TESIS DOCTORAL

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LA INFLUENCIA DE LA ALTERACIÓN DEL PAISAJE EN LAS INVASIONES POR PLANTAS EXÓTICAS

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Tesis Doctoral
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La Influencia de la Alteracion del Paisaje en las Invasiones por Plantas Exóticas

Memoria presentada por el Licenciado en Ciencias Ambientales
Pablo González Moreno para optar
al título de Doctor por la Universidad Pablo de Olavide

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CERTIFICO

Que Pablo González Moreno, Licenciado en Ciencias Ambientales por la Universidad de Málaga, ha realizado bajo mi dirección la presente Memoria de Tesis Doctoral, titulada “La influencia de la alteracion del paisaje en las invasiones por plantas exóticas”, y que a mi juicio reúne los méritos suficientes para optar al grado de Doctor por la Universidad Pablo de Olavide.

Y para que así conste, firmo el presente documento en Sevilla a 17 de noviembre de 2014.

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El autor, Pablo González Moreno, recibió del Ministerio de Economía y Competitividad (MINECO) una ayuda de Formación del Personal Investigador (BES-2010-035789) así como de cuatro ayudas destinadas a estancias breves. Así mismo, los trabajos contenidos en esta memoria se financiaron parcialmente a través de los proyectos del MINECO Consolider-Ingenio MONTES (CSD2008-00040) y RIXFUTUR (CGL2009-7515), del proyecto de excelencia de la Junta de Andalucía RNM-4031 y por el programa Severo Ochoa para centros de excelencia en R+D+I (SEV-2012-0262).

A mi familia
A María
A mis amigos

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RESUMEN

Las invasiones biológicas junto con la fragmentación del paisaje y la pérdida de hábitat son los principales factores asociados con la pérdida de biodiversidad. Las invasiones generan enormes impactos ecológicos tanto a escala local como regional, tales como la amenaza a la supervivencia de las especies nativas o la homogeneización biótica de las comunidades. Por ello, es fundamental conocer los patrones espaciales del grado de invasion (p.e. riqueza o abundancia de especies exóticas) y las variables que controlan el proceso de invasión de las especies exóticas. Durante mi doctorado, he profundizado en estos aspectos a través de una perspectiva macroecológica explorando cuáles son los factores que determinan el grado de invasión por plantas exóticas de hábitats terrestres a distintas escalas espacio-temporales. Las preguntas generales que se han planteado son las siguientes: ¿Cómo afecta la alteración humana del paisaje a la invasión en comparación con el clima y el tipo de hábitat? ¿El efecto de estas variables depende del contexto ecológico? Aunque en esta Tesis Doctoral se ha realizado un análisis de los patrones de invasión en una gran variedad de tipos de hábitats, se da un énfasis especial a los hábitats costeros por su especial vulnerabilidad.

A escala regional (España peninsular), tanto el clima como la alteración del paisaje presentan una importancia similar para explicar el grado de invasión por plantas exóticas. En cambio, a escalas intermedias (costa catalana y menorquina), encontramos una importancia relativa mayor de la alteración del paisaje que del clima o del tipo de hábitat. Dentro de las variables que caracterizan la alteración del paisaje, la abundancia y diversidad de cubiertas de suelo es el aspecto principal en comparación con la agregación espacial de esos mismos tipos de cubiertas. Es decir, la composición del paisaje es más importante que su configuración. La alteración del paisaje es también el factor principal asociado a la invasión de los bosques sumamente fragmentados de la comarca del Vallés en Cataluña. Si bien el monte Mediterráneo se considera relativamente resistente a la invasión por plantas exóticas, comprobamos en el Vallés como ciertas condiciones de perturbación y cercanía a las vías de comunicación facilitan el establecimiento de especies exóticas en el interior de los fragmentos.

Teniendo en cuenta esta importancia del paisaje en los patrones de invasión, es necesario reconocer que la dinámica temporal del paisaje puede también afectar al proceso de invasión. En este sentido, en la costa andaluza occidental observamos una asociación mayor del grado de invasión actual con la abundancia de área alterada en 1956 que con la de 2007. Este resultado sugiere un posible crédito de invasión, ya que áreas recientemente alteradas pueden presentar en la actualidad un grado de invasión menor al que les correspondería de acuerdo a su composición del paisaje. El crédito de invasión encontrado estuvo definido por la historia de introducción de las especies exóticas y de las prácticas humanas en el territorio. Por ejemplo, especies con un tiempo de residencia elevado y usadas frecuentemente en agricultura, son las que presentaron una mayor asociación con la cantidad de área agrícola en el pasado.

El efecto de la alteración del paisaje y del clima en el grado de invasión puede variar según el tipo de hábitat, la región biogeográfica y la fase del proceso de invasión. Para España peninsular, identificamos principalmente una interacción del clima con el tipo de hábitat al explicar el grado de invasión a nivel de comunidad, mientras que los patrones fueron similares entre regiones biogeográficas. Entre fases también observamos una interacción con el tipo de hábitat. Por ejemplo, los hábitats forestales presentaron un nivel intermedio de probabilidad de establecimiento de plantas exóticas pero una baja dominancia de las mismas. A nivel de especie, tomando como caso de estudio al geófito *Oxalis pes-caprae* L., encontramos diferencias entre las condiciones ambientales que definen su distribución en la región nativa, Sudáfrica, y las de la región Mediterránea donde ha sido introducida. En concreto, *Oxalis* ha sufrido una expansión del nicho climático hacia condiciones más frías no existentes en la región nativa muestreada. Por tanto, no podemos asegurar que la expansión del nicho se deba a una rápida evolución de la especie, ya que podría ser que la especie estuviera ya preadaptada a esas condiciones climáticas. Por otra parte, *Oxalis* presentó una ocupación parcial del nicho de perturbación al ocupar áreas con mayor perturbación a nivel local y de paisaje que en la zona nativa. Esto implica que la especie tiene aún el potencial de invadir zonas más naturales a medida que la invasión avance. En general, estos resultados a nivel de comunidad y de especie sugieren que el efecto del clima y de la alteración del paisaje en los patrones de invasión depende del tipo de hábitat y que su extrapolación entre regiones nativas y de introducción puede llevar a conclusiones erróneas.

La presente Tesis apunta a que es importante estudiar los patrones de invasión considerando las distintas escalas espaciales y fases en el proceso de invasión. Esta aproximación podría facilitar el manejo de especies invasoras al detectar el aspecto principal que controla el éxito de invasión (p.e. alteración del paisaje, clima y hábitat) exactamente en la escala espacial y la fase a la que actúa. A su vez, la importancia constatada de la alteración del paisaje en los patrones de invasión, puede ser utilizada en las estrategias de lucha y prevención contra las invasiones por plantas exóticas a través de una gestión que priorice áreas de actuación y especies en función del tipo de paisaje.

SUMMARY

Biological invasions, landscape fragmentation and habitat loss are the main factors associated with biodiversity loss. Invasions have enormous impacts both at local and regional scales, such as threatening native species or the biotic homogenization of communities. Thus, it is important to understand the aspects driving the spatial patterns of the degree of invasion (e.g. non-native species richness or abundance) and the invasion process of non-native species. During my PhD, I have focused on these aspects adopting a macroecological approach to explore which are the factors determining the degree of invasion by non-native plants in terrestrial habitats at different spatio-temporal scales. The general questions adopted include: What is the effect of human alteration of the landscape on non-native plants invasions in comparison to climate and habitat type? Does the effect of these variables depend on the ecological context? This Thesis considers a wide variety of habitats, giving special emphasis to coastal habitats due to their high vulnerability.

At regional scale (mainland Spain), climate and landscape alteration showed similar importance to explain the level of invasion by non-native plants. In contrast, at intermediate spatial scales (Catalonia and Menorca), we found a higher relative importance of landscape alteration to explain the local level of invasion in comparison to climate and habitat type. Within landscape alteration variables, the abundance and diversity of land-cover types (e.g. urban area) were the main factors driving invasion in comparison to their spatial arrangement (e.g. fragmentation). Briefly, landscape composition is more imporntant than its configuration. Landscape alteration was also the main factor controlling the invasion of forest fragments in the Vallés county in Catalonia, Spain. Although Mediterranean forests are considered relatively resistant to invasion by non-native plants, we identified that a certain level of perturbation and closeness to roads facilitate the establishment of non-native plants in the interior of these forest fragments.

Taking into account the importance of landscape characteristics on invasion patterns, it is relevant to recognize that the temporal dynamics of landscapes could affect the invasion process. In fact, we observed higher association of the current level of invasion with the abundance of altered area in 1956 than with the area in 2007. This finding suggests a potential invasion credit as areas recently altered might show a relatively lower level of invasion than the potential level associated to the actual landscape composition. The invasion credit founded was related to the history of non-natives introductions and the human practices in the territory. For instance, species with a large residence time and widely used in agriculture in the past showed high association with past cropland area.

The effect of landscape alteration and climate on the level of invasion could vary depending on the habitat type, the biogeographical region or the stage of the invasion process. For mainland Spain, we found an interaction between climate and the habitat type to explain the level of invasion at the community level, while invasion patterns were similar among biogeographical regions. Among stages of invasion we also identified an interaction with habitat type. For instance, woodlands had medium levels of non-native species establishment but very low dominance. At the species level and using the geophyte *Oxalis pes-caprae* L. as study case, we found differences between the environmental conditions defining its distribution in its native region (South Africa) and in the Mediterranean region where it has been introduced. *Oxalis* experienced an expansion of the climatic niche towards colder conditions not available in the sampled area of the native range. Nevertheless, we cannot assure unequivocally a rapid evolution of the species in these areas as the species could have been already preadapted to those colder conditions. On the other hand, the species showed an unfilling of the disturbance niche towards areas of higher disturbance rates at both local and landscape scales. This pattern suggests that *Oxalis* still has the potential to invade more natural areas as the invasion unfolds. In general, these results at community and species level imply that the effect of landscape alteration and climate on invasion patterns depends on the habitat type and that its extrapolation among native and introduced regions could result in misleading conclusions.

The results found in this PhD Thesis highlight that it is of major concern to study invasion patterns across different spatial scales and stages in the invasion process. This approach might help the management of non-native species by detecting the main aspect controlling the invasion success (e.g. landscape alteration, climate, or habitat type) at the scale and the stage where it actually occurs. Furthermore, the importance of landscape alteration on invasion patterns, might be used in the prevention and control of invasion by non-native plants through a management strategy at the landscape scale prioritizing areas and species of intervention based on the landscape type.

INTRODUCCIÓN, OBJETIVOS Y METODOLOGÍA

INTRODUCCIÓN

Las invasiones biológicas

Las invasiones biológicas junto con la alteración del paisaje son uno de los mayores problemas que afectan a la pérdida de biodiversidad (Sala et al., 2000). Las invasiones generan enormes impactos ecológicos tanto a escala local como regional tales como la amenaza directa de especies nativas o la homogeneización de la composición de las comunidades (Levine et al., 2003; Pino et al., 2009; Vilà et al., 2010a). Además, las invasiones pueden mermar la cantidad y la calidad de los recursos naturales de los que nos abastecemos (Pimentel et al., 2005). Por ello, es fundamental conocer los patrones de distribución y los procesos de invasión de las especies exóticas. En este sentido, no todas las especies exóticas llegan a ser invasoras ya que numerosos factores ecológicos pueden impedir su paso a un estadio de naturalización o de invasión propiamente dicho (ver definiciones en Caja 1). Conociendo la ecología de las especies exóticas y los factores que determinan su invasión se podrán diseñar estrategias apropiadas de gestión, y lo que es más importante, prevenirlas.

CAJA 1

De exótica a invasora (basado en Pyšek et al., 2004)

Planta exótica: taxones cuya presencia en una determinada área se debe al ser humano que las ha introducido de forma intencionada o no, o que han llegado sin la ayuda del ser humano proveniente de otras zonas en las que ya era exótica
Planta naturalizada: taxones exóticos que presenta poblaciones autosuficientes durante al menos 10 años sin la intervención directa del hombre a través del reclutamiento por semillas o partes de la planta (p.e. tallos, tubérculos, bulbos).
Planta invasora: taxones naturalizados que producen descendencia, frecuentemente en gran número, a distancias considerables de la planta madre y por tanto tienen el potencial de propagarse en una amplia área.
Neófitas: plantas exóticas cuya introducción fue posterior a 1500. Las plantas exóticas de introducción anterior se les denomina **arqueófitas**.

Si bien hay referencias a las invasiones y sus consecuencias en trabajos clásicos (Darwin, 1859), la preocupación por los fenómenos de introducción de especies exóticas y su impacto en la salud y las actividades humanas es lo que originó a mediados del siglo XX un interés creciente de las invasiones biológicas en Ecología (Elton, 1958; Davis et al., 2001). La investigación en ecología de las invasiones biológicas se ha centrado en dos aspectos principales: la caracterización del **potencial invasor de las especies** (Kolar & Lodge, 2001; Hayes & Barry, 2007) y **el estudio del grado de invasión de los ecosistemas** (Caja 2; Vilà et al., 2007; Chytrý et al., 2008a). Esta segunda rama de la ecología de las invasiones es la que quizá más importancia esté cobrando en la actualidad debido a su fácil implementación en los análisis de riesgo por invasión (Chytrý et al., 2009) y en la que se centrará la presente Tesis Doctoral. Estimar **el grado de invasión es relevante para facilitar la evaluación de la intensidad de las invasiones** biológicas en una determinada área, **reflejar la tendencia en la intensidad de las invasiones** a lo largo del espacio y tiempo y finalmente para **actuar como señal de alerta temprana** antes de la posible degradación del ecosistema (Catford et al., 2012).

CAJA 2

Conceptos clave

Grado de invasión: extensión o intensidad observada en las invasiones por especies exóticas en un ecosistema (Lonsdale, 1999; Chytrý et al., 2008a). Vendrá determinado por la combinación de presión de propágulos y la invasibilidad propia del ecosistema.

Invasibilidad (invasibility): susceptibilidad de una comunidad o hábitat al establecimiento y expansión de especies exóticas (Lonsdale, 1999; Alpert, 2000; Chytrý et al., 2008a).

Potencial invasor (invasiveness): capacidad de una especie para superar las diferentes barreras bióticas y abióticas y convertirse en invasora (Di Castri, 1989; Alpert, 2000).

Presión de propágulos: cantidad de semillas o partes viables de un organismo exótico que llegan a un determinado lugar y pueden llegar a desarrollar individuos adultos (Lonsdale, 1999; Chytrý et al., 2008a).

Dentro del estudio de las invasiones biológicas existe una **mayoría de trabajos centrados en plantas exóticas** en comparación con otros taxones (Pyšek et al., 2008; Jeschke et al., 2012). En un estudio realizado en 2006 se constató como de un total de 2670 artículos sobre invasiones, un 44% de los mismos se centraba en plantas (Pyšek et al., 2008). Considerando distintos grupos de plantas, de especial relevancia son los trabajos centrados en acacias (Richardson et al., 2011) y coníferas (Richardson & Rejmánek, 2004; Carrillo-Gavilán & Vilà, 2010). Además, una gran mayoría de los marcos conceptuales y desarrollos teóricos en el campo de las invasiones se han elaborado basándose en estudios sobre plantas (Kueffer et al., 2013). Considerando este último aspecto y la disponibilidad de información sobre distribución de plantas exóticas, esta Tesis utiliza como caso de estudio a las plantas exóticas para estudiar los patrones de invasión de los ecosistemas a distintas escalas espacio-temporales.

Los factores asociados con el proceso de invasión

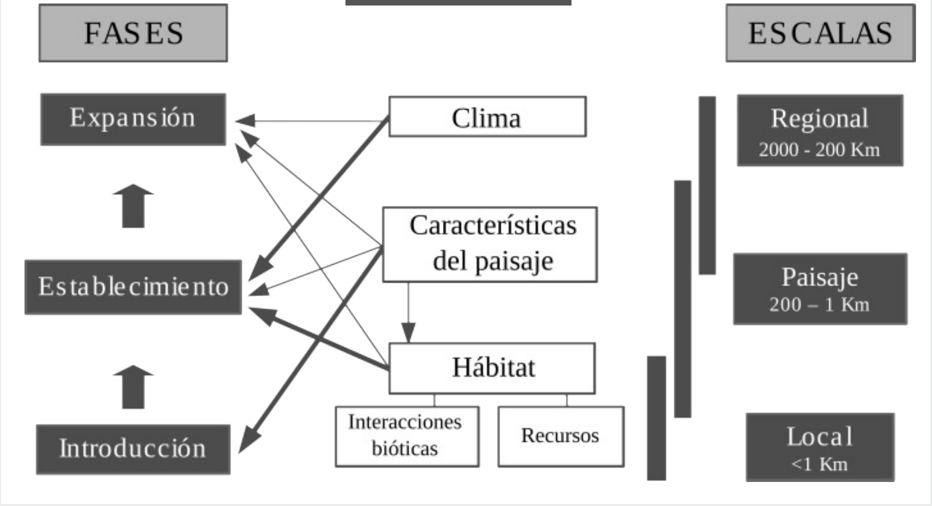
Las invasiones biológicas se ven afectadas por numerosos factores ecológicos, tales como el clima, la actividad humana, el tipo de hábitat o las interacciones bióticas, que pueden actuar a distintas escalas y fases en el proceso de invasión (Fig. 1; Catford et al., 2009; Milbau et al., 2009). Esta complejidad dificulta nuestra habilidad para comprender los mecanismos que controlan las invasiones biológicas y por tanto pronosticar su expansión futura. La presente Tesis se centrará en los factores **climáticos, de alteración del paisaje y del tipo de hábitat** por su relevancia para explicar el grado de invasión por plantas exóticas a escalas espaciales amplias (Chytrý et al., 2008a; Milbau et al., 2009). El efecto del clima es quizá el factor más estudiado dentro de las condiciones abióticas que determinan el proceso de invasión (Thuiller et al., 2005). Es sabido que el clima controla la distribución de las especies desde escalas continentales a regionales (Pearson & Dawson, 2003; Milbau et al., 2009). Por ejemplo, en climas templados las zonas más invadidas por plantas exóticas corresponden a áreas de mayor temperatura media anual y baja altitud, reflejando áreas ambientalmente favorables (Pino et al., 2005).

En un segundo nivel espacial, la **actividad humana a escala de paisaje puede afectar claramente a los patrones de invasión local** (Vilà & Ibáñez, 2011). Son numerosos los trabajos que relacionan la abundancia y diversidad de usos de suelo alterados con el grado de invasión por plantas exóticas (Pino et al., 2005;

Ibáñez et al., 2009b; Gavier-Pizarro et al., 2010). Así mismo, se ha propuesto que una mayor fragmentación del paisaje podría facilitar la dispersión de especies exóticas en detrimento de las especies nativas (Minor et al., 2009; pero ver Damschen et al., 2006). La alteración del paisaje a su vez afecta directamente a la biodiversidad a través de los bien estudiados procesos de fragmentación y pérdida de hábitat (Fischer & Lindenmayer, 2007). Teniendo en cuenta el efecto sinérgico que pueden ejercer la alteración del paisaje y las invasiones biológicas sobre la biodiversidad (Didham et al., 2007), es fundamental investigar de una manera más amplia el control que ejercen las distintas características del paisaje en los patrones de invasión (Vilà & Ibáñez, 2011).

A escala local, es decir, a nivel de comunidad, se ha comprobado como **el grado de invasión puede variar entre distintos tipos de hábitat** (Vilà et al., 2007; Chytrý et al., 2008b). Por ejemplo, hábitats con buenas condiciones de humedad y nutrientes tales como los bosques de ribera, parecen sufrir un mayor grado de invasión por plantas exóticas que hábitats de matorral o vegetación esclerófila (Alpert, 2000; Vilà et al., 2007; Affre et al., 2010). En general, los hábitats más

FIGURA 1



Marco conceptual de los determinantes ecológicos (clima, características del paisaje y tipo de hábitat) de los patrones de invasión por plantas exóticas que actúan a distintas escalas espaciales y fases del proceso de invasión. El grosor de las flechas indica la intensidad del efecto. Basado en Catford et al., (2009) y Milbau et al., (2009).

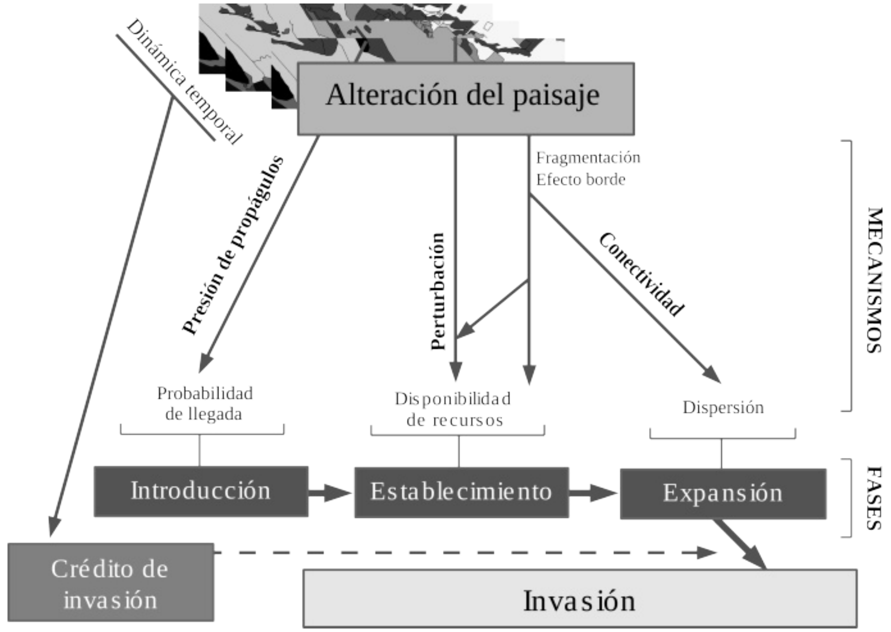
resistentes a la invasión tienden a presentar baja disponibilidad de nutrientes, alta competencia interespecífica, una larga trayectoria de adaptación a la actividad humana y estar en zonas con condiciones ambientales extremas (Alpert, 2000; Chytrý et al., 2008b). Hay dos aspectos fundamentales que promueven un grado de invasión diferente entre hábitats: la resistencia biótica y la fluctuación de los recursos. Por una parte, determinados tipos de hábitat pueden ofrecer una mayor resistencia biótica a la invasión debido por ejemplo a una alta competencia interespecífica que dificulta el establecimiento de nuevas especies (Levine et al., 2004). Por otra parte, un alto grado de perturbación local puede facilitar el establecimiento de especies exóticas al abrir “ventanas” de oportunidad asociadas a la existencia de nuevos recursos (p.e. nutrientes y espacio) (Hobbs & Huenneke, 1992; Davis et al., 2000). En otras palabras, un determinado episodio de perturbación puede romper la resistencia biótica de las comunidades y liberar recursos que aprovecharían las especies exóticas para establecerse (Hobbs & Huenneke, 1992).

Algunos modelos conceptuales desarrollados recientemente para comprender las invasiones biológicas sugieren que la importancia relativa del clima, las actividades humanas a escala de paisaje y el tipo de hábitat también dependen a su vez de la fase en la que se encuentre el proceso de invasión (Catford et al., 2009, 2011; Dawson et al., 2009; Leung et al., 2012). En una primera fase de introducción, la presión de propágulos estará sumamente relacionada con el tipo de paisaje del área de introducción. Así por ejemplo, la presencia de amplias zonas urbanas de baja densidad de construcción, como por ejemplo zonas residenciales, podría aumentar la probabilidad de llegada de plantas exóticas usadas en jardinería (Gavier-Pizarro et al., 2010). Una vez que los propágulos lleguen, es necesario que se reúnan las condiciones de clima y hábitat adecuadas para que la especie exótica pueda establecerse. Finalmente, la expansión de las especies exóticas vendrá determinada por una combinación adecuada de los tres grupos de variables: clima, alteración del paisaje y hábitat. El clima y el hábitat condicionarán el crecimiento poblacional y la abundancia local de las especies exóticas, mientras que la alteración del paisaje facilitará la dispersión de la especie a zonas próximas. Por tanto, **clima, alteración del paisaje y hábitat actuarán en las distintas fases del proceso de invasión actuando como filtros que limitarán el potencial de invasión de las especies exóticas** (Richardson et al., 2000).

Las invasiones por plantas exóticas y la alteración del paisaje

Los factores que controlan la influencia de la alteración del paisaje en el proceso de invasión son numerosos y actúan en la probabilidad de llegada de las especies exóticas, en su establecimiento en un determinado hábitat y en su posterior expansión dentro de este hábitat y otros adyacentes (Fig. 2).

Figura 2



Marco conceptual resumiendo el efecto de la alteración del paisaje en las invasiones por plantas exóticas. Basado en With, (2002) y Vilà & Ibáñez (2011). La inlfuencia de la alteración del paisaje en el proceso de invasión se puede explicar a través de tres mecanismos principales (i.e. incremento en la presión de propágulos, en el grado de perturbación y en la conectividad). A su vez es importante considerar la dinámica temporal en los cambios del paisaje y su efecto retardado en el grado de invasión o crédito de invasión.

En general, un mayor nivel de **alteración del paisaje:**

1. Potencia la **presión y diversidad de propágulos de especies exóticas** que pueden llegar (ver definición en Caja 2; Kumar et al., 2006). Por ejemplo, los usos de suelo con alta influencia humana tales como las áreas urbanas o agrícolas suelen estar asociados con un mayor grado de invasión por plantas exóticas en las zonas naturales vecinas (Ohlemüller et al., 2006; Gassó et al., 2009; Gavier-Pizarro et al., 2010). Los paisajes con un alto grado de urbanización pueden albergar numerosas plantas exóticas usadas en jardinería que tendrían una alta probabilidad de dispersarse e invadir zonas naturales cercanas (Gavier-Pizarro et al., 2010).

2. Desemboca en **mayores niveles de perturbación** a nivel de hábitat que facilitan el establecimiento de especies exóticas (ver fluctuación de recursos arriba). La alteración del paisaje conlleva la fragmentación de los hábitats y el incremento de hábitats de borde. Los bordes de las áreas naturales presentan unas condiciones microclimáticas y de perturbación que en general propician un mayor grado de invasión que en el interior de los fragmentos (Brothers & Spingarn, 1992; Vilà & Ibáñez, 2011).

3. Facilita la dispersión de especies exóticas (Hobbs, 2001; Borgmann & Rodewald, 2005; Bartuszevige et al., 2006) y consecuentemente su expansión en el territorio. La dispersión de plantas exóticas puede verse facilitada por la presencia de ambientes ruderales que de forma discontinua forman un corredor dentro de la matriz de hábitat natural (With, 2002). En este sentido, Minor et al., (2009) observaron como en paisajes fragmentados existe una limitación menor en la dispersión para las especies exóticas invasoras que para las nativas, que puede ser debida a una proporción mayor de especies zoócoras en el grupo de especies invasoras.

Componentes de la alteración del paisaje

Son numerosos los aspectos del paisaje que a priori pueden influir en los patrones de invasión por plantas exóticas (Vilà & Ibáñez, 2011). Las características del paisaje con mayor relevancia en los patrones de invasión están posiblemente relacionadas con la **composición del paisaje** (abundancia y diversidad de tipos de cubiertas de suelo) y en concreto con la abundancia de áreas altamente antropizadas tales como las zonas urbanas o las redes de comunicación (Sullivan et al., 2005; Gassó et al., 2009; Gavier-Pizarro et al., 2010). Otro tipo de variables menos estudiadas son las que caracterizan la **configuración del paisaje** (la distribución espacial de los tipos de cubiertas de suelo en el paisaje) y la **geometría de los parches de hábitat natural** (tamaño y complejidad de forma) (Deutschewitz et al., 2003; Kumar et al., 2006). La configuración del paisaje nos informa sobre aspectos relacionados con la fragmentación del paisaje (Bartuszevige et al., 2006; Kumar et al., 2006) mientras que la geometría de los parches se asocia con procesos de efecto de borde y de permeabilidad de las manchas a nivel local (Cully et al., 2003; González-Moreno et al., 2011). Tanto la configuración del paisaje como la geometría de los parches, normalmente ausentes en los estudios de riesgo de invasión, podrían ofrecer nuevas explicaciones a procesos de invasión secundarias desde otras zonas diferentes a las urbanas (Vilà & Ibáñez, 2011).

La dinámica temporal del paisaje

La alteración del paisaje es un proceso dinámico en el tiempo relacionado con la necesidad del ser humano de satisfacer su necesidad inmediata por determinados recursos naturales (Foley et al., 2005). Estas necesidades pueden variar a lo largo del tiempo resultando por tanto en un cambio de las prácticas humanas y de las características del paisaje. Debido a este componente dinámico del paisaje, el estudio del efecto combinado de la alteración del paisaje y las invasiones requiere además de un análisis temporal (Fig. 2). De hecho, el efecto que las transformaciones del paisaje puede tener sobre el grado de invasión solo llega a ser completamente evidente tras cierto tiempo de retraso (Jackson & Sax, 2010; Essl et al., 2011; Vilà & Ibáñez, 2011). De esta forma, la alteración reciente del

CAJA 3

Invasión y tiempo

Crédito de invasión: número de especies exóticas con potencial para colonizar un área tras una alteración del paisaje o en general cualquier perturbación, hasta que la comunidad del parche alcanza el equilibrio entre el grado de invasión y las características del paisaje (Cristofoli et al., 2010; Jackson & Sax, 2010; Vilà & Ibáñez, 2011).
Desfase temporal (time-lag): intervalo de tiempo entre la introducción de una especie exótica y su expansión (Kowarik et al., 1995; Larkin, 2012).
Legado del paisaje (land-use legacy): efecto de los usos de suelo pasados en el grado de invasión actual a nivel local. En general este concepto se aplica a los cambios de uso en un determinado parche de vegetación (Vilà et al., 2003; Pretto et al., 2010).

paisaje puede que no tengan un efecto inmediato en el grado de invasión actual si no que se vean reflejados en las comunidades florísticas venideras. Este **efecto retardado en la acumulación de especies exóticas en las comunidades** tras una determinada perturbación se denomina **crédito de invasión** o más generalmente crédito de inmigración (Vilà & Ibáñez, 2011; Caja 3) en contraposición a la bien estudiada deuda de extinción para especies en peligro de extinción local (Jackson & Sax, 2010).

Aunque es un concepto poco estudiado en sí mismo, el crédito de invasión parece ser una característica común en el proceso de invasión estrechamente relacionada con el **desfase temporal** que presentan las especies exóticas desde su introducción hasta su expansión definitiva (Kowarik et al., 1995). Por ejemplo, Essl et al., (2011) encontraron para Europa una mayor asociación entre el grado de invasión por países y las condiciones económicas de 1900 que con las condiciones económicas actuales, reflejando por tanto cierta evidencia de crédito de invasión en países con un elevado crecimiento económico reciente. A su vez, el crédito de invasión viene a complementar el concepto de **legados del paisaje que refleja el efecto que puede tener determinados cambios de uso de suelo en el grado de invasión local** (Vilà & Ibáñez, 2011). Es bien conocido por ejemplo, el efecto positivo que ejerce el abandono de áreas agrícolas en la proliferación de plantas exóticas que probablemente se habían introducido a modo de vallas entre propiedades o bien que se encontraban en el banco de semillas como "malas hierbas" (Aragón & Morales, 2003; Vilà et al., 2003). El crédito de invasión se podría cuantificar en este tipo de procesos como la diferencia entre el potencial máximo del grado de invasión tras el cambio de uso de suelo y los niveles antes de la transformación. De tal manera, el concepto de crédito de invasión puede ayudar a estudiar la dinámica de introducción de especies exóticas en un contexto de paisaje cambiante, facilitando a su vez la identificación del potencial de invasión futuro de las especies exóticas.

El proceso de invasión depende del contexto

El **clima, la alteración del paisaje y el tipo de hábitat podrían tener además un efecto interactivo en el proceso de invasión**, complicando de tal forma nuestro esfuerzo por comprender la importancia relativa de estos factores para explicar el grado de invasión local (Catford et al., 2009; Jiménez-Valverde et al., 2011). Por ejemplo, Gassó et al., (2012a) identificaron cómo el efecto de ciertas variables climáticas sobre la riqueza de especies de plantas exóticas variaba según el tipo de hábitat. Del mismo modo, es posible que estas interacciones varíen según el contexto biogeográfico, ya que por ejemplo el tipo de actividades humanas que impactan en el paisaje (p.e. tipo de agricultura o urbanismo) puede variar entre regiones biogegráficas y por tanto incidir en el tipo y cantidad de especies exóticas que se pueden establecer en una comunidad vegetal. Esta posible variabilidad entre regiones es sumamente relevante ya que impediría la extrapolación de los patrones de invasión entre regiones biogeográficas.

Otro aspecto relacionado con la variabilidad interregional es la posibilidad de que los factores que determinan la distribución de una especie sean similares o no entre el área nativa y el área de introducción. Cabría esperar que las especies exóticas ocuparan un nicho ambiental (ver Caja 4) similar entre ambas regiones (Broennimann et al., 2007; Pearman et al., 2008; Peterson, 2011). Sin embargo, **muchas especies no conservan su nicho ambiental entre el área de distribución nativa y la de introducción** (Gallagher et al., 2010), lo cual puede ser debido a una rápida adaptación de la especie a las nuevas condiciones ambientales y bióticas. Así, el **grado de invasión e incluso el potencial invasor** de determinadas especies exóticas **puede venir determinado por el contexto ecológico** de la comunidad receptora (Kolar & Lodge, 2001). Por tanto, es necesario desarrollar nuevas aproximaciones metodológicas que nos permitan comprender las numerosas interacciones que determinan el éxito de las especies invasoras.

CAJA 4

Conservación de nicho

Nicho ambiental: condiciones ambientales en las que una especie es capaz de establecerse y desarrollar poblaciones viables.
Expansión de nicho: ampliaciones del nicho de una especie al establecerse en condiciones ambientales de el área de introducción que no son ocupadas en el área nativa.
Ocupación parcial de nicho (unfilling): variaciones en el nicho observado debido a la ocupación de unas condiciones ambientales en el área de introducción más restringidas que en el área nativa.

OBJETIVOS Y ESTRUCTURA

La presente Tesis Doctoral se centra en determinar la **influencia de la alteración del paisaje en el grado de invasión por plantas exóticas en comparación con otros factores (clima y hábitat) y considerando la variabilidad debida al contexto ecológico**.

En concreto, esta Tesis Doctoral plantea las siguientes preguntas:
1. ¿Cuál es la importancia de la alteración del paisaje en la invasión por plantas exóticas en comparación con los factores climáticos y el tipo de hábitat?
2. ¿Cuáles son las características del paisaje más asociadas al grado de invasión por plantas exóticas?
3. ¿Existe relación entre el grado de invasión actual por plantas exóticas y las características del paisaje pasado?
4. ¿La influencia del clima y la alteración del paisaje en la invasión por plantas exóticas depende del contexto geográfico y del tipo de hábitat?

Estructura de la tesis

Para responder las preguntadas planteadas la investigación se divide en dos secciones:

La **Sección I, El paisaje y las invasiones por plantas exóticas**, engloba tres trabajos enfocados a comprender el papel de la alteración del paisaje en la invasión por plantas exóticas. En el **Capítulo 1** se estudia la importancia relativa de la alteración del paisaje en comparación con el clima y el hábitat sobre el grado de invasión en hábitats costeros de Cataluña y Menorca. A su vez, se descomponen cuales son las características del paisaje que más relevancia tienen sobre el grado de invasión. En el **Capítulo 2** se profundiza en la importancia de la alteración del paisaje tomando como caso de estudio los patrones de invasión desde el borde al interior de los fragmentos de bosques de la comarca del Vallés, en el área metropolitana de Barcelona. Estudiar la invasión de los fragmentos de bosque es sumamente interesante ya que en general la resistencia de los bosques a la invasión podría ser temporal y depender de la llegada de especies exóticas con capacidad para establecerse en condiciones de baja luminosidad (Martin et al., 2009). Es en relación a esta dinámica temporal de las invasiones en la que se centra el **Capítulo 3**. En este capítulo se considera el intenso proceso de cambio que ha sufrido el paisaje de la costa occidental andaluza, investigando si existe une crédito de invasión debido a alteraciones del paisaje en décadas pasadas.

La **Sección II, La importancia del contexto en las invasiones biológicas**, comprende dos capítulos que exploran la influencia del contexto geográfico y ecológico en el grado de invasión. El **Capítulo 4** analiza cómo el efecto del clima y la alteración del paisaje en el grado de invasión varían según la región biogeográfica y el tipo de hábitat considerando todo el gradiente ambiental de España peninsular. Finalmente, el **Capítulo 5** se centra en *Oxalis pes-caprae* L., un geófito herbáceo sudafricano, como modelo de estudio para entender las diferencias del efecto del clima, la alteración del paisaje y el tipo de hábitat en el grado de invasión de la Cuenca Mediterránea en comparación con su efecto en la región nativa en Sudáfrica.

CONSIDERACIONES METODOLÓGICAS

Las bases de datos florísticas

Esta Tesis **se basa en parte en la gran variedad de bases de datos de distribución de plantas exóticas** tanto en España como a nivel mundial. De especial relevancia es el Sistema de Información de Vegetación Ibérica y Macaronésica (SIVIM) (Font et al., 2012) con más de 50000 registros de inventarios fitosociológicos desde 1970 hasta la actualidad (Capítulo 4). Otra base de datos utilizada es la Infraestructura Mundial de Información en Biodiversidad (GBIF) que nos proporcionó información sobre la presencia de *Oxalis pes-caprae* a nivel global (Capítulo 5). Esta disponibilidad de datos nos ha permitido responder a cuestiones poco estudiadas sobre las invasiones biológicas abarcando un amplio espectro de hábitats y contextos geográficos.

El grado de invasión desde la introducción a la expansión

A pesar de que los patrones espaciales y temporales del grado de invasión es uno de los aspectos más estudiados sobre las invasiones biológicas, no existe homogeneidad en el uso de índices que lo estimen (Catford et al., 2012). Los índices más usados son la presencia o riqueza de especies exóticas (Lonsdale, 1999; Pino et al., 2005) y en menor medida, la abundancia de especies exóticas (Polce et al., 2011) o la abundancia o riqueza de exóticas relativa al total de especies (Catford et al., 2011). Estos diferentes índices pueden aportar distinta información sobre el proceso de invasión. La presencia de cualquier especie exótica puede considerarse un indicador del establecimiento mientras que la abundancia o riqueza de especies exóticas lo sería de una fase posterior de dominancia o expansión (Catford et al., 2011; Polce et al., 2011).

De todos los índices expuestos, la **abundancia y riqueza relativa de especies exóticas se consideran los índices más aconsejables** (Catford et al., 2012) ya que permiten la comparación entre taxones y lugares, y son independientes de la escala espacial. Entre estos dos índices, la abundancia podría reflejar en mayor grado la intensidad de la invasión ya que puede haber casos de comunidades pobres en especies exóticas (baja riqueza) pero con una o pocas especies muy dominantes y con mucho impacto. Sin embargo, ambos índices suelen estar correlacionados (Chytrý et al., 2009; Catford et al., 2011) con lo que en caso de falta de información sobre la abundancia de especies exóticas, se podría utilizar la riqueza de especie exóticas (Catford et al., 2012). Esta simplificación es una práctica predominante en los estudios sobre invasiones ya que en general, los datos sobre presencia de especies exóticas suelen tener una mayor disponibilidad y facilidad de muestreo. **En la presente Tesis se ha aspirando a cuantificar el grado de invasión a través de la abundancia o riqueza relativa** de especies exóticas en comparación con el resto de índices (Capítulo 2, 4 y 5). Sin embargo, la falta de información en algunas bases de datos sobre especies nativas ha llevado en algunos casos a utilizar el valor absoluto de riqueza de especies exóticas (Capítulos 1 y 3).

Además, existen divergencias en el uso de distintos grupos de especies considerando el periodo de introducción de referencia (neófitas y arqueófitas) o su carácter invasor (exóticas e invasoras) (ver Caja 1). Son frecuentes los estudios que analizan por separado arqueófitas y neófitas intentando reconocer patrones espaciales y temporales singulares a cada grupo de especie (p.e. Chytrý et al., 2008a; Polce et al., 2011). Sin embargo en muchos casos es difícil reconocer el carácter exótico de un arqueófito sino es mediante análisis genético o arqueológico (Khadari et al., 2005). De forma similar, aunque la definición de especie invasora es clara (p.e. Pyšek et al., 2004), no siempre es fácil conocer si una especie exótica es invasora si no se tienen registros del proceso de expansión desde que fue introducida (Catford et al., 2012). Unido a este aspecto, restringir el análisis del grado de invasión a especies invasoras, puede obviar el efecto de especies exóticas que se encuentran en una fase incipiente del proceso de invasión y que podrían tener un impacto en el futuro (Kowarik et al., 1995). Por tanto, para evitar confusiones, para **esta Tesis se ha restringido los análisis a especies neófitas exóticas**, evitando de tal manera posibles errores de clasificación de las especies en su carácter nativo, exótico o invasor.

La macroecología y sus métodos

La macroecología, disciplina que estudia los patrones de biodiversidad y procesos ecológicos a grandes escalas geográficas, ha tenido un verdadero auge en los últimos años. Este creciente interés ha ido acompañado de una mayor disponibilidad de datos sobre biodiversidad a escala regional y global, así como del desarrollo de sofisticados métodos estadísticos que permiten analizar los patrones subyacentes (Guisan & Thuiller, 2005; Elith et al., 2010). En el campo de las invasiones por plantas exóticas, la mayor parte de estudios **se centran en entender los patrones regionales del grado de invasión utilizando indicadores de riqueza o abundancia** (Gassó et al., 2009; Catford et al., 2011; Polce et al., 2011), con cierto paralelismo con los modelos clásicos de diversidad de especies nativas (Richerson & Lum, 1980). Esta aproximación macroecológica es la que se ha utilizado en la mayor parte de la Tesis (Capítulos 1 al 4).

A nivel de especies exóticas concretas es también frecuente la aplicación de modelos de nicho (Peterson, 2003; Ibáñez et al., 2009a; Jiménez-Valverde et al., 2011). Una de las principales singularidades de estos modelos es que muchas especies exóticas pueden no encontrarse en situación de equilibrio con el ambiente en el que han sido introducidos (Ibáñez et al., 2009a; Jiménez-Valverde et al., 2011). Por tanto, es fundamental considerar información sobre la distribución de las especies exóticas tanto en su área de distribución nativa como en la de introducción para asegurar una estimación adecuada del nicho (Jiménez-Valverde et al., 2011). Este aspecto se estudia en profundidad en el Capítulo 5 usando como caso de estudio a *Oxalis pes-caprae*. Otro aspecto relevante en la modelización de los patrones de invasión es que el éxito de las especies exóticas depende del contexto ecológico y geográfico (ver arriba) con lo cual es necesario adoptar métodos flexibles que permitan conocer el efecto puro y combinado de las variables que controlan el proceso de invasión.

Finalmente, la información disponible sobre grado de invasión local, generalmente presenta limitaciones inherentes al proceso de muestreo (p.e. sesgos geográficos y pseudoreplicaciones) o a los propios datos, como es el caso de la autocorrelación espacial, que pueden afectar a la interpretación de los resultados. Debido a estas complejidades, la modelización de los patrones de invasión requiere de métodos que se adapten a las circunstancias de cada estudio. **En esta Tesis se han adoptado principalmente dos marcos metodológicos** para satisfacer estas necesidades. Por una parte, los métodos de **inferencia multimodal** (Burnham & Anderson, 2002) y **partición de la devianza** (Borcard et al., 1992) han facilitado la comparación de la importancia de los distintos factores en los patrones de invasión a la vez que controlando por la complejidad de los modelos (Capítulos 1 al 3). Por otra parte, también se ha trabajado en un entorno de **modelización jerárquico y Bayesiano** (Gelman & Hill, 2007) para analizar el efecto interactivo de los predictores de los patrones de invasión (Capítulos 4 y 5). La estadística Bayesiana presenta ciertas ventajas respecto al tradicional método frecuentista: la flexibilidad que permite en la modelización, la posibilidad de incorporar información previa y la interpretación directa que ofrece sobre los intervalos de confianza (Clark, 2004; McCarthy, 2007). Si bien es una aproximación que en la actualidad presenta una reducida aplicación en Ecología, su potencialidad para estimar la distribución de las especies incorporando información previa y la flexibilidad para adoptar estructuras jerárquicas sugieren su uso generalizado en los próximos años (Diez et al., 2012).

SECCIÓN I

I. Quantifying the landscape influence on plant invasions in Mediterranean coastal habitats.
II. Landscape context modulates plant invasions in Mediterranean forest edges.
III. Association of plant invasions with past landscape characteristics provides evidence of invasion credit.

EL PAISAJE Y LAS INVASIONES POR PLANTAS EXÓTICAS

CAPÍTULO UNO

González-Moreno, P., Pino, J., Carreras, D., Basnou, C., Fernández-Rebollar, I. & Vilà, M. (2013) Quantifying the landscape influence on plant invasions in Mediterranean coastal habitats. Landscape Ecology, 28, 891–903.

QUANTIFYING THE LANDSCAPE INFLUENCE ON PLANT INVASIONS IN MEDITERRANEAN COASTAL HABITATS

RESUMEN

Las características del paisaje pueden ser un determinante fundamental de las invasiones por plantas exóticas, ya que explica en parte la disponibilidad de propágulos y el grado de perturbación. Nuestro objetivo fue explorar la importancia relativa de las características del paisaje y del parche, en comparación con el tipo de hábitat e influencia humana regional, para explicar los patrones de riqueza de plantas exóticas. Con este propósito, identificamos todas las plantas exóticas en 295 parches de cuatro tipos de hábitats costeros en tres regiones administrativas del Noreste de España con distinto grado de influencia humana. Para cada parche calculamos variables de geometría (tamaño y forma), composición del paisaje (abundancia y diversidad de los tipos de cubiertas del suelo) y configuración del paisaje (distribución espacial de los tipos de cubiertas). Los dos últimos grupos de variables fueron calculados considerando cinco radios diferentes alrededor de cada parche de muestreo. Las variables de composición fueron las más importantes para explicar la riqueza de especies exóticas. Áreas naturales rodeadas de paisajes diversos y urbanos tuvieron un alto número de especies exóticas, mientras que los paisajes agrícolas tuvieron el efecto inverso. La influencia humana regional estuvo también fuertemente asociada a la riqueza de especies exóticas, mientras que el tipo de hábitat fue el factor menos importante. La mayoría de de variables fueron más influyentes cuando se consideró un radio de 100 m alrededor de cada parche. Estos resultados sugieren que las características del paisaje deben ser consideradas para estimar el riesgo de invasión por plantas exóticas. Por tanto, el manejo de hábitats invadidos debe centrarse no sólo a escala de parche, sino también a escala de paisaje. Además, antes de considerar el paisaje en los planes de manejo, se deben realizar análisis de sensibilidad para evitar inconsistencias en el efecto de las variables.

ABSTRACT

Landscape pattern might be an important determinant of non-native plant invasions because it encompasses components influencing the availability of non-native plant propagules and disturbance regimes. We aimed at exploring the relative role of patch and landscape characteristics, compared to those of habitat type and regional human influence on non-native plant species richness. For this purpose, we identified all non-native plant species in 295 patches of four coastal habitat types across three administrative regions in NE Spain differing in the degree of human influence. For each patch, we calculated several variables reflecting habitat patch geometry (size and shape), landscape composition (abundance and diversity of land-cover categories) and landscape configuration (spatial arrangement of land-cover categories). The last two groups of variables were calculated at five different spatial extents. Landscape composition was by far the most important group of variables associated with non-native species richness. Natural areas close to diverse and urban landscapes had a high number of non-native species while surrounding agricultural areas could buffer this effect. Regional human influence was also strongly associated with non-native species richness while habitat type was the least important factor. Differences in sensitivity of landscape variables across spatial extents proved relevant, with 100 m being the most influential extent for most variables. These results suggest that landscape characteristics should be considered for performing explicit spatial risk analyses of plant invasions. Consequently, the management of invaded habitats should focus not only at the stand scale but also at the highly influential neighbouring landscape. Prior to incorporate landscape characteristics into management decisions, sensitivity analyses should be taken into account to avoid inconsistent variables.

INTRODUCTION

There is increasing interest in disentangling local and geographic effects on the distribution and abundance of non-native plant invasions (Chytrý et al., 2008a; Marini et al., 2009; Catford et al., 2011). Although significant advances have been made, several aspects remain largely unexplored. For instance, we still do not have a thorough understanding of the effects of patch and landscape characteristics (Vilà & Ibáñez, 2011) compared to those of the regional degree of human influence or habitat type (Chytrý et al., 2008a; Catford et al., 2011). Regions with heavy human influence have an overall increase in the probability of non-native plant arrival and establishment (Kueffer et al., 2010; Pyšek et al., 2010) that can be driven among other causes to a high use of ornamental species for gardening and restoration. Furthermore, within particular regions, the level of plant invasion among habitat types has proven to be different with water and nutrient rich habitats being more invaded than dry and stressful habitats (Chytrý et al., 2008b).

The main landscape characteristics associated with invasion are related to human land-cover such as built-up areas or transportation infrastructures edges (Sullivan et al., 2005; Gassó et al., 2009; Gavier-Pizarro et al., 2010). These human-altered areas are a common reservoir of non-native species (Ohlemüller et al., 2006; Gavier-Pizarro et al., 2010) that can enhance the non-native propagule pressure on nearby natural areas. Except landscape composition (i.e. abundance and diversity of land-cover categories), the analysis of other landscape characteristics related to its configuration (e.g. habitat fragmentation) and habitat patch geometry (e.g. size and shape) have received less attention (Deutschewitz et al. 2003; Kumar et al. 2006). The exploration of these variables could give new insights into secondary invasions from land-use areas other than urban (Vilà & Ibáñez, 2011).

Another aspect that still requires attention is the spatial extent (i.e. buffer area from the focal sampling unit) at which landscape characteristics influence local invasions (Kumar et al., 2006). It is well known that the influence of landscape characteristics on many ecological processes is dependent on the extent. For instance, the effect of habitat fragmentation on plant pollination and predation varies depending on the size of the landscape under consideration (Steffan-

Dewenter et al., 2001). In this case, the influence of habitat fragmentation on pollination occurred at an extent of up to 1000 m from the sampled patch, while the influence on predation took place at a larger extent (2500 m). The few studies exploring the effect of extent on plant invasions point to maximum influence at smaller extents (~250 m) (Bartuszevige et al., 2006; Kumar et al., 2006).

In this paper, we first explore the influence of patch and landscape characteristics on non-native species richness at different spatial extents and then we analyse their importance compared to the regional degree of human influence and habitat type controlling for climatic variability. The study was conducted in three coastal regions in Spain differing in their degree of human influence. Mediterranean coastal areas have a large number of habitats of high conservation concern which have been included in the Habitats Directive 92/43/EEC of the European Council (Campos et al., 2004). Nevertheless, Mediterranean coastal areas are in general heavily invaded and under intensive human use, especially tourism-related activities (Chytrý et al., 2008b; Sobrino et al., 2009). Specifically, we ask: (i) Are patch and landscape characteristics more important than the regional degree of human influence or habitat type in explaining non-native species richness?, (ii) Which patch and landscape characteristics are the most relevant to non-native species richness? And finally, (iii) at what spatial extent does landscape characteristics have maximum influence on non-native species richness?

METHODS

Study sites

The study was conducted in three administrative regions of Spain: Menorca Island, Girona, and Barcelona. The three regions were selected to represent a gradient from low to high human influence, respectively (Table 1). Menorca Island, declared Biosphere Reserve in 1993, belongs to the Balearic archipelago and it is located within the same latitude as the mainland regions. Balearic Islands are considered to be para-oceanic, as they were connected to the continent during the Messinian period (between 5.70 and 5.35 million years ago). Due to this pre-historical geographical connexion and the historical and current trade and transport between all these regions, they share an important component of both native and non-native flora. The climate of the three regions is typically

TABLE 1

GEOGRAPHIC CHARACTERISTICS OF THE THREE STUDY REGIONS

	Mainland		Island
	Barcelona	Girona	Menorca
Latitude (N)	41.2-41.6	41.7-42.4	39.8-40.1
Longitude (E)	1.7-2.8	2.8-3.2	3.8-4.2
Coast length (Km)	187.7	332.9	432.5
Population density (hab/Km^2)[a]	4711.3	335.8	136.5
Road length (Km/ Km^2)[b]	2.52	2.94	1.33
Urban area (Km^2/ Km^2)[b]	0.43	0.27	0.09
Mean temperature	16.3	15.9	16.8
Mean precipitation	636	609	608

[a] Coastal municipalities (Spanish National Statistics Institute 2011); [b] within 2000 m coastal strips

Mediterranean, with warm, dry summers and mild winters. They also share a similar cultural landscape as a result of the typical interaction between man and environment at the Western Mediterranean region. Forests and shrublands dominate the hilly areas, as a result of agricultural land abandonment in the mid-20th century. In contrast, lowlands and coastal areas are intensively cultivated or urbanised.

