UNIVERSIDAD DE OVIEDO

Departamento de Biología de Organismos y Sistemas

Programa de Doctorado: "Biología aplicada a la sostenibilidad de recursos naturales (Mención de calidad)"

"Dispersión de semillas y recolonización forestal en un paisaje fragmentado. Buscando la huella de mirlos y zorzales (*Turdus* spp.) más allá del bosque."

"Seed dispersal and forest recolonization in a fragmented landscape. Looking for the footprint of thrushes (*Turdus* spp.) beyond the forest."

TESIS DOCTORAL

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RESUMEN (en Inglés)

Frugivorous birds develop a key role in ecosystem functioning. They disperse seeds of many different plant species, being fundamental for maintaining and recovering plant communities, and developing thus an important ecosystem service. This ecological function renders frugivorous birds essential for conservation and restoration plans.

The consideration of an ecosystem service as part of environmental management programs must be based on a precise knowledge of the underlying ecosystem processes. To do that, ecosystem services should be studied from different complementary perspectives allowing to characterize the key organisms providing services, the environmental factor conditions provision, and the spatio-temporal scales at what services operate. Moreover, it must be assessed how human induced ecosystem degradation alters the provision of services.

The main objective of this PhD Thesis is to characterize the role of frugivorous birds in the regeneration process of zoochorous trees in a degraded forest landscape. The considered study system was the Cantabrian secondary forests, dominated by fleshy-fruited species whose main dispersers are thrushes (*Turdus* spp.).

Chapter 1 studies how landscape characteristics conditions the distribution of frugivorous birds. Fruit and forest cover availability affects their habitat use and, thus, the potential area influenced by avian service. As a starting hypothesis, it is suggested that the influence of both factors –fruits and forest cover- could be not independent from each other, with the effects of each one on frugivore habitat use being conditioned by the availability of the other.

Chapter 2 focuses on evidencing how the frugivory rate of individual trees depends on their ecological its neighborhood. These neighborhood effects determine the emergence of indirect plant-plant interactions, mediated by frugivores, which contribute to the structuration of tree community. Specifically, it is studied whether the temporal variability of the plant-frugivore system conditions the consistency and reciprocity of frugivore-mediated indirect interactions.

Chapter 3 studies how landscape structure conditions seed rain generated by frugivorous birds in deforested areas. The seed rain potentially driving the recolonization processes is characterized. It is assumed that fruiting landscapes widening bird's foraging areas could relax restrictions to seed dispersal within deforested areas.

Chapter 4 studies the effectiveness of frugivorous birds in the process of forest regeneration in a context of habitat loss. The bird contribution to tree regeneration is evidenced by means of an integrative

approach, considering the different stages of recruitment, and paying special attention to recolonization in deforested areas. It is hypothesized that habitat loss may condition frugivore's footprint directly, by affecting their spatial behavior, but also by conditioning the strength of post-dispersal environmental filters.

The result of this PhD Thesis evidence the service provided by frugivorous birds given their crucial contribution to forest maintenance and recolonization. Habitat degradation influences this service through different ways. Seed rain is nucleated under forest cover and few seeds arrive in deforested areas. Post-dispersal processes alters frugivore's footprint on regeneration. The presence of heather bushes within deforested areas, protecting seedlings from browsing, strengthens the initially weak bird footprint in the final patterns of recruitment. Results also show that the spatio-temporal heterogeneity of forest and the adaptive response of birds are key factors contributing to spread the service through the landscape. The conservation of frugivorous birds is needed for the maintenance of forest remnants. Forest extent recover will be achieved by implementing management measures to increase seed dispersal within deforested areas, while simultaneously preserving heathers that facilitate long-term tree establishment in these areas.

SR. DIRECTOR DE DEPARTAMENTO DE BIOLOGÍA DE ORGANISMOS Y SISTEMAS

A todos los que me han enseñado a aprender

y a aquellos de los que he aprendido a enseñar.

"*There are some who can live without wild things,*

and some who cannot.

These essays are the delights and dilemmas of one who cannot."

Aldo Leopold

A sand county almanac

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Introducción

Introducción general

Aves frugívoras, bosques y servicios ecosistémicos

Las aves desarrollan importantes funciones ecológicas en los sistemas naturales. Tienen un papel relevante como nodos en diferentes niveles de las redes tróficas, actúan como mutualistas fundamentales para numerosos grupos de plantas, pueden afectar a los flujos de nutrientes e incluso pueden actuar como ingenieros ecosistémicos (Sekercioglu 2006). La dispersión de semillas ha sido descrita como una de las principales funciones ecológicas que llevan a cabo estos organismos (Whelan et al. 2008; Wenny et al. 2011). Las aves frugívoras desempeñan un papel clave al dispersar las semillas de numerosas especies de plantas, con especial importancia en sistemas forestales tropicales y templados, en donde entre un 30 y un 90% de las especies de plantas son dispersadas por animales (Jordano 2000). La actuación de las aves frugívoras puede beneficiar a las plantas de muy diferentes maneras. Al retirar la pulpa de las semillas o por medio del tratamiento digestivo a las que las someten, la actividad de los frugívoros puede facilitar la germinación (Traveset y Verdú 2002). Los patrones espaciales de dispersión de semillas que generan (i.e. la lluvia de semillas; Nathan y Mueller-Landau 2000) tienen importantes repercusiones en la regeneración de las plantas. Transportando las semillas lejos de su árbol madre ayudan a que dichas semillas, y sus correspondientes plántulas, escapen de procesos de mortalidad densodependiente o debidos a efectos alelopáticos (Janzen 1970; Conell 1971; Harms et al. 2000). Dada la elevada movilidad de las aves, la dispersión de semillas favorece, además, el flujo génico en las poblaciones de plantas (Jordano y Godoy 2002; García et al. 2009a). Esa movilidad, junto con el alto grado de generalismo de las interacciones entre aves frugívoras y plantas (un mismo ave se relaciona con diferentes plantas y viceversa; Jordano 2000; Bascompte et al. 2003; Donatti et al. 2011), llevan a que también contribuyan a la estructuración de las comunidades vegetales (Harms et al. 2000; Levine y Murrell 2003). Por todo ello, y a través de los adultos que se establecen a partir de la lluvia de semillas, las aves frugívoras

dejan una huella significativa que resulta fundamental para el mantenimiento de la dinámica y estructuración de las poblaciones y las comunidades de plantas. Al hacer esto no sólo resultan fundamentales para el mantenimiento de los sistemas forestales, si no que desempeñan un importante servicio ecosistémico.

Los *servicios ecosistémicos* son todas aquellas condiciones o procesos determinados por los ecosistemas naturales, o las especies que los forman, que son necesarios para mantener el bienestar del ser humano (Daily 1997; Kremen 2005). Con la única aportación externa de la luz solar como energía que desencadena su funcionamiento, los ecosistemas generan ciclos biogeoquímicos que condicionan desde que dispongamos de oxígeno que respirar hasta que tengamos alimentos. Dada la gran variedad de beneficios que, directa e indirectamente, obtenemos de los sistemas naturales, y para una mejor comprensión de los mismos, se han diferenciado varias categorías de servicios ecosistémicos (Millennium Ecosystem Assessment 2003):

-*Servicios de provisión*: Engloban todos los bienes que obtenemos directamente de la naturaleza. Los ecosistemas nos proporcionan desde agua y alimentos (pesca, caza y frutos entre otros) hasta materiales de construcción, fibras, combustibles o productos químicos y farmacéuticos.

-*Servicios de regulación*: El funcionamiento de los ecosistemas regula procesos clave para nuestro bienestar, influenciando el clima, la calidad del aire y el agua, la erosión de los suelos o la incidencia de enfermedades humanas y animales y de plagas a cultivos.

-*Servicios culturales*: De ellos también obtenemos beneficios que son inmateriales, por medio de los valores estéticos, espirituales, culturales o recreativos que los ecosistemas representan para el ser humano.

-*Servicios de soporte*: Esta categoría engloba todos aquellos procesos que son necesarios para que el resto de servicios puedan mantenerse. En esta categoría se incluyen, por ejemplo, los ciclos de nutrientes, la creación de suelo, la producción primaria, la polinización o la dispersión de semillas.

Las aves benefician al ser humano de formas tanto directas como indirectas que van desde el control de enfermedades humanas y plagas agrícolas, hasta la fertilización del suelo, pasando por el turismo ornitológico (Whelan et al. 2008). La dispersión de semillas, aun teniendo un efecto indirecto, ha sido descrito como uno de los principales servicios que desarrollan (Whelan et al. 2008, Wenny et al. 2011). Al contribuir al funcionamiento de los sistemas forestales las aves frugívoras sustentan los servicios ecosistémicos que éstos generan. La producción de madera, como material de construcción o combustible, de frutos, caza o compuestos de interés farmacéutico son beneficios muy evidentes que obtenemos de estos ecosistemas, pero algunos de sus principales servicios no lo son tanto. Los bosques contribuyen a la creación y estabilización de los suelos, a regular los flujos hídricos (manteniendo la provisión de agua, pero también evitando inundaciones) y climáticos (influyendo en las precipitaciones, regulando la temperatura o aumentando el albedo) y son importantes sumideros de CO_2 (Myers 1997; Chazdon 2008). Estos servicios de regulación, fundamentales para nuestro bienestar, ganan aún mayor relevancia en el contexto actual de cambio global ya que pueden contribuir a mitigar sus efectos (Bonan 2008).

Servicios ecosistémicos en hábitats degradados

Las aves frugívoras no sólo son fundamentales para el funcionamiento de los sistemas forestales prístinos. Una función clave que desarrollan es la de contribuir a su mantenimiento y al de los servicios ecosistémicos que generan cuando éstos se encuentran degradados, llegando incluso a favorecer su recuperación. La gran movilidad de muchas especies de aves las convierte en elementos fundamentales de la resiliencia de estos ecosistemas, ya que pueden actuar como vínculos móviles (*mobile links*; Fig. I.1; Lundberg y Moberg 2003) transportando información entre diferentes áreas. Esta capacidad de movimiento les permite permanecer en paisajes fragmentados y seguir visitando rodales que por su tamaño o calidad no son capaces de albergar poblaciones estables de frugívoros y seguir desempeñando sus funciones en ellos (Lundber y Moberg

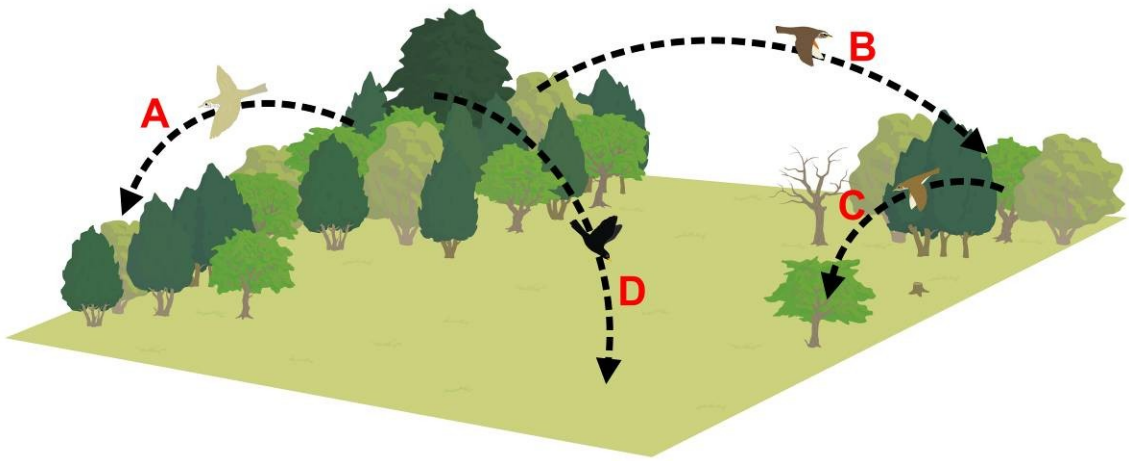


Fig. I.1. La capacidad de movimiento de las aves frugívoras es un rasgo clave para su función dentro de los ecosistemas forestales. No sólo mantienen las dinámicas de regeneración dentro del bosque (A), si no que también contribuyen al mantenimiento de las áreas degradadas, ya sea al visitarlas desde otros parches (B) o permaneciendo en ellas a pesar de su alteración (C). Incluso son capaces de favorecer la recuperación de áreas deforestadas al transportar semillas allí (D).

2003; Kremen et al. 2007; García et al. 2010; Rey 2011). Al ser capaces de transportar semillas entre diferentes rodales de bosque en paisajes fragmentados, promueven dinámicas metapoblacionales (García et al. 2009a) evitando así, en parte, los efectos negativos de los procesos de depresión genética por endogamia que pueden ocurrir en poblaciones vegetales pequeñas y aisladas (Ghazoul 2005). Pero su contribución puede ser más importante aún, al llevar semillas desde rodales de bosque remanente hasta las zonas completamente deforestadas, desencadenando el proceso de recolonización forestal en ellas (Fig. I.1D; Wunderle 1997; Lundberg y Moberg 2003; Cavallero et al. 2013). Estos hechos hacen que las aves frugívoras sean organismos de especial interés en planes de conservación, manejo y restauración de ecosistemas y de sus servicios (Sekercioglu 2006; Lundber y Moberg 2003; Kremen et al. 2007; Whelan et al. 2008). En el caso de los planes de restauración de ecosistemas degradados, la actuación de los frugívoros puede facilitar el que la recuperación forestal requiera escasa intervención (e inversión) o que llegue a producirse de forma pasiva (i.e. sin intervención humana; Chazdon 2008; Rey Benayas et al. 2008; Holl y Aide 2011).

La deforestación se encuentra entre los principales motores de cambio global (Sala et al. 2000; Lambin y Geist 2006; Meyfroidt y Lambin 2011). En el caso de los bosques europeos, su reducción ha sido el resultado de un largo proceso histórico de explotación por parte del ser humano. A la obtención de madera para su uso como material de construcción y combustible, y al aclareo de los bosques para obtener pastos para el ganado o tierras de cultivo se unieron, en tiempos modernos, la eliminación del bosque con finalidades industriales y su sustitución por monocultivos forestales, algunos de ellos con especies exóticas (Darby 1956; Behre 1988; Kaplan et al. 2009). Este proceso no sólo ha determinado una disminución de la superficie forestal, si no que ha dejado paisajes forestales altamente fragmentados (Wilcove et al. 1986), en los que los reductos de bosque están lejos de ser puramente naturales, mostrando una importante influencia de la actividad humana (Hannah et al. 1995), con pérdida de numerosas especies tanto animales como vegetales. Sin embargo, a día de hoy y en determinadas áreas del planeta, este proceso podría no sólo haberse detenido si no que también comenzado a revertirse (FAO 2011). La actual tendencia de despoblamiento en áreas rurales de Europa y Norte América, especialmente en zonas de montaña (MacDonald et al. 2000; FAO 2011; pero ver Blanco-Fontao et al. 2011), está dejando abandonadas tierras previamente dedicadas a prácticas agrícolas y ganaderas tradicionales que muestran grados de perturbación moderados y, por ello, con alto potencial para la recuperación forestal (Rey Benayas et al. 2007; Cramer et al. 2008; Navarro y Pereira 2012). Este proceso plantea una importante oportunidad para que se favorezca la *renaturalización* de estas áreas, lo que llevaría a un aumento de la superficie forestal y así como a un incremento de sus servicios (Chazdon 2008; Rey Benayas et al. 2009; Navarro y Pereira 2012). Entender cómo las aves frugívoras influencian los procesos naturales de mantenimiento y recolonización de los sistemas forestales puede ayudarnos a gestionar dichos procesos.

¿Qué necesitamos saber de los servicios ecosistémicos?

Considerar los servicios ecosistémicos dentro de programas y políticas de gestión y manejo medioambiental puede ser una buena herramienta a la hora de afrontar el proceso de cambio global. El lograr mantenerlos o potenciar su incremento contribuiría a paliar los efectos negativos que el cambio climático, los cambios de uso del suelo, las extinciones de especies o las invasiones biológicas acarrean (Kremen et al. 2007, Chazdon 2008). Sin embargo, estas actuaciones han de estar basadas, necesariamente, en un conocimiento preciso de los procesos ecológicos que subyacen a un servicio determinado (Kremen 2005, Carpenter et al. 2009). Kremen (2005) ha sugerido enfocar nuestro estudio de los servicios ecosistémicos desde puntos de vista complementarios que permitan alcanzar un conocimiento más global de la ecología de los servicios, integrando los diferentes procesos y componentes que los determinan (Fig. 2). Entre las principales necesidades de estudio destacó el caracterizar a los organismos que actúan como proveedores clave del servicio, el evaluar qué características ambientales condicionan su habilidad para suministrarlo y el ver sobre qué escala espacio-temporal actúan. Además, tanto Kremen como otros autores (Daily1997; Lundberg y Moberg 2003; Kremen 2005; Kremen et al. 2007; Tomimatsu et al 2013) han destacado la necesidad de que los servicios se estudien no sólo en los ecosistemas prístinos sino también en paisajes reales (i.e. alterados por la actividad humana), en los que el funcionamiento de los ecosistemas, y con ello de los servicios, puede verse seriamente alterado.

Estudiando a los organismos clave en un servicio ecosistémico podemos comprender cuáles de sus rasgos o funciones son los que determinan su importancia, y cómo su actividad condiciona la distribución del servicio (Fig. I.2). Como ya se expuso previamente, la relevancia que las aves frugívoras tienen para la regeneración forestal se debe al hecho de que actúan como dispersoras de semillas gracias a su movilidad (Fig. I.1). Sin embargo, y a pesar de su elevada capacidad de movimiento, esto no significa que la distribución de su servicio vaya a ser generalizada si no que estará limitada por la propia distribución de los

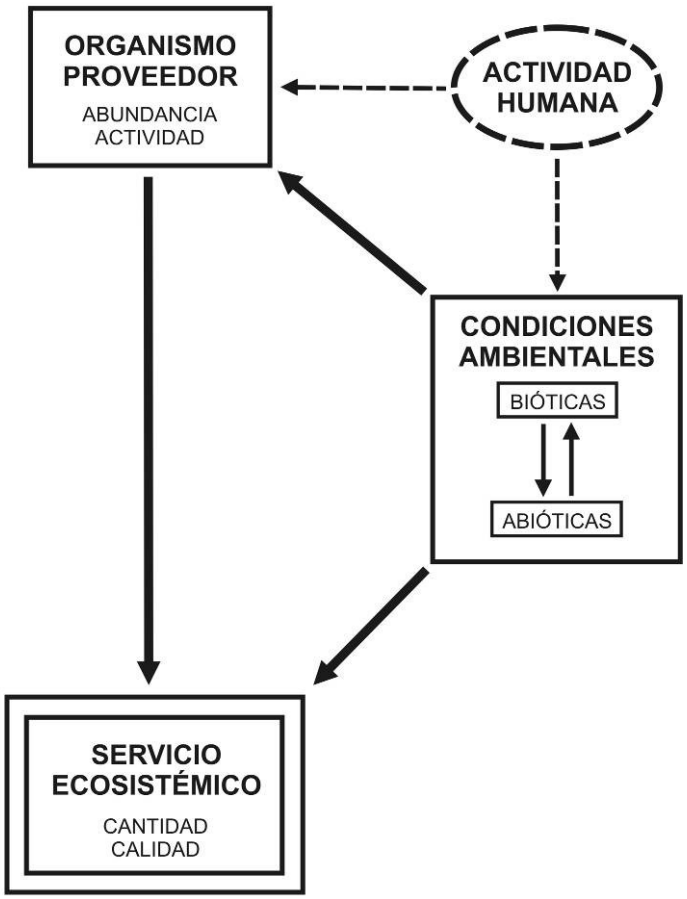


Fig. I.2. Diagrama conceptual mostrando los condicionantes de un servicio ecosistémico. Se consideran como proveedores del servicio a aquellos organismos responsables de desencadenarlo y, en gran medida, de su magnitud. Las condiciones ambientales bióticas y abióticas, también pueden ser relevantes para el servicio, ya sea por los efectos directos que tengan en él o por su influencia en el organismo proveedor. La actividad humana puede afectar tanto a los proveedores como a las condiciones ambientales, llevando a alteraciones de los servicios.

frugívoros y las funciones que desarrollen. La huella espacial que estos dejen estará mediada por las características ambientales que condicionan su uso del hábitat. Esta huella será la que determine el área potencial de influencia del servicio.

Las disponibilidades de frutos y cobertura forestal (actuando como protección) han sido descritas como las principales características del medio condicionando la actividad de las aves frugívoras (Herrera 1985; Cardoso da Silva et al. 1996; Alcántara et al. 2000; García et al. 2010; Blendinger et al.

2012). Respondiendo a la disponibilidad de ambos factores las aves optimizan su actividad a diferentes escalas (Sallabanks 1993; García y Ortiz-Pulido 2004), lo que determina desde su distribución a escala regional (Rey 1995; Tellería y Pérez-Tris 2003; Guitian y Munilla 2008) hasta su uso del hábitat dentro del paisaje local (Cordeiro y Howe 2003; Saracco et al. 2004; García et al. 2010). En el paisaje, las aves concentran su actividad en parches de bosque denso con abundante producción de frutos, evitando salir a zonas abiertas donde encuentran menos alimento y están más expuestas a los depredadores (Cardoso da Silva et al. 1996; Alcántara et al. 2000; García et al. 2010). Esto lleva a que la lluvia de semillas que generan esté concentrada generalmente bajo la cobertura del propio bosque, con sólo una pequeña parte de las semillas saliendo de él (Kollmann y Pirl 1995; Duncan y Chapman 1999; Alcántara et al. 2000; García et al. 2010). Frutos y cobertura condicionan además, en parte, la escala espacial a la que actúa el servicio de los frugívoros. Como norma general, los frugívoros que salen de la cobertura forestal se alejan poco de ella y por ello la cantidad de semillas dispersadas en áreas deforestadas disminuye rápidamente al alejarse del borde del bosque (Willson y Crome 1989; Aide y Cavelier 1994; Cubiña y Aide 2001). Pero la disponibilidad de estos dos factores influencia también el servicio al condicionar qué árboles concretos visitan los frugívoros, y con ello los patrones de lluvia de semillas a escala fina dentro del bosque (Nathan y Muller-Landau 2000; Carlo et al. 2007). Aunque los atributos de un árbol individual son importantes para que lo visiten (p.ej. el tamaño de cosecha; Sallabanks 1993; Blendinger et al. 2012), el vecindario ecológico en que se encuentra (i.e. las características ambientales de su entorno inmediato; Addicott et al. 1987) influye también en las decisiones de las aves, que optimizan su actividad alimentándose en árboles que disponen de abundante cobertura y frutos en su entorno (Sallabanks 1993; Saracco et al 2005; García y Chacoff 2007). La influencia del vecindario ecológico, además, está lejos de ser simple. En ocasiones, diferentes especies de plantas que comparten dispersores actúan como fuentes alternativas de alimento en un mismo vecindario. En los casos en los que esta diversidad condiciona en qué árbol comen los frugívoros, aparecen interacciones indirectas

(i.e. los efectos entre dos especies que están mediados por una tercera; Wootton 1994) entre las diferentes especies de plantas (Carlo et al. 2007 y referencias allí). Una planta podrá ver aumentada (Sargent 1990; Carlo y Aukema 2005; Blendinger et al. 2008) o disminuida (Manasse y Howe 1983; Alcántara et al. 1997; Saracco et al. 2005) la frecuencia de visita de las aves dependiendo de qué especies tengan por vecinas. Estos efectos de vecindario pueden tener importantes repercusiones para la estructuración de las comunidades forestales, ya que condicionan la distribución de la frugivoría (y por tanto del éxito reproductivo) entre distintas especies (Levine y Murrell 2003; Carlo et al. 2007) así como la lluvia de semillas a escala fina (Nathan y Muller-Landau 2000).

Las características ambientales no sólo condicionan los servicios ecosistémicos por medio de su influencia en los proveedores. En ocasiones, la huella que los organismos proveedores generan inicialmente con su actividad sufre un filtrado ambiental posterior, como resultado de otros factores tanto abióticos como bióticos, que condicionan que el servicio sea finalmente efectivo (Fig. I.2; Kremen 2005). Los frugívoros determinan el potencial de regeneración por medio de los patrones de lluvia de semillas que generan. Sin embargo esta huella inicial está lejos de ser el único determinante de los patrones finales de establecimiento de nuevos árboles adultos. Tras la dispersión, las semillas, y más tarde las plantas que germinan de ellas, quedan expuestas a múltiples influencias que condicionan el proceso de regeneración (Schupp y Fuentes 1995; Nathan y Mueller-Landau 2000; Schupp et al. 2010). Los patrones espaciales de deposición generados por los frugívoros pueden verse alterados por procesos de dispersión secundaria (Vander Wall y Longland 2005). La supervivencia y germinación de las semillas dependerán, en gran medida, de la actividad de los roedores y otros depredadores (Crawley 2000), pero también de las condiciones abióticas (luz, temperatura, humedad, etc.; Fenner 2000) en que se encuentren. Las plántulas emergidas de las semillas supervivientes, y posteriormente los individuos juveniles que estas generen, se verán afectados de nuevo por las condiciones abióticas en que se desarrollen, así como por la competencia con

otras plantas o el ataque de patógenos y herbívoros (Harms et al. 2000; Kitajima y Fenner 2000). Además, la influencia de los factores bióticos y abióticos no será necesariamente la misma para los diferentes estadios, de manera que el efecto inicial de los frugívoros no sólo disminuirá en intensidad si no que también podrá ver alterados sus patrones espaciales (Schupp y Fuentes 1995; Nathan y Mueller-Landau 2000). Este proceso secuencial de filtrado ambiental condicionará, pues, la efectividad de las aves frugívoras ya que no todas las semillas inicialmente dispersadas contribuirán al proceso final de regeneración forestal.

La degradación de los ecosistemas altera su funcionamiento, de manera que el conocimiento científico que dispongamos de los sistemas prístinos no será necesariamente extrapolable a las áreas degradadas, categoría que, a día de hoy, describiría a gran parte de los sistemas considerados como naturales. Para mantener y recuperar los servicios generados por estos ecosistemas necesitamos conocer qué alteraciones de funcionamiento presentan y comprender cómo estas afectan a los servicios (Lundberg y Moberg 2003; Kremen 2005; Kremen et al. 2007; Tomimatsu et al. 2013). La degradación de los sistemas naturales puede afectar a los servicios ecosistémicos a través de diferentes vías, teniendo efectos tanto en los proveedores del servicio como en los condicionantes ambientales del mismo (Fig. I.2). En el caso de la regeneración forestal mediada por las aves frugívoras, la degradación del medio puede reducir los tamaños de población de los dispersores, llevando a una disminución de la magnitud del servicio (García et al. 2010; Farwig y Berens 2012). La modificación de su hábitat, además, puede producir cambios en la actividad de las aves determinando alteraciones de los patrones de dispersión de semillas que generan (Cordeiro y Howe 2003; McConkey et al. 2012; Rey y Alcántara 2014). La efectividad de estos frugívoros también podrá verse afectada, incluso sin producir cambios en su abundancia o su actividad, si la degradación del sistema lleva a una alteración del filtrado ambiental de los estadios de regeneración post-dispersivos. Los cambios en las condiciones abióticas como la disponibilidad de luz, los regímenes hídricos o térmicos, o las características del suelo, tendrán importantes efectos sobre las

dinámicas de regeneración post-dispersiva (Kapos et al. 1997; Uriarte et al. 2010). Del mismo modo, las alteraciones en la incidencia de organismos antagonistas, como depredadores de semillas, patógenos o herbívoros, jugaran un papel importante en los patrones finales de regeneración (García y Chacoff 2007; González-Varo 2010; Puerta-Piñero et al. 2012). Comprender y gestionar el servicio realizado por las aves frugívoras en los ecosistemas requerirá de la consideración explícita de los principales factores que determinan los patrones finales de regeneración.

Objetivos

El objetivo general de esta tesis doctoral es caracterizar el papel de las aves frugívoras en el ciclo de regeneración de árboles de fruto carnoso en un paisaje forestal degradado, poniendo especial atención en la contribución a la recolonización forestal en áreas deforestadas. Los tres primeros capítulos abordan de forma crítica los principales paradigmas sobre los efectos de la estructura del hábitat en la actividad y el servicio de dispersión de los frugívoros. En concreto, se estudia la robustez de estos paradigmas frente a la variabilidad ambiental impuesta por la degradación del hábitat forestal así como por la variación interanual intrínseca de los paisajes de fructificación a los que se enfrentan las aves. Estos capítulos muestran la relación de las aves con las plantas en tres fases secuenciales, desde que las aves se enfrentan al paisaje a la hora de aprovisionarse de frutos, hasta que dispersan las semillas en él. El cuarto capítulo pretende llegar más allá, no sólo en lo que al ciclo de la planta se refiere, sino también en sus objetivos. En él se intenta evidenciar cuál es la huella final que dejan las aves en el proceso de regeneración forestal, lo que permitiría valorar el servicio real que desempeñan.

El **capítulo 1** "*Fine-tuning habitat use by frugivorous birds: interaction between protection and food availability*" estudia, sobre una serie interanual larga, el efecto de las características del paisaje sobre la distribución de las aves frugívoras. Se analiza el efecto conjunto de la disponibilidad de frutos y cobertura forestal en el uso del hábitat por parte de los frugívoros y, por tanto, en el área de distribución potencial del servicio dispersivo. Como hipótesis de partida se plantea que las influencias de ambos factores –frutos y cobertura forestal- podrían no ser independientes, si no que los efectos que cada uno tiene en el uso del hábitat de los frugívoros podrían estar condicionados por la disponibilidad del otro.

El **capítulo 2** "*Consistency and reciprocity of indirect interactions between tree species mediated by frugivorous birds*" tiene por objetivo evidenciar qué características del vecindario ecológico de un árbol influencian la magnitud de la frugivoría en él. A través de estos efectos de vecindario se estudia cómo las aves frugívoras determinan la aparición de interacciones indirectas entre las diferentes especies de fruto carnoso. Esta mediación implica que los frugívoros pueden estructurar las comunidades vegetales no sólo determinando dónde (bajo qué especie arbórea) se dispersan las semillas, sino también desde dónde (qué especie) lo hacen. En este capítulo se comprueba si la importante variabilidad temporal que caracteriza a los sistemas planta-frugívoro condiciona la consistencia y la reciprocidad de estas interacciones indirectas mediadas por las aves.

El **capítulo 3** "*Changes in fruiting landscapes relax restrictions on endozoochorous tree dispersal into deforested lands*" estudia cómo la estructura del paisaje condiciona los patrones de dispersión de semillas generados por las aves frugívoras. Más allá de únicamente comparar las diferencias entre el bosque y las áreas deforestadas, este capítulo caracteriza los patrones espaciales de dispersión de semillas en estas últimas áreas, ya que la limitación a la dispersión condiciona en gran medida el proceso de recolonización forestal en ellas. Se plantea que cambios en el paisaje de fructificación que amplíen las áreas de actividad de los frugívoros podrían contribuir a relajar la limitación a la dispersión de semillas en áreas deforestadas impuesta por la distancia al bosque.

El **capítulo 4** "*Footprint of seed dispersers in forest regeneration and recovery under habitat loss*" estudia la influencia de las aves frugívoras a través del proceso multifásico y global de regeneración, y cómo dicha influencia se ve afectada por la pérdida de hábitat. Integrando explícitamente los diferentes estadios secuenciales del ciclo de

regeneración, se evidencia la contribución de los frugívoros al proceso regeneración forestal, considerando de manera especial el proceso de recolonización en áreas deforestadas. Se plantea que la pérdida de hábitat puede condicionar la huella de las aves frugívoras no sólo mediante su influencia directa en ellas si no también afectando a su efectividad, al alterar el proceso de filtrado ambiental post-dispersivo.

Los resultados de estos trabajos permitirán lograr un mejor entendimiento de la contribución de las aves frugívoras a los procesos de mantenimiento y recuperación del bosque en un ambiente degradado, es decir, de su servicio ecosistémico. Los diferentes trabajos pretenden no sólo contribuir al conocimiento ecológico de las funciones de las aves y de los procesos que las condicionan, sino también ofrecer, además, información útil para la conservación y recuperación de los servicios ecosistémicos derivados.

Sistema y sitio de estudio

Sistema de estudio

El sistema de estudio considerado para el desarrollo de los trabajos de investigación de esta tesis doctoral es el bosque secundario montano cantábrico (norte de España). Este es un de hábitat frecuente en la Cordillera Cantábrica pero altamente fragmentado y que supone una baja cobertura a escala regional (García et al 2005a). El bosque secundario aparece frecuentemente como orla del bosque primario (principalmente de haya *Fagus sylvatica* o roble *Quercus* spp.), pero también de forma aislada, como rodales forestales de tamaño reducido o arboles individuales en el seno de pastizales y brezales-piornales (*Erica* spp., *Ulex europaeus*) dedicados a ganadería extensiva tradicional (principalmente razas autóctonas de vacuno y equino).

Los estudios se centraron en las acebedas-espineras, formaciones forestales dominadas por árboles productores de fruto carnoso. En dichas formaciones, acebo *Ilex aquifolium* y espino albar *Crategus monogyna* aparecen acompañados de ejemplares de tejo *Taxus baccata*, serbal de cazador *Sorbus aucuparia* y mostajo o serbal blanco *Sorbus aria*. Aunque estas especies suponen más del 70% de la cobertura arbórea (García et al. 2005b), junto a ellos también es frecuente encontrar avellano *Corylus avellana* así como, en ocasiones, ejemplares aislados de haya, fresno común *Fraxinus excelsior* o arce sicómoro *Acer pseudoplatanus*. Como especies de estudio se escogieron el acebo, el espino y el tejo (Fig. I.3) ya que ambos serbales son raros en la localidad de estudio (ver *Material y métodos generales*). Estas tres especies presentan frutos (semilla arilada en el caso del tejo) de morfología, tamaño y coloración similar (Fig. I.3) que maduran desde finales del verano, pudiendo permanecer en el árbol hasta finales del invierno.

