Efectos de la pérdida y fragmentación de hábitat en la ecología de poblaciones de *Primula vulgaris* L. en bosques cantábricos

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Resumen

Resumen

La alteración de los paisajes naturales por la acción humana es una de las principales causas de pérdida de biodiversidad a nivel mundial. Estos cambios en el paisaje comprenden varios procesos simultáneos e interdependientes: pérdida neta de hábitat, subdivisión del hábitat e incremento de la cantidad de borde en el hábitat remanente. La subdivisión del hábitat y los efectos de borde se agrupan generalmente como procesos de fragmentación, y muestran una fuerte interacción con la pérdida de hábitat. El cambio en el paisaje es por tanto un fenómeno complejo, que requiere una representación mediante modelos conceptuales realistas. Estos modelos deben integrar los distintos procesos y sus interrelaciones, además de considerar las respuestas de los diferentes organismos. En un principio, los paisajes fragmentados se representaban de forma binaria, con los fragmentos de hábitat inmersos en una matriz inhóspita. Sin embargo, actualmente se tiende a considerar el paisaje como gradientes continuos de adecuación de hábitat para cada especie o grupo de especies.

Los procesos de pérdida y fragmentación de hábitat afectan a la viabilidad de las poblaciones de plantas, ya sea de forma directa sobre los propios individuos, o bien indirecta, mediante la reducción de los tamaños poblacionales. Los cambios en el paisaje dan lugar a poblaciones pequeñas e aisladas donde la variabilidad genética y las interacciones planta-animal se ven alteradas, y esto afecta al éxito reproductivo. Los efectos directos de la pérdida y fragmentación de hábitat comprenden alteraciones en la polinización debido a la baja disponibilidad de hábitat, disminuciones del reclutamiento a causa del aislamiento de los fragmentos de hábitat, y alteraciones de varias tasas vitales e interacciones debido a los cambios en las condiciones ambientales en el borde de los fragmentos. En conjunto, los efectos de los cambios en el paisaje pueden llevar al colapso demográfico, incrementando la probabilidad de extinción de las poblaciones.

Las plantas forestales son un grupo de organismos especialmente sensible a los cambios en el paisaje, ya que la mayoría tienen una limitada capacidad de dispersión y unos requerimientos de hábitat muy específicos. El objetivo general de esta tesis es estudiar la respuesta ecológica de una planta forestal (*Primula vulgaris*) ante la pérdida y fragmentación de su hábitat. En concreto, analizamos los patrones de distribución y abundancia, los procesos de éxito reproductivo y reclutamiento, y finalmente los efectos globales del cambio en el paisaje en términos de dinámica poblacional.

En el **Capítulo 1** se estudia la respuesta de los patrones de distribución al cambio en el paisaje, y se analizan los diferentes modelos conceptuales que han sido propuestos para representar los paisajes alterados y las respuestas específicas. Concretamente, el **Capítulo 1a** demuestra la utilidad del modelo de paisaje continuo para el estudio de la respuesta de *P.*

vulgaris a la pérdida y fragmentación de hábitat, en términos de distribución, abundancia y estructura de edades de las poblaciones. Este modelo permite estudiar también la respuesta de la especie a otras variables ambientales y de su ciclo de vida que determinan su percepción del paisaje. Encontramos que la pérdida de hábitat es el proceso más perjudicial para *P. vulgaris*, y que su efecto es más patente en la presencia de la especie que en su abundancia y estructura de edades. Sin embargo, la especie no ocupa todo el hábitat forestal potencialmente adecuado, debido a sus restricciones a la dispersión y a cierto efecto de calidad de hábitat determinado por la pendiente topográfica. Las restricciones a la dispersión dentro del hábitat son tan importantes como el cambio en el paisaje a la hora de determinar la distribución a escala de paisaje de *P. vulgaris*. En el **Capítulo 1b** se hace un repaso histórico de los modelos conceptuales utilizados para el análisis de los procesos de cambio en el paisaje y de sus efectos en los organismos. Se distinguen modelos basados en patrones (modelo de islas, modelo de parche-matriz-corredor y modelo de paisaje abigarrado) frente a modelos basados en procesos (modelo de paisaje continuo). En este trabajo se discute la aplicabilidad de cada modelo, resaltando la utilidad del modelo de paisaje continuo mediante el ejemplo de *P. vulgaris* en bosques fragmentados.

En los **Capítulos 2** y **3** se estudia cómo afecta el cambio en el paisaje a dos procesos clave para la supervivencia de las poblaciones de plantas: la reproducción y el reclutamiento. En el **Capítulo 2** se evalúan los efectos de la pérdida y fragmentación de hábitat sobre el éxito reproductivo de *P. vulgaris*, distinguiendo efectos directos (efectos sobre los individuos independientemente de las características de las poblaciones) e indirectos (efectos en los individuos mediados por alteraciones del tamaño poblacional). La producción de flores y frutos disminuyó con la pérdida de hábitat, y la producción de frutos aumentó con la cantidad de borde forestal. La pérdida de hábitat disminuyó la producción de semillas debido a que redujo el tamaño poblacional. Los efectos observados fueron diferentes entre años, desapareciendo o incluso cambiando de signo, probablemente en relación con variaciones en la dureza invernal que determinan la duración de la floración. Estos resultados muestran que la medida de manejo más efectiva para incrementar la reproducción de esta especie sería incrementar la cobertura forestal alrededor de las poblaciones existentes. El potencial papel aditivo de la variabilidad climática debe ser también considerado en las propuestas de manejo. En el **Capítulo 3** se evalúa la importancia de diferentes mecanismos limitantes del reclutamiento de *P. vulgaris* (limitaciones a la dispersión vs. limitaciones al establecimiento) en distintos momentos del desarrollo, y cómo estas limitaciones se relacionan con alteraciones ambientales derivadas de la pérdida y fragmentación del hábitat. Para ello, se establece un experimento de adición de semillas en un gradiente de alteración paisajística. Observamos una severa limitación a la dispersión, que existe independientemente de las alteraciones del paisaje, aunque las reducciones en producción de semillas por pérdida de hábitat o los incrementos de la subdivisión del hábitat la incrementarían. La calidad del hábitat restringió la supervivencia y el crecimiento de las plántulas durante su primer año de vida. Las modificaciones del hábitat y de la población que resultan del cambio en el paisaje determinaron estas limitaciones al establecimiento, y muchos de sus efectos fueron interdependientes. Por lo tanto, la pérdida y fragmentación de hábitat pueden comprometer el reclutamiento de las plantas, ya que actúan incrementando las limitaciones a la dispersión y desencadenando las limitaciones al establecimiento.

En el **Capítulo 4** se integra la información sobre efectos en procesos de los dos capítulos anteriores para evaluar los efectos del cambio en el paisaje en la dinámica poblacional de *P. vulgaris*. Se estudia la respuesta de las diferentes tasas vitales (supervivencia, crecimiento, reproducción y reclutamiento) y de la tasa de crecimiento poblacional (lambda) ante la pérdida y fragmentación de hábitat, teniendo en cuenta la magnitud y variación del efecto de cada tasa vital en el crecimiento global. La pérdida de hábitat tuvo efectos negativos en diferentes procesos del ciclo vital, aunque la intensidad de estos efectos varió dependiendo de la tasa vital y el intervalo anual considerado. Las poblaciones situadas en zonas con elevada cobertura forestal mostraron tendencias positivas de crecimiento, debido a incrementos de la supervivencia y reproducción de plántulas y del reclutamiento, mientras que las poblaciones en sitios muy deforestados mostraron tendencias negativas. Sin embargo, poblaciones en áreas con cierto grado de fragmentación (aquellas con mucha cantidad de borde forestal) pueden tener tasas de crecimiento elevadas, debido al efecto positivo del borde forestal en la supervivencia de los adultos. Por lo tanto, los diferentes procesos de alteración tienen efectos balanceados en la dinámica poblacional. Aunque existe variación entre años, a largo plazo, un aumento de los períodos de crecimiento elevado puede incrementar las diferencias en dinámica poblacional a lo largo de los gradientes de alteración paisajística. Son necesarios estudios a largo plazo para elucidar las interacciones entre respuestas demográficas, patrones de paisaje y variabilidad climática.

Los resultados de este estudio muestran que los diferentes procesos de cambio en el paisaje influyen en procesos que ocurren a una escala mucho más pequeña, como es la de la población o incluso la de la planta individual. La pérdida y fragmentación de hábitat influyen en los procesos que determinan la dinámica poblacional de las plantas, y en conjunto son parcialmente responsables de la distribución de la especie. Los efectos de cada uno de los procesos de alteración difieren en cuanto a intensidad y signo, y la pérdida de hábitat puede tener una influencia directa, o bien indirecta, es decir, a través de reducciones del tamaño de población. Además de la pérdida y fragmentación de hábitat, la aplicación del modelo de paisaje continuo revela que otros factores ambientales y la limitación a la dispersión también determinan la distribución de la especie. *P. vulgaris* está claramente asociada al hábitat forestal

en nuestra área de estudio, sin embargo, nuestros resultados confirman que cierto grado de fragmentación forestal no es perjudicial para la especie. Al contrario, contribuye a incrementar la producción reproductiva, y en último término, la tasa de crecimiento poblacional. Por lo tanto, la viabilidad de esta especie está favorecida en paisajes con alta disponibilidad de hábitat forestal, compuestos por una red de parches interconectados, y con abundantes zonas de borde forestal. Estos resultados pueden extrapolarse a otras plantas herbáceas perennes de bosques templados.

Introducción General

Procesos de cambio en el paisaje: pérdida y fragmentación de hábitat

Los procesos ecológicos, y en último término, la distribución de las especies, dependen en gran medida de la estructura del paisaje. La heterogeneidad del paisaje controla muchos de los procesos que ocurren en todos los niveles de organización biológica. Por lo tanto, los cambios en la estructura del paisaje darán lugar a alteraciones en estos procesos y en los consecuentes patrones de distribución de especies. En concreto, el cambio en el paisaje generado por acción humana da lugar a alteraciones en la cantidad, calidad y configuración espacial de los hábitats naturales. La alteración de los paisajes naturales se considera como una de las principales causas de pérdida de biodiversidad a nivel mundial (Wilson 1985; Hanski 2005; Lindenmayer y Fischer 2006a; Krauss et al. 2010), siendo actualmente una prioridad de investigación dentro de la biología de la conservación. El cambio paisajístico puede considerarse un fenómeno complejo, que actúa a diferentes escalas espaciales, y que comprende varios procesos de alteración del hábitat simultáneos e interdependientes. En este contexto, Lindenmayer and Fischer (2006a) definieron el término “hábitat” como “el entorno adecuado para una especie concreta, y por tanto una entidad específica de especie”. De este modo, el cambio en el paisaje y los procesos que lo conforman deberían considerarse desde el punto de vista de cada especie que habita en el paisaje y de sus preferencias de hábitat. El proceso más evidente de cambio paisajístico es la pérdida neta de cantidad de hábitat, que se deriva de la reducción del área del paisaje adecuada para cada especie, ya sea por disminución del tamaño de los fragmentos de hábitat existentes, o por desaparición completa de algunos de estos fragmentos. La pérdida de hábitat en un paisaje conduce irremediablemente a la fragmentación de dicho hábitat. Entendemos por fragmentación de hábitat la división progresiva de un hábitat original, relativamente continuo, en un conjunto de fragmentos progresivamente empequeñecidos, que quedan aislados entre sí por una matriz de hábitat degradado, que puede presentar distintos grados de diferencia cualitativa con respecto al hábitat original (Haila 2002). En muchos estudios se ha incluido la pérdida de hábitat dentro del proceso de fragmentación, sin embargo, ambos procesos pueden tener efectos independientes en la biodiversidad, y sólo separándolos obtendremos una visión clara de la importancia de cada uno de ellos. Algunos autores incluso sostienen que el término fragmentación es conceptualmente ambiguo, y que se ha convertido en una “panacea” bajo la cual se incluyen genéricamente toda una serie de patrones y procesos de cambio en el paisaje causados por la acción humana (Haila 2002; Lindenmayer y Fischer 2006b). En este caso se seguirá la recomendación de Fahrig (2003) y se distinguirá la pérdida de hábitat de la fragmentación del mismo, reservando este término para los cambios en la configuración del hábitat. La fragmentación comprende dos procesos principales que afectan a la biodiversidad: la subdivisión del hábitat y los efectos de borde. La subdivisión de un fragmento de hábitat puede dar lugar a dos o más fragmentos independientes, que muestran distinto grado de aislamiento entre sí, dependiendo de la distancia existente entre ellos, pero también de las características de la matriz que los separa (por ejemplo, del grado de similitud entre la matriz y el hábitat original), que pueden influir en el aislamiento efectivo de los fragmentos (Ricketts 2001) y en el grado de conectividad entre ellos (Tischendorf y Fahrig 2000). Los efectos de borde engloban cambios en las condiciones ambientales en las zonas periféricas de los fragmentos de hábitat, debidos a la influencia de la matriz de hábitat degradado. Estos cambios afectan a las condiciones físicas y biológicas de las zonas cercanas al borde de los fragmentos, dando lugar por ejemplo a diferencias microclimáticas y a alteraciones en las interacciones entre especies (Murcia 1995; Ries et al. 2004).

La interdependencia entre pérdida y fragmentación de hábitat da lugar generalmente a relaciones de tipo cuadrático entre las medidas de subdivisión del hábitat (por ejemplo, el número de fragmentos) o de cantidad de borde y las de cantidad de hábitat (Fig. I.1). Si la cantidad de hábitat es muy pequeña, encontraremos un número bajo de fragmentos con poca cantidad de borde. Por otro lado, si el área de hábitat es muy grande, observaremos solamente un fragmento, o varios fragmentos grandes, y la cantidad de borde total será también reducida. Es decir, que tanto en las situaciones de grave pérdida de hábitat, como en aquellas donde el área de hábitat es muy extensa, encontramos menor número de fragmentos y menor cantidad de borde. Sin embargo, con valores intermedios de pérdida de hábitat observamos un mayor número de fragmentos y una mayor cantidad de borde. Esta interacción entre distintos procesos de cambio en el paisaje tiene fuertes repercusiones biológicas, ya que una especie que viva en un paisaje alterado sufrirá generalmente tanto efectos de pérdida como de fragmentación de su hábitat, ya que ambos procesos son interdependientes. Además, esta cuestión tiene también repercusiones analíticas, ya que si no se separan los efectos netos de cada proceso, podríamos sobreestimar, por ejemplo, los efectos de la fragmentación debido a su correlación con la pérdida de hábitat. A pesar de su importancia a la hora de separar los efectos de los distintos procesos de cambio paisajístico, estas relaciones han sido frecuentemente ignoradas en la literatura (Fahrig 2003).

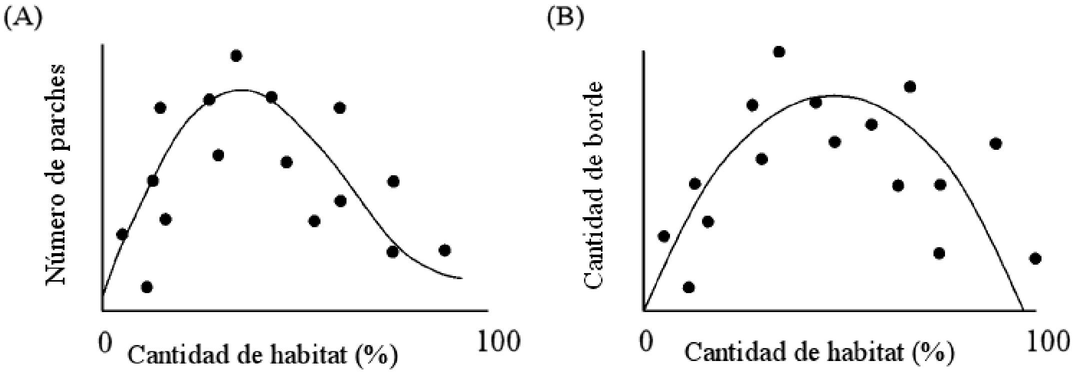

Figura I.1: Relaciones observadas típicamente entre cantidad de hábitat y (A) número de parches, (B) cantidad de borde. Modificado de (Fahrig 2003).

Conceptualización del cambio en el paisaje

Los modelos de paisaje son herramientas conceptuales que proporcionan una terminología y una representación visual que puede utilizarse para comunicar y estudiar cómo están distribuidos los organismos en el espacio (Lindenmayer y Fischer 2006a). La complejidad que conllevan los cambios en el paisaje requiere del desarrollo de modelos conceptuales que integren los diferentes procesos de cambio y sus interrelaciones, y que sean aplicables a la diversidad de paisajes que encontramos en el mundo real. Además, hay que tener en cuenta la especificidad del término “hábitat”, que implica la existencia de respuestas diferenciales de cada organismo a la alteración del paisaje. En los inicios de la investigación sobre pérdida de hábitat y fragmentación, los paisajes se representaban mediante una aproximación binaria (Fig. I.2), que consideraba sólo dos tipos de elementos en el paisaje: los fragmentos de hábitat y la matriz homogénea e inhóspita que los rodea (Haila 2002; Watling y Donnelly 2006). Esta conceptualización no tiene en cuenta las posibles diferencias entre especies en cuanto a la percepción del paisaje, ya que establece que los fragmentos de hábitat son igualmente adecuados para todas las especies de la comunidad, al igual que la matriz se considera totalmente inhóspita para todas ellas. Actualmente sabemos que esta concepción de hábitat frente a “no-hábitat” difícilmente aparece en los paisajes reales, ya que en la mayoría de los casos las transiciones entre los distintos elementos del paisaje no son tan abruptas, sino graduales, reflejando gradientes continuos de adecuación de hábitat, en los que lo que anteriormente se consideraba matriz puede tener distintos grados de permeabilidad a la dispersión de los organismos (Kupfer et al. 2006). Además, estos gradientes ambientales son específicos de especie, ya que la adecuación del hábitat está determinada por la capacidad de percepción y respuesta de cada especie ante los cambios en el paisaje y ante otros gradientes ambientales con efectos en los procesos biológicos (agua, nutrientes, luz, etc., Manning et al. 2004b). Para ser capaces de representar adecuadamente la realidad de la mayoría de los paisajes alterados de nuestro planeta, los modelos de paisaje necesitan ir más allá de las visiones binarias (Fig. I.2), y considerar las respuestas a los gradientes ambientales que son percibidos por cada especie.

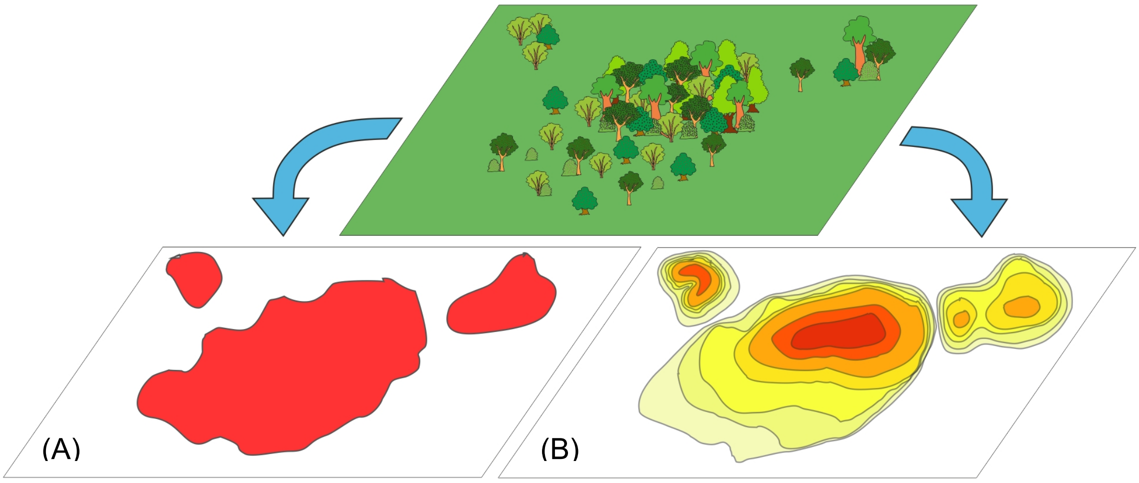

Figura I.2: Dos representaciones para un mismo paisaje forestal alterado: (A) Paisaje representado de forma binaria, donde el color rojo indica hábitat totalmente adecuado (fragmentos de bosque), y el color blanco, hábitat totalmente inhóspito (matriz deforestada); y (B) Paisaje representado como un gradiente continuo de adecuación de hábitat para una especie determinada, desde el hábitat más adecuado (rojo) hasta el menos adecuado (blanco).

Ecología de poblaciones en paisajes alterados

Los procesos de cambio paisajístico anteriormente descritos dan lugar a cambios en todos los niveles de organización ecológica, desde los organismos individuales a los ecosistemas. Esta tesis se centra en el estudio de las respuestas poblacionales de plantas frente a los cambios en el paisaje. La pérdida y fragmentación de hábitat dan lugar a reducciones en los tamaños poblacionales (Fahrig 2003) y en el potencial reproductivo individual (Aizen y Feinsinger 1994; Aguilar et al. 2006). Esto puede llevar a alteraciones de las dinámicas de reclutamiento, y en último término, al colapso demográfico, incrementando la probabilidad de extinción de las poblaciones. Sin embargo, la extinción es el resultado de un proceso de cambio prolongado, que comprende una serie de modificaciones en la biología de la población (Simberloff 1988), en las que se incluyen tanto cambios en procesos intrínsecos de la población, como en las interacciones entre especies (Lindenmayer y Fischer 2006a). Los cambios en el paisaje pueden alterar las interacciones de competencia (Bowers y Harris 1994), depredación (García y Chacoff 2007), herbivoría (Augustine y Frelich 1998; Tscharntke y Brandl 2004) y mutualismos como la polinización (Aizen y Feinsinger 1994; Lennartsson 2002) y la dispersión de semillas (Herrera y García 2010).

Los diferentes procesos de cambio en el paisaje pueden afectar a la viabilidad de las poblaciones de plantas, ya sea de forma directa, o bien indirecta, a través de reducciones de su tamaño poblacional y de incrementos en el aislamiento espacial entre poblaciones. Los tamaños de población se ven reducidos en paisajes alterados debido a la pérdida de hábitat, o debido a disminuciones en la capacidad dispersiva de los organismos (Schtickzelle et al. 2006) y del flujo génico (Young et al. 1996), generadas como consecuencia de la subdivisión del hábitat. Por lo tanto, estas alteraciones paisajísticas dan lugar a la aparición de poblaciones pequeñas y aisladas, que pueden sufrir pérdidas de variabilidad genética y altos niveles de endogamia (Culley y Grubb 2003; González-Varo et al. 2010; Van Rossum et al. 2002). Por otro lado, la diferenciación genética entre poblaciones puede aumentar debido a la disminución del flujo génico entre ellas (Young et al. 1996). En poblaciones pequeñas, puede existir una relación positiva entre la eficacia biológica y la densidad de la población (efecto Allee, Courchamp et al. 1999). Además, el pequeño tamaño y el aislamiento de las poblaciones pueden afectar también a interacciones importantes para el ciclo de vida de las plantas, como la polinización, que en muchos casos es un factor limitante de la reproducción. Tanto la diversidad como el comportamiento de los polinizadores pueden verse alterados en poblaciones pequeñas y aisladas, afectando al éxito reproductivo de las plantas (Aizen y Feinsinger 1994; Didham et al. 1996; Jacquemyn et al. 2002; Steffan-Dewenter y Tscharntke 1999). Sin embargo, la pérdida y subdivisión del hábitat pueden ejercer también efectos directos, es decir, no mediados por reducciones del tamaño de población e incrementos del aislamiento, sobre las poblaciones de plantas. Por ejemplo, la pérdida de hábitat puede reducir la tasa de visita y modificar el comportamiento de los polinizadores, resultando en un menor cuajado de semillas en las plantas (Goverde et al. 2002). La subdivisión del hábitat puede dar lugar a disminuciones del reclutamiento, ya que las semillas pueden ser incapaces de desplazarse entre los fragmentos de hábitat adecuado debido al incremento del aislamiento entre ellos (Ehrlén y Eriksson 2000). Por otro lado, el incremento de la cantidad de borde de los fragmentos de hábitat puede alterar directamente la densidad, reproducción, crecimiento y mortalidad de las poblaciones de plantas (Hobbs y Yates 2003; Lienert y Fischer 2003; Tomimatsu y Ohara 2004), ya sea debido a cambios en las condiciones abióticas (viento, temperatura, luz, nutrientes, etc.), o a cambios en las interacciones con animales. En general, la mayor cantidad de borde se ha asociado con el incremento de interacciones negativas como la depredación de semillas (Jules y Rathcke 1999) y la herbivoría (Wirth et al. 2008), aunque también se han documentado efectos de borde positivos (Carlson y Hartman 2001; Laurance et al. 2001; Montgomery et al. 2003).

Aunque hasta la fecha existen numerosos trabajos que tratan de explicar las respuestas ecológicas de las especies de plantas al cambio en el paisaje, la mayoría de ellos son parciales, en el sentido de que no consideran el efecto de todos los procesos de cambio, no son capaces de distinguir efectos netos de cada proceso, o estudian la respuesta de un único proceso ecológico (reproducción, reclutamiento, etc.). Existe por tanto la necesidad de estudiar de forma integradora los efectos de los distintos procesos de cambio en el paisaje (pérdida y subdivisión de hábitat y efectos de borde) sobre distintos tipos de respuestas ecológicas de las especies de plantas. En esta tesis se estudia la respuesta de varios aspectos clave de la ecología de poblaciones de plantas, concretamente, de la distribución y abundancia a escala de paisaje, el éxito reproductivo, el reclutamiento y la dinámica poblacional, a los cambios en el paisaje. Este trabajo podría considerarse como una aproximación “orientada a especie” (según Lindenmayer y Fischer 2006a), ya que trata de considerar la perspectiva de una especie concreta en vez de analizar el paisaje desde una perspectiva humana. Sin embargo, las conclusiones obtenidas del presente trabajo pueden ser aplicables a un amplio número de especies con características similares.

El estudio de los efectos del cambio en el paisaje puede abordarse desde dos perspectivas diferentes: estudiando los patrones de distribución de las poblaciones, o bien estudiando la respuesta de los procesos generadores de estos patrones. En la presente tesis hemos utilizado las dos aproximaciones. En primer lugar, se estudian los patrones de distribución y abundancia de una especie en un paisaje fragmentado, lo que nos permite tener una visión general de cómo responde la especie ante la estructura del paisaje. Después, se evalúan los efectos de las alteraciones paisajísticas en la reproducción y el reclutamiento, dos procesos del ciclo vital de las plantas que son extremadamente importantes en paisajes alterados. Finalmente, se estudian los efectos del cambio en el paisaje en términos de dinámica poblacional, integrando la respuesta de todos los procesos del ciclo vital ante las alteraciones paisajísticas, y determinando la importancia de cada uno de estos procesos para el crecimiento de la población.

Plantas forestales perennes y cambio en el paisaje

Las plantas forestales poseen una serie de rasgos que las hacen especialmente sensibles a la pérdida y fragmentación de su hábitat (Honnay et al. 2005), y por lo tanto interesantes como especies focales en estudios sobre los efectos del cambio en el paisaje. Recientemente, estas plantas han despertado interés debido a que muchas especies han pasado a ser raras o a estar amenazadas debido a la alteración del paisaje y a la destrucción de su hábitat. Las características comunes de su ciclo vital pueden interpretarse como una adaptación evolutiva al ecosistema forestal, relativamente estable y con perturbaciones poco frecuentes y localizadas. En este tipo de ecosistemas, generalmente no es necesario invertir en una elevada producción de semillas, bancos de semillas persistentes o estructuras que faciliten la dispersión a larga distancia. La mayoría de las plantas herbáceas forestales son perennes, de larga vida (Ehrlén y Lehtilä 2002), y aunque su reproducción es mayoritariamente sexual, presentan en muchos casos posibilidades de reproducción clonal (Klimeš et al. 1997). La producción de semillas es generalmente baja (Bierzychudek 1982; Hermy et al. 1999) y éstas no suelen permanecer durante mucho tiempo en el suelo (esto es, no hay bancos de semillas). La mayoría de especies carece de adaptaciones para la dispersión a larga distancia, por lo que las distancias de dispersión suelen ser de unos pocos metros (Whigham 2004), aunque en raras ocasiones pueden ocurrir eventos de dispersión a larga distancia (Vellend et al. 2003). La limitada capacidad de dispersión, junto con la baja producción de semillas y la limitada capacidad competitiva (Hermy et al. 1999), hacen que estas especies tengan poca capacidad de colonización de nuevos hábitats. Esta característica las hace especialmente vulnerables y propensas a la extinción en situaciones de pérdida y fragmentación de hábitat, y retrasa en gran medida su recuperación después de un declive poblacional.

Además de estas limitaciones, la calidad del hábitat también puede afectar especialmente a estas especies, ya que tienen requerimientos muy específicos en cuanto a disponibilidad de luz, humedad, condiciones del suelo y otros factores (Kolb y Diekmann 2004). Esto puede impedir que sean capaces de establecerse en determinados fragmentos de hábitat debido a su baja calidad.

Debido a la larga vida de estas especies, en ocasiones puede transcurrir una cantidad de tiempo considerable hasta que las poblaciones en declive desaparezcan después de las alteraciones ambientales. Este retraso en la extinción local es lo que se denomina deuda de extinción (Kuussaari et al. 2009), y es especialmente común en plantas herbáceas forestales (Honnay et al. 2005). La deuda de extinción es un factor importante a tener en cuenta en la conservación, ya que puede dar lugar a que se subestimen las consecuencias del cambio en el paisaje, debido a que sus efectos en las poblaciones no se observan inmediatamente después de que ocurran las alteraciones.

Objetivos y estructura de la tesis

El objetivo general de esta tesis doctoral es estudiar la respuesta de la ecología de poblaciones de una planta forestal (*Primula vulgaris*) frente a los cambios en el paisaje derivados de la pérdida y fragmentación de hábitat por acción humana. Para ello, se han evaluado de forma observacional las respuestas poblacionales en términos de distribución y abundancia, éxito reproductivo y viabilidad poblacional, a lo largo de gradientes de cambio paisajístico, y se han determinado de forma experimental los mecanismos que limitan el reclutamiento de la especie en paisajes alterados.

El **Capítulo 1** (*“Species distribution patterns in altered landscapes: conceptual models and specific responses”*) se centra en el estudio de los patrones de distribución de las plantas a escala de paisaje en respuesta a la pérdida y fragmentación de su hábitat, y de los diferentes modelos conceptuales que se han desarrollado para representar los paisajes alterados y las respuestas de las especies. En el **Capítulo 1a** (*“Applying a continua landscape approach to evaluate plant response to landscape change:* Primula vulgaris *in the Cantabrian mountains”*) se utiliza un modelo conceptual recientemente desarrollado, el modelo de paisaje continuo, para evaluar la respuesta de la herbácea perenne forestal *P. vulgaris* a la pérdida y fragmentación de hábitat, en términos de distribución, abundancia y estructura demográfica de las poblaciones. El carácter específico de este modelo permite estudiar también la respuesta de la especie a otras variables que determinan su percepción del paisaje; en este caso hemos considerado variables topográficas y la capacidad de dispersión. En el **Capítulo 1b** (*“Modelos de cambio en el paisaje: de la biogeografía de islas a la aproximación de paisaje continuo”*) se hace un repaso histórico de los distintos modelos conceptuales que se han utilizado para el análisis de los procesos de cambio paisajístico y sus efectos en los organismos, discutiendo la aplicabilidad de cada uno de ellos y haciendo hincapié en la utilidad del modelo de paisaje continuo mediante el ejemplo de *P. vulgaris* en bosques fragmentados.

En los **Capítulos 2** y **3** se estudia cómo afecta el cambio en el paisaje a dos procesos clave para la supervivencia de las poblaciones de plantas: la reproducción y el reclutamiento. En el **Capítulo 2** (*“Direct and indirect effects of landscape change on the reproduction of a temperate perennial herb”*) se evalúan los efectos de la pérdida y fragmentación de hábitat sobre el éxito reproductivo de *P. vulgaris*, distinguiendo efectos directos de los procesos de cambio paisajístico en la producción reproductiva individual, y efectos indirectos mediados por alteraciones de características poblacionales, como el tamaño de población. En el **Capítulo 3** (*“Mechanisms limiting* Primula vulgaris *recruitment in a fragmented landscape”*) se intenta distinguir la importancia de diferentes mecanismos limitantes del reclutamiento de *P. vulgaris* (limitaciones a la dispersión vs. limitaciones al establecimiento) en distintos momentos del desarrollo, y evaluar cómo estas limitaciones se relacionan con una serie de alteraciones ambientales derivadas de la pérdida y fragmentación de hábitat. Para ello, se establece un experimento de adición de semillas en un gradiente de alteración paisajística.

El **Capítulo 4** (*“Landscape change alters population growth of a perennial forest herb: integrative effects of landscape processes across multiple life-cycle stages”*) integra la información recogida en los dos capítulos anteriores sobre efectos en procesos, para evaluar cómo afecta el cambio paisajístico a la dinámica global de las poblaciones de *P. vulgaris*. En este capítulo se estudia la respuesta de las diferentes tasas vitales (supervivencia, crecimiento, reproducción y reclutamiento) y de la tasa de crecimiento poblacional ante la pérdida y fragmentación de hábitat, teniendo en cuenta la magnitud y variación del efecto de cada tasa vital en el crecimiento global.

Área y especie de estudio

La presente tesis doctoral se llevó a cabo en bosques templados de la cordillera Cantábrica (Asturias, Noroeste de España, Fig. I.3). Estos sistemas forestales son un excelente ejemplo de bosques templados europeos con un alto grado de alteración derivado de un proceso histórico de explotación humana, encaminado a disponer de pastizales para la ganadería extensiva de montaña. Este proceso ha conllevado una importante pérdida de hábitat forestal, unida irremediablemente a la fragmentación de dicho hábitat, lo que ha hecho que las grandes extensiones boscosas anteriormente presentes hayan dado paso a un paisaje más heterogéneo, donde los parches remanentes de bosque se entremezclan con zonas de pastizal, brezal y roquedos. El escenario forestal actual a escala de la vertiente asturiana de la cordillera Cantábrica se caracteriza por una baja cobertura forestal (22%), distribuciones de tamaños de fragmento muy sesgadas hacia los valores pequeños (<10 ha), una gran irregularidad en la forma de los fragmentos que conlleva efectos de borde generalizados, y fuertes diferencias entre distintos tipos de masas forestales en los patrones generales de fragmentación (García et al. 2005b).

El trabajo de campo en el que se basan los diferentes capítulos de esta tesis se ha realizado en la Sierra de Peña Mayor (Fig. I.3, 43º17'N, 5º30'W, perteneciente a los concejos de Bimenes, Nava y Laviana). En esta zona el paisaje se caracteriza por la presencia de unos pocos fragmentos grandes de bosque maduro de haya (*Fagus sylvatica* L.), donde también está presente el fresno (*Fraxinus excelsior* L.), junto con bosques de orla y muchos fragmentos pequeños de bosque secundario compuestos por especies de fruto carnoso (acebo *Ilex aquifolium* L., espino albar *Crataegus monogyna* Jacq., tejo *Taxus baccata* L., serbal de cazadores *Sorbus aucuparia* y mostajo *Sorbus aria*) y avellanos *Corylus avellana* L. Todos estos fragmentos se encuentran embebidos en una matriz no forestal que cubre alrededor del 70 % del área de estudio, y que puede contener densidades variables de árboles aislados.

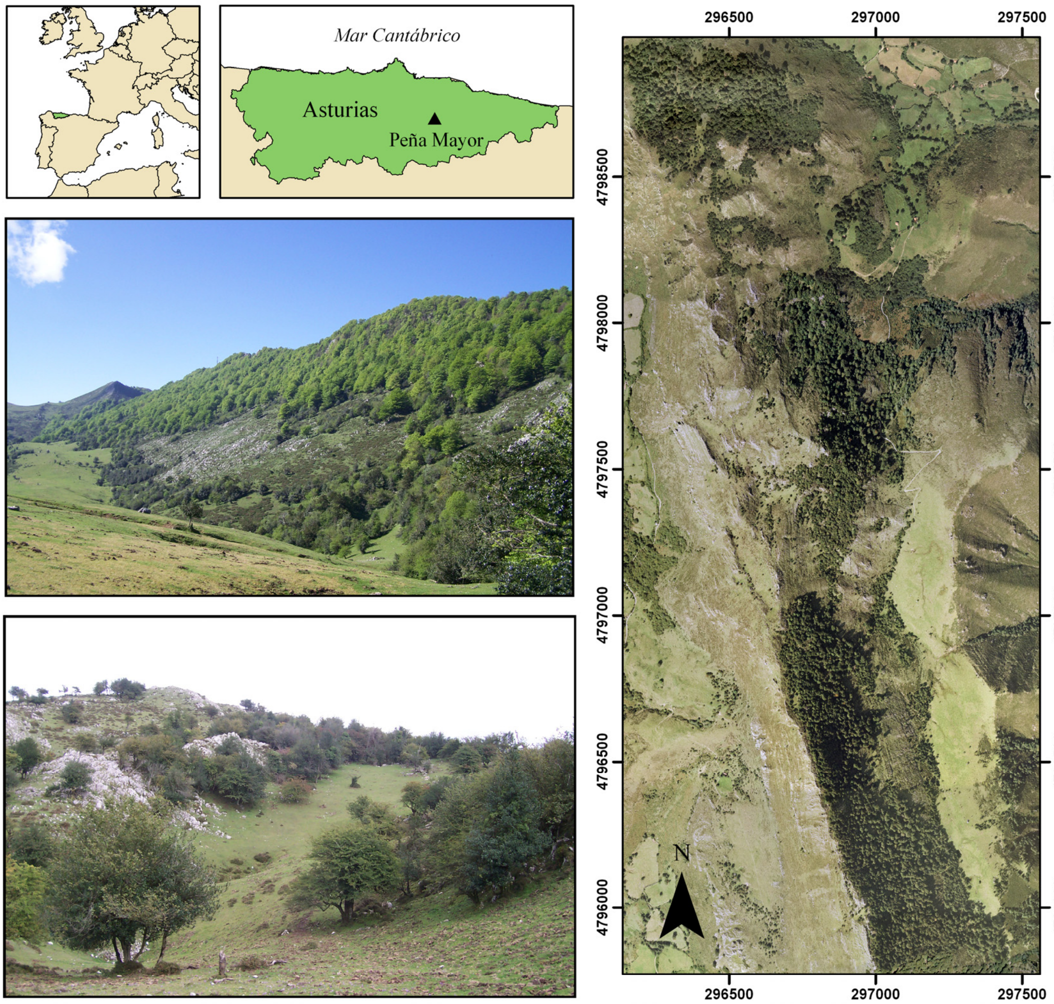

Figura I.3: Área de estudio. Izquierda, arriba: Localización geográfica. Derecha: Ortofotografía de la Sierra de Peña Mayor, mostrando el área donde se llevó a cabo el trabajo de campo correspondiente a todos los capítulos de esta tesis. Izquierda, centro: Vista de uno de los grandes parches de bosque maduro, junto con zonas de roquedo, brezal, bosque de orla y pastizal. Izquierda, abajo: Vista de un pequeño rodal de bosque secundario, intercalado con pastizal y roquedos.

