Plant invasion success in Spain: A macroecological approach

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Èxit de les invasions de plantes a Espanya: Una aproximació macroecològica

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Agraïments

He posat punt i final a aquesta tesi i encara no m'ho crec. Fa quatre anys vaig iniciar aquest aprenentatge enriquidor i esgotador en el món de la recerca, i ja fa quatre mesos que va començar el final. El final més llarg de la meva vida. En les tesis, el temps i la feina són relatius, es comprimeixen o s'expandeixen a un ritme força atzarós. Només el que ha passat per un procés d'aquestes característiques ho pot entendre.

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Introducció general

Les invasions biològiques: definició i conceptes principals

Les invasions biològiques tenen lloc quan les espècies són transportades des de la seva regió nativa a una altra on aconsegueixen mantenir poblacions autosostenibles sense intervenció humana directa i produir descendència a considerables distàncies dels organismes parentals; i així, tenen el potencial d'expandir-se a través grans àrees (Pyšek *et al.* 2004). Les invasions no són noves, però l'acceleració i la intensificació d'activitats humanes com el comerç global, el turisme i les migracions han estat acompanyades del transport intencionat o involuntari d'espècies a regions llunyanes a les seves àrees de distribució naturals (McNeely *et al.* 2001, Levine i D'Antonio 2003, Kowarik 2005). Algunes d'aquestes espècies transportades poden esdevenir invasores (di Castri 1989, Williamson 1996, Richardson i Pyšek 2000, Kowarik 2003), i algunes d'aquestes invasores poden ocasionar impactes ecològics com ara alteracions dels règims de pertorbació (D'Antonio i Vitousek 1992), alteracions del funcionament dels ecosistemes (Vitousek 1994, Brooks *et al.* 2004), i amenaces a la biodiversitat nativa (Lodge 1993, Mack *et al.* 2000, Sala *et al.* 2000), i per tant, poden causar l'homogeneïtzació de les biotes terrestres (Atkinson i Cameron 1993). Els béns econòmics també són alterats per les invasions biològiques perquè les invasions tenen impacte en l'agricultura, la silvicultura i la salut, per exemple disminuint la producció de les collites i de fusta o augmentant les malalties infecciones transmeses per vectors animals al·lòctons (Pimentel *et al.* 2001, Soulé 1992). A causa de l'acceleració i la intensificació de les invasions biològiques (di Castri 1989), i de les seves conseqüències adverses, aquest fenomen és considerat actualment un dels majors components del canvi global (Vitousek *et al.* 1997, Dukes i Mooney 1999, Vilà *et al.* 2006, Thuiller *et al.* 2007a).

El procés pel qual una espècie esdevé invasora pot ser il·lustrat com una seqüència d'estadis successius (Figura 1.1; Duncan *et al.* 2003, Pyšek *et al.* 2004, Sol *et al.* 2005). Primer, l'espècie ha de ser transportada des de la seva àrea nativa fins a una nova localitat. Segon, ha de ser alliberada o escapar-se en aquest nou ambient. Tercer, després de la introducció, ha d'aconseguir establir una població autosostenible. Quart, les espècies que aconsegueixen establir-se amb èxit han d'augmentar en abundància i expandir-se més enllà del punt d'introducció: l'abast d'aquesta expansió defineix el seu rang geogràfic en el nou ambient (Veure Quadre 1.1 per definicions detallades segons Pyšek *et al.* 2004). La dinàmica temporal d'aquest procés és un dels aspectes més difícils de la predicció de les invasions (Crooks i Soulé 1999, Simberloff 2003, Crooks 2005), ja que les latències temporals (i.e. intervals d'alentiment entre dos processos) són cada vegada més reconegudes durant qualsevol dels estadis del procés d'invasió (Kowarik 1995, Crooks i Soulé 1999, Binggeli 2001, Crooks 2005, Caley *et al.* 2008).

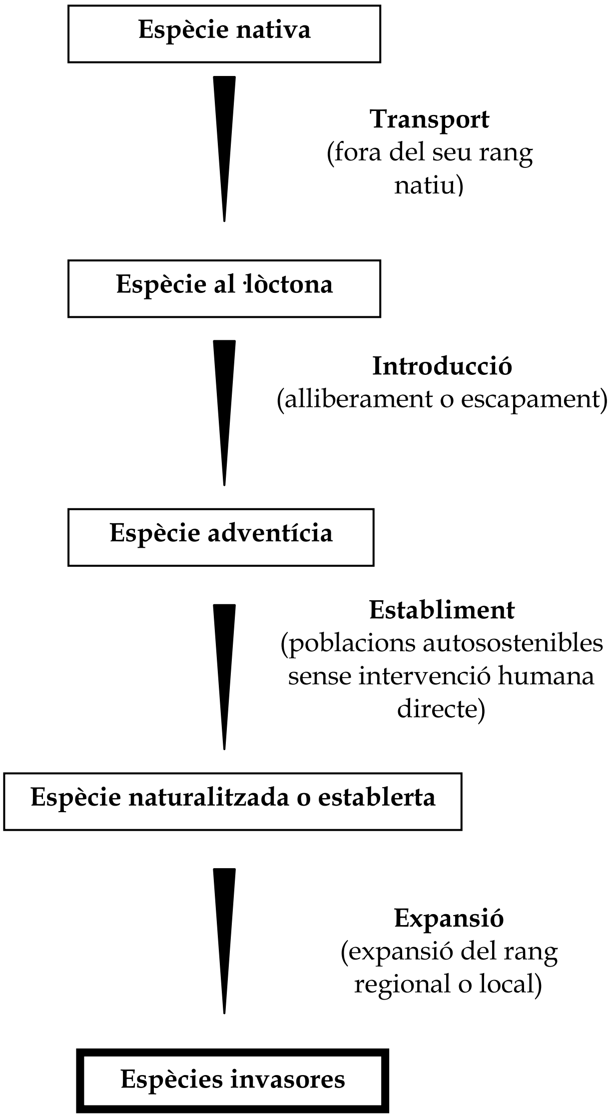

Figure 1.1 Esquema del procés d'invasió adaptat de Pyšek *et al.* 2004 and Duncan *et al.* 2003. See Box 1 for definition of terms.

Quadre 1.1 Definicions de la terminologia referent a l'estatus de les espècies segons Pyšek *et al.* (2004).

Espècies natives:
Espècies que han estat originades en una àrea determinada sense implicació humana o que hi han arribat sense intervenció humana intencionada o involuntària a partir d'una regió en la qual també són natives.

Espècies al·lòctones:
Espècies que són presents en una determinada regió (ex. continent, illa, ecoregió, o qualsevol unitat administrativa) degut a la intervenció intencionada o involuntària, o que han hi arribat sense l'ajuda humana a partir d'una area on són al·lòctones.

Espècies adventícies:
Espècies al·lòctones que poden florir (en el cas de les plantes) o que inclús es reprodueixen ocasionalment fora de cultiu o captivitat en una area, però que finalment moren perquè no formen poblacions autosostenibles, i necessiten introduccions repetides per la seva persistència.

Espècies naturalitzades o establertes:
Espècies al·lòctones que mantenen poblacions autosostenibles com a mínim durant 10 anys sense la intervenció directe de la gent (o tot i la intervenció humana).

Espècies invasores:
Espècies naturalitzades que produeixen descendència reproductiva, sovint en grans quantitats, a distàncies considerables dels individus parentals, i així tenen el potencial per expandir-se en grans àrees.

L'ecologia de les invasions

L'ecologia de els invasions és l'estudi de les introduccions d'organismes en àrees fora de les seves àrees de distribució natural ocasionades per les activitats humanes (Mack *et al.* 2000, Davis 2006, Richardson i Pyšek 2006). Aquest camp de l'ecologia estudia l'habilitat d'aquestes espècies per establir-se, naturalitzar-se i expandir-se en la regió d'introducció, les seves interaccions amb els organismes residents a les noves localitats, les característiques dels hàbitats i les regions on s'expandeixen, i considera els costos i beneficis de la seva presència i abundància en referència al valor dels sistemes naturals (Richardson i van Wilgen 2004, Pyšek *et al.* 2006, Richardson 2006). Diversos naturalistes del segle XIX, especialment Charles Darwin, Alphonse de Candolle, Joseph Hooker i Charles Lyell, van anomenar les espècies invasores en els seus escrits. No obstant això, les espècies naturalitzades i invasores eren, a l'època, essencialment curiositats i no eren percebudes com una amenaça per a la biodiversitat global.

Les invasions biològiques van començar a ser molt més extenses a la primera meitat del segle XX, però els biòlegs van ser lents en focalitzar la seva atenció en el fenomen (Richardson i Pyšek 2007). El llibre d'en Charles S. Elton (1958) titulat *The ecology of invasions by animals and plants* és generalment reconegut com el punt de partida per centrar l'atenció científica en les invasions biològiques (Richardson i Pyšek 2008). L'ecologia de les invasions ha crescut enormement des que va aparèixer el llibre de Elton (Pyšek *et al.* 2006, Richardson i Pyšek 2007, 2008).

Actualment, la majoria dels investigadors estan d'acord amb el fet que, donat que quan una espècie al·lòctona s'ha establert en una nova regió és extremament difícil d'eradicar o controlar, el mètode més efectiu per minimitzar el seu impacte és prevenir, en el primer lloc, l'establiment o l'expansió (Ricciardi i Rassmusen 1998, Mack *et al.* 2000). Aquesta aproximació requereix entendre l'ecologia del procés d'invasió i els factors subjacents a l'èxit en els diferents estadis, per tal de poder identificar situacions on hi ha un alt risc d'invasió (Duncan *et al.* 2003). Concretament, és necessari predir quins són els factors que permeten l'establiment i expansió de certes espècies quan són introduïdes en localitats externes al seu rang natural, i quines àrees són les més propenses a la invasió.

L'èxit de les espècies invasores

L'èxit de les espècies invasores és un dels temes centrals de l'ecologia de les invasions (Richardson i Pyšek 2008). Ens hem de preguntar per què algunes espècies naturalitzades han estat capaces d'aconseguir grans distribucions mentre d'altres es mantenen restringides. Normalment, l'èxit d'invasió s'estima comparant com les espècies difereixen en la seva abundància o rang de distribució. L'èxit d'invasió es pot estudiar a diverses escales espacials, des de parcel·les a regions, a tota la Terra.

S'han suggerit diversos factors no excloents que es relacionen amb l'èxit dels invasors (Figura 1.2):

- Concordança ambiental (Brown 1989, Williamson 1996).
- Capacitat invasora o potencial invasor de les espècies: abast de la capacitat intrínseca d'una espècie per superar diverses barreres biòtiques i abiòtiques i esdevenir invasora (di Castri 1989).

- Factors del fet introductiu com la pressió de propàgul, el temps des de la introducció, i factors estocàstics (Rejmánek *et al.* 2005a, Pyšek and Richardson 2007).
- Invasibilitat o vulnerabilitat del nou ecosistema a l'establiment d'espècies al·lòctones introduïdes. La invasibilitat depèn de factors biòtics i abiòtics (Lonsdale 1999).

Concordança ambiental

Una de les hipòtesis més freqüents en la bibliografia de biologia de les invasions és que les espècies haurien de tenir millors oportunitats d'establir-se si el clima i les condicions físiques del lloc d'introducció i de l'àrea de distribució natural de l'espècie concorden (Brown 1989, Panetta i Mitchell 1991, Scott i Panetta 1993, Williamson 1996). Regions en latituds similars o dintre de la mateixa regió biogeogràfica són més propenses a ser similars quant a condicions climàtiques i hàbitat, per tant, les espècies de latituds o regions biogeogràfiques similars tindran més èxit (Sol *et al.* 2005). Hi ha diversos estudis que reforcen aquesta hipòtesi (Curnutt 2000, Blackburn i Duncan 2001b, Cassey 2003), i que fins i tot la utilitzen com a punt de partida per a models de risc d'invasió (Thuiller *et al.* 2005). En una revisió recent, Hayes i Barry (2008) han arribat a la conclusió que la concordança de clima o hàbitat és la única característica que es pot associar amb l'èxit de les invasores, mesurat com a mida del seu rang de distribució en tots els tàxons.

Així mateix, alguns estudis han arribat a la conclusió que les espècies amb rangs geogràfics més grans són més propenses a establir-se (Rejmánek 1995, Goodwin *et al.* 1999, Blackburn i Duncan 2001a, Duncan *et al.* 2001). Les espècies tenen un rang geogràfic més gran quan poden explotar un rang més gran de condicions (tenen una gran tolerància de nínxol; Duncan *et al.* 2003, Booth *et al.* 2003 Vázquez 2006), o utilitzar condicions més extenses en el territori (tenen una posició de nínxol comú; Gaston 1994b).

Capacitat invasora

La majoria dels treballs inicials en invasions estaven dirigits a recopilar característiques d'història de vida de les espècies associades a l'èxit d'invasió (Booth *et al.* 2003). Molts estudis han intentat perfilar les espècies invasores amb més tendència a l'èxit, començant per l'intent de Herbert Baker d'identificar els trets d'una "*mala herba ideal*" (Baker 1965). Més tard, s'ha demostrat que això és difícil (Alpert *et al.* 2000). Tot i així, aquestes característiques són un ingredient crucial per explicar (i després predir) les invasions (Rejmánek 1996), i sembla que s'han començat a consolidar algunes generalitzacions al respecte (Kolar i Lodge 2001).

En l'àmbit dels ocells, Duncan et al. (2003) han identificat tres tipus de trets influents en l'èxit d'establiment d'una espècie : (a) trets que preadapten l'espècie al nou ambient (ex : flexibilitat del comportament; Sol 2003), (b) trets que afavoreixen l'increment de la població a partir d'un nombre baix de població (ex : trets d'història de vida i succedanis del creixement poblacional ; Primm 1991), i (c) trets que dificulten l'èxit d'establiment (ex : comportament migratori i dimorfisme sexual en el color ; Sol et al. 2002). Referent a l'èxit d'expansió, s'ha suggerit que les espècies amb taxes ràpides de creixement demogràfic tenen rangs més grans perquè són menys vulnerables a l'extinció local quan colonitzen espais vacants (Gaston 1988).

En l'àmbit de les plantes, hi ha hagut esforços recents per resumir els factors relacionats hipotèticament amb l'èxit d'invasió: forma de vida, alçada, creixement clonal, sistema reproductiu, mida de la llavor, vectors de pol·linització i dispersió, fenogàmia de la floració, potencial reproductiu i preferències d'hàbitat. Molts trets han estat testats freqüentment, però els estudis no han arribat a conclusions sòlides (Daehler 2003, Richardson i Pyšek 2006, Pyšek i Richardson 2007). D'acord amb aquestes revisions recents sobre trets més rellevants en el procés d'invasió, hi ha moltes fonts de biaixos que poden estar emmascarant l'efecte dels trets, com per exemple: la filogènia, el temps de residència, la pressió de propàgul, l'escala de l'estudi, i l'estadi del procés d'invasió analitzat. Pyšek i Richardson (2007) van demostrar que els factors socials i econòmics són crucials en l'estadi d'introducció, els factors biogeogràfics i ecològics en l'estadi de naturalització, i els factors ecològics i evolutius són mediadors crucials per a l'expansió. A més a més, diferents definicions d'invasora i diferents tipus de dades i metodologies afegeixen més inconsistències als estudis (Hayes i Barry 2008). Així que el paper que tenen els trets vitals de les espècies en el procés d'invasió deu ser específic del tàxon, l'estadi d'invasió, l'hàbitat i el context (Pyšek i Richardson 2007, Hayes i Barry 2008).

Factors del fet introductiu: pressió de propàgul i temps de residència

La pressió de propàgul i el temps de residència són els dos factors principals que difereixen en cada grup d'organismes introduit (Blackburn i Duncan 2001a, Duncan *et al.* 2003). La pressió de propàgul o l'esforç d'introducció (Blackburn i Duncan 2001a) és una mesura composta pel nombre d'individus d'una espècie alliberats en una regió de la que no en són nadius (Carlton 1996). Aquesta mesura incorpora estimacions del nombre absolut d'individus involucrats en cada un dels alliberaments (mida del propàgul) i el nombre d'alliberaments (nombre de propàguls) (Lockwood *et al.* 2005). La pressió de propàgul podria ser el factor clau per entendre per què l'èxit d'invasió és tan idiosincràtic (Lockwood *et al.* 2005). Tot i així, és molt difícil de mesurar, especialment en plantes. S'han fet servir diverses estimacions quantitatives amb un èxit raonable, entre les quals hi ha el nombre de visitants en les reserves naturals (Lonsdale 1999, McKinney 2002a), la mida o densitat de la població humana (McKinney 2001, 2002a, Pyšek *et al.* 2002, 2003, Taylor i Irwin 2004), la quantitat de comerç i turisme (Thuiller *et al.* 2005), o l'activitat econòmica (Taylor i Irwin 2004).

El temps de residència (temps des de la introducció) integra aspectes de la pressió de propàgul relacionats amb el ritme de la invasió: com més temps fa que l'espècie és a la regió, més gran és la mida del banc de propàguls, i més gran la probabilitat de dispersió, establiment i fundació de noves poblacions (Rejmánek *et al.* 2005b). L'impacte d'una espècie introduïda a la comunitat envaïda també creix amb el temps de residència (Collier *et al.* 2002). Com que majoritàriament no es coneix exactament quan una espècie va ser introduïda, s'ha proposat el terme "temps mínim de residència" (MTR) (Rejmánek 2000). L'MTR explica no només el rang i la freqüència de les distribucions actuals, sinó també l'estatus d'invasió d'una espècie. D'aquesta manera, és crucial la consideració del MTR en els estudis que avaluen els determinants de la capacitat invasora (Pyšek i Jarošik 2005). L'MTR està estretament associat amb la fase de latència que sovint precedeix l'invasió d'espècies al·lòctones –

el retard entre l'inici de la invasió i la fase típica de creixement exponencial (Baker 1965, Kowarik 1995)-.

El fenomen de les fases de latència té implicacions importants a l'hora de predir i gestionar les invasions, perquè invasions precedides de fases llargues de latència temporal determinarien que els patrons que observem avui són el resultat net de les introduccions i de les condicions i processos predominants en el passat (Hulme 2003). Una implicació pràctica de les fases de latència és que les invasions biològiques tenen una inèrcia intrínseca –el nombre d'espècies naturalitzades i invasores incrementarà en el futur encara que no hi hagi introduccions addicionals (Kowarik 1995)-.

Invasibilitat: el paper de la diversitat d'espècies natives, les interaccions interespecífiques i les pertorbacions

La invasibilitat és la resistència que l'ecosistema receptor ofereix a la invasió. A la pràctica, la invasibilitat es mesura a partir d'aquells factors abiòtics i biòtics que limiten l'establiment i la supervivència de les espècies al·lòctones (Lonsdale 1999). La diversitat d'espècies, les interaccions interespecífiques i la pertorbació han estat els tres principals factors examinats per detectar diferències en invasibilitat.

La hipòtesi de la resistència biòtica va sorgir amb Elton (1958), i suggereix que hi ha una relació negativa entre la diversitat d'espècies natives i la invasibilitat de la comunitat. Nombrosos estudis han detectat, en efecte, que les comunitats riques en espècies contenen menys espècies al·lòctones (ex. Rejmánek 1989, Tilman 1997, 1999, Knops *et al.* 1999, Levine 2000, Naeem *et al.* 2000, Dukes 2002, Kennedy *et al.* 2002), però d'altres han conclòs que les àrees amb elevada biodiversitat nativa contenen moltes espècies al·lòctones (Timmins i Williams 1991, Planty-Tabacchi *et al.* 1996, Stohlgren *et al.* 1999, Lonsdale 1999, Stadler *et al.* 2000, Pyšek *et al.* 2002, McKinney 2001).

Alguns tests experimentals que utilitzen conjunts d'espècies artificials que varien segons la diversitat donen suport a la hipòtesi de la resistència biòtica. Aquesta discrepància entre observacions i experiments és majoritàriament deguda a l'escala espacial dels estudis (Fridley *et al.* 2004, Herben *et al.* 2004), i pot ser explicada fent variar els factors externs (Shea i Chesson 2002). A gran escala espacial, les mateixes condicions abiòtiques que promouen una alta diversitat d'espècies natives (ex. clima, substrat, heterogeneïtat de l'hàbitat, etc.) també sosté diversitat d'al·lòctones en les flores; en altres paraules, el que és bo per les natives és bo per les al·lòctones. Mentre que a escala local els experiments avaluen l'efecte del veïnatge de les especies sobre l'establiment i la supervivència de les al·lòctones.

L'èxit de les espècies al·lòctones invasores ha estat sovint atribuït a l'escapament dels seus enemics naturals a la regió receptora (Elton 1958, Crawley 1987). En l'àmbit de les plantes, estudis que comparen el dany d'herbiboria o l'atac per patògens en plantes al·lòctones entre el rang natiu i el d'introducció han donat suport, generalment, a aquesta hipòtesi (Wolfe 2002, Mitchell i Power 2003, Maron i Vilà 2007).

Les interaccions biòtiques dintre de la comunitat nativa, com els mutualismes (ex. relacions planta-animal en la pol·linització o en la dispersió de llavors) poden afavorir la integració de les espècies al·lòctones a la comunitat, però també poden ser modificades per la presència d'aquestes espècies (Bjerknes *et al.* 2007, Richardson *et al.* 2000, Traveset i Richardson 2006, Bartomeus *et al.* 2008, Traveset *et al.* 2008).

Finalment, les pertorbacions naturals intrínseques o extrínseques a l'hàbitat com el foc, les inundacions, les pràctiques agrícoles, el drenatge de zones humides, les alteracions de salinitat o els nivells de nutrients en rius i llacs, així com les pertorbacions d'origen antròpic poden causar problemes a les espècies natives i incrementar la probabilitat d'establiment de les al·lòctones (Mack *et al.* 2000, McKinney 2002b). Generalment, en ambients pertorbats, els factors abiòtics semblen ser més determinants de la invasibilitat que els factors biòtics (Richardson i Bond 1991, Hood i Naiman 2000). A més a més, amb les pertorbacions, els fluxes de recursos i els nínxols es tornen disponibles per ser explotats per les al·lòctones. Les pertorbacions són, de fet, vistes com a « finestres obertes a la invasió » (Hobbs i Huenneke 1992, Davis *et al.* 2000, Davis i Pelsor 2001).

El grau d'invasió

Les variacions en el grau d'invasió (és a dir, abundància i riquesa d'espècies al·lòctones) entre localitats podrien simplement ser degudes a diferències en la pressió de propàgul (Williamson 1996, Lonsdale 1999, Chytrý *et al.* 2005, Hierro *et al.* 2005) o a la identitat de les espècies introduïdes, però també a diferències d'invasibilitat (Figura 1.2). Per saber si una regió, comunitat o hàbitat, és més envaïble, ens hem de preguntar no només si té més espècies al·lòctones, sinó també si és intrínsicament més susceptible a les invasions (Lonsdale 1999). Lonsdale (1999) va proposar una equació senzilla per definir el grau d'invasió d'una regió (E; nombre d'espècies al·lòctones), en funció de la pressió de propàgul (I; nombre d'introduccions) i invasibilitat (S; supervivència de les espècies introduïdes): $E = I \times S$

Els estudis a escala global i regional que s'han focalitzat en el grau d'invasió han detectat patrons regionals robustos:

- Les illes estan més envaïdes que els continents (Darwin 1845, cited by Cassey 2003, Rejmánek 1996, Lonsdale 1999, Denslow 2003).
- El Nou Món esta més envaït que el Vell Món (di Castri 1989).
- El grau d'invasió incrementa amb la latitud en els continents però no en les illes (Lonsdale 1999), i per tant, les àrees tropicals estan menys envaïdes que les regions extratropicals (Rejmánek 1996), però les espècies naturalitzades en els tròpics tenen rangs geogràfics més grans (Sax 2001).
- Les regions de baixa altitud contenen més espècies al·lòctones que les regions de molta altitud (Arévalo *et al.* 2005).
- Les àrees costaneres tendeixen a estar més envaïdes que les de terra endins (Pino *et al.* 2005).
- Els llocs temperats agrícoles, urbans o de ribera són zones molt envaïdes (Pino *et al.* 2005 , Kühn i Klotz 2006, Vilà *et al.* 2007, Chytrý *et al.* 2008b).

Tanmateix, si aquests patrons estan o no estan explicats per diferències d'invasibilitat encara està per testar.

Quadre 1.2 Definicions de la terminologia referent a l'èxit d'invasió segons diverses fonts bibliogràfiques.

Capacitat invasora:
Capacitat intrínseca d'una espècie per superar diverses barreres biòtiques i abiòtiques i esdevenir invasora (di Castri 1989).

Invasibilitat:
Propietats de l'ecosistema d'introducció que afecten la supervivència de les espècies al·lòctones (Lonsdale 1999).

Pressió de propàgul:

- *Des del punt de vista de les espècies:* Nombre d'individus d'una espècie alliberats en una region en la que no són natius (Carlton 1996). Incorpora una estimació del nombre absolut d'individus involucrats en cada un dels alliberaments (mida del propàgul) i del nombre d'alliberaments (nombre de propàguls) (Lockwood *et al.* 2005).
- *Des del punt de vista de la regió*: Nombre d'espècies al·lòctones introduïdes en una regió (Williamson 1996, Lonsdale 1999).

Temps mínim de residència:
Temps que ha passat des de la primera citació de l'espècie a la regió (Rejmánek 2000).

Avaluació del risc d'invasió

Predir l'èxit de les espècies al·lòctones ha estat un dels objectius principals de la recerca ecològica des que les invasions van ser reconegudes com una qüestió rellevant de conservació (Rejmánek i Richardson 1996, Reichard i Hamilton 1997, Smith *et al.* 1999, Kolar i Lodge 2001, Pyšek 2001, Caley *et al.* 2006). Donat que una vegada una espècie al·lòctona és establerta en una nova regió és molt difícil d'eradicar o controlar (Rejmánek *et al.* 2005a), prevenir la introducció d'espècies amb un risc elevat d'esdevenir invasores és, de lluny, el mitjà més efectiu, pel que fa als costos, per limitar futurs problemes amb espècies invasores (Duncan *et al.* 2003). El paper essencial de la prevenció ha estat destacat en estratègies polítiques recents, com la Convenció per la Diversitat Biològica (http://www.biodiv.org/) i l'Estratègia Global del Programa Global d'Espècies Invasores (McNeely *et al.* 2001). Així mateix, també ha estat destacat el fet que es requereixen mesures preventives després de la introducció. El potencial invasor de les espècies al·lòctones recentment introduïdes necessita tornar-se a avaluar regularment, ja que moltes espècies al·lòctones experimenten una fase clara de desajust, de vegades durant dècades després de la introducció, abans de mostrar cap signe d'esdevenir invasora (Crooks i Soulé 1999).

Moltes espècies al·lòctones que ja són presents en una regió i que actualment no mostren cap signe de ser invasores ho seran en el futur.

Identificar futures espècies invasores és enormement difícil. El coneixement científic acumulat dels trets dels invasors i les característiques dels hàbitats envaïts, i la informació de si una espècies és invasora en altres parts del món, especialment en àrees amb condicions ambientals similars (Westbrooks 1981, Rejmánek 2000, Union of Concerned Scientists 2001, Thuiller *et al.* 2005, Richardson i Thuiller 2008), han estat el fonament per desenvolupar esquemes d'avaluació de risc que intenten predir l'èxit d'espècies al·lòctones en una regió d'introducció (Mcneely *et al.* 2001, National Invasive Species Council 2001, Wittenberg i Cock 2001, Leung *et al.* 2002, Keller *et al.* 2007a, Gordon *et al.* 2008).

Com que el risc té dos components, la probabilitat d'invasió i les seves conseqüències (ex. impactes ecològics o socioeconòmics), els esquemes d'avaluació de risc intenten identificar la fracció de les espècies introduïdes amb una alta probabilitat d'esdevenir invasores, i preveure la seva expansió i els seus efectes perjudicials (Andersen *et al.* 2004). A més a més, hi ha evidències que la implementació de protocols d'avaluació de risc produeix beneficis econòmics nets (Keller *et al.* 2007b). En diverses parts del món s'han desenvolupat protocols d'exploració (Tucker i Richardson 1995, Daehler *et al.* 2004, Gordon *et al.* 2008), que aprofiten un ampli ventall d'informació, inclòs el coneixement d'invasions d'aquesta espècie en altres territoris, i diverses mesures proposades per avaluar el potencial de les espècies per ajustar-se a les característiques de l'ambient en qüestió (Rejmánek *et al.* 2005a). Els sistemes d'avaluació de risc haurien d'ajudar-nos a resoldre les cinc prioritats de prevenció i gestió de les noves invasions: recerca, monitoreig, legislació, mitigació de l'impacte i informació pública (Genovesi 2000, Myers *et al.* 2000, Genovesi i Shine 2002, Sol *et al.* 2005).

Macroecologia i anàlisis comparatives com a marc de la tesi

Tot i l'esforç conjunt, el camp de l'ecologia de les invasions ha estat criticat per la seva manca d'èxit en la prevenció i per la incapacitat d'oferir orientació a la gestió en el control d'espècies invasores (Ehrlich 1989, Vermeij 1996, Mack *et al.* 2000).

Els experiments són la millor aproximació per establir relacions causals, i per tant, són fonamentals per entendre els mecanismes d'invasió (Schoener i Spiller 1999, Levine 2000, Levine *et al.* 2003). Tot i així, els experiments són insuficients per entendre completament les invasions. A causa de la variabilitat immensa dels sistemes ecològics, una problemàtica dels experiments és la limitació dels resultats, que no poden ser generalitzats, i només es poden relacionar amb l'àrea en particular, el període de temps o les espècies concretes seleccionades com a cas d'estudi. A més a més, no totes les qüestions de les invasions poden ser afrontades amb l'experimentació: per exemple, aquelles on intervé la resistència de regions senceres als invasors. Finalment, els experiments no sempre són possibles per a tàxons com plantes de vida llarga o vertebrats per raons legals, ètiques i logístiques (Sol *et al.* 2008).

Una alternativa a l'aproximació experimental és l'anàlisi comparativa d'introduccions passades (Kolar i Lodge 2001, Fisher i Owens 2004, Cadotte *et al.* 2006). En les últimes dècades, l'ús de l'aproximació comparativa ha augmentat molt la nostra comprensió del procés d'invasió, destapant algunes de les regles generals que governen l'establiment i l'expansió de les espècies introduïdes en regions noves (Brown 1989, Lodge 1993, Kolar i Lodge 2001, Duncan *et al.* 2003, Fisher i Owens 2004, Cadotte *et al.* 2006). Un dels principals avantatges de l'aproximació comparativa és que pot ajudar a dibuixar els principis generals que s'apliquen en regions àmplies i en una gran diversitat de tàxons, aportant així generalitats suficientment realistes per ser utilitzades en avaluacions de risc dels futurs invasors. Així mateix, proporcionen també el punt de partida per determinar la gestió de les invasions existents (Kolar i Lodge 2002, Settele *et al.* 2005).

La macroecologia depèn molt del mètode comparatiu per identificar patrons a gran escala i per testar hipòtesis alternatives que puguin generar els patrons observats (Cadotte *et al.* 2006). Amb l'accessibilitat a grans bases de dades electròniques d'espècies, els ecòlegs han començat a buscar generalitats, i a examinar hipòtesis ecològiques a gran escala relacionades amb temes centrals com el rang, l'abundància i la diversitat dels invasors. Les anàlisis d'inventaris regionals d'espècies al·lòctones poden contribuir a identificar situacions associades amb un alt risc d'invasió (Cadotte *et al.* 2006).

L'aproximació macroecològica vinculada a nous i sòlids mètodes estadístics comparatius pot ajudar-nos a integrar les aproximacions de les espècies invasores i els ecosistemes envaïts (Chong 2006, Thuiller 2006) (Figura 1.2). Fent servir metodologies estadístiques apropiades, podem tractar diversos efectes de confusió, principalment el biaix filogenètic i la dependència espacial (Sol *et al.* 2008).

Biaix i dependència filogenètica

La importància de considerar les relacions filogenètiques quan comparem espècies ha estat àmpliament reconeguda (Felsenstein 1985, Harvey i Pagel 1991, Freckleton *et al.* 2002). No totes les espècies, gèneres i famílies al·lòctones s'han mogut de la mateixa manera (Richardson i Pyšek 2006), o sigui que les oportunitats de naturalitzar-se i envair no són iguals entre tàxons. Les espècies al·lòctones estan distribuïdes, no per atzar, dintre dels grups taxonòmics més grans, tant en l'àmbit global (Daehler 1998a, Pyšek 1998b), com continental (Weber 1997), i regional (Williams *et al.* 2002, Wu *et al.* 2004, Pauchard i Alaback 2004, Villasenor i Espinoza-Garcia 2004). Aquest patró té un marc filogenètic: Les espècies estretament relacionades comparteixen molts trets morfològics, comportamentals, fisiològics i ecològics a causa d'un ancestre comú en lloc d'una evolució independent (Felsenstein 1985, Harvey i Pagel 1991, Freckleton *et al.* 2002). Si aquests trets compartits afecten la probabilitat d'establiment, aleshores el resultat de la introducció estarà agrupat segons el grau de relació filogenètica o taxonòmica. Si no tenim en compte les relacions filogenètiques entre espècies, sobreestimem els graus de llibertat en l'anàlisi i incrementem la probabilitat d'obtenir falsos positius. A més a més, el grau de relació filogenètic que se solapa amb les influències ambientals (ex. a causa del conservadorisme de nínxol) interfereix amb les variables ambientals i pot menar a una mala estimació dels paràmetres.

Dependència espacial

Algunes regions deuen ser més fàcils d'envair (Williamson 1996, Shea i Chesson 2002), però si és més fàcil d'establir-se en algunes localitats que d'altres, aleshores, el resultat de les introduccions a la mateixa localitat estarà correlacionat (Duncan *et al.*

2003). Això vol dir que introduccions fetes a la mateixa regió probablement no representen indicis independents de la influència d'un factor en l'èxit d'establiment, perquè hauríem d'esperar resultats similars (èxit o fracàs) per totes les espècies introduïdes a la mateixa localitat, violant així l'assumpció fonamental dels tests estadístics estàndards. La pseudoreplicació que sorgeix si la probabilitat d'èxit en la introducció és més similar entre regions properes que entre regions més distants és l'anomenada autocorrelació. L'autocorrelació espacial pot ser particularment problemàtica en estudis que intenten caracteritzar els factors que fan algunes regions més resistents als invasors que d'altres (Sol *et al.* 2008).

Preguntes principals i estructura de la tesi

L'objectiu general d'aquesta tesi és analitzar els factors associats a l'èxit de les invasions de plantes a Espanya utilitzant mètodes comparatius a escala macroecològica (Figura 1.2). En particular, a través dels cinc capítols que segueixen aquesta introducció general, es tracten les qüestions següents:

Des del punt de vista de l'èxit de les espècies

- Hi ha trets específics que afavoreixin l'èxit dels invasors? (Capítol 1)
- Com de grans i extensos són els rangs potencials de les invasores? Han aconseguit ocupar-los? Amb quina taxa s'expandeixen? (Capítol 2)
- Els trets específics estan relacionats amb la taxa d'expansió de les invasores? (Capítol 2)

Des del punt de vista del grau d'invasió

- Hi ha factors climàtics, geogràfics o de paisatge associats al grau regional d'invasió? (Capítol 1)
- Hi ha factors de context regional que influencien el grau local d'invasió en diferents tipus d'hàbitat? (Capítol 3)

Integrant l'èxit de les espècies amb el grau d'invasió

- Com és l'organització regional i la composició de les agrupacions d'espècies invasores a Espanya? (Capítol 4)
- Com d'extensos són els nínxols ecològics dels invasors? (Capítol 4)
- Els nínxols ecològics de les espècies invasores estan condicionats pels trets de les espècies? (Capítol 4)

Avaluació del risc d'invasió per plantes

- És acurat predir les invasions per plantes a Espanya fent servir el protocol *Weed Risk Assessment*? (Capítol 5)

Els quatre capítols estan basats essencialment en la informació de *l'Atlas de las Plantas Alóctonas Invasoras de España* (Sanz-Elorza *et al.* 2004) i el capítol restant es refereix a un àmbit regional més petit, fent servir la base de dades catalana FLORACAT (Font i Ninot 1995). Els cinc capítols es presenten en format d'article científic, la qual cosa comporta algunes redundàncies en les descripcions de les bases de dades i les regions, però les referències han estat agrupades al final. Els capítols estan íntegrament escrits en anglès, excepte el resum, que està traduït al català. La discussió final de la tesi es presenta en les dues llengües, igual que aquesta introducció general.

