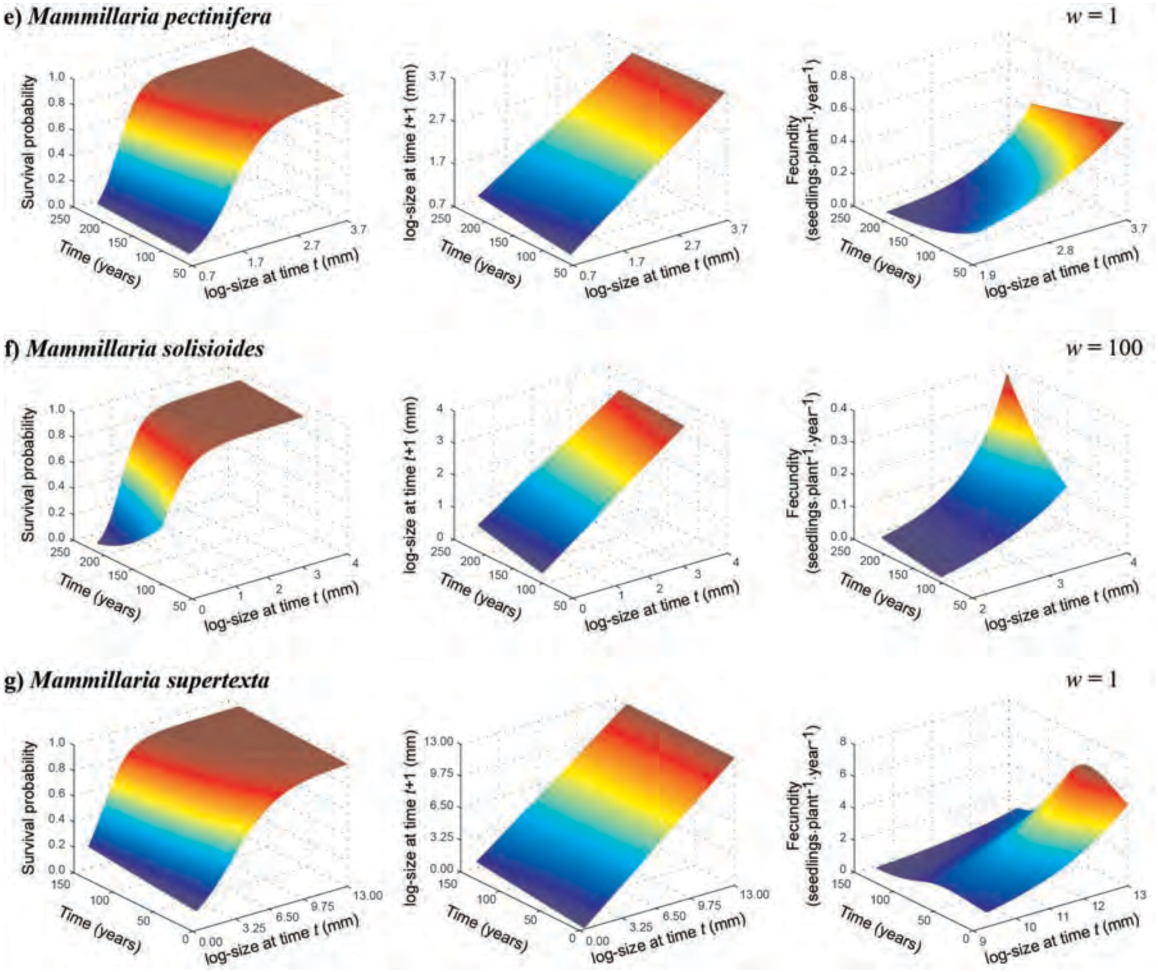


Figure 1 (*cont.*) Reconstructed vital rates of seven cacti species of the genus *Mammillaria* and their change through time due to chronic anthropogenic disturbance. The value of the parameter *w* (see equation 4) is the one with which the reconstruction was obtained.

The changes through time of the vital rates reconstructed by the model translate into changes in the population dynamics, measured via λ_t. In one species, *M. dixanthocentron*, λ_t declines through time as CAD accumulates, mainly due to CAD's negative effect on fecundity (Fig. 2a). In five species, *M. hernandezii*, *M. kraehenbuehlii*, *M. pectinifera*, *M. solisioides* and *M. supertexta*, λ_t increased with higher CAD intensities (Fig. 2b, c, e–g). This increment was mainly due to the positive effect CAD had on survival. Finally, in *M. napina* CAD had opposite effects on survival and fecundity, this resulted in a total effect on λ_t where the species first benefits from CAD, but after 50 years of its presence, the negative effect on survival outweighs that on fecundity (Fig. 2d), entailing population decline after 135 years of CAD accumulation.