Floristic survey

Non-native plant species (according to Bolós et al., 1993) were identified at the patch level in four types of coastal habitats: dunes (sand-covered shorelines), rock-outcrops (sea cliffs), shrublands (evergreen sclerophyllous shrub vegetation) and forests (pine/oak woodlands). The vegetation patches were selected from the most recent land-cover map for each region: the Land-Cover Map of Catalonia (www.creaf.uab.cat/mcsc, based on images from 2005) for Barcelona and Girona, and the Land-Cover Map of Menorca (http://www.obsam.cat/, based on images from 2002) for Menorca. These land-cover maps depict any distinct vegetation patch with a minimum area of 500 m^2.

First, we randomly selected an initial set of 50 patches of the land-cover maps for each habitat and study region with at least 60% of their area within a 500-m strip along the coast. Second, within this initial set, between 23 and 28 patches per habitat type and study region were selected to set up a gradient of patch area and human influence in the surroundings (percentage of urban and road area within 1 km radius). In Barcelona, we were able to sample only 16 rock-outcrop patches due to availability and accessibility constraints. Finally, a total of 295 patches ranging from 0.05 to 80 ha were sampled.

Patches were sampled from April to June 2010 depending on the regions, starting with the warmest (Menorca and southern Barcelona) and ending with the coldest (northern Barcelona and Girona). Within each region, patches were also sampled from south to north following the plant phenology. We performed an intensive prospection of each patch to identify all non-native species growing therein. Prospection was done by three or more trained botanists walking through all its area with no time limit, to be reasonably sure that none non-native species was missed. Only neophytes (i.e. introduced after 1500 a.c.) were considered. We did not consider archaeophytes (i.e. introduced before 1500 a.c.) due to the controversy of classifying some of them as native or non-native (Khadari et al., 2005). We then calculated non-native species richness per patch (i.e. total number of non-native species) as this is a good estimator of the level of plant invasion (Catford et al., 2011).

Explanatory variables

We characterized each patch with several patch and landscape variables (Table 2) commonly found to be associated to plant invasions at both grid and plot level (Deutschewitz et al., 2003; Pino et al., 2005; Kumar et al., 2006; Ohlemüller et al., 2006; Gavier-Pizarro et al., 2010). Patch and landscape variables were inferred from the most recent land-cover map for each region mentioned above. We calculated a set of patch variables, describing the geometry of the sampled patches; landscape composition variables, indicating the diversity and abundance of main land-cover categories; and landscape configuration variables, reflecting the spatial arrangement of land-cover categories in the landscape surrounding the sampled patches (Table 2).

Table 2

Variables used as predictors of non-native species richness in coastal habitats with indication of the landscape extent (i.e. buffer area from the focal patch) selected.

Variable	Extent (m)	Description	Data source
Habitat type		Four coastal habitats: dunes, rock-outcrops, shrublands and forests	
Region		Three regions to represent a gradient of human influence: Barcelona, Girona and Menorca	
Patch characteristics			
Patch edge (m)		Perimeter of the focal patch	Land-cover Map of Catalonia 2005 and Land-cover Map of Menorca 2002
Patch area (ha)*		Area of the focal patch	
Patch fractal index (dim.)*		Two times the logarithm of the patch perimeter divided by the logarithm of patch area	
Patch shape index (dim.)		Perimeter of the patch divided by the minimum perimeter possible of a circle of the corresponding patch area	
Landscape composition			
Natural land-cover (%)		Forests, shrublands and open areas	
Low-density urban land-cover (%)*	100	Mixed garden and buildings areas such as single-family housing areas and touristy resorts	
High-density urban land-cover (%)*	100	Built areas such as villages and cities	
Agricultural land-cover (%)*	100		
Water land-cover (%)*	100		
Shannon land-cover diversity index			
Simpson land-cover diversity index*	100		
Land-cover richness		Number of land-cover types in the landscape	

*Variables included in the final analysis to avoid collinearity. dim: dimensionless.

TABLE 2

(CONT.) VARIABLES USED AS PREDICTORS OF NON-NATIVE SPECIES RICHNESS IN COASTAL HABITATS WITH INDICATION OF THE LANDSCAPE EXTENT (I.E. BUFFER AREA FROM THE FOCAL PATCH) SELECTED.

Variable	Extent (m)	Description	Data source
Landscape configuration			
Edge density (m/ha)*	100	Total length of edge in the landscape divided by the total landscape area	
Patch density		Number of patches in the landscape	
Landscape shape index (dim.)		Total length of edge in the landscape divided by the minimum total length of edge possible	
Mean patch area (ha)*	250	Mean area of all patches in the landscape	
Mean fractal index (adim.)*	250	Mean fractal index of all patches in the landscape	
Mean shape index (adim.)		Mean shape index of all patches in the landscape	
Climate			WorldClim (Hijmans et al. 2005)
Mean annual temperature (ºC)			
Mean minimum temperature (ºC January)*			
Mean maximum temperature (ºC July)			
Annual precipitation (mm)*			
Mean annual radiation (W.m-2)*			ASTER GDEM 2009

*Variables included in the final analysis to avoid collinearity. dim: dimensionless.

Patch variables included patch area, patch edge, and two shape complexity variables: patch shape index and patch fractal index. As composition variables we calculated the relative percentage of each land-cover type and three land-cover diversity indices: Shannon and Simpson indices and land-cover richness. Configuration variables have been rarely used in plant invasion studies. We selected two broadly used indices to quantify each of these relevant aspects: the amount of edge in the landscape (i.e. edge density and landscape shape index), the number and size of patches (i.e. patch density and mean patch area), and the mean patch-shape complexity (i.e. mean shape index and mean fractal index) (McGarigal et al., 2002).

We calculated configuration variables and land-cover diversity indices using a land-cover map with the following classification: urban, natural, water, and agricultural. For the rest of variables regarding landscape composition we split the urban land-cover into low-density urban (i.e. mixed garden and buildings areas such as single-family housing areas and tourist resorts) and high-density urban (mainly built-up areas) as we were interested in the relative importance of both predictors. We calculated composition and configuration variables at five buffer distances (hereafter extent) from each sampled patch edge (100, 250, 500, 1000 and 2000 m) using ArcGIS 9.2 and FRAGSTATS (McGarigal et al., 2002).

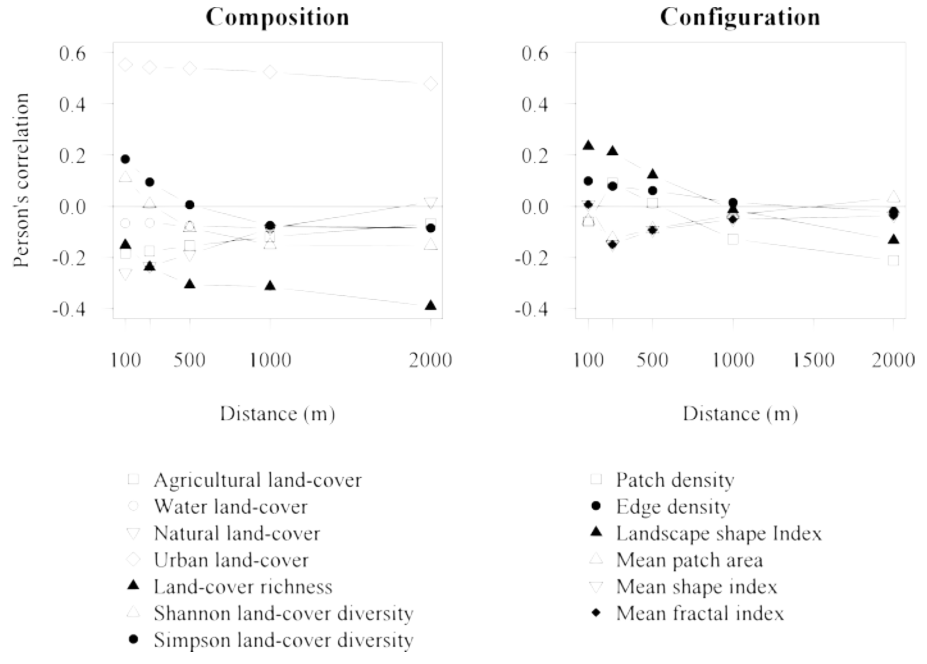
Finally, to control for climate variability, we calculated several climate variables. For the centroid of each patch, we obtained mean annual temperature, mean minimum temperature in the coldest month (January), mean maximum temperature in the hottest month (July), and annual rainfall from the WorldClim dataset (Hijmans et al., 2005) at 30 arc-second resolution (approximately 1 Km^2). We calculated mean annual solar radiation at the centroid of each patch in GRASS based on the ASTER Global Digital Elevation Model (http://gdem.ersdac.jspacesystems.or.jp) of 30 m resolution.

Statistical analyses

We used variance-partition techniques (Mood, 1969) and multimodel inference (Burnham & Anderson, 2002) of Generalized Linear Models (GLMs) to analyse the relationship between non-native species richness and region, landscape, habitat and patch variables. Climate variables were also included in the models as covariates to control their effect. We modelled the error terms of the GLMs using a negative binomial distribution, which is typically used for count data when overdispersion occurs (Gelman & Hill, 2007).

Prior to both the partitioning and the multimodel inference modelling, for each landscape variable, we selected the extent that was most influential on non-native species richness (Table 2). The selection was based on the Pearson's correlation coefficient between each landscape variable and non-native species richness at each buffer distance (Fig. 1). Then, we checked the collinearity among the selection of predictors by pair-wise Pearson's correlation tests (Appendix A). First, we selected variables that had a pair-wise correlation lower than 0.6 and

FIGURE 1



PEARSON'S CORRELATION COEFFICIENT BETWEEN NON-NATIVE SPECIES RICHNESS AND LANDSCAPE COMPOSITION (UPPER PART) AND CONFIGURATION VARIABLES (BOTTOM PART) AT EACH SPATIAL EXTENT (100, 250, 500, 1000, 2000 m AROUND SAMPLED PATCH). FOR CONFIGURATION VARIABLES, THE LAND-COVER CLASSIFICATION USED CONSIDERS URBAN, AGRICULTURAL, NATURAL AND WATER LAND-COVERS.

then selected the ones with best ecological meaning and explanatory power. With regard to patch variables, patch area was correlated with patch edge and patch shape index with the fractal index. For final models, we used the non-correlated indices patch area and patch fractal index. Taking landscape composition variables into account, we found natural land-cover to be negatively correlated to urban land-cover and land-cover diversity. Thus, we kept high- and low-density urban land-cover, agricultural land-cover and water land-cover. The three land-cover diversity indices were correlated. We selected only the Simpson diversity index. Most landscape configuration variables were also highly correlated. We selected edge density, mean patch area and mean fractal index. Climate variables were highly correlated and thus we selected only mean annual precipitation, mean minimum temperature in the coldest month and mean annual solar radiation.

Deviance partitioning

Variance-partition techniques indicate the variability explained by the single and shared effects of different groups of variables (Mood, 1969). Assuming that the deviance is a good measure of the variability explained by a model, we set up GLMs including a different subset of non-collinear variables: patch and landscape variables (i.e. including variables regarding patch geometry, landscape composition and landscape configuration), only regions, only habitat type, only climate variables and the combination of the four groups of variables. The deviance explained by each model was then used to identify the single and shared effects on non-native species richness by simple equation systems (Carrete et al., 2007). Following the same approach, we also partitioned the deviance of non-native species richness accounted by patch and landscape characteristics within patch geometry, composition and configuration variables.

Multimodel inference

Multimodel inference is a model selection method that allowed us to identify the best possible models and to rank all independent variables according to their influence on non-native species richness (Burnham & Anderson, 2002). We performed multimodel inference based on the all-subsets selection of GLMs using Akaike's Information Criterion corrected for a large number of predictors (AICc).

We selected the best model (smallest AICc) for each block of non-collinear predictors (i.e. patch geometry, composition, configuration, and climate). Then, we repeated the procedure, combining the best variables of each block and the factors habitat type and region to establish the set of best candidate models. For each candidate model in the final selection, we calculated the Akaike weight of evidence (Wi) to rank the predictors in order of importance (i.e. the closest to 1) in their relation to non-native species richness (Burnham & Anderson, 2002; Grueber et al., 2011). The weight of evidence was calculated within the set of best models given the selected predictors: all models within 4 AICc units from the best model. This threshold is within the limits adopted in other studies (Grueber et al., 2011), and allowed the presence of all groups of variables.

Moreover, to avoid a possible correlation between the predictor and the response variable due to random or unexpected noise, we performed a permutation procedure (100 times) to calculate the unbiased weight of evidence (D_{w+i}) (Thuiller et al., 2007). Only predictors with D_{w+i} higher than zero had a certain explanatory power on the dependent variable (Thuiller et al., 2007).

We also used multimodel inference to estimate regression coefficients and their confident intervals (with the adjusted standard error) within the best models subset (delta<4) (Burnham & Anderson, 2002, 2004). We calculated the coefficient for a given predictor as the sum across all possible models where the predictor was present, of the predictor's coefficient multiplied by the wi (Burnham & Anderson, 2002).

To explore the differences in non-native species richness among coastal habitat types and regions, we used the best candidate model (smallest AICc), including the factors habitat type and region. We tested significant differences among levels within each factor using a post hoc normal test with multiplicity correction by the joint distribution of all the statistics (Westfall, 1997).

Due to the characteristics of the data and the generally aggregated pattern of plant invasions, it is very likely to find spatial autocorrelation in the residuals of the GLMs. Spatial autocorrelation could generate an underestimation of the confidence intervals in the regression coefficients. In preliminary analyses using the Moran's Index, we detected significant spatial autocorrelation in the model's residuals at distances smaller than 1000 m. Thus, for each GLM in the multimodel inference procedure we tested the spatial autocorrelation in the model's residuals by the Moran's index. When the spatial autocorrelation was proven to be significant ($p<0.05$) we included a spatial autocovariate in the model considering the inverse distance among patches up to 1000 m (Augustin et al., 1996; Dormann et al., 2007). All statistical analyses were performed with the R-CRAN software. We used the package MuMIn for some procedures of the multimodel inference method and the package VEGAN as the base code for deviance-partition.

RESULTS

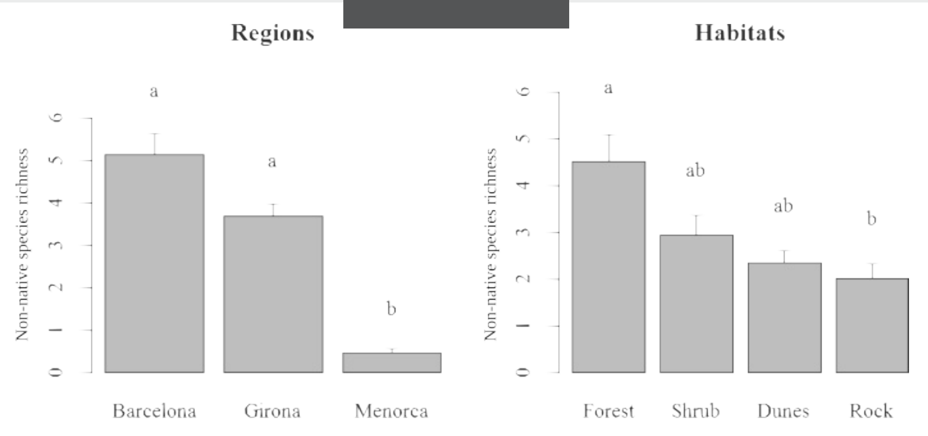
Differences on non-native species richness among regions and among habitat types

Across all the regions, we found 125 non-native species. The most abundant species were *Carpobrotus edulis* (L.) L. Bolus, *Agave americana* L., *Pittosporum tobira* (Thunb.) W.T. Ayton and *Opuntia ficus-indica* (L.) Mill., which occur in 31%, 26%, 24% and 23% of the patches, respectively. Considering the best model that included habitat type and region (Appendix A), non-native species richness of patches was significantly higher in the two mainland regions, Barcelona and Girona, than in Menorca Island (Fig. 2). However, we found no differences in non-native species richness between Barcelona and Girona. Invasion across coastal habitat types was significantly different (Fig. 2). Non-native species richness was greater in forests than in rock-outcrops, while the richness of shrublands and dunes was not significantly different from those two.

Partitioning the influence of region, patch and landscape characteristics and habitat type on plant invasions

The variability of non-native species richness was explained mainly by patch and landscape variables, and by region (Fig. 3). Both sets of predictors also had a high shared effect. In contrast, habitat type had very low single effect and its explanatory power was shared mainly with patch, landscape and region variables (Fig. 3).

FIGURE 2



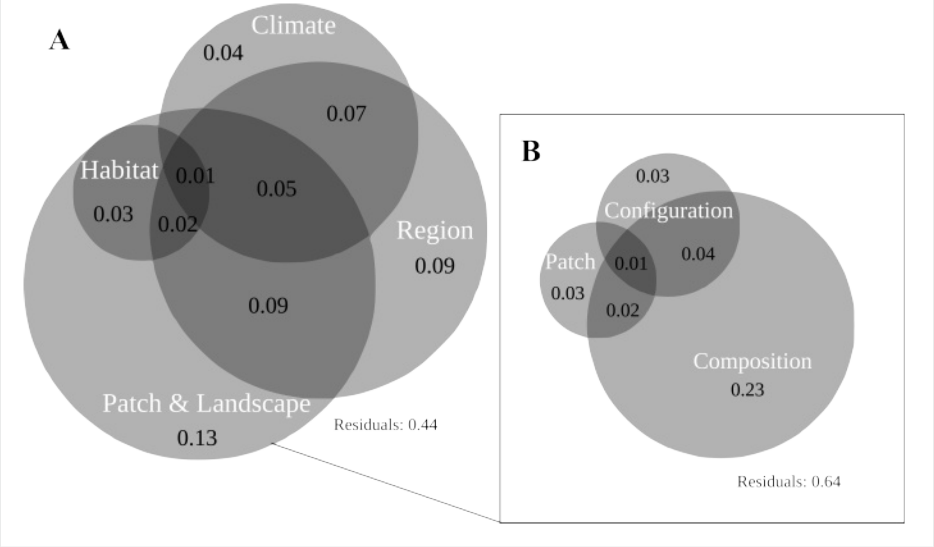
MEAN (±SE) NON-NATIVE SPECIES RICHNESS FOR EACH REGION AND HABITAT TYPE. LETTERS INDICATE SIGNIFICANT DIFFERENCES ($p<0.05$) BETWEEN REGIONS AND BETWEEN HABITATS ACCORDING TO POST-HOC TEST CORRECTED FOR MULTIPLE HYPOTHESIS BASED ON THE BEST MODEL INCLUDING HABITAT, REGION, LANDSCAPE AND CLIMATE VARIABLES SELECTED BY AICC CRITERIA.

Considering patch and landscape variables separately, the deviance-partition analysis revealed that the composition of the landscape surrounding the patch explained most of the deviance (Fig. 3). Patch geometry and configuration variables showed very little single effect on non-native species richness and a similar amount was shared with composition variables.

Patch and landscape characteristics influencing plant invasions

The best patch and landscape predictors explaining non-native species richness were Simpson land-cover diversity index, percentage of agricultural land-cover, and mean fractal index (Table 3). Land-cover diversity showed a positive association with non-native species richness while the association with agricultural land-cover and mean fractal index was negative. Patch area, edge density and percentage of urban land-cover also had a significant positive effect on non-native species richness. Regarding the percentage of urban land-cover, low-density urban land-cover showed higher importance than high-density land-cover (Table 3).

FIGURE 3



DEVIANCE PARTITIONING OF NON-NATIVE SPECIES RICHNESS USING GENERALIZED LINEAR MODELS AMONG (A) REGION, CLIMATE, HABITAT TYPE, AND PATCH AND LANDSCAPE PREDICTORS, AND (B) PATCH AND LANDSCAPE PREDICTORS: PATCH GEOMETRY, LANDSCAPE COMPOSITION, AND LANDSCAPE CONFIGURATION. EACH CIRCLE CORRESPONDS TO A GROUP OF VARIABLES. NUMBERS WITHIN CIRCLES ARE THE PROPORTION OF DEVIANCE EXPLAINED BY EACH SET OF PREDICTORS ALONE (NON-OVERLAPPED PART OF CIRCLES) OR SHARED. RESIDUALS INDICATE THE DEVIANCE NON-EXPLAINED BY THE MODELS.

The landscape extent relevant to plant invasions

Landscape composition and configuration variables showed different patterns of influence on non-native species richness, depending on the spatial extent. The most influential extent for landscape composition variables was 100 m around patches with a slight linear decrease in influence at larger radii (Fig. 1). By contrast, for configuration variables changes were more diverse (Fig. 1). A group of variables including mean shape complexity in the landscape (i.e. mean shape and fractal index) and patch density showed an unimodal response with maximum influence at 250-500 m. Edge density and landscape shape index showed a linear response. Landscape shape index and patch density had a positive effect on non-native species richness at smaller extents but changed to negative above 1000 m.

MULTIMODEL INFERENCE RESULTS: NON-CORRECTED AND UNBIASED WEIGHT OF EVIDENCE, AVERAGED AND STANDARDIZED COEFFICIENT ESTIMATES (BETA AVERAGED) AND CONFIDENCE INTERVALS (95% CI) OF REGION, HABITAT, LANDSCAPE (CONFIGURATION AND COMPOSITION), AND CLIMATE FOR NON-NATIVE SPECIES RICHNESS IN MEDITERRANEAN COASTAL HABITATS. PREDICTORS ARE SORTED BY IMPORTANCE ACCORDING TO THE UNBIASED WEIGHT OF EVIDENCE. REGRESSION COEFFICIENTS FOR THE CATEGORICAL VARIABLES HABITAT AND REGION ARE NOT SHOWN. SIGNIFICANT AVERAGED COEFFICIENTS ARE SHOWN IN BOLD. SEE TABLE 2 FOR A COMPLETE DESCRIPTION OF VARIABLES.

TABLE 3

Variable	Type	Weight	Unbiased Weight	Beta averaged	Adjusted SE	Lower CI	Upper CI
Intercept				**1.103**	0.182	0.747	1.460
Spatial autocovariate				**0.074**	0.015	0.045	0.104
Region	Region	1	0.82	-	-	-	-
Agricultural cover	Composition	1	0.784	**-0.243**	0.083	-0.405	-0.082
Patch area	Patch	0.976	0.736	**0.097**	0.041	0.017	0.177
Simpson land-cover diversity index	Composition	1	0.713	**0.263**	0.078	0.111	0.414
Mean fractal index	Configuration	1	0.711	**-0.158**	0.052	-0.26	-0.057
Edge densiy	Configuration	0.856	0.645	**0.148**	0.068	0.014	0.282
Low-density urban cover	Composition	0.79	0.591	**0.117**	0.057	0.006	0.227
High-density urban cover	Composition	0.674	0.411	0.096	0.05	-0.002	0.195
Habitat type	Habitat	0.587	0.354	-	-	-	-
Patch fractal index	Patch	0.457	0.243	-0.83	0.057	-0.194	0.028
Mean min. temperature	Climate	0.231	0.015	0.110	0.0126	-0.138	0.357

DISCUSSION

The relative importance of patch and landscape characteristics influencing plant invasions

Plant invasions could be seen as a spatial hierarchical process where ecological factors affect invasions at different scales (McDonald & Urban, 2006; Milbau et al., 2009). For instance, regional human influence and climate might control variability in non-native species richness at the regional scale (2000-200 km), landscape characteristics might influence from the landscape to the local scale (200-1 km), while patch characteristics and habitat type influence invasion at the local scale. Following this hierarchical approach, we found patch and landscape characteristics the most important group of variables influencing non-native species richness in comparison to regional human influence and habitat type. The importance of landscape characteristics found is in line with the medium spatial scale of the study area (<200 km) (Milbau et al., 2009). Coarser scales such as continental, would probably found a more relevant role of climate (Pearson et al., 2004) or regional human influence. The effect of landscape variables is mainly related to an increased propagule pressure from fragmented human-altered areas (Chytrý et al., 2008a; Catford et al., 2011; Vilà & Ibáñez, 2011). Human-altered areas such as gardens, artificial edges or communication networks are usually heavily invaded (Vilà et al., 2007; Chytrý et al., 2008b) and can easily become the source of propagules to nearby natural areas.

The identity of the region was, after patch and landscape variables, the most important factor explaining non-native species richness in Mediterranean coastal habitats. Non-native species richness was higher in Barcelona and Girona regions than in the Menorca Island. This result was also found for a broader geographic area in Catalonia and Balearic regions using a regional database of vegetation relevés and it was attributed to the higher human influence in the mainland regions than in Menorca (Vilà et al., 2010b). Stronger regional human influence could encompass factors known to increase non-native plant invasions such as higher propagule pressure from human-altered habitats and an intense use of non-native plants for ornamental or restoration purposes (Simberloff, 2009a). Indeed, density of human population and that of road networks are larger in Catalonia than in the Balearic Islands (Table 1; Vilà et al. 2010). However, in Menorca, these effects might be confounded with insularity, which might alter the arrival and establishment of non-native plant species. Classical works suggested that islands tend to be more heavily invaded than their mainland counterparts (Elton, 1958; Lonsdale, 1999; Pyšek & Richardson, 2006). However, other studies confirm our findings supporting that communities in non-oceanic islands tend to be less invaded by non-native plants than in the mainland (Teo et al., 2003; Atwood & Meyerson, 2011). Furthermore, even when islands were found to be more invaded these differences could be explained by other factors not directly linked to insularity, but to differences in anthropic disturbances (Yiming et al., 2006). Thus, after accounting for landscape characteristics and climate differences, our results suggest that the difference in regional human influence is the most important aspect explaining the differences in plant invasions across regions. Other factors not explored in this study that could account for difference in invasion might be related to differences in invasion history (Teo et al., 2003; Yiming et al., 2006; Vilà et al., 2010a). However, its relative importance should be considered rather low due to the intensive trade and transport among regions.

Although we found significant differences among habitats, habitat type alone did not explain a high amount of deviance in non-native species richness. On the contrary, previous studies have found habitat type to be the foremost factor explaining differences in plant invasions (Chytrý et al., 2008a; Gassó et al., 2012a). One reason for this discrepancy could be the environmental similarity among the habitats assessed in our study. Furthermore, habitat type encompasses a range of factors known to affect plant invasions (Catford et al., 2009; Chytrý et al., 2009). The partition analyses revealed that habitat type shared its explained deviance with landscape, region and climatic variables. Therefore, although habitat type might not be the most important predictor, it might be used as a simple estimate of invasion risk when information on the landscape or climate is scarce.

Patch and landscape characteristics influencing plant invasions

Landscape composition variables were more important predictors of non-native species richness than landscape configuration or patch variables. The importance of landscape composition on plant invasions has been widely confirmed in many studies (Vilà & Ibáñez, 2011). Land-cover diversity and the percentage of urban and agricultural land-cover were the most important landscape predictors of non-native species richness. Highly diverse landscapes support the idea that a larger gradient of environmental conditions allows the establishment and spread of many different non-native species. In turn, these landscapes could provide a greater pool of non-native species with the potential to reach natural vegetation patches (Pino et al., 2005; Marini et al., 2009).

Urban land-cover usually has a positive effect on plant invasion both at plot and grid level (Pino et al., 2005; Gassó et al., 2009; Gavier-Pizarro et al., 2010; Vilà & Ibáñez, 2011). However, not all urban areas contribute the same to plant invasion. Patches surrounded by low-density urban areas showed higher non-native species richness than high-density urban areas. These results support previous findings by Gavier-Pizarro et al. (2010) within administrative regions in New England (USA). The low-density urban land-cover is characterized by fragmented and disturbed natural areas within a loose matrix of gardening and housing areas. Therefore, the probability of non-native ornamental species spreading from gardening and housing areas into adjacent natural areas is higher in a low-density urban landscape matrix.

Agricultural land-cover was negatively associated with non-native species richness, as found in other studies (Ibáñez et al., 2009b; Marini et al., 2009). The effect of agricultural land-cover depends on the surrounding landscape and habitat type (Vilà & Ibáñez, 2011). In human-influenced landscapes, as in our study, agriculture could act as a buffer against invasion. Especially in forests, where invasion into the interior is driven mainly by shade-tolerant ornamental species, agriculture areas could act as a barrier to their expansion (Cadenasso & Pickett, 2001). Furthermore, non-native species of agricultural origin may not invade natural areas but remain as weeds in crops (Vilà et al., 2004).

The effect of landscape configuration and patch characteristics on plant invasions has been traditionally less explored (Vilà & Ibáñez, 2011). The low importance of these variables found in contrast to landscape composition variables underpins their idiosyncratic effects on plant invasions. As in previous works by Bartuszevige et al., (2006) and Kumar et al., (2006), we found that patches surrounded by fragmented landscapes (i.e. high edge density) underwent heavier invasions. Edges are usually highly invaded and thus might play an important role both as sources and sinks of non-native propagules (Vilà & Ibáñez, 2011). Mean landscape-shape complexity (i.e. mean fractal index) had a negative association with non-native plant richness. To our knowledge, the only study available exploring this attribute found a positive association (Kumar et al., 2006). Our opposite finding might be explained by less shape complexity of anthropogenic landscapes (mainly urban and agricultural) than natural landscapes. In fact, there was a negative correlation between mean shape complexity and urban land-cover (Appendix A).

Finally, the only patch characteristic influencing non-native species richness was patch area. The positive relationship found between patch size and non-native species richness might be simply trivial (i.e. the larger patch area the more opportunities for random establishment of non-native species), but it might also reflect higher microhabitat diversity of large patches compared with that of small ones. This finding contradicts previous studies where the relationship was not significant (Cully et al., 2003) or even negative (Guirado et al., 2006; Ohlemüller et al., 2006). The lack of effect of patch shape complexity is in line with other studies (Bartuszevige et al., 2006; Vilà & Ibáñez, 2011; but see Ohlemüller et al., 2006). These results confirm the variability of the influence of patch characteristics on non-native species richness in comparison to propagule pressure proxies such as landscape composition variables.

The landscape extent relevant to plant invasions

We found high variability in the association of landscape characteristics with non-native species richness considering the spatial extent of study. The sensitivity of landscape indices to the spatial extent is a major concern when trying to elucidate the importance of landscape characteristics in ecological processes (Baldwin et al., 2004; Kumar et al., 2006; Bailey et al., 2007). While previous studies have found 250 m to be the most influential extent in plant invasions (Sullivan et al., 2005; Bartuszevige et al., 2006; Kumar et al., 2006), our findings suggest that the major influence occurs at smaller spatial extents (100 m) for most of the variables. In highly altered systems such as in our study area, the immediate neighbouring space is probably the most relevant extent to invasion because it might reflect a direct link with disturbance and species dispersal. For example, adjacent urban areas might facilitate the arrival of ornamental plant species without the need of long-distance dispersal events or an increase in human frequentation.

We also found that landscape configuration variables caused more diverse changes across spatial extents than did landscape composition variables. While composition variables showed slightly linear decrease in association, most of the configuration variables showed also unimodal responses to the extent (i.e. maximum association at 200-250 m). This finding reinforces the idiosyncratic effect of landscape configuration variables on non-native species richness, and the importance of performing sensitivity analyses to detect the most relevant landscape extent for each landscape predictor (Kumar et al., 2006). Other aspects on the sensitivity of landscape indices not explored in this study that might require further research are the type of landscape (e.g. urban vs. agriculture landscapes), the landscape thematic resolution (i.e. classification scheme of land-cover types) and the sampling resolution (Baldwin et al., 2004; Kumar et al., 2006).

Conclusions

Landscape composition was the most important determinant of non-native plant invasions in Mediterranean coastal areas. Natural areas close to diverse and urban landscapes are highly vulnerable to plant invasions while surrounding agricultural areas could buffer this effect. Within highly invaded systems the effect of landscape composition is clearly more evident than the variability in regional human influence, habitat type, patch geometry or landscape configuration. The prevalence of this pattern might also depend on the range of climatic conditions, habitat similarity and the stage of invasion under consideration. Thus, our findings indicate that invasion-risk analyses must take into account the landscape matrix, especially in terms of land-cover diversity and human alteration (Hulme, 2006).

Our study also advocates that plant-invasion risk analyses considering landscape characteristics should include sensitivity analyses in order to test differences across spatial extents (Kumar et al., 2006; Pauchard & Shea, 2006). Our study yielded a wide variability in the strength of association of landscape variables with non-natives species richness at different spatial extents. Thus, a measure of landscape characteristics at a single spatial extent might lead to erroneous conclusions about the susceptibility of an area to invasion. Once the spatial extent that maximizes plant invasions is identified, it could be used to target the management of non-native species. Usually, the management of non-native species focus on the stand scale (Pauchard & Shea, 2006) although other approaches have been applied at the landscape scale (e.g. vehicles or weed cleaning) or even at broader scales (e.g. import regulation). Our study suggests that management of the neighbouring landscape (i.e. 100-250 m) should be a priority to control plant invasions at the local scale.

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APPENDIX A

TABLE A.1

PEARSON’S CORRELATION COEFFICIENTS AMONG THE PREDICTORS USED TO MODEL THE LEVEL OF PLANT INVASION IN COASTAL HABITATS.
SIGNIFICANCE: P<0.001: ***; P<0.01: **; P<0.05:*.

	Patch fractal index	Patch area	Annual precipation	Mean min. temperature	Radiation	water cover	High-density urban covei	Low-density urban cover	Agriculture cover	Edge density
Patch area	-0.1									
Annual precipation	-0.11 *	-0.02								
Mean minimum temperature	0.06	-0.13 *	-0.2 ***							
Radiation	0.08	-0.11	0.18 **	0.05						
Water cover	0.03	-0.02	-0.09	0.19 **	-0.01					
High-density urban land-cover	-0.08	0.04	0.21 ***	-0.05	0.09	-0.11				
Low-density urban land-cover	-0.15 **	0.04	0.31 ***	-0.43 ***	-0.03	-0.1	0.03			
Agricultural land-cover	-0.09	-0.04	0.03	0.22 ***	0	-0.01	0.01	-0.16 **		
Edge density	0.04	-0.01	0.09	0.14 *	0.09	0.01	0.21 ***	0.08	0.45 ***	
Mean patch area	-0.01	-0.06	-0.09	0.06	-0.16 **	0.01	-0.12 *	-0.11	-0.23 ***	-0.49 **
Mean fractal index	0.04	-0.12 *	-0.05	0.12 *	0.09	0.01	-0.13 *	-0.15 **	0.06	0.13 *
Simpson land-cover diversity index	-0.03	0.03	0.1	0.12 *	0.06	0.18 *	0.23 ***	0.26 ***	0.34 ***	0.53 ***

Selection of best models considering AICc criteria (Delta<4: all models within 4 AICc units from the best model) for alien species richness considering landscape, climate, region and habitat. In bold the best model including region and habitat.

Table A.2

Model	df	logLik	AICc	Delta	Weight
1+2+3+4+5+7+8+9+10+11	13	-519.59	1066.48	0	0.13
1+2+3+4+6+7+8+9+10+11	15	-517.87	1067.46	0.98	0.08
1+2+3+4+7+8+9+10+11	12	-521.27	1067.65	1.17	0.07
1+2+3+4+5+7+8+9+10+11+12	14	-519.16	1067.81	1.33	0.07
1+2+3+4+5+6+7+8+9+10+11	16	-517.23	1068.41	1.93	0.05
1+2+3+4+6+7+10+11	13	-520.56	1068.42	1.95	0.05
1+2+3+4+6+7+9+10+11	14	-519.49	1068.48	2	0.05
1+2+3+4+7+8+9+10+11+12	13	-520.72	1068.73	2.25	0.04
1+2+4+6+7+8+9+10+11	14	-519.66	1068.82	2.34	0.04
1+2+3+4+6+7+8+10+11	14	-519.7	1068.9	2.42	0.04
1+2+3+4+6+7+8+9+10+11+12	16	-517.51	1068.97	2.49	0.04
1+2+3+4+5+7+9+10+11	12	-522	1069.12	2.64	0.04
1+2+3+4+5+6+7+9+10+11	15	-518.78	1069.28	2.8	0.03
1+2+3+4+5+6+7+10+11	14	-519.89	1069.29	2.81	0.03
1+3+4+6+7+10+11	12	-522.39	1069.88	3.4	0.02
1+2+3+4+5+6+7+8+10+11	15	-519.08	1069.88	3.41	0.02
1+2+3+4+6+7+9+10+11+12	15	-519.13	1069.99	3.51	0.02
1+2+4+5+7+8+9+10+11	12	-522.44	1069.99	3.51	0.02
1+2+3+4+5+6+7+8+9+10+11+12	17	-516.92	1070.04	3.56	0.02
1+2+4+6+7+9+10+11	13	-521.38	1070.05	3.57	0.02
1+2+4+6+7+10+11	12	-522.55	1070.21	3.73	0.02
1+2+4+7+8+9+10+11	11	-523.7	1070.33	3.85	0.02
1+2+3+4+6+7+10+11+12	14	-520.43	1070.37	3.89	0.02
1+2+3+4+5+7+9+10+11+12	13	-521.58	1070.46	3.98	0.02
1+2+4+5+6+7+8+9+10+11	15	-519.37	1070.47	3.99	0.02

1: Spatial autocovariate; 2: Patch area; 3: Edge density; 4: Mean fractal index; 5: Patch fractal index; 6: Habitat; 7: Agricultural land-cover; 8: High-density urban land-cover; 9: Low-density urban land-cover; 10: Simpson land-cover diversity index; 11: Region; 12: Mean minimum temperature

TABLE A.3

COEFFICIENT ESTIMATES FOR BEST MODEL FROM THE MULTIMODEL INFERENCE SELECTION FOR ALIEN SPECIES RICHNESS INCLUDING HABITAT TYPE AND REGION.
SIGNIFICANCE: P<0.001: ***; P<0.01: **; P<0.05:*.

Variable	Estimate	Std. Error	z value	Pr(>|z|)	
Intercept	1.142	0.138	8.301	0	***
Spatial autocovariate	0.075	0.015	5.076	0	***
Patch area	0.09	0.037	2.411	0.0159	*
Edge density	0.133	0.069	1.91	0.0562	
Mean fractal index	-0.156	0.05	-3.112	0.0019	**
Habitat: Forest-Shrub	-0.23	0.125	-1.835	0.0665	
Habitat: Forest-Dunes	-0.221	0.145	-1.521	0.1281	
Habitat: Forest-Rock	-0.38	0.153	-2.483	0.013	*
Agriculture cover	-0.244	0.077	-3.182	0.0015	**
High-density urban land-cover	0.087	0.048	1.814	0.0696	
Low-density urban land-cover	0.099	0.052	1.912	0.0559	
Simpson land-cover diversity index	0.246	0.071	3.449	0.0006	***
Region: Barcelona-Girona	-0.035	0.115	-0.305	0.7605	
Region: Barcelona-Menorca	-1.673	0.194	-8.642	0	***

CAPÍTULO DOS

González-Moreno, P., Gassó, N., Pino, J. & Vila, M. (2013) Landscape context modulates plant invasions in Mediterranean forest edges. Biological Invasions, 15, 547–557.

LANDSCAPE CONTEXT MODULATES PLANT INVASIONS IN MEDITERRANEAN FOREST EDGES

RESUMEN

Los hábitats naturales en paisajes alterados son especialmente vulnerables a las invasiones biológicas. Nuestro objetivo fue entender la influencia del paisaje y las características locales en el nivel de invasión por plantas exóticas y sus rasgos en bordes forestales de paisajes altamente urbanizados. Identificamos todas las especies de plantas en 73 pares de parcelas en el borde y 50 m hacia el interior del bosque. Exploramos la asociación de la riqueza de especies exóticas y la similitud en la composición de especies entre las parcelas de borde e interior, con variables locales y de paisaje mediante modelos generalizados y técnicas de partición de la devianza. También implementamos un análisis Fourth-corner para explorar la asociación entre los rasgos de las plantas exóticas y las variables locales y de paisaje. Al contrario que para riqueza de nativas, la riqueza de exóticas estuvo más afectada por el paisaje vecino que por las características locales del borde. La proximidad a carreteras fue el factor más influyente para la riqueza y la proporción de exóticas, mientras que la perturbación fue la variable más importante para la riqueza de nativas. Los rasgos de las especies exóticas también estuvieron asociados a las características del paisaje. Por ejemplo, especies Mediterráneas introducidas a través de la agricultura estuvieron asociadas a paisajes agrícolas. Por tanto, nuestros resultados sugieren que para pronosticar áreas con alto grado de invasión e identificar invasores potenciales, los análisis de riesgo de invasión deben considerar el contexto paisajístico.

ABSTRACT

Natural habitats in human-altered landscapes are especially vulnerable to biological invasions. We aim to understand the influence of landscape and local characteristics on biological invasions by exploring the level of plant invasion and alien species traits in forest edges in highly urbanized landscapes. We identified all plant species in 73 paired plots in the edge and 50 m towards the interior of the forest. We explored the association between alien species richness and similarity in species composition between edge and interior plots with landscape and local variables, using generalized linear models and deviance partitioning techniques. Then, we performed Fourth-corner analyses to explore the association between alien plant traits and local and landscape variables. In contrast to native species richness, alien species richness was more affected by the surrounding landscape than by the local characteristics of the edge. Road proximity was positively associated with alien species richness and proportion and was its most important correlate, whereas disturbance was negatively associated with native species richness and was its most influential factor. Alien plant traits were also primarily associated with landscape characteristics. For instance, species of Mediterranean origin and introduced for agriculture were associated with higher agriculture use in the landscape. Our findings suggest that risk analyses of habitat vulnerability to invasion must consider the landscape context in order to successfully predict highly invaded areas and identify potentially successful invaders.

INTRODUCTION

Biological invasions and human-induced landscape changes are two major drivers of global change, affecting biodiversity both independently and synergistically (Didham et al., 2007). For example, human-derived land-uses can facilitate plant invasions in their surrounding natural habitats because they directly promote human frequentation and habitat disturbances that favour alien plant establishment (Hobbs & Huenneke, 1992; Guirado et al., 2006). Furthermore, these human-derived land-uses can also increase propagule pressure from the human-transformed land matrix to the remaining patches of natural habitat (Deutschewitz et al., 2003; Ohlemüller et al., 2006; Gassó et al., 2009). Peri-urban forest edges offer an excellent study system to explore the synergistic effect of human-driven landscape alteration and plant invasion given that the urban-forest edge is the invasion front for many alien species. Due to their specific environmental conditions, edges are usually highly invaded in comparison to the forest interior (Harper et al., 2005; Vilà & Ibáñez, 2011). The suitability of this habitat combined with high propagule pressure of specific alien plant species from urban areas (e.g. shade-tolerant species of gardening origin) might lead to further invasion of natural areas (Martin et al., 2009).

The adjacent landscape matrix might greatly influence the level of plant invasion in forest edges (Cadenasso & Pickett, 2001; Harper et al., 2005; Ewers & Didham, 2006; Vilà & Ibáñez, 2011). A higher number of alien species have been found in forest edges adjacent to urban areas compared to agriculture areas (Guirado et al., 2006) given that these areas may provide propagules from a larger number of ornamental species. Other landscape characteristics that might positively affect the level of invasion include, for example, the proximity of roads (e.g. Bradley & Mustard, 2006; Ibáñez et al., 2009b) and land-use diversity (e.g. Pino et al. 2005; Kumar et al. 2006). Furthermore, landscape alteration may also affect differences in the level of invasion between the forest edge and the interior due to changes in species' percolation. Although this hypothesis is inherent to some neutral landscape approaches derived from percolation theory (With, 2004), it remains largely unexplored. Highly altered landscapes supporting high alien propagule pressure might increase the percolation of alien species and therefore reduce the similarity in species composition between edge and interior forest communities.

Despite the recent evidence for the relevance of landscape shaping plant invasions (Vilà & Ibáñez, 2011), the relative importance of landscape characteristics versus local characteristics in forest edges remains unclear (Bartuszevige et al. 2006). Local characteristics operating at the edge, such as microclimate conditions (e.g. light conditions) and species interactions (e.g. seed dispersal), could affect alien species establishment and spread (Harper et al., 2005).

The success of alien species in the process of invasion (i.e. invasiveness) has been related to particular biological and life-history species traits (Hayes & Barry, 2007; Pyšek & Richardson, 2007; Gassó et al., 2009). However, few studies have linked these traits with environmental factors at the invaded sites (Thuiller et al., 2006; Jauni & Hyvönen, 2012), and to our knowledge, none have examined the relationship between specific alien plant traits and the local and landscape characteristics of forest edge habitats. Extrinsic traits such as the introduction pathway could determine the invasion success in forest edges. For example, Brothers & Spingarn, (1992) observed that alien species introduced for agriculture were limited to the first few meters of the forest edge, whereas species used for gardening were mainly found in the forest interior probably due to a combination of dispersal and light limitations. Understanding these associations might be important to the improvement of invasion risk analyses customized for different habitats or landscape characteristics.

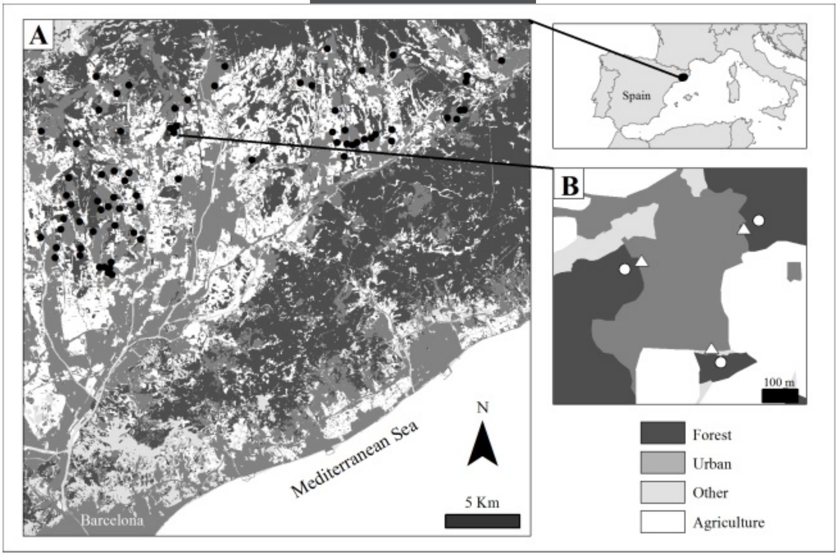
To provide insights on landscape and habitat management towards the prevention of plant invasions in forest edges, we compared plant invasion patterns between forest edges and forest interior in highly fragmented peri-urban forest areas. Specifically, we asked the following questions: (1) What are the main landscape and local factors explaining the level of plant invasion in forest edges? (2) Do landscape and local characteristics affect species similarity between the forest edge and the interior? (3) Are there differences in alien species traits between the forest edge and the interior? And finally, (4) are alien plant traits in forest edges related to landscape and local characteristics?

METHODOLOGY

Study site

The study area covers 35 000 ha in Vallès county (Catalonia, North-East Spain), located 25 km north of Barcelona city (Fig. 1). Elevation ranges from 130 to 815 m a.s.l. and mean annual precipitation ranges from 600 to 800 mm. During the last century, the landscape of this region has gone through a significant transformation, primarily due to agriculture abandonment and increasing urban sprawl related to the expansion of Barcelona's Metropolitan area (Olarieta et al., 2008). This land-use change has shaped a complex landscape mosaic with highly fragmented forests nested within a matrix of low-density urbanized and agricultural lands.

FIGURE 1



Location of the study area in Vallès county, Catalonia, NE Spain and sampling protocol (European Datum 1950). A) Black dots correspond to surveyed vegetation plots. B) White circles indicate forest interior plots and white triangles edge plots.

Plant species survey

We selected, by ortho-image interpretation of landscapes, 73 forest patches with contrasting human influence, ranging from agroforestry mosaics to urban surroundings (Fig. 1). Forests corresponded to mixed stands of pine *(Pinus halepensis* Mill., *P. pinea* L., *P. nigra* Arn.), the evergreen *Quercus ilex* L. and the deciduous *Q. cerrioides* Willk. In the most invaded location of each patch edge we set up a 10 m radius plot and another plot 50 m towards the forest interior (Fig. 1). Plant community effects are suggested to mostly disappear 50 m into the forest (Brothers & Spingarn, 1992; Fraver, 1994), although other effects could persist up to 100-500 m (Harper et al. 2005; Guirado et al. 2006). This setup might bias the comparison of species richness between the forest edge and interior, however, it should not affect the species traits occurrence or the predictors explaining plant community structures which constitute part of our main objectives. For each plot, we identified and classified all plant species as native or alien according to Bolós et al., (1993) and we calculated native and alien species richness and alien species proportion. We also calculated Sørensen's species similarity index (S) for native and alien species between edge and interior plots (McCune & Grace, 2002):

$$S = 2C / A + B$$

where A and B are the number of species in the edge and interior plots, respectively, and C is the number of species shared by the two plots. The Jaccard's similarity index was also calculated and used in the analyses, but as it yielded similar results to Sørensen's index, we do not present the results for simplicity.

A set of plant species traits and factors related to the introduction history (traits hereafter) known to be related to invasion success in Mediterranean regions were registered for each alien species (Lloret et al., 2005; Gassó et al., 2009): dispersal syndrome (zoochorous/non-zoochorous), vegetative reproduction (yes/no), life-form classification (trees – buds 25 cm above soil level, shrubs – buds no more than 25 cm above soil level, geophytes – buds below ground, annual plants and vines), introduction pathway (gardening/agriculture/forestry/weed) and biogeographical region of origin. We obtained all the above information

(Appendix A - Table A1) from Castroviejo et al., (1986), Bolós et al., (1993) and Sanz-Elorza et al., (2004).

Landscape and local variables

We characterized each plot with 9 landscape and local variables commonly used to explain plant invasion patterns (Deutschewitz et al., 2003; Pino et al., 2005; McDonald & Urban, 2006). The landscape characteristics were relative percentage of forest, urban and agriculture use, Shannon's diversity index of land uses and minimum distance to main roads and motorways (i.e. opposite to road proximity). We calculated all landscape variables within 250, 500, 1000 and 2000 m buffer areas from the edge plot using ArcGIS 10. These distances are within the range (250-1500 m) used in studies on alien plants (Sullivan et al., 2005; Bartuszevige et al., 2006; Kumar et al., 2006). The percentage of land use and the diversity index were based on the 3rd version of the Land Cover Map of Catalonia (www.creaf.uab.cat/mcsc), obtained by digitizing 2005 colour ortho-images. We obtained road proximity using the 1:50 000 topographic map of Catalonia (ICC, 2004).

The selected local variables were aspect, disturbance level, forest type (mixed/deciduous, oak/evergreen, oak/pine) and edge type (closed/open). We obtained aspect for each pair of plots. To facilitate interpretation, we transformed aspect into a NE-SW axis (Beers et al., 1966) with values of 0 at the NE aspect where radiation and evapotranspiration are expected to be lower and values of 2 at the SW orientation. Slope and aspect could interact to change radiation levels in forest edges. As slopes never exceeded 12º, we regarded aspect as a sufficient indicator of light penetration. We visually quantified disturbance level for each plot using a categorical range of 6 levels: undisturbed, very low (e.g. animal trampling), low (e.g. sporadic debris), medium (e.g. moderate human trampling and debris), high (e.g. high human trampling and accumulation of debris) and very high (e.g. dumping, logging and high soil disturbance). We also visually classified the edge type as open or closed depending on understory height and density.