La especie objeto de estudio en esta tesis es la primavera *Primula vulgaris* L. (Fig. I.4), una planta herbácea forestal de hábito perenne, hemicriptófita, con hojas en roseta basal y flores de color amarillo pálido (para descripción más detallada sobre la especie ver Jacquemyn et al. 2009). Las hojas son producidas continuamente a lo largo de la estación de crecimiento hasta el final del verano. La floración es temprana, en nuestra zona de estudio ocurre desde el final del invierno (Febrero) hasta el final de la primavera (Junio), siendo el pico de floración en Abril. La reproducción ocurre eminentemente por medio de semillas, aunque la reproducción

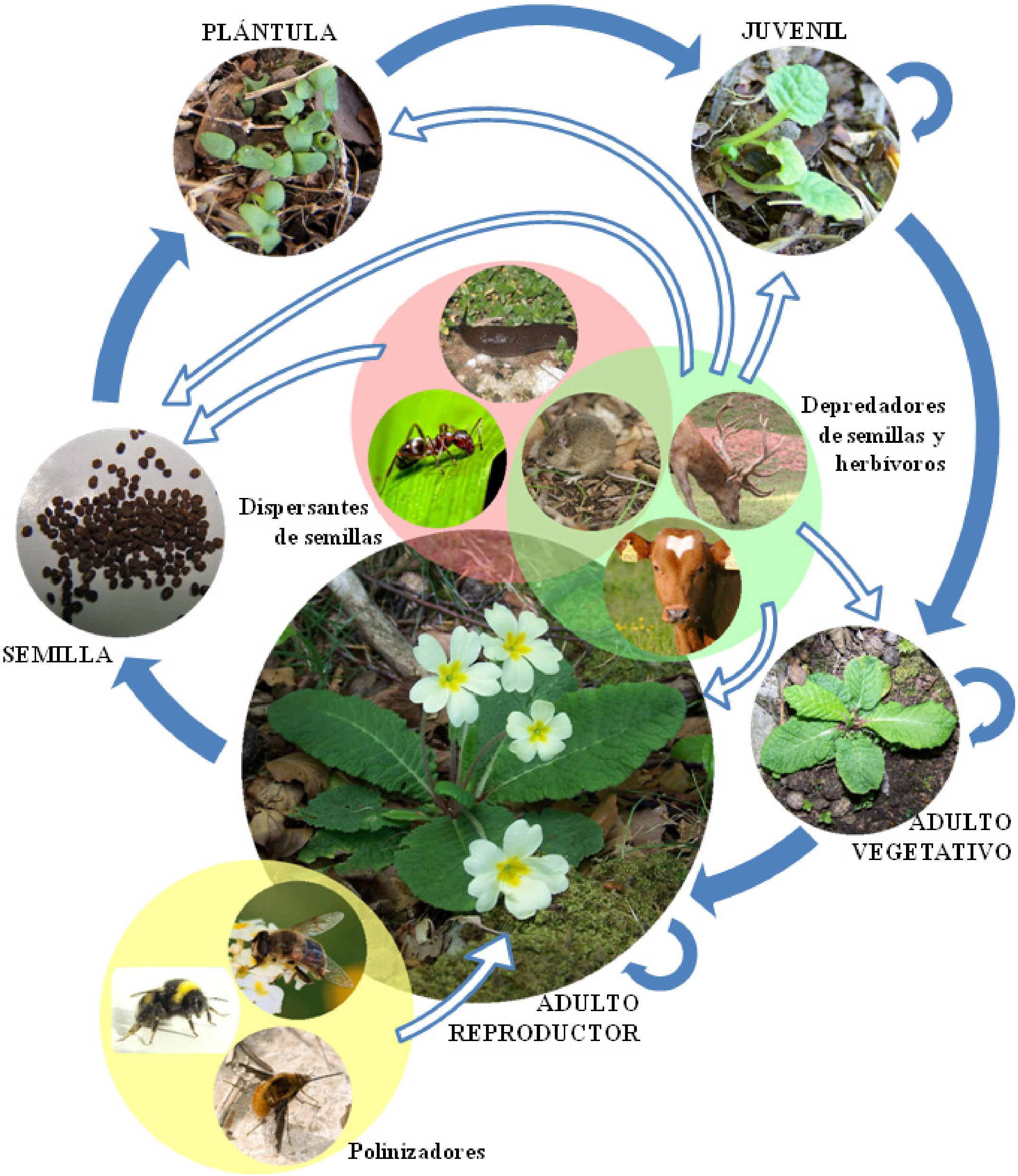

Figura I.4: Ciclo de vida de *Primula vulgaris* y principales organismos que interaccionan con la especie (ver texto para más detalles). Las flechas azules indican las transiciones del ciclo vital, mientras que las flechas con relleno blanco señalan a qué estadios afecta cada tipo de interacción.

vegetativa puede ocurrir en ocasiones debido a la producción de rosetas laterales a cortas distancias de la planta madre. Son plantas longevas, pudiendo vivir 10-30 años según (Boyd et al. 1990), y hasta 48 años según (Ehrlén y Lehtilä 2002). Su sistema reproductivo es autoincompatible: presentan distilia con morfos florales *pin*, o de anteras basales en el tubo de la corola, y *thrum*, con las anteras extendiéndose sobre el extremo del tubo de la corola, de base genética. Sólo la polinización entre morfos resulta eficiente en el cuajado de las semillas, aunque soporta ciertos niveles de autofertilización (Boyd et al. 1990; Endels et al. 2002a). Los frutos son cápsulas ovaladas, con pedicelos decumbentes en la madurez, haciendo que caigan hacia la superficie del suelo cuando están maduros (entre finales de Junio y principios de Julio en nuestra zona de estudio). Las semillas (30-50 por fruto) miden 2-2.5 mm de diámetro y presentan un elaiosoma.

Los polinizadores más frecuentes son Himenópteros (especialmente abejorros *Bombus* spp.) y Dípteros de las familias Bombilidae y Syrphidae (Fig. I.4), aunque también puede ser visitada por Lepidópteros (e.g. *Gonepteryx rhamni*) y otras especies (ver lista en Jacquemyn et al. 2009). Las hojas, flores y frutos son consumidos por ungulados silvestres, ganado y roedores. Las semillas parecen dispersarse sobre todo por barocoria (por su propio peso), aunque hay evidencias de que hormigas, roedores y babosas son agentes dispersantes (Valverde y Silvertown 1995, datos no publicados).

1 Species distribution patterns in altered landscapes: conceptual models and specific responses

1a

Applying a continua landscape approach to evaluate plant response to landscape change: *Primula vulgaris* in the Cantabrian mountains

Valdés,A. and García,D. (2009). Applying a continua landscape approach to evaluate plant response to fragmentation: *Primula vulgaris* in the Cantabrian mountains. *Applied Vegetation Science* **12:** 504-515.

ABSTRACT

The *continua* landscape approaches conceptualize the effects of landscape change on the biota by considering the altered landscape as continuous gradients, departing from the binary view of habitat as either suitable (fragment) or unsuitable (matrix). They also consider the ecological gradients or the *Umwelt* (species-specific perception of the landscape) to represent the processes that ultimately limit organisms' ability to colonize and persist within habitat remnants. We aim to ascertain if these approaches are suitable for evaluating the response of plant species to landscape change in fragmented mid-elevation temperate forests of the Cantabrian Range (North-western Spain).We sampled the presence, abundance and demographic structure of populations of the perennial herb *Primula vulgaris* across a continuous extent of 100 ha, subdivided into 400, 50 x 50 m sampling units. These variables were related to forest availability, forest subdivision and edge density, topography and the spatial clumpiness of populations (a measure of plant dispersal constraints and, hence, a major surrogate of plant Umwelt). We found that landscape change processes, especially habitat loss, negatively affect *P. vulgaris*, with a stronger effect on presence than on abundance and demography. Despite the importance of habitat availability, *P. vulgaris* does not occupy all potentially suitable forest habitat, mostly due to dispersal constraints. A positive effect of slope on plant presence also suggests some effect of habitat quality in determining establishment and, ultimately, occupancy of forest landscape. This study highlights that within-habitat dispersal constraints are as important as landscape change in determining the landscape-scale distribution of *P. vulgaris*. By assessing the relative role of the diverse alteration processes, and of the species' landscape perception, a continua landscape approach proves to be a valuable tool for predicting plant response to landscape change.

RESUMEN

Las aproximaciones de paisaje continuo conceptualizan los efectos del cambio en el paisaje en la biota considerando al paisaje alterado como gradientes continuos, más allá de la visión binaria del hábitat como adecuado (fragmento) o no adecuado (matriz). También consideran los gradientes ecológicos del *Umwelt* (percepción del paisaje específica de especie) para representar los procesos que finalmente limitan la habilidad de los organismos para colonizar y persistir en los remanentes de hábitat. Intentamos determinar si estas aproximaciones son adecuadas para evaluar la respuesta de las especies de plantas al cambio en el paisaje en bosques templados fragmentados de altitudes medias de la Cordillera Cantábrica (Noroeste de España). Muestreamos la presencia, abundancia y estructura demográfica de poblaciones de la planta perenne *Primula vulgaris* a lo largo de una extensión continua de 100 ha, subdividida en 400 unidades de muestreo de 50 x 50 m. Estas variables se relacionaron con la disponibilidad y subdivisión del bosque, la densidad de borde forestal, la topografía y la agregación espacial de las poblaciones (una medida de restricciones a la dispersión de las plantas y por lo tanto representativa de su *Umwelt*). Encontramos que los procesos de cambio en el paisaje, especialmente la pérdida de hábitat, afectaron negativamente a *P. vulgaris*, con un efecto más fuerte en la presencia que en la abundancia y demografía. A pesar de la importancia de la disponibilidad de hábitat, *P. vulgaris* no ocupa todo el hábitat forestal potencialmente adecuado, sobre todo debido a sus restricciones a la dispersión. El efecto positivo de la pendiente en la presencia de las plantas sugiere también cierto efecto de la calidad de hábitat en la determinación del establecimiento y, en último término, en la ocupación del paisaje forestal. Este estudio pone de manifiesto que las restricciones a la dispersión dentro del hábitat son tan importantes como el cambio en el paisaje a la hora de determinar la distribución a escala de paisaje de *P. vulgaris*. Al evaluar el papel relativo de los diversos procesos de alteración y de la percepción específica del paisaje, la aproximación de paisaje continuo ha demostrado ser una herramienta valiosa para predecir la respuesta de las plantas al cambio en el paisaje.

INTRODUCTION

Human-caused landscape change is considered a major cause of plant biodiversity loss worldwide (Eriksson and Ehrlén 2001; Hobbs and Yates 2003; Honnay et al. 2005; Cousins 2009). Landscape change includes three different but interdependent processes (Fahrig 2003) each of which may lead to the extinction of plant populations through specific mechanisms: 1) habitat loss, the area of original habitat decreasing due to destruction, may lead to direct reductions of population size (e.g. Jacquemyn et al. 2002; Leimu et al. 2006); 2) habitat subdivision, habitat remnants becoming more and more isolated within a degraded matrix, can lead to indirect reductions of population size due to metapopulation disruption (e.g. Graae 2000; Dupré and Ehrlén 2002); and 3) edge increase, the perimeter/area ratio of habitat fragments increasing as a result of their smaller size and more irregular shape, may result in fitness reduction in remnant habitat species due to the percolation of harmful matrix conditions (i.e. edge effects, e.g. Jules 1998, Lienert and Fischer 2003). Although the effects of landscape change have been widely reported, the models aiming to conceptualize its effects are still weak on representing real-world landscapes and on integrating the diverse landscape change processes (Haila 2002; Lindenmayer et al. 2008). The “island” (Laurance 2008) and “patch-matrix-corridor” (Forman and Godron 1986, see also Forman 1995) models defend a binomial classification of habitats, where the remnant patches of suitable habitat, sometimes connected by corridors, are equivalent to islands embedded in a dominant, highly contrasting matrix. However, most altered landscapes worldwide do not easily fit these models for several reasons. Firstly, many landscapes are actually mosaics of patches, each subject to a different degree of habitat destruction (McIntyre and Barrett 1992, Bennett et al. 2006). Secondly, the boundaries between original and degraded habitats are frequently gradient-like rather than sharp transitions (McIntyre and Hobbs 1999). Thirdly, the background matrix of many fragmented landscapes, otherwise classified as inhospitable, is frequently perceived as suitable habitat for many species (García and Bañuelos 2003; Murphy and Lovett-Doust 2004). Thus, McIntyre and Barrett (1992) advocated a “variegation” model that classifies degraded landscapes within a continuum depending on the degree of habitat modification, i.e. intact, variegated, fragmented, or relictual landscapes. Nevertheless, all these landscape views emerge from human-defined landscape patterns, and ultimately consider that some original habitats are always suitable for some individual species, independently of the ecological processes underpinning species-specific distributions (Manning et al. 2004b; Fischer and Lindenmayer 2007).

The “continua” landscape approaches (*continua* and *Umwelt* approach, Manning et al. 2004b; *continuum* approach, Fischer and Lindenmayer 2006, 2007) have been presented as an alternative to classic landscape change models. They try to explain organisms’ responses to landscape change by representing landscape characteristics in the form of continuous gradients, a fact that makes it easier to discern the separate effects of habitat availability, isolation and edge density. More importantly, they highlight that other processes, apart from landscape change, ultimately limit organisms' ability to colonize and persist within habitat remnants. These processes may be represented by means of life cycle or behavioural traits that condition the species-specific perception of the landscape (e.g. movement ability), and conceptualized as the species *Umwelt* (i.e. the environment that is perceived and used by each species, von Uexküll 1934; see Manning et al. 2004b). Alternatively, limiting processes may be expressed as species-specific ecological gradients like resource availability or climatic constraints (Fischer and Lindenmayer 2006, 2007). Originally thought for studying animals' response to landscape change, continua approaches have not been yet applied to plants (but see other approaches in Dupré and Ehrlén 2002; Kolb and Diekmann 2004; Kunstler et al. 2007). In this sense, it is widely accepted that seed dispersal may limit the extent to which the distribution of plants follows that of their suitable habitats at local and regional scales (e.g. Primack and Miao 1992; Ehrlén and Eriksson 2000; Svenning and Skov 2002; McEuen and Curran 2004), and thus, dispersal potential together with the response to climatic, edaphic or topographic gradients should be considered a surrogate of *Umwelt* in plants.

Perennial herbs of temperate and boreal have been suggested to show specific forest habitat requirements (Dupré and Ehrlén 2002; Kolb and Diekmann 2004) and to be susceptible to habitat loss and edge effects (Jules and Rathcke 1999; Honnay et al. 2002). However, they also show low colonization capacity due to restricted dispersal even within undisturbed forest habitats (Ehrlén and Eriksson 2000; Honnay et al. 2005). Due to the combination of forest disturbance susceptibility and dispersal limitation, they are a suitable group of plants for the evaluation of forest loss and fragmentation effects under continua approaches. In this work, we study the primrose (*Primula vulgaris* L.) in the montane forest of the Cantabrian Range (N Spain), a habitat suffering a high degree of fragmentation (García et al. 2005b). Our main objective is to apply a continua and Umwelt approach to discern how the presence, abundance, and demographic structure of *P. vulgaris* are affected by landscape change. Specifically, we seek to answer the following questions: 1) Which process of landscape change (habitat loss, habitat subdivision, edge increase) affects *P. vulgaris* most? 2) Which ecological trait of *P. vulgaris* (presence, abundance or demographic structure) is the most sensitive to landscape change effects? and 3) How important are the characteristics of the altered landscape in determining *P. vulgaris* distribution and demography, in relation to the surrogates of species *Umwelt*, such as other landscape characteristics and dispersal constraints?

METHODS

Study site

Our study was carried out in the Sierra de Peña Mayor, Asturias, Spain (43º17' N – 5º30' W, elevation 900 m a.s.l., Fig. 1.1), a mountain which is part of the Cantabrian Range. The climate of the region is Atlantic, with a mean annual temperature of 13 ºC and annual rainfall of ca. 1300 mm. As in many other parts of the Cantabrian Range (García et al. 2005b), historical deforestation for cattle grazing has transformed the once extensive temperate forests of the site into a heavily fragmented wood-pasture habitat. Topography might also partially determine forest configuration and fragmentation. For example, limestone rocky outcrops may prevent soil formation, negatively affecting forest development (García et al. 2005b).

The spatial extent of the study was a continuous area covering 100 ha (over a surface approx. 3000 m long and 1000 m wide) along a North-South axis through the site, which was divided into 400 landscape sampling units (50x50 m square plots, Fig. 1.1). The physiognomy of the area is a highly variegated forest landscape (*sensu* McIntyre and Hobbs 1999). That is, it presents a mosaic composed of a few large forest fragments with hardwood species (beech *Fagus sylvatica* L. and ash *Fraxinus excelsior* L.), fringe fleshy-fruited, bird-dispersed trees (holly *Ilex aquifolium* L., hawthorn *Crataegus monogyna* Jacq., yew *Taxus baccata* L., and rowans *Sorbus* spp.) and hazel (*Corylus avellana*), as well as numerous small forest fragments mostly composed of fleshy-fruited trees, and a dominant (ca. 75% cover) matrix of stony pastures and heathlands (*Erica* spp., *Ulex europaeus* L.) with variable densities of scattered remnant trees (mostly hawthorns).

Study species

Our target species is *Primula vulgaris* L. (Primulaceae), a perennial, early-flowering herb, typically living in moist open habitats in Europe (Endels et al. 2002b), but restricted to temperate forests in some parts of its range (Jacquemyn et al. 2009). In our region it behaves mainly as a forest species, although it can be also found in some other moderately shaded locations, like road and path slopes. It grows producing basal rosettes of leaves every year, and vegetative spread is possible over very short distances through the production of lateral rosettes. Flowers are pale yellow and borne on separate stalks. Flowering in our study area lasts from late winter (February) to late spring (June), peaking in April. *P. vulgaris* is distylous and it has a self-incompatibility system with two genetically determined floral morphs: "pin", with anthers sunk in the corolla tube, and "thrum", with anthers extending beyond the corolla tube. Only between-morph pollination is efficient for seed set, although the system allows for certain levels of self-fertilisation (Endels et al. 2002a). Biased morph frequency in small populations leads to reduced reproductive output (Brys et al. 2004). The most common pollinators are Hymenoptera and

Diptera. Fruits (capsules containing 30-50 small seeds with an elaiosome) are consumed by ungulates, rodents and Lepidoptera larvae. Seeds are thought to be dispersed mainly by barochory, but there is also some evidence of occasional dispersal by ants (Valverde and Silvertown 1995; authors' unpublished data).

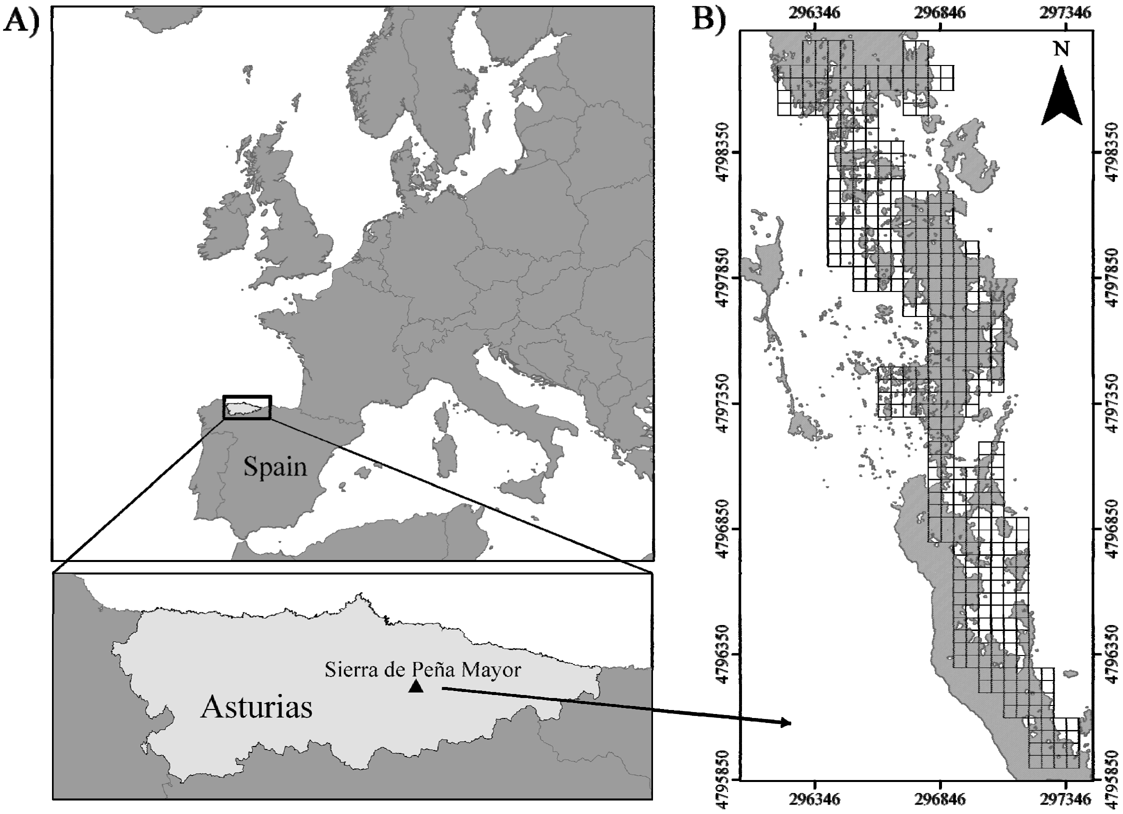

Figure 1.1: A) Geographic location of the study site, and B) representation of the sampling extent (grid of 400 50x50 m sampling units, forest cover represented in grey, numbers are UTM coordinates).

Measures of landscape change and other landscape characteristics

We developed a Geographic Information System (GIS) of the study area using ArcGIS 9.1, incorporating forest cover as a layer by carefully digitizing each of the forest patches revealed by digital orthophotographies (scale 1:5000). This allowed us to calculate, for each sampling unit, the following variables representing the degree of landscape change: the percentage of forest cover, a measure of habitat availability and an inverse measure of habitat loss; the number of forest patches, a measure of habitat subdivision; and the density of forest perimeter, a measure of edge density. Moreover, we were interested in distinguishing to what extent the forest sampled was representative of the availability of mature, hardwood forest habitat, so, in March 2008, we performed field sampling to estimate the abundance of beech trees (*F.*

sylvatica) with DBH (diameter at breast height) > 30 cm in each sampling unit. A topographical map with level curves was incorporated as a layer into the GIS to build a Digital Elevation Model (DEM) with cell size of 50 m. This provided us with a value of elevation, slope and aspect interpolated for each sampling unit.

Primula vulgaris presence and abundance

In April-May 2007, during the peak of *P. vulgaris* flowering in the study site, we determined the presence/absence of this species in each sampling unit by carefully searching for individuals in a systematic zig-zag walk covering the whole surface. For those sampling units where the species was detected, we drew a schematic map of all *P. vulgaris* patches representing their size and spatial arrangement, individual patches being defined as those clumps of plants clearly separated from each other by more than 20 m. Field maps were then used to create a digitized layer of *P. vulgaris* cover in the GIS, from which we obtained the percent cover and the number of patches of *P. vulgaris* for each sampling unit. The percent cover of the species was calculated by summing the areas of every patch, and then relating this to the total area of the unit. Those patches of *P. vulgaris* extending over more than one sampling unit in the field were drawn as a single patch in the GIS layer, but subsequently broken into different patches to calculate the cover corresponding to each sampling unit. The usefulness of percentage of *P. vulgaris* cover as a measure of abundance was validated by previous abundance sampling in 75 units containing the species, which showed that this percentage was strongly positively correlated to the abundance of all individuals per sampling unit (Pearson correlation coefficient $r = 0.920$, $P < 0.0001$; $N = 75$). Thus, the percentage of cover of *P. vulgaris* was considered to be a surrogate for population size in further analyses, and the number of patches, a measure of population subdivision.

As a surrogate of both the abundance of neighbour seed sources and the degree of clumpiness of the population at a spatial scale intermediate between the population patch and the landscape, we have used the percentage of *P. vulgaris* cover in the neighbouring area. From the GIS we estimated this percentagefor each sampling unit, the neighbourhood being the area covered by the eight 50x50 m quadrats bordering the four sides of the targeted sampling unit. As *P. vulgaris* cover was exclusively sampled within the 100-ha extent, in those sampling units situated on the perimeter of the sample area, the percentage of *P. vulgaris* neighbouring cover was obtained from between 3 and 7 quadrats, depending on location. The smaller sampling extent of these peripheral units had a negligible effect on the representativeness of the percentage of cover of *P. vulgaris* in the neighbourhood (a comparison of *P. vulgaris* cover values provided by, respectively, the eight neighbouring quadrats *versus* five, randomly chosen, neighbouring quadrats, around 50 central sampling units, evidenced no statistical differences between sampling extents). A positive response of *P. vulgaris* presence or population size to the percentage of cover in the neighbouring area (i.e. units showing a larger abundance of seed sources in their periphery having a stronger probability of containing the species, or hosting larger abundances) would be indicative of significant dispersal constraints (for similar procedures see Svenning 2001; Svenning and Skov 2002).

***Primula vulgaris* population structure**

We were interested in estimating the demographic structure of *P. vulgaris* populations as a surrogate of the intensity of recruitment within the population. Therefore, in those units where the species was present, we set up a systematic sampling protocol. We examined the group of plants that was nearest to the centre of the sampling unit, and assigned the first one-hundred individuals to one of the following developmental stages, by size differences (rosette diameter) and other biological attributes (Valverde and Silvertown 1998; Endels et al. 2002b): 1) juveniles, i.e. immature plants without cotyledons and only one rosette of leaves (distinguished from vegetative adults with one rosette by means of size differences; an individual was considered an adult when its rosette diameter was similar to the average diameter of flowering adults in the same population); 2) vegetative adults, i.e. individuals without flowers and without cotyledons, often showing signs of overwintering leaves, and whose rosette diameter was comparable to that of reproductive adults in the same population; and 3) reproductive adults, i.e. plants showing one or more flowering stalks. Although present, we decided not to take into account individuals at the seedling stage (tiny individuals with cotyledons still present), owing to their low detectability. We considered that the proportion of juveniles relative to the total number of sampled individuals was a representative enough measure of the long-term cumulative demographic structure and recruitment potential of *P. vulgaris* in our site (see also Brys et al. 2003).

Morph imbalance in small populations negatively affects reproductive ability in this species (Endels et al. 2002a), so we wished to assess the effect of the proportion of floral morphs on demographic trends. To this end, we calculated the pin-thrum ratio as the quotient of the absolute difference between the number of pin and thrum individuals divided by the total number of flowering adults.

Statistical analyses

To analyse the response of *P. vulgaris* presence, abundance and population subdivision (response variables) to the predictor variables of landscape characteristics (landscape change and topographic variables) and dispersal constraints (*P. vulgaris* cover in the neighbouring area), we set up multiple regression models. We also performed a regression model with the proportion of *P. vulgaris* juveniles as response variable, and, as predictor variables, landscape characteristics, percentage of cover of the species (as a measure of abundance) and pin-thrum ratio. A combined stepwise multiple logistic regression was used for the model using presence, whereas combined stepwise multiple linear regressions were used for the rest of the models. The model for presence included all sampling units ($N = 400$) whereas the rest of the models were run exclusively with those units in which the species was present ($N = 120$).

Variation in habitat availability (in our case, the percentage of forest cover) through the landscape is known to inherently influence the patterns of variation of other landscape change measures such as fragment isolation and edge density (Fahrig 2003). Thus, to statistically remove the effect of forest cover in the remaining landscape change parameters, we fitted quadratic regression models considering the number of forest patches and the edge density as response variables and the percentage of forest cover as predictor variable. We then used the residuals of these regressions as predictor variables in the multiple regression models mentioned above (see similar procedures in Hargis et al. 1998; Villard et al. 1999), together with the percentage of forest cover. Furthermore, we were interested in distinguishing the effect of the forest cover accounted for by mature forest (i.e. beech) from that accounted for by secondary fringe forest dominated by other tree species (fleshy-fruited trees and hazel). Thus, we fitted the percentage of forest cover (response variable) to the abundance of beech (predictor variable) with a quadratic regression model. We then used the residuals of this model together with the abundance of beech in the multiple regression models rather than the raw percentage of forest cover. Prior to multivariate models, we checked for colinearity among the biological variables included as predictors (see Appendix A). If two predictors were strongly correlated ($r > 0.70$), only the one that best fitted (based on R^2 values) the response variable in univariate models was included in the multiple regressions.

Given the spatial structure of our sampling framework, the presence of spatial autocorrelation in the data may violate the assumption of independently distributed errors in the regression models (Legendre and Legendre 1998). As a consequence, the effects of explanatory variables might be exaggerated (Legendre et al. 2002). In order to identify, and control for the effect of large-scale spatial structures in the data base, we applied a Trend Surface Analysis (TSA, Legendre and Legendre 1998) that incorporated, as potential predictors in the linear models, spatial terms in the form of a third-order polynomial of the spatial Cartesian geographic coordinates X-Y of the centroid of the sampling units (extracted from UTM coordinates) and their cross-product terms. Moreover, the measure of cover of *P. vulgaris* in the neighbouring area incorporated in the models for evaluating the role of dispersal constraints was considered as a small-scale spatial autocorrelation term (Svenning 2001). Despite the incorporation of TSA and the cover of *P. vulgaris* in the neighbouring area in the models, we still checked for the presence of significant spatial autocorrelation in the residuals of all linear models by means of Moran's *I* correlograms (Legendre and Legendre 1998). Those linear models showing a significant spatial structure in their residuals were repeated by performing spatially explicit regression models (autologistic models and lagged autoregressions, Rangel et al. 2006) which incorporated additional spatial autoregressive terms accounting for spatial structures at all scales (see also Svening and Skov 2007).

We evaluated the fit of the models on the basis of Akaike's information criteria (AIC, Akaike 1973), which allows the comparison of models with different numbers of parameters. Prior to running regression models, data were transformed to achieve normality and reduce heterocedasticity (arcsine of square root for proportions, and ln(x+1) for the rest of the data). Statistical analyses were carried out with JMP 7.0.1 (SAS 2007) and SAM 3.0 (Rangel et al. 2006).

RESULTS

P. vulgaris presence, abundance and demographic structure

P. vulgaris was present in 120 of the 400 sampling units (30%), and where it was present its percentage cover ranged from 0.9 to 100% (mean value of 40.0 ± 2.5 SE). The number of *P. vulgaris* patches varied between 1 and 7 (mean value of 1.6 ± 0.1 SE). Pin-thrum ratio) ranged between 0 and 1 (mean value of 0.23 ± 0.02 SE). The proportion of juveniles varied between 0 and 0.81 (mean value of 0.31 ± 0.01 SE). The proportion of vegetative adults relative to the total number of adults ranged between 0 and 0.78 (mean value of 0.48 ± 0.01 SE). Figure 1.2 shows the variation of some of these parameters along the study area and their frequency distributions.

Response of *P. vulgaris* to landscape characteristics and dispersal constraints

The multiple logistic model explained ca. 63% of the variance of the presence of *P. vulgaris* in the study area (Table 1.1). The probability of occurrence increased with the percentage of cover of the species in the neighbouring area, beech abundance, forest cover of other trees and slope, and decreased with the number of forest patches within the sampling unit. Two of the TSA spatial terms (Y, Y^2) also had a significant positive effect on the probability of presence, indicating that *P. vulgaris* occurrence increased slightly moving northwards along the study site, whilst also showing a quadratic spatial trend, with larger occurrence probabilities at the centre of the study site (Table 1.1, Fig. 1.2). The importance of species cover in the neighbouring area and the TSA terms in this model suggested the existence of significant fine- and broad-scale spatial structures in our data. Despite the inclusion of these spatial parameters, we still detected a significant degree of spatial structure in the residuals of the multiple logistic model (significant Moran's *I* coefficients at several distance classes, data not shown). Therefore, the logistic model was repeated, incorporating a spatial auto-covariate term that accounted for this spatial autocorrelation, and this autologistic model showed a similar degree of fit, with all main effects remaining significant (Table 1.1). The one difference being that the effect of species cover in the neighbouring area was reduced in importance relative to landscape parameters (Table 1.1), suggesting that the importance of dispersal constraints on the presence of *P. vulgaris* was inflated by spatial autocorrelation in the database. In this spatially explicit model, the parameters related to forest habitat availability were revealed to be the main predictors.

	Logistic regression			Autologistic regression		
Independent variables	β	Wald χ^2	P	β	t	P
% cover *Pv* in the neighbourhood	5.64	26.49	< 0.0001	5.40	3.23	0.001
Nº beech trees	1.43	30.49	< 0.0001	1.43	5.52	< 0.001
% forest cover (other trees) [1]	2.83	17.52	< 0.0001	2.81	4.13	< 0.001
Nº forest patches [2]	-1.76	6.05	0.0139	-1.74	-2.42	0.015
Slope	6.35	8.18	0.0042	6.32	2.84	0.005
Y	8.94e-4	7.86	0.0051	< 0.001	2.61	0.009
Y^2	1.24e-6	9.46	0.0021	< 0.001	2.48	0.013
yW (spatial auto-covariate term)	-	-	-	0.955	0.19	0.847

[1] Residuals of the raw percentage of forest cover against the number of beech trees

[2] Residuals against the raw percentage of forest cover

Table 1.1: Summary of the best fit of the logistic and autologistic regression models for the presence of *P. vulgaris* (N = 400, R^2 = 0.633, $\chi^2 \geq 309$, $P < 0.0001$, for both models; df = 7 and 8, respectively). For each independent variable included in the models, the partial regression coefficients (β), and their associated statistics (Wald chi-square in logistic regression and *t*-value in autologistic) and significance levels (*P*-values) are shown.

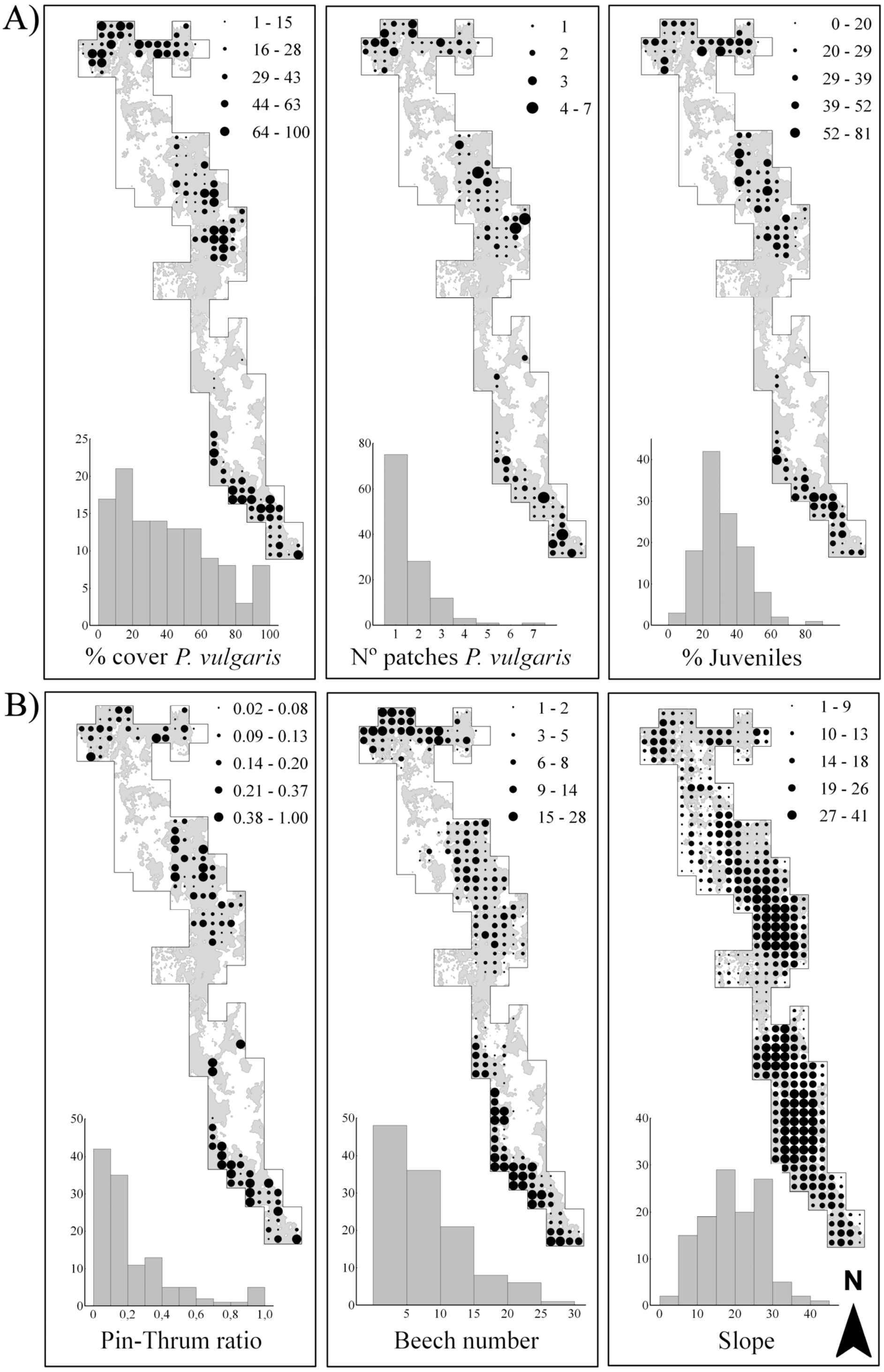

Figure 1.2: Raw data values for some response variables (A) and predictor variables (B) across the sampling area. Grey background represents forest cover. The magnitude of the variables is represented by the size of the black dots according to their respective ranges. No dots means that the value is zero. Each map is accompanied by the histogram of frequencies (no. of sampling units) of the corresponding variable.

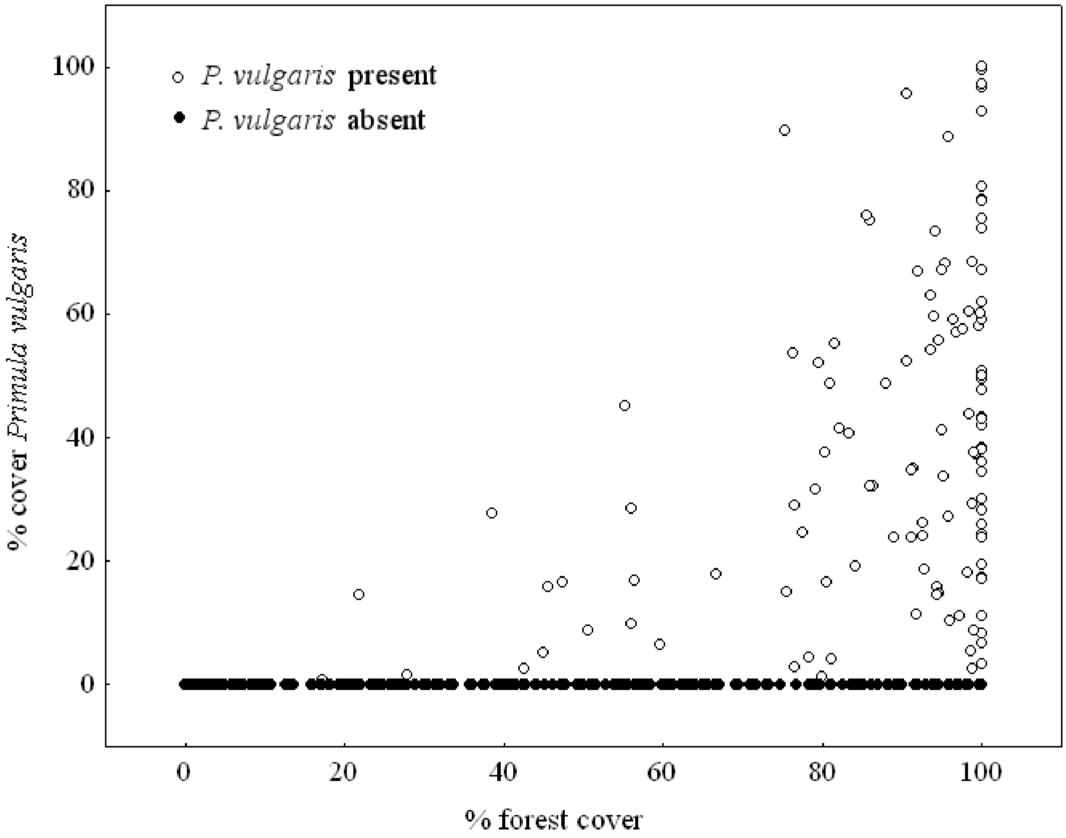

Figure 1.3: Percentage cover of *P. vulgaris* as a function of percentage of forest cover in the 400 sampling units.