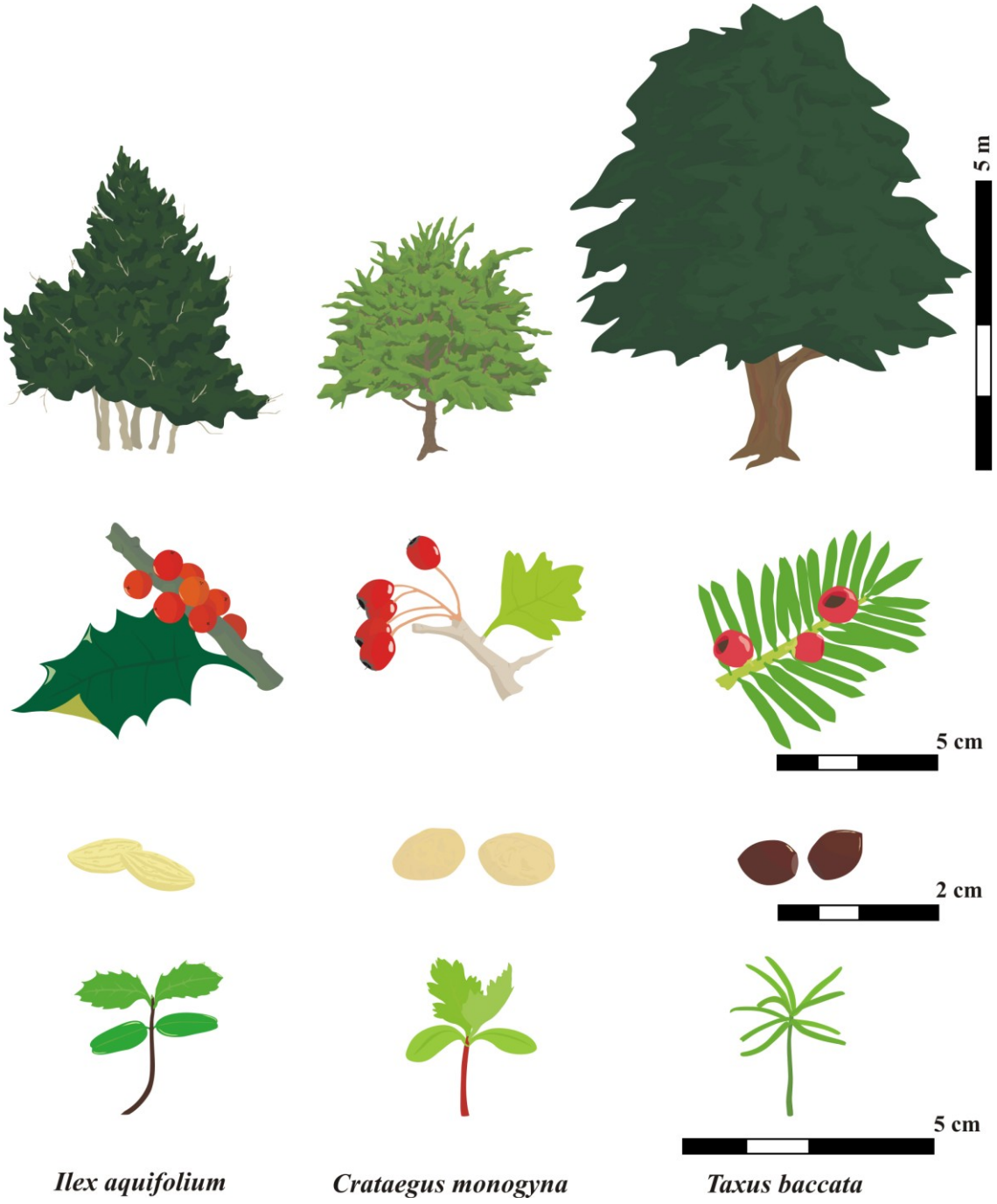


Fig. I.3. Diagrama mostrando el porte del individuo adulto, las hojas y los frutos (semillas ariladas en el tejo), las semillas y las plántulas de las tres especies arbóreas de estudio. La escala de representación varía entre estadios, por ello se incluye una escala aproximada en la figura para cada uno de ellos. En cada estadio la escala de representación es la misma para las diferentes especies de planta.

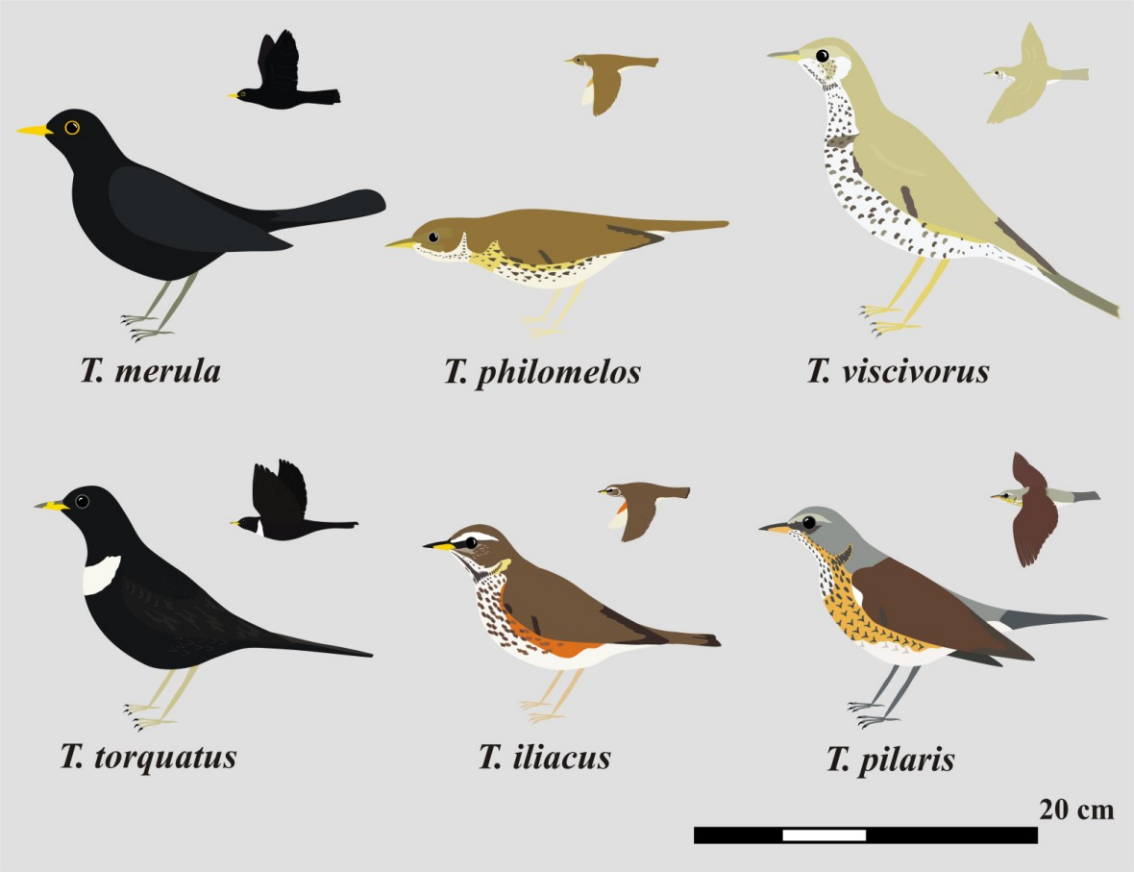


Fig. I.4. Especies de aves del género *Turdus* presentes en el sistema de estudio durante otoño e invierno. En la fila superior se muestran las especies residentes y en la inferior las invernantes. Para cada especie se muestra la vista del ave posada y en vuelo. Las diferentes especies aparecen representadas a la misma escala (se incluye escala aproximada para la vista del ave posada).

Mirlos y zorzales (*Turdus* spp.) son los principales frugívoros de estas especies (Martínez et al. 2008). En el área de estudio aparecen las seis especies de este género (Fig. I.4) presentes en Europa occidental: mirlo común *Turdus merula*, zorzal común *T. philomelos*, zorzal real *T. pilaris*, zorzal charlo *T. viscivorus*, zorzal alirrojo *T. iliacus* y mirlo capiblanco *T. torquatus*. Mientras que los zorzales alirrojo y real y el mirlo capiblanco son invernantes en el área cantábrica (criando en áreas del centro y norte de Europa), el mirlo y los zorzales común y charlo son especies residentes cuyas poblaciones se ven aumentadas durante otoño e invierno con individuos migradores procedentes de poblaciones más septentrionales (Ashmole 1962a,b). Aunque estas aves son mayoritariamente insectívoras y territoriales durante primavera y verano, su comportamiento pasa a

ser gregario en el otoño y el invierno (formando bandos mono- y multiespecíficos), periodo durante el cual su dieta está basada en frutos (Snow y Snow 1988). Aunque para algunas especies de zorzal se han descrito ciertas preferencias por especies concretas de frutos (p.eg. alirrojo-acebo; Guitián y Bermejo 2006), mirlos y zorzales pueden mostrar una considerable amplitud de dieta (Snow y Snow 1988; García et al. 2014), y en el área de estudio su alimentación parece estar condicionada en gran medida por la disponibilidad específica de frutos que encuentran cada año (García et al. 2013). Mirlos y zorzales ingieren los frutos enteros defecando las semillas intactas, actuando así como dispersores legítimos (Jordano 2000) para los árboles del sistema de estudio. Ciertas especies de mamíferos, como tejones *Meles meles*, zorros *Vulpes vulpes* o martas y garduñas *Martes* sp., también contribuyen a la dispersión de semillas de los árboles cantábricos (López-Bao y González-Varo 2011), aunque con menor importancia cuantitativa que mirlos y zorzales (Martínez et al. 2008; Peredo et al. 2013). Otras aves como la paloma torcaz *Columba palumbus*, diferentes córvidos, el petirrojo *Erithacus rubecula* o currucas *Sylvia* spp. se alimentan ocasionalmente de estos frutos, aunque los últimos tienden a actuar como depredares de pulpa (Snow y Snow 1988). Páridos *Parus* spp. y camachuelo común *Pyrrhula pyrrhula* actúan como depredadores de las semillas de los árboles aquí estudiados (Snow y Snow 1988).

Investigaciones previas en este sistema de estudio evidencian que la regeneración de los árboles depende fundamentalmente de la disponibilidad de semillas (i.e. sufren de limitación a la dispersión) en el sistema de estudio (García et al. 2005b). La lluvia de semillas está constituida principalmente por las semillas dispersadas por las aves, y en menor medida por las semillas contenidas en los frutos que caen bajo los doseles arbóreos. Las semillas dispersadas por las aves son depredadas principalmente por el ratón de campo *Apodemus sylvaticus* y el leonado *A. flavicollis* (García et al. 2005b,c), que también comen las semillas directamente de los frutos caídos (observación personal). La depredación de los roedores sobre el banco de semillas ocurre principalmente durante el invierno,

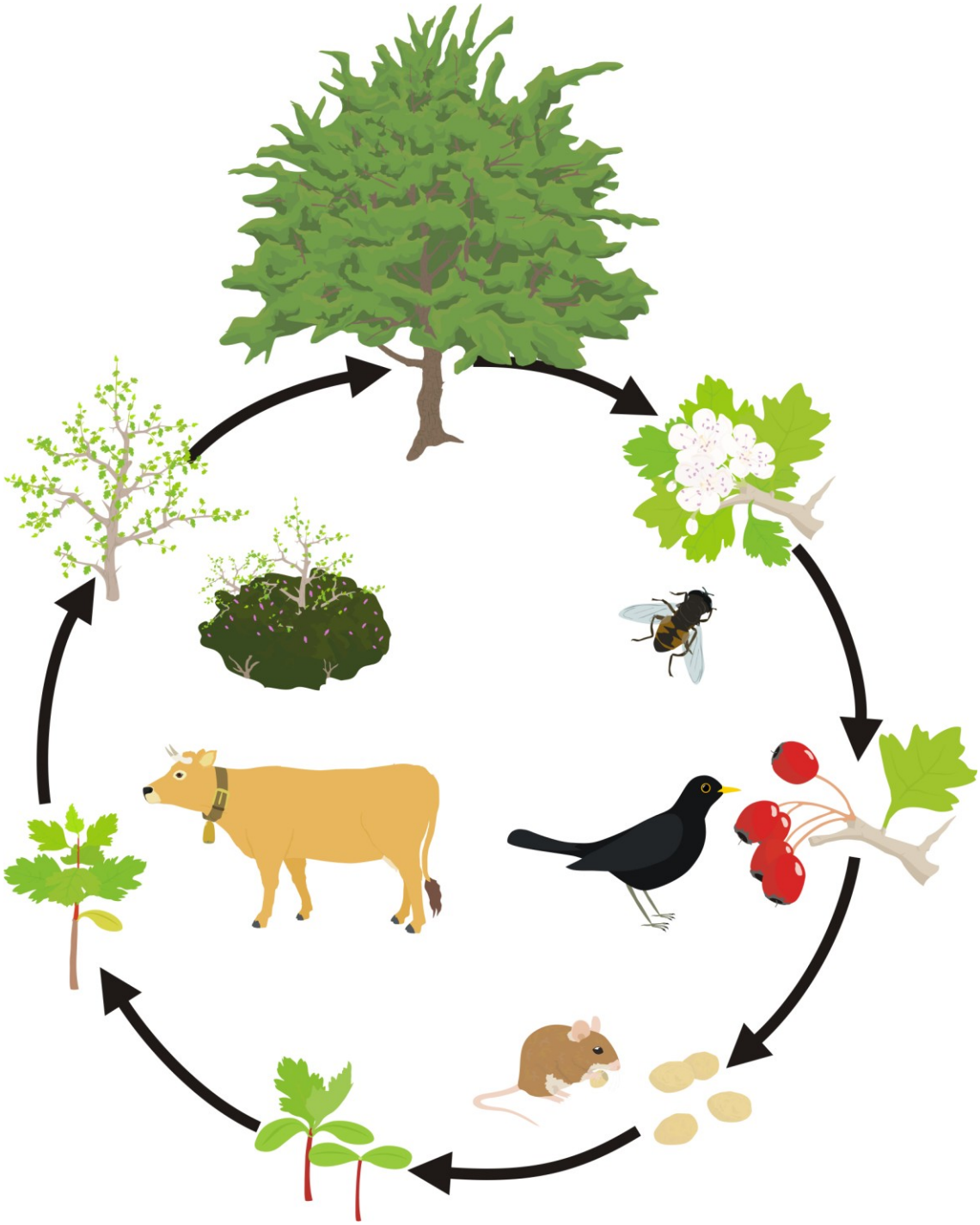


Fig. I.5. Esquema del ciclo de regeneración de las especies arbóreas de estudio, ejemplificadas por medio del espino albar *Crataegus monogyna,* y principales organismos que interactúan con estas especies (ver texto para detalles). Los interactores aparecen situados frente a la transición demográfica (flechas negras) a la que afectan. En el caso de los ungulados sus efectos influyen desde el estadio de plántula hasta el establecimiento de los nuevos adultos.

teniendo mayor incidencia bajo la cobertura forestal que en áreas abiertas (García et al 2005b). El banco de semillas es transitorio en las tres especies estudiadas y la germinación de la mayor parte de las semillas (ca. 70%) se produce tras 18 meses, durante la segunda primavera (entre abril y junio) tras la dispersión (D. García, *datos no publicados*). Las plántulas sufren una elevada mortalidad por ramoneo y pisoteo por ungulados (García y Obeso 2003; García et al. 2005b). Trabajos previos han demostrado que, al menos en el caso del tejo, el establecimiento puede verse favorecido por el dosel protector de árboles y arbustos espinosos (García y Obeso 2003).

Sitio de estudio

Los cuatro estudios que componen esta tesis doctoral se llevaron a cabo en una misma localidad situada en la Sierra de Peña Mayor, entre los concejos de Nava, Bimenes y Laviana (1000 m s.n.m.; 43º 17’ 59” N, 5º 20’ 29” W; Fig. M.1), en el Principado de Asturias (Fig. I.6A). En ella las especies arbóreas de estudio aparecen de forma dispersa en el sotobosque del bosque primario (hayedo), y mayormente como formaciones de orla y rodales independientes inmersos en la matriz deforestada que domina el paisaje. En esta localidad se estableció una parcela de estudio rectangular de 400 × 440 m principalmente cubierta por pastizales, brezales y afloramientos rocosos (suponiendo más del 70% de la cobertura; Fig. I.6 y Fig. I.7). En ella el bosque secundario aparece creando un gradiente de cobertura que va de masas continuas a pequeños fragmentos forestales y árboles asilados en la matriz (Fig. I.6B,C,D,E y Fig. I.7). La estructura de la parcela permitió disponer de un amplio rango de contextos difiriendo en las características del hábitat a escala fina.

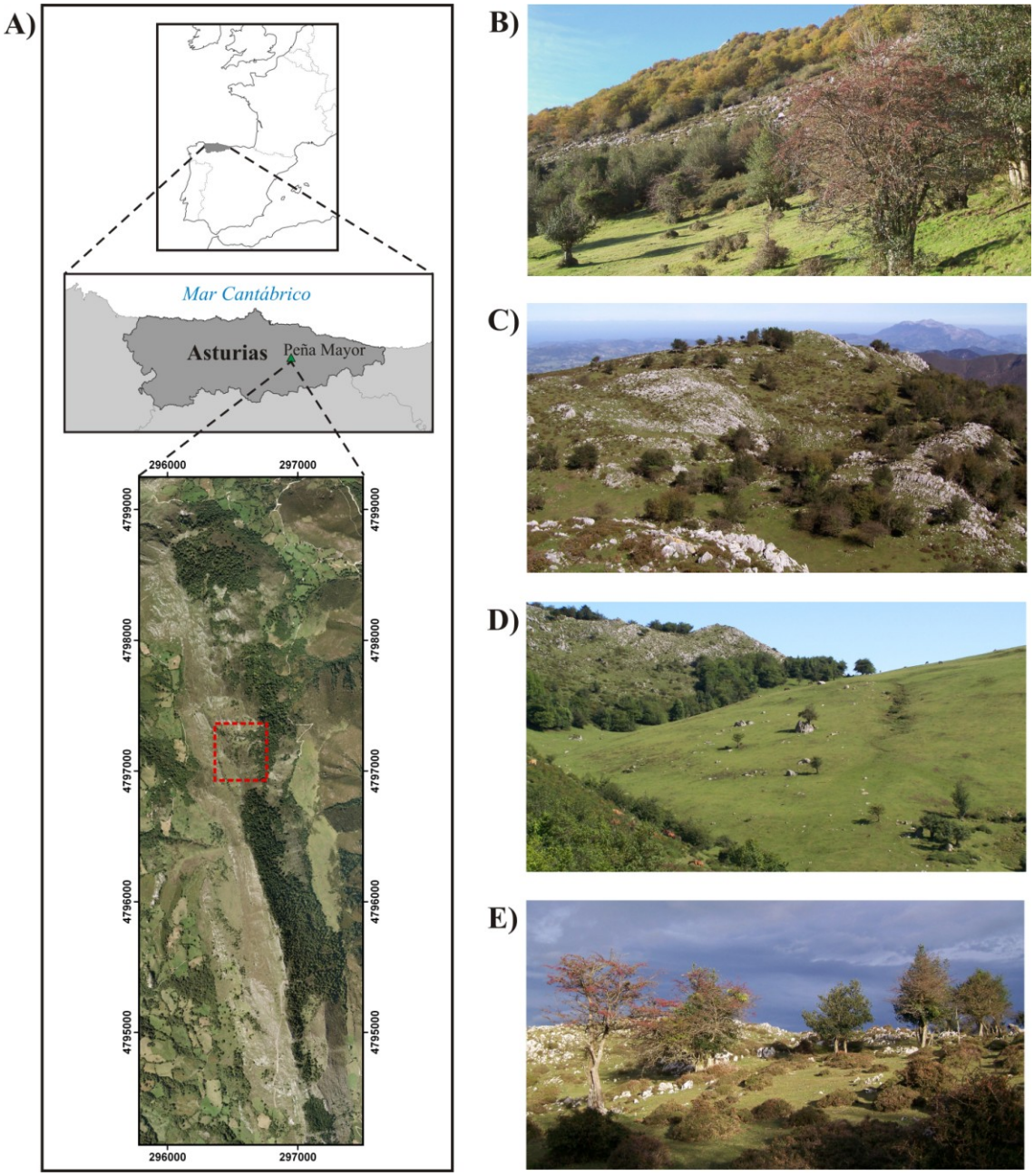


Fig. I.6. A) Localización geográfica del sitio de estudio. La ubicación de la parcela de estudio está señalada por rectángulo rojo sobre el ortofotomapa de la sierra de Peña Mayor. B) Aspecto de la localidad de estudio, presentando una acebeda-espinera (bosque secundario) en primer término y hayedo (bosque primario) en segundo plano en la parte alta de la ladera. C) Estructura fragmentada del bosque secundario en la parcela de estudio. D) Áreas con alto grado de deforestación dominadas por pastizales. E) Ejemplares de espino y acebo aislados un área deforestada con presencia de matorrales.

Métodos generales

Para tener un mejor manejo de la información espacial, la parcela fue subdivida en 440 celdas de 20 × 20 m (Fig. I.7). Estudios previos han demostrado que la extensión de la parcela y el tamaño de grano de la celda componen una escala de muestreo adecuada para representar la variabilidad espacial en los patrones de cobertura forestal, producción de frutos, actividad de aves, dispersión de semillas y germinación de plántulas (Herrera y García 2010; García y Martínez 2012; García et al. 2013). El total de los datos utilizados para los diferentes estudios fueron recogidos desde comienzos del otoño de 2007 hasta el final del verano de 2012, aunque el periodo de tiempo abarcado por cada capítulo no fue el mismo (para más detalles ver capítulos concretos).

Caracterización del hábitat forestal

Se creó un Sistema de Información Geográfiga (SIG, representado por las siglas en GIS en las partes del texto que se presentan en inglés) de la parcela de estudio basado en ortofotografías recientes (2009) de escala 1:5000. Se generó una capa basada en información georeferenciada exacta sobre la localización y dimensiones de la parcela, incluyendo la división en 440 celdas. Para representar la localización y extensión de la cobertura forestal se creó una capa de polígonos a partir de una digitalización precisa de su distribución en las ortofotografías (Fig. I.7). La capa de cobertura forestal incluyó la proyección del dosel de todos los árboles presentando un diámetro a la altura del pecho mayor de 10 cm y una altura mayor a 1.5 m, incluyendo los individuos aislados localizados en pastos y brezales. En aquellos casos en que el área de la cobertura forestal resultara dudosa sobre las ortofotografías, se comprobó *in situ* en el campo la extensión exacta de la misma.

En septiembre de 2007 se recorrió la superficie completa de la parcela mapeando la posición exacta de cada árbol presente en la misma, e identificándolo a nivel de especie (ver en Capítulo 2, Fig. C2.2B). Los árboles

productores de fruto carnoso de la parcela fueron principalmente el acebo (1633 individuos), el espino (662) y el tejo (103), apareciendo escasos individuos de las dos especies de serbal (16) que supusieron una proporción muy reducida de la producción de frutos en la parcela (< 3%) durante todos los años de estudio. La presencia de otras plantas de fruto carnoso cuyo periodo de fructificación esté solapado con el de las especies de estudio fue también muy reducida, no habiendo encontrado ejemplares de rosal silvestre *Rosa* spp. y pocas manchas aisladas y de muy escasa extensión de zarza *Rubus fruticosus/ulmifolius.* En octubre de cada año de estudio, entre 2007 y 2011, se estimó visualmente el tamaño de cosecha de cada uno de los árboles productores de fruto carnoso previamente mapeados, usando una escala semilogarítmica (*Fruit Abundance Index* FAI: 1= 1-10 frutos; 2 = 11-100; 3 = 101-1000; 4 = 1001-10000; 5 > 10000; Saracco et al. 2005). Tanto en el sistema como en la localidad de estudio, la fructificación de las diferentes especies de estudio es sincrónica y los frutos maduran a lo largo de uno o dos meses, permaneciendo después en el árbol entre 1 y 3 meses. Por ello se consideró que un único muestreo de la producción de frutos a comienzos de la temporada ofrecía una estima apropiada tanto de la abundancia como de la distribución espacial de los frutos disponibles para las aves.

Usando el SIG, se calculó el área de cobertura forestal y la cantidad de frutos producido por las diferentes especies en cada celda. La abundancia de frutos se obtuvo sumando los tamaños de cosecha de los diferentes árboles encontrados en cada celda. Para ello primero se estimó de un modo más preciso el tamaño de cosecha de una muestra de los árboles de la parcela, contando en cada uno el número de frutos producidos en 15 ramas (distribuidas por toda la copa del árbol) y extrapolándolo a la copa completa a partir del número total de ramas del árbol. Esto permitió realizar un ajuste entre el tamaño real de la cosecha y el FAI correspondiente, siguiendo una ecuación alométrica (*Tamaño de cosecha* = $1.765^{1.924\,FAI}$; $R^2 = 0.80$; $N = 136$; Herrera et al. 2011a).

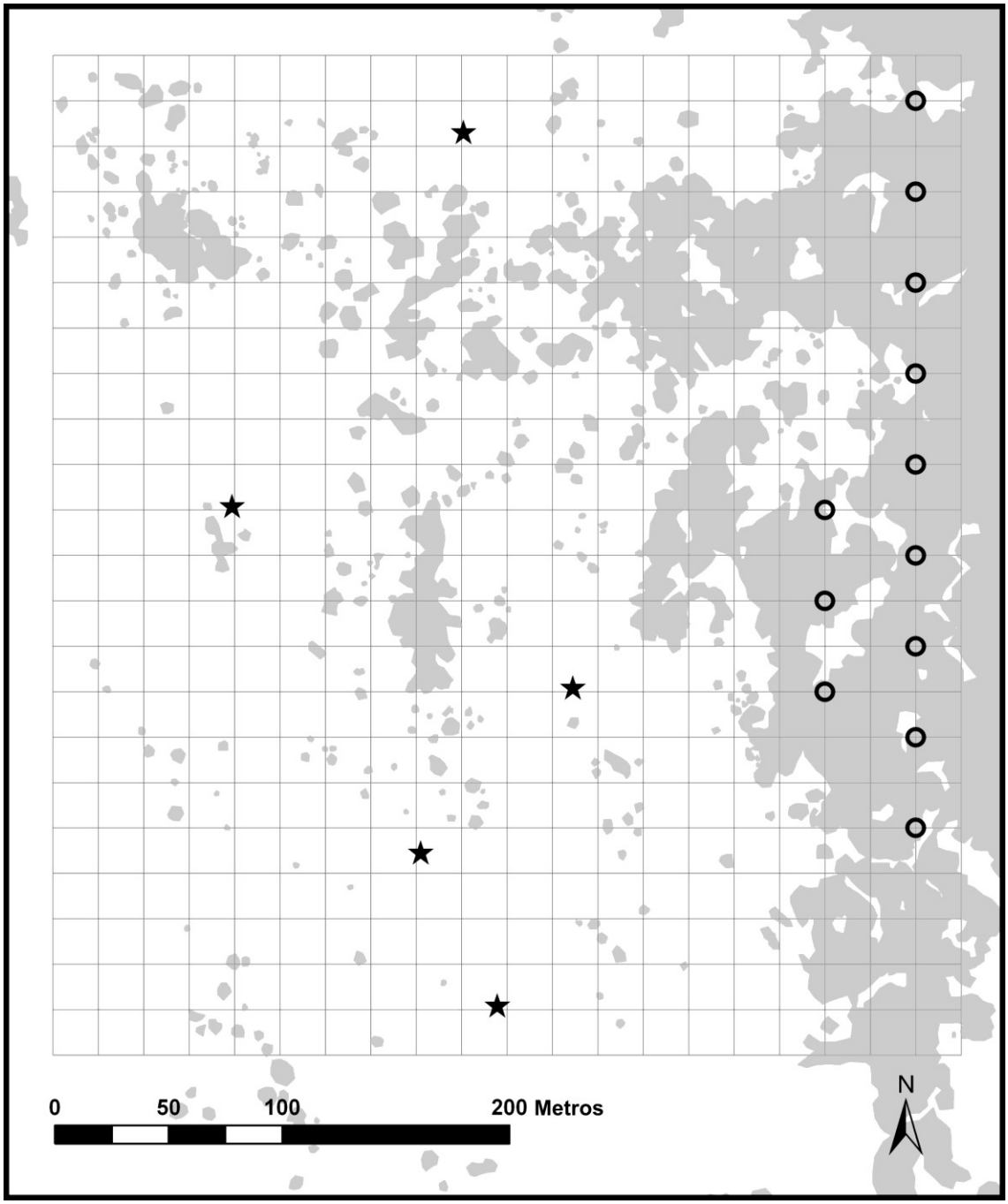


Fig. I.7. Mapa de la parcela de estudio, subdividida en celdas de 20 × 20 m, mostrando la extensión forestal (área en gris), y los puntos de observación de aves elevados (estrellas negras) y dentro del bosque (círculos).

Censos de aves frugívoras

Realizamos censos en la parcela para cuantificar la abundancia de mirlos y zorzales durante la época de fructificación. Se establecieron cinco puntos de observación directa en localizaciones elevadas situadas a lo largo del eje central de la parcela (Fig. I.7). Las observaciones se realizaron entre octubre y febrero cada temporada de estudio (2008-09 a 2011-12), con periodos de observación de una hora en cada punto, y repartiendo el tiempo de forma balanceada entre los diferentes puntos a lo largo de la temporada. En cada periodo de observación, el observador, ayudado por prismáticos (de 8 × 30), contó todos los zorzales vistos y oídos en diferentes las diferentes celdas georeferenciadas situadas dentro del campo de visión (con la ayuda de mapas impresos). En algunos casos, el avistamiento consecutivo de individuos de una misma especie podría corresponder al mismo individuo permaneciendo dentro de una celda determinada, o volviendo en ella tras pasar por otra. En estos casos, consideramos como independientes aquellas observaciones separadas por al menos 5 minutos.

La posición elevada de los puntos de observación (situados cubriendo un gradiente de 70 m de altura), junto con la estructura mayoritariamente parcheada y dispersa de la cobertura forestal en el paisaje, permitieron una alta detectabilidad visual y acústica de los mirlos y zorzales en la mayor parte de la superficie de la parcela, incluso en celdas situadas a distancias considerables. Sin embargo, debido a una mayor densidad de la cobertura forestal y a la topografía, la detectabilidad de las aves fue menor en algunas de las celdas más orientales de la parcela. Por ello se establecieron doce puntos de observación complementarios dentro del bosque en estas zonas, con cada punto localizado en el centro de cuatro celdas (Fig. I.7; ver García y Martínez 2012 y García et al. 2013 para utilización del mismo procedimiento). En estos puntos los censos se realizaron en periodos de diez minutos, contándose el número de mirlos y zorzales vistos u oídos en las cuatro celdas adyacentes. El objetivo de los censos no era evaluar el tamaño de población de los frugívoros, si no dar una medida de su abundancia en

términos funcionales, i.e. una estima de la actividad de los mirlos y zorzales a lo largo de la temporada en la parcela de estudio. Para ello se calculó la abundancia de aves por celda como el número acumulado de zorzales y mirlos vistos u oídos en cada celda a lo largo de la temporada. Se dividió el número acumulado de aves entre el tiempo total de observación para cada celda, calculando el número total de aves por cada 10 horas de observación. El ponderar por el tiempo total por celda permite la comparación de abundancia entre celdas, al corregir la sobreestimación en aquellas celdas observadas desde distintos puntos (y que, por lo tanto, contaban con mayores tiempos de observación) pero también entre años con diferente esfuerzo de observación.

Muestreo de semillas dispersadas

Se evaluó la lluvia de semillas generada por las aves en estaciones de muestreo distribuidas por toda la parcela en las temporadas de otoño-invierno de 2009-10 y 2010-11. Se situaron diez estaciones de muestreo, separadas cada una de la siguiente por dos metros, a lo largo del eje central norte-sur de 220 celdas de la parcela seleccionadas siguiendo un diseño de tablero de ajedrez (Fig. I.8) En cada estación se estableció un cuadrado de 50 × 50 cm en el suelo en el que se recogieron todas las semillas dispersadas por las aves en dos muestreos consecutivos (uno a finales de noviembre y otro en enero). Las semillas dispersadas por las aves son inequívocamente identificables: aparecen limpias de restos de pulpa, a diferencia de las que provienen de frutos caídos bajo los árboles, y en pequeños grupos (lo que las distingue de las que aparecen en las deposiciones de mamíferos), siendo atribuibles casi exclusivamente a los mirlos y zorzales (Martínez et al. 2008). Se estimó la abundancia de semillas dispersadas en las estaciones de muestreo como la suma de las encontradas en los dos muestreos, expresando su densidad como el número de semillas por metro cuadrado. Trabajos previos han demostrado que la pérdida de semillas dispersadas por la actividad de depredadores como roedores es baja durante el periodo de muestreo, con mayor incidencia avanzado el invierno (García et al. 2005c). Para cada estación de muestreo se recogió información de la estructura

del hábitat en que estaba situada, distinguiendo dos categorías de hábitat: bajo cobertura forestal y en áreas deforestadas (Fig. I.8B).

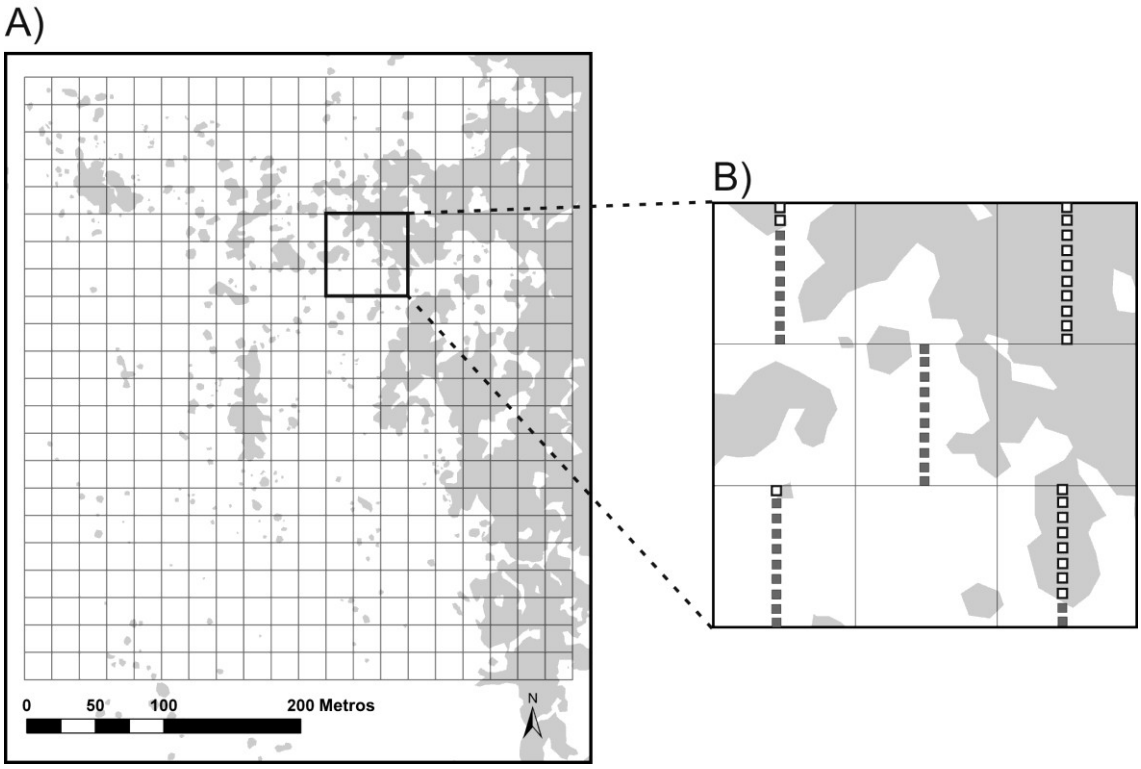


Fig. I.8. A) Parcela de estudio mostrando un detalle del diseño de tablero de ajedrez (B) utilizado para el muestreo de dispersión de semillas. Las estaciones de muestreo bajo cobertura forestal aparecen representadas por cuadrados pequeños blancos, mientras que las situadas en áreas deforestadas aparecen en gris oscuro.

