UNIVERSITAT DE BARCELONA

The role of species niche, species dispersal and landscape factors in the assembly of novel woody communities in metropolitan Mediterranean regions

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"The role of species niche, species dispersal and landscape factors in the assembly of novel woody communities in metropolitan Mediterranean regions"

Memoria presentada por Nancy Gamboa Badilla para optar al grado de Doctora
por la Universitat de Barcelona, programa de Biodiversitat,
con la aprobación del Dr. Joan Pino Vilalta Director de Tesis.

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Índice general

Índice de tablas

Índice de figuras

1. Introducción general

Cambio de usos del suelo y ensamblaje de nuevas comunidades

Los cambios ambientales inducidos por el hombre están provocando graves amenazas sobre la biodiversidad a escala global (Vitousek 1994; Sala et al. 2000). Así, la mayoría de los ecosistemas mundiales han sufrido cambios en su estructura, composición, funcionamiento o dinámica por la actividad humana en mayor o menor medida (Vitousek et al. 1997; Sanderson et al. 2002). Entre los diversos componentes de este cambio global de origen antrópico destaca por su carácter indicador el cambio en los usos y las cubiertas del suelo (Wickham et al. 2000; Lambin et al. 2001; Pereira & Cooper 2006; Gerard et al. 2010). Sin embargo, sus efectos sobre la biodiversidad son muy diferentes, por un lado, es responsable de la pérdida de gran número de hábitats, con la consiguiente extinción de especies (Sala et al. 2000), mientras que por el otro genera oportunidades para la aparición de nuevas comunidades y ecosistemas, y con ellos el establecimiento y la expansión de determinadas especies tanto nativas como exóticas (Hobbs et al. 2006, 2009).

Esta antropización del paisaje, con cambios en la cubierta y el uso del suelo, conlleva un proceso de ensamblaje de las comunidades de plantas, del cual surgen importantes cuestionamientos tales como ¿Qué factores intervienen en el ensamblaje de especies en una comunidad? ¿Estos cambios de origen antrópico en el paisaje pueden afectar a los mecanismos de ensamblaje de las comunidades bióticas? Es obvio que los cambios en la biodiversidad condicionan y son condicionados por el funcionamiento de los ecosistemas y por diversos factores abióticos (Loreau et al. 2001). A pesar de ello, los mecanismos que estructuran la mayor parte de dichas comunidades no están todavía bien identificados, lo que limita las posibilidades de respuesta y reduce las capacidades de gestión ante los riesgos planteados por el cambio global (Zavala 2004). Tradicionalmente se han propuesto dos aproximaciones para explicar el ensamblaje de las comunidades bióticas: modelos de nicho y neutros (Tilman 2004). Los modelos de nicho se fundamentan en el equilibrio de la competencia por los recursos y la segregación o exclusión ecológica, donde la diversidad y heterogeneidad del hábitat puede permitir que las especies coexistan (MacArthur & Levins 1967; Chase & Leibold 2003; Tilman 2004). Por su parte, los modelos neutros se fundamentan en los patrones de dispersión de las especies y en factores estocásticos, lo cual supone que las especies son ecológicamente equivalentes en sus respuestas a los condicionantes ambientales, por lo que la diversidad podría predecirse a partir del equilibrio entre la especiación y la extinción por reducciones en el tamaño de las poblaciones (Bell 2001; Hubbell 2001, 2006; Tilman 2004). La importancia relativa de los procesos de nicho o neutros en el ensamblaje de las comunidades depende de complejos factores ecológicos y evolutivos que favorecen o dificultan la coexistencia de especies ecológicamente equivalentes (Leibold & McPeek 2006).

En este contexto, el componente espacial toma una gran relevancia, pues influye en la dinámica del ensamblaje de las comunidades, condicionando los procesos de extinción y colonización (Bell 2001; Leibold & McPeek 2006; Ricklefs 2008). Por ello resulta necesario considerar la escala de paisaje para entender este ensamblaje de las comunidades, tanto en lo que respecta a la riqueza como a la composición de especies. Los patrones de extinción y colonización asociados a los cambios en los hábitats, sean inmediatos o diferidos, se ven afectados por la estructura espacial histórica y actual del paisaje, lo cual tiene influencia sobre la diversidad de las especies y la conectividad entre los diversos fragmentos de hábitat. Ésta facilita la dispersión efectiva de los diversos organismos, creando poblaciones regionales más grandes y persistentes (Hanski 1999); además, mantienen una mayor riqueza de especies, pues se induce la colonización y las tasas de extinción se ven disminuidas posiblemente por un efecto de rescate (Brown & Kodric-Brown 1977; Lindborg & Eriksson 2004). Por otra parte, luego de una alteración en la estructura del paisaje, los sitios conectados mantendrían mayor diversidad, lo que podría determinar efectos diferidos sobre la riqueza de especies (Eriksson 1996; Lindborg & Eriksson 2004).

Desfases entre los cambios en los hábitats y la sustitución de especies: deudas de extinción y créditos de colonización

Por otra parte, los efectos de los cambios ambientales sobre el ensamblaje de las comunidades pueden no ser inmediatos. Lo que podría resultar en asincronías entre el momento de la perturbación, como es el caso de los cambios en las cubiertas, los usos del suelo y la estructura del paisaje, y los efectos sobre la extinción y la colonización de las especies (Jackson & Sax 2010). Por ejemplo, los efectos conocidos del deterioro, la reducción y el aislamiento de los hábitats sobre la rarefacción y extinción local de especies (p.e. Loreau et al. 2001; Bierregaard 2001), pueden manifestarse mucho tiempo después de la aparición de estas presiones (Eriksson 1998; Dupouey et al. 2002; Lindborg & Eriksson 2004; Vellend et al. 2006), lo que ha venido a denominarse deuda de extinción (Tilman et al. 1994; Kuussaari et al. 2009). Un efecto de dicha deuda sobre las comunidades bióticas es que la riqueza de especies sea temporalmente mayor de lo esperado en términos de área y conectividad (Hermy & Verheyen 2007; Krauss et al. 2010; Piqueray et al. 2011). Esta situación podría causar extinciones futuras (en el momento en que se restablezca la relación especies-área inicial), aunque las especies tienen la capacidad de responder ante estos cambios en función de sus atributos biológicos y ecológicos, así como por su capacidad de dispersión desde poblaciones vecinas (Eriksson & Ehrlén 2001; Jacquemyn et al. 2003; Flinn & Vellend 2005; Lindborg et al. 2005, 2011; Kuussaari et al. 2009; Krauss et al. 2010; Bagaria et al. 2012). La identificación de las deudas de extinción en la naturaleza es determinante para precisar la capacidad que tienen los paisajes para mantener la biodiversidad, así como aproximar el tiempo que podrían tardar las poblaciones y comunidades en alcanzar el equilibrio con una estructura dada de paisaje después de la perturbación. Por su parte, evaluar el cambio histórico del paisaje se torna relevante para predecir la afectación en la distribución de especies debida a posibles cambios futuros en el uso del suelo (Vellend et al. 2006).

El caso opuesto a la deuda de extinción es la asincronía entre el surgimiento o formación de nuevos hábitats y el establecimiento de nuevas especies, denominada crédito de inmigración o de colonización (Hanski 2000; Cristofoli et al. 2010; Jackson & Sax 2010). Durante este tiempo de desfase, las nuevas manchas de hábitat muestran una riqueza de especies inferior a la esperada por su área y conectividad (Piqueray et al. 2011). En resumen, los cambios en los hábitats a escala de paisaje conllevan una notable incertidumbre en el ensamblaje de las comunidades. Un desafío interesante es analizar el balance entre los créditos de colonización y las deudas de extinción cuando ocurren de forma simultánea, dando lugar a excedentes o déficits temporales de especies según sea la importancia de cada uno de estos procesos (Jackson & Sax 2010; Cristofoli et al. 2010; Piqueray et al. 2011; Bagaria et al. 2015).

Invasión por especies exóticas en hábitats antropizados

Los ecosistemas resultantes de la acción humana, inmersos en paisajes altamente transformados, están frecuentemente modelados por nuevas reglas de ensamblaje y poseen composiciones de especies que no han ocurrido previamente dentro de un bioma determinado (Vitousek et al. 1997; Levine et al. 2003; Hobbs et al. 2006). En los denominados nuevos ecosistemas, gran parte de las colonizaciones pueden ser protagonizadas por estas especies (Vilà & Ibáñez 2011). Estudios recientes muestran la importancia de la estructura y la dinámica del paisaje en la invasión de estos nuevos hábitats por especies exóticas (Vilà et al. 2003; Pino et al. 2006; DeGasperis & Motzkin 2007), sugiriendo que la invasibilidad de los hábitats por estas especies se asocia a la fluctuación de recursos y al régimen de perturbaciones (Vilà et al. 2007; Chytry et al. 2008; Pyšek et al. 2010), pero que a su vez es modulada por el paisaje circundante. Así, hábitats naturales y seminaturales situados en paisajes muy antropizados presentan mayores invasiones que grandes áreas naturales continuas (Guirado et al. 2006; McKinney 2006), debido principalmente a la presión de propágulo asociada a la actividad humana y a una mayor frecuencia de perturbaciones que generan “ventanas de oportunidad” para el establecimiento de las nuevas especies (Vilà & Ibáñez 2011).

Por otra parte, muchos trabajos constatan que los cambios en la estructura y la composición del paisaje a lo largo del tiempo favorecen la invasión por especies exóticas en hábitats muy diversos (Doménech et al. 2005; Pino et al. 2006; DeGasperis & Motzkin 2007; Vilà & Ibáñez 2011). En general, los hábitats más inestables son los que registran un mayor grado de invasión por especies exóticas, aunque de nuevo, se observan asincronías entre estos cambios y la colonización y establecimiento de las nuevas especies. Este fenómeno se ha denominado crédito o deuda de invasión (Vilà & Ibañéz 2011; Essl et al. 2015; Clotet et al. 2016).

El cambio en las cubiertas y usos del suelo de las regiones metropolitanas mediterráneas: efectos sobre el ensamblaje de comunidades

La Europa mediterránea ha sufrido importantes cambios en las cubiertas y usos del suelo durante los últimos siglos, lo anterior fruto de los cambios socioeconómicos acaecidos (Debussche et al. 1999; Alados et al. 2004; Gerard et al. 2010; Parcerisas et al. 2012). Especialmente en el último siglo, como consecuencia de la intensificación agrícola en las zonas llanas y fértiles y el éxodo rural hacia las ciudades, los cultivos y los pastos de las zonas menos accesibles se han reducidoe notablemente y están siendo colonizados por nuevas formaciones leñosas (Gerard et al. 2010; Basnou et al. 2013). Esto está comportando la proliferación de nuevos bosques y matorrales, así como la desaparición de los mosaicos agroforestales tradicionales en muchos paisajes mediterráneos, con consecuencias notables sobre la biodiversidad (Preiss et al. 1997; Petit et al. 2001; Lambin & Meyfroidt 2011). Así, la superficie forestal en España ha aumentado notablemente durante la segunda mitad del siglo XX (Kauppi et al. 2006). Trabajos recientes sitúan en un 25% la proporción de bosques aparecidos en el último medio siglo como consecuencia de este cambio de usos del suelo en algunas regiones (Basnou et al. 2013).

Así pues, los paisajes mediterráneos europeos se caracterizan por la existencia de bosques y matorrales de formación relativamente reciente. Consecuentemente, en medio de este proceso surgen preguntas respecto a los factores que determinan el ensamblaje de dichas comunidades. Estudios previos realizados en plantas de bosques templados destacan el papel de la dispersión en el proceso de ensamblaje de los nuevos bosques más allá de su condición ecológica (Hermy & Verheyen 2007). Honnay et al. (2002), indican que la colonización por plantas de las nuevas manchas de bosque depende en gran medida de su conectividad, dado que en su investigación se mostró cómo paisajes altamente conectados (42% de cobertura forestal) presentaron mayor éxito de colonización que paisajes con baja conectividad (7% cubierta forestal). Por tanto, cambios en la estructura del paisaje, derivados de la fragmentación del hábitat, afectan a las especies forestales más sensibles, reduciendo su probabilidad de dispersión entre parches (Saunders et al. 1991; Meffe & Carroll 1994; Hanski 1999; Guirado et al. 2007). En este contexto, los bosques antiguos juegan un papel muy importante como fuentes de propágulo, incidiendo en la recuperación de la diversidad de especies vegetales en los bosques recientemente originados (Jacquemyn et al. 2003; Vellend 2003).

Hasta hace poco tiempo existía escasa información sobre la estructura, composición y la dinámica de estos nuevos bosques mediterráneos, a diferencia de lo que ocurre en los ecosistemas boreales o templados (Honnay et al. 2002; Svenning et al. 2009). En la actualidad, se tiene un cierto conocimiento de los patrones de distribución espacial y de la estructura de dichos bosques, así como de su riqueza y composición de plantas leñosas (Guirado et al. 2007, 2008; Basnou et al. 2016). A escala local, se ha observado que los nuevos bosques están asociados a áreas relativamente llanas y hasta tiempos recientes deforestadas, que en algunos casos tienen un clima menos adecuado para el crecimiento del bosque (Basnou et al. 2013, 2016). A pesar de ello, estos nuevos bosques presentan biomasas medias similares a las de los bosques preexistentes e incluso tasas de crecimiento netamente superiores (Vilà-Cabrera et al. 2015), lo que sugiere condiciones locales (topografía, profundidad de suelo, etc.) favorables para su crecimiento, en gran parte a causa de que muchos de estos bosques se asientan sobre antiguos cultivos o pastos. Por otra parte, algunos estudios recientes en dichos bosques muestran la existencia de créditos de colonización para el conjunto de plantas forestales (Bagaria et al. 2015), así como para especies leñosas dispersadas por vertebrados (Basnou et al. 2016).

El componente metropolitano

Finalmente, conviene destacar que muchos de estos bosques y matorrales se recuperan en paisajes metropolitanos, caracterizados por su elevada transformación antrópica. En este caso, el cambio de usos y cubiertas del suelo es especialmente complejo, puesto que se combina la urbanización de las zonas más bajas y accesibles con el abandono agrícola y posterior aforestación en las zonas marginales, como ha ocurrido en la región metropolitana de Barcelona (Basnou et al. 2013). El resultado de este proceso es la aparición de un paisaje dual en el que las nuevas áreas urbanas entran frecuentemente en contacto con los bosques y matorrales preexistentes, así como con los resultantes de la aforestación. Ello ha comportado cambios en la riqueza y composición de especies de dichos hábitats (Brotons & Herrando 2001; Guirado et al. 2007; Basnou et al. 2015). En particular, la proximidad a las áreas habitadas determina un aumento notable de las perturbaciones y de la presión de propágulo de las especies de tendencia antropófila, tanto nativas como exóticas, sobre estas formaciones forestales (Guirado et al. 2006, 2007; Basnou et al. 2015; Clotet et al. 2016; González-Moreno et al. 2013b). Todavía se desconoce en gran medida cómo estas presiones pueden afectar al ensamblaje de las comunidades forestales metropolitanas. En el caso de las plantas, se sabe que las perturbaciones de origen antrópico crean oportunidades para la colonización y expansión de especies exóticas de carácter pionero (Pino et al. 2013), si bien dichas condiciones favorables tienden a remitir con el avance de la sucesión, lo que conlleva la expulsión de estas especies de la comunidad. No obstante, el efecto de dichas perturbaciones puede prolongarse durante décadas, dando lugar a una especie de deuda de extinción en dichas invasiones (González-Moreno et al. 2017). Por otro lado, muchas especies exóticas de uso ornamental y frecuentes en las áreas urbanizadas adyacentes son propias de fases más avanzadas de la sucesión y son efectivamente diseminadas por vertebrados, por lo que pueden colonizar formaciones forestales menos alteradas y persistir e incluso medrar en dichas condiciones (Martin et al. 2009).

Hipótesis de investigación

En este escenario nos planteamos avanzar en el conocimiento de los patrones de ensamblaje de las comunidades de plantas en bosques y matorrales aparecidos en el área metropolitana de Barcelona durante el último siglo. Se plantean las siguientes hipótesis generales:

1. El grado de transformación antrópica de los paisajes metropolitanos puede determinar cambios importantes en los patrones de ensamblaje de las nuevas comunidades leñosas que albergan, con una disminución de las especies propias de dichas comunidades y un aumento de las especies antropófilas, tanto nativas como exóticas, en relación a las comunidades preexistentes.

2. Los cambios históricos del paisaje pueden haber dejado su huella en el proceso de ensamblaje de estas nuevas comunidades, con efectos diferidos (deudas de extinción y créditos de colonización) sobre la riqueza y composición de especies.

3. El establecimiento y propagación de gran parte de las especies pueden estar fuertemente condicionados por la dispersión de sus propágulos por parte de los vertebrados, los cuales pueden responder a determinados patrones de paisaje.

Objetivos generales

Dichas hipótesis generales se abordan de manera conjunta en tres capítulos con los siguientes objetivos concretos:

1. Analizar el efecto del legado histórico de cambios de uso del suelo en los patrones de ensamblaje en matorrales, en términos de estructura, riqueza y composición de especies (*Capítulo 3)*.

2. Evaluar el efecto de la antropización del paisaje, especialmente la urbanización, sobre el proceso de ensamblaje de las comunidades vegetales en los nuevos bosques periurbanos (*Capítulo 4*).

3. Analizar los patrones de invasión por plantas exóticas y la influencia del mecanismo de dispersión, las variables ambientales y la antropización del paisaje en estos mismos bosques periurbanos de reciente formación (*Capítulo 5*).

2. Zona de estudio y conjuntos de datos utilizados

La zona de estudio

La investigación realizada en este documento de tesis se ha desarrollado dentro de la provincia de Barcelona en Cataluña (NE de España). Dicho territorio presenta un notable gradiente climático, topográfico y de paisaje desde la costa mediterránea al Pre-pirineo. Fruto del gradiente climático encontramos comunidades leñosas típicamente mediterráneas (que ocupan más de la mitad de la provincia), submediterráneas, eurosiberianas e incluso subalpinas (Ruiz de la Torre 1990-1999; Rivas-Martínez 2011). Por otra parte, la provincia muestra también un claro gradiente de transformación antrópica del paisaje, desde la región metropolitana de Barcelona (con 3240 km2 y casi 4.8 millones de habitantes) hacia su interior dominado por paisajes agrícolas y forestales, con una densidad de población muy inferior (el resto de la provincia cuenta con 4480 km2 y 770000 habitantes; http://www.idescat.cat).

Para la realización de la presente tesis ha sido de vital importancia diferenciar de forma precisa las formaciones leñosas nuevas (es decir, de aparición reciente) del resto. La provincia de Barcelona cuenta con cartografía detallada de las cubiertas del suelo históricas y actuales, lo que ha permitido cartografiar los cambios en dichas cubiertas en los últimos 50 años (Figura 2.1). Así, cuenta con el Mapa de Cubiertas del Suelo de la Provincia de Barcelona del año 1956 (MCS56_B; www.sitxell.eu/es/default.asp) y con diversas ediciones (la última de 2009) del Mapa de Cubiertas del Suelo de Cataluña (MCSC, www.creaf.uab.es/mcsc). Ambos mapas han sido producidos por el CREAF mediante la fotointerpretación de imágenes (fotos aéreas de 1956-1957 geo-referenciadas en el primer caso y orto-imágenes en el segundo) a una escala muy detallada (inferior a 1:5000) y son por tanto totalmente comparables entre sí. La comparación de ambos mapas (Figura 2.2) permite constatar que las cubiertas leñosas de la provincia se han incrementado un 10% en el último medio siglo, con un aumento especialmente importante en el caso del bosque (19%). Además, un 30% de los bosques actuales son de aparición posterior a 1956, mientras que un 27% de los matorrales actuales se originaron a partir de cultivos abandonados después de dicha fecha. En el caso de la región metropolitana de Barcelona, dicho proceso se ha combinado con una importante urbanización del territorio, que se ha concentrado especialmente en las zonas bajas (Basnou et al. 2013).

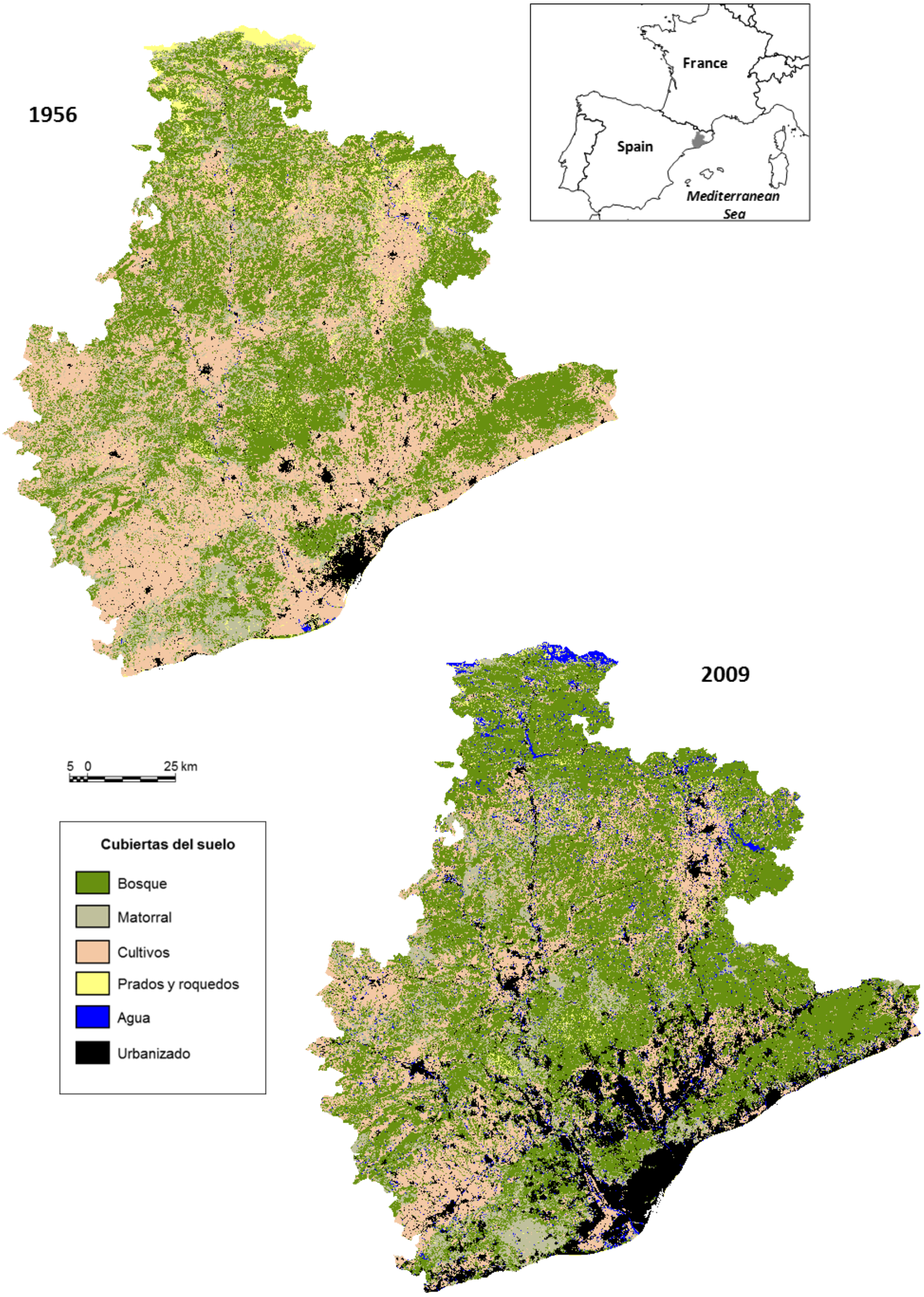

Figura 2.1. Cubiertas del suelo de 1956 y 2009 de la provincia de Barcelona. Fuente: MCSC56_B y MCSC 2009.

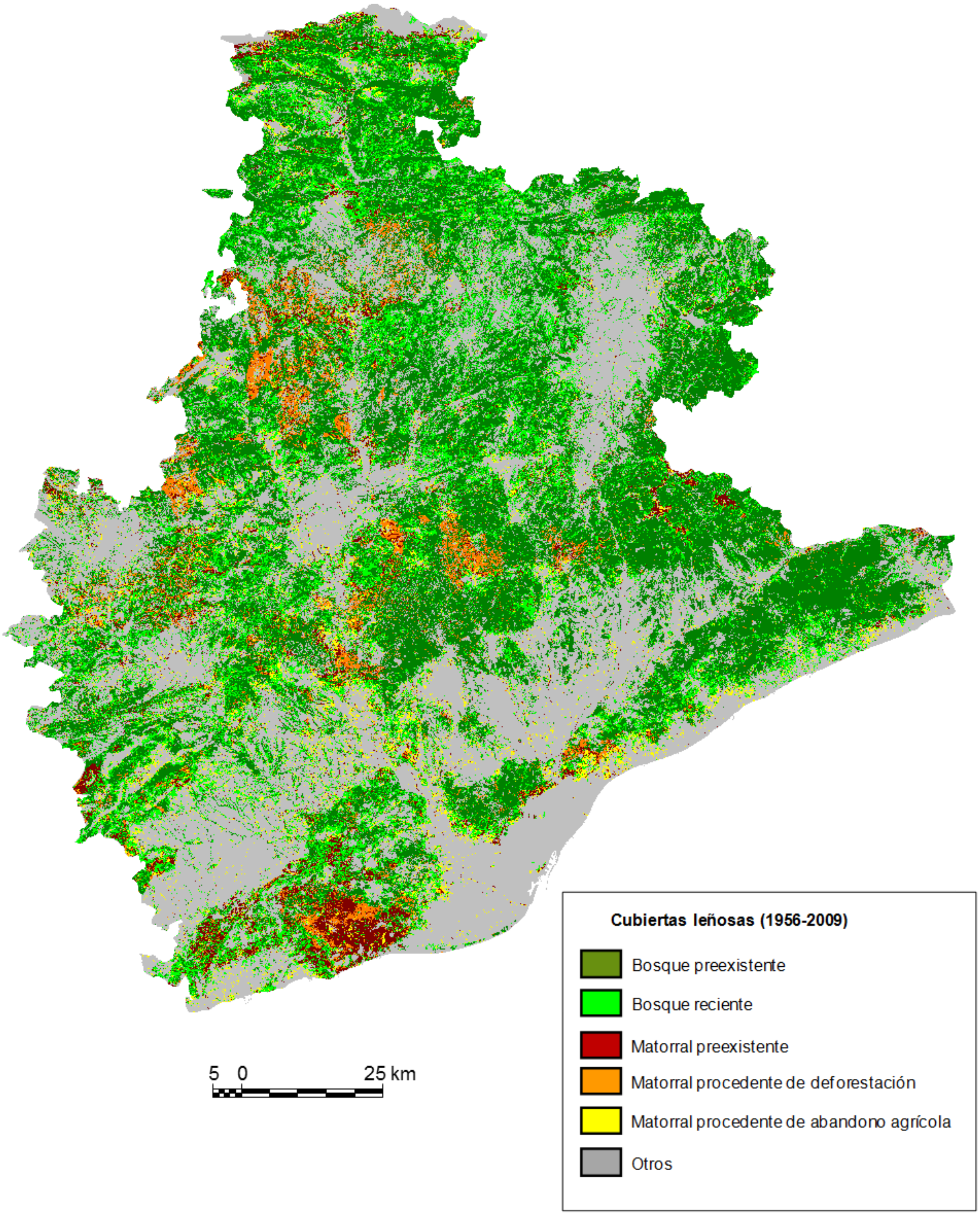

Figura 2.2. Bosques y matorrales de la provincia de Barcelona clasificados según su evolución entre 1956 y 2009. Fuente: MCSC56_B y MCSC 2009.