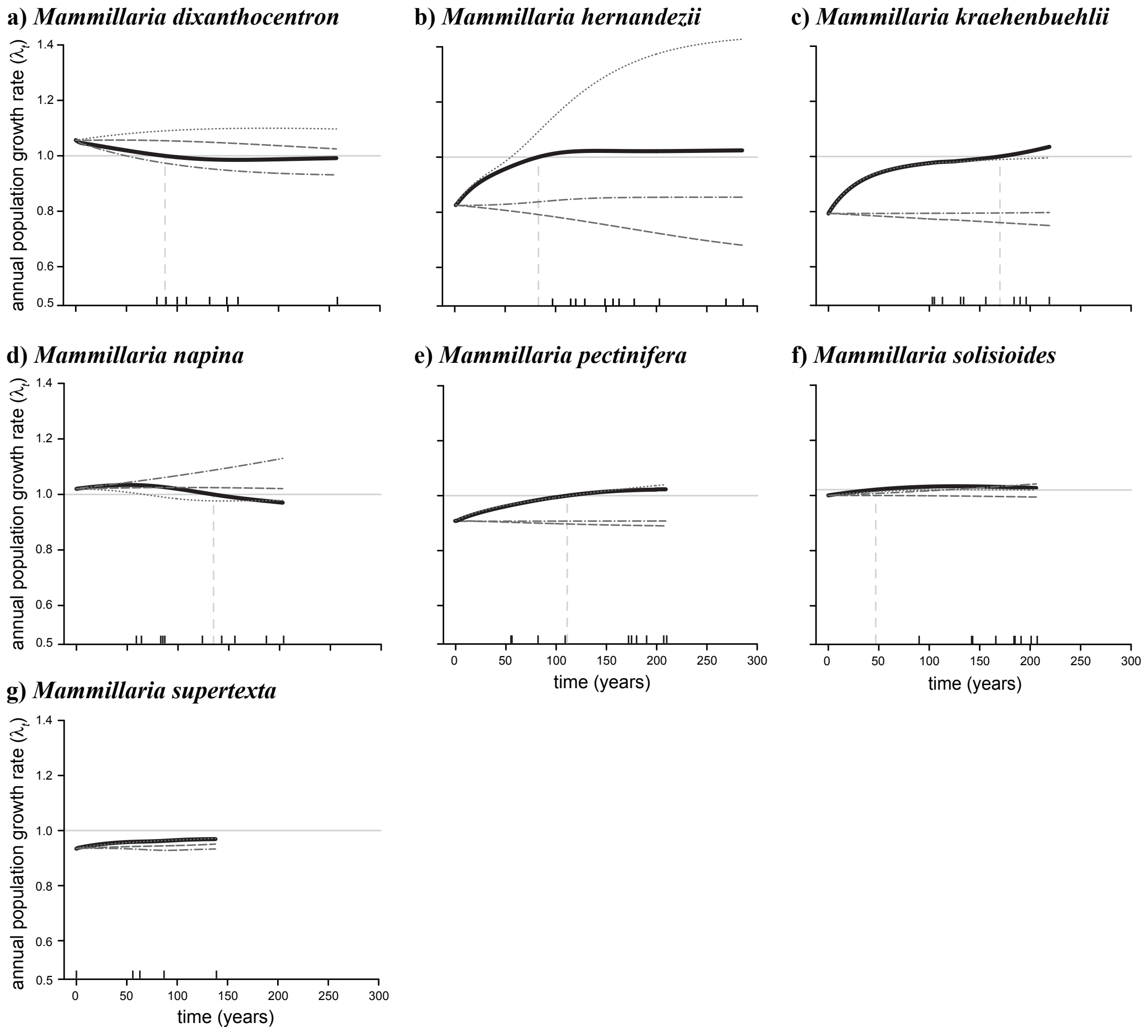


Figure 2. Change over time of the estimated annual population growth rate (λ_t) of seven cactus species as chronic anthropogenic disturbance (CAD) increases in intensity. The change in λ_t was analysed for the cases when the vital rates affected by CAD were: all (solid black), only survival (dotted), only growth (dashed), and only fecundity (dotdash). The line of no change in the estimated population growth rate ($\lambda_t = 1$) is in solid grey, and the time at which this occurs for the case where CAD affects all vital processes is in dashed grey. Inward-facing tick marks are the points at which data were collected.

Discussion

The reconstructed population dynamics for the seven cactus species we studied show different responses to CAD: four benefit from it, two benefit only from low disturbance intensities, and one is vulnerable to any form of CAD (Fig. 2, solid lines). These trends are, for most species, due to the long-term impact of CAD on survival (Fig. 2, dotted lines).

The vital rates most affected by CAD for the seven cactus species were survival and fecundity according to the reconstructed vital rates obtained by the model (Fig. 1). In the case of survival, the individuals showing the largest changes in their survival over time were the smallest ones, *i.e.* seedlings, though such changes were species-specific. Seedlings are known to be the stage most sensible to environmental changes and usually experience the highest mortalities (Godínez-Álvarez *et al.*, 2003). CAD would be expected to change the seedling microhabitat detrimentally by reducing plant cover, which in turn reduces humidity in the soil, a fundamental requirement for seedling survival (Godínez-Álvarez *et al.*, 2003; Jiménez-Sierra *et al.*, 2007). This is known to happen for *M. dixanthocentron*, and for other cacti (Contreras & Valverde, 2002; Godínez-Álvarez *et al.*, 2003; Ureta & Martorell, 2009; González & Martorell, 2013). However, seedlings of some cactus species could benefit from intermediate CAD intensities. The reduction of plant cover would be beneficial for those species whose seedlings do not require nurse plants to establish, but rather abiotic ones, such as rocks and gravel (Godínez-Álvarez *et al.*, 2003; Peters *et al.*, 2008). Also, by removing potential competitors, CAD may be increasing the availability of favourable sites for the establishment of cactus seedlings (Wilson & Keddy, 1986). This could be the case for the species identified by Martorell & Peters (2009) as ruderals: *M. hernandezii*, *M. kraehenbuehlii*, *M. napina*, *M. pectinifera* and *M. solisioides*. In these species, except for *M. napina*, the reconstructions showed that CAD did not negatively affect their seedlings.

In the case of fecundity, changes due to CAD were also particular to the species: three (*M. dixanthocentron*, *M. hernandezii* and *M. pectinifera*) decreased their fecundity over time, three (*M. kraehenbuehlii*, *M. napina* and *M. solisioides*) increased it, and one (*M. supertexta*) presented highest fecundities at intermediate CAD intensities (Fig. 1, third column). As fecundity is expressed as the mean number of seedlings produced by an individual per year, this process integrates both the fecundity of the reproductive individual along with the probabilities involved in the germination and establishment of new individuals. Thus, its interpretation is not simple. As with seedling survival, CAD would affect both germination and establishment through the removal of plant cover (Martorell *et al.*, 2012). However, only three species displayed the same trends in their fecundity and seedling survival. In the rest of the species, seedling survival and fecundity presented opposite behaviours. This could be due to a compensation process during the optimization process where a certain number of observed seedlings are the product of a large number of new individuals with high mortality or vice versa.