Statistical analysis

Invasion patterns in edge and interior plots and their relation to landscape and local characteristics

We explored the association of alien and native species richness, proportion of alien species and Sørensen's similarity index with landscape and local variables by multimodel inference (Burnham & Anderson, 2002) and variance partitioning techniques (Mood, 1969) based on Generalized Linear Models (GLM). For both analyses, we built independent GLMs for edge and interior plot data subsets with the exception of the models for the similarity indices which combine information from both plot types. We modelled the error terms of species richness variables using a Poisson distribution, which is typically used for count data (Gelman & Hill, 2007). For similarity indices and alien species proportion we used normal and binomial distributions, respectively. None of the GLMs exhibited spatial autocorrelation in the residuals according to Moran's index ($I < 0.4$).

Prior to modelling we identified the most influential buffer distance for each variable according to Pearson's correlation coefficients (Appendix A - Table A2). We selected 1000 m as the best compromise for all variables across buffer distances. We then checked the independent variables for collinearity using pairwise correlation tests, excluding correlation values higher than 0.6 (Appendix A - Table A3).

Variance partitioning techniques indicate the variability explained by the single and shared groups of variables (Mood 1969). Assuming that deviance is a good measure of the variability explained by a model, we set up a GLM for each dependent variable incorporating only landscape variables, only local variables and both of types of variables together. The deviance explained by each model was then used to identify the pure and mixed effects by simple equation systems (Carrete et al. 2007).

Multimodel inference is a model selection method that allowed us to identify the best possible models and rank all independent variables according to their influence on each dependent variable. We performed multimodel inference based on all-subsets selection of GLMs using Akaike's Information Criterion corrected for small samples or large number of predictors (AICc) (Burnham & Anderson 2002). For each combination of predictors we calculated the Akaike weight of evidence (Wi). Considering the best models given the selected predictors (delta<2: all models within 2 AICc units from the best model), the weight of evidence (Wi) of each predictor can be estimated as the sum of the model AICc weights across all models in which the selected predictor appeared (Burnham & Anderson, 2002). The predictor with the highest Wi (i.e. the closest to one) gets the highest weight of evidence to explain the response variable with the given data compared to the rest (i.e. the highest relative importance).

We also used multimodel inference to estimate regression coefficients and their unconditional confidence intervals (with the adjusted standard error) within the best models subset (delta<2) (Burnham & Anderson 2002). We calculated the coefficient for a given predictor as the sum of the predictor's coefficient multiplied by the weight of evidence, across all possible models where the predictor is present (Burnham & Anderson 2002).

Alien plant traits and their relation to landscape and local characteristics

We explored the differences in alien trait proportions (i.e. % of species with zoochorous dispersal, vegetative reproduction, and gardening/agriculture pathway of introduction) between invaded edge and interior plots by paired Wilcoxon's signed-rank tests, after verifying the absence of normality (n = 48). Then, we used the Fourth-corner method (Legendre et al., 1997; Dray & Legendre, 2008) to explore the association of landscape and local variables with alien plant traits at edge plots. This type of multivariate analysis allows the quantification of the relation between two matrices, R - landscape and local characteristics at each edge plot and Q - alien species traits, through a third matrix, L, which stores the distribution of species among edge plots. We used the permutation model q1/I, where cell values were permuted within the columns of the L-matrix (species) (Legendre et al., 1997; Aubin et al., 2009). This model tests the null hypothesis that species traits are randomly distributed with respect to characteristics of the sites. The alternative hypothesis states that individuals with specific traits are distributed according to their environmental preferences. Specifically, we expected an association of annual species with disturbed sites and close to roads (Lake & Leishman, 2004; Jauni & Hyvönen, 2012), as well as a significant relationship between the relative proportion of land uses and the pathway of introduction. The later association might reflect the effect of landscape type on propagule diversity arriving to the edge. We corrected probabilities of all statistics with the Holm's procedure after 9999 permutations.

We performed all statistical analyses with the R software using the ADE4 package for the Fourth-corner method (Dray & Dufour, 2007), the package MuMIn for some procedures of the multimodel inference method and the package VEGAN as the base code for deviance partitioning.

RESULTS

Invasion patterns in edge and interior plots and their relation to landscape and local characteristics

The total pool of native and alien species found in the plots was 150 and 48, respectively. The mean (±SE) proportion of alien species was 16% (±1.10) and the mean (±SE) species richness per plot was 16.04 (±0.42) for native species and 2.48 (±0.16) for alien species.

Alien species identity varied between edge and interior plots: 25 alien species were found only in the edge plots while four species were found only in the interior plots (Appendix A-Table A1). The most abundant alien species in edge plots were *Celtis australis* L. (46% of plots), *Lonicera japonica* Thunb. (34%) and *Ligustrum japonicum* Thunb. (31%), while in interior plots *Celtis australis* (39%), *Ligustrum japonicum* (24%), *Prunus domestica* L. (11%) and *Solanum chenopodioides* Lam. (11%) were the most abundant alien species.

The GLMs for species richness and proportion of alien species explained a small proportion of the variance (Table 1). The major correlates (i.e. higher weight of evidence) for alien species richness were edge type and road proximity (Table 1). Specifically, we found both higher alien species richness and proportion in closed edges at high road proximity (i.e. low minimum distance to main roads). Major correlates for native species richness were disturbance and edge type (Table 1). In contrast to alien species richness, higher native species richness was found in the least disturbed open edges. The variables best explaining alien species richness were similar for edge and interior plots.

TABLE 1

INFLUENCE OF LANDSCAPE AND LOCAL VARIABLES ON ALIEN/NATIVE SPECIES RICHNESS AND THE SIMILARITY OF ALIEN/NATIVE SPECIES COMPOSITION IN FOREST EDGE AND INTERIOR PLOTS. FOR EACH VARIABLE THE SIGN AND SIGNIFICANCE OF THE AVERAGED COEFFICIENT (C) AND ITS RELATIVE IMPORTANCE (W) ARE PROVIDED. THE DEVIANCE PARTITIONING OF THE PURE EFFECT OF LOCAL AND LANDSCAPE VARIABLES AND THEIR MIXED EFFECTS AND RESIDUALS ARE ALSO PRESENTED.

		LOCAL								LANDSCAPE										DEVIANCE PARTITIONING			
		Disturbance		Forest type		Closed Edge		Aspect		Distance to roads†		Forest use		Urban use		Agriculture use		Land use diversity		Local	Mixed	Landscape	Residuals
		C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W				
Edge	Native		0.74			-***	1						0.43		0.58		0.27			**0.14**	0.04	0.05	0.76
	Alien						0.2		0.76		0.89						0.49			0.05	0.00	**0.08**	0.88
	Alien proportion		0.20			+*	1		0.40		0.86		0.15		0.09		0.43		0.12	**0.11**	0.00	0.08	0.83
Interior	Native	-*	**1**				0.08		0.24		0.24		0.15				0.07		0.72	**0.10**	0.02	0.04	0.83
	Alien		0.30			+**	1		0.46	-***	1		0.22				0.18			0.11	0.00	**0.23**	0.74
	Alien proportion					+**	**1**		0.18	-***	**1**		0.17				0.13		0.16	0.09	0.00	**0.22**	0.76
Similarity	Native		0.79			+***	**1**		0.43		0.16				0.17				0.31	**0.23**	0.04	0.04	0.68
	Alien		0.07				0.35		0.13	-**	1		0.06		0.06		0.46		0.07	0.05	0.04	**0.19**	0.80

Note: the sign +/- indicates the positive/negative relationship between variables. Significant coefficients: *$P>0.05$; **$P<0.01$; ***$P<0.001$. The higher explaining block of factors is shown in bold. † Lower distance to roads implies higher road proximity

Species similarity between edge and interior plots was lower for alien (S = 0.24 ±0.03) than for native species (S = 0.59 ±0.01; W = 862.50, P < 0.0001), although this could be an artefact of Sørensen's index as it yields lower similarity values when species richness is low. Nevertheless, this bias should not affect the relationship to landscape and local variables. Similarity in alien species was mainly related to higher road proximity, whereas similarity in native species was associated with closed edges (Table 1).

Although the deviance partitioning analysis also showed a low explanatory strength of the selected variables, it yielded a clear pattern: the pure effects of the landscape predictors on alien species richness were higher than the effects of the local predictors. The opposite was observed for native species richness (Table 1). The mixed effects of the landscape and local groups of predictors were very small.

Alien plant traits in forest edges and their relation to landscape and local characteristics

Most alien species occurring in the edge plots were trees (50% of species found), with zoochorous dispersal (60%), native to East Asia (18%) and introduced for gardening (66%). Furthermore, half of the alien species had vegetative reproduction. Alien species found in the interior plots showed a similar spectrum of traits to those occurring in the edge plots: 61% of species were trees, 82% zoochorous, 36% came from East Asia and 68% were introduced through gardening. Comparing invaded paired plots, the proportion of zoochorous species was significantly higher in the interior plots (0.92 ± 0.03) than in the edge (0.82 ± 0.03; W = 68, P < 0.01). The same pattern occurred for species coming via agricultural introduction (Interior: 0.48 ± 0.05; Edge: 0.21 ± 0.03, W = 179, P < 0.0001). However, the proportion of species was higher in the edge plots than those in the interior for species with vegetative reproduction (Interior: 0.10 ± 0.03; Edge: 0.32 ± 0.04, W = 497.50, P < 0.0001) and introduced for gardening (Interior: 0.48 ± 0.06; Edge: 0.65 ± 0.04, W = 727.50, P < 0.01).

Fourth-corner analyses revealed a clear association between species traits and both landscape and local variables (Table 2, Appendix A - Table A4). All variables except forest type and urban use were correlated with at least one alien species trait (Table 2). Life form was related to disturbance, percentage of

TABLE 2

RELATIONSHIP AMONG PLANT TRAITS' LEVELS AND LOCAL AND LANDSCAPE VARIABLES. ONLY SIGNIFICANT CORRELATIONS AT THE 5% SIGNIFICANCE LEVEL AFTER HOLM CORRECTION ARE PRESENTED. THE SIGN INDICATES IF THE STATISTIC IS ABOVE (+) OR BELOW (-) THE EXPECTED VALUE BASED ON THE MEAN OF 9999 PERMUTATIONS.

	Closed edge	Disturbance	Aspect	Distance to roads	Forest use	Agriculture use	Land use diversity
Life form							
Shrub							+
Geophyte		+					
Annual						+	
Vine		-					
Pathway							
Agriculture				-	-	+	
Gardening				+	+	-	
Unintentionally						+	
Reproduction							
Vegetative						-	
Dispersion							
Zoochorous			+			+	
Region of origin							
America				+		-	
Europe		+					
South America				-			
East Asia	+			+			
Mediterranean						+	
South Africa						-	

agriculture use and land use diversity (Table 2). For instance, geophytes were present in more disturbed sites while vines were concentrated in the least disturbed areas (Table 2). Introduction pathway was only related to landscape variables (Table 2). For example, species of Mediterranean origin introduced through agriculture were positively associated with a high percentage of agriculture in the surrounding landscape matrix. In contrast, the presence of gardening species was positively associated with the percentage of forest use and negatively associated with road proximity (i.e. positive association with minimum distance to main roads) (Table 2).

DISCUSSION

Landscape characteristics are highly associated with plant invasions in forest edges

In contrast to native species richness, alien species richness demonstrated a stronger association with landscape characteristics than with local properties. The main landscape correlate related to the level of invasion (i.e. alien species richness and proportion) was road proximity. This association has also been found at different spatial scales of resolution from landscape to regional studies (Pino et al., 2005; Bradley & Mustard, 2006; Ibáñez et al., 2009b; Souza et al., 2011). High road density or proximity to roads might facilitate seed dispersal by humans or vehicles and therefore increase alien species spread (Bradley & Mustard 2006).

The local characteristic with the largest association with invasion was edge type. Alien species richness and proportion of alien species were larger in closed edges. This association could be explained by two non-exclusive effects. First, the closed structure in forest edges could be the result of the rapid growth of established alien species that build a wall of vegetation (Brothers & Spingarn 1992). Second, closed edges offer lower radiation but higher water availability and thus provide less stressful conditions than open forest edges (Didham & Lawton, 1999), thereby facilitating the establishment of shade-tolerant species commonly introduced via gardening which are expanding in very diverse forests (Martin et al., 2009).

Similarity of alien species composition between the forest edge and the interior also showed a stronger association with characteristics of the landscape than with local properties. Similarity of alien species was also associated with a landscape predictor, namely road proximity. Nearby roads may provide more opportunities for edge disturbance and propagule pressure from edges to the interior. On the other hand, similarity of native species was higher in closed forest edges. Closed edges promote low contrasting local conditions between the edge and the interior (e.g. comparable water and light conditions) that facilitates the establishment of similar native plant communities (Didham & Lawton 1999; Harper et al. 2005). These findings suggest that in contrast to native species, the establishment of alien plants in the forest interior is not highly limited by the local conditions. In fact, the forest interior may be invaded at high levels of propagule pressure demonstrating that forest edges are not a barrier to invasion (Guirado et al. 2006).

The association between alien plant traits and landscape

Many studies have pointed out that alien species traits related to successful invasion are habitat dependent (Kolar & Lodge, 2001; Lake & Leishman, 2004; Lloret et al., 2005; Jauni & Hyvönen, 2012). We found that some alien species traits were related to specific local variables such as disturbance, edge type and aspect. Nevertheless, our findings are not entirely consistent with previous studies, indicating that the association between species traits and habitat might be relatively idiosyncratic. For instance, alien species in disturbed plots tended to be geophytes, which is contrary to previous suggestions that annual plants should be more abundant (Lake & Leishman 2004; Jauni & Hyvönen 2012). However, this observation is consistent with the fact that herbaceous perennial plants with underground structures are good invaders because these structures are often associated with effective clonal growth mediated by disturbance (Gassó et al. 2009). Nevertheless, we observed differences in species traits between alien species occurring in edge and interior forest habitats. Agriculture and zoochorous species were found more frequently in the interior, while species with vegetative reproduction or with a gardening pathway of introduction were in the edge. This finding partially agrees with previous studies which suggest zoochorous and gardening species are concentrated in the forest interior (Brothers & Spingarn 1992; Cadenasso & Pickett 2001). The authors of the above mentioned investigations based their conclusions on observations of species occurrence or dispersal distances, although they did not statistically compare proportions or cumulative abundances between edge and interior. In fact, it seems difficult to find general patterns of alien traits dominance between the forest edge and interior. First, the predominance of alien species traits in the forest edge or interior may depend on the gardening and agriculture practices of the area. In our study area most agricultural alien species are fruit trees so it is possible that individuals found in the forest interior were legacies from former agriculture land. Second, alien species are rarely in equilibrium with their environment and as we observed, their spread depends heavily on constant propagule pressure from the nearby landscape. Thus, it is also possible that gardening species are still in the process of expansion and that they have not yet reached their potential penetration into the forest interior (Martin et al. 2009).

The Fourth-corner analysis also suggested that most predominant alien species traits, and probably the most successful ones in our study area, are linked to the landscape characteristics surrounding forest edges. Plots with higher agricultural area in the surrounding landscape primarily had annual species introduced for agriculture, of Mediterranean origin and without vegetative reproduction. These traits are commonly shared by crop species. Surprisingly, gardening origin was significantly associated with forest use but not with urban use. As transects were placed on urban-forest edges, it is possible that this setup represented a limited gradient of the percentage of urban land-use in the landscape. On the other hand, as gardening species could successfully establish themselves in the forest edge, forest habitats could be also a source of propagules for these species. Currently, most risk analyses to identify invasive plants focus on species traits (Kolar & Lodge 2001; Lloret et al. 2005; Hayes & Barry 2007) and the degree of climate match between the native and recipient area (Scott & Panetta, 1993; Thuiller et al., 2005). Our results indicate that risk analyses must also explore the characteristics of the landscape of the recipient area because it highly defines the most likely origin of potential invasive species.

Conclusions

Invasion in forest edges could be seen as a spatial hierarchical process where landscape characteristics control main differences in the level of invasion, which is also influenced by local site-specific conditions such as the edge structure (McDonald & Urban, 2006; Milbau et al., 2009). Overall we found alien species richness, proportion of alien species and composition differences between the forest edge and interior to be highly dependent on the landscape surrounding the edge. This finding suggests that invasion at these sites is a dynamic process primarily related to the propagule pressure from the surrounding landscape. High human-alteration of the landscape contributes to further expansion of alien plant species from forest edges into the interior. The global trend towards forest fragmentation, which increases the length of the interfaces between urban and forest areas, will exacerbate plant invasions by gardening species (Martin et al. 2009). Thus, management of plant invasion must also consider the landscape adjacent to natural areas in order to reduce the propagule pressure from human-derived land-uses. Possible landscape management measures could include changes in gardening practices or constant monitoring of plant invasion in urban-forest interfaces.

The analysis of plant traits related to invasiveness has been one of the main focuses in invasion biology (Hayes & Barry 2007; Pyšek & Richardson 2007) and the basis for invasion risk analysis. However, identifying general patterns is complicated as many plant traits associated with invasion are dependent on the habitat type and the stage of invasion (Kolar & Lodge 2001; Lloret et al. 2005; Gassó et al. 2009; Jauni & Hyvönen 2012). Our results indicate that these risk analyses should also include characteristics of the landscape matrix of the recipient region because successful or more abundant alien plant traits are likely to be different depending on the surrounding landscape (Vilà & Ibáñez 2011).

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APPENDIX A

Pearson's correlation coefficients between the level of invasion by alien species and landscape variables across buffer distances (250, 500, 1000 and 2000 m) around edge and interior forest plots.

TABLE A.1

	Edge				Interior			
Buffer distances	250	500	1000	2000	250	500	1000	2000
Alien								
Land use diversity	0.13	0.16	0.15	0.18	0.11	0.04	0.14	0.26 *
Urban use	0.03	0.07	0.08	0.14	-0.13	-0.12	0.03	0.05
Agriculture use	-0.30 *	-0.15	-0.12	-0.18	0.09	0.22	0.2	0.2
Forest use	0.31 **	0.04	0	0.03	0.1	-0.08	-0.22	-0.21
Native								
Land use diversity	-0.02	-0.14	0	0.06	0	-0.2	-0.18	-0.17
Urban use	0.07	0.17	0.17	0.22	-0.1	-0.01	0.06	-0.02
Agriculture use	0.03	0.06	0.14	0.17	0.1	0.09	0.13	0.16
Forest use	-0.18	-0.28 *	-0.26 *	-0.27 *	0.04	-0.09	-0.14	-0.11
	Sorensen Alien				Sorensen native			
Land use diversity	0.06	-0.09	-0.06	-0.17	-0.02	0.09	0.19	-0.03
Urban use	-0.12	0.03	0.07	-0.02	0.09	0.1	0.01	-0.09
Agriculture use	0.1	-0.14	-0.28 *	-0.27 *	-0.04	0.03	0.09	-0.02
Forest use	-0.01	0.1	0.19	0.21	-0.05	-0.15	-0.13	0.04

Significant coefficients: *P>0.05; **P<0.01; ***P<0.001.

ALIEN SPECIES LIST INCLUDING PLANT SPECIES TRAITS AND FACTORS RELATED TO THE INTRODUCTION HISTORY (TRAITS) AND THEIR OCCURRENCE IN THE FOREST EDGE OR INTERIOR.

TABLE A.2

	Traits					Presence	
Species	Life form	Native region	Introduction pathway	Biotic dispersal	Vegetative repr.	Edge	Interior
Acacia dealbata	Tree	Oceania	Gardening	No	Yes	No	No
Acacia melanoxylon	Tree	Oceania	Silviculture	No	Yes	No	No
Acanthus mollis	Geophyte	Med	Gardening	No	Yes	Yes	No
Acer negundo	Tree	Namerica	Gardening	No	No	Yes	No
Agave americana	Shrub	Namerica	Gardening	Yes	Yes	Yes	No
Ailanthus altissima	Tree	Easia	Gardening	No	Yes	No	No
Aloe arborescens	Tree	Safrica	Gardening	No	Yes	Yes	No
Aptenia cordifolia	Shrub	Safrica	Gardening	Yes	Yes	Yes	No
Araujia sericifera	Vine	Samerica	Gardening	No	Yes	Yes	Yes
Arundo donax	Tree	Asia	Agriculture	No	Yes	Yes	No
Canna indica	Geophyte	Samerica	Gardening	Yes	Yes	Yes	No
Carpobrotus edulis	Shrub	Safrica	Gardening	Yes	Yes	Yes	No
Celtis australis	Tree	Med	Agriculture	Yes	No	Yes	Yes
Cortaderia selloana	Geophyte	Samerica	Gardening	No	No	No	No
Cotoneaster lacteus	Tree	Easia	Gardening	Yes	No	Yes	Yes
Cotoneaster pannosus	Tree	Easia	Gardening	Yes	No	Yes	Yes
Cupressus sempervirens	Tree	Med	Gardening	No	No	Yes	No
Datura innoxia	Annual	Samerica	Unintentionally	Yes	No	Yes	No
Eriobotrya japonica	Tree	Easia	Gardening	Yes	No	Yes	Yes
Ficus carica	Tree	Med	Agriculture	Yes	No	Yes	No
Ipomoea indica	Vine	America	Gardening	No	Yes	Yes	No
Ipomoea sagittata	Vine	America	Unintentionally	No	Yes	Yes	No
Iris germanica	Geophyte	Europe	Gardening	No	Yes	Yes	Yes
Juglans regia	Tree	Eurasia	Agriculture	Yes	No	No	Yes
Lampranthus multiradiatus	Shrub	Safrica	Gardening	No	Yes	No	No
Ligustrum japonicum	Tree	Easia	Gardening	Yes	No	Yes	Yes
Lilium candidum	Geophyte	Africasia	Gardening	No	Yes	Yes	No
Lonicera japonica	Vine	Easia	Gardening	Yes	No	Yes	Yes
Mahonia japonica	Tree	Easia	Gardening	Yes	No	Yes	Yes
Myoporum tenuifolium	Tree	Oceania	Gardening	Yes	No	No	Yes

(Cont.) Alien species list including plant species traits and factors related to the introduction history (traits) and their occurrence in the forest edge or interior.

Table A.2

	Traits					Presence	
Species	Life form	Native region	Introduction pathway	Biotic dispersal	Vegetative repr.	Edge	Interior
Opuntia maxima	Tree	America	Gardening	Yes	Yes	Yes	No
Oxalis debilis	Geophyte	Samerica	Unintentionally	No	Yes	Yes	Yes
Parthenocissus inserta	Vine	Namerica	Gardening	Yes	Yes	Yes	No
Paspalum dilatatum	Geophyte	Namerica	Unintentionally	Yes	Yes	No	No
Phoenix canariensis	Tree	Namerica	Gardening	Yes	No	Yes	Yes
Phyllostachys aurea	Tree	Easia	Gardening	No	Yes	Yes	No
Phytolacca americana	Geophyte	Namerica	Gardening	Yes	Yes	Yes	No
Pittosporum tobira	Tree	Easia	Gardening	Yes	No	Yes	Yes
Prunus cerasifera	Tree	Eurasia	Gardening	Yes	No	Yes	Yes
Prunus domestica	Tree	Asia	Agriculture	Yes	No	Yes	Yes
Prunus persica	Tree	Easia	Agriculture	Yes	No	Yes	No
Pyracantha angustifolia	Tree	Easia	Gardening	Yes	No	Yes	Yes
Pyrus malus	Tree	Eurasia	Agriculture	Yes	No	No	Yes
Robinia pseudoacacia	Tree	Namerica	Gardening	No	Yes	Yes	Yes
Senecio angulatus	Vine	Safrica	Gardening	No	Yes	Yes	No
Senecio mikanioides	Vine	Safrica	Gardening	No	No	Yes	No
Senecio pterophorus	Shrub	Safrica	Unintentionally	No	No	Yes	No
Solanum chenopodioides	Annual	Samerica	Unintentionally	Yes	No	Yes	Yes
Solanum nigrum	Annual	Eurasia	Unintentionally	Yes	No	Yes	No
Sorghum halepense	Geophyte	Africasia	Unintentionally	No	Yes	Yes	Yes
Tipuana tipu	Tree	Samerica	Gardening	No	No	No	No
Tradescantia fluminensis	Geophyte	Samerica	Gardening	Yes	Yes	Yes	Yes
Vicia faba	Annual	Asia	Agriculture	Yes	No	No	Yes
Xanthium spinosum	Annual	Samerica	Unintentionally	Yes	No	No	No
Yucca gloriosa	Tree	Namerica	Gardening	Yes	Yes	Yes	No
Zantedeschia aethiopica	Geophyte	Safrica	Gardening	Yes	Yes	Yes	No

Table A.3

Pearson's correlation coefficients between local and landscape variables (1000 m buffer distance) used for modeling alien species richness for edge and interior forest plots.

	Disturbance	Aspect	Distance to roads	Forest use	Urban use	Agriculture use
Edge						
Aspect	-0.075					
Distance to roads	-0.017	0.059				
Forest use	0.059	0.086	-0.352**			
Urban use	-0.135	0.057	0.014	-0.267*		
Agriculture use	-0.013	-0.108	-0.348**	-0.066	-0.347**	
Land use diversity	0	0.055	0.376**	0.064	-0.524***	-0.538***
Interior						
Aspect	0.037					
Distance to roads	-0.096	0.059				
Forest use	0.052	0.086	-0.352**			
Urban use	-0.059	57	0.014	-0.267*		
Agriculture use	-0.168	-108	-0.348**	-0.066	-0.347**	
Land use diversity	0.137	0.055	0.376**	0.064	-0.524***	-0.538***

Significant coefficients: *P>0.05; **P<0.01; ***P<0.001.

RELATIONSHIP BETWEEN ALIEN SPECIES TRAITS AND LANDSCAPE AND LOCAL VARIABLES AND ALIEN SPECIES TRAITS BY FOURTH-CORNER ANALYSIS. ONLY SIGNIFICANT RELATIONS ARE SHOWN.

TABLE A.4

Variable	Trait	Statistic	Value	Probability	
Edge type	Region	Chi2	242233	0.0014	**
Disturbance	Life form	F	216101	0.0392	*
Aspect	Dispersion	F	358302	0.0422	*
Distance to roads	Region	F	244238	0.0059	**
Agriculture use	Life form	F	292575	0.0102	*
Agriculture use	Pathway	F	686969	0.0001	***
Agriculture use	Reproduction	F	115911	0.0003	***
Agriculture use	Dispersion	F	534554	0.0153	*
Agriculture use	Region	F	392457	0.0001	***
Forest use	Pathway	F	441204	0.0034	**
Forest use	Region	F	171281	0.0430	*
Land use diversity	Life form	F	247956	0.0233	*

CAPÍTULO TRES

González-Moreno, P., Pino, J., Cózar, A., García de Lomas, J. & Vilà, M. Association of plant invasion with past landscape characteristics provides evidence of invasion credit.

ASSOCIATION OF PLANT INVASIONS WITH PAST LANDSCAPE CHARACTERISTICS PROVIDES EVIDENCE OF INVASION CREDIT

RESUMEN

Las actividades humanas a escala de paisaje incrementan las invasiones al ser una fuente de propágulos de especies exóticas y ofrecer condiciones favorables para su establecimiento. Debido al desfase temporal en el proceso de invasión, la alteración del paisaje podría mostrar un efecto retardado en el grado de invasión local, configurando el denominado crédito de invasión. Al ser un concepto poco estudiado, nuestro objetivo fue comprobar si existe crédito de invasión en comunidades vegetales costeras afectadas por una intensa alteración del paisaje. Identificamos todas las plantas exóticas en un transecto a lo largo de 809 celdas (250 x 250 m) cubriendo aproximadamente 500 km del sudoeste español. Así mismo, caracterizamos estas especies según su tiempo de residencia y modo de introducción. Analizamos la asociación del grado de invasión (riqueza y abundancia de exóticas) y la presencia y abundancia de las especies exóticas más frecuentes, con el porcentaje de categorías de cubiertas de suelo antrópicas en 1956, 1991 y 2007 como indicadores de alteración del paisaje, controlando por el clima y las condiciones del hábitat. Los mejores modelos que explicaron el grado de invasión consideraron el paisaje de 1956, demostrando la presencia de crédito de invasión. Este patrón se basó principalmente en la asociación entre el grado de invasión y el porcentaje de área agrícola en 1956. Especies con un tiempo de residencia largo y usadas frecuentemente en agricultura en el pasado, también mostraron una asociación con el área agrícola pasada. Este crédito de invasión asociado a las características del paisaje pasado indica una posible infravaloración del grado de invasión en paisajes recientemente alterados. El crédito de invasión está enormemente influido por la idiosincracia del proceso de invasión ya que el conjunto de especies exóticas de una región está constituido por especies con una enorme variabilidad en el tiempo de residencia y con modos de introducción asociados a distintas cubiertas de suelo. Por tanto, aunque el crédito de invasión podría ser un fenómeno frecuente, el resultado exacto de la alteración del paisaje dependerá del tipo de paisaje y de la historia de introducción de especies exóticas. Considerar el crédito de invasión, podría ayudar en la evaluación del riesgo de invasión asociado a la alteración del paisaje.

ABSTRACT

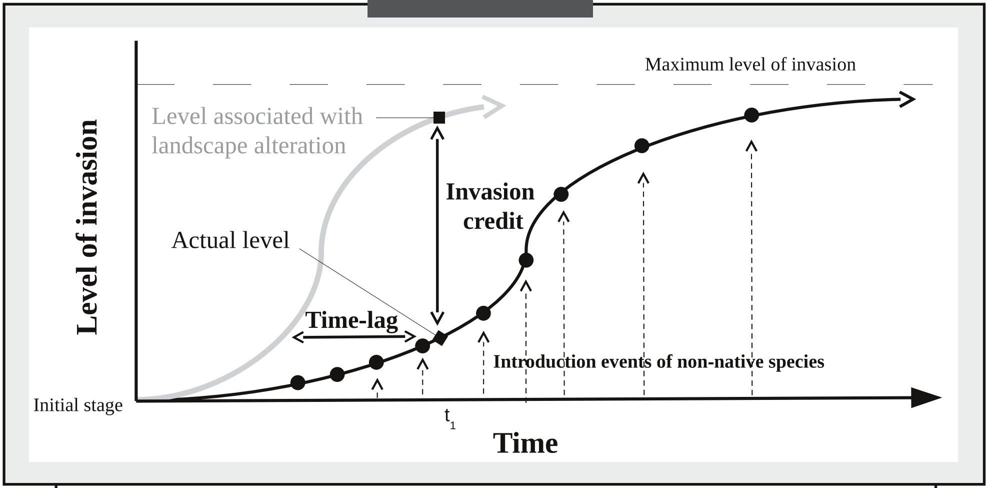
Human activities at the landscape scale increase invasions by acting as a source of non-native propagules and providing favourable conditions for their establishment. Due to time-lags in the invasion process, landscape alteration might show a delayed effect on the local level of invasion, shaping the commonly referred invasion credit. Yet accounting with scarce empirical evidence of this concept, we aimed to detect whether there is an invasion credit in coastal plant communities affected by intense landscape alteration. We identified all non-native plant species in a transect along 809 grid cells (250 x 250 m) covering approximately 500 km of the SW coast of Spain, and characterized these species regarding their residence time and introduction pathway. We analysed the association of the level of invasion (i.e. non-natives richness and abundance) and the presence and abundance of most frequent non-native species with the percentage of human land-cover categories in 1956, 1991 and 2007 as proxies of landscape alteration while controlling for climate and local habitat conditions. Best models explaining the level of plant invasion accounted for human land-cover categories in 1956, revealing a significant invasion credit. This pattern was mainly based on the association between the current invasion and cropland percentage in 1956. Species with large residence time and widely used in agriculture in the past showed also an strong association with past cropland area. We detected an invasion credit associated with past landscape characteristics, suggesting an underestimation of the level of invasion in recently altered landscapes. Invasion credit is highly influenced by the dynamic process of invasions. Non-native species pools are build up by species of contrasting residence times and with pathways related to different land-cover types. Thus, although invasion credit might be a widespread phenomenon, the exact outcome of recent landscape alteration depends on the landscape type as well as on the history of non-native species introductions. Accounting for invasion credit could help to assess the invasion risk related to landscape alteration.

INTRODUCTION

Landscape structure and composition strongly influence the vulnerability of ecosystems to invasions (Capítulo 1; Vilà & Ibáñez, 2011). Specifically, human land-cover areas such as cropland, urban and forest plantations, encompass an increase in propagule pressure and disturbance, favoring the establishment of non-native plant species (Ohlemüller et al., 2006; Gavier-Pizarro et al., 2010). Nevertheless, landscapes are highly dynamic, with changes at different time scales that might determine variations in the level of invasion (DeGasperis & Motzkin, 2007; Ficetola et al., 2010). Indeed, changes in the composition of native communities derived from landscape alteration often become evident only after long time periods (Kuussaari et al., 2009; Jackson & Sax, 2010). Analogously, as there is a time-lag between the different stages in the process of invasion (Kowarik et al., 1995), recent landscape alteration might not have an immediate effect on the current level of plant invasion in natural habitats, but might reflect community changes in the following decades. This delay will be also related to the pool of non-native species that altered areas accumulate through time (e.g. maturity and size of gardening areas). The difference between the current level of invasion in natural habitats and the potential level associated with the actual landscape alteration (e.g. pool of species in altered areas) is called the invasion credit (sensu Vilà & Ibáñez, 2011; Fig. 1). Despite the lack of empirical studies dealing with the invasion credit concept, its application can provide new insights about the dynamics of biological invasions that could be used in invasion risk analyses (Essl et al., 2011; Vilà & Ibáñez, 2011).

Invasion credit is an analogous concept to colonization or immigration credit (Cristofoli et al., 2010; Piqueray et al., 2011), which presumes a time-lag between habitat recovering and native species colonization. However, while it is assumed that colonization credit is "accrued" through the static pool of species present at the beginning of habitat recovering (i.e. the regional pool of native species), the invasion credit could be highly influenced by the identity of non-native species and the history of their invasions (i.e. introduction time and pathway) (Fig. 1). The pool of non-native species arriving to a specific region is highly dynamic due to a complexity of factors such as changes in human practices or commercial routes (Pyšek et al., 2003). This dynamism hampers the identification of invasion credit processes at the community level, since the

FIGURE 1



Conceptual framework of invasion credit. The gray line shows the expected level of invasion based on the landscape alteration of the area starting from a an initial stage of zero alteration. The black line indicates the actual level of invasion in the same area. After landscape alteration, each introduction event will increase the actual level of invasion. For a certain time (t_1) the difference in vertical between gray and black lines indicates the amount of invasion credit and the difference in horizontal, the time-lag.

composition of non-native species at a given time could be related to different past changes in the landscape. We would expect, for instance, an association between agricultural species and past cropland area, while gardening species would be related to past urban area (Capítulo 2). Therefore, we expect that exploring the association patterns with landscape alteration for most frequent non-native species could reveal patterns in the invasion dynamics not evident at the community level.

The detection of invasion credit might depend on the selected metrics to assess the invasion level (i.e. presence, richness and abundance). We expect low evidence of invasion credit for non-native species presence after landscape alteration as there is high probability that at least one species might become established. Furthermore, we hypothesize a higher signal of invasion credit for non-native species abundance than for richness due to time-lags between introduction and spread (Kowarik et al., 1995; Pyšek et al., 2003; Crooks, 2005; Gassó et al., 2009). Thus, older landscape alteration would imply relatively higher abundance of non-native species irrespectively of the potential non-native species richness.

In this study, we used an extensive field survey of non-native plants along the Southwestern coast of Spain to test the evidence of invasion credit in plant communities with different histories of landscape alteration. In the last 50 years, Spanish coastal areas have been exposed to an intense urbanization process linked to a substantial increase of plant invasions (Capítulo 1; Sobrino et al., 2009). A multi-model inference approach was used to unravel the effects of landscape alteration from 1956 to 2007 on the current level of plant invasion, and in the distribution of most frequent non-native plant species. Finally, we discuss the results providing a theoretical framework baseline about the invasion credit concept and its implications.

METHODS

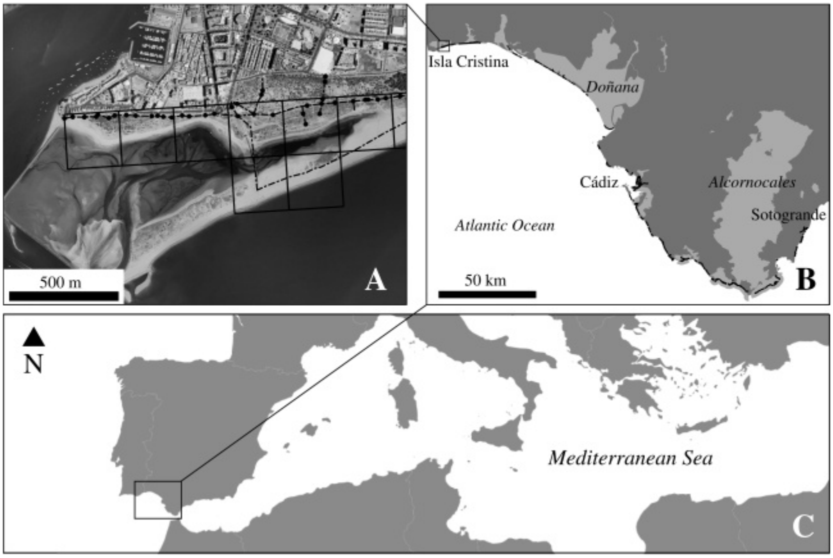
Study area

The study was conducted on the Southwestern coast of Spain covering ~500 km of the Atlantic coastline including Isla Cristina (7º19'50"W,37º11'40"N) on the West to Sotogrande (5º15'10"W,36º18'43"N) on the East (Fig. 2). The climate of the study region is typically Mediterranean, with warm and dry summers and mild winters. The coast is characterized by large sandy areas with sketchy rocky areas, particularly towards the East. The coastline includes discontinued by several large wetland systems (Guadalquivir and Odiel marshlands), urban areas ports and industries. The adjacent landscape has undergone an intense transformation process during the last century. Most urban expansion has occurred in the last 20 years, with the development of abundant residential areas. *Eucalyptus* and *Pinus pinea* plantations are also relatively frequent in the West as the result of intense forestry programs between 1940 and 1970.

Vegetation data

In spring 2010 and 2011 the level of invasion was quantified by sampling the coastal vegetation along a transect parallel to the coastline at an approximate distance of 50 m from the shoreline. Due to accessibility problems we sampled around 326 km of these 500 km. All non-native plants were identified walking along the transect within a strip of 25-50 m wide at each side. Sampling effort

FIGURE 2



A) Sampling protocol with indication of the transect (dashed line), the presence of non-native species (black dots) and 250 x 250 m cells (squares). B) Study area on the Southwestern coast of Spain. Black dots indicate cells used in the analyses (at least with 250 m of transect). Grey areas delimit protected areas. C) Location of the study area in the Western Mediterranean Basin.

was proportional to the detectability of non-native plants within the strip, which could depend on the slope and vegetation cover. For each patch of non-native species, we recorded its locality. As indicator of non-native plant abundance, the total area occupied by each non-native species was quantified for a subset of the transect. The total area occupied by each species was estimated by the polygon area (m^2) delimited by the external border of all neighbouring individuals within the transect area. For both presence and abundance, we only took into account neophyte species (i.e. introduced after 1492) according to Valdés et al., (1987).

The transect was divided into pieces using 250 m x 250 m grids cells following the UTM system to standardize the data (Fig. 2). The transect length within each cell was variable due to the sinuosity of the coastline. We tested different minimum transect length criteria to remove those cells with low sampling effort, resulting 250 m the best compromise between total cells sampled and the number of cells invaded. Thus, we selected 809 cells with a minimum transect length of 250 m (mean 403 m; maximum 1180m) (All dataset). In each cell, we calculated the presence of any non-native species and the total non-native species richness. Information about species' total area was available for 647 cells (Abundance dataset). Thus, as an indicator of non-native species abundance by cell, we calculated the sum of the total area of all non-natives (hereafter accumulated abundance).

We selected most frequent species, present in more than 30 cells, for a detailed analysis. From this list of species, we eliminated *Conyza bonariensis* (L.) Cronquist, annual species with maximum growth in summer, as it could have been underrepresented in our spring sampling. For the final list of species, we characterized the pathway and time of introduction as well as the continent of origin (Table 1). Finally, we calculated their presence-absence and total area (hereafter species abundance) in each cell considering the datasets above.

Detection of invasion credit

Evidence of invasion credit was estimated from the relation between the current level of invasion and temporal data of variables explaining invasion (Essl et al., 2011). Following this approach, invasion credit related to landscape alteration is evident if there is stronger association of the current level of invasion with past landscape characteristics than with current ones. Although this method does not quantify the exact magnitude of the invasion credit (i.e. the actual difference between the current level of invasion and its potential due to recent landscape alteration; Fig. 1), it indicates whether the invasion credit is significant, and highlights the appropriate temporal scale of environmental information needed to perform biological invasion projections (Ficetola et al., 2010). Following this approach we studied the association between the overall level of plant invasion and invasion of most frequent non-natives considering landscape alteration variables for 1956, 1991 and 2007, while controlling for habitat type, management practices and climate conditions.

Explanatory variables

Human landscape alteration in each cell was calculated using the Land-cover and vegetation maps of Andalusia of 1956, 1991 and 2007 based on aerial ortophotos and Landsat images (Moreira et al., 2010). The interpretation scale was 1:25,000 for 1956 and 2007 and 1:50,000 for 1991. Within each cell (i.e. zero distance) we calculated the percentage of area occupied by each land-cover type in each year and in a buffer of 250, 500, 1000, 2000, 3000, 4000 and 5000 m from the cell border (i.e. spatial extent). We considered four land-cover classes related to landscape alteration by human activities: cropland, low-density urban (i.e. mixed garden and buildings areas such as single-family housing areas and tourism resorts), high-density urban (mainly built-up areas) and Eucalyptus spp. plantations (hereafter plantations).

Table 1

List of most frequent non-native species with indication of the number of cells where it was found (n = 809) and its abundance (n = 647). Mean abundance ± standard error in the invaded cells for each species is calculated considering the total area occupied in the sampled transect.

					All data	Abundance data	
Species	Pathway	Origin	Introduction	Reference	Cells	Cells	Abundance
Carpobrotus edulis	Gardening Restoration	South Africa	1900 (Study area)	Sanz-Elorza et al. (2004)	113	80	546.49 ±168.71
Opuntia dillenii	Agriculture Gardening	America	1874 (Study area)	Colmeiro (1874)	82	49	167.74 ±45.04
Agave spp.	Agriculture Gardening	America	1576 (Spain)	Quer (1762); Ramón-Laca (1999); Guillot et al. (2009)	61	57	107.61 ±27.90
Arctotheca calendula	Gardening	South Africa	1925 (Study area)	Sanz-Elorza et al. (2004)	59	25	124.22 ±53.92
Eucalyptus spp.	Forestry	Australia	Mid 19th c. (Spain)	Sanz-Elorza et al. (2004)	40	31	138.60 ±34.11
Acacia saligna	Gardening	Australia	19th c. (Spain)	Sanz-Elorza et al. (2004)	39	39	182.94 ±59.94
Solanum sodomeum	Unintentionally	South Africa	1939 (Study area)	Coutinho (1939)	38	26	19.47 ±8.52
Yucca aloifolia	Agriculture Gardening	America	1803 (Spain)	Cavanilles (1803)	29	25	31.47 ±9.19

To control for current vegetation types within the cell, we quantified the percentage of area occupied in 2007 by the two main habitat types in the sampling area: wetland and dunes land-cover as we expected these two variables to be relatively constant across years, and to reflect the local ecological conditions within the cells. Similarly, to control for differences in the management of non-native species across space, we calculated the percentage of protected areas within each cell and at the seven buffer distances. Finally, climate data were obtained from the UNEX Spatial Data Infrastructure (http://ide.unex.es), which provides average monthly precipitation, minimum and maximum temperature at 1-km grid across Spain for the period 1971-2007. From this dataset we extracted 19 bioclimatic variables for each cell using the R-package DISMO.

VARIABLES CONSIDERED IN THE ANALYSES. FOR LANDSCAPE ALTERATION, PROTECTION STATUS AND HABITAT VARIABLES THE FINAL BUFFER DISTANCE TO CELL BORDER USED IS INDICATED FOR ALL THE DATASET (PRESENCE AND RICHNESS MODELS) AND THE SUBSET WITH ABUNDANCE INFORMATION (ABUNDANCE MODELS).

TABLE 2

Variable	Buffer selected	
	All data	Abundance data
Landscape alteration		
% High density urban	500 m	2000 m
% Low density urban	500 m	2000 m
% Cropland	500 m	2000 m
% Forest plantations	250 m	Within cell
Protection status		
% Protected area	Within cell	Within cell
Habitat		
% Dunes	Within cell	Within cell
% Wetlands	Within cell	Within cell
Climate		
Min Temperature of Coldest Month		
Annual Precipitation		
Precipitation of Warmest Quarter		

Selection of independent variables

Prior to modelling the level of invasion, for each landscape alteration variable and percentage of protected area, we selected the spatial extent that was most influential for non-native metrics (Table 2). The selection was based on the Pearson's correlation coefficient between each variable and non-native species richness and accumulated abundance at each buffer distance to the cell border (Appendix A – Fig A1). For cropland and urban land-cover variables, we selected 500 m for non-natives richness and 2000 m for accumulated non-native cover. For plantations, we selected 250 m from the limit of the cell to explain non-native richness and within the cell to explain accumulated cover. For protected area, we kept the value within the cell for both metrics.

We checked the collinearity among the selection of land-cover and climatic predictors by pair-wise Pearson's correlation tests (Appendix A–Table A1-2). First, we selected variables with a pair-wise correlation lower than 0.7, and then selected those with best ecological meaning and explanatory power on the metrics of invasion (based on Pearson's correlation). All variables were selected for land-cover and protected area variables, while minimum temperature of the coldest month (i.e. minimum temperature), annual precipitation and summer precipitation were selected among the climate variables (Table 2).

Statistical analyses

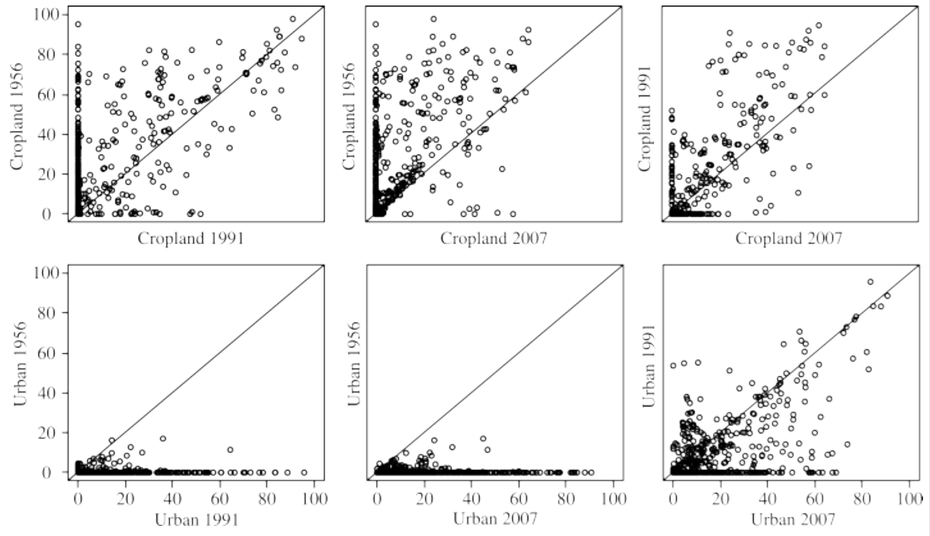
Generalized Linear Models (GLMs) were used to identify best models explaining the overall level of plant invasion (i.e. non-natives presence, richness and accumulated abundance) and invasion of most frequent non-natives (presence and abundance) considering landscape alteration variables for each of the following years: 1956, 1991 and 2007. Transect length, climate variables, percentage of protected area, and percentage of wetland and dunes habitats were included in the models as covariates to control their effect. Models were compared using the Akaike's Information Criterion corrected for a large number of predictors (AICc) (Burnham & Anderson, 2002). Lower AICc indicates better fit of the model. First, we selected the best models for each invasion metric including only the covariates mentioned above (local model). Second, we implemented separately the models with landscape alteration variables for each year including as fixed the variables selected in the previous local model (landscape alteration model). For this second type of models, we implemented four variants: all landscape alteration variables, only-cropland, only-plantations and only-urban land-covers. Third, we compared the goodness of fit of the best landscape alteration models for each year. Better fit of models considering landscape alteration variables of 1956 or 1991 than models of 2007 indicates that the level of invasion have higher association with the past landscape than the current landscape, suggesting a significant invasion credit (Essl et al., 2011; Lira et al., 2012).

We modeled the error terms of the GLMs explaining non-natives richness using a negative binomial distribution. This distribution is indicated for count data when over-dispersion occurs. For non-native accumulated abundance and most frequent species' abundance we used a log-normal error distribution while for non-natives presence a binomial distribution. All predictors were standardized and centered to facilitate interpretation of model coefficients. Preliminary analyses using the Moran's Index, indicated no relevant spatial autocorrelation in the models' residuals ($I<0.3$) (Appendix A-Fig. A2). Furthermore, adopting any method to reduce autocorrelation (e.g. Dormann et al., 2007) could bias our results as most of them consider adding covariates that are very likely to correlate with the land-cover variables of interest (e.g. spatial autocovariate; Hawkins, 2012). Besides, other methods add covariates that are calculated differently for each model, thus making impossible to compare among models for each year (e.g. eigenvector spatial filtering). Additionally, the main effect of spatial autocorrelation is on the standard errors of the model's coefficients (Dormann et al., 2007; Hawkins, 2012), thus not altering the main results of the study. Therefore, we proceeded without implementing any strategy to reduce spatial autocorrelation.

RESULTS

Most sampled cells showed an increase in urban area and a reduction of cropland from 1956 to 2007 (Fig. 3). This trend was less relevant from 1991 to 2007. From 1956 to 2007 and considering all sampled cells, there was an average reduction of 8.7% in cropland area, a 0.24% increase in plantations area and an increment of 3% and 10.7% for high-density urban and low-density urban area, respectively.

FIGURE 3



SCATTER PLOTS FOR CROPLAND AND LOW-DENSITY URBAN LAND-COVER PERCENTAGES RELATIONSHIPS IN 809 COASTAL CELLS (250 X 250 m) FOR 1956, 1991 AND 2007.

In total we found 60 non-native species. At least one non-native species was identified in 45 % of the 809 sampled cells. When including empty cells, non-native richness per cell was 0.93 ± 0.05 (mean ± standard error), with 10 species as maximum. Non-natives accumulated abundance in the subset of 647 cells was on average 2100 ± 564.68 m2. The most frequent and abundant species were *Carpobrotus edulis* L., *Opuntia dilenii* Ker-Gawl. Haw., *Agave* spp., *Arctotheca calendula* L., and *Eucalyptus* spp. (Table 1).

Present and past human influence on the level of plant invasion

Using all landscape alteration variables (i.e. percentage area of cropland, urban and plantations), the best model explaining non-natives richness included land-cover variables of 1956 (Table 3). In contrast, the best model explaining non-natives presence considered land-cover variables of 2007. For accumulated abundance all models showed similar results. Considering the models separately for each land-cover type across the different invasion metrics, only-cropland models were generally better for 1956 than the other years, while only-urban models were better for 2007 (Table 3). The only exception was found for richness models considering all the dataset, which showed better fit in only-urban models for 1956 (Table 3).

Table 3

Comparison of the goodness of fit (AICc values) of the models explaining current non-native species presence, richness and accumulated abundance considering human landscape alteration variables for 1956, 1991 and 2007 and two separate datasets. We present separately four models variants depending on the landscape alteration variables used: only-cropland, only-plantations, only-urban and all together. Lower AICc values indicate better goodness of fit. Bold values indicate models within 4 AICC (similar support) for each model type, non-native index and dataset across years.