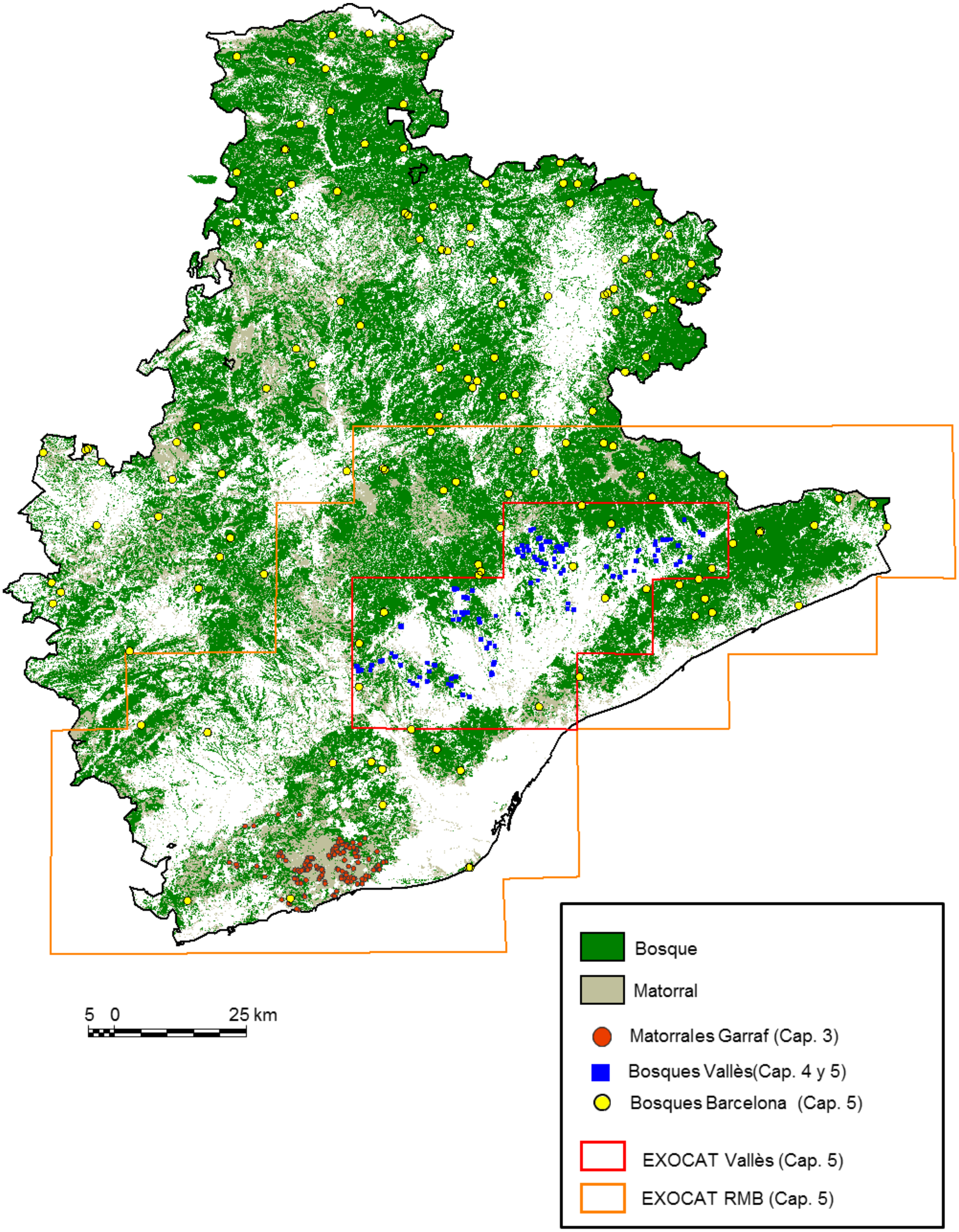

Figura 2.3. Fuentes de datos utilizadas en los diversos capítulos de la tesis.

Los diversos capítulos de la tesis se han centrado en dos regiones de la provincia de Barcelona especialmente antropizadas, como son el llano del Vallès y el Macizo del Garraf, donde se han utilizado datos específicos. Sin embargo, también se han utilizado datos más generales correspondientes a la Región Metropolitana de Barcelona y al conjunto de la provincia. Dichos conjuntos de datos se ilustran en la Figura 2.3 y se describen a continuación:

Los matorrales del macizo del Garraf

Los datos utilizados para analizar el ensamblaje de las comunidades de matorrales (Capítulo 3) se obtuvieron por parte de A Segura y J Pino en una campaña de campo en el Macizo del Garraf en 2013, realizada con el apoyo de mapas históricos y relativamente recientes de las cubiertas del suelo. A tal efecto se consideraron el MCSC56_B y el MCSC de 2009, reclasificados en cuatro categorías (bosques, matorrales, cultivos y otras cubiertas). Dichos mapas se combinaron en un mapa de cambios de cubiertas del suelo del período 1956-2009, del cual se seleccionaron tres categorías de matorrales actuales: boque-matorral, matorral-matorral y cultivo-matorral, considerando el uso del suelo en el año 1956 y en el 2009 respectivamente.

Este mapa de cambios en los matorrales se utilizó para la selección de parcelas de muestreo en la zona de estudio. En cada una de las categorías de bosque-matorral y matorral-matorral se seleccionaron dos grupos de 24 a 36 parcelas, correspondientes a parcelas con y sin antiguas terrazas de cultivos presumiblemente abandonadas a finales del siglo XIX o inicios del XX (año 1900 aproximadamente). En la categoría de cultivo-matorral sólo se seleccionó un grupo de 36 parcelas, asumiendo que los cultivos también estaban presentes en el año 1900. Con base en lo anterior, se muestreó un total de 150 parcelas distribuidas en cinco trayectorias de cambios en las cubiertas del suelo en los matorrales del Garraf (Tabla 2.1).

En cada punto de muestro se estableció una parcela circular de 50 m de radio, donde se colectó el grupo de datos utilizados en el primer capítulo de la presente investigación. Se anotó el recubrimiento de las especies de plantas leñosas y se midieron diversas variables ambientales.

Tabla 2.1. Trayectorias de cambio de usos del suelo en los matorrales de Garraf (entre paréntesis se indica la nomenclatura utilizada en el trabajo).

Trayectoria	**n**	**1900**	**1956**	**2009**
Cultivos recientes	36	Cultivo	Cultivo	Matorral
Bosques cultivados antes de 1956	28	Cultivo	Bosque	Matorral
Matorrales cultivados antes de 1956	26	Cultivo	Matorral	Matorral
Bosques no cultivados antes de 1956	24	No cultivo	Bosque	Matorral
Matorrales no cultivados antes de 1956	36	No cultivo	Matorral	Matorral

Los bosques del llano del Vallès

Los efectos de la conectividad forestal y la urbanización del paisaje sobre el ensamblaje general de las comunidades vegetales y la invasión por plantas exóticas de los nuevos bosques periurbanos se analizaron en el llano del Vallès (Capítulos 4 y 5). Dicho muestreo fue llevado a cabo por N Gamboa-Badilla, con la colaboración de E Álvarez. Mediante la combinación del MCSC56_B y el MCSC de 2009 en formato ráster, los bosques de la zona de estudio se clasificaron en pre-existentes (si existían en 1956 y 2009) y recientes (si correspondían a otra cubierta distinta del bosque en 1956). Con el objetivo de reducir la variación ambiental observada en estudios previos y responsable de variaciones notables en la composición vegetal de los bosques de la zona (Guirado et al. 2007), el estudio se limitó a las áreas con sustrato calcáreo y situadas a menos de 400 m de altitud. Dicha selección se llevó a cabo utilizando mapas geológicos y modelos digitales de elevaciones del ICGC.

La zona de estudio fue seleccionada también por la existencia de fuertes gradientes de conectividad forestal y de urbanización del paisaje, desde el centro del llano (donde se ubican las zonas más urbanizadas y menos conectadas al bosque) a las zonas de contacto con las sierras litoral y prelitoral (donde la conectividad forestal es elevada y la urbanización escasa). Utilizando métodos de *moving window* y de interpolación cartográfica y con el objetivo de seleccionar parcelas de muestreo a lo largo de dichos gradientes, se pusieron a punto modelos continuos de la proporción de cobertura forestal y urbana en un buffer de 500 m alrededor de cada punto del paisaje. Estos modelos se obtuvieron con el SIG MiraMon, calculando las coberturas actuales de bosque y urbanas (obtenidas del MCSC 2009) alrededor de 20000 puntos distribuidos regularmente (cada 250 m) en el área de estudio. Seguidamente, los valores se interpolaron en forma de mapas continuos (ráster) de 10 m de tamaño de píxel para toda la cobertura de bosque del año 2009, utilizando la inversa de la distancia como peso de interpolación.

Los mapas resultantes se utilizaron para seleccionar un total de 128 parcelas de muestreo distribuidas equitativamente en bosques preexistentes y recientes. Se seleccionaron tres categorías de conectividad forestal (alta, media y baja) y dos de urbanización (media y baja), que se combinaron entre sí produciendo un total de 8 categorías (la conectividad forestal y la urbanización del paisaje no son independientes por lo que no es posible a la vez una conectividad forestal y una urbanización elevadas; Figura 2.4). En cada categoría de combinación se distribuyeron al azar 16 parcelas circulares de 10 m de radio, 8 en cada tipo histórico de bosque. En cada una de dichas parcelas se anotó el recubrimiento de las diversas especies de plantas, clasificadas en función de su ecología, su origen y sus mecanismos de dispersión. También se recogieron datos de la estructura del bosque y de diversas variables ambientales.

Los bosques de la provincia de Barcelona

El estudio del grado de invasión de los bosques periurbanos (Capítulo 5) se llevó a cabo combinando los datos obtenidos en el llano del Vallès (punto anterior) con otras parcelas forestales distribuidas por los bosques de la provincia de Barcelona. Estas parcelas se obtuvieron de un muestreo realizado por Clotet et al. (2016) sobre el conjunto de hábitats de la provincia de Barcelona. Dicho muestreo contiene un total de 531 parcelas distribuidas por los principales hábitats de la provincia obtenidos por reclasificación de la cartografía de hábitats de Cataluña (http://mediambient.gencat.cat/ca/05_ambits_dactuacio/patrimoni_natural/sistemes_dinformacio/habitats/). Del total de parcelas 146 corresponden a bosques, con 46 ubicadas dentro de la región metropolitana de Barcelona (RMB) y las otras 100 fuera de ella. En cada una de dichas parcelas, de 5 m de radio, se registró el recubrimiento de las especies de plantas exóticas presentes y se midieron diversas variables ambientales y de paisaje actual e histórico.

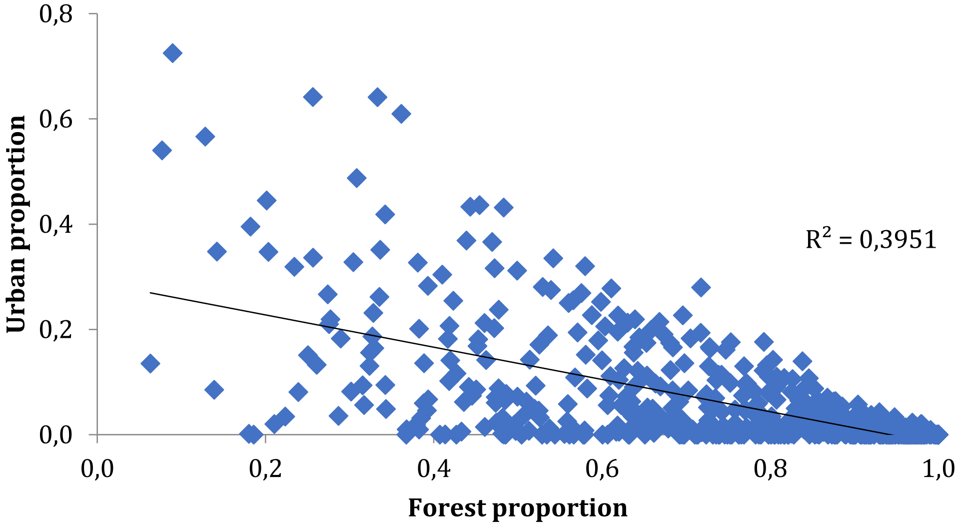

Figura 2.4. Muestras aleatorias en el área de estudio (= 20000) que señalan la relación entre la proporción de cobertura forestal y urbana en los paisajes de 500 m de radio en las tierras bajas del Vallès.

Las especies exóticas en la Región Metropolitana de Barcelona y el llano del Vallès

El estudio del grado de invasión de los bosques periurbanos por plantas exóticas (Capítulo 5) se complementó con un análisis del *pool* de dichas especies en el llano del Vallès y en la RMB. Los datos se obtuvieron de la base de datos EXOCAT, que reúne las citaciones conocidas de las especies exóticas en Cataluña por cuadrículas UTM de 10x10 km (http://exocat.creaf.cat/). La base de datos es el resultado de una exhaustiva revisión bibliográfica de varios años y de la colaboración de técnicos, expertos y naturalistas de Cataluña (Andreu & Pino 2013).

Para la presente investigación se extrajeron los registros de plantas exóticas de las cuadrículas correspondientes a la RMB y al llano de Vallès (Figura 2.3). Seguidamente se procedió a completar el conjunto de datos con las especies registradas en el muestreo de campo y que no estaban incluidas en EXOCAT: *Cedrus libani*, *Coronilla valentina*, *Cotoneaster lacteus*, *C. pannosus*, *Lonicera japonica*, *Lunaria annua*, *Oxalis latifolia*, *Pittosporum tobira*, *Prunus cerasifera*, *Prunus cerasifera var. Pissardii*, *Prunus domestica*, *Prunus dulcis*, *Pyracantha angustifolia*, *Solanum chenopodioides* y *Ulmus pumila*. Adicionalmente se incluyó a *Laurus nobilis* a pesar de ser nativa de Cataluña, pues se considera no nativa en la RMB y el Vallès. Por el contrario, *Pinus pinea* no se incluyó por cuestionarse su procedencia exótica (Martínez & Montero 2004).

3. Niche factors and land-use history mostly drive woody local-scale community assembly in Mediterranean scrublands

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Abstract

Despite there is a large consensus that signals of land use legacy might persist for a long time in plant communities, the role of this historical component on species presence and abundance compared with that of niche factors and species dispersal remains largely unknown. We compared the role of these factors on the assembly of Mediterranean scrub communities in the Garraf Massif (Barcelona, NE Spain) subjected to diverse land-cover pathways in the last century. Woody species cover was estimated in 150 scrubland plots distributed in five historical land use pathways. For each plot, woody and herbaceous vegetation cover, soil stoniness and depth, elevation, annual radiation and geographic position were also recorded. GLMs were used to examine the effect of historical land cover pathways and environmental factors on woody species richness, diversity and evenness. Relationships between species composition and environmental and historical variables were studied using Canonical Correspondence Analysis (CCA), with variance partition methods. Spatial effects at community and species level were assessed, respectively, through autocorrelation analyses on the residuals of species richness, diversity and evenness, and Mantel tests exploring the influence of geographical distances in species presence and cover. Woody species richness and diversity were associated to both elevation and historical land use pathways, while woody species evenness was only associated to elevation. The study failed to detect any spatial effects attributable to dispersal. Variance partition showed that environmental variables explained around 21% and 17%, and historical land use variables, 19% and 17% of the variance in species distribution, in cover and presence respectively. Results indicate that historical land use pathways and environmental (niche) factors equally drive local-scale woody community assembly in Mediterranean scrublands, while dispersal seems to play a minor role on this process.

Keywords: Environmental factors; Garraf massif; Land-cover pathways; Landscape changes; Land-use legacies; Woody species richness; Woody species diversity; Woody species composition.

Introduction

There is increasing evidence that the historical legacy of changes in habitats determines a deep footprint in plant community assemblages, both native (e.g. Hermy & Verheyen 2007; Vellend et al. 2007; Bagaria et al. 2015; Basnou et al. 2016) and alien (Vilà & Ibánez 2011; Basnou et al. 2016), which can last for a very long time (e.g. Dambrine et al. 2007). The underlying mechanisms driving community reassembly along habitat change are under debate since MacArthur & Wilson (1967). Classically, species colonization and persistence in communities have been attributed to niche differentiation (e.g. MacArthur & Levins 1967; Chase & Leibold 2003; Tilman 2004; Leibold & McPeek 2006), but more recently the role of stochastic processes (Körner et al. 2008; Poschlod & Biewer 2005), and species dispersal and propagule availability (Levin 1974; Hubbell 2001, 2006; Leibold & McPeek 2006) in these processes has been emphasized. Alternatives to the classical niche approach are coupled with the hypothesis that community assembly frequently takes place under non-equilibrium situations (Rohde 2005), which is supported by increasing evidence. In particular, time-lags (i.e. relaxation times) between habitat change and the subsequent shifts in species' presence and richness, called extinction debts and colonization credits (Tilman et al. 1994; Jackson & Sax 2010), have been increasingly reported (Kuussaari et al. 2009; Krauss et al. 2010; Cristofoli et al. 2010; Piqueray et al. 2011; Purschke et al. 2012; Guardiola et al. 2013; Bagaria et al. 2015). These lags in species' responses to habitat change are caused by different mechanisms (e.g. metapopulation dynamics, dispersal limitation, successional dynamics, habitat development, biological inertia; Hanski & Ovaskainen 2002; Hylander & Ehrlén 2013; Svenning & Sandel 2013), most of which are insufficiently known. Timing and relative importance of extinction debts and colonization credits in former and new communities, respectively, are presumed to affect both species richness and composition along habitat change (Jackson & Sax 2010; Cristofoli et al. 2010; Bagaria et al. 2015; Basnou et al. 2016), sometimes for centuries (Vellend et al. 2006; Cousins & Vanhoenacker 2011).

In any case, accumulated effects on species' responses might determine a complex signal of habitat change history in community structure, species richness and composition. Particularly, habitat change trajectories across time seem to play a major role in community assembly, yet this has been seldom explored. It is known that these trajectories influence plant invasion patterns in habitats (Hobbs 2000; Vilà et al. 2003; Pino et al. 2006; Domènech et al. 2005). There are also a number of studies indicating that the colonization by native species in new forest patches can be modulated by historical land use (Verheyen et al. 2003; Vellend 2004, 2005; Svenning et al. 2009; Puerta-Piñero et al. 2012; Navarro-González et al. 2013). However, the role of this historical trajectory of land use change on species presence and abundance compared with that of niche factors and species dispersal remains largely unknown.

Woody plant communities in the Mediterranean Basin have been subjected to extensive clearing over the past several centuries, due to grazing and agricultural expansion (Grove & Rackham 2001). In the past century, changes in traditional land uses and lifestyles have resulted in the abandonment of large cropland and farmland areas, thus leading to substantial woodland recovery (Lepart & Debussche 1992; Lasanta & García-Ruiz 1996; Di Pasquale et al. 2004; Bonet & Pausas 2004; Meyfroidt & Lambin 2011; Basnou et al. 2013). Despite the relevance of these processes, the role of past landscape and its recent dynamics on plant community assembly in Mediterranean woodlands is much less known, as previous studies have been mostly focused in the effects of present landscape (Montoya et al. 2008; Martín-Queller et al. 2011). It is known that time since abandonment determines woody species richness and cover in abandoned crops (Bonet & Pausas 2004). More recently, Basnou et al. (2016) detected the existence of colonization credits (i.e. lower species richness) in recent forests, but limited to vertebrate-dispersed species, probably due to ecological and dispersal constraints. Previous land use is associated to species richness and composition, and to post-fire recovery in forests affected by large wildfires (Puerta-Piñero et al. 2012). Moreover, the colonization of major Mediterranean tree species like *Quercus ilex* (Navarro-González et al. 2013) and several alien species (e.g. *Opuntia* spp.; Vilà et al. 2003) is also found to be modulated by past land use.

The relative effect of historical legacy of habitat changes on community assembly, compared with that of niche factors and species dispersal, is particularly unknown. In this work, we explore the role of a set of historical trajectories of habitat change, compared with that of environmental factors, on woody species assembly in Mediterranean scrublands. The study has been performed at landscape scale, at which dispersal effect is expected to be substantially reduced. We have addressed the following questions: (i) what is the effect of historical land use changes in community assembly compared with niche factors? And (ii) are species richness, diversity and composition equally affected by this historical component?

Methods

Study area

The study has been performed in the Garraf Massif (Barcelona, NE Spain; Figure 3.1), in the Spanish Mediterranean coast, which approximately covers 10000 ha and wich has a maximum elevation of about 600 m a.s.l. The climate is coastal Mediterranean, with annual rainfall between 600 and 700 mm and average temperature from 7 to 9 °C in winter and from 22 to 24 °C in summer (Meteorological Service of Catalonia, www.meteo.cat/servmet/index.html). Vegetation is dominated by calcicolous scrubs (>70% of total area; 2009), like *Chamaerops humilis*, *Pistacia lentiscus*, *Quercus coccifera*, *Rosmarinus officinalis* and chamaephytic grasses like *Ampelodesmos mauritanica* among other species. In some areas in the north face of the massif, less affected by large fires in the last 30 years, the landscape is dominated by *Pinus halepensis* forests with a dense scrubby understory. Agricultural areas, yet widespread throughout the massif in the past, are currently concentrated around towns and in the massif foothill.

While Garraf is currently dominated by limestone scrublands, it accounts for a recent history of deep changes in land use. Until the 19th century, it was dominated by Holm oak (*Q. ilex*) and Aleppo pine (*P. halepensis*) forests, but the arrival of phylloxera plague in Europe determined a large expansion of vineyards in the massif, as in many other Spanish Mediterranean regions, due to the high demand for wine (Badia-Miró et al. 2010). At the end of the 19th century, coinciding with the recovery of vineyards in Europe, these low-productive lands were abandoned while crops only persisted in the lowland areas and valley bottoms, mostly reconverted into olive, almond and carob tree crops. However, croplands were progressively abandoned in the mid-20th century, as a result of industrial and touristic development of the Barcelona Metropolitan Area. In addition, the massif was affected by large wildfires in 1982 and 1991, causing a strong reduction of the forest area. Thus, current scrublands are mostly derived from crop abandonment during the last century and forest degradation by repeated wildfires in the last decades.

Sampling

In 2013, we selected 150 plots distributed in five historical land cover pathways in current Garraf scrublands (Figure 3.1). Plots were selected considering three time steps (c.a. 1900, 1956 and present day; Table 3.1), combining historical and current land cover maps and fieldwork. Recent land cover pathways were considered using the 1956 Land Cover Map of the Barcelona province (www.sitxell.eu/en/mapa_historics.asp) and the 2009 Land Cover Map of Catalonia (www.creaf.uab.es/mcsc). Both were generated by photo-interpretation at a scale of 1:5000, and they were reclassified into four categories (forests, scrubs, crops, and other). Then, they were combined in a 1956-2009 land cover change map, from which three categories were selected: forest-scrub, scrub-scrub and crop-scrub. A set of plots were pre-selected over these categories (80 in the two first and 40 in the last), which were concentrated in relatively accessible areas (i.e. those with either unpaved or paved roads in their vicinity). Final selection was done through fieldwork, during which two groups of 24 to 36 plots were selected for both forest-scrub and scrub-scrub categories. These groups corresponded to plots with and without old crop terraces, assuming that these scrubs were formerly cropped (likely until the end of the 19th century, Badia-Miró et al. 2010) and non-cropped, respectively. In the crop-scrub category, only a single group (of 36 plots) was selected as we assumed that crops were also present in 1900. Thus, five land-cover pathways were finally identified in present-day Garraf scrublands (Table 3.1): recent (at least until 1956) crops (RC), formerly (before 1956) cropped forests (FCF) and scrublands (FCS), and non-cropped forests (NCF) and scrublands (NCS).

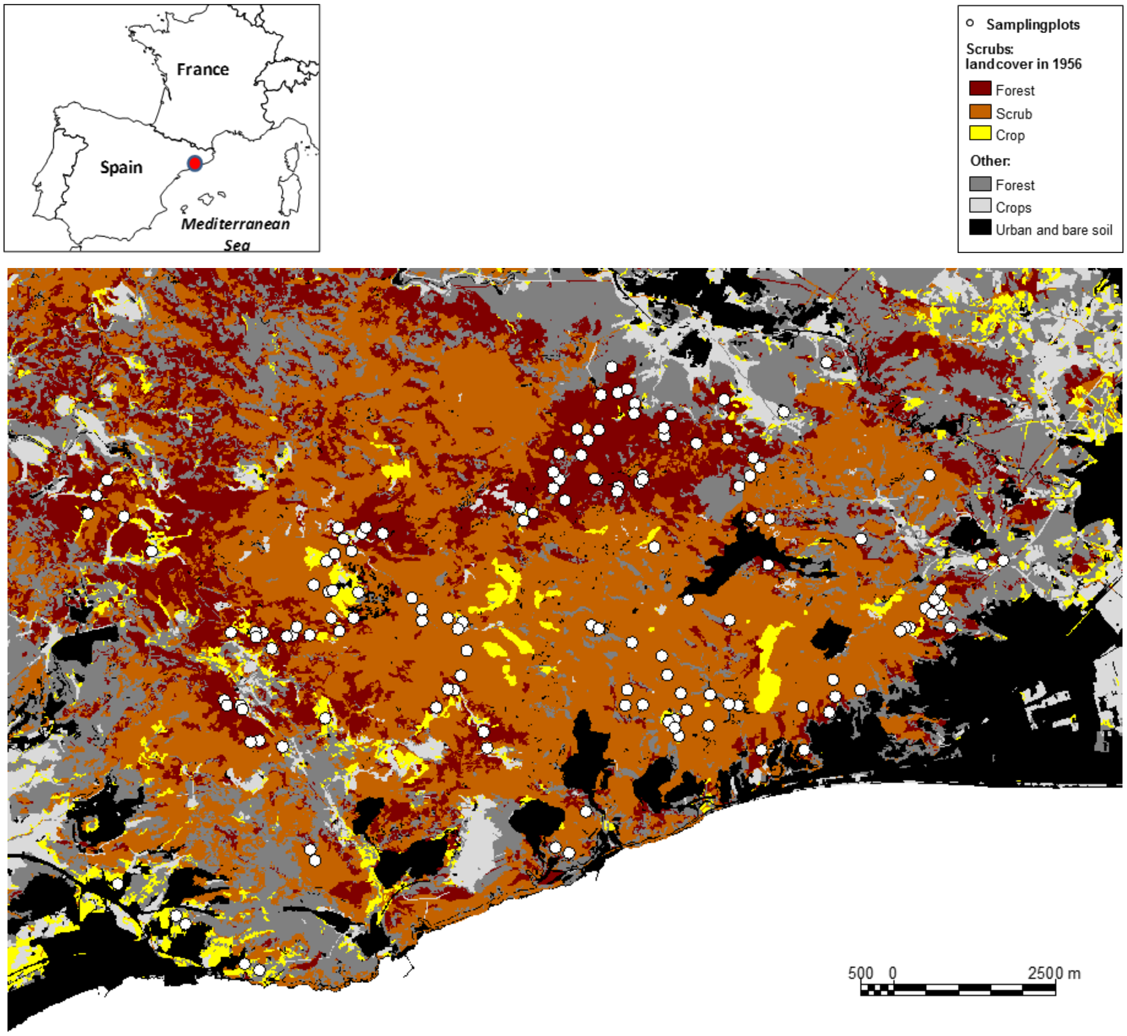

Figure 3.1. Study area in the Garraf Massif showing main current (2009) land cover categories. Land cover of 1956 in scrublands and the distribution of sampling plots are shown.

In each sampling point, vegetation was recorded in a 5-m radius plot. Total woody and herbaceous vegetation cover and that of each woody species were visually assessed using the Braun-Blanquet (1979) scale. Species sampling included *A. mauritanica*, a perennial tussock grass with a woody branched stem system at soil surface. Mean soil depth was measured from four measurements at each plot, made using a 1-m iron stake. Elevation and annual radiation in each plot were obtained from a Digital Elevation Model (DEM) with 30 m of pixel size, generated by the Cartographic Institute of Catalonia (ICC) and from the Climatic Atlas of Catalonia (www.opengis.uab.cat/acdc/catala/radiacio).

Table 3.1. Historical landuse pathways according to the land cover in 1900, 1956 and present, in Garraf shrublands (number of sampling plots).

	c.a. 1900	**1956**	**Present**	**No. of plots**
Non cropped forests (NCF)	non-crop	forest	scrub	24
Non cropped scrubs (NCS)	non-crop	scrub	scrub	36
Formerly cropped forests (FCF)	crop	forest	scrub	28
Formerly cropped scrubs (FCS)	crop	scrub	scrub	26
Recent crops (RC)	crop	crop	scrub	36

Statistical analyses

For each plot, we calculated woody species richness and the Shannon diversity and evenness indices. The relative influence of the historical land use trajectories and a set of environmental variables in these community parameters were analysed using general linear models (GLM) after checking for normality. The environmental variables mentioned above were included in models with plot geographic location (UTM coordinates). A model selection was then performed based on AICc increase (delta) compared to the best model (lowest AICc), and all models with delta of less than 2 were selected. Then, a final model was obtained only including the significant predictors present in more than 50% of the selected models. Normality of the residuals of these models was assessed and their spatial autocorrelation was tested based on the Moran's Index. Finally, the association of species richness, diversity and evenness with land use pathways was tested through pair wise comparison of means between the five land-cover pathways using a Tukey test for each model. Additional ANOVA tests, considering land cover in 1956 (forest, scrub and crop) and in 1900 (crop and non-crop) as separate factors, were finally performed to test the specific role of recent versus far past land use on community parameters.