For *M. dixanthocentron* and *M. hernandezii*, a validation of the effect of CAD on the vital rates was possible. González & Martorell (2013) already showed that the model correctly reconstructed the vital rates of *M. dixanthocentron*. In the case of *M. hernandezii*, González *et al.* (2013) reported the vital rates of two of the populations studied here, which were surveyed over six years. Comparing their results with our reconstructions, we can see that survival was correctly reconstructed, showing the largest increases in survival at the smallest individuals; growth was correctly reconstructing as increasing regardless of the size of the plant; and fecundity as decreasing with higher CAD intensity, especially for the largest individuals. For the remaining species, none of their populations' vital rates have been registered.

The changes in the vital rates over time integrate into shifts in the annual population growth rate (λ_t). In four species (*M. kraehenbuelli*, *M. pectinifera*, *M. solisioides* and *M. hernandezii*) populations are only viable (*i.e.*, $\lambda_t = 1$) under high CAD intensities (Fig. 2, solid lines), and thus may be considered ruderal because they increase their numbers in the presence of disturbance (Morris, 1992). *M. napina* and *M. dixanthocentron* could also be viewed as ruderal because their populations are capable of growing as CAD increases, but their λ_t-values eventually fall below one. Thus, both species begin to decline once disturbance has become too harsh. This is in line with what Martorell & Peters (2009) found for these species, which attained their highest densities at intermediate CAD intensities. In *M. solisioides* there was also an agreement between the reconstructed λ_t and the analysis of Martorell & Peters (2009): in both cases, populations keep growing as CAD increases. Nevertheless, the reduction in the population densities with high CAD observed in *M. kraehenbuelli*, *M. pectinifera*, and *M. hernandezii* were not detected by our method. This discrepancy could be due to our decision to restrict the response of the vital rates to CAD to a monotonic function, perhaps limiting the likelihood of λ_t to attain a maximum at intermediate CAD intensities. This inability to detect reductions in population sizes would have consequences on the conservation decisions derived from the use of the method. Under such a reconstruction, species considered as ruderal could be left without surveillance, even after the point were CAD starts to have a negative effect on a population's viability. Nevertheless, suggesting that a species should not be protected as it tolerates any CAD intensity is an untenable statement, and thus managers should always keep in mind that species will have a maximum CAD intensity tolerance threshold.

M. supertexta displays a completely different behaviour. Though its λ_t-values increase slightly over time, it never reaches a point where its population numbers increase (*i.e.* $\lambda_t > 1$ after some particular *t*-value). This means that the population would decrease rapidly over time, in agreement with the observed exponential decrease in density with CAD (Martorell & Peters, 2009).

With the sole exception of *M. dixanthocentron*, the vital rate whose change due to CAD affected most largely the population growth of these species was primarily the same: survival. In agreement with this, demographic studies in cacti have shown that changes in the survival probability of large individuals have larger effects on λ than those in fecundity or growth (Contreras & Valverde, 2002; Esparza-Olguín *et al.*, 2002; Godínez-Álvarez *et al.*, 2003; Valverde & Zavala-Hurtado, 2006; Avendaño-Calvo *et al.*, 2013; Jiménez-Sierra *et al.*, 2007). This means that conservation efforts should be focused towards understanding and controlling the mortality of established plants. In the case of *M. dixanthocentron*, the decline over time of λ_t was reconstructed as due to a decreased fecundity. However, the comparison of two of its populations, studied over six years, identified survival as the vital rate whose change most largely affected λ (González *et al.*, 2013). Therefore, although correctly reconstructing the decline of λ_t over time, the model for *M. dixanthoncentron* apparently incorrectly identified the vital rate most responsible for such decline.

The model also allows identifying the levels of CAD intensity that a ruderal species requires to live at a certain site or the maximum disturbance that a vulnerable species can withstand. Therefore, for a given population, the model can determine if it is in a state of decline, stability or increase in its numbers; it can also determine the vital rates affected by CAD that lead to such state. These are key knowledge elements in the design of conservation and management plans. Given that these plans usually are applied to several populations subject to different intensities of human disturbance, it is important to have an idea of the particular demographic status of each of them in order to make decisions about whether to eliminate or keep a certain amount of disturbance at a certain area on a case-by-case basis.

For our cacti species, their heterogeneous responses to CAD would require different management strategies. In all the populations of *M. supertexta* CAD should be stopped and a more direct intervention should be performed to increase its numbers, focusing efforts on the survival of individuals (Fig. 2g). In most of *M. dixanthocentron*'s populations CAD should be reduced, given that the level of CAD six of its eight populations are experiencing is above the threshold of population viability (Fig 2, bold lines). A direct intervention on its populations to increase its numbers should also be focused on the survival of their individuals (Fig. 2a). Conversely, given that *M. hernandezii*, *M. kraehenbuehlii*, *M. pectinifera* and *M. solisioides* were found to be ruderal species, their populations could be adequately managed with the present human activities in the region.

It is relevant to note that the model reconstructs the transient behaviour of the species as CAD increases its intensity. This behaviour will not necessarily equate to the one obtained through a traditional long-term asymptotic analysis (Fox & Gurevitch, 2000; Caswell, 2007; Chirakkal & Gerber, 2010; Stott *et al.*, 2012), especially when the population is far from its stable state (Bierzychudek, 1999). This is relevant in a conservation/management framework as plans designed with our results will take into account the present state of the populations, and not stable states which would not be expected to be attained under CAD (Ezard *et al.*, 2010; Stott *et al.*, 2010).

Finally, the case of *M. supertexta* shows that an alternative structure of the information provided to the model leads to equally good results. In this species only five populations were sampled, compared with the ~10 populations in the other species. However, additional information was available in the form of flower production in these populations. This result suggests that the researcher can modify the sampling strategy to better suit it to the particular study system without worrying about not arriving to the sought reconstruction.