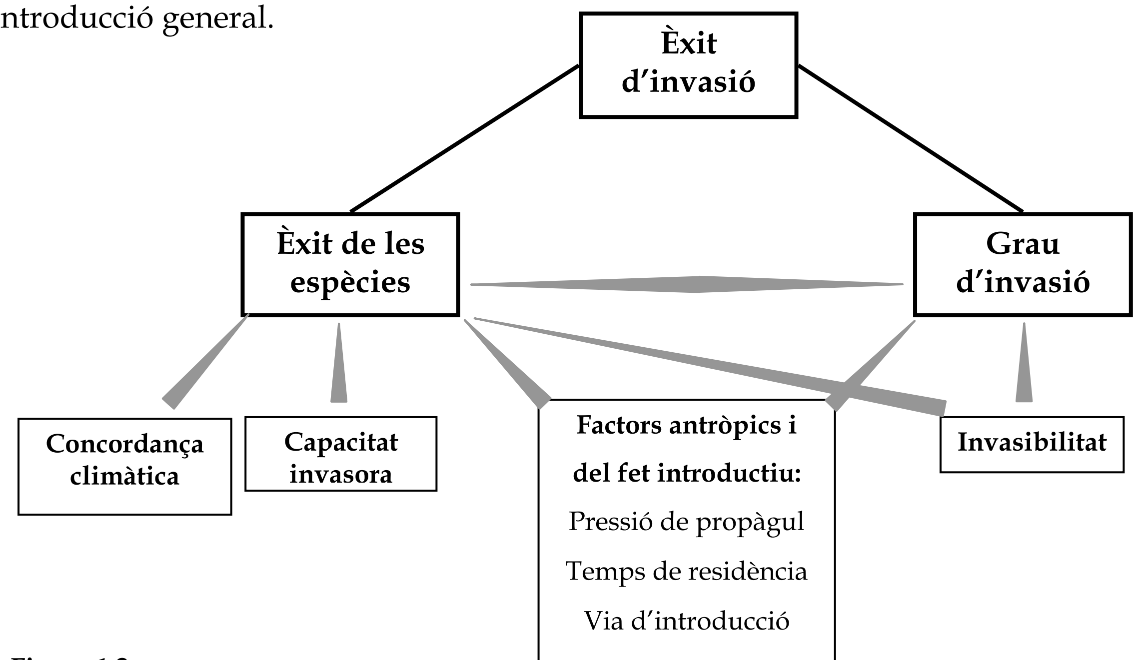

Figure 1.2
Esquema dels components de l'èxit d'invasió (èxit de les espècies i grau d'invasió) i els seus factors d'influència d'acord amb les hipòtesis destacades en aquesta introducció.

General introduction

Biological invasions: definition and main concepts

Biological invasions occur when species are transported to new regions where they manage to maintain self-sustainable populations without direct human intervention and produce offspring at considerable distances from the parent organisms, and thus, they have the potential to spread over large areas (Pyšek *et al.* 2004). Invasions are not novel but the acceleration and intensification of human activities such as global trade, tourism and people migration has been accompanied by the intentional or unintentional transport of species to regions far from their natural ranges (McNeely *et al.* 2001, Levine & D'Antonio 2003, Kowarik 2005). Some of these transported species might become invasive (di Castri 1989, Williamson 1996, Richardson & Pyšek 2000, Kowarik 2003), and some can cause ecological impacts such as altering disturbance regimes (D'Antonio & Vitousek 1992), altering ecosystem functioning (Vitousek 1994, Brooks *et al.* 2004), threatening native biodiversity (Lodge 1993, Mack *et al.* 2000, Sala *et al.* 2000), and thus, causing homogenization of Earth's biota (Atkinson & Cameron 1993). Human economic wealth is also altered by biological invasions because they impact on agriculture, forestry and health, for example, by decreasing crop and timber production or increasing infection diseases transferred by alien animal vectors (Pimentel *et al.* 2001, Soulé 1992). Due to the acceleration and intensification of the biological invasions phenomena (di Castri 1989), and their adverse consequences, they are considered as a major component of global change (Vitousek *et al.* 1997, Dukes & Mooney 1999, Vilà *et al.* 2006, Thuiller *et al.* 2007a).

The process by which a species become invasive can be illustrated as a sequence of stages (Figure 1.1; Duncan *et al.* 2003, Pyšek *et al.* 2004, Sol *et al.* 2005). First, the species must be transported from its native range to a new location. Second, it must be released or escaped into that environment. Third, following introduction, it must succeed in establishing a self-sustaining population. Fourth, species that establish successfully may increase in abundance and spread beyond the release point, and the extent of this spread defines their geographical range in the new environment (See Box 1.1 for detailed definitions following Pyšek *et al.* 2004). The temporal dynamics of this process is one of the most difficult aspects of invasion predictability (Crooks 2005, Crooks & Soulé 1999, Simberloff 2003). Lag times (i.e. interval of slowness between two processes) are increasingly recognized in any stage of the invasion process (Kowarik 1995, Crooks & Soulé 1999, Binggeli 2001, Crooks 2005, Caley *et al.* 2008).

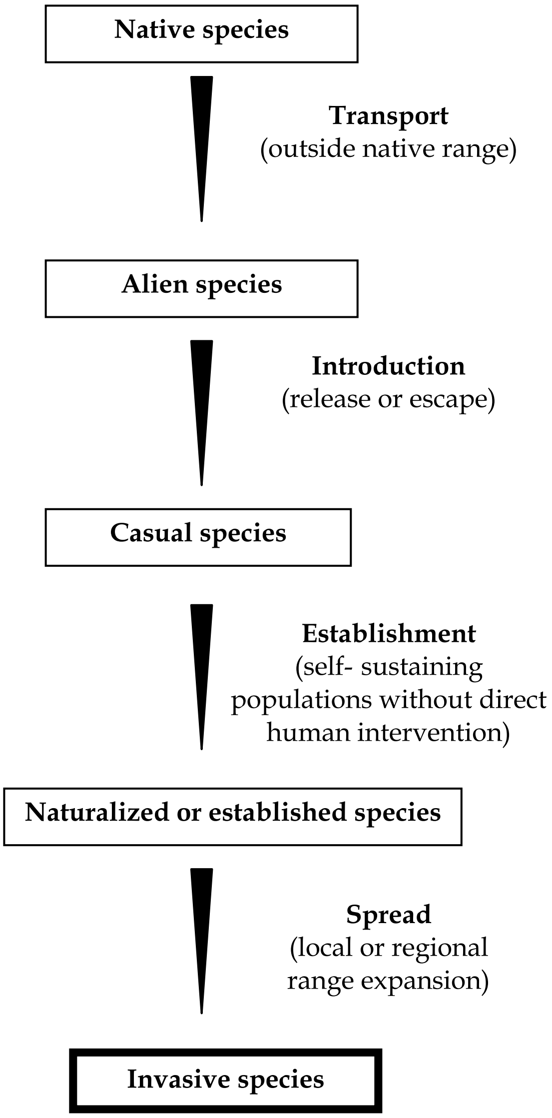

Figure 1.1 Human-caused invasion process scheme adapted from Pyšek *et al.* 2004 and Duncan *et al.* 2003. See Box 1 for definition of terms.

Box 1.1 Definition of species status terminology following Pyšek *et al.* 2004.

Native species:
Species that have been originated in a given area without human involvement or that have arrived there without intentional or unintentional human intervention from an area in which they are native.

Alien species:
Species in a given area (e.g. continent, island, eco-region, or any political entity) whose presence is due to intentional or unintentional human involvement, or which have arrived without the help of people from an area in which they are alien.

Casual species:
Alien species that may "flourish" in the case of plants or even reproduce occasionally outside cultivation or captivity in an area, but that eventually die out because they do not form self-sustaining populations, and rely on repeated introductions for their persistence.

Naturalized or established species:
Alien species that sustain self-replacing populations for at least 10 years without direct intervention by people (or in spite of human intervention).

Invasive species:
Naturalized species that produce reproductive offspring, often in very large numbers, at considerable distances from the parent individual, and thus have the potencial to spread over a large area.

Invasion ecology

Invasion ecology is the study of the human-mediated introduction of organisms to areas outside their natural distribution ranges (Mack *et al.* 2000, Davis 2006, Richardson & Pyšek 2006). This field of ecology addresses the ability of these species to establish, naturalize and spread in the introduced region, their interactions with resident organisms in the new locations, the characteristics of the habitats and regions where they spread, and the consideration of costs and benefits of their presence and abundance with reference to human value systems (Richardson & van Wilgen 2004, Pyšek *et al.* 2006, Richardson 2006). Several 19th century naturalists, notably Charles Darwin, Alphonse De Candolle, Joseph Hooker & Charles Lyell, mentioned invasive species in their writings. Naturalized and invasive species were, however, essentially curiosities at the time and were not perceived as a major threat to global biodiversity.

Biological invasions started becoming much more widespread in the first half of the 1900s, but biologists were slow to focus attention on the phenomenon

(Richardson & Pyšek 2007). Charles S. Elton's (1958) book on *The ecology of invasions by animals and plants* is generally acknowledged as the starting point for focussed scientific attention on biological invasions (Richardson & Pyšek 2008). Invasion ecology has grown enormously in the 50 years since Elton's volume appeared (Pyšek *et al.* 2006, Richardson & Pyšek 2007, 2008).

Nowadays, most researchers agree with the fact that, given that once an alien species is established in a new region it is extremely difficult to eradicate or control, the most effective method to minimize its impact is to prevent establishment or spread in the first place (Ricciardi & Rassmusen 1998, Mack *et al.* 2000). This approach requires that we understand the ecology of the invasion process and the factors underlying success at different stages, so that we can identify situations where invasion risk is high (Duncan *et al.* 2003). Specifically, it is needed to predict what are the factors that allow certain species to establish and spread when introduced to locations outside their natural range, and which areas are the most prone to be invaded.

Success of invaders

Success of invaders is one of the central topics of invasion ecology (Richardson & Pyšek 2008). One may ask why some naturalized species have been able to attain large distributions whereas others remain localized. Usually, invasion success is estimated by comparing how species differ in their abundance or distribution range, and it can be determined at several spatial scales, from plots to regions to the whole Earth.

Several non-exclusive factors have been suggested to be related with the success of invaders (Figure 1.2):

- Environmental matching (Brown 1989, Williamson 1996).
- Invasiveness or invasion potential of species: extent to which a species *per se* is able to overcome various biotic and abiotic barriers and become invasive (di Castri 1989).

- Introduction event factors such as propagule pressure, time since introduction, and stochastic events (Pyšek & Richardson 2007, Rejmánek *et al.* 2005a).
- Invasibility or the vulnerability of the new ecosystem to the establishment of introduced alien species. Invasibility depends both on biotic and abiotic factors (Lonsdale 1999).

Environmental matching

One of the most frequently stated hypotheses in the biological invasion literature is that species should have a better chance of establishing if the climate and physical conditions at the location of introduction and in the species' natural range are closely matched (Brown 1989, Panetta & Mitchell 1991, Scott & Panetta 1993, Williamson 1996). Regions at similar latitudes or within the same biogeographical region are more likely to be similar in climatic and habitat conditions, and so species exchanges between them will be successful (Sol *et al.* 2005). There are several studies that reinforce this hypothesis (Curnutt 2000, Blackburn & Duncan 2001b, Cassey 2003), and even use it as a basis for risk invasion models (Thuiller *et al.* 2005). In a recent cross x taxa review, Hayes & Barry (2008) have concluded that climate/habitat match is the only characteristic that is consistently associated with invader success, measured as range size, across taxa.

Related to this issue, some studies have found that species with larger geographic ranges are more likely to establish (Rejmánek 1995, Goodwin *et al.* 1999, Blackburn & Duncan 2001a, Duncan *et al.* 2001). Species may have large geographic ranges because they can exploit a broad range of conditions (they have large niche breadth; Booth *et al.* 2003, Duncan *et al.* 2003, Vázquez 2006), or because they use conditions that are themselves widespread (they have a common niche position in the given region; Gaston 1994b).

Invasiveness

Much of the early work on invasions was directed at collating species life-history traits associated with invasion sucess (Booth *et al.* 2003). Many studies have attempted to profile successful invaders, starting with Herbert Baker's attempt to identify the traits of an "ideal weed" (Baker 1965). Later, works have shown that identifying traits consistently associated with invasiveness is difficult (Alpert *et al.* 2000). However, such traits are a crucial ingredient for explaining (and therefore predicting) invasions (Rejmánek 1996). Kolar & Lodge (2001) concluded, from an analysis of plant and animal invasion studies, that some generalizations have emerged.

For birds, Duncan *et al.* (2003) identified three type of traits influencing establishment success of a species: (a) traits that pre-adapt species to the new environment (e.g. behavioural flexibility; Sol 2003), (b) traits that favour population increase from a low level (e.g. life history traits as surrogates of population growth; Primm 1991), and (c) traits that constrain establishment success (e.g. migratory behaviour and sexual colour dimorphism; Sol *et al.* 2002). In spreading success, it has been suggested that species with fast population growth rates have larger ranges because they may be less vulnerable to local extinction when colonizing unoccupied sites (Gaston 1988).

For plants, there have been recent efforts for summarizing factors hypothetized to be related with invasion success: growth form, plant height, clonality, breeding system, seed size, pollen and dispersal vectors, timing of flowering, reproductive potential, and habitat preferences. Many traits have been frequently tested but without consistent conclusions through studies (Daehler 2003, Richardson & Pyšek 2006, Pyšek & Richardson 2007). According to these recent reviews about traits that matter in invasion process, there are many sources of bias that can be masking off the effect of traits, such as: phylogeny, residence time, propagule pressure, the scale of the study, and the stage of the invasion process analysed. Pyšek & Richardson (2007) showed that social and economic factors are crucial in the introduction stage, biogeographical and ecological factors at the stage of naturalization, and ecological and evolutionary factors are crucial mediators of spread. Moreover, different definitions of invasive and different types of data set and methodologies used add more inconsistencies through works (Hayes & Barry 2008). Therefore, the role of species traits in the invasion process might be taxa-, stage-, habitat- and context-specific (Pyšek & Richardson 2007, Hayes & Barry 2008).

Introduction event factors: propagule pressure and residence time

Propagule pressure and residence time are the two main event level factors that differ for each introduced population (Blackburn & Duncan 2001a, Duncan *et al.* 2003). Propagule pressure or introduction effort (Blackburn & Duncan 2001a) is a composite measure of the number of individuals of a species released into a region to which they are not native (Carlton 1996). It incorporates estimates of the absolute number of individuals involved in any one release event (propagule size) and the number of discrete release events (propagule number) (Lockwood *et al.* 2005). Propagule pressure could be the key factor to understand why introduction success is so idiosyncratic (Lockwood *et al.* 2005). However, it is extremely difficult to measure, especially for plants. Various quantitative surrogates including the number of visitors to nature reserves (Lonsdale 1999, McKinney 2002a), human population size or density (McKinney 2001, 2002a, Pyšek *et al.* 2002, 2003, Taylor & Irwin 2004), the amount of trade and tourism (Thuiller *et al.* 2005) or economic activity (Taylor & Irwin 2004) have been used with reasonable success.

Residence time (i.e. time since introduction) integrates aspects of propagule pressure related to the timing of invasion: the longer the species is present in the region, the greater the size of the propagule bank, and the greater the probability of dispersal, establishment, and the founding of new populations (Rejmánek *et al.* 2005b). The impact of an introduced species in the invaded community also increases with residence time (Collier *et al.* 2002). As it is mostly not known exactly when a species was introduced, the term 'minimum residence time' (MRT) has been proposed (Rejmánek 2000). MRT explains not only the range and frequency of current distributions but also the invasion status of a species. Therefore, MRT is a crucial consideration in studies evaluating determinants of invasiveness (Pyšek & Jarošik 2005). MRT is closely associated with the lag phase that often precedes invasions of alien species – the delay between the start of invasion and the typical phase of exponential increase (Baker 1965, Kowarik 1995).

The phenomenon of lag phases have important implications for predicting and managing invasions, because large lag times preceding invasions determine that the patterns we observe today are the net result of introductions and prevailing conditions and processes from the past (Hulme 2003). A practical implication of lag phases is that biological invasions have a built-in inertia – the number of naturalized and invasive species will increase in the future even if no additional introductions are made (Kowarik 1995).

Invasibility: the role of native species diversity, interspecific interactions and disturbance

Invasibility is the resistance that the recipient ecosystem offers to invasion. In practice, it is measured as those abiotic and biotic factors that limit alien species establishment and survival (Lonsdale 1999). Species diversity, interspecific interactions and disturbance have been the three main factors examined to detect differences in invasibility.

The biotic resistance hypothesis raised by Elton (1958), suggested a negative relationship between native species diversity and community invasibility. Numerous studies have indeed found species rich communities to contain fewer alien species (e.g. Rejmánek 1989, Tilman 1997, 1999, Knops *et al.* 1999, Levine 2000, Naeem *et al.* 2000, Dukes 2002, Kennedy *et al.* 2002), but others have found that areas with a high native species diversity harbour more alien species (Timmins & Williams 1991, Planty-Tabacchi *et al.* 1996, Stohlgren *et al.* 1999, Lonsdale 1999, Stadler *et al.* 2000, McKinney 2001, Pyšek *et al.* 2002).

Experimental tests using synthetic species assemblages that vary in diversity support the biotic resistance hypothesis. This discrepancy between observations and experiments is mostly due to the spatial scale of study (Fridley *et al.* 2004, Herben *et al.* 2004), and can be explained by covarying external factors (Shea & Chesson 2002). At the large spatial scale, the same abiotic conditions that promote high diversity of native species (e.g. climate, substrate, and habitat heterogeneity) also support diverse alien floras; in other words, what is good for natives is good for aliens too; while at the local scale, experiments test for the neighbourhood effect of species diversity on the establishment and survival of aliens.

Success of invasive alien species has often been attributed to the release from their natural enemies in the recipient ecosystem (Elton 1958, Crawley 1987). For plants, studies comparing herbivory damage or attack by pathogens on alien plants in their native and introduced ranges have generally supported this hypothesis (Wolfe 2002, Mitchell & Power 2003, Maron & Vilà 2007).

Biotic interactions within the native community such us mutualisms (e.g. relationship plant-animal in pollination or propagule dispersal) can favour alien species integration in the community, but they can also be modified by the presence of such species (Richardson *et al.* 2000, Traveset & Richardson 2006, Bjerknes *et al.* 2007, Bartomeus *et al.* 2008, Traveset *et al.* 2008).

Finally, habitat intrinsic or extrinsic natural disturbances such as fire, floods, agricultural practices, drainage of wetlands, alterations of salinity or nutrient levels in streams and lakes, or man-made disturbances can cause problems to native species and can increase the probability of alien establishment (Mack *et al.* 2000, McKinney 2002b). Generally, in disturbed environments, abiotic factors seem to be more pivotal as determinants of invasibility than biotic factors (Richardson & Bond 1991, Hood & Naiman 2000). Moreover, with disturbances, resource pulses and niches become available to be exploit for aliens. Disturbances are in fact seen as "open windows to invasion" (Hobbs & Huenneke 1992, Davis *et al.* 2000, Davis & Pelsor 2001).

Level of invasion

Variations in the level of invasion (i.e. abundance and richness of alien species) among sites could be simply due to differences in the propagule pressure (Williamson 1996, Lonsdale 1999, Chytrý *et al.* 2005, Hierro *et al.* 2005) or the identity of introduced species, but also to differences in invasibility (Figure 1.2). To know whether a region, community or habitat has more risk of invasion, we need to ask not only whether it has more alien species, but whether it is intrinsically more susceptible to invasions (Lonsdale 1999). Lonsdale (1999) proposed a simple equation to define the level of invasion of a region (E; number of alien species), as a function of propagule pressure (I; number of introductions) and invasibility (S; survival of the species introduced): $E = I \times S$

Global and regional scale studies focusing on the level of invasion have found robust geographical patterns:

- Islands are more invaded than mainland (Darwin 1845, cited by Rejmánek 1996, Lonsdale 1999, Cassey 2003, Denslow 2003).
- The New World is more invaded than the Old World (di Castri 1989).
- The level of invasion increases with latitude on mainland but not on islands (Lonsdale 1999), so tropical areas are less invaded than extratropical regions (Rejmánek 1996), but species naturalized in tropics have larger geographical ranges (Sax 2001).
- Low altitude regions are found to contain more alien species than high altitude regions (Arévalo *et al.* 2005).
- Coastal areas tend to be more invaded than inland areas (Pino *et al.* 2005).
- Temperate agricultural, urban and riverine sites are highly invaded areas (Pino *et al.* 2005, Kühn & Klotz 2006, Vilà *et al.* 2007, Chytrý *et al.* 2008b).

Whether these patterns are explained by differences in invasibility remain to be tested.

Box 1.2 Definition of invasion success terms following several bibliographic sources

Invasiveness:
Extent to which a species *per se* is able to overcome various biotic and abiotic barriers and become invasive (di Castri 1989).

Invasibility:
Properties of the ecosystem of introduction that affect exotic species survival (Lonsdale 1999).

Propagule pressure:

- *From the species point of view:* Number of individuals of a species released into a region to which they are not native (Carlton 1996). It incorporates estimates of the absolute number of individuals involved in any one release event (propagule size) and the number of discrete release events (propagule number) (Lockwood *et al.* 2005).
- *From the region point of view*: Number of alien species introduced in a region (Williamson 1996, Lonsdale 1999).

Minimum residence time:
Time since the first citation of the species in the region (Rejmánek 2000).

Invasion risk assessment

Predicting the success of alien species has been a major aim of ecological research since invasions were recognized as an important conservation issue (Rejmánek & Richardson 1996, Reichard & Hamilton 1997, Smith *et al.* 1999, Kolar & Lodge 2001, Pyšek 2001, Caley *et al.* 2006). Given that once an alien species is established in a new region it is extremely difficult to eradicate or control (Rejmánek *et al.* 2005a), preventing the introduction of species that have a high risk of becoming invasive is by far the most cost-effective way of reducing future problems with invasive species (Duncan *et al.* 2003). The essential role of prevention is highlighted by recent policy strategies as the Convention on Biological Diversity (http://www.biodiv.org/) and the Global Strategy of the Global Invasive Species Programme (McNeely *et al.* 2001). Preventive measures are also required after introduction. The invasive potential of recently introduced alien species needs to be reassessed regularly, since many alien species undergo a clear 'lag phase', sometimes for decades following introduction, before the species shows any signs of becoming invasive (Crooks & Soulé 1999). Many alien species already present in a region and that currently show no signs of being invasive will invade in the future.

Identifying future invaders is hugely challenging. The accumulated scientific knowledge on invader traits together with the characteristics of invaded habitats, and information in whether a species is invasive in other parts of the world, especially in areas with similar environmental conditions (Westbrooks 1981, Rejmánek 2000, Union of Concerned Scientists 2001, Thuiller *et al.* 2005, Richardson & Thuiller 2008), has been the basis to develop risk assessment schemes that attempt to predict the success of alien species in a given region of introduction (Mcneely *et al.* 2001, National Invasive Species Council 2001, Wittenberg & Cock 2001, Leung *et al.* 2002, Keller *et al.* 2007a, Gordon et al 2008).

Because risk has two components: the likelihood of invasion and its consequences (e.g. ecological or socioeconomic impacts), risk assessment schemes attempt to identify the fraction of introduced species with a high likelihood of becoming invasive, and prevent their spread and their damaging effects (Andersen *et al.* 2004). So far, there is evidence that the implementation of risk assessment protocols produces net economic benefits (Keller *et al.* 2007b). Screening procedures have been developed in several parts of the world (Tucker & Richardson 1995, Daehler *et al.* 2004, Gordon *et al.* 2008). Such systems drew on a wide range of information, including whether a species is known to be invasive elsewhere, and various measures aimed at assessing the species' potential for dealing with features of the environment in question (Rejmánek *et al.* 2005a). Risk assessment systems should help us to deal with the five priorities for preventing and managing new invasions: research, monitoring, legislation, mitigating impact, and informing the public (Genovesi 2000, Myers *et al.* 2000, Genovesi & Shine 2002, Sol *et al.* 2005).

Macroecology and comparative analysis as thesis framework

Despite concerted effort, the field of invasion ecology has been criticized for its lack of success to predict invasions and to offer management guidance to control invaders (Ehrlich 1989, Vermeij 1996, Mack *et al.* 2000).

Experiments are the best approach to establish causal relationships, and hence are central to understanding the mechanisms of invasion (Schoener & Spiller 1999, Levine 2000, Levine *et al.* 2003). However, experiments are by itself insufficient to fully understand invasions. Due to the immense variability of ecological systems, one limitation of experiments is that the results might lack generality, being only related to the particular area, period of time or species selected as study case. Moreover, not all questions on invasions can be tackled by experimentation, for example those concerned to the resistance of entire regions to invaders. Finally, experiments are not always possible for taxa such as long-lived plants or vertebrates for legal, ethical or logistic reasons (Sol *et al.* 2008).

One alternative to the experimental approach is the comparative analysis of past introductions (Kolar & Lodge 2001, Fisher & Owens 2004, Cadotte *et al.* 2006). In the last decades, the use of the comparative approach has greatly broadened our understanding of the invasion process, uncovering some of the general rules that govern the establishment and spread of species introduced into foreign regions (Brown 1989, Lodge 1993, Kolar & Lodge 2001, Duncan *et al.* 2003, Fisher & Owens 2004, Cadotte *et al.* 2006). A major advantage of the comparative approach is that it can help draw general principles that can apply over broad regions and across a great diversity of taxa, and may thus provide generalities that are realistic enough to be used in risk assessment of future invaders as well as provide the starting place for determining management of existing invasions (Kolar & Lodge 2002, Settele *et al.* 2005).

Macroecology depends heavily on the comparative method to identify large-scale patterns and to test alternative hypotheses that might generate such patterns (Cadotte *et al.* 2006). With the accessibility of large electronic databases of species, ecologist have begun seeking generalities, and examining large-scale ecological hypotheses involving core themes of range, abundance and diversity of invaders. The analyses of regional inventories of alien species can contribute to identify situations associated with high risk of invasion (Cadotte *et al.* 2006).

The macroecological approach linked to new and robust statistical comparative methods can help us to integrate the invasive species and the invaded region approaches (Chong 2006, Thuiller 2006) (Figure 1.2). Moreover, following appropriate statistical methodologies we can deal with confounding effects, mainly phylogenetic bias and spatial non-independence (Sol *et al.* 2008).

Phylogenetic bias and non-independence

The importance of considering phylogenetic relationships when comparing species has long been recognized (Felsenstein 1985, Harvey & Pagel 1991, Freckleton *et al.* 2002). Not all alien species/genera/families have been moved around to the same extent (Richardson & Pyšek 2006), so opportunities to become naturalized and invasive are not even among taxa. Alien species are non-randomly distributed within higher taxonomic groups, whether considered globally (Daehler 1998a, Pyšek 1998b), continentally (Weber 1997), or regionally (Williams *et al.* 2002, Wu *et al.* 2004, Pauchard & Alaback 2004, Villasenor & Espinoza-Garcia 2004). This pattern has a phylogenetic background. Closely related species share many morphological, behavioural, physiological and ecological traits due to common ancestor rather than independent evolution (Felsenstein 1985, Harvey & Pagel 1991, Freckleton *et al.* 2002). If these shared traits affect the likelihood of establishment, then introduction outcomes will be clustered by phylogenetic or taxonomic relatedness. Not taking into account the phylogenetic relationship between species overestimates the degrees of freedom in the analysis and increases the chance to obtain false positives. Additionally, phylogenetic relatedness that overlaps with environmental influences (e.g. due to niche conservatism) may interfere with such variables and lead to wrong parameter estimates.

Spatial non-independence

Some regions might be easier to invade (Williamson 1996, Shea & Chesson 2002), but if it is easier to establish at some locations than others, then the outcome of introductions to the same location will be correlated (Duncan *et al.* 2003). This means that introductions in the same region are unlikely to represent independent pieces of evidence for the influence of a factor on establishment success, because we should expect similar outcomes (either success of failure) for all species introduced to the same location, violating a core assumption of standard statistical tests. The pseudo-replication that arises if the probability of success in introductions is more similar between near-by regions than it is between more distant regions is the so-called spatial autocorrelation. Spatial autocorrelation can be particularly problematic in studies trying to characterize the factors that make some regions more resistant to invaders than others (Sol *et al.* 2008).

Main questions and structure of the thesis

The general objective of this thesis is to analyse the factors associated to plant invasion success in Spain using comparative methods at macroecological scale (Figure 1.2). In particular, through the five chapters that follow this general introduction, we address the following questions:

Accounting for species success

- Are there species traits that favour invader success? (Chapter 1)
- How large and widespread are the potential distribution ranges of invaders? Have invaders reached to occupy them? At which rate do invaders spread? (Chapter 2)
- Are there species traits related to invader spread rate? (Chapter 2)

Accounting for level of invasion

- Are there climatic, geographic or landscape factors associated to the regional level of invasion? (Chapter 1)
- Are there regional context factors that influence the local level of invasion in different habitat types? (Chapter 3)

Integrating species success with level of invasion

- How is the regional organization and composition of invader species assemblages through Spain? (Chapter 4)
- How broad are the ecological niches of invaders? (Chapter 4)
- Are invader ecological niches conditioned by species traits? (Chapter 4)

Assessing plant invasion risk

- Is it accurate to predict plant invasions in Spain using the Weed Risk Assessment protocol? (Chapter 5)

Four chapters are mostly based on the information of the Atlas of Alien Plant Species in Spain (Sanz-Elorza *et al.* 2004) and one refers to a smaller regional level, using the Catalan database FLORACAT (Font & Ninot 1995). The five chapters are presented in scientific paper format, what entails some dataset and region descriptions redundancies, but the references have been assembled at the end. The chapters are written entirely in English, except the abstract, which is translated to the Catalan. The final discussion of the thesis is presented on both languages as this general introduction.

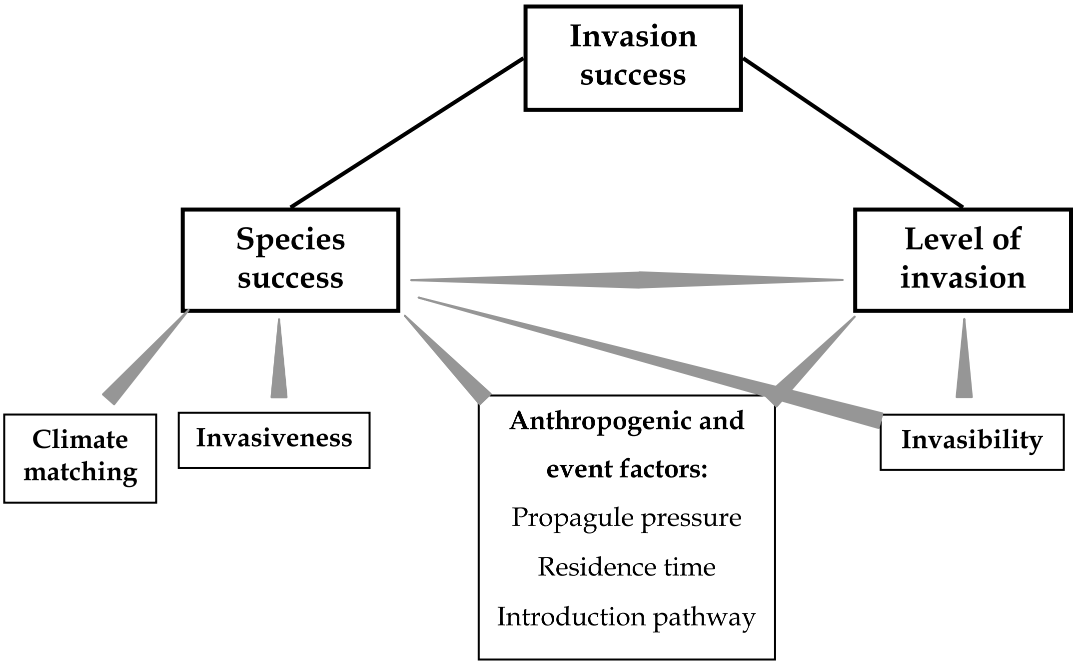

Figure 1.2
Scheme of the invasion success components (i.e. species success and level of invasion) and their factors of influence according to the hypothesis highlighted on this introduction.

Chapter 1

Exploring species attributes and site characteristics to assess plant invasions in Spain[1]

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[1] This chapter has been accepted in *Diversity and Distributions* on March 2008.
Authors: Núria Gassó, Daniel Sol, Joan Pino, Elías D. Dana, Francisco Lloret, Mario Sanz-Elorza, Eduardo Sobrino, Montserrat Vilà.

Resum

Explorant atributs d'espècies i característiques regionals per avaluar les invasions per plantes a Espanya

Les invasions biològiques són un component fonamental del canvi global amb efectes creixents en els ecosistemes naturals i les societats humanes. Les dificultats per predir acuradament el destí d'una introducció concreta han portat a un increment de l'interès per identificar situacions on el risc d'invasió sigui particularment elevat. Amb aquest propòsit, hem fet servir dues aproximacions diferents per tal d'analitzar els patrons regionals d'invasions per plantes a l'Espanya peninsular com a punt de partida per desenvolupar protocols de risc d'invasió espacials i escenaris d'invasions de plantes a la regió mediterrània en front de l'escalfament global. Des de la perspectiva de les espècies, hem testat quins trets d'història de vida i vies d'introducció estan relacionats amb l'extensió de la distribució regional de les plantes invasores. Des de la perspectiva de la regió envaïda, hem testat quins factors paisatgístics, geogràfics i climàtics estan associats a la riquesa regional d'espècies de plantes invasores. Els nostres resultats indiquen que, des del punt de vista de les espècies, tenint en compte els efectes de la taxonomia, la dispersió pel vent i el temps mínim de residència semblen afavorir l'èxit de les espècies mesurat com el nombre d'UTMs on és present l'espècie. Des del punt de vista de la regió envaïda, hem identificat l'alta pertorbació antròpica, la baixa altitud, la proximitat a la costa i el clima sec i càlid són els principals factors correlacionats amb la riquesa d'invasores per UTM. D'acord amb aquests resultats, una creixent importància dels ecosistemes antròpics i l'escalfament global a la regió mediterrània hauria de facilitar l'expansió de les plantes invasores, especialment les espècies dispersades pel vent, i que dóna com a resultat l'acumulació d'espècies invasores en alguns llocs (punts calents d'invasió).

Abstract

Biological invasions are a major component of global change with increasing effects on natural ecosystems and human societies. The difficulties to accurately predict the fate of a given introduction has led to increased interest in identifying situations where the risk of invasion is particularly high. With this purpose, we used two different approaches to analyze regional patterns of plant invasions in mainland Spain as a baseline to develop spatially explicit invasion risk protocols and scenarios of plant invasions in the Mediterranean region in the face of global warming. From the species perspective, we tested which life history traits and pathways of introduction are related to the extent of the regional distribution of plant invaders. From the invaded site perspective, we tested which landscape, geographic, and climatic factors were associated to regional invader species richness. From the species perspective, when taxonomic effects were accounted for, wind dispersal and minimum residence time appeared to favour invasion success measured as the number of UTM grid cells where present. From the invaded site perspective, we identified high anthropogenic disturbance, low altitude, short distance to the coastline, and dry, hot weather as the main correlates to UTM grid cell invader richness. According to these results, an increasing importance of man-modified ecosystems and global warming in the Mediterranean region should facilitate the expansion of plant invaders, especially wind-dispersed species, leading to the accumulation of invasive species in some sites (i.e. invasion hot-spots).

Introduction

Biological invasions are a major component of global environmental change (Vitousek *et al.* 1997, Dukes & Mooney 1999, Vilà *et al.* 2006, Thuiller *et al.* 2007a), with increasing effects on the loss of biodiversity (Lodge 1993), alteration of disturbance regimes (D'Antonio & Vitousek 1992), changes in the biogeochemical cycles (Vitousek 1994) and homogenization of Earth's biota (Atkinson & Cameron 1993). Given that once an alien species is established in a new region it is extremely difficult to eradicate or control, the most effective method to minimize its impact is to prevent establishment or spread in the first place (Duncan *et al.* 2003). For this purpose it is needed to predict which alien species have the highest risk to invade and which areas are the most prone to be invaded.

Analyses of regional inventories of alien species can contribute to identify situations associated with high risk of invasion (Cadotte *et al.* 2006). From a species perspective (species approach, hereafter), one may ask why some naturalized species have been able to attain large distributions whereas others remain localized. This is related to the species potential to invade according to their life history characteristics (i.e. invasiveness) and introduction event factors such as the pathway of introduction or time since introduction (Pyšek & Richardson 2007). From an invaded site perspective (site approach, hereafter), one may wonder why invaders are more common in some regions than in others. The regional level of invasion is related to the properties of the region of introduction that facilitate the survival of non-indigenous species (i.e. invasibility; Lonsdale 1999) and the intensity to which this species has been introduced (i.e. propagule pressure; Kühn *et al.* 2003).