Regarding species composition, we first assessed the distance decay in community similarity using Mantel tests on species presence and cover. Distance in species presence was assessed through the complementary of the Jaccard's index (i.e. subtracting this index from 1), while that in species cover was calculated using the Mahalanobis distance to remove correlations between species. These tests were performed using R statistical software, version 3.1.1 (R Development Core Team 2014). Still, the association of species presence and cover with the land cover change pathways and the studied environmental variables was explored by Canonical Correspondence Analysis (CCA) and variance partitioning, using CANOCO 4.5. Only species present in at least 10 of the total plots were taken into account.

Results

Plot factors

Plots in the diverse land-cover pathways exhibit several significant differences in the mean values of the diverse environmental variables (Table 3.2). The highest herbaceous cover was found in plots belonging to recent crops (RC) and formerly cropped forests of 1956 (FCF), while the lowest woody cover occurred in RC and non-cropped scrubs of 1956 (NCS). This pathway (NCS) also showed significantly lower soil depth than the rest of categories. Elevation was significantly lower in RC than in the rest of pathways but in formerly cropped scrubs (FCS), while annual radiation was lower in formerly cropped forests (FCF) than in the rest but in FCS. Regarding geographic position, longitude (i.e. UTM X) in RC plots was significantly different to those of the rest of land cover pathways, while latitude did not differ among pathways.

Table 3.2. Mean values of predictor variables in each land cover pathway in the Garraf Massif scrublands. Different letters correspond to significant ($p<0.05$) differences between means for the Tukey test.

Land cover pathways	**Non cropped forests (NCF)**	**Formerly cropped forests (FCF)**	**Non cropped scrubs (NCS)**	**Formerly cropped scrubs (FCS)**	**Recent crops (RC)**
Woody cover (%)	81.7 ± 10.7 ^{a}	81.9 ± 7.2 ^{a}	77.1 ± 10.8 ^{ab}	81.7 ± 6.5 ^{a}	70.9 ± 17.0 ^{b}
Herbaceous cover (%)	6.3 ± 2.2 ^{a}	10.7 ± 7.7 ^{ab}	9.1 ± 9.4 ^{a}	8.7 ± 5.0 ^{a}	16.9 ± 15.3 ^{b}
Soil depth (cm)	26.9 ± 15.52 ^{a}	17.2 ± 9.0 ^{a}	8.1 ± 15.4 ^{b}	16.9 ± 10.8 ^{a}	25.7 ± 10.1 ^{a}
Altitude (m)	317.1 ± 146.4 ^{a}	307.0 ± 103.0 ^{a}	320.3 ± 146.6 ^{a}	240.0 ± 108.3 ^{ab}	229.2 ± 98.1 ^{b}
Annual radiation (10kJ*m-2day-1)	1418.3 ± 131.5 ^{ab}	1391.3 ± 84.5 ^{b}	1468.3 ± 117.3 ^{a}	1433.8 ± 69.8 ^{ab}	1428.2 ± 59.6 ^{ab}
UTM X (m)	408241 ± 3252 ª	406137 ± 2775 ª	407971 ± 4772 ª	408852 ± 3776 ª	403849 ± 4708 ^{b}
UTM Y (m)	4572132 ± 2324 ª	4572433 ± 1856 ª	4571317 ± 1682 ª	4571452 ± 864 ª	4571623 ± 3144 ª

Species richness, diversity and evenness

The selected GLM showed that woody species richness was only significantly associated to elevation (with negative association) and to the historical land use pathways (Table 3.3). According to the Tukey test, this variable was significantly higher in scrublands that were forests in 1956 (FCF and NCF) than in the rest of land cover pathways (Figure 3.2). As species richness, species diversity was significantly higher in FCF and NCF than in the rest of pathways and it was negatively associated to altitude. In contrast, species evenness was not significantly different among pathways and it was only significantly associated to elevation, showing a negative relationship. None of these community variables was associated to geographical coordinates, thus showing that their values showed no spatial trends in the study area.

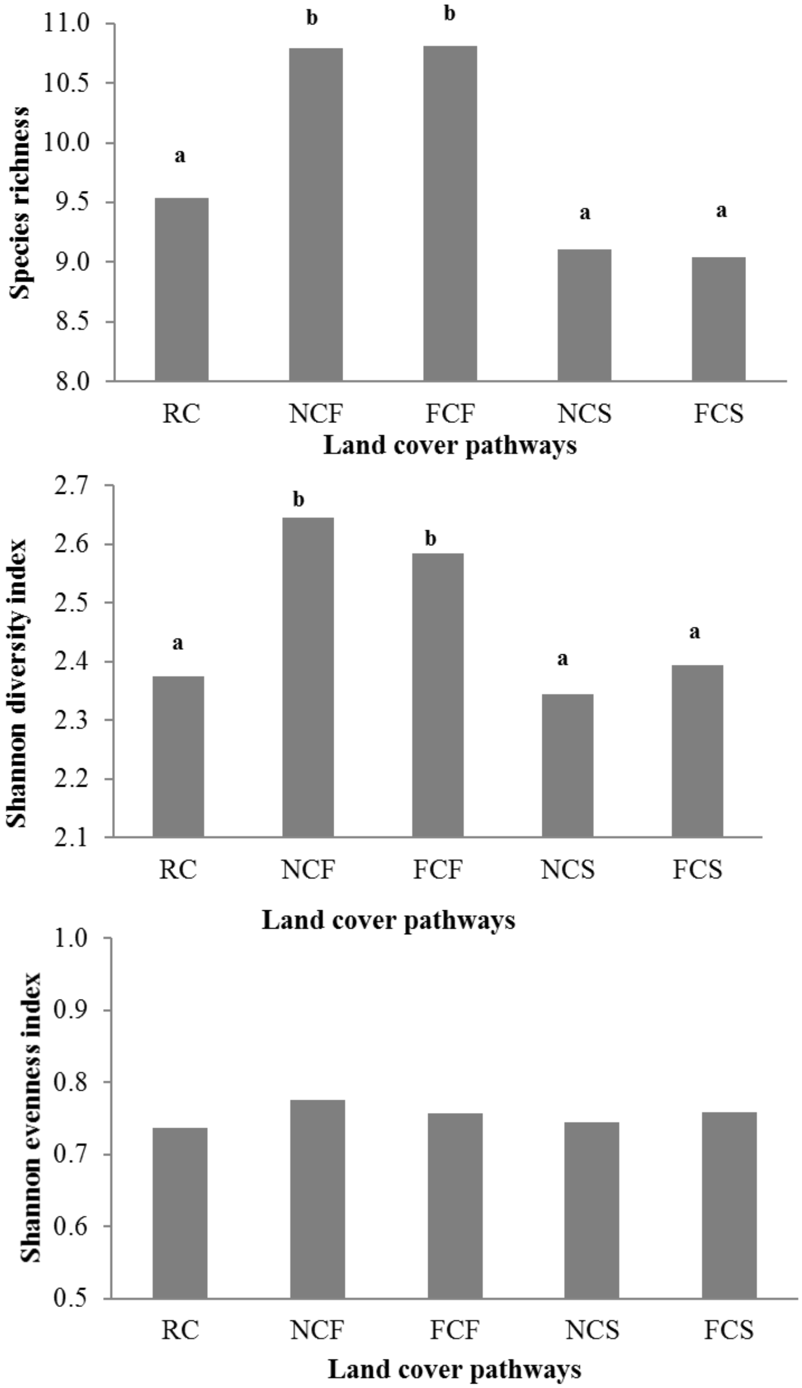

Figure 3.2. Mean woody species richness (top), diversity (middle) and evenness (bottom) in sampling plots by historical land cover pathway in the Garraf scrublands. Different letters correspond to significant ($p<0.05$) differences between means for the Tukey tests. RC: recent crops, NCF: non cropped forests, FCF: formerly cropped forests, NCS: non cropped scrubs, FCS: formerly cropped scrubs.

No significant spatial autocorrelation was detected in the residuals of the model of any community variable but in species diversity (Moran's I=0.01, p=0.09 for species richness; I=0.024, p=0.03 for species diversity; I= 0.009, p=0.16 for species evenness). In any case, values of I are small and changes in residual autocorrelation with distance are non-relevant for all response variables (see Appendix A.1). Additional ANOVA tests showed that species richness and diversity are associated to 1956 land cover (F=11.29, p<0.001 and F=7.03, p<0.01 respectively; df=2) but not to old (1900) land cover (F=0.02, p=0.87 and F=0.07, p=0.78 respectively; df=1), while species evenness is not associated to any land use factor (F=0.07, p=0.57, df=2 for 1956 and F=0.04, p=0.85, df=1 for 1900 land cover data, respectively).

Table 3.3. Results of General Linear Models for woody species richness, diversity and evenness (Significance: * p<0.05; ** p<0.01, *** p<0.001).

	Species richness		**Species diversity**		**Species evenness**	
	Estimate	t value	Estimate	t value	Estimate	t value
Non cropped forests (NCF)	12.348	20.986***	2.994	28.557***	0.799	45.256***
Formerly cropped forests (FCF)	-0.030	-0.059	-0.072	-0.785		
Non cropped scrubs (NCS)	-1.668	-3.056**	-0.297	-3.057**		
Formerly cropped scrubs (FCS)	-2.132	-3.770***	-0.336	-3.337**		
Recent crops (RC)	-1.551	-2.914**	-0.324	-3.420***		
Altitude	-0.005	-3.612***	-0.001	-4.550***	-0.0001	-2.654**

Species composition

Species frequency and cover in each land cover pathway is summarized in Appendix A.2. Mantel tests failed to detect any significant association of geographical distance with species frequency (r^2=0.045; p=0.257) and cover (r^2= 0.003; p= 0.932). We found 29 species present in more than 10 plots. CCA shows that 37% of variance in the presence of these species is explained by the studied environmental variables and land cover pathways. Variance partition shows that environmental variables and historical land cover variables explained the same amount of variation (17%) in species presence. About 2% of the variance is explained by unknown variables. In the case of species cover, the explained variance is 42%, with environmental variables explaining 21% and historical land use, 19% of this variance. Near 2% of the variance is again explained by unknown variables.

Ordination diagrams of both species presence and cover (Figure 3.3) show that this species is distributed in scrublands according whether they were cropped or not in 1956 and before this date, and depending on environmental factors. In the case of species presence, the first axis separates forests and scrublands that were cropped before 1956 (left side) from those non-cropped (right side), while the second axis separates scrublands that were crops in 1956 (top) from the rest (bottom). The ordination of species cover is similar to that of species presence, but showing some rotation in the axes and the species being more spread along them. This suggests that differences in species distribution in relation to environmental variables and land cover pathways are more important in species cover than in species presence.

Regarding environmental variables, RC scrublands are positively associated to soil depth, while those that were non-cropped forests or scrublands in 1956 (NCF and NCS) are positively associated with annual radiation. All categories showed some association with elevation and geographic coordinates, being these especially relevant between latitude and formerly cropped categories (FCF and FCS).

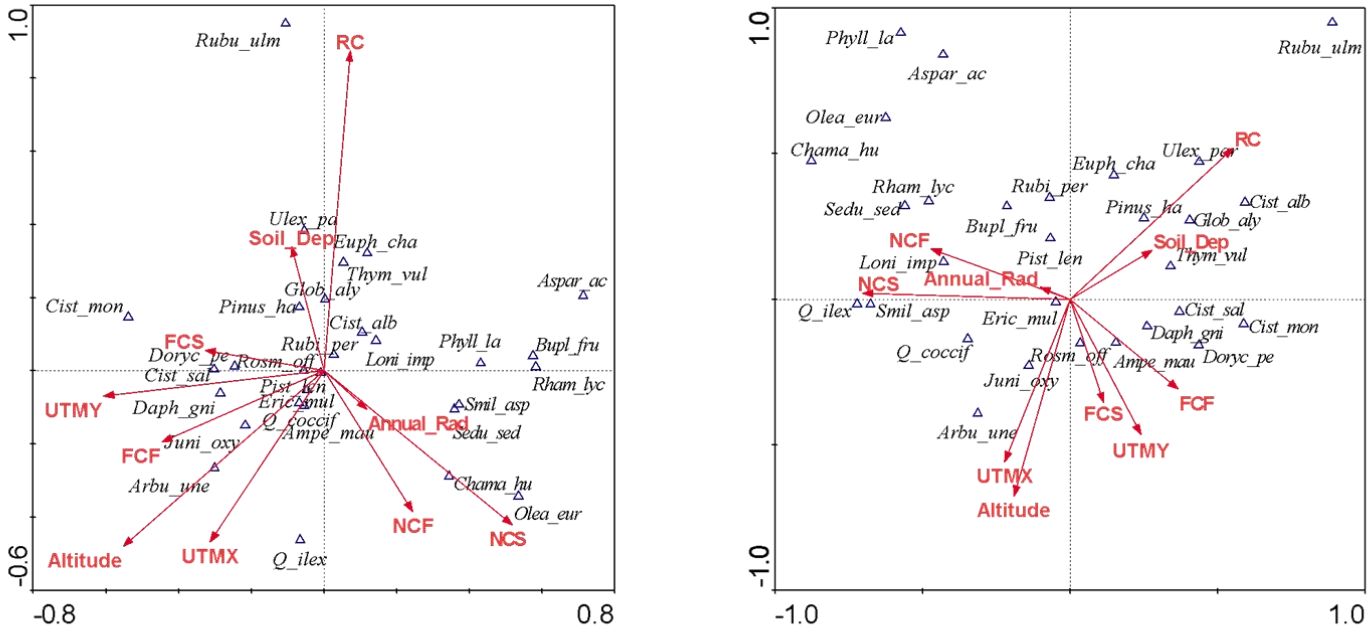

Figure 3.3. Canonical ordination diagram (CCA) of species presence (left) and cover (right) in Garraf scrublands. The species are represented by triangles and the arrows represent the historical land use variables (NCF: non cropped forests, FCF: formerly cropped forests, NCS: non cropped scrubs, FCS: formerly cropped scrubs, RC: recent crops) and environmental variables (UTMX: latitude, UTMY: longitude, altitude, soil depth and annual radiation). See Appendix A.2, material for species abbreviations.

In the case of species presence, the association of particular species with land cover pathways is generally weak, except for some species like *Ulex parviflorus, Euphorbia characias* and *Rubus ulmifolius* for RC, *Olea europaea* and *C. humilis* for NCF and NCS, or *Cistus spp., Dorycnium pentaphyllum, Arbutus unedo* and *Juniperus oxycedrus* for FCF and FCS. As previously indicated, the association with land-cover pathways is clearer for species cover. *Cistus albidus, E. characias, Globularia alypum, P. halepensis, U. parviflorus* and *Thymus vulgaris* are especially associated to RC. *A. mauritanica, D. pentaphyllum, Cistus* spp., and *Daphne gnidium* are especially abundant in FCF and FCS, while *C. humilis, O. europaea, Phyllirea angustifolia,* Rhamnus lycioides, *Quercus* spp. and *Lonicera implexa*, among others, are mostly abundant in NCF and NCS.

Discussion

Our study shows that both land cover change legacy and current environment determine complex, local-scale effects on current woody species assembly in Mediterranean scrublands. First, historical land use pathways and diverse environmental variables are significantly associated to community indicators such as woody species richness and diversity. Also, when taking into account community composition, environmental and historical factors equally contribute to explain species presence and abundance in the studied scrublands. And last, these effects are quite independent on the spatial distribution of scrublands, as indicated by the weak association of species richness, diversity and composition with distance and the lack of spatial autocorrelation in the residuals of the GLM.

As previously mentioned, effects of land use legacy on scrubland community assembly coexist with those of current environment. In fact, both factor types are commonly not independent from each other, as land use history strongly affects environmental factors (and vice-versa) like soil properties, which in turn determine a set of niche effects responsible for local species filtering (Dupouey et al. 2002). Batriu et al. (2015) observed that past agricultural uses determined an increase in soil fertility in Mediterranean marshlands compared with stable ones, and suggested that this strongly affected plant species composition in these communities. In our case, land cover pathways are clearly related with several environmental factors: recently cropped scrublands (RC) are associated to high soil depth, probably because crop fields with the best soils are commonly the last to be abandoned (e.g. Debussche et al. 1999), and they are characterized by lower and higher woody and herbaceous cover, respectively. Also, they are concentrated in lower, more accessible areas than the rest, and especially in the western part of the study area, because of the presence of rocky (carstic) areas less adequate for the agriculture in the east. Conversely, non-cropped scrubland categories (NCF, NCS) are associated to high solar radiation, and this suggests that these scrublands with no evidence of cropping are concentrated in the most exposed areas, which are the least suitable for agriculture under Mediterranean conditions.

As also previously stated, our study also indicated a lack of local spatial structure in the community assembly of Mediterranean scrublands, as there was no significant spatial autocorrelation for the community parameters (except species diversity, which had a negligible but significant autocorrelation) or between species presence and abundance at community level and geographic distance. Community similarity tends to decrease as the distance between sites increases (Nekola & White 1999), especially at large biogeographic scales, but this might not be the general case at local scales. Batriu et al. (2011) found that differences in plant species abundance in Mediterranean marshlands are more explained by environmental variables than by site and spatial position. These and our results suggest a key role of species' niches and a secondary role of species dispersal in the local assembly patterns in these communities. Thus, species dispersal seems to be unable to compensate the signal of historical land uses and the associated niche specificities at the studied scales. However, our results contrast with those by Huxel and Hastings (1999), Bagaria et al. (2012) and Jacquemyn et al. (2003) who found significant effects of distance in the distribution of plant species in fragmented habitats.

Thus, our findings showed that land use legacy affects woody species richness and, associated to it, species diversity. However, the observed patterns are no coincident with those expected according to recent literature. It is known for long that effects of habitat changes on biodiversity might not be immediate, and delayed species extinctions and colonizations might occur. This might lead to a temporal disequilibrium in species richness, called colonization credit, following settlement of novel habitats (Jackson & Sax 2010). Previous studies indicated that Mediterranean woody plant communities are strongly influenced by recent changes in land use (Dupouey et al. 2002; Puerta-Piñero et al. 2012; Navarro-González et al. 2013; Batriu et al. 2015; Basnou et al. 2015), as in other biomes (e.g. Verheyen et al. 2003; Vellend 2004, 2005; Svenning et al. 2009). Stand age determines woody species richness and composition in Mediterranean forests (Basnou et al. 2015) and their resilience to wildfires. Land use history strongly affects even some of the most relevant species in these forests, Holm oak (*Q. ilex*). Indeed, Navarro-González et al. (2013) showed that Holm oak regeneration in pine plantations in southeast Spain strongly depends on past land use intensity and, secondarily, on propagule availability. The more intense past land use, the less regeneration of oak stands under pine canopies.

However, our study does not provide evidence for these credits in Mediterranean scrublands, as species richness is not associated to scrubland age but to former habitat type. Thus, scrublands that were forests in 1956 (NCF and FCF types) exhibit the highest species richness, independently whether they were cropped or not in the old past. In addition, scrublands that were crops in 1956 (RC) do not exhibit lower species richness than those that were scrublands (NCS and FCS), despite they might be much younger (especially than NCS stands). This predominant association of species richness with land use of 1956 might reflect the already known effects of both habitat structure and resource availability (Pausas & Austin 2001). On the other hand, previous works failed to detect noticeable colonization credits in similar plant communities. Cristofoli et al. (2010) and Piqueray et al. (2011) found limited colonization credits in recently restored heathlands and grasslands in Belgium. Bonet & Pausas (2004) found an increase in woody species richness only for the first years along a 60-year chronosequence from old crops to scrublands in arid Mediterranean conditions. In addition, Bagaria et al*.* (2015) did not find any significant colonization credit for forest plant specialists at a local scale along a grassland-forest transition, while Basnou et al. (2016) found some colonization credit of woody plant species in novel forests compared with pre-existing ones at regional scale, yet this credit was only observed for vertebrate-dispersed species. All these results suggest that colonization credits are rapidly accrued in Mediterranean woody communities, yet it should be noted that the long history of human disturbance in the Mediterranean region, and especially of woody habitats (Grove & Rackham 2001), might have reduced the potential differences in species richness between recent stands and pre-existing ones taken as reference.

Maybe the most striking result of this study is that, while community parameters (i.e. species richness and diversity) are affected by recent past (1956) land cover, those regarding species composition (i.e. presence and abundance) are mostly associated to far past (pre-1900) land-cover. The spatial component of landscape structure and its temporal heterogeneity have far-reaching effects on plant species occurrence (Fahrig 1992; Hanski 1994; Hiebeler 2000; Jacquemyn et al. 2003). Life-history traits seem to play a key role in species colonization and persistence along heterogeneous landscape mosaics made up by patches of contrasting land use legacies, as found in Mediterranean marshlands (Batriu et al. 2015) and temperate forests (Verheyen et al. 2003; Vellend 2004, 2005). In our case, no deep analysis of species traits *versus* land-cover pathways has been performed, while some general trends can be observed. Thus, the youngest scrublands (RC) corresponding to recent crops on deep soils are dominated by pioneer scrubs with short life-spans and high growth rates (e.g. *C. albidus, E. characias, G. alypum, U. parviflorus* and *T. vulgaris*) and by pioneer trees (*P. halepensis*). In contrast, never cropped stands (NCS and NCF) concentrate large species with longer life-spans and slower growth rates (e.g. *C. humilis, O. europaea, Phyllirea angustifolia, R. lycioides*, and *Quercus* spp.) while those cropped long time ago (FCF and FCS) are mostly dominated by species with an intermediate strategy.

To conclude, we have found that historical land use legacy and current environmental factors help to maintain high diversity patterns of woody plant species at local scale in Mediterranean scrublands. These results might have both theoretical and applied implications. From a theoretical point of view, they stress the role of local niche and history on species sorting along metacommunities, and suggest that dispersal might often play a relatively minor role on local community assembly, especially if it occurs at a slower rate than local dynamics (Leibold et al. 2004; Mihaljevic 2012). From an applied point of view, the study highlights the need of including patch dynamics into habitat conservation schemes, as it might determine a large part of heterogeneity in the presence and abundance of particular species, and in the ecological interactions they carry out. Spatially explicit approaches, combining historical and current habitat maps using GIS, are especially indicated for this purpose.

4. Species balance in plant community assembly in novel periurban forests: the role of dispersal type and of habitat and landscape factors

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Abstract

This study explores the association of forest patch history, landscape pattern (i.e. forest connectivity and urbanization) and habitat condition with plant species richness and composition in peri-urban Mediterranean forests. We randomly selected 128 plots of 314 m2 stratified by forest historical type and forest connectivity (i.e. forest cover) and urbanization (i.e. urban cover) of the surrounding landscape. We determined forest historical type by combining land cover maps of 1956 and 2009, and we classified forests in pre-existing (i.e. those occurring in 1956 and 2009) and recent (only occurring in 2009). Also, we assessed forest and urban cover from the 2009 map. We then recorded cover of all vascular plant species in plots, and we assigned them to these groups: forest, scrubland-grassland, synanthropic and other. Still, we classified forest species into vertebrate-dispersed species and other. We assessed habitat condition through a set of climatic and habitat variables, obtained from field work and digital cartography. We then performed GLMs to find the effects of these factors on richness and cover of total species and those of the studied groups. Results show that habitat (e.g. climate, soil depth and tree density) and landscape structure (especially forest cover in the landscape) are the main drivers of plant community assembly. However, there is a secondary effect of forest historical type, shaped in (i) extinction debt of scrubland-grassland species, (ii) higher colonization of synanthropic species, and (iii) colonization credit of cover of vertebrate-dispersed forest species in recent forests compared with pre-existing ones. Thus, community assembly in recent forests is characterized by the remaining of some species from previous habitats, rapid colonization of habitat specialists, and a transient increase in synanthropic species. Results also highlight the importance of managing landscape structure for favoring forest specialists in plant community assembly in novel peri-urban forests.

Keywords: extinction debt; forest connectivity; immigration credit; landscape urbanization; Mediterranean forests; plant species richness; site condition.

Introduction

It is known for long that land use and cover change (LUCC) is affecting biodiversity patterns worldwide (e.g. Sala et al. 2000). The underlying processes driving community assembly along the subsequent changes in habitats are, however, under debate since MacArthur & Wilson (1967), with contrasting positions stating a key role of either species niche (e.g. MacArthur & Levins 1967; Chase & Leibold 2003; Tilman 2004; Leibold & McPeek 2006) or species dispersal (Levin 1974; Hubbell 2006). In addition, community assembly is strongly affected by land use legacy, which often determines historical signals in current communities (e.g. Hermy & Verheyen 2007; Vellend et al. 2007). This is partially due to the fact that effects of land use changes on biodiversity often are delayed, determining both extinction debts (Tilman et al. 1994; Kuussaari et al. 2009) of species from vanishing habitats and colonization credits (Cristofoli et al. 2010; Jackson & Sax 2010) of those from the new habitats. Depending on the timing and magnitude of these processes, transient species surpluses or deficits might be recorded during habitat changes independently of the final balance (i.e. the difference in species richness between original and final habitats; Jackson & Sax 2010). In the case of plants, this balance might be affected by a plethora of life-history traits affecting species' life-cycle (Lavorel & Garnier 2002; Kuussaari et al. 2009; Díaz et al. 2009), but especially by seed dispersal (Verheyen et al. 2003; Flinn & Vellend 2005; Karst et al. 2005; Ozinga et al. 2005; Svenning et al. 2009; Myers & Harms 2009; Götzenberger 2012) and seedling establishment processes (Clark et al. 1998; Öster et al. 2009; Marteinsdóttir 2014). The role of these processes in species' persistence and colonization across habitat change might be, in turn, modulated by the spatial pattern of habitat patches and their surrounding landscapes (Díaz et al. 2009; Svenning et al. 2009; Martín-Queller et al. 2011).

Recent forest transition in European Mediterranean regions provides a good case study of community assembly in new habitats resulting from LUCC. Forests in these regions have partially recovered in the last 50 years from old croplands and pasturelands, due to regional and international socio-political drivers (Grove & Rackman 2001; Basnou et al. 2013; Tomaz et al. 2013). Bagaria et al. (2015) found a predominance of extinction debt of grassland and scrubland species over colonization credit of forest plants along habitat change gradients from open habitats to forests. This drives to transient biodiversity surpluses (*sensu* Jackson & Sax 2010) of vanishing grassland/scrubland species, yet this pattern is largely dependent on a number of local and landscape factors. Basnou et al. (2016), in a study focused on woody plants, found colonization credits limited to vertebrate-dispersed species in recently grown forests, and suggested that niche and landscape constraints affect seed dispersal and seedling establishment of these species. At more local scale, Navarro-González et al. (2013) found that landscape pattern and history modulates dispersal and establishment of *Quercus ilex,* a dominant tree species, in pine plantations.

Forest recovery is also occurring in Mediterranean peri-urban regions as part of complex landscape change patterns, as it often coincides with intense urban sprawl (Catalan et al. 2008). This drives to the replacement of traditional rural-urban landscape gradients by sharp contacts between forests and the new urban peripheries (Basnou et al. 2013). These changes presumably affect metropolitan forests, whose structure, functioning and species composition are strongly determined by human activity (Nowak 1993; Heynen & Lindsey 2003; Guirado et al. 2007, 2008; Dobbs et al. 2011, 2013; Ramage et al. 2013). Thus, novel (*sensu* Hobbs et al. 2006) community assembly rules might be operating in human-altered landscapes because of its degree of transformation and LUCC rates. Previous works have found that plant species richness and composition in metropolitan forests are mostly determined by local disturbance and landscape transformation, suggesting that these factors might favor extinction of forest specialists and colonization by non-forest species (Hobbs 1988; Honnay et al. 1999; Hobbs 2000; Godefroid & Koedam 2003; Guirado et al. 2007). Structure and dynamics of the surrounding landscape also drive invasion by alien plants in metropolitan habitats (Basnou et al. 2015). In any case, it is largely unknown how these processes coexist with the general forest community assembly, and how they affect structure, composition, and functioning in novel forests.