Capítulo 1

Fine-tuning habitat use by frugivorous birds: interaction between protection and food availability

Afinando el uso del hábitat por aves frugívoras: interacción entre protección y disponibilidad de alimento

Abstract

Frugivorous animals contribute to plant regeneration, but the provision of this ecosystem services is spatially filtered by the environmental factors limiting frugivore habitat use. Understanding how this filter acts in real-world landscapes is crucial for predicting possible impacts of Global Change on seed dispersal services. Fruits and forest cover are the main determinants of frugivorous birds habitat use. The degree of spatial segregation between these habitat features is expected to determine a trade-off for frugivores between finding food and being safe. Nevertheless little is known on how such a trade-off may finally affect frugivore habitat use. We studied frugivorous bird habitat use in a landscape representing a gradient of forest loss and fragmentation. For four years we evaluated the spatial patterns of the abundances of frugivorous bird, fruits, and forest cover. Both fruits and forest cover influenced bird habitat use every year. However, we found an interaction between the effects of forest cover and fruits, with variations on the relevance of each factor depending on the availability of the other one. Namely, frugivore dependence on forest cover increased in landscape sectors with scarce fruits, but weakened when fruits were abundant. Similarly, birds preferentially used fruit-rich patches when being in those areas where forest cover was low, but relaxed fruit search in densely forested areas. The simultaneous consideration of the different environmental factors limiting frugivore habitat use revealed complex landscape effects, which are expected to cascade into fine-grained variability of seed rain.

Resumen

Los animales frugívoros contribuyen a la regeneración de las plantas, pero la provisión de este servicio se encuentra filtrada especialmente por aquellos factores que limitan el uso del hábitat por los frugívoros. Comprender como actúan estos filtros en los paisajes reales resulta crucial para predecir el posible impacto del proceso de Cambio Global en los servicios de dispersión de semillas. La distribución de los frutos y la cobertura forestal son los principales determinantes del uso del hábitat por parte de las aves frugívoras. Es esperable que el grado de segregación espacial entre frutos y cobertura de bosque determine un importante *trade-off* para los frugívoros entre encontrar alimento y protección. Estudiamos el uso del hábitat por parte de las aves frugívoras en un paisaje con un gradiente de pérdida y fragmentación forestal. Durante cuatro años evaluamos los patrones espaciales de la abundancia de aves frugívoras, frutos y cobertura forestal. Frutos y cobertura de bosque influenciaron el uso del hábitat de las aves todos los años. Sin embargo, encontramos una interacción entre los efectos de la cobertura y los frutos, con variaciones en la importancia de cada factor dependiendo de la disponibilidad del otro. La dependencia de los frugívoros de la cobertura forestal fue mayor en los sectores del paisaje con escasos frutos, pero se debilitó cuando los frutos fueron abundantes. De un modo similar, las aves usaron preferentemente las zonas con abundantes frutos al estar en sectores del paisaje con baja cobertura forestal, pero su búsqueda de frutos fue menos intensa en áreas de bosque denso. El considerar simultáneamente cómo diferentes factores ambientales limitan el uso del hábitat de las aves frugívoras permitió revelar efectos complejos del paisaje, que es esperable que repercutan en la variabilidad de los patrones de lluvia de semillas a escala fina.

Introduction

Frugivorous animals, by contributing to seed dispersal and the concomitant plant regeneration, provide an important ecosystem service (Whelan et al. 2008; Kremen et al. 2007; Farwig and Berens 2012). They take seeds away from mother plants, decreasing density dependent mortality (Hammond and Brow 1998; Metz et al. 2010), favoring gene flow (Hamrick et al. 1993; Jordano and Godoy 2002) and, when depositing seeds in degraded areas, promoting vegetation recovery (Wunderle 1997; Cavallero et al. 2013). Nevertheless this service is not delivered elsewhere, but spatially shaped by the environmental factors that ultimately filter frugivore distribution, by conditioning the availability of their suitable habitat (Nathan and Muller-Landau 2000; García et al. 2010). In order to predict seed dispersal under the potential scenarios of Global Change, it is, thus, mandatory a deeper understanding of the environmental filtering processes affecting frugivores in real-world landscapes (Naeem and Wright 2003; Kremen 2005; Tomimatsu et al. 2013). In the case of frugivorous birds, a major group of seed dispersers in temperate and tropical forests (Sekercioglu 2006), fruit abundance and woody plant cover have been described as major drivers of habitat use. Birds are able to optimize their foraging by tracking fruit abundance through space and time, resulting in more intense use of fruit-rich patches (Herrera 1985; Rey 1995; Saracco et al. 2004; Blendinger et al. 2012). The protection against predators, often provided by dense woody plant cover, is also a fundamental habitat condition for frugivorous birds, who avoid open areas where they are more vulnerable (Cardoso da Silva et al. 1996; Cordeiro and Howe 2003; García et al. 2010). In many landscapes, both food and protection co-occur, as fruits are concentrated in dense cover areas dominated by fleshy-fruited plants (e.g. García et al. 2010). However, in some habitats, especially those affected by anthropogenic alterations, frugivores must cope with spatially segregated food and protection (like in deforested areas with remnant fruiting trees, or in logged or plantation forest devoid of fruiting trees; Cleary et al. 2007; Herrera and García 2009). In these uncoupling cases, frugivores should optimize their habitat use according to a trade-off between

tracking fruits and staying within denser forest cover (Howe 1979; Fedriani and Boulay 2006). Despite their potential relevance in frugivore habitat use, the trade-offs have been poorly evaluated explicitly (but see García et al. 2011 for a scale-dependent approach). Due to interactive effects mediated by frugivore optimization behavior, it would be expected a lower weight of food or protection on habitat use when, respectively, the other factor is widely available (e.g. frugivores would be less reluctant to visit risky sites in those areas still providing much fruits; García et al. 2013).

In this study, we evaluated how fruit abundance and forest cover shaped simultaneously the habitat use of frugivorous birds in a fragmented landscape of the Cantabrian Range. For that purpose, we related the spatial patterns of bird abundance with that of forest cover and fruit abundance, during four consecutive years. Specifically we sought to answer the following questions: 1) What factor (fruit abundance *vs.* forest cover) influenced the most the abundance of frugivorous birds? 2) Was the relative relevance of both factors constant across years? And 3) Did the effect of forest cover on bird abundance varied depending on small-scale fruit availability and *vice versa*?

Specific materials and methods

The study was carried out over four consecutive years: autumn-winter season 2008-09, 2009-10, 2010-11 and 2011-12 (hereafter, respectively 2008, 2009, 2010 and 2011).

Frugivorous bird censuses

For this chapter we considered bird abundances obtained from observations performed in the study plot during 2008, 2009, 2010 and 2011fruiting seasons (for further explanation see *Métodos generales* section). The cumulative observations time from the vantage positions was of 103, 105, 156 and 215 h for 2008, 2009, 2010 and 2011, respectively. Observation time from each point

count was 165, 110, 195 and 230 min for 2008, 2009, 2010 and 2011, respectively.

Forest cover and fruit counts

We quantified forest cover area and fruit abundance in each plot cell, for 2008, 2009, 2010 and 2011 as specified in *Métodos generales* section.

Statistical analyses

Between-year variations in fruit abundance and in the abundance of birds were tested by means of Generalized Linear Models (GLM) with a quasi-Poisson error distribution and *log* link function.

To asses frugivore habitat selection we compared the actual distribution of plot cells according to their forest structure with that of cells in the same categories but where bird presence was detected. Independent comparisons were made for each year by means of Pearson's Chi^2 test.

To assess the influence of forest cover and fruit abundance on bird abundance we used Zero-inflated GLMs with Poisson error distribution and *log* link function. An independent model was built for each study year. All models included, as predictor variables, forest cover and fruit abundance, together with the interaction term forest cover × fruit abundance, and bird abundance (nº birds per 10-h of observation) as response variable. Correlation between the predictor variables was $r < 0.7$ (Pearson´s coefficient) in all models.

When significant interaction terms occurred in the Zero-inflated GLMs, *a posteriori* analyses were performed to evaluate the effect of a given predictor (forest cover or fruit abundance) on the response variable at different levels of the other predictor. To do that, we performed lineal regressions confronting the values of the response variable predicted by the original whole model against the partial residuals of each predictor (i.e. the residuals of one predictor against the

other), at different levels of the other predictor (Quinn and Keough 2002; Lamina et al. 2012). We differentiated two levels: low, with values from 0 to the respective mean of the distribution; and high, with values over the mean of the distribution. Statistical comparison between regression coefficients were done following Zar (1996). All the analyses were performed by using R 2.15 (R 2013), with *pscl* package for Zero-inflated GLMs.

Results

Fruit abundance varied between years (Fig. C1.1; GLM: F= 1904, $p < 0.0001$, DF= 1756), with a lower fruit production in 2008 (10.25 ± 1.14 fruits per square meter per cell) than in subsequent years (between groups differences *t* test in the GLM; Fig. C1.1). Bird abundance varied between years too (Fig. C1.1; GLM: F= 44.02, $p < 0.0001$, DF= 1756). The lowest abundance was observed during 2010 and the maximum in 2011, while 2008 and 2009 showed intermediate values (Fig. C1.1).

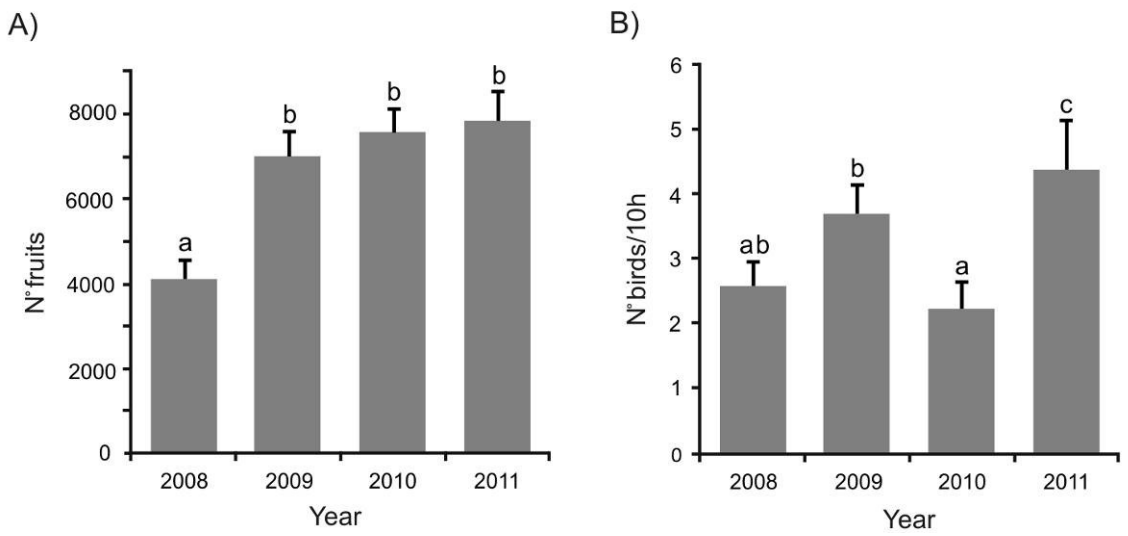


Fig. C1.1. A) Mean fruit abundance per cell (± Standard Error, SE) across years. B) Mean abundance of frugivorous birds per cell (nº birds/10h, ± SE) across years. In both parameters, significantly different years are denoted with different letters.

The presence of birds was distributed unequally between cells with different forest structure (Chi^2 test: F > 38, d.f. = 2 and $p < 0.001$ for all years; Fig. C1.2). Birds occurred more frequently than expected in those cells with both

forest cover and fruits. Conversely, birds significantly avoided open cells and, in a lesser extent, cells with forest cover but no fruits.

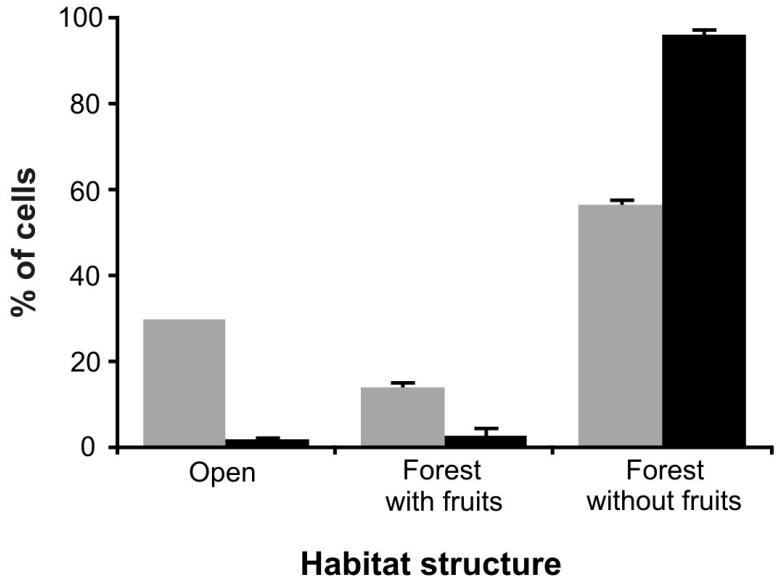


Fig. C1.2. Distribution of cells in which bird presence was recorded (black) according to their habitat characteristics (Open: with no forest cover) compared with that of all cells in the plot (gray). Mean values of four study years (± SE) are shown.

GLM models showed that forest cover and fruit abundance influenced bird abundance all years, with consistently stronger effects for forest cover than for fruit abundance (Table C1.1). Nevertheless we found a significant interaction between the effects of both predictors every year (Table C1.1). As evidenced by partial lineal regressions, the positive effects of forest cover on bird abundance differed between low and high fruit abundance levels, as they were stronger in areas of low fruit abundance (Table C1.2, differences between slopes: $t > 1.96$, $p < 0.05$ and $N = 440$ for all the cases). The effects of fruit availability on bird abundance also differed across levels of forest cover. Fruit abundance influenced positively bird abundance in cells with low forest cover, but, unexpectedly a negative effect appeared at high cover levels, in three out four study years (Table C1.2, differences between slopes: $t > 1.96$, $p < 0.05$ and $N = 440$ for all the cases).

Table C1.1. Effects of forest cover and fruit abundance on the abundance of frugivorous birds. Independent Zero-Inflated GLMs were performed for each study year. Maximum likelihood estimates, their standard errors, the values of the *z* statistic and *p* values are shown.

2008				
	Estimate	Std. Error	z	*p*
Intercept	5.526	0.005	1071.5	< 0.001
Forest cover	0.736	0.003	231.2	< 0.001
Fruit abundance	0.109	0.007	16.2	< 0.001
Forest cover × fruit abundance	-0.116	0.004	-26.4	< 0.001
2009				
	Estimate	Std. Error	z	*p*
Intercept	5.823	0.004	1382.5	< 0.001
Forest cover	0.645	0.003	225.5	< 0.001
Fruit abundance	0.389	0.004	96.9	< 0.001
Forest cover × fruit abundance	-0.137	0.002	-63.5	< 0.001
2010				
	Estimate	Std. Error	z	*p*
Intercept	5.209	0.006	856.2	< 0.001
Forest Cover	0.847	0.004	230.8	< 0.001
Fruit abundance	0.268	0.005	56.6	< 0.001
Forest cover × fruit abundance	-0.176	0.003	-57.8	< 0.001
2011				
	Estimate	Std. Error	z	*p*
Intercept	5.734	0.004	1291.7	< 0.001
Forest Cover	1.026	0.003	372.1	< 0.001
Fruit abundance	0.274	0.004	68.9	< 0.001
Forest cover × fruit abundance	-0.235	0.002	-103.7	< 0.001

Table C1.2. Partial effects of predictors from Zero-Inflated GLMs (Table C1.1) on the abundance of frugivorous birds (predicted values from GLMs in Table C1.1). β values (± SE) of the linear regressions between partial residuals of each predictor and bird abundance, at low and high levels of the other predictor, are shown for the study years ($p < 0.05$ in all cases).

Year	Forest Cover		Fruit Abundance	
	Low fruit abundance	High fruit abundance	Low forest cover	High forest cover
2008	17.33 ± 0.24	13.86 ± 0.69	2.07 ± 0.17	-3.91 ± 0.88
2009	19.01 ± 0.27	5.31 ± 2.36	8.40 ± 0.39	6.29 ± 1.23
2010	16.89 ± 0.25	11.28 ± 0.83	3.42 ± 0.11	-3.61 ± 0.89
2011	44.75 ± 0.90	30.47 ± 1.99	5.69 ± 0.42	-12.88 ± 1.96

Discussion

In this study we evaluated how forest cover and fruit abundance shaped the habitat use of frugivorous birds along a gradient of forest fragmentation in the Cantabrian Range. Our results showed that birds concentrated their activity in forested areas providing fruits. These results agree with previous findings showing that few frugivorous birds visit deforested areas (Cardoso da Silva et al. 1996; Cordeiro and Howe 2003; García et al. 2010). In fact, forest cover influenced the most habitat use by birds every year (Tables C1.1 and C1.2) suggesting that birds used habitat more limited by safety than by food availability (see also Brown 2000). Moreover, forest cover may also mean more than just protection for thrushes, given that the presence of dense forest could also be acting as a first cue for birds, when looking for the food provided by fleshy-fruited trees. In any case, our results also evidenced that birds tracked fruit availability across the studied landscape, as suggested for other frugivorous birds in temperate and tropical habitats (e.g. Lehouck et al. 2009; García et al. 2010; Blendinger et al. 2012). In our study system, the aggregative flocking behavior of most thrush species, together with their almost exclusively fruit-based diet (Guitián et al. 2000; Martínez et al. 2008), would be traits promoting active fruit resource tracking.

Beyond the general positive effects of forest cover and fruit availability on the abundance of frugivorous birds, our four-year data suggest that the effects of these environmental features on frugivore habitat use varied through the landscape, as the limitations imposed by each feature depended on the magnitude of the other one (Tables C1.1 and C1.2). Namely, frugivore dependence on forest cover increased in those landscape sectors with scarce fruits, but weakened when fruits were abundant and widespread. This pattern was probably related to a trade-off in bird behavioral decisions, with birds being mostly driven by search of protection when fruits are scarce, but overcoming their reluctance to visit low cover areas when these still provide much fruits, as it happens in remnant trees with big crop sizes (Herrera and García 2009).

In the case of the effects of fruit availability, we found that birds used more frequently fruit-rich patches when forest cover was low but, unexpectedly, they avoided fruit-rich sites in highly forested landscape sectors. This negative trend could be explained by strong competition between birds in fruit-rich areas. However, although some negative interactions (e.g. defense of fruiting trees by individual birds) may occur in the studied system (*authors' personal observations*; see also Snow and Snow 1984), they are sporadic and operate at a very fine spatial scale (i.e. different branches within the same tree). In fact, the relative abundances of the different thrush species are frequently correlated in our study system (García and Martínez 2012), suggesting interspecific facilitation (see also Saracco et al. 2004).

A post-hoc evaluation of the characteristics of the sites with dense forest cover but few fruits in the study plot revealed a differential feature: the occurrence of big trees whose tops overgrow the average forest canopy. These tall trees provided much cover (forest cover was > 50 % in cells presenting a big tree) and, in most years, were associated to a decrease in fruit abundance (as they were non fleshy-fruited individuals, like male yews, or species, like beech or ash)

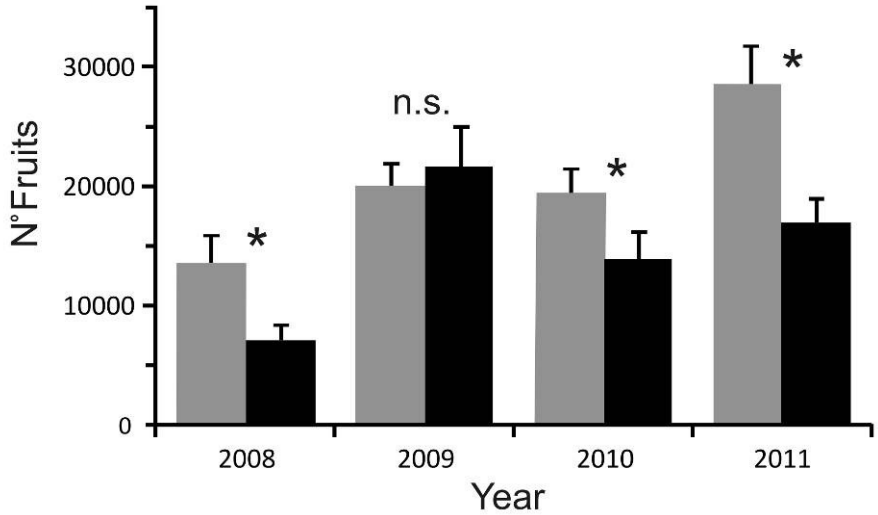


Fig. C1.3. Mean fruit abundance per cell (± SE) in cells presenting large trees (n = 50; black) respective to those devoid of big trees (n = 54, gray) but presenting similar forest cover extent (> 50 % forest cover for both cell types). Between type of cell differences on the number of fruits have been highlighted (Wilcoxon test; *: $p < 0.05$; n.s.: no significant).

in the plot cells where they occurred (Fig. C1.3). Thrushes frequently perched on these big trees, maybe using them as watchtowers for predator vigilance (authors´ unpublished data; see also García 2001). In order to control how the occurrence of big trees affected the interactive effects of forest cover and fruit abundance in the abundance of frugivorous birds, we repeated the previous models excluding those cells presenting big trees. We still found forest cover as the main factor on birds' habitat use, with stronger effects in poor-fruit areas (Fig. C1.3; Tables C1.3 and C1.4). The effects of fruit availability on the abundance of frugivorous birds were also still stronger and positive at low cover levels, but positive or null at high cover levels (Fig. C1.3; Table C1.4). In sum, the dilution of the effects of fruit availability on the abundance of frugivorous birds along the gradient of forest cover also suggested small-scale optimization of habitat use (Howe 1979; Brown 2000; Mayor et al. 2009). Namely, frugivores would strongly track fruit resources if not being enough protected, but relax fruit search in low-risk areas. This pattern may be also determined by a potential frugivore satiation in high cover areas (Hampe 2008), as they usually provide the

densest fruiting patches across the landscape. The fact that birds were unresponsive to fruit abundance in the years with highest fruit production at the whole plot scale (2009 and 2010; Fig. C1.1) would support this rationale.

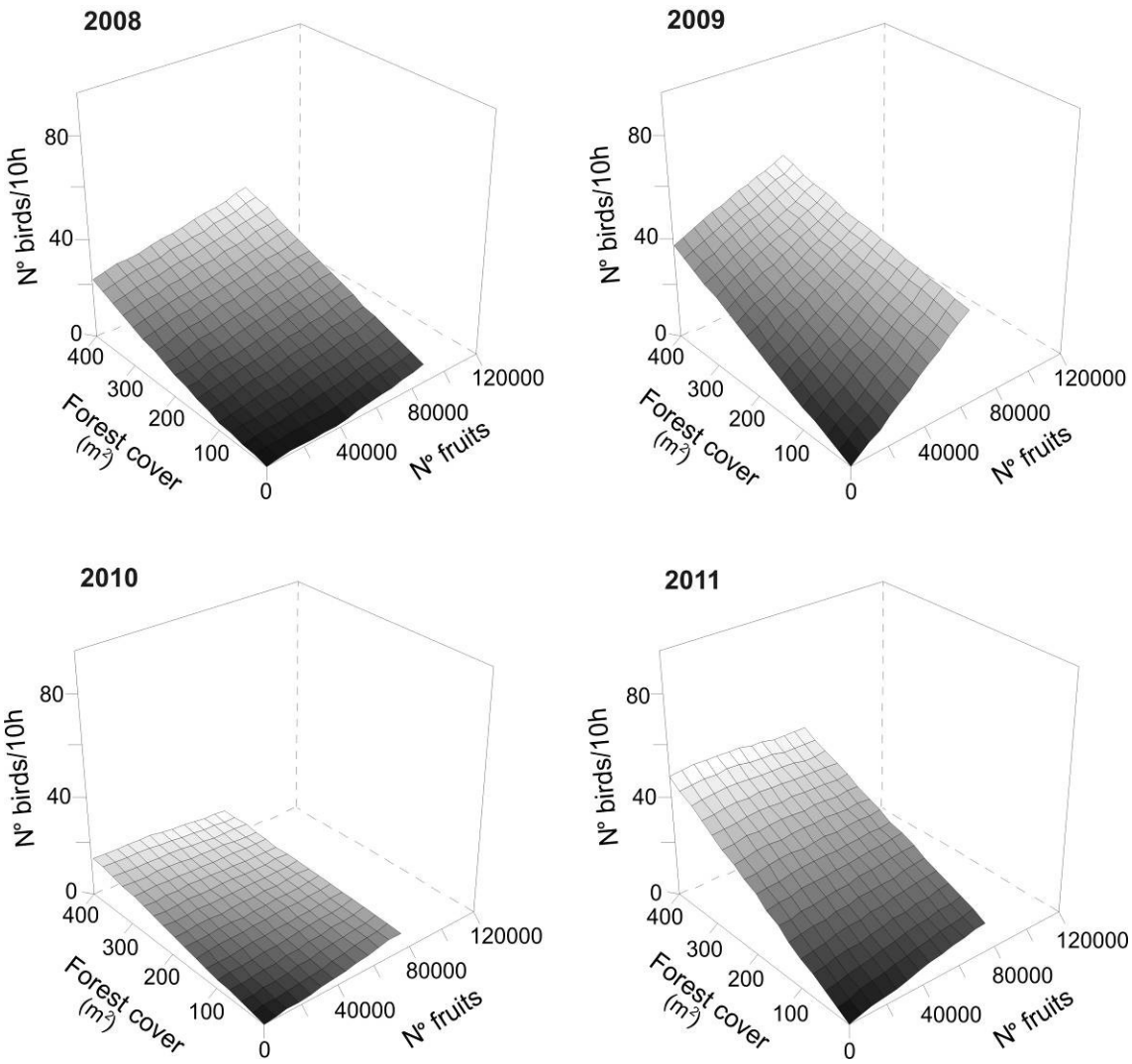


Fig. C1.3. Expected values of bird abundance for combination of different values of forest cover and fruit abundance, for different study years. Variations are highlighted in a gray-toned scale, with darker tones representing lower values. Trend surfaces were obtained by interpolation of the predicted values extracted from the Zero-Inflated GLMs (cells with big trees excluded).

Table C1.3. Effects of Forest cover and Fruit abundance on bird abundance considering only those cell not presenting large trees (n = 390). Independent Zero-Inflated GLMs were performed for each study year. Maximum likelihood estimates, their standard errors, the values of the *z* statistic and *p* values are shown.

2008				
	Estimate	Std. Error	z	*p*
Intercept	5.453	0.005	1025.1	< 0.001
Forest cover	0.506	0.004	111.8	< 0.001
Fruit abundance	0.113	0.007	16.2	< 0.001
Forest cover × fruit abundance	-0.028	0.005	-5.8	< 0.001
2009				
	Estimate	Std. Error	z	*p*
Intercept	5.808	0.004	1325.2	< 0.001
Forest cover	0.502	0.004	113.7	< 0.001
Fruit abundance	0.469	0.005	96.9	< 0.001
Forest cover × fruit abundance	-0.264	0.004	-69.3	< 0.001
2010				
	Estimate	Std. Error	z	*p*
Intercept	5.066	0.006	805.8	< 0.001
Forest cover	0.326	0.007	48.4	< 0.001
Fruit abundance	0.155	0.006	25.4	< 0.001
Forest cover × fruit abundance	-0.149	0.005	-27.1	< 0.001
2011				
	Estimate	Std. Error	z	*p*
Intercept	5.479	0.005	1094.1	< 0.001
Forest cover	0.749	0.005	156.3	< 0.001
Fruit abundance	0.325	0.005	70.6	< 0.001
Forest cover × fruit abundance	-0.237	0.003	-82.5	< 0.001

Table C1.4. Partial effects of predictors from Zero-Inflated GLMs (Table C1.3) on the abundance of frugivorous birds (predicted values from GLMs in Table C1.3) considering only those cell not presenting large trees. β values (± SE) of the linear regressions between partial residuals of each predictor and bird abundance, at low and high levels of the other predictor, are shown for the study years (n.s.= no significant, $p < 0.05$ in all other cases).

Year	**Forest Cover**		**Fruit Abundance**	
	Low fruit abundance	High fruit abundance	Low forest cover	High forest cover
2008	7.38 ± 0.08	5.96 ± 0.75	1.77 ± 0.17	1.11 ± 0.63
2009	12.49 ± 0.20	4.95 ± 0.27	10.25 ± 0.58	2.75 ± 1.11
2010	3.49 ± 0.05	0.97 ± 0.18	2.18 ± 0.07	n.s.
2011	15.68 ± 0.03	8.37 ± 1.31	4.94 ± 0.37	n.s.

Conclusions

In this study we contribute to the fine-tuning of current understanding of the environmental filtering of frugivorous bird habitat use. Our results evidence that simultaneously considering the influence of different environmental factors may reveal more complex landscape effects than those expected by studying them independently. Adaptive frugivore behavior determines interactions between the effects of different factors that simultaneously condition their habitat use. Environmental filtering of animal distribution at small scale is expected to cascade into the ecosystem services that they provide (Kremen 2005; Kremen and Ostfeld 2005). This fine-tuned knowledge of frugivores habitat use is expected to help us to better understand, and thus predict, fine-grained spatial variability in seed rain templates through the landscape. It will be expected that quite small forest patches andisolated trees standing within deforested areas will have a disproportionate effect on seed rain when presenting high fruit crops.

Capítulo 2

Consistency and reciprocity of indirect interactions between tree species mediated by frugivorous birds

Consistencia y reciprocidad de interacciones indirectas entre especies arbóreas mediadas por aves frugívoras

Abstract

Despite the recognized importance of indirect plant-plant interactions for community structure, we still need to improve our current knowledge on how their outcomes are consistent in space and time, as well as reciprocal between participating species. These caveats are especially relevant in the case of indirect interactions mediated by animals, whose behavior may show high variability. We studied consistency and reciprocity of frugivore-mediated interactions between fleshy-fruited trees. For three years we examined the influence of crop size and neighborhood characteristics (con- and heterospecific fruit abundance and forest cover) on frugivory rates on *Crataegus monogyna* and *Ilex aquifolium*, two coexisting species in the secondary forests of the Cantabrian range that share a guild of frugivorous birds. Crop size and neighborhood characteristics influenced frugivory on *C. monogyna* and *I. aquifolium*. Both con- and heterospecific fruit abundance affected frugivory, evidencing the occurrence of indirect interactions between trees, although the strength and sign of these effects varied between tree species as well as across years within species. By showing complex temporal patterns in the consistency and reciprocity of indirect interactions, this study emphasizes the need for multispecific, long-term studies to assess the actual contribution of animal-mediated plant-plant indirect interactions to community dynamics.

Resumen

A pesar del reconocimiento de la importancia de las interacciones indirectas entre plantas para la estructuración de las comunidades, aún necesitamos mejorar el conocimiento actual de cómo sus resultados son consistentes en el espacio y el tiempo, al mismo tiempo que recíprocos entre las especies implicadas. Estas carencias de conocimiento son especialmente importantes en el caso de las interacciones indirectas mediadas por animales, cuyo comportamiento puede mostrar alta variabilidad. Estudiamos la consistencia y la reciprocidad de interacciones indirectas mediadas por frugívoros entre árboles productores de fruto carnoso. Durante tres años examinamos la influencia del tamaño de cosecha y las características del vecindario ecológico (producción de frutos homo- y heteroespecíficos y cobertura forestal) en las tasas de frugivoría en el espino albar y el acebo, dos especies coexistentes en los bosques secundarios cantábricos, y con un gremio compartido de aves frugívoras. El tamaño de cosecha y las características del vecindario influenciaron la frugivoría en ambas especies. La abundancia de frutos tanto homo- como heterospecíficos afectaron a la frugivoría, evidenciando la existencia de interacciones indirectas entre árboles, aunque su fuerza y signo varió entre especies de planta y años. Al mostrar los complejos patrones de consistencia temporal y reciprocidad de las interacciones indirectas, este estudio subraya la necesidad de estudios multiespecíficos y a largo plazo para evidenciar el verdadero papel de las interacciones indirectas en la dinámica de las comunidades vegetales.

Introduction

Direct interactions (i.e. those where the effect of one species is transmitted without intermediaries to another), maybe by being more conspicuous or intuitive, have been the center of most studies of plant-plant interactions. However indirect interactions, in which the effect of one species on another is mediated by a third (Wooton 1994; for example, a plant species that suffers increased herbivory due to its co-occurrence with another, highly palatable, species; Barbosa et al. 2009), have been revealed as community drivers of equal, or even greater importance than direct interactions (Holt 1984; Strauss 1991; Schoener 1993; Vandermeer et al. 1995; Bailey and Whitham 2007). Nevertheless, despite this recognized relevance, a general community framework is still short on information on how consistent, and how reciprocal among participating species, the outcomes of plant-plant indirect interactions are (Holt and Lawton 1994; Chaneton and Bonsall 2000).

Following on from early studies, it has been shown that the effects of indirect interactions are not necessarily constant across space (Holt 1984; Holt 1988) or time (Holt and Lawton 1994; Miriti 2006), disappearing or even changing their sign, and leading to variations in community dynamics (Holt 1984). For example, Kitzberger and collaborators (2007) found, during a bamboo masting event in the Patagonian forest, that the initial positive effects of bamboo seeds on those of *Nothofagus* and *Autrocedrus* became negative after three months. Moreover, reciprocity in the performance of indirect effects, defined, in a broad sense, as the ocurrence of two-way indirect interactions between species, irrespective of their sign, is also important. Different community dynamics are expected when indirect interactions simultaneously affect all participants rather than simply a single species (Chaneton and Bonsall 2000). Caccia et al. (2006) evidenced that the presence of the mice-preferred *Austrocedrus* seeds increased predation on the seeds of *Nothofagus*, but there was not a reciprocal effect of *Nothofagus seeds* on those of *Austrocedrus*. Nevertheless, very few of the studies focusing on indirect interactions have actually considered reciprocity (Chaneton

and Bonsall 2000). The assessment of consistency and reciprocity is especially pertinent in those plant-plant relationships mediated by animal species. Given that animals may respond to spatio-temporal variation in environmental conditions, irrespective of plant response, and may interact simultaneously with co-occurring plants (at least in the case of generalist consumers), low consistency but high reciprocity may be expected for most animal-mediated, indirect plant-plant interactions.