As a conclusion, we can state that the application of the model we developed in González & Martorell (2013) allows identifying how CAD affects the vital rates and the population dynamics of the cacti species we studied. However, the fact that the present version of the model involves describing the vital rates as monotonic functions of time, although producing seemingly correct reconstructions of the vital rates, does not guaranty that further analyses of the population dynamics derived from such rates will be highly reliable. Thus, such analyses should be carefully pondered against the existing knowledge of population responses to CAD.

References

Avendaño-Calvo, T., A. Flores Martínez & G. Manzanero Medina. 2013. Estudio poblacional de *Mammillaria supertexta* Mart. Ex Pfeiff. en el Valle de Cuicatlán, Oaxaca, México. In: Estudios en Zonas Áridas de Oaxaca. M. Briones-Salas, G. Manzanero Medina & G. González Pérez, eds. Santa Cruz Xoxocotlán, Oaxaca: Instituto Politécnico Nacional, CIIDIR Unidad Oaxaca. Pp. 44-56.

Bhat Jahangeer, A., K. Munesh, K. Negi Ajeet, & N. P. Todaria. 2012. Anthropogenic pressure along altitudinal gradient in a protected area of Garhwal Himalaya, India. Journal of Environmental Research And Development 7: 62-65.

Bierzychudek, P. 1999. Looking backwards: assessing the projections of a transition matrix model. Ecological Applications 9: 1278–1287.

Binford, M. W., M. Brenner, T. J. Whitmore, A. Higuera-Gundy, E. S. Deevey, & B. Leyden. 1987. Ecosystems, paleoecology and human disturbance in subtropical and tropical America. Quaternary Science Reviews 6: 115–128.

Casas, A., A. Valiente-Banuet, J. L. Viveros, J. Caballero, L. Cortés, P. Dávila, R. Lira, & I. Rodríguez. 2001. Plant resources of the Tehuacán-Cuicatlán Valley, Mexico. Economic Botany 55: 129–166.

Caswell, H. 2001. Matrix population models. Construction, analysis, and interpretation. 2nd edition. Sinauer: Sunderland, Massachusetts. 722 p.

Caswell, H. 2007. Sensitivity analysis of transient population dynamics. Ecology Letters 10: 1–15.

Chirakkal, H., & L. R. Gerber. 2010. Short- and long-term population response to changes in vital rates: implications for population viability analysis. Ecological Applications 20: 783–788.

CITES. 2013. Convention on International Trade in Endangered Species of Wild Fauna and Flora. Appendices I,II and III. Retrieved from http://www.cites.org/eng/app/appendices.php.

Contreras, C., & T. Valverde. 2002. Evaluation of the conservation status of a rare cactus (*Mammillaria crucigera*) through the analysis of its population dynamics. Journal of Arid Environments 51: 89–102.

Easterling, M. R., S. P. Ellner, & P. M. Dixon. 2000. Size-specific sensitivity: applying a new structured population model. Ecology 81: 694–708.

Esparza-Olguín, L., T. Valverde, & E. Vilchis-Anaya. 2002. Demographic analysis of a rare columnar cactus (Neobuxbaumia macrocephala) in the Tehuacan Valley, Mexico. Biological Conservation 103: 349–359.

Ezard, T. H. G., J. M. Bullock, H. J. Dalgleish, A. Millon, F. Pelletier, A. Ozgul, & D. N. Koons. 2010. Matrix models for a changeable world: the importance of transient dynamics in population management. Journal of Applied Ecology 47: 515–523.

Flores-Martínez, A., G. I. Manzanero-Medina, J. Golubov, C. Montaña, & M. C. Mandujano. 2010. Demography of an endangered endemic rupicolous cactus. Plant Ecology 210: 53–66.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, & J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27: 233–249.

Fox, G. A., & J. Gurevitch. 2000. Population numbers count: tools for near-term demographic analysis. The American Naturalist 156: 242–256.

Godínez-Álvarez, H., T. Valverde, & P. Ortega-Baes, 2003. Demographic trends in the Cactaceae. Botanical Review 69: 173–203.

González, E. J., & C. Martorell. 2013. Reconstructing shifts in vital rates driven by long-term environmental change: a new demographic method based on readily available data. Ecology and Evolution 3: 2273–2284.

González, E. J., M. Rees, & C. Martorell. 2013. Identifying the demographic processes relevant for species conservation in human-impacted areas: does the model matter? Oecologia 171: 347–356.

Guo, Q. 2004. Slow recovery in desert perennial vegetation following prolonged human disturbance. Journal of Vegetation Science 15: 757–762.

Hannah, L., J. Carr, & A. Lankerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation 4: 128–155.

Hernández, H. M., & H. Godínez-Álvarez. 1994. Contribución al conocimiento de las cactáceas mexicanas amenazadas. Acta Botanica Mexicana 26: 33–52.

Jiménez-Sierra, C., M. Mandujano, & L. Eguiarte. 2007. Are populations of the candy barrel cactus (*Echinocactus platyacanthus*) in the desert of Tehuacán, Mexico at risk? Population projection matrix and life table response analysis. Biological Conservation 135: 278–292.

Karanth, K., L. Curran, & J. Reuning-Scherer. 2006. Village size and forest disturbance in Bhadra Wildlife Sanctuary, Western Ghats, India. Biological Conservation 128: 147-157.

MacNeish, R. S. 1967. A summary of the subsistence. In: R. S. MacNeish, J. Brunet & J. E. Anderson, eds. The prehistory of the Tehuacan Valley: Environment and Subsistence. Vol. 1. University of Texas Press. Pp. 290-331.

Martorell, C. 2013. Ciencia espinosa: Algunas reflexiones en torno a la investigación con plantas suculentas en México. In: M. Briones-Salas, G. Manzanero Medina & G. González Pérez, eds. Estudios en Zonas Áridas de Oaxaca. Oaxaca, Mexico: Instituto Politécnico Nacional, CIIDIR Unidad Oaxaca. Pp. 87-98.