		1956	1991	2007		1956	1991	2007
All dataset		Presence			Abundance dataset	Accumulated abundance		
	All	1028.56	1035.45	**1023.72**		**3431.78**	**3431.35**	**3433.71**
	Cropland	**1039.81**	1047.13	1047.13		**3449.23**	3462.32	3462.32
	Plantation	**1047.13**	**1044.04**	**1047.13**		3462.32	**3461.1**	**3357.87**
	Urban	1035.98	1038.8	**1023.72**		3445.46	3452.62	**3435.32**
		Richness				Richness		
	All	**2056.39**	2067.66	2068.86		**1492.71**	1499.4	1499.69
	Cropland	**2074.26**	**2076.57**	**2076.57**		**1507.07**	1521.93	1521.93
	Plantation	**2075.78**	**2076.5**	**2075.77**		**1520.13**	**1521.93**	**1520.52**
	Urban	**2059.97**	2067.66	2068.86		1510.57	1507.05	**1499.69**

Present and past human influence on the most frequent non-native species

Presence and abundance of most frequent species showed a variable association with present and past landscape variables. Presence of *Opuntia*, *Agave* and *Yucca aloifolia* L. was better explained by models considering all landscape alteration variables for 1956 and specifically taking into account the percentage of cropland area (Table 4). This pattern was slightly different for their abundance (Table 4). *Opuntia* and *Yucca* abundance showed also better fit with the 1956 model but taking into account both plantations and cropland percentages. In contrast, *Agave*

Comparison of goodness of fit (AICc values) of the models explaining the presence and abundance of most frequent non-native species considering human landscape alteration for 1956, 1991 and 2007. We present separately four models variants depending on the landscape alteration variables used: only-cropland, only-plantations, only-urban and all together. Lower AICc values indicate better fit of the models. Bold values indicate models within 4 AICc (similar support) for each model type, species and non-native index across years. See table 1 for full name of species.

Table 4

		PRESENCE			ABUNDANCE		
		1956	1991	2007	1956	1991	2007
Carpobr.	All	596.59	**578.53**	587.41	**2813.44**	2821.06	2832.99
	Cropland	**604**	**605.87**	**605.5**	**2835.21**	2876.42	2876.85
	Plantation	605.87	**596.02**	605.87	**2871.07**	**2869.22**	2876.12
	Urban	599.23	**588.51**	**587.41**	2861.28	2848	**2838.97**
Opuntia	All	**433.1**	444.31	444.31	**2529.13**	2545.16	2543.22
	Cropland	**436.53**	444.31	444.31	**2546.91**	**2548.27**	**2548.27**
	Plantation	**441.45**	**444.31**	**444.31**	**2535.73**	2548.27	2546.83
	Urban	**442.36**	**444.31**	**444.31**	**2542.07**	**2545.16**	**2545.6**
Agave	All	**405.44**	413.94	411.75	**2554.44**	2566.01	**2554.37**
	Cropland	**408.24**	413.94	413.94	**2564.12**	**2566.5**	**2566.5**
	Plantation	**411.61**	**413.94**	**413.94**	**2555.34**	**2566.5**	**2564.95**
	Urban	**412.71**	**413.94**	**411.75**	2566.5	2566.04	**2554.37**
Arctoth.	All	**362.45**	**366.11**	368.78	**2210.7**	**2220.87**	**2225.3**
	Cropland	**369.67**	**367.52**	**369.31**	**2225.3**	**2225.3**	**2225.3**
	Plantation	**369.67**	**369.67**	**369.42**	**2225.3**	**2225.3**	**2225.3**
	Urban	**362.45**	367.63	369.67	**2210.7**	**2220.87**	**2225.3**
Eucalypt.	All	303.62	307.3	**290.96**	2435.69	2422.22	**2402.37**
	Cropland	**308.92**	**308.44**	**306.98**	**2441.97**	**2441.97**	**2441.1**
	Plantation	307.18	307.89	**296.22**	2441.97	2433.95	**2413.69**
	Urban	**305.6**	**308.29**	**304.95**	2435.69	2429.47	**2424.96**
Acacia	All	265.56	255.84	**247.93**	2443.45	**2434.13**	2408.53
	Cropland	**268.99**	**269.76**	**269.76**	2449.94	2445.32	**2442.01**
	Plantation	**269.76**	**269.76**	**269.76**	**2444.33**	2449.94	**2445.02**
	Urban	266.64	257.54	**247.93**	2447.98	2434.13	**2413.39**
Solanum	All	**300.69**	**297.08**	**297.68**	**1823.43**	**1820.41**	**1821.24**
	Cropland	**300.69**	**300.69**	**300.69**	**1824.42**	**1824.18**	**1823.98**
	Plantation	**300.69**	**299.27**	**300.69**	**1824.42**	**1824.42**	**1824.42**
	Urban	**300.69**	**298.39**	**297.68**	**1823.43**	**1821.7**	**1821.24**
Yucca	All	**220.7**	226.32	231.87	**1932.78**	1952.89	1954.37
	Cropland	**227.35**	237.57	237.57	**1956.98**	1977.61	1981.62
	Plantation	**237.53**	**236.04**	**237.57**	**1957.08**	1985.84	1976.6
	Urban	**232.97**	**230.06**	**232.24**	1985.84	**1968.48**	1973.25

abundance was similarly explained by the 1956 and 2007 models. *Carpobrotus* and *Arctotheca* presence was also mainly explained by past landscape alteration variables. The former was mainly associated with plantations in 1991 and the latter with urban areas in 1956. Regarding their abundance, we did not find any difference across dates for *Arctotheca*, while for *Carpobrotus*, the best model was obtained with cropland area in 1956. *Eucalyptus* and *Acacia saligna* (Labill.) H. Wendl. were more strongly associated with landscape alteration variables in 2007 (Table 4). Specifically, the higher differences were found for plantations in Eucalyptus and urban land-cover percentages for *Acacia*. Finally, *Solanum sodomeum* L. showed similar association with human land-cover categories across the three dates analyzed.

DISCUSSION

We generally found higher association of current plant invasions with past landscape characteristics than with current ones, indicating a significant invasion credit in coastal habitats. This pattern varied depending on the metric used to quantify the level of invasion. Furthermore, this association was highly dependent on the landscape dynamics (Ficetola et al., 2010) and on the particularities of the introduction event and time since introduction (Kowarik et al., 1995).

The influence of present and past landscape alteration on invaded communities

Since the level of plant invasion was explained better using landscape characteristics in 1956 than 1991 or 2007, we can expect a relatively higher level of invasion in past altered areas than in those with recent alteration. It is in the latter areas where we expect an invasion credit as non-native species are still spreading thanks to relatively recent disturbance events and propagule pressure. Some studies have been also found invasion credit at wider spatial contexts and accounting for different drivers (Essl et al., 2011, 2012; Vilà & Ibáñez, 2011). Essl et al., (2011) showed that the number of non-native species per country in Europe is more closely related to indicators of socioeconomic activity from the past century than to those from last decade. Similarly, other studies have reported invasion to be associated with land-use legacies at the local scale. For instance, secondary forests resulting from crop abandonment generally are more invaded than undisturbed forests (Aragón & Morales, 2003; Vilà et al., 2003). These patterns suggest that plant invasions are closely linked to the temporal dynamics of human activities both at the local and at the landscape scales.

The type and intensity of human activities at landscape scale often changes across time, having probably delayed consequences on invasion patterns (Fig. 1). In Southwestern Spain, the transformation of coastal areas from cropland to urban land-cover decades ago matches with the current level of plant invasion. Indeed, areas with high agricultural activity in 1956 harbour relatively higher level of invasion than recently altered areas. This pattern is probably the result of the traditional use of non-native plants in agriculture (e.g. green fences and fibre providers) and the accidental introduction and spread of weedy species. In contrast, urban areas most likely became a source of non-natives around 90s-00s, when gardens started to be extensively associated with new urbanizations and included a large number of ornamental non-native species. Considering this trend, we expect an increase of the level of invasion in the following decades associated to this urbanization process (Capítulo 2).

The patterns found for invasion credit were not homogeneous across the metrics used to estimate the level of invasion. Considering full models for each year, only non-native species richness showed invasion credit in relation to 1956. In contrast, non-native species presence and accumulated abundance showed no clear evidence of invasion credit. No evidence of invasion credit for presence is likely due to the high probability that at least one species become established after landscape alteration. However, we hypothesized higher signal of invasion credit for species abundance than for richness as non-native species commonly show a delay between establishment and spread (Kowarik et al., 1995; Gassó et al., 2009). Here, we suggest two non-exclusive possible causes for this finding. On one hand, the delay between the scenarios studied, on a scale of decades, might have not been wide enough to drive a steady change in the abundance. On the other hand, the abundance of non-native species might be particularly affected by factors not taken into account in the models (e.g. local or short-term disturbance such as trampling or mechanized cleaning), which would result in significant fluctuations in the abundance at small time scales. In contrast, the richness would be mainly related to the propagule pressure at landscape scale, included in the models in the form of land-cover area variables.

The idiosyncratic nature of invasion credit

In this study, the observed invasion credit patterns were related to the biological attributes and the characteristics of the introduction of the most frequent species. We found three types of non-native species based on their relation with landscape alteration and continent of origin: 1) non-native species of American origin, with long residence time (since 16th-19th century), and showing association with agricultural areas of 1956 (Opuntia, *Agave* and *Yucca*), 2) non-native species of Australian origin, with medium residence time (since 19th century) and related to recent plantations or urban areas (*Eucalyptus* and *Acacia*), and 3) recent non-native species (since early 20th century) of South African origin and showing association with past altered areas (*Carpobrotus* and *Arctotheca*). These groups of non-native species emerge from different trends in the history of international trade in Spain as well as in the dynamics of human-driven landscape alteration. The former is evident in the species origin. Among most frequent species, we found that older species had an American origin while recent species were Australian or South African. This pattern is related to the intensive trade between Spain and Latin America since the XVI century, while the increment in global trade has occurred in the last centuries. This relation between introduction time and continent of origin has been also found in other studies. For example, Pyšek et al., (2003) identified a gradient in introduction time for non-native plants establishing in Czech Republic from oldest introductions corresponding to European and Asian species to recent introductions originated in Australia and Africa. Furthermore, these groups of non-native species also mirror the different events in the history of human-driven landscape alteration. The first group of species was widely used in agriculture in the last century and consequently have their maximum establishment probability in areas with high cropland area in 1956. These species are likely shaping the invasion credit at community level associated with past cropland area (see previous section). The second and third groups are characterized by species associated with other uses than agriculture such as gardening (e.g. *Arctotheca* and *Acacia*), forestry (e.g. *Eucalyptus*) or dune fixation (e.g. *Acacia* and *Carpobrotus*). Most of these species are associated with more recent landscape alteration, which likely explains the lack of invasion credit associated with past urban area at community level. These results stress the importance of choosing the adequate propagule pressure proxies and time-lags to identify invasion credit at community level (Ficetola et al., 2010).

As we have shown, the high variability in the characteristics of the introduction event and time since introduction of particular non-native species might hide invasion credit patterns at community level (Fig. 1). This inherent characteristic of invasion credit is not considered in the more general immigration credit concept, as the latter is usually associated with a rather constant regional pool of native species with potential to arrive (Cristofoli et al., 2010). In contrast, the pool of non-native species is highly dynamic with new non-native species constantly arriving to any given area due to changes in human practices (Fig. 1). Species with high residence time will have high probability of local establishment (early introductions events in Fig. 1). Therefore, the actual invasion credit of an area would be defined by both the time-lag of old invaders and the arrival of new comers. As a result, it is very complex to predict the identity of the non-native species that will arrive in the future and their link with landscape alteration. For instance, the presence of *Arctotheca*, an ornamental species widely used in gardening, is associated with the amount of urban land-cover area in 1956, indicating a significant invasion credit. Nevertheless, this species could be replaced by others in gardening. Consequently, the urban area will not further act as a source of propagules of the species. In brief, we found a consistent association between past landscape characteristics and plant invasions at community level, but the particular changes in the use patterns of each non-species species put insurmountable problems to identify invasion credit at species level.

Understanding invasion credit and its consequences

Temporal dynamics in biological invasions is increasingly considered a key aspect in biological invasions (DeGasperis & Motzkin, 2007; Ficetola et al., 2010; Vilà & Ibáñez, 2011). Nevertheless, among the different approaches to study the temporal component of invasion, the invasion credit concept has rarely being tested. Invasion credit is in some aspects a parallel concept to the well known time-lag for recently established non-native species (Kowarik et al., 1995; Gassó et al., 2009). We see two main differential aspects. First, invasion credit is always defined with a baseline scenario related to certain human alteration at any spatial scale, while time-lag is generally based on the first introduction event. Second, invasion credit is applied to invasion metrics at community level (e.g. non-native species richness) while time-lag is especially designed for single species. Based on these advantages we encourage the applicability of the invasion credit concept to other taxa and systems in order to understand in a broader sense the temporal dynamics of invasion at community level.

In the present work, we show how invasion credit can be a useful approach to highlight the intrinsic temporal component of biological invasions. We identified invasion credit associated with human landscape alteration originated 50 years ago. This wide time-lag might result in a potential mismatch between human perceptions and the actual expansion rate of invasive species. These differences could ultimately derive in undesirable management strategies such as the protection of old invasive species threatened outside their native range (Clavero, 2014). Furthermore, not accounting for the existence of invasion credit and the dynamic character of invasions (e.g. changing pool of arriving species) could lead to the underestimation of the invasion risk associated with landscape alteration (Crooks, 2005). Thus, we advocate for the systematic use of past landscape characteristics in the modeling of biological invasions.

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APPENDIX A

TABLE A.1

PEARSON'S CORRELATION TABLE AMONG ALL PREDICTOR VARIABLES USED TO MODEL NON-NATIVE PLANT SPECIES RICHNESS ACROSS 809 CELLS (250 X 250 M) ALONG THE SW SPANISH COAST. BOLD VALUES INDICATE CORRELATIONS ABOVE 0.6 (R^2=0.36).

ALL DATA	Transect length	Non-natives richness	Minimum temperature	Annual precipitation	Summer precipitation	%Plantation 1956	%Cropland 1956	%High-density urban 1956	%Low-density urban 1956	%Plantation 1991	%Cropland 1991	%High-density urban 1991	%Low-density urban 1991	%Dunes 2007	%Wetland 2007	%Plantation 2007	%Cropland 2007	%High-density urban 2007	%Low-density urban 2007
Transect length	0.18																		
Non-natives richness	0.08	-0.20																	
Minimum temperature	0.10	-0.13	0.46																
Annual precipitation	-0.13	0.10	-0.43	0.04															
Summer precipitation	0.05	0.15	0.02	-0.05	-0.05														
%Plantation 1956	0.07	0.16	-0.02	-0.06	-0.05	0.14													
%Cropland 1956	0.03	-0.01	0.00	-0.10	-0.06	-0.02	0.19												
%High-density urban 1956	-0.01	0.17	0.03	0.19	0.11	-0.02	0.01	-0.02											
%Low-density urban 1956	0.07	0.04	0.04	0.03	-0.05	-0.01	-0.06	-0.02	-0.02										
%Plantation 1991	0.06	0.09	-0.15	-0.05	-0.09	0.01	**0.70**	0.00	-0.04	-0.05									
%Cropland 1991	0.00	0.09	-0.14	-0.15	0.08	-0.02	0.30	0.48	-0.04	-0.03	0.09								
%High-density urban 1991	0.01	0.17	0.08	-0.09	-0.02	0.21	0.21	0.13	0.11	0.03	-0.09	0.06							
%Low-density urban 1991	0.04	0.08	-0.33	-0.04	0.24	0.00	-0.05	-0.04	-0.02	-0.06	0.00	0.01	-0.03						
%Dunes 2007	-0.14	-0.10	0.10	-0.25	-0.03	-0.04	-0.18	-0.05	-0.06	-0.04	-0.09	-0.07	-0.09	-0.22					
%Wetland 2007	0.03	0.07	0.06	0.09	0.02	0.33	0.02	-0.03	-0.01	0.29	-0.07	-0.02	0.08	-0.05	-0.06				
%Plantation 2007	0.09	0.05	-0.08	0.03	-0.10	0.00	**0.64**	-0.01	-0.04	-0.04	**0.82**	0.01	-0.06	-0.02	-0.12	-0.04			
%Cropland 2007	0.06	0.07	-0.04	-0.18	0.01	-0.03	0.21	0.52	-0.04	-0.03	0.09	**0.78**	0.23	-0.03	-0.04	-0.04	-0.02		
%High-density urban 2007	0.06	0.19	-0.03	-0.08	-0.10	0.25	0.53	0.00	0.09	0.02	0.34	0.10	**0.68**	-0.02	-0.15	0.05	0.21	0.13	
%Low-density urban 2007	-0.08	-0.20	0.32	0.01	-0.12	-0.11	-0.41	-0.18	-0.06	0.05	-0.45	-0.24	-0.31	-0.20	0.28	-0.03	-0.40	-0.30	-0.49

TABLE A.2

PEARSON'S CORRELATION TABLE AMONG ALL PREDICTOR VARIABLES USED TO MODEL NON-NATIVE PLANT SPECIES ABUNDANCE ACROSS 647 CELLS (250 x 250 m) ALONG THE SW SPANISH COAST. BOLD VALUES INDICATE CORRELATIONS ABOVE 0.6 (R^2=0.36)

ABUNDANCE DATA	Transect length	Non-natives abundance	Minimum temperature	Annual precipitation	Summer precipitation	%Plantation 1956	%Cropland 1956	%High-density urban 1956	%Low-density urban 1956	%Plantation 1991	%Cropland 1991	%High-density urban 1991	%Low-density urban 1991	%Dunes 2007	%Wetland 2007	%Plantation 2007	%Cropland 2007	%High-density urban 2007	%Low-density urban 2007
Transect length	0.03																		
Non-natives abundance	-0.06	-0.07																	
Minimum temperature	0.03	-0.09	0.27																
Annual precipitation	-0.07	0.04	-0.17	0.32															
Summer precipitation	0.06	0.06	-0.01	-0.06	-0.01														
%Plantation 1956	0.13	0.03	-0.33	-0.21	-0.02	0.14													
%Cropland 1956	0.08	0.01	0.02	-0.27	0.01	-0.03	0.08												
%High-density urban 1956	-0.05	0.04	0.09	-0.08	0.01	0.04	0.03	0.44											
%Low-density urban 1956	0.05	0.00	0.00	0.02	-0.03	-0.01	-0.07	-0.05	-0.02										
%Plantation 1991	0.09	0.00	-0.42	-0.21	-0.14	0.00	**0.84**	0.03	-0.02	-0.05									
%Cropland 1991	0.06	0.03	-0.13	-0.25	0.01	-0.03	0.29	**0.81**	0.54	-0.04	0.19								
%High-density urban 1991	0.08	0.11	-0.09	-0.19	0.09	0.27	0.17	0.17	0.23	0.03	-0.14	0.13							
%Low-density urban 1991	0.13	0.04	-0.22	0.11	0.17	0.02	0.16	-0.03	0.14	-0.05	0.11	0.06	0.10						
%Dunes 2007	-0.16	-0.02	0.05	-0.33	0.04	-0.03	-0.22	0.00	-0.03	-0.03	-0.17	-0.04	-0.04	-0.19					
%Wetland 2007	0.06	0.05	0.03	-0.02	-0.01	0.59	0.06	-0.04	0.02	0.15	-0.05	-0.04	0.18	-0.03	-0.04				
%Plantation 2007	0.08	-0.01	-0.37	-0.14	-0.11	0.01	**0.80**	0.02	-0.03	-0.05	**0.96**	0.15	-0.16	0.11	-0.19	-0.04			
%Cropland 2007	0.10	0.07	-0.03	-0.30	-0.02	-0.03	0.23	**0.61**	0.16	-0.05	0.16	**0.65**	0.32	-0.06	0.02	-0.05	0.12		
%High-density urban 2007	0.13	0.10	-0.45	-0.22	0.14	0.21	0.51	0.13	0.25	0.01	0.29	0.25	**0.77**	0.23	-0.16	0.13	0.19	0.20	
%Low-density urban 2007	-0.05	-0.02	0.47	0.01	-0.11	-0.07	-0.50	-0.17	-0.12	0.05	-0.53	-0.24	-0.33	-0.25	0.32	-0.02	-0.50	-0.29	-0.55

Standardized coefficients of best models explaining current non-native species presence, richness and accumulated abundance considering all human landscape alteration variables for 1956, 1991 and 2007 (% cropland, low density urban, high density urban and forest plantations) and controlling for habitat type (% wetland and dunes), management practices (% protected area), climatic conditions (Minimum temperature of coldest month, annual precipitation and precipitation of warmest quarter) and transect length. Variables not shown were not included in the model selection process. Best models are shown for the two datasets used in the analyses, all (n=809) and abundance datasets (n=647).

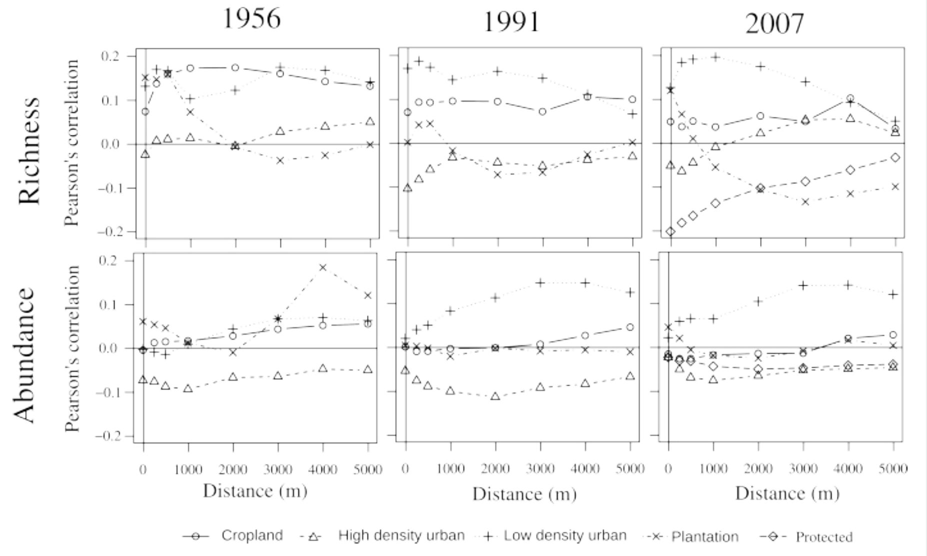
Table A.3

ALL DATASET	Richness			Presence		
	1956	1991	2007	1956	1991	2007
Intercept	-0.92***	-0.92***	-0.91***	-1.41***	-1.38***	-1.40***
% Cropland	0.13*			0.27**	0.15	
% Low density urban	0.18***	0.16**	0.17**	0.3**	0.31***	0.46***
% High density urban	-0.1			-0.12		
% Forest plantations					0.19	
Min temperature of coldest month	-0.16*	-0.22**	-0.18*	-0.24*	-0.32***	-0.33***
Annual precipitation	-0.23***	-0.13*	-0.16*	-0.27**	-0.16	-0.15
Precipitation of Warmest Quarter	0.09	0.1	0.14*			
% Wetlands	-0.09	-0.09	-0.07	-0.11	-0.11	-0.1
% Protected area	-0.17**	-0.15*	-0.12	-0.03	0.04	0.11
Transect length	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***

ABUNDANCE DATASET	Richness			Accumulated abundance		
	1956	1991	2007	1956	1991	2007
Intercept	-1.16***	-1.14***	-1.15***	0.73*	1.03**	1.00**
% Cropland	0.27***	0.19**		0.65***		
% Low density urban	0.17***	0.27***	0.3***	0.69***	0.9***	0.89***
% High density urban	-0.11	0.14**		-0.36*	0.34*	
% Forest plantations					0.23	0.26
Annual precipitation	-0.11	0.001	-0.02	-0.72***	-0.46**	-0.56***
Precipitation of Warmest Quarter				0.46**	0.26	0.29
% Wetlands	-0.1	-0.1	-0.1	-0.26	-0.25	-0.27
% Protected area	-0.15*	-0.05	-0.1	0.01	0.2	0.14
Transect length	0.001***	0.001***	0.001***	0.01***	0.001***	0.001***

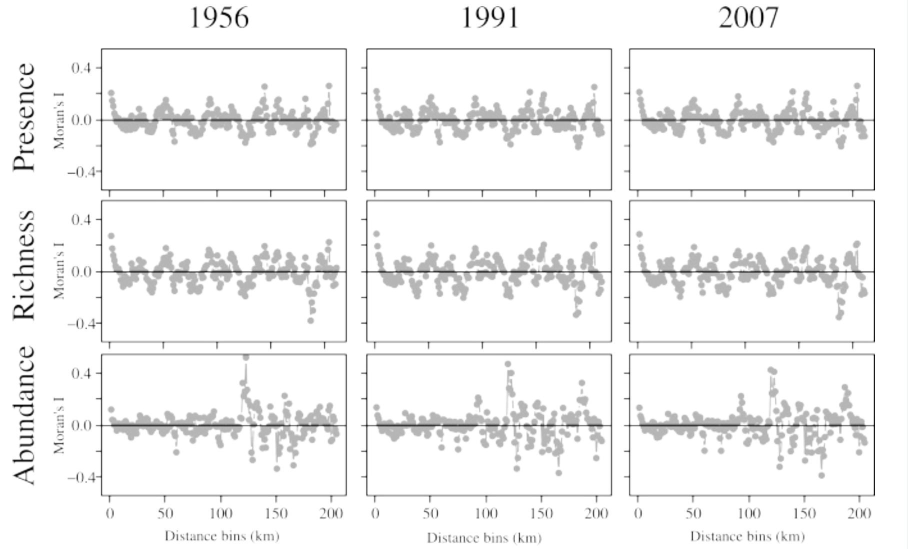
$*P<0.05$; $**P<0.01$; $***P<0.001$

FIGURE A.1



Pearson's correlation coefficient among non-native plant species richness and abundance with percentage of land-cover categories reflecting human alteration of landscape for 1956, 1991 and 2007 at different radius distances from 809 cells (250x250 m) on the SW Spanish coast. Zero distances corresponds to percentages calculated within the cell.

FIGURE A.2



MORAN'S INDEX CALCULATED IN 1 KM BINS FOR THE MODELS EXPLAINING THE PRESENCE, RICHNESS AND ABUNDANCE OF NON-NATIVE PLANTS USING ALL VARIABLES REFLECTING LANDSCAPE ALTERATION (I.E. PERCENTAGE OF HUMAN LAND-COVER CATEGORIES) FOR 1956, 1991 AND 2007 AND CONTROLLING FOR CLIMATE AND HABITAT TYPE.

SECCIÓN II

IV. Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat.

V. Beyond climate: disturbance niche shifts in invasive species.

LA IMPORTANCIA DEL CONTEXTO EN LAS INVASIONES BIOLÓGICAS

CAPÍTULO CUATRO

González-Moreno, P., Diez, J.M., Ibáñez, I., Font, X. & Vilà, M. (2014) Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. Diversity and Distributions, 20, 720–731.

PLANT INVASIONS ARE CONTEXT-DEPENDENT: MULTISCALE EFFECTS OF CLIMATE, HUMAN ACTIVITY AND HABITAT

RESUMEN

Entender las condiciones que favorecen las invasiones biológicas es un paso fundamental para desarrollar estrategias de manejo adecuadas. Sin embargo, el nivel de invasión local se ve afectado por complejas relaciones con los factores ambientales que podrían cambiar según el tipo de hábitat y la región. Nuestro objetivo fue cuantificar la asociación contexto dependiente del clima y la actividad humana a escala de paisaje (perturbación y presión de propágulos) con el nivel de invasión local. Basándonos en una extensa base de datos de parcelas de vegetación (~50,000), usamos modelos jerárquicos Bayesianos para estudiar como el clima y la actividad humana (variables de cubiertas del paisaje) se asocian con el establecimiento (presencia) y dominancia (riqueza y abundancia relativa en parcelas invadidas) de plantas exóticas, considerando nueve tipos de hábitat y tres regiones bioclimáticas. La asociación entre clima y establecimiento y dominancia de plantas exóticas varió dependiendo del tipo de hábitat pero no de la región bioclimática. Estas asociaciones también variaron según la fase de invasión. Por ejemplo, el establecimiento de exóticas estuvo más relacionado con la cercanía a la costa mientras que la dominancia aumentó en áreas continentales cálidas y con alta precipitación. Las variables de actividad humana estuvieron asociadas con el establecimiento y la dominancia de forma similar entre las regiones bioclimáticas. En general, el establecimiento y la abundancia de exóticas tuvo su máximo en paisajes alterados. Los hábitats mostraron diferente susceptibilidad al establecimiento de exóticas respecto a la dominancia (p.e. los hábitats forestales presentaron unos niveles medios de establecimiento pero muy baja dominancia). Este estudio destaca como la interacción entre el clima, la actividad humana y el tipo de hábitat puede determinar los patrones de invasión. Por tanto, un manejo adecuado de las invasiones por plantas exóticas requiere tener en cuenta los efectos del tipo de hábitat en las diferentes fases del proceso de invasión.

ABSTRACT

Understanding the conditions that promote biological invasions is a critical step to developing successful management strategies. However, the level of invasion is affected by complex interactions among environmental factors that might change across habitats and regions making broad generalizations uninformative for management. We aimed to quantify the context-dependent association of climate and human activity at landscape scale (i.e. disturbance and propagule pressure) with the level of plant invasion at local scale across different stages of invasion, habitat types and bioclimatic regions. Based on an extensive database of vegetation plots (~50,000) we used hierarchical Bayesian models to test how climate and human activity at a landscape scale (i.e. land-cover variables) are associated with establishment (i.e. presence) and dominance (i.e. relative species richness and abundance in invaded plots) of non-native plants across nine habitat types and three bioclimatic regions. The association of climate with establishment and dominance of non-native plants varied depending on habitat type but not bioclimatic region. These associations also varied depending on the stage of invasion under consideration. Establishment of non-native species was more likely close to the coast, while their dominance increased in wet and warm continental areas. Human activity variables were associated with establishment and dominance similarly across bioclimatic regions. Non-native species establishment and abundance peaked in human-altered landscapes. Different habitats showed different susceptibilities to establishment versus dominance by non-native species (e.g. woodlands had medium levels of establishment but very low dominance). This study highlights how complex interactions among climate, human activity, and habitats can determine patterns of invasions across broad landscapes. Successful management of plant invasions will depend on understanding these context-dependent effects across habitats at the different stages of the invasion process.

INTRODUCTION

Biological invasions pose a major threat to the native biota and ecosystem functioning (Vilà et al., 2011). Thus, prevention and management of invasions are critical for the conservation of natural and semi-natural ecosystems. Successful management of biological invasions relies on understanding the mechanisms behind the invasion process. Recent conceptual models have suggested that invasions are affected by multiple interacting factors, including abiotic conditions, human activity, and habitat type, which may act at different scales and stages of invasion (Chytrý et al., 2008a; Catford et al., 2009; Milbau et al., 2009). Such complexity hampers our ability to disentangle the mechanisms underlying invasions and thus the forecasting of future invasions. Climatic effects on invasion are perhaps the most commonly studied within abiotic factors. This approach can be successful at large scales to the extent that climatic patterns shape the macro-environmental conditions determining species distribution from continental to regional scales (Pearson & Dawson, 2003; Thuiller et al., 2005; Milbau et al., 2009). Human activity can also clearly affect patterns of invasion (Capítulo 1; Ibáñez et al., 2009a; Vilà & Ibáñez, 2011). For example, human land-covers types such as built-up areas or crops are highly associated with plant invasions due to the increased propagule pressure and disturbance that benefit non-natives establishment (Ohlemüller et al., 2006; Gassó et al., 2009; Gavier-Pizarro et al., 2010). In addition, the level of plant invasion has also been shown to vary among habitat types at a local scale (Vilà et al., 2007; Ibáñez et al., 2009a) with anthropogenic, mesic, and nutrient rich habitats being more invaded than natural, dry, and nutrient poor habitats (Chytrý et al., 2008b). These differences among habitats, partly explained by biotic interactions and human influence at a local scale, highlight the paramount importance of habitat type for influencing invasions on top of the combined effects of climate and human activity at larger spatial scales.

The effects of climate, human activity and habitat type on plant invasions are likely interactive rather than additive, further complicating efforts to understand the relative importance of the different drivers of invasion (Catford et al., 2009; Jiménez-Valverde et al., 2011). Patterns of invasion appear highly idiosyncratic when different habitats types are modelled separately. For example, identical climates may result in a different level of invasion depending on the habitat type and bioclimatic region (i.e. biogeographical region sensu EEA, 2008) (Ibáñez et al., 2009b). In addition, the effects of human activity, derived from land-cover variables, may also vary across bioclimatic regions. For example, regions often have distinct landscape compositions as a result of the interaction of human activities and their climatic drivers. In regions with a predominance of agricultural land and dispersed human settlements, crops may be the most important source of non-native propagules. In contrast, in highly urbanized regions, ornamental plants may be the source of most non-native plants while crops could help to buffer the spread of these species into natural habitats (Capítulo 1). Given these complex interactions, a comprehensive understanding of the invasion process is critical and may even require new analytical approaches that account for those interactions.

Ecological theory and conceptual models of invasions also suggest that the relative importance of climate, human activity and habitat type shaping invasions will depend on the stage of the invasion process under consideration (Catford et al., 2009; Leung et al., 2012). For example, initial establishment of a single species may be driven by propagule pressure from the neighbouring landscape (i.e. human activity), while subsequent dominance may be more dependent on the existence of suitable climatic and local conditions (i.e. habitat type) for plant and population growth (Catford et al., 2009; Leung et al., 2012). The framework of invasion stages for single species can also be applied to groups of non-native species invading plant communities (Catford et al., 2011; Polce et al., 2011). Following the initial establishment of a particular non-native species within a community, this species might increase in abundance at the time that new non-native species are establishing and becoming abundant (i.e. increase in non-native species richness and abundance respectively). Developing a better understanding of how the combination of climatic conditions, human activity, and habitat characteristics affect both the establishment and dominance of non-native species in the community will be critical to inform more targeted management actions (Polce et al., 2011; Leung et al., 2012).

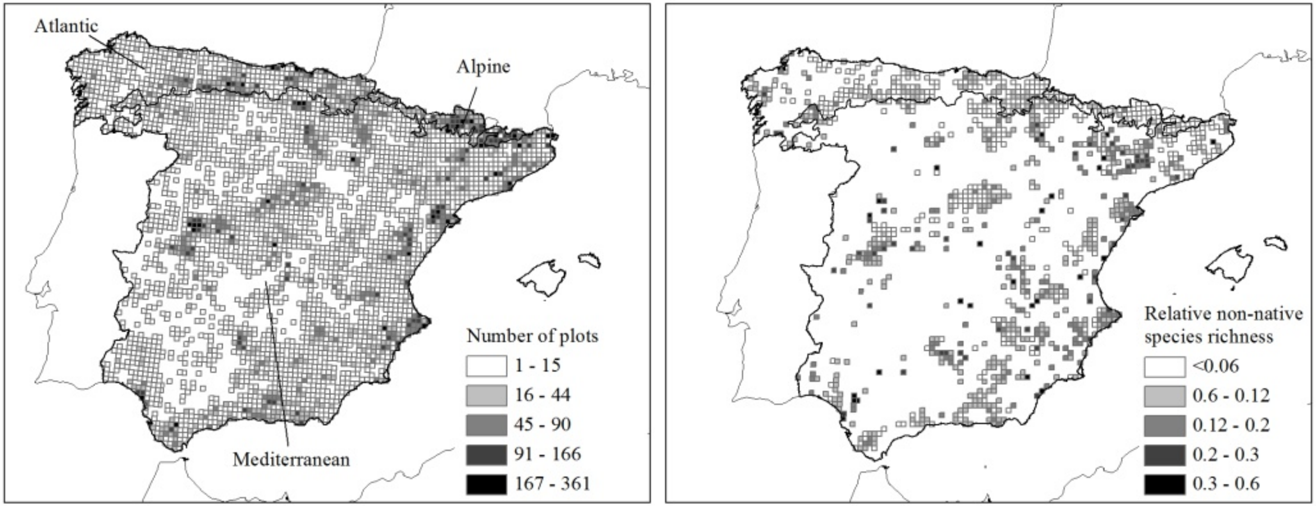
In this study we used an extensive database of vegetation plots (~50000) and hierarchical Bayesian statistical models to investigate how climate, human activity and habitat type interact to explain local patterns of non-native species establishment (i.e. presence) and dominance (i.e. richness and abundance) across mainland Spain. We used data on native and non-native plant species presence and abundance as proxy of invasion success (Catford et al., 2012). Specifically, we asked the following questions: (1) Does the relationship between climate and plant invasions vary across bioclimatic regions and habitats? (2) Does the association of human activity (in terms of land-cover variables) with plant invasions depend on the regional bioclimatic context? And finally, (3) Do these associations and the relative importance of climatic conditions and human activity depend on the metric of invasion (presence, richness and abundance of non-natives, as surrogates of the invasion stages establishment and dominance)? To answer these questions we compared the results of two modelling approaches: a hierarchical model (context-dependent) that nested the effects of climate across bioclimatic regions and habitat types and allowed variation of human activity variables along bioclimatic regions and a classical non-hierarchical model (non context-dependent) that included the different driving variables in an additive and independent fashion. Finally, we discuss the benefits of hierarchical models to investigate current determinants of the level of plant invasion and the potential to identify the current and future incidence of plant invasions.

METHODS

Plant species dataset

In order to quantify plant invasions across mainland Spain, we used data from the Information System of Iberian and Macaronesian Vegetation (SIVIM) (Font et al., 2012); see Appendix A for database characteristics). We gathered 53 345 relevés (plots, hereafter) from 1970 to 2011 that had a phytosociological alliance assignment and location accuracy at least of 10 Km UTM. Our selection covers most environmental gradients across mainland Spain and therefore a wide range of plant communities. A higher density of plots was located in mountain and coastal areas compared to plateau and large valleys (Fig. 1). According to a survey gap analysis based on multivariate environmental similarity surface index (MESS) (Elith et al., 2010; Rossi, 2012) the dataset provided a good coverage of the entire environmental conditions of the study area with only exceptions in rare areas with extremely high precipitation (North western Spain), urban development (Madrid) and agriculture cover (Guadalquivir basin in Southern Spain). Plot size was variable but with ranges per habitat type following

FIGURE 1



Number of vegetation plots and mean relative non-native species richness at invaded plots per 10-Km UTM grid in mainland Spain.

European standards (Appendix A). Despite the long time frame of the dataset, we found little association between level of invasion and time of collection (Appendix A). Furthermore, we did not find any significant bias in the sampling through time across different habitats, regions or geographical areas.

TABLE 1

SUMMARY OF CLIMATE (AVERAGES PERIOD 1971-2007) AND HUMAN ACTIVITY AT LANDSCAPE SCALE CHARACTERISTICS (CORINE LAND-COVER MAPS) IN DIFFERENT BIOCLIMATIC REGIONS IN MAINLAND SPAIN.

	Alpine	Atlantic	Mediterranean
Annual precipitation (mm)	965.56	1301.72	552.38
Summer precipitation (mm)	218.42	173.43	70.99
Winter minimum temperature (º C)	-5.56	1.1	0.77
Temperature seasonality (sd)	6.46	4.85	6.46
Urban cover (%)	1	5.38	7.13
Agriculture cover (%)	3.53	12.12	30.63
Grassland cover (%)	47.72	45.41	29.11
Woodland cover (%)	28.85	29.78	17.12
Land cover diversity	1.07	1.08	1.26

For each plot we identified the bioclimatic region (i.e. Alpine, Atlantic and Mediterranean; Fig.1, Table 1, details in Appendix A (EEA, 2008) and the habitat type following a classification based on the Level 1 of the European Nature Information System of 2007 (EUNIS). We identified the habitat type using a crosswalk table between the phytosociological alliance assigned in SIVIM and the most likely EUNIS habitat type as in Vilà et al., (2007) and Chytrý et al., (2008b): coastal, aquatic (inland surface waters), grasslands, scrubland including heathlands, woodlands, rocky, ruderal, agriculture and saline habitats (Appendix B). This classification informs both the type of native community and the human influence at a local scale. We developed the crosswalk table using expert knowledge and habitat information provided by Rivas-Martínez et al., (2002) and Rodwell et al., (2002). Our expertise on the species composition of the phytosociological alliances guaranties the validity of grouping them in broad habitat types.

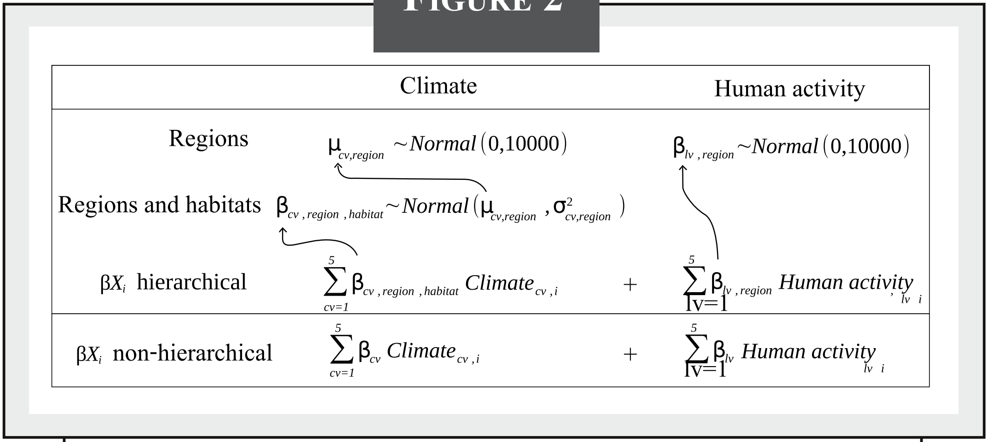
Relaying on the strong association between the number of introductions and the incidence of invasive species (Catford et al., 2011, 2012; Polce et al., 2011) we calculated three widely used metrics in invasion ecology: (i) presence-absence of non-native species in all plots, (ii) relative non-native species richness in invaded plots, calculated as the number of non-native species within a plot in relation to the total number of species, and (iii) relative non-native abundance in invaded plots calculated as the accumulated percentage of non-native vegetation cover divided by the cover of all species. Only non-natives introduced after 1500 a.c. were considered. We did not restrict the study to only invasive species as we might have missed species limited to early stages in the invasion process (Catford et al., 2012). These different metrics are surrogates for different stages of invasion, with presence (i) representing the establishment stage and richness (ii) and abundance (iii) indicating a dominance stage (Polce et al., 2011; Catford et al., 2011). The presence-absence of any non-native plant would inform about the likely of recruitment of at least an individual plant irrespective of its ability to reproduce and become naturalized. In contrast, an increase in abundance of the species or the recruitment of new species would inform about a later phase in the invasion process where given suitable ecological conditions, non-native species are expanding and ultimately becoming dominant in the community.

Climate and human activity data

We selected several climatic and land-cover variables (our proxy for human activity at landscape scale). All variables selected have been commonly used in plant invasion studies (description in Appendix B). The geographic location of each plot was only known within the 10-km UTM grid. We therefore characterized the climate and human activity context of each plot at the grid level. We discarded UTM grids with size lower than 60 km^2 or less than 60% of land (versus ocean) to ensure comparable values of predictors and to avoid possible misplacement of plots located at UTM borders.

We obtained climate data from the UNEX Spatial Data Infrastructure (http://ide.unex.es), which provides average monthly precipitation, minimum and maximum temperature at 1-km grid across Spain for the period 1971-2007. From this dataset we extracted the following biologically-relevant climate variables per UTM grid using the R-package DISMO: annual precipitation, summer precipitation (i.e. warmest quarter of the year), precipitation seasonality (i.e. coefficient of variation), annual temperature, winter minimum temperature (i.e. coldest month), summer maximum temperature (i.e. warmest month) and temperature seasonality (i.e. standard deviation). We also calculated the distance from each grid cell border to the coast to reflect a gradient in climate continentality.

FIGURE 2



	Climate	Human activity
Regions	$\mu_{cv,region} \sim Normal(0,10000)$	$\beta_{lv,region} \sim Normal(0,10000)$
Regions and habitats	$\beta_{cv,region,habitat} \sim Normal(\mu_{cv,region}, \sigma^2_{cv,region})$	
βX_i hierarchical	$\sum_{cv=1}^{5} \beta_{cv,region,habitat}\, Climate_{cv,i}$	$+ \sum_{lv=1}^{5} \beta_{lv,region}\, Human\ activity_{lv,i}$
βX_i non-hierarchical	$\sum_{cv=1}^{5} \beta_{cv}\, Climate_{cv,i}$	$+ \sum_{lv=1}^{5} \beta_{lv}\, Human\ activity_{lv,i}$

MODEL STRUCTURE THAT DEFINES THE VECTOR OF COEFFICIENTS ASSOCIATED WITH EACH CLIMATE AND HUMAN ACTIVITY PREDICTOR (βX_i) USING BOTH HIERARCHICAL AND NON-HIERARCHICAL APPROACHES. IN THE HIERARCHICAL SECTION, THE LEVEL REGION DEFINES THE ASSOCIATION OF EACH CLIMATE AND HUMAN ACTIVITY VARIABLE IN EACH BIOCLIMATIC REGION. THE LEVEL REGION AND HABITATS REPRESENTS THE VECTOR OF COEFFICIENTS ASSOCIATED WITH EACH COMBINATION OF CLIMATE VARIABLES ACROSS REGIONS AND HABITAT TYPES.

Finally, we extracted the following human activity variables for each grid from the CORINE Land-cover Map (2006): percentage of urban (including major transport infrastructures), agriculture, woodland and grasslands land-cover and the Shannon diversity index of these land-cover types (land-cover diversity, hereafter).

Model development

We modelled initial establishment of non-native species (i.e. presence data in 53345 plots) and subsequent dominance (i.e. richness and abundance data in 8146 invaded plots) in order to test whether these different stages are associated with different variables (Catford et al., 2011; Polce et al., 2011). For each of these two stages of invasion we constructed hierarchical Generalized Linear Models (HGLMs) in order to allow the associations with climate to vary among bioclimatic regions and habitats, and human activity variables to depend on bioclimatic region. We compared the results of this model structure with a more traditional approach using non-hierarchical Generalized Linear Models (GLMs) in which we included all the sets of variables and models with only habitat, climate or human activity variables. In contrast to the context-dependent associations considered in the HGLMs, GLMs just test the independent effects of the variables included. We fit all models using a Bayesian framework, which is useful for complex models or when sample sizes within sub-groups are highly variable (Clark, 2004; Gelman & Hill, 2007).

Modelling the presence of non-native species

The presence-absence of non-native species at each plot was estimated from a Bernoulli distribution with probability of being present p_i:

$$N_i \sim \text{Bernoulli}\ (p_i);\ \text{Logit}(p_i) = \alpha_{\text{habitat (i)}} + \beta X_i + e_{\text{g (i)}}$$

where α_{habitat} represents the intercept for each habitat type. Random effects for each UTM grid, g, were estimated from the same grid level distribution. The matrix of explanatory variables, X_i, included all the climate and human activity variables and their associated coefficients, β, were estimated using a hierarchical and non-hierarchical approach (Fig. 2).

Modelling the richness and abundance of non-native species

Non-native species richness at each plot, $NNSR_i$, was modelled using a Binomial distribution with parameters TR_i , total species richness, and q_i. , the probability of being non-native:

$$NNSR_i \sim \text{Binomial}(q_i, TR_i);\ \text{Logit}(q_i) = \alpha_{habitat(i)} + \beta X_i + e_{g(i)}$$

To ensure positive values, and also improve convergence, non-native species relative abundance, $NNSRA_i$: $NNSA_i/Ta_i$, (non-native species abundance/total vegetation abundance), was modelled using a Log-Normal distribution with mean μ_{Ai} and variance σ_A:

$$NNSRA_i \sim \text{Log-Normal}(\mu_{Ai}, \sigma^2_A);\ \mu_{Ai} = \alpha_{habitat(i)} + \beta X_i + e_{g(i)}$$

The habitat-related intercepts, αhabitat, the vector of coefficients associated with climate and human activity variables, β, and the plot level random effects, eg, were modelled following the same approach described above.

Variable selection

We tested the collinearity among the predictors using pair-wise Pearson's correlation tests (Appendix B). First, we selected variables that had a pair-wise correlation lower than 0.75 in both datasets (i.e. in all plots and in invaded plots). Among the variables with correlations greater than 0.75, we selected those with the strongest ecological meaning and explanatory power. This process resulted in the following climate variables: annual precipitation, summer precipitation, winter minimum temperature, temperature seasonality and distance to the coast. Human activity variables were not highly correlated, and thus we included them all. All variables were standardized by subtracting the mean (centred) and dividing by the standard deviation (standardized) in order to improve model convergence and aid interpretation of coefficient estimates (Gelman & Hill, 2007).

Model comparison and validation

We implemented four non-hierarchical (GLM) models: 1) only climate variables, 2) only human activity variables, 3) only habitat type, and 4) all variables (i.e. full model). We compared these models with the hierarchical model (HGLM), which included all variables but allowed climate effects to vary among habitats and regions and human activity effects among regions. We used the Deviance Information

Criteria (DIC) to compare the performance of the models (Spiegelhalter et al., 2002). First, we compared the performance of the five models to identify the best-fit model. Then, we compared the first three models to quantify the relative importance of climate variables, human activity variables and habitat type on the presence, richness and abundance of non-natives. Finally, we compared the relationships estimated using the HGLM with those of the GLMs in order to test for the importance and differences of context-dependent relationships versus independent ones.

Preliminary analyses using the Moran's Index, did not detect significant spatial autocorrelation in the models' residuals at any distance bigger than 10 km (I<0.1). Therefore we proceeded without modelling spatial random effects. It is possible that there is spatial autocorrelation in patterns of invasion within 10-km grid cells, but we could not test this because we lacked more precise information for plots location.

We randomly set apart 20% of total plots for model validation and calibrated the models with the remaining 80%. Goodness of fit of the validation data was calculated using the sum of squares errors (SSE, Predicted-Observed) for each model. Models that minimized this value were considered to fit better the data. For the presence model we also calculated the Area Under the Curve (AUC), a widely used method to evaluate presence-absence data models (Jiménez-Valverde et al., 2011). Models with AUC>0.5 discriminate the presences and absences better than chance. Final models were run in OpenBUGS 3.2.1 (Lunn et al., 2009). Models were run until convergence of the parameters was ensured (~50,000 iterations), after which posterior distributions of the parameters were calculated from 100,000 iterations (code of the models in Appendix C).

RESULTS

Model comparison

The hierarchical model (HGLM) considering all context-dependent effects performed better than all classical non-hierarchical models (GLMs) across all metrics according to DIC values (i.e. smallest DIC value, Table 2). Differences were greater for the presence of non-native species than for richness or abundance. Validation of the models with independent data yielded similar model rankings, except for richness (Table 2).

TABLE 2

COMPARISON OF MODELS USED TO EXPLAIN PRESENCE, RELATIVE RICHNESS AND ABUNDANCE OF NON-NATIVE PLANT SPECIES AT INVADED PLOTS IN MAINLAND SPAIN USING HABITAT TYPE, CLIMATE AND HUMAN ACTIVITY VARIABLES. BEST INDICATORS FOR EACH PLANT INVASION METRIC ARE SHOWN IN BOLD.

		Calibration				Validation	
Model	DIC	DIF	pD	AUC	SSE	AUC	SSE
PRESENCE							
All hierarchical	**30150**	0	1059	**0.82**	**4254.61**	**0.78**	**1147.83**
All non-hierarchical	30830	0.02	1038	0.81	4379.33	0.77	1169.46
Habitat	30940	0.03	1147	0.82	4367.25	0.77	1170.76
Climate	33200	0.1	1150	0.78	4753.87	0.71	1263.78
Human activity	33260	0.1	1174	0.78	4753.92	0.71	1261.99
RICHNESS							
All hierarchical	**16660**	0	297.6		4804.64		1077.34
All non-hierarchical	16670	0	280.4		4839.52		**1064.28**
Habitat	16780	0.01	382.5		**4596.59**		1091.85
Human activity	17100	0.03	381.9		4988.25		1094.51
Climate	17110	0.03	399.2		4962.87		1098.45
ABUNDANCE							
All hierarchical	**-20100**	0	494.9		**116.64**		**28.55**
All non-hierarchical	-20000	0	439.3		120.92		28.99
Habitat	-19980	0.01	456.5		121.24		29.04
Human activity	-19510	0.03	446.6		129.67		30.93
Climate	-19510	0.03	466.4		130.43		31.31

DIC: Deviance Information Criteria, DIF: increment in relative DIC compared to best model; pD: effective number of parameters, AUC: Area Under the Curve, SSE: Sum of Square Errors.