The aim of the present study was to assess the importance of dispersal type, habitat and landscape factors on plant community assembly in recent peri-urban forests. We took advantage of a previous general assessment in the metropolitan region of Barcelona (Guirado et al. 2007), showing a primary effect of local habitat condition and a secondary role of landscape on plant species richness and composition in these forests. Here, using a space-for-time approach, we have combined historical (1956) and present-day (2009) land cover maps to identify recent (post-1956) and preexisting (pre-1956) forests, and to compare their species richness and composition (i.e. richness of habitat and dispersal types) while considering site conditions and landscape traits related to forest connectivity and urbanization. Then, the study was aimed at exploring the following hypotheses:

1. Plant community assembly in recent peri-urban forests is mostly driven by habitat factors as suggested by Guirado et al. (2007) in the overall forest set. However, the surrounding landscape might play a modulating role on this assembly process, with forest connectivity and urbanization favoring and limiting forest plants, and determining the opposite effects on non-forest ones.
2. Time-lags in species extinction and colonization are expected along plant community assembly in these novel forests, with extinction debts of species from the previous habitats and colonization credits of forest specialists.
3. The interplay between landscape structure and species dispersal type might also modulate this assembly process, especially in the case of forest species dispersed by vertebrates as suggested by Basnou et al. (2016).

Methods

Study site

The study was performed in the Vallès lowland (35 500 ha), in the metropolitan area of Barcelona (Catalonia, NE of Spain; Figure 4.1). Climate is typically Mediterranean, with mild winters and warm and dry summers. Mean annual temperature ranges from 13 to

15 ºC and mean annual precipitation from 630 to 830 mm, according to the Digital Climatic Atlas of Catalonia (www.opengis.uab.cat/acdc/). The area is characterized by a strong climatic gradient, with an increase in annual rainfall and a decrease in mean temperature from SW to NE (Guirado et al. 2007).

Major land-use changes have occurred during the last decades in this area (Guirado et al. 2008; Basnou et al. 2013) as a result of a gradual increase of industrial and urban areas, as well as crop abandonment. Indeed, the Vallès area has undergone a gradual increase of industrial and urban areas since a high immigration flux during the 60's and 70's in the last century, triggered by the proximity to Barcelona. This fact, added to crop abandonment, generated a highly man-modified and fragmented landscape. Some forest areas have been reduced by urbanization, despite others showed a noticeable forest regeneration after pasture and crop abandonment (Basnou et al. 2013).

Plot selection and data set

Sampling design was performed to select recent and preexisting forests along the climatic, forest connectivity and landscape urbanization gradients in the Vallès lowland (Figure 4.1). Non-calcareous areas (which are relatively rare in the Vallès) and those located above 400 m a.s.l. (which we considered out of the Vallès lowlands) were avoided, in order to reduce the environmental variation observed in previous studies and responsible for high variation in plant species composition (Guirado et al. 2007). In the remaining areas, a total of 128 plots were selected and randomly distributed in two groups of 64, corresponding respectively to preexisting and recent forests. These forest historical types were identified by combining land cover maps of 1956 and 2009. Thus, preexisting forests were those present in both maps, while recent forests were only present in that of 2009 (Figure 4.2a; Basnou et al. 2013).

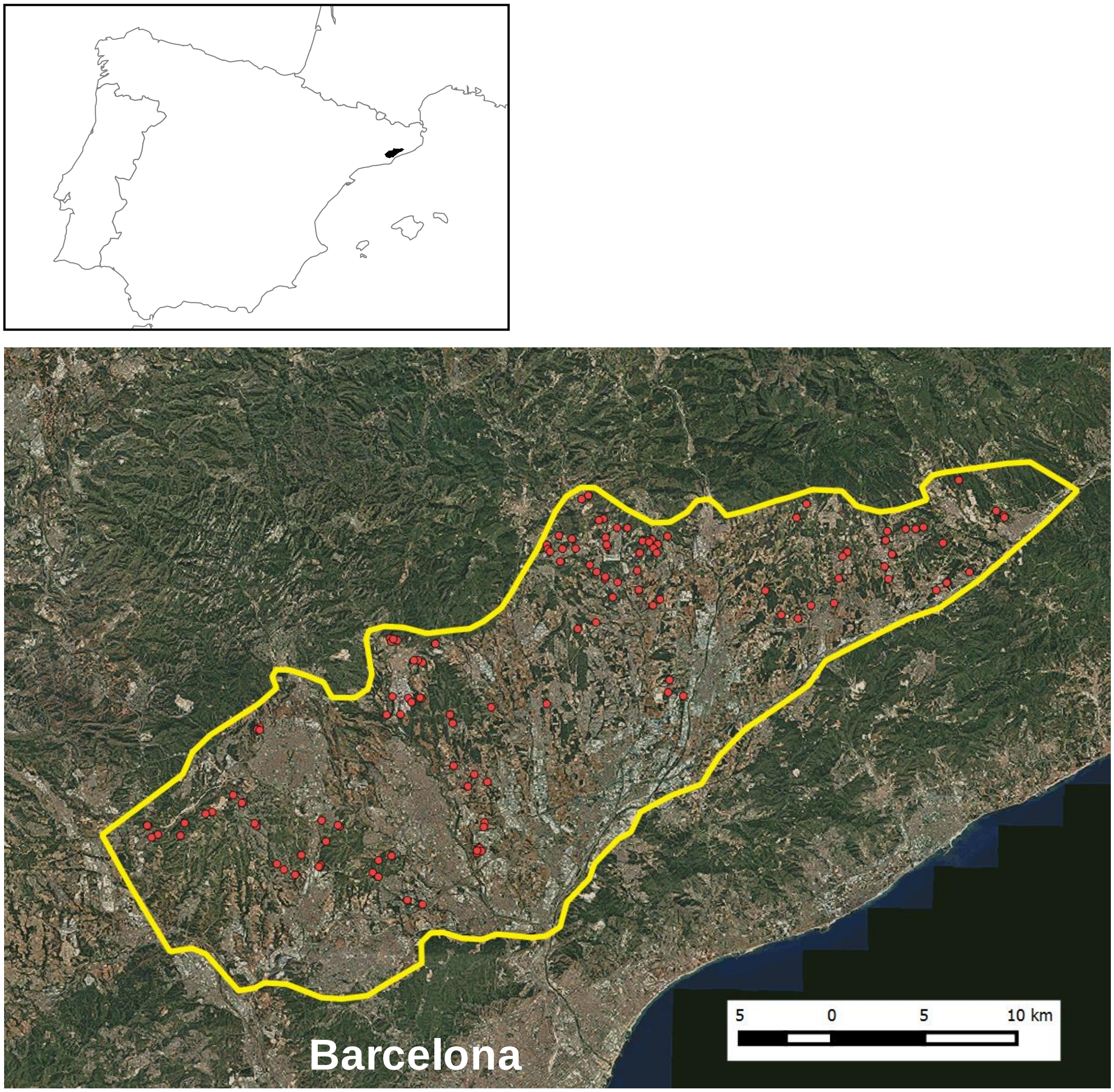

Figure 4.1. Location of the study area and plots in the metropolitan area of Barcelona (NE of Spain). Polygon approximately indicates the Vallès Lowland.

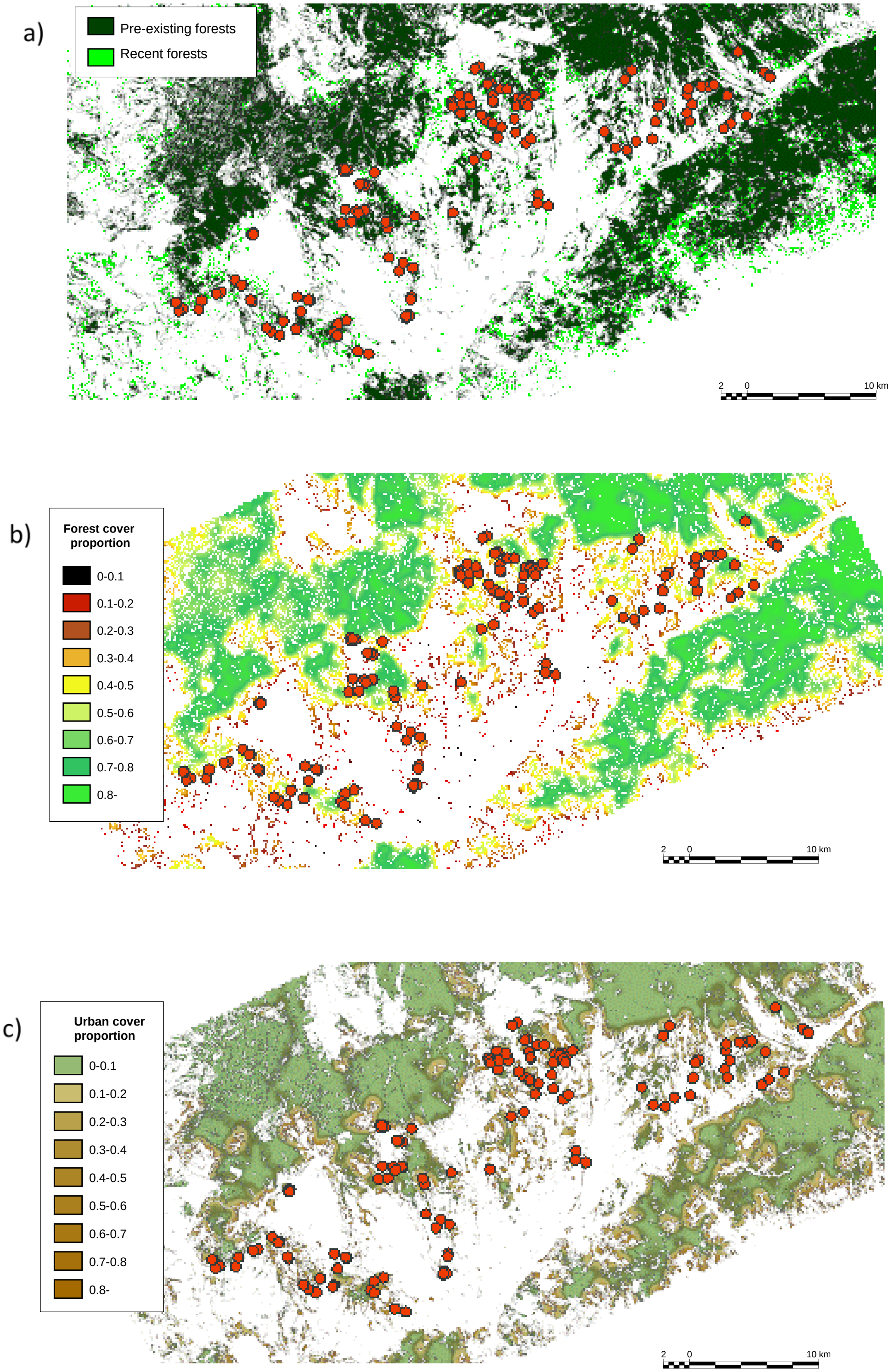

Figure 4.2. Historical types (a), current forest cover (b) and current urbanization cover (c) in a 500-m buffer around the studied forests.

Current (2009) forest connectivity (Figure 4.2b) and urbanization (Figure 4.2c) were estimated by obtaining respective models of forest and urban cover proportion in a buffer of 500 m around a given point across the landscape. These variables were calculated using the MiraMon GIS (Pons 2000). We selected a set of 20000 points regularly distributed across the study area, every 250 m, for which values were calculated. Then, values were interpolated at 10-m pixel size across the 2009 forest area using the inverse of distance as interpolation weight. Since forest connectivity and urbanization are not independent (see Chapter 2 and Figure 2.4 for details), we have tried to select both pre-existing and recent forest samples across a combination of forest and urban cover (low, medium, high). On each category combination were equally distributed 16 plots in the surrounding 500-m radius landscape.

Complementary environmental variables

Habitat condition was characterized by a number of habitat variables recorded in the selected plots by field work (Appendix B.1). Slope and aspect were measured using a clinometer and a compass. Forest structure was assessed by measuring the DBH of all trees of more than 5 cm in diameter within the same radius. The percentage of photosynthetically active radiation (PAR) reaching forest understory was estimated by comparing the mean values of two measures per plot obtained beneath and outside forest canopy, using a ceptometer (AccuPAR LP-80; Decagon Devices, Inc., Pullman, WA). Stoniness (i.e. percentage of stones in soil) was visually evaluated. Mean soil depth was estimated as the mean of four measurements made at each plot, using a 1 m long iron stake.

Human disturbance and management were also qualitatively assessed. Similarly to Guirado et al. (2007), human disturbance was scored as low, moderate or high, depending on the evidence of trampling and presence of refuse. Management was assessed from time since the last forest management scored as: recent management (cutting), when we found cut branches; old management, when traces were only cut stumps; or null management, when we did not find any traces of management. Climatic and geographic attributes of sampling plots were obtained from digital cartography. Mean temperature and annual rainfall were obtained from the Digital Climatic Atlas of Catalonia (www.opengis.uab.cat/acdc/) while plot elevation was inferred from the official Digital Elevation Model (DEM) of Catalonia (Cartographic Institute of Catalonia). Sampling plots were geo-referenced in the field by using a GPS and set up in a geo-referred point layer, which was combined with the climatic and DEM layers using the MiraMon GIS tools (Pons 2000).

The mean values of all environmental variables were compared between pre-existing and recent forests using T-tests for quantitative variables and Chi Square tests for the categorical independent variables (aspect, disturbance and management), Bonferroni correction was also applied. These tests showed little differences between forest historical types, as only management was significantly different between pre-existing and recent forests (Appendix B.1 and B.2).

Plant species data

Cover percentage of all vascular plants was recorded in a radius of 10 m around the plot center, using the semiquantitative scale of Braun-Blanquet (+,<5%; 1, 5-10%; 2, 10-25%; 3, 25-50%; 4, 50-75%; 5, >75%). Following previous studies (Guirado et al. 2006, 2007), plants were classified into four habitat types (Appendix B.3) based on local floras (Bolòs et al. 1990): forest, scrubland-grassland, synanthropic (associated to human activity, like ornamental, crop and ruderal species, either native or alien), and other. Species were also classified in two major dispersal types: vertebrate-dispersed (i.e. those producing fleshy or dry fruits specifically adapted to be dispersed through endozoochory or diszoochory) and non-vertebrate-dispersed (including those species potentially dispersed through ectozoochory). Species richness (i.e. the number of species) and mean species abundance (i.e. average species cover) per plot were calculated for each group.

Statistical analyses

We first explored if forest age determines changes in the importance of the different plant dispersal types. Thus, we evaluated the association between dispersal and forest historical types in terms of species frequency using a chi-square test, and that of species cover with dispersal and habitat types and their interaction using ANOVA tests.

We then used Generalized Linear Models (GLM) to assess the association of forest historical type (pre-existing vs. recent), habitat (including habitat condition, climate, latitude and longitude) and landscape (forest connectivity and landscape urbanization) factors with species richness and cover of each habitat type per plot. In the case of forest species, this was also assessed between dispersal types. Linear Pearson´s correlation coefficients were used for continuous independent variables in order to reduce multicollinearity. The threshold value used for deciding on redundancy was $|r| = 0.75$. Elevation and UTM Y were discarded because they were highly correlated to temperature ($|r| = 0.960$) and UTM X ($|r| = 0.783$), respectively. Levene test was used to test homogeneity of variances. In GLM models, Poisson distribution of errors was used for species richness while Gaussian distribution was used for species cover. Categorical variables (aspect, disturbance, management and forest historical type) were included in the models as dummy variables.

Results

Habitat types

A total of 226 plant species were recorded in the study (see Appendix B.3 for details), which were classified into the habitat type groups as follows: 64 as forest species, 89 as scrubland-grassland species, 67 as synanthropic species, and 6 as other. Forest, scrubland-grassland and synanthropic species make up 54.8, 28.5 and 12.2%, respectively, of total richness in recent forests, while these percentages are 64.3, 19.0 and 11.6% respectively in preexisting forests.

On average, there were 21.5 species per plot, ranging from 9 to 46 species (SD ± 6.5), per plot (see means and SD in Figure 4.3). Mean species richness per plot was 23.2 and 19.9 in recent and preexisting forests, respectively. Those of forest, scrubland-grassland and synanthropic species were respectively 13.5, 6.6, and 2.8 in recent forests, and 13.7, 3.8 and 2.3 in preexisting forests. On average, species cover was 18.1% (SD ± 6.6), ranging from 5.4 to 37.5% per plot. Forest, scrubland-grassland and synanthropic species showed a mean cover of 20.7, 12.4 and 6.4%, respectively. Species of these habitat types showed respectively a mean cover of 19.8, 14.9 and 5.7% in recent forests, while these percentages are 21.5, 9.9 and 6.4% respectively in old forests.

Regarding species richness, the model for total species accounted for 30% of total variance (Table 4.1), with species richness being negatively associated to tree density and mean temperature, and positively associated to UTM X coordinate, stoniness and recent forest. Total species richness also shows a marginally significant association with W aspect. The model for total forest species captured 15% of total variance, being species richness positively associated to UTM X coordinate and to the percentage of forest surrounding the patch. The model for scrubland-grassland species accounted for 45% of total variance, being species richness negatively associated to mean temperature, tree density, mean soil depth, percentage of PAR, and the percentage of both forest and urban areas surrounding the patch. It is also positively associated to recent forests, annual rainfall and, marginally, to stoniness. It is, still, positively associated to W aspect, old management and negatively to medium and low disturbance. The model for synanthropic species richness captured 43% of variance, with species richness being positively associated to recent forests, UTM X coordinate and stoniness, and negatively to rainfall, northern aspect, tree density and forest cover in the surrounding landscape.

The model for total species cover captured 38% of variance (Table 4.2). Species cover was positively associated to forest cover in the landscape, soil depth, stoniness, mean temperature and low disturbance compared with the reference level (high disturbance), while it was negatively associated to UTM X coordinate and, marginally, to recent management compared with the reference level (null management). The model for forest species cover accounted for 26% of variance, with soil depth, stoniness, mean temperature and low disturbance (compared with the reference value, high disturbance) being positively associated to species cover. In contrast, recent forests are negatively associated to species cover. In the case of scrubland-grassland species, the model accounted for 21% of variance. Recent forests, UTM X coordinate and percentage of urban cover in the surrounding landscape are negatively associated, while mean annual temperature is positively associated to species cover. The model for synanthropic species explained 23% of variance, with UTM X being positively associated while forest cover in the landscape, rainfall and tree density being negatively associated to species cover.

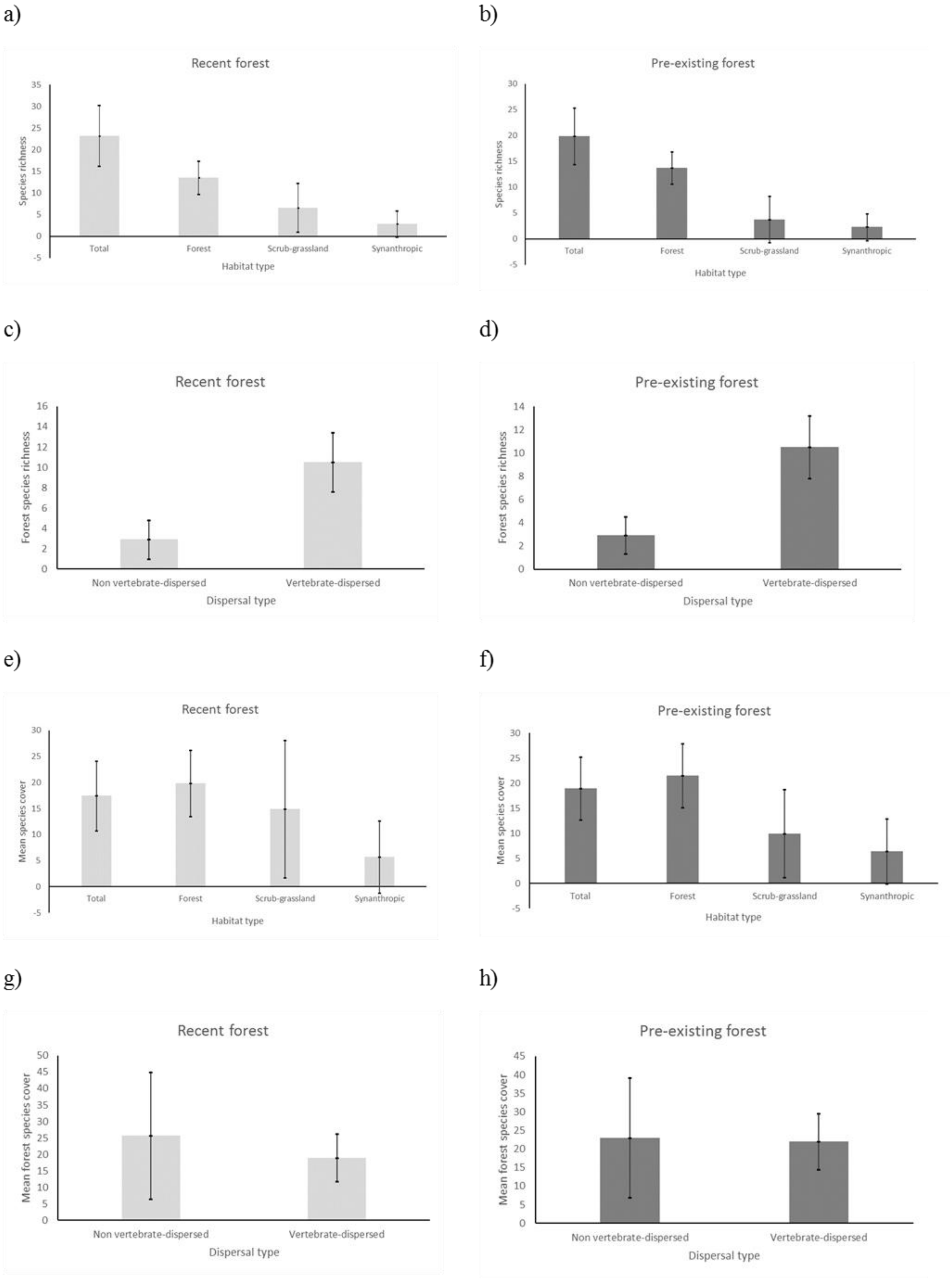

Figure 4.3. Mean and standard deviation of species richness and mean cover by habitat and dispersal (in the case of forest species) types per forest historical type.

Table 4.1. Results of Generalized Linear Models for richness of total species and those of the main habitat types. Pseudo-r^2 values have been calculated as the opposite of the ratio between residual and model deviances. Only significant and marginally variables are shown (significance: · P<0.1; * P<0.05; ** P<0.01; *** P<0.001).

	Estimate	SE	Z-value	Sig.
Total species (pseudo r^2= 0.30)				
UTM X	1.10E-05	2.44E-06	4.515	***
Aspect-W	1.08E-01	5.56E-02	1.938	.
Stoniness	4.42E-03	1.64E-03	2.698	**
Mean temperature	-1.08E-01	4.66E-02	-2.323	*
Tree density	-4.45E-03	1.27E-03	-3.495	***
Forest historical type-Recent	1.19E-01	4.08E-02	2.912	**
Forest species (pseudo r^2= 0.15)				
UTM X	5.91E-06	2.05E-06	2.885	**
Forest cover in landscape	3.04E-01	1.35E-01	2.259	*
Scrub-grassland species (pseudo r^2= 0.45)				
Forest cover in landscape	-0.755459	0.259688	-2.909	**
Urban cover in landscape	-0.879247	0.259472	-3.389	***
Aspect-W	0.538516	0.124497	4.326	***
PAR	-0.898285	0.225249	-3.988	***
Mean soil depth	-0.014217	0.006129	-2.319	*
Stoniness	0.006195	0.003262	1.899	.
Annual rainfall	0.002214	0.001097	2.017	*
Mean temperature	-0.859323	0.104413	-8.23	***
Tree density	-0.013423	0.002968	-4.523	***
Disturbance-Low	-0.274505	0.11107	-2.471	*
Disturbance-Medium	-0.210314	0.117066	-1.797	.
Forest-Recent	0.478039	0.091716	5.212	***
Management-Old	0.220194	0.095928	2.295	*
Synanthropic species (pseudo r^2= (0.43)				
UTM X	7.83E-05	1.06E-05	7.406	***
Forest cover in landscape	-1.28E+00	3.70E-01	-3.462	***
Aspect-N	-3.56E-01	1.73E-01	-2.06	*
Stoniness	1.77E-02	5.03E-03	3.518	***
Annual rainfall	-6.42E-03	1.71E-03	-3.754	***
Tree density	-1.37E-02	3.64E-03	-3.77	***
Forest historical type -Recent	2.25E-01	1.14E-01	1.967	*

Table 4.2. Results of Generalized Linear Models for cover of total species and those of the main habitat types. Pseudo-r2 values have been calculated as the opposite of the ratio between residual and model deviances. Only significant and marginally variables are shown (significance: · P<0.1; * P<0.05; ** P<0.01; *** P<0.001).

	Estimate	**SE**	**t-value**	**Sig.**
Total species (r^2=0.38)				
UTM X	-2.34E-04	6.60E-05	-3.548	***
Forest cover in landscape	6.14E+00	2.71E+00	2.266	*
Mean soil depth	1.61E-01	7.42E-02	2.168	*
Stoniness	9.77E-02	4.28E-02	2.282	*
Mean temperature	5.78E+00	1.24E+00	4.664	***
Disturbance-Low	3.83E+00	1.30E+00	2.939	**
Management-Recent	-3.74E+00	2.03E+00	-1.84	.
Forest species (r^2= 0.26)				
Mean soil depth	1.83E-01	7.73E-02	2.373	*
Stoniness	1.20E-01	4.33E-02	2.775	**
Mean temperature	3.88E+00	1.26E+00	3.067	**
Disturbance-Low	3.64E+00	1.37E+00	2.657	**
Forest-Recent	-2.16E+00	1.01E+00	-2.135	*
Scrub-grassland species (r^2= 0.21)				
UTM X	-2.60E-04	7.79E-05	-3.338	**
Urban cover in landscape	-1.08E+01	4.99E+00	-2.164	*
Mean temperature	4.09E+00	2.17E+00	1.883	.
Forest historical type - Prexisting	-4.46E+00	1.85E+00	-2.407	*
Synanthropic species (r^2= 0.23)				
UTM X	2.65E-04	6.73E-05	3.934	***
Forest cover in landscape	-6.75E+00	2.91E+00	-2.321	*
Annual rainfall	-5.06E-02	1.35E-02	-3.761	***
Tree density	-6.12E-02	3.38E-02	-1.809	.

Dispersal types

Species frequency per dispersal type (vertebrate- *versus* non vertebrate-dispersed) is significantly associated to forest historical types (Chi-squared 61.26, df 3; p<0.001). The majority (62.5%) of forest species are vertebrate-dispersed, while this percentage is considerably lower in scrubland-grassland (33.8%) and much lower in synanthropic species (4.3%). Of total species, only 28.7% are vertebrate-dispersed, being species cover significantly associated to habitat type (F=6.28; df=3; p<0.001) but not to dispersal type (F=0.35; df=1; p=0.55) or to its interaction (F=0.21; df=1; p=0.81).

Models of forest species richness per dispersal type explained a low percentage of variance (between 13 and 16%; Table 4.3). Richness of vertebrate-dispersed species is positively related with mean temperature and the percentage of forest in the surrounding landscape, and marginally with annual rainfall. In contrast, that of non-dispersed by vertebrates is only related with X coordinate and, marginally, to tree basal area, showing positive associations in both cases. As for species cover, models explained between 23 and 35% of variance. Cover of vertebrate-dispersed species is positively associated to preexisting forests, to the percentage of forest in the surrounding landscape, and to a set of habitat variables including soil depth, stoniness and mean temperature. It is also positively related with low and medium disturbance levels, but these associations are only marginally significant. Still, it is negatively associated to recent management compared with the reference value (null management). In the case of species not dispersed by vertebrates, species cover is positively associated to low disturbance compared to the reference value (high disturbance), and negatively associated to X coordinate, tree basal area, and urban cover in the landscape (in this case, the association is only marginally significant).

Table 4.3. Results of Generalized Linear Models for the richness and cover of forest species classified according dispersal types (vertebrate *versus* non vertebrate-dispersed). Pseudo-r^2 values have been calculated as the opposite of the ratio between residual and model deviances. Only significant and marginally variables are shown (significance: · $P<0.1$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$).