Martorell, C., & E. M. Peters. 2005. The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. Biological Conservation 124: 199–207.

Martorell, C., & E. M. Peters. 2009. Disturbance-response analysis: a method for rapid assessment of the threat to species in disturbed areas. Conservation Biology 23: 377–387.

Martorell, C., P. P. Garcillán, & F. Casillas. 2012. Ruderality in extreme-desert cacti? Population effects of chronic anthropogenic disturbance on *Echinocereus lindsayi*. Population Ecology 54: 335–346.

Martorell, C., D. M. Montañana, C. Ureta & M. C. Mandujano. Unpublished. Cows, looters, or greenhouse gases? Testing the different hypotheses for the threatened status of cacti using *Coryphantha werdermannii* as a model species.

McAuliffe, J. R., P. C. Sundt, A. Valiente-Banuet, A. Casas, & J. L. Viveros. 2001. Pre-columbian soil erosion, persistent ecological changes, and collapse of a subsistence agricultural economy in the semi-arid Tehuacán Valley, Mexico's 'Cradle of Maize'. Journal of Arid Environments 47: 47–75.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-Being. Washington, D.C.: Island Press. 109 pp.

Montañana, D. M. 2009. Respuesta poblacional de *Coryphantha werdermannii* a diferentes intensidades de disturbio antropogénico en Cuatro Ciénegas, Coahuila. Tesis de licenciatura. Facultad de Ciencias. Universidad Nacional Autónoma de México. 50 pp.

Morris, C. G. 1992. Academic press dictionary of science and technology. San Diego: Academic Press. 2432 pp.

Murali, K. S., U. Shankar, R. U. Shaanker, K. N. Ganeshaiah, & K. S. Bawa. 1996. Extraction of non-timber forest products in the forests of Biligiri Rangan Hills, India. 2. Impact of NTFP extraction on regeneration, population structure, and species composition. Economic Botany 50: 252–269.

Pereira, H. M., P. W. Leadley, V. Proenca, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarres, M. B. Araújo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D. Cooper, E. L. Gilman, S. Guenette, G. C. Hurtt, H. P. Huntington, G. M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila, & M. Walpole. 2010. Scenarios for Global Biodiversity in the 21st Century. Science 330: 1496–1501.

Pérez-Negrón, E., & A. Casas. 2007. Use, extraction rates and spatial availability of plant resources in the Tehuacán-Cuicatlán Valley, Mexico: The case of Santiago Quiotepec, Oaxaca. Journal of Arid Environments 70: 356-379.

Peters E. M., C. Martorell, & E. Ezcurra. 2008. Nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti (*Mammillaria*) in the Tehuacan Valley, Mexico. Journal of Arid Environments 72: 593-601.

Portilla-Alonso, R. M., & C. Martorell. 2011. Demographic consequences of chronic anthropogenic disturbance on three populations of the endangered globose cactus *Coryphantha werdermannii*. Journal of Arid Environments 75: 509–515.

Reynolds, J. F. J., D. M. S. D. Smith, E. F. E. Lambin, B. L. B. Turner, M. M. Mortimore, S. P. J. S. Batterbury, T. E. T. Downing, H. H. Dowlatabadi, R. J. R. Fernández, J. E. J. Herrick, E. E. Huber-Sannwald, H. H. Jiang, R. R. Leemans, T. T. Lynam, F. T. F. Maestre, M. M. Ayarza, & B. B. Walker. 2007. Global desertification: building a science for dryland development. Science 316: 847–851.

Rundel, P. W. 1999. Disturbance in Mediterranean-climate shrublands and woodlands. In: L. R. Walker, ed. Ecosystems of disturbed ground. Amsterdam: Elsevier. Pp. 271–285.

Sala, O. E. O., F. S. F. Chapin, J. J. J. Armesto, E. E. Berlow, J. J. Bloomfield, R. R. Dirzo, E. E. Huber-Sanwald, L. F. L. Huenneke, R. B. R. Jackson, A. A. Kinzig, R. R. Leemans, D. M. D. Lodge, H. A. H. Mooney, M. M. Oesterheld, N. L. N. Poff, M. T. M. Sykes, B. H. B. Walker, M. M. Walker, & D. H. D. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Santini, B. 2007. Efecto de la heterogeneidad temporal y el disturbio sobre la dinámica poblacional de dos especies raras del género *Mammillaria* (Cactaceae). Tesis de licenciatura. Facultad de Ciencias, UNAM. 63 pp.

SEMARNAT, 2002. Norma Oficial Mexicana NOM-059-ECOL-2001. Protección ambiental, especies nativas de México de flora y fauna silvestres, categorías de riesgo y especificaciones para su inclusión, exclusión o cambio, lista de especies en riesgo. En: Diario Oficial de la Federación. 6 de marzo de 2002. Segunda Sección.

Singh, S. P. 1998. Chronic disturbance, a principal cause of environmental degradation in developing countries. Environmental Conservation 25: 1–2.

Stott, I., M. Franco, D. Carslake, S. Townley, & D. J. Hodgson. 2010. Boom or bust? A comparative analysis of transient population dynamics in plants. Journal of Ecology 98: 302–311.

Stott, I., D. J. Hodgson, & S. Townley. 2012. Beyond sensitivity: nonlinear perturbation analysis of transient dynamics. Methods in Ecology and Evolution 3: 673–684.

Ureta, C., & C. Martorell. 2009. Identifying the impacts of chronic anthropogenic disturbance on two threatened cacti to provide guidelines for population-dynamics restoration. Biological Conservation 142: 1992–2001.

Valverde, P. L., & J. A. Zavala-Hurtado. 2006. Assessing the ecological status of *Mammillaria pectinifera* Weber (Cactaceae), a rare and threatened species endemic of the Tehuacán-Cuicatlán Region in Central México. Journal of Arid Environments 64: 193–208.