The representation of the percentage of cover of *P. vulgaris* as a function of the amount of forest habitat revealed the absence of the species in sites having less than 20 % forest cover (Fig. 1.3). Moreover, sites with moderate and high values of forest cover showed either presence or absence of *P. vulgaris*, and great variation in its abundance. A multiple regression model showed that abundance (response variable) was significantly positively related to species cover in the neighbouring area as well as to total forest cover (regression coefficients, respectively, $\beta = 0.63$, $P < 0.0001$ and $\beta = 0.38$, $P = 0.0002$). This model explained ca. 28% of abundance variance ($N = 120$, df = 2, $F = 23.19$, $P < 0.0001$). Other landscape characteristics were unrelated to the abundance of *P. vulgaris*. The residuals of the regression model for cover in the neighbouring area and forest cover showed a random spatial pattern (data not shown), so no further spatially explicit analysis was performed. The model for population subdivision, with the number of *P. vulgaris* patches as the response variable, did not indicate a significant effect of any predictor variable.

A small amount of variance (9 %) of the proportion of *P. vulgaris* juveniles was accounted for by total forest cover (β = 0.18, *P* = 0.0007). The proportion of juveniles was lower in areas of low forest cover, but it was highly variable where higher levels of suitable habitat were available. No significant spatial autocorrelation was detected for the residuals of this model.

DISCUSSION

The aim of this work was to predict the presence, abundance and demographic structure of *P. vulgaris* as a function of continuous gradients of habitat loss and fragmentation, other landscape characteristics, and the spatial clumpiness of populations. The response of *P. vulgaris* to the availability of forest cover and to the number of forest patches indicated that this species responds to both habitat loss and habitat subdivision at the landscape scale. As judged by the degrees of fit and the number of landscape change parameters included in the regression models, landscape change effects were, nevertheless, stronger on presence than on abundance, abundance in turn suffering a stronger effect than demographic structure. This response to landscape change, however, does not mean that the species occupies all the potentially suitable remnant habitat. In fact, there was only a partial match between the spatial distribution of *P. vulgaris* and that of the potential forest habitat. This may happen because the species is not able to reach all remnant habitat, due to dispersal limitation or, alternatively, because some habitat sectors, despite colonization, are not suitable for the long-term persistence of the species.

Effects of forest loss and fragmentation on *P. vulgaris*

In the montane areas of the Cantabrian Range, *P. vulgaris* behaves as a strict forest species, being fully dependent on the presence of forest cover. As this species has also been found to occur in undisturbed, non-forested habitats in central Europe (Endels et al. 2002b), it seems that its requirements for forest conditions are indirect, and relatively unrelated to shade tolerance or vernal habit. In this sense, the avoidance of non-forest habitats in our site may relate to the low abundance of highly competitive graminoids on the forest floor (Jacquemyn et al. 2003), or to the lower risk of browsing and trampling damage by domestic cattle than in the pasture-heathland matrix (García and Ehrlén 2002, Leimu et al. 2002, both with *P. veris*).

We found a positive response of *P. vulgaris* presence, abundance and demographic structure to forest habitat availability, suggesting habitat loss has a pivotal role as a major driver of negative landscape change effects. This agrees with previous research that suggested a correlation between habitat loss and decreased population viability, conditioned by the biased flower morph ratios, and hence reduced seed production, in small populations (Brys et al. 2004; Endels et al. 2002a, b). This does not, however, seem to be the case for our populations, in which no effect of morph imbalance was detected and thus, we would expect a direct link between habitat loss and actual population size.

In relation to habitat availability, our results suggest the existence of a critical amount of forest cover (ca. 20%) below which *P. vulgaris* seems unable to occur (Fig. 1.3). This cover value is notably similar to the theoretical threshold below which the effects of landscape change become exponential, a result of the emergence of the disrupting effects of habitat subdivision (Fahrig 2003). In fact, our study also shows a negative effect of habitat subdivision on the presence of *P. vulgaris*, although weaker than that of habitat loss. Conversely, we failed to detect any potential independent edge effect, as none of the species parameters measured were affected by edge density. This contrasts with previous studies demonstrating a clear negative response of other perennial herbs to the proximity of forest edges (e.g. Jules 1998; Lienert and Fischer 2003). These contrasting results may be partially explained by the scale differences between studies (small-scale distance to the edge gradient vs. the large-scale landscape gradient considered in our study). Thus, there is a need for complementary multi-scaled approaches enabling the interpretation of edge effects within a landscape context (Ewers et al. 2007).

Our results suggest that the effects of landscape change were not equally strong for all of the ecological traits analyzed: there was a decrease in the magnitude of landscape change effects, from presence to abundance to demography. This difference could be partially attributable to sampling effects, namely, a smaller sample size and a narrower gradient of sampled landscape in the models for abundance and demography relative to the presence model. In addition, we found that the proportion of juveniles was low in areas of low forest cover, but along a broad portion of the gradient of habitat availability it was highly variable. This suggests that small-scale environmental factors and stochasticity, not detected by our sampling grain, may be accounting for a large proportion of the variability in the abundance and the demographic structure of *P. vulgaris*. For example, it is known that the demography of *Primula* sp. depends on the presence of small gaps in the forest canopy (Valverde and Silvertown 1995, 1998), as well as on ground-level disturbance (Ehrlén et al. 2005).

Forest availability and habitat suitability

In our study site, *P. vulgaris* only occupied a part of its potential distribution area, as judged by the distribution of the fragmented forest cover (Figs. 1.2 and 1.3). The species only appeared when forest cover was above 20%, but there were also many sites with moderate or high levels of forest cover in which it was absent or very scarce.

Incorporation in the analytical models of a term explicitly representing the degree of clumpiness of the populations suggests that dispersal constraints have an important effect on habitat occupancy, irrespective of the increased dispersal limitations imposed by habitat subdivision. In other words, as evidenced for other perennial herbs of temperate and boreal forests (Primack and Miao 1992; Ehrlén and Eriksson 2000), *P. vulgaris* cannot establish in many forested sites because seeds are not able to reach and colonize them. In fact, the dispersal mode (barochory and/or myrmecochory) of this species probably prevents seeds from being deposited more than a few metres away from the mother plant (Valverde and Silvertown 1995). Long distance dispersal events carried out by ungulates have been demonstrated in other perennial herbs (Vellend et al. 2006), but, if they exist at all, seem to be very rare in the case of *P. vulgaris*, judging by the aggregated structure of the populations at the landscape scale. At the same time, dispersal limitation is expected to inhibit the filling of potentially suitable habitats even in a scenario of progressive recovery of historically fragmented forest habitats, as currently happens in many forest landscapes of Europe (Honnay et al. 2005). In such a case, the distribution of herbs sensitive to habitat loss and fragmentation may in fact represent the distribution of suitable habitat at the moment of lowest forest availability (Helm et al. 2006; Cousins et al. 2006). Our results suggest, however, that this was not the case of *P. vulgaris* in the Cantabrian Range, since it was equally affected by the availability of mature forest as by the availability of secondary-growth and fringe forest.

This study also suggests some effect of establishment limitation, in addition to dispersal constraints, on the partial occupancy of the fragmented forest by *P. vulgaris*. In other words, low habitat quality in some sections of the landscape may prevent population establishment, despite the presence of viable seeds. In this sense, the significant effect of other landscape characteristics, namely the slope, in the species' occurrence was indicative of habitat suitability playing such a role. We may expect a direct, positive effect of slope on forest suitability if steep areas are less frequented by natural enemies of this species, such as domestic and wild ungulates (enemy-free-sites hypothesis, Haig et al. 2000). Steep slopes may also exert an indirect, positive effect by enhancing dispersal and concomitant colonization and persistence: the tiny *P. vulgaris* seeds (mean weight in mg from sample of seeds from our study area is 0.81 ± 0.02 SE) may have some degree of secondary dispersal by wind, down-hill rolling or dragging by superficial water (Oshawa et al. 2007). Finally, although our regression models evidenced an effect of slope independent of the role of landscape change, there may also be some indirect effect accounted for by the correlation between forest cover and slope, as less altered forests occur in steeper areas which are inherently more difficult to exploit from a human perspective, (Fig. 1.2, García et al. 2005b, see also Silva et al. 2007).

Concluding remarks

This work provides evidence that dispersal constraints and some landscape characteristics that determine habitat suitability are almost as important as forest loss and fragmentation in determining the landscape-scale distribution of *P. vulgaris* in the Cantabrian Range. This is equivalent to acknowledging that landscape change is a spatially non-random process and that not all fragmented forest habitat is suitable for this perennial herb. Moreover, it illustrates the advantages of applying a continuum landscape view to explain plant response to landscape change, compared to other approaches relating life-history traits and dispersal syndromes to the response to landscape alterations (e.g. Hewitt and Kellman 2002; Kolb and Diekmann 2004; Kunstler et al. 2007). Firstly, the continuum landscape approach highlights the fact that plants are affected by the continuous gradients of landscape modification caused by different, although simultaneous, alteration processes. Secondly, it enables the incorporation and explicit evaluation of the relative role of the *Umwelt*, or perceptual landscape, of plant species in fragmented scenarios. In our case, we propose that the *Umwelt* of *P. vulgaris* in Cantabrian fragmented landscapes was represented, primarily, by dispersal ability, since seed dispersal determined the range of environmental heterogeneity actually perceived by the plant, and, complementarily, by topography, which may determine to some extent the persistence by fostering establishment limitations. In summary, by looking at the landscape as spatial and environmental continua, and by discerning the relative roles of landscape change processes, dispersal constraints and habitat quality, the continua landscape approach overcomes the weakness of classic landscape change models and proves itself to be a more robust and integrative tool for predicting future plant responses to human-caused landscape degradation.

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1b Modelos de cambio en el paisaje: de la biogeografía de islas a la aproximación de paisaje continuo

Valdés, A. (*en prensa*). Modelos de paisaje y análisis de fragmentación: de la biogeografía de islas a la aproximación de paisaje continuo. *Ecosistemas*.

ABSTRACT

The study of landscape change, and the management of the environmental problems that it leads to, requires conceptualizing landscapes in a realistic way. This entails not only establishing theoretical frames representing species loss and collapse of ecological processes in habitat loss and fragmentation gradients, but also representing these gradients adjusted to real-world landscapes and to the heterogeneity in the response capacity of organisms. In this article I revise, from an historical perspective, the different models utilized for the analysis of landscape change. These include pattern-based models, as the model based on island biogeography theory, the patch-corridor-matrix model and the variegated landscape model, and process-based models, as the recently proposed continuum landscape model. I illustrate the utility of this last model with the case of *Primula vulgaris* in fragmented forests of the Cantabrian Range. I discuss the applicability of the different models for the study of landscape change, and finally I highlight the integrative capacity of the continuum model, as it allows to simultaneously evaluate the effects of different landscape change processes, other environmental features and life-cycle traits, giving a more complete view of species' response to habitat alteration than previous models.

RESUMEN

El estudio del cambio en el paisaje, y la gestión de los problemas ambientales que este proceso acarrea, requiere conceptualizar el paisaje de forma realista. Esto conlleva no sólo establecer marcos teóricos que representen la pérdida de especies y el colapso de los procesos ecológicos en los gradientes de pérdida y fragmentación de hábitat, sino también representar dichos gradientes ajustados a los paisajes del mundo real y a la heterogeneidad en la capacidad de respuesta de los organismos. En este artículo se repasan, desde una perspectiva histórica, los distintos modelos de paisaje utilizados para el análisis del cambio en el paisaje. Estos incluyen modelos basados en patrones, como el modelo basado en la teoría de biogeografía de islas, el modelo de parche-corredor-matriz y el modelo de paisaje abigarrado, y modelos basados en procesos, como el recientemente propuesto modelo de paisaje continuo. Se ejemplifica la utilidad de éste último modelo con el caso de *Primula vulgaris* en bosques fragmentados de la Cordillera Cantábrica. Se discute la aplicabilidad de los diferentes modelos para el estudio del cambio en el paisaje, y finalmente se pone de manifiesto la capacidad integradora del modelo continuo, que permite evaluar simultáneamente los efectos de diferentes procesos de cambio en el paisaje, otras características ambientales y rasgos del ciclo de vida de las especies, proporcionando una visión más completa de la respuesta de las especies a la alteración de su hábitat que modelos anteriores.

INTRODUCCIÓN

La investigación en pérdida y fragmentación de hábitats es desde hace años uno de los campos más desarrollados dentro de la biología de la conservación (Fazey et al. 2005), ya que este proceso está afectando a la biodiversidad a nivel mundial (Sala et al. 2000). Los cambios en el paisaje por acción humana dan lugar a la división progresiva de un hábitat *a priori* relativamente continuo en un conjunto de fragmentos aislados y de menor tamaño, que quedan embebidos en una matriz de hábitat degradado, cualitativamente muy diferente al original (Saunders et al. 1991). En realidad, el cambio en el paisaje es un fenómeno complejo que engloba tres procesos simultáneos e interdependientes de alteración, debido a los cuales se incrementa el riesgo de extinción de las poblaciones de los hábitats originales: (1) La continua reducción de la superficie de los fragmentos origina una pérdida de hábitat que puede dar lugar a reducciones directas de los tamaños poblacionales. Esto implica un aumento de la estocasticidad demográfica y ambiental que puede inducir al colapso demográfico (Turner 1996); (2) La separación progresiva de los fragmentos de hábitat conduce al aislamiento creciente de las poblaciones que albergan, con lo que disminuye la capacidad de dispersión (Fahrig y Merriam 1994), y se reducen de forma indirecta los tamaños de población; (3) Los efectos de borde, resultantes del incremento de la relación perímetro/superficie de los fragmentos, consisten en cambios en las condiciones biológicas y físicas en las zonas cercanas a los límites de los fragmentos, y pueden alterar los ciclos de vida de las especies que viven en ellos (Murcia 1995). Estos tres procesos están interrelacionados, y en general la subdivisión del hábitat y los efectos de borde son mayores en áreas con disponibilidad de hábitat intermedia (Fahrig 2003).

La complejidad que suponen los cambios en el paisaje requiere llevar a cabo una modelización realista, que sea capaz de integrar los diferentes procesos y las relaciones existentes entre ellos, junto con la diversidad de esquemas de alteración que aparecen en los paisajes del mundo real. Además, hay que tener en cuenta que los diferentes organismos pueden tener respuestas muy distintas frente al proceso de cambio paisajístico, dependiendo de su capacidad para percibir las alteraciones en el paisaje, que está condicionada por los rasgos particulares de su ciclo vital (Solon 2005). En este artículo se repasan los diferentes modelos conceptuales de cambio en el paisaje que han sido propuestos hasta el momento, evaluando su capacidad para representar los distintos paisajes alterados y las respuestas de las diferentes especies. Se señalan las ventajas de cada modelo con respecto a los anteriores, y se ejemplifica la utilidad del más reciente con un estudio sobre los efectos del cambio en el paisaje en una planta herbácea forestal.

MODELOS CONCEPTUALES DE PAISAJE

Modelo de islas

El *modelo de islas* (Fig. 1.4A) está basado en la teoría de biogeografía de islas (MacArthur y Wilson 1967), que extrapola el concepto de "insularidad" a todos los hábitats naturales que son disgregados debido a la influencia antrópica. La teoría de biogeografía de islas ha tenido un gran impacto en ecología y biología de la conservación (por ejemplo, para el diseño de reservas, Higgs 1981), estimulando en gran medida la investigación sobre fragmentación de hábitats.

Este modelo considera a los parches de hábitat fragmentado como *islas* embebidas en un *mar* constituido por hábitat inhóspito, denominado generalmente *matriz*. La matriz es considerada como un medio totalmente hostil para todos los organismos. Además, este modelo propone una transición clara y abrupta entre esta matriz y los parches remanentes de hábitat, y supone que las condiciones ambientales previas al cambio paisajístico son homogéneas, al igual que las existentes dentro de los parches. Esta uniformidad espacial lleva implícita la existencia de una consistencia temporal; es decir, se ignora la existencia de fluctuaciones temporales en las poblaciones que puedan hacer variar su distribución dentro del paisaje fragmentado.

Modelo de parche-matriz-corredor

Este modelo (Fig. 1.4B) es en realidad una extensión del *modelo de islas*, ya que incorpora el concepto de corredor a la concepción binaria de "hábitat adecuado" frente a "matriz inhóspita" propuesta por el modelo de islas. Sin embargo, el *modelo de parche-matriz-corredor* no se centra tanto en las diferencias en riqueza de especies, sino sobre todo en la configuración geográfica del paisaje fragmentado. Considera también que puede existir cierta heterogeneidad en la matriz, aunque no se le da gran importancia a este factor.

En este modelo, el paisaje fragmentado se considera compuesto por estos tres elementos discretos. Según Forman (1995), cada punto de un paisaje está situado dentro de un *parche*, de un *corredor* o de la *matriz*. Los parches son áreas de hábitat original que pueden tener diferentes tamaños y formas. Los corredores son elementos lineales de hábitat que conectan parches y pueden variar en longitud y anchura. Los parches y corredores están embebidos en una matriz que puede tener distinta extensión.

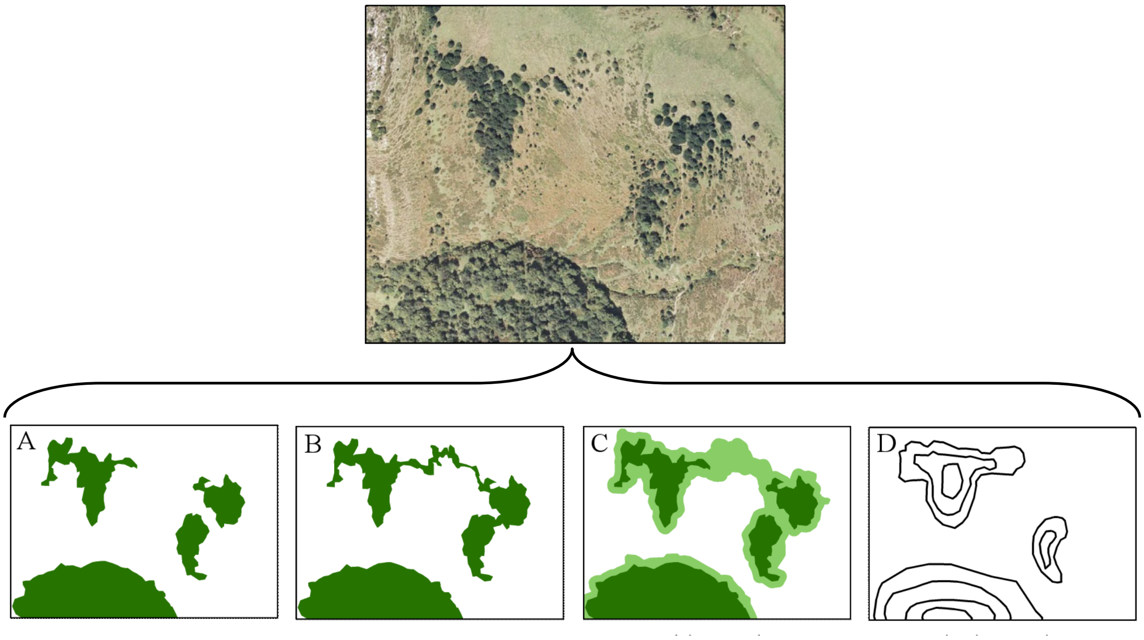

Figura 1.4: Interpretación de un mismo paisaje fragmentado mediante los cuatro modelos conceptuales de cambio en el paisaje existentes: (a) modelo de islas; (b) modelo de parche-matriz-corredor; (c) modelo de paisaje abigarrado; (d) modelo continuo.

Modelo de paisaje abigarrado

En general, la mayoría de los paisajes fragmentados que observamos en el mundo real no se ajustan a la concepción binaria de “hábitat” y “no-hábitat” que proponen los modelos anteriores, en los que las transiciones entre los diferentes elementos del paisaje se definen como abruptas, y la influencia de la matriz es ignorada. Los modelos anteriores asumen también que las comunidades que viven en los fragmentos de hábitat están únicamente influidas por las presiones opuestas de colonización y extinción local, sin tener en cuenta la influencia de la matriz circundante, que puede dar lugar a diversos fenómenos físicos y biológicos asociados con cambios en las condiciones abióticas y bióticas en las zonas periféricas de los fragmentos (“efectos de borde”, Murcia 1995). Los efectos de borde muestran una clara relación con la pérdida de hábitat, e introducen nuevos factores a tener en cuenta al analizar un paisaje fragmentado, como la forma del fragmento (formas más irregulares implican una mayor relación perímetro/área y por tanto la influencia del borde será más acusada, Ewers y Didham 2007). La propia naturaleza de la matriz también es ignorada por los modelos anteriores, que suponen que las consecuencias del cambio en el paisaje son independientes del tipo de matriz (urbana, agrícola, etc.) que rodea a los fragmentos. Sin embargo, los diferentes tipos de matriz ofrecen distinta resistencia a la dispersión de los organismos (Ricketts 2001, Tischendorf y Fahrig 2000), determinando el grado de aislamiento efectivo de los fragmentos de hábitat, que no depende sólo de la distancia existente entre ellos, sino también de la resistencia o permeabilidad de la matriz a la dispersión de los organismos (Herrera, en prensa).

El modelo de *paisaje abigarrado* (variegated lanscape, *sensu* McIntyre y Barrett 1992, Fig. 1.4C) propone que el paisaje fragmentado está formado por un mosaico de hábitats que representan distintos grados de modificación con respecto a la situación original, generando gradientes de adecuación de hábitat. Por lo tanto, la matriz puede presentar distinto grado de permeabilidad para los diferentes organismos; es decir, puede no representar una barrera, sino ser utilizada en mayor o menor grado dependiendo de la especie considerada y la escala a la que dicha especie utilice el ambiente. Este modelo tiene en cuenta también pequeños elementos de hábitat, como árboles aislados en el caso de paisajes forestales fragmentados (Fischer y Lindenmayer 2002), que serían probablemente incluidos dentro de la matriz en los modelos de islas y parche-matriz-corredor, y que podrían servir como “piedras de paso” para facilitar el movimiento de los organismos dentro del paisaje, incrementando la permeabilidad de la matriz. En relación a las limitaciones a la hora de que el modelo de paisaje represente la percepción de distintas especies, McIntyre y Barrett (1992) propusieron identificar grupos de especies con requerimientos de hábitat comunes, como alternativa intermedia entre considerar la respuesta al cambio en el paisaje de toda la comunidad o de cada una de las especies por separado. Más tarde, McIntyre y Hobbs (1999) propusieron un marco conceptual en el que se incorpora una componente temporal a los cambios en el paisaje, distinguiéndose cuatro estados secuenciales situados a lo largo de un continuo de destrucción del hábitat: intacto, abigarrado, fragmentado y relicto (Fig. 1.5). Estos estados se combinan luego con gradientes de modificación del hábitat remanente, que dependen también en cierta medida del grado de destrucción del hábitat (generalmente, en los hábitats fragmentados y relictos el grado de modificación interna del hábitat remanente es mayor que en los intactos y abigarrados). Estos autores dan un primer paso en la visión del paisaje como un continuo de destrucción y degradación del hábitat original. También sugieren que la interpretación del paisaje que realizan las diferentes especies puede ser muy diferente del punto de vista humano; por ejemplo, un paisaje que nosotros visualizamos como fragmentado puede ser percibido como relativamente continuo por especies con mucha movilidad o capacidad de dispersión.

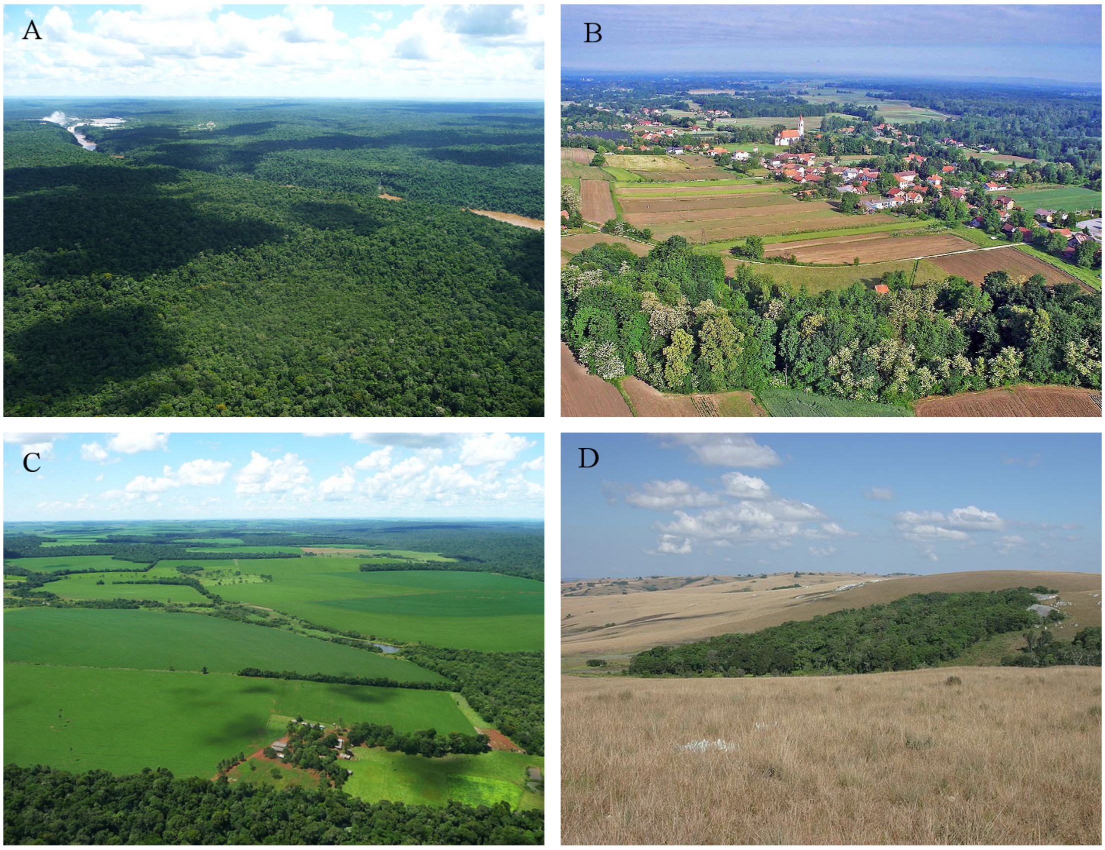

Figura 1.5: Ejemplos de los cuatro estados de alteración del paisaje descritos por McIntyre y Hobbs (1999): (a) selva intacta cerca de las cataratas del Iguazú, Argentina; (b) paisaje abigarrado con bosques y campos de cultivo en Razkrižje, Eslovenia; (c) bosques fragmentados para plantaciones en Brasil; (d) parche relicto de bosque montano en la meseta de Nyika, Malawi. (a) y (c): fotografías de dominio público. (b): Vojko Prah. (d): Dr. Thomas Wagner, Environmental and Agricultural Consulting and Research, bajo licencia CC-BY-SA 3.0 Unported.

Modelo de paisaje continuo

Todos los modelos anteriores asumen implícitamente que una misma clasificación de los patrones paisajísticos puede ser válida para todas las especies, pero es bien sabido que muchos organismos no perciben el paisaje de la misma forma (Lindenmayer et al. 2003). El modelo de continuo temporal y espacial propuesto por McIntyre y Hobbs (1999) propone la existencia de diferencias entre grupos de especies en cuanto a requerimientos de hábitat. Sin embargo, la definición de los gradientes de paisaje y de los estados de destrucción del hábitat se sigue haciendo en último término desde el punto de vista humano, basándose en los patrones físicos del paisaje, y sin tener en cuenta los procesos que generan las distribuciones reales de los organismos o los rasgos específicos que influyen en la percepción del paisaje por distintos organismos. Sin embargo, existe la necesidad de considerar la visión que cada especie tiene del paisaje fragmentado y de integrar en los modelos conceptuales rasgos del ciclo de vida de los organismos que puedan determinar esta percepción.

Recientemente el modelo de paisaje continuo (*Continua* and *Umwelt*, Manning et al. 2004b; modelo continuo, Fischer y Lindenmayer 2006, Fig. 1D) ha sido propuesto para paliar estas deficiencias. Fischer et al. (2004) habían resaltado previamente la utilidad de conceptualizar el paisaje por medio de una superposición de mapas de contornos que representaran la adecuación del hábitat para cada especie en concreto, teniendo en cuenta las diferentes escalas espaciales de percepción y respuesta al paisaje. Este modelo engloba la definición del continuo paisajístico presentada por McIntyre y Hobbs (1999), pero incorpora también el concepto de *Umwelt* (von Uexküll 1926). El *Umwelt* se refiere a la percepción y respuesta individual de cada especie, no sólo frente al gradiente continuo de hábitat sino también frente a otros gradientes de factores ambientales que influyen en procesos biológicos, y teniendo en cuenta la escala espacial y temporal de percepción de cada organismo. Así, además de los gradientes de hábitat, Fischer y Lindenmayer (2006) consideran en concreto los gradientes de alimento, refugio, espacio y condiciones climáticas, ya que estos factores están estrechamente ligados a procesos ecológicos, y por lo tanto deberían estar relacionados con los patrones de distribución de las especies. Las variables respuesta utilizadas en los modelos estadísticos basados en este modelo conceptual están generalmente relacionadas con la especie individual, más que con la riqueza de especies de la comunidad, como ocurría en los anteriores modelos.

APLICACIÓN DEL MODELO DE PAISAJE CONTINUO AL ESTUDIO DE LA RESPUESTA AL CAMBIO EN EL PAISAJE DE *PRIMULA VULGARIS* EN LA CORDILLERA CANTÁBRICA

Para estudiar la respuesta de la planta forestal perenne *Primula vulgaris* al proceso de pérdida y fragmentación del bosque en la Cordillera Cantábrica, utilizamos una aproximación basada en el modelo de paisaje continuo (Capítulo 1a). Esta conceptualización nos permitió evaluar el efecto de los distintos procesos asociados al cambio paisajístico, junto con otros factores que representan la percepción que la especie tiene del paisaje (gradientes topográficos y restricciones a la dispersión), en la presencia, la abundancia y la estructura demográfica de la especie. La elección de esta especie fue debida a que en general, las plantas perennes tienen requerimientos de hábitat específicos (Dupré y Ehrlén 2002), son susceptibles a la pérdida de hábitat y a los efectos de borde (Jules y Rathcke 1999; Honnay et al. 2002), y tienen una dispersión muy restringida incluso dentro del hábitat forestal (Honnay et al. 2005). Por lo tanto, es esperable que la pérdida y fragmentación del hábitat les afecte de forma negativa.

El estudio se realizó en la Sierra de Peña Mayor (cordillera Cantábrica), una zona que ha sido deforestada desde tiempos históricos (García et al. 2005b) y en la que actualmente encontramos bosques altamente fragmentados, con dominancia de una matriz de pastos (75 % de cobertura), formando un paisaje de tipo abigarrado (según McIntyre y Hobbs 1999). Consideramos una superficie de 100 ha, que dividimos en 400 unidades de muestreo (cuadrados de 50x50 m), y construimos un Sistema de Información Geográfica (SIG) en el que incorporamos capas con la digitalización de la cobertura forestal y de la cobertura de *P. vulgaris*, además de un Modelo Digital de Elevaciones (MDE). Para cada unidad de muestreo, obtuvimos tres variables descriptoras del proceso de fragmentación: a) el porcentaje de cobertura forestal (como medida de disponibilidad de hábitat y medida inversa de pérdida de hábitat), b) el número de rodales forestales (como medida de la subdivisión del hábitat), y c) la longitud de perímetro de bosque (como medida de la cantidad de borde). Obtuvimos también variables topográficas para cada unidad de muestreo (elevación, pendiente y orientación). La presencia o ausencia de *P. vulgaris* fue determinada en cada unidad de muestreo, y su abundancia estimada mediante el porcentaje de cobertura de la especie. Además, calculamos su cobertura en el entorno formado por los 8 cuadrados que rodean a cada unidad de muestreo, y la utilizamos como medida de la abundancia de fuentes de semillas adyacentes; una respuesta positiva de la presencia o abundancia de *P. vulgaris* a esta variable nos indicaría la existencia de restricciones a la dispersión (Svenning 2001; Svenning y Skov 2002). Por último, en las unidades con presencia de la especie realizamos un muestreo aleatorio de 100 individuos que se clasificaron como *juveniles*, *adultos vegetativos* o *adultos reproductores* basándose en diferencias de tamaño, presencia de elementos reproductores y otros atributos biológicos. Como medida de la estructura demográfica, obtuvimos la proporción de juveniles relativa al total de individuos muestreados (Brys et al. 2003). Mediante modelos de regresión múltiple, evaluamos la respuesta de la presencia, abundancia y estructura demográfica de *P. vulgaris* a las características del paisaje (variables de fragmentación y topográficas) y a las restricciones a la dispersión (cobertura en el entorno). Utilizamos una regresión logística en el caso de la presencia, y regresiones lineales en el caso de la abundancia y estructura demográfica.

Los resultados de los análisis indicaron que la presencia de la especie se incrementa con la disponibilidad de hábitat forestal y, en menor medida, disminuye cuanto mayor es el número de parches forestales (es decir, cuanto más subdividido está el hábitat). Esto nos indica que la especie responde sobre todo a la pérdida, pero también a la subdivisión del hábitat a escala de paisaje, independientemente de la pérdida de hábitat. Estos efectos fueron más acusados con la presencia de la especie que con su abundancia o estructura demográfica, que quizás estén más influidas por otros factores ambientales que actúan a una escala espacial más fina. El efecto de la cobertura de la especie en el entorno fue positivo y, al menos en el caso de la presencia, similar en importancia al de las variables de fragmentación. Por eso, a pesar del fuerte efecto ejercido por la cantidad de hábitat, la especie no ocupa todo el hábitat disponible, ya que hay zonas de alta cobertura forestal en las que no está presente. Esto puede deberse a que no es capaz de alcanzar todo el hábitat remanente, dada su limitación a la dispersión. Sin embargo, también puede ocurrir que algunos sectores de paisaje, a pesar de poder ser colonizados, sean inadecuados para la persistencia de la especie, y que su establecimiento se vea limitado en estas zonas debido a la baja calidad del hábitat. La presencia de estas limitaciones al establecimiento se pone de manifiesto mediante el efecto positivo de la pendiente topográfica en la presencia de la especie: las áreas más escarpadas pueden representar sitios más "seguros" para la planta, por ejemplo, debido a que son de difícil acceso para los herbívoros. Este desajuste entre la distribución de la especie y la distribución del hábitat fragmentado se refleja en la Figura 1.6, donde se representa, en forma de gradiente, la probabilidad de presencia que predice el modelo de regresión logística para el área muestreada, superpuesta a la distribución de la cobertura forestal. La probabilidad de presencia se calcula a partir de la ecuación extraída del modelo logístico, en la que están incluidas todas las variables con un efecto significativo sobre la presencia. Este patrón, donde la distribución predicha de la especie coincide sólo parcialmente con la de su hábitat, es una consecuencia directa de la aplicación del modelo de paisaje continuo, mediante el cual la distribución se explica en base a otros factores, además de las características del paisaje alterado. En este caso, la ausencia de la planta de muchas zonas potencialmente adecuadas en cuanto a cantidad de hábitat (Fig. 1.6) se debe a características propias del *Umwelt* de esta especie, representado por su limitada capacidad de dispersión y por su dependencia de características topográficas. Las zonas de cobertura elevada y baja probabilidad de presencia de la especie en la Figura 1.6 corresponderán con zonas donde la especie no ha sido capaz de dispersarse, o bien donde el hábitat es de baja calidad debido a sus características topográficas.

La utilización del modelo de paisaje continuo en este estudio supone ventajas frente a otros modelos que sólo tienen en cuenta patrones de paisaje para explicar la respuesta de los organismos a la pérdida y fragmentación del hábitat, y que nos ofrecerían solamente una visión parcial de la respuesta de *P. vulgaris* ante los cambios paisajísticos. Además, consideramos que este marco conceptual puede ser adecuado para estudiar la respuesta de otras especies de plantas forestales ante el proceso de cambio en el paisaje, ya que todas ellas comparten características de su ciclo biológico (sobre todo en cuanto a la limitada capacidad de dispersión) y tienen similares requerimientos de hábitat (Honnay et al. 2005).

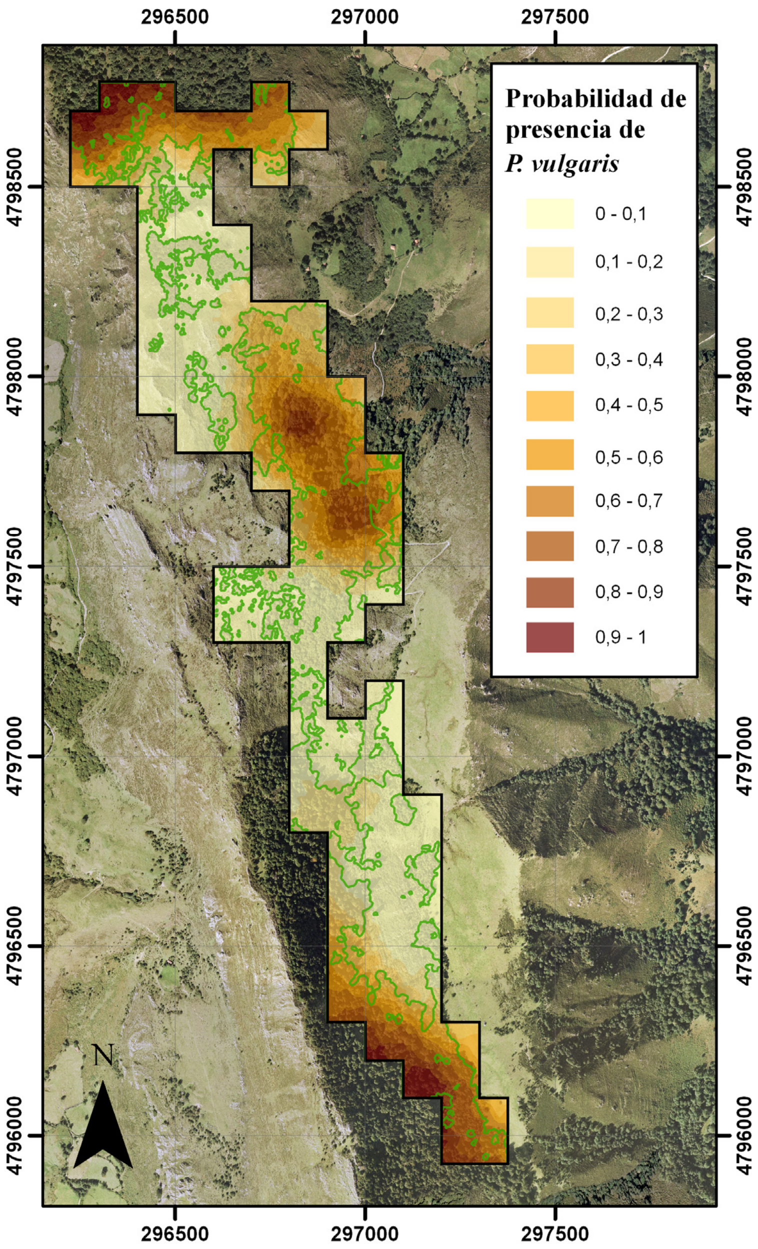

Figura 1.6: Ortofotografía de la zona de estudio y modelo de predicción de presencia de *Primula vulgaris*. El área de muestreo (100 ha) aparece delimitada en negro. El gradiente de color representa la probabilidad de presencia de *P. vulgaris* extraída mediante una regresión logística. La cobertura forestal dentro del área de muestreo está delimitada en verde.