Despite the considerable effort that has been devoted in the past to identify the traits that underpin the invasiveness of introduced species (Pyšek & Richardson 2007) or the characteristics that make some regions more vulnerable to invasion than others (Ohlemüller *et al.* 2006), surprisingly there have been few studies that included both species and site perspectives (Thuiller *et al.* 2006b) or even to focus on both aspects for a single region (Chong *et al.* 2006, at local scale). Here, we use the species and site approaches, as two different ways to comprehend the distribution and invasion extent of invasive plants in Spain as the basis to develop spatially explicit invasion risk protocols and scenarios of plant invasions in the Mediterranean region. In particular, we use empirical models to examine how some life history traits are related to the regional distribution of invasive plants once introduction event factors and phylogenetic effects are accounted for. We also test a number of climatic, landscape, topographic and anthropogenic factors that could account for variation in invader richness within the study region.

Methods

Study region

Spain occupies 493,486 km^2 of the Iberian Peninsula. Its geography is characterized by two central plateaus crossed by three main rivers (Duero, Tajo and Guadiana). These plateaus are surrounded by mountains and two main depressions in the NE and in the S (the Ebro and Guadalquivir rivers, respectively). It is a mountainous country where elevations over 1500 m a.s.l. are common and the highest peak achieves 3480 m a.s.l. These geographical features condition the distribution of agricultural areas (50.3%, mainly in the centre of the plateaus, along the main river valleys and the coastal plains. The remaining territory is occupied by forests (17.5%, mainly in the N half), scrublands (20.5%), grasslands (7%), and artificial areas (1.3%) (CORINE Land Cover Map of Spain, http://www.fomento.es).

Spain houses a heterogeneous climatic mosaic with three main climatic types: oceanic Mediterranean continental and Mediterranean maritime (Ninyerola *et al.* 2000). Furthermore, mountainous systems impose sharp topographic-climatic gradients where these three climatic types gradually change to Mountain climate, characterized by cold, strong winds and abundant rainfall or snowfall. Oceanic climate prevails in the NW and it is characterized by relatively mild winters, warm summers, and generally abundant rainfall spread out over the year. Mediterranean continental climate covers the majority of mainland Spain and it is characterized by wide diurnal and seasonal variations in temperature and by low, irregular rainfall with high rates of evaporation. Finally, Mediterranean maritime climate dominates the Eastern and Southern coast and it is characterized by rainfall concentrated in spring and autumn, and the moderating effect of the sea over the temperatures. Therefore, in Spain there are up to three main climatic gradients: N-S, from lowland to summits and from the coast to inland.

Due to its geographical, topographic, climatic and geologic characteristics, Spain has a high landscape diversity; and despite a large number of protected areas, natural ecosystems are rather fragmented and deteriorated (Costa *et al.* 1900, Valladares *et al.* 2005). Around the middle of the 20th century, large reforestation programs were performed to increase the productivity of the Spanish forests, following a crisis of the rural world and its consequent generalized agricultural field abandonment. Currently, human population in Spain is mostly concentrated in metropolitan areas (e.g. Madrid and Barcelona with 5.6 and 4.6 million inhabitants, respectively), and coastal areas, where urban cover has highly increased in the last 20 years and it is even expanding towards adjacent areas.

Species approach

The identity and distribution of the 106 vascular plant invaders analyzed in this study were obtained from the most recently published atlas of alien plant species in Spain (Sanz-Elorza *et al.* 2004). The cartographic information in the atlas was generated through a five years work compilation of bibliographic and herbarium records. The selected list included all vascular neophytes (i.e. established aliens introduced after 1500) identified for Spain, and represent 10.6% of the total number of alien plants listed in the above mentioned atlas. Sanz-Elorza *et al.* (2004) considered that a plant was invasive according with the definition by Pyšek *et al.* (2004), that is; an alien species with self-sustainable populations without direct human intervention that produces offspring at considerable distances from the parent plants, and thus has the potential to spread over large areas. For each species we calculated the size of the area of distribution (hereafter range size) as the number of occupied cells in the 10x10 km UTM (Universal Transverse Mercator) grid (see Appendix G.I for cartography). This variable was used as an estimation of the degree of invasion success of the species.

We built a database with six biological and ecological plant traits that, according to the literature (Pyšek *et al.* 1995, Rejmánek 1995, Goodwin *et al.* 1999, Lloret *et al.* 2003), are potentially related with the invasion success of alien species and for which we had sufficient data: seed size (very large (>10mm), large (5-10mm), medium (2-5mm), small (1-2mm), very small (<1mm)), clonality (yes, no), longevity (annual, biennial, perennial), life-form (Raunkiaer system), dispersal syndrome (wind, animal, water) and pollination type (wind, animal, water). Three factors related to the introduction event were also included in the database: region of origin (America, Asia, Africa, Europe, Middle East, Oceania, Cosmopolitan (i.e. native to more than one continent), pathway of introduction (agriculture, gardening, forestry, unintentionally), and minimum residence time (i.e. year of first bibliographic or herbarium record in Spain). All the above information was taken from Castroviejo *et al.* (1986-2000), Casasayas (1989, 1990), Bolós *et al.* (1993) and Sanz-Elorza *et al.* (2004).

We adopted the framework of the Generalized Linear Mixed Models (GLMM) (e.g. Blackburn & Duncan 2001a) to model variation in range size between species as a function of the predictors described above. There was a clear taxonomic bias in the set of invasive species, with over 34% of species belonging to just two families (Asteraceae and Poaceae). Because species are linked by phylogeny (Harvey & Pagel 1991), using species as independent data points may inflate the degrees of freedom (Brändle *et al.* 2003) and increase the Type-I error. Therefore, we accounted for phylogenetic effects by allowing the incorporation of taxonomic categories as nested random factors in the GLMM as a surrogate for phylogenetic relationships. In this way, the likely non-independence of response values of closely related species is, at least partly, controlled by assuming a common positive correlation between introduction outcomes for species within nested taxonomic groups (genera and family, in our case), but a zero correlation between introduction outcomes for species in different groups (a variance components model). There are more sophisticated procedures that allow implementing the complete phylogenetic structure in the statistical models, but we could not use such methods because there was no possibility to have a robust phylogenetic tree that reflected the complete phylogenetic structure. Even if this approach has limitations, we are confident that it contributes to mitigate the problem that invasive species are a non-random subset of all species introduced (see Blackburn & Duncan 2001a).

The response variable (i.e. range size) was right-skewed and could not be normalised with logarithmic or any other transformation. This precluded the use of models with error structure based on the normal distribution. As an alternative, we decided to model invasion success with a Poisson distribution of errors (Crawley 2002). Poisson errors are recommended to deal with integer (count) variables, which are often right-skewed (Crawley 2002). The inspection of the residuals showed that this error structure adjusted well to our response variable.

We started modelling invasion success with a model that contained all our predictors and their quadratic terms. Using a backward selection process, we next simplified the model so as to leave only significant predictors (minimum adequate model). The model was run in the glmmPQL procedure of the MASS library on the R statistical package (Venables & Ripley 2002, R Development Core Team 2006).

Site approach

We determined invader plant species richness as the number of species present in each 10x10 km UTM grid as the dependent variable. For each UTM cell, we estimated 18 variables concerning landscape, topography, climate and human settlement (see Appendix G.II for cartography). Several authors have highlighted the influence of these variables on the number of invasive plant species in a given area (Pyšek et al. 2002, Kühn *et al.* 2003, Pauchard & Alaback 2004, Pino *et al.* 2005, Stohlgren *et al.* 2005). All the GIS procedures involving the set up of the explicative variables and their combination with invasive species richness were performed using the in-house software MiraMon (Pons 2000), but mapping was done with ArcView (ESRI 1992-2006).

Landscape variables were calculated from the CORINE Land Cover Map of Spain (http://www.fomento.es). We used this map to calculate the following relative ground covers per UTM cell: built-up areas, agricultural areas, forests, scrub-herbaceous vegetation, open spaces, wetlands and water bodies. Land cover diversity was estimated by calculating the Shannon index of the above mentioned land cover categories.

Topographic variables were obtained from the official Digital Elevations Model (DEM) of 100 m pixel size (http://www.opengis.uab.es). We calculated mean altitude (m) and altitude range (difference between maximum and minimum) per UTM cell and, through MiraMon distance algorithms, mean distance to the coastline (m) for each UTM cell.

Climatic variables were calculated from the Digital Climatic Atlas of Spain (Ninyerola *et al.* 2005; http://opengis.uab.es/wms/iberia/index.htm), a grid of 200 m pixel size generated from the existing network of meteorological stations and DEM. We calculated the mean values per UTM cell of mean annual temperature (ºC), annual temperature range (i.e. difference between maximum temperature in July as the hottest month, and minimum temperature in January, the coldest month), annual rainfall (mm), summer rainfall (sum of the rainfall in June, July and August), and annual solar radiation (KJ $\cdot m^{-2} \cdot day^{-1} \cdot \mu m^{-1}$).

Human settlement variables were calculated from maps obtained in the official server of the Spanish Ministry (http://www.cnig.es). Road length (m) and railway length (m) were also calculated per each UTM cell. We considered human settlement variables as a measure of human footprint (Sanderson *et al.* 2002) and a surrogate for propagule pressure (Pyšek *et al.* 2002). Percentage of built-up areas was already calculated as a landscape variable.

Due to the potential heterogeneity of sampling effort within the region and the consequent difficulty to distinguish between absence of invasive species and missing data, the analyses were limited to UTM cells with at least 1 invasive species present. We also excluded UTM cells with a land proportion of less than 60%. Then, from the total pool of 10506 UTM cells that cover Spain, only 2517 of them were taken into account in our analysis. To reduce the colinearity in explicative variables, a Pearson's correlation matrix was calculated. Because environmental data are *per se* highly correlated at the regional scale, a tolerance of a pairwise $|r| > 0.75$ was used to determine unacceptable colinearity between explicative variables, as previous studies have done (Pino *et al.* 2005). After revising the Pearson's correlation matrix, we excluded mean annual temperature, which was a model whose estimation involved a DEM and thus exhibited a trivially high correlation with mean altitude ($r = -0.79$,

$p<0.001$) and summer rainfall ($r = -0.74$, $p<0.001$).

We started modelling invader species richness as a function of the predictors with Generalized Linear Models (GLM). We used Moran's *I* correlograms (Legendre & Legendre 1998) to evaluate the amount of spatial autocorrelation of the residuals. Moran's *I* is an autocorrelation coefficient and could be regarded as spatial equivalent to Pearson's correlation coefficient. Significance was assessed after 1000 permutations (Bjørnstad 2004).

Autocorrelated data violate the assumption of independence of most standard statistical procedures, so when positive autocorrelation is present Type I errors may be strongly inflated (Legendre 1993). Moreover, Lennon (2000) pointed out that spatial autocorrelation can alter parameter estimates of linear models by influencing the variance-covariance matrix (Anselin 1988, Anselin & Bera 1998), and these biases may seriously distort our understanding of the processes involved in generating the observed ecological patterns. Therefore, with the purpose to control for spatial autocorrelation, we next performed a Generalized Linear Mixed Model (GLMM) with a Poisson distribution of errors and a defined correlation structure. We tested different autocorrelation structures, as described in Crawley (2002), and used spatial correlograms to select the one that most effectively eliminated the spatial autocorrelation. The models were run using the glmmPQL procedure of the MASS library on the R statistical package (Venables & Ripley 2002, R Development Core Team 2006). As before, we simplified the final model in order to obtain a minimum adequate model with only significant variables.

Results

Species approach

Invasive plants in Spain largely varied in their range size. On average, species range size was of 131.27 UTM cells, ranging from 1 to 824. However, many species had restricted ranges (e.g. *Opuntia monacantha*, *Leucaena leucocephala*, *Pennisetum setaceum*), whereas a few showed extensive distributions (e.g. *Sorghum halepense*, *Amaranthus retroflexus*, and *Robinia pseudoacacia*) (Fig 2.1) and Appendix D.I ang G.I.

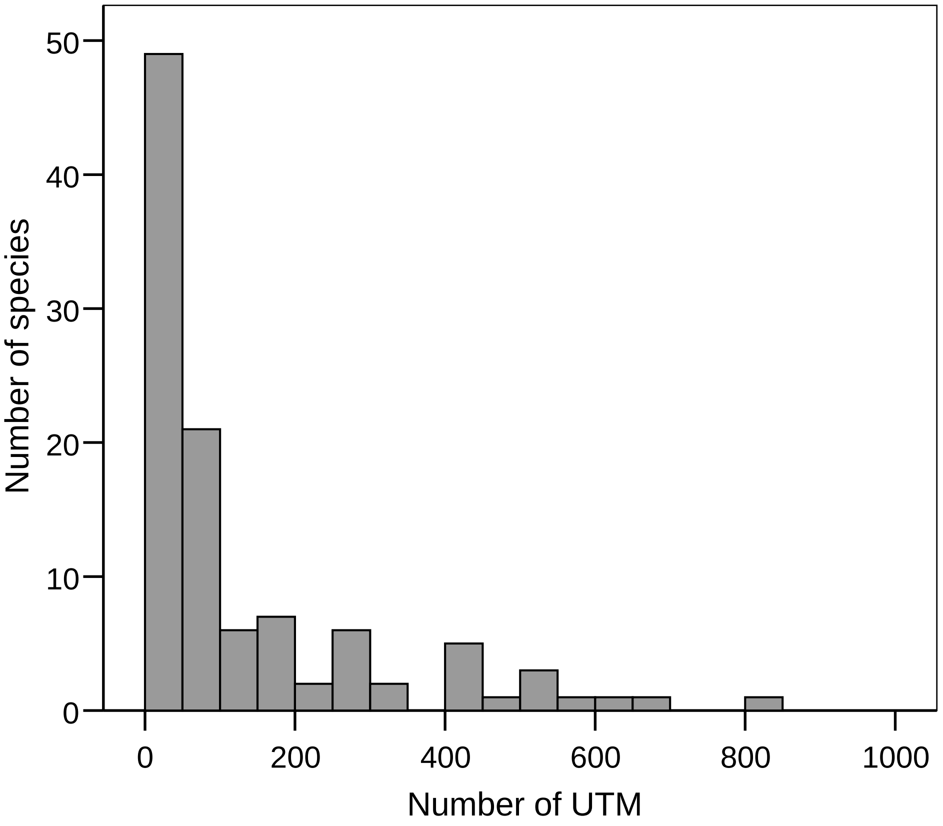

Figure 2.1
Frequency distribution of range size (nº of 10 x 10 km UTM cells where the species is present) of each plant invader.

Family of the invasive species did not explain any proportion of the variance in range size, while genera explained 48.5% of the variation. After accounting for taxonomic differences, we found that only two out of our nine predictors were significantly related with range size (Table 2.1), and none of the quadratic terms was significant. First, wind was the dispersal vector related to the largest ranges, followed by animal dispersal (Fig 2.2). Second, minimum residence time and range size showed a positive relationship (Fig 2.3). Closer inspection showed that, while range size increased with time in species introduced in the last 100 years ($r^2=0.272$, $p<0.0001$), the relationship turned out non-significant for species introduced between 500 and 100 years ago ($r^2=0.091$, $p=0.142$).

Table 2.1 Minimum adequate mixed model accounting for variation in range size of invasive plants in mainland Spain (N=106 species), controlling for taxonomic relationships. Family and Genus of the species were included as nested random factors in the model (not shown) to deal with taxonomic autocorrelation. Dispersal syndrome is a categorical variable with three levels (Water, Wind, and Animal); the estimates represent differences of each level with respect to Animal dispersion, which is given a value of zero (Crawley 2002).

Variable	Category	Estimate	Standard error	t-value	*P*
Intercept		3.611	0.242	14.909	<0.001
Dispersal syndrome	Water	-1.721	0.880	-1.955	0.059
	Wind	0.568	0.256	2.219	0.033
Residence time		0.004	0.000	5.623	<0.001

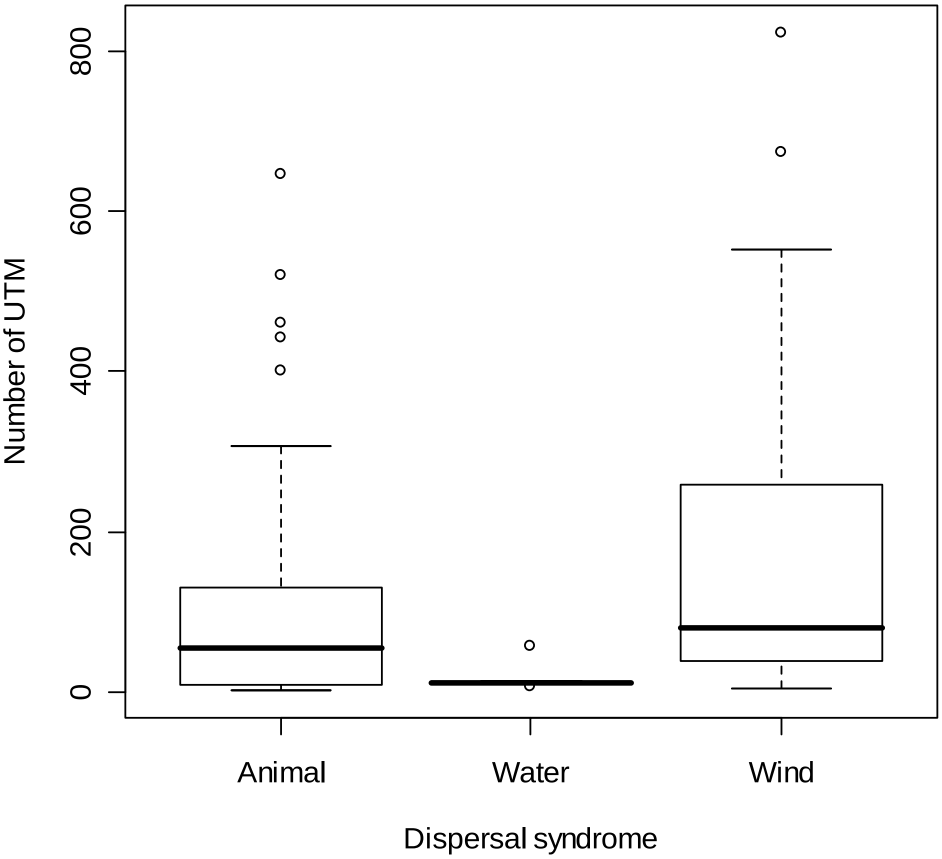

Figure 2.2
Range size (nº of 10 x 10 km UTM cells where the species is present) of invasive plant species in mainland Spain according to their dispersal syndrome (i.e. animal, 58 species; water, 5 species; wind, 43 species). Box width indicates the interquartile range, the dark line inside the box indicates where is the median, whiskers arrive until the largest and smallest non-outlier observations, and the small circles represent the observations considered as outliers.

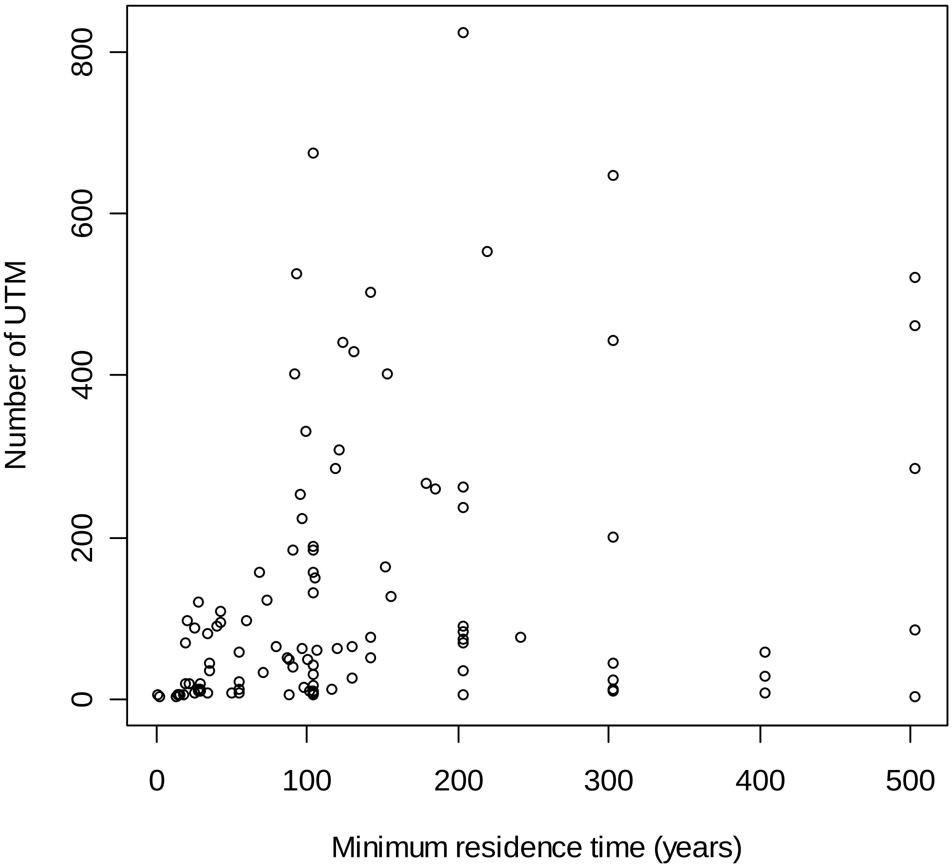

Figure 2.3
Relationship between minimum residence time and range size (nº of 10 x 10 km UTM cells where the species is present) of invader plant species in mainland Spain. Range size increased with time in species introduced in the last 100 years (r^2=0.272, p<0.0001), the relationship turned out non-significant for species introduced between 500 and 100 years ago (r^2=0.091, p=0.142).

Site approach

On average, only 2.49 invasive species were found per 10x10 km UTM cell, with values ranging from 1 to 54 species. However, most UTM cells (35.9 %) had only 1 invader. In general, the coastal UTM cells had the highest values of invasive species richness, especially along the Eastern side of mainland Spain, with hot-spots (i.e. arbitrarily set up to values higher than 50 species per UTM cell) in the Northern Mediterranean coast (Fig 2.4).

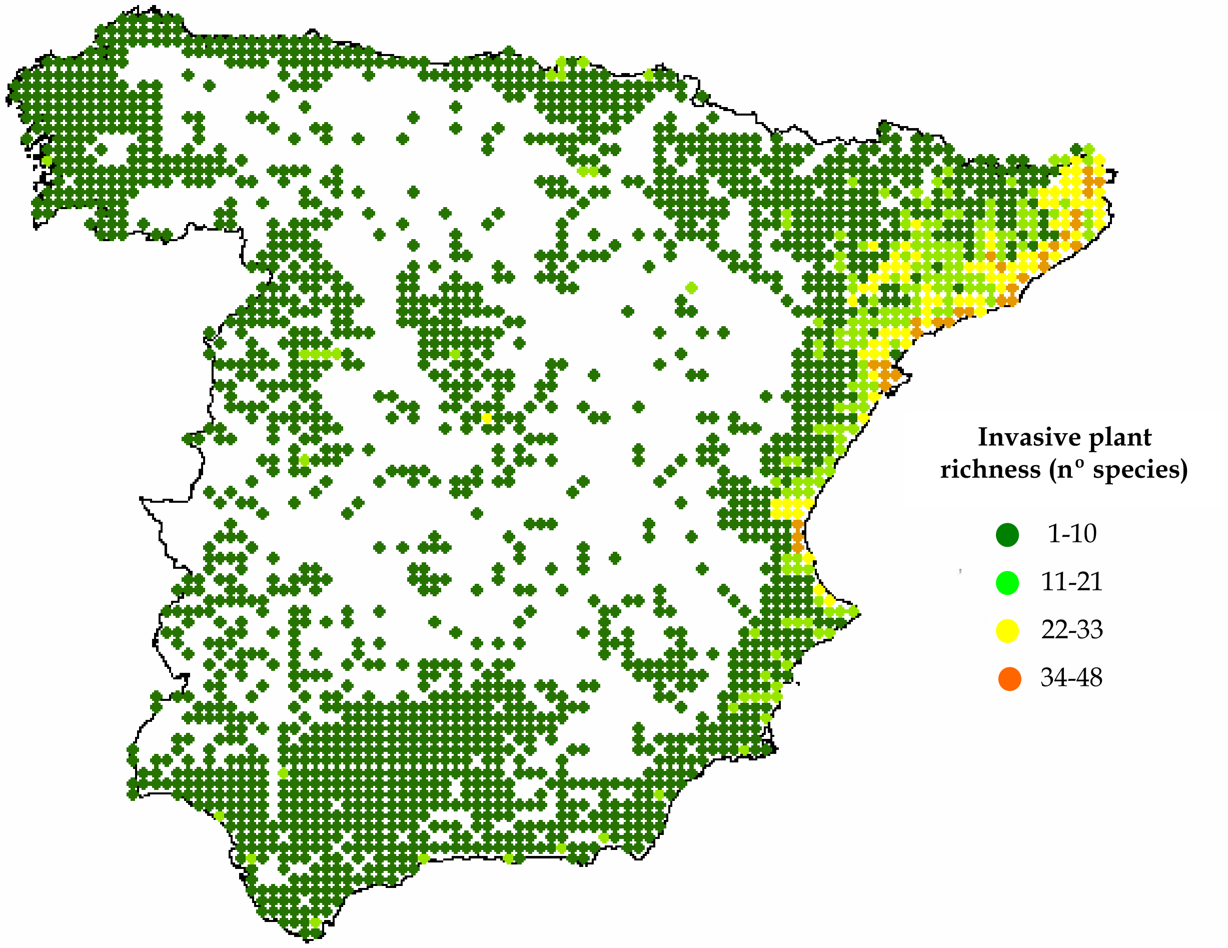

Figure 2.4
Invasive plant species richness (number of species) per 10x10km UTM cell in mainland Spain. White areas have not been considered in the analysis.

A high spatial autocorrelation was detected in the residuals of the initial GLM (Moran's $I = 0.70$). Thirty percent of this autocorrelation could be removed by using a spatially-based GLMM with Gaussian correlation structure. We could not find any model that completely removed the spatial autocorrelation, and thus the results presented here may be conditional on the model adopted. However, we note that the remaining autocorrelation was small (Moran's $I < 0.50$). The minimum adequate model showed that six out of 18 predictor variables were significantly related to invasive plant richness. Percentage of built-up areas, road and railway length were all positively related with invasive plant richness, while distance to the coastline, mean altitude and annual rainfall were negatively related with invasive plant richness (Table 2.2).

Table 2.2 Minimum adequate mixed model accounting for variation in regional invasive species richness in mainland Spain (N = 2517 10 x 10 km UTM cells), incorporating Gaussian spatial correlation structure.

Variable	Estimate	Standard error	t-value	*P*
Intercept	1.349	0.032	41.390	<0.001
Built-up areas	0.122	0.013	9.127	<0.001
Road length	0.051	0.016	3.210	0.001
Railway length	0.049	0.016	3.025	0.002
Distance coast	-0.522	0.039	-13.358	<0.001
Mean altitude	-0.186	0.034	-5.391	<0.001
Annual rainfall	-0.169	0.028	-5.876	<0.001

Discussion

Our two approaches allowed for the identification of several factors that underpin the range size of invasive plant species and make some sites more susceptible to invaders than others. Before discussing these findings in detail, we draw attention on an historical factor that can alter our perception of invasion success: the time since the species was first introduced. Species recently introduced showed more restricted distributions because they have had less opportunity to expand their range. Residence time also represents a dimension of propagule pressure: the longer the species is present in the region, the more propagules are spread by human activities and the probability of founding new populations increases (Hamilton *et al.* 2005, Pyšek & Jarosík 2005, Rejmánek *et al.* 2005b). Moreover, time since introduction or residence time could not be necessarily the same than time since the first record, as we have assumed on this work, because for species introduced at the same moment, the ones that are more invasive are likely to be recorded earlier. Therefore, time since first record might depend on invasiveness. However, our analysis also reveals that the relationship between invasion success, measured in terms of range size, and time since the first record disappears when considering species introduced more than 100 years ago. This result could be due to the fact that these species would have already reached their maximum spreading area in Spain, according to their potential invasiveness and the characteristics of the recipient-area, or it could be a consequence of the lack of highly reliable historical data before 100 years ago.

Only a few traits seem to be consistently associated with invasion success in plants (Pyšek & Richardson 2007). From the nine traits we examined, besides minimum residence time, only propagule dispersal syndrome appeared to be related with range size. After correction for minimum residence time and taxonomic affiliation, species dispersed by wind (i.e. anemochory) have the widest range size. Dispersal syndrome has classically been screened as an important determinant of invasiveness (Vermeij 1996, Richardson *et al.* 2000, Kolar & Lodge 2001). In many regional analysis, wind dispersal has been found to be the most effective for invaders to spread (Prinzing *et al.* 2002, Lloret *et al.* 2003).

Besides dispersal, none of the other traits classically considered to be associated with invasion success were significant in our analyses. Thus, successful plant invaders do not seem to be characterized by their seed size, clonal strategy, longevity, life-form or pollination mechanism. The general failure to identify features of successful invaders are in line with suggestions that the outcome of invasions is highly idiosyncratic, although it can also indicate that the ecological attributes of successful alien invaders are not general but habitat-dependent (Thompson *et al.* 1995). General features of successful invaders, if they exist, should not be many, as adaptations that are useful in some environments are not necessarily appropriate for other environments. Thus, it would seem more likely to find pre-adaptations to invade specific habitats, rather than a wide variety of habitats (Sol 2007). Although our analyses consider many of the main hypotheses put forward to explain invasion success in plants, the possibility that we have missed the traits that really matter because they could not be found in the literature or have to be assessed experimentally, should not be completely ruled out.

Compared to the species-level approach, our attempt to identify factors that make some regions more susceptible to invasion than others was much more successful. Even if we did not manage to eliminate completely spatial autocorrelation, it was reduced until a level that it should not alter our main conclusions. The hot spots of invasive plants richness in Spain were localized in coastal NE areas, consistent with a previous analysis of a subregion (Pino *et al.* 2005). These areas have concentrated an historical and up to date high level of development, trading and tourism activities, and hence should be associated with higher rates of species introductions. In agreement with this hypothesis, the coastal NE areas accumulate most of the first records of alien species in Spain (Casasayas 1989, 1990).

The importance of anthropogenic disturbance is represented by percentage of built-up areas, road and railway length. Man-induced disturbances have been traditionally considered a key factor for land cover diversity, and, in turn, for the invasion process (Elton 1958, Kowarik 1990, Jenkins 1996, Pyšek 1998a, Hobbs 2000). In consequence, flora of urban areas and their surroundings is usually richer in alien species than natural areas (Stadler *et al.* 2000, Chocholouškova & Pyšek 2003). Man-modified habitats such as human settlements, old fields, roadsides, rangelands and areas near croplands or plantations are more prone to invasion than natural or seminatural habitats, as found in other studies (Kowarik 1990, Tyser & Worley 1992, Pyšek 1998a, Hobbs 2000, Vilà *et al.* 2003).

With regard to topographic and climatic factors, mean altitude and annual rainfall were negatively related with invasive plant richness, as it has also been found, at regional and landscape scales, in Central Europe (Mihulka 1998, Pyšek *et al.* 2002), in South Central Chile (Pauchard & Alaback 2004), United States (Stohlgren *et al*. 2005, Chong *et al.* 2006). Low altitudes have been found to have higher propagule pressure (Becker *et al.* 2005). A recent study (Kleunen *et al.* 2007) found that plants from low altitudes in their native ranges have a higher naturalization success and more opportunities to be introduced elsewhere because they are used in horticulture. Therefore, the higher invasive species richness in low altitudes might be due to a combination of high propagule pressure and the introduction of plant species adapted to low altitude conditions and dispersed intentionally by humans. Moreover, mean altitude is negatively correlated with mean annual temperature, which has also been found to be closely related with invasive plant richness in other studies (Pino *et al.* 2005). Therefore, warm and dry climates seem to be advantageous for invasive plants. Spanish invasive flora is mainly dominated by species of tropical and subtropical origin, most of them presumably unable to complete their life-cycle in cold or high altitude areas (Casasayas 1989, 1990, Sanz-Elorza *et al.* 2004).

The negative association of invader richness with altitude, coupled with distance to the coast, is also an indicator for the importance of anthropogenic land uses such as built-up and agricultural areas for invasion because they are clumped at low elevations. Thus, elevation was not only an indicator of microclimate but also indirectly represented the gradient of land use intensity from built-up and intensively managed agricultural areas at low elevations to forest, shrub and herbaceous associations, and extensive farming at high elevations. Given these previous findings, it should not come as a surprise that distance to the coastline was negatively related with invasive plant richness. Close to the coastline we find the mildest climates, and high human presence and therefore, a high propagule pressure and disturbance.

Despite the limitations of our study in terms of reduced number of species traits analyzed, potential variation in sampling effort and limitations to consider all country area, by using species and site approaches at regional scale, we have been able to identify some features that underpin range size of invasive species and make some sites more vulnerable to invasion than others. The dispersal syndrome seems to be central in understanding variation among species in their geographical spread, whereas anthropogenic disturbance, propagule pressure and mild climate are all factors explaining patterns of variation in alien species richness, what seems consistent at different scales and regions, as discussed above. Therefore, an important implication of our finding is that an increasing importance of man-modified ecosystems and global warming would facilitate plant invasions (Dukes & Mooney 1999), increasing the opportunities for the accumulation of invasive plant species in hot-spots. Such information is critical to develop invasion risk protocols for future global change scenarios in the Mediterranean region.

Chapter 2

Spread of invasive plant species: Just a matter of time?[2]

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[2] This chapter is in review in *Ecology* in June 2008.
Authors: Núria Gassó, Wilfried Thuiller, Joan Pino, Montserrat Vilà.

Resum

Expansió de les espècies de plantes invasores : és només qüestió de temps ?

L'èxit de les espècies invasores ha estat sovint mesurat segons l'abundància local o regional o el rang de distribució actual a les regions envaïdes. Tot i així, aquestes mesures no tenen en compte el rang potencial adequat a l'espècie, i per tant, només mostren una fotografia del patró d'invasió en un moment determinat. Estudis recents han desenvolupat models basats en el nínxol per avaluar la conveniència d'una regió per una espècie invasora determinada i el seu potencial per expandir-s'hi. En aquest estudi, els nostres objectius principals són estimar: (1) el rang de distribució potencial de 78 plantes invasores descrites a l'*Atlas de las plantas aloctonas invasoras de España*, (2) la proporció del rang de distribució que ocupen actualment, (3) la taxa d'expansió de cada espècie, i (4) quins trets de les espècies estan associats a la taxa d'expansió. Hem descobert que la majoria d'espècies encara no han ocupat la meitat dels seus rangs potencials geogràfics. Les espècies introduïdes més d'hora han ocupat, de mitjana, una proporció més gran dels seus rangs potencials de distribució, i les espècies amb la taxa d'expansió més elevada no són necessàriament aquelles que han omplert el seu rang potencial. Finalment, hem detectat que només el síndrome de dispersió i el creixement clonal són importants per la taxa d'expansió. Des del punt de vista de la gestió, hauríem de parar més atenció a aquelles espècies de plantes amb rangs de distribució potencial amples però amb un grau d'ocupació baix, perquè pot ser només és una qüestió de temps que assoleixin la seva màxima àrea de distribució.

Abstract

Success of invasive species has been usually measured as local or regional abundance or current distribution range in the invaded regions. However, these measures do not account for the suitable potential range of the species, so they only show a picture of the invasion pattern for a given time step. Recent studies have developed niche-based models to assess the suitability of a region for a given invasive species and its potential to spread through it. On this study, our main objectives are to estimate: (1) The potential distribution range of 78 major plant invaders described in the atlas of invasive plant species in Spain, (2) The proportion of it that they currently occupy, (3) The spread rate of each species, and (4) Which species traits are associated to spread rate. We found that most of the species have not yet occupied half of their potential geographic ranges. Species introduced earlier have, on average, occupied a higher proportion of their potential distribution ranges, and species with the highest spread rate are not necessary those which have already filled out their potential range. Finally, we found that only dispersal syndrome and clonality were of importance for spread rate. From a management point of view, we should pay more attention to those plant species with a large potential distribution range but a low occupancy, because it might be only a matter of time that they reach their maximum area of distribution.

Introduction

The acceleration and intensification of human activities such as global trade, tourism and migration have been accompanied by the intentional or unintentional transport of species to regions far from their natural ranges (McNeely *et al.* 2001, Levine and D'Antonio 2003). Several of these species introduced to new regions become invasive (Pyšek *et al.* 2004). Invasive species have become of major conservation concern, by threatening native species (Mack *et al.* 2000), altering ecosystem functioning (Brooks *et al.* 2004), and affecting human economic wealth by impacting on agriculture, forestry and health (Pimentel *et al.* 2001). As a consequence, a major challenge for researchers is to understand the drivers of distribution range extension, rate and magnitude of invasive species spread (Ewel *et al.* 1999, Sakai *et al.* 2001, Wittenberg & Cock 2001).