Frugivory has a key role in plant community dynamics (Wang and Smith 2002; Levine and Murrell 2003). Fruit removal is the first filter as to the relative number of propagules that many plant species introduce into the community. Removal of the fruits from one plant will not only depend on the traits of the species, but also on the surrounding environmental context, which is frequently shaped by the occurrence of other plant species (Carlo et al. 2007 and references therein). Thus, plant-plant interactions mediated by frugivores will emerge as a result of, first, the wide generalism of plant-frugivore assemblages (with many plant species sharing frugivores within the community, Bascompte et al. 2003; Donatti et al. 2011) and, second, the ability of frugivores to optimize their foraging by selecting collective fruiting patches over individual fruiting plants (Sallabanks 1993; García and Ortíz-Pulido 2004). In fact, this scale-dependent behavior generates neighborhood effects (Sargent 1990; Carlo et al. 2007). For a given plant, these effects may mean apparent competition if the presence of fruiting neighbors leads to a decrease in fruit removal from that plant (Manasse and Howe 1983; Alcántara et al. 1997; Saracco et al. 2005), whereas they will, conversely, imply apparent mutualism if the result is an increase in fruit removal (Sargent 1990; Carlo and Aukema 2005; Blendinger et al. 2008). These variations in frugivory patterns may be translated into imbalances in the magnitude of seed dispersal for the different plant species, presumably cascading down through the subsequent stages of their regeneration cycles (Levine and Murrell 2003), and potentially leading to variations in plant species populations and community dynamics (Hubbell et al. 2001, Wang and Smith 2002).

In this work, we study the consistency and the reciprocity of frugivore-mediated, plant-plant interactions, defined as those involving both intra- and interespecific effects within tree neighborhoods. For this purpose we monitored the influence of neighboring fruit production on fruit removal in two co-occurring species of fleshy-fruited trees linked by a shared guild of frugivorous birds for 3 years. Neighborhood effects were estimated by taking into account that individual removal rates may also be affected by plant traits (crop size; Sallabanks 1993) and by other features of the surrounding context (forest cover acting as protection; Sapir et al. 2004). Specifically, we tested the occurrence of apparent competition and mutualism mediated by shared frugivores through answering the following questions: 1) How variable across species and years were fruit removal rates, individual crop sizes and the production of con- and heterospecific fruits (as neighborhood characteristics which potentially influence birds' foraging activity)?; and 2) Which environmental features (crop size, neighborhood) affected frugivory rate across species and years, and how (positive or negatively)? We expected that the inherent variability of fruit-frugivore interactions, derived from interannual changes in fruit crop and frugivore abundances (Levey and Benkman 1999; Jordano 2000), would also occur in our system, potentially affecting consistency and reciprocity of the frugivore-mediated indirect interactions.

Specific materials and methods

The study was carried out over three consecutive years: the autumn-winter season in 2007-08, 2008-09 and 2009-10 (hereafter, respectively 2007, 2008 and 2009). The study plot represented a gradient of secondary forest cover, from dense forest areas to scattered trees isolated within the non-forest matrix, that provided a wide range of neighborhood characteristics for individual trees, both in terms of forest cover and fruit abundance (Fig. I.7).

Frugivory

At the beginning of the fruiting season of each year (October), we selected 16 individual fruiting trees (hereafter focal trees) of each species. They were distributed throughout the entire plot to reflect a complete range of neighborhood characteristics in the field, from isolated trees to trees embedded in forest fruit-rich patches (Fig C2.1). The identity of focal trees changed from one year to another as many trees failed to bear fruits in consecutive years (see *Appendix A* for more information). Before the fruit consumption by birds began, for each focal tree, we counted the number of fruits on 15 branches (arbitrarily distributed through the whole accessible crown of the tree) and the total number of branches per tree. We estimated the individual crop size by multiplying the average

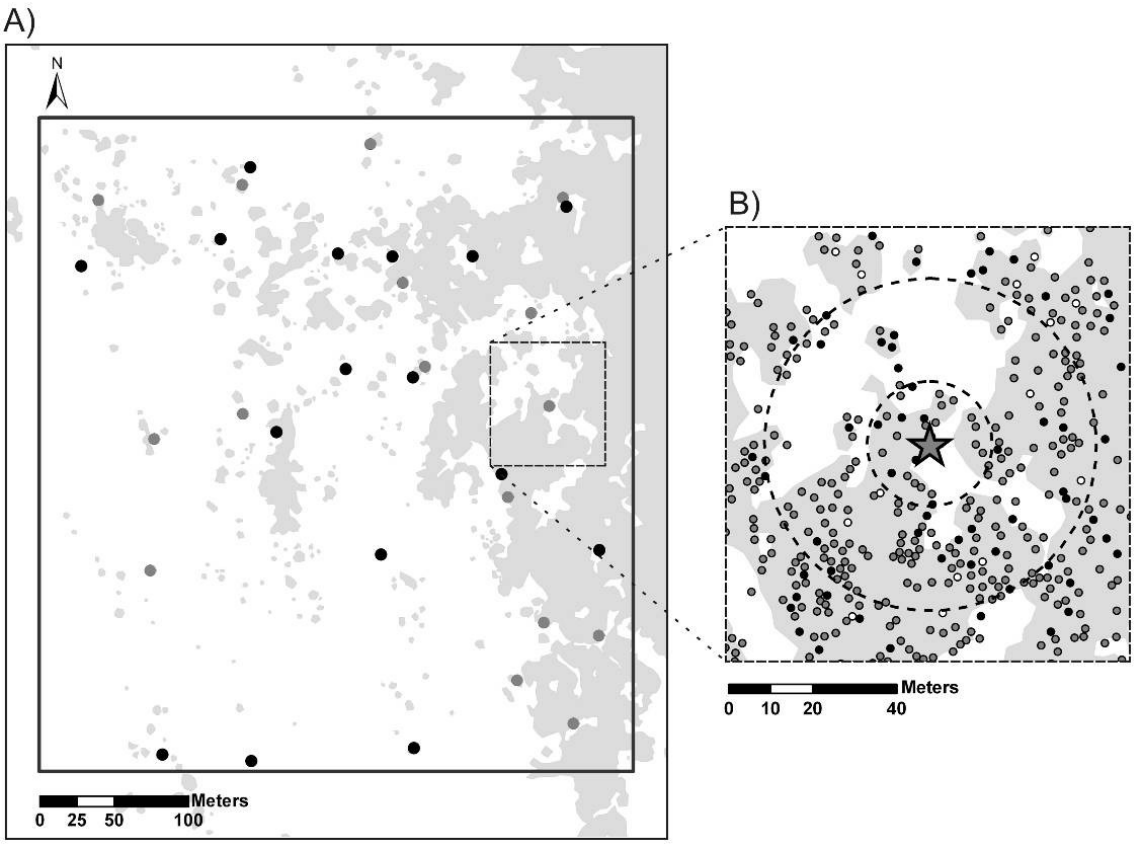


Fig. C2.1. A) Map of the study plot in 2008 sampling period, showing focal trees (black dots: *Crataegus monogyna; gray dots: Ilex aquifolium*) and the extent of forest cover (light gray area). B) A detail of the inner circle (15 m radius) and outer ring (15 to 40 m radius), both indicated with a dashed line, chosen to represent ecological neigborhoods around a central focal tree (dark grey star). Fleshy-fruited trees are represented as dots (black: *C. monogyna*; dark gray: *I. aquifolium*; white: *Taxus baccata*).

number of fruits per branch by the number of branches per tree. At the same time, we labeled 5 fruiting branches per tree, and counted the initial number of fruits. To avoid bias in frugivory estimations, labeled branches were selected so as to be arbitrarily distributed through the whole accessible crown of the tree, and to contain from 60 to 120 fruits. When standing fruits are removed by Cantabrian thrushes, their stalks remain attached to the branch for a long time afterwards (*authors' personal observation*; Fig. C2.2), whereas when fruits fall to the ground through natural abscission or the action of wind or rain, their stalks fall with them. This enabled us to distinguish fruits picked and removed by thrushes from those falling to the ground through abiotic causes. Labeled branches were surveyed fortnightly from October to February of each sampling season, and the number of standing fruits and the number of bare stalks remaining on branches were recorded each time. Bare stalks were removed with scissors after each survey to avoid recounting. For each tree, we estimated frugivory as a fruit removal rate by considering the labeled branches and dividing the number of bare stalks observed throughout the season by the initial number of standing fruits.

Abortion of fruits in the studied species happens at an early stage of fruit development (June-August; Obeso 2004; Chacoff et al. 2008). Fruit counts, on all fruiting trees as well as on the labeled branches, were done at the beginning of fruit ripening, so abortions did not cause any bias in the frugivory estimates. The activity of non-disperser pulp-eaters was also considered. Those fruits attacked by pulp eaters were easily distinguishable, presenting partial depulpation while retaining the seeds. The impact of the activity of pulp eaters, such as small passerines (*Erithacus rubecula*, *Parus* spp., etc.), on the frugivory estimates was negligible too, affecting less than 0.6% of labeled fruits (*authors' unpublished data*). We assumed that almost all fruits picked from branches were actually swallowed by thrushes (and hence their seeds were dispersed), and that only a small proportion of picked fruits fell under trees or were consumed by other animals (e.g. Guitián et al. 2000; García et al. 2013). We further considered that

the dropping of fruits by thrushes was unrelated to the characteristics of neighborhood or fruit size constraints, but rather due to thrushes' rejection of infested fruits (Manzur and Courtney 1984) or handling failures (Guitián et al. 2000).

Fig. C2.2. Fruited branches of A) *Crataegus monogyna* and B) *Ilex aquifolium* showing intact fruits and bare stalks (indicated by white arrows) after foraging by birds.

Neighborhood metrics

To measure neighborhood characteristics, we used GIS to delimit two non-overlapping sectors around each focal tree (Fig. C2.1B): an inner circle of 15-m radius (hereafter R15) and a surrounding ring with a circumference ranging from 15 to 40 m radii (hereafter R15-40). We considered that each of these two sectors represented a neighborhood context at a different spatial scale (Hubbell et al. 2001; García and Chacoff 2007). As neighborhood metrics for each sector, we calculated forest cover (m^2) and the abundance of fruits of *C. monogyna*, *I. aquifolium* and *T. baccata* i.e., the sum of crop sizes of all fruiting trees per species.

Statistical analysis

Between-year variations in removal rates, crop sizes and abundance of different fruits at R15 and R15-40 of focal trees were tested by using Generalized Linear Models (GLMs), with a Normal error distribution and a log link function. In addition we performed the same analyses for forest cover at R15 and R15-40 to assess whether focal trees represented similar neighborhood gradients, year on year, within the whole gradient of forest cover across the study plot (*Appendix A*). Independent analyses were performed for each focal species.

We also used GLMs to analyze the effects of crop size and neighborhood parameters on frugivory. Independent models were built for each "*species*" x "*year*" combination, given that a different set of focal trees were sampled every year, and that strong between-year variation in total and relative fruit abundances have been found in the study system (García et al. 2013). Each model incorporated the crop size of the focal tree, the amount of forest cover (m^2) and the number of *C. monogyna*, *I. aquifolium* and *T. baccata* fruits as predictor variables. Due to the scarcity of adult fruiting trees of the species in the plot, it was only possible to incorporate *T. baccata* fruit abundance in models at the R15-40 extent. Instead of the raw values of forest cover, the residuals of the linear regression between fruit abundance (predictor) and forest cover (response) were incorporated in the models. In this way, we sought to avoid the potential effects of non-independence between predictors in the multivariate models (Quinn and Keough 2002; Pearson correlation forest cover - fruit abundance: r = 0.77, $P \leq 0.0001$, N = 96) while achieving a measure of forest cover variability that was independent of fruit abundance (as many trees such as hazel, male holly, and male yew, do not bear fleshy-fruits; see Hargis et al. 1998; Villard et al. 1999 for a similar procedure in forest fragmentation studies). We assumed that this residual variable represented the protection of frugivorous birds against their own predators, as it accounted for the effects of forest cover independent of food provision (García et al. 2011). The GLMs were constructed with Normal error distribution for the response variable (frugivory). We tested different link

functions and raw and log transformed data on predictor variables to find the best-fit model for each case, as judged by deviance G^2 as a goodness-of-fit statistic (lower values indicating a better fit; Quinn and Keough 2002). All statistical analyses were performed with JMP 7.0 (SAS Institute 2007).

Results

We found strong variation between years in frugivory rates, individual crop sizes and most neighborhood characteristics (GLM: $\chi^2 > 2.92$, $N = 48$, for all tests; Fig. C2.3). The average proportion of removed fruits per plant in *I. aquifolium* increased from 2007 to 2009, but intermediate values were observed in *C. monogyna* in all years. The crop size of focal trees and the abundance of fruits in their neighborhoods differed significantly between years in both species. *C. monogyna* and *I. aquifolium* fruit abundances showed opposite tendencies: while the former decreased from 2007 to 2008, the latter increased. No between years variations were found in the abundance of *T. baccata* fruits. The values of forest cover around both species at either R15 or R15-40 neighborhood scales were similar between years (*Appendix A*, Fig. A.1).

Crop size and neighborhood effects on frugivory

GLM models showed significant effects of crop size and neighborhood characteristics on the fruit removal rates of *C. monogyna* and *I. aquifolium*. Crop size and forest cover effects were, however, inconsistent in time (Table C2.1). The abundance of fruits in the neighborhood significantly affected fruit removal rate in focal trees in all study cases (species by year combinations). The effects of the different neighbor fruits on frugivory varied across years, both in occurrence and sign (Table C2.1, Fig. C2.4). We also found that the between year consistency of these neighborhood effects was not similar for *C. monogyna* and *I. aquifolium* (Table C2.1, Fig. C2.4). Neighborhood effects varied not only between years and species, but also between scales for each species within year (Table C2.1).

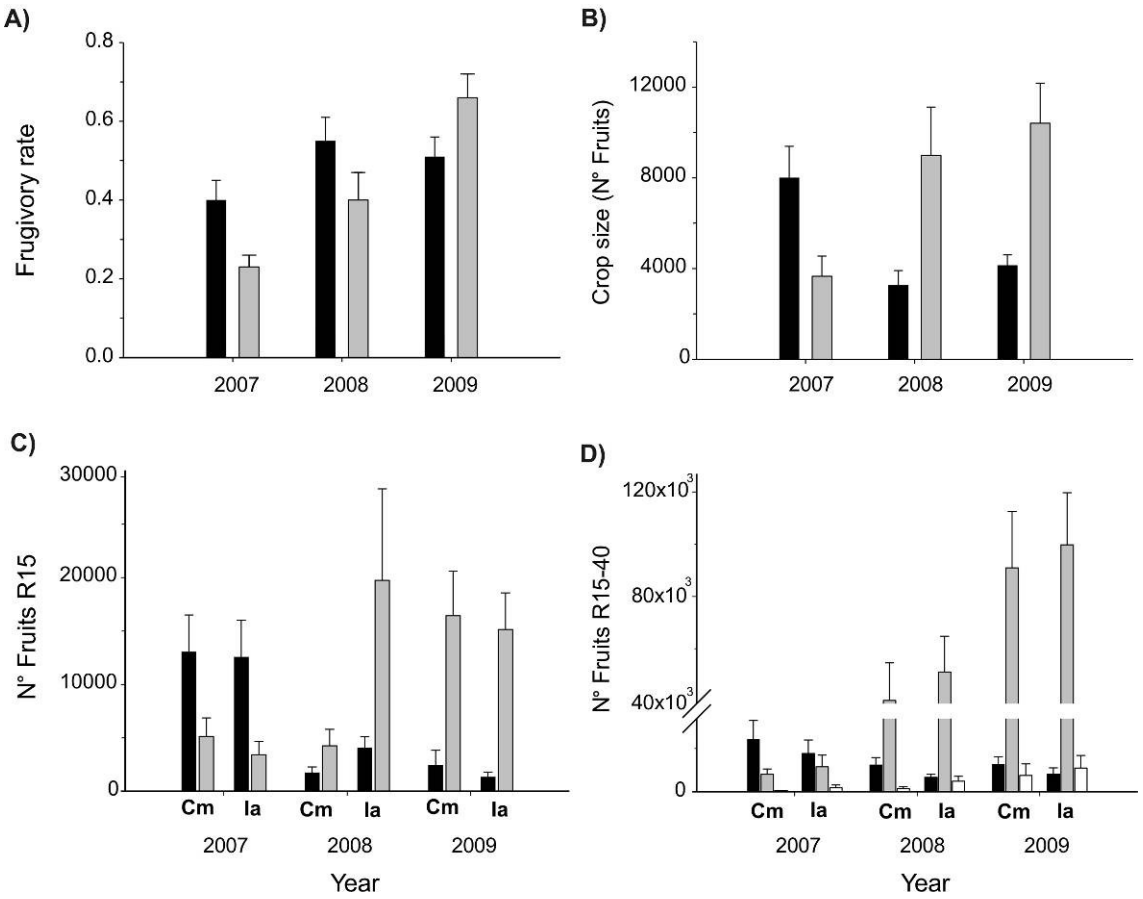


Fig. C2.3. A) Mean frugivory rate (proportion of fruits removed from labeled branches) on focal trees (n=16) ± standard error (SE) on *Crataegus monogyna* (black bars) and *Ilex aquifolium* (grey bars) for the three years studied. B) Mean crop size (number of fruits produced) on focal trees (*N* = 16) ± SE on *C. monogyna* (black) and *I. aquifolium* (gray) for the three years studied. C) and D) Mean fruit abundance ± SE of the different species producing fruits in the inner circle (15 m radius, R15) and outer ring (15 to 40 m, R15-40 radius), respectively, chosen to represent ecological neighborhoods of *C. monogyna* (**Cm**) and *I. aquifolium* (**Ia**) focal trees (N = 16). *C. monogyna* fruits are represented by black bars, *I. aquifolium* by gray bars and *T. baccata* by white bars (no *T. baccata* fruits were found in any R15).

Table C2.1. Summary of GLM models evaluating the effect of crop size and neighborhood characteristics on the frugivory rate of *Crataegus monogyna* and *Ilex aquifolium* trees in different years. Predictor variables include the crop size of the focal tree, and forest cover and the abundance of fleshy fruits of different species (Cm: *C. monogyna;* Ia: *I. aquifolium*; Tb: *Taxus baccata*) in the inner circle, (radius 15 m, R15) and outer ring (radius15 to 40 m, R15-40), which were chosen to represent different ecological neighborhoods. No *T. baccata* fruits were found at R15 in any year so this factor was not taken into consideration in the models. The case was the same in 2007-08 around *C. monogyna* at R15-40. In all models: Normal distribution, Log link function, degrees of freedom (*d.f.*) = 8 (except in *C. monogyna in* 2007 where *d.f.* = 7), $\chi^2 > 2.2$ and $P < 0.05$. Raw predictor variables were used in the models except for *C. monogyna* 2008-9 and 2009-10 where the best fit was found to be with log transformed variables. The maximum likelihood estimates (*estimate*, in bold when $P < 0.05$) and χ^2 values testing the partial effect of each predictor variable on the model are shown. * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

		2007-08		2008-09		2009-10	
C. monogyna							
Parameter		**estimate**	χ^2	**estimate**	χ^2	**estimate**	χ^2
Crop size		**8.38 x10^{-5}**	10.60 ***	**0.19**	3.99 *	0.04	0.04
R15	Forest cover	**4.33 x10^{-3}**	10.09 **	0.05	0.09	-0.09	0.18
	Fruits Cm	**-1.50 x10^{-5}**	3.85 *	**-0.16**	5.55 *	-0.03	0.79
	Fruits Ia	**2.33 x10^{-5}**	3.49 *	**0.08**	6.16 *	**0.08**	5.19 *
R15-40	Forest cover	**-5.84 x10^{-4}**	7.45 **	-0.05	0.11	-0.40	3.13
	Fruits Cm	**-1,90 x10^{-5}**	11.07 ***	**0.19**	4.09 *	0.01	0.09
	Fruits Ia	-1.82 x10^{-5}	1.46	-0.04	2.59	0.04	0.70
	Fruits Tb	-	-	**0.09**	6.40 *	-0.04	1.55
I. aquifolium							
Parameter		**estimate**	χ^2	**estimate**	χ^2	**estimate**	χ^2
Crop size		**5.03 x10^{-5}**	8.91 **	7.73 x10^{-6}	<0.01	**-4.20 x10^{-5}**	5.95 *
R15	Forest cover	**4.19 x10^{-3}**	34.88 ***	-8.73 x10^{-3}	0.16	**2.31 x10^{-3}**	6.49 *
	Fruits Cm	**-1.67 x10^{-5}**	6.65 **	-3.04 x10^{-4}	2.94	**1.31 x10^{-4}**	3.77 *
	Fruits Ia	**1.54 x10^{-4}**	26.73 ***	**-2.72 x10^{-4}**	8.19 **	1.42 x10^{-5}	2.30
R15-40	Forest cover	**-4.84 x10^{-4}**	27.22 ***	-1.12 x10^{-3}	0.44	-3.66 x10^{-5}	0.07
	Fruits Cm	-3.42 x10^{-6}	0.87	**3.13 x10^{-4}**	7.26 **	-1.59 x10^{-5}	2.49
	Fruits Ia	**-5.34 x10^{-6}**	3.55 *	3.38 x10^{-6}	0.45	-2.23 x10^{-6}	2.63
	Fruits Tb	**-1.63 x10^{-4}**	26.46 ***	**1.11 x10^{-3}**	9.30 **	**-2.56 x10^{-5}**	11.00 ***

Discussion

Indirect interactions between plants have traditionally been considered as important drivers of plant community dynamics (Bailey and Whitham 2007). In this study, we widen the current framework of plant-plant indirect interactions by showing how shared plant consumers may lead to reciprocal indirect effects between plant species, which can change from negative (competitive) to positive (mutualistic). Specifically, we show that the reproductive success of fleshy-fruited trees, estimated as the rate of fruit removal by legitimate dispersers, was determined not only by intrinsic plant traits, but also by the presence of con- and heterospecific fruiting trees in the neighborhood of individual plants (Manasse and Howe 1983; Alcantara et al. 1997; Saracco et al. 2005). By reciprocally influencing frugivore visitation and fruit consumption, neighbor trees may generate apparent mutualistic and competitive processes with the potential to shape tree recruitment and, hence, community dynamics (Carlo et al. 2007; Sasal and Morales 2013). Nevertheless, the ultimate, community-level consequences of these indirect interactions will strongly depend on how constant in time (Holt and Barfield 2003; Kitzberger et al. 2007), and generalized across species, their effects are (Chaneton and Bonsall 2000). Here, by studying two plant species over three consecutive years, we overcome the limitations of single-species or short-term studies and assess frugivore-mediated interactions in terms of species reciprocity and temporal consistency. In the following sections, we interpret the plant-plant interaction outcomes by looking at birds as a resource for plant reproduction, but discuss the contingencies of these interactions by considering how frugivores react to fruit resources and habitat structure.

Crop size effects

Crop size is frequently a major determinant of frugivory rate as frugivores are disproportionally attracted to plants with big crops, because these are more conspicuous or more profitable (Sallabanks 1993; Blendinger et al. 2008) and we expected these mechanisms to be operating in the cases of *C. monogyna* and *I. aquifolium* (see also Martínez et al. 2007). However, the crop size effects found

in the present study varied between years. Birds did remove proportionally more fruits from those trees bearing bigger crops in 2007 (Table C1.1), a year in which the total local fruit abundance was comparatively smaller and fruiting trees were more heterogeneously distributed across the landscape (García et al. 2013). These two facts might have led thrushes to optimize their foraging by selecting where to feed at a very fine spatial scale: the individual tree. However, we found negative effects of crop size on frugivory rate (*I. aquifolium* in 2009, a year of very high fruit production; Fig. C2.3D). This situation suggests satiation effects, as proposed by Hampe (2008), with higher overall crop production resulting in a decreased proportion of fruits being consumed.

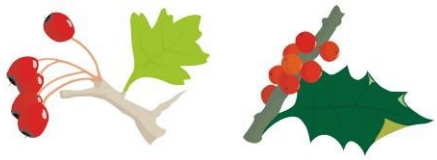
Forest cover effects

Frugivorous birds often concentrate their activity on high-cover forest patches, searching for perching places and protection from predators (Sapir et al. 2004; García et al. 2011; *Capítulo 1*), leading to fruiting trees in dense neighborhoods having higher visitation rates. In our case, the amount of forest cover in the immediate vicinity of the fruiting tree positively influenced fruit removal in *C. monogyna* and *I. aquifolium*. These results corroborate previous findings from indirect measurements of bird activity, like seed deposition, within the same system, which suggest an effect of forest cover independent of fruit abundance (Martínez et al. 2008; Herrera et al. 2011a). Similarly, we show here that forest cover influence varied strongly between years, not exerting an influence on frugivory by birds in every year (Herrera et al. 2011a; García et al. 2013; see also Caccia et al. 2006 for a similar results on seed predation). Forest cover extent was constant over time in the study plot and around the focal trees (*Appendix A*). Thus, the dilution of forest cover effects must be related to variations in other neighborhood features like fruit availability (Herrera et al. 2011a) or other ecological factors not considered by our design, like the abundance of predators of frugivorous birds (Howe 1979).

Indirect interactions between fruiting neighbors

Our results show that, while feeding on individual *C. monogyna* and *I.* aquifolium trees, birds were influenced by the presence of con- and heterospecific fruits in the immediate vicinity. As judged from the sign of the relationship between neighboring fruit abundance and fruit removal, *C. monogyna* only competed with conspecific neighbors, whereas *I. aquifolium* suffered both intra- and interspecific apparent competition. However, we also found apparent mutualism, as birds fed more on *C. monogyna* trees when they were surrounded by many *I. aquifolium* fruits. By contrast, mutualism in *I. aquifolium* was performed by con- and heterospecific plants, as was the case for this species in relation to apparent competition. Even though other studies have revealed these indirect interactions (e.g. Alcántara et al. 1997; Blendinger et al. 2008), we are not aware of previous evidence of the influence of con- and heterospecific fruiting neighborhoods on different co-occurring focal species within a community.

We also found that different co-occurring plant species showed different patterns of temporal consistency (Fig. C2.4). Some interaction outcomes were consistent between years in *C. monogyna*, which was affected by interspecific facilitation each year and, simultaneously, by intraspecific competition in two out of the three years of the study. Conversely, in *I. aquifolium,* the influence of con- and heterospecific neighbors varied between years in both occurrence and sign. We cannot explain these temporal inconsistencies based on the scenarios proposed for direct interactions, such as those linked to strong environmental biotic variations (e.g. competition-facilitation transitions along stress gradients; Pugnaire y Luque 2001; Holzapfel et al. 2006), or those derived from variations associated with the ontogenetic development of interacting plants (Miriti 2006). We would thus argue here that the temporal patterns shown in the present work must derive from the between year variation in the large-scale characteristics of the whole plant-frugivore system. In this sense, the abundances of both fruits and



		C. monogyna	*I. aquifolium*
Intraspecific	Competition	**2007**	2007
		2008	**2008**
		2009	2009
	Mutualism	2007	**2007**
		2008	2008
		2009	2009
Interspecific	Competition	2007	**2007**
		2008	2008
		2009	2009
	Mutualism	**2007**	2007
		2008	2008
		2009	**2009**

Fig. C2.4. Summary of observed intra- and interspecific neighborhood indirect interactions on *Crataegus monogyna* and *Ilex aquifolium* in different years, interpreted from the effect of fruit abundance at R15 neighborhood and frugivory rate (in bold black, years with significant effect; in gray, years with no effect). Consistency in the intra- and interspecific effects can be seen by following the vertical columns. Reciprocity in interspecific effects can be seen in the lower square.

thrushes and their landscape-scale spatial distribution changed between years (García et al. 2013; *Capítulo 1*), which means that frugivores have to cope with quite different neighborhoods from year to year. Namely, frugivores will be

conditioned to optimize their foraging according to different fruiting scenarios, both at the neighborhood and the landscape scale, and thus the role of the different neighborhood characteristics may not be the same across years (Van Ommeren and Witham 2002; Kitzberger et al. 2007; García et al 2013). With regard to the inter-specific discordances in consistency patterns, they do not seem to be related with any of the ecological factors considered in this study. We suggest that minor phenological mismatches (with *C. monogyna* ripening earlier than *I. aquifolium*), combined with variations in the bird community through the season (with migratory species arriving sequentially), could underpin the differential frugivory outcomes between plant species.

Even though new studies of indirect interactions have been published following that by Chaneton and Bonsall (2000), who reported on the paucity of research relating to reciprocity in indirect interactions, this still remains a poorly explored matter. We have found no evidence of any study considering reciprocity in the indirect effects between fruiting plants (but see Östamn and Ives 2003 and Caccia et al. 2006 for good examples of insect and seed predation respectively). We, however, did find reciprocity in the performance of indirect interactions in our study systems (Fig. C2.4). While feeding on *C. monogyna,* birds are influenced by the fruits of neighbor *I. aquifolium* trees, and, reciprocally, hawthorn fruits influence bird foraging on holly trees (Fig. C2.4). Nonetheless, this reciprocity also changed between years, both in terms of occurrence and in the symmetry of the effects (same or different sign). Its coexistence with *I. aquifolium,* consistently enhanced frugivory on *C. monogyna*, while the effect of this latter species on the former showed considerable variability. We would expect that consistency in the outcomes of one species, even with no long-term reciprocity, would lead to demographic imbalances between species (similar to that suggested by Schnurr et al. 2004 and Caccia et al. 2006), ultimately promoting coexistence, with *C. monogyna* individuals reproducing better when surrounded by few conspecifics but by many *I. aquifolium*.

Finally, our multi-scaled neighborhood approach also enabled us to observe the inconsistent outcomes (occurrence and sign) of frugivore-mediated interactions across spatial scales. These inconsistencies suggest that landscape features differentially determine frugivore foraging decisions at different scales (García and Ortíz-Pulido 2004; García et al. 2011). In our study, considering a broader scale also meant that we could show the relevance of the effects of another plant species involved in the indirect interactions, *T. baccata* (Table C2.1), which had scarce influence in the immediate neighborhood, maybe due to its scattered distribution through the landscape.

Conclusions

In this study we have shown that even within a small assemblage of fleshy-fruited plants and their shared frugivores, environmental variability led to a high degree of complexity in the outcome of indirect interactions between tree species at neighborhood and landscape scales. Over a short time scale important variations in the consistency and reciprocity of these indirect effects were found, with species dependent singularities. We argue that these results, based on a straightforward fruit-frugivore case study, may be applied to many other temperate and tropical systems, hosting both richer and more generalist plant-frugivore assemblages, and also to other interactions mediated by animal consumers, such as pollination.

Short-term, species-centered studies are useful tools for identifying the factors determining the occurrence of indirect interactions, but usually fail to reveal the balances which determine their consistency. In addition, the reciprocal and symmetrical effects for the different species involved in these interactions should not be taken for granted. Thus, if we aim to understand the real impact of indirect interactions on plant communities we need to explicitly consider the different sources of variability affecting them, by using long-term, multispecific approaches.

Capítulo 3

Changes in fruiting landscapes relax restrictions on endozoochorous tree dispersal into deforested lands

Cambios en los paisajes de fructificación relajan las restricciones a la dispersión endozoócora de árboles a zonas deforestadas

Abstract

Passive forest restoration is based on the natural recovery of degraded habitats. However, tree recruitment is frequently hampered in such areas. Tree seed dispersal is scarce and spatially constrained, confining the potential of forest regeneration to a narrow spillover band surrounding forest remnants. Understanding how landscape configuration can favor seed dispersal into deforested areas is thus crucial to recover forest extent and the concomitant ecosystem services. We studied tree seed dispersal by frugivorous birds from secondary forests into montane pastures of the Cantabrian Range. For two years, we evaluated the patterns of fruit production, bird movement and seed dispersal through the landscape. The large-scale spatial distribution of fruits varied strongly between years, with a relatively higher fruit production in isolated trees within pastures in the second year, when birds were more frequently observed perching on isolated trees. In both years, few seeds were dispersed into deforested areas, and those dispersed occurred close to forest cover. Nevertheless, seed arrival at longer distances increased during the second year. When more fruits were produced within the pastures, birds more often overcame their reluctance to leave the forest, and this change in frugivore foraging patterns cascaded into the spatial patterns of seed dispersal. By influencing frugivore activity, fruiting-derived landscape dynamism can relax the restriction of tree seed dispersal into deforested areas. Landscape biological dynamism should be taken into account in order to manage rewilding in European temperate forests.

Resumen

La restauración pasiva se basa en la recuperación natural de los hábitats degradados. Sin embargo, la regeneración de especies arbóreas en estas áreas es muy limitada. La dispersión de semillas es escasa y su distribución espacial constriñe el potencial de regeneración forestal a una estrecha banda de avance entorno a los remanentes de bosque. Entender cómo la configuración del paisaje puede favorecer la dispersión de semillas a las áreas deforestadas es crucial para la recuperación de los bosques y de sus servicios ecosistémicos. Estudiamos la dispersión de semillas de árboles por aves frugívoras desde bosques secundarios a pastos montanos de la Cordillera Cantábrica. Durante dos años evaluamos la producción de frutos, los movimientos de las aves y la dispersión de semillas a lo largo del paisaje. La distribución de los frutos a escala amplia varió entre años, con un incremento relativo de la producción de frutos en árboles aislados en los pastizales durante el segundo año, cuando las aves visitaron estos árboles con mayor frecuencia. Muy pocas semillas llegaron a los prados ambos años, y las que llegaron aparecieron muy cerca del bosque. Sin embargo, durante el segundo año aumentó la llegada de semillas a puntos más lejos del bosque. Las aves superaron su reticencia a dejar el bosque el año en el que los árboles aislados en los prados produjeron más frutos. Este cambio en sus patrones de actividad repercutió en los patrones espaciales de la lluvia de semillas. Al influenciar la actividad de los frugívoros, el dinamismo del paisaje derivado de la producción de frutos puede atenuar las restricciones a la dispersión de semillas arbóreas a áreas deforestadas. El dinamismo biológico en el paisaje debe de ser considerado en el manejo de la recolonización de los bosques templados europeos.