UTILIDAD DE LOS DIFERENTES MODELOS Y GENERALIZACIÓN EN LA APLICACIÓN DEL MODELO CONTINUO COMO BASE CONCEPTUAL EN LOS ESTUDIOS DE CAMBIO EN EL PAISAJE

Los diferentes modelos conceptuales anteriormente expuestos se han aplicado para estudiar una gran variedad de paisajes alterados. Sin embargo, el enfoque de estos estudios ha sido diferente según el modelo utilizado, y la cantidad de trabajos que lo aplican es menor cuanto más recientemente se ha propuesto el modelo. El *modelo de islas* ha sido aplicado (implícita o explícitamente) en gran cantidad de estudios observacionales, y en la mayoría de los estudios experimentales sobre perdida y fragmentación de hábitat (revisados en Debinski y Holt 2000). En muchos casos se han comparado fragmentos de distintos tamaños y/o distinto grado de aislamiento en cuanto a riqueza de especies (Stouffer y Bierregaard Jr 1995), abundancia de individuos (Collins et al. 2009), estructura demográfica (Bruna y Kress 2002), interacciones interespecíficas (Goverde et al. 2002), reclutamiento (Cordeiro y Howe 2001), etc. No obstante, la investigación actual sobre pérdida y fragmentación de hábitat tiende a ir más allá de este modelo (Laurance 2008). El *modelo de parche-matriz-corredor* se ha utilizado en numerosos estudios centrados en el papel de los corredores biológicos (ver revisión de Haddad y Tewksbury 2006) y de varios trabajos donde se investiga el papel de los setos como corredores (revisados en Davies y Pullin 2007). El *modelo de paisaje abigarrado* ha sido la base de muchos trabajos que han resaltado la importancia de la matriz (Manning et al. 2004a; Fischer et al. 2005) y sus características (Rodewald 2003; Watson et al. 2005; Umetsu y Pardini 2007), así como de otros elementos del paisaje, como árboles aislados (Manning et al. 2004a), aspectos que fueron básicamente ignorados por los modelos anteriores. El *modelo de paisaje continuo* ha sido aún poco utilizado. Los estudios que lo han aplicado (e.g. González-Varo et al. 2008; Lees y Peres 2008; Deconchat et al. 2009; González Varo 2010) se han centrado sobre todo en la evaluación de la respuesta de la distribución y abundancia de aves frente a entornos fragmentados. Sin embargo, este modelo tiene un elevado potencial para ser aplicado en el estudio de los efectos del proceso de cambio paisajístico en otros tipos de organismos.

El modelo de islas, el modelo de parche-matriz-corredor y el modelo de paisaje abigarrado se agrupan generalmente bajo el término *modelos basados en patrones*. El modelo de paisaje continuo, por el contrario es un *modelo basado en procesos* que pueden afectar a cada especie diferencialmente. Los modelos basados en patrones tratan de reducir la complejidad que supondría analizar la respuesta de cada especie por separado. Aunque es necesario cierto grado de simplificación de la realidad para llevar a cabo estudios en paisajes fragmentados, en algunos casos este tipo de modelos consideran patrones ecológicos demasiado sencillos, suponiendo que ciertos parches (definidos como “hábitat” desde el punto de vista humano) son adecuados para todas las especies que coexisten en un paisaje. Estos modelos pueden mejorarse evaluando la respuesta de grupos concretos de especies de acuerdo con su utilización del paisaje modificado: en hábitats forestales fragmentados se ha hablado frecuentemente de "especies de interior de bosque", "especies de borde" y "especies generalistas" (Urbina-Cardona et al. 2006); o bien se han clasificado los parches de hábitat en "fuentes", que proporcionan dispersantes y "sumideros", donde la mortalidad supera a la reproducción (Pulliam et al. 1992).

El modelo de paisaje continuo no está basado en patrones de paisaje, sino en los procesos que dan lugar a las distribuciones de especies concretas. Sin embargo, llevar a cabo la evaluación de los efectos concretos de la pérdida y fragmentación de hábitat en todas y cada una de las especies existentes en un paisaje es, en la mayor parte de los casos, inabarcable. Una manera de llevar a cabo cierta generalización es agrupar especies diferentes que representen respuestas comunes a gradientes ambientales, y analizar así la distribución de "grupos" de especies. Por ejemplo, se puede evaluar la respuesta al cambio paisajístico de grupos de especies con requerimientos de hábitat similares, como pájaros forestales (McGarigal y McComb 1995), o con los mismos requerimientos tróficos, como insectos del suelo (Golden and Crist 2000). Así, definiríamos una especie de "*Umwelt* multiespecífico", que constituiría la percepción y respuesta conjunta de cada uno de estos grupos funcionales de especies frente a los diferentes gradientes ambientales.

Recientemente se ha debatido en varias ocasiones sobre la utilidad de ambos tipos de modelos (Lindenmayer y Fischer 2006; Fischer y Lindenmayer 2007; Price et al. 2009). Estos autores coinciden en que ambas aproximaciones son útiles y complementarias, y que la elección de una u otra depende de varios factores, entre ellos el paisaje estudiado, la especie a considerar, la escala espacial y los objetivos del estudio. Sin embargo, desde un punto de vista sintético, hay que destacar la capacidad integradora del modelo continuo, que permite evaluar la distribución de una especie considerando el efecto de los distintos procesos que la determinan, teniendo en cuenta tanto variables externas (gradientes de pérdida y fragmentación de hábitat y otros factores ambientales), como internas (rasgos del propio ciclo de vida de la especie). Esto nos proporciona una visión más completa de la respuesta de la especie frente al paisaje que la que nos darían los modelos basados únicamente en patrones. El punto débil de este modelo, que es su dificultad de aplicación, puede solucionarse considerando como objeto de estudio a un grupo de especies, en vez de a cada especie por separado. Por ejemplo, como se mencionó anteriormente, nuestro estudio con *P. vulgaris* podría generalizarse para el grupo de plantas forestales perennes. De esta manera, si nos interesa incluir a todas las especies de un paisaje en nuestro estudio, la aplicación del modelo es más factible, ya que podemos definir una serie de grupos de los que estudiaremos su respuesta, en vez de centrarnos en todas y cada una de las especies que viven en ese paisaje. Por lo tanto, este modelo constituye una base conceptual sólida sobre la que desarrollar estudios de cambio en el paisaje, ya sean a escala de especie, de grupo de especies, o de una comunidad completa, y creo que debería sustituir a las aproximaciones puramente basadas en patrones físicos, que nos proporcionan una visión sesgada de la realidad.

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2 Direct and indirect effects of landscape change on the reproduction of a temperate perennial herb

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ABSTRACT

The harmful effects of landscape change on species reproduction may be direct, when habitat loss and fragmentation affect individual performance within habitat remnants, but also indirect, when reproductive collapse derives from the effect of landscape alterations on population traits. Although the distinction between direct and indirect effects is crucial for species effective management, studies looking at both are scarce. To assess the mechanisms and the temporal consistency of landscape change effects on reproduction, we quantified flowering, fruiting and seed set of the perennial herb *Primula vulgaris* through a gradient of forest loss and fragmentation, in two years with different climatic conditions. We used Structural Equation Modelling to relate, at the landscape scale, forest habitat availability and subdivision, forest edge length, population size and subdivision, and flower, fruit and seed production. We also evaluated the effects of light availability, plant abundance and aggregation on reproduction at the local scale. Flower and fruit production decreased in landscape regions with lower forest habitat availability, and fruit production decreased in areas with a smaller amount of forest edge. There was also a negative indirect effect of habitat loss on seed production, through population size reduction. These effects mostly emerged at the landscape scale and operated in all reproductive stages, but were also transmitted across stages, as flower and fruit production quantitatively influenced seed output. Landscape change effects on reproduction differed between the two years, becoming evident after a mild winter that favoured long-lasting flowering, but disappearing, or even changing sign, when winter harshness shortened flowering. Disentangling the relative importance of direct and indirect effects of landscape change in plant reproduction is a novel approach to distinguishing between populations and habitats as the required management targets. In our study system, increasing *P. vulgaris* population sizes within small forest patches seems less effective than increasing forest cover around existing populations (even small ones), in order to enhance individual reproduction. The contrasting effects of the different processes of landscape change and the potential additive role of climatic variability must also be considered in management purposes.

RESUMEN

Los efectos perjudiciales del cambio en el paisaje en la reproducción de las especies pueden ser directos, cuando la pérdida y fragmentación de hábitat afectan al rendimiento individual dentro de los remanentes de hábitat, pero también indirectos, cuando el colapso reproductivo se deriva del efecto de las alteraciones del paisaje en rasgos poblacionales. Aunque la distinción entre efectos directos e indirectos es crucial para el manejo efectivo de las especies, los estudios evaluando ambos tipos de efectos son escasos. Para estudiar los mecanismos y la consistencia temporal de los efectos del cambio en el paisaje en la reproducción, cuantificamos la floración, fructificación y cuajado de semillas de la planta perenne *Primula vulgaris* a lo largo de un gradiente de pérdida y fragmentación de bosque, en dos años con diferentes condiciones climáticas. Utilizamos Modelos de Ecuaciones Estructurales para relacionar, a escala de paisaje, la disponibilidad y subdivisión del hábitat forestal, la longitud del borde forestal, el tamaño y subdivisión de la población, y la producción de flores, frutos y semillas. También evaluamos los efectos de la disponibilidad lumínica, abundancia de plantas y agregación en la reproducción a escala local. La producción de flores y frutos disminuyó en sectores del paisaje con baja disponibilidad de hábitat forestal, y la producción de frutos disminuyó en zonas con poca cantidad de borde forestal. Apareció también un efecto negativo indirecto de la pérdida de hábitat en la producción de semillas, a través de la reducción del tamaño poblacional. Estos efectos emergieron sobre todo a escala de paisaje y operaron en todas las fases reproductivas, pero se transmitieron también entre fases, ya que la producción de flores y frutos influyó cuantitativamente la producción de semillas. Los efectos del cambio en el paisaje en la reproducción fueron diferentes entre los dos años, siendo evidentes después de un invierno suave que favoreció la larga duración de la floración, pero desapareciendo, o incluso cambiando de signo, cuando la dureza invernal acortó la floración. Descifrar la importancia relativa de los efectos directos e indirectos del cambio en el paisaje en la reproducción de las plantas es una aproximación novedosa para distinguir entre poblaciones y hábitats como objetivos de manejo. En nuestro sistema de estudio, incrementar los tamaños de población de *P. vulgaris* dentro de parches forestales pequeños parece menos efectivo que incrementar la cobertura forestal alrededor de las poblaciones existentes (incluso de las pequeñas), con el fin de aumentar la reproducción individual. Los efectos diferenciales de los distintos procesos de cambio en el paisaje y el papel aditivo potencial de la variabilidad climática deben ser también considerados en las propuestas de manejo.

INTRODUCTION

Landscape change has been shown to be severely detrimental for the persistence of many species (Lindenmayer and Fischer 2006a). Considerable empirical evidence attributes the harmful effects of habitat loss and fragmentation to the collapse of landscape-scale dispersal dynamics (Fahrig 2003). Moreover, population declines may also arise from altered individual reproduction within remnant habitat patches (Kolb 2005). This has been highlighted in the case of plants (e.g. Aguilar et al. 2006; Leimu et al. 2010), as it has been assumed that local population dynamics may depend more on the net outcomes of reproduction than on immigration and gene flow (Honnay et al. 2005; but see Bruna et al. 2009).

The causal links between landscape change and reproductive disruption are difficult to predict as they derive from three interdependent and simultaneous processes: habitat loss (Andrén 1994), habitat subdivision (Doak 2000) and edge increase (Tomimatsu and Ohara 2002), the latter two usually termed fragmentation processes. Each of these processes may hamper plant reproduction in two ways. Firstly, they may compromise reproduction by directly affecting individual plant performance, irrespective of population traits. For example, the change in microenvironmental conditions associated with the proximity of forest edges may reduce individual reproductive output through decreases in pollination (Jules and Rathcke 1999) or increases in herbivory (Wirth et al. 2008). Secondly, landscape change may indirectly affect plant reproduction by modifying population traits such as population size (i.e. Allee effects, Matsumura and Washitani 2000) or the spatial distribution of individuals (Fischer and Matthies 1997), with subsequent effects on reproductive success. For example, in small, subdivided populations, fruit and seed set may be reduced due to either decreased pollinator visitation, which diminishes the quantity of pollen arriving to flowers (Ågren 1996), or to higher inbreeding levels, which reduces the genetic quality of pollen (Chacoff et al. 2008). Ascertaining the relative contribution of direct and indirect effects on reproductive disruption is an important step in the conservation of species suffering landscape change, as it helps in the complicated balancing act of choosing the appropriate target for management, be that at the habitat, population or individual plant level. For example, population-oriented tools, such as increasing population size, may not prove fruitful when reproduction depends mostly on the effects of landscape features on individual plants.

Besides the diversity of organization levels over which landscape change operates, an additional complexity in the prediction of its effects comes from the temporal dimension of plant reproduction. In this sense, landscape change effects may differ between years due to the control exerted by large-scale processes, like climatic conditions, on local reproduction. For example, the effects of population size on reproduction may vary greatly between years with different weather conditions (Tomimatsu and Ohara 2002). Ascertaining the interactions between landscape change and climatic variability is a priority in developing management tools for populations under the simultaneous action of different global change drivers (Brook et al. 2008).

Despite the large body of research demonstrating the negative effects of habitat loss and fragmentation on plant reproduction (e.g. Aguilar 2006, but see also Mustajärvi et al. 2001 for positive effects), studies discerning the relative importance of direct *versus* indirect effects of different landscape change processes, from flowering to seed set, are lacking (but see Ågren et al. 2008). Similarly, despite the importance of integrating the effects of landscape alteration in a context of global environmental changes (Leimu et al. 2010), studies across years are scarce (Rabasa et al. 2009). In this paper, we used an integrative approach to evaluate the effects of landscape change on the reproduction of the perennial herb *Primula vulgaris* in the highly fragmented forests of the Cantabrian range (Northwestern Spain). Over two years with contrasted climatic conditions, we linked landscape change gradients to the reproductive success of *P. vulgaris*. Specifically, we sought to answer the following questions: 1) What are the principal processes (habitat loss, habitat subdivision, edge increase) and levels of organization (populations, individuals) through which landscape change affects *P. vulgaris* reproduction? 2) Does landscape change affect flower production, fruit set, and seed set equally? and 3) Are landscape change effects consistent across reproductive years with contrasted climatology?

MATERIALS AND METHODS

Study species

We focused on the perennial, early-flowering herb *Primula vulgaris* L. (primrose, Primulaceae). This species lives in moist open habitats of central Europe (Jacquemyn et al. 2009). In our region, it is mainly restricted to the forest understorey, although it is able to live in shady environments such as the banks of roads and paths. It flowers mainly from late winter (February) to late spring (June), with a peak from late March to early April (authors' unpublished data). Flowering is possible in early winter in warm, dry years. It is distylous and self-incompatible, with two floral morphs. Only between-morph pollination is efficient for seed set, although certain levels of self-fertilization are found (Endels et al. 2002a). Pollinators are Hymenoptera (bumblebees) and Diptera (beeflies and hoverflies). Fruit consumers include ungulates, rodents and Lepidoptera larvae (Jacquemyn et al. 2009). Seeds have an elaiosome and are dispersed mainly by barochory (Valverde and Silvertown 1995).

A previous study (Chapter 1) suggested strong effects of landscape structure on the presence and the demography of this species in the Cantabrian forests. Other studies with *Primula* spp. have shown that reductions in population size due to habitat alteration hamper reproduction (Jacquemyn et al. 2002), which is also thought to depend on habitat quality (Valverde and Silvertown 1995; 1998).

Spatio-temporal framework

This study was conducted in the Sierra de Peña Mayor, Asturias, Spain (43º17' N – 5º30' W, elevation 900 m a.s.l.), a mountainous area of the Cantabrian Range. The climate of the region is Atlantic, with a mean annual temperature of 13 ºC and annual rainfall of ca. 1300 mm. Historically, as in many other parts of the Cantabrian Range (García et al. 2005b), deforestation for cattle grazing occurred here, and the landscape has suffered considerable change; from the original continuous temperate forests to a heavily fragmented wood-pasture habitat.

This study was carried out in an area of 3000 x 1000 m in size (Fig. 2.1), containing a few large forest fragments with hardwood species (beech *Fagus sylvatica* L. and ash *Fraxinus excelsior* L.), many fringe forest patches dominated by fleshy-fruited, bird-dispersed trees (holly *Ilex aquifolium* L., hawthorn *Crataegus monogyna* Jacq., yew *Taxus baccata* L., rowan *Sorbus aucuparia* and whitebeam *Sorbus aria*) and hazel *Corylus avellana* L., as well as numerous small forest fragments mostly composed of fleshy-fruited trees, embedded in a matrix of stony pastures and heathlands (*Erica* spp., *Ulex europaeus* L.). The matrix covers ca. 60% of the area.

This study took place during 2008 and 2009, two years with contrasting weather conditions during winter (Appendix B): the nearest meteorological station (Oviedo, Asturias, 232 m a.s.l.) registered a mean temperature of 9.4 ºC and a cumulative precipitation of 243.1 mm for winter 2007-2008 (December to March), and mean temperature of 7.9 ºC and cumulate precipitation of 443.5 mm for the same period in 2008-2009. In addition, lower temperatures and heavier precipitation produced much more frequent and abundant snowfalls, and an increased persistence of snow cover in winter 2008-2009, resulting in a delayed start to flowering and a much shorter flowering season in 2009 (Appendix B).

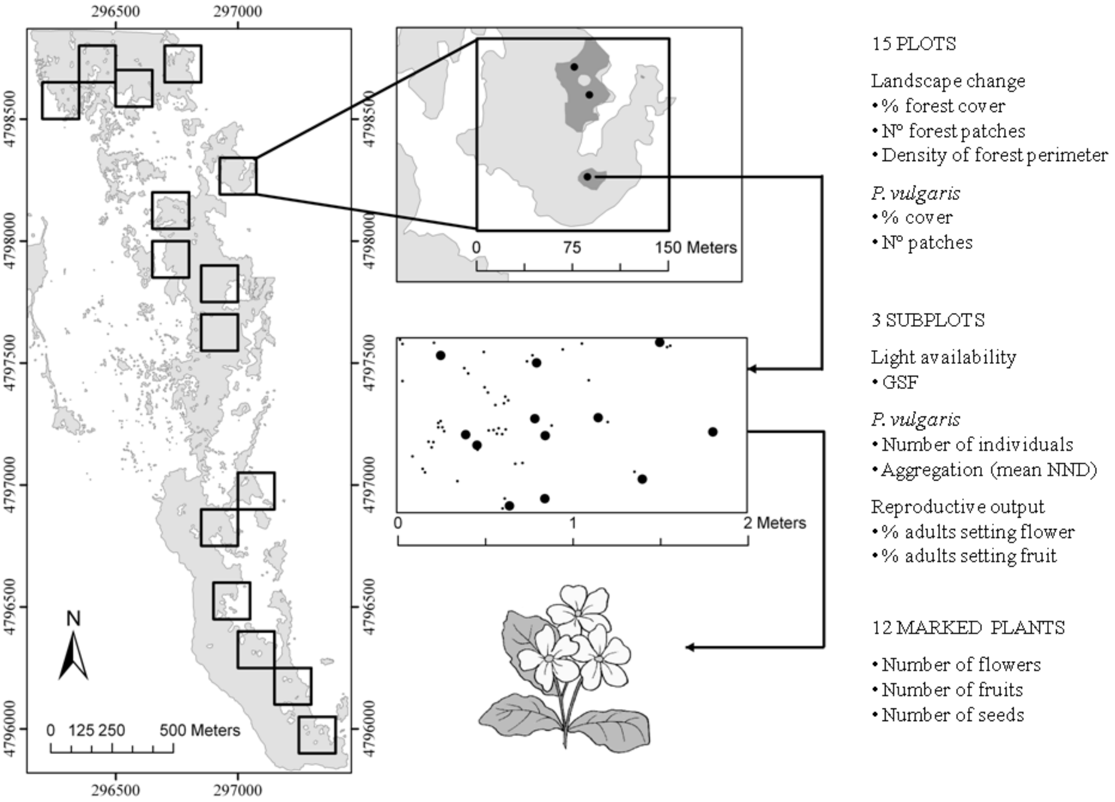

Figure 2.1: Outline of the framework for sampling landscape change parameters, population traits and reproductive output at different spatial scales (GSF = Global Site Factor, a measure of light availability; NND = Nearest Neighbour Distance) see text for details on variable calculation). Light grey area represents forest cover and dark grey in the box, *P. vulgaris* cover.

Landscape change parameters and fine-scale habitat features

A previous study (Chapter 1) found that *P. vulgaris* is absent from highly deforested areas (forest cover < 20%), but that it may also be absent from high-cover areas. In fact, large forest patches may contain several groups of isolated *P. vulgaris* populations. With these patterns in mind, for the present study we delimited, in autumn 2007, 15 square plots (150x150 m) for the sampling of landscape structure and *P. vulgaris* population features across the study area (Fig. 2.1). We selected this sampling grain size (22500 m^2) as a compromise, enabling us to cover the spatial variability in both population features and processes (e.g. population patchiness, Chapter 1; pollinator range, Osborne et al. 1999) and forest landscape structure, whilst employing feasible logistical effort. Plot locations were selected arbitrarily in order to contain the species, to avoid overlapping, to cover a large extent of the local landscape, and to represent sufficiently wide gradients of habitat loss, habitat fragmentation and *P. vulgaris* population features (see below).

The degree of landscape change in these plots was measured from a Geographic Information System (GIS) of the study area created with ArcGIS 9.1 (see details in Chapter 1), where we included a layer representing forest cover. For each of the plots, we calculated three major landscape change descriptors: the percentage of forest cover (a measure of habitat availability and an inverse measure of habitat loss); the number of forest patches (a measure of habitat subdivision); and the length of forest perimeter (a measure of edge amount). All these parameters showed considerable variation across plots (Appendix C).

To evaluate habitat features at a fine scale, we established three permanent 2 x 1 m subplots in each of the 15 plots (Fig. 2.1). In each subplot, we measured light availability, based on the Global Site Factor (GSF, Rich 1990), in July 2008 (the time of year with maximum foliar expansion). We took a hemispherical photograph of the forest canopy in each subplot and analysed all photographs with Hemiview 2.1 (Delta T Devices Ltd, Cambridge). For each subplot, we obtained a GSF value, which is the proportion of global solar radiation at a given location relative to that in the open, varying between 0 (totally closed canopy) and 1 (totally open sites).

Abundance and subdivision of *P. vulgaris* populations

The GIS also included a layer with *P. vulgaris* cover estimated from schematic maps drawn in the field during a previous study (Chapter 1) which found that the percentage of species cover was strongly positively correlated to plant abundance. In the current study we therefore used cover as a surrogate of the species' abundance. We also noted the number of *P. vulgaris* patches (defined as clumps of plants separated from each other by more than 20 m) in each plot, as a measure of population subdivision. Both species cover and number of patches showed considerable variation across plots (Appendix C).

At the fine scale, we estimated abundance as the number of adults in each subplot in late May of 2008 and 2009. As a measure of plant aggregation, we also calculated the mean nearest neighbour distance (NND) between adults in each subplot.

Sampling of reproductive output

In 2008 and 2009, we sampled reproductive output in reproductive plants (i.e. those showing flower buds), including both early and late flowering individuals. In each subplot, we marked 8 reproductive plants at the beginning of the flowering season (January 2008, February 2009) and 4 in the middle of the season (April). Marked plants were surveyed fortnightly during the flowering and fruiting season (January-July) and every two months for the rest of the year. In each survey, we counted the number of flower buds, open and dead flowers, and intact and preyed fruits per plant. Each year, we took a sample of ripe fruits and counted the number of seeds per fruit.

This species shows a very long ($\geq$ 15 days) individual flower lifespan (the amount of time flowers remain receptive and attractive to pollinators), and an extended flowering period. Thus, by the end of the flowering season a plant may still simultaneously present flower buds, receptive flowers and developing fruits. This is not a handicap in estimating the total number of flowers produced by an individual each year, as flowers that do not set fruit remain attached to the plant for a long time. An exact count of the total number of flowers produced (for example, by labelling individual buds) was logistically unfeasible, so we estimated this as the maximum recorded count, per plant and per year, of the sum of buds, and open and dead flowers. The number of fruits per marked plant and year was estimated as the maximum of the sum of intact and preyed fruits. The number of seeds per marked plant and year was calculated as the number of seeds per fruit times the estimated total number of fruits. A mean value of number of flowers, fruits and seeds in marked plants was obtained for each subplot and year.

During the flowering season we also calculated the proportion of adults in each subplot setting flower and fruit. Combining these proportions with the average number of flowers, fruits, and seeds per marked plant, we were able to estimate the average number of flowers, fruits and seeds per adult per subplot; the three main sequential measures of reproductive output. These small-scale reproductive measures were averaged between subplots to obtain broad-scale measures of reproductive output for each of the 15 plots.

Statistical analyses

Our goal was to evaluate landscape change effects on reproductive output using an integrative approach, that is, by distinguishing the relative effects of different alteration processes acting through the modification of population traits and/or the change in individual plant performance, across different reproductive stages. For this, we used Structural Equation Modeling (SEM, namely path analysis, Quinn and Keough 2002), which assesses causality without experimental tests, and allows the consideration of cascading effects across consecutive reproductive stages. We related landscape change parameters (percentage of forest cover, number of forest patches and density of forest perimeter), *P. vulgaris* population traits (size and subdivision) and reproductive output (mean number of flowers, fruits and seeds per adult) at the plot scale, for each year. Path analysis starts by building an *a priori* path scheme; an analytical model representing all the hypothetic causal links between predictors and response variables, based on previous knowledge of the ecological system. In our case, this saturated model included the links representing expectable effects of fragmentation and population traits on reproduction which had been proven to operate at the landscape scale. Path analysis enables the exploration of the direct and indirect effects of predictors on response variables, taking into account the possible collinearities among predictors and among responses. Thus, we sought to evaluate the direct effects of landscape change parameters in reproductive output at different stages (i.e. effects on individual performance), the indirect effects of landscape change on final reproductive output (seeds per adult) mediated by previous effects on early reproductive stages (flowers and fruits per adult), as well as the indirect effects of landscape change on reproductive output mediated by the modification of population traits. Direct effects are measured by standardized partial regression coefficients between a predictor and a response, whereas indirect effects are calculated as the sum of the products of all standardized partial regression coefficients over all paths between a predictor and a response. These coefficients were estimated by Maximum Likelihood procedures, as recommended for small sample sizes (Iriondo et al. 2003).

We conducted separate analyses for each year, considering possible alternatives to the saturated model by constructing nested models sharing the same causal structure. We did this by running a stepwise specification search in Amos 16.0 (SPSS, Chicago, IL) choosing the final model for each of the two years on the basis of Akaike Information Criterion (AIC, Akaike 1973). The fit of each model to the data was assessed using a likelihood chi-squared value, which tests the null hypothesis that the covariance matrix implied by the model reproduces the observed covariance matrix. A significant goodness of fit test indicates that the model is a poor description of the observed covariance among variables, while a non-significant value indicates that the predicted pattern of covariance is not distinguishable from that observed. As our design considered each plot as an experimental replicate in order to properly represent landscape-scale processes, our sample size was small (N = 15). Thus, we also tested goodness of fit by means of Bentler's comparative fit index (CFI; Iriondo et al. 2003). CFI > 0.9 indicates an acceptable fit between the model and the data.

In order to assess the small-scale effects of habitat suitability and population traits on reproduction, we evaluated the effects of light availability, plant abundance and aggregation on reproductive output at the subplot scale using multiple regression models. We used number of flowers, fruits and seeds per adult as response variables and GSF, adult abundance and mean NND between adults as predictors. The model for the number of fruits also considered the number of flowers as a covariable, as did the model for the number of seeds with respect to the number of flowers and fruits. Given the spatial structure inherent in the empirical design (three subplots within each sampling plot), there could be some bias in the determination of the effects of predictors and covariables due to spatial autocorrelation. Thus, our multiple regression models incorporated a spatial autoregressive term (Simultaneous Autoregressive Regression, SAR; Keitt et al. 2002). We set up a model for each response variable and year, with SAM 3.0 software (Rangel et al. 2006).

Prior to analysis, data were transformed to achieve normality and reduce heteroscedasticity (arcsine of square root for proportions, and ln (x + 1) for the rest of the data).

RESULTS

P. vulgaris reproductive output strongly differed between the two study years (Fig. 2.2). Mean number of flowers, fruits and seeds per adult were significantly higher in 2008 than in 2009 (paired t-test: t = - 6.46, $P < 0.0001$ for flowers; t = - 3.64, $P = 0.0027$ for fruits; and t = - 3.78, $P = 0.0020$ for seeds). All reproductive parameters varied along the gradient of landscape change, increasing with forest cover, especially in 2008 (Fig. 2.3).

The best-fit SEMs explained a large amount of the variation in reproductive output (Fig. 2.4). In 2008, predictors explained 32.5 % of the variation in flowers per adult, 73.2 % for fruits and 89.2 % for seeds. These values were somewhat lower in 2009, explaining 18.8 % of variation in flowers, 62.6 % in fruits and 58.3 % in seeds. In both cases there was a good fit between the model and the data (2008: chi-square = 13.19, df = 16, $P = 0.65$, CFI = 1.00; 2009: chi-square = 14.14, df = 18, $P = 0.72$, CFI = 1.00).The best-fit path models (Fig. 2.4) included negative correlations of forest cover with amount of edge and number of forest patches, suggesting that decreases in habitat cover result in increased edge density and habitat subdivision. In addition, models showed significant effects of landscape change on *P. vulgaris* population traits, as bigger populations occurred in high-cover forest plots, whereas highly subdivided populations occurred in high-cover and edge-rich areas (Fig. 2.4). These relationships were the same in both years; as landscape change parameters and population traits were constant.

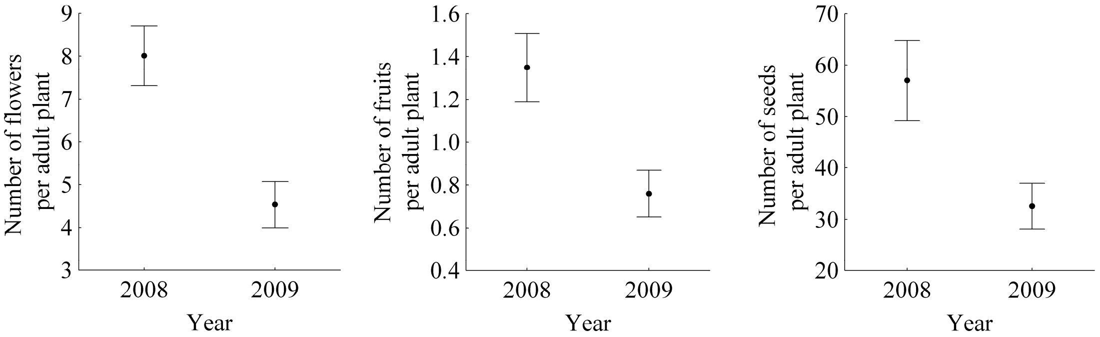

Figure 2.2: Average (± SE) of the number of flowers, fruits and seeds per adult *P. vulgaris* plant in 2008 and 2009 (N = 15 plots).

The SEM model for 2008 revealed that landscape change directly affected the different stages of reproduction (Fig. 2.4), these being the most important effects observed. Production of flowers and fruits per adult was higher in plots with more forest cover. Fruit production was also higher in plots with high forest edge density. Seed production was higher in high-cover plots as a consequence of these plots hosting bigger populations. Additionally, the reproductive stages were interdependent. More fruits per adult were set in plots where more flowers per adult were produced. Similarly, seed production was positively influenced by fruit production. However, more flowers per adult resulted in reduced number of seeds per adult, although the total effect of flower number on seed number (direct plus indirect through fruit number) was positive (see Appendix D). There were no direct effects of landscape change on seed production; but more seeds per adult were produced in high-cover and edge-rich plots due to indirect effects of these measures acting through flower and fruit production. Seed production depended mostly on habitat availability, through the effect of forest cover on earlier reproductive stages.

In 2009, forest cover did not influence any of the reproductive stages, either directly or through effects on population traits. Furthermore, the effect of amount of edge in fruit production changed sign: fewer fruits were produced per adult in plots with high forest edge density. This negative effect of edge was also present in flower production, though not significant. Finally, fruit production per adult was higher in plots where the forest habitat was more subdivided. As in the previous year, flower production positively influenced fruit production, although the effect was not significant. More seeds per adult were produced where fruit production was high, but the direct negative effect of flower production on seed production disappeared. Thus, there were no direct effects of landscape change on seed production, but more seeds per adult were produced in plots with low density of forest edge and high forest subdivision, as a result of indirect effects acting through fruit production, with forest edge exerting the major influence.

Small-scale SAR models explained between 13 and 86 % of the variance in reproductive output (Table 1.1). The degree of spatial autocorrelation in the measured parameters was generally low, as revealed by the small difference in the amount of variance explained by the predictor variables and that explained by predictors plus space (see R^2 values in Table 1.1). The model for number of flowers per adult was never significant while those for number of fruits and seeds were significant in both years. Number of fruits per adult increased when plants were more sparse (higher NND) in 2008, and, in both years, when more flowers per adult were produced. In addition, number of seeds per adult increased as fruits per adult increased.

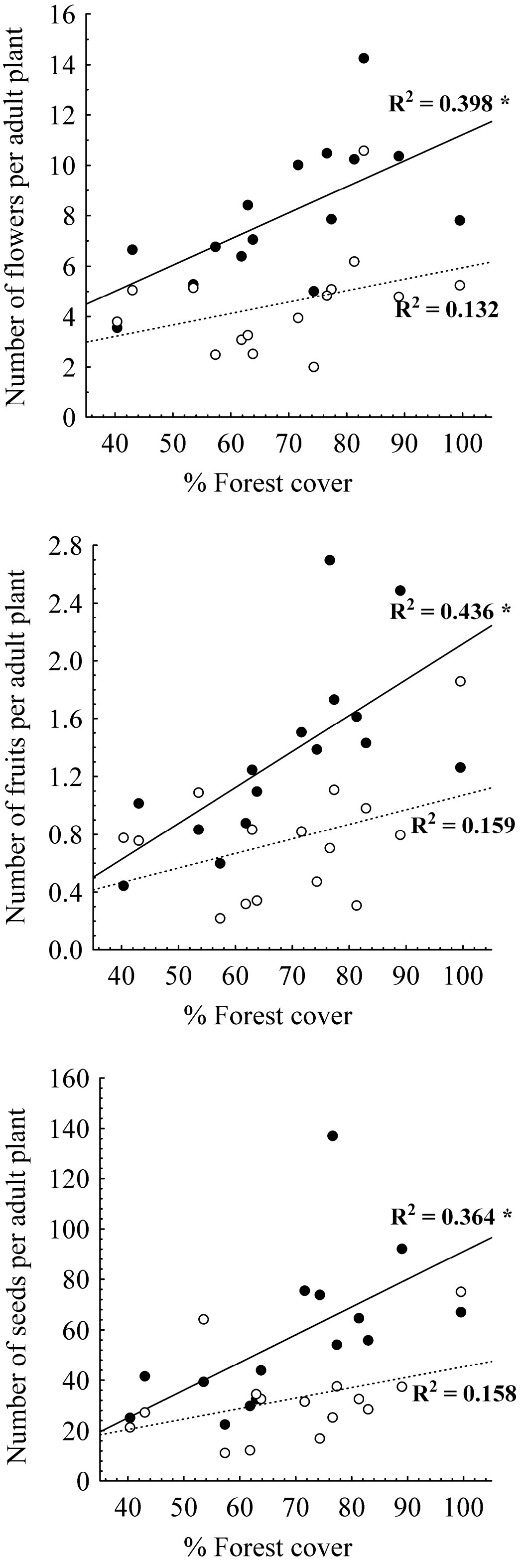

Figure 2.3: Effects of percentage of forest cover on the number of flowers, fruits and seeds per adult of *P. vulgaris* in the 15 plots, with filled circles representing data for 2008 and open circles representing data for 2009. Lines and R^2 values for linear regression fits are shown (asterisks indicate significance at $P < 0.05$).

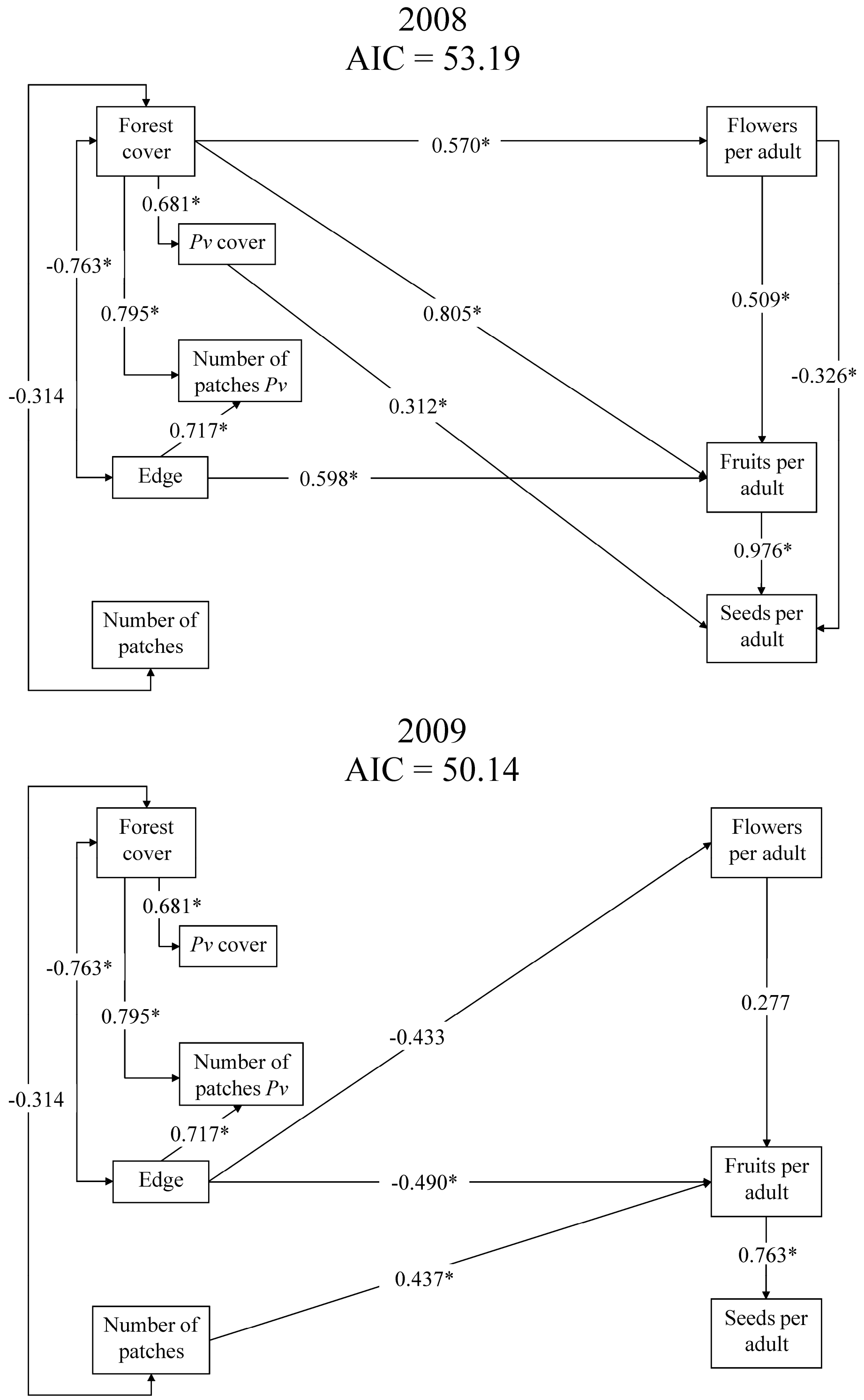

Figure 2.4: Path models showing the direct and indirect effects of landscape change variables and population traits on reproductive output of *P. vulgaris* (*Pv*) per adult in 2008 and 2009. Values of standardized partial regression coefficients and correlation coefficients are shown. Asterisks indicate significance ($P < 0.05$). The AIC value for each model is shown.