Valverde, T., S. Quijas, M. López-Villavicencio, & S. Castillo. 2004. Population dynamics of *Mammillaria magnimamma* Haworth.(Cactaceae) in a lava-field in central Mexico. Plant Ecology 170: 167–184.

Villagra, P., G. Defosse, H. del Valle, S. Tabeni, M. Rostagno, E. Cesca, & E. Abraham. 2009. Land use and disturbance effects on the dynamics of natural ecosystems of the Monte Desert: Implications for their management. Journal of Arid Environments 73: 10–10.

Vitousek, P., H. Mooney, J. Lubchenco, & J. Melillo. 1997. Human domination of Earth's ecosystems. Science 277: 494–499.

Wilson, S. D., & P. A. Keddy. 1986. Species competitive ability and position along a natural stress/disturbance gradient. Ecology 67: 1236–1242.

Zavala-Hurtado, J., & P. Valverde. 2003. Habitat restriction in *Mammillaria pectinifera*, a threatened endemic Mexican cactus. Journal of Vegetation Science 14: 891–898.

Discusión general y Conclusiones

El método desarrollado en la presente tesis para la reconstrucción del cambio en las tasas vitales a lo largo del tiempo parte de una serie de estructuras y densidades poblacionales observadas en distintos momentos en el tiempo. Al garantizar que el efecto de la forma funcional del modelo no interferiría en los resultados arrojados por el método (capítulo 1), se desarrolló y validó el método tanto con datos generados artificialmente como con datos reales de una cactácea globosa sujeta a disturbio antropogénico crónico (DAC; capítulo 2). Posteriormente, se aplicó el método a datos de otras seis cactáceas sujetas a este disturbio (capítulo 3). Los resultados muestran que el método es capaz de reconstruir de manera cualitativa las tasas vitales y sus cambios en el tiempo (capítulo 2). Igualmente, el método logra identificar aquella tasa vital responsable del cambio en el tiempo de la tasa de crecimiento poblacional (capítulo 3). Sin embargo, la estimación del valor numérico de dicha tasa, tal como se demostró en el capítulo 1, depende de la estructura particular del modelo demográfico usado. Las estructuras de tamaño y las densidades poblacionales ofrecen la información necesaria para reconstruir correctamente las tasas vitales a nivel cualitativo; no obstante, al ser limitada, dicha información no logra estimar las tasas con precisión.

Partiendo del método desarrollado en mi tesis de maestría (González, 2008), hice algunas modificaciones que permitieron mejorarlo. En dicha tesis la única fuente de información proveída al modelo eran las estructuras de tamaños. Así, al aplicarlo a datos de poblaciones de *Mammillaria dixanthocentron* sujetas a DAC, los resultados obtenidos fueron, en retrospectiva, deficientes, pues no se logró reconstruir correctamente la mayor fecundidad que presentan los individuos de mayor tamaño en esta especie (*i.e.* se obtuvo una solución tipo-1 de acuerdo con la nomenclatura presentada en el capítulo 2). De esta manera, la primera modificación que se le hizo al modelo fue la incorporación de una fuente de información adicional a las estructuras de tamaños: la densidad poblacional. Esta variable es fácil de evaluar, pues únicamente requiere estimar el área en la que están distribuidos los individuos medidos. Además, el hecho de que en modelos con fines similares también se haya incorporado la densidad (Fournier *et al.*, 1998; Gross *et al.*, 2002; Maury, 2005), confirma la utilidad de esta información para lograr nuestro objetivo.

Sin embargo, la incorporación de la densidad poblacional al método introdujo un nivel de subjetividad: el valor asignado a w. Este factor pondera el ajuste de las densidades poblacionales contra el de las estructuras de tamaños, y debe ser elegido por el usuario. Dicho valor se puede establecer de manera subjetiva a partir de una evaluación de la calidad relativa que ofrecen ambos conjuntos de datos, incrementando el valor del factor cuando se tuviera mayor confianza en la calidad de los datos de las estructuras de tamaños, y disminuyéndolo de lo contrario. No obstante, en los capítulos 2 y 3 se siguió un procedimiento más sistemático: iniciar con un valor de w igual a uno, aplicar el método y, de no obtenerse una reconstrucción biológicamente factible, incrementar dicho valor un orden de magnitud hasta obtener dicha reconstrucción. Es decir, bajo este procedimiento damos preferencia a la información dada por las estructuras poblacionales; sin embargo, muchas veces las estructuras poblacionales no presentan un patrón claro de cambio en su forma a medida que el tiempo pasa, por lo que es necesario aumentar la importancia relativa de las densidades poblacionales. Este procedimiento parece, hasta el momento, dar buenos resultados.

El segundo cambio que se le hizo al método fue modificar la función de supervivencia para hacerla más realista a nivel biológico. Recientemente se ha reconocido que la función logística puede fácilmente alcanzar la cota de uno en los modelos integrales de proyección (IPMs), prediciendo así que los individuos grandes sean inmortales (Merow *et al.*, 2014). Debido a que nosotros originalmente modelamos la supervivencia con una función logística, se introdujo una asíntota variable menor a uno para evitar este problema.

Los datos de *Mammillaria dixanthocentron*, un cacto globoso sujeto a DAC, fueron usados en ambas tesis, lo que permite comparar los resultados obtenidos con la incorporación de ambas modificaciones. En la tesis de maestría (González, 2008: Fig. 4.10), el principal problema a nivel biológico fue que no se reconstruyó correctamente cómo cambia la fecundidad al incrementar el tamaño de los individuos. En la presente tesis (Capítulo 2, Fig. 4), el método sí identificó que los individuos más grandes tienen mayor fecundidad, aunque esta fue menor a la observada. Asimismo, la supervivencia tuvo una asíntota menor a uno que, aunque mayor a la observada, refleja mejor la biología de la especie. Esta disparidad con respecto a lo observado se debe a una compensación entre el tamaño y número de plántulas producidas y la supervivencia de estas (capítulo 2). Así, aunque no se obtuvieron reconstrucciones exactas, ambas modificaciones redundaron en mejores resultados que los arrojados por la versión del modelo presentada en la tesis de maestría.