Success of invasive species has been traditionally measured as local or regional abundance or current distribution range in the invaded regions (Mack *et al.* 1996). These measures show a picture of the invasion pattern for a given time step. However, they do not account for the suitable potential range of the species and therefore they do not inform about the position of this picture within the invasion process in a given region.

Recent studies have developed niche-based models to assess the suitability of a region for a given invasive species and its potential to spread through (Peterson 2003, Rouget *et al.* 2004, Guisan & Thuiller 2005, Thuiller *et al.* 2005). These models are mainly based on the climate matching approach (Curnutt 2000, Pauchard *et al.* 2004). However, the level of invasion of a region is not only related to climate but also to landscape and anthropic conditions of the invaded region (Pino *et al.* 2005, Gassó *et al.* 2008), so these factors should be included when calculating potential distribution ranges.

Residence time (i.e. time since first introduction) has been postulated to be one of the main factors influencing invasion success (Hamilton *et al.* 2005, Pyšek & Jarosík 2005, Rejmánek *et al.* 2005b, Gassó *et al.* 2008), as it represents a dimension of propagule pressure: the longer the species is present in the region, the more propagules are spread and the probability of founding new populations increases

(Lockwood *et al.* 2005).

Success of invaders also depends upon their invasiveness; extent to which a species *per se* is able to overcome various biotic and abiotic barriers, establish with self-sustaining populations, proliferate and disperse in a new environment (Richardson & Pyšek 2006). In vascular plants, some reproductive traits are correlated to invasion success (Hamilton *et al.* 2005, Pyšek & Richardson 2007) but it highly depends on the scope and scale of the analysis (Daehler 2003).

All these factors might determine the current distribution range of a species, and they might also influence their potential distribution range (Guisan & Thuiller 2005). Here we calculated, for 78 major plant invaders described in the atlas of invasive plant species in Spain (Sanz-Elorza *et al.* 2004), the potential distribution ranges of the species in Spain using climatic, topographic and land use conditions of the current distribution ranges. Therefore, we go a step further in the concept of invasion success by estimating the proportion of potential distribution range currently occupied. We hypothesize that species that have reached a bigger proportion of their potential ranges are those more anciently introduced.

Furthermore, following the recent concern about temporal dynamics of biological invasions (Crooks 2005, Pyšek & Hulme 2005, Williamson *et al.* 2005, Wilson *et al.* 2007), and therefore, accounting for the invasion process, we calculated the spread rate of each species in function of their current and potential distribution ranges, and residence time in Spain, by using a model proposed by Wilson *et al.* (2007). Finally, we tested which species traits are associated to the spread rate of species. In summary, we address the following questions: (1) What is the occupancy (i.e proportion of potential distribution range currently occupied) of plant invaders in Spain? (2) Is occupancy associated to the residence time or to the spread rate of the species? (3) Is the spread rate explained by species traits?

Methods

Species distribution and selection of predictors

Our study focused on invasive alien plant species: alien species with self-sustainable populations without direct human intervention that produces offspring at considerable distances from the parent plants, and thus have the potential to spread over large areas Pyšek *et al.* (2004).

Distribution data and minimum residence time (i.e. earliest date on which a given species was recorded in Spain) were compiled from the Atlas of invasive plant species in Spain (Sanz-Elorza *et al.* 2004). This Atlas contains spatially explicit presence records for over 100 invasive alien plant species at a resolution of 10x10 km UTM (Universal Transverse Mercator) grid. Due to the potential heterogeneity of sampling effort across the country and the consequent difficulty to distinguish between absence of invasive species and missing data, the analyses was limited to UTM cells with at least 1 invasive species present. Furthermore, from the initial database, we only selected neophytes (i.e. established aliens introduced after 1500) recorded in more than 10 UTMs. We also excluded UTM cells with a land proportion of less than 60%. Overall, our analysis is based on 2401 UTM cells and 78 invasive species (Appendix D.II). For each species we explored the following list of factors that have been evoked in the literature (Pyšek *et al.* 1995, Rejmánek 1995, Goodwin *et al.*1999, Lloret *et al.* 2005) to explain invasiveness (i.e. invasion potential of an alien): seed size (very large (>10mm), large (5-10mm), medium (2-5mm), small (1-2mm), very small (<1mm)), clonality (yes, no), longevity, life-form (*sensu* Raunkiaer), dispersal and pollination syndromes (wind, animal, water), and nitrogen fixation capacity (yes, no).

Estimating potential distribution ranges

Environmental data

According to previous works, we selected an initial set of nineteen environmental predictors (10 landscape, 6 climatic and 3 topographic) of proven association with regional alien species richness (Pyšek et al. 2002, Kühn *et al.* 2003, Pauchard &

Alaback 2004, Pino *et al.* 2005, Stohlgren *et al.* 2005, Gassó *et al.* 2008). These variables were obtained from different data sources (Table 3.1) and aggregated at 10x10 km UTM grid cell scale. All the GIS procedures involving the set up of the environmental variables were performed using MiraMon (Pons 2000), but mapping was done with ArcView (ESRI 1992-2006).

We reduced the dimensionality of the correlated landscape variables from10 to 5 using a principal component analysis and keeping the first five orthogonal axes (cumulated explained variance = 80%). In addition, we selected 3 climatic (minimum temperature in winter, annual temperature range, and summer rainfall), and one topographic variable, distance to the coastline, expected to be strongly related to the distribution of alien plant species at regional scale (Gassó *et al.* 2008). Distance to coastline is expected to measure a complex interaction between mild climate and intense human pressures in the Iberian Peninsula. Coastal areas concentrate the tourism, trading and transport centres and, in turn they accumulate most of the first records of alien species (Casasayas 1990). However, because of the natural topography of Spain (high plateau in the centre), this variable is strongly correlated to annual temperature range. In order to keep distance to coastline into the model despite the confounding information coming from annual temperature range, we adjusted distance to coastline for temperature annual range by fitting univariate non-linear regressions (generalised additive model with 4-degrees of freedom) describing the average relationship between temperature annual range and distance to coastline. We then used the residuals of the univariate regression as a predictor. We followed the same strategy for summer rainfall which was correlated with minimum winter temperature and annual temperature range (for more details on the approach, see Thuiller *et al.* 2006a, Leathwick *et al.* 2007).

Table 3.1 Initial set of environmental predictors (see Appendix G.II for cartographic information). Landscape variables were reduced from 10 to 5 using a principal component analysis and keeping the first five orthogonal axes (cumulated explained variance = 80%). One topographic and 3 climatic variables were also selected to be used in the potential distribution models. However, for distance to the coastline we used the residuals from regression with annual temperature range, and for summer rainfall, we used the residuals from multiple regression with annual temperature range and minimum winter temperature.

Variables	Data source	Transformation and use in the potential distribution model
Landscape		
Percentage of built-up areas	CORINE Land Cover Map of Spain (http://www.fomento.es)	PCA
Percentage of agricultural areas		PCA
Percentage of forests		PCA
Percentage of scrub and herbaceous associations		PCA
Percentage of open spaces		PCA
Percentage of wetlands		PCA
Percentage of water bodies		PCA
Land cover diversity (Shannon Index)		PCA
Roads length (m)	Official server of the Spanish Ministry (http://www.cnig.es)	PCA
Railway length (m)		PCA
Topography		
Mean altitude (m)	Digital Elevations Model (DEM) (http://www.opengis.uab.es)	Not used
Altitude range (maximum-minimum; m)		Not used
Mean distance to the coastline (m)		Residuals
Climate		
Mean annual temperature (ºC)	Digital Climatic Atlas of Spain (http://opengis.uab.es/wms/iberia/index.htm)	Not used
Temperature range (max July - min January; ºC)		Used
Minimum winter temperature (ºC)		Used
Annual rainfall (mm)		Not used
Summer rainfall (mm)		Residuals
Annual solar radiation (KJ/m^2 ·dia ·µm)		Not used

Modelling strategy

Because the native distribution was not known for most of the selected species, we estimated the potential range of each species using their current distribution in Spain (see Wilson *et al.* 2007 for more details). However, this does not assume that species are in "equilibrium" with the environment, but that they have had sufficient time to sample a wide variety of habitats and climates in their introduced range. If this assumption was false, then there may be a relationship between residence time and potential range size (which did not exist, see Results).

The potential distribution range of each species was modelled in function of the nine selected variables. All the modelling process was performed using the

BIOMOD application (Thuiller 2003) implemented under the R software. We calibrated 4 models usually described as the most powerful approaches available (Elith *et al.* 2006, Prasad *et al.* 2006): generalised linear models (GLM) using a stepwise regression with AIC criteria, generalised additive models (GAM) with four degree of smoothing using a stepwise regression with AIC criteria, Random Forest (RF) with 2000 trees, Generalised Boosting Models (GBM) with 3000 trees and an interaction depth of 2. Models were calibrated using a 70% of the initial data sets and evaluated on the remaining 30% using the Relative Operating Characteristic (ROC) curve procedure.

To avoid the usual trouble of selecting one particular model and as recently recommended by Araujo & New (2007) and Marmion *et al.* (2008), we performed a weighed averaging procedure across our four models. For each species the four models were ranked according to the area under the ROC curve (AUC) values, and only the best three predictions (i.e. from the best three models) were conserved and were awarded 3, 2 or 1 point(s) respectively and then standardized to produce a vector of weights whose elements sum to unity. Final projections consist in weighted average of these three simulations (Hartley *et al.* 2006). Then, for each species, we transformed the averaged predictions into presence–absence using a threshold maximizing the percentage of presence and absence correctly predicted (Pearce & Ferrier 2000). For these averaged predictions, the accuracy of the simulations was assessed using the area under the ROC curve (AUC). We used the following conservative rough guide for the AUC: AUC<0.8, null model; 0.8<AUC<0.9, good model and AUC>0.9, very good model.

Calculating occupancy and spread rate

The proportion of potential distribution range currently occupied (i.e. occupancy, hereafter) by each species was expressed as a binary variable with the first column containing the number of UTM cells currently occupied and the second column the number of potentially suitable UTM cells not yet occupied.

The spread rate (*r;* UTM/year) was calculated for each species according to the logistic model proposed by Wilson *et al.* (2007) as follows:

$$r = \frac{1}{t} \cdot \ln\left[\frac{N_t \cdot (K - N_0)}{N_0 \cdot (K - N_t)}\right]$$

where N_t is the number of UTMs where the plant species was found in 2004 (i.e. current distribution range); N_0, the number of UTMs in Spain to which the plant was introduced, assumed to be 1; t was the number of years since the earliest record of the plant in Spain (i.e. minimum residence time); and K is the number of suitable UTMs for the species (i.e. potential distribution range).

Statistical analyses

We developed two statistical analyses: one to express occupancy as a function of minimum residence time and the other to express spread rate as a function of species traits. Minimum residence time and spread rate were log transformed to meet the assumptions of parametric analysis.

Because species are linked by phylogeny (Harvey & Pagel 1991), using species as independent data points may inflate the degrees of freedom (Brändle *et al.* 2003) and increase the Type-I error. We used Generalized Linear Mixed Models (GLMM) to deal with the phylogenetic effects by allowing the incorporation of taxonomic categories as nested random factors (Family/Genus). Several sophisticated procedures are available to implement the complete phylogenetic structure in the model, but, in our case, there was not any robust phylogenetic hypothesis available for the studied species. Moreover, the approach we used helped to mitigate the problem that invasive species are a non-random subset of all species introduced (see Blackburn & Duncan 2001a).

All analyses were conducted in the open source R software version 2.5.1 (R Development Core Team, 2005). We modelled occupancy with a binomial distribution of errors using the glmmPQL procedure of the MASS library on the R statistical package (Venables & Ripley 2002, R Development Core Team 2006).

Spread rate was modelled using the *lme* procedure of the nlme library on R statistical package (Pinheiro & Bates 2000). Stepwise regression-backward, forward or both, is an obvious method for examining the relative importance of each species trait to explain spread rate. However, using usual stepwise regression to find the optimal combination of explanatory variables to model a response is often considered to be a high-variance operation because small perturbations of the response data can sometimes lead to vastly different subsets of the variables (Burhman & Anderson 2002). To avoid this problem, and to measure the actual power of each variable over spread rate, we used multimodal inference based on all-subsets selection of the GLMM using the AIC measure.

The weight of evidence (w_{pi}) of each predictor can be simply estimated as the sum of the model AICs weights over all models in which the selected predictor appeared (Burham & Anderson 2002, Brooks *et al.* 2004, Link *et al.* 2006, Thuiller *et al.* 2007b). The predictor with the highest w_{pi} (the closest to 1) gets the highest weight of evidence to explain the response variable (the highest relative importance). This approach based on a set of multiple models is far more robust than inferring variable importance based on a single stepwise selected model (Burham & Anderson 2002, Link *et al.* 2006). Moreover, to be sure that a correlation between a predictor and the response variable are not due to random or unexpected noises, we performed a permutation process. Randomization is here an important step to make sure the weight of evidence in favour of a set of models and subsequent variables is robust and ecologically meaningful and can be further used to make inferences. We randomly permutated each predictor separately within the data set, re-calculating w_{pi}, and repeated this procedure 100 times for each predictor. The absolute weight of evidence (Dwp) was then calculated by subtracting the median value of the 100 randomized wpi from the original wpi. Only predictors with Dwp higher than zero have a certain explanatory power on spread rate (see Thuiller *et al.* 2007b for more details).

Results

Potential distribution range and occupancy

Species were assumed to have had sufficient time to sample a wide variety of habitats and climates in their introduced range because there was not a relationship between minimum residence time and potential distribution range ($R^2=0.05$, $p>0.05$).

Therefore, potential distribution models were based on current distribution of species, and we found, as expected, a positive relationship between CDR (i.e. current distribution ranges) and PDR (i.e. potential distribution ranges) (PDR = 309.3 + 0.89CDR, R^2=0.53, p<0.001). However, current distribution ranges only explained half of the variance of the potential distribution ranges. There is a set of species, especially those that currently occupy less than 200 UTM that, according to our models, would have the potential to spread through larger areas than the expected by the linear relationship (Fig 3.1).

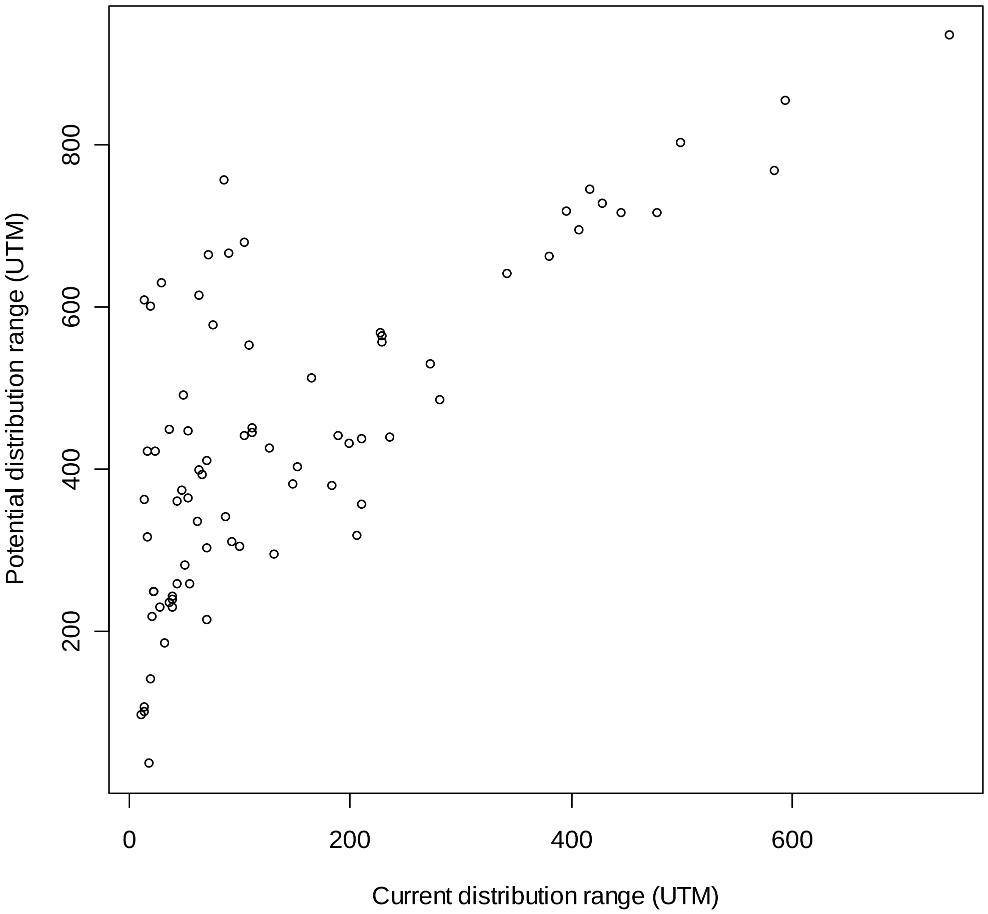

Figure 3.1

Relationship between current (CDR) and potential (PDR) distribution ranges of the invasive species in Spain. A linear regression between both variables shows that current distribution rage only explained half of the variance of potential distribution range (PDR = 309.3 + 0.89CDR, R^2=0.53, p<0.001).

Most of the species have not yet occupied half of their potential geographic ranges (Fig 3.2) (see Appendices D.II and G.I for more details). The two species with the highest occupancy were the deciduous tree *Robinia pseudoacacia* (72.79%) and the grass *Sorghum halepense* (72.09%), and the two species with the lowest occupancy were the shrub *Senecio inaequidens* (2.83%) and the herb *Tradescantia flumminensis* (2.30%) (Fig 3.3).

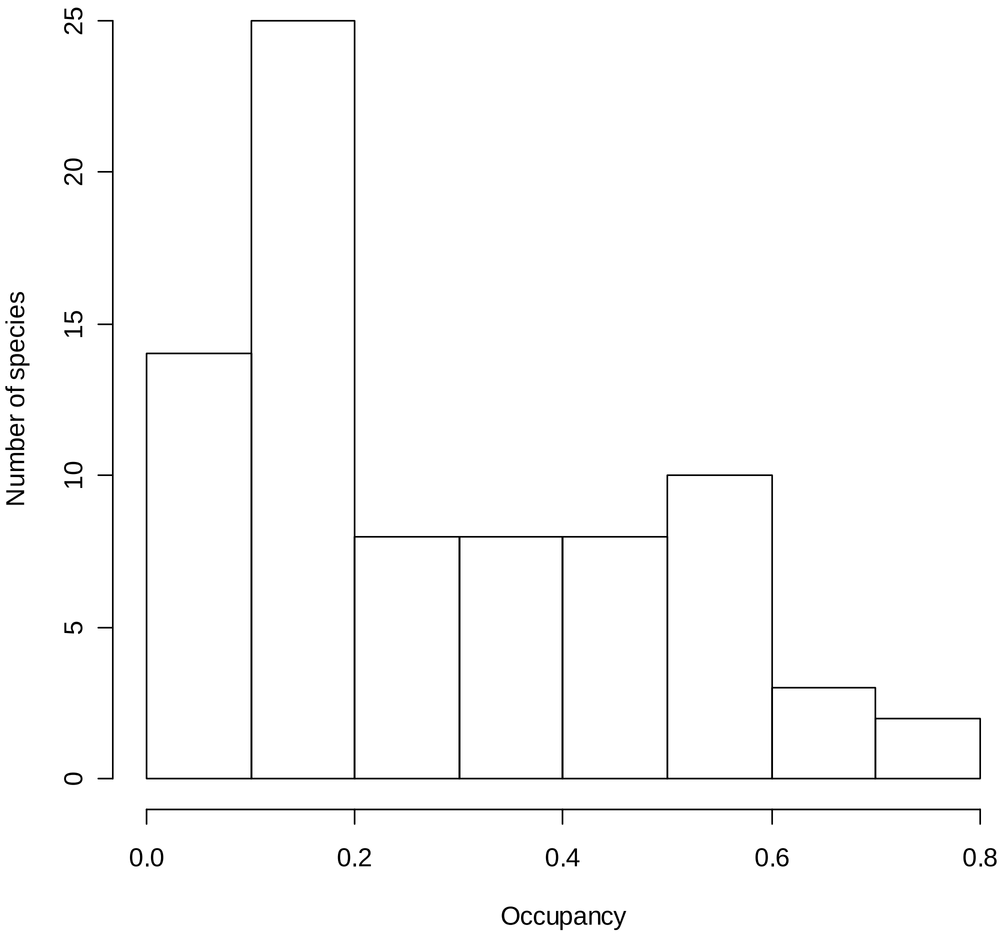

Figure 3.2
Frequency distribution of Occupancy (i.e. proportion of the potential distribution range currently occupied) by 78 invasive plant species in Spain.

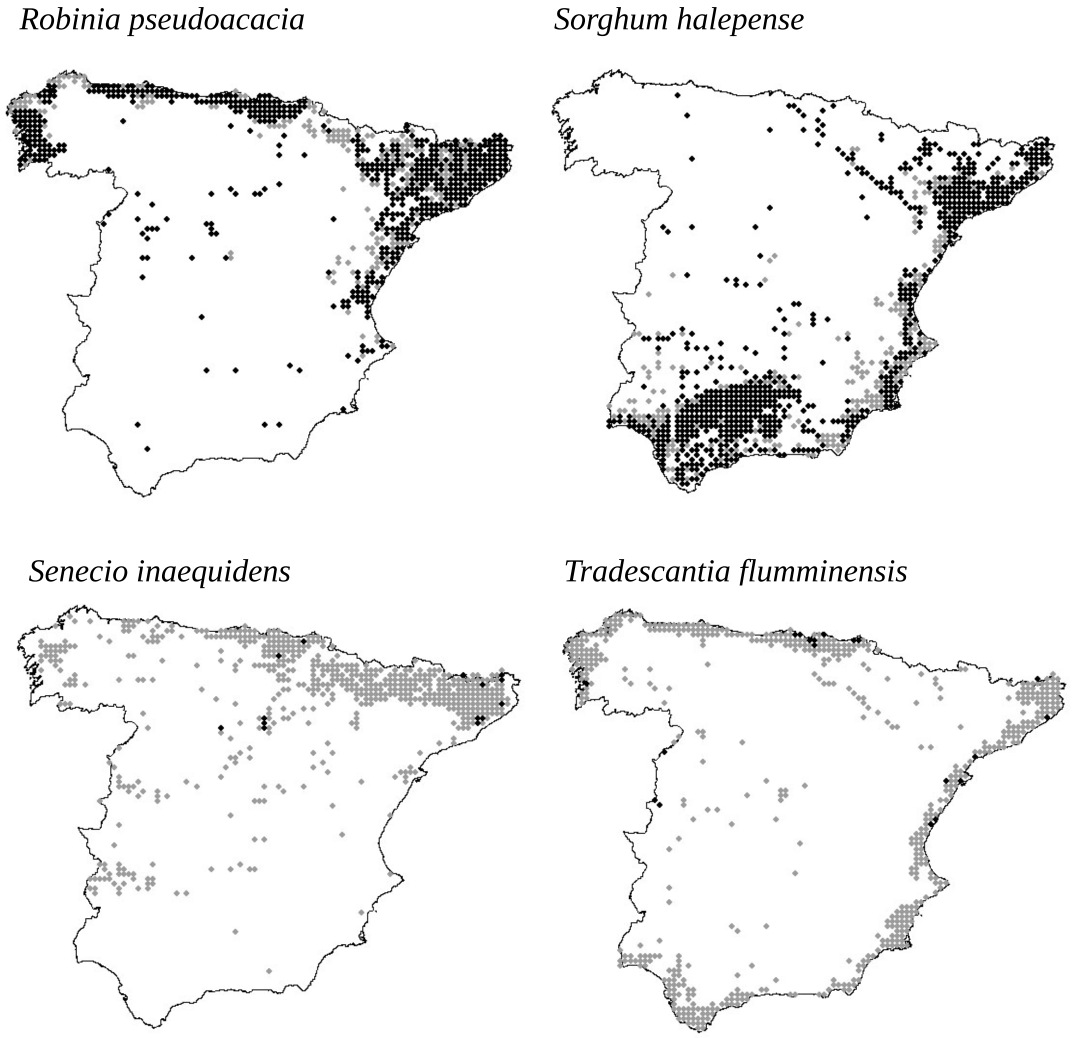

Figure 3.3
Maps of current distribution range (black) over potential distribution range (grey) of four invasive plant species in Spain. The two species on top are the ones with the highest occupancy (i.e. proportion of the potential distribution range currently occupied) and the ones at the bottom the ones with the lowest.

Relationship between occupancy and minimum residence time

Having accounted for the potential phylogenetic effects, the glmmPQL showed that minimum residence time explained a significant portion of occupancy variance (t=3.9, p<0.0001). Species introduced earlier have, on average, occupied a higher proportion of their potential distribution range (Fig 3.4). It is interesting to note that the relationship is however non linear but triangular, with some species introduced long time ago having still a very restricted distribution in respect to their potential modelled suitable habitat.

Relationship between occupancy and spread rate

Interestingly, species with the highest spread rate are not necessary those which have already filled out their potential range (t=-0.67, p=0.50, Fig 3.4). The species with the fastest spread rates are: *Amaranthus powellii* (*r*=0.221 UTM/y) and *Austrocylindropuntia subulata* (*r* = 0.205 UTM/y), and the slowest are *Sophora japonica* (*r* = 0.008 UTM/y) and *Tropaeolum majus* (*r* = 0.007 UTM/y).

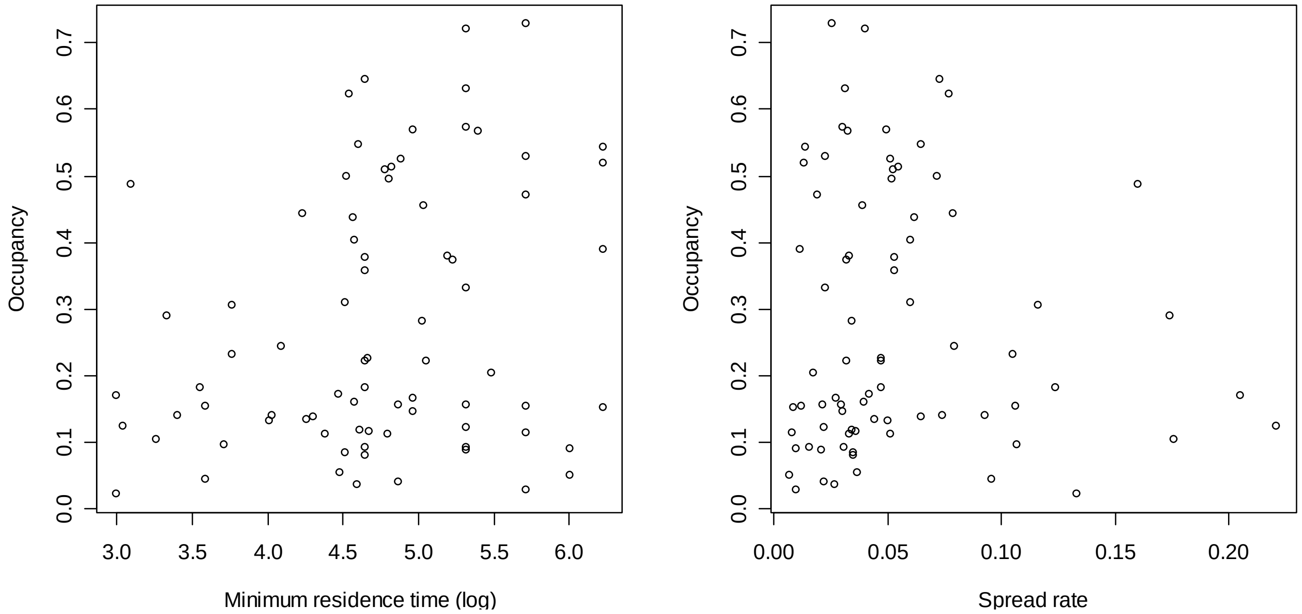

Figure 3.4
Relationship between occupancy (i.e. proportion of the potential distribution range currently occupied) and, from left to right, minimum residence time (log(years)) and spread rate (*r* ; UTM/year) of 78 invader plant species in Spain. Having accounted for the potential phylogenetic effects, the glmmPQL showed that minimum residence time explained a significant portion of the variance (t=3.9, p<0.0001) of occupancy, but it did not exist a significant relationship between occupancy and spread rate (t=-0.67, p=0.50).

Relationship between spread rate and biological traits

Amongst the seven biological traits expected to be related with plant spread rate, only two of them were of importance. The inference-based model, after permutation, showed that dispersal syndrome was by far the predictor with the highest absolute weight of evidence (weight = 0.71) followed by clonality (weight = 0.14) (Fig 3.5). Species dispersed by wind (Fig 3.6) and with clonal growth spread faster.

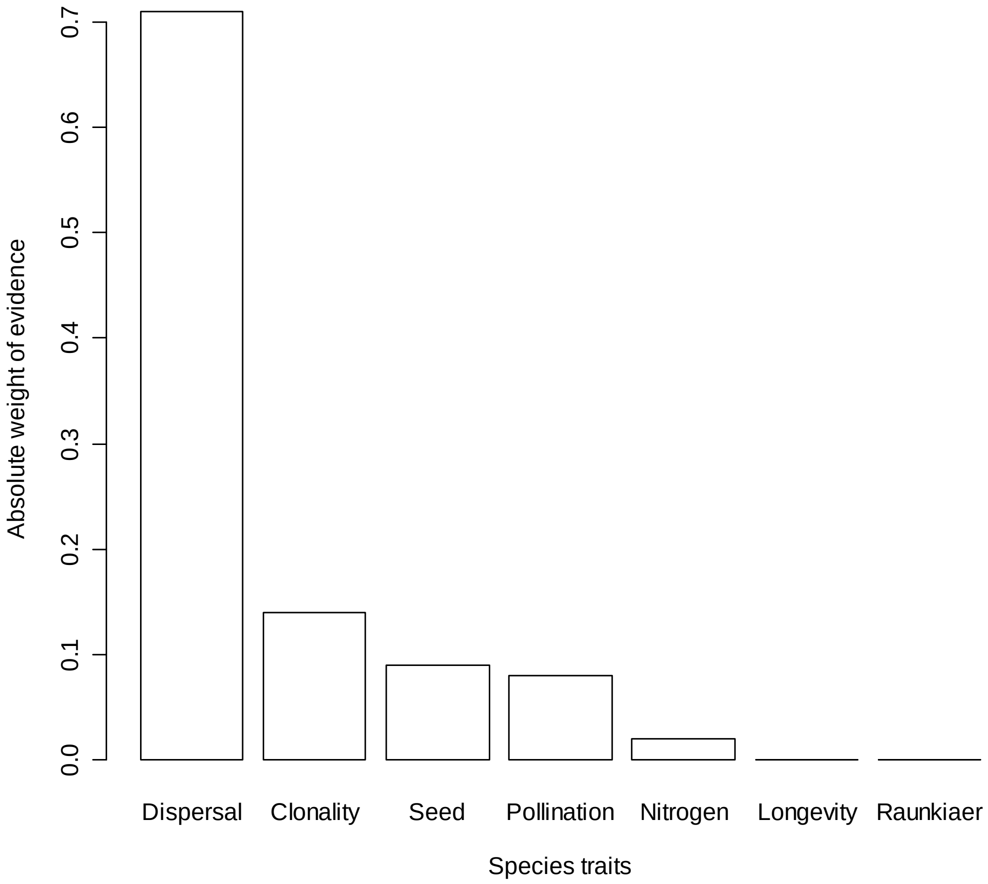

Figure 3.5
Absolute weights of evidence of 7 species traits predicting the spread rate (*r;* UTM/year) of 78 invasive plant species in Spain. This measure gives an unbiased estimation of the weight of evidence after accounting for random artefacts.

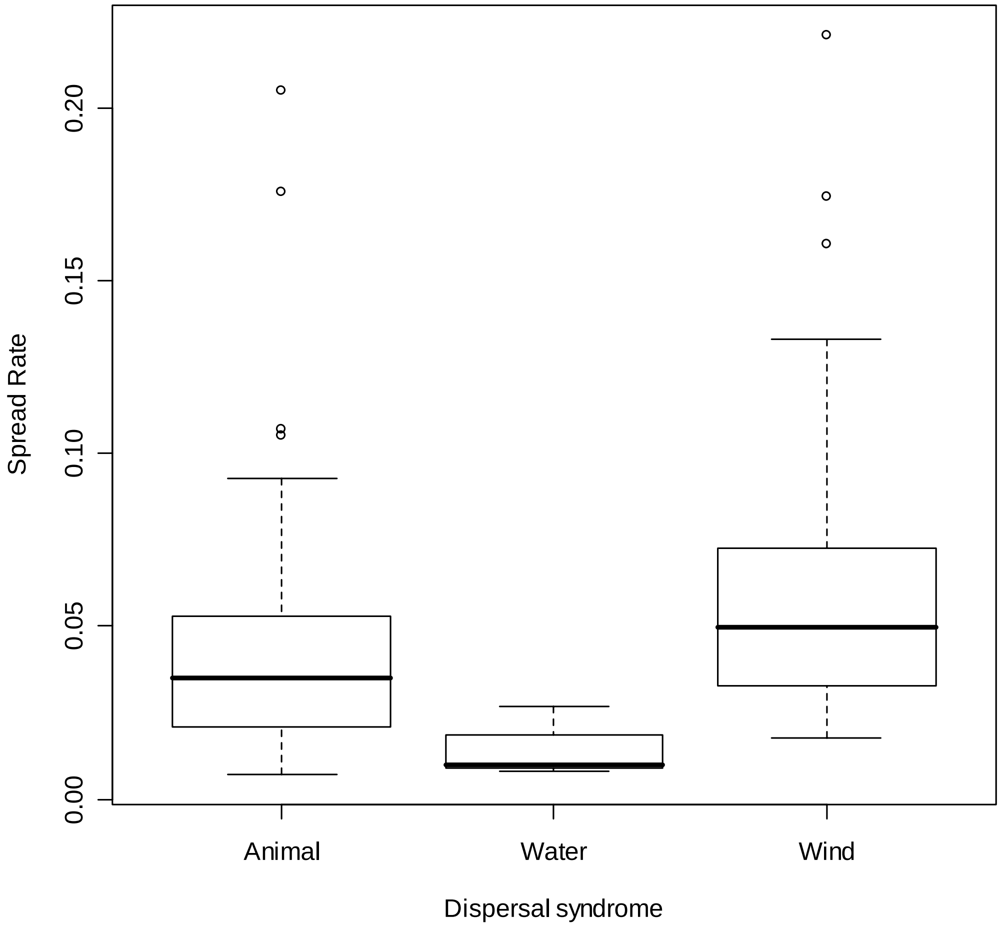

Figure 3.6
Spread rate (*r* ; UTM/year) of invasive plant species in Spain according to their dispersal syndrome. Box width indicates the interquartile range, the dark line inside the box indicates where is found the median, whiskers arrive until the largest and smallest non-outlier observations, and the small circles represent the observations considered as outliers.

Discussion

In general, invasive plants in Spain seem to be at an early stage of invasion, because most of the species have not yet reached half of their potential distribution ranges. There are large differences between species which might be explained by differences in their niche breadth (Thuiller *et al.* 2005) and the availability of suitable places. The plants with the widest potential distribution ranges are *Sorghum halepense,* considered as one of the top weeds of the world (Holm 1977) and *Amaranthus retroflexus*, also a worldwide invader, both of them invading many different habitat-types and growing in disturbed coastal places (Sanz-Elorza *et al.* 2004). These two species were introduced more than 100 years ago and exhibit wide current distribution ranges, being spread already in more than half of their potential distribution range.