	Estimate	**SE**	**Z-value**	**Sig.**
Species richness				
Vertebrate-Dispersed species (pseudo r^2=0.16)				
Forest cover in landscape	0.3572787	0.1483717	2.408	*
Annual rainfall	0.0008615	0.0004647	1.854	.
Mean temperature	0.1387025	0.0691301	2.006	*
Non vertebrate-Dispersed species (pseudo r^2=0.13)				
UTM X	1.74E-05	4.35E-06	3.992	***
Tree basal area	5.47E-07	3.08E-07	1.775	.
Species cover				
Vertebrate-Dispersed species (r^2=0.35)				
Forest-Preexisting	3.72E+00	1.25E+00	2.977	**
Forest cover in landscape	1.17E+01	3.66E+00	3.197	**
Mean soil depth	2.19E-01	8.92E-02	2.453	*
Stoniness	9.81E-02	5.12E-02	1.917	.
Disturbance-Low	-3.24E+00	1.69E+00	-1.916	.
Disturbance-Medium	2.55E+00	1.37E+00	1.866	.
Management.-Recent	-7.39E+00	2.44E+00	-3.033	**
Mean temperature	5.67E+00	1.49E+00	3.796	***
Non vertebrate-Dispersed species (r^2=0.23)				
UTM X	-6.20E-04	1.26E-04	-4.934	***
Urban cover in landscape	-1.46E+01	7.84E+00	-1.869	.
Disturbance-Low	1.29E+01	4.13E+00	3.113	**
Tree basal área	-2.12E-05	9.95E-06	-2.132	*

Discussion

The ultimate goal of this study was to understand plant community assembly in novel periurban forests resulting from recent land use and cover change (LUCC) in periurban landscapes. Using a space-for-time approach, we have compared plant species richness and cover for a set of species groups between recent (appeared after 1956) and pre-existing forests in landscapes with contrasting urban and forest cover, and while considering a set of concomitants, environmental factors. Complementary tests confirm that these forest historical types show scarce differences in their habitat and landscape variables (Appendix B.1) and results obtained from their comparison are, therefore, fully consistent.

Our study complements a previous work by Guirado et al. (2006, 2007) performed in the same study area but focused on the association between present landscape structure and plant biodiversity. A main result of our study is that forest historical type plays a secondary role in plant community assembly in peri-urban forests compared with habitat and landscape factors. Indeed, overall plant species richness and abundance and those of the studied groups are especially determined by current forest cover in the landscape, but also by a set of habitat factors. In any case, there is a significant effect of forest history that is reflected in the following results: recent forests exhibit (i) some extinction debt of species from previous scrublands and grasslands, (ii) a (transient) surplus of synanthropic species, and (iii) some colonization credit in the case of forest species, yet limited to species cover of vertebrate-dispersed. Combined, these processes determine a likely transient species surplus (i.e. higher total species richness) in recent forest compared with the pre-existing ones.

Relevance of landscape and site condition

As hypothesized, plant community assembly in peri-urban forests is mostly associated to habitat condition and landscape variables, particularly to those related with forest condition and connectivity, and human-induced disturbance. Forest cover in the surrounding landscape is positively associated to forest species richness. It is a proxy of habitat connectivity, which is considered a key driver of community assembly (e.g. Diaz et al. 1998; Bailey 2007; Montoya et al. 2008; Svenning et al. 2009; Martín-Queller et al. 2011). However, forest cover also includes other patch and landscape traits like landscape grain (i.e. mean patch size), patch connectivity (i.e. distance between patches), and edge effects (i.e. distance from the forest edge). A decrease in forest cover usually leads to forest fragmentation, with a decrease in patch size and connectivity and an increase in the proportion of forest edges. These changes in the forest spatial pattern affect the exchange of habitat specialists between forest patches, and this in turn affects plant species richness and composition (Holt et al. 1995; Hanski 1999; Bascompte & Rodríguez 2001; Vellend 2003; Guirado et al. 2007). We have also shown that forest cover is negatively associated to both scrubland-grassland and synanthropic species richness. Changes in forest spatial pattern associated to forest loss and fragmentation enhance the colonization of non-forest species through forest edges, which become more abundant (e.g., Hobbs 1988, 2000; Wiens 1992; Murcia 1995; Guirado et al. 2006; González-Moreno et al. 2013b). Forest edges are particularly suitable for open habitat species, e.g. due to light availability (Godefroid & Koedam 2003), and they are especially vulnerable to invasion by synanthropic species coming from the adjacent human-transformed habitats (Hobbs 1988; Wiens 1992; Murcia 1995; Hobbs 2000; Guirado et al. 2006, González-Moreno et al. 2013b). Forest cover in the landscape is also associated to total and synanthropic species cover, with positive and negative associations respectively. These effects might be, however, due to the known effects of forest fragmentation on forest disturbance due to human frequentation (Godefroid & Koedam 2003; Guirado et al. 2006).

Our study failed to detect urban cover in the landscape as a prominent correlate of plant species richness and cover. It is largely known that landscape urbanization strongly affects plant community assembly in peri-urban forests (Guirado et al. 2007; González-Moreno et al. 2013b), preventing forest plants from colonizing newly created forest patches and also promoting the colonization of ruderal and garden plants, both native and exotic (Brothers & Spingarn 1992; Hobbs 2000). In our case, however, urban cover is only related to scrubland-grassland species richness and cover, with negative associations in both cases. Guirado et al. (2007) found that scrubland-grassland species richness increases with distance to roads, suggesting that human-induced disturbance associated to landscape pattern might especially affect these species. Surprisingly, urban cover was not significantly associated to either synanthropic species richness or cover; this might indicate that the high disturbance characterizing peri-urban landscapes makes urban cover in the adjacent landscape scarcely relevant for synanthropic species invasion, contrarily to that suggested in previous works (Guirado et al. 2007).

A number of habitat condition factors are related with species richness and cover, in total and per groups, but most recurrent habitat factors in models are tree density, soil depth and stoniness, which are typical indicators of site condition in forest stands. Tree density is negatively associated to total species richness and to richness and cover of non-forest (scrubland-grassland and synanthropic) species. This matches with the fact that these species are especially favored by non-dense forests, as they are generally less shade-tolerant than forest ones (Deconchat & Balent 2001; Pauchard & Alaback 2004; Guirado et al. 2007). Soil depth increases both total and forest mean species cover, due to the higher amount of water and resources. It should be noted that stoniness increases both species richness and cover in total and forest species, and even synanthropic species richness. Soil stoniness might increase micro-scale heterogeneity thus favoring species diversity, as found by Harner & Harper (1976) in *Juniperus* stands, but also reducing size inequalities among species thus increasing mean species cover. Both theoretical and empirical (e.g. Lundholm 2009) evidence exists for a positive relationship between environmental heterogeneity and species diversity, through heterogeneity in productivity and disturbance (Huston 1994), especially when neutral models in community assembly are considered (Hubbell 2001).

Our study has also considered direct measures of human disturbance and management in forests, but its effect on plant species richness and cover was quite limited. In addition, low disturbance increases mean total and forest species cover when compared with the reference value (high disturbance). These results match with the intermediate disturbance hypothesis (Connell 1978), which states that diversity of competing species is expected to be maximized at intermediate frequencies and/or intensities of disturbance or environmental change. However, this hypothesis has been questioned on both empirical and theoretical grounds (e.g. see Fox 2013), and it appears to be strongly dependent on habitats and species types. For example, we have found that scrub-grassland species richness is negatively affected by both low and medium disturbance levels compared to high one and this suggest that these species, mostly early successional and shade-intolerant, are benefited from high disturbance in forests. In contrast, we have not found this trend for synanthropic species, which are of ruderal habit. In contrast, Guirado et al. (2007), found a positive association of high disturbance with synanthropic species richness and cover in the same study area, while and limiting the study to the eastern Vallès.

The study also detected some effects of regional and climatic gradients in plant community assembly in the study forests, yet results are sometimes contradictory. Total, forest and synanthropic species richness increase eastwards, probably due to a complex set of factors including climate gradients (as mentioned above, it becomes colder and rainier eastwards), general history of land use but also a decrease in the "metropolitan effect" of Barcelona that might have determined the historical disturbance regime in forests. In some cases, climatic variables reinforce this statement: scrub-grassland species richness is negatively associated to mean temperature and positively associated to annual rainfall. In contrast, synanthropic species richness is negatively associated to rainfall, suggesting that land use rather than climate factors might be associated to this pattern. For example, the agroforestry mosaics in the east limit of the study area might provide a larger species pool of synanthropic species than the periurban areas in the west, despite no data are available to test this statement. In contrast, mean cover of total, forest, and scrubland-grassland species are positively associated to mean temperature and that of synantropic species is negatively associated to rainfall, suggesting that mean species cover increases in dry, hot climates were forest canopy cover tend to be lower (Selkimäki et al. 2012). This would explain the decrease eastwards in cover of these species groups. Again, however, synanthropic species break this pattern, suggesting the concurrence of local land use factors.

The role of forest history

Despite the prevalence of current habitat and landscape factors, forest historical type also plays some role on plant community assembly in the studied periurban forests. We have hypothesized that recent forests exhibit lower species richness and cover than pre-existing forests, due to the existence of colonization credits (Basnou et al. 2016). However, we have observed higher richness of scrubland and grassland species in recent forests, which can be interpreted as an extinction debt of species from previous habitats (i.e. crops, pastures and scrublands of 1956), as suggested by Bagaria et al. (2015) in vanishing grasslands subjected to forest encroachment. Similarly, we have found that synanthropic species richness is positively associated to recent forests. Peri-urban forests are especially affected by ruderal, cultivated and alien species associated to human activity (Guirado et al. 2007). Even so, previous studies have reported the replacement of native species with non-native ones following disturbance, even leading to the extinction of some forest specialists and to biotic homogenization (Chapin III et al. 2000; McKinney 2006; Kowarik 2011; Guirado et al. 2007; Barrico et al. 2012). We have not dealt with alien species specifically (but see chapter 5), yet synanthropic species include some proportion of aliens. Since land use changes provide transient windows of opportunity for the establishment of alien species, we expect an increase in synanthropic species in novel forest assemblages that can disappear after a relaxation time, as reported in previous studies (e.g. Kuppinger et al. 2010; Pino et al. 2013).

Also, we have found that overall richness and cover and those of habitat specialists, i.e. forest plant species, were non-significantly associated to forest historical type. These findings disagree with those from temperate forests, where the immigration credit of particular species might persist for decades or even centuries (Hermy et al. 1999; Hanski 2000; Honnay et al. 2002; Jacquemyn et al. 2003: Vellend 2003; Flinn & Vellend

2005; Vellend et al. 2006; Naaf & Kolk 2015).Thus, contrary to some authors who supported that equilibrium is rarely achieved quickly in biodiversity dynamics and that centuries will be required for certain plant species to reestablish populations in recent forests (Peterken 1996; Bellemare et al. 2002; Vellend 2003; Jackson & Sax 2010), our study shows a rapid immigration (<50 years), almost equalizing most of the plant groups in recent and pre-existing forests. This matches with that observed in other woody habitats like recently restored heathlands (Cristofoli et al. 2010). Two main explanations have been proposed. First, that Mediterranean forests have a long history of human disturbance (Rackham & Grove 2001; Marull et al. 2010), and this might have altered natural site conditions thus decreasing the expected forest species richness and the possible colonization credits in novel community assemblages. As forest alteration might be especially important in peri-urban areas (Guirado et al. 2007), the potential differences in species richness between pre-existing and recent forests might be still more reduced in these forests. On the other hand, the lack of colonization credit might be partially due to a rescue effect (Brown & Kodric-Brown 1977; Piessens et al. 2004) of populations from adjacent open habitats, as many of forest species often grow in scrublands and hedgerows (Bolòs et al. 2005). Thus, colonization of recent forests by these species might be immediate in the case of forests originated from scrublands, but also promoted by nearby hedgerow populations in those forests originated from abandoned croplands. Also, the species richness of this group is positively related with forest cover (Table 4.1), suggesting that propagule constraints due to forest scarcity affect the colonization of these species in both pre-existing and recent forests. Thus, rapid colonization of forest species and persistence of scrubland-grassland plants would determine the observed biodiversity surplus (Jackson & Sax 2010). In absence of further disturbance this surplus is expected to disappear after some relaxation time, during which species are committed to eventual extinction, especially in remote areas with low disturbance regimes (Pino et al. 2013; Bagaria et al. 2015). However, this might not be case of metropolitan regions, where high frequency and intensity of disturbance continuously opens windows of opportunity for the establishment of non-forest species (Guirado et al. 2006, 2007).

In any case, our study detected some colonization credit for forest species, but limited to mean cover of vertebrate-dispersed species (Table 4.3). This partially corroborates, for the specific case of periurban forests, the results obtained by Basnou et al. (2016) only for woody species and for the overall Barcelona region (including forestry, agroforestry and peri-urban areas). We have found that forest cover in the surrounding landscape positively affects species richness and cover of these species, and this suggests a modulating role of landscape on the behavior of dispersers, as also pointed out by other authors (e.g. see Puerta-Piñero et al. 2012 and Navarro-González et al. 2013 for *Q. ilex*). On the other hand, species cover is related to some habitat variables suggesting niche constrains of species establishment (e.g. mean soil depth and PAR; Table 4.3).

Conclusions and implications for management

We can conclude that plant community assembly in peri-urban forests is mostly driven by site condition and landscape factors, with a preeminent role of forest connectivity that promotes colonization of habitat specialists (i.e. forest species) while it prevents that of non-forest species. Forest historical type plays a secondary role in community assembly, despite new forests exhibit (i) extinction debt of species from previous open habitats (grasslands and scrublands), (ii) high colonization of synanthropic species, and (iii) some colonization credit of habitat specialists but constrained to vertebrate–dispersed species. The resulting biodiversity surplus is expected to decrease after some relaxation time when extinction and colonization events have occurred (Bagaria et al. 2015), but this outcome might be unachieved in peri-urban forests, where fragmentation often causes forest instability and enhances establishment of non-forest species (Guirado et al. 2006, 2007), thus increasing again the biodiversity surplus.

Results emphasize the importance of forest connectivity for managing plant species assemblage in peri-urban forest patches, as indicated by Guirado et al. (2006). On the other hand, they highlight the need of considering the recent history of forest patches for managing time-lags in biodiversity change in highly dynamic landscapes. A key avenue for effective forest restoration and management is obtaining reliable information on these time lags and their association to habitat deterioration, connectivity loss, and to the susceptibility of plant species to genetic deterioration and to environmental and demographic stochasticity (Hylander & Ehrlén 2013).

5. Alien plant invasion in novel metropolitan forests: the role of vertebrate dispersal

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Abstract

Forest invasion by alien plants is still largely unknown despite it might drive plant community assembly in novel forests resulting from recent land use changes, especially in human-transformed landscapes. We explored the plant invasion pattern in the metropolitan forests of the Barcelona Province (NE of Spain) through a specific sampling in the Vallès lowland combined with a set of previous databases for the province. Sampling was aimed at comparing presence, richness and abundance of total alien species and those of both vertebrate and non-vertebrate-dispersed species in recent and pre-existing forests, taking landscape and environmental correlates into account. Results show that metropolitan forests are more invaded than those of the rest of the province. Moreover, alien flora in these forests is dominated by vertebrate-dispersed species, yet the regional species pool shows a bias towards non-vertebrate-dispersed ones. Forest fragmentation is positively associated to presence, richness and cover of vertebrate-dispersed plants, while urban cover is positively associated to cover of non-vertebrate-dispersed species. There is a clear association between forest historical type and plant dispersal syndromes, with vertebrate-dispersed species being mostly concentrated in old forests and vice versa. In contrast, the study failed to detect any clear association of forest historical type or landscape structure with alien species composition, being this mostly associated with environmental factors. The study warns about the high invasion degree of metropolitan forests by alien plants and the high proportion of vertebrate-dispersed species, most of them being able to colonize relatively undisturbed forests and persist or even expand along succession.

Keywords: forest connectivity; invasion debt; landscape urbanization; Mediterranean forests, Barcelona Metropolitan Region.

Introduction

Habitat invasion by non-native species is a determinant component of global environmental change affecting ecological, economic and social systems (Vitousek et al. 1996; Davis et al. 2000; Hobbs 2000; Sala et al. 2000; Vilà et al. 2006; Vilà & Ibañez 2011). It is a highly idiosyncratic process (Pyšek et al. 2004; Blackburn et al. 2011) while depending on species invasiveness, habitat invasibility and some attributes of the invasion process (e.g. introduction time and pathway, and propagule pressure; Alpert et al. 2000; Richardson & Pyšek 2006; Gassó et al. 2009).

Habitat invasibility is largely due to intrinsic habitat properties, yet modulated by a large number of factors operating at local, landscape and regional scales (Shea & Chesson 2002; Vilà et al. 2007; Gassó et al. 2012; González-Moreno et al. 2013b, 2014). At local level, previous studies have emphasized the role of resource availability and disturbance regime in habitat susceptibility to invasion by alien plants, being human settlements, old fields, roadsides, rangelands, plantations and croplands among the most invaded habitats (e.g. Vilà et al. 2007; Chytrý et al. 2008). Both current and historical landscape context also affects habitat invasibility, and this determines a high risk of invasion of natural habitats embedded in human-transformed landscapes (Pyšek 1998). Indeed, a large number of studies show that the current landscape and its historical changes are key drivers of plant invasion in contrasting Mediterranean habitats (Vilà et al. 2003; Domènec et al. 2005; Guirado et al. 2006, 2007; Gassó et al. 2012; González-Moreno et al. 2013b; Basnou et al. 2016; Clotet et al. 2016).

Habitat invasion by alien plants is also influenced by species invasiveness (Pyšek & Richardson 2007; Gassó et al. 2009), which strongly depends on species traits (e.g. González-Moreno et al. 2013a). In particular, dispersal type has been considered a determinant trait of plant invasiveness (Vermeij 1996; Richardson et al. 2000; Gassó et al. 2009). Both dispersal by wind and by vertebrates have been identified among the most effective plant dispersal types (Rejmánek 1996; Lake & Leishman 2004) despite there is some controversy about what is the most successful one. Wind-dispersed species have been found as the most effective plant invaders in several large-scale studies (Lloret et al. 2005; Prinzing et al. 2002; Gassó et al. 2009), being especially well represented in regional alien floras (Vilà et al. 2001; Lloret et al. 2005). It has been suggested that dispersal by wind is part of a strategy of gap detection, expected to be frequent in pioneer species associated to habitat disturbance. As it is assumed that undisturbed plant communities exhibit a so-called biotic resistance against invasions (Levine et al. 2004; Martin et al. 2009), this often neglects the possibility that other plant ecological types, namely late-succesional, shade-tolerant species, might play a relevant role in the invasion of closed habitats less subjected to frequent disturbance (Martin et al. 2009).

Forests are among the least invaded habitats in the Mediterranean Region (Vilà et al. 2007), and also across Europe (Chytrý et al. 2008). Classic works (e.g. Di Castri 1990) even suggested that Mediterranean forests are particularly resistant to invasion due to their environmental harshness and changes across recent millennia. Despite this, a set of previous studies showed that human-induced disturbance promotes forest invasion (e.g. Chytrý et al. 2008; Martin et al. 2009). Thus, early-successional species, both native and alien (Guirado et al. 2006, 2007; Pino et al. 2013), are especially favored by forest disturbance in Mediterranean forests, yet this colonization is often limited in time while high resource availability is maintained (Pino et al. 2013). In any case, other studies have begun to question this paradigm and show that an important subset of invasive forest species is neither dependent on disturbance nor restricted to early successional life strategies (Gilbert & Lechowicz 2005; Martin & Marks 2006). Thus, many alien plant species have invaded deeply shaded, relatively undisturbed forest understories, in both temperate and tropical regions around the world (Martin et al. 2009). These species are commonly dispersed by vertebrates (mostly birds, but also mammals), which are known to be key actors in Mediterranean forest assembly (e.g. Basnou et al. 2016). They are often favored by increasing propagule pressure and disturbance due to anthropogenic processes, but they can also spread across succession and under natural disturbance regimes (Martin & Marks 2006; Martin et al. 2009).

Mediterranean forests have partially recovered in the last 50 years from old croplands and rangelands (Grove & Rackham 2001). This forest increase also occurs in peri-urban regions taking part of complex land use change processes including urban sprawl (Catalan et al. 2008; Basnou et al. 2013). Community assembly of new forests under such conditions is especially unknown, yet novel (*sensu* Hobbs et al. 2006) assembly rules might determine changes in forest structure and composition. Particularly, high propagule pressure associated to landscape urbanization might determine an increase in forest invasion by alien plants. Previous studies showed that forests embedded in such highly altered landscapes are especially susceptible to invasion by alien plants (Murcia 1995; Guirado et al. 2006; Gassó et al. 2012; González-Moreno et al. 2013b). However, the importance of plant invasions in forest community assembly under contrasting environmental contexts and especially the role of wind- and vertebrate-dispersed species in the invasion process is largely unknown.

In this work, we study the invasion process of forests in the metropolitan area of Barcelona, comparing the invasion pattern in recent and preexisting forests, and exploring the role of species dispersal, the association with land-use history, and the influence of environmental factors on their alien species richness and composition. Recent and preexisting forests were identified from comparing 1956 and 2009 land cover cartography (Basnou et al. 2016; see Chapter 2 for details) while their invasion degree was assessed from diverse datasets on floristic composition at regional and local levels. A set of questions were addressed: (1) Are peri-urban forests more invaded than the rest in the Barcelona province? (2) Is forest history more important than habitat and landscape traits in the invasion of peri-urban forests? (3) Are vertebrate dispersed species more prone than non-vertebrate-dispersed ones to invade peri-urban forests? (4) Are recent and preexisting forests invaded by specific species pools?

We expect that forests embedded in the metropolitan landscape are more prone to be invaded than non-metropolitan ones because of high disturbance and propagule pressure characterizing human-altered landscapes (Gassó et al. 2012; Basnou et al. 2016). We also expect a relevant role of vertebrate-dispersed species due to their acknowledged ability to colonize low disturbed habitats as forests in general (Martin et al. 2009). However, invasion in novel forests can be less than expected and strongly modulated by habitat and landscape attributes, as shown by Basnou et al. (2015) for native woody species. Environmental differences between recent and preexisting forests also determine changes in their alien species pools, as suggested by the observed contrasting ecological types of native plants in these forests.

Methods

Study area

The study has been performed combining data at three spatial scales in the Barcelona province (Catalonia, NE of Spain): the overall province, the Metropolitan Region of Barcelona and the Vallès lowland (Figure 5.1). The Barcelona Province covers an area of 7725 km^2 with highly variable environmental conditions, resulting from its topography and geographical situation. Elevations range from 0 m a.s.l. in its southern border in the Mediterranean coast, to 2590 m a.s.l. in the north in the Pyrenees. Climate is mostly Mediterranean but with a strong NE-SW gradient (Ninyerola et al. 2000), with rainfall increasing and average temperature decreasing north- and eastwards, following the elevation gradients. As a result, Mediterranean-type biomes gradually change with latitude to temperate, subalpine and even alpine. In addition, landscape structure shows a N-S rural-urban gradient, with forests being the dominant land-cover category (50 % of the province), followed by croplands (21 %), built-up areas (12.8 %) and scrublands (11 %; Land Cover Map of Catalonia, LCMC 2009: www.creaf.uab.cat/mcsc/). The northernmost mountain ranges are covered by forest, while the coastal and pre-coastal areas are dominated by built-up areas, mainly close to the city of Barcelona, and croplands. The rest of the province is made up by a set of coastal and pre-coastal mountain ranges mostly covered by forests and scrublands in the east and west, respectively, combined with a set of inland plains and plateaus mostly occupied by croplands (Clotet et al. 2016).

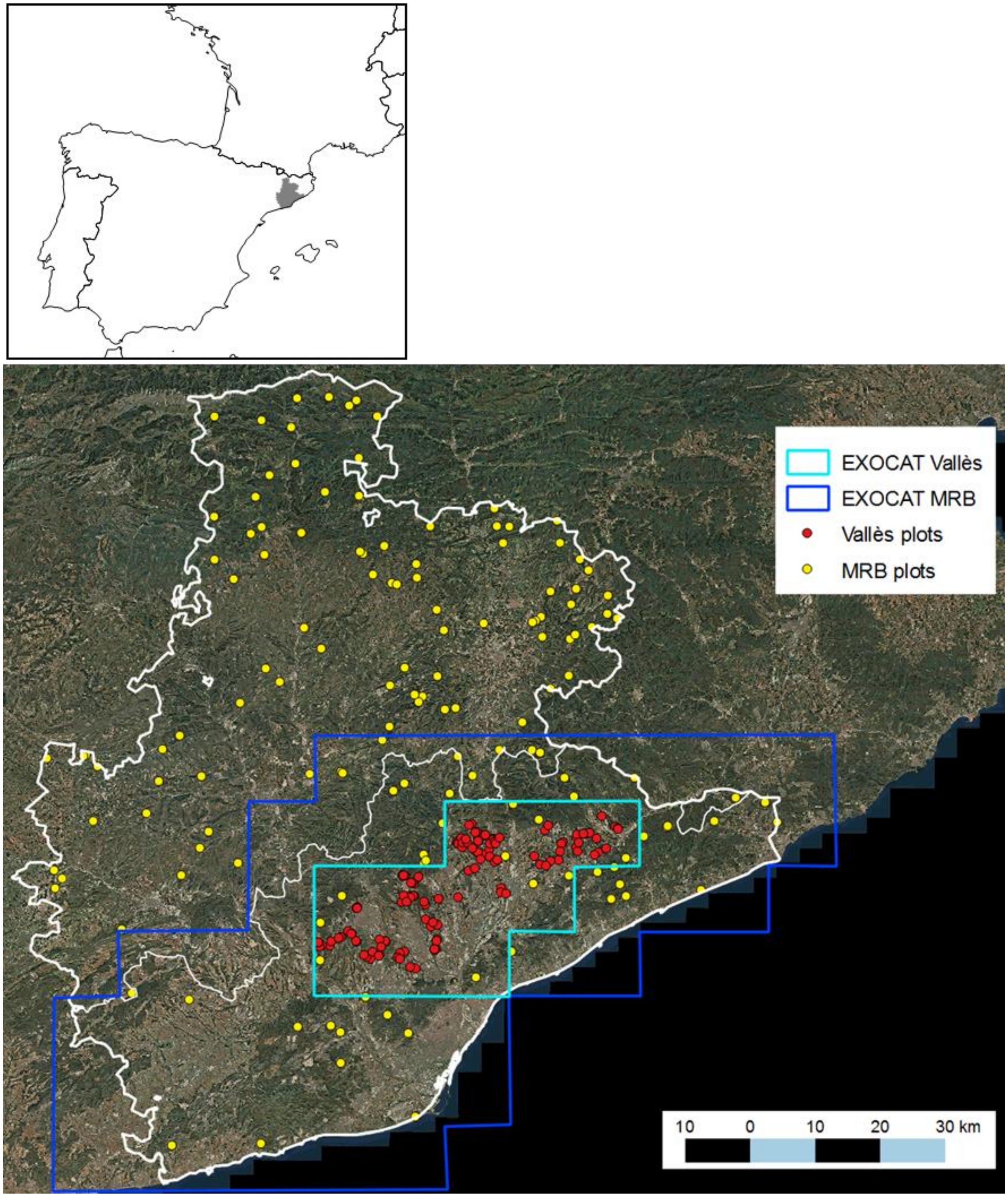

Figure 5.1. The Barcelona province and the Metropolitan Region of Barcelona (MRB) with their corresponding sets of sampling plots, and the areas of the MRB and the Vallès lowlands from which EXOCAT data were selected for the study.

The Metropolitan Region of Barcelona (MRB; 3200 km^2) corresponds to the southern half of the Barcelona province between the pre-coastal range and the Mediterranean Sea. With a population of 5.5 million inhabitants, the MRB is among the densest, most urbanized regions in Europe, yet houses a number of remnant natural areas featuring considerable ecological diversity and value. Variability in topography (elevation ranges from 0 to 1700 m a.s.l.) and climate (with the abovementioned NE– SW climate gradient) is responsible for landscape heterogeneity. Climate is typically Mediterranean with mean annual rainfall ranging between 550 and 1000 mm and mean annual temperature between 14.5 and 16.6 °C (Ninyerola et al. 2005). As common in metropolitan areas, landscape is extremely dynamic with sustained urbanization, but also deforestation and afforestation processes, the first concentrated in lowlands and the two lasts in ranges (Marull & Mallarach 2005; Basnou et al. 2013).