Introduction

The extent of European natural forests has been severely reduced due to historical exploitation for timber and firewood, clearing for pastures and arable lands, and their replacement with timber plantations (Darby 1956; Behre 1988; Kaplan et al. 2009). Despite historical forest loss, the current abandonment of montane rural areas throughout Europe (MacDonald et al. 2000; FAO 2011), and the concomitant release of fertile ground once devoted to extensive traditional practices, is opening up opportunities for natural forest recovery (Navarro and Pereira 2012). Understanding and favoring this rewilding process is crucial to recover the ecosystem services provided by forests (ranging from climate modulation or soil stabilization to CO_2 storage; Myers 1997; Chazdon 2008), especially in the context of global change mitigation (Bonan 2008).

Passive restoration is based on the natural, i.e. unassisted, recovery of forests affected by disturbance, once the disturbance agent disappears (Rey Benayas et al. 2008; Holl and Aide 2011). Allowing natural succession in abandoned lands can be the simplest way to recover forest, but this process is often spatially restricted, slow in time, and may even be arrested (Martínez-Garza and Howe 2003; Cramer et al. 2008). Both the tempo and the mode of forest recovery depend on the different environmental filters affecting the initial stages of the tree regeneration cycle in the disturbed environment (e.g. factors driving dispersal, predation and germination of seeds, and survival of seedling and saplings; Holl et al. 2000). As the first step in tree regeneration, effective seed dispersal from remnant forests to abandoned lands has been described as one of the main limiting processes in forest recovery in both tropical and temperate regions (e.g. Debussche and Lepart 1992; Holl et al. 2000; Duncan and Chapman 2002; Bustamante-Sánchez and Armesto 2012). Seed arrival in deforested lands depends mostly on two landscape features, namely, the distance from seed sources to recovering sites, and the quantity of surrounding seed sources, usually represented by the cover of remnant forest (Kunstler et al. 2007; Rey Benayas et al. 2008; García et al. 2010; Holl and Aide 2011). In addition, the spatial

distribution of dispersed seeds (i.e. the seed rain) is also affected by the landscape-scale configuration of forested and unforested patches. As a generalized spatial pattern, has been evidenced a sharp decline in seed arrival with increasing distance from the edge of remaining forest patches (Willson and Crome 1989; Aide and Cavelier 1994; Cubiña and Aide 2001) and, consequently, dispersal limitation restricts further forest regeneration to a narrow spillover band surrounding the remnant forest cover (Günter et al. 2007). Such a distance constraint occurs even in those plants dispersed by animal vectors, as frugivorous animals frequently show behavioral barriers to forage in open areas, far from forest cover (Cardoso da Silva et al. 1996; Duncan and Chapman 2002; García et al. 2010). Only when some isolated trees stand in such open areas, offering fruits or perching sites, do frugivores overcome their reluctance to leave the forest (McDonnell and Stiles 1983; Cardoso da Silva et al. 1996; Duncan and Chapman 2002) and disperse seeds into the deforested matrix more often (Herrera and García 2009; Carlo et al. 2013). However, even in these cases, seed deposition is narrowly restricted to the area beneath the canopy of remnant trees, thus resulting in a pattern of cover-associated seed rain similar to that found in forest areas (Duncan and Chapman 1999; Carrière et al. 2002; Bustamante-Sánchez and Armesto 2012). Whether the patterns of distance- and cover-sequestered seed deposition may relax in response to environmental change, leading to liberated seed dispersal into deforested ground, is largely unknown.

When studying the potential of animal-generated seed dispersal for passive restoration we have to consider that plant-frugivore interactions are inherently variable in space and time (Levey and Benkman 1999; Jordano 2000). Between years variation is typical in both quantity of fruits and their large-scale spatial distributions (i.e. the fruiting landscape), determining strong changes in the foraging scenarios found by frugivorous animals (*Capítulo 1*). As such, this source of landscape-scale dynamism often leads to important variations in the magnitude of seed dispersal in fragmented landscapes (Hampe et al. 2008; García et al. 2013; Perea et al. 2013). For example, seed dispersal is strongly biased to

large forest patches when fruits mostly occur in dense forests, but it is enhanced under isolated masting trees, which contribute to widening the distribution of fruits across the whole landscape (Herrera and García 2009). Previous studies have shown that inter-annual changes in fruiting landscape affect the probability of seed dispersal from forest into pastures (García et al. 2013). Nevertheless, no study has yet explicitly evaluated how the temporal dynamism of fruit-frugivore systems modulates the distance constraint of seed dispersal into deforested land. We hypothesize that distance constraints on seed dispersal should weaken when fruiting landscapes widen the foraging ranges of frugivores.

In this paper, we evaluated the spatio-temporal variability in tree fruit availability, frugivorous bird abundance and activity, and tree seed dispersal by birds from forest patches to the surrounding matrix of deforested pastures, in a fragmented landscape of the Cantabrian Range. Specifically we sought to answer the following questions: 1) Does the landscape context, in terms of forest cover extent and isolation, affect seed deposition into pastures? 2) Do these landscape-context effects change between years? And, if so: 3) Can interannual changes in seed dispersal be interpreted as a result of the different responses of birds to the fruiting landscape?

Specific materials and methods

The study was carried out over two consecutive years: autumn-winter season 2009-10 and 2010-11 (hereafter, respectively 2009 and 2010). From the perspective of pastures as sites of seed deposition, the fragmented landscape in the plot represents a wide range of contexts which differ in their quantity of, and their distance to, surrounding forest cover.

Frugivorous bird censuses

For this chapter we considered bird abundances obtained from observations performed in the study plot during 2009-10 and 2010-11 fruiting seasons (for further explanation on methodology see *Métodos generales* section; observation

efforts are shown in Chapter 1). For each bird observation we detailed the microhabitat where the bird was resting. We distinguished between three different microhabitats (Fig. C3.1D-F) depending on the structure of the forest cover: forest (in the main forest cover), remnant tree (in isolated trees within the pastures) and open ground (with no tree cover at all). We considered as an isolated tree each tree-like plant, showing a minimum trunk diameter of 10 cm and taller than 1.5 m, standing alone or together with a maximum of two other individuals (evidenced by direct observation on the field), and showing a minimum distance of 5 m to the main forest cover (estimated by using the GIS). We calculated the number of birds per cell in different microhabitats by the same procedure used by the abundance of birds per cell (see *Métodos generales* section).

Forest cover and fruit counts

For this chapter we quantified forest cover area and fruit abundance in each plot cell for 2009 and 2010, as specified in *Métodos generales* section.

Sampling of dispersed seeds

Seed rain was quantified in a subset of 220 plot cells (Fig. C3.1B), for 2009 and 2010. According to the structural characteristic of the cover where each quadrat was located, we determined the habitat of the sampling station, assigning it to the category of either covered (under woody canopy) or open (uncovered by woody canopy) (Fig. C3.1B). This design resulted in 541 sampling stations in covered microhabitat and 1659 in open microhabitat.

Characterization of forest context around sampling stations

The position of all sampling stations was geo-referenced and introduced as a layer in the GIS. For each open habitat sampling station we estimated (from the GIS) *distance to forest* (m) as the lineal distance to the nearest forest cover, and *forest cover* (m^2) as the area covered by forest in a 25-m radius extent around each station (Fig. 3.1C). Previous studies have proven this radius to be an appropriate scale to represent variability in, simultaneously, habitat cover and

seed dispersal, across a local landscape (García and Chacoff 2007; Carlo et al. 2013).

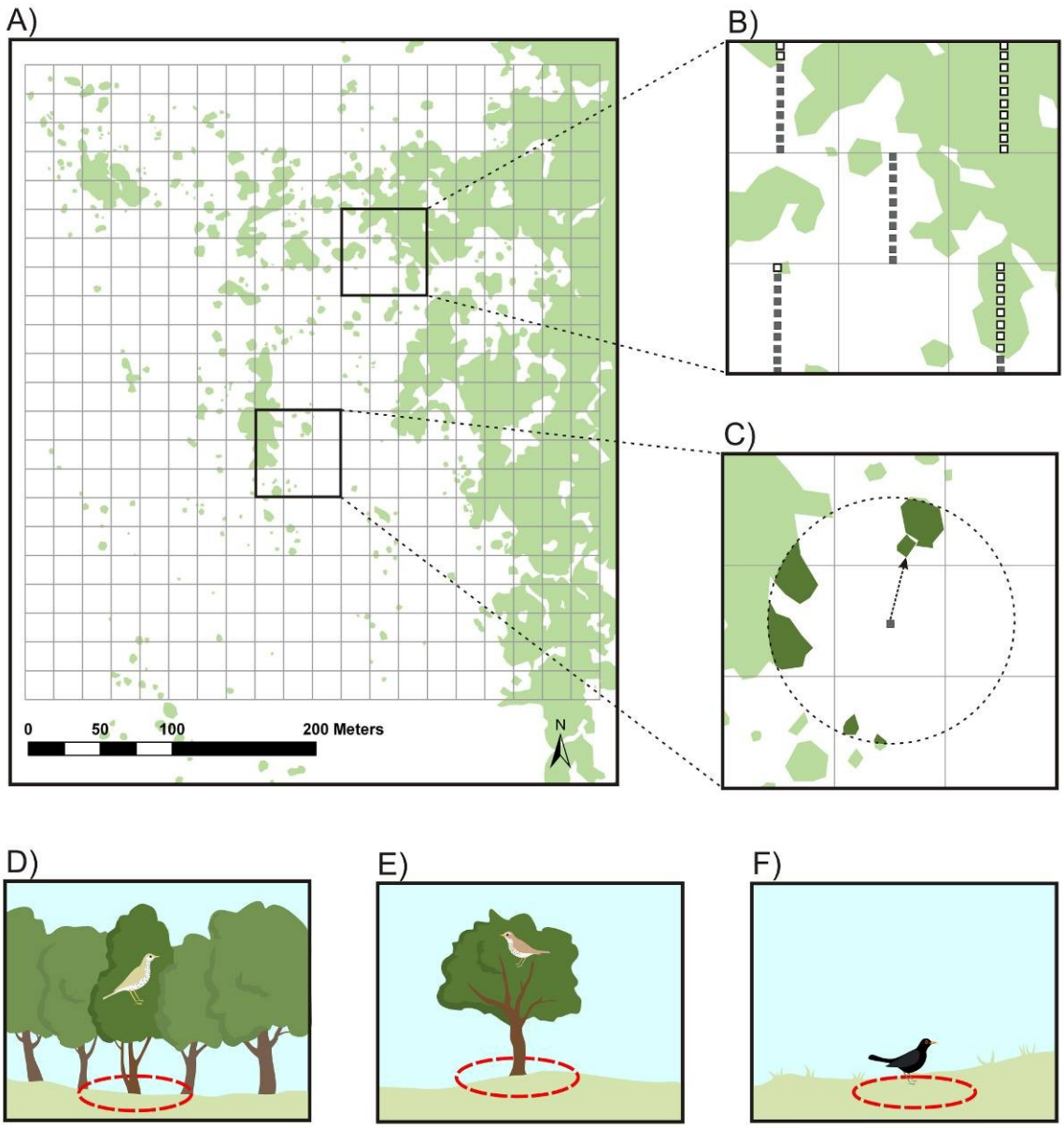


Fig. C3.1. A) Map of the study plot, subdivided into 20 × 20 m cells, showing the extent of forest cover (light green area). B) Detail showing the chess-board design for seed dispersal sampling. Sampling stations located in *open* habitats are represented as dark gray quadrats while those under forest cover are in white. C) Detail representing the forest context metrics for an open sampling station (dark gray quadrat): the minimum distance to forest cover (dashed arrow) and the forest cover (dark green extent in a surrounding 25-m radius circumference). Microhabitats considered for bird observations are shown on the bottom line: D) forest, E) remnant tree and F) open ground.

Statistical analysis

Fruit abundances in the study plot were compared between years (2009-2010) by using Generalized Linear Models (GLMs) with a quasi-Poisson distribution of errors and *log* link function. To describe the distribution of fruits along a gradient of forest cover we grouped the cells into exclusive categories according to forest cover, considering eight 50-m^2 wide intervals (i.e. 0-50, 51-100,..., 351-400 m^2), and summed the fruit abundance from all cells within each category. We compared the distributions of fruits between years by using a χ^2 test.

Between years differences in bird abundance at the whole plot scale were checked by using GLMs (quasi-Poisson distribution, *log* link). Similar models were applied to each of the cell subsamples corresponding to the different perching microhabitats.

Two descriptors of seed dispersal were considered: *seed arrival* (presence/absence of seeds in a given sampling station), and the *number of dispersed seeds* per sampling station. Between-year variations in seed dispersal at the whole plot scale were analyzed by using GLMs (Binomial distribution and *probit* link for seed arrival; quasi-Poisson distribution and *log* link for number of dispersed seeds). The model for number of dispersed seeds considered only those sampling stations containing any dispersed seeds.

We sought to examine the effect of forest context on seed dispersal into open habitats across years. Due to the correlation between distance to forest and forest cover (Pearson Correlation: $r = -0.85$, $P < 0.0001$, $N = 1659$), we constructed independent GLMs for these two variables. These models only included those sampling stations in open habitats. We first assessed how seed arrival was affected by the distance to forest, the year, and the interaction *distance* × *year* (Binomial distribution, *probit* link function). A second model considered as predictors forest cover, year and the interaction *forest cover* × *year*. Two equivalent GLMs (quasi-Poisson distribution, *log* link) were applied to the

number of dispersed seeds as a response variable. Predictor variables were standardized in all models. The present sampling design may suffer from spatial non-independence in the estimation of landscape effects on seed dispersal, given that the study plot represented a gradient of forest cover (Fig. C3.1A), and that sampling stations were clustered on a per-cell basis (Fig. C3.1B). Thus, in order to obtain estimates of main effects in GLMs which were free of spatial autocorrelation bias, we applied a Spatial EigenVector Mapping approach (SEVM; Griffith and Peres-Neto, 2006; Dormann et al., 2007). This methodology explicitly accounts for the influence of space in the dependent variable by including these spatial effects as additional independent variables in GLMs. For a given original GLM, uncorrelated explicative eigenvectors are obtained from the decomposition of the spatial autocorrelation (SAC) found in model residuals, by using the eigenfunction decomposition of spatial connectivity matrices (Griffith and Peres-Neto, 2006). Once obtained, eigenvectors are sequentially added to the GLM model, until no significant SAC is found in the residuals (measured by Moran's *I* statistic). A final GLM model is then recalculated, including the matrix of selected eigenvectors as additional predictors.

When significant interaction terms (distance × year; forest cover × year) occurred in the GLMs above, *a posteriori* analyses were performed to compare seed dispersal between years, at different sections of the gradients of distance or forest cover. To do that, we sub-divided the distributions of *distance to forest* and *forest cover* into three different categories (short, medium and long for distance; low, medium and high for cover). We considered short/low values as those ranging from 0 to the respective medians of the distribution of distance and cover. Medium values were grouped from above the median to the 90th percentile. Those values above 90% of the distribution were respectively considered long/high (Fig. 3.3; *Appendix B,* Fig B.1). Between-year differences in seed arrival and in the number of dispersed seeds were checked by using

Fischer tests for each section of the respective distance and forest cover gradients.

All the analyses were performed by using R 2.15 (R Development Core Team), with *spdep* package for SEVM.

Results

Total fruit abundance was similar between years in the study plot (Table C3.1; GLM: $t = 0.65$, $p = 0.52$; DF = 879), but the relative contribution of the different tree species varied between years (GLM: $t = -6.31$ for *I. aquifolium*, and $t = 9.68$ for *C. monogyna*; $p < 0.0001$; DF = 879). *I. aquifolium* accounted for 81.2% of total fruit abundance in 2009, but for only 25.5% in 2010, when *C. monogyna* was numerically dominant (Fig. C3.2). *T. baccata* fruits accounted for < 10% of total fruit abundance, with no differences between years (GLM: $t = 0.82$, $p = 0.41$, DF = 879). Associated with the variation in the relative abundances, the distribution of fruits along the gradient of forest cover also changed from year to year ($\chi^2 = 7.57 \cdot 10^4$, $p < 0.0001$, DF = 7). Namely, fruit abundance was mostly concentrated in high forest cover areas in 2009, whereas it was more widely distributed in 2010, with fruits appearing in both high and in low forest cover areas (Fig. C3.2).

The abundance of frugivorous birds was significantly lower in 2010 than in 2009, at the whole plot scale (GLM: $t = -2.48$, $p = 0.01$, DF = 879; Table C3.1). When considering bird abundance in the different microhabitats, a lower number of birds was found in forest in 2010 relative to 2009 (GLM: $t = -2.48$, $p = 0.01$, DF = 351; Table C3.1), but abundances were similar between years in remnant trees and in open ground (GLM: $t = -0.26$, $p = 0.8$, DF = 283 for remnant trees; $t = -1.55$, $p = 0.12$, DF = 653 for open ground; Table C3.1). While bird sightings in forest accounted for 88.3 % of the total abundance in 2009, this decreased to 83.2% in 2010. Conversely, the proportion of birds observed in remnant trees increased from 8.7% in 2009 to 13.6% in 2010.

The arrival of dispersed seeds in sampling stations decreased from 2009 to 2010 (GLM with SEVM approach: $z = -3.76$, $p < 0.001$, DF = 4399; Tables C3.1 and 2).The number of dispersed seeds also decreased from 2009 to 2010 (GLM: $t = -5.63$, $p < 0.0001$, DF= 1623; Tables C3.1 and C3.2). Both decreasing trends were stronger under forest cover than in open habitats (Table C3.1).

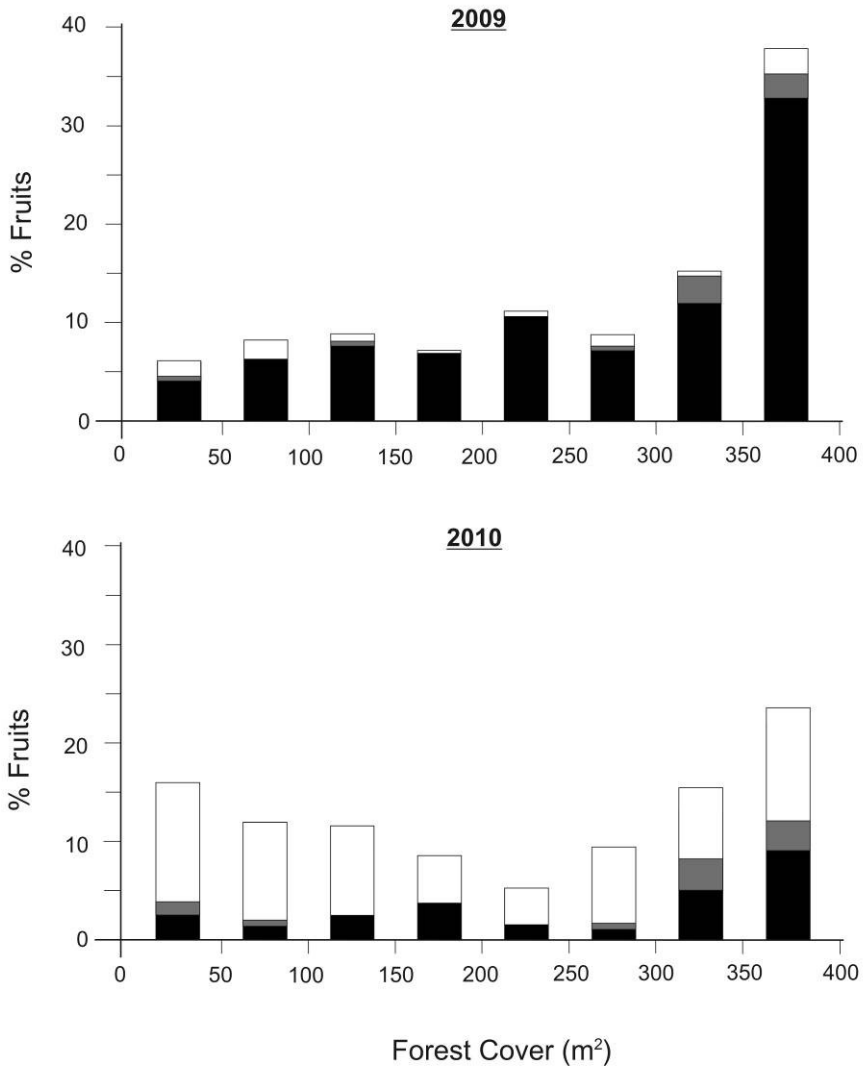


Fig. C3.2. Percentage of each fruit, as a proportion of total fruit production, produced in cells of different categories of forest cover in the study plot, for both study years. Each bar is sub-divided into the proportion of fruits produced by *C. monogyna* (white), *T. baccata* (gray) and *I. aquifolium* (black).

Table C3.1. Summary of abundance of fruits and frugivorous birds, rate of seed arrival and the abundance of dispersed seeds, for different study years; average values are shown ± standard error. **Fruits**: number of fruits per m^2 per cell. **Birds**: abundance of frugivorous birds per cell per 10 hours, and abundance in different microhabitats. **Seeds**: Seed arrival rate as the percentage of sampling stations showing dispersed seeds (from a total of 2200 stations), and their arrival in *forest* (541 stations) and *open* (1659 stations) habitats. Number of dispersed seeds per m^2 for all sampling stations, and distinguishing between stations in *covered* and *open* habitats.

Year		**2009**	**2010**
Fruits	**Nº fruits/m^2**	17.4 ± 1.5	18.8 ± 1.5
Birds	**Nº birds/10h**	3.79 ± 0.46	2.25 ± 0.39
	forest	3.34 ± 0.46	1.87 ± 0.39
	isolated tree	0.33 ± 0.06	0.31 ± 0.05
	open	0.12 ± 0.03	0.07 ± 0.01
Seeds	**Seed arrival**	39.4%	34.6%
	covered	72.4%	64.3%
	open	24.7%	21.5%
	Nº dispersed seeds /m^2	62.5 ± 5.4	27.0 ± 2.7
	covered	205.5 ± 20.5	88.4 ± 10.3
	open	3.2 ± 0.3	2.8 ± 0.3

Seed arrival in open habitats was negatively affected by distance to forest, drastically decreasing with increasing distance from the forest edge, but it was similar between years (Table C3.2). A significant interaction between distance and year also occurred (Table C3.2). *A posteriori* analyses showed that this interaction resulted from a decrease in seed arrival at short distances but an increase at long distances in 2010, with respect to 2009 (Fisher tests: short distances: odds ratio = 0.73, p = 0.004; medium distances: odds ratio = 0.78, p = 0.07; long distances: odds ratio= 2.64, p = 0.03; Fig. C3.3A).

The GLM evaluating the effect of forest cover on seed arrival in open habitats suggested a significant decrease in seed dispersal probability in low-cover and deforested areas (Table C3.2). Again, we found no effect of the year

Table C3.2. Effects of Distance to forest and Forest cover (evaluated by independent analyses) on A) Seed arrival and B) Number of seeds dispersed into open habitats. *Year* was included as a predictor variable for both seed dispersal descriptors. Spatial eigenvectors (obtained by SEVM) describing the spatial autocorrelation of the response variable were included as predictors only for Seed arrival. Maximum likelihood estimates, their standard errors, the values of the *z* and *t* statistics and *p* values are shown.

A) Seed arrival				
	Distance to forest			
	Estimate	Std. Error	z	Pr(>|z|)
Intercept	-1.592	0.080	-19.9	< 0.001
Distance to forest	-1.043	0.107	-9.7	< 0.001
Year	-0.122	0.109	-1.1	0.262
VecC1	-0.343	0.060	-5.7	< 0.001
VecC2	-0.238	0.049	-4.8	< 0.001
VecC3	-0.197	0.052	-3.8	< 0.001
Distance×Year	0.331	0.142	2.3	< 0.001
	Forest cover			
	Estimate	Std. Error	z	Pr(>|z|)
Intercept	-1.587	0.078	-20.2	< 0.001
Forest cover	1.154	0.091	12.6	< 0.001
Year	-0.047	0.106	-0.4	0.658
VecD1	-0.292	0.052	-5.6	< 0.001
VecD2	-0.188	0.051	-3.7	< 0.001
Cover×Year	-0.506	0.117	-4.3	< 0.001
B) Number of seeds dispersed				
	Distance to forest			
	Estimate	Std. Error	t	Pr(>|t|)
Intercept	1.062	0.058	18.2	< 0.001
Distance to forest	-0.247	0.073	-3.4	< 0.001
Year	-0.119	0.088	-1.3	0.180
Distance×Year	0.102	0.100	1	0.311
	Forest cover			
	Estimate	Std. Error	t	Pr(>|t|)
Intercept	1.033	0.059	17.5	< 0.001
Forest cover	0.293	0.069	4.2	< 0.001
Year	-0.082	0.088	-0.9	0.353
Cover×Year	-0.107	0.095	-1.1	0.262

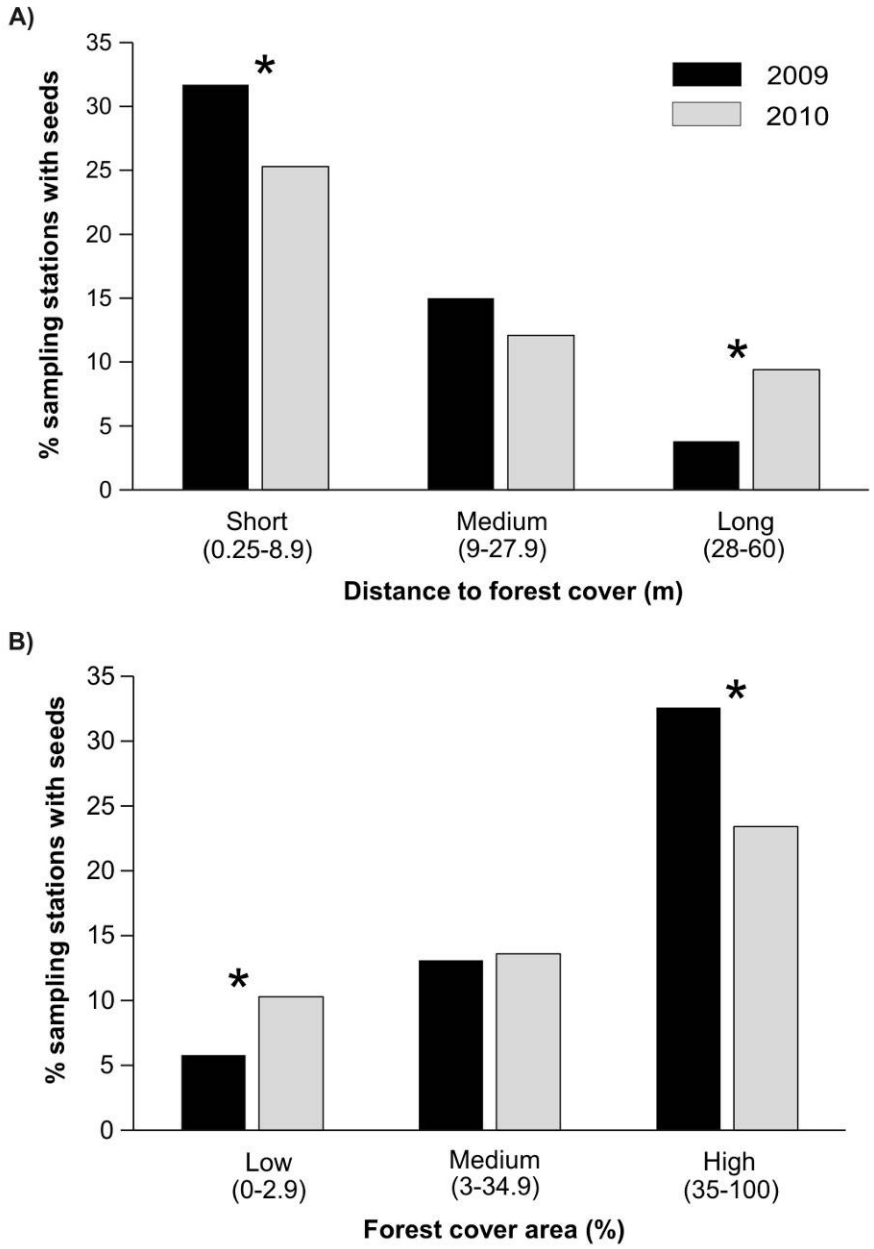


Fig. C3.3. Seed arrival (percentage of sampling stations receiving dispersed seeds) in different categories of distance to forest (A) and forest cover (B) for different years. Between years differences in a given category after a Fisher test are highlighted (*: $p < 0.05$).

but a significant interaction between forest cover × year (Table C3.2). *A posteriori* analyses evidenced a decrease in seed arrival in high covered areas from 2009 to 2010, at the same time as an increase into those areas devoid of forest cover (Fisher test: low cover: odds ratio= 2.36, $p = 0.03$, medium cover:

odds ratio = 1.04, p = 0.86, high cover: odds ratio = 0.63, p < 0.0001; Fig. C3.3B).

As shown for seed arrival, the number of seeds dispersed into open habitats decreased sharply with distance to forest edge, but was significantly higher when the sampling stations were surrounded by high forest cover (Table C3.2). No effect of year or interaction between forest context descriptors and year were found (Table C3.2).

Discussion

In this study, we evaluated the patterns of bird-generated, community-wide seed dispersal into deforested habitats (i.e. pastures) in a montane locality of the Cantabrian Range. The characteristics of the forest context surrounding pastures highly influenced seed dispersal. This main result accords with those from tropical forest ecosystems, where animals dispersed low proportions of tree seeds into pastures, and deposited most seeds in areas surrounded by high levels of forest cover, and, in addition, close to the cover (Willson and Crome 1989; Aide and Cavelier 1994; Cubiña and Aide 2001). Nevertheless, we found that this restriction relaxed in one of the study years, resulting in a higher proportion of seeds being delivered into pastures and at further distances from forest cover. We argue that this variation in the effects of forest context resulted from the temporal dynamism of the plant-frugivore system, with frugivore foraging varying in response to inter-annual changes in the fruiting landscape.

Patterns of seed dispersal into pastures

In this study, frugivorous birds carried seeds into less than 25% of the sampling stations in pastures, but to more than 65% of stations under forest cover (Table C3.1). Similar to previous findings (e.g. Kollmann and Pirl 1995; Holl et al. 2000; Duncan and Chapman 2002), we found that seeds did not only arrive at fewer sites in pastures, but were also deposited there in considerably lower numbers. In fact, the quantity of seeds arriving in open areas was two orders of

magnitude lower than under forest cover (Table C3.1; see also García et al. 2013). The early recruitment of the tree species studied here is supposed to be more limited by seed density than by the availability of suitable microsites for seedling establishment (García et al. 2005b), and, thus, we consider that the potential for forest regeneration in these open areas is quite scant. Nevertheless, even though we observed a strong difference in seed deposition between open and forested areas in both years, we also found some temporal variability in the magnitude of this difference. Namely, a significant decrease in both seed arrival and seed number took place in forested areas from 2009 to 2010. Despite this, we found that the magnitude of seed dispersal remained constant in the open areas (Table C3.1). This actually meant a two-fold increase in the relative importance of seed dispersal into deforested habitats, as seeds in open arriving there accounted for 4.5% of the total seed rain in 2009 but this increased to 8% in 2010 (Table C3.1). Previous works in this study system have also suggested between year variations in the magnitude of seed deposition (Herrera and García 2009; García et al. 2013), enlarging the temporal scope of the present data.

A negative effect of distance from forest edge in shaping the spatial pattern of seed dispersal into pastures has been reported previously in tropical ecosystems (Willson and Crome 1989; Aide and Cavelier 1994; Cubiña and Aide 2001). Here, we show that this pattern can be extended to our temperate system, as the number of dispersed seeds decreased sharply with increasing distance to forest cover. Although some seeds arrived as far as 50 m away from the forest cover, more than the 75% of dispersed seeds did not get further than 11 m away in either year. Thus, the potential for tree regeneration in these Cantabrian pastures is not only low but also spatially restricted to a narrow spillover band surrounding the remnant forest (see also Günter et al. 2007). In 2010, however, we detected a relaxation of this forest cover effect, as suggested by the increased probability of seed arrival at long distances from forest as well as in low forested landscape sectors (Fig. C3.3). We also found a lower proportion of the dispersed seeds deposited in highly covered areas, close to the forest edge.

Mechanisms behind variable seed dispersal patterns

Changes in the influence of forest context on seed dispersal into deforested habitats have been explained as a result of the local variability in the presence of isolated trees or other structures acting as perches (with pastures with more isolated trees receiving more seeds; McDonnell and Stiles 1983; Holl et al. 2000), or as a consequence of the differences in the structure of the forest context itself (with pastures in areas with higher or more complex forest cover receiving more seeds; Kollmann and Pirl 1995; Cole et al. 2010). Our study was carried out in a study plot with no between years variation in the extent or the spatial configuration of forest cover. Thus, the abovementioned cover-related factors do not seem to be determining the variations in forest context effects observed here. We suggest that this variability in fact results from the important dynamism of the plant-frugivore system, namely that concerning the abundance and the spatial distribution of fruits and frugivores (García et al. 2013). Our study did not find variations in total fruit abundance, but the spatial pattern of fruit abundance markedly changed from one year to the next (Fig. C3.2). While in 2009 the distribution of fruits in the study plot was strongly skewed towards highly forested areas, in 2010 it was better shared between these areas and those devoid of forest, dominated by pastures with few isolated remnant trees (Fig. C3.2). This shift in the large-scale spatial template of fruits reflects a change in the identity of the dominant fruiting species (Fig. C3.2), since *I. aquifolium* was mainly restricted to densely forested areas whereas *C. monogyna* appeared both in the forest and in the pastures as isolated trees.

The pattern of activity of birds across different habitats within the landscape changed from one year to the next, mirroring the change in fruiting spatial templates. In 2010 a lower proportion of birds was observed in the forest, while visits to isolated trees increased (Table C3.1). The present study only covered two years, but previous works in the same system have evidenced similar inter-annual changes in the fruiting landscape, with concomitant changes in frugivory and seed dispersal (Herrera and García 2009; García et al. 2013).

Taken together, our present and previous results suggest, over a longer time period, that frugivorous birds perceived the large-scale landscape context and optimized their foraging activity according to the fruiting scenario they found each year (see also Tellería et al. 2008; García et al. 2013). In other words, when fruit production is low in the forest but comparatively high in small stands and isolated trees within the pastures, frugivorous birds would need to leave the forest to forage in open areas more often. This habitat-use change would consequently lead to variations in the seed rain that frugivores generate (Nathan and Muller-Landau, 2000; Culot et al. 2010), and a higher proportion of seeds could be expected to be dispersed at longer distances into pastures, as, in fact, we demonstrate in the present study.