	Dep. vars.	Flowers per adult				Fruits per adult				Seeds per adult			
2008		F	*P*	R^2_p	R^2_{p+s}	F	*P*	R^2_p	R^2_{p+s}	F	*P*	R^2_p	R^2_{p+s}
		2.42	0.080	0.150	0.166	10.99	<0.001	0.523	0.528	36.32	<0.001	0.862	0.856
		β	t	P		β	t	P		β	t	P	
	GSF	0.55	1.93	0.061		-0.26	-1.07	0.290		0.28	0.78	0.440	
	Abund.	-0.25	-1.74	0.089		0.15	1.13	0.264		-0.09	-0.42	0.676	
	NND	-1.38	-0.41	0.687		11.97	3.97	<0.001		-0.96	-0.20	0.845	
	Fl/adult					0.57	4.95	<0.001		-0.04	-0.18	0.859	
	Fr/adult									2.14	10.34	<0.001	
2009		F	*P*	R^2_p	R^2_{p+s}	F	*P*	R^2_p	R^2_{p+s}	F	*P*	R^2_p	R^2_{p+s}
		1.74	0.174	0.113	0.129	5.22	0.002	0.343	0.345	35.81	<0.001	0.852	0.853
		β	t	P		β	t	P		β	t	P	
	GSF	0.48	1.47	0.147		0.14	0.64	0.525		-0.20	-0.57	0.574	
	Abund.	-0.12	-0.76	0.453		0.16	1.35	0.184		0.13	0.68	0.499	
	NND	-4.97	-1.34	0.189		4.55	1.74	0.090		1.00	0.24	0.811	
	Fl/adult					0.46	4.48	<0.001		-0.13	-0.72	0.480	
	Fr/adult									2.71	11.97	<0.001	

Table 1.1: Summary of the spatial simultaneous autoregressive (SAR) models considering, as predictors, Global Site Factor (GSF; a measure of light availability), *P. vulgaris* plant abundance and nearest neighbour distance (NND), and, as response variables, flowers, fruits and seeds per adult in 2 x 1 m subplots. F and *P*-values and the coefficients of determination for predictor variables (R^2_p) and for predictor variables plus space (R^2_{p+s}) are shown for each model, and partial regression coefficients (β, t and *P*-values are shown for the predictors (N = 45; df = 3).

DISCUSSION

In this study, we used an integrative approach to demonstrate how *P. vulgaris* reproduction was affected by forest landscape structure in the Cantabrian Range. We found that the different processes of landscape change exerted direct effects on individual reproductive potential. To a lesser extent, variations in habitat availability modified plant population size, which also affected individual reproduction. Both direct and indirect habitat alteration effects mostly emerged at a large scale, as habitat features or population traits scarcely affected fine-scale variability in plant reproduction. Moreover, landscape change differentially affected the successive stages of reproduction, but also had effects cascading from flowering to seed setting, as flower and fruit production quantitatively influenced seed output. Finally, landscape change effects were temporally inconsistent, disappearing or even changing sign between the two years.

Direct, indirect and cumulative effects of landscape change on reproduction

Habitat alteration greatly affected *P. vulgaris* reproduction in its different stages through the direct effect of landscape changes. This was especially evident in 2008, when the amount of forest habitat affected flower, fruit and seed production independently. Sites with low forest availability seem suboptimal for *P. vulgaris* reproduction for several reasons. First, plants in deforested sites may have fewer resources for flowering than plants in highly-forested, more humid sites (Jacquemyn et al. 2009). Second, the positive effect of forest cover on fruit set, irrespective of flower number, suggests some effect of forest cover favouring pollination and outcrossing (*P. vulgaris* is limited by pollination, Boyd et al. 1990). Large forest patches may promote longer pollinator movements than small patches, increasing pollen load quality (Goverde et al. 2002). Also, a proportionally greater pollinator abundance in larger patches is expected, as forest habitats account for most floral resources in the late-winter and early-spring across the fragmented landscape (Hegland and Boeke 2006). Finally, there was also a direct positive effect of edge density on fruit production. These edge effects were found even when considering a reduced analytical variability for edge length in SEM (as correlation with forest cover was significant), indicating that our estimations of edge effects are, in fact, conservative. Although fragmentation paradigms predict negative effects of edges on individual fitness (i.e. edge effects, Murcia 1995), they may benefit some pollinators (Montgomery et al. 2003) so enhancing pollen deposition and outcrossing.

Besides these direct effects of habitat loss and fragmentation on *P. vulgaris* reproduction, we also found indirect effects, mediated by modifications in population traits. The links between landscape gradients and population features were, however, complex since forest availability favoured plant abundance but, simultaneously, forest cover and edge density both favoured population subdivision. Thus, the larger the forest habitat availability, the bigger, but more subdivided, the plant populations. Irrespective of the processes linking landscape configuration with population traits, we found reproductive consequences of population variability in the fragmented scenario. Namely, plants produced more seeds in large than in small populations, and this effect was independent of fruit production, thus highlighting some mechanism affecting seed development. As suggested above in relation to increased fruit set, improved seed set may be related to quantitatively and qualitatively enhanced pollination in larger populations. For example, higher flower visitation rates and stronger outcrossing are expected in larger populations due to increased pollinator visitation, and higher and more diverse pollen loads (Ågren 1996), leading to increased seed production (Aizen and Harder 2007).

Our integrative approach also revealed the cascading effects of landscape change, from flowering to seed maturation. Greater seed output was ultimately found in less altered areas, resulting from the overall positive effect of flower production on seed set and explained by the strong effect of fruit production on seed set, counterbalancing the apparent trade-off between flower production and seed set (higher flower production led to higher fruit production, but the number of seeds per fruit decreased; Primack 1987).

Finally, landscape change effects on *P. vulgaris* reproduction were scale-dependent, as habitat suitability and population traits poorly explained the fine-scale variability in reproduction, indicating that these features operated by and large at the landscape scale. In 2008, fruit production per adult was higher in subplots with low plant aggregation, suggesting effects of intra-specific pollinator or resource competition (Zimmerman 1980), but also increased inbreeding (short pollinator movements in clumped patches would lead to low-quality pollen transfer; Goverde et al. 2002).

Temporal variability in reproduction and landscape change effects

The magnitude of *P. vulgaris* reproduction was remarkably different in the two years studied. As suggested for other forest perennials (De Frenne et al. 2010), mild winter temperatures, low precipitation and early snow melt during the first year (Appendix B) facilitated an early-start to flowering which extended over a long period, resulting in higher reproductive output. The extended flowering season in 2008 may well have produced more pollination opportunities, which would have increased fruit and seed production (Alonso 2004). Conversely, the delayed start to, and shortening of, the reproductive season due to the more adverse meteorological conditions in 2009 resulted in a much lower and more homogeneous reproductive output (see error bars in Fig. 2.2).

Landscape change effects on reproduction also varied between years, with most disappearing and some changing sign from 2008 to 2009. The lowered reproductive ability imposed by the shorter flowering period seemed to buffer the ability of plants to track for the large-scale environmental heterogeneity derived from habitat change. Alternatively, landscape configuration effects might be stronger early in the season, and thus mostly emerge when more plants are flowering early, as occurred in 2008. For example, gradients of soil temperature, which affect flowering in vernal plants (Dahlgren et al. 2007), may be more marked across the fragmented landscape (with warmer and less variable soils in more forested sectors) in late winter than during spring. Our data support this possibility, as reproductive output was more influenced by habitat availability in plants that flowered early (data not shown).

The positive effect of forest edge on reproduction in 2008 was replaced by the opposite trend in 2009: more fruits per adult were produced in areas with less edge. The same happened with flowers. In this case, the phenology of proximate factors affecting reproduction and its interaction with landscape gradients may also underpin these interannual differences, resulting in detrimental edge effects when the plants flower later. The abundance of edge may favour cattle entering the forest in mid-spring (*pers. obs.*), resulting in plants suffering from increased herbivory and trampling (e.g. Wirth et al. 2008). Herbivores may reduce plant reproduction directly by affecting resource allocation and by consuming reproductive tissue, as well as indirectly by disrupting plant-pollinator interactions (Vázquez and Simberloff 2004). Furthermore, in 2009 more fruits were produced where the forest habitat was scattered through a higher number of forest patches. This could also be related to pollination, as habitat subdivision may make pollinators move between patches and thus carry pollen over longer distances, reducing inbreeding and increasing fruit set (Goverde et al. 2002; Aizen and Harder 2007). This effect was probably diluted in 2008 by the high abundance of flowers and flowering individuals, which would favour outcrossing even with short pollinator movements.

In conclusion, we wish to highlight that the temporal variability shown here suggests an interaction between landscape change and the large-scale effects of regional climatic conditions. In this sense, an increased frequency of mild winters, like that established by scenarios of climate warming, seems to enhance *P. vulgaris* reproduction (as reported by De Frenne et al. 2010 for *Anemone nemorosa*), but also seems to make landscape change effects more pronounced, increasing the demographic difference between populations in highly altered habitats and those in continuous forests. In other words, if the interaction detected in our short-term study were to be maintained over subsequent years, landscape change could prevent the effects of warming by keeping reproductive output in highly altered sites consistently low (see Fig. 2.3). Clearly, longer-term studies are needed to confirm this interaction.

Implications for management

Reproduction is a target process when developing conservation or management plans for perennial herbs in fragmented landscapes (Honnay et al. 2005; Leimu et al. 2010), as it may condition genetic variability within populations, local population growth, and regional patch dynamics through seed dispersal. In the case of *P. vulgaris*, reproductive disruption leads to genetic impoverishment (Van Geert, Van Rossum and Triest 2008) and seems to contribute markedly to large-scale dispersal limitation (Chapter 1). Moreover, the contribution of recruitment to the *P. vulgaris* population growth rate in our study site (Chapter 4) suggests that reproduction plays a relevant role in population dynamics and future population size. We therefore consider that our results on *P. vulgaris* reproduction may help to establish guidelines for the conservation of endangered perennial herbs and, ultimately, for the preservation of plant biodiversity in fragmented habitats. Our results may, in addition, be applied to the management of *P. vulgaris* populations in other parts of its distribution range, where extinction risk is much higher (e.g. Endels et al. 2002b).

We would like to present recommendations to conservation practitioners from three major considerations. First, we would argue that disentangling the relative importance of direct and indirect effects of landscape change in reproduction is a novel way to distinguish between populations and habitats as the required management targets. In the case of *P. vulgaris* in the Cantabrian forests, population-oriented measures, such as increasing population sizes within small forest patches, would be less effective than habitat-oriented management, such as increasing forest cover around existing populations (even small ones), in order to increase individual reproduction. Secondly, we highlight here the complexity of landscape change effects, given that habitat loss, habitat subdivision and edge increase may have contrasting effects on plant reproduction, which may even be inconsistent over time. In this sense, preventing further loss of forest habitat may be compatible with accepting some degree of forest fragmentation, as increased edge may be beneficial for reproduction. This can be achieved by promoting networks of interconnected and edge-rich forest patches, rather than single, regular forest stands. And thirdly, we urge the consideration of the potential additive role of landscape change and climatic variability, under an integrative framework of the effects of different global change drivers, on species persistence (see also Brook, Sodhi and Bradshaw 2008; Leimu et al. 2010). To achieve this goal, simulation modelling based on long-term monitoring of target parameters (i.e. harshness of winter, flowering and fruiting over gradients of landscape modification) would be required to assess the synergistic effects of global warming and habitat fragmentation.

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3

Mechanisms limiting *Primula vulgaris* recruitment in a fragmented landscape

Valdés, A. and García, D. (*in prep.*). Mechanisms limiting *Primula vulgaris* recruitment in a fragmented landscape.

ABSTRACT

Plant recruitment may be limited by dispersal, if seeds cannot arrive at potential recruitment sites, and by establishment, due to a low availability of good-quality sites for recruitment. Habitat loss and fragmentation may foster these limitations both directly and indirectly, by altering plant population traits affecting recruitment. Seed-sowing experiments, scarcely applied along gradients of landscape alteration, are useful to assess these limitations. Experiments are usually monitored until germination, but further monitoring is needed to evaluate if the suitability of a site changes between recruitment stages. Forest plants are very sensitive to habitat loss and fragmentation, and prone to suffer from recruitment limitations because of their low dispersal ability and specific habitat requirements. In this study, we perform a landscape-scale seed-sowing experiment to disentangle the importance of dispersal and establishment limitations in different stages of recruitment of *Primula vulgaris* in fragmented forests of the Cantabrian range (Northwestern Spain). We evaluated the influence of environmental changes associated with habitat loss and fragmentation (modifications of habitat amount at different scales, changes in distribution of the species and in the activity of seed predators and seedling herbivores) on seedling emergence, survival and growth from seeds to one-year seedlings. We found strong evidences of severe dispersal limitation, as seedling emergence in experimental replicates where no seeds were added was very low. Dispersal limitation was strong independently of landscape alterations. There was no limitation for seedling emergence, apart from the number of germinated seeds in first spring increasing in sectors were large-scale habitat amount was low. The availability of safe-sites for recruitment constrained the subsequent phases of seedling life, both the survival and growth of seedlings during their first year of life. Habitat and population modifications resulting from landscape change determined establishment limitations for seedling survival and growth, many of their effects being interdependent. Thus, habitat loss and fragmentation can compromise plant recruitment by sequentially increasing dispersal limitations and triggering establishment limitations.

RESUMEN

El reclutamiento de plantas puede estar limitado por la dispersión, si las semillas no pueden llegar a los sitios potenciales de reclutamiento, y por el establecimiento, debido a una baja disponibilidad de sitios de buena calidad para el reclutamiento. La pérdida y fragmentación de hábitat pueden promover estas limitaciones de forma directa e indirecta, alterando rasgos de las poblaciones de plantas que afectan al reclutamiento. Los experimentos de adición de semillas, raramente aplicados a lo largo de gradientes de alteración del paisaje, son útiles para evaluar estas limitaciones. Son monitorizados generalmente hasta la germinación, pero se necesita un seguimiento posterior para evaluar si la idoneidad de un sitio cambia entre los estadios del reclutamiento. Las plantas forestales son muy sensibles a la pérdida y fragmentación de hábitat, y propensas a sufrir limitaciones al reclutamiento debido a su baja capacidad dispersiva y requerimientos de hábitat específicos. En este estudio, llevamos a cabo un experimento de adición de semillas a escala de paisaje, para averiguar la importancia de las limitaciones al reclutamiento y al establecimiento en diferentes estadios del reclutamiento de *Primula vulgaris* en bosques fragmentados de la cordillera Cantábrica (Noroeste de España). Evaluamos la influencia de cambios ambientales asociados a la pérdida y fragmentación de hábitat (modificaciones de la cantidad de hábitat a diferentes escalas, cambios en la distribución de la especie y en la actividad de depredadores de semillas y herbívoros) en la emergencia, supervivencia y crecimiento desde las semillas hasta las plántulas de un año de edad. Encontramos fuertes evidencias de una severa limitación a la dispersión, ya que la emergencia de plántulas en réplicas experimentales donde no se añadieron semillas fue muy baja. La limitación a la dispersión es fuerte independientemente de las alteraciones del paisaje. No hubo limitación para la emergencia de semillas, aparte de que la cantidad de germinación en la primera primavera se incrementó en sectores donde la cantidad de hábitat a gran escala fue baja. La disponibilidad de sitios adecuados para el reclutamiento restringió las siguientes fases de la vida de las plántulas, tanto la supervivencia como el crecimiento durante su primer año de vida. Las modificaciones del hábitat y de la población que resultan del cambio en el paisaje determinaron las limitaciones al establecimiento para la supervivencia y crecimiento de plántulas, y muchos de sus efectos fueron interdependientes. Por lo tanto, la pérdida y fragmentación de hábitat pueden comprometer el reclutamiento de las plantas, ya que secuencialmente incrementan las limitaciones a la dispersión y desencadenan las limitaciones al establecimiento.

INTRODUCTION

Seed dispersal and seedling recruitment are key steps of plant life cycles, as they condition plant distribution, population growth and colonization of new areas (Ehrlén and Eriksson 2000; Wang and Smith 2002). Plant recruitment at early stages can suffer from two different limiting processes which act sequentially (Baeten et al. 2009). First, *dispersal limitation* (also called *seed limitation*) is due to the failure of seeds to arrive at saturating densities at all potential recruitment sites (Eriksson and Ehrlén 1992; Nathan and Muller-Landau 2000). This can happen either because seed production is too low to saturate potential recruitment sites, even if seeds are able to reach all of them, or because not enough seeds reach all recruitment sites, even though enough are produced to saturate them (Clark et al. 1998; Terborgh et al. 2011). Secondly, *establishment limitation* (also called *microsite limitation*) is due to a low availability and quality of sites for establishment, and acts between seed deposition and recruitment into the adult population (Clark et al. 1998; Nathan and Muller-Landau 2000). Although both types of processes have been well documented, and all plants suffer to some extent from dispersal and establishment limitations, there is a variation between species in the relative importance of both kinds of recruitment limitation (Verheyen and Hermy 2001; Kolb and Barsch 2010).

Anthropogenic disturbances, such as habitat loss and fragmentation, may exacerbate recruitment limitations, leading to plant populations to severe decline or even extinction (Bruna et al. 2009). Anthropogenic landscape change may increase recruitment limitations by affecting differentially the different recruitment processes such as seed dispersal, germination, or seedling establishment. For example, dispersal limitation in fragmented landscapes may increase because fragmentation decreases seed production by reducing population sizes (Aguilar et al. 2006; Chapter 2), or because fragmentation increases isolation between habitat remnants, and seeds are not able to reach fragments of suitable habitat which are too far away from seed sources (e.g. Cordeiro and Howe 2003, Herrera and García 2011). On the other hand, establishment limitations may be fostered by the low habitat quality and the new environmental conditions imposed by the fragmentation process (e.g. edge effects, Tomimatsu and Ohara 2004). In this sense, habitat loss and fragmentation may increase seed predation (Farwig et al. 2009; García and Chacoff 2007) and seedling herbivory (Benitez-Malvido 1995), hamper seed germination (Bruna 1999), and restrict seedling survival by altering the quality of safe-sites for recruitment (Uriarte et al. 2010). In sum, landscape alterations may increase recruitment limitations in plants both directly (i.e. causing direct alterations in recruitment processes; Bruna et al. 2009) and indirectly (by altering plant population traits, such as population size, with an effect on recruitment; Chapter 2). In spite of these findings, studies integrating dispersal and establishment restrictions, and evaluating the relative importance of the different limitations in altered landscapes are scarce, and eminently observational (Cordeiro and Howe 2003; Kunstler et al. 2007; McEuen and Curran 2004; Uriarte et al. 2010).

Seed-sowing experiments (reviewed in Clark et al. 2007; Turnbull et al. 2000) provide a direct and convenient way of assessing the relative importance of these limitations, but they have been scarcely applied along gradients of landscape alteration. Observing experimentally sowed seeds of a given species producing recruits in sites where this species is known to be absent indicates that its recruitment is limited by seed availability. However, seed arrival and seed germination do not guarantee successful recruitment into the seedling stage, let alone successful development into adults, as the suitability of a site for recruitment might change between the seed, seedling and adult life stages Thus, seed sowing experiments monitored only until seed germination might miss establishment limitations occurring in further developmental phases. Specifically, the transition from seed to an established seedling has been acknowledged to be an important demographic bottleneck for some forest herbs (Albrecht and McCarthy 2009).

Forest plants are very sensitive to habitat loss and fragmentation, and especially prone to suffer from recruitment limitations, as they are adapted to the relatively stable forest ecosystem, with infrequent and localized disturbances (Honnay et al. 2005). Thus, most of them have typical seed dispersal distances of a few meters, and produce low amounts of seeds that are not very persistent in the soil (no seed bank, Whigham 2004). All these traits may result in a strong dispersal limitation which may be exacerbated in altered landscapes. On the other hand, due to their specific habitat requirements (i.e. light availability, humidity, soil moisture; Jacquemyn et al. 2009), forest plants may fail to establish in many low-quality habitat fragments.

In this study, we perform a landscape-scale seed-sowing experiment in order to disentangle the processes limiting the recruitment of a perennial forest herb (*Primula vulgaris*) in the highly fragmented forests of the Cantabrian range (Northwestern Spain). A previous study (Chapter 1) showed evidences of landscape-scale dispersal constraints in this species, together with some effect of habitat quality in determining establishment. Besides, landscape change has been shown to decrease seed production due to an indirect effect of habitat availability reducing population size (Chapter 2). Here, we seek to assess the importance of dispersal and establishment limitations in different stages from dispersed seeds to one-year seedlings. We evaluated the influence of environmental changes associated with habitat loss and fragmentation (modifications of habitat amount at different scales, changes in distribution of the species and in the activity of seed predators and seedling herbivores) on seedling emergence, survival and growth. Specifically, we seek to answer the following questions: 1) Is seedling emergence of *P. vulgaris* limited by dispersal, by establishment, or by both? 2) How is seedling survival of the species affected by changes resulting from habitat loss and fragmentation (habitat amount, presence of the species, seed predation and seedling herbivory) in both summer and winter periods? and 3) How do these factors influence plant size at one-year age?

METHODS

Study site

Our study was carried out in Sierra de Peña Mayor, Asturias, Spain (43º17' N – 5º30' W, 900 m a.s.l.), within the Cantabrian Range. The climate of the region is Atlantic, with a mean annual temperature of 13 ºC and annual rainfall of ca. 1300 mm. This area has suffered from historical deforestation for cattle grazing, as many other parts of the Cantabrian Range (García et al. 2005b). As a result, the landscape has changed from continuous temperate forests to a heavily fragmented wood-pasture habitat.

The experimental area (Fig. 3.1) comprises a highly variegated forest landscape (sensu McIntyre and Hobbs 1999). That is, it presents a mosaic composed of a few large forest fragments with hardwood species (beech: *Fagus sylvatica* L. and ash: *Fraxinus excelsior* L.), fringe fleshy-fruited, bird-dispersed trees (holly: *Ilex aquifolium* L., hawthorn: *Crataegus monogyna* Jacq., yew: *Taxus baccata* L., rowan: *Sorbus aucuparia* and whitebeam: *Sorbus aria*) and hazel (*Corylus avellana* L.), as well as numerous small forest fragments mostly composed of fleshy-fruited trees, and a matrix of stony pastures and heathlands (*Erica* spp., *Ulex europaeus* L.), covering ca. 60% of the area.

Study species

Our target species is *Primula vulgaris* L. (Primulaceae), a perennial, early-flowering herb, typically living in moist open habitats in Europe (Endels et al. 2002b), but restricted to temperate forests in some parts of its range. In the Cantabrian Mountains (Northwestern Spain) it behaves mainly as a forest species, although it can be also found in some other semi-shaded locations, like roadsides and trails. It grows through the production of leaves in basal rosettes, and vegetative spread is uncommon but possible through lateral rosettes. Flowers are pale yellow and borne on separate stalks. Fruits are capsules containing 30-50 small seeds with an elaiosome. Fruit ripening occurs in late June and early July in our study area (*pers. obs.*). Seeds are delivered when capsules prostrate on the ground after the bending of the pedicels, and open by five top-valves. Seeds are thought to be dispersed mainly by barochory, but there is also some evidence of occasional dispersal by ants, rodents and slugs (Jacquemyn et al. 2009;

Valverde and Silvertown 1995; authors' unpublished data). It is thought that seeds are short-lived (Thompson et al. 1996) and that most of the seedlings recruited in a population during a given season emerge from seeds delivered in the previous year's seed production rather than from a long-lived seed pool (Valverde and Silvertown 1995).

Experimental design

The experimental design was based on a Geographic Information System of the study area (ArcGIS 9.1, see Chapter 1 for details), where forest cover and *P. vulgaris* cover were represented. We looked for experimental locations showing contrasting environmental and population parameters as a result of landscape alteration. In July 2009, we chose 6 sites within the experimental area (Fig. 3.1). Each site comprised a pair of 50x50 m plots, with a separation of 50-80 m between them. In sites 1, 3 and 6, the pair of plots was located in an area with low forest habitat amount (2-46 % forest cover in the plot), whereas in sites 2, 4 and 5, they were located in an area with high forest habitat amount (73-100 % forest cover in the plot). *P. vulgaris* plants were absent from one of the plots of each pair and present in the other one. Into each of these plots we placed 4 sampling stations: 2 of them were located under dense forest canopy (under canopy stations) and another 2 were located in open areas or in forest canopy gaps (open stations). Each of these stations comprised a set of 3 seed-sowing treatments (experimental replicates): *Exclusion* (20 seeds sown in two rows on a 10x10 cm surface of mown soil, covered with a 4-mm pore wire mesh box, preventing access by seed predators and herbivores like small vertebrates, such as rodents and birds, and large invertebrates such as slugs and carabid beetles), *Open* (20 seeds sown on a similar, uncovered surface) and *Control* (similar surface with no seeds added, to account for emergence from the natural seed bank). Seeds were collected from ripe fruits in *P. vulgaris* populations of the study area and were sown immediately. All treatments were permanently marked.

We monitored all the sampling stations from the sowing till April 2011 (22 months; monitoring was made on a monthly basis till June 2010, and after that surveys were made in August 2010, February and April 2011). The first seedling emergences were observed in March 2010. After that, we counted the number of emerged seedlings in every treatment of each sampling station in each survey, taking also photographs of the experimental replicates in order to be able to follow each plant individually, and distinguish new emergences from seedlings that had appeared in previous surveys. In April 2011, we measured all the remaining individuals (we estimated plant size by means of plant basal area, assuming an elliptical shape, and measuring its major and minor diameters). Individuals were stage-classified on the basis of their size and other biological attributes (see Endels et al. 2002b for a similar classification). We distinguished

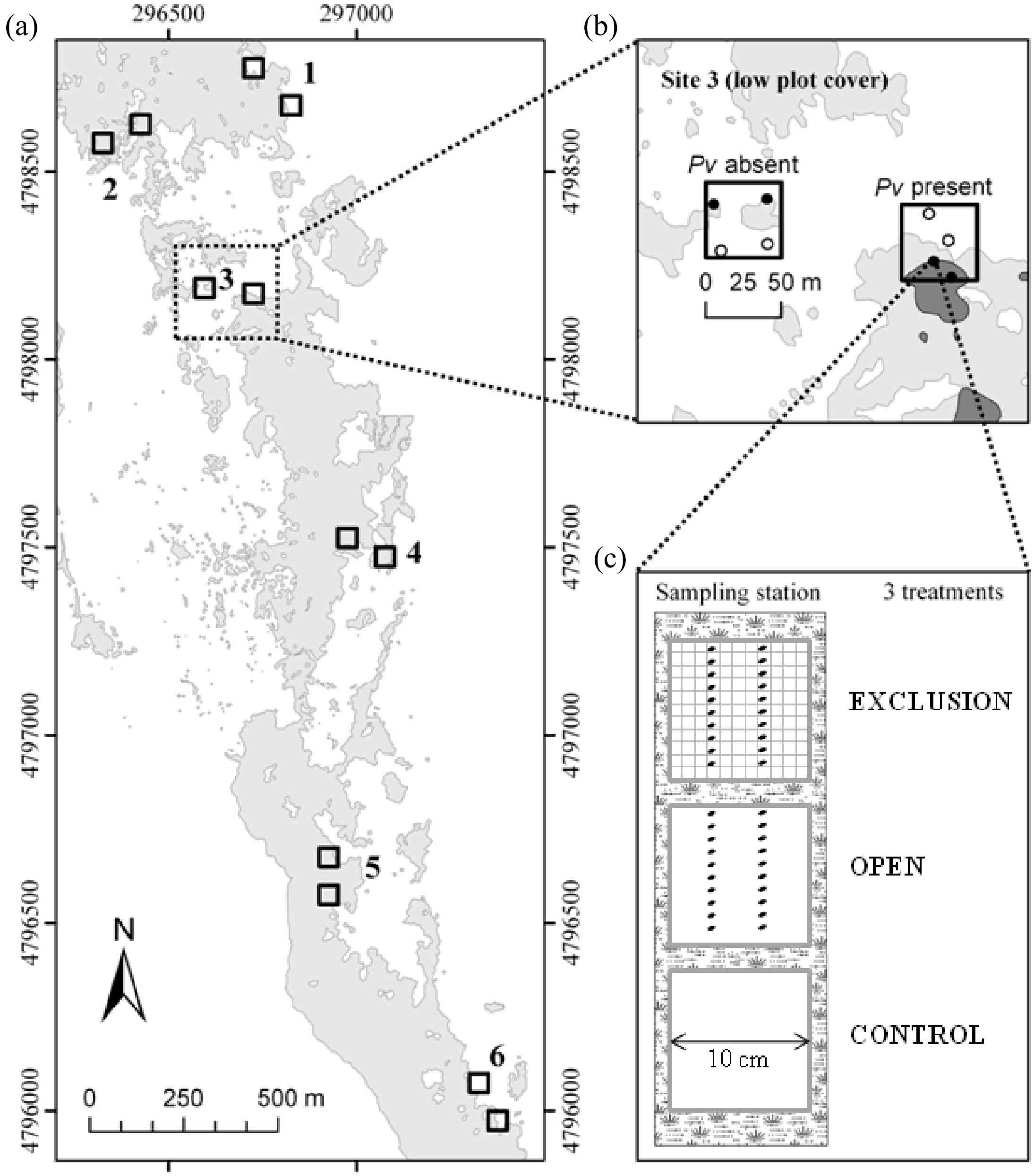

Figure 3.1: Outline of the sampling framework. (a) Location of the six sampling sites along the study area. Light grey area represents forest cover. Sites 1, 3 and 6 contain low-cover plots, and sites 2, 4 and 5 contain high-cover plots. (b) Detail of one of the sites. Dark grey area represents *P. vulgaris* cover. Each site contains one 50x50 m plot where *P. vulgaris* is absent and one where it is present. Each plot contains four sampling stations: two under canopy (black dots) and two in open areas (white dots). (c) Station with 3 treatments (experimental replicates, see text for details).

four stages: seedlings (with cotyledons still present), juveniles (without cotyledons, with only one rosette of leaves and with a rosette diameter smaller than the average of flowering individuals observed in nearby populations), vegetative adults (without cotyledons and with a rosette diameter comparable to that of flowering individuals in nearby populations) and reproductive adults (with flowers and/or flower buds).

Data analysis

We considered three key survey dates for our analyses: May 2010 (to account for the cumulate germination by the end of the first spring), August 2010 (to account for first-summer mortality) and April 2011 (to account for first-winter mortality and possible second-spring germination).

From our count data and growth measures, we constructed a series of response variables to be used in our analyses, trying to take into account the sequential phases of the recruitment process, from seed germination to seedling survival and growth. These variables were estimated on a per-experimental-replicate basis, as we were mostly interested in evaluating the effects of large- and medium-scale factors (habitat amount in the 50x50 plots and in the microhabitat of the sampling station, presence of the species, predator and herbivore activity) on recruitment. This is, the experimental replicates (each of the treatment surfaces), rather than individual seeds or seedlings, were the sampling units in analyses. First, we constructed a binary variable called *emergence*, which took the value 1 if there had been any emergence in the experimental replicate (irrespective of the number of emerged seedlings) until each of the three survey dates considered, and 0 if there were no emergences until that date. Thus, this variable represented the occurrence of emergence events. Second, we calculated the *number of emergences*, as the total number of seedlings emerged until each date in each experimental replicate (irrespective of if they were still alive or not). From August 2010 survey, we calculated the *survival after first summer* as the number of individuals counted on this survey, divided by the total number of emergences occurred until this date. The *survival after first winter* was calculated as the number of individuals counted in April 2011 survey (excluding those newly emerged from August 2010 onwards) divided by the count in August 2010. Finally, the *size at one-year age* was calculated as the average size from all alive individuals within each experimental replicate on April 2011.

We wanted to assess the response of all these variables in models incorporating the same set of predictors: the *plot cover* (as a measure of habitat amount at the 50x50 m plot scale, coded as low or high), the *presence* of the species in the experimental plot (coded as binary, with 1 = presence and 0 = absence), the *microhabitat* where the sampling station was located (under canopy or in the open), and the *experimental treatment* (E = exclusion, O = open or C = control). These models also included the second- and third-order interactions between these predictors. Experimental site was not included as a predictor because previous analyses showed that variation between sites in all the response variables was negligible.

We fitted Generalized Linear Models (GLMs) with R 2.13.0 (R Development Core Team 2011) with different probability distributions and link functions depending on the response variable considered (see Table 3.1 for details). The choices of probability distributions for each model were made following Crawley (2007), in order to correct for potential overdispersion in the data. Separate models were fitted for emergence at each of the three survey dates and including all treatments. These models were then repeated excluding the replicates corresponding to the *Control* treatment. We assumed, in the first case, that a significant decrease of emergence in the *Control* treatment, relative to the other treatments, would be indicative of strong dispersal limitation, as it would mean that emergence from the natural, unmodified seed bank is low, and that emergence is much more probable when seeds are added (*Exclusion* and *Open* treatments). In the second case, removing the replicates from *Control* treatment allowed us to explore more deeply the effect of the rest of the predictors in terms of establishment limitation occurring between seed deposition and early emergence (e.g. due to seed predation). The model for number of emergences was fitted after removing the replicates from the *Control* treatment. The models for survival after first summer and winter, and that for size at one-year age, were fitted including only those experimental replicates where any individual was found at the considered survey date.

In all cases we fitted first a full model with the whole set of predictors and their second- and third-order interactions. Then we used stepwise combined model selection based on BIC (Bayesian Information criterion) to choose the most informative model. In models with quasibinomial distribution, model selection was made by successively removing factors from the full model, as BIC is not defined for this sort of models.

RESULTS

From the 1920 seeds sown, 414 germinated during the study period (22 %). More than 75 % of emergences happened before the May 2010 survey. Emergence from the natural seed bank was observed only in 4 (8 %) of the 48 experimental surfaces assigned to the *Control* treatment, with 54 emergences observed in total (from which 50 were found in the same experimental replicate). All of these emergences in the *Control* treatment occurred in plots where *P. vulgaris* was present.

The binomial GLMs revealed that the probability of emergence differed between treatments in the three survey dates considered (Table 3.1, Fig. 3.2). In all of them the *Control* treatment had a significant negative effect on emergence, and in August 2010 also the *Exclusion* had a significant positive effect. When the *Control* treatment was removed, all the predictors included in the model were not significant (and in August 2010 none of them was included in the model, Table 3.1). The number of emergences in May 2010 was higher when plot cover was low, but in the rest of the surveys it was not related to any of the predictors (Table 3.1).

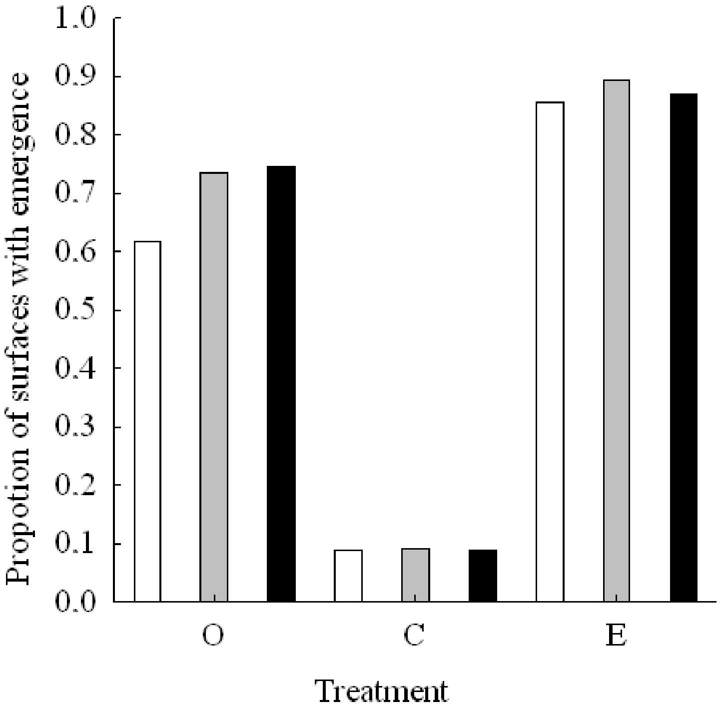

Figure 3.2: Proportion of experimental replicates where there was any emergence represented against treatment for each of the three surveys considered. White bars represent data for May 2010, grey bars data for August 2010 and black bars data for April 2011.

From the 414 emerged seedlings, 169 were still alive in August 2010 (41 %), and 134 in April 2011 (32 %). Survival responded differently to the set of predictors depending on the date considered (Table 3.1). After first summer, there was a positive effect of *P. vulgaris* presence, of the open microhabitat and of the *Exclusion* treatment, but the significance of these effects was due to the significance of their interactions (Table 3.1). This means that the effect of the experimental treatment on survival after first summer depended on the microhabitat and on the presence of the species (Fig. 3.3a). The experimental exclusion from predators and herbivores increased significantly seedling survival in those replicates located far from adult populations and under canopy cover. However, survival was higher in the *Open* than in the *Exclusion* treatment for replicates located under canopy and where *P. vulgaris* was present (although this difference was only marginally significant, see Table 3.1). On the other hand, survival after first winter was only related to the microhabitat, being higher in open habitats (Table 3.1, Fig. 3.3b).

Of the 134 emerged individuals which were still alive in April 2011, 86 were still considered as seedlings, due to the presence of cotyledons. The rest of individuals were classified as juveniles (39), vegetative adults (8) and reproductive adults (1). The size of individuals at one-year age was significantly larger in the *Exclusion* treatment and when the plot cover was low, although the significance of this last effect was due to the significance of its negative interaction with the presence of the species (Table 3.1). Size was significantly higher in plots with low cover when *P. vulgaris* was absent of the plot, but when it was present, the opposite trend was observed (although the difference between high and low-cover plots was only marginally significant, Fig. 3.4).

Response variable (distribution, link)		Dependent variables	May 2010		August 2010		April 2011	
			Estimate	p	Estimate	p	Estimate	p
Emergence (binomial, logit)	*Control* included	microhabitat (open)	0.17	0.7680				
		treatment (C)	-2.28	**0.0021**	-3.19	**<0.0001**	-3.39	**<0.0001**
		treatment (E)	0.55	0.3672	1.16	**0.0309**	0.62	0.2207
		microhabitat (open) x treatment (C)	-1.36	0.3058				
		microhabitat (open) x treatment (E)	17.50	0.9895				
	Control removed	microhabitat (open)	0.29	0.6280			-0.06	0.9319
		treatment (E)	0.55	0.3670			$1.98e^{-16}$	1.0000
		microhabitat (open) x treatment (E)	17.39	0.9900			17.52	0.9899
No. emergences (neg. binomial, log)[1]		plot cover (low)	0.51	**0.0279**				
Survival after first summer / winter (quasibinomial, logit)[1,2]		presence (1)			3.20	**0.0028**		
		microhabitat (open)			1.63	0.1234	1.31	**0.0258**
		treatment (E)			4.29	**0.0003**		
		presence (1) x microhabitat (open)			- 3.40	**0.0087**		
		presence (1) x treatment (E)			5.89	**<0.0001**		
		microhabitat (open) x treatment (E)			3.83	**0.0046**		
		presence (1) x microhabitat (open) x treatment (E)			5.88	**0.0005**		
Size at one-year age (negative binomial, log)[1,2]		presence (1)					0.51	0.3506
		plot cover (low)					1.15	**0.0054**
		treatment (E)					2.36	**<0.0001**
		presence (1) x plot cover (low)					-3.17	**<0.0001**

[1] *Control* treatment removed

[2] Included only experimental surfaces where any individual was found at the survey date considered

Table 3.1: Summary of the GLM results. Only final models resulting from model selection are shown. Boldface indicates significance (α = 0.05).