The Vallès lowland (approx. 355 km^2) is located in the NW of the MRB, and corresponds to one of the most transformed and populated areas in this region. Elevation ranges from 115 to approx. 485 m a.s.l., mean annual rainfall from 630 to 830 mm and mean temperature from 13 to 15 °C (Digital Climatic Atlas of Iberian Peninsula, http://opengis.uab.es/wms/iberia/). It exhibits a complex mosaic of urban areas, croplands and forests, mostly dominated by *Quercus ilex, Quercus suber, Quercus cerrioides*, *Pinus halepensis* and *Pinus pinea* (Guirado et al. 2007, 2008), which show complex and highly dynamic fragmentation and recovering processes (Pino et al. 2008).

Sampling

First, we have compared the invasion degree of forests in the MRB and those of the rest of the Barcelona province, using a previous survey on alien plant presence and abundance in the main habitats in the province (Clotet et al. 2016). This survey was made up by 531 circular plots (5-m radius) randomly distributed across the most widespread habitat types along the Barcelona province (coastal habitats, broad-leaved forests, coniferous forests, croplands, meadows, riparian habitats, rock outcrops, scrublands, urban habitats and wetlands). Of these plots, 146 correspond to forests, with 46 and 100 of them inside and outside the province, respectively.

Second, the role of forest history versus habitat and landscape properties on forest invasion (i.e. richness and composition) was addressed by a specific sampling in the Vallès lowland. Total alien species richness and that of vertebrate- and non-vertebrate-dispersed were compared between pre-existing and recent forests under urbanization and forest connectivity gradients, and considering a set of climatic, topographic and forest stand attributes. A total of 126 plots were selected and distributed in two groups of 63, corresponding respectively to pre-existing and recent forests identified by combining land cover maps of 1956 and 2009, both generated by 1:5000 photo-interpretation orthoimages. Thus, pre-existing forests were those present in both maps, while recent forests were only present in that of 2009 (Basnou et al. 2013). Non-calcareous areas and those higher than 400 m a.s.l. were avoided, in order to reduce the environmental variation observed in previous studies and responsible for high variation in plant species composition (Guirado et al. 2007). For all the study area, current forest connectivity and urbanization of the surrounding landscape were estimated from the 2009 land cover map, by obtaining respective models of forest and urban cover proportions in a buffer of 500 m around a given point across the study area. These variables were calculated from a set of 20000 points selected regularly (every 250 m) and distributed in the current forest through the landscape. Then, they were interpolated at 10 m pixel size across the 2009 forest area using the inverse of distance as interpolation weight. Since forest connectivity and urbanization are not independent, both pre-existing and recent forest plots were selected across a combination of forest and urban connectivity (low, medium, high; see chapter 2, Figure 2.4 for details). All the tasks were performed using MiraMon GIS (Pons 2000).

In addition to forest history, habitat and landscape factors, local variables were obtained in each plot through field work (Appendix C.1 and C.2). Slope and aspect (N, W, S, E) were measured using a clinometer and a compass respectively. The DBH of all trees with diameter over 5 cm were measuring to assess forest structure. Mean soil depth was estimated by the average from four random measures obtained with a 1-m iron stack. The percentage of photosynthetically active radiation (PAR) was obtained by comparing the mean values of two measures per plot recorded beneath and outside forest canopy, using a ceptometer (AccuPAR LP-80; Decagon Devices, Inc., Pullman, WA). Stoniness (i.e. percentage of stones covering the ground) was visually estimated. Additionally, human disturbance and management were qualitatively scored on each plot (see Guirado et al. 2007). Disturbance (low, moderate, high) was scored depending on evidence of human trampling and presence of refuse. Management was rated depending on signals of logging activities and classified as recent (presence of cut branches), old (former timber harvesting traces, like cut stumps) or null (absence of forestry evidences). Elevation of each plot were obtained from a Digital Elevation Model (DEM) of 30 m pixel size, generated by the Cartographic Institute of Catalonia (ICC), while annual rainfall and temperature were obtained from the Digital Climatic Atlas of Iberian Peninsula (http://opengis.uab.es/wms/iberia/). Comparison of mean values and frequencies of categories of these variables showed little differences between forest historical types.

In each plot, cover of each plant species was measured using the Braun Blanquet semiquantitative scale. For this study, we selected native species which were classified by their dispersal strategy (vertebrate or non-vertebrate dispersal), despite total species richness per plot was also included as predictor (Appendix C.3). Presence, richness and cover of all alien species and of those vertebrate and non-vertebrate dispersed were calculated per plot as response variables.

The question whether vertebrate-dispersed species are more prone than non-vertebrate-dispersed ones to invade peri-urban forests was addressed through comparing the local pool of alien species in the Vallès lowland plots with the regional pools in both the Vallès lowland and in the MRB. We produced the alien species lists for these areas by extracting all the records of alien plant species included in the EXOCAT database, which summarizes the records of all known alien species in Catalonia (http://exocat.creaf.cat/), and corresponding to these geographic areas. Also, we completed the lists with the species recorded in the field and not present in the EXOCAT database for either the MRB or the Vallès lowland. These included *Cedrus libani, Coronilla valentina, Cotoneaster lacteus, Cotoneaster pannosus, Lonicera japonica, Lunaria annua, Oxalis latifolia, Pittosporum tobira, Prunus cerasifera, Prunus cerasifera var. pissardii, Prunus domestica, Prunus dulcis, Pyracantha angustifolia, Solanum chenopodioides* and *Ulmus pumila. Laurus nobilis* was also included in the list as it is non-native in the MRB and in the Vallès, despite it is considered native in Catalonia and therefore not included in EXOCAT. In contrast, *P. pinea* was not included in the list because its alien status has been largely questioned (Martínez & Montero 2004).

Statistical analyses

First, a chi-square test was performed to compare alien species richness in sampling plots inside *versus* outside the MRB at the Barcelona province. Also, regional pools of vertebrate- and non-vertebrate-dispersed species were compared in terms of species frequency (i.e. number of citations) in the MRB and in the Vallès Lowlands, through t-tests.

The invasion patterns in periurban forests in the Vallès lowland and their association with forest history were assessed through different approaches. Frequency of invaded plots by vertebrate- and non-vertebrate-dispersed species were compared using a t-test, while the association between forest type (pre-existing and recent) and dispersal strategy of alien species (vertebrate and non-vertebrate dispersal) was assessed using a chi-square test on species presence. ANOVA tests were also performed to compare the effect of forest history and dispersal type on alien species richness and cover in plots. Still, separate general linear models (GLM) were done to assess the relative influence of forest history and the studied landscape, environmental and forest stand factors in presence, richness and cover of total alien species and of vertebrate and non-vertebrate dispersed ones. For each response variable (i.e. presence, richness and cover of each species group) a full model was built, on which model selection was performed based on AICc increase (delta). All models with delta of less than 2 were selected. Then, an adjusted model was obtained only including the significant predictors present in more than 50% of the selected models.

Still, the effect of forest historical type, landscape factors and environmental and forest stand variables on alien species composition was evaluated for a set (n=11) of alien species occurring in more than 126 plots in the Vallès lowland forests. Presence and cover of these species were related with the predictor variables using redundancy analyses (RDA). All data analyses were performed using the R statistical software, version 3.1.1 (R Development Core Team 2014) except RDA which were performed using CANOCO 4.5.

Results

Regional patterns of alien species invasion

About 10.3% of forest plots sampled across the Barcelona province are invaded by alien species. The percentage of invaded plots is higher inside (23.9%) than outside (4.0%) the Metropolitan Region (X^2= 14.74, df=1; P<0.001). In the case of Vallès lowlands, 71.4% of sampled plots are invaded by alien species, yet this figure cannot be compared with those obtained for the overall province as plot areas are different.

Regional pool of alien species is made up, respectively, by 35.8% and 64.2% of vertebrate- and non-vertebrate-dispersed species in the MRB, and by 25.8% and 74.2% in the Vallés lowland. Regarding alien species citations in the EXOCAT database, no significant differences among dispersal strategies were found in either the MRB (vertebrate-dispersed: 12.02; non-vertebrate-dispersed: 17.85; t=0.80, 112 df, p>0.05) or the Vallès lowland (vertebrate-dispersed: 18.44; non-vertebrate-dispersed: 13.02; t=-0.42, 18 df, p>0.05).

Alien species patterns per dispersal type in forest plots

In the Vallès lowland, results obtained at habitat scale contrast with those obtained from the EXOCAT database: from 34 species recorded in forest plots, 18 (52.9%) are dispersed by vertebrates while 16 (47.1%) are not. In addition, vertebrate-dispersed species are more frequent in plots (mean frequency 9.06) than non-vertebrate-dispersed species (3.19), being these differences marginally significant ($t=-1.847$; $p=0.079$). Forest history is significantly associated to plant dispersal type ($X^2= 5.72$; $df=1$; $P<0.05$), with vertebrate-dispersed species being more frequent in preexisting forests and vice-versa for non-vertebrate-dispersed plants (Figure 5.2a). Dispersal type is also significantly associated with alien species richness per plot (Figure 5.2b; $F_{1,248}=37.63$, $P<0.001$), and values are higher in vertebrate-dispersed species than in the rest. In contrast, forest history and the interaction between both factors have no significant influence on species richness (Forest: $F_{1,248}=0.50$, $P> 0.05$; Forest*Dispersal type: $F_{1,248}=2.35$, $P>0.05$). Similarly, alien species cover is significantly associated to dispersal type being higher in vertebrate-dispersed species than in the rest (see Figure 5.2c; $F_{1,248}=22.75$, $P<0.001$) but not to forest type or the interaction of both factors ($F_{1,248}=0.15$, $P>0.05$; Forest*Dispersal type: $F_{1,248}=0.22$, $P>0.05$).

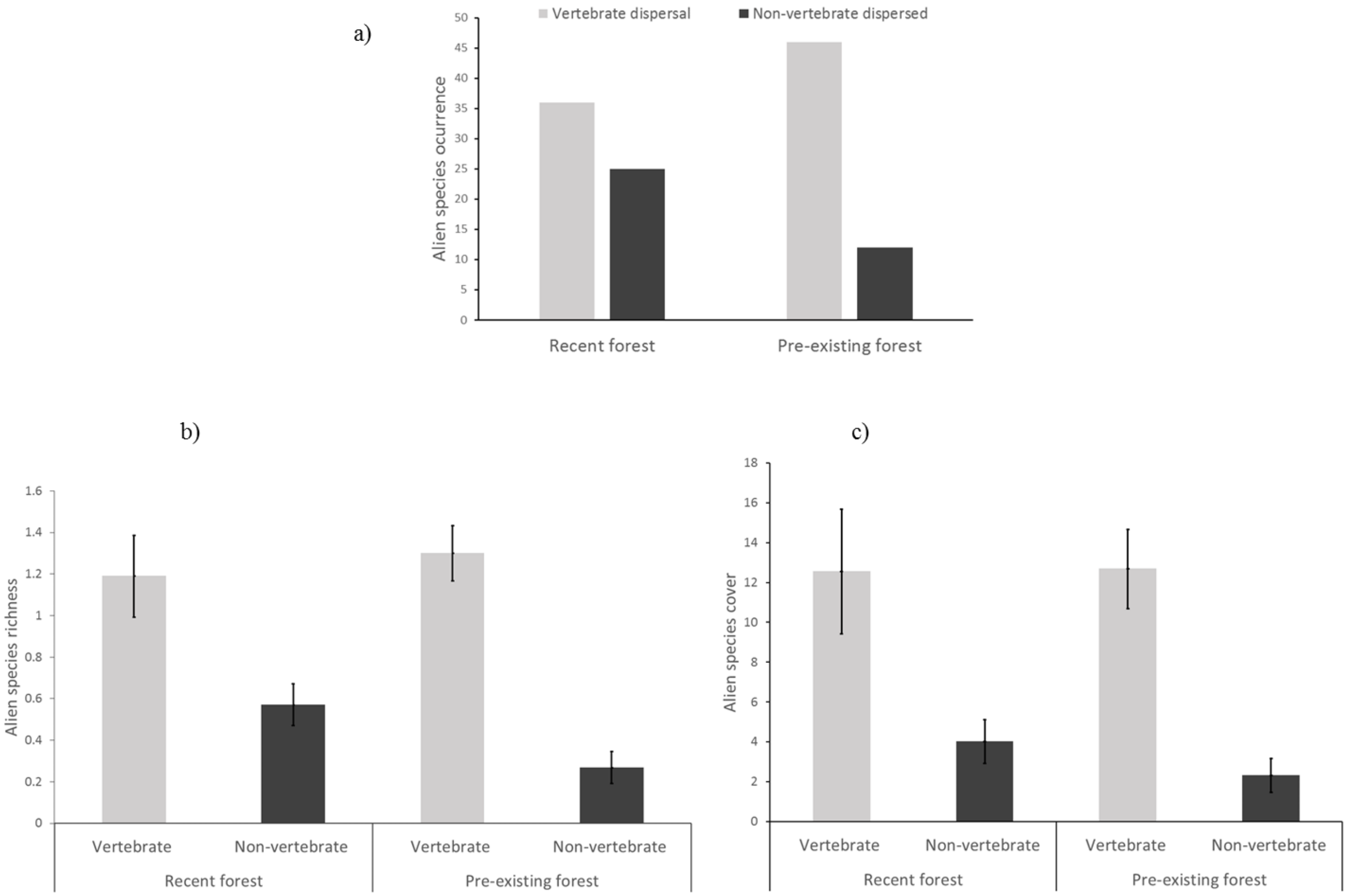

Figure 5.2. Occurrence (a), richness (b) and cover (c) of vertebrate and non-vertebrate dispersed species in recent and pre-existing forest at the Vallès lowlands. Occurrence corresponds to number of plots while richness and cover correspond to mean values per plot (±SE) in each species type.

The role of forest historical type versus landscape and environmental factors

GLM models on alien species presence, richness and mean cover explain a moderate amount of variance, with r^2 usually between 0.30 and 0.41, yet some models show lower values (Tables 5.1 to 5.3). In the case of alien species presence, GLM showed a positive association of this variable with UTM X for all species groups (Table 5.1). Mean annual rainfall is negatively associated to the occurrence of total and non-vertebrate-dispersed species but positively associated to that of vertebrate-dispersed species. The percentage of forest in the adjacent landscape and forest type (old) were associated to the occurrence of vertebrate-dispersed species, with negative and positive associations respectively. Native species richness was positively associated to the occurrence of alien species not dispersed by vertebrates. In the case of total species, occurrence is marginally associated to the percentage of forest in the adjacent landscape and to native species richness. For non-vertebrate-dispersed species, presence was marginally associated to forest density, forest type and percentage of urban areas in the adjacent landscape.

As in alien species presence, UTM X is positively associated to species richness for all species groups (Table 5.2). Forest density and the percentage of forest in the adjacent landscape are negatively associated to richness of both total and vertebrate-dispersed species, while there is only a marginally significant association with forest density in non-vertebrate-dispersed species. Mean annual rainfall and native species richness are positively and negatively associated, respectively, to richness of non-vertebrate-dispersed species, while the last variable is marginally associated to total species richness. The rest of variables show marginally significant associations with richness of the diverse species groups: forest management with total and vertebrate-dispersed species, the percentage of urban areas in the adjacent landscape with total and non-vertebrate-dispersed species, and forest type with this last group.

In the case of mean alien species cover (Table 5.3), we found that longitude is positively associated to total and non-vertebrate-dispersed species, and marginally to vertebrate-dispersed ones. The percentage of forest in the surrounding landscape is negatively related to cover of both total and vertebrate-dispersed species. In addition, mean annual rainfall and native species richness are negatively and positively associated, respectively, to the mean cover of non-vertebrate-dispersed species. Still, there are some variables with marginally significant effects, as tree density on total species, elevation on vertebrate-dispersed species, and stoniness on non-vertebrate-dispersed ones.

Table 5.1. General Linear Models for alien species presences in the Vallès lowlands, including the interactions between dispersal strategy and the rest of predictors (Significance: .p<0.1; *p<0.05; **p<0.01; ***p<0.001).

Parameters	**Estimate**	**P**
Total species		
Adjusted r^2=0.36		
Percentage of forest in the landscape	-0.3861	.
Mean annual rainfall	-0.003425	***
Native richness	0.01203	.
UTMX: Longitude	0.00002867	***
Vertebrate-dispersed species		
Adjusted r^2=0.34		
Percentage of forest in the landscape	-0.6134	**
Forest type: old	0.1642	*
Mean annual rainfall	0.003095	**
UTMX: Longitude	0.00002428	***
Non vertebrate-dispersed species		
Adjusted r^2=0.39		
Tree density	-0.004126	.
Forest type: old	-0.1311	.
Mean annual rainfall	-0.002386	*
Native richness	0.02583	***
Percentage of urban areas in the landscape	0.3321	.
UTMX: Longitude	0.00001978	***

Table 5.2. General Linear Models for alien species richness in the Vallès lowlands, including the interactions between dispersal strategy and the rest of predictors (Significance: .p<0.1; *p<0.05; **p<0.01; ***p<0.001).

Parameters	**Estimate**	**P**
Total species		
Adjusted r^2=0.41		
Tree density	-0.0196	*
Percentage of forest in the landscape	-2.289	**
Management: null	-0.3498	.
Richness of native species	0.03956	.
Percentage of urban areas in the landscape	1.332	.
UTMX: Longitude	0.00006602	***
Vertebrate-dispersed species		
Adjusted r^2=0.38		
Tree density	-0.01405	*
Percentage of forest in the landscape	-2.298	***
Management: null	-0.2866	.
UTMX: Longitude	0.0000454	***
Non vertebrate-dispersed species		
Adjusted r^2=0.32		
Tree density	-0.006104	.
Forest type: old	-0.2001	.
Mean annual rainfall	-0.003242	*
Richness of native species	0.03465	**
Percentage of urban areas in the landscape	0.613	.
UTMX: Longitude	0.0000279	***

Table 5.3. General Linear Models for alien species cover in the Vallès lowlands, including the interactions between dispersal strategy and the rest of predictors (Significance: .p<0.1; *p<0.05; **p<0.01; ***p<0.001).

Parameters	**Estimate**	**P**
Total species		
Adjusted r^2=0.28		
Tree density	-0.2347	.
Percentage of forest in the landscape	-0.3651	**
UTMX: Longitude	0.0007658	*
Vertebrate-dispersed species		
Adjusted r^2=0.30		
Percentage of forest in the landscape	-33.16	***
UTMX: Longitude	0.0004715	.
Altitude	-0.04534	.
Non vertebrate-dispersed species		
Adjusted r^2=0.18		
Mean annual rainfall	-0.03788	*
Native richness	0.253	*
Stoniness	0.1051	.
UTMX: Longitude	0.0002510	*

Effects on alien species composition

Celtis australis, L. nobilis, Ligustrum lucidum, Conyza sumatrensis, P. domestica, Araujia sericifera, *S. chenopodioides*, *C. pannosus*, *C. lacteus*, *Pyracantha angustifolia* and *Senecio pterophorus* are the most frequent species in plots (present in a range of 42 to 6), with a mean cover per plot between 15 to 4.45% (Appendix C.1). Eight of these dominant species are dispersed by vertebrates. RDA shows that the 17% of variance in the presence of these alien species is explained by the forest type and the set of environmental variables (canonical coefficient=0.173; p<0.01). In the case of the alien species cover, the explained variance is 12% (canonical coefficient=0.127; p<0.01). The associated diagrams (Figure 5.3) of both species presence and cover show that the most frequent alien species in the studied area are distributed according to environmental variables like temperature, soil depth, PAR and longitude, and slope in the specific case of species presence. The association of particular species with forest historical type is weak on both alien species presence and cover.

Considering alien species cover first axis links *C. australis*, *A. sericifera*, *Pyracantha angustifolia*, *S. pterophorus* and *L. lucidum* with temperature, and *P. domestica*, *S. chenopodioides* and *C. sumatrensis* with longitude, PAR and soil depth (right side). *C. pannosus, C. lacteus* and *L. nobilis* are related with the rest of the environmental variables (bottom). Regarding alien species presence, ordination diagram matched *C. australis, A. sericifera,* and *S. pterophorus* with temperature (first axis) and *P. domestica*, *Pyracantha angustifolia, L. nobilis* and *C. sumatrensis* with soil depth, PAR, longitude and also slope in a smaller grade (right side). *C. lacteus*, S. *chenopodioides* and *C. pannosus* are related with the rest of the environmental variables (bottom). It is noted that the ordination diagrams of alien species presence and cover are essentially the same, but they show some rotation in axes and species. Differences in species distribution in relation to environmental variables and forest type are more defined in species cover than in species presence.

Discussion

Our study first shows that metropolitan forests are more invaded by alien plants than the rest in the Barcelona province, likely due to the high disturbance and the large propagule characterizing human-transformed landscapes (Pino et al. 2005; Guirado et al. 2007). Our plot data indicate that the majority and a substantial proportion of these forests are invaded by alien plants in the Vallès lowland and in the MRB, respectively. This result is especially relevant, as former studies suggested that Mediterranean forests are especially resistant to plant invasion (e.g. Di Castri 1990). The hypothesis of low forest invasibility had been supported by studies based on vegetation surveys at Spanish and European scales (Vilà et al. 2007; Chytrý et al. 2008). However, several previous studies (Guirado et al. 2006, 2007) already indicated the high presence of synanthropic species, including exotic plants, in the Vallès forests. Martin et al. (2009) performed a review of the invasion status of forests worldwide, in which they concluded that forests stands are frequently invaded by a given set of alien species.

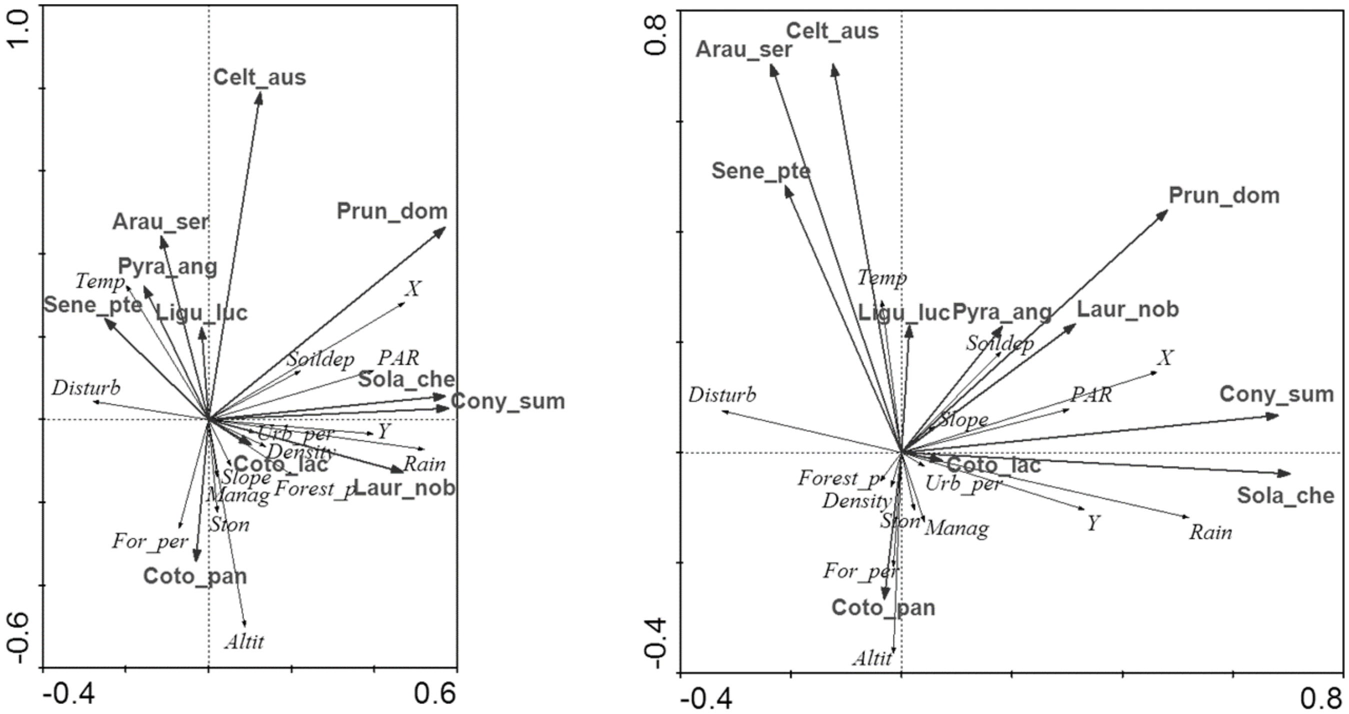

Figure 5.3. Redundancy analysis diagram (RDA) of alien species presence (left) and cover (right) in recent and pre-existing forest plots at the Vallès lowland. Included code variables Forest_p: pre-existing forest, For_per: forest percentage, Urb_per: urbanization percentage, UTMX: latitude, UTMY: longitude, Soildep: soil depth, Temp: temperature, PAR: photosynthetically active radiation, Ston: stoniness, Manag: management, Altit: altitude, disturb, slope, density, rain. See Appendix C.3 for species abbreviations.

What is especially new in our study the contrasting importance of the diverse dispersal types on alien species pools across spatial scales: while non-vertebrate-dispersed species are dominant in the regional species pools in the MRB and the Vallès lowland, vertebrate-dispersed species are more frequent (yet differences are marginally significant) and they appear in higher number and cover than non-vertebrate-dispersed plants at forest plot scale. Dispersal by vertebrates has been acknowledged as an effective mechanism of invasive plant colonization and spread in previous studies, yet estimates of its importance are extremely variable (Gosper et al. 2005; Buckley et al. 2006). Our results suggest the existence of a set of ecological filters favoring the colonization, establishment and spread of these vertebrate dispersed species in forests (Martin et al. 2009) yet these filters are largely unknown. As dispersal by vertebrates is also a primary mechanism of plant community assembly in Mediterranean scrublands (Herrera 1984) and forests (Basnou et al. 2016), these filters might be at least partially shared with native species. In any case, specific interactions between fruit and frugivore traits might strongly determine the success of the subsequent native or alien species colonization (Herrera 2002; Gosper et al. 2005) and, consequently, plant community assembly might be extremely idiosyncratic.

Our results corroborate the effect of already known correlates of plant invasion in the Metropolitan Area of Barcelona. In particular, there is a positive effect of longitude, which can be attributed to the regional pattern of alien species richness and its socio-economic drivers (Pino et al. 2005; Clotet et al. 2016). Negative effects of tree density and rainfall can be related to a closer forest canopy: as found by Guirado et al. (2007), increasing canopy cover affects synanthropic species richness in the Vallès forests. Mean annual rainfall has a negative effect on total alien species richness, but also on native woody species richness as found by Basnou et al. (2016), and this might be the cause of the positive, yet marginally significant, association between native and alien species richness detected in our study. In addition, our results also highlight the role of the adjacent landscape on forest colonization by alien plants in urban regions. Previous studies already showed that woody Mediterranean habitats embedded in urbanized landscapes are especially invaded by alien plants (e.g. Guirado et al. 2007; Gassó et al.

2012; González-Moreno et al. 2013b; Basnou et al. 2015; Clotet et al. 2016). Our study shows that the percentage of forest in the surrounding landscape negatively affects total alien species presence, richness and cover, while urban cover positively affects total species richness. Forest fragmentation increases the amount of forest edges in the landscape, which are particularly prone to be invaded by alien plants (González-Moreno et al. 2013a). On the other hand, the surrounding human-transformed landscape provides high propagule pressure to the adjacent forest edges and are responsible for high disturbance sources (e.g. due to land use change but also to human frequentation) that might especially promote species establishment, thus increasing species richness (Guirado et al. 2006; Godefroid & Koedam 2007; Basnou et al. 2015).