Integrating landscape dynamic structure and seed dispersal into deforested lands

Frugivorous animals acting as mobile links (moving seeds between different landscape patches, from forest into pastures; Lundberg and Moberg 2003) have frequently been considered as important tools in vegetation passive restoration plans (Wunderle 1997; Holl et al. 2000; Cavallero et al. 2013). An equivalent role may be attributed to frugivorous birds in our study system, in which seed availability has been suggested to strongly limit tree recruitment (García et al. 2005 b). Furthermore, birds' reluctance to use open habitats constrains the initial potential for tree regeneration in pastures to a narrow *halo* surrounding the remaining forest. Fruiting landscape dynamics, like those observed here, confer variability to the behavior of frugivorous birds, and, subsequently, to seed dispersal patterns (Cardoso da Silva et al. 1996; García et al. 2013). In certain years, responding to landscape-scale widespread fruit distributions, birds forage outside the forest more frequently, carrying more seeds, and carrying them further distances, into pastures. We suggest that a relaxing of distance constraints on seed arrival, similar to that we have evidenced here, would also take place during other events of within forest fruit shortage. If this is true, the spatial pattern of forest regeneration in pastures which can be expected in the long-term

will be shaped by the summed templates of different spillover bands, in the form of *tides* of seeds within the pastures (Fig. C3.4). While most years seed arrival will occur quite near to the forest edge (Fig. C3.4A), in other years *spring tides* of seeds would take place, spreading wider the initial potential of forest recolonization within pastures (Fig. C3.4B). Indeed, between 2009 and 2010 we observed an increment of 2 m in the average distance at which seeds arrived. This widening of the spillover band would also contribute to an enlargement of the scale at which forest regeneration potentially operates as, translated into surface terms, it represents an increase of 10% in the unforested surface of the study plot affected by seed dispersal.

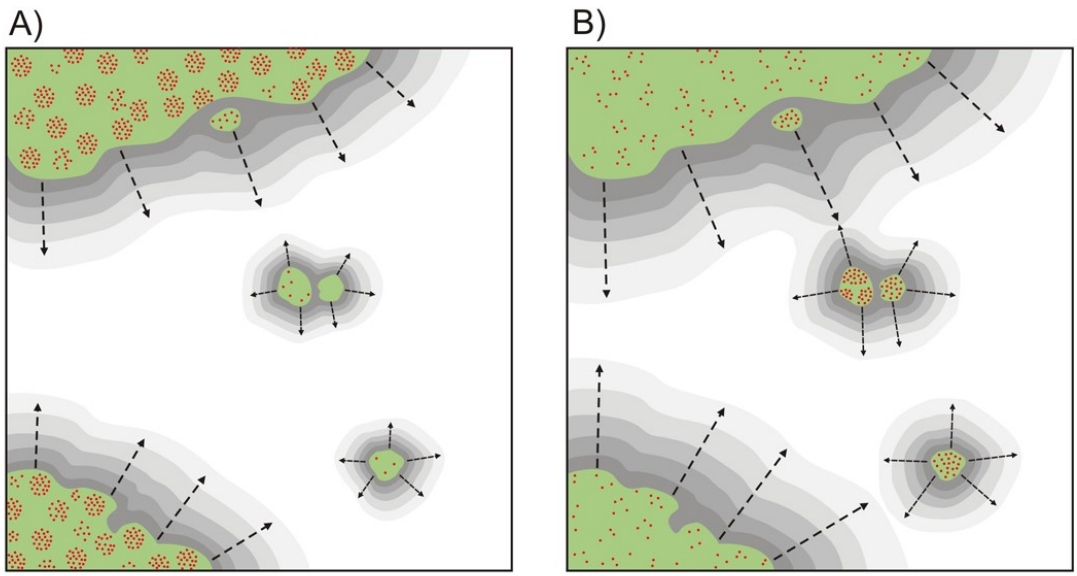


Fig. C3.4. Representation of between-years variations in seed dispersal from forest cover into pastures. Forest is represented in green and pasture in white (with isolated remnant trees as small green polygons). Fruits are represented as red spots within forest cover. Seed arrival in pastures is represented as a decreasing gradient from forest edge (gray tones). A) When fruits are concentrated in large forest patches, seed dispersal is constrained to a narrow spillover band surrounding forest cover. B) When fruits are widespread across the whole landscape, and even more abundant in isolated remnant trees than in large forest patches, birds visit deforested land more frequently, widening and spreading the spillover band of seed dispersal.

The present study nonetheless has some limitations that must be considered in relation to the interpretation of results. First, we focused on the raw, community-wide potential for forest recolonization, without considering potential differences between tree species. We found that, in 2009, the different tree species occurred in the same relative frequencies in open and in covered stations, but, in 2010, the proportion of seeds of *I. aquifolium* decreased, while that of *C. monogyna* increased, in open with respect to covered stations (data not shown). These species-specific patterns may also affect recolonization dynamics through effects on vegetation composition. Second, even though seed dispersal spatially constrains the potential for forest recovery, final recolonization templates may differ from those initially determined by seed rain. Environmental filtering which affects subsequent plant regeneration stages may blur the seed dispersal footprint (Holl et al. 2000). Third, this study is based on a single locality, restricting the extrapolation of our results over larger extents. That said, we consider that the local conditions of our study system are frequently replicated through the region, as both the the plant-frugivore assemblage (e.g. Guitián et al. 2000) and the patterns of forest loss and fragmentation -due to regional processes of exploitation- (e.g. García et al. 2005a) are highly predictable across the Cantabrian Range. Indeed, high habitat loss and fragmentation degrees are generalized in many mature and secondary forests of other mid-mountain areas in Europe (Darby 1956; Behre 1988; Kaplan et al. 2009).

Conclusions

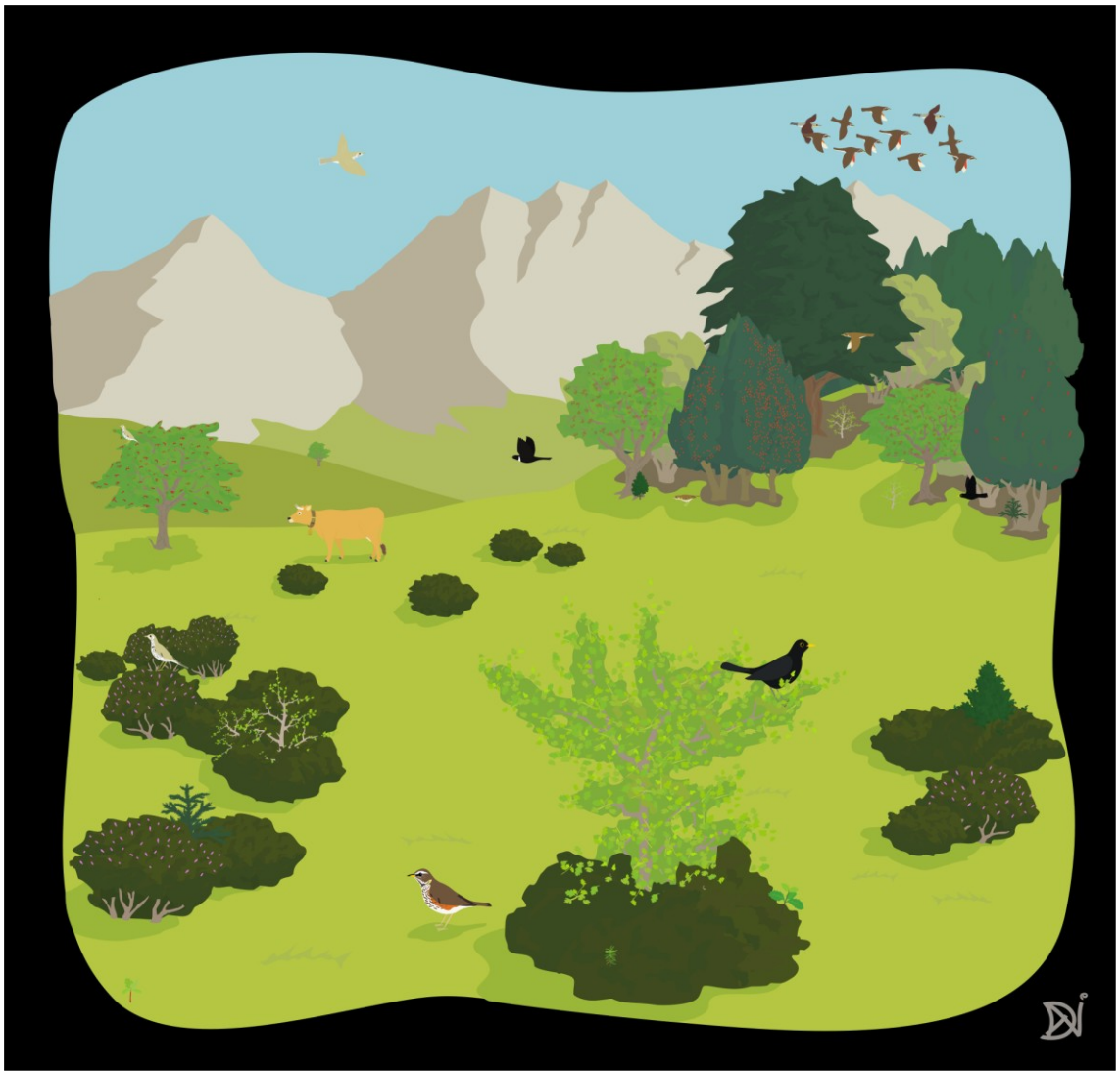
As proposed by Holl and Aide (2011), some important factors should be taken into account for the effectiveness of natural recolonization as a strategy for restoring vegetation in degraded areas. The success of passive restoration plans will rely on the intrinsic recovery capacity of the system (the ecosystem resilience), on the level of degradation suffered and, also, on the characteristics of the landscape context surrounding the area. Our study system seems to be a perfect candidate for achieving significant forest recovery, as it retains the

potential for natural tree regeneration. Areas available to recover are extensive livestock grazing pastures with low levels of soil perturbation and moderate-to-high fertility and, thus, they are potentially suitable sites for seedling establishment once seeds have arrived. Even when the matrix is mainly open, some forest patches and isolated trees still remain, acting also as seed sources for regeneration. Moreover, the main forest tree species are all dispersed by mobile animal vectors that contribute to their spreading. Here, in addition, we show that the spatio-temporal variability inherent to this system is an important source of forest resilience (see also García et al. 2013). Dynamic landscapes, like that found here, derived from large-scale variable fruiting patterns, can contribute to relaxing the restrictions that limit forest recovery in degraded areas. We thus encourage the consideration of this type of landscape biological dynamism when aiming to manage rewilding in European temperate forests (Navarro and Pereira 2012).

Capítulo 4

Footprint of seed dispersers in forest regeneration and recovery under habitat loss

Huella de los dispersores de semillas en la regeneración y recuperación forestal en un escenario de pérdida de hábitat



Abstract

Frugivorous animals perform relevant services in forest ecosystems. As seed dispersers, they may leave a spatial footprint in the tree regeneration patterns, but this contribution is conditioned by environmental factors affecting post-dispersal regeneration stages. Human-induced ecosystem degradation can seriously compromise frugivore services. However few studies have considered that these detrimental effects can be the result of simultaneously altering frugivore initial footprint and its post-dispersal environmental filtering. Here, we evaluated how habitat loss conditioned the contribution of avian seed dispersers to tree regeneration and forest recovery in degraded lands. By using an integrative approach we dissected habitat loss effects, distinguishing between the direct influence on bird abundance and activity and the indirect effects through the modification of post-dispersal filtering. Habitat alteration highly conditioned dispersers activity, mainly restricting seed dispersal to highly forested areas. Tree recruitment was severely reduced during early regeneration stages but forest-confined, bird-mediated regeneration patterns were maintained. Late environmental filters conditioning sapling establishment drastically altered regeneration spatial patterns. Unfavorable conditions for long-term sapling survival occurred both under tree canopy and within deforested areas. Nevertheless the protective role of protective scrubs in deforested areas equalized the late tree recruitment magnitude between forest and deforested areas. In terms of large-scale forest regeneration, frugivorous birds reinforced the forest-skewed recruitment patterns exacerbated by habitat loss. Nevertheless, in terms of the recovery of deforested lands, and despite restricted seed dispersal, the long-term role of birds is crucial to generate a bank of samplings associated to nurse scrubs. Our results evidence that an integrative approach can help to understand the different ways through which habitat alteration affects frugivore ecosystem services. Revealing them will help to develop management plans that optimize the frugivore contribution to restoration programs.

Resumen

Los animales frugívoros desempeñan importantes servicios en los sistemas forestales. Como dispersores de semillas, dejan una huella espacial en los patrones de regeneración arbórea, pero su contribución se encuentra condicionada por factores ambientales que afectan a los estadios de regeneración post-dispersiva. La degradación antrópica de los ecosistemas puede comprometer seriamente los servicios de los frugívoros. Sin embargo escasos estudios han considerado que estos efectos negativos pueden ser el resultado de que alteren simultáneamente la huella inicial de los frugívoros y el filtrado ambiental post-dipersivo. En este estudio evaluamos como la pérdida de hábitat condicionó la contribución de las aves dispersoras de semillas a la regeneración y recuperación forestal en áreas degradadas. Mediante el uso de una aproximación integradora, diseccionamos los efectos de la pérdida de hábitat diferenciando los resultantes de su influencia directa en las aves de aquellos debidos a la modificación del filtrado postdispersivo. La alteración del hábitat condicionó en gran medida la actividad de los dispersores, restringiendo los patrones de dispersión de semillas principalmente a áreas de cobertura forestal densa. El reclutamiento arbóreo se redujo de forma severa durante los estadios de regeneración temprana pero mantuvo los patrones de regeneración asociados a la cobertura forestal mediados por las aves. Los filtros ambientales que condicionaron el establecimiento de juveniles alteraron drásticamente los patrones de regeneración. Condiciones desfavorables para la supervivencia alargo plazo ocurrieron tanto dentro del bosque como en las áreas deforestadas. En términos de la regeneración forestal a escala amplia, las aves frugívoras reforzaron los patrones de reclutamiento sesgados hacia el bosque agravados por la pérdida de hábitat. Sin embargo, en cuanto a la recuperación forestal, y a pesar de la restringida dispersión de semillas, el papel a largo plazo de los frugívoros es crucial para crear un banco de individuos juveniles asociados a matorrales nodriza. Nuestros resultados evidencian que una aproximación integradora puede ayudar a entender las diferentes vías a través de las cuáles la alteración del hábitat afecta a los servicios ecosistémicos. El revelarlas ayudará a desarrollar planes de manejo que

optimicen la contribución de los frugívoros en programas de restauración ambiental.

Introduction

Frugivorous animals acting as seed dispersers have been recognized to develop key ecological functions within natural ecosystems (Lundberg and Moberg 2003; Howe and Miriti 2004; Farwig and Berens 2012). By taking seeds away from mother plants frugivores decrease density dependent mortality (Harms et al. 2000), favor within population gene flow (Jordano and Godoy 2002; García et al. 2009a), take part in plant community assembly (Harms et al. 2000; Levine and Murrell 2003) and, when accomplishing long distance dispersal events, contribute to metapopulation dynamics (García et al. 2009a). Furthermore, because of their essential role in structuring plant communities, they contribute to sustain biodiversity and maintain ecosystem functioning (Bascompte and Jordano 2007; Schleuning et al. *under revi*ew). Moreover, as essential components of the ecological memory (Lundberg and Moberg 2003), they promote ecosystem recovery after disturbances, when dispersing seeds from undisturbed habitats and favor vegetation recolonization in disturbed ones (Wunderle 1997; Cavallero et al. 2013). By performing these functions they accomplish crucial ecosystem services (Lundberg and Moberg 2003, Kremen et al. 2007), as they contribute to sustain processes affecting human well-being, such as soil stabilization, flood control, CO_2 storage, and climate regulation, among others (Daily 1997).

Frugivores create the seed deposition template (i.e the seed rain; Nathan and Mueller-Landau 2000), determining the distribution of early potential for plant regeneration (e.g. Suárez-Esteban et al. 2013; Wenny 2000; García et al. 2009b). Frequently, this template may be far from representing the final pattern of adult distribution, and frugivore footprint is hardly distinguishable, or even totally disappears (Schupp and Fuentes 1995; García 2001; Rey and Alcántara 2014). Namely, the initial regeneration potential determined by frugivores is filtered by environmental factors affecting seed survival, seedling emergence and establishment and sapling survival (Schupp et al. 2010). When these post-dispersal filters are weak and spatially homogeneous the initial template will be maintained. On the contrary, when they involve strong demographic sieves with

heterogeneous spatial patterns that do not match the seed rain, frugivore footprint will be blurred on the final recruitment (Schupp and Fuentes 1995; García et al. 2005b). The effectiveness of frugivorous animals as seed dispersers will depend on the quantity of seeds dispersed but also on the quality of dispersal, which is highly conditioned by these environmental constraints on seed fate (Schupp et al. 2010). Then, discerning the actual role of frugivores in ecosystems can be only accomplished by explicitly considering the filtering effects of environment in plant recruitment.

Studying frugivore services will be critical in real-world ecosystems, i.e. those degraded by human activity, where the provision of services could be seriously compromised (Kremen 2005; Kremen et al. 2007). Habitat degradation is expected to affect the effectiveness of frugivores by altering the quantity and the spatial patterns of seed deposition, as result of its detrimental influence on, respectively, frugivore population size and behavior (Pejchar et al. 2008; García et al. 2010; Rey and Alcántara 2014). But it can also alter frugivore effectiveness by modifying post-dispersal seed and seedling fate through changes in abiotic conditions, such as light, humidity or temperature (Kapos et al. 1997; Uriarte et al. 2010), and/or in the behaviour of seed and seedling predators (García and Chacoff 2007, González-Varo 2010). These different effects must be studied together by considering integrative approaches allowing to evidence how and why habitat degradation alters the ecosystem services provided by frugivores. Understanding these matters would be especially relevant for an effective management of those services as a way to promote vegetation recovery on degraded areas.

In this study, we evaluate the contribution of avian seed dispersers to the processes of forest regeneration and recovery in a context of habitat loss. We dissected the influence of habitat alteration on long-term tree recruitment, discerning between effects on frugivore activity and seed dispersal and effects in post-dispersal seed fate. For that purpose we linked the large-scale spatial

patterns of habitat cover, bird abundance and four sequential tree regeneration stages (seed, emerged and established seedlings, and saplings) by means of an integrative approach. Specifically we sought to answer the following questions: 1) Which habitat characteristics influence post-dispersal regeneration stages? 2) How do post-dispersal processes alter the initial regeneration patterns determined by the seed rain? 3) Do frugivorous bird contribute to tree recolonization within the deforested habitat?

Specific materials and methods

Habitat characteristics

Habitat characteristics were quantified in a subset of 220 plot cells, selected following a chess-board design (Fig. C4.1B). We calculated from GIS forest cover area and fruit abundance in each cell. We also assessed in the field the presence/absence of big trees whose tops overgrew the average forest canopy, as previous studies in the same site have evidenced that these hints influence bird activity (see Chapter 1). In addition, we quantified in the field the cover of scrubs (mostly heather, but also gorse) and the cover of pasture per cell. In summer 2011, we visually estimated the proportion of scrub cover in ten 1m-radius areas randomly distributed in each cell, and extrapolated the average value of these areas to the total cell area. Scrubs rarely grow under tree canopy in our study site, and thus pasture cover per cell was calculated as the surface of each cell minus forest and scrub covers.

Frugivorous bird censuses

For this chapter we considered bird abundances obtained from observations performed in the study plot during 2009-10 and 2010-11 fruiting seasons (for further explanation on the methodology of bird censuses see *Métodos generales* section; observation efforts are shown in Chapter 1)

Sampling of tree regeneration stages

We considered four consecutive tree regeneration stages: seed (dropped by birds and in fallen fruits), emerged seedlings (i.e. presenting cotyledons but no leaves, knots or lignification of the stem), established seedlings (i.e. those emerged seedlings surviving after summer), and established saplings (i.e. pre-reproductive individuals ≥ 10 cm tall or with a stem basal diameter ≥ 0.5 cm). Seeds and seedlings were studied by following two consecutive yearly cohorts from fruit production to seedling establishment. The first cohort ranged from autumn 2009 (fruit stage) till late summer 2011 (established seedling stage), the second cohort from autumn 2010 till late summer 2012. Tree sapling stage was studied through a single monitoring, covering individuals of different ages, not assignable to a given cohort.

We assessed seed availability in sampling stations across the whole plot, at the end of the seed dispersal seasons (January 2010 and 2011). Ten 50 × 50 cm sampling stations were placed in each of the 220 chess-board cells (Fig. C4.1B). In each station, we collected and counted all fleshy fruits fallen directly from trees and fleshy-fruited tree seeds deposited by birds during the dispersal season. We estimated the contribution of fallen fruits to seed availability by extrapolating the number of seeds inside fruits to the quadrat surface. *C. monogyna* fruits and *T. baccata* ariles are single seeded. *I. aquifolium* fruits contain 2-4 seeds and, thus, we considered three seeds as the average value. We estimated total seed density per sampling station as the sum of bird-dispersed seeds and fruit-contained seeds, expressing this density as number of seeds per square meter. We considered seeds of both origins together, as previous studies have suggested that seeds from fallen fruits also account for a part of seedling emergence in the studied tree species (Herrera and García 2010).

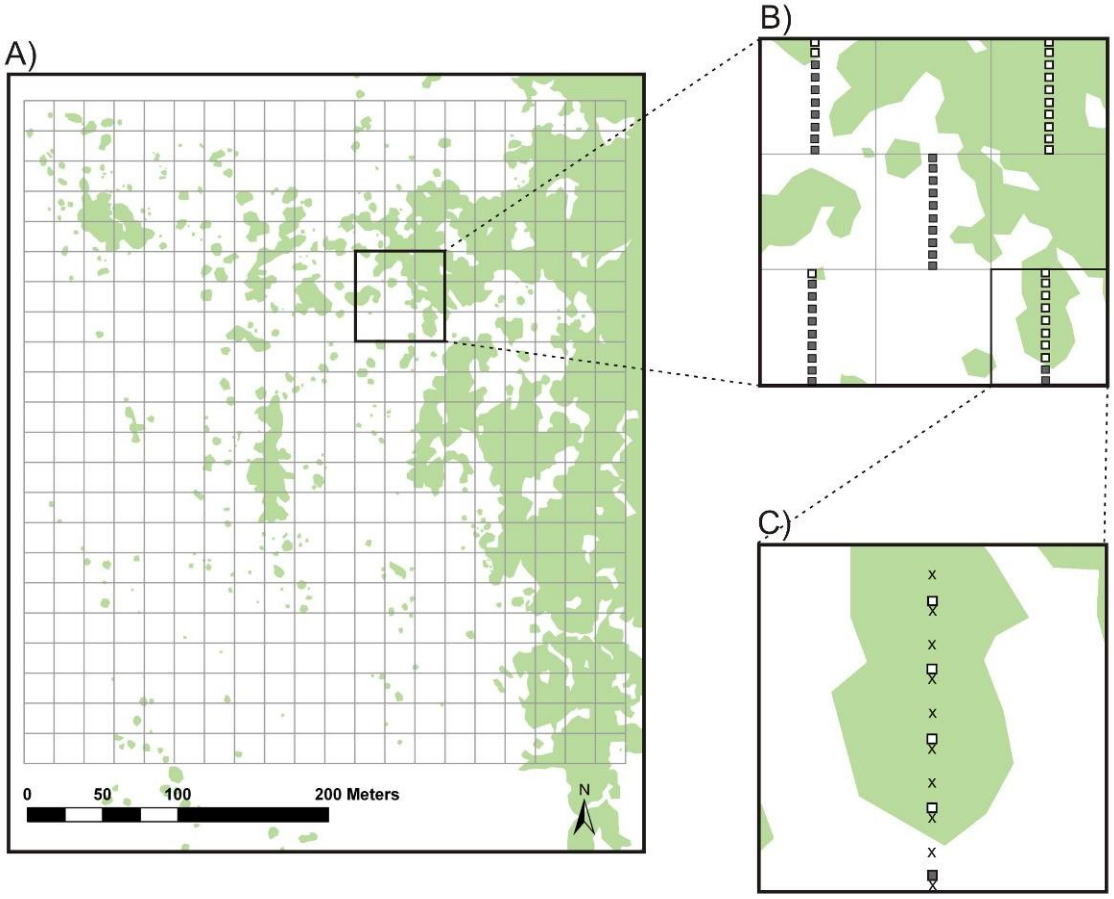


Fig. C4.1. A) Map of the study plot, subdivided into 20 × 20 m cells, showing the extent of forest cover (light green area). B) Detail of the chess-board design for the sampling of tree regeneration stages, showing the distribution of seed-rain sampling stations within 20 x 20 m cells. C) Detail of a cell showing the distribution of seedling sampling stations located adjacent to seed rain stations (represented by crosses). In both B) and C), sampling stations located in *open* habitats are represented as dark gray quadrats while those *covered* (under forest cover) are in white.

We assessed seedling emergence and establishment in sampling stations across the whole plot in 2011 and 2012. Five sampling stations were placed in each of the 220 chess-board cells, separated from each other by 4 meters, and located next to one of the seed availability sampling stations (Fig. C4.1C). In each station, we set up a permanently labeled 50 × 50 cm quadrat on the ground, and checked the emergence of all fleshy-fruited tree seedlings during spring (April-May). Emerged seedlings are distinguishable by the presence of cotyledons but no leaves, knots or lignifications on the stem. The seedlings of the

three tree species studied are easily distinguishable by cotyledons shape and color, and stem color (Fig. I.3). For each sampling station, we individually distinguished each emerged seedling by positioning it within the quadrat with x, y coordinates, mapping it on a drawing template. Survival of emerged seedlings was monitored monthly through spring and summer, until late August. We considered as established seedlings those surviving by the end of the summer, as preliminary surveys showed that the summer period concentrates most of seedling mortality through the whole year (*authors' personal observation*). We counted the cumulative number of emerged seedlings and the number of established seedlings and expressed their densities as number of seedlings per square meter.

We determined the habitat and the microhabitat for each seed and seedling sampling station. Habitat was determined according to the major structural characteristic of the cover where the quadrat was located, considering the categories of either covered (under tree canopy) or open (uncovered by tree canopy). Microhabitats were classified according to the fine-grain structural characteristic of the cover, maintaining the covered category for areas under tree, but distinguishing between scrub (under the canopy of scrubs) and pasture (with herbaceous vegetation) in open habitat.

In each of the 220 chess-board cells, we surveyed the entire surface recording the total abundance of established saplings of fleshy-fruited tree species. We considered as a sapling any pre-reproductive individual $\geq$ 10 cm tall or with a stem basal diameter $\geq$ 0.5 cm. For oldest individuals, we verified the absence of flowers and fruits in the following spring and autumn respectively. We performed a single sampling (summer 2011) aimed to represent the long-term, cumulative tree recruitment in the study site, as the sapling category gather individuals of different ages. We classified the microhabitat where each sapling was standing according to the same categories used for seeds and seeding sampling stations. During 2011 sampling we labeled 386 individuals equally

distributed between microhabitats (covered, pasture and scrub) and species (holly, hawthorn and yew), and covering the whole extent of the study plot. We checked the survival of labeled saplings in late summer (September) 2012. Sapling survival was very high (97.15%) and mortality was widespread cross the plot, and across different microhabitats and species (authors' unpublished data). We then considered that the magnitude and the spatial template of sapling establishment represented a good proxy to long-term tree recruitment.

For each cell and cohort (2009 and 2010) we calculated the average density of seeds and emerged and established seedlings per m^2. Sapling density per cell was estimated as the number of individuals per square meter. Also, for each cell and cohort, we estimated the densities of seeds, emerged seedlings, established seedlings and saplings in deforested habitat by considering exclusively the data from those sampling stations (or individuals in the case of saplings) in open microhabitats (Fig. C4.1B,C).

Statistical analyses

Between-habitats (*covered* vs. *open*) density differences were tested for the different regeneration stages, by means of independent Generalized Linear Models (GLM) for each stage, considering quasi-Poisson error distributions and *log* link functions. Analyses concerning seed availability, seedling emergence and seedling establishment were based in densities at sampling station scale, whereas those concerning sapling establishment used density estimated on a per-cell basis.

We compared the distribution of individuals across microhabitats (*covered*, *scrub* and *pasture*) between different stages by means of contingency tables and chi-square tests (for paired stages). We also compared the distribution of individuals of each stage with the availability of the microhabitats within the study plot (from the total frequencies of microhabitats across all sampling stations).

Our objective was to evaluate the role of avian seed dispersers in forest regeneration process, taking explicitly into account the influence of habitat characteristics on both the activity of birds and the different tree regeneration stages. For this purpose, we used Structural Equation Modeling (SEM, Grace 2006), which allows to evaluate complex (i.e. multivariate) relationships, including cascading effects, across parameters representing causal processes and consecutive patterns (e.g. habitat effects and regeneration stages). Structural equation models are initially built as saturated causal schemes, or path diagrams, representing all potential causal links between different predictors and response variables, based on previous knowledge of the ecological system. Path analysis enables to measure both direct and indirect effects between variables across the whole scheme. Direct effects are represented by links between consecutives predictor and response variables, and measured by standardized partial regression coefficients between them. Indirect effects are calculated as the sum of the products of all standardized partial regression coefficients over all paths between non-consecutive predictor and response variables.

We primarily sought to represent the effect of avian seed dispersal on forest regeneration process across the whole habitat loss gradient. For this purpose, we constructed independent models for studying factors influencing, on the one hand, the emergence of seedlings from different cohorts and, on the other hand, the recruitment of saplings (as saplings were not assignable to a particular cohort). In the first case, the path model of each cohort (2009 and 2010) included emerged seedling and seed densities, abundance of birds and habitat characteristics (forest cover, big tree presence, fruit abundance and scrub cover) on a per-cell basis (220 chess-board cells subset). In the second case, the path model included densities of emerged seedlings (averaged between cohorts), established seedling (averaged between cohorts) and established saplings and habitat characteristics (forest cover, big tree presence, fruit abundance and scrub cover) on the same per-cell basis ($N = 220$).

Moreover, we were interested in evaluating the role of avian seed dispersal in forest recolonization, i.e. tree recruitment in deforested habitat. For this purpose, we repeated the above models but only considering data of tree regeneration stages obtained from stations in open microhabitats. We only incorporated in these models those cells presenting, at least, four and two stations in open microhabitats for, respectively, the seed and seedling samplings (N = 183 cells). No big trees appeared within these cells, and thus this variable was excluded for these models.

We considered possible alternatives to the saturated model by constructing nested models sharing the same causal structure. Final models were chosen on the basis of Akaike Information Criterion (AIC). The fit of each model to the data was assessed using a likelihood χ^2 value, with non-significant values indicating fit between model and the data. To avoid the effects of deviations from multivariate normality in both parameter estimates and overall model χ^2 value, we applied Satorra-Bentler corrections (Satorra and Bentler 1994).

All analyses were performed by using R 2.15 (R 2013), with *lavaan* package for SEMs (Rosseel 2012).

Results

Habitat characteristics represented clear inverse gradients on their spatial templates (Fig. C4.2), with forest cover, big trees (only appearing within forest) and fruits appearing segregated from scrub spatial distribution. While the templates of bird abundance and the densities of seeds, emerged seedlings (almost identical than that of emerged seedlings) and established seedlings highly matched the gradient of habitat loss, sapling establishment template appeared as a combination of both forest and scrub gradients.

Table C4.1. Summary of the abundance of individuals in different tree regeneration stages (on white background) and the probability of transition between them (on gray background). The densities of seeds, emerged seedlings and established seedlings are shown for different study cohorts. Established sapling density corresponds to a single sampling. For all stages, the average values in the whole data set, and distinguishing between *covered* and *open* habitats, are shown ± standard error. Values for seeds and seedlings were calculated at the sampling stations scale while those for saplings at the cell scale. Transition probabilities were calculated as the rate of change in density of individuals between two consecutives regeneration stages, and expressed as a percentage. The probabilities of seedling emergence and seedling survival are shown for different study cohorts. Seedling-to-sapling survival was calculated by considering the averaged density of established seedlings between cohorts. For all transitions, the probability in the whole data set, and distinguishing between *covered* and *open* habitats, are shown.

Cohorts		**2009**	**2010**
Seeds/m^2		81.29 ± 13.75	43.89 ± 6.79
	covered	323.13 ± 24.76	160.29 ± 13.91
	open	5.32 ± 0.55	6.72 ± 0.68
Emergence		4.40%	12.46%
	covered	3.81%	11.11%
	open	8.27%	15.48%
Emerged seedlings/m^2		3.58 ± 0.46	5.47 ± 0.57
	covered	12.31 ± 1.63	17.81 ± 1.90
	open	0.44 ± 0.07	1.04 ± 0.16
Seedling survival		43.57 %	32.90 %
	covered	44.59 %	33.86 %
	open	34.09 %	25.96%
Established seedlings/m^2		1.56 ± 0.21	1.80 ± 0.23
	covered	5.49 ± 0.77	6.03 ± 0.79
	open	0.15 ± 0.04	0.27 ± 0.06
Seedling-to-sapling survival		3.57%	
	covered	1.74%	
	open	19.05%	
Established Saplings/m^2		0.06 ± 0.004	
	covered	0.10 ± 0.010	
	open	0.04 ± 0.004	

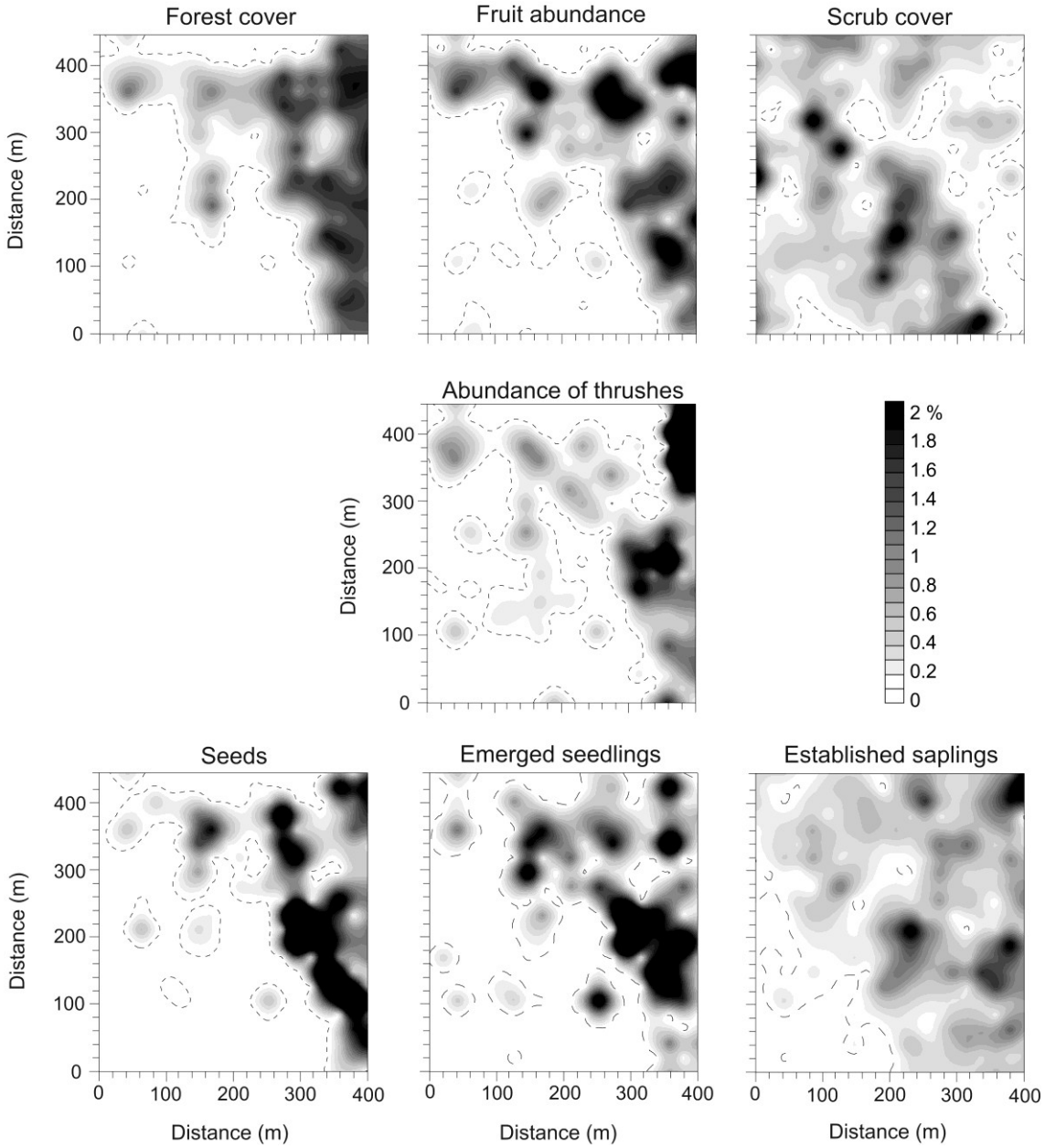


Fig. C4.2. Distribution of forest and scrub cover, the abundance of fruits, the abundance of thrushes and densities of seeds, emerged seedlings and established saplings in the study plot. Medium value of the two study years is represented for fruits, thrushes, seeds and emerged seedlings. Grey-scaled contours represent the percentage of the total sum of each variable in the plot accounted for by each cell. Dashed lines surrounding the minimum value considered (0.1%) and the grey scale are shown.