Models including the three groups of variables together (i.e. climate, human activity and habitat type) performed better than models considering only a group of variables for all non-native plant metrics (Table 2). The difference in DIC between climate and human activity models was rather low in comparison to the difference with the habitat model for all metrics. Validation of the models with independent data yielded similar results.

The association of climate, human activity and habitat type with non-native plant metrics

The two types of models, GLMs and HGLM, provided different insights about the association of non-native plant metrics with climate, human activity, and habitat type. The hierarchical model tested regional and habitat dependent association of these variables with non-native plant metrics, while the classical non-hierarchical model estimated their association independently. In the following subsections we compare the results for both types of models.

Association of climate with non-native plant metrics

Considering independent effects (i.e. non-hierarchical model), the significance of the climate predictors varied between the presence of non-native species and the richness and abundance of non-native species models (Fig 3). Presence of non-native species was positively correlated to summer precipitation and proximity to the coast (Fig 3). In contrast, both richness and abundance were positively associated with high annual precipitation and negatively with summer precipitation (Fig 3). Furthermore, richness was also positively associated with temperature seasonality and winter minimum temperature (Fig 3).

Although the independent effects of some climate variables on non-native plant metrics were not significant (Fig 3), the hierarchical analyses revealed significant associations within specific habitat types (Table 3, Appendix B Table B8-B10). For instance, the effect of annual precipitation on presence was different among habitat types: in grasslands, rocky and agriculture habitats, presence was associated with low annual precipitation while in coastal, scrubland, woodland and ruderal habitats it was associated with high annual precipitation (Table 3). These habitat-specific associations were more prevalent with presence than with richness or abundance of non-native species (Table 3).

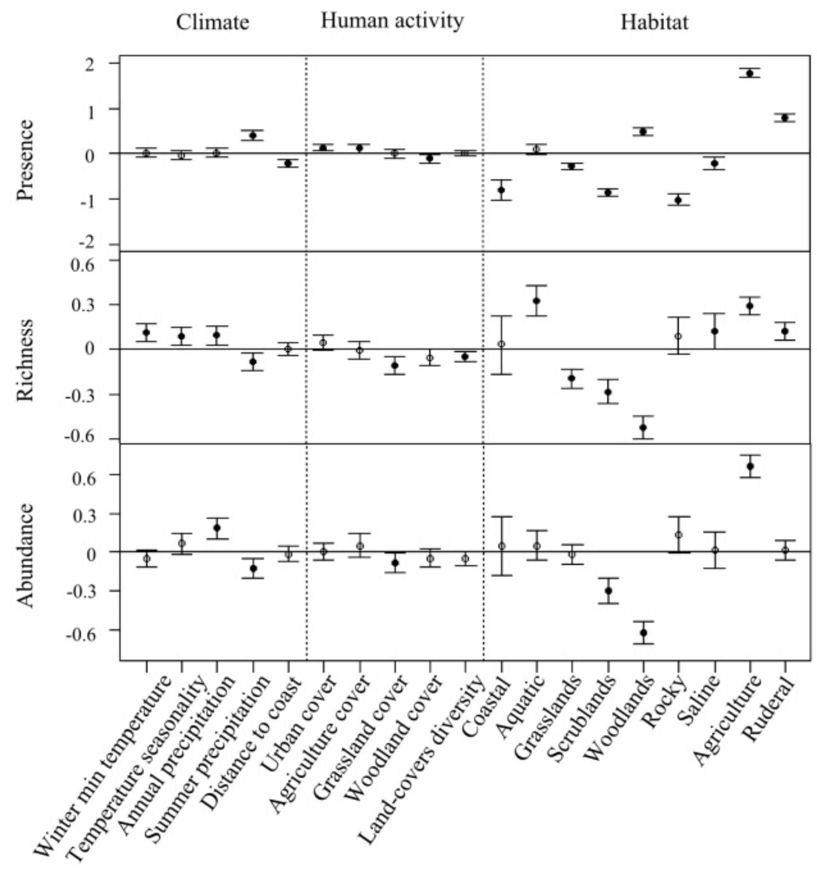
Table 3

Sign of the coefficients for climate variables across bioclimatic regions and habitat types in the full hierarchical models explaining presence of non-native species, relative richness and abundance at invaded plots in mainland Spain. Only results for combinations of climate variables and bioclimatic region with at least one significant coefficient for habitat type are shown. For full results see Appendix B.

Habitat type	Winter Minimum temperature		Temperature seasonality		Annual precipitation			Summer precipitation			Distance to coast	
	Atl	Med	Atl	Med	Alp	Atl	Med	Alp	Atl	Med	Alp	Med
Presence												
Coastal	n.s.	-	n.s.	n.s.	n.s.	+	n.s.	n.s.	-	+	n.s.	n.s.
Aquatic	-	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Grassland	+	n.s.	n.s.	+	-	-	-	n.s.	n.s.	+	n.s.	-
Scrubland	+	n.s.	n.s.	n.s.	n.s.	+	n.s.	n.s.	-	+	n.s.	n.s.
Woodland	-	n.s.	n.s.	+	n.s.	n.s.	+	n.s.	n.s.	+	n.s.	n.s.
Rocky	n.s.	n.s.	n.s.	n.s.	n.s.	-	-	n.s.	n.s.	+	n.s.	-
Agriculture	n.s.	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.	+	+	n.s.	-
Ruderal	n.s.	+	n.s.	+	n.s.	+	n.s.	n.s.	n.s.	+	-	-
Richness												
Grassland	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.
Scrubland	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.
Saline	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.
Agriculture	n.s.	+	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ruderal	+	+	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Abundance												
Coastal	n.s.	n.s.	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Aquatic	n.s.	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Grassland	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Scrubland	n.s.	n.s.	+	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Woodland	n.s.	-	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Rocky	n.s.	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Saline	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.
Agriculture	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	+	-	n.s.	n.s.	n.s.	n.s.
Ruderal	n.s.	+	n.s.	n.s.	n.s.	n.s.	+	-	n.s.	n.s.	n.s.	n.s.

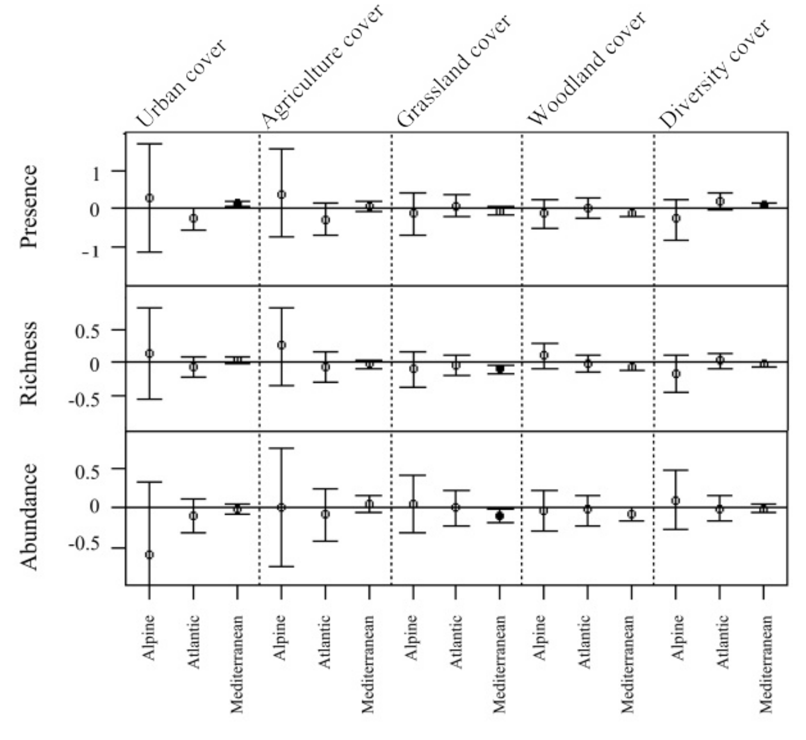
Alp: Alpine; Atl: Atlantic; Med: Mediterranean; +: positive association; -: negative association; n.s.: non-significant association

FIGURE 3



POSTERIOR MEANS (WITH CREDIBLE INTERVALS) OF THE INDEPENDENT MEAN COEFFICIENTS FOR HABITAT, CLIMATE AND HUMAN ACTIVITY VARIABLES IN THE NON-HIERARCHICAL MODELS FOR THE PRESENCE OF NON-NATIVE SPECIES AND THEIR RELATIVE RICHNESS AND ABUNDANCE AT INVADED PLOTS IN MAINLAND SPAIN. FILLED DOTS INDICATE THAT THE 95% CREDIBLE INTERVAL AROUND THE PARAMETER MEAN VALUES DID NOT INCLUDE ZERO. TO FACILITATE COMPARISON, HABITAT COEFFICIENTS ARE CENTRED AROUND THE MEAN OF ALL HABITAT COEFFICIENTS.

FIGURE 4



POSTERIOR MEANS (WITH CREDIBLE INTERVALS) OF THE COEFFICIENTS FOR HUMAN ACTIVITY VARIABLES ACROSS BIOCLIMATIC REGIONS IN THE HIERARCHICAL MODELS FOR THE PRESENCE OF NON-NATIVE SPECIES AND THEIR RELATIVE RICHNESS AND ABUNDANCE AT INVADED PLOTS IN MAINLAND SPAIN. FILLED DOTS INDICATE THAT THE 95% CREDIBLE INTERVAL AROUND THE PARAMETER MEAN VALUES DID NOT INCLUDE ZERO.

The effect of climate across regions was very consistent for non-native plant metrics within each habitat type (Table 3). We only found divergence in the association of summer precipitation with presence, which was positive in the Mediterranean region for most habitats and highly variable in the Alpine and Atlantic regions (Table 3, Appendix B Table B8).

Association of human activity with non-native plant metrics

Considering independent associations (i.e. non-hierarchical model), the presence of non-native species was positively associated with agriculture and urban land-cover and negatively with woodland land-cover (Fig. 3). The pattern was different for richness and abundance of non-native species, which were negatively associated only with grassland land-cover (Fig. 3). Richness also showed a negative association with land-cover diversity.

For human activity variables we hypothesized that their association with non-native plant metrics would vary regionally. We found that most associations were in fact only significant in the Mediterranean region (Fig. 4). For instance, presence of non-native species was only associated with urban land-cover and land-cover diversity in the Mediterranean region.

Non-native plant metrics across habitat types

Presence, richness and abundance of non-natives were significantly different among habitat types in the non-hierarchical model (Fig. 3, Appendix B - Table B6). Agriculture and ruderal habitats had the highest presence, richness and abundance of non-native species while scrublands had the lowest. Differences among several habitats varied depending on the non-native plant metric under consideration (Fig. 3). For instance, woodlands showed medium presence values of non-native species but very low richness and abundance; aquatic habitats had medium presence and abundance values but rather high richness. These trends were similar for the hierarchical model (Appendix B: Fig. B2 and Table B7).

DISCUSSION

Conceptual models to explain invasion success have pointed to the combination of having enough propagules and a suitable environment, biotic and abiotic (Chytrý et al., 2008a; Catford et al., 2009). In our work, climate was used to estimate abiotic suitability (Thuiller et al., 2005), human activity at a landscape scale was used as a proxy for propagule availability (Capítulo 1; Chytrý et al., 2008a), and habitat type represented both characteristics of the native community and the human influence at a local scale (Chytrý et al., 2008a). Among these variables, we found habitat type to be the single most important factor associated with invasion. Furthermore, these factors are likely interactive rather than additive and might act at different spatial scales and stages (Catford et al., 2009; Milbau et al., 2009; Jiménez-Valverde et al., 2011). However, few empirical studies have quantified these complex patterns (Gassó et al., 2012a). Here, we have explored how a hierarchical modelling approach can quantify the context-dependent association of these variables with the presence and abundance of non-native plants (i.e. our proxy for plant invasion). We found that the associations of climate and human activity with non-natives patterns were mainly dependent on the habitat type but not on the bioclimatic region. Furthermore, non-native plant metrics across habitats varied depending on the metric of invasion. As the different metrics could be considered surrogates for different stages of invasion, our results reinforce that different stages might be controlled by different factors (Catford et al., 2009, 2012; Polce et al., 2011)

Climate and plant invasions

At large scales, climate is the most important abiotic aspect shaping non-native species distribution (Thuiller et al., 2005; Broennimann et al., 2007). In our study, non-native species were more likely to be present in areas with high summer precipitation and close to the coast (i.e. the Atlantic part of the study area), reflecting higher presence in mesic areas without extreme seasonality (Polce et al., 2011). Presence of non-natives in coastal areas could also be enhanced by the increased propagule pressure associated with higher human influence in these regions (Capítulo 1; Gassó et al., 2009). Still, we already accounted by human activity by adding the land-cover variables and considered distance to the coast as a good proxy for low seasonality. In contrast, higher richness and abundance of non-natives was associated with higher climate seasonality, but also with higher wet and warm conditions. Thus, although it is more likely to find at least one non-native species close to the coast, wet areas towards the interior are also hubs for non-native species diversity and abundance.

Climate variables that were not significantly associated with non-native plant metrics independently (i.e. non-hierarchical model), were found to be important in specific habitats (i.e. hierarchical model). Climatic effects on plant invasions are mediated by the ecological characteristics of different habitats such as biotic resistance or abiotic constraints. For instance, we found higher presence of non-native species with low annual precipitation in grasslands, rocky and agriculture habitats while the opposite trend was relevant in coastal, scrubland, woodlands and ruderal habitats. In contrast to more open habitats, an increase in annual precipitation might counteract the competition for water in woody habitats and the excess of salinity in coastal habitats. Although the mechanisms underlying these interactions require further research, our results suggest that considering habitat-dependent effects seems fundamental to understand and predict plant invasions (Gassó et al., 2012a).

There was high consistency in the associations of climate variables with all non-native plant metrics across bioclimatic regions. Within specific habitat types, only the association of summer precipitation with presence showed divergences for coastal and scrubland habitats. In the humid Atlantic region, presence was enhanced in relative drier environments (lower summer precipitation) while in the drier Mediterranean region we found the opposite trend. This finding agrees with plant invasion being enhanced in mesic conditions (i.e. intermediate temperature and moisture levels) (Polce et al., 2011).

Human activity and plant invasions

Besides suitable climatic conditions, plant invasions are facilitated by increasing disturbance levels and propagule pressure of non-native species from regional to landscape scales. Such patterns are highly associated with human land-covers (i.e. agriculture or urban), while natural areas (i.e. higher grassland and woodland cover) might act as a buffer to plant invasions (Ohlemüller et al., 2006; Carboni et al., 2010). We found the same pattern for all non-native plant metrics: invasive plants were negatively associated with natural areas and positively associated with human-altered areas. Unlike other studies (Capítulo 1; Pino et al., 2005; Kumar et al., 2006; Marini et al., 2009), we found a negative association of land-cover diversity and non-native richness. Diverse landscapes usually enhance local non-native species richness by increasing variability of ecological conditions, however if the number of land-covers characterized is low, land-cover diversity could show the pattern of the most predominant land-cover type (i.e. agriculture land-cover).

As for the relationships with climate variables, we also found that the relationships between invasion and human activity were highly consistent spatially, exhibiting similar relationships across bioclimatic regions. In fact, we found that human activity variables were only significant in the Mediterranean region probably due to its higher human alteration and disproportionate number of plots (five times more samples in the Mediterranean than in the Atlantic). Considering the high consistency found for climate and human activity effects across bioclimatic regions, we suggest that broad patterns of plant invasion could be feasibly extrapolated among neighbouring regions.

Habitat types and plant invasions

Following previous studies, anthropogenic habitats (i.e. agriculture and ruderal) yielded the highest values of non-natives metrics (Vilà et al., 2007; Chytrý et al., 2008b). Nevertheless, for several habitats there were some discrepancies. For instance, woodlands showed high non-native species presence but extremely low richness and abundance. The few shade-tolerant non-native species that could overcome the he limitation of light availability in woodlands are very likely to survive even if it is in low numbers (Martin et al., 2009). However, the species able to invade woodlands are generally rare or might be still in an incipient phase of expansion (Capítulo 2; Martin et al., 2009), reflecting low local richness and abundance. Thus, further research should confirm if the potential differences between the presence and abundance of non-native plants is mediated by their different traits in relation to the habitat they invade or by the stage of the invasion process.

Analysis of multi-species invasion

Several metrics have been proposed to quantify the level of plant invasions such as the richness or abundance of non-native species (Catford et al., 2012). We have found different patterns of climate, human activity, and habitat type associations with each metric, suggesting that different variables control the overall presence and abundance of non-native species, our proxies for establishment and dominance during multispecies invasions (Catford et al., 2011; Polce et al., 2011). We expected higher importance of human activity at a landscape scale (i.e. proxy for propagule pressure) than climate (i.e. defining suitable abiotic conditions) in the establishment stage. Nevertheless, both groups of variables showed similar importance for predicting the establishment and dominance of non-native species. Further studies could explore if these patterns are also similar in other stages of the invasion process such as transport or expansion (Blackburn & Duncan, 2001; Leung et al., 2012) or consider the human activity predictors at a finer scale (Capítulo 1).

Modelling strategies to understand the context-dependence of invasions

Our model results have shown how a hierarchical approach better reflects plant invasions than non-hierarchical models. Although proven a powerful modelling strategy (Pearson et al., 2004; Diez & Pulliam, 2007; Vicente et al., 2011), hierarchical modelling has been rarely used to model biological invasions (Ibáñez et al., 2009a, 2014; Diez et al., 2012). Hierarchical modelling can accommodate the frequently proposed issue of considering the invasion process across spatial scales (Collingham et al., 2000; Pearson & Dawson, 2003; Milbau et al., 2009). Climate, topography and human activity at regional level might drive invasion variability at large scales while local variability may be determined by changes in biotic interactions, disturbance or microclimate which are highly associated with habitat type (Milbau et al., 2009).

Hierarchical models can also be used to test the consistency in the associations of plant invasions and environmental variables. Context-dependent associations are usually assessed by calibrating the same model with different datasets (Broennimann et al., 2007; Gassó et al., 2012a). This modelling strategy is problematic when the number of categories is large due to the increasing number of parameters to estimate, the unbalanced number of samples per category, and the difficulty to interpret differences. Hierarchical models can partially solve these problems, especially when the data have a nested structure, and when partial pooling of information across groups is likely to be helpful. Because these are common characteristics of ecological studies, hierarchical approaches may be widely useful for quantifying context-dependent patterns of invasion and developing predictions of invasion risk.

Concluding remarks

It is important to consider the stage of the invasion process when managing new introductions (Simberloff, 2009b). Areas with high establishment probability might not be the ones with higher dominance of non-native species (Catford et al., 2011). These invasion hot spots regarding establishment might be colonized by only a few widespread species but not highly abundant because of environmental constraints. Screening non-native species presence together with richness and abundance provide a simple method to anticipate successful plant invasions and not only potential establishment.

Although future patterns of invasions will not necessarily mirror past invasions, given our stage of knowledge, the information we can obtain from past invasions is our best bet on how future invasions may develop. Given this information, hierarchical models can help management of plant invasions through a better accountability of context-dependent effects (i.e. the interactions between climate suitability, human activity and the conditions of the local habitat). The outputs from these models might be used to develop invasion risk scenarios within particular habitats and bioclimatic regions, delivering more detailed information to prevent future invasions.

ACKNOWLEDGEMENTS

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APPENDIX A – DATABASE CHARACTERISTICS

The Information System of Iberian and Macaronesian Vegetation (SIVIM) accounts for ca. 2180618 floristic records and 130066 phytosociological relevés from 1970 to 2011 organized following a 10 km UTM grid.

Biogeographical regions

SIVIM covers the three bioclimatic regions in mainland Spain: Alpine, Atlantic and Mediterranean. The Alpine region is restricted to the Pyrenees mountain range with altitudes up to 3404 m above sea level. The urban development in the region is restricted to the lowest part of the valleys with intense agricultural areas and grasslands for grazing surrounding them (Mottet et al., 2006). Grasslands in the higher altitudes are also used for grazing as common pastures. The Atlantic region is located in the Northern area of Spain and it is characterized by a humid and mild climate. The relief is very uneven with steep slopes and narrow valleys. The landscape type is rather patchy with small-scale agricultural systems and urban areas mostly concentrated in the lower parts of the slopes. In the upper part, grasslands are used as pastures and are well integrated with natural vegetation. Recently these areas are being replaced by conifer and eucalyptus (Atauri et al., 2004). Finally, the Mediterranean region is characterized by intense agricultural areas on the large valleys and coastal areas while the urban development is concentrated towards the coast. The interior of the region is a large plateau of ~600 m above sea level with mostly extensive dryland agriculture and sparsely populated (except Madrid metropolitan area).

Phytosociological data

Phytosociological databases have been widely used in plant ecology including studies about non-native species (Chytrý et al., 2005; Pino et al., 2005; Vilà et al., 2007; Chytrý et al., 2008a,b). These databases are based on relevés (plots hereafter) gathered by expert botanists where all plant species are identified (Dengler et al., 2008). The characterization of species as non-native is done a posteriori using a list of all non-native species known to the Iberian Peninsula (Appendix B). The list was constructed based on expert knowledge and information from vegetation Flora and Atlas (Castroviejo et al., 1986; Sanz-

Elorza et al., 2004). Three major aspects could affect the quality of phytosociological data: plot size, location accuracy and sampling method.

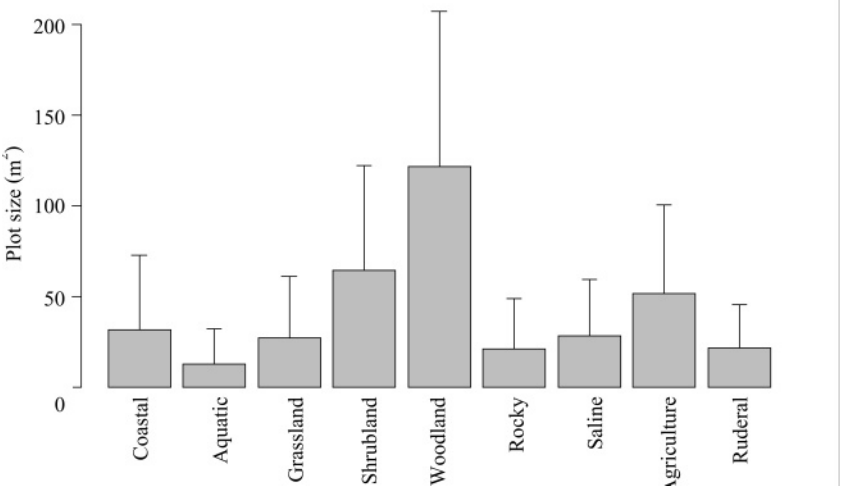
Plot size: mean size of plots with available information (33032 plots) was significantly different among habitats ($F=21.47$, $p<0.001$). Aquatic habitats had the smallest plots and woodlands the biggest plots (Fig. A1). Nevertheless, mean plot size within habitats followed the standards used in pytotosociological data in Europe (Chytrý & Otýpková, 2003; Vilà et al., 2007). Therefore, we assume similar plot size within each habitat type making reliable the comparisons in the level of invasion among habitats and in the habitat-dependent associations.

Location accuracy of all plots was assured restricting the precision to the 10 km UTM grid. Plots without location at that level were excluded from the analyses.

Sampling method: sampling method in phytosociological data follows a preferential method where botanists target specific vegetation types or areas. Regarding vegetation types at the local scale, it is assumed that botanist would target natural vegetation consistently avoiding invaded areas. However, a recent study by Michalcová et al., (2011) shows comparable or even higher values estimators of non-native metrics in preferential sampling versus stratified-random methods in woodland habitats. Considering sampling bias at large scale, a higher density of SIVIM plots was located in mountain and coastal areas compared to plateau and large valleys (Fig. 1). This pattern was consistent across habitat types. Only agriculture habitat had a more homogeneous distribution across whole Spain. We also performed a survey gap analyses using multivariate environmental similarity surface index (MESS) (Elith et al., 2010; Catford et al., 2011) for each 10 Km UTM grid. MESS quantifies the similarity between the environmental conditions (i.e. variables used in the models) in mainland Spain with the conditions represented in all plots of the database. Positive MESS values indicate that the full range of conditions are included in the data with higher values indicating areas that are better represented by data (maximum value = 100). Negative values indicate conditions not included in the data where the models are extrapolating (Elith et al., 2010). For the SIVIM data MESS values ranged from -1 to 100 (mean: 52.1 sd: 28.4) indicating a very good coverage of the environmental conditions in Spain. Considering climate, extrapolation areas were restricted to a very limited location in North western Spain with very high precipitation rates. For human influence variables extrapolation areas were located in several grids in Madrid area (completely urban cover and maximum distance to coast) and in the central part of the Guadalquivir river basin in Southern Spain (extremely high agriculture cover).

In summary, the systematic approach used by phytosociologists enhances the possibilities of using SIVIM to test interesting ecological questions such as in the growing field of invasion Ecology. Despite its mentioned limitations, the large size of the database and consistent patterns found suggest a good reliability of the results drawn from the analyses and configures SIVIM up to now as the best current database about vegetation in Spain.

Figure A.1



Mean plot size across habitats in the Information System of Iberian and Macaronesian Vegetation.

Time

Considering the long time frame of the database (1970 to 2011), it is possible that invasive species abundance could increase with time. However we did not find any important association between invasion and time of collection across all dataset (GLMs - Presence: R^2=0.024, Abundance R^2=0.06, Richness R^2=0.02). Thus, it is very unlikely that including time of collection in the models will change the results.

On the other hand, as we are interested in the degree of invasion at habitat and region levels, time could affect our findings if through time there is bias in the sampling across different habitats, regions or geographical areas. Thus, we performed three different preliminary analyses to detect potential bias:

Are there plots geographically stratified through time? We found little spatial structure of the data in relation to time of collection (trend surface GLMs explaining time of publication: R^2=0.05 for all data, R^2<0.13 for most habitat types and R^2<0.49 for coastal and saline habitats). The spatial structure of the latter habitats is evident and not related to sampling bias.

Are habitats sampled in a similar intensity through time? Most habitats had the maximum of sampling intensity in the 90s with lower intensity in both earlier and later years (quadratic GLMs relating number of plots and time of collection: R^2>0.16 for most habitat types). Only coastal habitats showed similar sampling intensity through time (R^2=0.12 for coastal habitats).

Are regions sampled in a similar intensity through time? All bioclimatic regions had the maximum of sampling intensity in the 90s (quadratic GLMs relating number of plots and time of collection: R^2 >0.24).

APPENDIX B

Crosswalk table between the phytosociological alliance assigned in the Information System of Iberian Vegetation (SIVIM) and the most likely European Nature Information System (EUNIS) habitat type (in brackets official coding).

Table B.1

Coastal (B)
Agropyro-Minuartion peploidis
Alkanno-Malcolmion
Alkanno-Malcolmion parviflorae
Alkanno-Maresion nanae
Ammophilion arundinaceae
Ammophilion australis
Anthyllido hamosae-Malcolmion lacerae
Asplenion marini
Brassicion oleraceae
Cakilion maritimae
Coremation albi
Crithmo-Armerion maritimae
Crithmo-Daucion halophili
Crithmo-Limonion
Crithmo-Staticion
Crucianellion maritimae
Euphorbio portlandicae-Helichrysion maritimae
Helichrysion picardii
Hyperico elodis-Sparganion
Juniperion turbinatae
Koelerion albescentis
Lavaterion maritimae
Linarion pedunculatae
Medicagini citrinae-Lavaterion arboreae
Medicagini-Lavaterion arboreae
Rubio longifoliae-Coremation albi
Saginion maritimae
Sporobolion arenarii
Aquatic(C)
Agrostion salmanticae
Batrachion aquatilis
Batrachion fluitantis
Calamagrostion pseudophragmitis
Callitricho-Batrachion
Cardaminion amarae
Cardamino-Montion
Caricion remotae
Charion fragilis
Charion vulgaris
Chenopodion rubri
Cicendion
Cratoneurion commutati
Eleocharition acicularis
Filipendulion ulmariae
Glycerio-Sparganion
Hydrocharition
Imperato cylindricae-Erianthion ravennae
Imperato-Erianthion
Isoetion
Lemnion minoris
Lemnion trisulcae
Littorellion uniflorae
Lycopodo-Cratoneurion commutati
Magnocaricion elatae
Magnopotamion
Myosotidion stoloniferae
Nanocyperion
Nasturtion officinalis
Nitellion flexilis
Nymphaeion albae
Parvopotamion
Phragmition australis
Phragmition communis
Potamion
Potamion pectinatae
Potamogetonion eurosibiricum
Preslion cervinae
Ranunculion aquatilis
Ranunculion fluitantis
Ranunculion omiophyllo-hederacei
Riellion helicophyllae
Ruppion maritimae
Sphagno-Utricularion
Swertio-Anisothecion squarrosi
Utricularion
Utricularion vulgaris
Zannichellion pedicellatae
Grassland (E)
Adenocarpion decorticantis
Aegilopion
Agropyro pectinati-Lygeion sparti
Agropyro-Lygeion
Agrostio castellanae-Stipion giganteae
Agrostion castellanae
Agrostion stoloniferae
Alopecurion pratensis
Alysso granatensis-Brassicion barrelieri
Alysso-Festucion pallentis
Alysso-Sedion
Alysso-Sedion albi
Aphyllanthion
Arabidion caeruleae
Arabidion coeruleae
Arabidopsion thalianae
Armerion cantabricae
Armerion eriophyllae
Arrhenatherion
Arrhenatherion elatioris
Artemisio albae-Dichanthion ischaemi
Asplenio serpentini-Armerion
Berberidion vulgaris
Brachypodion phoenicoidis
Calthion palustris
Campanulo herminii-Nardion strictae
Cnidion
Corynephorion canescentis
Corynephoro-Malcolmion patulae
Cynosurion cristati
Deschampsion mediae
Elynion medioeuropaeum
Festucion burnatii

Table B.1

(Cont.) Crosswalk table between the phytosociological alliance assigned in the Information System of Iberian Vegetation (SIVIM) and the most likely European Nature Information System (EUNIS) habitat type (in brackets official coding).

Festucion elegantis
Festucion eskiae
Festucion gautieri
Festucion scariosae
Festucion scopariae
Festucion spadiceae
Festucion supinae
Festucion valesiacae
Filipendulenion
Frangulo alni-Pyrion cordatae
Genistion floridae
Genistion purgantis
Geranio pusilli-Anthriscion caucalidis
Helianthemion guttati
Helianthemo-Festucion pallentis
Hieracio castellani-Plantaginion radicatae
Hyparrhenion hirtae
Hyperico-Scleranthion
Juncion acutiflori
Juncion trifidi
Koelerion glaucae
Koelerio-Phleion phleoidis
Laserpitio nestleri-Ranunculion thorae
Laserpitio-Ranunculion
Laserpitio-Ranunculion thorae
Lonicero-Berberidion hispanicae
Lythrion tribracteati
Mesobromion erecti
Minuartio-Festucion curvifoliae
Molinerion laevis
Molinio-Holoschoenion vulgaris
Molinion caeruleae
Mucizonion sedoidis
Nanocyperion flavescentis
Nardion strictae
Nardo-Agrostion tenuis
Nardo-Caricion rigidae
Nardo-Juncion squarrosi
Omphalodion commutatae
Ononidion striatae
Oxytropido-Elynion
Paspalo-Agrostion verticillati
Paspalo-Polypogonion
Paspalo-Polypogonion semiverticillati
Petasition officinalis
Phlomidio-Brachypodion retusi
Plantagini discoloris-Thymion mastigophori
Plantagini-Festucion
Plantaginion serrariae
Plantaginion thalackeri
Poion supinae
Polygono-Trisetion
Poo bulbosae-Astragalion sesamei
Potentillion anserinae
Potentillo montanae-Brachypodion rupestris
Primulion intricatae
Prunion spinosae
Pruno-Rubion radulae
Pruno-Rubion ulmifolii
Ptilotrichion purpurei
Ranunculion bullati
Resedo lanceolatae-Moricandion
Rubion subatlanticum
Salicion herbaceae
Sambuco-Salicion capreae
Sarothamnion scoparii
Saturejo-Hyparrhenion hirtae
Sedion anglici
Sedion caespitosi
Sedion micrantho-sediformis
Sedion pyrenaici
Sedo-Ctenopsion gypsophilae
Sedo-Scleranthion
Senecion fluviatilis
Seslerio-Festucion pallentis
Sideritido fontquerianae-Arenarion aggregatae
Stipion capensis
Stipion parviflorae
Stipion retortae
Stipion tenacissimae
Taeniathero-Aegilopion geniculatae
Teesdaliopsio-Luzulion caespitosae
Thero-Airion
Thero-Brachypodion
Thero-Brachypodion ramosi
Trachynion distachyae
Trifolio subterranei-Periballion
Triseto velutini-Brachypodion boissieri
Triseto-Polygonion bistortae
Tuberarion guttatae
Ulici-Ericion ciliaris
Veronico-Lysimachion
Violion caninae
Violion cornutae
Xerobromion erecti

Scrubland (F)

Aeonio-Euphorbion canariensis
Andryalion agardhii
Anthyllido terniflorae-Salsolion papillosae
Arbuto unedonis-Laurion nobilis
Argyranthemo suculenti-Calendulion maderensis
Asparago albi-Rhamnion oleoidis
Astragalion tragacanthae
Calluno-Genistion
Carthamo arborescentis-Salsolion oppositifoliae
Cistion ladaniferi
Cistion laurifolii
Cistion mediomediterraneum
Cytision oromediterranei

(Cont.) Crosswalk table between the phytosociological alliance assigned in the Information System of Iberian Vegetation (SIVIM) and the most likely European Nature Information System (EUNIS) habitat type (in brackets official coding).

Table B.1

Cytision oromediterraneo-scoparii
Daboecion cantabricae
Dactylido maritimae-Ulicion maritimi
Echinospartion horridi
Ericion arboreae
Ericion tetralicis
Ericion umbellatae
Eryngio-Ulicion erinacei
Euphorbio-Callunion
Genistion haenselero-polyanthi
Genistion lobelii
Genistion micrantho-anglicae
Genistion occidentalis
Genistion pilosae
Genistion polygaliphyllae
Genisto retamoidis-Phlomidion almeriensis
Genisto versicoloris-Juniperion hemisphaericae
Genisto-Vaccinion
Gypsophilion
Gypsophilion hispanicae
Hammado articulatae-Atriplicion glaucae
Helianthemo italici-Aphyllanthion monspeliensis
Hypericion balearici
Hypericion ericoidis
Juniperion nanae
Launaeion cervicornis
Launaeo arborescentis-Schizogynion sericeae
Lavandulion lanatae
Lavandulo-Echinospartion boissieri
Lepidion subulati
Loiseleurio-Vaccinion
Myrico fayae-Ericion arboreae
Oleo-Ceratonion siliquae
Periplocion angustifoliae
Pinion mugo
Pruno prostratae-Juniperion sabinae
Resedo constrictae-Helianthemion syriacae
Retamion monospermae
Retamion sphaerocarpae
Rhamno lycioidis-Quercion cocciferae
Rhododendro-Vaccinion
Rosmarinion officinalis
Rosmarino-Ericion
Rubo ulmifolii-Nerion
Rubo ulmifolii-Nerion oleandri
Salicion cinereae
Salicion eleagno-daphnoidis
Salicion incanae
Salicion pedicellatae
Salicion pentandrae
Salicion salviifoliae
Salicion silesiacae
Salicion triandrae
Salicion triandro-fragilis
Salicion triandro-neotrichae
Salsolo vermiculatae-Peganion harmalae
Securinegion buxifoliae
Sideritidion bourgaeanae
Sideritido incanae-Salvion lavandulifoliae
Soncho-Sempervivion
Staehelino-Ulicion baetici
Stauracanthion boivinii
Tamaricion africanae
Tamaricion boveano-canariensis
Telinion monspessulano-linifoliae
Teucrio pyrenaici-Bromion erecti
Thymo longiflori-Sideritition
Thymo moroderi-Sideritidion leucanthae
Thymo-Sideritition leucanthae
Thymo-Teucrion verticillati
Ulici argentei-Cistion ladaniferi
Ulici europaei-Cytision striati
Vaccinion
Xeroacantho-Erinaceion

Woodland (G)

Abieti-Piceion
Aceri granatensis-Quercion fagineae
Alnion glutinosae
Alnion incanae
Alno-Padion
Alno-Ulmion
Artemisio glutinosae-Santolinion rosmarinifoliae
Athyrio-Piceion
Avenello ibericae-Pinion ibericae
Betulion carpatico-pubescentis
Betulion fontqueri-celtibericae
Betulion pubescentis
Carici piluliferae-Epilobion angustifolii
Carpinion
Cisto-Pinion canariensis
Corylo-Populion tremulae
Deschampsio-Pinion
Dicrano-Pinion
Erico-Pinion
Eriophoro vaginati-Pinetum mugo
Fagion sylvaticae
Fraxino-Carpinion
Galio rotundifolii-Abietion albae
Genisto germanicae-Quercion
Ilici-Fagion
Juniperion cedri
Juniperion thuriferae
Junipero intermediae-Pinion catalaunici
Luzulo-Fagion

TABLE B.1 (CONT.) CROSSWALK TABLE BETWEEN THE PHYTOSOCIOLOGICAL ALLIANCE ASSIGNED IN THE INFORMATION SYSTEM OF IBERIAN VEGETATION (SIVIM) AND THE MOST LIKELY EUROPEAN NATURE INFORMATION SYSTEM (EUNIS) HABITAT TYPE (IN BRACKETS OFFICIAL CODING).

Nicotiano glaucae-Ricinion communis
Osmundo-Alnion
Paeonio broteroi-Abietion pinsapo
Piceion excelsae
Pino acutisquamae-Juniperion phoeniceae
Pino ibericae-Juniperion sabinae
Pino rotundatae-Sphagnetum
Pino-Juniperion sabinae
Populion albae
Pulmonario longifoliae-Quercion roboris
Quercion broteroi
Quercion fruticosae
Quercion ilicis
Quercion pubescenti-petraeae
Quercion pubescenti-sessiliflorae
Quercion pyrenaicae
Quercion robori-petraeae
Quercion roboris
Querco rotundifoliae-Oleion sylvestris
Rubio periclymeni-Rubion ulmifolii
Salicion albae
Seslerio caeruleae-Pinion uncinatae
Tilio-Acerion

Rocky (H)

Adenocarpion argyrophylli
Adiantion
Adiantion capilli-veneris
Agrostion alpinae
Androsacion alpinae
Androsacion ciliatae
Androsacion vandellii
Andryalo ramosissimae-Crambion filiformis
Andryalo-Glaucion
Anomodontion europaeum
Antirrhinion asarinae
Arenarion balearicae
Asplenio celtiberici-Saxifragion cuneatae
Asplenion glandulosi
Asplenion petrarchae
Asplenion serpentini
Bartramio-Polypodion australis
Bartramio-Polypodion serrati
Brassico balearicae-Helichrysion rupestris
Calamagrostion arundinaceae
Campanulion velutinae
Centrantho-Parietarion
Cheilanthion hispanicae
Cosentinio bivalentis-Lafuenteion rotundifoliae
Cystopteridion
Dryopteridion oreadis
Galeopsion
Galeopsion pyrenaicae
Glaucion flavi
Gymnocarpion robertiani
Homalothecio-Polypodion serrulati
Hymenophyllion tunbrigensis
Hypno-Polypodion vulgaris
Iberidion spathulatae
Iberido-Linarion propinquae
Jasionion foliosae
Linario saxatilis-Senecionion carpetani
Linarion filicaulis
Melico-Phagnalion intermedii
Parietario-Centranthion rubri
Parietario-Galion muralis
Petrocoptidion glaucifoliae
Phagnalo saxatilis-Cheilanthion maderensis
Phagnalo-Cheilanthion fragrantis
Pimpinello-Gouffeion
Pinguiculion longifoliae
Platycapno saxicolae-Iberidion granatensis
Platycapno saxicolae-Iberidion lagascanae
Polypodion serrati
Potentillion caulescentis
Rumici indurati-Dianthion lusitani
Sarcocapnion enneaphyllae
Sarcocapnion pulcherrimae
Saxifragion camposii
Saxifragion continentalis
Saxifragion mediae
Saxifragion nevadensis
Saxifragion praetermissae
Saxifragion trifurcato-canaliculatae
Saxifragion willkommianae
Scrophularion sciophilae
Senecionion leucophylli
Stipion calamagrostis
Teucrion buxifolii
Valeriano longiflorae-Petrocoptidion
Violo biflorae-Cystopteridion alpinae

Agriculture (I)

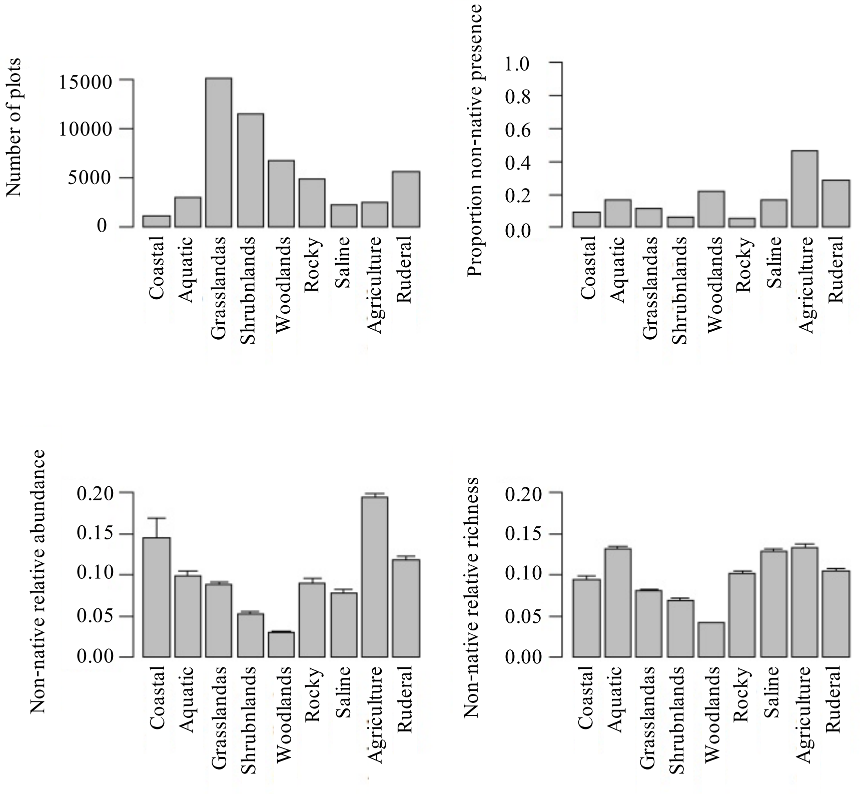
Agropyrion pungentis
Arthrocnemion fruticosi
Arthrocnemion glauci
Atriplicion littoralis
Cypero-Spergularion salinae
Frankenion pulverulentae
Glauco maritimae-Juncion maritimi
Hordeion marini
Juncion maritimi
Limoniastrion monopetali
Limonion catalaunico-viciosoi

(CONT.) CROSSWALK TABLE BETWEEN THE PHYTOSOCIOLOGICAL ALLIANCE ASSIGNED IN THE INFORMATION SYSTEM OF IBERIAN VEGETATION (SIVIM) AND THE MOST LIKELY EUROPEAN NATURE INFORMATION SYSTEM (EUNIS) HABITAT TYPE (IN BRACKETS OFFICIAL CODING).

TABLE B.1

Limonion confusi
Limonion galloprovincialis
Loto-Trifolienion
Lygeo sparti-Limonion angustebracteati
Lygeo-Lepidion cardamines
Microcnemion coralloidis
Oenanthion fistulosae
Plantaginion crassifoliae
Puccinellion caespitosae
Puccinellion limosae
Salicornion dolichostachyo-fragilis
Salicornion europaeo-ramosissimae
Salicornion fruticosae
Salicornion patulae
Scirpion compacti
Scirpion maritimi
Scorzonero-Juncion gerardii
Spartinion maritimae
Suaedion braun-blanquetii
Suaedion brevifoliae
Thero-Salicornion
Thero-Suaedion
Ruderal (E5 & H5.6)
Aphanion
Caucalidion
Caucalidion lappulae
Caucalidion platycarpae
Cerintho majoris-Fedion cornucopiae
Diplotaxion erucoidis
Fumario-Euphorbion
Fumarion wirtgenii-agrariae
Gaudinio verticicolae-Hordeion bulbosi
Lycio europaei-Ipomoeion purpureae
Oryzo sativae-Echinochloion oryzoidis
Panico-Setarion
Polycarpion tetraphylli
Polygono-Chenopodion polyspermi
Roemerion hybridae
Scleranthion annui
Secalion mediterraneum
Sherardion
Spergulo-Oxalidion
Saline (A2.5, D6 & E6)
Adenostylion alliariae
Aegopodion podagrariae
Agropyro-Rumicion crispi
Arction
Arction lappae
Atropion belladonae
Balloto-Conion maculati
Bidention tripartitae
Bromo ramosi-Eupatorion
Bromo ramosi-Eupatorion cannabini
Bromo-Hordeion
Bromo-Oryzopsion miliaceae
Calamagrostion villosae
Carduo carpetani-Cirsion odontolepidis
Carrichtero-Amberboion
Chenopodion glauci
Chenopodion muralis
Cirsion flavispinae
Cirsion richterano-chodati
Convolvulion sepium
Convolvulo arvensis-Agropyrion repentis
Convolvulo-Agropyrion
Dauco-Melilotion
Dryopterido-Athyrion
Echio plantaginei-Galactition tomentosae
Echio-Galactition
Epilobion angustifolii
Eragrostion
Euphorbion peplis
Euphorbion prostratae
Galio-Alliarion
Geranion sanguinei
Glaucio-Cakilion
Hordeion leporini
Linario polygalifoliae-Vulpion alopecuroris
Linarion niveae
Linarion triornithophorae
Malvion neglectae
Matricario-Polygonion arenastri
Mentho-Juncion inflexi
Mesembryanthemion crystallini
Onopordion acanthii
Onopordion arabici
Onopordion castellani
Origanion virentis
Parietarion lusitanico-mauritanicae
Polygonion avicularis
Poo chaixii-Deschampsion
Rumicion alpini
Rumicion pseudalpini
Saginion procumbentis
Salsolion ruthenicae
Salsolo-Peganion
Sambucion ebuli
Santolinion pectinato-canescentis
Sclerochloo durae-Coronopodion squamati
Silybo-Urticion
Sisymbrion officinalis
Trifolio fragiferi-Cynodontion
Trifolio-Cynodontion
Trifolion medii

FIGURE B.1



NUMBER OF PLOTS, PROPORTION OF PLOTS WITH PRESENCE SPECIES AND MEAN (+SE) RELATIVE RICHNESS AND ABUNDANCE OF NON-NATIVE SPECIES AT INVADED PLOTS ACROSS HABITAT TYPES IN MAINLAND SPAIN.

LIST OF NON-NATIVE SPECIES INCLUDED IN THE DATABASE.

TABLE B.2

Abutilon theophrasti
Acacia cyclops
Acacia dealbata
Acacia farnesiana
Acacia melanoxylon
Acacia saligna
Acer negundo
Achyranthes sicula
Aeonium arboreum
Aesculus hippocastanum
Agave americana
Ageratina adenophora
Ailanthus altissima
Aloe arborescens
Alternanthera caracasana
Amaranthus albus
Amaranthus blitoides
Amaranthus blitum
Amaranthus cruentus
Amaranthus deflexus
Amaranthus hybridus
Amaranthus hypochondriacus
Amaranthus muricatus
Amaranthus powellii
Amaranthus retroflexus
Amaranthus spinosus
Amaranthus viridis
Ambrosia artemisiifolia
Ambrosia coronopifolia
Ammannia coccinea
Ammannia robusta
Araujia sericifera
Arctotheca calendula
Artemisia annua
Artemisia verlotiorum
Asparagus setaceus
Aster lanceolatus
Aster pilosus
Atriplex suberecta
Azolla caroliniana
Azolla filiculoides
Baccharis halimifolia
Bidens aurea
Bidens bipinnata
Bidens frondosa
Bidens pilosa
Bidens subalternans
Boussingaultia cordifolia
Bromus willdenowii
Buddleja davidii
Capsicum annuum
Carpinus betulus
Carpobrotus acinaciformis
Carpobrotus edulis
Casuarina cunninghamiana
Cenchrus ciliaris
Cercis siliquastrum
Chamaesyce maculata
Chamaesyce polygonifolia
Chamaesyce prostrata
Chamaesyce serpens
Chamomilla suaveolens
Chenopodium ambrosioides
Chenopodium capitatum
Chenopodium multifidum
Chenopodium pumilio
Chloris gayana
Cleome violacea
Commicarpus africanus
Conyza bonariensis
Conyza canadensis
Conyza primulaefolia
Conyza sumatrensis
Coronopus didymus
Cortaderia selloana
Cotula australis
Cotula coronopifolia
Crassula lycopodioides
Crataegus azarolus
Crepis bursifolia
Cucurbita pepo
Cupressus arizonica
Cuscuta campestris
Cyperus eragrostis
Cyperus michelianus
Datura ferox
Datura innoxia
Datura stramonium
Dichondra micrantha
Digitaria debilis
Duchesnea indica
Echinochloa hispidula
Echinochloa oryzoides
Eclipta prostrata
Einadia nutans
Elaeagnus angustifolia
Eleocharis bonariensis
Eleusine indica
Eleusine tristachya
Eragrostis curvula
Eragrostis pectinacea
Erigeron annuus
Erigeron karvinskianus
Eriobotrya japonica
Eucalyptus camaldulensis
Eucalyptus globulus
Euonymus japonicus
Eupatorium adenophorum
Euphorbia lathyris
Fallopia baldschuanica
Fallopia dumetorum
Fraxinus ornus
Galinsoga ciliata
Galinsoga parviflora

Table B.2 (Cont.) list of non-native species included in the database.