More interestingly, the study shows differential effects of landscape structure and some components of its dynamics (i.e. forest history) on the spread of alien species depending on their dispersal type. Indeed, the negative association of forest cover in the landscape with alien species presence, richness and cover is constrained to vertebrate-dispersed species, while the positive effect of urban areas on some of these parameters only appears in non-vertebrate-dispersed ones. These results reveal the complexity of the invasion process in metropolitan forests: by one hand, landscape pattern might strongly influence animal presence and movement affecting populations of dispersers and determining, in turn, the colonization patterns of vertebrate-dispersed species (Santos & Tellería 1994; Silva & Tabarelli 2000). It is already known, for example, that frugivorous birds are especially concentrated in forest edges. Therefore, edge increase resulting from habitat fragmentation will favor plant invasions (Cordeiro et al. 2004; González-Moreno et al. 2013a). However, habitat fragments might offer contrasting opportunities for establishment of these species due to differences in environment and disturbance regimes (Buckley et al. 2006), thus modulating the positive effect of edge increase. On the other hand, the positive association of non-vertebrate-dispersed species with urban cover in the landscape might be associated to the fact that most of them are pioneer, disturbance-dependent species that exhibit a strategy of gap detection (Martin et al. 2009), being favored by high frequentation and disturbance regime associated to forest edges (Guirado et al. 2006).

Also, interesting in the study is that forest history is associated to plant dispersal type, with vertebrate-dispersed species being more frequent in preexisting forests and vice-versa for non-vertebrate-dispersed plants. In addition, vertebrate-dispersed species show some invasion debt in pre-existing forests, as their presence is significantly lower in these forests than in recent ones (Table 5.1). This pattern matches by that observed in native species (Basnou et al. 2016) and it is indicative for invasion debt (*sensu* Essl et al. 2015). Despite our data do not confirm this, other works have shown some invasion debt of the whole alien species pool in Mediterranean habitats: Basnou et al. (2015) and González-Moreno et al. (2017) found that total alien species richness in diverse coastal habitats is related with current but also historical landscape variables in the surrounding landscape, suggesting that the habitat invasion following land use changes might be in part immediate and in part time-delayed. Clotet et al. (2016) found, also in Mediterranean habitats, that this invasion debt interacts with habitat type suggesting that the invasion process after disturbance takes place at diverse speed depending on habitat types. In any case, the diversity of results regarding invasion debt in these recent works highlights the fact that this invasion debt is driven by the specific time-lags in species' responses to habitat change, which in turn depend on the specific attributes (biology and ecology, but also residence time and invasion pathways) of alien species making up the regional species pool (González-Moreno et al. 2017).

It should also be noted that non-vertebrate-dispersed species show an opposite pattern that the expected under the invasion debt paradigm, as they exhibit higher presence and richness in recent than in pre-existing forests. This pattern is indicative for extinction debt, a particularly widespread process among native plant specialists (Krauss et al. 2010) but also suggested for alien species following land use change (González-Moreno et al. 2017). Extinction debt of alien species might be especially frequent among pioneer species with a strategy of gap detection, which commonly take profit of disturbance events that provide the so-called windows of opportunity for species establishment and spread. This is the case of several species colonizing forests after wildfires, where the subsequent vegetation recovery constraints species persistence (Keeley et al. 2005; Pino et al. 2013). In our study, higher presence and richness of non-vertebrate-dispersed species in new that in preexisting forests suggests then many, if not most, of these species colonized these new forests stands in the early stages of forest assembly, and that will be extirpated from these stands along succession.

Lastly, the study failed to detect any relevant effect of forest history and environmental and landscape variables on either the presence or abundance of the most frequent alien species. Species ordination mostly matches with a set of main environmental variables according to species ecology, while it is weakly associated to forest historical type for both species presence and cover. Basnou et al. (2015) found, in a larger scale study involving a set of contrasting coastal habitats, a primary effect of habitat type, and a secondary effect of climate (temperature) and of history of the surrounded landscape on alien species composition. Thus, changes in land use and in the surrounding landscape seem to have a secondary role on alien species composition, and this reinforces again the idiosyncrasy of plant invasion process in a given area along the history (González-Moreno et al. 2017).

6. Discusión general

A lo largo de la presente tesis doctoral se han explorado diversos determinantes del ensamblaje de las comunidades leñosas mediterráneas en la región metropolitana de Barcelona. Para ello se han comparado bosques y matorrales de reciente formación con otros más estables a lo largo de la historia reciente de dicha región, teniendo en cuenta distintos factores ambientales y del paisaje. Los resultados ponen de manifiesto el papel central del paisaje actual y de los mecanismos de dispersión de las especies en el proceso de ensamblaje de dichas comunidades. La estructura del paisaje es responsable de cambios en la composición de especies, principalmente porque los patrones de fragmentación y de urbanización característicos de los paisajes metropolitanos determinan cambios notables en la disponibilidad de propágulos, especialmente por lo que respecta a las especies propias de los hábitats y a las más antropófilas, incluidas las exóticas. Sin embargo, parece que las reglas de ensamblaje siguen siendo esencialmente las mismas, con un predominio de las especies dispersadas por vertebrados tanto entre las especies nativas como entre las exóticas.

Por otra parte, el estudio también muestra un cierto papel, aunque más secundario, del historial reciente de cambios en el ensamblaje de dichas comunidades. Ello se traduce en un cierto cambio en la composición de especies entre estas formaciones recientes y el resto, y en la persistencia de modestas deudas de extinción de las especies de los hábitats preexistentes y de créditos de colonización de las especies propias de los nuevos hábitats. Seguidamente se discuten con detalle algunos de estos resultados.

Los efectos del hábitat y del paisaje circundante en las comunidades vegetales periurbanas

En bosques, los resultados obtenidos (capítulos 4 y 5) corroboran otros trabajos previos en la zona (Guirado et al. 2006, 2007) que resaltan el papel central de los factores de hábitat y del paisaje actual en el ensamblaje de las comunidades vegetales.

Así, la riqueza total y por grupos ecológicos se ve condicionada por la conectividad forestal –que afecta positivamente a la riqueza y abundancia de las especies forestales y negativamente al resto- y por el grado de urbanización –que afecta negativamente a las especies de hábitats abiertos. La riqueza también se ve afectada por gran número de factores asociados a la cobertura forestal a escala local y al grado de perturbación de los bosques. Estudios previos identifican la conectividad forestal como un factor determinante del ensamblaje de las comunidades de leñosas en bosques (por ejemplo, Díaz et al. 1998; Bailey 2007; Montoya et al. 2008; Svenning et al. 2009; Martín-Queller et al. 2011). La fragmentación del bosque conlleva una disminución del tamaño de las manchas y un aumento en la proporción de bordes de dicho bosque, lo cual perjudica a las especies propiamente forestales y favorece, en cambio, a las de los hábitats agrícolas y urbanos adyacentes (Holt et al. 1995; Hanski 1999; Bascompte & Rodríguez 2001; Vellend 2003; Guirado et al. 2007). Así, la fragmentación convierte a los bosques en hábitats especialmente vulnerables a la colonización por especies antropófilas, tanto nativas como exóticas (Hobbs 1988, 2000; Wiens 1992; Murcia 1995; Hobbs 2000; Guirado et al. 2006; González-Moreno et al. 2013b).

La invasión de los bosques metropolitanos por especies exóticas

Las exóticas son un caso especial de dichas especies antropófilas. Paradójicamente, estudios previos realizados a escala regional sugieren que las formaciones leñosas mediterráneas son especialmente resistentes a las invasiones por plantas exóticas (Di Castri 1990; Vilà et al. 2007; Chytrý et al. 2008). Sin embargo, otros estudios a escala local en la región de Barcelona (González-Moreno et al. 2013b, Basnou et al. 2015) ya destacaron la invasión por especies exóticas en los hábitats forestales metropolitanos, probablemente debido al alto grado de perturbación y a la presión de propágulo que caracteriza a estos paisajes. Así mismo, los procesos de fragmentación del hábitat aumentan el número de manchas de bosque en el paisaje, lo que provoca un aumento de los bordes forestales altamente susceptibles a ser invadidos por plantas exóticas (González-Moreno et al. 2013a). Los resultados del Capítulo 5 refuerzan estos trabajos previos y revelan por primera vez que los bosques del llano del Vallès y de la Región Metropolitana de Barcelona están más invadidos por plantas exóticas que los del resto de la provincia. Por otra parte, destacan que el porcentaje de bosque en el paisaje circundante afecta negativamente a la presencia, riqueza y cobertura de especies exóticas, posiblemente debido a que la fragmentación incrementa la cantidad de perímetro especialmente vulnerable a la invasión (González-Moreno et al. 2013a) y pone en contacto a las manchas de bosque con las fuentes de propágulo de las zonas agrícolas y urbanas (Basnou et al. 2015). Muchas de estas especies exóticas son pioneras, dependientes de disturbios y tolerantes a la luz, viéndose favorecidas por la frecuencia de las alteraciones y el régimen de perturbación de los paisajes antropizados (Guirado et al. 2006). Sin embargo, algunos autores (Martin et al. 2009) alertan sobre la excesiva atención puesta sobre las especies exóticas de carácter pionero, y ponen de manifiesto que los bosques, especialmente los de ambientes muy antopizados, pueden estar notablemente invadidos por especies de estadios más avanzados de la sucesión y tolerantes a la sombra, capaces por tanto de invadir hábitats poco perturbados.

El efecto del legado histórico del cambio en los hábitats

La historia de cambios en los hábitats determina una profunda huella en las comunidades vegetales, tal como ponen de manifiesto gran número de trabajos previos centrados en especies nativas (e.g. Hermy & Verheyen 2007; Vellend et al. 2007; Bagaria et al. 2015; Basnou et al. 2016) y exóticas (Vilà & Ibánez 2011). Otros estudios han puesto de manifiesto la influencia de la historia de cambios de los usos del suelo en las comunidades de plantas leñosas mediterráneas actuales (Dupouey et al. 2002; Navarro-González et al. 2013; Batriu et al. 2015; Basnou et al. 2015). Dichos efectos se observan también para las especies dominantes en dichas comunidades, como es el caso de la encina (*Quercus ilex*), cuya regeneración en plantaciones de pino depende fuertemente de la intensidad de los usos del suelo pasados y de la disponibilidad de propágulos en el paisaje adyacente (Navarro-González et al. 2013).

Nuestros trabajos realizados en matorrales metropolitanos (capítulo 3) sugieren también que el ensamblaje de estas comunidades arbustivas está parcialmente determinado por el cambio en los usos del suelo, el cual afecta a la riqueza, diversidad y composición de especies leñosas. Los efectos de este legado coexisten con los propios de los diversos factores propios del nicho ecológico de las especies y que a su vez son frecuentemente modulados por los cambios mencionados en los usos del suelo (Dupouey et al. 2002; Batriu et al. 2011). Sin embargo, los resultados obtenidos en bosques (capítulos 4 y 5) muestran un efecto mucho menor de los cambios en los hábitats, los cuales se concentran sobre la riqueza, pero también sobre la importancia de los diversos grupos de especies. Basnou et al. (2016) detectaron también efectos moderados sobre dicha composición para el caso particular de las especies leñosas.

Por otra parte, los efectos de estos cambios en los usos del suelo ocurren frecuentemente de forma diferida. Así, se observan desfases en las colonizaciones y extinciones de especies cierto tiempo después de que estos cambios hayan tenido lugar, denominados respectivamente créditos de colonización y deudas de extinción (Jackson & Sax 2010). Cristofoli et al. (2010) y Piqueray et al. (2011) encontraron limitados créditos de colonización en brezales y praderas recién restauradas en Bélgica. Bonet & Pausas (2004) observaron un aumento en la riqueza de las especies leñosas, coherente con el concepto de crédito de colonización, en una cronosecuencia de 60 años de matorrales mediterráneos procedentes del abandono de cultivos. Por el contrario, nuestros trabajos en matorrales (Capítulo 3) no proporcionan ninguna evidencia de dichos créditos de colonización para una cronosecuencia más larga. Por lo que respecta a los bosques (Capítulo 4), únicamente se observa un cierto crédito de colonización en la abundancia de determinados grupos de especies como las forestales y, dentro de éstas, las dispersadas por vertebrados. Basnou et al. (2016), en un estudio para toda la Región Metropolitana de Barcelona, encontraron un crédito de colonización en la riqueza de plantas leñosas de los bosques nuevos, otra vez limitado a las especies dispersadas por vertebrados. Así pues, debemos concluir que dichos créditos de colonización son muy limitados en las comunidades leñosas mediterráneas, quizá porque el proceso de colonización de las nuevas formaciones es muy rápido o quizá porque las formaciones de referencia (las preexistentes) sobre las que se evalúa dicho crédito están muy simplificadas por la reiterada acción antrópica.

Un concepto similar al de crédito de colonización es el de crédito (Vilà et al. 2011) o deuda (Essl et al. 2015) de invasión, que define el desfase entre el cambio en los hábitats y su invasión por especies exóticas. Basnou et al. (2015) y González-Moreno et al. (2017) observaron que la riqueza total de especies exóticas en hábitats costeros está parcialmente relacionada con la estructura histórica del paisaje, lo que sugiere la existencia de esta deuda de invasión. Por su parte, Clotet et al. (2016) encontraron que ésta depende del tipo de hábitat. Nuestros resultados en bosques periurbanos (Capítulo 4) también indican la presencia de esta deuda de invasión, aunque limitada a las especies dispersadas por vertebrados como también ocurría en las especies nativas. Esta diversidad de resultados pone en evidencia la complejidad de dicha deuda de invasión, que depende de la interacción entre los atributos de las especies exóticas y de los hábitats receptores y el historial de cambios de los mismos (González-Moreno et al. 2017).

Cabe destacar finalmente algunos de los resultados obtenidos en bosques recientes, que son coherentes con la existencia de deudas de extinción. Por un lado, dichos bosques muestran una mayor riqueza de especies de matorrales y prados que el resto (Capítulo 4). Resultados similares fueron observados por Bagaria et al. (2013) en montañas mediterráneas. Combinada con los escasos créditos de colonización anteriormente comentados, dicha deuda de extinción determina un excedente de especies en los nuevos bosques, que probablemente es transitorio (Jackson & Sax 2010) y conducirá a la extinción de dichas especies a medida que las condiciones forestales de los nuevos bosques se vayan consolidando. Por otro lado, una conclusión similar puede desprenderse de la mayor presencia y riqueza de plantas exóticas no dispersadas por vertebrados en los bosques recientes (Capítulo 5): probablemente esto es debido a la proliferación de especies pioneras que se irán extinguiendo a medida que vayan consolidando las condiciones forestales de los nuevos bosques, tal como se observa después de determinadas perturbaciones como el fuego (Pino et al. 2013).

El papel de la dispersión por vertebrados en el ensamblaje de los nuevos bosques

Es sobradamente conocido el papel central de la dispersión por vertebrados – especialmente aves y micromamíferos - en el ensamblaje de las formaciones leñosas nativas mediterráneas, tanto matorrales (Herrera 1984) como bosques (Basnou et al. 2016). Por otra parte, diversos trabajos reconocen que este tipo de dispersión es un mecanismo especialmente eficaz en la colonización y propagación de las especies invasoras en los hábitats naturales (Gosper et al. 2005; Buckley et al. 2006). La presente tesis pone de manifiesto la importancia de la dispersión por vertebrados y su interacción con la estructura y la dinámica del paisaje reciente en el ensamblaje de las comunidades de plantas nativas de los bosques periurbanos (Capítulo 4). Así, se observa que la conectividad forestal es determinante en la riqueza y abundancia de las especies forestales nativas dispersadas de este modo, completando así los resultados de Guirado et al. (2007), que indicaban lo mismo para la riqueza del conjunto de especies forestales. En cambio, la fragmentación del bosque favorece la presencia y riqueza de plantas exóticas con este mecanismo de dispersión en bosques periurbanos (Capítulo 5). Esta disparidad de resultados entre especies nativas y exóticas evidencia la complejidad de este proceso de colonización: se ha sugerido que la estructura del paisaje tiene gran influencia en la abundancia y comportamiento de los dispersores y determina así los patrones de colonización de las especies dispersadas (Santos & Tellería 1994; Silva & Tabarelli 2000). Sin embargo, descartando que las plantas nativas y las exóticas sean dispersadas por organismos distintos (no existen datos al respecto), nuestros resultados sugieren que la estructura del paisaje podría estar condicionando la colonización de especies nativas y exóticas en dichos bosques a través de sus efectos sobre la presión de propágulo.

Donde sí que coinciden nativas y exóticas dispersadas por vertebrados es en el hecho de que su presencia y abundancia se ven favorecidas por la edad del bosque. Dicho patrón se había descrito previamente para las especies nativas leñosas de los bosques metropolitanos (Basnou et al. 2016) pero se desconocía para las especies exóticas. Este resultado sugiere que la llegada y el establecimiento de dichas especies están condicionados por la estructura del bosque, a través de requerimientos de nicho de las especies de plantas o de sus organismos dispersores (Basnou et al. 2016). Por otra parte, también sugieren la existencia de un conjunto de filtros ecológicos que favorecen o seleccionan el establecimiento de las especies dispersadas por vertebrados en los bosques (Martin et al. 2009). Éstos, combinados con las interacciones entre los atributos de los frutos y sus agentes dispersores, podrían determinar el éxito de la colonización de especies nativas o exóticas (Herrera 2002; Gosper et al. 2005) y en consecuencia conducir los patrones de ensamblaje de las comunidades leñosas mediterráneas.

Efectos sobre la composición de especies

Las teorías clásicas predicen cambios en la composición de especies a lo largo del proceso de sucesión, en los cuales los atributos biológicos y ecológicos de las especies juegan un papel fundamental. En consecuencia, es esperable una variación en la composición y los atributos de las especies en bosques y matorrales con trayectorias de cambio distintas (Guirado et al. 2008). Nuestros resultados muestran un cierto cambio en la riqueza de especies de los diversos grupos ecológicos, por ejemplo en bosques (Capítulo 4). Sin embargo, los cambios son relativamente menores (más debidos a la abundancia que a la presencia) y a largo plazo en la composición de especies en función de la edad de los hábitats. Ello se ha observado en la composición de especies leñosas en matorrales (Capítulo 3) y estudios previos lo corroboran para el caso de los bosques (Basnou et al. 2016). Ello sugiere que el proceso de sustitución a lo largo de la sucesión es muy gradual o que los estados de referencia (los bosques y matorrales más antiguos) mantienen un notable grado de perturbación que impide su evolución hacia estados más estables (Basnou et al. 2016).

Por otra parte, la composición de las especies exóticas en los bosques metropolitanos parece estar asociada principalmente a un conjunto de variables ambientales según la ecología de las especies y de manera más secundaria al tipo histórico o edad del bosque (Capítulo 5). Investigaciones realizadas por Basnou et al. (2015) en hábitats costeros corroboran estos resultados. Esto apunta a suponer que el proceso de invasión de dichos hábitats es altamente idiosincrático y depende en gran medida de las características, mientras que los cambios en el uso del suelo y el paisaje circundante juegan un papel más secundario (González-Moreno et al. 2017).

Implicaciones para la conservación de las comunidades vegetales

La presente tesis aporta datos de cómo los factores ambientales y de paisaje modulan el proceso de ensamblaje de las comunidades de plantas en las nuevas formaciones leñosas mediterráneas. Algunos de estos resultados pueden ser especialmente interesantes para mejorar la gestión de dichas formaciones con objeto de mejorar la conservación de su biodiversidad vegetal.

En matorrales mediterráneos, los resultados indican que es necesario considerar la dinámica de manchas -resultante de los patrones espaciotemporales de cambio de usos- porque determinan la beta-diversidad de especies leñosas en el paisaje y las interacciones ecológicas que conllevan. En bosques, los resultados muestran la importancia del paisaje actual –en particular la fragmentación del bosque y la antropización de la matriz territorial- y de la dispersión por vertebrados en el ensamblaje de las comunidades de plantas en las nuevas formaciones forestales. Por tanto, es determinante una gestión del paisaje forestal metropolitano especialmente encaminada a evitar el contacto entre dichos bosques y las áreas urbanas, creando áreas de amortiguamiento (*buffers*) y manteniendo o restaurando los gradientes de uso propios de los mosaicos agroforestales tradicionales (Santos et al. 2008).

Un énfasis especial debe ponerse en la gestión de las plantas invasoras que colonizan dichos bosques. Hay un predominio de especies dispersadas por vertebrados tolerantes a la sombra y propias de estados relativamente avanzados de la sucesión que no responden por tanto al síndrome típico de las plantas exóticas del territorio (Clotet et al. 2016). A diferencia de estas últimas, que desaparecen de los bosques perturbados cuando se produce la recuperación del dosel (Pino et al. 2013), estas especies es más probable que persistan o incluso incrementen su presencia a lo largo de la sucesión vegetal. Por tanto, la gestión de estas especies precisa de una estrategia específica, que pasa por la identificación de las principales fuentes de propágulo y de los requerimientos ecológicos para su establecimiento y expansión.

7. Conclusiones generales

Capítulo 3: Efectos del legado histórico de cambios de uso del suelo en los patrones de ensamblaje en matorrales

Las trayectorias históricas de uso del suelo y los factores ambientales (asociados al nicho ecológico de las especies) son los factores principales que explican el ensamblaje de las comunidades leñosas en matorrales mediterráneos. En cambio, la dispersión de las diversas especies parece jugar un papel más secundario en este proceso.

Mientras que la riqueza y diversidad de especies de dichos matorrales son afectadas por el uso del suelo del pasado reciente (1956), la composición de las especies en estas comunidades (por ejemplo, presencia y abundancia) se relaciona principalmente con usos del suelo más antiguos (1900 aproximadamente).

La riqueza y la diversidad de especies leñosas son afectadas tanto por la altitud como las trayectorias históricas del uso del suelo. En cambio, la equitatividad sólo se relaciona con la altitud, y este patrón parece debido a la predominancia de determinadas especies (*Q. coccifera*) en las zonas elevadas del macizo. La variación en la presencia y la cobertura de las especies leñosas se explica de forma similar por las variables ambientales y las trayectorias históricas del uso del suelo.

Los resultados indican que es necesario considerar la dinámica de manchas en las estrategias de conservación de estos matorrales ya que podría determinar la variabilidad en la presencia y abundancia de especies particulares y en las interacciones ecológicas que conllevan.

Capítulo 4: Efecto de la antropización del paisaje sobre el proceso de ensamblaje de las comunidades vegetales en los nuevos bosques periurbanos

Las condiciones del hábitat y los atributos del paisaje determinan el ensamblaje de las comunidades vegetales en los bosques periurbanos. En particular, la conectividad del bosque propicia la colonización por parte de especies leñosas y dificulta la de plantas propias de los hábitats antropizados adyacentes.

La edad del bosque (considerando bosques de reciente formación y bosques prexistentes) determina un cierto efecto sobre la riqueza de especies total y la de algunos grupos. En los nuevos bosques se observa una mayor riqueza de especies, que se puede relacionar con una deuda de extinción de las especies de hábitats abiertos previos (pastizales y matorrales) y un cierto crédito de colonización de las especies de bosque, limitado a las plantas dispersadas por vertebrados.

La llegada e instalación de especies dispersadas por vertebrados se ve especialmente dificultada en los nuevos bosques, lo que conlleva la aparición de los créditos de colonización anteriormente mencionados. Este resultado sugiere que la colonización de dichas especies está condicionada por la estructura del bosque, a través de requerimientos de nicho de las especies de plantas o de sus dispersores.

La conectividad forestal es un aspecto clave para el manejo del ensamblaje de las comunidades de plantas en los fragmentos de bosque periurbano, puesto que la fragmentación del bosque favorece la llegada de especies antropófilas y reduce las posibilidades de colonización y establecimento de las estrictamente forestales en paisajes tan dinámicos y antropizados.

Capítulo 5: Patrones de invasión por plantas exóticas en bosques periurbanos de reciente formación

Los bosques metropolitanos son especialmente susceptibles a la invasión por plantas exóticas. Son especialmente frecuentes y abundantes las especies dispersadas por vertebrados, aunque éstas no dominen en la flora exótica del territorio. Esto sugiere la existencia de filtros ecológicos que favorecen particularmente la colonización de los bosques por este grupo de especies.

Las condiciones del paisaje y el tipo histórico de bosque (reciente o prexistente) modulan los patrones de invasión. En particular, los bosques prexistentes localizados en paisajes fragmentados presentan una mayor susceptibilidad a la invasión por especies exóticas dispersadas por vertebrados.

La mayor proporción de especies dispersadas por vertebrados, tolerantes a la sombra y propias de estados relativamente avanzados de la sucesión, constituye un reto importante para la conservación de la biodiversidad en bosques periurbanos. En contraste con las especies exóticas pioneras, que pueden llegar a ser erradicadas de los bosques perturbados mediante la recuperación del dosel, estas especies es más probable que persistan o incluso incrementen su presencia a lo largo de la sucesión vegetal.

En un contexto metropolitano, el manejo a escala de paisaje para reducir la fragmentación del bosque podría coadyuvar a mitigar los procesos de invasión de las exóticas dispersadas por vertebrados. Además, estas acciones de manejo pueden ayudar a recuperar a las especies leñosas vulnerables a la alteración del hábitat y a la frecuente perturbación humana en los bordes de los parches de bosque, lo que contribuiría a la conservación de la biodiversidad y del funcionamiento ecológico de estos bosques metropolitanos.

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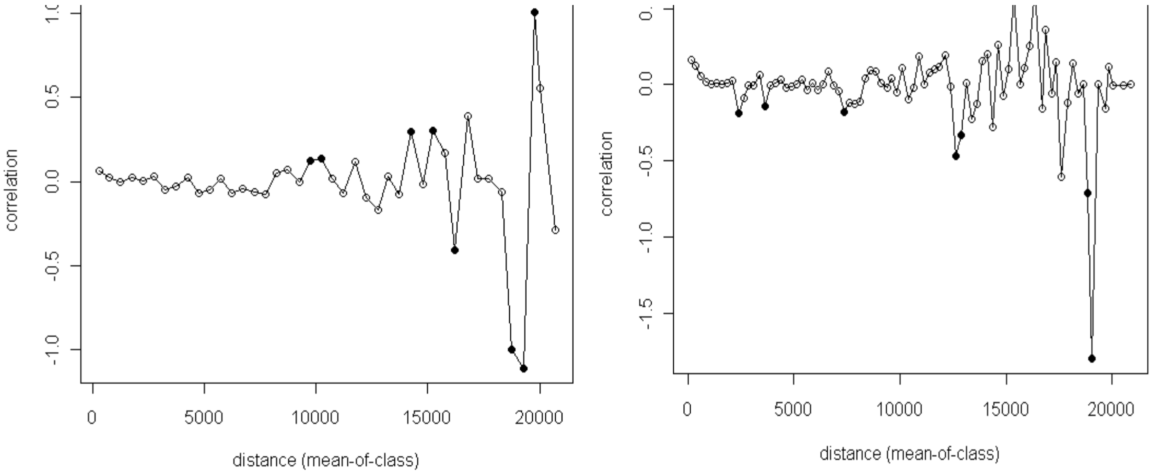
9. Apéndices

A. Niche factors and land-use history mostly drive woody local-scale community assembly in Mediterranean scrublands

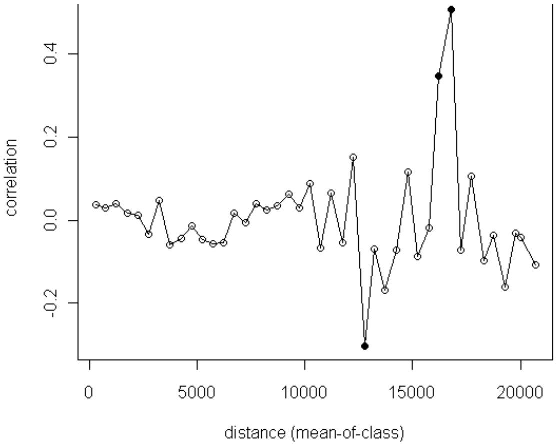
Appendix A.1. Correlograms (Moran's I) obtained from the residuals of the GLM regarding species richness, diversity and evenness.



Woody species richness

Woody species diversity

Woody species evenness



Appendix A.2. Species mean cover and frequency (percentage of plots) in each land cover pathway, and total plots in which each species has been found.