The density of the studied tree regeneration stages was different between habitats (GLM, $| t | > 5$ and $p < 0.0001$ in all cases), with all stages presenting higher densities in covered than in open habitat (Table C4.1). Their distributions across microhabitats differed significantly from that of microhabitat availability in the study plot ($\chi^2 > 5.99$, $p < 0.05$ in all cases). We also found different microhabitat distributions between stages, excepting when comparing those of dispersed seeds and established seedlings ($\chi^2 = 3.39$, $p = 0.18$; $\chi^2 > 5.99$, $p < 0.05$ in all other cases). The distributions of seeds, emerged seedlings, and established seedlings were strongly biased towards covered microhabitats, whereas a half of saplings appeared in open areas, with most of the standing within scrubs (Fig. C4.3). That happened even when covered and scrub where the least abundant microhabitats.

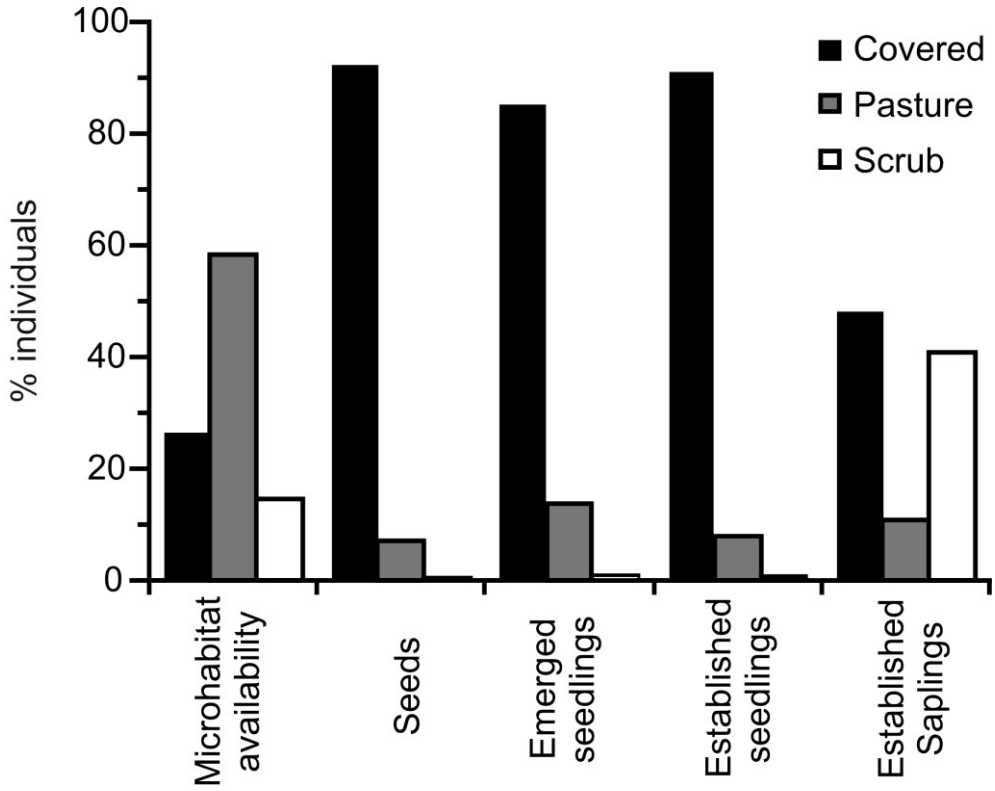


Fig. C4.3. Distribution of the percentage of individuals of each tree regeneration stage in different microhabitats. The availability of the microhabitats in the study plot is also shown.

The best-fit SEMs for seedling emergence included all considered predictors except scrub cover, while those for the sapling establishment included all considered predictors except fruit abundance, for both forest regeneration and recolonization models (Fig.C4. 4 and C4.5).

SEMs representing forest regeneration (i.e. those including the whole data set) did not find relationship between the abundance of thrushes and the density of seeds, which was directly affected by habitat characteristics of the cell (Fig. C4.4). Namely, forest cover and fruit abundance had direct positive influence in the density of seed in both cohorts, while big trees only showed direct, but negative effects in the 2009 cohort. These models also evidenced that the density of emerged seedlings was, in turn, directly influenced by both the density of seeds and forest cover. The density of established seedling was not directly influenced by habitat characteristics, being only related to the density of emerged seedlings. Contrastingly, the density of sapling establishment was unrelated to previous regeneration stages but positively influenced by forest and scrub cover. As judged by the values of the standardized path coefficients, forest cover influenced the most the variability in the densities of established saplings.

SEMs representing forest recolonization (i.e. those including the data from open sampling stations) revealed that, besides forest cover and fruit abundance, the abundance of thrushes had significant positive direct effects on the density of seeds. These effects on seed density cascaded into the density of emerged seedlings in open habitats, for both cohorts, as this response variable was unaffected by any environmental preditor (Fig. C4.5). Path structure for sapling establishment in open habitats was similar to that in the regeneration model, but with scrub cover as the main predictor of sapling density in these areas.

For a detailed breakdown of direct, indirect and total effects in SEMs see *Appendix C* (tables C.1 and C.2).

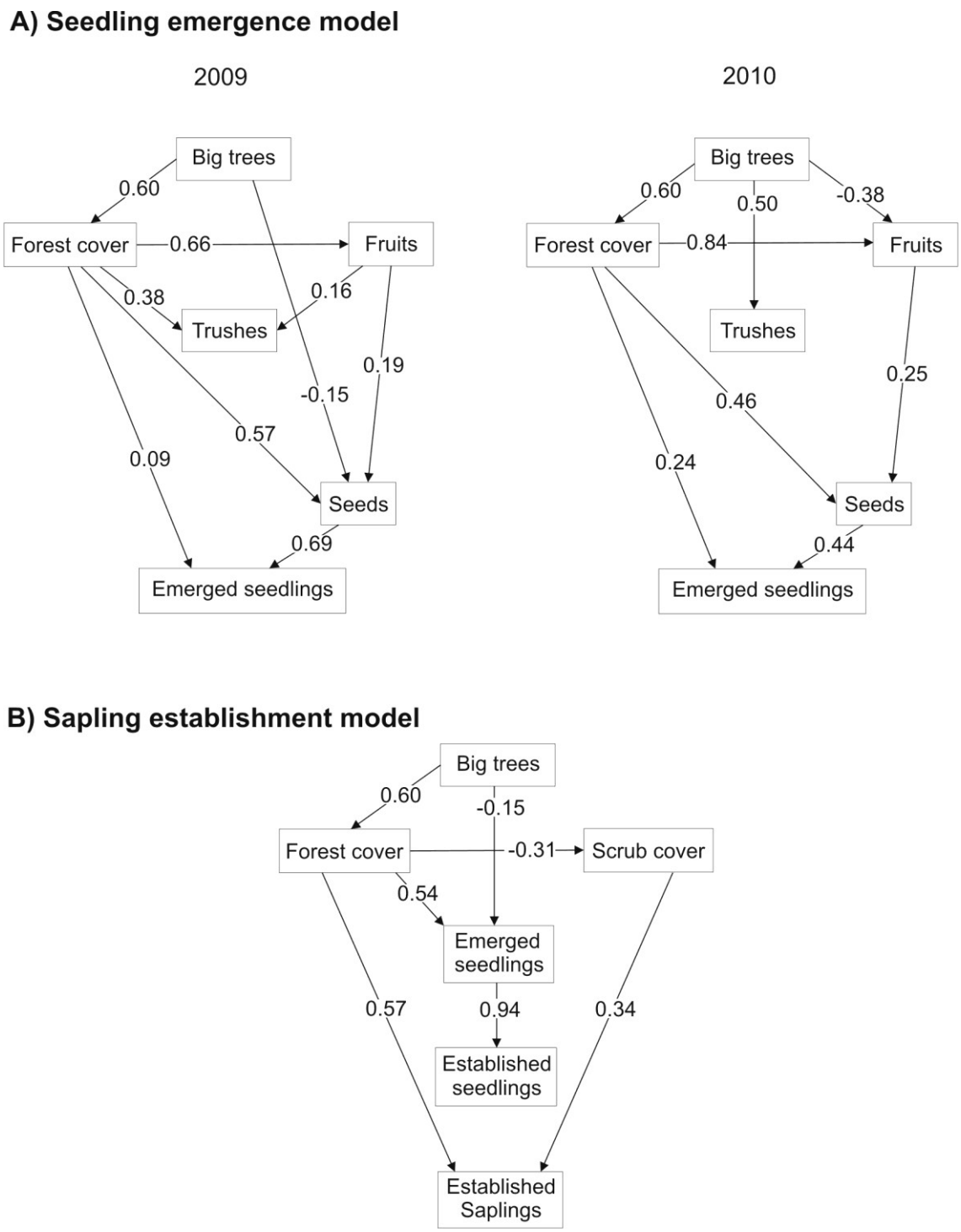


Fig. C4.4. Path diagrams of the best-fit structural equation models showing the effects of habitat characteristics and the abundance of thrushes on tree regeneration stages for the forest regeneration model (N = 220 cells). Values of standardized partial regression coefficients are shown. A) Models for habitat and avian seed disperser (Thrushes) influence on the densities of seeds and emerged seedling, for the studied cohorts. B) Model for habitat influence on the densities of established seedlings and saplings.

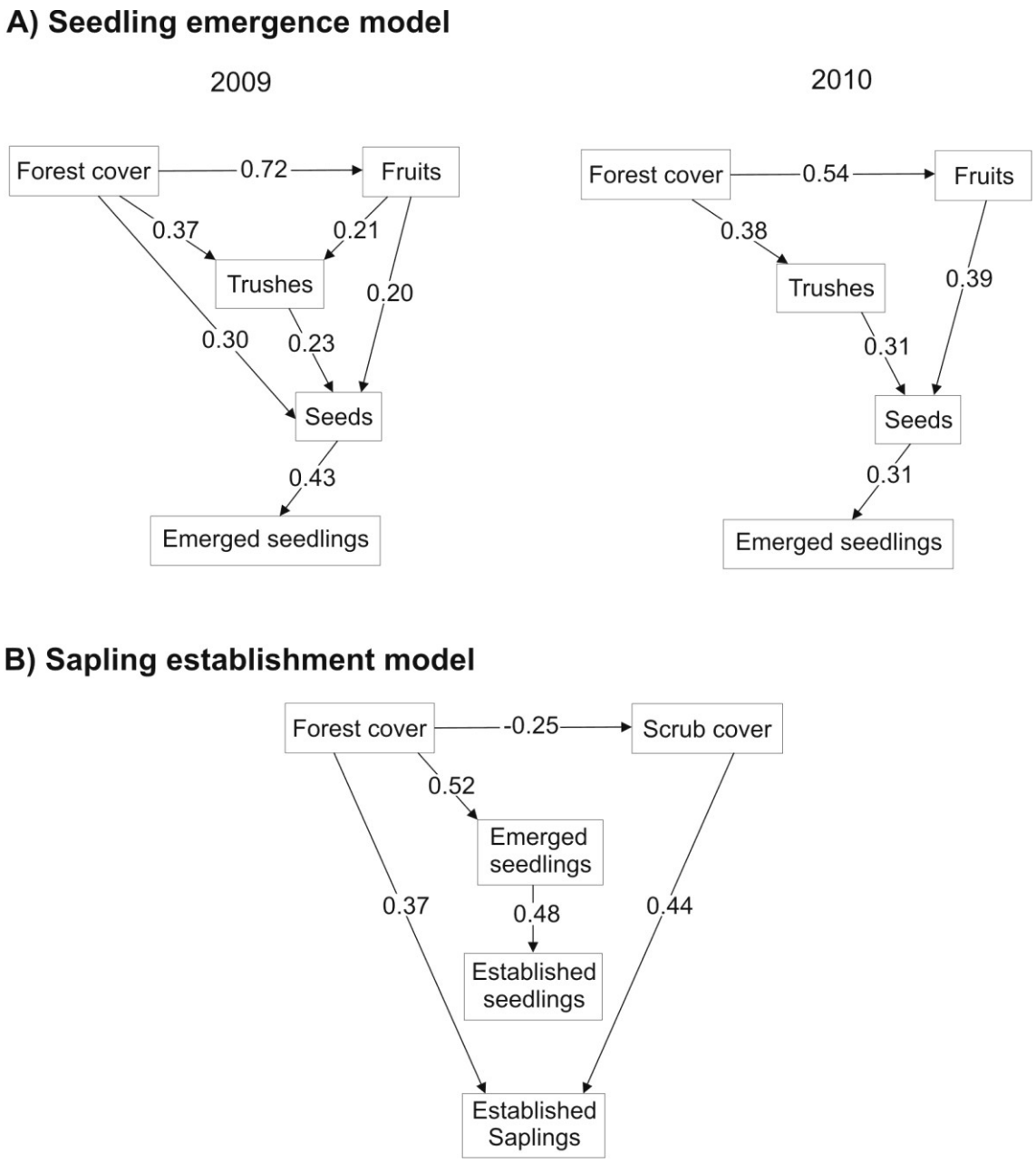


Fig. C4.5. Path diagrams of the best-fit structural equation models showing the effects of habitat characteristics and the abundance of thrushes on tree regeneration stages, for the forest recolonization model (N = 183 cells). Values of standardized partial regression coefficients are shown. A) Models for habitat and avian seed disperser (Thrushes) influence on the densities of seeds and emerged seedling, for the studied cohorts. B) Model for habitat influence on the densities of established seedlings and saplings.

Discussion

In this study we evaluated the demographic and spatial footprint of frugivorous birds on forest regeneration and recovery in a context of habitat loss. Habitat structure conditioned the effectiveness of frugivorous birds by influencing their distribution and, hence, the provision of seed dispersal service, through the landscape, but also by determining the fate of post-dispersal regeneration stages. Frugivores biased heavily early tree regeneration towards forested areas. Nevertheless environmental filtering on late regeneration stages altered the bird footprint equalizing, at the long term, the late tree recruitment magnitude between forest and deforested areas.

Forest regeneration

Habitat structure highly influenced the forest regeneration process when considered through the whole landscape. Forest cover favored regeneration by directly influencing different stages, but also indirectly by modifying other components of the system that are relevant for the regeneration process (Fig. 4; *Appendix C*, table C.1). Thus, even when most of the surface of the study area was deforested, tree regeneration stages appeared highly biased to forest areas.

Seed availability was concentrated under forest cover, strongly constraining the templates for the subsequent regeneration stages. This pattern was the result of trees providing seeds through fallen fruits, but also of bird activity being mainly nucleated within forest cover (Fig. C4.2 and C4.4). The spatial distribution of seed availability at the whole plot scale was independent of the variability in the abundance of birds. But this does not mean that birds do not contribute to tree regeneration, as they generated more than 50% of seed rain (data not shown), but that the number of birds *per se* is not enough for explaining the large-scale variability in tree regeneration. Birds would be foraging for longer periods in highly protected and fruit rich areas, leading to intense seed deposition independently of frugivore abundance (Fig. C4.2 and C4.4; García et al. 2010).

Even when an important demographic filtering took place during the seed-to-seedling transition, with emergence rates under 15% (Table C4.1), the spatial template of seed availability was the main predictor of the spatial patterns of seedling emergence (Fig. C4.4). It has been previously evidenced that the magnitude of seed predation by rodents is high in the studied tree species (García et al. 2005b,c) but it also has been found to be stronger under tree cover than in open areas (García et al. 2005c). Certain alteration of spatial patterns occurred during this transition, with a low increase of the relevance of regeneration in open areas (Table C4.1; Fig. C4.3), but the high concordance between regeneration stages suggests that the environmental constraints affecting seed survival were spatially more homogeneous than seed availability (Schupp and Fuentes 1995; García et al. 2005b). Between habitats differences in seed predation in the study years could have not being strong enough to alter the forest-sequestered regeneration pattern determined by the seed availability but, also, other environmental factors would be favoring germination within forest (Holl et al. 2000) counteracting the spatial bias generated by rodents. Mortality of seedlings during their first summer meant the lowest demographic loss through the regeneration cycle, with more than 25% of individuals surviving after that period (Table C4.1). Similar to what happened during seed-to-seedling transition, regeneration patterns resulting from the environmental filtering affecting seedling establishment did not depart from those determined by previous stages. Seedling establishment templates were highly concordant with spatial patterns of seedling emergence. In fact, the initial pattern of seed rain was recovered during seedling establishment, as the mortality of emerged seedlings was higher in open areas (Table C4.1; Fig. C4.3), probably due to competition with grasses and higher browsing in pastures (Holl et al. 2000).

On the contrary, seedling-to-sapling transition did not only mean a drastic decrease in the number of individuals, but also an alteration of forest-sequestered early regeneration templates. Sapling establishment patterns at the plot scale did not match established seedlings templates and, even when there was still a high

number of individuals under forest cover (Table C4.1), most of saplings appeared in open areas (Fig. C4.3). The fact that the sampled saplings did not belong to the same cohorts of early regeneration studied here could explain that mismatch. Nevertheless, the differences between stages in their distribution across microhabitats (Fig. C4.2 and C4.3) suggest the existence of a strong environmental filtering during late recruitment that decoupled the sampling template from that of seedlings. Sapling recruitment pattern could be explained by the influence of different filters in open and forested areas. Most saplings standing in deforested areas grew within scrubs (Fig. C4.3), and, as evidenced by SEMs, the large scale distribution of saplings mirrored that of scrub cover, two facts that suggest some kind of facilitation effect for saplings. Scrubs can have positive effect on tree recruitment by buffering the environmental stress associated to climate (e.g. summer drought; Holmgren et al. 1997; Gómez-Aparicio et al. 2004). This does not seem to be the case here, as summer drought is rare under the Atlantic climate conditions of our study site. Similarly to the role of other shrubs in our study system (García and Obeso 2003), scrubs would act as nurse plants for tree saplings by protecting them from intense browsing by ungulates, very abundant in the study site. Similarly to that happened in previous stages, forested areas showed the highest density of saplings, although sapling establishment rate was quite low there (under 2%, in contrast with 19% in open areas; Table C4.1). Even when browsing by ungulates is probably having detrimental effects within forest too, saplings presented lower damage levels in forest than in pastures (authors' personal observation). Thus, we consider that the main reason leading to a lower sapling recruitment rate in this habitat would be competition for light and/or nutrients with adult trees (Lewis and Tanner 2000; Dupuy and Chazdon 2006).

Recolonization of deforested areas

The influence of habitat structure in forest recolonization was quite similar to that found for regeneration across the whole plot, with forest cover and the abundance of fruits in the surroundings favoring tree recruitment in open areas

(Fig. C4.5). Noteworthy, a larger number of birds visiting open areas led to an increased seed deposition there (Fig. C4.5), as bird presence is infrequent in these areas and few trees act as seed sources there. As suggested for the forest regeneration process, the abundance of forest cover and fruits in the surroundings would entail longer stays of birds, contributing too to an increase seed deposition in pastures, irrespective of changes in bird number. Again, seedling establishment in deforested areas mirrored seedling emergence, while the distribution of sapling abundance was unrelated to that of seedlings but influenced by forest and scrub cover. Indeed, scrub cover was the most important predictor of sapling occurrence in the deforested areas, evidencing the importance of plant-plant facilitation for the recolonization process.

Frugivorous bird footprint

The activity of frugivorous birds in our study system, like in many other temperate and tropical ecosystems (Kollmaann and Pirl 1995; Duncan and Chapman 2002; García et al. 2010), is highly conditioned by forest cover, restricting their seed dispersal service to highly forested areas. Although this service could be spatially redundant with abiotic seed dispersal, birds provide a high-quality seed rain. In this sense, previous studies have evidenced that thrushes drop many seeds under low crop or even not fruited trees (Martínez et al. 2008), where density-dependent seed and seedling mortality is expected be lower (Harms et al. 2000). Frugivore-mediated seed movement through the forest landscape would favor gene flow within and between tree populations, a process especially relevant in fragmented landscapes, like the one under study (Jordano and Godoy 2002; Aguilar et al. 2008; García et al. 2009a). In addition, by feeding on different co-occurring fleshy-fruited species, birds promote multi-specific seed rain under mother trees (García et al. 2007), what would contribute to within-forest tree community dynamics (Harms et al. 2000; Levine and Murrell 2003). Even when the magnitude of demographic bird footprint decreases through seed-to-seedling transitions, seedling establishment keeps the initial bird-generated template (Fig. C4.2). Nevertheless, bird footprint is blurred

in the seedling-to-sapling transition. Unfavorable conditions for long-term survival under tree canopy would screen-off frugivore spatial effect within the forest, whereas ungulate browsing would filter tree recruitment in deforested areas, biasing survival to those saplings growing under the protective canopy of scrubs. Most of these saplings are indeed the demographic outcome of bird activity, as scrubs seldom receive seeds from fallen fruits (only when growing very close to fruiting trees), and saplings can be found even tens of meters away from any tree (Fig. C4.2).

Conclusions

Frugivorous bird abundance has been proposed as a surrogate of landscape-scale seed dispersal function for forest management and restoration programs (García et al. 2010). In this work, we widen this concept by considering the long-term demographic effect of avian seed dispersal through the whole tree recruitment process, evidencing that frugivore effectiveness can be seriously compromised by post-dispersal environmental filters. Our study demonstrates that, in a context of forest loss, forest habitat features are the best predictors of tree regeneration through the whole landscape, but bird abundance is still an effective surrogate of tree recolonization in deforested landscape sectors. More importantly, passive restoration of these deforested lands will be conditioned by the presence of nurse scrubs within pastures. Conserving populations of frugivorous birds would be necessary for maintaining remnant forests and their associated ecosystem services. But this will not be enough if we aim to recover these services by passively restoring the lost forest. For that purpose it will also be necessary to favor the characteristics of the system contributing to reduce seed dispersal limitation (Holl et al. 2000; Duncan and Chapman 2002; Cavallero et al. 2013) together with those promoting the overcome of restriction to establishment (nurse scrubs in our study system).

Discusión general

Al actuar como dispersoras de semillas, las aves frugívoras desempeñan un papel clave en el proceso de regeneración de los sistemas forestales, y con ello proveen un importante servicio ecosistémico (Sekercioglu 2006; Whelan et al. 2008; Wenny et al. 2011). Este hecho las convierte en organismos de especial interés para programas de conservación e incluso recuperación de sistemas forestales degradados (Wunderle 1997; Lundber y Moberg 2003; Cavallero et al. 2013). Pero, cualquier acción de manejo o gestión de dicho servicio ecosistémico debe de estar basada en un conocimiento adecuado de los procesos ecológicos que lo determinan (Kremen 2005). Es necesario entender cómo las aves contribuyen al proceso de regeneración forestal, bajo qué factores ambientales, y cuál es el alcance del servicio. Además esta información debe de provenir de los propios sistemas degradados, ya que en ellos el funcionamiento ecosistémico puede estar seriamente alterado y, por ello, los conocimientos desde los sistemas prístinos no son necesariamente extrapolables.

Los resultados de esta tesis doctoral demuestran la importancia del servicio prestado por las aves frugívoras en un paisaje forestal degradado. Las aves son fundamentales para el mantenimiento de los remanentes de bosque y, además, su contribución resulta determinante para desencadenar el proceso de recolonización en áreas deforestadas. La estructura del hábitat condiciona la actividad y el servicio de dispersión de los frugívoros en este sistema degradado. Sin embargo, los resultados obtenidos evidencian que las restricciones impuestas por el hábitat, según son descritas por los paradigmas actuales, pueden mostrar una importante variabilidad. La respuesta adaptable de los frugívoros ante la heterogeneidad espacio-temporal del ambiente (resultante de la degradación del hábitat forestal y la variación interanual de los paisajes de fructificación) permite que su huella se expanda por gran parte del paisaje. Así mismo, el uso de una aproximación integradora ha permitido revelar los factores que condicionan la efectividad de las aves como proveedoras del servicio ecosistémico, ofreciendo información relevante para lograr una adecuada conservación y manejo del mismo.

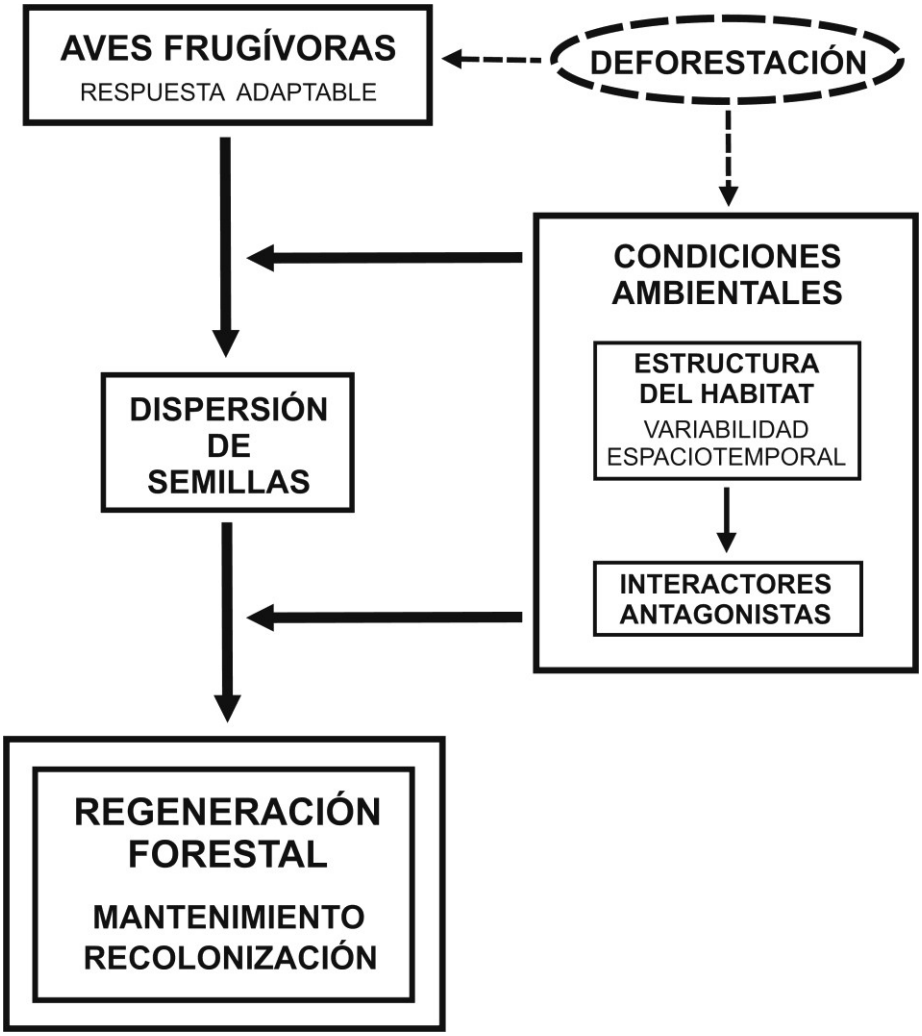


Fig. D.1. Diagrama que muestra los factores que condicionan el proceso de regeneración forestal mediado por las aves frugívoras estudiados en los diferentes capítulos de la tesis.

Condicionantes ambientales sobre las aves

El sistema estudiado en esta tesis doctoral no es una excepción en cuanto a los principales factores que condicionan la actividad de las aves frugívoras. Estudios previos han descrito que la actividad de los zorzales está muy influenciada por la disponibilidad de alimento y protección. Estas aves prefieren permanecer en áreas de bosque denso con frutos abundantes (García et al. 2010; García y Martínez 2012; García et al. 2013), y es allí donde se alimentan principalmente (García y Chacoff 2007; Morales et al. 2013). Por ello, la lluvia de semillas que generan aparece concentrada, en su mayor parte, bajo árboles con frutos en el interior del bosque (García et al. 2010; Herrera y García 2010; García y Martínez

2012; Carlo et al. 2013; García et al. 2013; Morales et al. 2013), y muy pocas semillas alcanzan las áreas degradadas (García y Martínez 2012; Carlo et al. 2013; García et al. 2013; Morales et al. 2013). Este condicionamiento por parte de la cobertura con frutos ha sido descrito de forma generalizada en sistemas forestales tanto templados como tropicales y por ello es considerado como un paradigma en el proceso de dispersión de semillas por aves (Herrera 1985; Holl et al. 2000; Nathan y Mueller-Landau 2000; Duncan y Chapman 2002; Carlo y Morales 2008; García et al. 2010; McConkey et al. 2012; Sasal y Morales 2013). De este paradigma se deduce que el papel de las aves en la regeneración forestal, aunque de suma importancia, muestra un alcance limitado debido a que su área de influencia en el paisaje se encuentra muy restringida (Cardoso da Silva et al. 1996; Wunderle 1997; Holl et al. 2000; Duncan y Chapman 2002). Sin embargo, por medio de una aproximación crítica a este paradigma, los resultados obtenidos revelan que cobertura y frutos pueden presentar mayor variabilidad como condicionantes de la dispersión de lo considerado. A continuación se expone cómo el condicionamiento que ambos factores ambientales imponen muestran variaciones tanto espaciales como temporales que permiten que el potencial de regeneración determinado por las aves, a partir de la lluvia de semillas que generan, alcance gran parte del paisaje.

Variabilidad espacial

La heterogeneidad que muestra el sistema forestal degradado determina que las aves frugívoras se enfrenten a configuraciones del paisaje en las que la disponibilidad de frutos y cobertura forestal pueden aparecer segregadas en el espacio (Fig. I.7, C3.2 y C4.2). La respuesta de las aves a esta segregación supondrá un importante compromiso, teniendo que elegir entre obtener alimento y disponer de protección. El estudiar el efecto simultáneo de frutos y cobertura forestal en el uso del hábitat por las aves en un sistema degradado ha permitido revelar un alto grado de adaptabilidad comportamental de las aves ante estas situaciones. Las aves son capaces de enfrentarse a estos escenarios, y la escasez de uno de estos dos factores en un área del paisaje puede ser compensada, en

términos de abundancia de aves, en parte, por una alta disponibilidad del otro (Capítulo 1). Así, las aves permanecen en áreas de cobertura forestal densa con escasos frutos y, más importante aún, son capaces de superar su reticencia a visitar las áreas con pocos árboles si allí encuentran suficiente cantidad de frutos como recompensa (Capítulos 1 y 3).

La heterogeneidad a escala fina determinada por los vecindarios multi-específicos de frutos influye también en la actividad trófica de las aves. La disponibilidad de frutos de diferentes especies en el entorno inmediato de un árbol concreto condiciona su magnitud de interacción con las aves frugívoras. Así, árboles situados en entornos con abundancias totales de frutos y cobertura semejantes no contribuirán por igual a la lluvia de semillas debido a la identidad de sus vecinos (Capítulo 2; Carlo et al. 2007; Blendinger et al. 2012). Estas desigualdades creadas por las aves determinan la aparición de interacciones indirectas de facilitación y competencia entre las especies arbóreas, con importantes repercusiones potenciales en la estructuración de la comunidad forestal (Hubbell et al. 2001; Wang and Smith 2002; Carlo et al. 2007). Pero más aún, estas variaciones en la visita de los frugívoros a árboles concretos, también se traducirán en diferencias en la abundancia de semillas que reciban bajo su dosel (Carlo et al. 2007; Rodríguez-Pérez et al. 2014).

En cualquier caso, la respuesta de las aves a la heterogeneidad espacial a distintas escalas contribuye a aumentar la variabilidad de la lluvia de semillas dentro del bosque, haciendo que no sólo provenga y se concentre bajo aquellos árboles situados en áreas con más cobertura y frutos. El efecto de los dispersores se distribuirá entre diferentes árboles, incluso aquellos situados en zonas de escasa producción de frutos o parcialmente deforestadas (Herrera y García 2009). Así, esta heterogeneidad espacial, además de afectar a los patrones de lluvia de semillas dentro del bosque, también contribuye a la llegada de semillas a áreas degradadas. La fragmentación de la cobertura forestal y la variabilidad espacial en los paisajes de fructificación determinan que para poder buscar recursos a lo

largo del paisaje las aves crucen, o incluso se detengan, en la matriz deforestada, lo que propicia la deposición de semillas en el hábitat abierto (Capítulo 3; Cardoso da Silva et al. 1996; García y Martínez 2012; García et al. 2013). Todo ello determina que la huella de las aves frugívoras se expanda en relación a lo esperable en función de la cobertura forestal, ampliando su distribución a lo largo del paisaje (Capítulos 1, 2 y 3).