Gamochaeta subfalcata
Gleditsia triacanthos
Gomphocarpus fruticosus
Gymnostyles stolonifera
Gypsophila pilosa
Helianthus annuus
Helianthus tuberosus
Heliotropium curassavicum
Hibiscus trionum
Impatiens balfourii
Impatiens glandulifera
Impatiens noli-tangere
Ipomoea batatas
Ipomoea indica
Ipomoea purpurea
Ipomoea sagittata
Ipomoea stolonifera
Ixia paniculata
Jasminum nudiflorum
Juncus tenuis
Lepidium perfoliatum
Lepidium virginicum
Ligustrum lucidum
Ligustrum ovalifolium
Lindernia dubia
Lonicera japonica
Ludwigia grandiflora
Lychnis coronaria
Lycium barbarum
Lycopersicon esculentum
Melia azedarach
Mentha spicata
Mesembryanthemum crystallinum
Mirabilis jalapa
Mollugo verticillata
Nicotiana glauca
Nothoscordum inodorum
Oenothera biennis
Oenothera glazioviana
Oenothera rosea
Opuntia dillenii
Opuntia maxima
Opuntia tuna
Oxalis articulata
Oxalis latifolia
Oxalis pes-caprae
Panicum capillare
Panicum dichotomiflorum
Panicum miliaceum
Parthenocissus quinquefolia
Paspalum dilatatum
Paspalum urvillei
Paspalum vaginatum
Pennisetum setaceum
Pennisetum villosum
Phaseolus vulgaris
Phoenix canariensis
Phyla nodiflora
Physalis philadelphica
Phytolacca americana
Pinus canariensis
Pinus radiata
Pontederia cordata
Populus deltoides
Prunus cerasifera
Prunus laurocerasus
Pseudotsuga menziesii
Pyrus communis
Quercus rubra
Reynoutria japonica
Ribes rubrum
Robinia pseudoacacia
Rumex cristatus
Salix babylonica
Salvia microphylla
Salvinia natans
Senecio angulatus
Senecio inaequidens
Senecio mikanioides
Setaria faberi
Setaria geniculata
Setaria italica
Setaria pumila
Setaria viridis
Sida spinosa
Silene dichotoma
Solanum chenopodioides
Solanum melongena
Solanum sodomeum
Solanum sublobatum
Solanum tuberosum
Solidago altissima
Solidago canadensis
Sophora japonica
Sorghum halepense
Spartina alterniflora
Spartina densiflora
Spartina patens
Sporobolus indicus
Stenotaphrum secundatum
Tagetes minuta
Tetragonia tetragonoides
Trachycarpus fortunei
Tradescantia fluminensis
Tropaeolum majus
Ulmus pumila
Verbena supina
Veronica persica
Vitis vulpina
Xanthium spinosum
Xanthium strumarium
Zantedeschia aethiopica
Zea mays

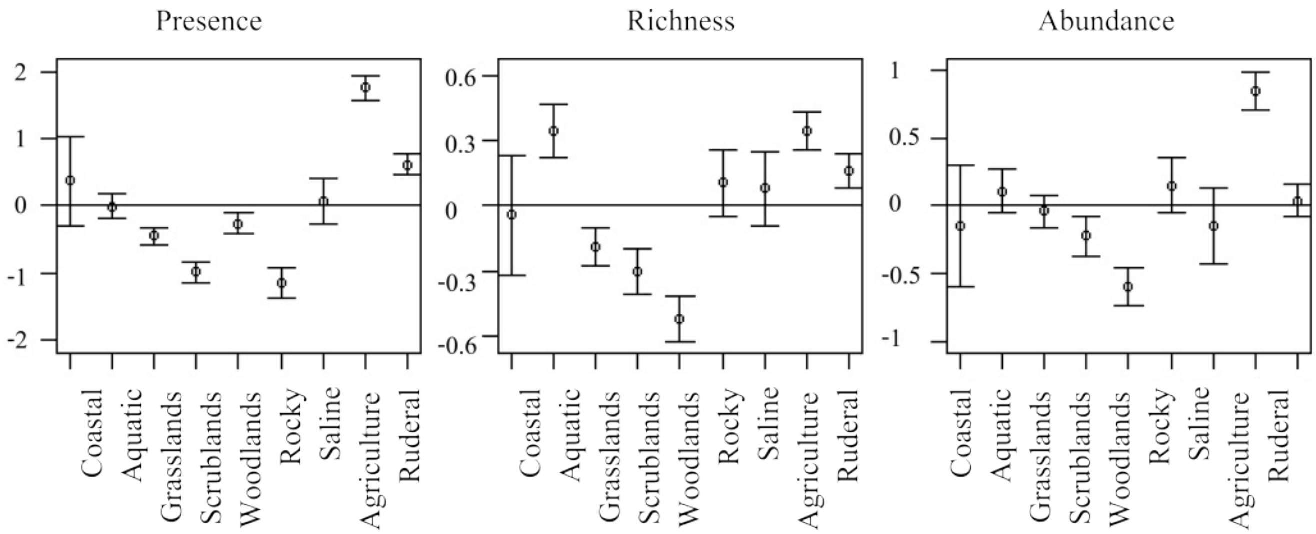
Variables used as predictors of to explain presence, relative richness and abundance of non-native plant species. For each variable we provide examples of previous research including them.

Table B.3

Variable	Description	References
Habitat type		(Vilà et al., 2007; Chytrý et al., 2008b,a)
Bioclimatic region		
Climate		
Mean annual temperature (ºC)	Mean temperature	(Pino et al., 2005; Ohlemüller et al., 2006; Gassó et al., 2009; Marini et al., 2009; Polce et al., 2011)
Winter min. temperature (ºC)*	Min. temperature of coldest month	(Ibáñez et al., 2009b; Catford et al., 2011)
Summer max. temperature (ºC)	Max. temperature of warmest month	(Ibáñez et al., 2009b; Catford et al., 2011)
Temperature seasonality (ºC)*	Standard deviation of annual temperature	(Gassó et al., 2009)
Annual precipitation (mm)*	Total precipitation per year	(Pino et al., 2005; Gassó et al., 2009; Ibáñez et al., 2009b; Marini et al., 2009; Carboni et al., 2010)
Summer precipitation (mm)*	Precipitation in warmest quarter	(Gassó et al., 2009; Catford et al., 2011)
Precipitation seasonality (mm)	Standard deviation of annual precipitation	(Gassó et al., 2009)
Distance to coast (Km)*	Continentality measure	(Pino et al., 2005; Gassó et al., 2009)
Human activity		
Shrubland land-cover (%)*		(Deutschewitz et al., 2003; Sullivan et al., 2005; Ohlemüller et al., 2006; Ibáñez et al., 2009b; Marini et al., 2009)
Woodland land-cover (%)*		(Deutschewitz et al., 2003; Sullivan et al., 2005; Ohlemüller et al., 2006; Ibáñez et al., 2009b; Marini et al., 2009)
Urban land-cover (%)*	Including build-up areas and transportation infrastructures	(Pino et al., 2005; Sullivan et al., 2005; Marini et al., 2009; Carboni et al., 2010; Polce et al., 2011; Catford et al., 2011)
Agricultural land-cover (%)*		(Deutschewitz et al., 2003; Ibáñez et al., 2009b; Marini et al., 2009; Souza et al., 2011)
Shannon land-cover diversity*		(Pino et al., 2005; Kumar et al., 2006; Marini et al., 2009)

*Variables included in the final analysis to avoid collinearity

FIGURE B.2



POSTERIOR MEANS (WITH CREDIBLE INTERVALS) OF THE MEAN COEFFICIENTS FOR HABITAT TYPE IN THE HIERARCHICAL MODELS FOR THE PRESENCE OF NON-NATIVE SPECIES AND THE RELATIVE RICHNESS AND ABUNDANCE AT INVADED PLOTS. TO FACILITATE COMPARISON, HABITAT COEFFICIENTS ARE CENTERED AROUND THE MEAN OF ALL HABITAT COEFFICIENTS.

Table B.4

Pearson's correlation coefficients among climate and human activity variables used to model the level of plant invasion

All plots	Winter minimum temperature	Temperature seasonality	Annual precipitation	Summer Precipitation	Distance to coast	Urban cover	Agriculture cover	Grassland cover	Woodland cover
Temperature seasonality	-0.35								
Annual precipitation	-0.30	-0.52							
Summer Precipitation	-0.56	-0.31	0.69						
Distance to coast	-0.37	0.67	-0.12	-0.17					
Urban cover	0.40	-0.17	-0.19	-0.15	-0.17				
Agriculture cover	0.44	0.27	-0.57	-0.53	0.05	0.21			
Grassland cover	-0.40	-0.16	0.48	0.44	0.03	-0.49	-0.64		
Woodland cover	-0.37	-0.15	0.45	0.44	-0.03	-0.41	-0.58	0.25	
Land-cover diversity	0.31	0.04	-0.29	-0.32	-0.02	0.15	0.17	-0.30	-0.12
Invaded plots									
Temperature seasonality	-0.37								
Annual precipitation	-0.26	-0.59							
Summer Precipitation	-0.50	-0.34	0.73						
Distance to coast	-0.45	0.64	-0.15	-0.17					
Urban cover	0.48	-0.16	-0.27	-0.22	-0.26				
Agriculture cover	0.43	0.33	-0.60	-0.59	0.05	0.26			
Grassland cover	-0.44	-0.17	0.52	0.48	0.08	-0.59	-0.66		
Woodland cover	-0.42	-0.18	0.54	0.53	0.03	-0.50	-0.62	0.38	
Land-cover diversity	0.26	0.11	-0.33	-0.35	0.02	0.07	0.24	-0.29	-0.19

TABLE B.5

NUMBER OF ALL PLOTS AND INVADED PLOTS FOR EACH COMBINATION OF HABITAT TYPE AND BIOCLIMATIC REGION.

Habitat	Number of plots			Number of invaded plots		
	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit
Coastal	0	514	612	0	36	65
Aquatic	126	367	2561	26	98	390
Grassland	2081	1468	9407	220	129	1136
Scrubland	832	1680	11337	53	214	739
Woodland	1126	1453	4231	362	634	516
Rocky	661	956	3340	15	69	210
Agriculture	99	126	2367	43	86	1080
Ruderal	542	634	4515	167	175	1301
Saline	0	262	2053	0	38	344

Confidence intervals of paired habitat coefficient differences for the non-hierarchical model. In bold comparison between habitats whose mean coefficients are significantly different.

Table B.6

	Coastal	Aquatic	Grassland	Shrubland	Woodland	Rocky	Saline	Agriculture
PRESENCE								
Aquatic	**(0.61,1.19)**							
Grassland	**(0.25,0.79)**	**(-0.51,-0.25)**						
Shrubland	(-0.35,0.21)	**(-1.12,-0.81)**	**(-0.7,-0.48)**					
Woodland	**(1.01,1.56)**	**(0.23,0.53)**	**(0.66,0.86)**	**(1.23,1.47)**				
Rocky	(-0.52,0.08)	**(-1.31,-0.93)**	**(-0.89,-0.59)**	(-0.31,0.01)	**(-1.66,-1.35)**			
Saline	**(0.28,0.88)**	**(-0.51,-0.13)**	(-0.11,0.23)	**(0.47,0.82)**	**(-0.88,-0.52)**	**(0.58,1.01)**		
Agriculture	**(2.31,2.88)**	**(1.53,1.86)**	**(1.95,2.2)**	**(2.52,2.8)**	**(1.18,1.44)**	**(2.64,2.99)**	**(1.83,2.2)**	
Ruderal	**(1.33,1.87)**	**(0.56,0.84)**	**(0.98,1.17)**	**(1.55,1.78)**	**(0.21,0.42)**	**(1.66,1.97)**	**(0.85,1.19)**	**(-1.12,-0.87)**
RICHNESS								
Aquatic	**(0.05,0.53)**							
Grassland	(-0.46,0)	**(-0.64,-0.4)**						
Shrubland	**(-0.55,-0.08)**	**(-0.74,-0.47)**	(-0.19,0.01)					
Woodland	**(-0.78,-0.33)**	**(-0.97,-0.72)**	**(-0.41,-0.24)**	**(-0.35,-0.13)**				
Rocky	(-0.2,0.31)	**(-0.4,-0.06)**	**(0.14,0.43)**	**(0.22,0.53)**	**(0.46,0.77)**			
Saline	(-0.16,0.34)	**(-0.37,-0.03)**	**(0.18,0.46)**	**(0.25,0.56)**	**(0.5,0.79)**	(-0.15,0.22)		
Agriculture	**(0.03,0.48)**	(-0.15,0.09)	**(0.41,0.57)**	**(0.48,0.67)**	**(0.72,0.91)**	**(0.06,0.35)**	**(0.03,0.31)**	
Ruderal	(-0.13,0.31)	**(-0.32,-0.08)**	**(0.24,0.4)**	**(0.31,0.5)**	**(0.55,0.73)**	(-0.11,0.18)	(-0.14,0.14)	**(-0.25,-0.09)**
ABUNDANCE								
Aquatic	(-0.07,0)							
Grassland	(-0.07,0)	(-0.02,0.02)						
Shrubland	**(-0.11,-0.04)**	**(-0.06,-0.02)**	**(-0.05,-0.03)**					
Woodland	**(-0.12,-0.05)**	**(-0.06,-0.03)**	**(-0.06,-0.04)**	(-0.02,0.01)				
Rocky	(-0.07,0)	(-0.02,0.02)	(-0.02,0.02)	**(0.02,0.06)**	**(0.03,0.07)**			
Saline	**(-0.12,-0.05)**	**(-0.07,-0.02)**	**(-0.07,-0.03)**	(-0.03,0.01)	(-0.02,0.02)	**(-0.07,-0.02)**		
Agriculture	**(0.02,0.08)**	**(0.07,0.11)**	**(0.08,0.1)**	**(0.11,0.14)**	**(0.12,0.15)**	**(0.07,0.11)**	**(0.12,0.15)**	
Ruderal	(-0.05,0.01)	(0,0.03)	(0,0.03)	**(0.04,0.07)**	**(0.05,0.08)**	(0,0.04)	**(0.04,0.08)**	**(-0.09,-0.06)**

TABLE B.7

Confidence intervals of paired habitat coefficient differences for the hierarchical model. In bold comparison between habitats whose mean coefficients are significantly different.

	Coastal	Aquatic	Grassland	Shrubland	Woodland	Rocky	Saline	Agriculture
PRESENCE								
Aquatic	(-1.15,0.38)							
Grassland	**(-1.58,-0.07)**	**(-0.63,-0.25)**						
Shrubland	**(-2.13,-0.6)**	**(-1.19,-0.77)**	**(-0.7,-0.38)**					
Woodland	(-1.4,0.13)	**(-0.46,-0.05)**	**(0.03,0.34)**	**(0.55,0.9)**				
Rocky	**(-2.31,-0.73)**	**(-1.4,-0.86)**	**(-0.93,-0.46)**	(-0.4,0.09)	**(-1.13,-0.63)**			
Saline	(-1.12,0.51)	(-0.33,0.49)	**(0.13,0.91)**	**(0.66,1.46)**	(-0.07,0.73)	**(0.77,1.66)**		
Agriculture	(0.61,2.15)	**(1.52,2.01)**	**(2.01,2.4)**	**(2.53,2.96)**	**(1.8,2.24)**	**(2.62,3.18)**	**(1.27,2.1)**	
Ruderal	(-0.53,1)	**(0.42,0.82)**	**(0.92,1.2)**	**(1.43,1.77)**	**(0.71,1.04)**	**(1.51,2)**	**(0.15,0.93)**	**(-1.35,-0.94)**
RICHNESS								
Aquatic	**(0.06,0.72)**							
Grassland	(-0.46,0.17)	**(-0.68,-0.38)**						
Shrubland	(-0.58,0.06)	**(-0.81,-0.48)**	(-0.24,0.02)					
Woodland	**(-0.8,-0.15)**	**(-1.03,-0.7)**	**(-0.46,-0.21)**	**(-0.37,-0.08)**				
Rocky	(-0.19,0.49)	**(-0.44,-0.03)**	**(0.11,0.47)**	**(0.21,0.6)**	**(0.43,0.82)**			
Saline	(-0.23,0.48)	**(-0.48,-0.04)**	**(0.07,0.47)**	**(0.17,0.59)**	**(0.39,0.82)**	(-0.27,0.23)		
Agriculture	**(0.07,0.7)**	(-0.15,0.15)	**(0.41,0.64)**	**(0.51,0.77)**	**(0.73,0.99)**	**(0.05,0.41)**	**(0.05,0.46)**	
Ruderal	(-0.11,0.52)	**(-0.33,-0.04)**	**(0.24,0.45)**	**(0.33,0.58)**	**(0.56,0.8)**	(-0.12,0.23)	(-0.12,0.27)	**(-0.29,-0.07)**
ABUNDANCE								
Aquatic	(-0.28,0.78)							
Grassland	(-0.4,0.62)	(-0.33,0.04)						
Shrubland	(-0.59,0.44)	**(-0.54,-0.12)**	**(-0.35,-0.01)**					
Woodland	(-0.96,0.08)	(-0.89,-0.49)	**(-0.71,-0.39)**	**(-0.55,-0.18)**				
Rocky	(-0.25,0.84)	(-0.22,0.31)	(-0.04,0.42)	**(0.12,0.62)**	**(0.49,0.98)**			
Saline	(-0.57,0.57)	(-0.59,0.1)	(-0.43,0.22)	(-0.26,0.41)	**(0.11,0.78)**	(-0.67,0.08)		
Agriculture	**(0.47,1.51)**	**(0.53,0.94)**	**(0.71,1.05)**	**(0.87,1.25)**	**(1.24,1.62)**	**(0.44,0.94)**	**(0.66,1.32)**	
Ruderal	(-0.33,0.69)	(-0.25,0.12)	(-0.06,0.22)	**(0.09,0.43)**	**(0.46,0.79)**	(-0.35,0.12)	(-0.14,0.5)	**(-0.97,-0.64)**

TABLE B.8

POSTERIOR MEAN WITH 95% CONFIDENCE INTERVALS (C.I.) OF THE COEFFICIENTS FOR CLIMATE VARIABLES ACROSS BIOCLIMATIC REGIONS AND HABITAT TYPES IN THE HIERARCHICAL MODEL OF THE RELATIVE ABUNDANCE OF NON-NATIVE SPECIES AT INVADED PLOTS. IN BOLD SIGNIFICANT COEFFICIENTS.

Habitat		Winter Min. temperature			Temperature seasonality			Annual precipitation			Summer precipitation			Distance to coast		
		Alpine	Atlantic	Medit	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit
Coastal		0.05	0.06	-0.17	0.15	0.16	0	0.36	**1.39**	-0.17	-0.36	-0.71	-0.22	0.18	1.27	0
	C.I	0.64,0.75	-0.4,0.43	-0.56,0.22	1.02,1.33	0.59,0.81	-0.36,0.3	0.58,1.42	**0.82,1.96**	0.73,0.25	-1,0.23	2.06,0.07	-0.7,0.18	0.82,1.36	0.69,3.69	0.14,0.16
Aquatic		0.03	0.05	**-0.25**	0.23	0.18	0	0.34	0.26	0.11	-0.32	-0.42	-0.23	0.17	-0.33	0.03
	C.I	0.63,0.69	0.34,0.38	**0.04**	0.75,1.27	-0.47,0.8	0.21,0.18	0.36,1.03	0.24,0.75	0.17,0.39	-0.79,0.15	1.03,0.11	-0.5,0.02	0.66,1.01	1.81,1.14	0.08,0.18
Grassland		0.06	0.11	0.03	0.16	0.07	**0.18**	0.27	-0.06	-0.2	-0.28	-0.11	0.15	0.15	-0.34	0
	C.I	-0.57,0.7	0.21,0.44	-0.13,0.2	0.71,1.05	0.41,0.53	**0.02,0.34**	0.34,0.85	0.42,0.29	-0.41,0	-0.69,0.15	0.63,0.56	-0.02,0.33	0.49,0.81	1.38,0.74	0.09,0.09
Shrubland		0.07	0.15	-0.17	0.04	**0.71**	-0.08	0.39	**0.74**	0.08	-0.37	-0.33	-0.13	0.26	-0.07	0
	C.I	0.59,0.75	0.17,0.49	-0.37,0.02	1.04,1.05	**0.16,1.28**	0.28,0.11	0.28,1.14	**0.36,1.11**	0.13,0.29	-0.86,0.09	1.07,0.37	-0.33,0.06	0.51,1.24	-1.3,1.23	-0.11,0.1
Woodland		0.05	0.08	**-0.28**	0.13	**0.42**	0	0.35	0.11	0.23	-0.28	-0.21	-0.06	0.08	-0.82	-0.01
	C.I	0.58,0.68	0.22,0.38	**0.07**	0.75,1.01	**0.05,0.8**	0.19,0.17	0.15,0.87	0.14,0.35	0.01,0.48	-0.68,0.11	0.58,0.16	-0.23,0.1	0.48,0.63	-1.66,0	-0.13,0.1
Rocky		0.04	0.04	**-0.49**	0.32	0.07	-0.01	0.24	0.44	0.03	-0.34	-0.52	-0.15	0.1	-0.39	0.01
	C.I	0.63,0.71	0.36,0.38	**0.24**	0.69,1.53	0.67,0.74	0.25,0.19	0.68,0.93	-0.29,1.2	0.31,0.34	-0.84,0.15	1.35,0.13	-0.43,0.13	0.84,0.94	-1.9,1.15	0.11,0.16
Saline		0.05	0.05	0.02	0.15	0.21	-0.05	0.36	0.31	0.11	-0.36	-0.35	**-0.52**	0.19	-0.33	0.02
	C.I	0.64,0.75	0.45,0.43	-0.3,0.34	1.04,1.36	0.51,0.89	0.33,0.16	0.62,1.43	0.48,1.05	0.28,0.51	-1,0.21	1.12,0.37	**-0.96,-0.11**	0.83,1.35	2.06,1.33	-0.1,0.18
Agriculture		0.08	0.13	-0.14	0.01	0.43	0.11	0.64	0.3	**0.31**	**-0.52**	-0.08	-0.1	0.43	-0.37	-0.01
	C.I	0.58,0.78	0.23,0.56	-0.3,0.03	1.17,1.06	-0.12,1	0.03,0.25	0.13,2.03	0.31,0.88	**0.13,0.5**	**-1.12,-0.05**	0.74,0.87	-0.28,0.09	0.35,1.57	-1.89,1.1	-0.1,0.09
Ruderal		0.04	0.11	0.08	0.13	-0.33	0.06	0.34	0.15	**0.21**	-0.41	-0.39	-0.12	0.1	0.46	-0.02
	C.I	0.59,0.69	-0.2,0.41	-0.08,0.24	0.79,1.07	0.99,0.27	0.08,0.19	0.19,0.89	0.22,0.51	**0.03,0.39**	-0.86,-0.01	0.95,0.12	-0.28,0.05	0.55,0.72	-0.9,1.97	0.13,0.07

Table B.9

Posterior mean with 95% confidence intervals (C.I.) of the coefficients for climate variables across bioclimatic regions and habitat types in the hierarchical model of the presence of non-native species. In bold significant coefficients.

Habitat		Winter Minimum temperature			Temperature seasonality			Annual precipitation			Summer precipitation			Distance to coast		
		Alpine	Atlantic	Medit	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit
Coastal		-0.33	0.31	**-0.77**	-0.98	-0.46	0.01	-0.11	1.43	0.25	0.33	**-3.07**	**0.61**	-0.94	0.78	-0.3
	C.I	-1.6,1.08	-0.75,1.43	**-1.47,-0.13**	-2.59,0.7	-1.42,0.27	-0.56,0.55	-3.4,3.43	0.75,2.14	-0.34,0.89	-0.8,1.38	**-4.67,-1.46**	**0.14,1.13**	-3.54,1.57	-1.59,3.65	-0.77,0.04
Aquatic		-0.45	**-0.91**	**-0.35**	-1.02	-0.77	-0.25	-0.63	0	-0.11	0.44	0.21	0.27	-1.04	1.17	-0.18
	C.I	-1.46,0.56	**-1.7,-0.18**	**-0.6,-0.1**	-2.37,0.39	-1.98,0.03	-0.53,0.01	-1.89,0.5	-0.89,0.84	-0.43,0.21	-0.39,1.23	-0.96,1.44	-0.08,0.59	-2.44,0.27	-0.8,3.94	-0.37,0.01
Grassland		-0.57	**0.55**	0.07	-1.19	-0.19	**0.26**	**-1.02**	**-0.42**	**-0.33**	0.35	0.38	0.53	0	-0.3	**-0.25**
	C.I	-1.47,0.33	**0.08,1.02**	-0.1,0.25	-2.4,0.03	-0.74,0.44	**0.09,0.42**	**-1.83,-0.21**	**-0.84,-0.01**	**-0.54,-0.12**	-0.37,1.01	-0.28,1.05	0.35,0.71	-0.99,1.01	-1.61,0.98	**-0.37,-0.13**
Shrubland		-0.15	**0.65**	0.09	-0.96	-0.22	-0.11	-0.74	0.79	-0.2	0.34	**-2.6**	**0.52**	-0.74	-1.3	-0.04
	C.I	-1.16,0.96	**0.15,1.16**	-0.12,0.3	-2.27,0.49	-0.81,0.45	-0.31,0.09	-1.87,0.38	0.32,1.24	-0.43,0.03	-0.48,1.17	**-3.73,-1.55**	**0.31,0.74**	-2.09,0.62	-3.06,0.33	-0.2,0.13
Woodland		-0.34	-0.48	-0.02	-0.75	-0.27	**0.27**	0.68	0.31	**0.31**	0.63	0.19	**0.51**	-0.56	-0.54	-0.04
	C.I	-1.21,0.63	-0.93,-0.03	-0.25,0.22	-1.92,0.58	-0.75,0.22	**0.06,0.5**	-0.01,1.47	-0.03,0.64	**0.03,0.59**	-0.08,1.31	-0.33,0.72	**0.3,0.71**	-1.39,0.29	-1.64,0.54	-0.22,0.14
Rocky		-0.14	0.43	-0.09	-0.89	-0.04	-0.07	-0.79	**-1.31**	**-0.81**	0.23	1.19	**0.48**	-1.29	-1.25	**-0.23**
	C.I	-1.18,1.03	-0.24,1.11	-0.39,0.19	-2.27,0.66	-0.78,1.11	-0.36,0.2	-2.24,0.62	**-2.42,-0.36**	**-1.2,-0.42**	-0.68,1.07	-0.12,2.57	**0.16,0.79**	-2.86,0.24	-3.72,0.6	**-0.46,-0.01**
Saline		-0.32	-0.43	-0.26	-0.98	-0.21	-0.13	-0.1	0.23	0.41	0.33	-0.79	-0.13	-0.93	-0.21	-0.17
	C.I	-1.58,1.09	-2.15,0.96	-0.7,0.14	-2.62,0.72	-0.98,0.74	-0.49,0.21	-3.47,3.36	-0.74,1.15	-0.18,1.07	-0.78,1.36	-2.17,0.54	-0.8,0.51	-3.54,1.58	-2.83,2.22	-0.42,0.09
Agriculture		-0.05	-0.21	-0.01	-1	-0.37	-0.02	1.47	**-1.14**	-0.11	0.13	**1.68**	**0.69**	-1.16	-0.31	**-0.19**
	C.I	-1.12,1.19	-1.11,0.64	-0.25,0.24	-2.42,0.48	-1.24,0.43	-0.22,0.17	-0.29,3.75	**-1.99,-0.35**	-0.37,0.14	-0.82,0.96	**0.41,3.08**	**0.42,0.98**	-2.89,0.35	-2.63,1.99	**-0.34,-0.03**
Ruderal		-0.55	0.26	**0.28**	-1.04	-0.55	**0.24**	0.3	**0.77**	-0.09	0.17	-0.88	**0.65**	**-1.83**	1.71	**-0.4**
	C.I	-1.48,0.41	-0.25,0.74	**0.08,0.49**	-2.31,0.25	-1.38,0.1	**0.06,0.43**	-0.54,1.21	**0.29,1.24**	-0.32,0.14	-0.61,0.88	-1.78,0.02	**0.45,0.87**	**-2.94,-0.73**	-0.16,3.77	**-0.56,-0.25**

TABLE B.10

POSTERIOR MEANS WITH 95% CONFIDENCE INTERVALS (C.I.) OF THE COEFFICIENTS FOR CLIMATE VARIABLES ACROSS BIOCLIMATIC AND HABITAT TYPES IN THE HIERARCHICAL MODEL OF THE RELATIVE RICHNESS OF NON-NATIVE SPECIES AT INVADED PLOTS. IN BOLD SIGNIFICANT COEFFICIENTS.

Habitat	Winter Min. temperature			Temperature seasonality			Annual precipitation			Summer precipitation			Distance to coast		
	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit	Alpine	Atlantic	Medit
Coastal	-0.23	0.21	0.11	-0.33	0.08	0.09	-0.08	0.03	0.03	-0.25	-0.07	-0.1	0.18	-0.4	0.01
C.I	0.77,0.42	0.08,0.51	0.01,0.26	1.25,0.55	0.22,0.33	0.17,0.34	0.69,0.51	0.15,0.22	-0.15,0.2	-0.62,0.1	-0.4,0.3	0.36,0.14	0.67,1.14	1.05,0.17	0.09,0.14
Aquatic	-0.21	0.17	0.1	-0.29	0.13	0.13	-0.17	0.01	0.04	-0.27	-0.14	-0.12	0.22	-0.37	-0.01
C.I	0.72,0.43	-0.1,0.43	-0.02,0.2	1.17,0.51	-0.13,0.4	0.02,0.27	-0.76,0.3	0.19,0.18	0.11,0.18	0.61,0.05	0.44,0.15	0.29,0.04	-0.4,0.98	-1,0.18	0.09,0.08
Grassland	-0.24	**0.23**	0.09	-0.25	0.09	-0.01	-0.09	0	0.02	-0.23	-0.08	**-0.11**	0.05	-0.41	-0.01
C.I	0.77,0.39	**0,0.47**	0.02,0.18	1.05,0.48	0.18,0.32	-0.13,0.1	0.58,0.35	0.18,0.16	0.11,0.13	0.52,0.07	0.38,0.24	**-0.23,0**	0.47,0.54	-1,0.13	0.08,0.06
Shrubland	-0.22	0.15	**0.12**	-0.38	0.14	0.05	-0.07	0.03	0.05	-0.27	-0.09	**-0.16**	0.14	-0.37	0
C.I	0.74,0.43	-0.11,0.4	**0.01,0.23**	1.22,0.42	0.11,0.39	0.09,0.18	0.61,0.45	0.14,0.21	0.07,0.17	-0.6,0.06	0.41,0.26	**0.04**	0.55,0.85	0.98,0.17	0.08,0.08
Woodland	-0.26	0.18	0.1	-0.25	0.18	0.06	-0.07	0.02	0.03	-0.2	-0.09	-0.09	0.07	-0.33	-0.02
C.I	0.78,0.36	-0.05,0.4	-0.03,0.2	1.05,0.45	0.05,0.43	0.08,0.21	0.52,0.31	0.14,0.16	0.12,0.15	-0.48,0.1	0.34,0.16	-0.2,0.03	0.37,0.51	0.88,0.16	0.12,0.06
Rocky	-0.22	0.2	0.1	-0.34	0.09	0.12	-0.08	0.03	0.07	-0.26	-0.07	-0.01	0.18	-0.41	0.01
C.I	0.74,0.43	0.06,0.47	0.03,0.21	1.19,0.45	-0.2,0.35	0.06,0.29	0.62,0.45	0.16,0.23	0.07,0.25	0.59,0.07	0.38,0.26	0.18,0.22	0.51,0.98	1.04,0.13	0.07,0.14
Saline	-0.23	0.2	0.11	-0.33	0.12	0.12	-0.09	0.02	0.01	-0.25	-0.1	**-0.23**	0.17	-0.36	0.01
C.I	0.77,0.43	0.11,0.51	0.02,0.23	1.24,0.56	0.15,0.38	0.06,0.29	-0.7,0.5	0.17,0.22	0.19,0.16	-0.61,0.1	0.42,0.24	**0.03**	-0.64,1.1	0.98,0.21	0.07,0.15
Agriculture	-0.22	0.21	**0.1**	-0.43	0.17	**0.28**	0	0.01	0.07	-0.26	-0.11	-0.03	0.34	-0.29	-0.01
C.I	0.74,0.43	0.07,0.51	**0.01,0.2**	1.31,0.39	0.07,0.44	**0.18,0.37**	0.52,0.59	0.19,0.18	-0.04,0.2	0.58,0.05	0.42,0.22	-0.15,0.1	0.26,1.19	-0.91,0.3	0.08,0.05
Ruderal	-0.22	**0.28**	**0.13**	-0.33	0.13	**0.12**	-0.09	-0.01	0.03	-0.26	-0.19	-0.1	0.23	-0.28	0
C.I	0.73,0.41	**0.05,0.53**	**0.04,0.24**	1.14,0.41	0.15,0.38	**0.02,0.22**	0.54,0.31	0.18,0.15	0.07,0.14	0.57,0.04	-0.54,0.1	-0.21,0	-0.28,0.8	0.84,0.34	0.06,0.08

APPENDIX C- MODELLING DETAILS AND SOFTWARE CODE

Modelling details

Presence of non-native species

The presence-absence of non-native species at plot “i” (N_i) was estimated from a Bernoulli distribution with probability of being present p_i:

Likelihood: N_i ~Bernoulli (p_i)
Process model: $\text{logit}(p_i) = \alpha_{\text{habitat (i)}}+\beta X_i + e_{g\ (i)}$

where αhabitat represents the intercept for each habitat type. Each intercept was given a non-informative prior distribution, α~Normal(0,100). Random effects for each UTM grid, g, were estimated from the same grid level distribution, where $e_{g(i)}\sim$ Normal (μ_e, σ^2_e) with $\mu_e\sim$Normal(0, 10000) and $\sigma_e\sim$ Uniform (0,100). The design matrix of explanatory variables, Xi, included all the climate and human activity variables. The vector of coefficients associated with each climate and human activity variable, β, was estimated using both a hierarchical and non-hierarchical approach (Fig. 2). In the latter case (GLM model), each coefficient was given non-informative normal distributions, β~Normal(0,10000).

For the hierarchical approach (HGLM model) the coefficients associated with each climate variable were grouped within regions and habitat type to understand the interaction among them (Fig. 2). The effect of each climate variable (cv) was estimated for each habitat, nested within regions: $\beta_{\text{cv,region,habitat}}\sim$ Normal($\mu_{\text{cv,region}}$, $\sigma^2_{\text{cv,region}}$). Due to the small number of regions the mean effect of climate variables for each bioclimatic region were given independent non-informative prior distributions (Gelman & Hill, 2007): $\mu_{\text{cv,region}}\sim$ Normal(0,10000) and $\sigma_{\text{cv,region}}\sim$Uniform(0,100). Similarly, the effect of each human activity variables (lv) was estimated for each region from non-informative prior distributions:

$\beta_{\text{lv,region}}\sim$Normal(0,10000).

Richness and abundance of non-native species

Non-native species richness at each plot, $NNSR_i$, was modelled using a Binomial distribution with parameters TR_i , total species richness, and qi. , the probability of being non-native:

Likelihood: $NNSR_i \sim$ Binomial (q_i ,TR_i)
Process model: Logit(q_i) = $\alpha_{habitat(i)} + \beta X_i + e_{g(i)}$

To ensure positive values, and also improve convergence, non-native species relative abundance, $NNSRA_i$: $NNSA_i/TA_i$,(non-native species abundance/total vegetation abundance), was modeled using a Log-Normal distribution with mean μ_{Ai} and variance σ_A:

Likelihood:$NNSRA_i$~Log-Normal(μ_{Ai}, σ^2_A)
Process model: $\mu_{Ai} = \alpha_{habitat(i)} + \beta X_i + e_{g(i)}$

where σ_A was estimated from a non-informative distribution, $\sigma_A \sim$ Uniform (0,100). The habitat-related intercepts, $\alpha_{habitat}$, the vector of coefficients associated with each climate and human activity variables, β, and the plot level random effects, e_g, were also modelled following the same approach described for the presence model.

Openbugs codes

Modelling the presence of non-native plant species

Openbugs codes to model the presence probability of non-native plant species using 53345 plots (NP) and 3158 UTM grids (NG)

Non-hierarchical model{

```
###########
 ##Likelihood
###########
for (i in 1:NP) {
   y[i] ~ dbern (p.bound[i])
   p.bound[i]  <-  max(0,  min(1,  p[i]))
   logit(p[i]) <- xbeta[i] + alpha[grid[i]]
```

```
   xbeta[i] <-  betaH[HABITAT[i]] + beta[1]*TMIN1[i] + beta[2]*TSEAS[i] + beta[3]*PTOT[i]
+beta[4]*PWARQ[i] +beta[5]*DCOAST[i] +betaG[1]*URBANO[i] + betaG[2]*AGRIC[i] + betaG[3]*GRASS[i]
+betaG[4]*FOREST[i]+betaG[5]*SH_COV[i]
###########
# Priors
##########
#Random effect for grid level.
for (g in 1:NG) {
   alpha[g] ~ dnorm(alpha.mean,alpha.tau)
 }
   alpha.mean ~ dnorm(0, 0.0001)
   alpha.tau <- pow(alpha.sigma, -2)
   alpha.sigma ~ dunif(0,100)
# Hyperprior for Habitat
for (j in 1:9)  {
   betaH[j] ~ dnorm(0, betaH.tau)
   betaH.adj[j] <- betaH[j] - mean(betaH[])
}
   betaH.tau <- pow(betaH.sigma, -2)
   betaH.sigma ~ dunif(0, 100)
 # Independent effect of climate variables
for (v in 1:5)  {
   beta[v] ~ dnorm(0, 0.0001)
}
# Independent effect of human activity variables
for (v in 1:5)  {
      betaG[v] ~ dnorm(0, 0.0001)
 }    }
```

Hierarchical model{

```
###########
#Likelihood
###########
for (i in 1:NP) {
y[i] ~ dbern (p.bound[i])
p.bound[i]  <-  max(0,  min(1,  p[i]))
logit(p[i]) <- xbeta[i] + alpha[grid[i]]
xbeta[i] <-  betaH[HABITAT[i]] + beta[1,REGION[i],HABITAT[i]]*TMIN1[i] +
beta[2,REGION[i],HABITAT[i]]*TSEAS[i] + beta[3,REGION[i],HABITAT[i]]*PTOT[i]
```

```
+beta[4,REGION[i],HABITAT[i]]*PWARQ[i] +beta[5,REGION[i],HABITAT[i]]*DCOAST[i]
+betaG[1,REGION[i]]*URBANO[i] + betaG[2,REGION[i]]*AGRIC[i] + betaG[3,REGION[i]]*GRASS[i]
+betaG[4,REGION[i]]*FOREST[i]+betaG[5,REGION[i]]*SH_COV[i]
}

###########
# Priors
##########
#Random effect for grid level.
for (g in 1:NG) {
alpha[g] ~ dnorm(alpha.mean,alpha.tau)
   }
alpha.mean ~ dnorm(0, 0.0001)
alpha.tau<- pow(alpha.sigma, -2)
alpha.sigma ~ dunif(0,100)

# Hyperprior for Habitat
for (j in 1:NH)  {
betaH[j] ~ dnorm(0, betaH.tau)
betaH.adj[j] <- betaH[j] - mean(betaH[])
}
betaH.tau<- pow(betaH.sigma, -2)
betaH.sigma ~ dunif(0, 100)

# Climate across regions and habitats (hierarchical)
for (v in 1:5)  {
for ( k in 1:3)  {
        #Effect of climate across regions
betaCR.mean[v,k] ~ dnorm(0, 0.0001)
betaCR.tau[v,k] <- pow(betaCR.sigma[v,k], -2)
betaCR.sigma[v,k] ~ dunif(0,100)
for ( j in 1:9)  {
              # Effect of climate across habitats
beta[v,k,j] ~ dnorm(betaCR.mean[v,k], betaCR.tau[v,k])
            }
   }
}
# Human activity across regions (non-hierarchical)
for (v in 1:5)  {
```

```
for ( j in 1:3)  {
            # Effect of human activity across regions
betaG[v,j] ~ dnorm(0, 0.0001)
           }
}   }
```

Modelling the relative richness and abundance of non-native plant species

Openbugs codes to model relative richness and abundance of non-native plants at invaded plots using 8146 plots (NP) and 1605 UTM grids (NG)

```
Non-hierarchical model{
###########
##Likelihood
###########
for (i in 1:NP) {
   RICH_NEOF[i] ~ dbin(pb[i],RICH_TOTAL[i])
   pb[i] <- pb.raw[i]
   logit(pb.raw[i]) <-  xbeta.PR[i] + alpha.PR[grid[i]]
   xbeta.PR[i] <-  betaH.PR[HABITAT[i]] + beta.PR[1]*TMIN1[i] + beta.PR[2]*TSEAS[i] + beta.PR[3]*PTOT[i]
+beta.PR[4]*PWARQ[i] +beta.PR[5]*DCOAST[i] +betaG.PR[1]*URBANO[i] + betaG.PR[2]*AGRIC[i] +
betaG.PR[3]*GRASS[i] +betaG.PR[4]*FOREST[i]+betaG.PR[5]*SH_COV[i]

   ABUND[i] ~ dlnorm(abund.hat[i],abund.tau)
   abund.hat[i] <- abund.hat.raw[i]
   abund.hat.raw[i] <-  xbeta.AB[i] + alpha.AB[grid[i]]
   xbeta.AB[i] <-  betaH.AB[HABITAT[i]] + beta.AB[1]*TMIN1[i] + beta.AB[2]*TSEAS[i] +
beta.AB[3]*PTOT[i] +beta.AB[4]*PWARQ[i] +beta.AB[5]*DCOAST[i] +betaG.AB[1]*URBANO[i] +
betaG.AB[2]*AGRIC[i] + betaG.AB[3]*GRASS[i] +betaG.AB[4]*FOREST[i]+betaG.AB[5]*SH_COV[i]
}

###########
# Priors
##########
abund.tau <- pow(abund.sigma, -2)
abund.sigma ~ dunif(0,100)

#Random effect for grid level.
for (g in 1:NG) {
```

```
    alpha.PR[g] ~ dnorm(alpha.mean.PR,alpha.tau.PR)
    alpha.AB[g] ~ dnorm(alpha.mean.AB,alpha.tau.AB)
    }
    alpha.mean.PR ~ dnorm(0, 0.0001)
    alpha.tau.PR <- pow(alpha.sigma.PR, -2)
    alpha.sigma.PR ~ dunif(0,100)
    alpha.mean.AB ~ dnorm(0, 0.0001)
    alpha.tau.AB <- pow(alpha.sigma.AB, -2)
    alpha.sigma.AB ~ dunif(0,100)


# Hyperprior for Habitat
for (j in 1:9)  {
    betaH.PR[j] ~ dnorm(0, betaH.tau.PR)
    betaH.adj.PR[j] <- betaH.PR[j] - mean(betaH.PR[])
    betaH.AB[j] ~ dnorm(0, betaH.tau.AB)
    betaH.adj.AB[j] <- betaH.AB[j] - mean(betaH.AB[])
}
    betaH.tau.PR <- pow(betaH.sigma.PR, -2)
    betaH.sigma.PR ~ dunif(0, 100)
    betaH.tau.AB <- pow(betaH.sigma.AB, -2)
    betaH.sigma.AB ~ dunif(0, 100)

# Independent effect of climate variables
for (v in 1:5)  {
    beta.PR[v] ~ dnorm(0, 0.0001)
    beta.AB[v] ~ dnorm(0, 0.0001)
}

 # Independent effect of human activity variables
for (v in 1:5)  {
    betaG.PR[v] ~ dnorm(0, 0.0001)
    betaG.AB[v] ~ dnorm(0, 0.0001)
}   }
```

```
Hierarchical model{
##Likelihood
for (i in 1:NP) {
   RICH_NEOF[i] ~ dbin(pb[i],RICH_TOTAL[i])
logit(pb [i]) <-  xbeta.PR[i] + alpha.PR[grid[i]]
   xbeta.PR[i] <-  betaH.PR[HABITAT[i]] + beta.PR[1,REGION[i],HABITAT[i]]*TMIN1[i] +
beta.PR[2,REGION[i],HABITAT[i]]*TSEAS[i] + beta.PR[3,REGION[i],HABITAT[i]]*PTOT[i]
+beta.PR[4,REGION[i],HABITAT[i]]*PWARQ[i] +beta.PR[5,REGION[i],HABITAT[i]]*DCOAST[i]
+betaG.PR[1,REGION[i]]*URBANO[i] + betaG.PR[2,REGION[i]]*AGRIC[i] +
betaG.PR[3,REGION[i]]*GRASS[i]
+betaG.PR[4,REGION[i]]*FOREST[i]+betaG.PR[5,REGION[i]]*SH_COV[i]

ABUND[i] ~ dlnorm(abund.hat[i],abund.tau)
abund.hat [i] <-  xbeta.AB[i] + alpha.AB[grid[i]]
xbeta.AB[i] <-  betaH.AB[HABITAT[i]] + beta.AB[1,REGION[i],HABITAT[i]]*TMIN1[i] +
beta.AB[2,REGION[i],HABITAT[i]]*TSEAS[i] + beta.AB[3,REGION[i],HABITAT[i]]*PTOT[i]
+beta.AB[4,REGION[i],HABITAT[i]]*PWARQ[i] +beta.AB[5,REGION[i],HABITAT[i]]*DCOAST[i]
+betaG.AB[1,REGION[i]]*URBANO[i] + betaG.AB[2,REGION[i]]*AGRIC[i] +
betaG.AB[3,REGION[i]]*GRASS[i]
+betaG.AB[4,REGION[i]]*FOREST[i]+betaG.AB[5,REGION[i]]*SH_COV[i]
}
###########
# Priors
##########
abund.tau<- pow(abund.sigma, -2)
abund.sigma ~ dunif(0,100)

#Random effect for grid level.
for (g in 1:NG) {
alpha.PR[g] ~ dnorm(alpha.mean.PR,alpha.tau.PR)
alpha.AB[g] ~ dnorm(alpha.mean.AB,alpha.tau.AB)
   }
alpha.mean.PR ~ dnorm(0, 0.0001)
alpha.tau.PR<- pow(alpha.sigma.PR, -2)
alpha.sigma.PR ~ dunif(0,100)
alpha.mean.AB ~ dnorm(0, 0.0001)
alpha.tau.AB<- pow(alpha.sigma.AB, -2)
alpha.sigma.AB ~ dunif(0,100)
```

```
# Hyperprior for Habitat
for (j in 1:9)  {
betaH.PR[j] ~ dnorm(0, betaH.tau.PR)
betaH.adj.PR[j] <- betaH.PR[j] - mean(betaH.PR[])
betaH.AB[j] ~ dnorm(0, betaH.tau.AB)
betaH.adj.AB[j] <- betaH.AB[j] - mean(betaH.AB[])
}
betaH.tau.PR<- pow(betaH.sigma.PR, -2)
betaH.sigma.PR ~ dunif(0, 100)
betaH.tau.AB<- pow(betaH.sigma.AB, -2)
betaH.sigma.AB ~ dunif(0, 100)

# Climate across regions and habitats (hierarchical)
for (v in 1:5)  {
for ( k in 1:3)  {
    #Effect of climate across regions
betaCR.mean.PR[v,k] ~ dnorm(0, 0.0001)
betaCR.mean.AB[v,k] ~ dnorm(0, 0.0001)
betaCR.tau.PR[v,k] <- pow(betaCR.sigma.PR[v,k], -2)
betaCR.sigma.PR[v,k] ~ dunif(0,100)
betaCR.tau.AB[v,k] <- pow(betaCR.sigma.AB[v,k], -2)
betaCR.sigma.AB[v,k] ~ dunif(0,100)
for ( j in 1:9)  {
       # Effect of climate across habitats
beta.PR[v,k,j] ~ dnorm(betaCR.mean.PR[v,k], betaCR.tau.PR[v,k])
beta.AB[v,k,j] ~ dnorm(betaCR.mean.AB[v,k], betaCR.tau.AB[v,k])
}
  }
}

# Human activity across regions (non-hierarchical)
for (v in 1:5)  {
for ( j in 1:3)  {
       # Effect of human activity across regions
betaG.PR[v,j] ~ dnorm(0, 0.0001)
betaG.AB[v,j] ~ dnorm(0, 0.0001)
      }
 }
}
```

MESS code

We adapted the code by Rossi, (2012) to compute the multivariate environmental similarity surface index (MESS) in R (Elith et al., 2010; Catford et al., 2011) using as input dataframes instead of RasterStack objects. MESS quantifies the similarity between the value of certain variables for a plot and the value of the same variables in a group of reference plots. Positive MESS values indicate that the full range of conditions are included in the data with higher values indicating areas that are better represented by data (maximum value = 100). Negative values indicate conditions not included in the data where the models are extrapolating (Elith et al., 2010).

X: dataframe with plots to calculate MESS. In survey gap analysis the entire environmental conditions.
V: dataframe with reference plots. In survey gap analysis the environmental conditions for all plots in the survey database.
full: if TRUE, it returns a dataframe with the MESS value for each variable and if FALSE, it returns a dataframe with the minimum MESS value of all variables.

```
mess<-function(X,V,full=TRUE){
messi<-function(p,v){ # function to calculate MESS for each plot
   niinf<-length(which(v<=p)) ;   f<-100 * niinf / length(v)
   if(f==0) simi<-100*(p-min(v))/(max(v)-min(v))
   if(0<f & f<=50) simi<-2*f
   if(50<=f & f<100) simi<-2*(100-f)
   if(f==100) simi<-100*(max(v)-p)/(max(v)-min(v))
   return(simi)}
E<-X ; r_mess<-X
for (i in 1:(dim(E)[2])) {
   e<-data.frame(E[,i]) ; v<-V[,i] # select data for each column
   r_mess[,i]<-apply(X=e, MARGIN=1, FUN=messi, v=v) #calculate the function  }
rmess <-apply(X=r_mess, MARGIN=1, FUN=min)
if(full==TRUE) {
   out <- cbind(r_mess,rmess) # It returns dataframe with the MESS value for each variable
   names(out)<-c(names(X),"mess")
}
if(full==FALSE) out <- rmess
return(out) # It returns dataframe with the minimum MESS value of all variables}
```

CAPÍTULO CINCO

González-Moreno, P., Diez, J.M., Richardson, D.M. & Vilà, M. (2014) Beyond climate: disturbance niche shifts in invasive species. Global Ecology and Biogeography. In press.

BEYOND CLIMATE: DISTURBANCE NICHE SHIFTS IN INVASIVE SPECIES

RESUMEN

Para entender los factores que controlan la distribución de las especies y anticipar posibles expansiones de las especies invasoras es necesario analizar como los nichos de las especies varían entre el rango nativo y el de introducción. La mayoría de los estudios realizados hasta la fecha, han considerado sólo el nicho climático, basándose en la correlación entre los comúnmente utilizados datos de presencia de las especies y el clima regional. En este estudio, usamos datos de presencia y abundancia de Oxalis pes-caprae, una especie nativa de Sudáfrica e invasora en muchas regiones del globo, para entender como los cambios de nicho pueden estar influenciados por el grado de perturbación a la vez que por el clima. Usamos datos de presencia de la especie a nivel global y también llevamos a cabo un muestreo intensivo de la abundancia de Oxalis (~11,000 parcelas) a lo largo de diferentes hábitats en Sudáfrica y en su rango de introducción en la cuenca Mediterránea. Para identificar posibles cambios en los nichos climáticos y de perturbación, ampliamos los análisis de ordenación (PCA) utilizando GLMs Bayesianos. Encontramos una considerable expansión del nicho climático hacia condiciones de mayor estacionalidad y menor temperatura en el rango de introducción. Sin embargo, esta expansión se redujo enormemente al considerar las condiciones comunes a ambos rangos. Oxalis ocupa paisajes relativamente naturales en el rango nativo que permanecen no ocupados en el rango de introducción ("ocupación parcial del nicho"). Al contrario que en el rango nativo, donde encontramos abundancias similares de la especie entre el rango nativo y de introducción, Oxalis es más abundante en hábitats perturbados en el rango de introducción. La enorme expansión del nicho climático que encontramos, refleja más bien la propia plasticidad de la especie que una posible rápida evolución. Por otro lado, la ocupación parcial del nicho de perturbación en el rango de introducción, sugiere un alto potencial de la especie para invadir nuevas áreas naturales. En conjunto, estos resultados sugieren que la caracterización del nicho de las especies invasoras basándonos sólo en el clima o en información parcial de su distribución, puede conducir a una infravaloración del potencial de estas especies para expandirse en el futuro.

ABSTRACT

Analysing how species' niches shift between native and introduced ranges is a powerful tool for understanding the determinants of species distributions and for anticipating range expansions by invasive species. Most studies only consider the climatic niche, by correlating widely available presence-only data with regional climate. However, habitat characteristics and disturbance also shape species' niches, thereby potentially confounding shifts attributed only to differences in climate. Here, we used presence and abundance data for Oxalis pes-caprae, a species native to South Africa and invading areas globally, to understand how niche shifts may be influenced by disturbance at habitat and landscape scales in addition to climate. We used available presence-only data and also conducted extensive surveys of the abundance of Oxalis (~11,000 plots) across different habitats in South Africa and in the introduced range in the Mediterranean Basin. We extended PCA methods for measuring niche shifts by using Bayesian GLMs to identify climatic and disturbance niche shifts. We found a large climatic niche expansion towards higher seasonality and lower temperature in the introduced range, but this expansion was greatly reduced when considering only conditions available in both ranges. Oxalis occupied more natural landscapes in the native range that remained unoccupied in the introduced range ("niche unfilling"). In contrast to the similar abundances in natural and disturbed habitats in its native range, Oxalis was more abundant in disturbed habitats in the introduced range. The large climatic niche expansion most likely reflects significant plasticity of Oxalis rather than rapid evolution. Furthermore, the unfilling of its disturbance niche in the introduced range suggests high potential for further invasion of natural areas. Together, these findings suggest that characterizations of invasive species' niches based only on climate or partial information of their distribution risk underestimating their potential for future spread.