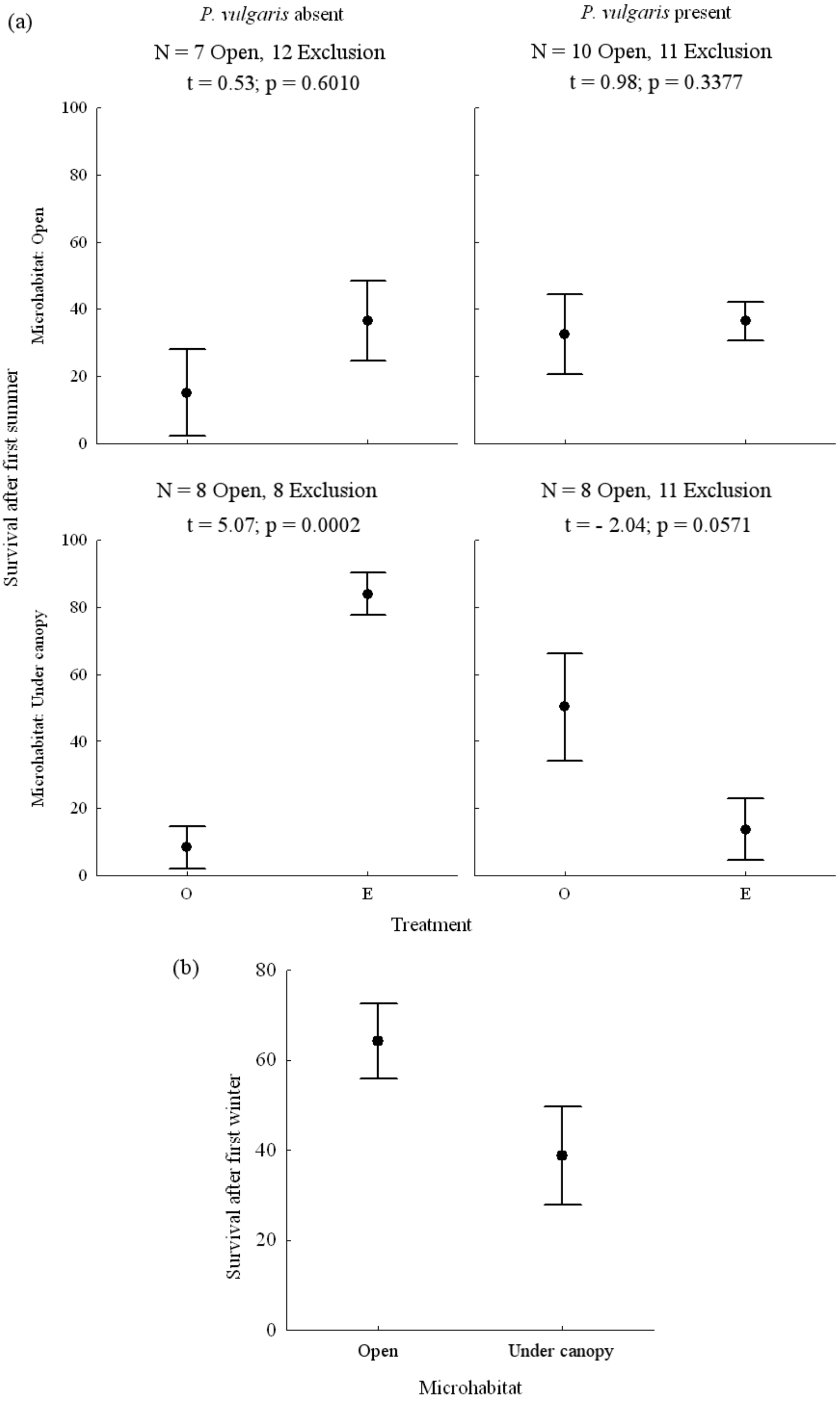

Figure 3.3: (a) Average (± SE) of survival after first summer by treatment, plotted separately for each combination of *P. vulgaris* presence and microhabitat (N, t- and p-values resulting from a GLM fit with distribution = quasibinomial and link = logit are shown in each case), and (b) Average (± SE) of survival after first winter by microhabitat (N = 23 open, 17 under canopy).

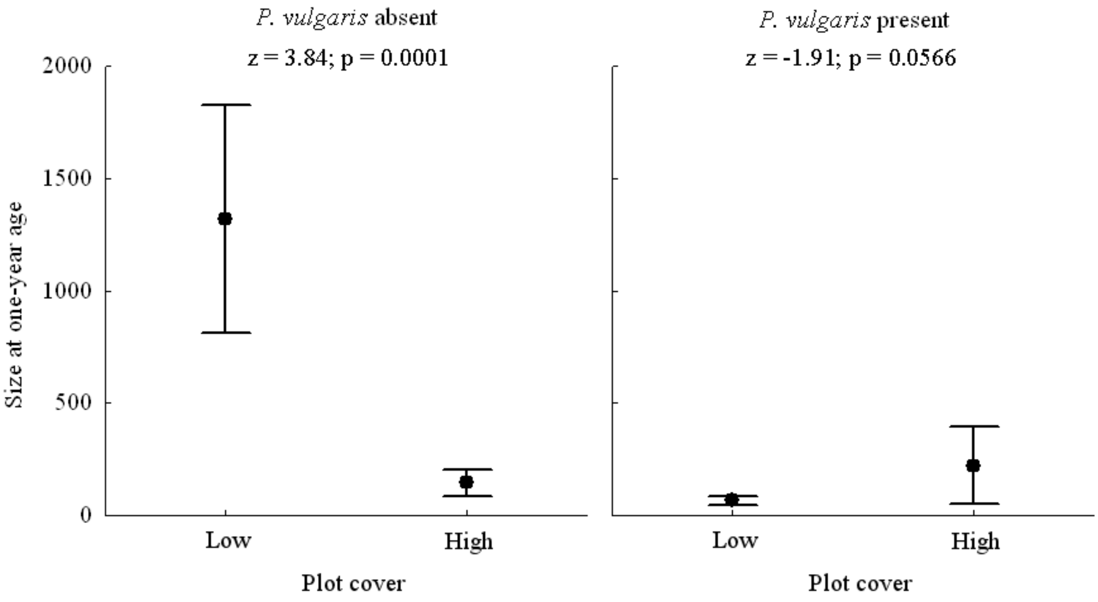

Figure 3.4: Average (± SE) of size at a year of age by plot cover, plotted separately for plots with *P. vulgaris* absent (N = 9 low, 9 high) and present (N = 7 low, 11 high), z- and p-values resulting from a GLM fit (distribution = negative binomial, link = log) in each case are shown.

DISCUSSION

In this study, we experimentally assessed the mechanisms limiting recruitment during several phases of early development in *P. vulgaris* in a fragmented landscape. We have found strong evidences of severe dispersal limitation, as seedling emergence in those experimental replicates where no seeds were added was very low, even in those located in plots where reproductive adults of the species were naturally present. Thus, dispersal limitation seems to be strong independently of landscape alterations, although reductions in seed production or increases in habitat subdivision would contribute to foster even more this limitation. After accounting for the effect of dispersal limitation, no limitation was apparent for the occurrence of seedling emergence, although the amount of seed germination by the end of the first spring comparatively increased in sectors were large-scale habitat amount was low. Nevertheless, the limitations associated to the availability of safe-sites for recruitment seemed to affect the subsequent phases of seedling life, both the survival and the growth of seedlings during the first year of life. Some of these establishment limitations interact with local and large-scale habitat amount, and with population features and the plant-animal interactions potentially resulting from landscape changes.

Dispersal limitation of seedling emergence

As very few natural emergences were observed in *Control* surfaces, our results suggest that recruitment in this species is highly restricted by seed availability during the phase of seedling emergence. The existence of strong dispersal limitation at the landscape scale was already suggested in a previous study with this species (Chapter 1), where probability of presence and abundance of *P. vulgaris* in a 50x50 m area was positively correlated with nearby plant abundance in a 150x150 m neighborhood (reflecting the abundance of nearby seed sources, Jacquemyn et al. 2001; Verheyen and Hermy 2001). Thus, dispersal limitation is the major limitation for recruitment of *P.* vulgaris, and it seems to be happening at both local (within plots with *P. vulgaris* populations) and broad scales, and this could limit local population size and plant distribution (Ehrlén and Eriksson 2000). Dispersal restrictions occur irrespective of the degree of landscape alteration, although habitat loss and subdivision can represent severe barriers for recruitment (Cordeiro and Howe 2001; Kunstler et al. 2007; McEuen and Curran 2004), due to the poor capacity of seeds to be dispersed over large distances between habitat fragments.

Seed limitation in *P. vulgaris* at our study site seems to be both due to the low seed production derived from population size reductions associated to habitat loss (the local seed sources do not saturate available microsites with seeds, Chapter 2, Ehrlén and Eriksson 2000), and to restricted seed dispersal at a local and broad scale. Previous studies have reported that dispersal distances are generally no more than a few centimeters from the maternal plant in this species (Cahalan and Gliddon 1985; Campagne et al. 2008). Ants seem rather ineffective in dispersing seeds of *P. vulgaris*, as they harvest only a limited proportion of the seeds available (Valverde and Silvertown 1995). This was confirmed by a previous field experiment performed in the same study area (*authors' unpublished data*) where we evaluated myrmecochory by placing Petri dishes with seeds each along a gradient from closed canopy to open sites. Ants (but not rodents or bigger animals) could enter into the dishes. After 15 days, only 22% of seeds disappeared from Petri dishes, highlighting the ineffectiveness of ant as seed dispersers. It has been demonstrated that slugs could also play a role in seed dispersal of forest herbs (Türke et al. 2010), and a slug seed feeding experiment (*authors' unpublished data*) showed that slugs (*Arion* spp.) are able to swallow and defecate seeds of *P. vulgaris* (mean percentage of seeds swallowed was 75%), but further studies should be performed in order to ascertain if this behavior occurs in field conditions. Finally, rodents have been documented to remove a high percentage of seeds in other studies (Valverde and Silvertown 1995). The higher probability of emergence in the *Exclusion* surfaces in the August 2010 survey could be reflecting a protective effect against seed removal by rodents, but this is not important in the other surveys (and we have to note that more than 75 % of emergences happened before May 2010). In summary, it seems that animal dispersal is scarce in this species in our study area, and that seed dispersal distances are small. Thus, the available seed pool might not be able to reach potential suitable sites for recruitment. Although long-distance dispersal events have been reported to occur in some forest herbs (Vellend et al. 2003), and Valverde and Silvertown (1995) considered rodents as long-distance dispersers of *P. vulgaris*, this kind of events seem to be particularly improbable for this species in our study area, as none of the *Controls* located in plots unoccupied by *P. vulgaris* showed any recruitment at all.

We have demonstrated that the emergence of seedlings from seeds was almost exclusively only limited by seed availability, as removing the *Control* treatment from the emergence model turned the rest of the factors not significant. However, the number of emergences increased in plots where forest cover was low, showing some sort of response of germination to habitat amount at a broad scale, probably due to higher light availability in these areas (Valverde and Silvertown 1995). There are no other establishment limitations acting at the phase of germination, and it seems that predispersal seed predation is not very important in our system, as revealed by the low importance of the effect of the *Exclusion* treatment. This contrasts with results from other species where pre- and postdispersal seed predation is very important for recruitment (Fedriani et al. 2004). In fact, rodents have been documented to be important predispersal predators by attacking fruits of *P. vulgaris*, removing the whole capsules and leaving only the stalks and occasional capsule remains on the ground (Brys et al. 2004; Valverde and Silvertown 1995). This has not been evaluated specifically in the present study, but previous field observations suggest that fruit predation is scarce in our study area. However, this low predispersal predation cannot be attributed to a low predator abundance, as suggested by the strong seed predation by rodents suffered by woody species in the same area (García et al. 2005a).

Establishment limitation of seedling survival and growth

Although establishment limitation was not very important for seedling emergence, our data demonstrated that several environmental constraints affected the subsequent phases of seedling life. Survival of seedlings after first summer was maximized in the *Exclusion* treatment in experimental stations located under canopy and in areas where *P. vulgaris* was absent. The exclusion treatment enhanced survival in areas lacking *P. vulgaris*, thus revealing that animal damages to seedlings (browsing, trampling, etc.) could be an important factor decreasing survival probability in these areas. However, damage by animals seems to be less important in areas hosting populations of *P. vulgaris*, as in fact in these areas survival tended to be higher in the *Open* treatment. The spatial variation in the contrast between the *Exclusion* and *Open* treatments, and in the magnitude of net effects of the exclusion on survival, suggest that other mortality factors, different to animal predators excluded by the boxes, were also taking part in generating establishment limitations across the fragmented landscape. In this sense, mortality by specific pathogens like fungi (Bell et al. 2006), more prone to occur in areas where adults are abundant, could explain the difference in the effects of exclusion on survival between areas with and without *Primula*.

The *Exclusion* treatment did not provide any benefit in areas where there are established populations of the species, and damages to seedlings by animals seem to be less frequent in these areas than in areas without *P. vulgaris*, where the experimental seedlings can be much more conspicuous and prone to herbivore attack. Increased survivorship of seedlings in areas where many adult plants are present has been attributed to satiation of herbivores (Schupp 1992), and this could make seedlings in our experimental surfaces escape from herbivory in areas where the species is present. This could be true for small herbivores like invertebrate larvae, slugs or rodents but not for larger ones like deer or cattle. But this sort of positive denso-dependence with established plants might also be due to positive environmental effects (habitat favorability, *sensu* Uriarte et al. 2010), reflecting underlying soil quality or other environmental factors not evaluated in this study. This was only evident for survival after summer, but not after winter, probably because of the higher abundance of cattle, which grazes and tramples on *P. vulgaris*, during the summer period (*pers. obs.*).

Seedling establishment has been documented to increase with light levels below a threshold value, but to fail above certain threshold of light availability due to increased risk of seedling desiccation and mortality (Uriarte et al. 2010). Our results show that seedling survival after the first summer is generally high in stations located under cover, but on the other hand, survival after winter increases in open stations. This is probably due to above-threshold levels of photosynthetically active radiation in open areas during the summer period, causing seedling mortality because of water stress, but below-threshold values in these areas during winter, seedling survival increasing with light availability during this period (Valverde and Silvertown 1995).

Individual growth was lower in *Open* surfaces, leading to smaller plant sizes, and revealing some negative effect of animal damages on growth. Herbivory has been acknowledged to have an indirect effect on seedling growth (Meiners and Handel 2000), as partial consumption generally does not kill the seedling, but it reduces its competitive abilities. We believe that the same might happen with trampling. Individual size responded to large-scale habitat amount mostly when there were no nearby populations of *P. vulgaris*. This shows that some kind of negative denso-dependence is present, probably due to resource competition (for light, water or nutrients) with conspecific adults or other forest plants, reducing seedling growth (Tyler and D' Antonio 1995; Wright 2002). We also found negative denso-dependence effects on reproduction, as individual fruit production at the local scale increased in areas with low plant aggregation (Chapter 2). There was also some effect of forest availability at a large scale: sites with low habitat amount are also more fragmented, and this could increase light input received by individuals growing in these areas.

Concluding remarks

As it has been found for some other perennial herbs, including other species of this genus (*P. elatior*, Verheyen and Hermy 2001), *P. vulgaris* recruitment is limited by both seed dispersal and seedling establishment. In this study, we highlight that these limitations occur sequentially. Seedling emergence is nearly only limited by seed availability, and it seems that seeds are able to germinate in some percentage irrespective of the environmental conditions of the site where they arrive, although higher amounts of seeds germinate when habitat amount at a broad scale was low. Nevertheless, herbivory, presence of established populations of the same species and habitat amount at local and large scales played a significant role in the following phases of development, many of their effects being interdependent. It seems that dispersal limitations are not dependent on habitat loss and fragmentation, as they occur independently of the landscape and local habitat context. However, these processes are especially detrimental for recruitment if plants are dispersal-limited. On the other hand, habitat and population modifications resulting from landscape change can trigger some kind of establishment limitations, compromising plant recruitment in altered landscapes (Bruna 2002; Uriarte et al. 2010).

We have evaluated *P. vulgaris* recruitment until germinated plants reached approximately one year of life from emergence (see Methods). As the bottleneck of recruitment occurs after seedling emergence (Ehrlén and Eriksson 2000), it has been acknowledged that short-term recruitment studies may overestimate habitat suitability; this is, they may state that some kind of habitat is suitable for plant recruitment when in fact it is only suitable for the first stages of plant development, but not for later stages or for adult plants. We have tried to go beyond seedling emergence and record further seedling survival in two seasonal periods together with seedling size, as a surrogate of growth capacity. Our results show that mortality is higher during germination (78 %) than during the seedling phase (59% after summer and 68% after winter). However, seedling emergence, although low, was generally widespread in our experimental surfaces with added seeds, but when regarding seedling survival and growth, some environmental restrictions resulting from habitat loss and fragmentation arose. Further monitoring of surviving individuals is needed in order to find out if there are other major environmental obstacles in the development till the adult stage, as by April 2011 only around 7 % of the emerged individuals in our experimental surfaces had reached the adult stage. *P. vulgaris* presence, abundance, reproduction and population growth rate have been shown to increase in areas with high percentages of forest cover in previous landscape-scale studies (Chapter 1, 2, 4), and thus it seems that established populations perform better in forest habitats. Even seedling survival from one year to the next has been documented to show a strong increase with forest cover (Chapter 4). This is not contradicted by our current finding of higher seedling survival in open microhabitats after first winter, because the former studies have only measured landscape-scale forest cover. Our finding agrees with previous studies on these species reporting the benefits of higher light availability in small-scale forest canopy gaps for seedling establishment (Valverde and Silvertown 1995). However, seedling size was higher in plots with low broad-scale habitat amount, and this might reflect a change in habitat requirements between 1-year seedlings and adult individuals (life stage conflicts, *sensu* Schupp 1995, or ontogenetic niche shifts, *sensu* Young et al. 2005).

ACKNOWLEDGEMENTS

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4

Landscape change alters population growth of a perennial forest herb: integrative effects of landscape processes across multiple life-cycle stages

Valdés, A., García, D., García, M. B. and Ehrlén, J. (*in prep.*). Landscape change alters population growth of a perennial forest herb: integrative effects of landscape processes across multiple life-cycle stages.

ABSTRACT

Landscape change affects the demographic performance of plant species via habitat loss, habitat subdivision and edge increase. Studies up to date have been mostly partial, focusing on single landscape processes or life-cycle phases, but there is a need of ascertaining the differential effects of different processes on each vital rate conforming the plant life cycle and driving overall population growth. This knowledge will be useful to effectively assess and manage the current and long-term viability of plant populations under global change scenarios. We also need to evaluate the effect that changes in each vital rate cause on population growth, and how this influence changes along the gradients of landscape modification. In this study, we evaluate the effect of landscape change on survival, growth, reproduction and recruitment, and the overall population dynamics over three years, of a perennial forest plant (*Primula vulgaris*) in a historically managed landscape, performing also simulations to predict future population responses to different global change scenarios. Habitat availability and edge amount contributed to increase many vital rates for the interval 2008-2009. Highly-forested, but moderately-fragmented areas showed higher population growth rates, especially due to the positive effects of forest cover on seedling survival, reproduction and recruitment, and of forest edge length on reproductive adult survival. However, demographic effects were weaker for the period 2009-2010, when recruitment no longer contributed to the observed variation in population growth. Simulations showed that population growth rate in the long run responded similarly to forest habitat availability and forest edge length, and increased when there was a high frequency of high-growth intervals. The different processes of landscape alteration show counterbalanced effects on plant population dynamics: population growth was hampered by habitat loss, but some degree of fragmentation may be beneficial. Larger forest patches represent a high-quality habitat for survival and reproduction, and hence for population growth. Although population growth shows strong between-year variation, probably related to climatic variability, an increased frequency of high-growth events would increase the differences in population dynamics across the landscape change gradients. Thus, we advocate for further long-term studies elucidating the possible interactions between plant demographic responses, landscape patterns and climatic variability.

RESUMEN

El cambio en el paisaje afecta al comportamiento demográfico de las especies de plantas a través de la pérdida y subdivisión del hábitat y del incremento en la cantidad de borde. Los estudios hasta la fecha han sido generalmente parciales, centrándose en un solo proceso de cambio o en determinadas fases del ciclo vital, pero existe la necesidad de establecer los efectos diferenciales de distintos procesos en cada tasa vital que forma parte del ciclo de vida de las plantas y que determina el crecimiento global de la población. Estos conocimientos serán útiles para evaluar y gestionar de forma efectiva la viabilidad presente y futura de las poblaciones de plantas ante escenarios de cambio global. También necesitamos evaluar el efecto que los cambios en cada tasa vital causan en el crecimiento poblacional, y cómo esta influencia cambia a lo largo de los gradientes de modificación del paisaje. En este estudio, evaluamos el efecto del cambio en el paisaje en la supervivencia, crecimiento, reproducción y reclutamiento, y en la dinámica poblacional global a lo largo de tres años de una planta forestal perenne (*Primula vulgaris*) en un paisaje históricamente manejado, realizando también simulaciones para predecir las respuestas poblacionales futuras ante diferentes escenarios de cambio global. La disponibilidad de hábitat y la cantidad de borde contribuyeron a incrementar muchas tasas vitales en el intervalo 2008-2009. Poblaciones en áreas con elevada cantidad de bosque, pero moderadamente fragmentadas, mostraron mayores tasas de crecimiento, especialmente debido a efectos positivos de la cobertura forestal en la supervivencia y reproducción de plántulas y en el reclutamiento, y de la longitud de borde forestal en la supervivencia de los adultos reproductores. Sin embargo, los efectos demográficos fueron más débiles en el período 2009-2010, cuando el reclutamiento no contribuyó a la variación observada en el crecimiento poblacional. Las simulaciones mostraron que la tasa de crecimiento poblacional a largo plazo respondió de forma similar a la disponibilidad de hábitat forestal y a la longitud de borde, y se incrementó cuando existió una alta frecuencia de intervalos de crecimiento elevado. Los diferentes procesos de alteración del paisaje muestran efectos balanceados en la dinámica poblacional de las plantas: el crecimiento poblacional se redujo con la pérdida de hábitat, pero cierto grado de fragmentación resultó beneficioso. Los parches grandes de bosque representan un hábitat de alta calidad para la supervivencia y reproducción, y por tanto para el crecimiento poblacional. Aunque existe fuerte variación entre años, probablemente relacionada con la variabilidad climática, un aumento de la frecuencia de períodos de crecimiento elevado puede incrementar las diferencias en dinámica poblacional entre los gradientes de paisaje. Por lo tanto, son necesarios estudios a largo plazo para elucidar las posibles interacciones entre respuestas demográficas de las plantas, patrones de paisaje y variabilidad climática.

INTRODUCTION

Large-scale habitat degradation and fragmentation are among the major causes of biodiversity loss worldwide (Wilson 1985; Fahrig 2003; Sutherland et al. 2009). The alterations of landscape structure driven by these anthropogenic disturbances may affect the demographic performance of plant species in original remnant habitats, leading populations to severe declines (Hobbs and Yates 2003), or even to local extinction (Fischer and Stöcklin 1997). The demographic effects of landscape change derive from the simultaneous and interdependent occurrence of three different processes: habitat loss, which leads to direct reductions of population sizes (Swift and Hannon 2010); habitat subdivision, which increases isolation between populations, causing disruptions in individual dispersal capacity and gene flow resulting in indirect reductions of population sizes (Graae 2000); and edge increase, which changes the environmental conditions on habitat boundaries due to the influence of the degraded habitat matrix, altering, among others, microclimate or species interactions (Ries et al. 2004).

The consequences of landscape change on plant individual fitness components and on overall species abundances and distributions have been extensively studied (Saunders et al. 1991; Fahrig 2003; Lienert 2004). However, approaches trying to elucidate demographic effects have been partial, as most studies only consider single landscape processes (mostly habitat loss, represented by habitat availability or size of the habitat fragments) as the drivers of demographic collapse (Bruna and Oli 2005; García and Chacoff 2007; Cordeiro et al. 2009). Moreover, empirical studies usually focus on single phases or stages of the life cycle, commonly reproduction (Chapter 2; Aizen and Feinsinger 1994; Cunningham 2000; Rabasa et al. 2009), or they estimate effects on the basis of static measures of demographic inputs (seed or seedling number, Herrera and García 2010; Uriarte et al. 2010). Therefore, little is known about the differential effects of habitat loss and fragmentation processes on the complete set of vital rates conforming the whole life cycle of plants (i.e. including survival, growth, and reproduction) and driving overall population growth. Achieving such an integrative mechanistic understanding is a requisite to develop effective tools for managing the current growth of plant populations in altered landscapes, but also to predict their long-term viability under global change scenarios, characterized by the synergistic action of landscape alteration and climate warming (Leimu et al. 2010).

Understanding how landscape alteration affects plant population growth first requires identifying which landscape processes affect each demographic vital rate. For example, seed production and seedling survival are known to be negatively affected by habitat loss and increased habitat isolation (Steffan-Dewenter and Tscharntke 1999; Kolb 2005), whereas individual growth seems to be hampered due to the abiotic changes imposed by edge increase (Bruna et al. 2002). However, a significant landscape effect on a given vital rate does not necessarily translate into an altered population dynamics, given that not all the vital rates affect equally to population growth. For example, the populations of many perennial plants may persist over long periods, even when habitat fragmentation disrupts reproduction and seed production, if adult survival is the major driver of population dynamics (e.g. Colling and Matthies 2006). Thus, associating the alterations of vital rates to specific landscape processes is not enough, and it must be completed with the identification of the key vital rates having a highest influence on population growth along the gradients of landscape modification (Bruna et al. 2009). Analyses oriented to determine the vital rates that mostly account for the response of population growth rate to landscape features are essential to fully understand the ultimate mechanisms by which landscape change drives population dynamics to collapse, but also to manage extinction debts, that is, situations where population collapse is delayed with respect to the changes in landscape structure (Honnay et al. 2005; Vellend et al. 2006).

In this study, we integrate the complex effects of the multiple landscape change processes (habitat loss, habitat subdivision and edge increase) acting over multiple life-cycle stages. We evaluate the effect of landscape change on survival, growth, reproduction and recruitment, and the overall population dynamics over three years (comprising thus two yearly intervals), of a perennial forest plant (*Primula vulgaris*) in a historically managed landscape. As the effect of landscape change and other large-scale environmental conditions (i.e. climate) on population growth may vary across years, we also perform simulations to predict future population responses to different scenarios accounting for different levels of landscape change and climatic variability. Specifically, we seek to answer the following questions: (1) Which processes of landscape change (habitat loss, habitat subdivision, edge increase) have important effects on the different vital rates? (2) Which are the overall effects of these processes on actual population growth rate and the long-term viability? (3) Which are the vital rates that mostly account for the response of population growth to landscape change?

METHODS

Study species

Our target species is *Primula vulgaris* L. (Primulaceae), a perennial, early-flowering herb, typically living in moist open habitats in Europe (Endels et al. 2002b), but restricted to temperate forests in some parts of its range (Jacquemyn et al. 2009). In the Cantabrian mountains (Northwestern Spain, our study region) it behaves mainly as a forest species, although it can be also found in some other semi-shaded locations, like roadsides and trails. It grows through the production of leaves in basal rosettes, and vegetative spread is uncommon but possible through lateral rosettes. Flowers are pale yellow and borne on separate stalks. Flowering in our study area lasts from late winter (February) to late spring (June), peaking at the end of March-beginning of April (authors' unpublished data). *Primula vulgaris* is distylous and only between-morph pollination (mainly by Hymenoptera and Diptera) results in seed production, although the system allows for certain levels of self-fertilization (Endels et al. 2002a). Biased morph frequency in small populations leads to reduced reproductive output (Brys et al. 2004). Fruits (capsules containing 30-50 small seeds with an elaiosome) are consumed by ungulates, rodents and Lepidoptera larvae. Seeds are thought to be dispersed mainly by barochory, but there is also some evidence of occasional dispersal by ants and slugs (Valverde and Silvertown 1995; authors' unpublished data).

Study site

Our study was carried out in Sierra de Peña Mayor, Asturias, Spain (43º17' N – 5º30' W, 900 m a.s.l.), within the Cantabrian Range. The climate of the region is Atlantic, with a mean annual temperature of 13 ºC and annual rainfall of ca. 1300 mm. This area has suffered from historical deforestation for cattle grazing, as many other parts of the Cantabrian Range (García et al. 2005b). As a result, the landscape has changed from continuous temperate forests to a heavily fragmented wood-pasture habitat.

The sampling area (Fig. 4.1) is located along a North-South axis through the study site. It covers approx. 3000 m long and 1000 m wide and comprises a highly variegated forest landscape (sensu McIntyre and Hobbs 1999). That is, it presents a mosaic composed of a few large forest fragments with hardwood species (beech: *Fagus sylvatica* L. and ash: *Fraxinus excelsior* L.), fringe fleshy-fruited, bird-dispersed trees (holly: *Ilex aquifolium* L., hawthorn: *Crataegus monogyna* Jacq., yew: *Taxus baccata* L., rowan: *Sorbus aucuparia* and whitebeam: *Sorbus aria*) and hazel (*Corylus avellana* L.), as well as numerous small forest fragments mostly composed of fleshy-fruited trees, and a matrix of stony pastures and heathlands (*Erica* spp., *Ulex europaeus* L.), covering ca. 60% of the area. Within this area, in 2008 we chose 15 square plots (150x150 m, Fig. 4.1) containing *P. vulgaris*, representing a landscape-scale gradient of habitat loss and fragmentation, where landscape sampling and population censuses were performed.

Sampling design

We based our landscape analyses on a Geographic Information System (Hargis et al.) of the study area (ArcGIS 9.1, see Valdés and García 2009 for details), where we incorporated a layer representing forest cover. For each 150x150 m plot, we calculated three variables describing the degree of landscape change. The percentage of forest cover was used as a measure of habitat availability and an inverse measure of habitat loss. The number of forest patches was used as a measure of habitat subdivision. The length of forest perimeter was used as a measure of edge amount. There was considerable variation in these parameters (mean ± SD was 69.03 ± 16.54 for percentage of forest cover, 516,59 ± 205,79 m for edge length, and 2,07 ± 1,67 for number of patches).

It is well-known that fragmentation measures such as fragment isolation and edge length are usually dependent on habitat availability (Fahrig 2003), and in our data the length of forest edge showed a high correlation with forest cover ($r = -0.71$, $p = 0.0028$), as did the number of forest patches ($r = -0.55$, $p = 0.0318$). Thus, we fitted quadratic regression models of length of edge and number of forest patches against the percentage of forest cover, and used the residuals of these regressions in the rest of our analyses (see Hargis et al. 1998; Villard et al. 1999 for similar approaches). This allowed us to test for the effects of habitat subdivision and edge density independently of habitat loss effects. So hereafter, when we talk about the variables ‘length of forest edge’ and ‘number of forest patches’ we are always referring to the residual values of these regressions.

We carried out annual population censuses in three 2x1 m subplots within each of the 15 larger plots (Fig. 4.1), at the beginning of July 2008, 2009 and 2010. We were able to visually distinguish three types of individuals: seedlings, vegetatives and reproductives, although we considered four stage categories based on biological attributes (Valverde and Silvertown 1998; Endels et al. 2002b): seedlings (with cotyledons still present), juveniles (vegetative plants with one rosette and a smaller diameter than the average of reproductive individuals in the same population), vegetative adults (vegetative plants with one or two rosettes, a diameter comparable to that of reproductive individuals, and often showing signs of overwintering leaves, hereafter vegetatives), and reproductive adults (plants with flowers and/or flower buds, hereafter reproductives). We did not include a seed stage in our models because available information does not suggest the existence of a long-term seed bank in *P. vulgaris* (Thompson et al. 1997, pers. obs.).

We performed annual censuses at the beginning of July, just after fruit ripening and when seeds are being dispersed, but before germination. In July 2008, we made a map of each subplot. All the plants but seedlings were located by means of X-Y coordinates, and their stage category was recorded. Seedlings were counted and mapped in a subsample of the area of the subplot, covered by 4 randomly distributed permanent square plots (25x25cm each). In 2009 and 2010, each subplot was carefully inspected: mapped plants were relocated and their stage was assessed. The fate of seedlings from the previous year was determined in the small square plots, where new seedlings were also counted and mapped.

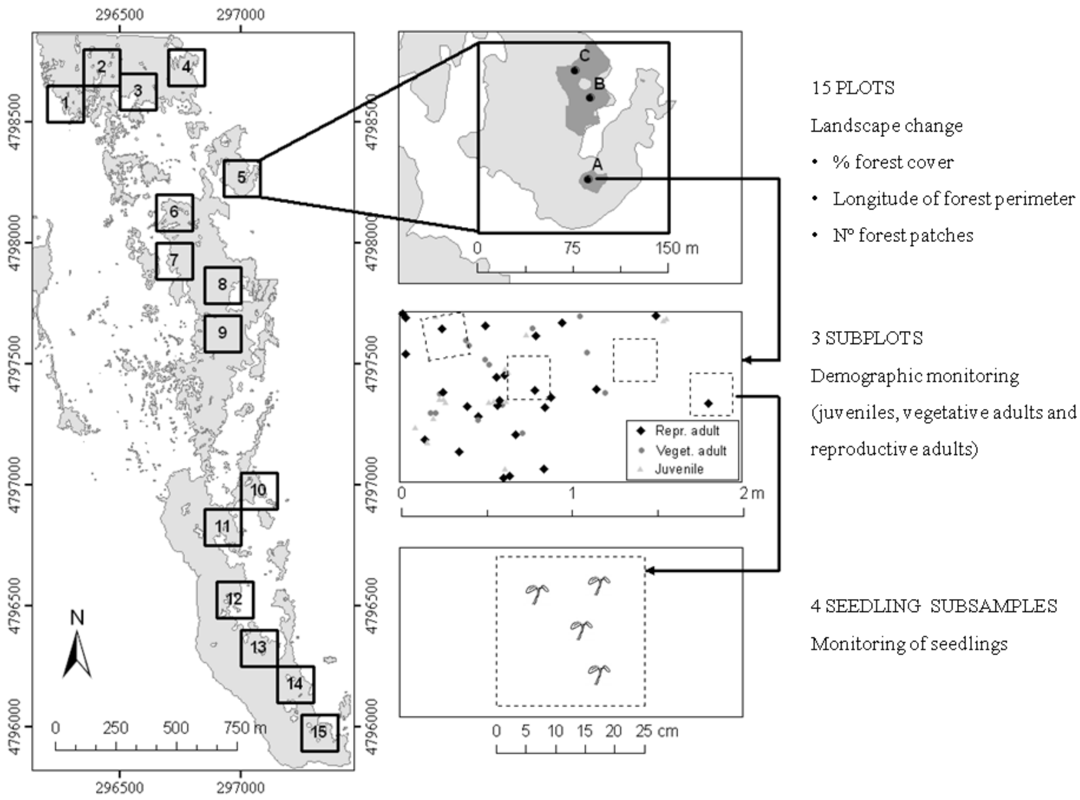

Figure 4.1: Outline of the framework for sampling landscape change and demographic parameters of *P. vulgaris* along a gradient of different landscape configurations. Grey area represents forest cover.

Data analysis

Calculation of vital rates

From the census data, we calculated vital rates for each stage category in each plot by pooling data from the 3 subplots. Specifically, we calculated the probabilities of survival (proportion of individuals in a stage at the previous census that were still alive at the following census), reproduction (proportion of reproductive individuals at each census related to the total number of individuals of all stages in the previous census), the probabilities of seedlings and juveniles growing to vegetatives (proportion of individuals at those categories that turned into vegetatives at the following census) and the recruitment rate (average number of seedlings produced per reproductive during the interval from one census to the next, calculated by dividing the number of seedlings found in a census by the number of reproductives found in the previous one).

When the number of individuals in the seedling stage at a given census was less than 10 within a plot (which occurred in 9 and 3 plots out of 15 in 2009 and 2010 respectively), we did not calculate the vital rates involving seedlings (probabilities of seedling survival, reproduction and growth to vegetative adult) for that plot, because we believe they could not be reliable with so few individuals.

We evaluated the differences in vital rates between the two yearly intervals by means of one-way ANOVAS.

Matrix construction, calculation of population growth rates and relationship with landscape change

We constructed stage-classified matrix models according to the standard procedure (Caswell 2001): $n(t+1)=An(t)$, where A is a matrix describing how individuals in each stage class of a population with a given abundance of plants in each class $n(t)$ contribute to a new population structure $n(t + 1)$. For each plot, we constructed two matrices (one for 2008-2009 and another for 2009-2010) from the estimated vital rates. Each matrix element was calculated as a combination of two or more underlying vital rates (Table 4.1). For the plots without information on seedling survival, we used values of the most similar plot in terms of forest cover and higher seedling abundance.

We also constructed a set of predicted matrices based on the relationships between estimated vital rates and landscape variables (for a similar approach see Kolb et al. 2007). We assessed the variation in vital rates along the gradient of alteration by fitting linear regressions of every vital rate against each of the three landscape change variables in the two yearly intervals (statistical significance level for regressions was set at $\alpha = 0.1$). For the 2008-2009 interval, five vital rates were significantly related to the percentage of forest cover, and other four vital rates to the forest edge length (Table 4.2). For 2009-2010, three vital rates were significantly related to forest cover and one vital rate to forest edge length (Table 4.2). None of the vital rates was significantly related to the number of forest patches. Regression functions were used to estimate predicted vital rates for each value of percentage of forest cover (units, from 40 to 100%) and length of forest edge (10-units intervals, from -300 to 300). For those vital rates unrelated to landscape variables we calculated the across-plot average value (N=15; all the plots with available values in the case of the vital rates involving seedlings). Predicted and averaged values of vital rates were used to calculate matrix elements, leading to predicted matrices for the whole landscape change gradient; this is, one predicted matrix for each value of percentage of forest cover, length of forest edge, and yearly interval.

We calculated the deterministic population growth rates (lambda, λ), defined as the dominant right eigenvalue of the matrix A (Caswell 2001), for each plot and yearly interval, as well as for each of the predicted matrices. Demographic growth rates were calculated using the PopTools add-in for Microsoft Excel (Hood 2009).

	Seedling	Juvenile	Veget. adult	Reprod. adult
Seedling				Re
Juvenile	Ss*(1-Sr)*(1-Sv)	Js*(1-Jr)*(1-Jg)		
Veget. adult	Ss*(1-Sr)*Sv	Js*(1-Jr)*Jg	Vs*(1-Vr)	Rs*(1-Rr)
Reprod. adult	Ss*Sr	Js*Jr	Vs*Vr	Rs*Rr

Table 4.1: Matrix elements of *P. vulgaris* expressed as combinations of vital rates (Ss = probability of seedling survival, Sr = probability of seedling reproduction, Sv = probability of seedlings growing to vegetative adults, Js = probability of juvenile survival, Jr = probability of juvenile reproduction, Jg = probability of juveniles growing (to vegetative adults), Vs = probability of vegetative adult survival, Vr = probability of vegetative adult reproduction, Re = average number of seedlings produced per reproductive adult, Rs = probability of reproductive adult survival, Rr= probability of reproductive adult reproduction).

We performed linear regressions to assess the effect of forest habitat availability and forest edge length on population growth rates in each of the two intervals studied. For regressions, we used the values of λ estimated from the original matrices of each plot (N=15) as well as the values of λ obtained from predicted matrices over the landscape change gradient (N=61 for each landscape variable and yearly interval).