Un cambio adicional que llevó a una mayor certidumbre sobre la identificación de la reconstrucción que maximiza el ajuste del modelo a los datos fue el uso del Automatic Differentiation Model Builder (ADMB; Fournier *et al.*, 2012), un software diseñado específicamente para ajustar modelos complejos. Anteriormente, dicha identificación se hizo utilizando un enfoque heurístico: el método de optimización por enjambre de partículas (Eberhart y Shi, 2001). La programación de este método la realicé en Matlab, un programa que a su vez corre sobre la plataforma Windows/MacOS. Por el contrario, ADMB es un programa basado en lenguaje C++, lo que agiliza la obtención de resultados.

Aún con estas mejoras, y como se mostró en el capítulo 2, el modelo que proporcione el mejor ajuste a los datos no necesariamente corresponderá a la mejor reconstrucción de las tasas vitales desde un punto de vista biológico. Esto implica que la selección de la mejor reconstrucción debe ser supervisada. Sin embargo, el conocimiento biológico necesario para hacer la selección es sumamente básico. Esto hace factible la amplia aplicación del método partiendo de un mínimo conocimiento biológico de la especie de interés.

Ghosh *et al.* (2012), al igual que mi método, utilizan estructuras de tamaño para reconstruir el IPM que las produce. La estructura del IPM que utilizan tiene la ventaja de que evita la multiplicidad de reconstrucciones y, por lo tanto de la selección supervisada del mejor modelo. Sin embargo, su estructura es muy diferente de la mía, pues estos autores no buscan reconstruir las tasas vitales. Estos autores, por el contrario, buscan proyectar estructuras poblacionales en el tiempo, sin importar que las funciones asociadas a las tasas vitales sean realistas a nivel de lo experimentado por los individuos de una población. Por ello nuestros resultados no son comparables. No obstante, lo importante del trabajo de Ghosh *et al.* (2012), junto con la presente tesis, es que demuestran que es posible construir IPMs partiendo de datos poblacionales, y no individuales como ha sido lo habitual hasta el momento.

Al analizar los resultados provistos por el método planteado en esta tesis, es importante tener en mente cuáles son sus debilidades y fortalezas. El capítulo 1 nos muestra que el impacto relativo de cada tasa vital sobre el crecimiento poblacional será correctamente identificado por el método, pero no así los valores exactos de dichos impactos o tasas. El grado de imprecisión en la estimación puede ser mayor si el IPM tiene una estructura sencilla (modelos lineales vs. modelos aditivos en las tasas vitales), conclusión a la cual también llegaron Dahlgren *et al.* (2012). Por lo tanto, el uso de una estructuras sencilla en mi método puede tener un impacto sustancial en la precisión de las tasas vitales reconstruidas. Todo lo anterior se refleja en los resultados obtenidos para las siete especies estudiadas (capítulo 3): la tasa vital con mayor impacto relativo sobre la tasa anual de crecimiento poblacional (λ_t) fue la supervivencia, lo que concuerda con la literatura existente para cactáceas (Contreras & Valverde 2002; Esparza-Olguín et al. 2002; Godínez-Álvarez et al. 2003; Valverde & Zavala-Hurtado 2006; Avendaño-Calvo 2007; Jiménez-Sierra et al. 2007), sugiriendo que el resultado es confiable. Por el contrario, los valores particulares de las λ_ts no fueron tan cercanos a los reportados para otros cactos (Godínez-Álvarez *et al.* 2003), y a veces no parecen realistas. Esto es relevante desde un punto de vista de conservación donde, en general, es más importante determinar las tasas vitales responsables de un cambio en el comportamiento poblacional, más que tener certidumbre sobre el valor exacto de λ (Crone *et al.*, 2013).

Otra limitación del método es que el usuario debe especificar el intervalo de valores biológicamente plausibles que puede tomar cada parámetro del modelo. Un problema que se observó al usar datos reales fue que en promedio un 57 % de los parámetros estimados se encontraron en los límites de dichos intervalos (capítulos 2 y 3). En consecuencia, las reconstrucciones dependen de las apreciaciones subjetivas del usuario al establecer los intervalos. Este fue el caso de los parámetros asociados al efecto del tamaño (79 % llegaron con a los límites) y de la interacción tamaño-DAC (75 %). Esto sugiere que la información suministrada al método no permite discriminar entre dichos efectos, posiblemente porque, como se planteó en el capítulo 3, las tasas vitales se pueden compensar entre sí y resultar en las mismas estructuras y tamaños poblacionales. Una solución sería entonces no incorporar la interacción tamaño-DAC en el modelo. Otra posible causa del problema es que, desde una perspectiva bayesiana, estamos suponiendo que la distribución de los valores de los parámetros es uniforme. Establecer distribuciones diferentes podría ser una solución, aunque también introduciría un sesgo que, *a priori*, no podríamos justificar en la mayoría de los casos.

Perspectivas

Diferentes aspectos del modelo y el posterior análisis de los resultados arrojados requieren de nuevas investigaciones. Entre estas se encuentran evaluar (1) la incorporación de términos cuadráticos a los modelos de las tasas vitales, (2) la significancia de los términos de estos modelos y (3) evaluar la sensibilidad y robustez del método.

Incorporar términos cuadráticos a las funciones que describen las tasas vitales aumentaría la diversidad de comportamientos que estas pueden tener tanto en el tiempo como entre individuos. A nivel temporal, el uso de un término cuadrático permitiría modelar el efecto de un DAC no lineal en el tiempo (Singh, 1998). A nivel del tamaño de los individuos, un término cuadrático permitiría, por ejemplo, una caída en la supervivencia de los individuos senescentes.