Variabilidad temporal

A diferencia de la heterogeneidad espacial, que es resultado de la pérdida de bosque y de diferencias entre especies arbóreas en la producción de frutos, la variabilidad temporal aquí estudiada atañe exclusivamente a la fructificación, y es debida a diferencias entre especies e individuos en ciclos interanuales de producción y vecería. Cada otoño, las aves frugívoras encuentran importantes cambios tanto en la distribución espacial de los frutos en el paisaje (Capítulo 3; Herrara y García 2009; García et al. 2013), como en la abundancia total de frutos (Capítulo 1), e incluso en la aportación relativa de las diferentes especies (Capítulos 2 y 3; García et al. 2013). Ante estas fluctuaciones en los paisajes de fructificación, las aves frugívoras cambian entre años sus patrones de actividad a escala paisajística (Capítulos 1, 2 y 3). Las aves frugívoras se enfrentan a los cambios en la distribución espacial de los frutos gracias a su capacidad de rastreo de recursos (Rey 1995; Saracco et al. 2004; Tellería et al. 2008). Por lo tanto, estas variaciones en los patrones de fructificación llevan a que las aves visiten, con distinta frecuencia, diferentes áreas del paisaje en distintos años (García et al. 2013). Las variaciones en la disponibilidad de frutos a escala amplia también pueden alterar el condicionamiento que este factor ejerce sobre el uso del hábitat por parte de las aves frugívoras. En años en que el alimento es abundante por todo el paisaje, las aves no se ven tan condicionadas por la disponibilidad de frutos y su área de influencia en el paisaje se expande (Capítulo 1).

Las variaciones en disponibilidad y distribución espacial de los frutos, y en la contribución relativa de las distintas especies fructificantes, influyen

también en la actividad de las aves alterando los vecindarios ecológicos de frutos multiespecíficos. Al optimizar su actividad en respuesta a la composición de estos vecindarios, las aves cambian de un año a otro el reparto de la frugivoría entre árboles individuales. Más aún, esta optimización altera los balances de facilitación/competencia intra- e inter-específica entre los diferentes árboles (Capítulo 2), significando una importante variabilidad para la contribución de las aves a la estructuración de la comunidad forestal. Cómo es esperable, esta respuesta adaptable de las aves a la heterogeneidad temporal en los paisajes de fructificación se traduce en cambios interanuales en la composición y la estructura de la lluvia de semillas dentro del bosque (García et al. 2013; Rodríguez-Pérez et al. 2014).

La variabilidad temporal en los paisajes de fructificación también puede alterar los patrones de lluvia de semillas en áreas deforestadas, al contribuir a relajar el condicionamiento impuesto por la cobertura forestal. En esta tesis se sugiere que en años en que los pequeños rodales de bosque y los árboles aislados producen tantos o más frutos que los rodales forestales grandes, las aves visitan las áreas degradadas con mayor frecuencia (Capítulo 3). Un seguimiento a largo plazo del sistema de estudio evidencia que los cambios en la actividad de los frugívoros en relación a la variación en el paisaje de fructificación, y sus consecuencias en la dispersión de semillas, son un fenómeno que ocurre de forma recurrente. Así, para una serie de ocho años consecutivos (2004-2011) de muestreo de la abundancia y distribución de frutos en el sistema estudio, se detectaron, en cinco ocasiones, paisajes con fructificación fuertemente concentrada en los grandes rodales forestales, y en tres ocasiones, paisajes con fructificación mucho más repartida entre bosque y matriz deforestada. En estos tres años, se encontraron evidencias comparables de una mayor actividad –y un mayor servicio ecológico- de los frugívoros en la matriz deforestada (Tabla D.1). Durante estos eventos, el secuestro de la cobertura forestal sobre la deposición de semillas se relaja (Capítulo 3; Herrera et al. 2011; Rodríguez-Pérez et al. 2014), y un mayor número de semillas llega a zonas de escasa cobertura (Herrera y García

2009) e, incluso, a las áreas deforestadas (Capítulo 3; García et al. 2013). Además, la mayor frecuencia de visita de los frugívoros a las áreas degradas del paisaje altera la distribución espacial de las semillas, ya que son dispersadas a mayor distancia del bosque (Capítulo 3), aumentando el área de influencia del potencial de recolonización (Fig. C3.4).

Condicionamiento ambiental post-dispersivo

Las aves frugívoras actúan como desencadenantes del proceso de regeneración al dispersar las semillas de los árboles, pero esto no asegura que su aporte inicial se traduzca en una contribución efectiva (Schupp et al. 2010). Los frugívoros podrían estar dispersando semillas a áreas en las que su supervivencia, o la de las plantas que se generan a partir de ellas, se encuentren comprometidas (Schupp y Fuentes 1995; Nathan y Mueller-Landau 2000; Schupp et al. 2010). Los resultados de esta tesis muestran que la huella final de las aves en el proceso de regeneración difiere de la inicialmente esperada. Tras la dispersión, menos del 0,1% de los propágulos de árboles alcanza el estadio juvenil (Tabla C4.1). Durante este proceso no sólo disminuye el potencial global de regeneración, sino que también se ven alterados sus patrones espaciales, ya que actúa un filtrado ambiental discordante con el que moldea la actividad de las aves y los patrones de dispersión consecuentes (Capítulo 4; Schupp y Fuentes 1995). Aunque la degradación ambiental también tiene efectos adversos en la regeneración durante los estadios post-dispersivos, finalmente la aportación de las aves contribuye, de forma determinante, tanto al mantenimiento de los remanentes forestales como a la recolonización de las áreas deforestadas.

Los resultados obtenidos evidencian que el filtrado post-dispersivo sobre la regeneración de árboles en los bosques secundarios cantábricos difiere del descrito en otros bosques ibéricos, también dominados por especies zoócoras. Así, a diferencia de lo que ocurre en bosques mediterráneos (Gómez-Aparicio et al. 2004; González-Varo et al. 2012; Puerta-Piñero et al. 2013), el

Año	Abundancia frutos	Distribución espacial de los frutos	Efectos en el proceso de dispersión de semillas	Fuente
2004	Alta	Concentrada en bosque	Abundancia de semillas depositadas bajo árboles aislados mucho menor que bajo árboles en bosque.	Herrera y García 2009
2005	Alta	Repartida entre bosque y pastos	Abundancia de semillas depositadas bajo árboles aislados semejante a bajo árboles en bosque.	Herrera y García 2009
2006	Alta	Concentrada en bosque	*Kernel* de dispersión fuertemente dependiente de la cobertura de bosque.	Herrera et al. 2011
2007	Baja	Repartida entre bosque y pastos	Abundancia de aves menos agregada espacialmente. Disminución de influencia de cobertura en la lluvia de semillas. *Kernel* de dispersión dependiente de la abundancia de frutos. Lluvia de semillas menos agregada espacialmente. Mayor aparición de semillas en áreas deforestadas.	Herrera et al. 2011 García et al 2013 Capítulo 2
2008	Baja	Concentrada en bosque	Abundancia de aves muy dependiente de cobertura de bosque.	García et al. 2013 Capítulos 1 y 2
2009	Alta	Concentrada en bosque	Abundancia de aves y lluvia de semillas muy dependiente de cobertura de bosque. Fuertes efectos de vecindario ecológico en dispersión dentro del bosque.	García et al. 2013 Rodríguez-Pérez et al. 2014 Capítulos 1, 2, 3 y 4
2010	Alta	Repartida entre el bosque y los pastos	Relajación de efectos de vecindario ecológico en dispersión dentro del bosque. Mayor proporción de aves visitando árboles aislados. Mayor proporción de semillas dispersadas a áreas deforestadas. Semillas en áreas deforestadas dispersadas a sectores del paisaje con menor cobertura remanente y más lejos con respecto a ella.	Rodríguez-Pérez et al. 2014 Capítulos 1, 3 y 4
2011	Alta	Concentrada en bosque	Abundancia de aves muy dependiente de cobertura de bosque.	Capítulo 1

Tabla D.1. Síntesis de resultados de diferentes trabajos de investigación basados en datos recogidos en la localidad de estudio entre los años 2004 y 2011. Para cada año se muestra la abundancia de frutos en el paisaje (Alta > 15 frutos/m^2) así como sus patrones de distribución espacial, diferenciando entre aquellos años en que la producción de frutos estuvo principalmente concentrada en las áreas de bosque denso y aquellos en que la distribución fue más homogénea por todo el paisaje, como resultado de una mayor importancia relativa de la fructificación de árboles aislados en los pastos. Se muestran los efectos de la variación en la configuración espacial del paisaje de fructificación en la distribución de aves frugívoras y la dispersión de semillas. Mientras que en 2004, 2008, 2009 y 2011 la producción de frutos estuvo dominada por el acebo, en 2005, 2007 y 2010 la especie dominante fue el espino. Durante 2006 la contribución de ambas especies a la producción total fue similar.

establecimiento de las plántulas no es el mayor cuello de botella demográfico a largo plazo. En el área Cantábrica, con clima de influencia atlántica, la sequía estival tiene escasa incidencia en la supervivencia de las plántulas recién emergidas (*observación personal*). Es durante el periodo que lleva al establecimiento de los juveniles cuando se da el mayor filtrado ambiental de la huella de las aves frugívoras. Este filtrado, al tiempo que supone una disminución drástica del potencial de regeneración creado por las aves, también altera sus patrones de distribución en el paisaje (Fig. C4.1 y C4.2). Condiciones adversas para el establecimiento en el interior del bosque (para procesos similares ver Lewis y Tanner 2000; Dupuy y Chazdon 2006), unidas al efecto nodriza de los matorrales en las áreas degradadas -que protegen a las plántulas frente a los herbívoros- determinan finalmente que la escasa huella inicial de las aves en estas áreas se magnifique en los patrones finales de reclutamiento. La distribución de los juveniles establecidos (con una mortalidad inferior al 3%; Capítulo 4) es un buen indicador de la que tendrán los futuros árboles adultos en este sistema. Los juveniles que sobreviven dentro del bosque contribuirán al mantenimiento de los remanentes forestales, mientras que los que crecen en las áreas deforestadas, constituirán el frente de recolonización del bosque.

Aunque los resultados de esta tesis no profundizan en la variabilidad temporal de la regeneración a largo plazo, es esperable que las variaciones entre cohortes en el filtrado ambiental durante las fases post-dispersivas (García et al. 2005b; Herrera y García 2010) se reflejen en los patrones espaciales de reclutamiento. En cualquier caso, es también esperable que gran parte de las variaciones temporales en los patrones espaciales de regeneración sean el resultado directo de la importante variabilidad interanual de la lluvia de semillas (ver sección anterior).

Síntesis

La variabilidad espacio-temporal descrita para este sistema será responsable, en gran medida, de la escala a la que actúa el servicio ecosistémico de las aves frugívoras. La regeneración forestal no ocurre de manera inmediata, si no que hay una importante demora desde la aportación inicial hasta que se genera la nueva cobertura forestal. El servicio final será el resultado de la aportación acumulada durante múltiples años consecutivos y que, por lo tanto, incorporará la variabilidad espacio-temporal intrínseca del sistema. La adición combinada de los diferentes patrones anuales de regeneración determinará un potencial global que alcanza a extenderse por el paisaje más que cada uno de los patrones individuales por separado. La figura C4.2 muestra cómo la distribución espacial de los individuos juveniles en la parcela de estudio aparece más extendida por el paisaje que la de los estadios de regeneración previos, ocupando la casi totalidad del área de estudio. Esta discordancia, además de ser resultado directo de diferencias en la influencia del hábitat en los distintos estadios (Schupp y Fuentes 1995), también refleja el hecho de que los juveniles son el resultado acumulado de la actividad de las aves durante múltiples años, y no de las dos cohortes concretas estudiadas para los otros estadios. La suma de los diferentes patrones anuales contribuirá, así mismo, a la diversidad de la comunidad forestal. En distintos años la lluvia de semillas proviene de árboles diferentes (Capítulo 2) lo que favorece la diversidad genética de las poblaciones de plantas (Aldrich y Hamrick 1998). Además ocurren variaciones en la diversidad de las especies que

son dispersadas cada año (Capítulos 2 y 3; García et al 2013) y en su lugar de deposición (a qué microhábitat; Capítulo 3; Rodríguez-Pérez et al. 2014), promoviendo una mayor riqueza a escala de paisaje.

La heterogeneidad espacio-temporal del sistema propicia que la regeneración del bosque se mantenga en este paisaje degradado y que incluso pueda recolonizar las áreas deforestadas. Esta fuente de resiliencia es el resultado de la acción conjunta de diferentes componentes del sistema (Nÿstrom y Folke 2001). Tanto la variabilidad espacial como la temporal de los paisajes de fructificación son el resultado directo de que el bosque esté compuesto por distintas especies de árboles productores de fruto. Aunque todas las especies muestran vecería, ésta no está sincronizada entre ellas (Capítulo 2; García et al. 2013). Esto determina que la producción de frutos, aunque varíe en magnitud, permanezca por encima de unos niveles mínimos todos los años (atrayendo a las aves) y que además aparezca distribuida en diferentes áreas del paisaje cada año. En este sistema, los árboles que permanecen en la matriz deforestada son, en su mayoría, espinos, quizás por un proceso de tala selectiva o por mayor tolerancia al ramoneo. Es esta especie, pues, la que actúa principalmente como legado biológico en las áreas degradadas, propiciando la salida de frugívoros fuera del bosque, y la que genera los episodios esporádicos de incremento del potencial de recolonización (Capítulo 3; Tabla D.1, Nyström y Folke 2001; García et al. 2013). Las aves frugívoras desempeñan un papel fundamental en la resiliencia del sistema al actuar como vínculos móviles (Lundberg y Moberg 2003; Kremen et al. 2007). Son capaces de mantener el funcionamiento ecosistémico en el paisaje degradado, conectando diferentes parches e incluso desencadenando el proceso de recolonización en las áreas deforestadas (Fig. I.1). La complementariedad de respuesta de las diferentes especies de aves ante la degradación forestal es también un factor importante para que el servicio se distribuya a lo largo de diferentes sectores paisaje cada año (Santos et al. 1999; Lehouck et al. 2009; García y Martínez 2012; Morales et al. 2013). A pesar de esta complementariedad, todas las especies muestran una respuesta común ante

las variaciones espaciotemporales de los paisajes de frutos, incluso aquellas consideradas frecuentemente forestales como el zorzal común (Rey 1995; Rey 2011; García et al. 2013). Esta respuesta común es la que determina el acoplamiento entre el paisaje de fructificación y los patrones espaciales de regeneración en las zonas deforestadas. Por último, sin los matorrales actuando como estadio sucesional intermedio, no sería posible la recolonización forestal en las áreas degradadas.

Recomendaciones de manejo

Los ecosistemas forestales suponen importantes beneficios para el bienestar humano (Myers 1997; Chazdon 2008), pudiendo incluso contribuir a paliar los efectos adversos del Cambio Global (Bonan 2008). Por ello, conservar los bosques remanentes y propiciar la recuperación de las masas forestales perdidas resulta de suma importancia. En la región Cantábrica, se estima que los bosques montanos, entre los que se encuentran los bosques secundarios de estudio, ocupan en la actualidad menos de un 23% de su área potencial (García et al. 2005a). Los remanentes forestales se encuentran, además, altamente empequeñecidos y aislados entre sí, siendo este proceso de fragmentación especialmente evidente en el sistema de estudio. Los resultados de esta tesis muestran cómo los zorzales contribuyen a la resiliencia (i.e. mantenimiento a largo plazo y recolonización) de las acebedas-espineras cantábricas en los ambientes degradados. Por ello, todo plan de conservación de estos sistemas forestales debe considerar, de forma explícita, la conservación de estas aves. La presión cinegética, especialmente importante en las especies invernantes, debe de ser controlada. Diversos estudios sugieren que los movimientos migratorios de los zorzales europeos parecen encontrarse en proceso de retracción, debido a que parte de sus poblaciones permanecen durante el otoño y el invierno en el norte de Europa, o hacen sólo migraciones de corta distancia (Rivalan et al. 2007; SEO/Birdlife 2012). Este proceso, asociable al calentamiento global, puede tener importantes repercusiones tanto para las acebedas-espineras cantábricas cómo para otros sistemas forestales del centro y sur de Europa, en los que los zorzales

son importantes dispersores (p.eg.: Herrera 1984; Snow y Snow 1988; Alcántara et al. 1997; Guitián et al. 2000; García 2001; Rumeu et al. 2008; González-Varo 2010).

El proceso de despoblamiento rural, con el consiguiente abandono de áreas agrícolas y ganaderas, puede ser una buena oportunidad para permitir una recuperación significativa de superficie forestal y con ello incrementar los servicios de los bosques (Chazdon 2008; Rey Benayas et al. 2009; Navarro y Pereira 2012). La consideración de planes de restauración pasiva o asistida (i.e. basados en un nivel bajo de intervención) puede ser de gran utilidad para dinamizar, a bajo coste, la recuperación de estos bosque. Ha de considerarse que la restauración pasiva del sistema tendrá efecto a largo plazo, ya que el proceso de recolonización es lento y tiene limitaciones. Planes de restauración asistida pueden ser más adecuados si se quiere aumentar y acelerar el proceso (Rey Benayas et al. 2008; Holl y Aide 2011). Así, además de medidas para la conservación de las aves, el plantar pequeños grupos de árboles de fruto carnoso en las áreas degradadas puede contribuir a atraer frugívoros y, en consecuencia, semillas (Duncan y Chapman 2002; Rey Benayas et al. 2008; Corbin y Holl 2012). Si estos grupos son multi-específicos, se propiciará además la producción continuada de frutos en distintos años y mayor constancia en su efecto de atracción. Pero estas medidas tendrán poca relevancia si no se considera también el papel de los matorrales nodriza. Los grupos de árboles deberían establecerse áreas del paisaje con abundantes matorrales que posibiliten que la aportación de las aves al proceso de restauración se haga efectiva. Por ello también deben de considerarse los brezos y otros matorrales como un objetivo de conservación. Es frecuente que estos arbustos prosperen en aquellas áreas del paisaje que han sufrido una disminución de la presión ganadera, o en las que pastos de siega y tierras de cultivo han sido abandonados. En la actualidad, el manejo de estas áreas se basa principalmente en rozas del terreno y subvenciones a las explotaciones ganaderas para evitar la matorralización, y así mantener un paisaje dominado por pastos. Una vía alternativa a la actividad ganadera deficitaria

podría ser el permitir, o incluso propiciar, la recuperación de la superficie forestal en estas áreas, aumentando así los servicios producidos por el bosque. En el caso en que las tierras no sean de propiedad pública (i.e. que no sean pastos comunales) esta práctica se podría ver incrementada con el pago de incentivos a aquellos propietarios que realicen un manejo del territorio que ayude a recuperar la superficie forestal (Sierra y Russman 2006; Wunder 2007; Pagiola 2008).

Las recomendaciones propuestas para el sistema de estudio tienen un alto potencial de extrapolación a otros sistemas forestales templados, e incluso tropicales, en los que el proceso de recolonización forestal está formado por un frente de avance de especies de árboles o arbustos dispersados por vectores animales (McDonell y Stiles 1983; Herrera 1984; Clout y Hay 1989; Debussche y Lepart 1992; McClanahan y Wolfe 1993; Kollmann 1995; Holl et al. 2000; Duncan y Chapman 2002; García et al. 2010; Cavallero et al. 2013; Suárez-Esteban et al. 2013). Incluso en aquellos sistemas como los mediterráneos, en los que la sequía estival es uno de los principales cuellos de botella para el ciclo de regeneración, la conservación de los arbustos que actúan como plantas nodriza resultará también clave (Castro et al. 2002; Gómez-Aparicio et al. 2004).

Líneas futuras de estudio

Esta tesis doctoral deja frentes abiertos para futuros estudios. Los diferentes capítulos se basan en estudios realizados en una única localidad. Sin embargo, sería necesario corroborar si las conclusiones de estos trabajos son extrapolables a diferentes localidades o si distintas configuraciones del paisaje determinan alteraciones en el servicio prestado por las aves frugívoras. Considerando localidades con diferente estructura en la cobertura forestal a escala de paisaje se podría comprobar si la distribución que muestran los parches forestales en el paisaje condiciona la magnitud de la dispersión de semillas fuera del bosque y, con ello, el proceso de recolonización. Dado que hay un importante efecto de la distancia a la cobertura condicionando este proceso de dispersión (Capítulo 3), sería esperable que para distintos paisajes con similar cantidad de bosque

remanente, haya una mayor regeneración en aquellos que muestren mayor conectividad para las aves (Manning et al. 2009). Esta información podría ser de utilidad para diseñar planes de restauración asistida, optimizando la distribución de los grupos de árboles a plantar en el paisaje. Una aproximación a escala geográfica también permitiría ver si el proceso de filtrado post-dispersivo condiciona de manera diferente la efectividad de las aves en distintas localidades (Fedriani et al. 2004; García et al. 2005b). Sería de especial interés ver cómo variaciones en la carga ganadera pueden afectar al proceso de recolonización forestal. Mientras que las metodologías empleadas en esta tesis serían adecuadas para mostrar las variaciones en regeneración entre localidades, el uso de series de datos y fotografías aéreas históricas sería de gran utilidad para evidenciar los cambios en el paisaje a lo largo del tiempo.

En esta tesis no se ha considerado la aportación que los mamíferos a la restauración del sistema. Aunque su papel como dispersores de las especies arbóreas aquí estudiadas no es equiparable al de las aves frugívoras, sí son importantes para otras especies arbóreas y arbustivas (López-Bao y González Varo 2011; Peredo et al. 2013). Además, parecen tener un papel complementario al de las aves tanto en las especies que dispersan como en el tipo de microhábitat dónde las dispersan, ya que las depositan preferentemente en hábitats abiertos (Peredo et al. 2013). Sería necesario estudiar cuál es la efectividad de los mamíferos como dispersores viendo qué destino sufren las semillas. Es probable que las especies arbóreas presenten las mismas limitaciones para su regeneración en hábitats abiertos que las dispersadas por las aves, pero, al dispersar también especies arbustivas que suelen ser pioneras (como la zarza y rosa), podrían estar contribuyendo a potenciar la aportación posterior de las aves.

Conclusiones

1. La actividad de las aves frugívoras, dispersoras de árboles de fruto carnoso en el bosque secundario cantábrico, depende de la cobertura forestal y la abundancia de frutos a escala de paisaje. Existe una interacción entre las limitaciones que la cobertura forestal y la abundancia de frutos imponen al uso del hábitat de las aves. La escasez de uno de los factores puede ser parcialmente compensada por niveles altos de disponibilidad del otro.

2. La producción de frutos por parte de diferentes especies en el vecindario ecológico de un árbol condiciona la frugivoría por aves en dicho árbol. La actividad de las aves al alimentarse en vecindarios de frutos multi-específicos determina la aparición de interacciones indirectas recíprocas entre las especies arbóreas de fruto carnoso.

3. La aparición y la reciprocidad de las interacciones indirectas entre árboles de fruto carnoso medidas por aves frugívoras muestran importantes inconsistencias temporales. La respuesta de las aves ante la variabilidad temporal de los paisajes de fructificación altera los balances de facilitación/competencia entre plantas.

4. Existen importantes restricciones a la dispersión de semillas por aves hacia áreas deforestadas. Una proporción reducida de las semillas es dispersada fuera del bosque y su distribución espacial está condicionada por la cobertura forestal remanente. La magnitud de la dispersión disminuye drásticamente a medida que aumenta la pérdida de hábitat, y al alejarse del bosque.

5. Cambios en los paisajes de fructificación pueden alterar los patrones de dispersión de semillas por aves en las áreas deforestadas. Un aumento de la producción de frutos en las áreas degradadas del paisaje incrementa la actividad de las aves en estas áreas. Como consecuencia de ello, una mayor proporción de

semillas es dispersada fuera del bosque, llegando a áreas con mayor grado de deforestación y a mayor distancia con respecto al bosque.

6. La estructura del hábitat condiciona la efectividad de las aves como dispersoras de semillas de árboles, al afectar a los estadios post-dispersivos. El potencial de regeneración determinado por la lluvia de semillas disminuye drásticamente a lo largo de las diferentes transiciones entre estadios demográficos. La discordancia entre la influencia de la estructura del hábitat en los patrones de lluvia de semillas y la que tiene en los patrones de regeneración post-dispersiva altera la huella espacial de las aves.

7. La presencia de matorrales actuando como nodrizas, protegiendo de los herbívoros a las plántulas establecidas de los árboles ornitócoros, es determinante para la recolonización del bosque en las áreas deforestadas.

8. La aportación de las aves dispersoras de semillas al ciclo de regeneración forestal tiene un papel relevante en el mantenimiento de los remanentes de bosque, y resulta fundamental para desencadenar la recolonización de áreas deforestadas.

9. Los bosques secundarios cantábricos presentan un elevado potencial para recolonizar áreas deforestadas. Si se quiere propiciar la expansión de estos bosques son necesarias medidas para conservar las poblaciones de aves dispersoras, para incrementar su actividad en las áreas deforestadas, así como para preservar los matorrales nodriza.

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Apéndices

Appendix A

Additional description of the estimation of forest cover around focal trees in Chapter 2

In the study plot, the total extent of forest cover at landscape scale remained constant throughout the study period (2007-2009), as no tree losses from logging, fires or other large-scale disturbances occurred, and tree fall from natural causes affected less than 0.1% of standing trees (*authors personal observation*). Focal trees were arbitrarily chosen throughout the entire plot each year in an attempt to represent a similar gradient of neighborhood forest cover between years. The identity of the focal trees selected for sampling changed from one year to another because some failed to fruit every season. We thus considered a scenario in which the amount of forest cover around focal trees remained constant across years, but varied between different focal trees.

We explicitly analyzed the between-year variations in forest cover at both R15 and R15-40 by using Generalized Linear Models (GLMs), with a Normal error distribution and a Log link function. Independent analyses were performed for each focal species. Based on measurements of the mean and dispersion values of the amount of forest in the neighborhood of focal trees (Fig C2.2), our study design assured that the spatial gradient of forest cover in the neighborhood of focal trees was equally broad across study years. Moreover, forest cover remained constant, on average, across study years, as no between years differences were found in the forest cover around either species at R15 or R15-40 neighborhood scales (GLM: $\chi^2 > 2.92$, $N = 48$, for all tests).

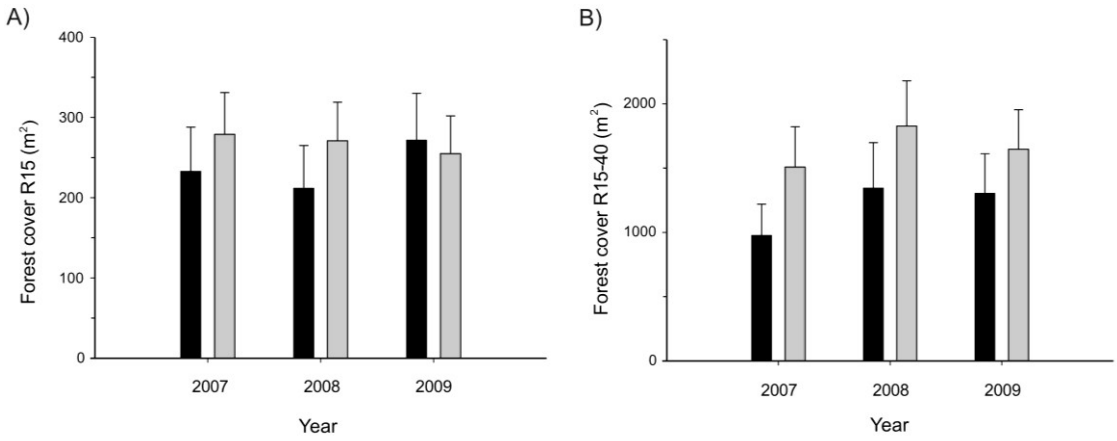

Figure A.1. Mean forest cover (m^2) ± SE in the concentric areas, at A) 15 m (R15) and B) 15 to 40 m (R15-40) radii, chosen to represent ecological neigborhoods around *Crataegus monogyna* (black bars) and *Ilex aquifolium* (gray bars) focal trees (*N* = 16).

Appendix B

Distributions of frequencies of sampling stations with respect to forest cover descriptors

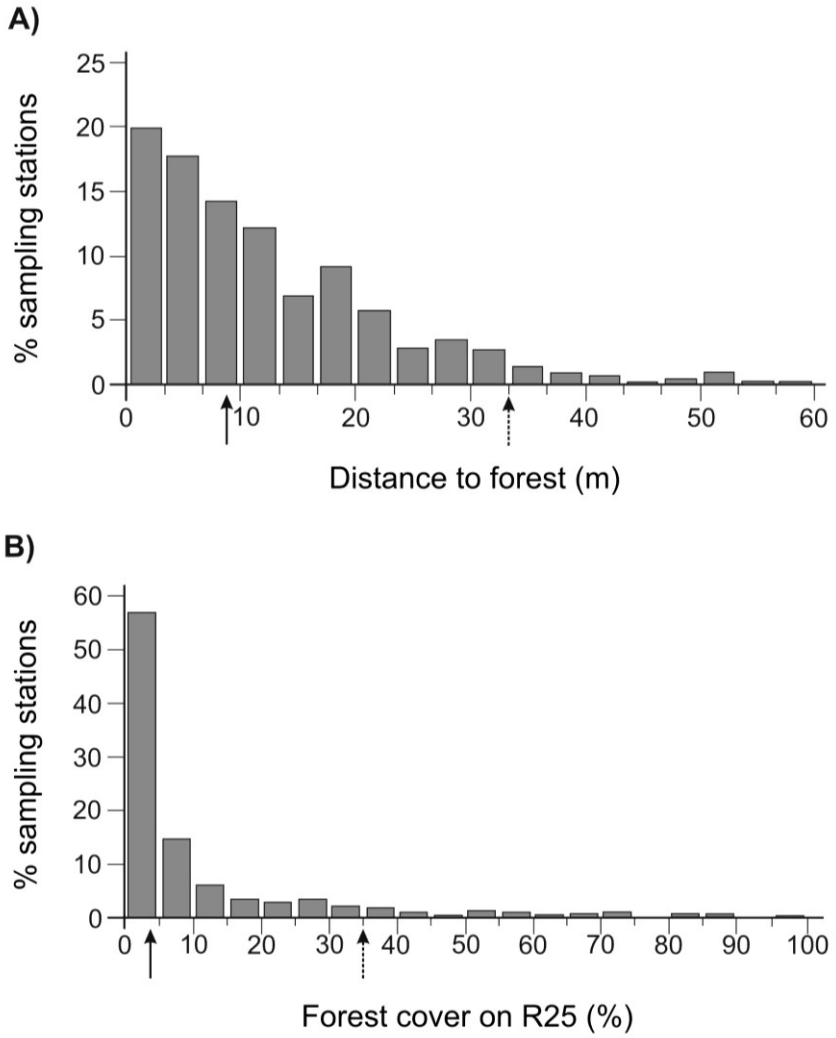

Fig. B.1. Distribution of sampling stations located in pastures along the gradient of forest cover on the study plot. A) Percent of sampling stations in different categories considering their distance to the forest edge. B) Percent of sampling stations in different categories considering the percent of forest cover within a 25 m radius (R25) surrounding each station. Values of the median and the 90th percentile of each distribution have been highlighted on the x axis with solid- and dashed arrows respectively.

Appendix C

Direct, indirect and total effects estimated in Structural Equation Models in Chapert 4.

Table C.1. Direct, indirect and total effects in the SEMs for the forest regeneration model. Direct effects are standardized path coefficients (see Fig. c4.4). Indirect effects are computed as the sum of products of the coefficients along all of the possible routes from the predictor to the response variable. Total effects are the sum of direct and indirect effects. A) Effects of habitat characteristics, the abundance of thrushes and seed availability in density of emerged seedlings, for 2009 and 2010 cohorts. B) Effects of landscape characteristics and density of emerged seedlings in densities of established seedlings and established saplings. Effects in gray tone indicates $p = 0.1$.

A) Seedling emergence model

		2009			2010		
Response	Predictor	Direct	Indirect	Total	Direct	Indirect	Total
Seeds	Big trees	-0.15	0.41	0.26	—	0.03	0.03
	Forest cover	0.57	0.12	0.69	0.46	0.21	0.67
	Fruits	0.19	—	0.19	0.25	—	0.25
	Thrushes	—	—	—	—	—	—
Emerged seedlings	Big trees	—	0.19	0.19	—	0.28	2.28
	Forest cover	0.09	0.48	0.57	0.24	0.29	0.53
	Fruits		0.13	0.13	—	0.11	0.11
	Thrushes	—	—	—	—	—	—
	Seeds	0.69	—	0.69	0.44	—	0.44

B) Sapling establishment model

Response	Predictor	Direct	Indirect	Total
Established seedlings	Big trees	—	0.30	0.30
	Forest cover	—	0.51	0.51
	Scrub cover	—	—	—
	Emerged seedlings	0.94	—	0.94
Established saplings	Big trees	—	0.26	0.26
	Forest cover	0.57	-0.13	0.44
	Scrub cover	0.34	—	0.34
	Emerged seedlings	—	—	—
	Established seedlings	—	—	—

Table C.2. Direct, indirect and total effects in the SEMs for the forest recolonization model (containing only data from regeneration in open microhabitats). Direct effects are standardized path coefficients (see Fig. C4.5). Indirect effects are computed as the sum of products of the coefficients along all of the possible routes from the predictor to the response variable. Total effects are the sum of direct and indirect effects. A) Effects of habitat characteristics, the abundance of thrushes and seed availability in the density of emerged seedlings, for 2009 and 2010 cohorts. B) Effects of landscape characteristics and density of emerged seedlings in densities of established seedlings and established saplings.

A) Seedling emergence model

		2009			2010		
Response	Predictor	Direct	Indirect	Total	Direct	Indirect	Total
Seeds	Forest cover	0.30	0.27	0.57	—	0.33	0.33
	Fruits	0.20	0.05	0.25	0.39	—	0.39
	Thrushes	0.23	—	0.23	0.31	—	0.31
Emerged seedlings	Forest cover	—	0.24	0.24	—	0.09	0.09
	Fruits	—	0.11	0.11	—	0.10	0.10
	Thrushes	—	0.10	0.10	—	0.08	0.08
	Seeds	0.43	—	0.43	0.25	—	0.25

B) Sapling establishment model

Response	Predictor	Direct	Indirect	Total
Established seedlings	Forest cover	—	0.25	0.25
	Scrub cover	—	—	—
	Emerged seedlings	0.48	—	0.48
Established saplings	Forest cover	0.37	-0.11	0.26
	Scrub cover	0.44	—	0.44
	Emerged seedlings	—	—	—
	Established saplings	—	—	—

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La investigación presentada en esta Tesis Doctoral se ha desarrollado en el Departamento de Biología de Organismos y Sistemas de la Universidad de Oviedo.

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