Simulations of population growth

As we found a significant variation on average λ values between the two yearly intervals, as well as strong differences in the climatic conditions, we sought to evaluate the long term effects of landscape change and temporal variability in population growth rate. To do this, we developed stochastic models to calculate the stochastic population growth rate (λ_s) for different combinations of landscape features (forest cover and edge length) and frequencies of occurrence of high-growth intervals (from 0 to 1, at 0.05 intervals). Stochastic population growth rates were calculated, based on simulations of 5000 iterations, for each combination of two values of landscape features and frequency of occurrence of high-growth intervals, to represent which is the most likely population growth rate over a sequence of years (Caswell 2001; Morris and Doak 2002). These analyses were performed with R (R Development Core Team 2011) using the popbio package (Stubben and Milligan 2007).

Sensitivity and LTRE analyses

In order to identify the vital rates that contributed the most to the observed variation in lambda along the landscape change gradient, we used a regression Life Table Response Experiment (LTRE, Caswell 2001).

Originally thought to determine how a treatment alters vital rates, and how observed changes affect population growth, LTRE may be applied to population matrices calculated along continuous gradients of factors like herbivory (Knight et al. 2009) or time since last fire (Kesler et al. 2008). Thus, this analysis enabled us to decompose the total effects of habitat availability (percentage of forest cover) and edge amount (forest edge length) on population growth rate into the effects via each vital rate. We performed separated analyses for each yearly interval, using the predicted values of those vital rates which showed significant linear relationships with habitat availability or forest edge length (see above and Table 4.2). Our analysis followed three consecutive steps, leading to three different estimators.

First, we calculated the sensitivities of population growth rate to changes in vital rates for each of the predicted matrices representing population dynamics along the landscape gradient. Sensitivity values represented to what extent lambda was influenced by the changes in a particular vital rate (Ehrlén and Van Groenendael 1998; Morris and Doak 2002; Franco and Silvertown 2004).

Second, we multiplied these sensitivities by the slope of the regression between the vital rate and the landscape change variable to which it was related (β values in Table 4.2). The results of these products were the slope coefficients of the relationship between population growth rate and landscape change variables, through each vital rate. These slope coefficients represented how lambda varied in response to landscape change variables through each particular vital rate, and thus are useful to decompose the effects of landscape on lambda into effects via different vital rates. Slope coefficients are calculated for all values along the landscape gradient. When plotted against forest cover or edge length, small, near-to-zero values of the slope coefficient indicate that landscape change has little effect on the vital rate, that lambda is not sensitive to changes in that vital rate, or both. Positive values indicate positive responses of lambda to landscape features.

And third, we estimated the actual LTRE contribution of each vital rate to the variation in population growth rate for all points along the landscape gradient, by multiplying the previously calculated slope coefficients by the values of the landscape feature (percentage of forest cover or forest edge length), centered on their respective means. These contributions show the differences in population growth rate due to each particular vital rate between the populations located at a given point of the landscape gradient with respect to to those populations located at the average value of the gradient (for, respectively, forest cover or edge length). When plotted against forest cover or edge length, small, near-to-zero values indicate non-significant and homogeneous effects of a given vital rate on population growth, irrespective of landscape features. At a given point of the landscape gradient, this value will be either negative or positive depending on whether the landscape change variable is below or above its mean value and on the sign of the slope coefficient of the relationship between population growth rate and the landscape feature. High absolute values indicate that a given vital rate accounts for a high part of the landscape effect on lambda. For example, in a below-average point of the forest cover gradient, a highly negative or a highly positive contribution would indicate that lambda is very sensitive to a given vital rate that, respectively, decreases or increases significantly at low forest cover values. This would be the opposite for above-average points of the gradient.

		% Forest cover		Length of forest edge	
Interval	Vital rate	β	R^2	β	R^2
2008-2009	Seedling survival	0.0049	0.3430		
	Seedling growth			-0.0008	0.8927
	Seedling reproduction	0.0102	0.4630		
	Juvenile growth			0.0009	0.3171
	Juvenile reproduction	0.0048	0.2101		
	Vegetative reproduction	0.0053	0.2356		
	Reproductive survival			0.0003	0.3368
	Reproductive reproduction			-0.0002	0.2740
	Recruitment	0.0400	0.3101		
2009-2010	Seedling survival	0.0030	0.5382		
	Seedling reproduction	0.0043	0.3539		
	Vegetative reproduction	0.0035	0.1873		
	Reproductive survival			0.0003	0.2652

Table 4.2: Relationships between vital rates and landscape change variables in the two yearly intervals studied. β and R^2 for significant linear regressions are shown ($\alpha = 0.1$; n=15, except for regressions of vital rates related to seedlings where n=6 for 2008-2009 and n=12 for 2009-2010).

RESULTS

Description of populations

The density of individuals of the different stage classes did not differ between intervals, except for the reproductives, which were more abundant in 2008-2009 than in 2009-2010 (Table 4.3). Vital rates showed considerable variation between intervals, and more seedlings survived and grew to vegetatives, more vegetatives and reproductives reproduced, and higher recruitment occurred, in 2008-2009 relative to 2009-2010. Conversely, more juveniles grew to vegetatives in 2009-2010 than in 2008-2009.

Stage		2008-2009		2009-2010		t	P > |t|
		Mean	CV	Mean	CV		
Seedling	Density at the beginning	29.33	0.64	44.44	1.23	1.11	0.2848
	Survival	0.18	0.75	0.11	0.73	-2.30	0.0375
	Reproduction	0.04	2.22	0.20	1.21	2.12	0.0634
	Growth to vegetative	0.13	1.22	0.03	3.46	-2.28	0.0486
Juvenile	Density at the beginning	17.62	0.41	16.92	0.45	-0.87	0.3988
	Survival	0.55	0.18	0.48	0.21	-2.06	0.0584
	Reproduction	0.27	0.63	0.19	0.52	-1.94	0.0726
	Growth to vegetative	0.22	0.96	0.71	0.19	8.62	<0.0001
Vegetative	Density at the beginning	6.22	0.46	7.63	0.52	1.74	0.1041
	Survival	0.69	0.14	0.72	0.15	0.73	0.48
	Reproduction	0.71	0.25	0.39	0.34	-7.06	<0.0001
Reproductive	Density at the beginning	17.50	0.30	22.03	0.29	10.47	<0.0001
	Survival	0.82	0.07	0.82	0.08	0.06	0.9565
	Reproduction	0.96	0.05	0.70	0.13	-11.48	<0.0001
	Recruitment	2.66	0.90	1.26	0.62	-2.35	0.0338

Table 4.3: Mean values and coefficients of variation (CV) of the density at the beginning (number of individuals per square meter) and the vital rates for each of the stages and intervals (N=15 plots). Results of paired t-tests comparing each parameter between intervals are also shown.

Population growth rates (λ) calculated from the matrices based on the original data from sampling plots ranged from 0.71 to 1.30 (mean 0.97 ± 0.04 SE) for 2008-2009 and 0.69 to 0.92 (mean 0.83 ± 0.02 SE) for 2009-2010. Lambdas estimated from matrices based on vital rates predicted along the complete landscape gradients ranged from 0.76 to 1.32 (mean 1.00 ± 0.00 SE) for 2008-2009 and 0.74 to 0.93 (mean 0.83 ± 0.00 SE) for 2009-2010. Population growth rates were significantly higher in 2008-2009 than in 2009-2010, for both types of matrices (paired t-test: $t = -4.22$, $P > |t| = 0.0009$ for original data, and $t = -95.09$, $P > |t| < 0.0001$ for predicted data).

Relationships between landscape features, vital rates and population growth rates

Seedling survival, the transition of seedlings, juveniles and vegetatives into reproductive plants, and recruitment rate were significantly higher in highly forested areas in 2008-2009 (Table 4.2). The same applies to 2009-2010, except for juveniles becoming reproductives and recruitment rate. Growth of juveniles to vegetatives and survival of reproductives increased significantly, while seedling growth and reproductive reproduction decreased, in areas with larger forest edge length in 2008-2009. In 2009-2010, reproductive survival increased with forest edge length.

Population growth rate varied along the gradients of landscape change, and larger lambda values were found in areas of higher forest cover and larger forest edge length (Fig. 4.2). In 2008-2009, forest cover accounted for 78 % of the variation in population growth rate, while this effect reduced to a 30 % in 2009-2010. Linear regressions showed significant positive effects of forest cover in lambda, both for lambda from matrices based on original data (2008-2009: $\beta = 0.009$, $F = 46.33$, $P < 0.0001$; 2009-2010: $\beta = 0.002$, $F = 5.70$, $P = 0.0328$) and those from matrices based on predicted vital rates (2008-2009: $\beta = 0.008$, $F = 1424.84$, $P < 0.0001$; 2009-2010: $\beta = 0.002$, $F = 53696.93$, $P < 0.0001$). Although not significant, there is also a positive relationship between lambda and forest edge length (Fig. 4.2).

Stochastic simulations showed that population growth rate in the long run (λ_s) was higher when both forest habitat availability and length of forest edge were high, and as expected, when there was a high frequency of high-growth intervals, this is, intervals with high lambdas (such as 2008-2009; Fig. 4.3). The highest the frequency of high-growth intervals across years, the stronger the differences in growth rate between populations located in areas of high forest cover and those in low cover sites.

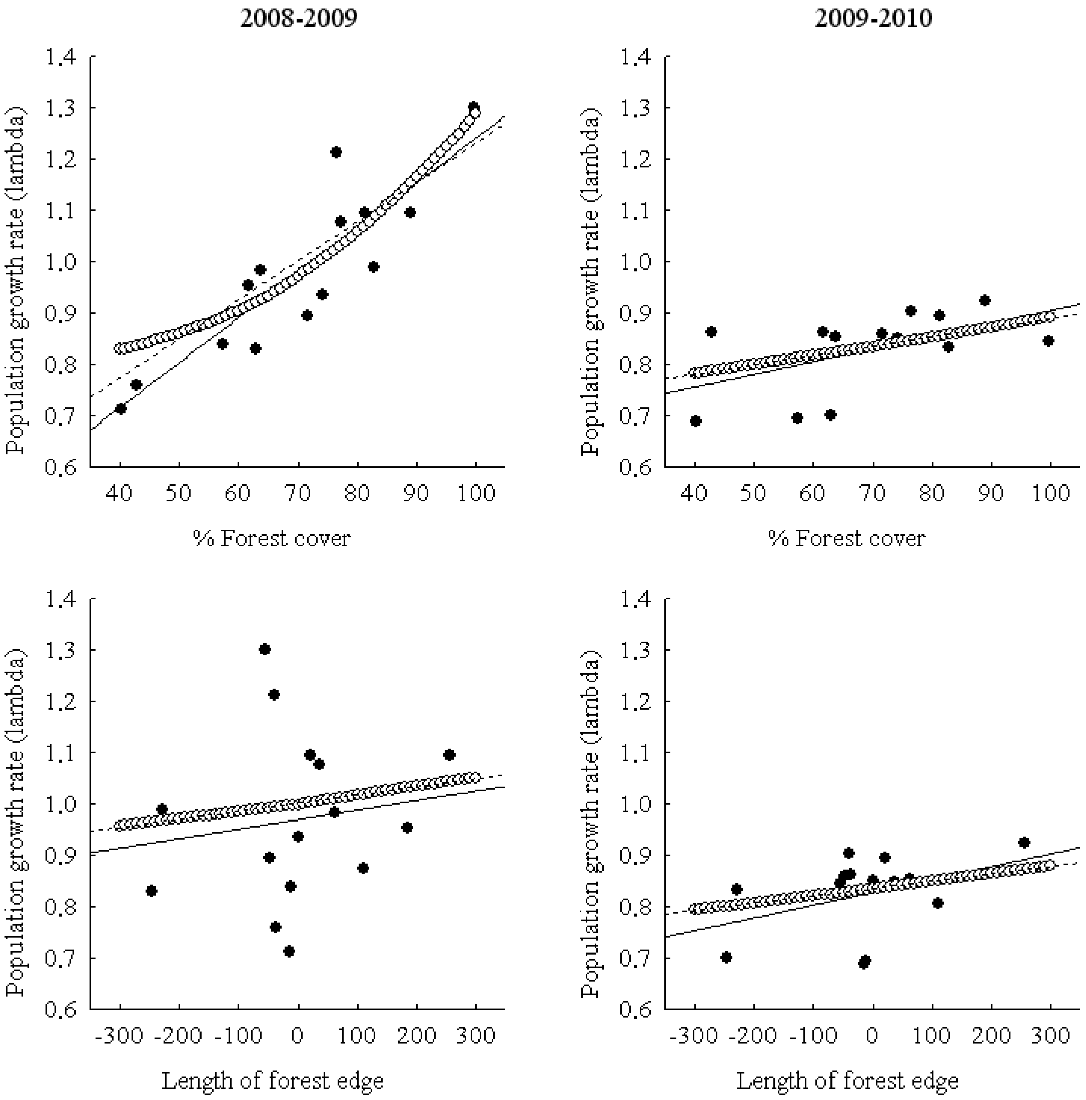

Figure 4.2: Relationships between population growth rate (lambda) and the percentage of forest cover (above) and the length of forest edge (below) for the two intervals studied. Filled circles are the results from matrices based on original data, and open circles are the results from matrices based on predicted vital rates. Lines from fitted regressions both for real (solid line) and predicted values (dotted line) are shown.

Sensitivity and LTRE analyses

Sensitivity estimates (data not shown) suggested that lambda was most sensible to changes in seedling survival and reproduction along the gradient of forest cover, and to changes in reproductive survival and reproduction along the gradient of forest edge, in 2008-2009. In 2009-2010, the highest sensitivities along the gradients of forest cover and edge were, respectively, those of seedling survival and reproductive survival.

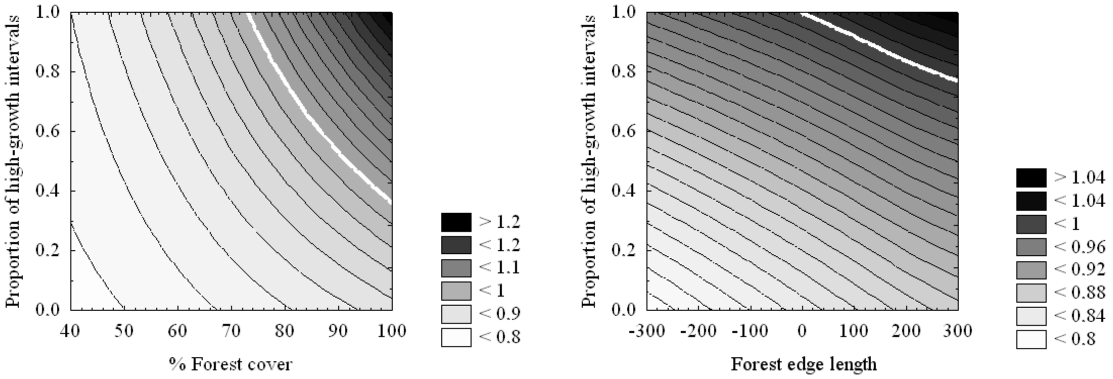

Figure 4.3: Contour plot showing the response of stochastic lambda (grayscale) to the proportion of high-growth intervals (similar to 2008-2009) together with the percentage of forest cover (left) and the length of forest edge (right). The white line indicates values of stochastic lambda higher than 1 (effective population growth).

The slope coefficients of the relationship between lambda and forest cover through different vital rates suggested that, in 2008-2009, the positive relationship between population growth rate and forest cover (Fig. 4.2) was mainly due to the contribution of seedling survival, recruitment and seedling reproduction (Fig. 4.4a). Although lambda was not very sensitive to changes in recruitment rate, this vital rate shows the highest variation along the gradient of forest cover (note the high β value in Table 4.2), and thus is responsible for a considerable amount of the increase in population growth rate with forest cover. This is, population growth rate increases with forest cover mostly due to a higher proportion of seedlings surviving and reproducing, and a higher recruitment rate in high-cover areas. However, the abovementioned slope coefficients were lower for low-cover areas than for high-cover areas (Fig. 4.4a), suggesting that the higher the forest cover, the stronger the response, in terms of population growth, to this landscape feature. In 2009-2010, due to the lower effect of forest cover on most vital rates (Fig. 4.4a), the slope coefficients for the relationships between forest cover and lambda were constant and generally low, the higher being that of seedling survival (Fig. 4.4a). This is, the variation of lambda along the forest cover gradient (Fig. 4.2) was mostly due to enhanced seedling survival at increasing levels of forest cover.

Regarding the response of lambda to the gradient of forest edge length, slope coefficients of this relationship through different vital rates indicated that, in 2008-2009, reproductive survival was the main vital rate responsible for lambda variability (Fig. 4.4a), having a positive and constant effect along the edge length gradient. This indicates that lambda increased in edge-rich areas mostly because the longest the forest edge, the highest the

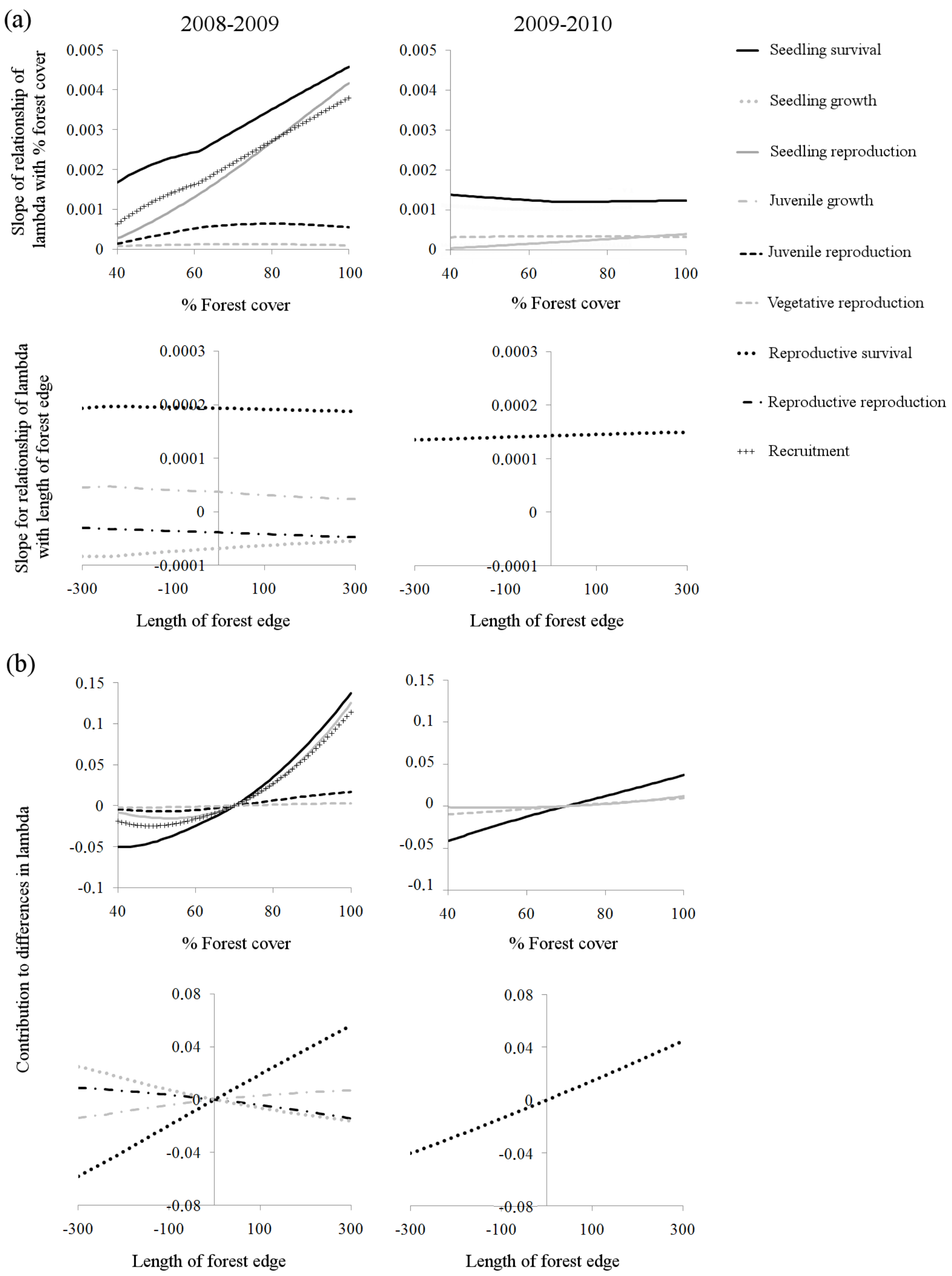

Figure 4.4: (a) Slope coefficients of the relationship between population growth rate and landscape change variables, through each vital rate, represented against percentage of forest cover (above) and length of forest edge (below), for each of the two yearly intervals studied. (b) Actual LTRE contribution of each vital rate to the variation in population growth against percentage of forest cover (above) and length of forest edge (below), for each of the two yearly intervals studied. Note the different scales used in the Y-axis. Only vital rates significantly related to landscape change variables were used for the analysis.

survival of reproductives. There were also constant and very low effects of seedling and juvenile growth, and reproductive reproduction on the relationship between lambda and edge length. In 2009-2010, a similar positive and constant effect of reproductive survival on the response of lambda to edge length was found (Fig. 4.4a).

The estimates of LTRE contributions of vital rates (Fig. 4.4b) suggested similar effects of the different vital rates on the variability of lambda across landscape gradients than those evidenced by the slope coefficients described above. Regarding the gradient of forest cover in 2008-2009, the net contributions of seedling survival, recruitment and seedling reproduction were stronger for high-cover populations that for low-cover populations, as revealed by the bigger absolute difference with the contribution at the gradient mean value (and the exponential trend of change of contributions along the forest cover axis, Fig. 4.4a). Juvenile and vegetative reproduction showed constant and quite low LTRE contributions, and therefore their increases with forest cover are not very important for the overall effect of this variable on lambda. The contributions of recruitment and juvenile reproduction disappeared in 2009-2010, and those of seedling and vegetative reproduction were constant and low. Regarding the response of lambda to edge length, in 2008-2009, reproductive survival showed the largest contribution to lambda variation. This effect also occurred in 2009-2010. Seedling and juvenile growth, and reproductive reproduction showed constant and quite low LTRE contribution values, only in 2008-2009.

DISCUSSION

In this study, we have applied an integrative approach to evidence how different processes of landscape change affect the population dynamics of *P. vulgaris* in the highly fragmented forests of the Cantabrian Range. We found that the loss of forest cover at the landscape scale exerted negative effects on different processes of the plant life-cycle (survival, growth and reproduction of individuals at different stages), although the intensity of these effects varied depending on the vital rate and the yearly interval considered. As a result, populations inhabiting highly forested areas showed positive trends of population growth, whereas populations in highly deforested sites showed trends of decreasing population size. Nevertheless, areas with some degree of forest fragmentation (i.e. those showing increased length of forest edge) may show high population growth rates. Thus, the different landscape structural alterations derived from the process of anthropogenic habitat degradation may have counterbalanced effects on plant population dynamics. Moreover, although population growth may vary strongly between years, in the long run, an increased frequency of high-growth events may exaggerate the differences in population dynamics along the gradients of landscape alteration. In the following sections, we will disentangle the ultimate mechanisms by which landscape change alters *P. vulgaris* population dynamics and discuss the potential long-term consequences of temporal variability in these landscape effects.

Linking landscape change, vital rates and population growth

Landscape change greatly affected *P. vulgaris* population growth, especially through the negative influence of habitat loss. Our LTRE analysis showed that the low population growth rates observed in highly deforested areas mostly resulted from the reduced survival of seedlings, the lowered probability of seedlings to reach quickly a reproductive status, and the decreased recruitment in these areas, compared to areas with high forest cover. Lower seedling survival rates in forest fragments compared to continuous forest have been also observed for a tropical understory herb (Bruna 2002), and this reduction was attributed, among other factors, to temperature stress and increased herbivory in fragments. Woody cover has also been demonstrated to offer an improved environment for seedling survival and recruitment in Mediterranean ecosystems (Ramírez et al. 2006). We can expect soil to be warmer in more forested sectors, and soil moisture, a factor limiting seedling survival (Albrecht and McCarthy 2009), to be higher. Besides, areas with low forest availability harbor smaller populations of *P. vulgaris* (Chapter 1), where lowered seedling survival may result from the genetic load of increased inbreeding (Kolb 2005; Van Geert et al. 2008). Regarding the other vital rates affecting population growth rate along the forest cover gradient, fast transitions from seedling to reproductive adult have been observed in other *Primula* species (*P. farinosa*¸ Toräng et al. 2010). In our populations, seedlings reaching reproductive status were more frequent in high- than in low-cover areas. This may be associated to the occurrence of those environmental conditions also favoring survival, such as more resources (water, nutrients) for flowering, and therefore for growth, in more forested areas (Jacquemyn et al. 2009). Finally, regarding the demographic role of recruitment along the forest cover gradient, a previous research in our study site evidenced that populations in low-cover areas showed lower reproductive outputs (i.e. flower, fruit and ultimately seed production) during the 2008 reproductive season than those in highly forested areas (Chapter 2). We believe that these differences in reproductive output must be largely responsible for the differences in recruitment along the forest cover gradient in the interval 2008-2009. The relationship of 2009 reproductive output with habitat availability was also positive, although not significant (Chapter 2), and this justifies that recruitment rate does not contribute to variation in lambda in the interval 2009-2010.

Population growth rate was higher in sites with longer forest edges (although the relationship was not significant). Positive effects of edge habitat have been sometimes documented on plant growth (Bach et al. 2005) and reproduction (Burgess et al. 2006), but according to our LTRE results, the increase in growth rates with increased edge length is mostly due to higher survival of reproductive adults. The fact that the survival of reproductive adults is relatively important for population growth is not unexpected, as the dynamic of this perennial species has been demonstrated to be strongly dependent on the persistence of adult stages in closed canopy areas (Valverde and Silvertown 1998, but see Lehtilä et al. 2006 for contrasting results with *P. veris*). A larger light availability in edge-rich forest patches could lead to stronger resource acquisition by adults in these areas, favoring resource accumulation (Schmucki and De Blois 2009) and, hence, re-growth ability and long-term survival in individual adults.

Variability in demographic effects of landscape change between intervals

We found considerable variation in vital rates and population growth between the two intervals studied. Higher lambdas were found in 2008-2009, when we found also higher seedling survival and recruitment rate, two of the vital rates of highest influence in lambda variation throughout the landscape change gradient. Variations between years in climatic conditions could explain these differences: for example, mean precipitation was higher for the interval 2008-2009 (authors' unpublished data), and some studies have positively related this variable with recruitment and seedling survival in tropical and temperate forests (e.g. Engelbrecht et al. 2005; Clarke 2002). On the other hand, 2008 winter was mild, with higher-than-average temperatures and a shorter snow cover period, which favored an early-starting and long-lasting reproductive season. This fact seemed to guarantee more opportunities for pollination and finally resulted in a larger reproductive output per adult than in 2009 (Chapter 2). Since recruited seedlings observed in the field emerged from seeds bore in the previous year, the differences in seed production between 2008 and 2009 would lead to a larger recruitment in 2008-2009 than in 2009-2010. Besides variation in population growth rates, the magnitude of the effects of forest loss on population growth also differed between the two intervals. This sort of temporal inconsistency in landscape change effects has been previously found regarding reproduction in our study system (Chapter 2), and also in other studies (Rabasa et al. 2009).

Population growth rate showed a non-linear trend of increase with habitat availability in 2008-2009 (Fig. 4.2), suggesting that the positive effect of forest cover was stronger at high- than at low-cover areas. This was explained by the strengthened effects of habitat availability on seedling survival, reproduction and recruitment at high forest cover levels. However, in 2009-2010 population growth rate increased linearly with habitat availability, mostly due to the also linear effects on this variable on seedling survival. Non-linear effects of habitat loss have been acknowledged mostly as threshold responses (Fahrig 2003, MacRaild et al. 2010), but we have found no previous evidence of these kind of exponential effects on survival, reproduction or recruitment. However, these non-linear effects seem to be triggered by other environmental factors: in our case, they could result from favorable climate for reproduction and survival.

On the other hand, the difference in growth rates between populations with high and low habitat availability is much more noticeable in the yearly interval where population growth is generally high. This is because population growth in areas with low habitat availability remains consistently low, but in sites with high habitat availability, there is considerable temporal variation in population growth. Hence, according to our results, it seems that habitat loss suppresses the effects of these temporally-variable, broad-scale factors, like could be climatic changes.

Our results may also help to understand how *P. vulgaris* may perform in future scenarios comprising further landscape changes together with alterations in other large-scale environmental conditions, such as climate warming. Our simulations along the whole gradient of landscape change showed that the stochastic population growth rate is, as expected due to our previous field-based results, higher in high-cover and edge-rich areas. Thus, the lower the availability of forest habitat and the length of forest edge, the higher the proportion of high-growth intervals needed to have effective population growth in the long run (this is, to reach stochastic lambda values higher than 1, Fig. 4.3). Moreover, the higher is the proportion of high-growth intervals, the broader are the differences in population growth rate between the extremes of the landscape gradient; this is, between low- and high cover sites, and between sites with low and high length of forest edge. This highlights that long-term landscape change effects on demography are dependent on the interaction between the degree of alteration and the magnitude of temporal variability in population growth, and can thus be conditioned by climate or other broad-scale factors. In this sense, Toräng et al. (2010) found that a future increase in the frequency of dry years due to climate change would reduce population growth of *P. farinosa* in Sweden, due to high mortality of all life stages in these years. According to our data, the increased frequency of mild winters predicted by future global change scenarios would, on the contrary, lead to an increase in population growth of *P. vulgaris* in our study area, especially due to an increased recruitment. Nevertheless, we acknowledge that our data on two yearly intervals are limited to develop thorough predictions about population responses to climate change. Studies based on longer temporal series (e.g. Nicolè et al. 2011) are needed to clarify the effect of the interplay between landscape modification and climate change on population demography, if aimed to predict the future of plant populations facing the new environmental conditions imposed by global change.

Concluding remarks

In this study, we have evaluated the effects of landscape change on the demography of a perennial forest plant during two yearly intervals, considering all the processes making up its life cycle and the final effect on population growth rate. Although landscape change may be sometimes irrelevant in demographic terms (e.g. Kolb et al. 2010), it is expected to affect plant population dynamics through the decreased population sizes, the increased isolation between population patches, and the negative effects of edge increases (Honnay et al. 2005). By assessing the role of different landscape processes on *P. vulgaris* demography, we found that landscape change was actually relevant, and demonstrated that habitat loss, and not habitat fragmentation *per se*, was the major driver of demographic collapse in the fragmented forest of the Cantabrian range. By distinguishing the transitions between the different life-cycle stages, we identify the key processes or vital rates responsible for population declines along the gradients of landscape change (Bruna et al. 2009). Namely, we evidence that habitat loss effects mostly derived from the decreased probabilities of seedling survival and individual reproduction. Some of these effects may be the indirect consequences of habitat loss on population size decreases and genetic bottlenecks. Nevertheless, our transition-based analysis strongly suggest a direct effect of landscape change on individual performance, large forest patches representing a high-quality habitat for individuals to survive and reproduce, and hence for populations to growth, irrespective of population size (see also Chapter 2). Finally, compared to other forest perennial herbs (Silvertown et al. 1993), the effect of *P. vulgaris* adult longevity on population dynamics was less important, and hence no long-term demographic inertia against landscape change (i.e. extinction debts; Honnay et al. 2005) are expected in this species under the current environmental setting. Thus, although the effects of landscape alteration may be inconsistent on time, and apparently interact with year-to-year climatic variability, strong population declines and even local extinction are expected under further landscape alteration. Clearly, long-term studies are needed in order to properly assess extinction probabilities, as well as to elucidate the possible interactions between plant demographic responses, landscape patterns and climatic variability.

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Discusión General

Consecuencias del cambio en el paisaje para las plantas herbáceas forestales

Los resultados obtenidos en la presente tesis doctoral demuestran que los diferentes procesos de cambio en el paisaje afectan a la ecología de poblaciones de *P. vulgaris*, y por extensión, a otras plantas forestales perennes con similares características. Ya sea de forma directa o indirecta, la pérdida y fragmentación del hábitat forestal influyen en todos los procesos poblacionales estudiados en los diferentes capítulos (Fig. D1). Sin embargo, los efectos de cada uno de los procesos de alteración (pérdida de hábitat, subdivisión, efectos de borde) difieren en cuanto a intensidad y signo. Los diferentes procesos poblacionales también dependen unos de otros (Fig. D.1), y en conjunto son responsables de la generación del patrón observado de distribución de la especie (Capítulo 1a).

La pérdida de hábitat parece ser el proceso de cambio paisajístico más perjudicial para la eficacia biológica y persistencia de nuestra especie de estudio. Esto concuerda con los estudios revisados por (Fahrig 2003), donde se documenta que los efectos negativos de la pérdida de hábitat sobre la biodiversidad son en general mucho más fuertes que los de la fragmentación en sí misma. En nuestro caso, la abundancia de *P. vulgaris* se reduce en zonas con poca cantidad de hábitat forestal (Capítulos 1a y 2). Esto da lugar a una cierta disminución del éxito reproductivo (Capítulo 2) y a alteraciones del reclutamiento mediadas por interacciones entre el tamaño poblacional y otros factores, como la herbivoría (Capítulo 3). Además, la disminución de los tamaños poblacionales en zonas con poca cantidad de hábitat puede conllevar una escasa variabilidad genética y altos niveles de endogamia (Van Rossum et al. 2002), que podrían contribuir en parte a la reducida supervivencia de algunos estadios del ciclo vital, como las plántulas, en estas zonas (Capítulo 4). Además de la reducción del tamaño poblacional y las consecuencias derivadas de ella, los efectos más importantes de la pérdida de hábitat sobre la ecología de poblaciones son directos. El éxito reproductivo (Capítulo 2) disminuye en zonas con baja disponibilidad de hábitat forestal, debido a reducciones en la disponibilidad de recursos y en la polinización. La cantidad de hábitat disponible a distintas escalas determina la disponibilidad lumínica, que influye en el reclutamiento de la especie e interacciona con otros factores limitantes del establecimiento (Capítulo 3). El resultado global a nivel de dinámica poblacional es que en las áreas con mayor cantidad de hábitat forestal, las tasas de crecimiento de las poblaciones son mayores, debido en gran parte a que existen condiciones ambientales favorables para la supervivencia, crecimiento y reproducción de diferentes estadios del ciclo vital (Capítulo 4).

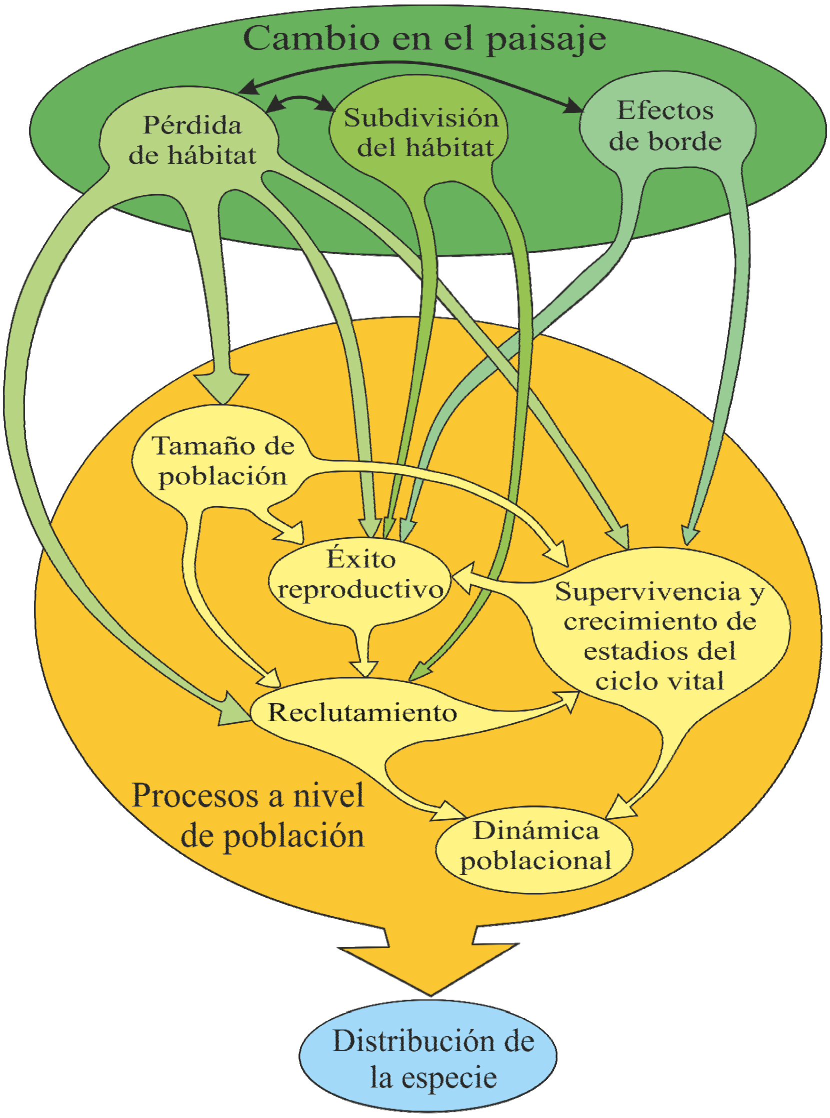

Figura D.1: Esquema que sintetiza las relaciones entre los procesos de cambio en el paisaje y los procesos poblacionales y patrones de distribución estudiados en los diferentes capítulos de la tesis.

En comparación con la pérdida de hábitat, los efectos de la fragmentación (evaluados como subdivisión del hábitat y aumento de la cantidad de borde) sobre las poblaciones de *P. vulgaris* son más débiles, y hemos encontrado tanto efectos positivos como negativos, coincidiendo también con lo sugerido por Fahrig (2003). La subdivisión del hábitat incrementó el éxito reproductivo, al menos en uno de los dos años de estudio, lo que atribuimos a un aumento de la calidad polínica en sitios con mayor número de fragmentos de bosque, resultante del movimiento de los polinizadores entre ellos. Por otro lado, aunque en el Capítulo 3 no se ha evaluado directamente el efecto de la subdivisión del hábitat en el reclutamiento, es esperable que las limitaciones a la dispersión observadas se agraven aún más en zonas donde el bosque está muy subdividido, ya que las semillas probablemente no serán dispersadas a lo largo de las distancias que separan los fragmentos de hábitat. Este hecho, resulta en una disminución del flujo génico (Nathan y Muller-Landau 2000), ya que los nuevos individuos establecidos dentro de un fragmento de hábitat corresponderán generalmente a la producción de semillas de plantas de ese mismo fragmento. Además, la subdivisión del hábitat impide la colonización de nuevos fragmentos donde la especie no esté presente. Por su parte, el incremento de la cantidad de borde forestal resultante del proceso de fragmentación mostró también efectos positivos y negativos. De hecho, el efecto de la cantidad de borde en el éxito reproductivo (Capítulo 2) cambió de signo dependiendo de la fenología de floración del año estudiado. Una mayor cantidad de borde parece incrementar el cuajado de frutos por efectos beneficiosos en la polinización (Montgomery et al. 2003) cuando la floración es temprana. Sin embargo, cuando ésta es tardía, predominan los efectos negativos, ya que la mayor cantidad de borde facilitaría la entrada de herbívoros. La presencia de borde también favorece la supervivencia de las plantas adultas (Capítulo 4), probablemente debido a que la mayor disponibilidad lumínica en zonas de borde favorece la adquisición de recursos (Schmucki y De Blois 2009), e incrementa otras tasas vitales en menor medida. Esto contribuye a aumentar la tasa de crecimiento poblacional en zonas con elevada longitud de borde forestal, aunque este efecto en dinámica poblacional es más débil que el ejercido por la cantidad de hábitat.