Species	Abbrev.	NCF		FCF		NCS		FCS		RC		Total plots
		Cover (%)	Plots (%)	Cover (%)	Plots (%)	Cover (%)	Plots (%)	Cover (%)	Plots (%)	Cover (%)	Plots (%)	
Ampelodesmos mauritanica	Ampe_mau	30.5	17	51.0	28	20.6	19	45.0	20	48.2	17	133
Arbutus unedo	Arbu_une	17.0	14	4.3	39	12.9	19	12.5	17	11.3	11	36
Asparagus acutifolius	Aspar_ac	8.8	29	2.5	11	6.1	25	.	.	5.0	36	28
Bupleurum fruticescens	Bupl_fru	10.8	29	26.3	10	11.1	33	.	.	10.4	29	21
Buxus sempervirens		.	.	.	.	2.5	100	.	.	.	.	1
Ceratonia siliqua		.	.	.	.	.	.	2.5	100	.	.	1
Chamaerops humilis	Chama_hu	9.4	21	2.5	14	8.4	44	5.0	12	2.5	9	43
Cistus albidus	Cist_alb	2.5	25	2.5	6	2.5	19	15.0	6	13.1	44	16
Cistus monspeliensis	Cist_mon	2.5	7	14.3	50	.	.	15.0	7	12.5	36	14
Cistus salviifolius	Cist_sal	2.5	6	4.1	50	.	.	2.5	25	6.7	19	16
Clematis flammula		2.5	33	.	.	5.6	44	.	.	8.8	22	9
Clematis vitalba		.	.	2.5	33	.	.	.	.	8.8	67	3
Coriaria myrtifolia		2.5	33	.	.	8.8	67	.	.	.	.	3
Coronilla minima		.	.	.	.	.	.	.	.	2.5	100	1
Crataegus monogyna		.	.	.	.	.	.	.	.	2.5	100	1
Cytisophyllum sessilifolium		2.5	100	.	.	.	.	.	.	.	.	3
Daphne gnidium	Daph_gni	4.3	15	6.9	43	2.5	4	4.6	26	4.6	13	47
Dorycnium hirsutum		.	.	2.5	56	.	.	2.5	11	2.5	33	9
Dorycnium pentaphyllum	Doryc_pe	2.5	10	7.9	40	2.5	8	6.0	21	8.4	20	84
Erica arborea		.	.	.	.	15.0	100	.	.	.	.	1
Erica multiflora	Eric_mul	10.9	20	10.7	32	10.4	15	11.5	16	9.0	18	95
Euphorbia characias	Euph_cha	2.5	6	2.5	11	2.5	22	2.5	17	2.5	44	18
Globularia alypum	Glob_aly	5.0	10	15.9	32	6.7	6	14.6	24	15.5	28	50
Helichrysum stoechas		2.5	100	.	.	.	.	.	.	.	.	1
Juniperus oxycedrus	Juni_oxy	5.9	19	4.2	39	7.9	12	5.0	18	4.3	12	57
Lithospermum fruticosum		.	.	2.5	100	.	.	.	.	.	.	1
Lonicera implexa	Loni_imp	5.0	24	8.8	19	11.3	19	15.0	5	2.5	33	21
Olea europea	Olea_eur	4.1	42	2.5	26	2.5	32	.	.	.	.	19
Phyllirea angustifolia		2.5	14	5.0	71	.	.	.	.	2.5	14	7
Phyllirea latifolia	Phyll_la	12.5	27	2.5	14	4.6	27	.	.	6.1	32	22
Pinus halepensis	Pinus_ha	17.1	13	16.4	27	9.4	9	8.3	19	15.7	32	100
Pinus pinea		2.5	100	.	.	.	.	.	.	.	.	1
Pistacia lentiscus	Pist_len	15.3	17	15.6	25	16.8	19	13.1	17	15.7	23	145
Quercus suber		.	.	.	.	.	.	.	.	2.5	100	1
Quercus cerrioides		2.5	14	2.5	29	2.5	14	2.5	29	2.5	14	7
Quercus coccifera	Q_coccif	32.3	19	20.4	28	39.3	19	29.3	17	12.4	18	124
Quercus ilex	Q_ilex	5.3	56	2.5	19	6.7	19	.	.	2.5	6	16
Rhamnus alaternus		.	.	.	.	.	.	.	.	2.5	100	3
Rhamnus lycioides	Rham_lyc	.	.	10.8	16	8.1	47	8.8	21	2.5	16	19
Rosa sempervirens		.	.	.	.	.	.	.	.	2.5	100	2
Rosmarinus officinalis	Rosm_off	11.8	14	25.6	25	22.7	18	30.9	21	15.0	22	125
Rubia peregrina	Rubi_per	2.5	20	2.5	28	4.1	15	2.5	9	3.3	28	54
Rubus ulmifolius	Rubu_ulm	.	.	.	.	.	.	2.5	8	8.0	92	12
Ruscus aculeatus		.	.	.	.	2.5	100	.	.	.	.	1
Sedum sediforme	Sedu_sed	2.5	25	2.5	11	3.9	32	2.5	11	2.5	21	28
Smilax aspera	Smil_asp	11.3	26	2.5	19	10.6	29	37.5	3	2.5	23	31
Spartium junceum		.	.	.	.	.	.	2.5	67	62.5	33	3
Thymus vulgaris	Thym_vul	6.7	10	4.6	19	2.5	16	10.8	10	6.5	45	31
Ulex parviflorus	Ulex_par	11.9	12	6.1	21	.	.	10.3	24	11.1	42	33
Viburnum tinus		15.0	100	.	.	.	.	.	.	.	.	1

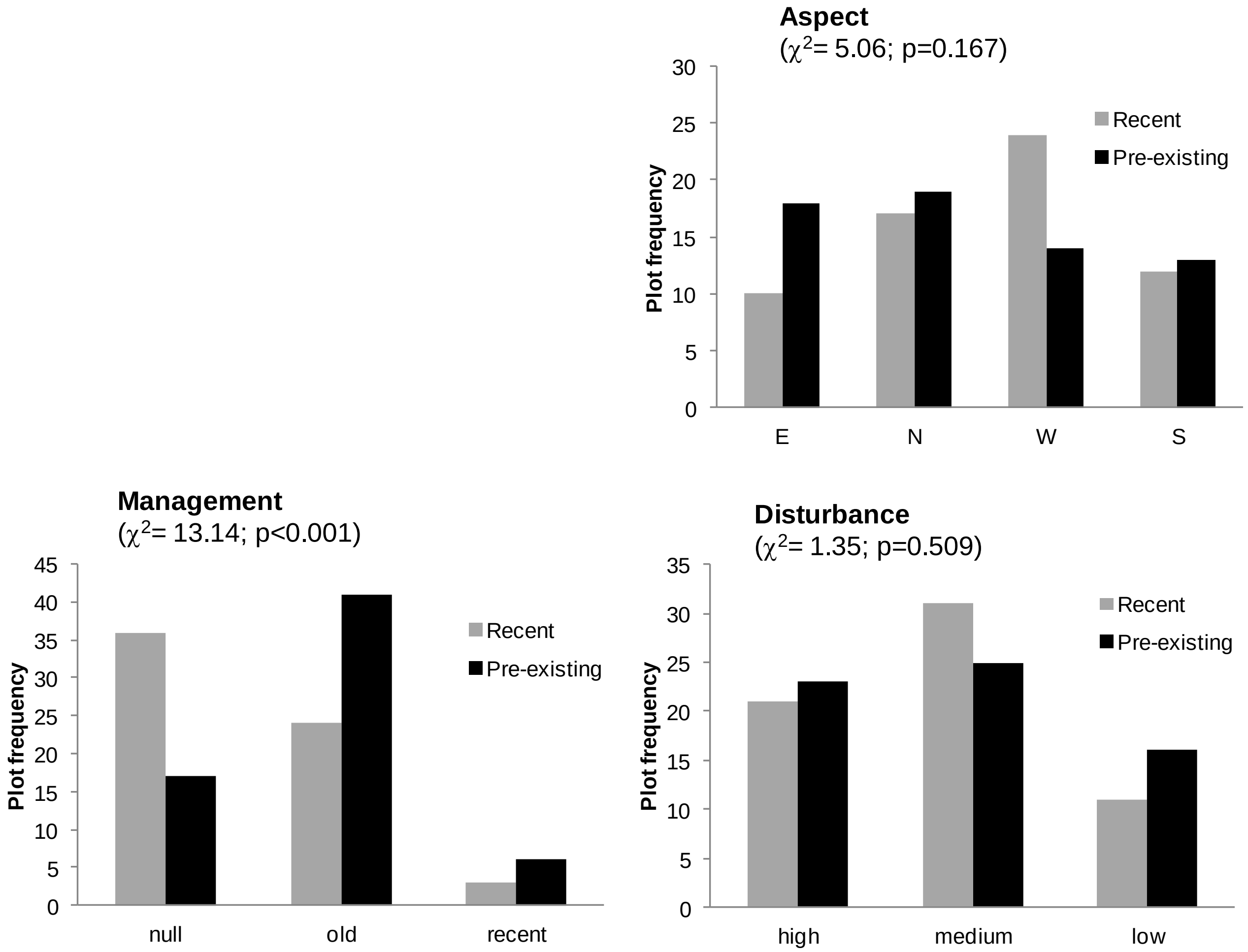
NCF: non-cropped forests, FCF: formerly cropped forests, NCS: non-cropped scrublands, FCS: formerly cropped scrublands, RC: recent crops

B. Species balance in plant community assembly in novel periurban forests: the role of dispersal type and of habitat and landscape factors

Appendix B.1. Mean values and SD of continuous predictors considered in the study in preexisting and recent forests. Significance of the corresponding T-tests, calculated with forest historical type as a factor and after Bonferroni correction, is also shown (significance: ns non significant; · $p<0.1$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$).

	Recent forests		Pre-existing forests			
	Mean	SD	Mean	SD	t-test	
Site condition						
Tree density (trees/plot)	33.24	17.4	32.59	17.41	0.210	ns
Basal area (m^{2}ha^{-1})	34.42	17.00	32.40	18.49	0.644	ns
Alien species richness	1.76	1.8	1.56	1.4	0.707	ns
Slope	22.98	13.7	25.6	16.33	-0.975	ns
Photosynthetically Active Radiation	0.23	0.3	0.32	0.32	-1.765	·
Mean annual rainfall (mm)	691.96	57.7	692.37	58.33	-0.039	ns
Mean annual temperature (°C)	14.16	0.5	14.16	0.37	-0.021	ns
Elevation (m)	262.79	82.6	262.64	68.24	0.011	ns
Soil depth (m)	43.45	6.2	44.3	5.93	-0.783	ns
Stoniness (%)	15.89	12.3	14.83	12.63	0.479	ns
Latitude (UTM X)	4607510.2	7455.4	4607073.7	6695.8	-0.348	ns
Longitude (UTM Y)	431963.2	11943.6	432091.4	12038.0	0.061	ns
Landscape structure						
% of patch perimeter surrounded by forest	0.36	0.2	0.36	0.19	0.150	ns
% of patch perimeter surrounded by urban	0.32	0.2	0.32	0.19	-0.178	ns

Appendix B.2. Frequencies of categories in preexisting and recent forests in the categorical predictors considered in the study. Significance of the corresponding chi-square tests, calculated with forest type as a factor and after Bonferroni correction, is also shown.



Appendix B.3. Species recorded in the study plots classified per habitat type. Vertebrate-dispersed species are indicated.

Species	**Habitat type**	**Vertebrate-Dispersed**
Arbutus unedo	Forest	*
Aristolochia longa	Forest	
Arum sp.	Forest	*
Asparagus acutifolius	Forest	*
Asplenium adiantum-nigrum	Forest	
Asplenium adiantum-nigrum subsp. onopteris	Forest	
Asplenium trichomanes	Forest	
Brachypodium sylvaticum	Forest	
Bupleurum fruticosum	Forest	
Campanula rapunculus	Forest	
Clematis flammula	Forest	
Clematis sp.	Forest	
Clematis vitalba	Forest	
Coriaria myrtifolia	Forest	*
Cornus sanguinea	Forest	*
Coronilla emerus	Forest	
Corylus avellana	Forest	*
Crataegus monogyna	Forest	*
Daphne gnidium	Forest	*
Euonymus europaeus	Forest	*
Fraxinus angustifolia	Forest	
Galium maritimum	Forest	
Geum urbanum	Forest	
Hedera helix	Forest	*
Juniperus communis	Forest	*
Lapsana communis	Forest	
Ligustrum vulgare	Forest	*
Limodorum abortivum	Forest	
Lithospermum purpurocaeruleum	Forest	
Lonicera etrusca	Forest	*
Lonicera implexa	Forest	*
Lonicera xylosteum	Forest	*
Myosotis arvensis	Forest	
Origanum vulgare	Forest	
Osyris alba	Forest	*
Phillyrea latifolia	Forest	*
Pinus halepensis	Forest	

Pinus pinaster	Forest	
Pinus pinea	Forest	*
Pistacia lentiscus	Forest	*
Polypodium vulgare	Forest	
Prunus avium	Forest	*
Prunus mahaleb	Forest	*
Prunus spinosa	Forest	*
Pyrus communis	Forest	*
Quercus cerrioides	Forest	*
Quercus ilex	Forest	*
Quercus suber	Forest	*
Rhamnus alaternus	Forest	*
Rosa sempervirens	Forest	*
Rosa canina.	Forest	*
Rubia peregrina	Forest	*
Rubus ulmifolius	Forest	*
Ruscus aculeatus	Forest	*
Sambucus nigra	Forest	*
Satureja calamintha	Forest	
Smilax aspera	Forest	*
Sorbus domestica	Forest	*
Sorbus torminalis	Forest	*
Tamus communis	Forest	*
Ulmus minor	Forest	
Ulmus sp.	Forest	
Viburnum tinus	Forest	*
Viola alba	Forest	
Agrimonia eupatoria	Scrub_grassland	
Anacamptis pyramidalis	Scrub_grassland	
Andryala integrifolia	Scrub_grassland	
Aphyllantes monspeliensis	Scrub_grassland	
Arctium minus	Scrub_grassland	
Argyrolobium zanonii	Scrub_grassland	
Arrhenatherum elatius	Scrub_grassland	
Astragalus monspessulanus	Scrub_grassland	
Astragalus sp.	Scrub_grassland	
Avenula bromoides subsp. bromoides	Scrub_grassland	
Avenula sp.	Scrub_grassland	
Blackstonia perfoliata	Scrub_grassland	
Brachypodium phoenicoides	Scrub_grassland	
Brachypodium retusum	Scrub_grassland	
Briza maxima	Scrub_grassland	
Bupleurum frutiscescens	Scrub_grassland	

Calicotome spinosa	Scrub_grassland	
Carduncellus monspelliensium	Scrub_grassland	
Carex flacca	Scrub_grassland	
Carex halleriana	Scrub_grassland	
Carex sp.	Scrub_grassland	
Carex vulpina	Scrub_grassland	
Centaurea aspera	Scrub_grassland	
Centaurea linifolia	Scrub_grassland	
Chondrilla juncea	Scrub_grassland	
Cistus albidus	Scrub_grassland	
Cistus monspeliensis	Scrub_grassland	
Cistus salviifolius	Scrub_grassland	
Convolvulus althaeoides	Scrub_grassland	
Convolvulus cantabrica	Scrub_grassland	
Coris monspeliensis	Scrub_grassland	
Dactylis glomerata	Scrub_grassland	
Dorycnium hirsutum	Scrub_grassland	
Dorycnium pentaphyllum	Scrub_grassland	
Erica arborea	Scrub_grassland	
Erica multiflora	Scrub_grassland	
Eryngium campestre	Scrub_grassland	
Euphorbia characias	Scrub_grassland	
Euphorbia mariolensis	Scrub_grassland	
Euphorbia serrata	Scrub_grassland	
Filago pyramidata	Scrub_grassland	
Foeniculum vulgare	Scrub_grassland	
Fumana ericoides	Scrub_grassland	
Galactites tomentosa	Scrub_grassland	
Galium lucidum	Scrub_grassland	
Galium verum	Scrub_grassland	
Genista scorpius	Scrub_grassland	
Globularia alypum	Scrub_grassland	
Helichrysum stoechas	Scrub_grassland	
Hieracium pilosella	Scrub_grassland	
Hyparrhenia hirta	Scrub_grassland	
Hypericum perforatum	Scrub_grassland	
Juniperus oxycedrus	Scrub_grassland	*
Knautia columbaria	Scrub_grassland	
Lathyrus sp.	Scrub_grassland	
Lavandula latifolia	Scrub_grassland	
Lavandula stoechas	Scrub_grassland	
Leontodon taraxacoides	Scrub_grassland	
Melica ciliata	Scrub_grassland	

Melica minuta	Scrub_grassland	
Olea europaea	Scrub_grassland	*
Ononis minutissima	Scrub_grassland	
Ophrys fusca	Scrub_grassland	
Orobanche hederae	Scrub_grassland	
Oryzopsis miliacea	Scrub_grassland	
Pallenis spinosa	Scrub_grassland	
Phagnalon saxatile	Scrub_grassland	
Phillyrea angustifolia	Scrub_grassland	*
Plantago lagopus	Scrub_grassland	
Plantago laceolata	Scrub_grassland	
Polygala rupestris	Scrub_grassland	
Psoralea bituminosa	Scrub_grassland	
Quercus coccifera	Scrub_grassland	*
Ranuculus bulbosus	Scrub_grassland	
Rosmarinus officinalis	Scrub_grassland	
Rumex obtusifolius	Scrub_grassland	
Ruta chalepensis	Scrub_grassland	
Sanguisorba minor	Scrub_grassland	
Scabiosa atropurpurea	Scrub_grassland	
Sedum rupestre	Scrub_grassland	
Sedum sediforme	Scrub_grassland	
Sideritis hirsuta	Scrub_grassland	
Sonchus tenerrimus	Scrub_grassland	
Spartium junceum	Scrub_grassland	
Teucrium chamaedrys	Scrub_grassland	
Teucrium polium	Scrub_grassland	
Thymus vulgaris	Scrub_grassland	
Ulex parviflorus	Scrub_grassland	
Urospermum dalechampii	Scrub_grassland	
Acer negundo	Synanthropic	
Ailanthus altissima	Synanthropic	
Anagallis arvensis	Synanthropic	
Araujia sericifera	Synanthropic	
Arundo donax	Synanthropic	
Avena barbata	Synanthropic	
Bromus madritensis	Synanthropic	
Bryonia dioica	Synanthropic	*
Cedrus libani	Synanthropic	
Celtis australis	Synanthropic	*
Chenopodium album	Synanthropic	
Chenopodium murale	Synanthropic	
Cirsium vulgare	Synanthropic	

Convolvulus arvensis	Synanthropic	
Conyza sp.	Synanthropic	
Conyza sumatrensis	Synanthropic	
Coronilla valentina	Synanthropic	
Cotoneaster lacteus	Synanthropic	*
Cotoneaster pannosus	Synanthropic	*
Cynoglossum creticum	Synanthropic	
Daucus carota	Synanthropic	
Dichondra micrantha	Synanthropic	
Diplotaxis erucoides	Synanthropic	
Echium vulgare	Synanthropic	
Eriobotrya japonica	Synanthropic	*
Erucastrum nasturtiifolium	Synanthropic	
Ficus carica	Synanthropic	*
Galium aparine	Synanthropic	
Geranium robertianum	Synanthropic	
Geranium rotundifolium	Synanthropic	
Juglans regia	Synanthropic	*
Laurus nobilis	Synanthropic	*
Ligustrum lucidum	Synanthropic	*
Lonicera japonica	Synanthropic	*
Lunaria annua	Synanthropic	
Mahonia aquifolium	Synanthropic	*
Marrubium vulgare	Synanthropic	
Medicago arabica	Synanthropic	
Medicago lupulina	Synanthropic	
Medicago sp.	Synanthropic	
Melissa officinalis	Synanthropic	
Mercurialis annua	Synanthropic	
Opuntia ficus-indica	Synanthropic	*
Oxalis articulata	Synanthropic	
Oxalis corniculata	Synanthropic	
Oxalis latifolia	Synanthropic	
Parietaria officinalis	Synanthropic	
Phytolacca americana	Synanthropic	*
Pittosporum tobira	Synanthropic	*
Potetilla reptans	Synanthropic	
Prunus cerasifera	Synanthropic	*
Prunus cerasifera var. pissardii	Synanthropic	*
Prunus domestica	Synanthropic	*
Prunus dulcis	Synanthropic	*
Pyracantha angustifolia	Synanthropic	*
Robinia pseudoacacia	Synanthropic	

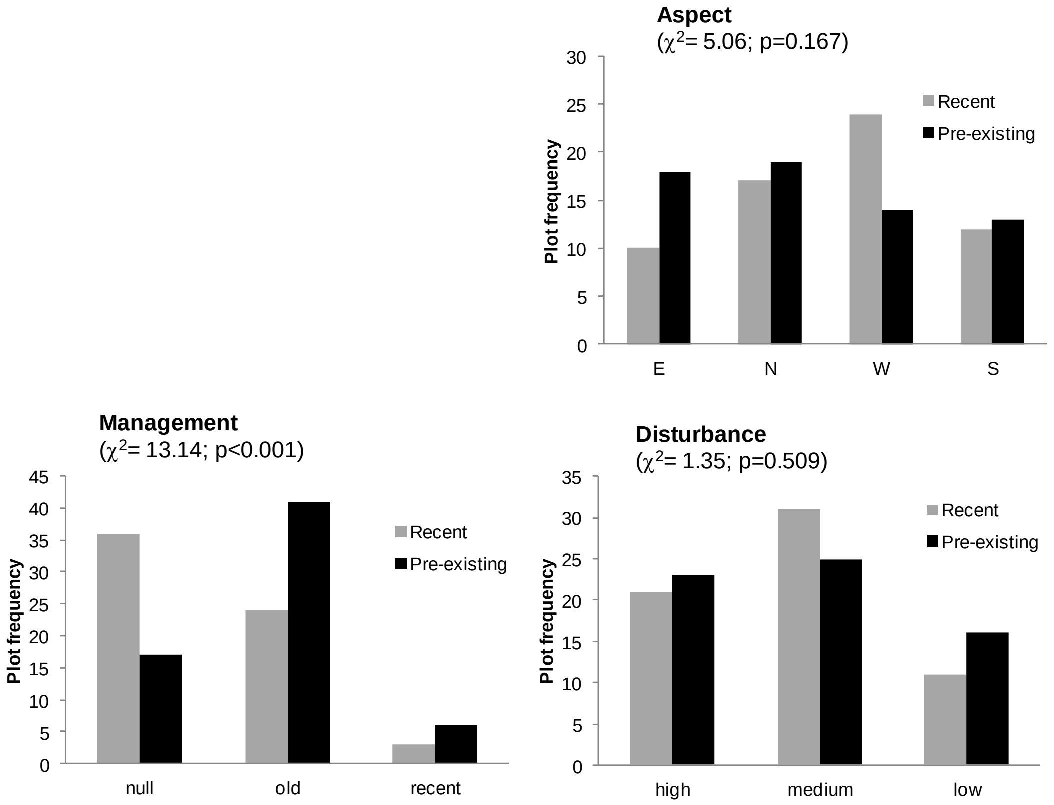
Senecio inaequidens	Synanthropic	
Senecio pterophorus	Synanthropic	
Solanum chenopodioides	Synanthropic	*
Solanum nigrum	Synanthropic	*
Solanum sp.	Synanthropic	*
Sonchus oleraceus	Synanthropic	
Stellaria media	Synanthropic	
Ulmus pumila	Synanthropic	
Urtica dioica	Synanthropic	
Vicia hybrida	Synanthropic	
Vitis vinifera	Synanthropic	*
Ceterach officinarum	Other	
Crepis sp.	Other	
Eleagnus pungens	Other	
Euphorbia sp.	Other	
Hieracium sp.	Other	
Holcus lanatus	Other	

C. Alien plant invasion in novel metropolitan forests: the role of vertebrate dispersal

Appendix C.1. Mean and SD values of measured variables in recent and pre-existing forests. T-test comparing mean values between forest types (significance: ns non-significant; ·p<0.1; * p<0.05; ** p<0.01; *** p<0.001).

	Recent forest		Pre-existing forest		t-test	
	Mean	SD	Mean	SD		
Tree density (trees/plot)	33.24	17.40	32.59	17.41	0.210	ns
Basal area (m^{2}ha^{-1})	34.42	17.00	32.40	18.49	0.644	ns
Native species richness	21.46	6.60	18.37	5.04	2.965	**
Alien species richness	1.76	1.80	1.56	1.40	0.707	ns
Slope	22.98	13.70	25.60	16.33	-0.975	ns
Photosynthetically Active Radiation (PAR)	0.23	0.30	0.32	0.32	-1.765	·
Mean annual rainfall (mm)	691.96	57.70	692.37	58.33	-0.039	ns
Mean annual temperature (°C)	14.16	0.50	14.16	0.37	-0.021	ns
Elevation (m)	262.79	82.60	262.64	68.24	0.011	ns
Soil depth (m)	43.45	6.20	44.30	5.93	-0.783	ns
Stoniness (%)	15.89	12.30	14.83	12.63	0.479	ns
Latitude (UTM X)	4607510.2	7455.4	4607073.7	6695.8	-0.348	ns
Longitude (UTM Y)	431963.2	11943.6	432091.4	12038.0	0.061	ns
% of the patch perimeter surrounded by forest	0.36	0.20	0.36	0.19	0.150	ns
% of the patch perimeter surrounded by urban areas	0.32	0.20	0.32	0.19	-0.178	ns

Appendix C.2. Frequencies of categories in preexisting and recent forests in the categorical predictors considered in the study. Significance of the corresponding chi-square tests, calculated with forest type as a factor and after Bonferroni correction, is also shown.



Appendix C.3. Mean cover and frequency of alien species at the Vallès lowlands by recent and pre-existing forest. Abbreviations of most frequent species are given.

Species	Abbrev	Dispersal strategy	Cover					Frequency				
			Pre-existing		Recent		Total	Pre-existing		Recent		Total
			Non-vert	Vert	Non-vert	Vert		Non-vert	Vert	Non-vert	Vert	
Acer negundo		Non vert			5.00		5.00			1		1
Ailanthus altissima		Non vert			27.50		27.50			2		2
Araujia sericifera	Arau_seri	Non vert	9.50		6.00		7.27	4		7		11
Arundo donax		Non vert	20.00		5.00		12.50	1		1		2
Cedrus libani		Non vert			20.00		20.00			1		1
Celtis australis	Celt_aust	Vert		14.48		11.71	13.10		21		21	42
Conyza sp.		Non vert			4.00		4.00			2		2
Conyza sumatrensis	Cony_suma	Non vert	5.50		5.40		5.43	4		10		14
Coronilla valentina		Non vert	4.00		3.00		3.50	1		1		2
Cotoneaster lacteus	Coto_lact	Vert		12.50		20.00	15.00		4		2	6
Cotoneaster pannosus	Coto_pann	Vert		9.50		2.60	5.67		4		5	9
Dichondra micrantha		Non vert	5.00				5.00	1				1
Eriobotrya japonica		Vert		5.00		5.00	5.00		2		1	3
Ficus carica		Vert				5.00	5.00				1	1
Laurus nobilis	Laur_nobi	Vert		8.19		8.20	8.20		26		15	41
Ligustrum lucidum	Ligu_luci	Vert		14.29		13.38	13.80		7		8	15
Lonicera japonica		Vert				40.00	40.00				2	2
Lunaria annua		Non vert	5.00		1.00		3.00	1		1		2
Mahonia aquifolium		Vert				5.00	5.00				1	1
Opuntia ficus-indica		Vert				1.50	1.50				2	2
Oxalis articulata		Non vert	3.00				3.00	1				1
Oxalis latifolia		Non vert	10.00				10.00	1				1
Phytolacca americana		Vert		7.50			7.50		2			2
Pittosporum tobira		Vert		5.00		10.00	7.50		1		1	2
Prunus cerasifera		Vert				10.00	10.00				1	1
Prunus cerasifera var. pissardii		Vert		5.00			5.00		1			1
Prunus domestica	Prun_dome	Vert		5.29		8.14	6.71		7		7	14
Prunus dulcis		Vert				5.00	5.00				1	1
Pyracantha angustifolia	Pyra_angu	Vert				11.57	11.57				7	7
Robinia pseudoacacia		Non vert	30.00		30.00		30.00	1		1		2
Senecio inaequidens		Non vert	5.00		1.00		3.00	1		1		2
Senecio pterophorus	Sene_pter	Non vert	5.00		5.40		5.33	1		5		6
Solanum chenopodioides	Sola_chen	Vert		3.83		5.20	4.45		6		5	11
Ulmus pumila		Non vert			10.00		10.00			1		1

Cubierta *Pistacia lentiscus*

Contracubierta *Ulex parviflorus*

Fotografías de H. Arias-LeClaire en Garraf, Barcelona