INTRODUCTION

Understanding the determinants of invasive species distributions is crucial for effective management. A common approach is to make predictions about the potential introduced range using the data of the species' distribution in the native or introduced range (Peterson et al., 2003; Thuiller et al., 2005). This approach relies on the assumption that species have similar niche characteristics in native and introduced ranges (i.e. niche conservatism) (Peterson et al., 2003; Alexander & Edwards, 2010). Recent studies have questioned this assumption for plants (Broennimann et al., 2007; Gallagher et al., 2010), insects (Fitzpatrick et al., 2007; Medley, 2010), amphibians (Urban et al., 2007) and fish (Lauzeral et al., 2011) by highlighting the potential importance of rapid evolution and altered biotic interactions during the invasion process. Nevertheless, species may have access to only a subset of the potentially suitable climatic conditions in their native ranges. Consequently, when analyses of climatic niche shifts are limited to those climates available in both native and introduced ranges (i.e. analogous conditions), there appear to be fewer real niche shifts (Petitpierre et al., 2012).

Knowing whether climatic niches are similar in the native and introduced range is extremely important for predicting species’ occurrences in new areas and in response to climate change (Alexander & Edwards, 2010). For example, observed shifts into novel climates in the introduced range that are not occupied in the native range (i.e. expansion) suggest that rapid evolution may have expanded a species’ climatic tolerances. Conversely, narrower climatic envelopes observed in the introduced range than in the native range (i.e. unfilling), suggest the importance of dispersal limitation, lag phases and/or evolutionary bottlenecks associated with introduction processes (Medley, 2010; Guisan et al., 2014). Furthermore, some processes, such as changes in biotic interactions between the ranges, may lead to either niche expansion or unfilling. Quantifying the prevalence of niche unfilling in the invaded range is critically important because it suggests the likelihood of further spread over time in the introduced range.

Niche conservatism in invasive species is typically tested using broad climatic niches, despite the fact that similar ideas may be applied to other aspects of a species' niche, such as disturbance regimes or habitat characteristics (Wiens et al., 2010; Guisan et al., 2014). For example, many invasive plant species are favoured by the nutrient-rich conditions provided by high levels of disturbance (Hobbs & Huenneke, 1992). It has been suggested that non-native species tend to colonize disturbed habitats in the early stages of the invasion process, and may then expand to more natural conditions as the invasion unfolds (Dietz & Edwards, 2006). The association of a species with disturbance (i.e. disturbance niche) may be related to local gradients from natural to ruderal habitats (Vilà et al., 2007), and also human alterations at the landscape scale (Capítulo 1). Although theory suggests a shift towards more altered habitats and landscapes in the introduced range, the roles of habitat and disturbance in mediating niche shifts have received much less attention than climatic niche shifts. Nonetheless, shifts in a species' disturbance niche are important to understand because they may contribute to the time lags that often characterize invasions (Geerts et al., 2013).

In this study, we used Oxalis pes-caprae L., a geophyte native to South Africa which has invaded Mediterranean-climate areas globally, to test for shifts in both climatic and disturbance niches between native and introduced areas. First, we quantified the climatic niche conservatism of the species using global data (30' resolution) and ordination methods. Second, we examined the climatic and disturbance niches using data on the abundance of the species from an extensive field sampling (~11000 plots; 30” resolution) throughout the native range in South Africa and across large parts of the introduced range in the Mediterranean basin. We hypothesized that different niche shifts may be apparent when considering abundance compared to the widely used occurrence data. We used a combination of PCA methods and GLMs within a Bayesian framework to provide a more detailed test of how the species’ climate and disturbance niches shift in the introduced region. We interpret the results to provide guidelines for more accurate modelling of invasive species and consider implications for the potential invasion of Oxalis into natural areas in the long term.

METHODS

Study species

Oxalis pes-caprae L. (hereafter **Oxalis**) is a small geophyte from South Africa which has invaded many Mediterranean areas globally (Weber, 2003). It was introduced to the Mediterranean Basin in 1796, and reached mainland Spain by 1825 and the Balearic Islands by 1870 (D'Austria, 1884). Despite its long history in the Mediterranean Basin, in Spain it only covers 46% of its potential distribution (Gassó et al., 2012). It generally flowers from late autumn to early summer and is heterostylic with three flower morphs (Castro et al., 2007). In its native range all three floral morphs occur and the species reproduces both sexually and asexually (Ornduff, 1987), while in the introduced range only one morph is dominant and the principal means of reproduction is via vegetative bulbils (Vilà et al., 2006; Castro et al., 2007).

Global climatic niche shift analyses

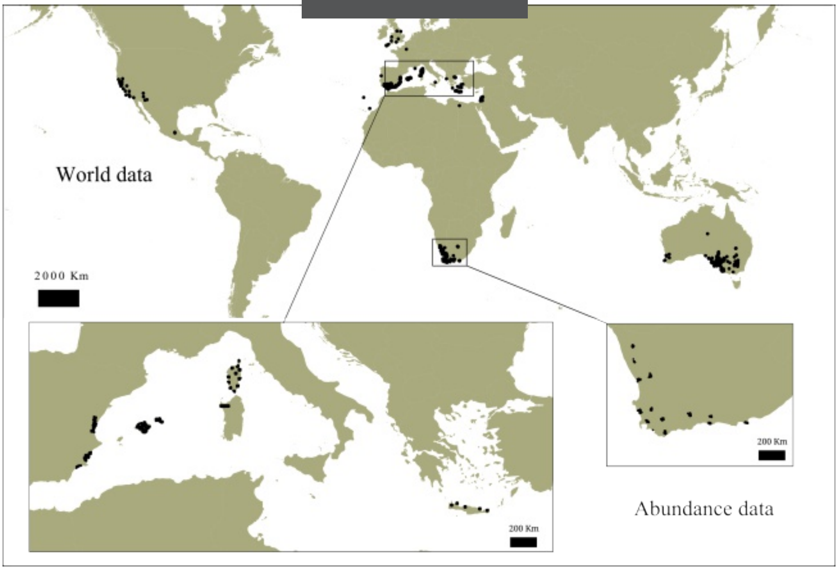
Plant Dataset

We collected all available presence-only data for **Oxalis** in GBIF (Fig. 1; 1818 plots); this provided good coverage for the native range (South Africa) and a large part of the introduced range (North America, Europe, and Australia). We kept those plots with at least 0.001º positional accuracy and excluded isolated locations outside its known distribution (most likely botanical gardens). In addition, we added 1852 occurrence plots from our surveys in South Africa and Europe (see section below).

Climate data

We extracted 19 bioclimatic variables from WorldClim (Hijmans et al., 2005) at 30' resolution (~50 km). We included as explanatory variables only the minimum combination of climatic variables identified as not collinear within each range (Appendix A-Table A.1): mean annual temperature, temperature seasonality, precipitation seasonality, winter precipitation (coldest quarter), minimum temperature of coldest month (minimum temperature) and temperature of driest quarter.

FIGURE 1



Oxalis pes-caprae plots used in the analyses. The upper part of the figure shows the localities of presence-only data used to test the global climatic niche shift. The panels in the lower half show the localities of plots where abundance data were collected in the introduced range (Mediterranean Basin, left) and in the native range (South Africa, right).

Statistical analyses

We identified climatic niche shifts for *Oxalis* between native and introduced ranges within the whole Mediterranean biome using the global occurrence data and the climatic data at 30' resolution. To avoid pseudo-replication we included only one plot for each 30'x30' grid cell (342 plots). Our analysis of niche shifts followed the three-step approach used by Broennimann et al., (2012) and Petitpierre et al., (2012). First, we delimited the Mediterranean biome (Olson et al., 2001) for both ranges and extracted all climate data at 30' resolution. Based on this data, we performed a Principal Component Analyses (PCA), and used its first two axes to characterize the environmental space within which we could compare the native and introduced niches (Appendix A–Fig. A.1). We then divided this environmental space into a grid of 100 x 100 cells as in Broennimann et al., (2012). Second, we used a kernel density function to convert *Oxalis* occurrences and the available climates in each range into densities in order to correct for sampling bias and environmental availability respectively, and to ensure that the results were independent of the grid resolution (Broennimann et al., 2012). Third, we calculated three indices of niche shifts: unfilling, stability and expansion (Petitpierre et al., 2012) considering either the common environmental space for native and introduced ranges or the whole environmental space. **Unfilling** is defined as the proportion of the densities in the native range located in different conditions than the introduced range, **stability** is the proportion of the densities in the introduced range overlapping with the native range, and **expansion** is the proportion of the densities in the introduced range located in different conditions than the native range. We calculated each index using the 75th percentile of the available environmental conditions in each range. This approach removes the marginal environments and avoids bias due to artefacts of the density function (Petitpierre et al., 2012). Finally, we calculated the median of the distribution density and the median of the available climatic space in both ranges in order to assess the overall direction of the shifts.

Mediterranean Basin niche shift analyses

Plant dataset

We obtained local abundance data in the introduced range from two different datasets in the Mediterranean Basin (Fig. 1): from Gimeno et al., (2006), conducted on two Balearic Islands (Mallorca and Menorca) and two adjacent coastal regions of mainland Spain (Valencia and Murcia), and from Affre et al., (2010), conducted on three Mediterranean Islands (Crete, Sardinia and Corsica). The two datasets were originally sampled using similar protocols: 1) five 10 x 10 km UTM cells were randomly chosen in each region. 2) Within each UTM cell 100 plots were sampled. In Gimeno et al. (2006) exact survey plots were selected by stopping every 1 km along several communication networks (from main roads to paths). In contrast, in Affre et al. (2010) the 100 plots were randomly located (GPS accuracy <10 m). Accessibility problems during sampling finally lead to fewer than 100 plots per block, so the final dataset included 1716 plots from Gimeno et al., (2006) and 1355 from Affre et al., (2010). 3) In each plot, dominant habitats falling within a 50-m radius were classified according to 10 categories that varied in the level of human influence (i.e. disturbance at the local scale): agriculture, coastal, forest, grassland, river, transport network (road and railway margins), rocky, ruderal (disturbed open areas), shrubland and urban (built areas), resulting in one or more data entries for each sampled plot. For all habitats surveyed at each plot, Oxalis cover was categorized using a six-point index based on percent cover: dominant (≥75%) = 5, abundant (75–50%) = 4, frequent (50–25%) = 3, occasional (25-5%) = 2, rare (≤5 - >0%) = 1 and absent (0%) = 0.

To characterize the distribution of Oxalis in its native range we followed the protocol by Gimeno et al. (2006). We sampled thirteen 10 x 10 km UTM cells (1033 plots) covering the whole gradient of climatic conditions where Oxalis occurs (as indicated by experts and herbarium data). We also considered the gradient of human influence by placing the grids close to urban nuclei of different sizes.

Climate and landscape data

As for the global analysis we extracted 19 bioclimatic variables from WorldClim for all plots, but at 30” resolution (~1 km). To avoid collinearity problems in the regression analyses we selected only poorly correlated variables (r<0.7): mean annual temperature, temperature seasonality, precipitation seasonality and winter precipitation.

To characterize human influence at the landscape scale for each plot we obtained the following land-cover variables (percentage of urban, agricultural and natural land-covers), minimum distance to roads and human footprint index. Land-cover data was obtained from the European CORINE Land-cover Map (2006, Crete from 2000) and the South African NLC2009. We resampled raster maps to 100-m resolution (minimum resolution of CORINE Map) and calculated land-cover percentage at three buffer distances from each plot: 250, 500 and 1000 m. Road network maps (restricted only for vehicles) were obtained from the global community-owned project OpenStreetMap. This dataset is highly accurate compared to corporate datasets (Neis et al., 2011) and we assume a similar error for all study areas. Finally, human-footprint index data were extracted from the Last of the Wild Project at 1-km resolution (WCS & CIESIN, 2005). Based on collinearity analyses we selected agricultural and urban land-covers, distance to roads and human footprint variables (Appendix A-Table A.1). We identified 1000 m as the most appropriate buffer distance based on Pearson's correlations between the Oxalis' abundance and land-cover variables across distances (Appendix A-Table A.2). All data extraction and manipulation was done using open-source GIS software (QGIS, GRASS and POSTGIS).

Statistical analyses

We used ordination (PCA) and Generalized Linear Models (GLMs) to test climate and disturbance niche conservatism of Oxalis between the native range (4862 data entries considering the habitats found in each of the 1033 plots) and across a large part of the introduced range in the Mediterranean Basin (6009 data entries corresponding to 3071 plots). Ordination allowed for the comparison of species niches for each range in a space defined by axes summarizing several variables. We used GLMs to compare the changes between ranges in the association of Oxalis' abundance with each variable and in the difference in local habitat suitability.

Ordination method - We used the same PCA approach as in the global analysis to quantify climatic and disturbance niche shifts between the introduced range in the Mediterranean basin and the native range in South Africa. We compared the niches for both ranges using all climatic (30" resolution) and disturbance (landscape scale) conditions as environmental space for all plots sampled irrespective of the occurrence of Oxalis. With this approach we assumed a good coverage of the available environmental space in the native range but it covers only a restricted portion of the introduced range in the Mediterranean basin. For the PCA we used the same climate variables as in the global analysis. However, we used those landscape variables selected by collinearity analyses plus natural land-cover as disturbance variables. The collinearity among variables does not affect the results and facilitates better distinction of the disturbance gradient. We analysed shifts using both presence and abundance data. For the abundance data, we adapted the method by replicating plots according to their level of abundance (1 to 5). This weights the species density by its abundance such that areas of the PCA where Oxalis shows higher abundance will proportionally include higher species density.

Modelling shifts using GLMs - We identified how climate and disturbance (habitat and landscape scales) affected shifts in Oxalis' abundance using Bayesian models that allowed regression coefficients to vary between the native and introduced ranges. The abundance of Oxalis in the dominant habitats of each plot (N=10871), was modelled using a Binomial distribution considering climate (30" resolution) and landscape variables that were not correlated for both ranges (details Appendix B). We corrected for the potential sampling bias arising from the roadside collection of some data by including the distance to roads as covariate. We also compared models that included only road sampling data with models including all data. Because results were very similar, we focus on results using all data ('road only' models in Appendix A).

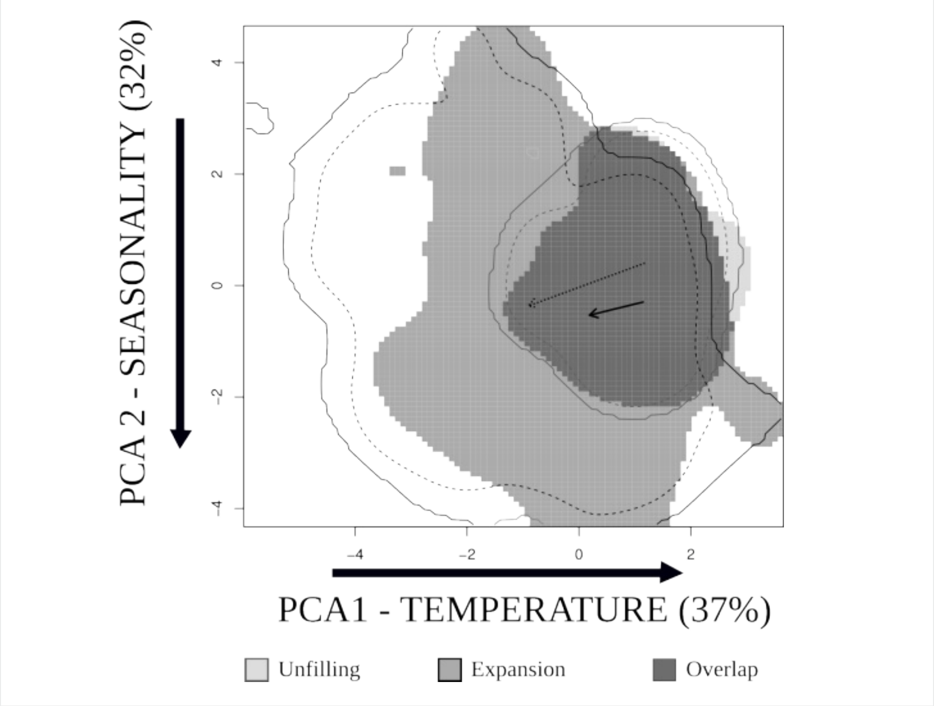
We calculated several aggregate indices based on the model coefficients to facilitate their interpretation. First, we calculated the overall suitability of disturbed habitats in each range as the sum of the coefficients of agricultural, transport network, urban and ruderal habitats. Similarly, we calculated the overall suitability of natural habitats for each range as the sum of the coefficients for coastal, forest, grasslands, river, rocky and shrubland habitats. Finally, to quantify the overall importance of disturbance variables at landscape scale in each range we calculated the sum of the absolute values of their coefficients.

We set apart a randomly selected 10% of plots for model validation and calibrated the models with the remaining 90%. Goodness of fit of the models was calculated using Deviance Information Criteria (DIC) (Spiegelhalter et al., 2002) for the whole model and mean squared errors (Predicted-Observed) of the validation plots for each range. Models that minimized both values were considered to better fit the data. In preliminary analyses, full models without quadratic terms were always equivalent to more simple models (within 2-4 DIC). Thus, we ran final models using all climate and landscape variables selected by collinearity analyses without quadratic terms. We did not detect significant spatial autocorrelation in the models' residuals at bins of 0.1º (Moran's Index<0.1). Final models were run in OpenBUGS 3.2.1 (Lunn et al., 2009) until convergence of the parameters was ensured (~25,000 iterations, convergence assessed visually), after which the parameters were calculated from another 25,000 iterations (code in Appendix B).

Predicting shifts

To visually compare Oxalis distribution in native and introduced ranges we made predictions of the abundance of the species in Southern Europe using GLMs calibrated with either native or introduced data (Reciprocal Distribution Modelling; Medley, 2010). We used the posterior parameter values of the best model to generate mean predictions at the central point of 1-km UTM grid resolution irrespective of the habitat type. We also identified non-analogue conditions to the calibrated data based on the Multivariate Environmental Similarity Surfaces index (MESS) (Elith et al., 2010) where models are extrapolating and predictions should be interpreted cautiously (Fitzpatrick & Hargrove, 2009).

FIGURE 2



Global climatic niche shift of *Oxalis pes-caprae* based on a PCA of climate variables. The light grey line delimits the entire range of conditions in the native range of *Oxalis* while the black line delimits the conditions in the introduced range (whole Mediterrean biome without considering South Africa). For both ranges, the continuous line corresponds to the whole climatic space while the dashed line indicates the 75% percentile. The overlapped space between grey and black lines corresponds to the common environmental space between ranges. Shaded areas represent the portion of these conditions actually occupied by *Oxalis*: medium grey for niche expansion (presence only in the introduced range), light grey for niche unfilling (presence only in the native range) and dark grey shows the conditions that are occupied in both ranges. The continuous black arrow shows the environmental distance between the median of the distribution density for each range. The dashed black arrow shows the environmental distance between the median of the available climatic space in each range. See Appendix A for detailed plots.

RESULTS

Global climatic niche shift

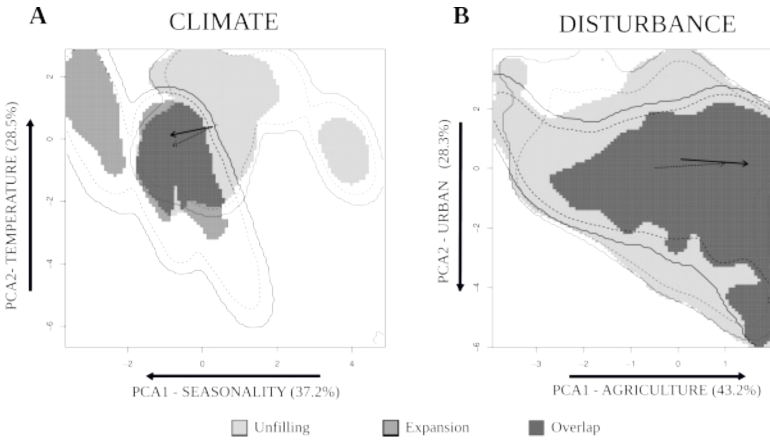
The climatic space of the whole Mediterranean biome was summarized by two PCA axes explained mainly by minimum temperature (36.9%) and precipitation seasonality (32.2%) (Appendix A–Fig. A.1). Using this climatic space we found that the median of Oxalis distribution in the introduced range moved towards lower temperature and slightly higher seasonality relative to the native range (Fig.2). More specifically, the climatic niche of Oxalis expanded into areas with both higher and lower precipitation seasonality, extending into some areas outside the climatic envelope of the Mediterranean biome (37.3% expansion). On the other hand, some small areas with higher temperature and medium seasonality were only occupied in the native range (3.1% unfilling). Taking into account only the common environmental space between the native and introduced range (overlap between black and grey lines in Fig.2), expansion and unfilling were reduced in both cases to just 3.5% and 0% respectively.

Mediterranean Basin niche shift

Comparing niche shifts in an ordination space

The climatic space across all abundance plots sampled was summarized by two axes corresponding mainly to precipitation seasonality (37.2%) and mean annual temperature (28.5%) (Appendix A–Fig. A.2). The median of Oxalis distribution shifted towards higher seasonality and slightly lower temperature in the introduced range (Fig.3A). The climatic niche of the species was expanded specially to areas with higher precipitation seasonality occurring in Malta (15% expansion). On the other hand, some areas with lower seasonality were only occupied in the native range (68% unfilling). Taking into account the common environmental space there was no expansion and unfilling was 10%. Results considering only presence data were very similar but with lower percentages (4% unfilling in the common space; Appendix A–Fig. A.4). These results are very similar to the global climatic niche shift but with higher rates.

FIGURE 3



Shifts in the climatic and disturbance niche of Oxalis pes-caprae (abundance) between South Africa and the Mediterranean basin based on separate PCAs for climate variables and disturbance variables at landscape scale. See legend in Figure 2 and Appendix A for detailed plots.

Mean and standard deviation (Sd) of the squared errors (Predicted-Observed) in the models explaining the abundance of Oxalis (Mediterranean Basin niche shift analyses) for the validation plots set apart (10%) for the native and introduced ranges (rows) calibrated with data from its own range or the other (columns). In bold, best model calibration for each range.

TABLE 1

	CALIBRATED WITH			
	Native range		Introduced range	
MODEL FOR	Mean	Sd	Mean	Sd
Native range	**0.67**	**1.67**	5.78	6.35
Introduced range	2.64	4.17	**1.48**	**2.55**

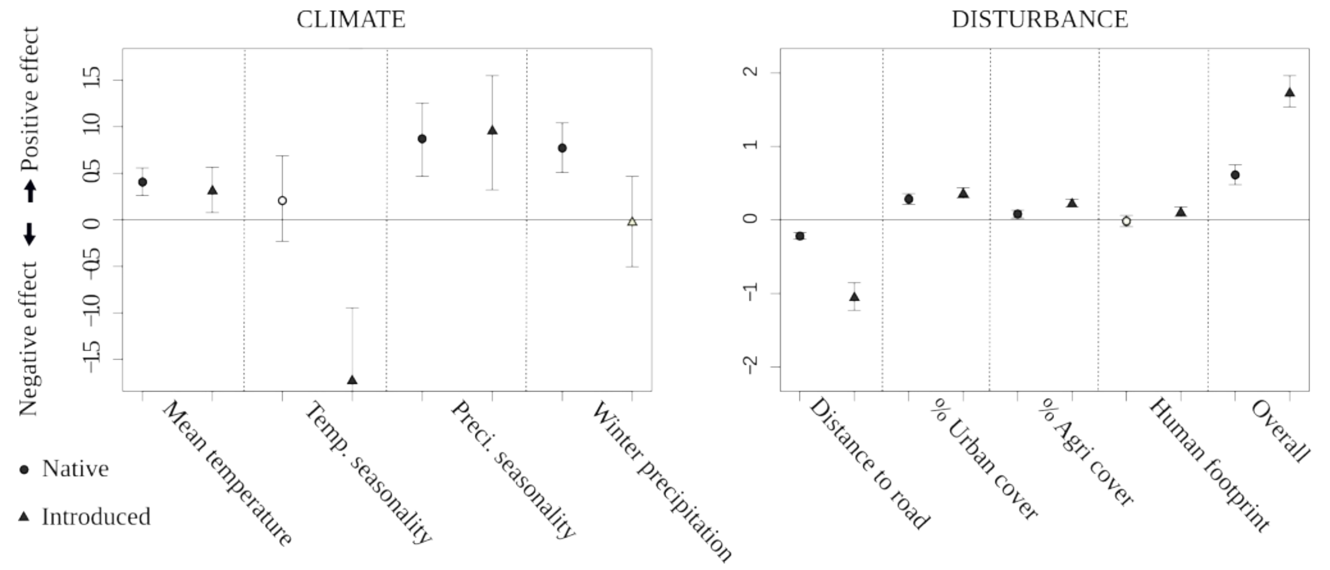
The disturbance space at the landscape scale was summarized by two axes corresponding to natural vs. agricultural areas (43.2%) and urban areas vs. distance to roads (28.3%) (Appendix A–Fig. A.2). Using this space, we found a shift of the median of *Oxalis* distribution in the introduced range towards higher disturbed areas (Fig. 3B) but that corresponded only to 0.9% of expansion to higher disturbed areas. This expansion occurred at a landscape configuration not available in the native range, corresponding to intense agricultural areas in eastern mainland Spain. Areas with the highest natural land-cover were only occupied in the native range (15% unfilling). When considering the common disturbance space, this unfilling was reduced to 8%. Results considering only presence data were very similar but with slightly lower percentages (6% unfilling in the common space; Appendix A–Fig. A.4).

Comparing niche shifts in a regression model

The final model showed rather low errors for the native range compared to the introduced range (Table 1). Half of the climatic variables showed similar associations with *Oxalis*' abundance in both ranges (Fig. 4). *Oxalis*' abundance increased at higher mean annual temperature and precipitation seasonality in both ranges. Nevertheless, precipitation in winter seems to be positively associated with *Oxalis*' abundance only in the native range, whereas temperature seasonality was negatively associated with abundance only in the introduced range.

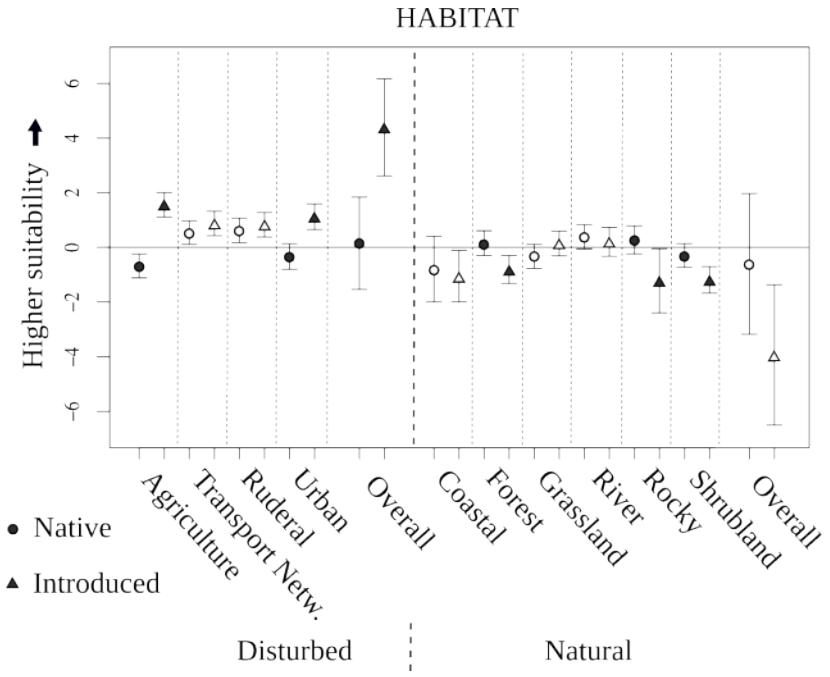
Proximity to roads, agricultural and urban land-covers were all positively associated with *Oxalis*' abundance in both ranges (Fig. 4). Furthermore, proximity to roads, urban cover and the human footprint index were all more strongly associated with *Oxalis*' abundance in the introduced range than in the native range (Fig. 4, Appendix A–Table A.3). The overall difference for disturbance variables at landscape scale was also significantly higher in the introduced range. In the native range, *Oxalis*' abundance was rather similar across habitats, although ruderal and transport network habitats showed slightly higher suitability (Fig. 5). In contrast, habitat suitability in the introduced range was significantly higher in disturbed habitats than in natural habitats (Fig. 5, Appendix A–Table A.4). For several natural habitats, suitability was significantly higher in the native range (i.e. forest, rocky, and shrubland), while for the rest of the habitats, differences were not significant (Fig. 5). On the other hand, for half of the disturbed habitats suitabilities were higher in the introduced range (i.e. agricultural and urban) and the rest showed not significant differences.

Figure 4



Posterior means (with Bayesian credible intervals) of the coefficients for climate and landscape variables at native (circles) and introduced (triangles) ranges in the GLM explaining the abundance of *Oxalis pes-caprae*. The "Overall" coefficient is the absolute sum of the four landscape coefficients. Filled symbols indicate that the 95% credible interval around the parameter mean values did not include zero (i.e. significant effect).

FIGURE 5

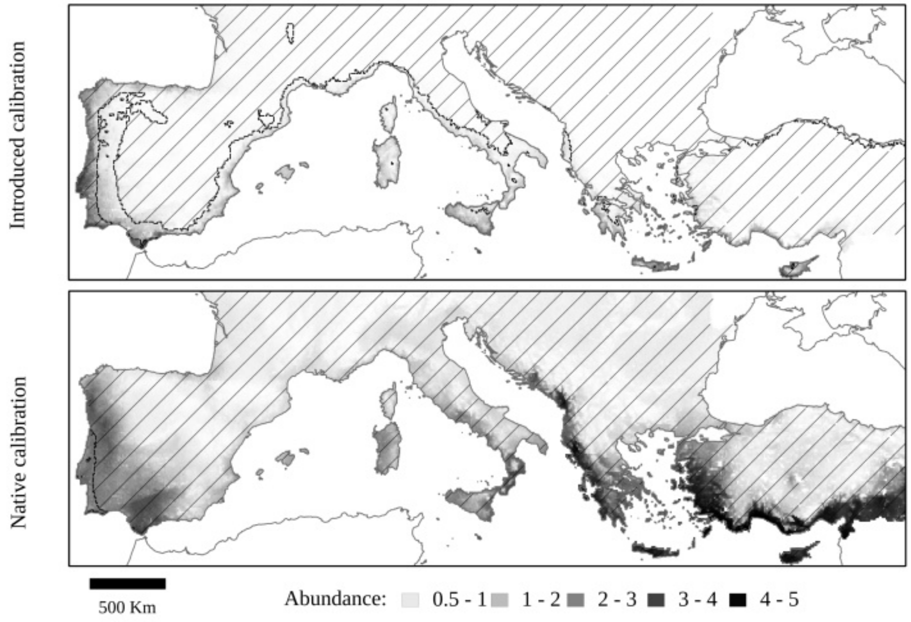


Posterior means (with credible intervals) of the coefficients for habitat type (disturbance at local level) at native (circles) and introduced (triangles) ranges in the GLM explaining the abundance of *Oxalis pes-caprae*. The "Overall" coefficients are the sum of the disturbed and natural habitats coefficients respectively. Filled symbols indicate that the 95% credible interval around the difference between coefficients of both ranges for each habitat did not include zero (i.e. significant difference).

Predicting shifts

Predictions in the introduced range from models calibrated with native range data showed larger potential distribution of *Oxalis* than models using only introduced range data (Fig.6). However, when considering only predictions for analogue conditions the potential distribution based on native range data was rather small (Fig.6, Appendix A–Fig. A.7).

FIGURE 6



Prediction maps of Oxalis pes-caprae abundance (from absent =0 to dominant = 5). Upper part: predictions with GLM calibrated only with data from the introduced range. Lower part: predictions with GLM calibrated only with data from the native range. Dashed line delimits analog conditions (positive values of MESS index) in relation to the calibrated data. Surface crossed with lines indicates non-analog conditions where models are extrapolating at least in one variable.

DISCUSSION

Estimating the strength of niche conservatism is extremely important for predicting the spread of introduced species (Alexander & Edwards, 2010; Petitpierre et al., 2012). Although most niche shifts studies consider only broad climatic niches, additional factors such as habitat and disturbance may also affect niche shifts for invasive species. For Oxalis, we found similar levels of climatic and disturbance niche shifts between native and introduced ranges, mainly related to different environmental availability between ranges and a time lag in the invasion process. Clearly, features other than broad climatic factors are also important for shaping species' niches.

Climatic niche shifts

The observed niche shift of Oxalis towards higher precipitation seasonality and lower temperatures in the introduced range is most likely a consequence of the availability of climatic conditions in the introduced range that are not present in the native range, rather than rapid evolution. The colder, more seasonal climates in the Mediterranean are simply not available in South Africa. When considering climates available in both ranges, expansion and unfilling metrics were greatly reduced (<10%), on par with percentages found for 86% of the Holarctic species studied by Petitpierre et al. (2012). Nonetheless, the large expansion observed when considering the whole climatic space suggests that the species might have significant plasticity in the niche not expressed in the native range (Alexander & Edwards, 2010). Similar patterns of expansion linked to high plasticity have been found for species introduced to Australia with ~75% of species studied experiencing novel biomes (Gallagher et al., 2010). These findings have important consequences for invasion risk analyses because models considering only the niche in the native range could greatly underestimate the invasion potential of non-native species (Hierro et al., 2009; Jiménez-Valverde et al., 2011).

Half of the climate variables showed similar associations with Oxalis' abundance in its native and introduced ranges suggesting a constant sensitivity to climate across its whole range. However, for the other half of the climate variables, the association was only important in one of the ranges. For example, temperature seasonality was only associated with Oxalis' abundance in the introduced range.

The negative association between temperature seasonality and abundance suggests higher abundances close to coastal areas, raising two possible mechanisms. On the one hand it could reflect the original niche in the native range, as *Oxalis* occupies areas in the native range with relatively lower seasonality than in the introduced range (Fig. 3). On the other hand, this pattern could be an artefact of the coastal locations of historical introductions and the insufficient time to spread further inland.

Precipitation in winter was only an important correlate of *Oxalis'* abundance in the native range. We had expected the same association in the introduced range because the species is a winter-growing geophyte (Ross et al., 2008). Two non-exclusive factors could explain this pattern. First, the species might be associated with artificial water sources in human-altered areas in the introduced range (personal observation), allowing the species to be less dependent on precipitation regimes. Second, differences could be an artefact of the collinearity between precipitation in winter and precipitation seasonality which occurs only in the introduced range. The different sensitivity of *Oxalis'* abundance to climate variables in the two ranges highlights the importance of understanding the biology of invasive species both in their native and introduced ranges rather than developing “blind” models from the “best” set of predictors.

Disturbance niche shifts

Oxalis prefers high levels of disturbance in both the native and introduced ranges. However, we found a clear shift towards higher levels of disturbance in the introduced range, both at landscape and local scales. In other words, *Oxalis* occupies more natural areas in the native range that remain unoccupied in the introduced range. Similar patterns have been described for other invasive species. For instance, *Rhododendron ponticum* L. occurs in well conserved forests in its native range but it is highly invasive in the British Isles where it is especially competitive in disturbed areas (Cross, 1975). Such evidence supports the hypothesis that invasive species may be associated with higher levels of disturbance especially in the beginning of the invasion process (Hobbs & Huenneke, 1992; Dietz & Edwards, 2006). This finding implicates that non-native species such as *Oxalis* could invade more natural habitats as the invasion unfolds (Dietz & Edwards, 2006). This possibility is further supported by the ecology of *Oxalis* in the introduced range. Due to the lack of local floral morph diversity in the introduced range its principal means of reproduction is by bulbis (Castro et al., 2007). This vegetative reproduction could partially explain the shift towards higher levels of disturbance as disturbance and rapid clonal spread are generally associated (Coffroth & Lasker, 1998). However, the recent discovery of populations with higher floral morph diversity (Castro et al., 2013) and the partial breakdown in the morph-incompatibility system in Portugal (Costa et al., 2014) suggest that the species may be able to take advantage of sexual reproduction and thereby adapt to more natural conditions.

Other factors intrinsic to specific habitats could affect changes in abundance between native and introduced ranges. For instance, Oxalis is more abundant in agricultural habitats in the introduced range, probably due to different crop systems. In Southern Europe, the reduction in profitability in modern agriculture (especially olive groves, which are not common in South Africa) promotes systems with lower inputs and weed control allowing higher Oxalis' abundance compared to similar habitats in South Africa. Biotic interactions could also limit Oxalis spread into natural habitats. For instance, Oxalis is a poor competitor against native grasses (Sala et al., 2007). In contrast, Vilà et al., (2006) found similar rates of Oxalis bulb predation and germination among ruderal, shrubland and old-field habitats. Although we lack knowledge of its success in later stages of the recruitment dynamics (Vilà et al., 2006), its “invasive” character in the native range suggests that the species might be able to expand into more natural habitats, profiting from local disturbances (e.g. forest gaps). This potential expansion could alter succession dynamics in natural habitats, thereby magnifying ecological impacts in the introduced range.

Understanding and modelling niche shifts

Climatic niche shifts are commonly tested using an aggregation of climate variables in an ordination space (e.g. Gallagher et al., 2010; Petitpierre et al., 2012). Although it is possible to reduce bias in sampling and frequency of environmental conditions by applying smoothing functions (Broennimann et al., 2012), this method still requires a priori knowledge of which variables are most important for determining range limits of the species. This is a major caveat of the method because sensitivities to different climatic variables are likely to vary among species. Furthermore we found slightly higher shifts considering abundance data than with occurrence data, which could partially explain the low shift values found in other studies. Another approach frequently used is Reciprocal Distribution Modelling in which the potential distribution of a species in the introduced range is predicted from the actual occurrence in the native range and vice versa (Fitzpatrick et al., 2007; Medley, 2010). This technique allows predictions to be mapped in geographical space and accepts categorical variables. Using this approach we have complemented the ordination method by identifying the variables that characterize Oxalis' niche and compared the conservatism in the association of single variables with the species' abundance. Despite its potential, it is important to consider possible bias arising from the selection of the variables (Strubbe et al., 2013) and uncertainties such as that associated with extrapolation into non-analogue conditions (Fitzpatrick & Hargrove, 2009). Therefore, for shift analyses we advocate a careful selection of biologically relevant variables, the use of both occurrence and abundance data and the combined implementation of ordination and distribution modelling approaches.

The relative merits of quantifying absolute shifts in environmental conditions between ranges, versus shifts within those conditions available in both ranges is currently under debate (Petitpierre et al., 2012). Limiting analyses to conditions common to both ranges allows shifts to be interpreted as “true” niche shifts versus simply the filling of a pre-adapted niche (Petitpierre et al., 2012). However, for invasive species this approach is likely to underestimate invasion risk because introduced ranges often contain environmental conditions not available in the native range. Further, our study highlights the importance of defining species' niches more broadly than simply by climate because other factors may have important effects on niche shifts (Wiens et al., 2010). For Oxalis, considering only common climatic conditions might underestimate its potential to invade colder, more seasonal and more natural areas. Evidence is mounting that estimations of invasion risk should not assume niche conservatism (Fitzpatrick et al., 2007; Gallagher et al., 2010), but rather incorporate multiple niche dimensions in both native and introduced ranges (Broennimann & Guisan, 2008; Jiménez-Valverde et al., 2011). Thus, while invasive species offer a unique chance to test basic biogeographic questions about niche shifts, understanding these basic processes also have important consequences for management of biodiversity.

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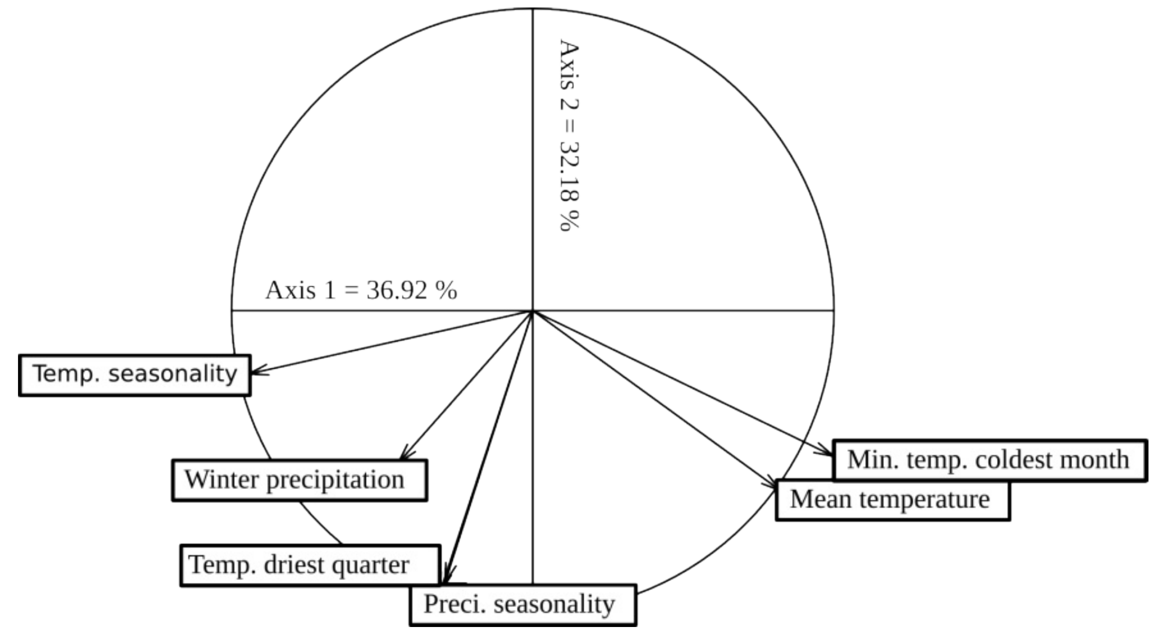
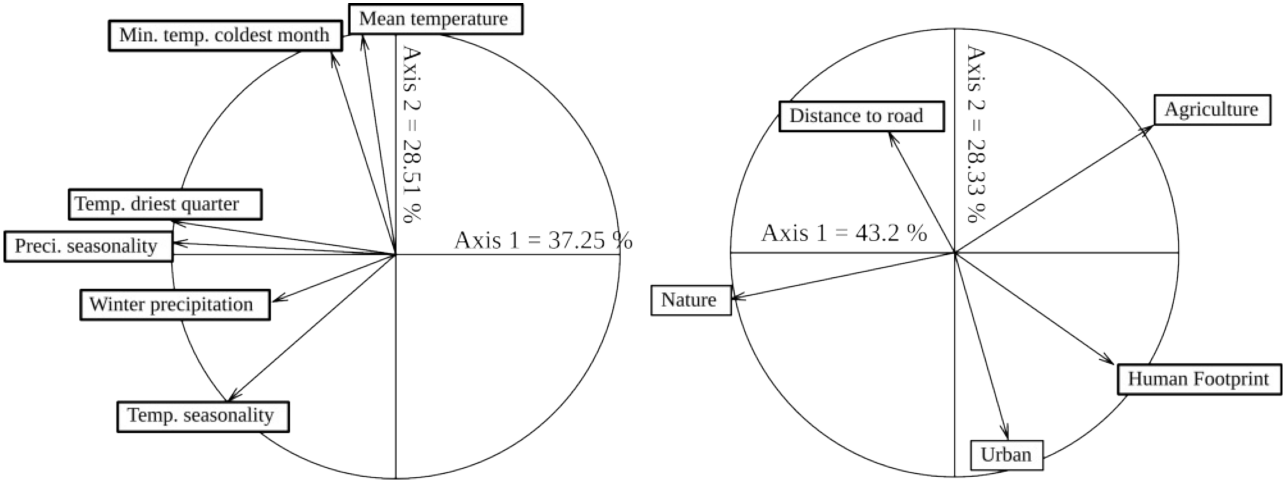
APPENDIX A – SUPPLEMENTARY TABLES AND FIGURES

FIGURE A.1



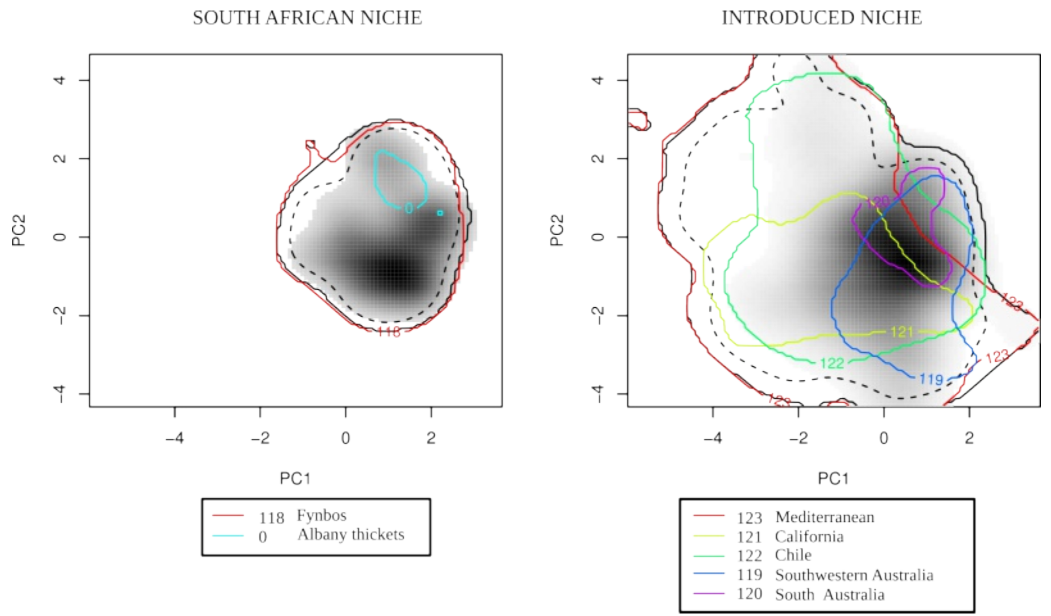
PRINCIPAL COMPONENT ANALYSIS PLOT OF THE WORLDWIDE MEDITERRANEAN SPACE SHOWING THE CONTRIBUTION OF EACH CLIMATIC VARIABLE TO THE FIRST TWO AXES.

FIGURE A.2



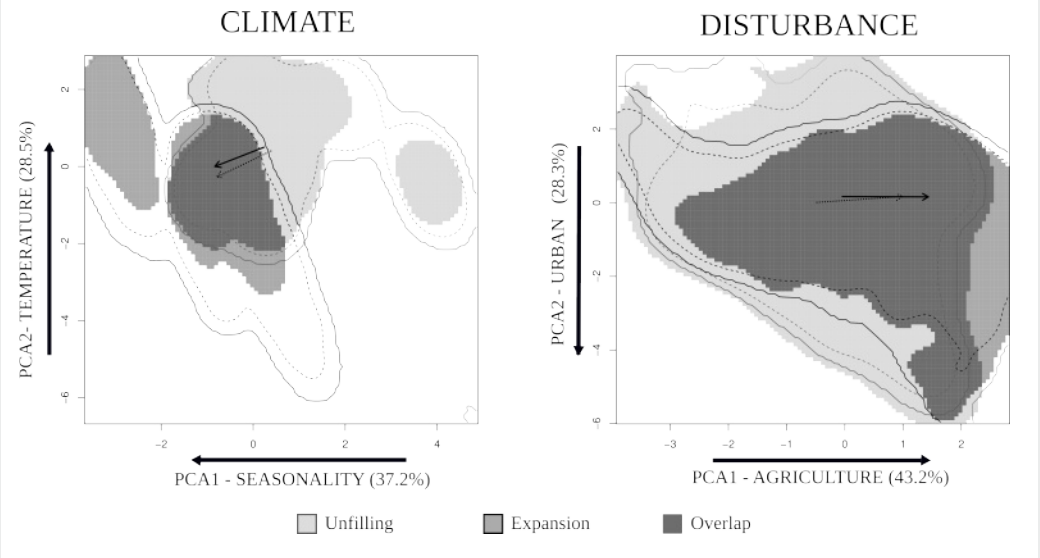
PRINCIPAL COMPONENT ANALYSIS PLOTS OF THE SAMPLED SPACE (MEDITERRANEAN BASIN AND SOUTH AFRICA) SHOWING THE CONTRIBUTION OF CLIMATE AND LANDSCAPE VARIABLES TO THE FIRST TWO AXIS.

FIGURE A.3



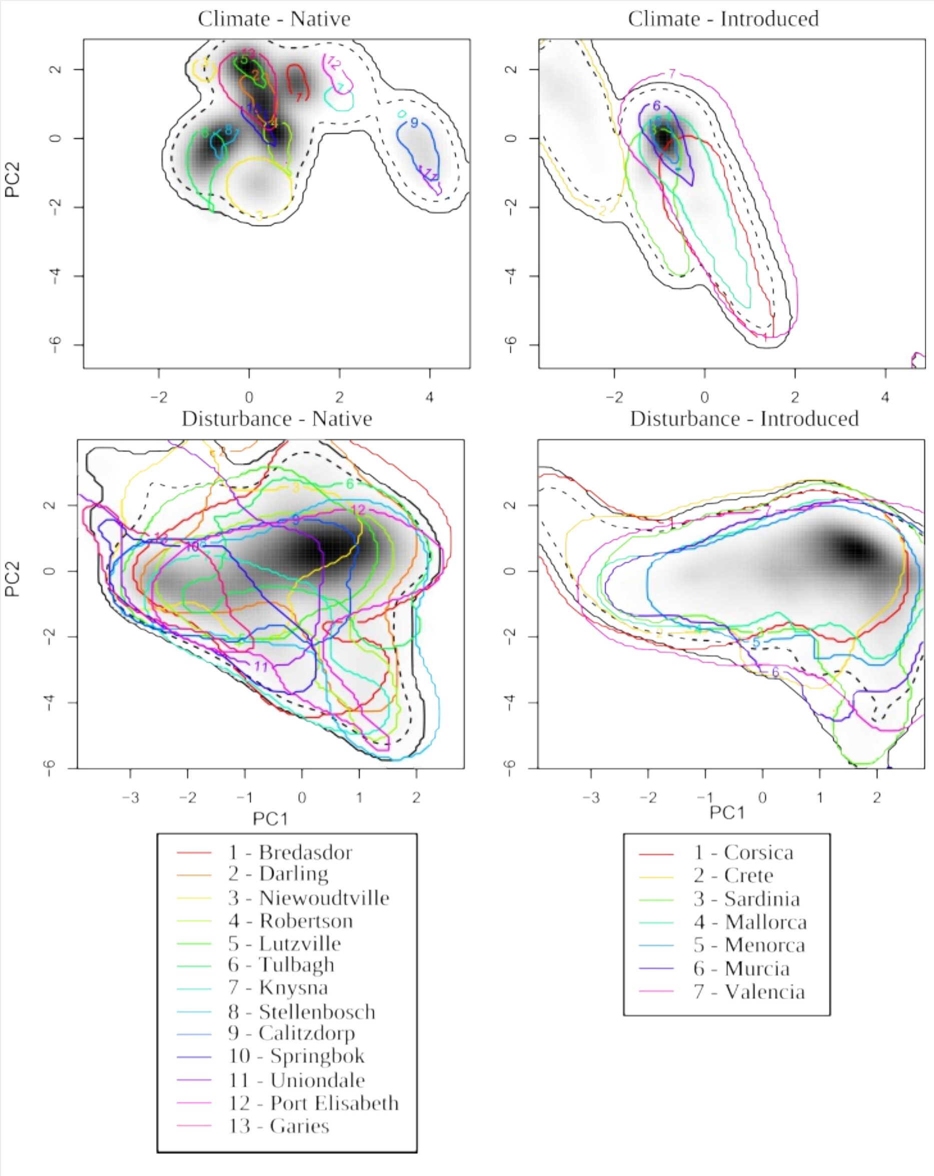
GLOBAL CLIMATIC NICHE OF *OXALIS PES-CAPRAE* IN NATIVE AND INTRODUCED RANGES. IN GRAY SHADE DISTRIBUTION DENSITY OF THE SPECIES. BLACK DASHED LINE CORRESPOND TO THE 75% PERCENTILE OF THE WHOLE CLIMATIC NICHE. LINES CORRESPOND TO DIFFERENT GEOGRAPHICAL AREAS.