Todos estos procesos contribuyen a generar el patrón de distribución de la especie a escala de paisaje (Capítulo 1a). Hemos visto que la probabilidad de presencia de la especie se incrementa con la disponibilidad de hábitat y disminuye con su subdivisión. Sin embargo, los efectos de borde no explican las diferencias observadas en presencia, a pesar de que sí afectan al éxito reproductivo y al crecimiento y supervivencia de varios estadios del ciclo vital (sobre todo a la supervivencia de adultos, ver Capítulo 4). Es decir, que el incremento de la cantidad de borde genera únicamente efectos de tipo directo sobre procesos concretos, que luego no se traducen en efectos sobre la distribución, al menos a la escala a la que nosotros la hemos estudiado y con el diseño de muestreo que hemos utilizado. Por otro lado, además de la respuesta de la especie a la pérdida y fragmentación del hábitat, la respuesta a otros gradientes abióticos independientes de la configuración del paisaje (pendiente topográfica), y sobre todo las elevadas limitaciones a la dispersión de *P. vulgaris* tienen un papel igualmente importante en la generación de su patrón de distribución, ya que son factores limitantes del reclutamiento. Las zonas de elevada pendiente favorecen la persistencia de la especie, y la limitación a la dispersión impide que las semillas sean capaces de alcanzar fragmentos de hábitat potencialmente adecuados para su establecimiento (ver también Capítulo 3). Esta interacción de factores exógenos (perdida y fragmentación de hábitat, topografía) y endógenos (limitación a la dispersión) en la determinación de la distribución de *P. vulgaris* solamente es detectable cuando se aplica la aproximación de paisaje continuo. Otros modelos (descritos en el Capítulo 1b) proporcionarían una visión parcial de la respuesta de las especies ante el paisaje, ya que sólo considerarían el efecto de los patrones de alteración, sin tener en cuenta otros gradientes ambientales que pueden influir en la presencia de las especies, ni las características específicas de los ciclos vitales que pueden determinar sus distribuciones.

La mayoría de los efectos de pérdida y fragmentación de hábitat, y de gradientes ambientales y poblacionales que hemos observado se han manifestado a escala de paisaje, aunque también hemos evaluado la importancia de algunos factores a escala local, como los efectos de la disponibilidad lumínica, la abundancia y la agregación de plantas conespecíficas en la reproducción (Capítulo 2), o los efectos del microhábitat en el reclutamiento (Capítulo 3). Sin embargo, estos efectos fueron mucho menos importantes, indicando que la escala operacional de los factores de alteración es sobre todo la escala de paisaje. No obstante, el paisaje está influyendo activamente en procesos que ocurren a una escala mucho más pequeña, como es la de la población o incluso la de la planta individual.

En conjunto, los resultados de esta tesis confirman que *P. vulgaris* está claramente asociada al estrato herbáceo del hábitat forestal en nuestra área de estudio. Esto contrasta con estudios realizados en otras partes de Europa, donde la especie se distribuye sobre todo en hábitats húmedos y de escasa competencia, como bordes de campos de cultivo, acequias, setos y otros elementos lineales asociados a paisajes agrícolas (Campagne et al. 2008; Endels et al. 2002b). Sin embargo, *P. vulgaris* también es una planta eminentemente forestal en Gran Bretaña (Jacquemyn et al. 2009; Valverde y Silvertown 1995). Nuestros resultados confirman además que cierto grado de fragmentación forestal puede beneficiar a la especie, ya que tanto la subdivisión del hábitat como la disponibilidad de borde forestal contribuyeron, al menos en uno de los años estudiados, a incrementar la producción reproductiva (Capítulo 2), y además la supervivencia de las plantas adultas, y en último término la tasa de crecimiento poblacional (Capítulo 4), fue mayor en zonas con mayor disponibilidad de borde. Por lo tanto, la viabilidad poblacional de *P. vulgaris* y de otras herbáceas forestales con similares características se verá más favorecida en paisajes con una elevada disponibilidad de hábitat forestal, compuestos por una red de parches forestales interconectados, y donde las zonas de borde forestal sean abundantes, que en paisajes con una única gran masa forestal continua.

Importancia de la variabilidad temporal

Algunos de los trabajos incluidos en esta tesis comprendieron varios años de estudio (2 en el Capítulo 2 y 3 en el Capítulo 4). En estos casos pudimos apreciar una importante variación entre años tanto en los resultados de los procesos estudiados (producción reproductiva, tasas vitales, tasa de crecimiento poblacional), como en la magnitud e incluso en el signo de los efectos del cambio en el paisaje sobre dichos procesos. Nuestra hipótesis es que esta variación se relaciona con los patrones de variación climática, y esto se debe sobre todo a que los inviernos con temperaturas suaves dan lugar a un adelantamiento temporal de la floración, lo que provoca que el período reproductivo sea más largo, y por tanto que la producción reproductiva por planta sea mayor. Esto se traducirá en un incremento del reclutamiento en la primavera siguiente, que contribuirá a incrementar la tasa de crecimiento poblacional. Además, las diferencias en precipitación entre años también pueden estar detrás de las variaciones observadas en supervivencia de semillas (Capítulo 4, Engelbrecht et al. 2005; Clarke 2002), que también contribuyen en gran parte a la variación observada en la dinámica poblacional. En años con inviernos suaves, los efectos del cambio en el paisaje en la reproducción y en la dinámica poblacional son más fuertes que en años de mayor dureza invernal, y las diferencias entre zonas muy alteradas y zonas de bosque continuo se intensifican. Esto parece indicar que el efecto de los cambios en el paisaje interacciona de forma aditiva con los efectos a gran escala de las condiciones climáticas, y que el potencial efecto positivo de la suavidad invernal en la reproducción y el subsecuente reclutamiento se vería contrarrestado por la mayor magnitud de los efectos de pérdida y fragmentación de hábitat. Es decir, que aunque las condiciones climáticas fueran favorables para la reproducción de la especie, su rendimiento en zonas muy alteradas sería igualmente muy bajo. Este resultado es especialmente interesante si consideramos que las predicciones actuales de cambio global sugieren la aparición de inviernos cada vez más suaves en el área Cantábrica. Sin embargo, aunque algunos autores ya han apuntado en esta dirección (Brook et al. 2008; Leimu et al. 2010), claramente se necesitan estudios a largo plazo para verificar que nuestra hipótesis sobre la interacción de diferentes factores de cambio global es correcta, y que los efectos aditivos que hemos observado se mantienen a lo largo de los años. El estudio de este tipo de interacciones entre factores globales que afectan a la biodiversidad constituye una línea de investigación con clara proyección futura, donde nuestros resultados podrían ser la base para desarrollar estudios de monitorización a largo plazo de parámetros poblacionales a lo largo de gradientes paisajísticos. Esta monitorización debería ir unida a un seguimiento de las condiciones climáticas, que permita evaluar la dependencia de las respuestas reproductivas y demográficas de factores como la dureza del invierno o la precipitación. En conjunto, estos datos tomados a largo plazo podrían utilizarse para plantear estudios de simulación, que nos permitan predecir de forma precisa la viabilidad futura de las poblaciones en distintos escenarios de cambio global.

Cabe destacar que la cantidad de borde mostró efectos opuestos en el éxito reproductivo, concretamente en la producción de frutos, en los dos años estudiados. Esta variabilidad interanual puede deberse a interacciones, en este caso, entre las respuestas fenológicas de factores bióticos que afectan a la reproducción y los patrones de cambio en el paisaje: las zonas de borde pueden favorecer la entrada de polinizadores en el bosque (Montgomery et al. 2003), lo que incrementaría el cuajado de frutos, pero también la entrada de ganado que consume y pisotea las plantas, llevando a una reducción del éxito reproductivo. El efecto global del borde puede cambiar de signo dependiendo de qué tipo de interactor sea más favorecido por estas zonas (polinizadores o herbívoros), de la intensidad relativa de los efectos de cada tipo de interactor en la reproducción, y de la abundancia relativa de interactores a lo largo del período reproductivo de la planta.

Además de la variabilidad global en la reproducción de las plantas, hemos observado que en el mismo evento reproductivo se puede apreciar bastante variabilidad fenológica entre los distintos individuos de la población, existiendo plantas que podríamos llamar “de floración temprana” frente a plantas “de floración tardía” dentro del período reproductivo. Estas diferencias se han tenido en cuenta a la hora de realizar los muestreos de los capítulos 2 y 4, incluyendo ambos tipos de plantas por igual en los diseños. Análisis no mostrados en dichos capítulos nos revelaron que las plantas de floración temprana producen generalmente mayor número de flores y frutos por planta, y que la diferencia con las plantas de floración tardía en cuanto a producción reproductiva es mayor en años donde el período de floración es más largo y tiene un inicio más temprano (es decir, en años con invierno suave). Además, encontramos también que el efecto de la disponibilidad de hábitat en el éxito reproductivo era más intenso en las plantas de floración temprana que en las de floración tardía. Es decir, que los efectos del cambio en el paisaje son más patentes al principio de la época de floración, lo que puede contribuir también al hecho de que su intensidad disminuya en años donde la floración se retrasa debido a condiciones climáticas adversas. Obviamente, estas conclusiones deberían verificarse también con estudios a más largo plazo que examinen la magnitud de la producción reproductiva y de los efectos de las alteraciones paisajísticas en plantas con diferente fenología de floración.

Directrices para futuros estudios

En los diferentes trabajos que componen esta tesis doctoral, en muchos casos no se han evaluado de forma directa los mecanismos próximos responsables de las respuestas biológicas de *P. vulgaris* a la alteración de su hábitat, aunque se ha tratado en todo momento de elucidar cuáles son esos mecanismos. Por ejemplo, el estudio de la respuesta reproductiva se hubiera enriquecido con un análisis explícito del proceso de polinización. De hecho, al mismo tiempo que se realizaron las observaciones de producción reproductiva, se llevaron a campo censos de polinizadores de forma intensiva durante los dos años de estudio, con la idea de evaluar la influencia de los factores de alteración del hábitat sobre la diversidad de polinizadores y la tasa de visita floral. Sin embargo, debido a la extremadamente baja tasa de visita floral, no se obtuvieron datos para llevar a cabo contrastes de hipótesis concluyentes. Dicha baja frecuencia de observación de visitantes florales en *P. vulgaris* ya se había documentado en otros estudios (Jacquemyn et al. 2009). Ya Darwin (1877) observó muy pocos insectos visitando las flores de *P. vulgaris* en hábitat forestal, y sugirió que la especie podría depender en gran medida de polinizadores nocturnos, como las polillas. Las flores de *P. vulgaris* presentan una serie de características que parecen ser importantes para la atracción de insectos nocturnos, como el color amarillo pálido de los pétalos, que facilita la visibilidad, el olor, que es más fuerte al final de la tarde y durante la noche, y el hecho de que la corola no presenta un ritmo diurno de apertura y cierre (Jacquemyn et al. 2009). Sin embargo, no se dispone de evidencias de polinización nocturna, excepto en condiciones muy artificiales (Boyd et al. 1990). Por lo tanto, en el futuro sería interesante ampliar nuestros estudios sobre reproducción con datos de polinización que incluyeran también a los posibles polinizadores nocturnos, ya que los censos de visitantes florales que hemos realizado hasta el momento han sido diurnos.

Aparte de los estudios reflejados en los diferentes capítulos de esta memoria, esta tesis se engloba dentro de un proyecto más amplio aún en desarrollo, y que incluye una serie de experimentos de campo orientados a evaluar, de forma directa, los mecanismos específicos que determinan la pérdida de rendimiento reproductivo y eficacia biológica de los individuos debido a efectos cuantitativos (tamaño de población) y estructurales (grado de degradación del hábitat). En uno de estos diseños, tratamos de evaluar el efecto del “tamaño de parche floral” en el resultado final de la reproducción y el reclutamiento, y en las interacciones planta-animal tanto positivas (polinización) como negativas (herbivoría). Para ello, se transplantaron individuos adultos producidos en invernadero para establecer poblaciones experimentales de tamaño “grande” y “pequeño” emparejadas en zonas de hábitat similares. Nuestra hipótesis era que las poblaciones grandes, al producir mayor cantidad de flores, atraerían a los polinizadores con mayor intensidad que las poblaciones pequeñas, con menor producción floral, incrementándose por lo tanto la tasa de cuajado de semillas por planta y el reclutamiento de plántulas en poblaciones de mayor tamaño. Estas poblaciones atraerían también a mayor cantidad de herbívoros, lo que podría afectar a su rendimiento. Sin embargo, los resultados obtenidos hasta el momento no han sido concluyentes, quizás debido a efectos de la plantación o a que las plantas necesitan mayor tiempo de aclimatación para que se estabilice su producción floral. Además, en algunos casos hemos observado que el “tamaño de parche floral” resultó ser mayor en las poblaciones pequeñas que en las grandes, probablemente a causa de efectos ambientales derivados de las condiciones del lugar de plantación (composición del suelo u otros factores no evaluados), y esto dificultó la obtención de resultados. Sin embargo, este tipo de diseño, con ciertas mejoras en el control de las condiciones ambientales y otros factores que puedan producir variabilidad no deseada, podría ser muy interesante para evaluar de forma fina el efecto aislado del tamaño de población en la reproducción y reclutamiento de plantas forestales. Por otro lado, la realización de censos de visitantes florales, incluyendo polinizadores nocturnos, en estas poblaciones experimentales situadas en zonas de hábitat similares, serviría para elucidar el efecto del tamaño de población en los polinizadores, independientemente de los efectos de calidad o cantidad de hábitat y configuración del mismo.

Otro de los mecanismos a evaluar es la pérdida de eficacia biológica que se produce en gradientes locales de degradación de hábitat relativos al borde forestal. Para ello, estamos trabajando también con poblaciones experimentales, en este caso situadas a lo largo de una zona de transición muy marcada entre bosque maduro y pastizal, en transectos con tres localizaciones: interior del bosque, borde forestal y pastizal. En este caso, los resultados preliminares nos indican que la producción de flores, frutos y semillas, y el crecimiento vegetativo, disminuyen según avanzamos desde el interior del bosque maduro hasta el pastizal, mientras que la tasa de herbivoría aumenta. El pastizal parece un hábitat totalmente hostil, ya que las plantas situadas en esta zona produjeron muy pocas flores y ningún fruto, sus hojas fueron muy consumidas por los herbívoros y su crecimiento vegetativo fue muy reducido. El borde forestal parece un hábitat medianamente adecuado para la floración, ya que las plantas situadas en esta zona produjeron una cantidad moderada de flores, sin embargo la subsiguiente producción de frutos fue bastante reducida, revelando que las condiciones ambientales de las propias zonas de borde quizás no son totalmente adecuadas para la polinización y cuajado de frutos. La herbivoría y el crecimiento vegetativo también son intermedios entre las zonas de pastizal y las de bosque. Una vez más, este trabajo confirma que el hábitat forestal es el más adecuado para *P. vulgaris* en nuestra área de estudio, ya que las poblaciones situadas en el interior del bosque tuvieron mayor producción reproductiva y crecimiento vegetativo, y las tasas de herbivoría fueron menores. Este estudio experimental demuestra que a escala local, las zonas de borde forestal no son beneficiosas para la especie, en contraste con los estudios previos (Capítulos 2 y 4), donde se observó que la abundancia de borde forestal a escala de paisaje favorecía en cierta medida la producción reproductiva, la supervivencia y el crecimiento poblacional. De esto se deriva que existe una discordancia de escalas, ya que el efecto positivo de la cantidad de borde se manifiesta únicamente a escala de paisaje. A esta escala, las zonas de borde pueden actuar favoreciendo la entrada de polinizadores y la penetración de ciertos recursos, como la radiación solar, hacia zonas más interiores del bosque, con condiciones adecuadas para la persistencia de estas especies.

Aunque en esta tesis no se han evaluado los efectos genéticos de la pérdida y fragmentación de hábitat, sabemos que éstos pueden estar detrás de algunas de las respuestas biológicas observadas en *P. vulgaris*. Las consecuencias genéticas de los procesos de alteración paisajística son bien conocidas (Van Geert et al. 2007; Van Rossum et al. 2002; Young et al. 1996). Claramente, sería interesante estudiar la estructura genética de *P. vulgaris* en nuestra área de estudio, para averiguar el grado de riqueza alélica, heterocigosidad y endogamia que sufren las poblaciones, y cómo esta variabilidad genética se relaciona con el tamaño de población, además de investigar si existe flujo génico entre poblaciones situadas a diferentes distancias. En este sentido, sería interesante también comprobar el grado de aislamiento polínico entre poblaciones mediante experimentos de polinización cruzada, en los que se observe la respuesta de los parámetros reproductivos a la adición de polen de poblaciones situadas a diferentes distancias. Esto nos permitiría inferir hasta qué punto los polinizadores pueden contribuir a mantener el flujo génico entre poblaciones, ya que sabemos que la dispersión de semillas limita fuertemente el establecimiento en fragmentos de hábitat muy alejados de los núcleos con plantas madre. Mediante este tipo de estudios genéticos podríamos comprobar si existe relación entre las respuestas demográficas observadas en esta tesis y la variación y estructura genética.

Implicaciones para la conservación

P. vulgaris es una especie común en el Noroeste de España, y no se encuentra dentro de ninguna categoría de protección, al no considerarse actualmente amenazada en nuestra zona de estudio. Sin embargo, esta especie es considerada rara y en declive en algunas partes de Europa, como en Bélgica (Endels 2004; Jacquemyn et al. 2003). En esta tesis doctoral se demuestra que la viabilidad de las poblaciones de esta especie podría verse comprometida por los cambios en el paisaje, especialmente a consecuencia de la pérdida de hábitat. Por extensión, esta afirmación podría extenderse a muchas otras especies de plantas herbáceas forestales, ya que la mayoría comparten unos mismos rasgos que las hacen altamente dependientes de su hábitat y sensibles a las alteraciones (ver Introducción General).

Una primera aplicación que podríamos extraer de los resultados de esta tesis, de cara a futuros estudios de cambio en el paisaje, es la ventaja que supone la utilización del modelo de paisaje continuo frente a otros modelos anteriores (comentados en el Capítulo 1b). El Capítulo 1a constituye la primera aplicación de este modelo hasta la fecha para el estudio de la respuesta de una planta ante la alteración del paisaje. La incorporación de este marco teórico en estudios futuros asegurará una correcta interpretación de la percepción que las diferentes especies tienen del paisaje, permitiendo conocer las causas reales de los declives poblacionales.

Por otro lado, nuestros resultados evidencian que la pérdida de hábitat es la principal amenaza para las plantas herbáceas forestales, y que la fragmentación no puede considerarse como perjudicial para su viabilidad poblacional. Al contrario, cierto grado de fragmentación puede incluso beneficiarlas en términos reproductivos y demográficos, debido a los efectos positivos de la disponibilidad de borde forestal. Sin embargo, si los fragmentos están muy separados unos de otros, el reclutamiento se vería altamente comprometido. Por lo tanto, las medidas de manejo a seguir para asegurar la persistencia de estas especies en nuestros bosques irían encaminadas a mantener un alto porcentaje de cobertura forestal a escala de paisaje, donde cierto grado de fragmentación sería tolerable, siempre que se mantenga la conectividad entre fragmentos. La conservación debería ir orientada a la mejora del hábitat, ya sea incrementando el tamaño de los fragmentos de bosque, o mediante la creación de nuevos fragmentos interconectados con los ya existentes, en los que estas especies sean capaces de establecerse. Las medidas orientadas directamente a las poblaciones, como el incremento del tamaño poblacional en los fragmentos pequeños de bosque, parecen menos adecuadas, ya que la mayoría de los efectos de las alteraciones paisajísticas que hemos observado son directos, y no mediados por el tamaño poblacional (ver Capítulo 2). Además, en el caso de establecerse medidas de conservación, sería imprescindible un seguimiento a largo plazo para evaluar la respuesta de las poblaciones al manejo del hábitat.

Conclusiones

1. La pérdida de hábitat es el proceso de cambio paisajístico que afecta en mayor medida a la presencia de *Primula vulgaris* a escala de paisaje. La abundancia y estructura de edades de las poblaciones también están determinadas, aunque en menor grado, por la cantidad de hábitat.
2. Las restricciones a la dispersión son tan importantes como los procesos de cambio en el paisaje en la determinación del grado de ocupación del hábitat forestal disponible por *P. vulgaris*. Existen también efectos de la calidad de hábitat, evaluada como pendiente topográfica, que limitan el establecimiento de la especie en zonas con suficiente cantidad de hábitat.
3. El modelo de paisaje continuo constituye una nueva aproximación teórica adecuada para el estudio de los efectos del cambio en el paisaje. Permite considerar la respuesta individual de una especie (o de un grupo de especies con rasgos similares) ante gradientes ambientales de pérdida y fragmentación de hábitat, distinguiendo los efectos de cada proceso concreto, e incluyendo también otros factores ambientales que influyen en procesos biológicos, junto con características propias del ciclo vital de la especie.
4. El éxito reproductivo de *P. vulgaris* disminuye en zonas con baja disponibilidad de hábitat forestal y poca cantidad de borde. Esto se debe a efectos directos de la pérdida y fragmentación de hábitat sobre la reproducción, y en menor grado, a efectos indirectos mediados por reducciones del tamaño poblacional. Para favorecer la reproducción de ésta y otras especies similares, un manejo orientado a incrementar la cobertura forestal alrededor de las poblaciones ya existentes parece más adecuado que un incremento de los tamaños poblacionales.
5. Los efectos del cambio en el paisaje en la reproducción de *P. vulgaris* fueron diferentes en los dos años estudiados, siendo más evidentes después de un invierno templado que alargó la época de floración, y desapareciendo o cambiando de signo tras un período de floración corto debido a una mayor dureza invernal.
6. El reclutamiento de *P. vulgaris* está altamente limitado por la dispersión, independientemente del grado de alteración del paisaje. La supervivencia y crecimiento de las plántulas están influidas por factores ambientales relacionados con el proceso de cambio en el paisaje, como la disponibilidad de hábitat a distintas escalas, la presencia de individuos de la misma especie y las interacciones antagónicas con animales.
7. La tasa de crecimiento poblacional de *P. vulgaris* se incrementa en zonas de elevada cantidad de hábitat y moderado grado de fragmentación, especialmente debido a los efectos positivos de la cantidad de cobertura forestal en la supervivencia y reproducción de las plántulas y en el reclutamiento, y de la cantidad de borde forestal en la supervivencia de los adultos reproductores.

8. Los efectos demográficos también mostraron variabilidad entre los dos períodos de estudio, siendo más débiles cuando el reclutamiento no contribuyó a la variación observada en el crecimiento poblacional.
9. A largo plazo, una elevada frecuencia de períodos de crecimiento elevado puede incrementar las diferencias en dinámica poblacional a lo largo de los gradientes de cambio en el paisaje.

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Apéndices

APPENDIX A:

Correlation matrix showing Pearson correlation coefficients (*r*) for all pairs of biological variables initially entered as predictors in the stepwise regression models for presence, abundance and population subdivision. Correlations higher than $r = 0.7$ are shown in bold.

	% forest cover	Beech abundace	Forest cover (other trees)	Nº forest patches	Edge density	Elevation	Slope	Aspect	% cover *Pv* in neighbourhood
% forest cover [1]	1.00								
Beech abundance	**0.70**	1.00							
Forest cover (other trees) [2]	**0.73**	0.05	1.00						
Nº forest patches [3]	0.00	-0.03	0.03	1.00					
Edge density [4]	0.00	-0.05	0.02	0.41	1.00				
Elevation	-0.20	-0.23	-0.08	0.03	0.11	1.00			
Slope	0.20	0.25	0.05	-0.09	-0.10	-0.10	1.00		
Aspect	-0.12	-0.11	-0.06	0.23	0.18	0.08	-0.32	1.00	
% cover *Pv* in neighbourhood	0.58	0.65	0.21	-0.01	-0.04	-0.27	0.30	-0.09	1.00

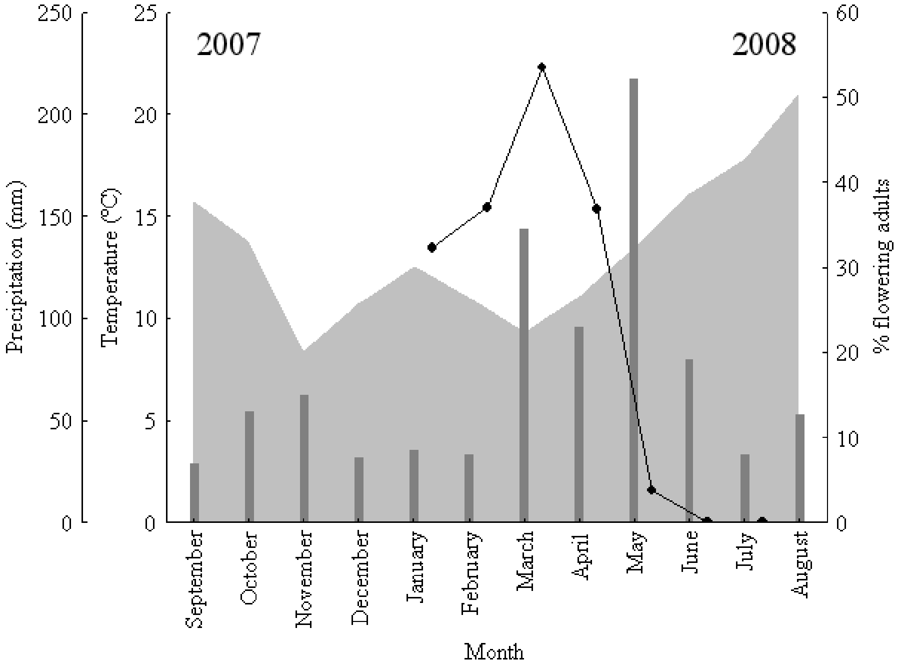
[1] Raw percentage of forest cover calculated from GIS

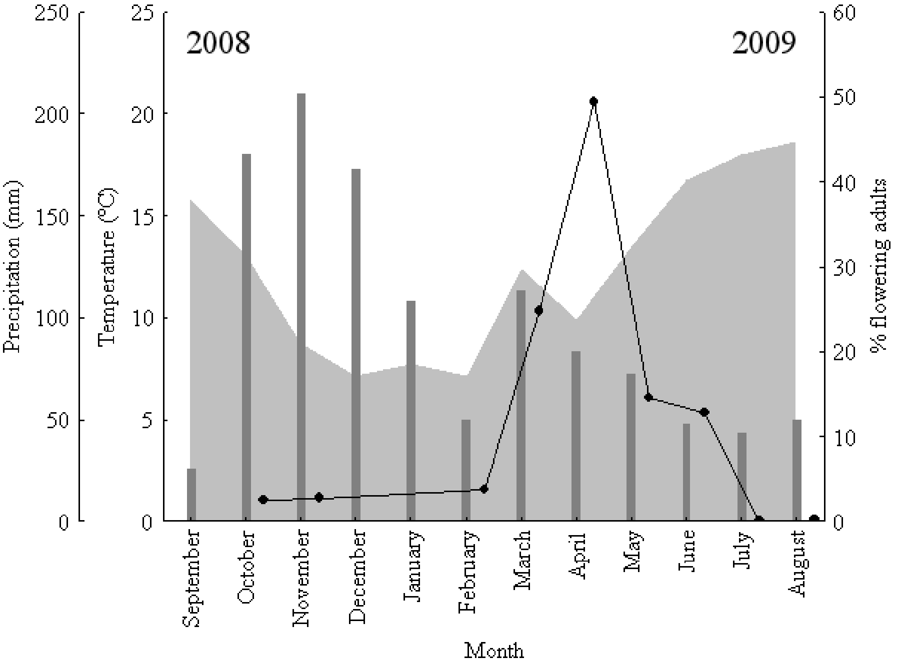
[2] Residuals of the raw percentage of forest cover against the number of beech trees

[3,4] Residuals against the raw percentage of forest cover

APPENDIX B:

Climatic diagrams representing the mean monthly temperature (light grey area) and the cumulated precipitation (dark grey bars), in the city of Oviedo (232 m a.s.l., 30 km from the study site), and the mean monthly percentage of flowering adults (black dots, flowering data recordings, start from January 2008).





APPENDIX C:

Descriptive statistics for the predictor variables considered in the landscape scale path analysis and in the local scale linear regressions. Min. = minimum value, Max. = maximum value, SE = standard error, CV = coefficient of variation, GSF = Global Site Factor, NND = Nearest Neighbour Distance.

			Mean	Min.	Max.	SE	CV
Landscape scale (n = 15)	Landscape change	% forest cover	69.03	40.36	99.58	2.97	23.54
		Nº forest patches	2.07	1	7	0.30	79.29
		Density of forest perimeter	516.59	47.64	807.25	36.92	39.14
	P. vulgaris	% cover	25.49	0.45	66.08	3.26	70.16
		Nº patches	3.87	1	10	0.41	57.52
Local scale (n = 45)	Light availability	GSF	0.17	0.01	0.55	0.02	82.16
	P. vulgaris	Number of adults	53.37	13	144	3.05	54.20
		Aggregation (mean NND)	0.08	0.04	0.15	0.00	30.54

APPENDIX D:

Direct, indirect and total effects of landscape change variables in flower, fruit and seed number per adult for 2008 and 2009. Boldface indicates significance (P < 0.05).

Resp. var.	Predictor var.	2008			2009		
		Direct	Indirect	Total	Direct	Indirect	Total
Flower number	Forest cover	**0.570**	-	**0.570**	-	-	-
	Edge	-	-	-	- 0.433	-	- 0.433
	Nº patches	-	-	-	-	-	-
Fruit number	Forest cover	**0.805**	0.290	**1.095**	-	-	-
	Edge	**0.598**	-	**0.598**	**- 0.490**	- 0.120	- 0.610
	Nº patches	-	-	-	**0.437**	-	**0.437**
	Flower number	**0.509**	-	**0.509**	0.277	-	**0.277**
Seed number	Forest cover	-	1.095	**1.095**	-	-	-
	Edge	-	0.584	**0.584**	-	- 0.466	**- 0.466**
	Nº patches	-	-	-	-	0.334	**0.334**
	Flower number	**- 0.326**	0.497	**0.171**	-	0.211	**0.211**
	Fruit number	**0.976**	-	**0.976**	**0.763**	-	**0.763**

Anexo: Publicaciones

Applied Vegetation Science 12: 504–515, 2009

Applying a continua landscape approach to evaluate plant response to fragmentation: *Primula vulgaris* in the Cantabrian mountains

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Abstract

Question: Continua landscape approaches conceptualize the effects of habitat fragmentation on the biota by considering fragmented landscapes as continuous gradients, departing from the view of habitat as either suitable (fragment) or unsuitable (matrix). They also consider the ecological gradients or the 'Umwelt' (species-specific perception of the landscape) to represent the processes that ultimately limit organisms' ability to colonize and persist within habitat remnants. Are these approaches suitable for evaluating the response of plant species to fragmentation?

Location: Fragmented mid-elevation temperate forests, Cantabrian range, Spain.

Methods: The presence, abundance and demographic structure of populations of the perennial herb *Primula vulgaris* were sampled across a continuous extent of 100 ha, subdivided into 400 50 m × 50 m sampling units. These variables were related to forest availability, forest subdivision and edge density, topography and the spatial clumpiness of populations (a measure of plant dispersal constraints and, hence, a major surrogate of plant Umwelt).

Results: Fragmentation processes, especially habitat loss, negatively affect *P. vulgaris*, with a stronger effect on presence than on abundance and demography. Despite the importance of habitat availability, *P. vulgaris* does not occupy all potentially suitable forest habitat, mostly owing to dispersal constraints. A positive effect of slope on plant presence also suggests some effect of habitat quality in determining establishment and occupancy of forest landscape.

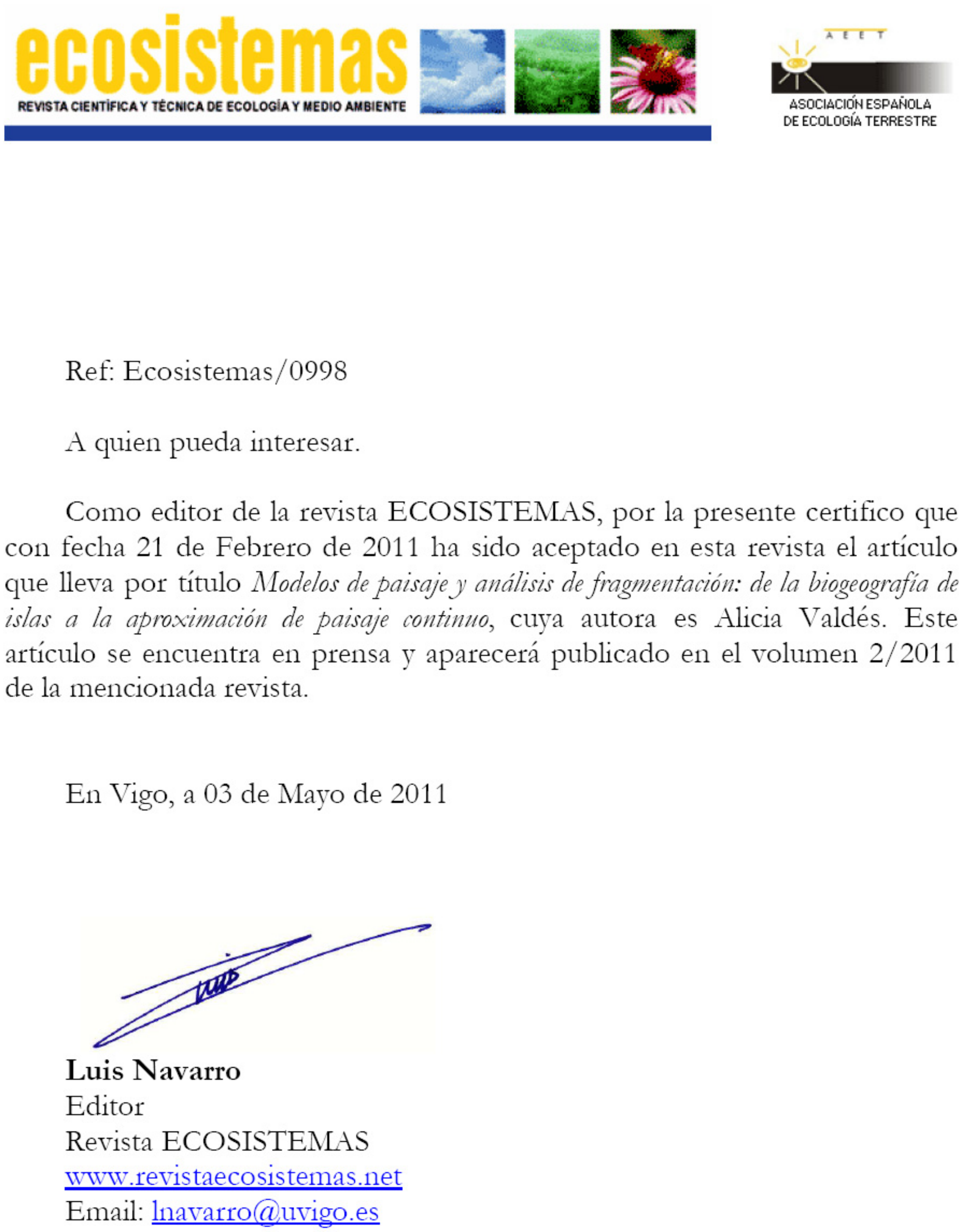
Conclusions: Within-habitat dispersal constraints are as important as forest fragmentation in determining the landscape-scale distribution of *P. vulgaris*. By assessing the relative role of the diverse fragmentation processes, and of the species' landscape perception, a continua landscape approach proves to be a valuable tool for predicting plant response to landscape change.

Keywords: Habitat availability; Habitat suitability; Land use; Landscape change; Landscape ecology; Montane forests; Northern Spain; Perennial herbs; Plant dispersal.

Nomenclature: Castroviejo et al. (1986).

Introduction

Fragmentation of natural habitats caused by human activity is considered a major cause of plant biodiversity loss worldwide (Eriksson & Ehrlén 2001; Hobbs & Yates 2003; Honnay et al. 2005; Cousins 2009). Fragmentation includes three different, but interdependent, processes of landscape change (Fahrig 2003), each of which may lead to the extinction of plant populations through specific mechanisms: (1) Habitat loss: the area of original habitat decreasing because of destruction, may lead to direct reductions of population size (Jacquemyn et al. 2002; Leimu et al. 2006), (2) Habitat subdivision, habitat remnants becoming more and more isolated within a degraded matrix, can lead to indirect reductions of population size due to metapopulation disruption (Graae 2000; Dupré & Ehrlén 2002), (3) Edge increase, the perimeter to area ratio of habitat fragments increasing as a result of their smaller size and more irregular shape may result in fitness reduction in remnant habitat species because of percolation of harmful matrix conditions (i.e. edge effects; Jules 1998; Lienert & Fischer 2003). Although the effects of habitat fragmentation have been widely reported, the models aiming to conceptualize fragmentation effects are still weak on representing real-world landscapes and on integrating the diverse fragmentation processes (Haila 2002; Lindenmayer et al. 2008). The 'island' (Laurance 2008) and 'patch-matrix-corridor' (Forman & Godron 1986, see also Forman 1995) models defend a



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A quien pueda interesar.

Como editor de la revista ECOSISTEMAS, por la presente certifico que con fecha 21 de Febrero de 2011 ha sido aceptado en esta revista el artículo que lleva por título *Modelos de paisaje y análisis de fragmentación: de la biogeografía de islas a la aproximación de paisaje continuo*, cuya autora es Alicia Valdés. Este artículo se encuentra en prensa y aparecerá publicado en el volumen 2/2011 de la mencionada revista.

En Vigo, a 03 de Mayo de 2011

Luis Navarro
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Direct and indirect effects of landscape change on the reproduction of a temperate perennial herb

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Summary

1. The harmful effects of landscape change on species reproduction may be direct when habitat loss and fragmentation affect individual performance within habitat remnants, but also indirect when reproductive collapse derives from the effect of landscape alterations on population traits. Although the distinction between direct and indirect effects is crucial for the effective management of species, studies looking at both are scarce.

2. To assess the mechanisms and the temporal consistency of landscape change effects on reproduction, we quantified flowering, fruiting and seed set of the perennial herb *Primula vulgaris* through a gradient of forest loss and fragmentation, in 2 years with different climatic conditions. We used structural equation modelling to relate, at the landscape scale, forest habitat availability and subdivision, forest edge length, population size and subdivision, and flower, fruit and seed production. We also evaluated the effects of light availability, plant abundance and aggregation on reproduction at the local scale.

3. Flower and fruit production decreased in landscape regions with lower forest habitat availability, and fruit production decreased in areas with a smaller amount of forest edge. There was also a negative indirect effect of habitat loss on seed production, through population size reduction. These effects mostly emerged at the landscape scale and operated in all reproductive stages, but were also transmitted across stages, as flower and fruit production quantitatively influenced seed output.

4. Landscape change effects on reproduction differed between the 2 years, becoming evident after a mild winter that favoured long-lasting flowering, but disappearing, or even changing sign, when winter harshness shortened flowering.

5. *Synthesis and applications*. Disentangling the relative importance of direct and indirect effects of landscape change in plant reproduction is a novel approach to distinguishing between populations and habitats as the required management targets. In our study system, increasing *P. vulgaris* population sizes within small forest patches seems less effective than increasing forest cover around existing populations (even small ones), to enhance individual reproduction. The contrasting effects of the different processes of landscape change and the potential additive role of climatic variability must also be considered in management purposes.

Key-words: Cantabrian range, habitat fragmentation, habitat loss, Northern Spain, *Primula vulgaris*, reproductive success, structural equation modelling, temperate forests, temporal variability

Introduction

Landscape change has been shown to be severely detrimental for the persistence of many species (Lindenmayer & Fischer 2006). Considerable empirical evidence attributes the harmful effects of habitat loss and fragmentation to the collapse of landscape-scale dispersal dynamics (Fahrig 2003). Moreover, population declines may also arise from altered individual reproduction within remnant habitat patches (Kolb 2005). This has been highlighted in the case of plants (e.g. Aguilar *et al.* 2006; Leimu *et al.* 2010), as it has been assumed that local population dynamics may depend more on the net outcomes of reproduction than on immigration and gene flow (Honnay *et al.* 2005; but see Bruna, Fiske & Trager 2009).

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