Results confirmed our hypothesis that occupancy was dependent on minimum residence time, reinforcing other studies which have used other estimations of invasion success (Hamilton *et al.* 2005, Pyšek & Jarosík 2005, Rejmánek *et al.* 2005b). In general, the more ancient an invasive species is in a region, the more it fills out its potential range because it has more opportunities to be introduced several times at various locations and to spread naturally by dispersal. In a previous work with the same data set (Gassó *et al.* 2008), a relationship between current distribution range and minimum residence time was found. However, there was a set of species introduced long time ago that were found in fewer places than expected. Thuiller *et al.* (2006) also found that residence time did not explain the distribution patterns of invaders in South Africa after a century of residence. There are several plausible explanations for these exceptions. It could be that those species had already reached the maximum of their potential ranges so they can not spread more. Nevertheless, as we showed, there is a triangular relationship between relative occupancy and minimum residence time: there are some species introduced long time ago (more than 100 years) that have not yet occupied their entire potential suitable habitat. For example; *Sophora japonica* was introduced 304 years ago, but it currently occupies only 11.1% of its potential distribution range demonstrating a very low spread rate. Slow spread could be related to the history of use of species by humans. *Sophora japonica* was first introduced in the country in the 18th century but it was not used commonly as an ornamental species until the 20th century (Sanz-Elorza *et al.* 2004). We can therefore suspect that in the case of some species formerly introduced and with a slow spread rate, there could be a substantial time lag between the date of first introduction and the actual start of the exponential phase of the invasion due to factors such as differences in the historical propagule pressure (Cousens & Mortimer 1995, Crooks *et al.* 2005). Following this hypothesis, these species could strongly rely on humans to spread over large regions because of inefficient natural dispersal ability, or because of the spatial distribution of suitable habitat (Wilson *et al.* 2007). Moreover, Crooks *et al.* (2005) showed that lag times in invasion dynamics can be masked of and they are difficult to detect and measure. There are several hypotheses to explain lag phases: the genotypic hypothesis (Hobbs & Humphries 1995), the demographic hypothesis (Cousens & Mortimer 1995), and the extrinsic hypothesis (Sakai *et al.* 2001). The lag phase may depend on the scale of observation. Therefore, although population growth rate may occur in a discrete area, at local scale, this may not correspond to the regional spread rate (Pyšek & Hulme 2005).

Furthermore, our results showed no relationship between occupancy and spread rate. Many species would follow the expected pattern of high spread rate versus high occupancy, such as *Achillea filipendulina,* introduced 22 years ago in the country and already occupying half of its potential distribution range, which is indeed very restricted (Appendices D.II and G.I). Alternatively, some particular species with a high occupancy have a very slow spread rate, such as *Robinia pseudoacacia,* which has only reached the 73% of its potential range in about two centuries; it was six times slower than *A. filipendulina*. This supports that spread rate might reflect better than occupancy the species invasiveness because occupancy does not account for residence time.

We found that dispersal syndrome and clonality influence species' spread rate. Dispersal syndrome has already been found an important determinant of invasiveness (Vermeij 1996, Richardson *et al.* 2000, Kolar & Lodge 2001, Lloret *et al.* 2005). Wind dispersed species (i.e. anemochory) might spread faster at the regional scale than animal or water dispersed species (Willson 1992, Lonsdale 1999). Clonality was also found to increase the spread rate as found by Pyšek (1997). Given that the weight of evidence of clonality was lower than for dispersal syndrome, we suspect that clonality might have an effect at the local scale, favouring populations to grow and spread at early invasion stages while wind dispersal contributes to create new foci of invasion.

Besides dispersal syndrome and clonality, none of the other predictors classically considered to be associated with invasion success were significant. Faster spreading plant invaders do not seem to be characterized by their seed size, longevity, pollination mechanism, life-form, or nitrogen fixing capacity. Although we can not rule out that we have missed traits that really matter, the general failure to identify plant features of successful or faster invaders suggest that the outcome of invasions is highly idiosyncratic (Richardson *et al.* 2000, Thuiller *et al.* 2006b), although it can also indicate that the ecological attributes of successful alien invaders are not general but habitat-dependent (Thompson *et al.* 1995, Lloret *et al.* 2005). General features of fast invaders, if exist, should not be many, as adaptations that are useful to spread in some environments are not necessarily appropriate for other environments. Another possible explanation would be that we mismatched the scales of the variables as we measured the spread rate at the regional scale while features that explain invasiveness would affect basically at local spreading (Lloret *et al.* 2005). Moreover, until now in the literature, while it is shown that species traits may be important in determining species establishment and naturalization rates (Daehler 2003), there is not evidence of a close relationship between the spread rate and traits of invasive species (Pyšek & Hulme 2005). Several studies have also indicated the importance of human activities, such as economy and tourism, and landscape features for the introduction, naturalization and spread of alien species (Vilà & Pujadas 2001, Pino *et al.* 2005, Williamson *et al.* 2005, Thuiller *et al.* 2006b, Gassó *et al.* 2008).

General conclusions and conservation implications

By integrating potential distribution range calculations with new and robust statistical techniques, we have been able to identify a few features that underpin the level of invasion and the speed to which plant species invade a region. Minimum residence time explains species occupancy, and dispersal syndrome and clonality explain their spread rate. Our results suggest that to understand invasion dynamics, research efforts should take into account historical event factors such as minimum residence time and factors influencing propagule pressure components such as dispersal mechanisms (both natural and human-induced).

From a management point of view, we should pay more attention to those plant species with a large potential distribution range but a low occupancy, because it might be only a matter of time that they reach their maximum area of distribution. So, one trivial but important conclusion is that the earlier an invasive plant is discovered, the better is the chance of its eradication. Our findings also highlight that management efforts should focus on avoiding introduction and controlling the populations already installed of clonal and wind disperser species taking into account that both factors might help the species to spread faster.

Finally, our modelling approach offers a good tool for invasion risk assessment as it can contribute estimating potential distribution ranges and rates of spread in future climatic and land-use scenarios. We believe that more research should be done on the direction of trying to link environmental global change with spreading of invasive species (Vilà *et al.* 2006).

Chapter 3

Regional context affects native and alien plant species richness across different habitat types[3]

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[3] This chapter has been submitted to *Biological Invasions* in June 2008.
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Resum

El context regional afecta la riquesa d'espècies de plantes natives i al·lòctones en diferents tipus d'hàbitats

Els hàbitats estan emmarcats en paisatges complexos i en una matriu ambiental que determina certes diferències en el seu grau d'invasió. Per tant, és necessari fer anàlisis precises de vulnerabilitat dels hàbitats que tinguin en compte el context paisatgístic, ambiental i humà. En aquest estudi, explorem l'efecte a gran escala del context pel que fa a la riquesa d'espècies de plantes natives i al·lòctones de parcel·les de vegetació classificades en diferents tipus d'hàbitat. En particular, ens preguntem: (1) la riquesa d'espècies natives i la d'al·lòctones en els hàbitats estan associades als mateixos factors de context? (2) com de consistent és la influència d'aquests factors en els diversos hàbitats?, i (3) com la composició d'espècies al·lòctones en els hàbitats modula la influència que tenen els factors de context sobre la riquesa d'espècies al·lòctones? Els resultats han demostrat que no hi ha una interacció consistent entre els tipus d'hàbitat, les variables de context i l'ecologia de les espècies, cosa que reforça la idea que la identitat de l'hàbitat és més important com a predictor de les invasions que altres variables ambientals o geogràfiques associades. De tota manera, hem descobert alguns patrons concrets, com per exemple la resposta diferent al context antropogènic en funció de l'ecologia de les espècies introduïdes, una dependència climàtica més gran en espècies natives que en al·lòctones, i una associació entre la pèrdua de coberta de vegetació llenyosa amb l'augment d'espècies al·lòctones i el descens de natives.

Abstract

Habitats are embedded in complex landscapes and in an environmental matrix that determine differences in their level of invasion. Precise analyses of habitat vulnerability to invasion taking into account landscape, environment and human context are needed. In the present study, we explore the effect on native and alien richness of large scale context around a set of vegetation plots classified in habitat types. We address the following questions: (1) Are native and alien species richness within habitats associated to the same regional context factors? (2) How consistent is the influence of these factors across habitats? and (3) How does alien species composition modulate the influence of regional context factors on alien species richness? Results showed complex and non consistent interaction between habitat types, context variables and species ecology, reinforcing that habitat identity is more important as a predictor of invasion than other associated environmental and geographic variables. We found, however, some patterns such as the different response to an anthropogenic context according to the ecology of the alien species introduced, a major dependence on climate by native species, and an association between woody land cover loss with an alien species increase and a native species decrease.

Introduction

Biological invasion is a large scale phenomenon caused by direct and indirect species introductions by humans (Kowarik 2005). The extent of invasion and its impact differs spatially depending on the region and habitat type (Sax 2001, Levine *et al.* 2003, Rejmánek *et al.* 2005b). For example, islands contain more invaders than adjacent mainland areas (Lonsdale 1999). In the case of plants, low altitude regions are found to contain more alien species than high altitude areas (Arévalo *et al.* 2005), as low altitude habitats harbour a greater extent of anthropogenic environments with a higher level of invasion compared to natural habitats (Vilà *et al.* 2007, Chytrý *et al.* 2008b).

Spatially explicit analyses of the level of invasion and its environmental correlates are of primary importance in order to diagnose the most invaded areas and to set up the basis for invasion risk assessment regarding future climate and land use changes (Ibáñez *et al.* 2006, Thuiller *et al.* 2006b). Extensive analysis of the level of invasion can be conducted at the coarse (regional) and fine (local-habitat) grained scale. At the coarse scale, regional analyses have focused on correlations between alien species richness and environmental variables (Deutschewitz *et al.* 2003, Pino *et al.* 2005, Stohlgren *et al.* 2005, Gassó *et al.* in press) for large geographic (e.g. UTM cells) or administrative areas (i.e. counties, protected areas). These analyses have identified climate mildness and surrogates of propagule pressure (i.e. intensity and frequency of introductions) such as population density and urbanization as key determinants of invasion (Deutschewitz *et al.* 2003, Pino *et al.* 2005, Kühn and Klotz 2006, Gassó *et al.* in press). At the fine grained scale, most studies are based on extensive analysis of large datasets of vegetation plots. These local scale analyses have identified anthropogenic habitat types as being the most invaded (Stholgren *et al.* 2005, Chytrý *et al.* 2006, Maskell *et al.* 2006, Vilà *et al.* 2007, Chytrý *et al.* 2008a).

Moreover, many surveys have found that habitats with a high number of alien plant species also harbour a high number of native species (Brown & Peet 2003, Stholgren *et al.* 2005). This is in accordance with the theory that invasion of alien plants and colonization of native plants might be driven by the same factors such as disturbance and resource availability (Levine & D'Antonio 1999). However, other studies have failed to detect any significant association between native and alien species for a great number of habitats (Vilà *et al.* 2007). Patterns of native and alien plant species across environmental gradients might not always be consistent because many alien species are recent colonizers (i.e. being established in the last hundred years) and thus their patterns of distribution and abundance are not yet influenced by historical factors (e.g.. glaciation events) and speciation rates in the recipient region (Sax 2001, Kühn *et al.* 2003). Furthermore, both the introduction and spread of alien species are intrinsically human mediated processes and therefore their occurrence and abundance might be more influenced by anthropogenic factors than native species are.

Finally, local scale analyses of plant invasions have found large spatial invasion differences within particular habitat types depending on their invasion history (Roy *et al.* 1999, Domènech *et al.* 2005, Guo *et al.* 2006). Clearly, habitats are embedded in complex landscapes and in an environmental matrix that determine differences in their level of invasion (McIntyre & Lavorel 1994). Therefore, precise analyses of habitat vulnerability to invasion taking into account the landscape, environment and the human context are needed.

Chytrý *et al.* (2008b) addressed this demand by analysing the effect of the immediate context on the degree of habitat invasion in the Czech Republic. In their work, a set of proxies for urban pressure obtained from habitat surroundings (i.e. a radius of 500 m around vegetation plots) showed a low but significant association with the number of alien plants per habitat. In the present study, we explore the effect of large scale context (areas of 10x10 km) around a set of more than 15,000 vegetation plots classified in EUNIS habitat types. This dataset is recorded in Catalonia, a region of 32,000 km^2 located in the NE of Spain with high plant species richness resulting from a heterogeneous climate, topography and geology (Bolòs *et al.* 2005). We address the following questions: (1) Are native and alien species richness within habitats associated to the same regional context factors? (2) How consistent is the influence of these factors across habitats? and (3) How does alien species composition modulate the influence of regional context factors on alien species richness?

Methods

Study region

Catalonia (32,000 km^2) is located in the northeast of Spain bounded in the north by the Pyrenees and on the east by the Mediterranean Sea . We chose this region for our analysis because of its contrasting topography, climate, dominant vegetation and land-uses. Elevation ranges from 0 to 3350 m a. s. l., and due to its geographical situation the area receives Mediterranean, Atlantic and even Saharan influences (Ninyerola *et al.* 2000). Catalonia is located in the boundary between the Eurosiberian and Mediterranean phytographic regions, in which the Pyrenees impose a sharp topographic-climatic gradient where Mediterranean and Eurosiberian-type biomes gradually change northwards, to sub-alpine and Alpine types. Rainfall decreases and average temperature increases southwards. A continental gradient can also be observed from the coast, with moist temperate climates, to inland, with contrasting dry conditions.

The landscape structure of Catalonia reflects the typical secular interaction between man and climate in Western Europe and the Mediterranean region. Forest currently occupies 40% of the Catalonian surface (Burriel *et al.* 2001). In recent decades, abandonment of marginal agricultural areas is leading to a progressive afforestation challenged by an increasing wildfire frequency. The most favourable plains and plateaux for human settlement exhibit a contrasting situation, with progressive crop intensification and urbanisation.

Vegetation plots

The high phytogeographic diversity of Catalonia results in a rich flora, estimated in more than 3,200 species (Bolòs *et al.* 2005). A remarkably long tradition in botany has permitted the accumulation of a great number of floristic records in Catalonia. In order to facilitate the development of surveys from the regional to continental level, the FLORACAT project (Font & Ninot 1995) has been devoted to the gathering, organisation and online exploitation (http://biodiver.bio.ub.es/biocat/homepage.html) of all these floristic data. FLORACAT accounts for about 1,200,000 floristic records and 17,000 phytosociological relevés organised following a UTM 10x10 km grid. We selected those relevés having phytosociological classification, and that were located in UTM cells with a land proportion of more than 60%. Relevés were assigned to a first or second hierarchical level of EUNIS habitat classification, through the phytosociological alliance they belong to (Appendix D.III). The plots differed in size from 1 m^2 to hundreds of m^2 (Table 4.1), following the within-habitats variation of the European standards for phytosociological relevés (Chytrý & Otypková 2003). Further details on the Catalonian data set are given in Vilà *et al.* (2007).

We assumed that the database covers all the studied area in a sufficiently uniform way, as there was a positive linear association (R^2=0.74, $p<0.001$) between the number of plots per EUNIS and the number of UTM cells they belong to (Fig. 4.1), indicating that the number of plots is a good measure of the geographical extent of a particular EUNIS habitat within the studied region. For each plot the number of native and neophyte (i.e. alien species introduced or naturalised after 1500 a.C.) species was recorded.

Table 4.1 Summary of habitat types with indication of the number of plots of each habitat type, number of UTM where they are present, mean (± SE) alien and native species richness and proportion of plots with at least one alien species. Habitat types in bold are those that were successfully modelled.

EUNIS Habitat	Plot size (interquartile range, m2)	No. of plots	No. of UTM	No. of alien species per plot (mean ± SD)	No. of native species per plot (mean ± SD)	Plots with at least 1 alien species (%)
I1 Arable land and market gardens	**30–90**	**362**	**90**	**1.49 ± 0.09**	**19.65 ± 0.49**	**59.95**
E5.6 Anthropogenic forb-rich habitats	**10–30**	**720**	**123**	**0.98 ± 0.06**	**16.65 ± 0.33**	**39.44**
H5.6 Trampled areas	**5–20**	**272**	**76**	**0.75 ± 0.07**	**14.71 ± 0.53**	**40.81**
F9.1 Riverine and lakeshore scrub	25–80	41	25	0.66 ± 0.17	23.78 ± 2.18	36.58
B1 Coastal dune and sand habitats	12–50	76	7	0.48 ± 0.07	10.15 ± 0.55	42.11
F9.3 Southern riparian galleries and thickets	25–80	41	14	0.43 ± 0.14	13.27 ± 0.97	26.83
E6 Inland saline grass and herb-dominated habitats	20–50	276	13	0.24 ± 0.02	7.42 ± 0.20	22.46
E3 Wet grasslands	**7–25**	**369**	**81**	**0.19 ± 0.03**	**16.29 ± 0.41**	**13.55**
B3 Coastal rocks	20–100	44	2	0.18 ± 0.05	12.81 ± 0.93	18.18
E2 Mesic grasslands	**18–50**	**310**	**58**	**0.11 ± 0.02**	**28.15 ± 0.70**	**10.65**
E1 Dry grasslands	**5–35**	**1964**	**169**	**0.09 ± 0.01**	**29.20 ± 0.26**	**8.71**
F3 Temperate and Mediterraneo-montane scrub habitats	**20–50**	**339**	**85**	**0.06 ± 0.01**	**19.67 ± 0.54**	**5.31**
G1 Deciduous woodland	**75–100**	**973**	**119**	**0.05 ± 0.01**	**27.43 ± 0.34**	**3.18**
F5 Maquis, matorral and thermo-Mediterranean brushes	50–100	252	55	0.02 ± 0.01	21.18 ± 0.50	1.58
H3 Inland cliffs, rock pavements and outcrops	4–20	452	82	0.01 ± 0.01	9.39 ± 0.20	1.55
G2 Broadleaved evergreen woodland	40–100	588	107	0.01 ± 0.01	21.75 ± 0.38	1.19

Predictor variables

Based on previous works (Pausas *et al.* 2003, Pino *et al.* 2005) we selected 10 predictors related with land cover composition, anthropogenic context, and climate from those significantly related with both native and alien species richness in Catalonia (Table 4.2). Because of the limitations of spatial resolution imposed by the FLORACAT dataset, all these variables were averaged for the UTM 10x10 km grid. All the GIS procedures involving the set up of environmental variables were performed using MiraMon software (Pons 2000).

Relative frequency (% area) of the main land cover categories (i.e. agricultural forests, scrub and grasslands) were calculated from the CORINE Land Cover Map of Spain (http://www.fomento.es).

Percentage of build-up areas, human population density and distance to the roads were considered as anthropogenic context pressures. We used the official urban settlement map of Catalonia (http://www.gencat.net/mediamb/sig/siga.htm) that includes the most recent (1999) population census to calculate the population density per UTM square. Miramon distance algorithms were used to calculate the mean distance of each 200 m side pixel to the main roads and motorways for each UTM square, applied on a selection of the motorways and major roads from the 1:50,000 topographic map of Catalonia.

Mean annual temperature (ºC) and annual rainfall (mm) were calculated from the climatic models of Catalonia, set up by Ninyerola *et al.* (2000) at a spatial resolution of 180 m using the existing network of meteorological stations and Digital Elevation (DEM) models. Mean annual temperature was strongly correlated with annual rainfall ($r = -0.84$, $p<0.0001$). In order to keep annual rainfall into the analysis despite the confounding information coming from mean annual temperature, we adjusted annual rainfall by fitting univariate non-linear regressions (generalised additive model with 4-degrees of freedom) describing the average relationship between mean annual temperature and annual rainfall. We then used the residuals of the univariate regression as a predictor (for more details see Thuiller *et al.* 2006a and Leathwick *et al.* 2006).

Table 2 Summary of predictor variables used in the analysis. All the variables were aggregated at UTM 10x10km grid cell scale.

UTM context variables	Data source
Land cover	
Percentage of built-up areas Percentage of agricultural areas Percentage of forests Percentage of scrub and grasslands	CORINE Land Cover Map of Spain (http://www.fomento.es)
Proxy of anthropogenic context	
Percentage of build-up areas Human population density (inhabitants/km^2) Distance to roads (m)	CORINE Land Cover Map of Spain Urban settlement map of Catalonia (http://www.gencat.net/mediamb/sig/siga.htm)
Climate	
Mean annual temperature (ºC) Mean annual rainfall (mm)	Digital Climatic Atlas of Spain (http://opengis.uab.es/wms/iberia/index.htm)

Statistical analyses

Native and alien species richness (i.e. species number per plot) were the dependent variables used for our analysis. Species richness might be potentially affected by different plot sizes, so other studies have used proportions (e.g. the number of aliens divided by the number of all species). However, as we performed different models for native and for alien species, it would have been redundant to use this type of correction. Moreover, assuming that plot sizes within habitats did not differ to the same extent as between habitats and followed the European standardization (Chytrý & Otypková 2003, Chytrý *et al.* 2008b), we considered it was appropriate to use species number per plot for within-habitat comparisons.

The association between alien and native species richness with the predictor variables was explored by Generalized Linear Mixed Models (GLMM) for each terrestrial habitat type with at least one alien species per plot using the open source R software version 2.5.1 (R Development Core Team 2005). As each plot belongs to a geographical well-delimited UTM cell, plots could not be used as fully independent data points and therefore UTM cells were considered as random factors in the model.

We modelled native species richness in the lme procedure of the nlme library on the R statistical package (Lindstrom & Bates 1988). Alien species richness was right-skewed and as it could not be normalised with logarithmic or any other transformation it was modelled with a Poisson distribution of errors (Crawley 2002). The models were run in the glmmPQL procedure of the MASS library on the R statistical package (Venables & Ripley 2002, R Development Core Team 2006).

Afterwards, we explored if it was possible to run the models for all terrestrial habitat types with at least 1 alien species in relation to a set of intrinsic habitat variables: mean and dispersion (SE) of both alien and native species richness, and the number of plots and UTM cells per habitat type. We then compared the mean values of these variables for successfully and unsuccessfully modelled habitat types, using a non-parametric test of ranks and the Mann-Whitney U statistics.

The successfully modelled habitats were 8 habitat types that could be grouped as anthropogenic (i.e. I1: arable land and market gardens, E5.6: anthropogenic forb-rich habitats, H5.6: trampled areas), grasslands (i.e. E1: seasonally wet and wet grasslands, E2: mesic grasslands, E3: dry grasslands), and woody (i.e. F3: temperate and Mediterraneo-montane scrub habitats, G1: broadleaved deciduous woodlands) (Table 4.1). The total number of plots for these 8 modelled habitats was 5,309.

We then classified the alien species found in each habitat type according to their weedy (i.e. mainly found in crops) or ruderal (i.e. mainly found in uncultivated disturbed habitats) ecological behaviour (Appendix D.IV). This classification was done through expert knowledge and following regional criteria (Bolós *et al.* 2005). We analysed the results of GLMM modelling in the light of habitat species composition (Appendix D.IV).

Results

Only 50% of habitat types were successfully modelled using GLMM because of dataset restrictions (i.e. not enough number of plots, UTM, or plots with at least 1 alien species). Modelled habitats did not show any significant difference from the rest concerning their mean and SE values for both alien and native species richness (Table 4.3). Conversely, they showed a significantly higher number of plots and they were present in significantly more UTM cells than those non modelled habitats (Fig 4.1). The three less invaded habitats (i.e. F5, H3, and G2) despite their large sample size and wide distribution across the region, had a very low occurrence of alien species (i.e. proportion of plots with at least one alien species); therefore the resulting models were too unbalanced towards plots without invaders and it was not possible to run them.

Table 4.3 Test of ranges comparing a set of descriptive statistics for unsuccessfully (i.e. "Non modelled" in the table) and successfully (i.e. "Modelled" in the table) modelled habitat types. Non parametric statistics were performed to test the differences between both categories of habitats.

	Non modelled (Rank sum)	Modelled (Rank sum)	Mann-Whitney U	Z	p-level
No. of plots	78.0	153.0	23.0	-2.25	0.024
No. of UTM	71.5	159.5	16.5	-2.71	0.007
Alien species (mean)	109.0	122.0	54.0	-0.07	0.944
Native species (mean)	84.0	147.0	29.0	-1.83	0.067
Alien species (SE)	116.5	114.5	48.5	0.45	0.647
Native species (SE)	125.0	106.0	40.0	1.06	0.291

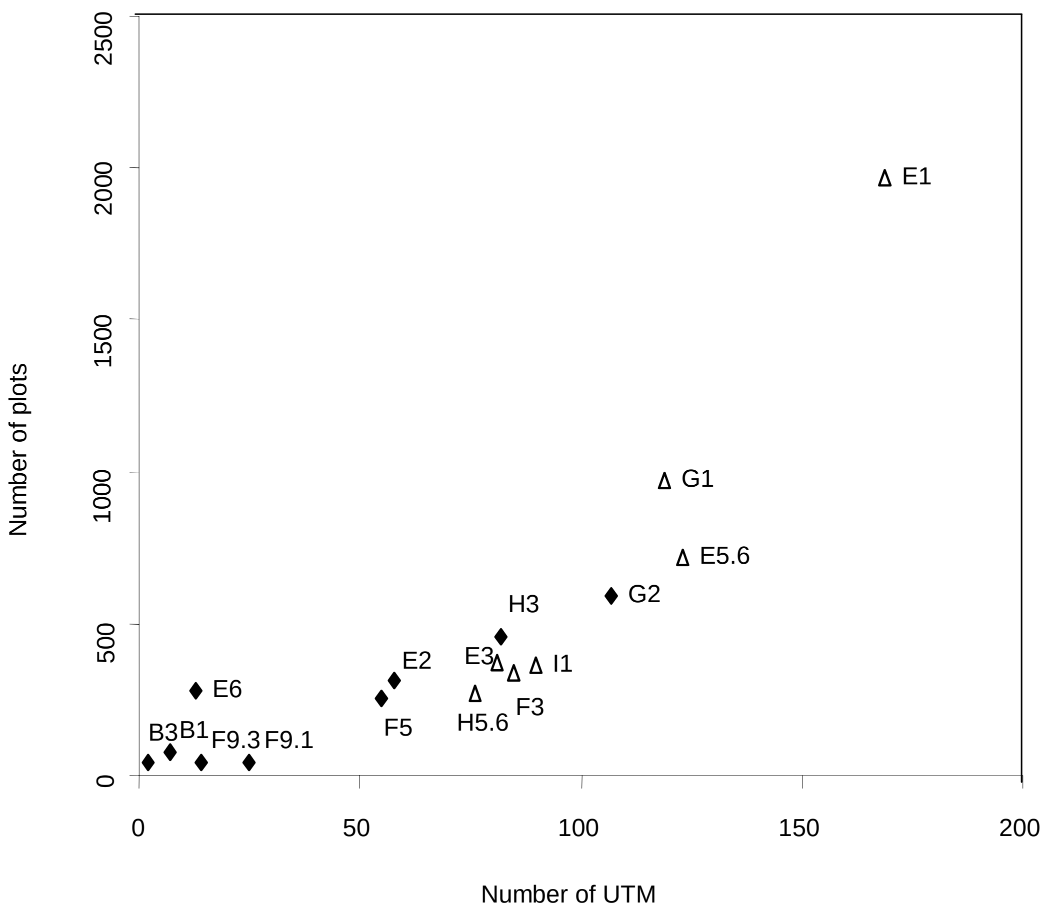

Figure 4.1

Number of plots *versus* number of UTM for each habitat type, separating those successfully (white triangle) and unsuccessfully (black rhombus) modelled. The exponential regression was significant ($y = 59.052e^{0.0216x}$, $R^2=0.83$, $p<0.001$). See table 4.1 for description of habitat types.

Alien species composition

A total of 77 different alien species were found distributed among the 8 successfully modelled habitat types (Appendix D.IV). The three most represented species were *Aster squamatus* (found in 87 plots), *Amaranthus retroflexus* (75 plots) and *Bromus catharticus* (68 plots). Anthropogenic habitats were those with more aliens (36 exclusive species, 65 taking into account the species shared with the other habitat types), followed a long way by grasslands and woody habitats. Only 5 species were common between the three groups of habitats (Fig 4.2). The highest proportion (59 %) of weedy species was in arable land and marked gardens (I1), while the other anthropogenic habitats, as well as grasslands, were mostly invaded by ruderal species. In woody habitats, most of the alien species were neither classified as weedy or as ruderal (Fig 4.3), being in many cases woody species (e.g. *Robinia pseudoacacia*) or species adapted to the shaded conditions of the understorey (e.g. *Lonicera japonica*) (Appendix D.IV).

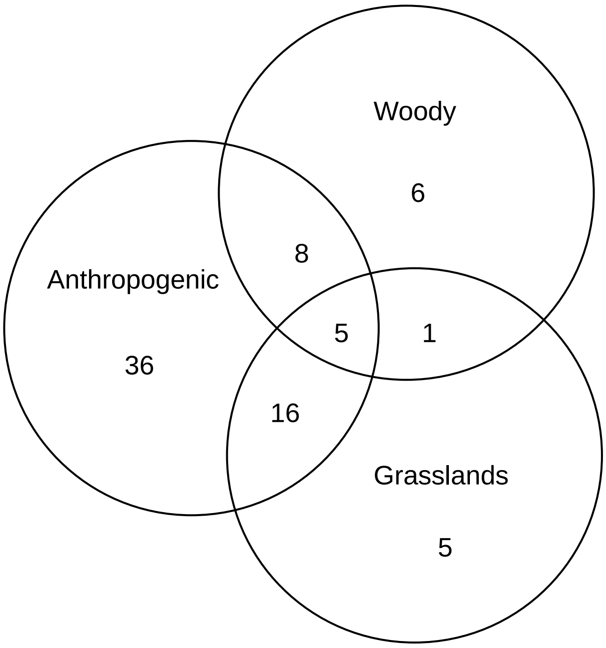

Figure 4.2
Non-proportional Venn diagram showing the number of shared and non-shared alien species among the three groups of habitat types successfully modelled. See table 1 for description of habitat types.

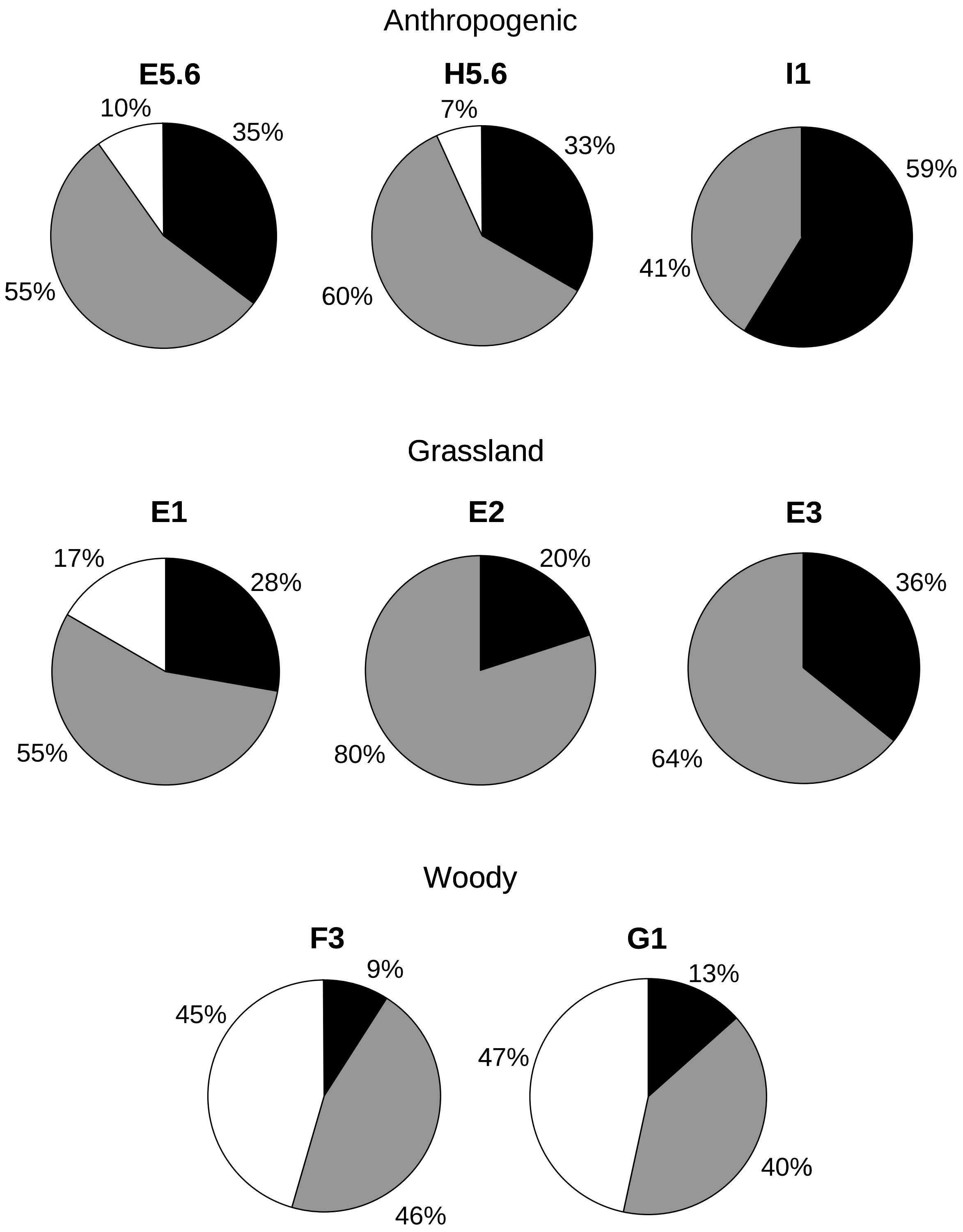

Figure 4.3
Proportion of weedy (i.e. mainly found in crops; black), ruderal (i.e. mainly found in uncultivated disturbed habitats; grey), and other (white) species for each EUNIS habitat type.

Predictors for alien and native species richness

Minimum adequate models on both alien and native species richness showed high variability in the resulting significant variables among habitat types (Table 4.4, Fig 4.2) indicating a complex interaction between habitat types, context variables and species ecology.

Climate variables were more associated to native than to alien species richness. Native species richness in the majority of habitats was positively associated to rainfall, and half of them were negatively associated to mean temperature. In contrast, temperature and rainfall were significant for alien species richness in only one and three habitat types, respectively.

Landscape variables showed a heterogeneous pattern with the native and alien species richness of habitat types. Native species richness was positively associated to forest cover in the majority of habitats, but it was associated to scrubland and cropland cover only in certain anthropogenic habitats. In contrast, alien species richness showed both positive and negative associations with forest, scrubland, and cropland covers depending on habitat type.

Built-up land cover proportion showed a significant association with both native and alien species richness only on anthropogenic habitats (i.e. E5.6 and H5.6). Distance to roads affected both native and alien species in a similar manner. However, the trend was more generalized in alien species richness. The association of alien species richness with distance to roads was negative for the majority of habitat types except for the most and the least weedy ones (i.e. I1, F3, G1), for which the association was positive or non-significant. Population density was only positively related with alien species richness in arable habitats (i.e. I1).

Table 4.4 Summary of the minimum adequate models for each habitat type when modelling (a) alien species richness and (b) native species richness. Only values of t-student statistic are shown for those variables that remained in the minimum adequate model, with significance. (*) when 0.01< p <0.05, (**) when 0.001< p <0.01, and (***) when p<0.001). See table 1 for description of habitat types.

a)

Eunis	% forest	% shrub	% agriculture	% built-up	Distance roads	Population density	Mean annual temperature	Annual rainfall
I1		-5.17***			2.79**	3.58***		
E5.6			5.75***	2.48*	-2.16*			3.28**
H5.6		2.02*		2.77**	-2.85**		5.91***	
E3	-4.31***				-2.24*			2.23*
E2								
E1					-2.79**			
F3	2.01*		3.65***					
G1	-10.56***	-7.35***	-4.70***					

b)

Eunis	% forest	% shrub	% agriculture	% built-up	Distance roads	Population density	Mean annual temperature	Annual rainfall
I1								
E5.6	3.36**	3.49***	2.31*	2.72**	-2.49*		-2.46*	3.51***
H5.6	2.25*	2.64*	3.06**	3.42**	2.01*			2.71**
E3	4.76***							2.05*
E2					-2.65*		-3.14**	4.68***
E1	3.78***	1.92*			-2.44*	3.22**		
F3							-5.73***	5.60***
G1	3.08**						-3.62***	3.11**

Discussion

We found that context variables in the 10x10 km neighbourhood area do have a significant effect on the degree of plant invasion in a habitat. This complements the view of Chytrý *et al.* (2008a) in Central Europe who found significant effects at a considerably lower spatial neighbourhood scale (500 m radius around plots). Context variables also affected native species richness. However, the effect of habitat context on native and alien plant species richness was, in some cases, very different or even opposite.

Typical Mediterranean habitats such as maquis, matorral and thermo-Mediterranean brushes (i.e. F5) and broadleaved evergreen woodland (i.e. G2) are the ones with the lowest level of invasion (Vilà *et al.* 2007). Almost 99% of these plots do not have alien species. These habitats are very common and well represented across the territory (i.e. high number of plots and UTM) indicating that woody habitats are very resistant to invasion (Chytrý *et al.* 2008b)), and reinforcing the hypothesis of the natural resistance of Mediterranean ecosystems to invasions (di Castri 1989, Casasayas 1990).

For the habitats modelled, we found that climate variables were more associated to native than to alien species richness. In most habitats, native species richness increased with annual rainfall and decreased with mean annual temperature. In a previous work on the same region, Pausas at al. (2003) also found a positive relationship between species richness and humid climate but a positive relationship with mean annual temperature. This opposite response to temperature might be due differences in the spatial scale of the studies or in the identity of the species assemblages. While Pausas *et al.* (2003) analysed the distribution patterns of all plant species in the region at the UTM scale, we have distinguished alien from native species pools. In contrast to these effects on native species, temperature and rainfall were only significant for the alien species richness in one and two habitat types, respectively. As in other studies (Pino *et al.* 2005, Chytrý *et al.* 2008a), temperature has been found to have a positive effect over alien species richness.