Figure A.4



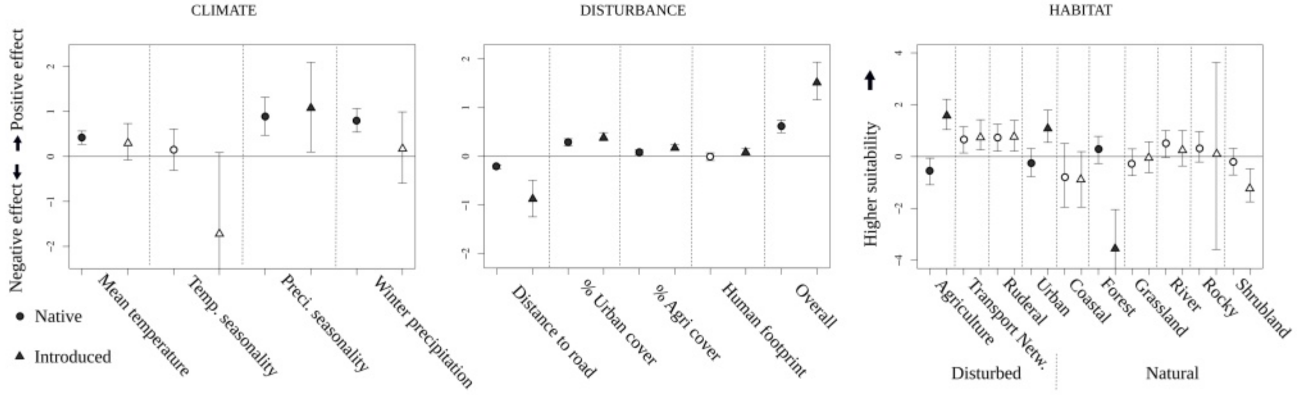
Shifts in the climatic and disturbance niche of *Oxalis pes-caprae* (occurrence) between South Africa and the Mediterranean basin based on separate PCAs for climate variables and disturbance variables at landscape scale. The light grey line delimits the entire range of conditions in the native range of *Oxalis* while the black line delimits the conditions in the introduced range (Mediterrean basin). For both ranges, the continuous line corresponds to the whole climatic space while the dashed line indicates the 75% percentile. Shaded areas represent the portion of these conditions actually occupied by *Oxalis*: medium grey for niche expansion (presence only in the introduced range), light grey for niche unfilling (presence only in the native range) and dark grey shows the conditions that are occupied in both ranges. The continuous black arrow shows the environmental distance between the median of the distribution density for each range. The dashed black arrow shows the environmental distance between the median of the available climatic space in each range.

FIGURE A.5



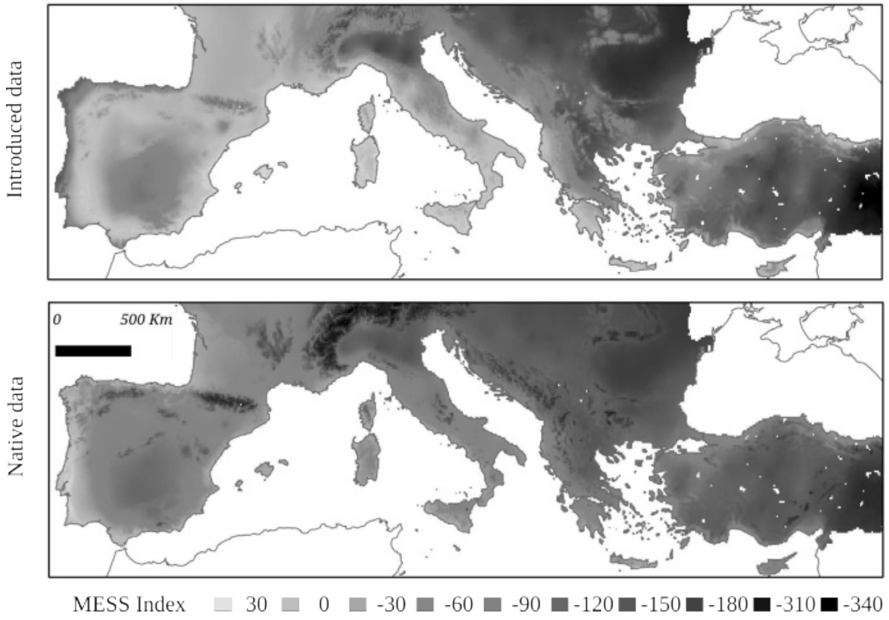
Climatic and disturbance niche of Oxalis pes-caprae based on abundance data in native and introduced ranges corresponding to the sampled space (Mediterranean Basin and South Africa). In gray shade distribution density of the species. Black dashed line correspond to the 75% percentile of the whole niche. Lines correspond to different geographical areas.

FIGURE A.6



Posterior means (with credible intervals) of the mean coefficients for climate and disturbance variables at native (circles) and introduced (triangles) ranges in the GLM explaining the abundance of *Oxalis pes-caprae* only from road sampling data. The "Overall" coefficient is the absolute sum of the four disturbance coefficients. In climate and disturbance coefficients, filled symbols indicate that the 95% credible interval around the parameter mean values did not include zero. In habitat coefficients filled symbols indicate that the 95% credible interval around the difference between coefficients of both ranges for each habitat did not include zero.

Figure A.7



Map of MESS values for predictions in the introduced range. MESS quantifies the similarity between the environmental conditions used to calibrate the models (upper part introduced range, lower part native range) with the conditions represented in all predicted points. Positive MESS values indicate that the full range of conditions are included in the data with higher values indicating areas that are better represented by data. Negative values indicate conditions not included in the data where the models are extrapolating (Elith et al., 2010).

Person's correlation coefficient of the association among all variables used in the analyses. In bold selected variables that were not intercorrelated in either of the ranges.

Table A.1

	Annual Mean Temperature	**Temperature Seasonality**	Min Temperature of Coldest Month	Mean Temperature of Driest Quarter	**Precipitation Seasonality**	**Precipitation of Coldest Quarter**	**Human footprint index**	**% Agriculture cover**	% Nature cover	**% Urban cover**	**Distance to road**
SOUTH AFRICA											
Temperature Seasonality (SD *100)	0.04										
Min Temperature of Coldest Month	0.26	-0.79									
Mean Temperature of Driest Quarter	0.39	0.27	0.20								
Precipitation Seasonality	0.20	0.51	-0.11	0.62							
Precipitation of Coldest Quarter	-0.47	0.00	0.10	0.21	0.17						
Human footprint index	0.08	-0.14	0.23	0.12	-0.08	0.24					
% Agriculture cover	-0.07	-0.03	0.13	0.20	0.12	0.32	-0.02				
% Nature cover	0.09	0.08	-0.20	-0.25	-0.08	-0.40	-0.21	-0.82			
% Urban cover	-0.06	-0.08	0.11	0.05	-0.08	0.11	0.41	-0.30	-0.21		
Distance to road	-0.09	-0.03	0.00	-0.03	0.10	-0.01	-0.21	0.19	-0.10	-0.15	
Oxalis abundance	0.09	0.08	0.04	0.20	0.21	0.14	0.03	0.22	-0.18	-0.05	-0.07
MEDITERRANEAN BASIN											
Temperature Seasonality (SD *100)	-0.01										
Min Temperature of Coldest Month	0.56	-0.66									
Mean Temperature of Driest Quarter	0.95	0.16	0.42								
Precipitation Seasonality	0.42	-0.14	0.65	0.39							
Precipitation of Coldest Quarter	-0.33	-0.33	0.41	-0.35	0.61						
Human footprint index	0.42	-0.04	0.14	0.37	-0.09	-0.38					
% Agriculture cover	0.38	-0.10	0.29	0.33	0.10	-0.09	0.33				
% Nature cover	-0.54	0.13	-0.36	-0.48	-0.11	0.20	-0.48	-0.85			
% Urban cover	0.23	0.00	0.09	0.21	0.02	-0.16	0.40	-0.18	-0.24		
Distance to road	-0.32	-0.04	-0.10	-0.29	0.17	0.34	-0.26	-0.23	0.30	-0.12	
Oxalis abundance	0.12	-0.26	0.32	0.06	0.14	0.13	0.14	0.22	-0.24	0.11	-0.12

TABLE A.2

PEARSON'S CORRELATION COEFFICIENT OF THE ASSOCIATION BETWEEN *OXALIS* ABUNDANCE AND LAND-COVER VARIABLES AT 250, 500 AND 1000 m.

	Distance		
	250	500	1000
% Agriculture cover	0.235	0.239	0.243
% Urban cover	0.011	0.020	0.032
% Nature cover	-0.234	-0.239	-0.241

TABLE A.3

CREDIBLE INTERVALES FOR THE DIFFERENCES BETWEEN NATIVE AND INVADED RANGE FOR EACH CLIMATE AND LANDSCAPE COEFFICIENTS IN THE GLM EXPLAINING THE ABUNDANCE OF *OXALIS PES-CAPRAE*. IN BOLD COMBINATIONS WHICH CONFIDENCE INTERVAL DO NOT INCLUDE ZERO.

Variable	Differences
Mean temperature	- 0.19, 0.36
Temperature seasonality	**0.99, 2.95**
Precipitation seasonality	- 0.78, 0.63
Precipitation winter	**0.23, 1.35**
Road distance	**0.64, 1.02**
Agriculture cover	- 0.18, 0.02
Urban cover	- **0.22, -0.08**
Human footprint	- **0.22, -0.03**
Overall disturbance	- **1.38, -0.89**

Differences of the posterior means (with credible intervals) of the coefficients for habitat type at native (NA) and introduced (IN) ranges in the GLM explaining the abundance of Oxalis pes-caprae. In bold combinations which credible interval which do not include zero (i.e. significant). The Disturbed and Natural coefficients correspond to the sum of the disturbed and natural habitats coefficients respectively.

Table A.4

	Agriculture – NA	Agriculture – IN	Coastal – NA	Coastal – IN	Forest – NA	Forest – IN	Grassland – NA	Grassland – IN	River – NA	River – IN
Agriculture – IN	**1.41,3.07**									
Coastal – NA	-1.32,1.08	-3.77,-0.94								
Coastal – IN	-1.54,0.79	-3.54,-1.7	-1.88,1.36							
Forest – NA	0.61,1.05	-2.25,-0.57	-0.27,2.16	0.04,2.38						
Forest – IN	-1,0.73	-2.67,-2.08	-1.45,1.42	-0.71,1.2	**-1.84,-0.09**					
Grassland – NA	0.17,0.53	-2.72,-1.06	-0.73,1.67	-0.44,1.89	-0.7,-0.26	-0.38,1.35				
Grassland – IN	-0.01,1.65	-1.55,-1.29	-0.48,2.35	0.27,2.13	-0.86,0.84	0.65,1.26	-0.37,1.31			
River – NA	0.86,1.27	-2.02,-0.35	-0.03,2.39	0.27,2.6	-0.01,0.47	0.33,2.06	0.51,0.91	-0.6,1.08		
River – IN	0,1.76	-1.7,-1.03	-0.44,2.44	0.28,2.24	-0.84,0.94	0.58,1.45	-0.35,1.41	-0.29,0.41	-1.06,0.7	
Transport – NA	1.07,1.36	-1.85,-0.2	0.13,2.54	0.44,2.75	0.19,0.58	0.49,2.21	0.72,1.02	-0.43,1.22	-0.01,0.33	-0.53,1.21
Transport – IN	0.72,2.38	-0.78,-0.6	0.25,3.08	1.01,2.85	-0.12,1.56	1.39,1.98	0.37,2.03	0.6,0.86	-0.34,1.33	0.33,1.01
Rocky – NA	0.61,1.29	-2.16,-0.42	-0.17,2.31	0.14,2.52	-0.24,0.48	0.18,1.99	0.26,0.94	-0.74,1.01	-0.46,0.25	-0.84,0.99
Rocky – IN	-1.9,0.8	-3.98,-1.6	-2.19,1.33	-1.62,1.28	-2.74,-0.03	-1.63,0.8	-2.25,0.45	-2.56,-0.18	-2.96,-0.26	-2.66,-0.2
Ruderal – NA	1.09,1.51	-1.78,-0.11	0.2,2.63	0.51,2.85	0.22,0.71	0.56,2.3	0.74,1.16	-0.36,1.32	0.01,0.47	-0.46,1.3
Ruderal – IN	0.67,2.34	-0.84,-0.62	0.21,3.04	0.96,2.81	-0.17,1.52	1.34,1.94	0.32,1.99	0.55,0.83	-0.39,1.28	0.28,0.97
Shrubland – NA	0.2,0.56	-2.69,-1.03	-0.71,1.7	-0.41,1.92	-0.67,-0.24	-0.35,1.37	-0.15,0.21	-1.27,0.39	-0.88,-0.49	-1.38,0.37
Shrubland – IN	-1.37,0.34	-2.99,-2.52	-1.82,1.03	-1.07,0.8	-2.21,-0.48	-0.74,-0.02	-1.72,-0.01	-1.58,-1.08	-2.43,-0.72	-1.79,-1
Urban – NA	0.08,0.6	-2.75,-1.05	-0.75,1.67	-0.45,1.89	-0.78,-0.2	-0.41,1.35	-0.27,0.25	-1.33,0.37	-1,-0.44	-1.43,0.35
Urban – IN	0.95,2.64	-0.64,-0.25	0.49,3.33	1.24,3.11	0.11,1.82	1.59,2.27	0.6,2.29	0.76,1.19	-0.11,1.58	0.54,1.29
Disturbed – NA	-0.42,2.08	-3.46,0.63	-0.95,2.84	-1,3.41	-1.27,1.26	-1.1,3.02	-0.78,1.74	-2.04,2.05	-1.5,1.04	-2.12,2.01
Disturbed – IN	2.95,7.18	1.51,4.13	2.72,7.64	3.67,7.21	2.11,6.36	3.83,6.57	2.6,6.83	2.92,5.57	1.89,6.12	2.81,5.56
Natural – NA	-2.11,2.25	-5.09,0.75	-1.89,2.27	-2.58,3.48	-2.93,1.41	-2.73,3.13	-2.45,1.89	-3.67,2.17	-3.16,1.18	-3.74,2.13
Natural – IN	-6.16,-0.35	-7.69,-3.3	-6.32,0.04	-5.05,-0.71	-7,-1.18	-5.31,-0.94	-6.52,-0.7	-6.27,-1.88	-7.22,-1.41	-6.33,-1.95

Table A.4

(Cont.) Differences of the posterior means (with credible intervals) of the coefficients for habitat type at native (NA) and introduced (IN) ranges in the GLM explaining the abundance of *Oxalis pes-caprae*. In bold combinations which credible interval which do not include zero (i.e. significant). The Disturbed and Natural coefficients correspond to the sum of the disturbed and natural habitats coefficients respectively.

	Transport – NA	Transport – IN	Rocky – NA	Rocky – IN	Ruderal – NA	Ruderal – IN	Shrubland – NA	Shrubland – IN	Urban – NA	Urban – IN	Disturbed – NA	Disturbed – IN	Natural – NA
Transport – IN	-0.49,1.16												
Rocky – NA	-0.59,0.06	-1.47,0.27											
Rocky – IN	-3.11,-0.42	-3.29,-0.91	**-2.88,-0.12**										
Ruderal – NA	-0.1,0.26	-1.09,0.58	0,0.7	0.5,3.2									
Ruderal – IN	-0.54,1.12	-0.15,0.06	-0.32,1.43	0.86,3.25	-0.63,1.05								
Shrubland – NA	-0.98,-0.7	-2,-0.34	-0.91,-0.24	-0.42,2.28	-1.13,-0.72	-1.96,-0.3							
Shrubland – IN	-2.58,-0.88	-2.3,-1.83	-2.36,-0.57	-1.16,1.23	-2.67,-0.96	-2.26,-1.78	**-1.74,-0.04**						
Urban – NA	-1.12,-0.64	-2.06,-0.36	-1,-0.22	-0.47,2.26	-1.24,-0.68	-2.01,-0.32	-0.3,0.22	-0.01,1.72					
Urban – IN	-0.26,1.41	0.05,0.44	-0.04,1.73	1.14,3.55	-0.35,1.34	0.09,0.49	0.58,2.26	2.02,2.6	**0.6,2.31**				
Disturbed – NA	-1.64,0.86	-2.77,1.32	-1.43,1.19	-0.94,3.7	-1.72,0.77	-2.72,1.37	-0.81,1.71	-0.71,3.4	-0.76,1.73	-3.02,1.08			
Disturbed – IN	1.74,5.96	2.2,4.82	1.98,6.24	3.61,7.62	1.65,5.88	2.25,4.87	2.57,6.8	4.23,6.92	2.6,6.84	1.96,4.58	**0.95,7.52**		
Natural – NA	-3.32,1.03	-4.4,1.44	-3.05,1.29	-2.49,3.74	-3.42,0.96	-4.36,1.49	-2.48,1.86	-2.35,3.51	-2.46,1.92	-4.65,1.2	-2.16,0.64	-9.15,-0.83	
Natural – IN	-7.38,-1.57	-7,-2.61	-7.13,-1.29	-4.86,-0.56	-7.46,-1.65	-6.96,-2.57	-6.54,-0.73	-4.93,-0.56	-6.51,-0.69	-7.26,-2.84	-8.17,0	-9.91,-6.73	-8.29,1.64

APPENDIX B

Modelling details

The categorical abundance of *Oxalis* in the dominant habitats of each plot i (N=10871), AB_i, was modelled using a Binomial distribution with trial size equal to 5 (maximum abundance category): $AB_i \sim \text{Binomial}(q_i, 5)$. The probability of being more abundant was modelled using a logit link function as:

$$\text{logit}(q_i) = \gamma + \alpha_{\text{habitat,range}(i)} + e_{g(i)} + \beta X_{(i)}$$

where γ is an overall intercept, $\alpha_{\text{habitat, range}(i)}$ is a random effect for each habitat type and range, $e_{g(i)}$ is a random effect for each UTM cell, g, and X is the design matrix of explanatory variables. All parameters were given non-informative prior distributions:

$\gamma \sim \text{Normal}(0,100)$
$\alpha_{\text{habitat,range}} \sim \text{Normal}(0,100)$
$e_g \sim \text{Normal}(0, \sigma^2_e)$; $\sigma_e \sim \text{Uniform}(0,100)$

The design matrix of explanatory variables, X, included the climate (30" resolution) and landscape variables that were not correlated for both ranges (see data section). The vector of coefficients associated with each climate and landscape variable, β, was estimated for each range given non-informative normal distributions,

$$\beta_{\text{var,range}(i)} \sim \text{Normal}(0,10000)$$

All predictors were centred and standardized in order to improve model convergence and aid interpretation (Gelman & Hill, 2007). Preliminary analyses using the Moran’s Index, did not detect significant spatial autocorrelation in the models’ residuals at distance bins of 0.1º (~10 km; I<0.1). Therefore we proceeded without implementing any spatial correction.

OpenBugs code

Openbugs code to model the abundance of Oxalis pes-caprae (5 abundance classes) in relation to habitat type (betaH), climate variables (betaC) and disturbance variables (betaD) using 10871 plots (NP) and 48 grids (NG) in the native and invaded ranges of the species (R)

```
   ##Likelihood


for (i in 1:NP) {
   ABUND[i] ~ dbin(pb[i],5)
   logit(pb[i]) <- mu + betaH[HABITAT[i],R[i]]+ xbeta[i]+alpha[grid[i]]
xbeta[i]<betaC[1,R[i]]*MEANTEMP[i]+betaC[2,R[i]]*TEMPSEAS[i]+betaC[3,R[i]]*PRECSEAS[i]
+betaC[4,R[i]]*PRECWINT[i]+betaD[1,R[i]]*ROAD[i]+betaD[2,R[i]]*AGRI[i]+betaD[3,R[i]]*URBAN[i]
+betaD[4,R[i]]*H[i]
}

 ###########
# Priors
##########
#Intercept
mu ~ dnorm (0, .0001)
mu_adj <- mu + mean(betaH[,])

#Random effect for grid level.
for (g in 1:NG) {
   alpha[g] ~ dnorm(0,alpha_tau)
   }
   alpha_tau <- pow(alpha_sigma, -2)
   alpha_sigma ~ dunif(0,100)

# Habitat
for (r in 1:2)  {
  for (j in 1:10)  {
     betaH[j,r] ~ dnorm(0, betaH_tau[r])
```

```
      betaH_adj[j,r] <- betaH[j,r] - mean(betaH[,]) #we subtract the mean to make them comparable
    }
      betaH_tau[r] <- pow(betaH_sigma[r], -2)
      betaH_sigma[r] ~ dunif(0, 100)
  }
  # Climate variables
  for (v in 1:4)  {
            for ( r in 1:2)  {
             betaC[v,r] ~ dnorm(0, 0.0001)  # Mean effect of climate within ranges
            }
     }
  # Disturbance variables
  for (v in 1:4)  {
            for (r in 1:2)  {
              betaD[v,r] ~ dnorm(0, 0.0001)  # Mean effect of disturbance within ranges
            }
        }
```

Discusión General y síntesis

DISCUSIÓN GENERAL Y SÍNTESIS

La importancia de la escala espacial en los factores que controlan el grado de invasión

Los patrones de invasión por plantas exóticas pueden ser debidos a un proceso jerárquico en el que numerosos factores actúan a distintas escalas espaciales (Milbau et al., 2009). Teniendo en cuenta clima, alteración del paisaje y el tipo de hábitat, **la alteración del paisaje es el factor más importante a la hora de determinar el grado de invasión de las comunidades vegetales a escalas intermedias o de paisaje** (<200 km). En el Capítulo 1 encontramos que las variables relacionadas con la alteración humana tanto a escala regional como de paisaje fueron los factores con una mayor asociación con el grado de invasión de zonas costeras, explicando en conjunto aproximadamente el 60% de la variabilidad en los patrones de invasión. En el Capítulo 2 encontramos un patrón similar. Las variables asociadas a la alteración del paisaje explicaron alrededor de un 20% de la variabilidad del grado de invasión en bosques fragmentados, en contraposición con menos de un 10% explicado por variables de carácter local tales como el tipo de hábitat, tipo de borde del fragmento o la orientación. Estos resultados concuerdan con numerosos trabajos en los que variables relacionadas con la abundancia o la distancia a usos de suelo alterados se identifican como factores clave para explicar el grado de invasión (Pino et al., 2005; Bartuszevige et al., 2006; Gassó et al., 2009; Gavier-Pizarro et al., 2010).

Sin embargo, no siempre la alteración del paisaje es el factor principal que controla el grado de invasión. En los Capítulo 4 y 5 observamos como el clima y la alteración del paisaje reflejaron un peso similar al explicar el grado de invasión. Esta diferencia en la importancia relativa se puede deber principalmente a la escala de estudio. Las variables climáticas cobran mayor importancia desde escalas regionales a continentales donde existe un gradiente climático amplio (Pearson & Dawson, 2003; Ibáñez et al., 2009b; Milbau et al., 2009). En este sentido, Pino et al., (2005) encontraron una mayor relevancia del clima analizando los patrones de invasión de Cataluña, región que engloba el área de estudio del Capítulo 2 y parte del área del Capítulo 1. Estos resultados apuntan a que **la influencia del clima en los patrones de invasión se observará en 1) amplios gradientes climáticos independientemente de la escala espacial y 2) condiciones ambientales extremas**. En relación al primer aspecto, un gradiente climático amplio también se puede encontrar en zonas de alta montaña, donde la variación de temperatura en distancias relativamente pequeñas determinará principalmente los patrones de riqueza de especies exóticas (Arévalo et al., 2005). Respecto al segundo aspecto, el grado de invasión en hábitats extremadamente áridos, estaría más influenciado por el clima que por la alteración del paisaje circundante. Por ejemplo en los ecosistemas dunares costeros, una mayor precipitación relativa podría contrarrestar el efecto negativo de la aridez y permitir el establecimiento de plantas exóticas (Carboni et al., 2010). Estos patrones se deben a que las especies exóticas suelen tener un mayor éxito invasor en condiciones ambientales moderadas y con escasa limitación de recursos (Polce et al., 2011).

La importancia de la fase en la que se encuentre el proceso de invasión

La importancia relativa de los factores que controlan los patrones de invasión puede variar dependiendo de la fase en la que se encuentre el proceso de invasión (Dietz & Edwards, 2006; Catford et al., 2009, 2011). Es decir, **los factores que determinan el éxito de introducción de una especie no son los mismos que determinan su éxito de expansión**. Por ejemplo, en el Trópico, Dawson et al., (2009) observaron como ciertos rasgos de las plantas exóticas (p.e. tamaño de las semillas o tipo de dispersión) y no la presión de propágulos, controlan su probabilidad de éxito según las distintas fases del proceso de invasión. Otros trabajos se han centrado en esta variabilidad considerando una aproximación multiespecie, en la que la presencia de cualquier especie exótica puede considerarse un indicador del establecimiento mientras que la abundancia de especies exóticas lo sería de una fase posterior de dominancia o expansión (Catford et al., 2011; Polce et al., 2011). Los pocos estudios que han profundizado en este aspecto no han encontrado diferencias claras en la importancia relativa de los factores climáticos y de alteración del paisaje tanto para el establecimiento como para la expansión de plantas exóticas (Catford et al., 2011; Polce et al., 2011; Capítulo 4). En cambio, sí que se han observado diferencias debidas al tipo de hábitat (Catford et al., 2011; Capítulo 4). En Australia, Catford et al., (2011) encontraron que la diferencia más significativa entre fases se debe a diferencias en la cobertura de vegetacion. Así, en zonas de alta cobertura de vegetación observaron una alta probabilidad de establecimiento de plantas exóticas pero una baja abundancia relativa. Del mismo modo, en el Capítulo 4 observamos como un mismo hábitat podía presentar diferencias entre la probabilidad de establecimiento y de dominancia. Por ejemplo, los hábitats forestales tuvieron una alta probabilidad de presencia de exóticas pero una extremadamente baja riqueza y abundancia. Estos resultados sugieren que **entre las fases de establecimiento y de expansión, el control es ejercido principalmente por el tipo de hábitat**, con una importancia similar del clima y la alteración del paisaje (Capítulo 4).

La alteración del paisaje y las invasiones biológicas

Las características del paisaje más asociadas al grado de invasión

De todos los aspectos que definen la alteración del paisaje, **la abundancia y la diversidad de los distintos tipos de cubiertas de suelo son los factores más importantes que caracterizan el grado de invasión** (Capítulo 1). Entre ellos, la abundancia de suelos urbanos y más concretamente los de baja densidad (p.e. urbanizaciones residenciales), es el componente principal. La asociación positiva entre área urbana y grado de invasión en áreas naturales se ha comprobado en numerosos trabajos atribuyéndose su importancia tanto a un aumento de la presión de propágulos como a una mayor perturbación relativa (Borgmann & Rodewald, 2005; Pino et al., 2005; Gassó et al., 2009; Marini et al., 2009). En concreto, la mayor importancia de las áreas residenciales se puede deber a la presencia de zonas ajardinadas que actúan como fuente de propágulos de plantas exóticas ornamentales (Gavier-Pizarro et al., 2010; Capítulo 1).

En contraposición, **la configuración del paisaje** es un factor poco estudiado en los análisis de los patrones de invasión por plantas exóticas (Vilà & Ibáñez, 2011) y que **ha resultado tener un papel minoritario y variable** en los pocos trabajos desarrollados hasta la fecha y en el que se presenta en esta Tesis (Capítulo 1). En general, los paisajes fragmentados parecen estar asociados a un mayor grado de invasión. Este patrón se debe principalmente a que una mayor densidad de hábitat de borde facilitaría el establecimiento y expansión de plantas exóticas (Brothers & Spingarn, 1992; Minor et al., 2009; Capítulo 1). Entre estas dos fases del proceso de invasión, la expansión es quizá la que podría tener una mayor asociación con la configuración del paisaje. Por ejemplo, Bartuszevige et al., (2006) encontraron una asociación significativa entre densidad de borde en el paisaje y la abundancia de *Lonicera maackii* pero no con la presencia de la especie, lo que sugiere un efecto positivo de la fragmentación tan sólo en la expansión de la especie. **Sería por tanto interesante profundizar en la**

importancia relativa de la composición y configuración del paisaje tanto en el establecimiento como en la expansión de especies exóticas, ya que podría ofrecer una explicación a la dispersión secundaria de determinadas especies exóticas una vez que son introducidas en áreas naturales.

Las invasiones en un paisaje cambiante

Los patrones de invasión que observamos en la actualidad son en parte el resultado del proceso de transformación del paisaje durante las últimas décadas. Por esta razón, el grado de invasión actual en determinadas áreas puede deberse no tanto a las características del paisaje actual sino a las características pasadas, conformando por tanto el denominado crédito de invasión (Vilà & Ibáñez, 2011). Si bien ha sido poco estudiado, **la existencia de crédito de invasión parece depender en gran parte de la transformación dominante del paisaje y del modo de introducción y tiempo de residencia de las especies exóticas** (Capítulo 3). En la costa andaluza occidental, donde en las últimas décadas se ha producido un importante proceso de urbanización de zonas agrícolas, observamos cierto crédito de invasión asociado a la abundancia de áreas alteradas en 1956 y dominado principalmente por especies asociadas a la agricultura (Capítulo 3). Un resultado similar se encontró en la costa Mediterránea catalana, donde se identificó una importancia relativa mayor del área agrícola en 1956 que de 2005 para explicar la abundancia de plantas exóticas (Basnou et al., bajo revisión.). Estos patrones sugieren que paisajes recientemente alterados presentan un grado de invasión relativamente inferior a los que le correspondería por su composición. Por tanto, se esperaría un incremento del grado de invasión en los próximos años.

La escasez de trabajos relacionados con el crédito de invasión se puede deber a la dificultad de obtener series temporales de información sobre patrones de invasión y características del paisaje. A su vez, la alta correlación entre la configuración del paisaje entre distintas fechas para una misma área de estudio fuerzan en algunos casos a elegir el paisaje más reciente, imposibilitando constatar de tal manera la existencia de crédito de invasión (p.e. Carboni et al., 2010). A pesar de este poco desarrollo, el marco conceptual del crédito de invasión puede ser relevante para estudiar la dinámica temporal de las invasiones. **Una adecuada aproximación metodológica incluiría un análisis a nivel de especie considerando la dinámica propia del paisaje del área de estudio y las características del evento de introducción** (p.e. fecha y modo de introducción).

Este tipo de estudios ofrecería información relevante para la prevención y detección temprana de especies invasoras al identificar tanto el nivel actual de invasión como su nivel potencial futuro.

La importancia del contexto en el grado de invasión

A nivel de comunidad

Son numerosos los factores que pueden interactuar para definir el grado de invasión de una comunidad. **Las características ecológicas de cada hábitat,** tanto bióticas como abióticas, **parecen tener un papel relevante a la hora de controlar la asociación de las variables climáticas y de alteración del paisaje con el grado de invasión** (Gassó et al., 2012a). La interacción del clima con el tipo de hábitat refleja en parte la importancia de la **resistencia biótica** en el control del grado de invasión local (Levine et al., 2004). En el Capítulo 4 observamos como una mayor precipitación anual se asociaba a un mayor grado de invasión en hábitats leñosos posiblemente al contrarrestar el efecto de la competencia interespecífica. Por el contrario, encontramos una asociación opuesta para hábitats "abiertos" tales como las praderas o los hábitats agrícolas. El tipo de hábitat también condiciona las **características abióticas** a nivel local (p.e. disponibilidad de recursos en el suelo) que pueden interaccionar con el efecto de otros factores sobre el grado de invasión. Por ejemplo, en determinados hábitats tales como los forestales, la abundancia de área agrícola a escala de paisaje presenta un efecto amortiguador del grado de invasión (Pino et al., 2005; Ibáñez et al., 2009b; Gavier-Pizarro et al., 2010; Capítulo 1). Este patrón podría estar relacionado con las condiciones de baja luminosidad del sotobosque que impediría la invasión de especies provenientes de agricultura, y por tanto mayoritariamente adaptadas a condiciones de alta luminosidad (Cadenasso & Pickett, 2001; Vilà et al., 2004). Por el contrario, considerando un rango de hábitats más amplio que incluya "hábitats abiertos" y ruderales, el efecto principal de la abundancia de área agrícola en el grado de invasión es positivo (Bradley & Mustard, 2006; Capítulos 4 y 5). Esta variabilidad refleja la idiosincrasia de los patrones de invasión y **la necesidad de considerar la interacción de variables que actúan a nivel local**, principalmente el tipo de hábitat, **con otras que afecten a nivel regional** (Gassó et al., 2012a).

El efecto del clima y la alteración del paisaje sobre el grado de invasión local también podrían variar según el contexto biogeográfico. Polce et al., (2011) identificaron un efecto positivo de la temperatura anual en el grado de invasión por plantas exóticas en distintos tipos de vegetación de Europa. Sin embargo a escala regional, las áreas con condiciones más moderadas fueron las que albergaron una mayor invasión. Es decir, mayor invasión en áreas relativamente cálidas de las regiones con clima atlántico y continental, y en áreas más frias de la región Mediterránea. Este patrón, estrechamente relacionado con la asociación de las especies exóticas a condiciones climáticas relativas moderadas (Rejmánek, 1989; Polce et al., 2011), no lo encontramos en España peninsular (Capítulo 4). A pesar de que distinguimos regiones sumamente diferentes como la Mediterránea y la Alpina, **los patrones debidos al efecto de las variables climáticas** fueron estables **y no dependieron de la región biogeográfica**. También encontramos un patrón similar para la alteración del paisaje, ya que su efecto sobre el grado de invasión también fue similar entre regiones biogeográficas (Capítulo 4). Estos resultados sugieren que al menos para la Península Ibérica, **los patrones generales de invasión por plantas exóticas pueden ser extrapolados entre regiones biogeográficas**.

A nivel de especie

Otro aspecto relacionado con la variabilidad interregional es la posibilidad de que los factores que determinan la presencia o abundancia de una especie (es decir, su nicho ambiental) sea similar o no entre el área nativa y la de introducción. En principio, el nicho ambiental de una especie debería ser similar entre la área nativa de la especie y la área de introducción (Peterson et al., 2003; Alexander & Edwards, 2010). Sin embargo, esta conservación del nicho no siempre es evidente. Varios estudios han identificado tanto procesos de expansión como de ocupación parcial del nicho (p.e. Broennimann et al., 2007; Fitzpatrick et al., 2007; Lauzeral et al., 2011). En el caso de expansión, los estudios sugieren la posibilidad de que las especies exóticas puedan sufrir procesos de evolución relativamente rápidos (Alexander & Edwards, 2010). **Para Oxalis pes-caprae, encontramos una expansión del nicho climático** en la área de introducción hacia condiciones más frías (Capítulo 5). La magnitud de la expansión climática se redujo considerablemente al considerar sólo las condiciones climáticas existentes tanto en la área nativa como en la de introducción. Por tanto, **no podemos asegurar que Oxalis haya sufrido una evolución o adaptación a nuevas condiciones climáticas**, ya que cabe la posibilidad de que la especie estuviera preadaptada a esas condiciones pero que no tuviera acceso a áreas de características similares en la área nativa (Petitpierre et al., 2012; Guisan et al., 2014). Para identificar estos procesos evolutivos sería necesario realizar experimentos en campo donde especímenes de la región nativa y de introducción crecieran en las mismas condiciones a lo largo de un gradiente ambiental (“common garden”; Alexander & Edwards, 2010). Por otra parte, **encontramos para la misma especie una ocupación parcial del nicho de perturbación** a nivel de paisaje y hábitat local. *Oxalis* ocupó paisajes y hábitats relativamente más naturales en la área nativa que en la de introducción (Capítulo 5). Este cambio de nicho concuerda con el desfase temporal que presentan las especies exóticas al establecerse primero en áreas perturbadas y saltar a zonas más naturales a medida que el proceso de invasión avanza (Dietz & Edwards, 2006). El nicho de perturbación no ha sido considerado en otros trabajos similares pero resalta la dinámica temporal del proceso de invasión y la posibilidad de que especies como *Oxalis*, invadan ecosistemas naturales en el futuro.

Implicaciones para la conservación y desarrollos futuros

Teniendo en cuenta la variabilidad en la importancia relativa de los factores que controlan los patrones de invasión **es fundamental estudiar estos patrones en otros contextos ecológicos considerando las distintas escalas espaciales** (Pauchard & Shea, 2006). Este tipo de estudios nos permitirán conocer los límites geográficos reales a partir de los cuales los patrones de invasión pasan de estar controlados principalmente por el clima a ser dominados por la alteración del paisaje o el tipo de hábitat. Del mismo modo, sería interesante complementar los estudios realizados en esta Tesis **incorporando un análisis de los factores que determinan el éxito de invasión a lo largo de todas las fases del proceso de invasión**, desde el transporte e introducción hasta el impacto ecológico. En general, modelizar los patrones de invasión utilizando una aproximación multiescala y multifase podría facilitar el manejo de especies invasoras al detectar el proceso principal que controla el éxito de invasión exactamente a la escala espacial y fase al que actúa (Pauchard & Shea, 2006).

Frente a la problemática de las especies invasoras, los gestores toman distintas medidas en función de la fase en la que se encuentre la especie exótica, su abundancia y el impacto que ocasione: prevención, detección precoz, control, erradicación y restauración (Dana & Rodríguez-Luengo, 2008). De todas las medidas posibles, la prevención es la más recomendada ya que permite eliminar la amenaza de la especie invasora antes de que su expansión por el territorio imposibilite su control. **Para una prevención adecuada, es necesario un análisis del riesgo de las especies potencialmente invasoras** basado en su biología, carácter invasor en otras regiones, nicho ambiental y posibilidad de introducción. Es en este análisis de riesgo donde **el tipo de paisaje puede tener un papel relevante ya que puede filtrar el tipo de plantas exóticas con mayor probabilidad de introducción** (Capítulo 2). Por ejemplo, en un paisaje principalmente agrícola esperaríamos encontrar en mayor proporción plantas exóticas de origen Mediterráneo, anuales y de dispersión zoocora (Capítulo 2). Este conocimiento puede ayudar a los gestores a identificar a priori qué especies tienen más probabilidad de establecerse en un territorio y desarrollar planes de prevención adecuados.

A su vez **una gestión adecuada requiere reconocer la dinámica temporal de las invasiones** (Kowarik et al., 1995; Vilà & Ibáñez, 2011; Capítulo 3 y 5). El grado de invasión potencial de un área o el potencial invasor de una especie puede no verse reflejado inmediatamente sino en décadas posteriores. **Identificar un posible crédito de invasión y el tipo de especies que lo conforman podría ayudar a prevenir una expansión futura de la invasión** (Capítulo 3). Del mismo modo, el elevado tiempo de residencia que pueden llegar a tener ciertas especies exóticas en un territorio, puede desembocar en un menosprecio de su carácter invasor a largo plazo o incluso en considerarlas nativas (Crooks, 2005; Clavero, 2014; Capítulo 3). Una estrategia apropiada debería centrarse en un seguimiento de las especies exóticas tanto de introducción reciente como de gran tiempo de residencia que permita la detección precoz de cambios importantes en su carácter invasor.

Finalmente, **en las tareas de control y erradicación es fundamental conocer a priori los patrones de invasión** para priorizar las áreas de interés y controlar las zonas fuente de especies exóticas. De los numerosos aspectos que pueden influir en los patrones de invasión, la alteración del paisaje es quizá uno de los que presentan mayor importancia relativa (Capítulo 1) y el que cobra mayor relevancia en la gestión de plantas invasoras. Al contrario que para el clima, **los gestores pueden actuar a nivel de paisaje estableciendo medidas correctoras específicas para cada uso de suelo o tipo de paisaje**. Por ejemplo, efecto del paisaje sobre el grado de invasión local parece ser máximo en una franja de 250-500 m alrededor del área de estudio (Capítulo 1) con lo que una estrategia eficiente pasaría por el control y seguimiento de las especies exóticas en esa franja del paisaje relativamente pequeña. Del mismo modo, la intensa asociación entre grado de invasión y abundancia de zona urbana de baja densidad, sugiere que el esfuerzo debe ir dirigido al interfaz urbano-forestal intentando reducir las prácticas de jardinería que promuevan el uso de plantas exóticas (Gavier-Pizarro et al., 2010; Capítulo 1 y 2).

CONCLUSIONES

Sección I – El paisaje y las invasiones por plantas exóticas

1. A escalas espaciales intermedias (<200 km), la alteración del paisaje es el factor más importante que determina el grado de invasión local por plantas exóticas en comparación con el tipo de hábitat y las condiciones climáticas. De los componentes del paisaje, la composición (abundancia y diversidad de tipos de cubiertas de suelo) es el grupo de variables más asociado al grado de invasión. En cambio, la configuración del paisaje (distribución espacial de los tipos de cubiertas) y la geometría de los parches poseen un asociación menor con el grado de invasión.

2. Los hábitats forestales Mediterráneos no están libres del riesgo de invasión por plantas exóticas. Cierta intensidad de perturbación y la cercanía a vías de comunicación pueden permitir la llegada y el establecimiento de especies exóticas en el interior de los bosques. Este patrón puede acentuarse debido al incremento de la interfaz urbano-forestal y al uso cada vez mayor de especies exóticas en jardinería.

3. Los patrones de invasión actuales por plantas exóticas están condicionados por la dinámica del paisaje, de forma que alteraciones pasadas pueden originar un crédito de invasión y por tanto un potencial mayor de grado de invasión en el futuro. El crédito invasión vendrá determinado por el tipo e historia del paisaje así como por las características de introducción de las plantas exóticas más frecuentes.

Sección II – La importancia del contexto en las invasiones biológicas

4. El patrón espacial del grado de invasión por plantas exóticas en España peninsular depende principalmente del tipo de hábitat y en menor medida del contexto geográfico. El tipo de hábitat es el factor más determinante a la hora de explicar el grado de invasión y a su vez para definir el tipo de asociación de las variables climáticas con el grado de invasión. En cambio, no se observa una variabilidad interregional en el efecto del clima o la alteración del paisaje.

5. Las especies exóticas pueden presentar un nicho ambiental diferente entre su área de distribución nativa y la de introducción. *Oxalis pes-caprae*, geófito nativo de Sudáfrica, presenta una expansión del nicho climático en su área de introducción en la cuenca Mediterránea. En cambio, observamos una ocupación parcial del nicho de perturbación. Esta ocupación parcial del nicho de perturbación indica una expansión potencial de la especie hacia zonas más naturales. Nuestros resultados sugieren por tanto, que la caracterización del nicho de especies exóticas sólo con variables climáticas o con información de una sola de las áreas de distribución puede llegar a subestimar el área potencial de invasión de las especies exóticas.

CONCLUSIONS

Section I – Landscape and plant invasions

1. At intermediate spatial scales (<200 km), landscape alteration is the most important factor determining the degree of invasion by exotic plants in comparison to habitat type and climate. From the different components of the landscape, the composition (i.e. abundance and diversity of the different land-cover types) is the group of variables with higher association with the degree of invasion. In contrast, landscape configuration (i.e. the spatial distribution of land-cover types) and patch geometry show lower association with the degree of invasion.

2. Mediterranean forest habitats are not out of risk of plant invasions. Certain degree of disturbance and closeness to roads allow the introduction and establishment of exotic species in the forest interiors. The global trend towards forest fragmentation, which increases the length of the interfaces between urban and forest areas, and the use of exotic species in gardening, might exacerbate plant invasion in the near future.

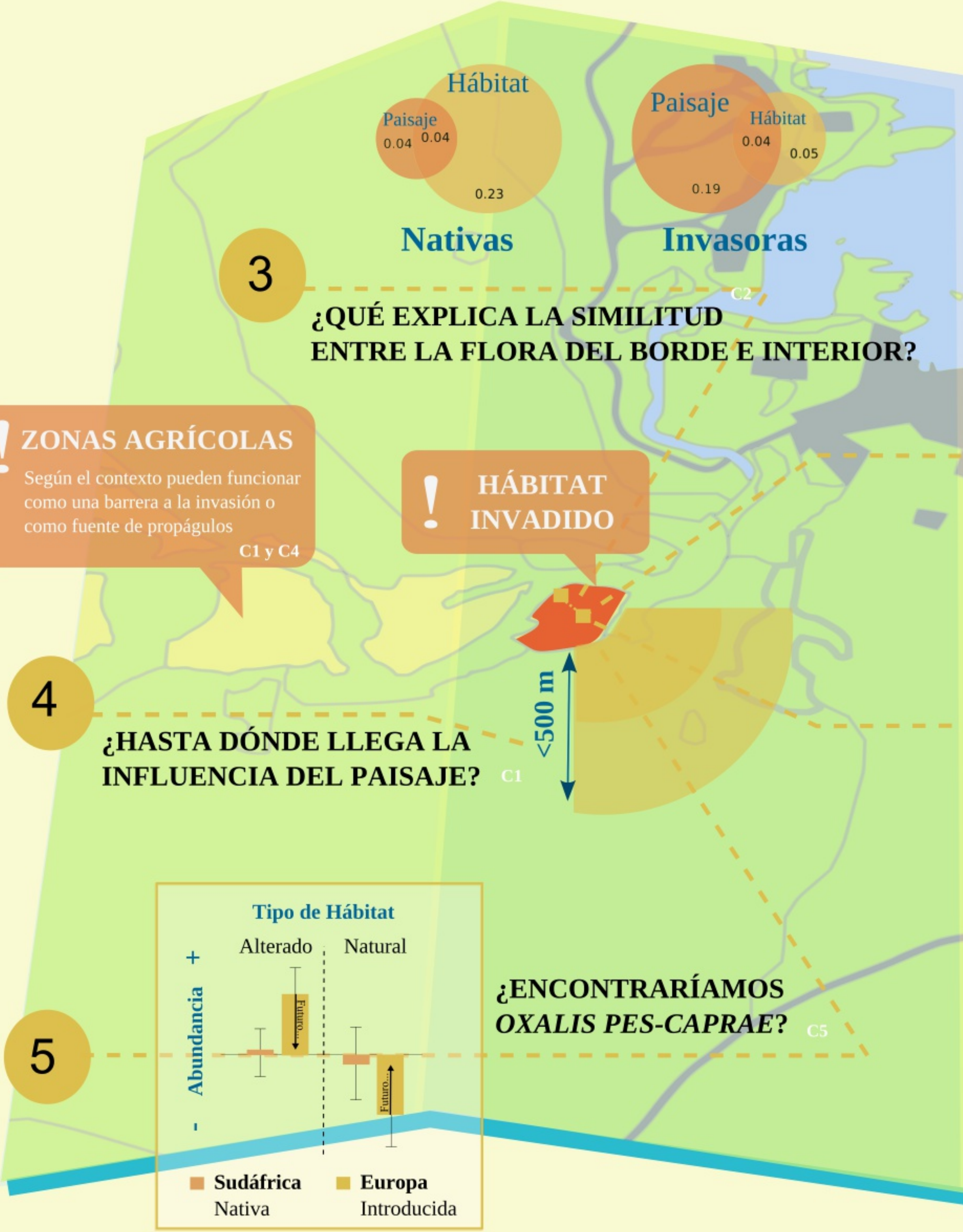
3. Current plant invasion patterns are affected by landscape dynamics. Human landscape alterations in the past could produce an invasion credit, and thus a higher potential degree of invasion in the future. The existence of invasion credit is conditioned by the landscape type and history, as well as by the introduction characteristics of most frequent exotic species.

Section II – Biological invasions are context-dependent

4. The spatial pattern of the degree of plant invasion in mainland Spain depends mainly on the habitat type and to a lesser extent on the geographical context. Habitat type is the single most important factor explaining plant invasions and at the same time, it controls the association between climatic variables and the degree of invasion. In contrast, there is no regional variability in the effect of climate or landscape alteration.

5. Exotic species can show a distinct environmental niche between native and introduced ranges. *Oxalis pes-caprae*, a geophyte native to South Africa, shows an expansion of the climatic niche in its introduced range in the Mediterranean Basin. On the contrary, it shows an unfilling of its disturbance niche. This unfilling implies a potential expansion of the species towards more natural areas. Therefore, our findings suggest that considering only the climatic niche or the information of one of the ranges could lead to the understimation of the invasion potential of exotic species.

INVASIONES Y PAISAJE



3

¿QUÉ EXPLICA LA SIMILITUD ENTRE LA FLORA DEL BORDE E INTERIOR?

C2

! ZONAS AGRÍCOLAS

Según el contexto pueden funcionar como una barrera a la invasión o como fuente de propágulos

C1 y C4

! HÁBITAT INVADIDO

4

¿HASTA DÓNDE LLEGA LA INFLUENCIA DEL PAISAJE?

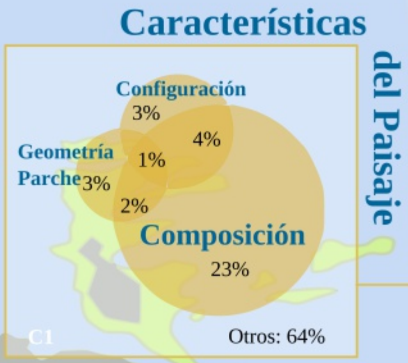
C1

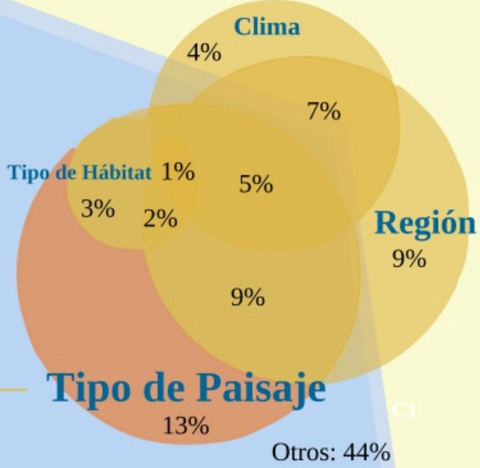
5

¿ENCONTRARÍAMOS *OXALIS PES-CAPRAE*?

C5

El Grado de Invasión por Plantas Exóticas





1

¿QUÉ EXPLICA SU GRADO DE INVASIÓN?

2

¿CAMBIA LA INVASIÓN SEGÚN EL TIPO DE HÁBITAT?

! URBANIZACIONES

Los jardines son el origen de numerosas introducciones

C1

AGRADECIMIENTOS

Aproximadamente 7680 horas de trabajo, 44730 km de vuelo y 2900 km de muestreo por carretera. Esas son las cifras que resumen cuatro años de trabajo investigando los patrones de invasión por plantas exóticas. Sin duda, mi primer agradecimiento tiene que ser para nuestra continuamente castigada Tierra ya que este estudio ha supuesto una emisión de aproximadamente 7850 kg de CO2. Si bien he intentado en todo lo posible reducir mi huella de carbono, mi aportación al cambio climático durante cuatro años de trabajo no es nada desdeñable, y puede ser considerada hasta paradójica si se tiene en cuenta que tanto cambio climático como invasiones biológicas son dos amenazas principales para la biodiversidad a nivel mundial. Espero que al menos, el presente trabajo y lo aprendido puedan compensar esta emisión a largo plazo, facilitando nuevos desarrollos que nos permitan minimizar nuestro impacto sobre la biodiversidad.

En la situación actual de crisis económica y política, creo que es fundamental hacer un ejercicio de transparencia y agradecer a todos los contribuyentes su apoyo a mi proyecto de investigación doctoral. En total, la inversión pública directa en mi trabajo ha sido de 98845€, de los que aproximadamente el 70% ha sido salario y el resto gastos de estancias de investigación en otros centros y formación. Gracias a una participación por contribuyente menor al céntimo de euro (0.002€ según datos de 2012), he podido formarme y aportar mi modesta contribución a la ciencia. Me puedo considerar un afortunado por haber investigado con libertad y en condiciones dignas, cosa que hasta hace unos años era una utopía y que casi se tambalea en el momento álgido de la crisis.

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La presente Tesis Doctoral pretende conocer la importancia relativa de la alteración del paisaje en comparación con el clima y el tipo de hábitat para explicar el grado de invasión por plantas exóticas, reconocer qué aspectos del paisaje actual y pasado son relevantes en el proceso de invasión y entender cómo el efecto de estos factores se modula dependiendo del contexto ecológico.

A PRESENTE TESIS DOCTORAL PRETENDE CONOCER
A IMPORTANCIA RELATIVA DE LA ALTERACIÓN DEL
AISAJE EN COMPARACIÓN CON EL CLIMA Y EL TIPO
E HÁBITAT PARA EXPLICAR EL GRADO DE INVASIÓN
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