Normalmente se desea evaluar la significancia estadística de los términos en un modelo demográfico con el fin de evaluar la importancia que tienen las diferentes variables explicativas en la dinámica poblacional. En mi caso, se podría evaluar si los términos de los modelos lineales que describen cada una de las tasas vitales son relevantes. Esto requeriría correr el método con y sin cada uno de estos términos y compararlos a través de su AIC. Esto puede potencialmente requerir mucho tiempo de cómputo y lo más probable sería que, dada la posibilidad de que los parámetros se estén compensando entre sí, los AICs no fuesen muy diferentes entre sí, simplificándose el modelo. De ser este el caso, el modelo simplificado dependería en última instancia del orden en el que se fueron eliminando los parámetros.

La sensibilidad y la robustez del método fueron dos aspectos que se planteó evaluar desde el inicio del proyecto, pero debido al tiempo de cómputo requerido para su realización, fueron aplazados para el momento en que se tuviese un método de rápida implementación. Al lograrse tiempos de ejecución menores, se favoreció la aplicación del método a las siete especies de cactáceas con el objeto de ejemplificar las capacidades del modelo. Queda como tarea pendiente evaluar estos dos aspectos del método. Evaluar la sensibilidad del método permitiría identificar aquellos aspectos del muestreo a los que es más sensible el modelo y, por lo tanto, a los que habría que ponerles mayor atención al momento de tomar las muestras. Evaluar la robustez identificaría la capacidad que tiene el modelo para dar resultados satisfactorios en caso de que los supuestos del modelo no se cumplan (los supuestos del modelo fueron enunciados en el apéndice 1 del capítulo 2). Permitiría de igual modo identificar aquellos supuestos cuya violación tendría mayor impacto sobre los resultados y, por lo tanto, sobre los que se tendría que poner más atención al momento de la implementación del método. Comparando los resultados obtenidos con datos artificiales y reales (capítulo 2), parece que el modelo es robusto a una falta de homogeneidad en el ambiente entre sitios, pues las poblaciones de *M. dixanthocentron* difieren en algunos atributos ambientales (*e.g.,* la altitud). Aún así resta por evaluarse, de una manera más sistemática, la violación de este y otros supuestos del modelo.

Literatura citada

Avendaño-Calvo, T. de J. 2007. Dinámica poblacional *Mammillaria supertexta* Mart. ex Pfeiff. en el Valle de Cuicatlán, Oaxaca, México. Tesis de Maestría. Instituto Politécnico Nacional. 90 pp.

Contreras, C., y T. Valverde. 2002. Evaluation of the conservation status of a rare cactus (*Mammillaria crucigera*) through the analysis of its population dynamics. Journal of Arid Environments 51: 89–102.

Crone, E. E., M. M. Ellis, W. F. Morris, A. Stanley, T. Bell, P. Bierzychudek, J. Ehrlén, T. N. Kaye, T. M. Knight, P. Lesica, G. Oostermeijer, P. F. Quintana-Ascencio, T. Ticktin, T. Valverde, J. L. Williams, D. F. Doak, R. Ganesan, K. McEachern, A. S. Thorpe y E. S. Menges. 2013. Ability of matrix models to explain the past and predict the future of plant populations. Conservation Biology 27: 968-978.

Dahlgren, J.P. y J. Ehrlén. 2011. Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. Oikos 120: 1183-1190.

Eberhart, R. C. y Y. Shi. 2001. Particle swarm optimization: developments, applications and resources. Proceedings of the Congress on Evolutionary Computation 2001. IEEE Press: Piscataway, New Jersey. Pp. 81-86.

Esparza-Olguín, L., T. Valverde, y E. Vilchis-Anaya. 2002. Demographic analysis of a rare columnar cactus (*Neobuxbaumia macrocephala*) in the Tehuacan Valley, Mexico. Biological Conservation 103: 349–359.

Fournier, D. A., J. Hampton, y J. R. Sibert. 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. Canadian Journal of Fisheries and Aquatic Sciences 55: 2105–2116.

Fournier, D.A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen y J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods Software 27: 233-249.

Godínez-Álvarez, H., T. Valverde, y P. Ortega-Baes, 2003. Demographic trends in the Cactaceae. Botanical Review 69: 173–203.

González, E. J. 2008. Modelación de la dinámica poblacional de cactáceas endémicas del Valle de Tehuacán a lo largo de un gradiente de disturbio antropogénico crónico. Tesis de Maestría. Facultad de Ciencias, UNAM: México, D. F. 101 pp.

Ghosh, S., A. E. Gelfand y J. S. Clark. 2012. Inference for size demography from point pattern data using integral projection models. Journal of Agricultural, Biological, and Environmental Statistics 17: 641-677.

Gross, K., B. A. Craig, y W. D. Hutchison. 2002. Bayesian estimation of a demographic matrix model from stage-frequency data. Ecology 83: 3285–3298.

Jiménez-Sierra, C., M. Mandujano, y L. Eguiarte. 2007. Are populations of the candy barrel cactus (*Echinocactus platyacanthus*) in the desert of Tehuacán, Mexico at risk? Population projection matrix and life table response analysis. Biological Conservation 135: 278–292.

Maury, O., B. Faugeras y V. Restrepo. 2005. FASST: A fully age-size and space-time structured statistical model for the assessment of tuna populations. Collective Volume of Scientific Papers ICCAT 57: 206-217.

Merow, C., J. P. Dahlgren, C. J. E. Metcalf, D. Z. Childs, M. E. K. Evans, E. Jongejans, S. Record, M. Rees, R. Salguero-Gómez y S. M. McMahon. 2014. Advancing population ecology with integral projection models: a practical guide. Methods in Ecology and Evolution. DOI: 10.1111/2041-210X.12146.

Singh, S. P. 1998. Chronic disturbance, a principal cause of environmental degradation in developing countries. Environmental Conservation 25: 1-2.

Valverde, P. L., y J. A. Zavala-Hurtado. 2006. Assessing the ecological status of *Mammillaria pectinifera* Weber (Cactaceae), a rare and threatened species endemic of the Tehuacán-Cuicatlán Region in Central México. Journal of Arid Environments 64: 193–208.