In most habitats, native species richness was positively related to the proportion of forest land cover and it was associated to scrubland and cropland cover only in anthropogenic habitats. Changes in native species richness associated to climatic and landscape variables can be determined by complex biogeographic patterns, but also by human effects that might cause the spread of generalist, ruderal species and the rarefaction of specialists (McKinney *et al.* 1999, 2006). In contrast, alien species richness was in general negatively associated to forest and shrub cover proportion. This finding reinforces that natural habitat loss favours the introduction and spreading of alien species (Brothers & Spingarn 1992) and highlights the resistance to invasions of woody Mediterranean ecosystems mentioned above.

Distance to roads affected both native and alien species richness, being, in most of the habitats, higher when closer to the roads. However, the trend is more generalized for alien species richness, as has already been shown in other studies (Tyser & Worley 1992, Lippe & Kowarik 2006). On average, there are more aliens in plots close to roads. However, the other surrogates of anthropogenic influence, urban-land cover and human population density, did not always show a significant effect on alien or native species richness. Human population density was only positively related to alien species richness in arable lands (i.e. I1) and built-up cover only in anthropogenic habitats (i.e. E5.6 and H5.6.). These results mirror those of Chytrý *et al.* (2008a) who found that propagule pressure proxy variables (i.e. anthropogenic context) were only of great importance for archaeophytes but of minor relevance for neophytes. In grasslands, native species richness was also positively related to human population density probably as a consequence of the influence of anthropogenic disturbances on grass colonization (Kühn & Klotz 2006).

The association of alien species richness with distance to roads was positive for the most invaded habitats: arable land and marked gardens (I1), and non-significant for woody habitats (F3 and G1). These three habitats are the ones with lowest proportion of ruderal alien plants. Ruderal plants, usually annual or perennial grasses, are typical in disturbed places because they are pioneers in plant succession (Prach *et al.* 2001), and roads and their surrounding habitats are their usual introduction and dispersal vectors (Schmidt 1989, Lippe & Kowarik 2006). However, in arable land and marked gardens (i.e. I1), the most frequent species are weedy, typically annual or perennial species with short life cycles (Boutin & Jobin 1998) and persistent seed banks (Thompson 1992), whose means of introduction might be independent of communication corridors. Weedy species are mostly introduced mixed with seed crop or in contaminated arable machines, and their ecology is highly related to the cyclic disturbances of arable land, which usually experiences a complete removal of above-ground biomass at least once per year (Mohler 2001). On the contrary, woody alien species from woody habitats are usually long-lived species, with more specific dispersal mechanisms such as endozoochory or anthropogenic mechanisms, compared to ruderal species from nearby areas using wind or external animal dispersal.

In conclusion, regional context factors do not have a consistent association between habitats on local alien and native species richness. This lack of consistency is especially striking for anthropogenic context variables, reinforcing that habitat identity is more important as a predictor of invasion than other associated environmental and geographic variables (Chytrý *et al.* 2008a). This complexity of responses among habitat types have, however, some patterns such as the different response to an anthropogenic context according to the ecology of the alien species introduced in each habitat, a major dependence on climate by native species, and the association between woody (i.e. forest and scrubland) land cover loss with alien species increase and native species decrease. More research is needed on the interaction of species requirements and traits with habitat and landscape characteristics. According to our study, these interactions are very diverse and complex but could be the key to a good prediction of habitat invasions.

Chapter 4

Ecological niche and species traits: key drivers of regional plant invader assemblages[4]

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[4] This chapter is planned to be submitted to Ecology
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Resum

Nínxol ecològic i trets de les espècies: agents clau dels grups de plantes invasores

Una aproximació integradora que lligui els trets de les espècies amb les condicions dels ecosistemes envaïts és fonamental per entendre la distribució espacial i l'expansió de les espècies invasores. La distribució espacial de les espècies a escala regional es pot explicar pels seus nínxols ecològics. Així doncs, argumentem que la mida del rang de distribució de les espècies invasores està relacionada amb la seva posició (condicions ecològiques mitjanes d'on es troba) i l'amplitud (rang de variació de les condicions ecològiques on es troba) del nínxol. Hem examinat la mida del rang de distribució de les espècies de plantes invasores a l'Espanya peninsular, els seus trets vitals i les característiques ambientals de les àrees que envaeixen amb la intenció de (1) testar si els grups d'espècies de plantes invasores a escala regional segueixen un patró imbricat, (2) inspeccionar la relació entre la mida del rang de distribució i la posició i l'amplitud de nínxol per testar si el patró imbricat és un producte del solapament del nínxol de les espècies; i finalment (3) examinar si els trets de les espècies estan relacionats amb la posició o l'amplitud de nínxol. Hem comprovat que, a escala regional, les plantes invasores a Espanya estan distribuïdes en subgrups imbricats, la qual cosa pot ser explicada parcialment per un solapament de nínxols, indicant que, en general, les espècies invasores amb rangs restringits no tenen requeriments ambientals particulars, sinó que es troben en àrees envaïdes per espècies generalistes i àmpliament distribuïdes. A més a més, hem detectat que les espècies restringides són menys tolerants a un rang ampli de condicions climàtiques i de tipus de vegetació que les espècies amb distribucions molt àmplies. Es distingeixen espècies amb posicions de nínxol comunes, que estan àmpliament distribuïdes perquè es troben en els llocs amb condicions ambientals molt comuns, i espècies amb una gran amplitud de nínxol, que poden estar àmpliament distribuïdes perquè tenen un potencial intrínsec per envair (capacitat invasora). Finalment, hem trobat que les espècies amb una gran amplitud de nínxol no són fixadores de nitrogen, tenen el cicle de vida curt i creixement clonal, mentre que la posició de nínxol en zones costaneres i antròpiques està relacionada amb el creixement clonal i l'origen de regions geogràfiques càlides.

Abstract

An integrative approach linking species traits and ecosystem conditions that favour biological invasions is fundamental to understand the spatial pattern of invasive species assemblages and invasion spread. The spatial distribution of species at the regional scale can be explained by their ecological niches. Therefore, we argue that the range size of invasive species is related to its niche position (i.e. mean ecological conditions where it occurs) and niche breadth (i.e. width of ecological conditions where it occurs). We examined the range size of invader plant species across mainland Spain, their biological traits and the environmental characteristics of areas that they invade with the purpose to (1) test whether invasive plant species assemblages at the regional scale follow a nested pattern, (2) inspect the relationship between range size and niche position and breadth to test whether the nested pattern is a product of species niche overlap; and finally (3) examine if species traits are related to niche position and niche breadth. We found that at the regional scale, invasive plant species assemblages in Spain are organized in nested subsets, what can be partially explained by a niche overlap, indicating that, in general, invasive species with restricted range do not have particular environmental requirements, but that they occur in areas invaded by generalist and widespread invaders. Moreover, we found that these restricted invaders are less tolerant to broad climatic and vegetation cover conditions than widespread invaders. We also distinguished between species with common niche position, which can be widespread because they occur in widespread environmental conditions, and species with wide niche breadth, which can be widespread because they have an intrinsic potential to invade (i.e. invasiveness). Finally, we found that wide niche breadth was conditioned by nitrogen non-fixation, short-life, and clonality, while a niche position in anthropogenic coastal areas was related to clonality and warm geographical origin.

Introduction

Mitigations of ecological and socio-economic impacts of invasive species require a comprehensive understanding of the factors driving invasions (Brooks *et al.* 2004, Mack *et al.* 2004, Pimentel *et al.* 2001, Soulé 1992). That is, determining their arrival, initial dispersal, establishment of self-sustaining populations and spread. Invasion ecology has mainly focused on the factors that make either a species an invader (Kolar & Lodge 2002, Hamilton *et al.* 2005) or an ecosystem prone to invasion (Pyšek et al. 2002, Pauchard & Alaback 2004, Pino *et al.* 2005, Stohlgren *et al*. 2005). However, these two approaches have been kept separately until recently, when species have began to be considered as a set of intrinsic and extrinsic traits that provide invasiveness (i.e. potential to invade) in certain environmental conditions (Chong 2006, Thuiller *et al.* 2006b). This merging approach is fundamental to understand the composition of invasive species assemblages, as both species properties and community features are known to determine the level of invasion in habitats and regions (Simberloff & Von Holle 1999).

Despite that biological invasions occur at large spatial scales, biogeographic approaches have still not been considered in depth to describe both the patterns of invasion and the mechanism behind them (Hierro *et al.* 2005). One might wonder whether within taxa, certain invaders require specific environmental conditions or if they have requirements common to almost all invaders and therefore they are highly widespread and their distribution ranges overlap. The exploration of native animal communities has found that species assemblages are highly nested: species-poor assemblages are subsets of the species assemblages present at species richest sites (Patterson & Atmar 1986). Put in other words, areas with few species tend to be built up with the most frequent ones, while the least frequent species are restricted to areas with a high number of species. Whether such nested pattern is also found in invader assemblages is unknown.

In the case of invasive plants, species distribution might be the outcome of a combination of factors such as residence time (Rouget & Richardson 2003, Pyšek & Jarosík 2005, Gasso *et al.* in press), propagule pressure (Lockwood *et al.* 2005), and their ecological requirements represented by their ecological niche (Thuiller *et al.*

2005, Vázquez 2006). Hutchinson (1957), suggested that the niche can be seen as a *n*-dimensional space, in which each dimension or axis represents the range of environmental conditions required to sustain viable populations. Fundamental niche is defined in absence of competition, predation, dispersal limitation, and natural or human disturbances (Pulliam 2000), what is very difficult to measure. Yet, we can quantify the realized niche, which describes that part of the fundamental niche actually occupied by the species under these constraints and defines the spatial distribution of species in a given community and study area (Austin & Smith 1989). Here, we quantified the realized niches of plant invaders.

Several studies have related species realized niches to bioclimatic, geological and land use conditions to describe and predict niche positions or to forecast the effects of climatic change on the dynamics and patterns of species distributions (Malanson *et al.* 1992). However, little studies have applied the niche theory to invasion biology (Peterson & Vieglais 2001, Thuiller *et al.* 2005, Vázquez 2006, Ficetola *et al.* 2007) and little effort has been done to establish a link between physiological, morphological and reproductive attributes of species and their niches (but see Niinemets 2001).

Within the framework of the niche theory, we argue that range size (i.e. the size of the distribution area) of an invader is related to its position and breadth in the *n*-dimensional space defining the realized ecological niche (Brown 1995, Gaston & Blackburn 2000, Gregory & Gaston 2000). Niche position is defined here as the mean of the ecological conditions in which a species occurs, while niche breadth is the variation of the ecological conditions in which a species occurs. A broader niche, for instance, might enable the species to become more widespread (Gaston & Blackburn 2000, Brown 1984, 1995, Brown *et al.* 1995, Kolb *et al.* 2000). Success of invader species has also been related to niche breadth (Vázquez 2006) what leads us to hypothesize that a nested pattern of species assemblages could be the result of a niche overlap among species (Gaston & Blackburn 2000), and differences among niches might be, in turn, a consequence of differences among species traits (Wright *et al.* 1998, Vázquez 2006, Thuiller *et al.* 2004).

We examined the range size of invader plant species across mainland Spain, their traits and the environmental characteristics of invaded areas with the purpose to (1) test whether invasive plant species assemblages at the regional scale follow a nested pattern, (2) inspect the relationship between range size and niche position and breadth to test whether the nested pattern is a product of species niche overlap; and finally (3) examine if certain species traits are related to niche position or niche breadth, and therefore, are related to the species potential of becoming widespread (i.e. species having a common niche position or a wide niche tolerance).

Methods

Study region

Spain is located in the SW of Europe and occupies 493,486 km^2 of the Iberian Peninsula. The region has a long history of exposure to alien plant species, enough for many species to be distributed across a wide range of environmental conditions (Sanz-Elorza *et al.* 2004). Spain has a heterogeneous climatic mosaic with four main climatic types: oceanic, alpine, Mediterranean continental and Mediterranean maritime (Ninyerola *et al.* 2000). Due to its geographic, topographic, climatic and geologic heterogeneity, Spain has a high landscape and habitat diversity (Costa *et al.* 1900, Valladares *et al.* 2005), including arid, Mediterranean, temperate and alpine ecosystems, providing a broad spectra of conditions to support a high diversity of plants.

Data set

Species and traits

Data on the distribution of invasive neophytes (i.e. established aliens introduced after 1500) were extracted from the Atlas of invasive plant species in Spain (Sanz-Elorza *et al.* 2004). Invasive species are considered following the definition proposed by Pyšek *et al.* (2004): alien species with self-sustainable populations without direct human intervention that produces offspring at considerable distances from the parent plants, and thus have the potential to spread over large areas. The Atlas contains presence records for over 100 species at a resolution of 10x10 km UTM (Universal Transverse Mercator) grid but, to perform accurate models, we restricted the analyses to 74 species found at least in 10 UTM cells. Due to the potential heterogeneity of sampling effort across the country and the consequent difficulty to distinguish between absence of invasive species and missing data, the analyses were also limited to UTM cells with at least one invasive species present. We also excluded coastal UTM cells with a land proportion lower than 60%. The final number of sites (i.e. UTM cells) included in the analyses was 2401.

For each species we calculated its range size as the number of occupied UTM cells and explored a list of intrinsic (i.e. seed size, clonality, longevity, life-form, dispersal and pollination syndromes, and nitrogen fixation capacity) and extrinsic traits (i.e. region of origin and pathway of introduction) that have been evoked at some point to explain invasiveness (Pyšek *et al.* 1995, Rejmánek 1995, Goodwin *et al.*1999, Lloret *et al.* 2005, Thuiller *et al.* 2006b, Pyšek *et al.* 2008) (Table 5.1).

Table 5.1 Intrinsic and extrinsic species traits taken into account to explain plant invader species niche position and breadth in Spain. The different categories for each trait and the code used in the figures are shown.

Intrinsic traits	Category	Code
Seed size	Very large (> 10 mm)	5
	Large (5-10 mm)	4
	Medium (2-5 mm)	3
	Small (1-2 mm)	2
	Very small (< 1 mm)	1
Clonality	Yes	1
	No	0
Longevity	Annual	1
	Biennial	2
	Perennial	3
Life-form	Chamaephyte	Ch
	Geophyte	Ge
	Hemicryptophyte	He
	Macrophanerophyte	Mc
	Mesophanerophyte	Ms
	Nanophanerophyte	Nn
	Therophyte	Th
	Vine	Vi
Dispersal syndrome	Anemochory	Wind
	Zoochory	Animal
	Hydrochory	Water
Pollination type	Anemophily	Wind
	Zoophily	Animal

Table 5.1. continuation

Extrinsic traits		
Region of origin	America	AM
	South America	SM
	North America	NM
	Asia	A
	Europe	E
	South Africa	SF
	North Africa	NF
	Oceania	O
Pathway of introduction	Agriculture	A
	Gardening	G
	Silviculture	S
	Weed	W
	Unintentional	U

Environmental modelling

Invader species realized niche models were based on the information of a set of nineteen environmental predictors (i.e. land cover, topography and climate) obtained from different cartographic sources (Table 5.2 and Appendix G.II). All the GIS procedures involving the set up of environmental variables were performed using MiraMon software (Pons 2000).

The proportion of main land cover categories (i.e. build-up areas, agricultural areas, forests, scrub and herbaceous vegetation, open spaces, wetlands and water bodies) were calculated from the CORINE Land Cover Map of Spain (http://www.fomento.es). Land cover diversity was estimated by calculating the Shannon index of the abovementioned land cover categories.

Road length (m) and railway length (m) were calculated from maps obtained in the official server of the Spanish Ministry (http://www.cnig.es). We considered these human settlement variables as a measure of human footprint (Sanderson *et al.* 2002) and a surrogates for propagule pressure (Pyšek et al. 2002).

Mean altitude (m) and altitude range (m) were calculated from the official Digital Elevations Model (DEM) of 100 m pixel size (http://www.opengis.uab.es). Mean distance to the coastline (m) was calculated using MiraMon distance algorithms.

Finally, six climatic variables were calculated from the Digital Climatic Atlas of Spain (Ninyerola *et al.* 2005; http://opengis.uab.es/wms/iberia/index.htm), a grid set of 200 m pixel size generated by modelling from the Spanish network of meteorological stations. We calculated the mean values per site of annual temperature (ºC), minimum winter temperature (ºC), temperature range (i.e. difference between maximum temperature in July as the hottest month, and minimal temperature in January, the coldest month), annual rainfall (mm), summer rainfall (sum of the rainfall in June, July and August), and annual solar radiation (KJ ·m^{-2} ·day^{-1} ·µm^{-1}).

Table 5.2 Environmental predictors and data source taken into account to determine plant invader species niche in Spain. See Appendix G.II for cartographic information.

Variables	Data source
Landscape	
Percentage of built-up areas	CORINE Land Cover Map of Spain (http://www.fomento.es)
Percentage of agricultural areas	
Percentage of forests	
Percentage of scrub and herbaceous associations	
Percentage of open spaces	
Percentage of wetlands	
Percentage of water bodies	
Land cover diversity (Shannon Index)	
Roads length (m)	Official server of the Spanish Ministry (http://www.cnig.es)
Railway length (m)	
Topography	
Mean altitude (m)	Digital Elevation Model (DEM) (http://www.opengis.uab.es)
Altitude range (maximum-minimum; m)	
Mean distance to the coastline (m)	
Climate	
Mean annual temperature (ºC)	Digital Climatic Atlas of Spain (http://opengis.uab.es/wms/iberia/index.htm)
Temperature range (max July - min January)	
Minimum winter temperature (ºC)	
Mean annual rainfall (mm)	
Summer rainfall (mm)	
Mean annual radiation (KJ/m^2 ·dia ·µm)	

Testing nestedness in species assemblages

We used a nestedness index to estimate the degree of association between species and sites. This procedure aims at evaluating if species composition in a given site is at random (low nestedness) or if sites with few species are mainly integrated by the most abundant invaders (high nestedness). The minimum requirement for nestedness is that habitat patches differ in their suitability, and species differ in their abilities to colonize and persist on them (Ryti & Gilpin 1987).

We built a matrix with the occurrence (i.e. presence or absence) of each species in each site. Then, to validate the existence of a nested structure among species and sites, we estimated the nestedness index (*N*) as $N = (100-T)/100$, where *T* is the Temperature index, which measures the matrix disorder with values ranging from 0^{o} to 100^{o} (Atmar & Patterson 1993). Because we were interested in emphasizing nestedness of order instead of disorder, we calculated the level of *N*, with values ranging from 0 (minimum *N*) to 1 (maximum *N*) (Bascompte *et al.* 2003). *N* was calculated using the Nestedness Calculator Software (Atmar & Patterson 1995). The Nestedness Calculator reorders the rows and columns of the matrix to minimize the unexpected occurrences and pack the matrix into a state of maximal nestedness (i.e. sites in descending order of species richness and species in decreasing order of range extension). Then, *T* is calculated as the sum of squared deviations from the isocline of perfect nestedness of unexpected presences and absences, divided by the maximum value possible for the matrix, multiplied by 100. To assess the significance of *T* we compared the observed value of *T* with a benchmark of 500 random matrices provided by a null model in which each cell in the matrix has the same probability of being occupied (Gaston & Blackburn 2000), which is an efficient way to test if the observed nestedness differed from a random pattern (Wright *et al.* 1998).

Determining species niches

Several methods have been used to describe and separate species realized niches in an environmental space, ranging from little sophisticated analysis (Green 1971, Austin *et al.* 1984), to canonical correspondence analysis (ter Braak 1986) as well as other related multivariate analyses (ter Braak 1987, Doledec *et al.* 2001, Thuiller *et al.*

2004). To separate invader species niches based on species distribution and the environmental variables selected (Table 5.2 and Appendix G.II), we used a method proposed by Doledec *et al.* (2000). This method uses the outlying mean index analysis (OMI, hereafter), a new multivariate method implemented in *ade4* library on the R statistical software (Chessel *et al.* 2004) that makes no assumption about the shape of species response curves to the environment, and gives equal weight to species-rich and species-poor sites. This method extracts the mean position of the species in the environmental space (i. e. niche position). It measures the propensity of the species to select a specialized environment. Following the main axes calculated from the environmental variables included in the OMI, we also extracted the variability of environment used by each species (i. e. ± SD; niche breadth) (see Thuiller *et al.* 2004).

Species niche as a predictor of range size

The niche concept states a three dimensional relationship between niche position, niche breadth and species abundance or range size in an assemblage (Shugart & Patten 1972). We modelled range size (i.e. number of UTM where each species is present) as a function of niche position and niche breadth on the two main gradients selected by the OMI. Previously, range size was log transformed to follow a normal distribution.

Because species are linked by phylogeny (Harvey & Pagel 1991), using species as independent data points may inflate the degrees of freedom (Brändle *et al.* 2003) and increase the Type-I error. Several sophisticated procedures are available to implement the complete phylogenetic structure in the model, but, in our case, there was not any robust phylogenetic hypothesis available for the studied species. Therefore, we used Generalized Linear Mixed Models (GLMM) to deal with the phylogenetic effects by incorporating taxonomic categories (Family/Genus) as nested random factors. The models were run with the *lme* procedure of the *nlme* library on R statistical package (Pinheiro & Bates 2000).

Species' traits explaining species niche

To analyze if niche properties are related to species traits, niche position and niche breadth on the two main niche axes were modelled using a GLMM that included taxonomic relationships as in the previous analysis with the *lme* procedure of the *nlme* library on R statistical package (Pinheiro & Bates 2000).

Stepwise regression is a commonly used method for examining the relative importance of each species trait to explain niche position and niche breadth. However, using stepwise regression to find the optimal combination of explanatory variables that model a response is often considered to be a high-variance operation because small perturbations of the response data can sometimes lead to vastly different subsets of variables (Burhman & Anderson 2002). To avoid this problem, and to measure the actual power of each species trait over niche position and niche breadth, we used multimodal inference based on all-subsets selection of the GLMM using the AIC measure.

The weight of evidence (w_{pi}) of each species trait as a predictor of niche position and niche breadth can be simply estimated as the sum of the model AICs weights over all models in which the selected predictor appeared (Burham & Anderson 2002, Brooks *et al.* 2004, Link *et al.* 2006, Thuiller *et al.* 2007b). The predictor with the highest w_{pi} (the closest to 1) gets the highest weight of evidence (i.e. the highest relative importance) to explain the response variable. This approach based on a set of multiple models is far more robust than inferring variable importance based on a single stepwise selected model (Burham & Anderson 2002, Link *et al.* 2006).

Results

Nested species assemblages

Site-species matrix temperature was 4.85°, which gives a level of nestedness (*N*) of 0.952. After comparing this value with a benchmark of 500 random matrices, with an averaged *T* of 29.9° ± 0.24 (i.e. a mean nestedness of 0.70), we found that the probability of a random replicate being equally or more nested than our study matrix is less than 0.0001. Therefore, there is a high level of nestedness in our site-species matrix, indicating that species present in sites with low invasive plant richness are a subset of species also occurring in richer sites.

Species niches

OMI successfully explained 96% of the total variability when separating species niches, with the first two axes explaining 77% (Table 5.3 and Fig 5.1). The first axis (anthropization hereafter) summarises a gradient of human transformation reflected by buit-up percentage area, road and railway length, low elevation, short distance to the coast and low temperature variation. The second axis (climate-landscape hereafter) summarises the differences between forested and cropland areas in Spain. Forested areas are associated to cold and humid mountainous areas within relatively diverse landscapes, while croplands are concentrated in lowlands with warm and dry climatic conditions. Species niche positions were widely distributed on the environmental ordination diagram (Fig 5.2 and Appendix G.I), mostly on the right side, which is related to areas with a high anthropization degree according to the interpretation of axis 1.

Table 5.3 Proportion of the variance explained by each OMI axes.

Axes	% Variance	% Cumulative variance
1- Anthropization	0.45	0.45
2- Climate and vegetation land cover	0.32	0.77
3- Climate	0.14	0.90
4- Topography and land cover	0.03	0.93
5- Land cover	0.02	0.96

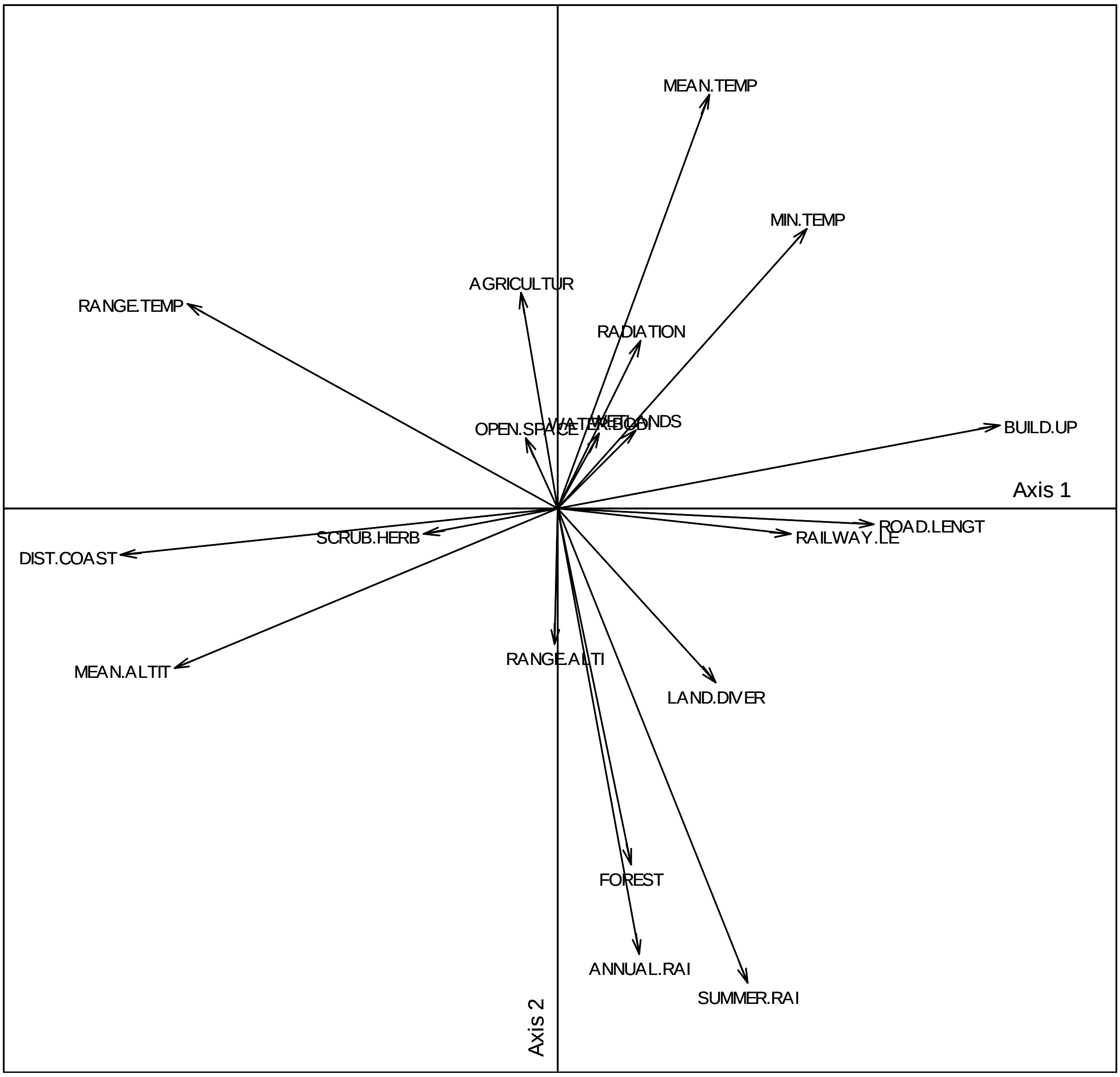

Figure 5.1
Ordination diagram on the first two axes of the OMI ordination analysis in invasive species niches. The first axis was the strongest gradient to affect species distributions and indicated a gradient of anthropization degree, represented by coastal and build up areas. The second axis is a gradient of climatic and land cover variability from forested areas to croplands.

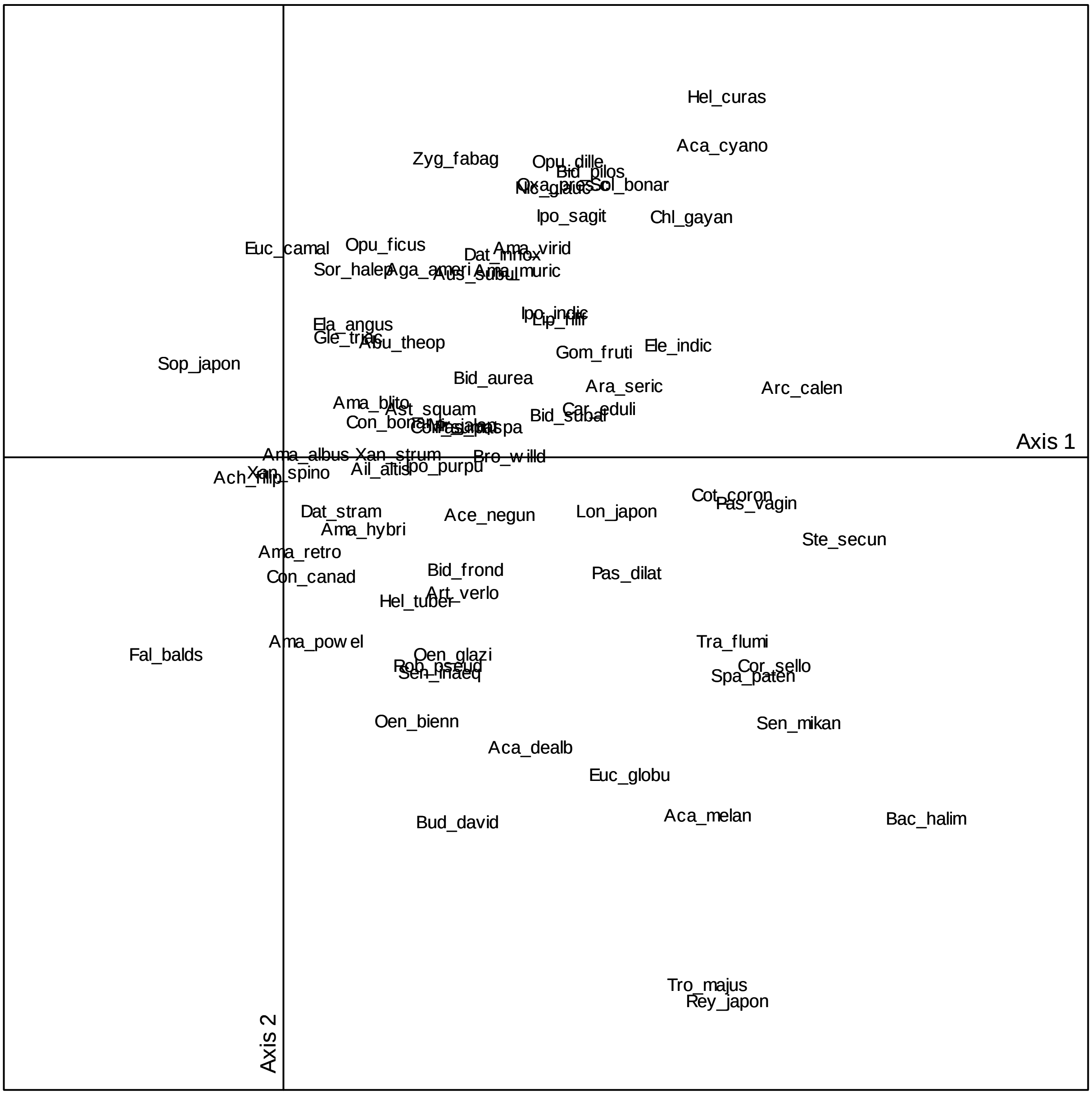

Figure 5.2 Niche position of the most invasive species in Spain represented on the environmental ordination diagram of the first two axes of the OMI ordination analysis. See Appendix D.V for species acronyms.

Species niche as a predictor of range size

The minimum adequate model of range size as a function of niche position and breadth, and controlling for taxonomic relationships, explained almost half of the variation in range size ($R^2 = 0.48$, $p<0.0001$) (Table 5.4).

In this model, range size is negatively related to position and breadth on axis 1: species with restricted distribution ranges are found in highly anthropic places and they have a wider tolerance over this axis. In contrast, range size was positively related with niche breadth on axis 2: species with wide distribution ranges are more tolerant to conditions driven by climate and vegetation land cover (Table 5.4).

Table 5.4 Minimum adequate model (i.e. only significative variables) accounting for variation in distribution range size of plant invasive species in Spain, as a function of their niche position and breadth of the main two axes of the OMI ordination. The model explained almost the half of the variation in range size ($R^2 = 0.48$, $p<0.0001$).

	Value	Std. Error	DF	t-value	p-value
Intercept	4.50	0.10	26	43.40	<0.0001
Axis 1 position	-0.63	0.11	20	-5.97	<0.0001
Axis 1 breadth	-0.35	0.11	20	-3.25	<0.01
Axis 2 breadth	0.32	0.11	20	2.99	<0.01

Species traits explaining species niches

Inferential models accounting for both position and breadth on axis 1 explained more variance than inferential models for axis 2 on the OMI ordination (Table 5.5).

Table 5.5 Summary for explained variance of inferential models accounting for niche position and niche breadth of plant invasive species in Spain in both axis 1 and axis 2 of the OMI ordination.

Model for	R^2	Adjusted R^2	F	p-value
Axis 1 position	0.83	0.83	362	<0.0001
Axis 2 position	0.63	0.62	122.8	<0.0001
Axis 1 breadth	0.78	0.77	253	<0.0001
Axis 2 breadth	0.34	0.33	36.53	<0.0001

Table 5.6 Relative importance (%) of each species trait over niche position and niche breadth on axis 1 and axis 2 of the OMI ordination. The three traits with the highest relative importance on each niche property are shown in bold.

Trait	Importance over axis 1 position	Importance over axis 1 breadth	Importance over axis 2 position	Importance over axis 2 breadth
Nitrogen fixation	**16.6**	**32.8**	**14.8**	14.0
Longevity	**18.5**	7.2	**14.9**	**22.1**
Dispersal syndrome	13.7	6.8	9.0	5.4
Pollination syndrome	16.4	**22.1**	11.6	11.1
Clonality	12.5	**19.7**	12.7	**14.9**
Seed size	0.9	0.1	1.9	3.3
Life-form	0.3	0.0	10.3	5.1
Origin	**19.1**	0.0	5.7	3.7
Pathway	2.0	11.3	**19.2**	**20.4**

In Table 5.6 we show each trait relative importance as explanatory variable for niche position and niche breadth on both OMI axis 1 and 2. The main results are as follows:

Species niche position over axis 1 is mainly conditioned by species origin (19.1%), longevity (18.5%), and nitrogen fixation (16.6%) (Table 5.6). Perennial, nitrogen non-fixers species from South America, Africa and Australia are those present in highly humanized places close to the coast (Fig 5.3).

Niche breadth over axis 1 is mainly affected by nitrogen fixation (32.8%), pollination (22.1%) and clonality (19.7%) (Table 5.6). Clonal species without the capacity of fixing nitrogen, and animal dispersed are the most tolerant to different levels of anthropization and distance to the coast (Fig 5.4).

Niche position over axis 2 is mainly related with the pathway of introduction (19.2%), longevity (14.9%), and again with nitrogen fixation (14.8%) (Table 5.6). Unintentionally introduced species, agricultural weeds, and crop plants are those present in hottest, driest and agricultural places. Species that live in such places are also perennial and nitrogen fixers (Fig 5.5).

Finally, species niche breadth over axis 2 is mainly affected by longevity (22.1%) and pathway (20.4%), followed by clonality (14.9%) (Table 5.6). Short-lived species (i.e. annuals and biennials) introduced through agriculture (i.e. crops and weeds), clonal and nitrogen non-fixers have more tolerance on different climatic and vegetation land cover conditions (Fig 5.6).

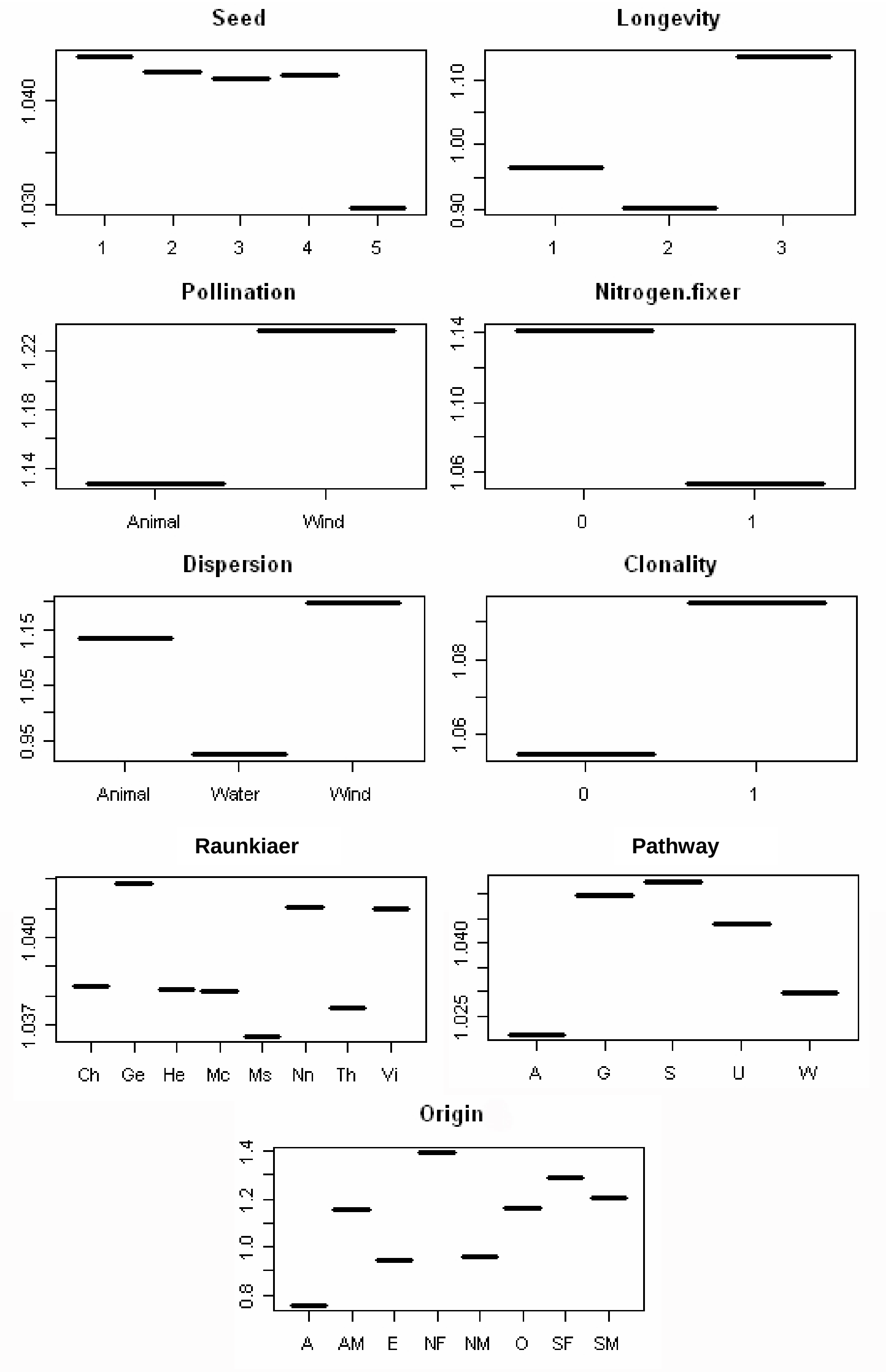

Figure 5.3 Plot for each species trait (x-axis) response to niche position on axis 1 of the OMI ordination (y-axis). See Table 5.1 for trait code and Table 5.6 for trait importance.

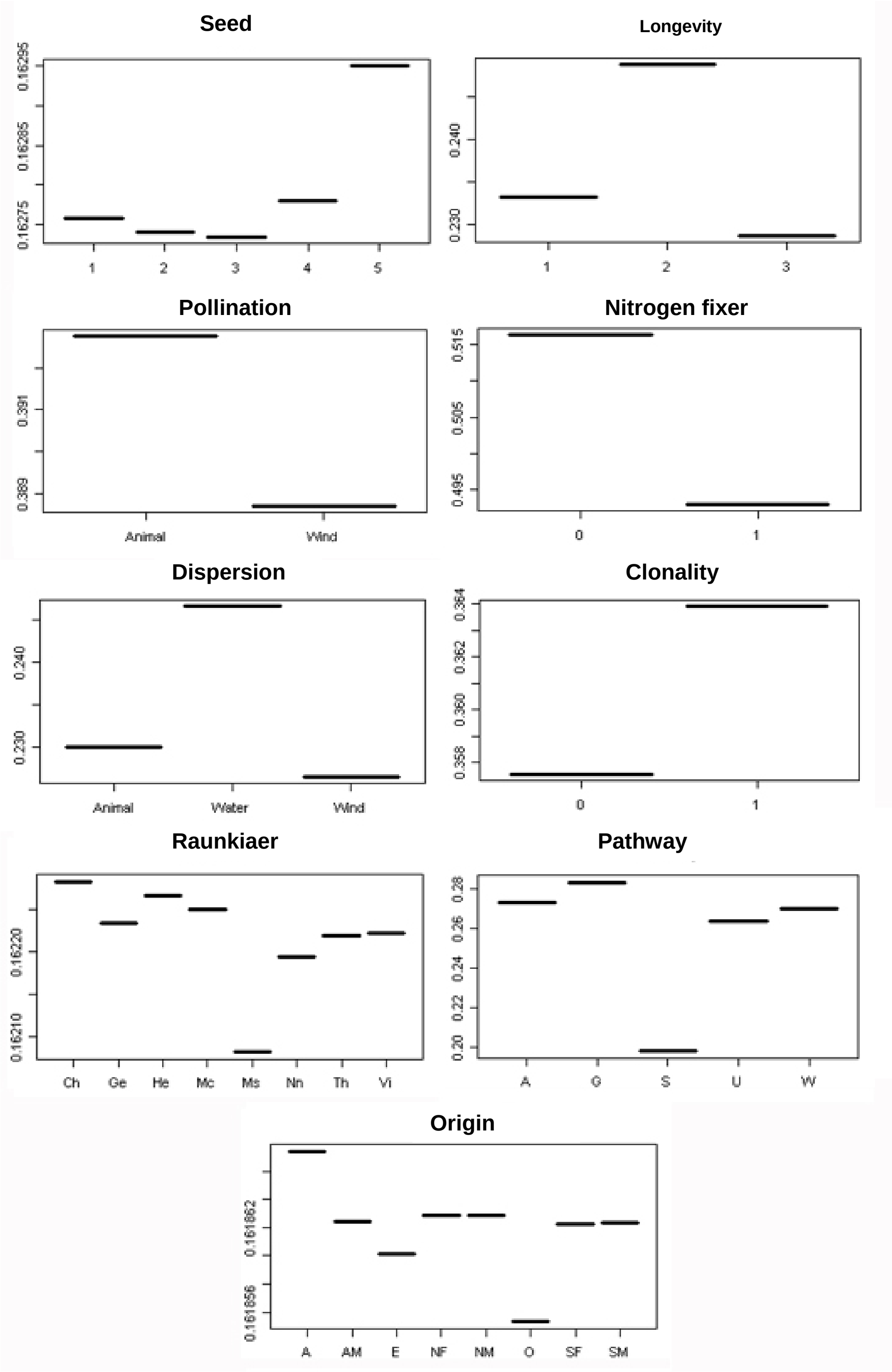

Figure 5.4 Plot for each species trait (x-axis) response to niche breadth on axis 1 of the OMI ordination (y-axis). See Table 5.1 for trait code and Table 5.6 for trait importance.

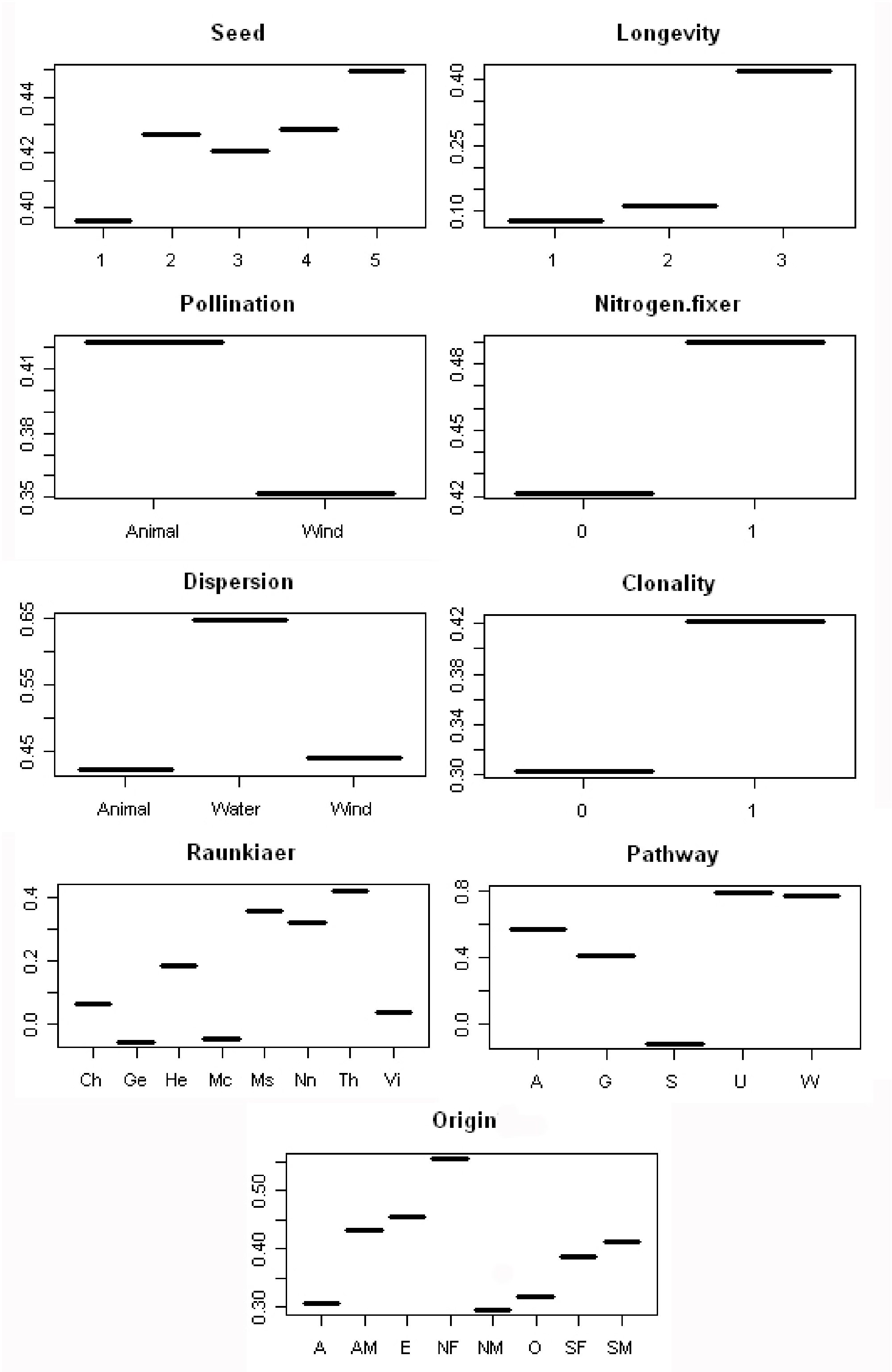

Figure 5.5 Plot for each species trait (x-axis) response to niche position on axis 2 of the OMI ordination (y-axis). See Table 5.1 for trait code and Table 5.6 for trait importance.

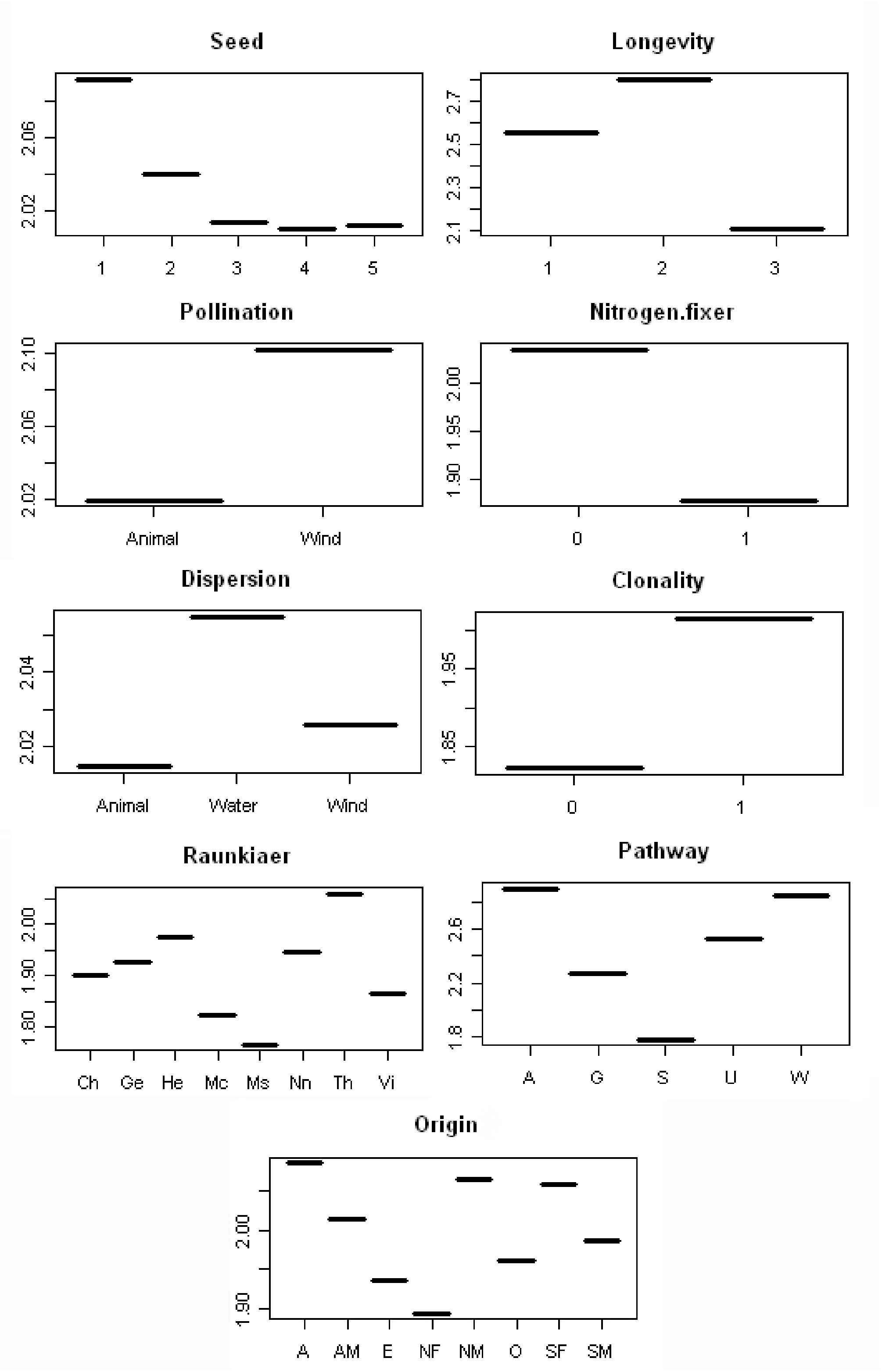

Figure 5.6 Plot for each species trait (x-axis) response to niche breadth on axis 2 of the OMI ordination (y-axis). See Table 5.1 for trait code and Table 5.6 for trait importance.

Discussion

Nested pattern and species niches

At the regional scale, invasive plant species assemblages in Spain are organized in nested subsets: species with restricted distribution ranges appear to be located in sites where invasive plant richness is high whereas in sites with few species these are widespread. Our hypothesis was that this nested pattern could be reflecting a species niche overlap. We found indeed that range size is related to niche position and breadth of the invaders, what leads us to think that there is a niche overlap among the species. However, this relationship is more complex than suspected. In addition, there are other several possible explanations for this nested pattern. First, it could be a mirror of the "invasional meltdown" hypothesis, which establishes that a group of invasive species in an assemblage would facilitate new invasions in the same recipient community by increasing the likelihood of survival, and even increase the ecological and magnitude of impact (Howarth 1985, Simberloff & Von Holle 1999). From this point of view, invasive species would be the drivers of change in a species assemblage (MacDougall & Turkington 2005). Alternatively, nestedness might be generated by factors such as passive sampling effect, patch area and isolation, and habitat distribution (Wright *et al.* 1998), or simply be an artefact of particular species distributions (Gaston & Blackburn 2000). In our database, there could be a passive sampling effect because the cartographic information of the Atlas of Invasive Plant Species in Spain (Sanz-Elorza *et al.* 2004) was generated through a five years work compilation of bibliographic and herbarium records. However, we tried to minimize this effect by taking only into account for the analysis those cells with at least one invasive species and by selecting only species recorded at least in 10 sites. Patch area did not have any influence on our results because we based the analysis in a grid cell of constant size (i.e. UTM 10x10km), still, habitat isolation could also cause nestedness because only species with the highest colonization ability will be able to reach the most remote habitat patches (Kadmon 1995, Conroy *et al.* 1999). Finally, distribution of the habitat required for each species can follow as well a nested pattern, what could result in a nested pattern of invasive species (Gaston &

Blackburn 2000).

Our analysis detected that all the invasive plant species studied had their niche positions from medium to highly anthropogenic sites, suggesting an association between invasion and human disturbance. Moreover, distribution range size was positively related to the coastal and highly humanized landscape. Thus, regionally rare species with restricted ranges are accumulated in highly anthropogenic areas, while widespread species have their niche positions closer to the average and widespread environmental conditions. Some other studies have already found a negative relationship between niche position and range size (Fuller 1982, Duncan *et al.* 1999, Gregory & Gaston 2000), concluding that species exploiting more widespread resources will themselves be more widespread. We think, therefore, that the high level of nestedness is a mirror of these "hotspots" located in anthropogenic and coastal areas where there is a high level of propagule pressure. Man-induced disturbances have been insistently considered a key factor to trigger and sustain invasions (Elton 1958, Kowarik 1990, Jenkins 1996, Pyšek 1998a, Hobbs 2000). In consequence, flora of urban areas and their surroundings is usually richer in alien species than natural areas (Stadler *et al.* 2000, Chocholouškova & Pyšek 2003). Coastal areas in Spain have a mild climate and intense human pressures and concentrate tourism, trading and transport centres and, in turn they accumulate most of the first records of alien species (Casasayas 1990). Furthermore, we found that restricted species with niche positions in highly humanized places had a high tolerance over this axis, what can pose a serious management problem because these species introduced in anthropogenic places could spread through more natural areas.

The second environmental gradient determining invasive species niches was defined by climate and vegetation cover. The lack of association between niche position on this niche gradient and range size, reinforces the idea of a relative independence of invasive species on climatic conditions, that is, rarely found invasive plants are not restricted to certain climatic conditions or vegetation types (Vilà & Pujadas 2001, Pino *et al.* 2005). Nevertheless, range size was positively related to niche breadth to this gradient , what implicates that broader niches on climate and vegetation land cover conditions enables a species to become more widespread, as also suggested by other studies (Brown 1995, Brow *et al.* 1995, Vázquez 2006).

Summarizing, we found that wide size ranges of invaders are a consequence of tolerance to wide climatic and vegetation cover conditions and that the most invaded sites are coastal and highly anthropogenic. These two relationships show how the nested pattern can be, at least partially, explained by a niche overlap. Curiously, widespread species are less tolerant to a wide range of anthropogenic conditions than restricted species, and their mean niche positions are located in sites with medium human disturbance levels, supporting that the intermediate disturbance hypothesis also holds for invader species richness (Hobbs & Huenneke 1992, McKinney 2002b).

The species with more common niche positions and with large niche breadth, such as *Sorghum halepense, Robinia pseudoacacia* or *Amaranthus retroflexus,* were also the species associated with the widest distribution ranges in Spain (Appendix D.V). The species with a higher level of specialization (i.e. extreme niche position and narrow niche breadth) had, in general, a nested niche inside the niche of more generalist species (see Fig 5.7 for an example).

We found, however, many exceptions to this general niche overlap pattern, what could be an explanation for the non-perfect nestedness of species assemblages in terms of spatial distribution. Species such as *Nicotiana glauca* or *Oxalis pes-caprae* have restricted niches but wide distribution ranges, and species such as *Achylea filipendulina* or *Tradescantia flumminensis* have very large niche breadth but their distribution range is quite restricted at the moment (Appendix D.V). This mismatch could be due to their short time since introduction (Gassó *et al.* in press).

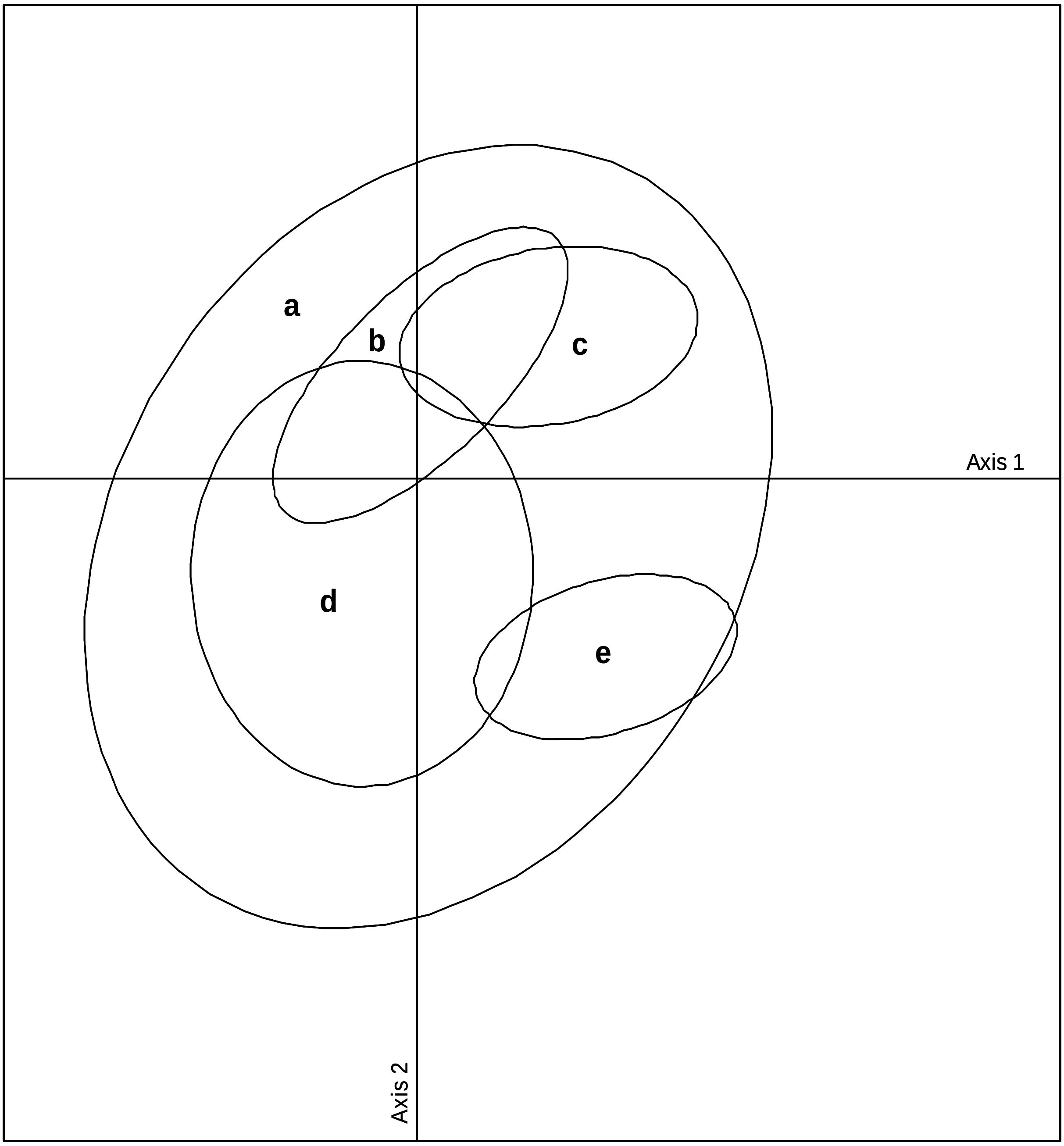

Figure 5.7 Graphical representation of niche of four species with restricted distribution ranges (**b**, *Eucalyptus camaldulensis;* **c**, *Opuntia dilleni;* **d**, *Fallopia baldsuanica;* **e**, *Acacia melanoxylon*) nested inside the niche of a species with a wide distribution range (**a**, *Conyza canadensis*). Niche position is the centre of each species elipse and the extend of the elipse is an estimation of niche breadth in function of the maximal deviation of site conditions from niche position.

Species niches and traits

An overview of the relationship between species niches and traits revealed that some intrinsic (nitrogen fixing capacity, life-form, clonality) and extrinsic (origin and pathway) traits are related with niche position and niche breadth. We should keep in mind, however, that some of these traits could be correlated or secondary explained by others that we did not take into account.

Nitrogen fixation capacity could be related with invasion success because of the competitive advantage that it represents in poor soils (Pyšek & Richardson 2007). However, the cost of this symbiosis cause a severe trade-off problem to nitrogen fixers and species can benefit from this capacity only in nitrogen deficient soils (Fitter 1997), what can explain that nitrogen non-fixers were mainly found in coastal places with high human pressure (i.e. soil enrichment), and that they had wider niche breadths (Fitter 1997) than nitrogen fixers.

Short-lived species have been suggested to be better invaders (Pyšek *et al.* 1995, Cadotte & Lovett-Doust 2001, Pyšek & Richardson 2007) over longer-lived due to the yearly reproduction or survival in adverse conditions as dormant seeds (Crawley 1997). We found that short-lived invasive species occurred in the most widespread environmental conditions and they showed a higher tolerance to climatic and vegetation cover variation.

Clonal capacity have been historically related to invasion success for its advantage in colonizing and competing in new communities (Pyšek 1997, Lloret *et al.* 2005, Pyšek & Richardson 2007), and our results support this hypothesis, because we found that clonal species were present in stressful conditions (i.e. coastal, highly anthropic, hot and dry places) and were more tolerant on both climatic and anthropic axes, so they are capable to colonize and survive in a wider environmental range.

Finally, we found that extrinsic traits recently taken into account in invasions studies (Thuiller *et al.* 2006b, Pyšek & Richardson 2007) are, indeed, important when explaining the niche of plant invaders. Geographical origin was highly related with anthropogenic niche position, being species coming from warm regions those present in highly anthropized-coastal places. To our surprise, pathway of introduction was more important to explain the position of the species according to the climatic gradient than to the anthropogenic gradient. Species introduced by agriculture (i.e. crops and weeds) and those unintentionally introduced were found in hot, dry, and logically, agricultural areas, and were more tolerant to a wide range of climatic and vegetation conditions than those introduced by other means.

Conclusions and conservation implications

In general, invasive species with restricted distribution do not have particular environmental requirements, but they occur in anthropogenic areas also invaded by generalist and widespread species. These restricted invaders are less tolerant to broad climatic and vegetation cover conditions than widespread invaders. Our approach allowed to distinguish between species that are widespread because they occur in widespread environmental conditions (i.e. common niche position), and species that are widespread because they have an intrinsic potential to invade (i.e. invasiveness) given by their wide niche breadth, which is, in turn, conditioned by species traits such as short-life and clonal growth. This distinction can be very useful when assessing species differences in invasion likelihood and risk. Moreover, our results showed that anthropogenic disturbances in coastal areas facilitate the introduction and establishment of invaders, especially clonal species coming from warm regions. These findings pose a serious management problem because these places seem not to be species-saturated and could serve as foci areas of infestation for species coming from similar climate regions that could spread towards inland natural areas.

Chapter 5

Predicting plant invaders in the Mediterranean through a Weed Risk Assessment system[5]

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[5] This chapter has been submitted to *Biological Invasions* in June 2008.
Authors: Núria Gassó, Corina Basnou, Montserrat Vilà.

Resum

Predir les plantes invasores a la Mediterrània amb un sistema d'avaluació de riscos

Els esquemes d'avaluació de riscos s'han desenvolupat per tal d'identificar les espècies potencialment invasores, prevenir la seva expansió i reduir els seus efectes nocius. Una de les eines més prometedores per detectar plantes invasores és l'esquema anomenat Weed Risk Assessment (WRA), desenvolupat a Austràlia. El nostre estudi explora si el WRA australià pot predir satisfactòriament l'estatus d'invasió de les plantes al·lòctones a la Mediterrània a partir de l'exploració d'una base de dades de plantes d'Espanya. A més a més, hem analitzat si els factors que es tenen en compte en el WRA estan lligats a la probabilitat d'invasió (estatus d'invasió) o als impactes que causa la invasió. La precisió global del WRA aplicat a Espanya va ser 57.65%, més baixa que el WRA aplicat en bases de dades d'altres regions. El resultat va ser que el 94% de les espècies invasores van ser rebutjades, el 50% de les espècies adventícies van ser acceptades, i el 29% de les adventícies necessitaven una avaluació més profunda. Creiem que el baix ajust del test a les nostres dades podria ser el resultat de: (1) una incorrecta classificació prèvia dels estatus de les espècies per part dels experts, (2) que l'WRA es basa tant en la probabilitat d'invasió com en els impactes potencials, i (3) que les espècies adventícies podrien tenir tendència a esdevenir invasores si aconseguissin superar un cert llindar de temps de residència.

Abstract

Risk assessment schemes have been developed to identify potential invader species, prevent their spread and reduce their damaging effects. One of the most promising tools for detecting plant invaders is the Weed Risk Assessment (WRA) scheme developed for Australia. Our study explores whether the Australian WRA can satisfactorily predict the invasion status of alien plants in the Mediterranean Basin by screening a plant dataset with information for 100 invasive and 100 casual alien plants in Spain. Furthermore, we analysed whether the factors taken into account in the WRA are linked to invasion likelihood (i.e. invasion status) or to impacts. The overall accuracy of the WRA applied to Spain was 57.65%, lower than the WRA tested in other regional datasets. The outcome was 94% of the invasive species were rejected, 50% of the casual species were accepted, and 29% of the casuals required further evaluation. We postulate that low accuracy could result from: (1) an incorrect "a priori" expert classification of the species status, (2) WRA scores based on invasion likelihood factors as well as potential impacts, and (3) casual species being prone to becoming invasive when reaching a minimum residence time threshold.

Introduction

Predicting the success of alien species has been a major aim of ecological research since invasions were recognized as an important conservation issue (Rejmánek & Richardson 1996, Reichard & Hamilton 1997, Smith *et al.* 1999, Kolar & Lodge 2001, Pyšek 2001, Caley *et al.* 2006). To this purpose, many studies have focused on finding which biological traits make a species invasive and the characteristics of invaded habitats (Goodwin *et al.* 1999, Daehler 2003, Heger & Trepl 2003, Richardson & Pyšek 2006). Since Baker (1965), the search for invader syndromes (i.e. suites of traits and abiotic factors associated to invasiveness following Agrawal & Fishbein (2006)) aims to improve our ability to predict the invasion success of alien plants in new regions (Richardson & Pyšek 2006). For example, Thuiller *et al.* (2006) have found that the spatial regional distribution of invasive alien species in South Africa is driven by life forms, reproductive traits and human uses.

The accumulated knowledge on invader traits together with the characteristics of invaded habitats has been used to develop risk assessment schemes that attempt to predict the success of alien species in the region of introduction (Wittenberg & Cock 2001, Keller *et al.* 2007a). For plants, only a small proportion of introduced alien species become invasive (Di Castri 1989, Williamson 1996). Because risk has two components: likelihood of invasion and consequences (e.g. ecological or socioeconomic impacts), risk assessment schemes attempt to identify this small fraction of species with a high likelihood of becoming invasive, and prevent their spread and their damaging effects. So far, there is evidence that the implementation of risk assessment protocols produces net economic benefits (Keller *et al.* 2007b).

Risk assessment schemes differ in the methods used and the phase of invasion process they target. Recently, taking advantage of the rapid increase in computing tools, facilities and database availability, new screening models have been developed. One of the most promising models as a tool for detecting plant invaders is the Australian Weed Risk Assessment (WRA, Pheloung 1995) which has also been tested for New Zealand (Pheloung 1999). The same screening model with modifications was successfully tested to work in Hawaii and other Pacific islands (Daehler & Carino 2000, Daehler *et al.* 2004). Křivánek & Pyšek (2006) compared the accuracy of several models for alien woody species suited to the Central European climate, concluding that Daehler´s WRA scheme was the most suitable for a wide range of geographical regions.

Our study explores whether the original Australian WRA scheme (Pheloung 1999) satisfactorily predicts the invasion success of alien plants in the Mediterranean region. For this purpose, we have chosen Spain as a representative Mediterranean region because of its climatic, geological, landscape and habitat heterogeneity and high species diversity (Medail & Quezel 1997). Moreover, we go a step further by analysing whether the factors taken into account in the WRA are those really involved in differentiating casual from invasive alien plants, considering status differences to be a consequence of invasion likelihood. We follow Richardson *et al.* (2000a) in defining invasion plant status. Invasive species are alien species with self-sustaining populations not requiring direct human intervention, that produce offspring at considerable distances from the parent plants and thus have the potential to spread over large areas. Casual species do not form self-replacing populations outside cultivation and rely on repeated introductions for their persistence. Specifically, our main questions are (1) Does the WRA have a high accuracy when adapted and applied to a Mediterranean region? and (2) What are the determining factors for an alien plant species to be considered invasive and do these correspond with the questions taken into account to calculate the WRA final score?

Methods

Weed Risk Assessment for Mediterranean regions

The scheme chosen for testing was the original Australian WRA (Pheloung 1995) because it is already designed to be applied in a region with Mediterranean climate influence (Appendix D.VI). The WRA system consists of 49 questions which encompass biogeography, undesirable plant attributes and biology/ecology (Pheloung *et al.* 1999). A high score (>6) identifies a species likely to be of high risk (weed) and rejects it for import; a low score (<1) accepts the plant for import (non-weed) and intermediate scores (1-6) require further evaluation. The WRA score ranges from -14 (benign taxa) to 29 (maximum risk).

From the original WRA we only modified question 5.03: " Nitrogen fixing woody plant" to "Nitrogen fixing plant", to include the non-woody nitrogen fixing plants. These are an important component of Spanish alien flora, many of such species being very abundant in ruderal, disturbed habitats (Sanz-Elorza *et al.* 2004).

Screened species and information sources

We screened a plant data set that was comprised of information about 100 invasive and 100 casual alien plants recorded in the Atlas of Invasive Plant Species in Spain (Sanz-Elorza *et al.* 2004), including herbaceous and woody species (Appendix D.VII). The chosen invasive species comprised all the most invasive species listed in the Atlas, while the casual species were selected randomly from the pool of 380 casual species recorded therein. Information was gathered from regional and local floras (Castroviejo *et al.* 1986-2000, Bolós *et al.* 2005), weed atlases (Sanz-Elorza *et al.* 2004), and Internet databases such as: BioFlor (http://www.ufz.de/biolflor), Plants for a Future (2002) (http://www.comp.leeds.ac.uk/pfaf), Hypermedia for Plant Protection – Weeds (http://www.dijon.inra.fr/hyppa), Poisonous Plants of North Carolina (http://www.ces.ncsu.edu/depts/hort/consumer/poison), species accounts from Plantas Invasoras en Portugal (http://www.uc.pt/invasoras), USDA Plants database (http://plants.usda.gov), International Survey of Herbicide Resistant Weeds (http://www.weedscience.org), Global Compendium of Weeds (http://www.hear.org/gcw) Global Invasive Species Database (http://www.issg.org/database/welcome), Weeds in Australia (http://www.weeds.gov.au), and Ecological Traits of New Zealand Flora (http://ecotraits.landcareresearch.co.nz).

Data analysis

We calculated the accuracy and reliability of WRA for Spain following Smith *et al.* (1999). Accuracy indicates the probability of correct classification, i.e. the proportion of known invasive species that would be correctly assessed as invasive and thus rejected [A_i=(I_r/I_t)x100; where I_r is the number of invaders that were rejected by the system, and I_t was the total number of invaders assessed], and that of known casual species which are accepted [$A_c=(C_a/C_t)\text{x}100$; where C_a is the number of casual species that were accepted and C_t was the total number of casual species assessed]. Overall accuracy [$A_o=(C_a + I_r)/(C_t + I_t)$] includes both components. Reliability takes into account that any sample of species rejected by a screening system will include a proportion of casual species wrongly classified as invaders (Křivánek & Pyšek 2006). It has two components: the probability that an accepted species would have been an invader, $P_{ai}=I_a/(C_a+I_a)$, and the probability that a rejected species would have been an invader, $P_{ri}=I_r/(C_r+I_r)$.

A Principal Components Analysis (PCA) was used to identify the main variables that characterize the pool of all tested alien species and to reduce the number of multivariate data for a posterior comparison between invasive and casual species characteristics. This linear method was chosen because the number of species was low (200) compared to the number of variables (30) and the length of the longest gradient from Detrended Correspondence Analysis was between 1 and 2 (Lepš & Šmilauer 2006). Ordination was performed using CANOCO for Windows 4.5.

We adopted the framework of the Generalized Linear Mixed Models (GLMM) (e.g. Blackburn & Duncan 2001a) to determine variation between species in invasion status (i.e. casual or invasive) and WRA score (i.e. two estimations of invasion risk) as a function of the 15 WRA variables best characterized by the first two principal components (Fig.2). Both GLMM analyses incorporated taxonomy to overcome potential phylogenetic biases. Because species are linked by phylogeny (Harvey & Pagel 1991), using species as independent data points may inflate the degrees of freedom (Brändle *et al.* 2003) and increase the Type-I error. GLMM deals with phylogenetic effects by allowing the incorporation of taxonomic categories as nested random factors. In this way, the likely non-independence of response values of closely related species is controlled by assuming a common positive correlation between introduction outcomes for species within nested taxonomic groups (genera and family, in our case). Conversely a zero correlation is assumed between introduction outcomes for species in different groups (a variance components model). There are more sophisticated procedures that allow implementing the complete phylogenetic structure in the model (Sol *et al.* 2008), but we could not use such methods because there was no robust phylogenetic hypothesis available for the species studied. In addition, the approach we used helped to mitigate the problem of invasive species being a non-random subset of all species introduced (Blackburn & Duncan 2001a).

We modelled invasion status with a Binomial distribution of errors (Crawley 2002), because the response variable was binary (i.e. casual(0)/invasive(1)) . Invasion risk (i.e. WRA score) followed a normal distribution and did not need transformation to achieve the requirements of parametric analysis, so we modelled it with a Normal distribution of errors. In both cases, the inspection of the residuals showed that error structures adjusted well to our response variables.

We started modelling invasion status with a full model that contained all our predictors. Using a backward selection process, we next simplified the model so as to leave only significant predictors (minimum adequate model). The model was run in the glmmPQL procedure of the MASS library on the R statistical package (Venables & Ripley 2002, R Development Core Team 2006).

Results

We were able to answer a mean of 43 questions (range 29-49 questions) out of 49. While only one invasive species (*Chloris gayana*) was accepted, the system accepted 21 % of casual species. Surprisingly, half of the casual species were rejected and many of them needed further evaluation (Fig 6.1).

Overall accuracy for the WRA was 57.65%, being 93.94% for invasive species and 20.62% for casual species. Results for reliability showed that the probability that an accepted species would become an invader was very low (4.76%), and that the probability that a rejected species is an invader was high (65.49%).

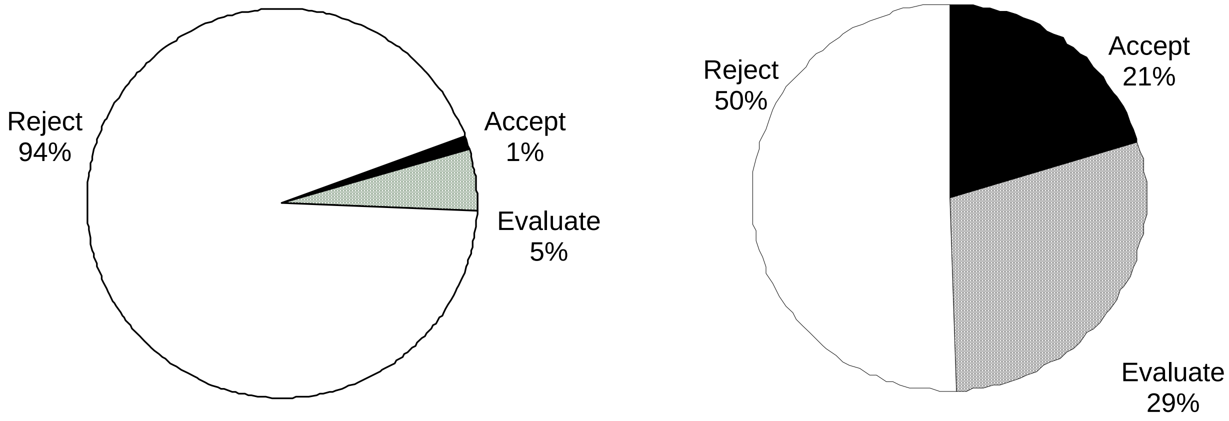

Figure 6.1 Results of the Australian Weed Risk Assessment system of Pheloung *et al.* (1999) applied to 100 invasive and 100 casual plant species in Spain. Percentage of species rejected, accepted or suggested for further evaluation is indicated.

When performing the Principal Components Analysis, the first two principal components explained 24% of the variability in the species data. Out of the 49 WRA questions, there were only 15 that were best characterised by the first two principal components, so they were the ones that better predicted the total of alien plant species variation. The PCA biplot (Fig 6.2) indicates invasion-related traits, which are assembled in 3 different groups. The first group contains crop and gardening plants (D1, W2, M2, P4), most of them nitrogen fixing (T3) and bird dispersed (M6), forming dense thickets (UT12). Many species included in this cluster belong to the genus *Acacia, Opuntia* and *Lonicera.* The second group comprises species of Mediterranean origin (C1) and species that may create a fire hazard (UT8), such as *Gleditzia triacanthos* and *Eucalyptus globulus*, respectively. Finally, the last cluster is mainly composed of grasses (T2) (i.e. *Eleusine indica, Sorghum halepense,* and species belonging to Asteraceae and Amaranthaceae, also species which are wind dispersed (M4) or potentially dispersed as a contaminant (M3).

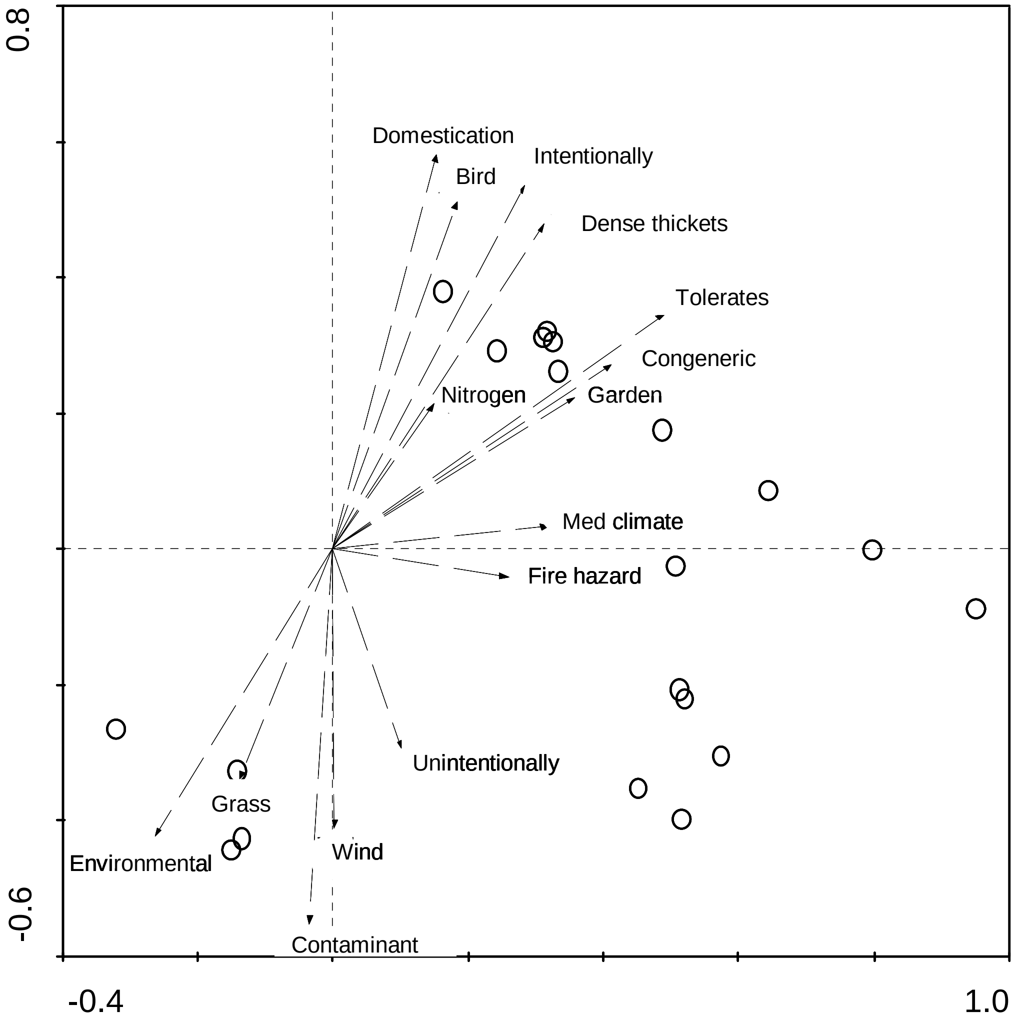

Figure 6.2 Alien species – WRA (Australian Weed Risk Assessment) variables ordination biplot (PCA Axes 1-2). Alien species fit > 20 % and variables fit > 40 %. Only the first 15 WRA variables that are best characterized by the first two principal components are displayed in the figure. See Appendix D.VI for explanation of variables.

There was a clear taxonomic bias in the set of alien species, with 33% of species belonging to just three families; Asteraceae (12%), Fabaceae (11%), and Poaceae (10%). Thus, clustering the species according to taxonomic relationships throught the GLMM analysis, we found that only 5 out of the 15 PCA predictors were significantly related with the invasion status of the species: existence of congeneric weeds (W4), creating fire hazard (UT8), intentional introduction (M2), introduced as contaminant (M3), and bird dispersed (M6) (Table 6.1). In contrast, we found that the WRA score was significantly related with more predictors: 13 out of the 15 (Table 6.2). These variables were mainly related to domestication, climate and area of distribution, undesirable traits, dispersal mechanisms, and persistence attributes.

Table 6.1 Minimum adequate mixed model accounting for variation in invasion status (i.e. invasive or casual species). A positive estimate value indicates a positive relationship with the invasion status. See Appendix D.VI for explanation of variables.

Variable	Estimate	Standard error	DF	t-value	P
Intercept	-1.249	0.653	60	-1.912	n.s.
Congeneric	2.476	0.519	42	4.767	<0.0001
Fire hazard	-1.700	0.795	42	-2.137	<0.05
Intentionally	-1.312	0.558	42	-2.349	<0.05
Contaminant	1.557	0.544	42	2.861	<0.01
Bird	1.214	0.583	42	2.082	<0.05

Table 6.2 Minimum adequate mixed model accounting for variation in WRA final score. A positive estimate value indicates a positive relationship with WRA score. See Appendix D.VI for explanation of variables.

Variable	Estimate	Standard error	DF	t-value	*P*
Intercept	-8.875	1.787	48	-4.966	<0.0001
Domestication	-3.894	0.891	24	-4.368	<0.001
Med climate	2.764	0.601	24	4.595	<0.0001
Fire hazard	2.769	1.118	24	2.476	<0.05
Dense thickets	3.516	0.755	24	4.655	<0.0001
Garden	4.570	0.785	24	5.820	<0.0001
Environmental	5.154	0.721	24	7.150	<0.0001
Congeneric	6.107	0.746	24	8.185	<0.0001
Tolerates	2.651	0.730	24	3.629	<0.001
Unintentionally	3.644	0.804	24	4.530	<0.0001
Intentionally	2.140	0.907	24	2.360	<0.05
Contaminant	2.240	0.758	24	2.956	<0.01
Wind	2.040	0.846	24	2.412	<0.05
Bird	3.632	0.816	24	4.451	<0.001

Discussion

The WRA scheme developed for Australia and New Zealand (Pheloung *et al.* 1999) has been recognized as potentially suitable for a wide range of geographical regions (Daehler & Carino 2000, Daehler et al. 2004, Křivánek & Pyšek 2006). When applied to Hawaii, the modified WRA rejected 99% of invasive species, and in other Pacific islands, 95% of invasive species were rejected and 85% of non-invasive species accepted (Daehler & Carino 2000). The results were even better when applying the WRA model in the Czech Republic, with all invasive woody species rejected and 83.8% of non-invasive species accepted (Křivánek & Pyšek 2006). We obtained similar encouraging results for Spain as a Mediterranean region when screening invasive species, 94% of which were rejected. However, only 21% of casual species were accepted and 50% of them were rejected. Therefore, the overall accuracy of the WRA for Spain was considerably lower (57.7%) than when it was applied in other territories (e.g. 86% in Křivánek & Pyšek 2006). These differences in accuracy between regions might be due to differences in the invasion status definition, which can contribute to misunderstandings of results, making it difficult to compare them. Pheloung *et al.* (1999) distinguished between non-weed, minor weed and major weeds; Daehler & Carino (2000) screened a dataset of naturalized plants, distinguishing between non-pest and pest; and Křivánek & Pyšek (2006) used a dataset of woody alien species classified in 4 invasion status groups (i.e. not escaped from cultivation, casual, naturalized non-invasive, and invasive). The dataset that we have used contains alien plants of different life forms and we distinguished casual from invasive species.

Overall, the level of misclassifications tends to be higher for species that will probably never become invasive than for harmful invaders. The poorer performance of the WRA for casual species has already been found to occur in other studies such as in Daehler & Carino (2000) and Křivánek & Pyšek (2006). There are several non-exclusive explanations to this finding. First, the species rejected could be in fact potential invaders with small residence time or with long lag phases, therefore, needing more time to pass from casual to invasive status (Crooks 2005). As other authors have demonstrated, minimum residence time is one of the most important factors that should be considered in evaluating invasion success (Pyšek & Jarosík 2005). Another reason could be inappropriate classification of species as casual in the Atlas of Invasive Plant Species in Spain (Sanz-Elorza *et al.* 2004) when they could be considered invasive. For example, the casual classified *Ligustrum lucidum* has recently experienced a high population growth in localities near Barcelona (Gassó, unpublished data) and could be locally classified as invasive. Finally, another explanation for the large number of casual species misclassifications could be a consequence of the high weighting that the WRA gives to some variables that are not those most related with invasion status (Table 6.1). In fact, risk has two components: likelihood of invasion and consequences. While the likelihood of invasion is related to the invasion status, the consequences of the invasion are related to actual or undesired impacts. However, other studies have shown that quantitative risk evaluation systems only based on invasion likelihood would have almost the same performance as the current WRA (Caley & Kuhnert, 2006).

Characteristics related to dispersal capacity are highly related to invasion status. Contaminant and bird dispersed species are prone to becoming invasive, as previous studies have demonstrated (Rejmánek & Richardson 1996, Richardson *et al.* 2000b, Lloret *et al.* 2005). On the other hand, intentional dispersal by humans is related with casual status. Species intentionally introduced in new regions (e.g. for agricultural purposes or as ornamentals) often manage to jump into natural ecosystems and survive; becoming casual species, but their persistence depends on the constant influx of more individuals. This result is in accordance with the intention of the first question of the WRA; "Is the species highly domesticated?". If answering "yes" to this question, the final score becomes lower, so the more domesticated is an species, the lower the invasion risk, considering that plants selected and bread by humans for many generations to grow in a cultivated environment have a handicap that might limit the species survival in the wild (Daehler & Carino 2000). However, a species that is highly domesticated might have a higher propagule pressure, and many studies have demonstrated that propagule pressure is one of the most important factors related to invasion success (Williamson 1996, Lockwood *et al.* 2005). For example, Pyšek *et al.* (2005) found frequent planting to be correlated to invasive success, because the more times the species has been introduced (i.e. high domestication), the higher its probability of being successfully dispersed and spread. Thus considering propagule pressure, there is a positive relationship between intentional dispersal (question 7.02) and the final WRA score. Indeed, we consider that there is a contradiction between the question regarding intentional dispersal and the one addressing domestication (question 1.01). More research is needed to elucidate the effects of domestication and propagule pressure on invasion likelihood, so that non-contradictory questions can be incorporated into the WRA.

We obtained a conspicuous result concerning the difference between invasion likelihood and impact: the capacity of creating a fire hazard was negatively related to invasion status. Therefore, fire risk generation does not appear to be a factor that increases the probability of spread, as there are more species with fire generation capacity among casual species than among invasive. Nevertheless, the capacity of creating a fire hazard is positively related to the WRA score, because it is an undesirable trait, especially in the Mediterranean region where fire is an important inherent disturbance and plants with this capacity could cause major impacts. So, with this example, we can highlight the importance of including impact questions in a Risk Assessment, because many plants currently classified as casuals, if spread in the future, could generate significant impacts.

Finally, concerning the viability of applying the WRA scheme, we would like to stress that many questions require very specific information that in many cases, especially for casual species, has not been documented yet. Those species that are widely invasive over the world have been studied considerably, thus there is generally more information about invasive species than casual species. For some characteristics, information is lacking or is very difficult to obtain for most of the taxa even if there is clear evidence of their importance in successful invasions. Examples of such traits are hybridization (Vilà *et al.* 2000), allelopathy (Callaway & Ridenour 2004), release of natural enemies (Colautti *et al.* 2004), self compatibility (Daehler 1998b), and potential impacts (e.g. pest and pathogens).

In conclusion, we found that the WRA scheme is quite accurate to discriminate invasive species but not so for casual species when applied to the Mediterranean region. Moreover, having detected some incongruities between invasion likelihood questions and impact questions, we suggest that a separate analysis should be done to evaluate these two risk components, as this would provide more useful information, especially for management. Concerning invasion likelihood, more research is needed to determine if differences between casual and invasive are due to differences in biological traits, or whether it is a matter of propagule pressure and residence time. This study represents a first step towards the construction of a Mediterranean Basin WRA.

Discussió general

Mesura de l'èxit de les invasions

L'èxit d'invasió és un concepte amb dos components: l'èxit de les espècies al·lòctones a l'àrea receptora i el grau d'invasió d'un lloc determinat. En aquesta tesi, hem integrat aquests dos components utilitzant diferents aproximacions i diferents escales espacials per aclarir quins factors ecològics els afecten i com estan relacionats.

Hem estimat el grau d'invasió com la riquesa de plantes invasores a escala regional (UTM 10x10 km), en l'àmbit espanyol, i com a riquesa de plantes al·lòctones a escala local (parcel·les) en diferents tipus d'hàbitat, en l'àmbit català. A escala regional, hem detectat que les àrees amb el grau d'invasió més elevat d'Espanya es troben a la costa del nord-est, d'acord amb dades prèvies de Catalunya (Pino *et al.* 2005). A escala local, estudis anteriors (Vilà *et al.* 2007) ja havien demostrat que els hàbitats antròpics tenen la riquesa d'espècies al·lòctones més elevada. A aquesta escala, el nostre estudi ha contribuït a demostrar que els factors de context mesurats a escala d'UTM poden modificar el grau d'invasió en els hàbitats.

L'èxit de les espècies invasores ha estat tradicionalment mesurat segons l'abundància local o regional, o rang de distribució actual en la regió envaïda (Mack *et al.* 1996). Hi ha un ampli ventall de mesures per estimar l'èxit dels invasors, variant l'escala espacial i l'estadi del procés d'invasió (Pyšek *et al.* 2006). La majoria d'aquestes mesures són estàtiques; mostren una fotografia del patró d'invasió en un moment donat, però no ens informen de la posició d'aquesta fotografia dintre del procés d'invasió en una regió donada. En aquesta tesi, hem utilitzat diverses aproximacions per valorar l'èxit de les espècies des d'un punt de vista estàtic i dinàmic, i a diferents escales espacials. Aquesta tesi s'ha focalitzat pricipalment en l'últim estadi de la invasió: l'expansió de l'espècie. Des d'un punt de vista estàtic, hem avaluat l'èxit de les espècies en relació a la mida del rang actual, mesurat segons el número d'UTMs on l'espècie és present actualment a Espanya. Per incrementar la fiabilitat i la precisió de la mesura de l'èxit de les espècies, proposem utilitzar el grau d'ocupació (proporció del rang de distribució potencial actualment ocupat). Des d'un punt de vista dinàmic, hem calculat la taxa d'expansió, una mesura que integra els rangs actuals i potencials amb el temps de residència. Aquests descriptors utilitzats per mesurar l'èxit de les espècies classifiquen les espècies invasores de manera diferent (taula 7.1). Aquestes diferències mostren les dificultats per definir l'èxit de les espècies i la seva dependència d'una complexa xarxa de factors que poden afavorir-lo de diverses maneres.

Table 7.1 Classificació de les cinc espècies invasores amb més èxit i les cinc amb menys èxit a Espanya d'acord amb els diversos descriptors que hem fet servir en aquesta tesi.

	Rang actual	Grau d'ocupació	Taxa d'expansió
Més èxit	*Sorghum halepense*	*Robinia pseudoacacia*	*Amaranthus powellii*
	Robinia pseudoacacia	*Sorghum halepense*	*Austrocylindropuntia subulata*
	Amaranthus retroflexus	*Amaranthus retroflexus*	*Fallopia baldschuanica*
	Conyza canadensis	*Eucalyptus globulus*	*Araujia sericifera*
	Amaranthus blitoides	*Amaranthus blitoides*	*Achillea filipendulina*
Menys èxit	*Baccharis halimifolia*	*Echinochloa oryzoides*	*Lippia filiformis*
	Senecio inaequidens	*Elodea canadensis*	*Tradescantia fluminensis*
	Reynoutria japonica	*Opuntia dillenii*	*Datura innoxia*
	Elodea canadensis	*Tradescantia fluminensis*	*Sophora japonica*
	Sophora japonica	*Senecio inaequidens*	*Tropaeolum majus*

La figura 7.1 il·lustra els components de l'èxit d'invasió i els seus factors d'influència i interaccions a través d'una extensió del diagrama de la figura 1.1. Algunes d'aquestes interaccions han estat analitzades en aquesta tesi per la primera vegada, com per exemple: (1) la relació entre l'èxit d'invasió i el grau d'invasió, (2) la interacció entre l'amplitud i la posició de nínxol de les espècies, i (3) l'efecte dels trets vitals de les espècies en l'amplitud i la posició de nínxol. D'acord amb el que hem detectat, els factors humans són els determinants més importants de l'èxit de les invasions, no només quant a la introducció de noves espècies sinó també pel que fa a la seva expansió a través d'accions humanes i pertorbacions antròpiques. La pressió de propàgul, el temps de residència, i la pertorbació antròpica són, per tant, els factors que més condicionen l'èxit de les espècies i el grau d'invasió a Espanya. Tot i així, els factors tradicionalment considerats característiques de les espècies i condicions ambientals (clima i paisatge) s'ha descobert que tenen un paper secundari, però tanmateix important, en la variació de l'extensió i la magnitud d'aquestes invasions. En les seccions següents exposarem les troballes més importants de la tesi en relació amb les connexions presentades en el diagrama de la figura 7.1.

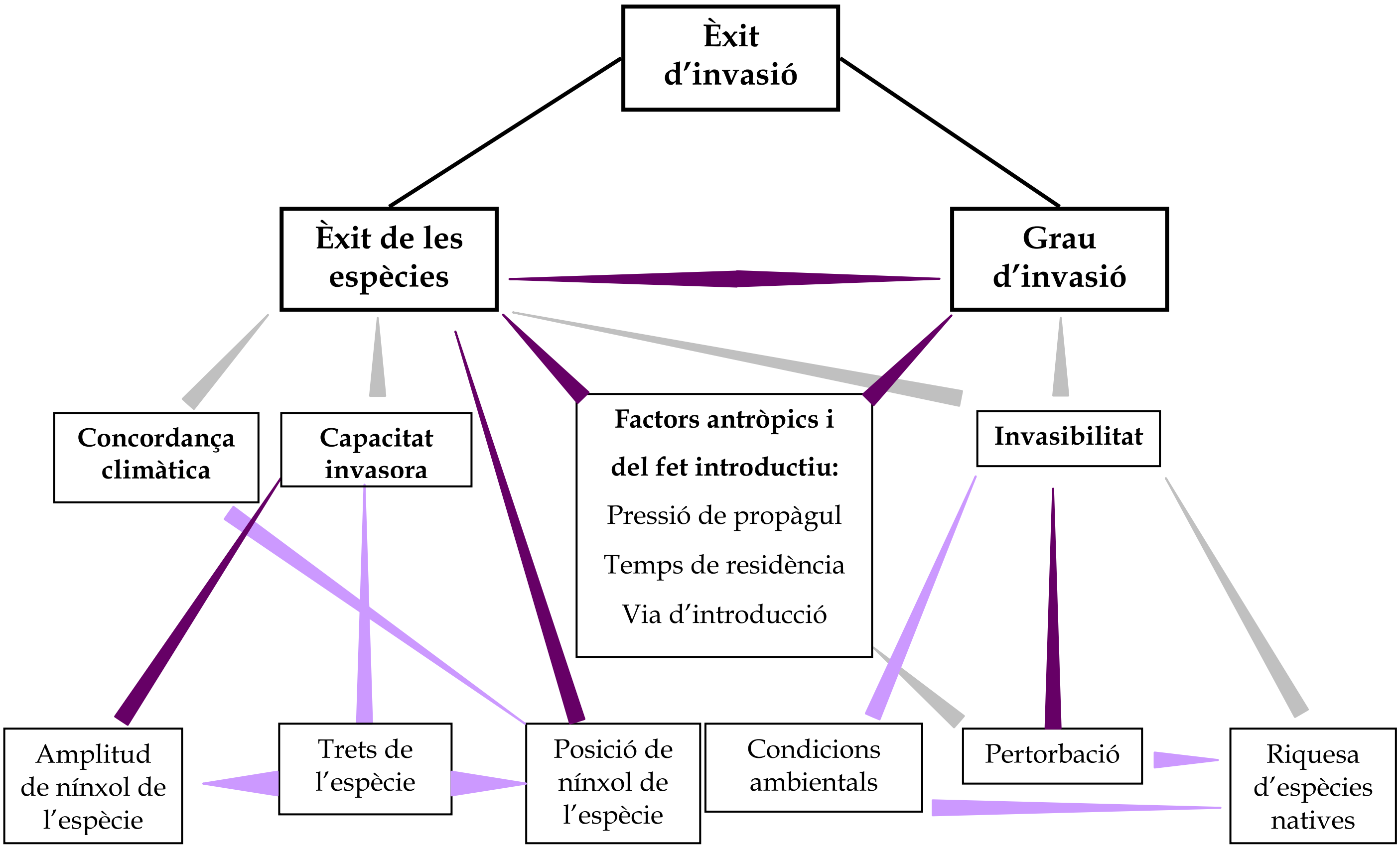

Figure 7.1 Diagrama dels components de l'èxit de les invasions (èxit de les espècies i grau d'invasió) and ecological factors of influence. Les fletxes grises indiquen les relacions hipotètiques que no han estat testades en aquest treball (o no significatives en el cas de la concordança climàtica i l'èxit de les espècies). Les fletxes porpres indiquen relacions directament testades. La intensitat del porpre incrementa amb la importància de cada associació d'acord el que s'ha trobat en aquesta tesi.

Factors associats a l'èxit de les espècies invasores

Factors del fet introductiu

El temps de residència és un factor històric que, d'acord amb els nostres resultats, hauria de ser tingut en compte quan s'avalua la capacitat invasora d'una espècie. Les espècies recentment introduïdes mostren distribucions més restringides perquè han tingut menys oportunitats d'expandir els seus rangs. El temps de residència representa una dimensió de la pressió de propàgul: com més temps fa que una espècies està present en una regió, més propàguls seran disseminats per les activitats humanes i més grans serà la seva expansió espacial i la probabilitat de fundar noves poblacions (Hamilton *et al.* 2005, Pyšek i Jarosík 2005, Rejmánek *et al.* 2005a). Les nostres anàlisis inicials van revelar que la relació entre el temps de residència i la mida del rang desapareix quan es consideren espècies introduïdes fa més de 100 anys (capítol 1). Hem hipotetitzat, aleshores, que aquest resultat podria ser degut al fet que aquestes espècies haurien arribat ja a la seva àrea màxima d'expansió a Espanya, d'acord amb la seva capacitat invasora potencial i les característiques de l'àrea receptora. Tanmateix, tot i que els resultats han confirmat la nostra hipòtesi que el grau d'ocupació depèn del temps mínim de residència, hi ha un grup d'espècies introduïdes fa molt de temps (més de 100 anys) que no ha ocupat tot el seu hàbitat potencial. Aquest fenomen podria ser explicat per diferències en les seves taxes d'expansió. Hem constatat, en efecte, que les espècies introduïdes antigament i amb baixa ocupació s'expandeixen lentament, la qual cosa podria estar relacionada amb la història de l'ús que els humans fan d'aquestes espècies; un temps de latència entre la data de la primera introducció i l'inici real de la fase exponencial de la invasió (Cousens i Mortimer 1995, Crooks *et al.* 2005). Les fases de latència podrien dependre de l'escala d'observació: encara que la taxa de creixement poblacional tingui lloc a escala local, pot no correspondre a la mateixa taxa d'expansió regional (Pyšek i Hulme 2005).

Des del punt de vista de l'efecte directe de la pressió de propàgul, hem trobat que la dispersió intencionada per part dels humans està relacionada amb l'estatus d'espècie adventícia (capítol 5). Les espècies introduïdes de manera intencionada en noves regions (amb finalitats agrícoles o ornamentals) sovint aconsegueixen saltar als ecosistemes naturals i sobreviure, esdevenint així espècies adventícies. La seva persistència, però, depèn del flux constant de més individus introduïts pels humans. A més a més, hem detectat molts altres factors relacionats amb la pressió de propàgul que són importants pel grau d'invasió regional i local. Els exposem a continuació i discutim en les seccions següents que fan referència al grau d'invasió.

Concordança climàtica: l'efecte de l'origen geogràfic

Més de la meitat de les plantes invasores d'Espanya venen de regions mediterrànies, tropicals o subtropicals (Sanz-Elorza *et al.* 2004). En les nostres anàlisis, l'origen geogràfic està molt relacionat amb la posició de nínxol: les espècies procedents de regions càlides seran presents en zones costaneres molt humanitzades amb poca variació de temperatura entre hivern i estiu. La influència de l'origen en la posició de nínxol dóna suport a la teoria de la concordança climàtica (Brown 1989, Williamson 1996, Panetta i Mitchell 1991, Scott i Panetta 1993), segons la qual les espècies que venen de regions amb condicions climàtiques similars a les de la regió envaïda seran més propenses a l'èxit.

Trets de les espècies

D'acord amb les nostres anàlisis (veure capítols 1, 2, i 4) i d'acord amb altres autors (Pyšek i Richardson 2007), només algunes característiques vitals semblen estar consistentment associades a l'èxit d'invasió en plantes. Els patrons generals que hem detectat són:

El tipus de dispersió ha estat clàssicament considerada un determinant important de la capacitat invasora (Vermeij 1996, Richardson *et al.* 2000, Kolar i Lodge 2001): En moltes anàlisis regionals, la dispersió pel vent (anemocòria) s'ha demostrat que és la més efectiva per l'expansió dels invasors (Prinzing *et al.* 2002, Lloret *et al.* 2003). Nosaltres hem constatat, en efecte, que les espècies invasores dispersades pel vent són les més àmpliament esteses a Espanya, i que tenen la taxa d'expansió més ràpida. De tota manera, no hem trobat cap indici de relació entre el tipus de dispersió i l'amplitud de nínxol de les espècies.

També hem conclòs que el creixement clonal està relacionat amb la taxa d'expansió de les espècies invasores i amb la seva tolerància climàtica. El creixement clonal afecta l'èxit de les espècies a escala local afavorint el creixement i l'expansió de les poblacions en estadis inicials de la invasió, mentre que la dispersió per vent contribueix a crear nous focus d'invasió i expansió a escala regional (Pyšek 1997, Lloret *et al.* 2005, Pyšek i Richardson 2007).

Les espècies de vida curta han estat considerades millors invasores que les espècies de vida llarga (Pyšek *et al.* 1995, Cadotte i Lovett-Doust 2001, Pyšek i Richardson 2007) a causa de la reproducció anual o de la supervivència en condicions adverses gràcies a la dormició de les llavors (Crawley 1997). Nosaltres hem resolt que les espècies invasores de vida curta es troben en les condicions ambientals més extenses en el territori i mostren una tolerància més gran a la variació climàtica i al tipus de vegetació que les espècies de vida llarga.

La capacitat de fixació de nitrogen podria considerar-se relacionada amb l'èxit de les espècies, a causa de l'avantatge competitiu que representa en sòls pobres (Pyšek i Richardson 2007). Tanmateix, el cost d'aquesta simbiosi causa un problema de compromisos als fixadors de nitrogen, i així les espècies poden beneficiar-se d'aquesta capacitat només en sòls deficients en nitrogen (Fitter 1997). Aquesta és la raó per la qual hem detectat més espècies sense la capacitat de fixar nitrogen en llocs costaners amb gran pressió humana, on normalment el sòl no és pobre en nitrogen, i que els no fixadors de nitrogen tenen amplituds de nínxols més grans (Fitter 1997) que els fixadors.

Factors associats al grau d'invasió

Factors antròpics

Les alteracions induïdes pels humans han estat tradicionalment considerades un factor clau per la diversitat de cobertes del sòl, i també, pel procés d'invasió (Elton 1958, Kowarik 1990, Jenkins 1996, Pyšek 1998a, Hobbs 2000). Com a conseqüència, la flora de les àrees urbanes i els seus voltants és habitualment més rica en espècies al·lòctones que la flora de les àrees naturals (Stadler *et al.* 2000, Chocholouškova i

Pyšek 2003). Tal i com altres estudis han apuntat (Kowarik 1990, Tyser i Worley 1992, Pyšek 1998, Hobbs 2000, Vilà *et al.* 2003), els ecosistemes modificats pels humans, com els assentaments humans, els camps abandonats, les vores de camins i carreteres, les vores i àrees properes a cultius o plantacions, són més propenses a la invasió que els hàbitats naturals o seminaturals.

Nosaltres hem trobat, en efecte, que la riquesa regional d'espècies invasores és més elevada en àrees construïdes amb una alta densitat de carreteres i vies ferroviàries (capítol 1). A escala local, la distància a les carreteres afecta a la riquesa d'espècies natives i al·lòctones, essent, en la majoria dels hàbitats, més alta com més a prop de les carreteres (capítol 3) es troba. Tot i així, la tendència és més generalitzada pel que fa a la riquesa d'espècies al·lòctones, com s'ha demostrat prèviament en altres estudis (Tyser i Worley 1992, Lippe i Kowarik 2006). Les plantes al·lòctones ruderals, normalment herbes anuals o perennes, són típiques de llocs alterats perquè són pioneres en la successió vegetal (Prach *et al.* 2001), i les carreteres i els hàbitats que les envolten són els seus vectors habituals d'introducció i dispersió (Schmidt 1989, Lippe i Kowarik 2006).

Topografia, clima i paisatge

L'altitud mitjana i la pluviositat anual afecten adversament la riquesa de plantes invasores a escala regional, com també s'ha constatat en altres regions com Europa Central (Mihulka 1998, Pyšek *et al.* 2002), a Xile (Pauchard i Alaback 2004), i a Estats Units (Stohlgren *et al.* 2005, Chong *et al.* 2006): Les zones de baixa altitud estan exposades a una pressió de propàgul més alta que les zones muntanyoses (Becker *et al.* 2005). A més a més, l'altitud mitjana afecta negativament la temperatura mitjana anual, que també està estretament relacionada amb la riquesa de plantes invasores (Pino *et al.* 2005, Chytrý *et al.* 2008a). D'aquesta manera, climes càlids i secs semblen ser avantatjosos per les plantes invasores a Espanya. La distància a la costa condiciona desfavorablement la riquesa de plantes invasores. Prop de la costa trobem climes més suaus i una alta presència humana, i per tant, una alta pressió de propàgul i grau de pertorbació.

A escala local, constatem que les variables climàtiques estan més associades a la riquesa d'espècies natives que la d'al·lòctones. En la majoria dels hàbitats, la riquesa d'espècies natives incrementa amb la pluviositat anual i decreix amb la temperatura mitjana anual. Contràriament, temperatura i pluviositat només són significatives per la riquesa d'espècies al·lòctones en un o dos tipus d'hàbitats, respectivament.

En la majoria dels hàbitats, la riquesa d'espècies natives afecta positivament la proporció de coberta forestal i només s'associa als matollars i els cultius en hàbitats antròpics. Els canvis en la riquesa d'espècies natives associats a variables climàtiques i de paisatge poden ser determinats per patrons biogeogràfics complexos, però també per accions humanes que causen l'expansió de les espècies generalistes i ruderals i enrareixen les especialistes (McKinney *et al.* 1999, 2006). Per contra, la riquesa d'espècies al·lòctones s'associa desfavorablement amb la proporció de cobertes forestals i de matollar. Encara que el nostre estudi està basat en diferències de grau d'invasió i no en diferències d'invasibilitat (Lonsdale 1999), el que hem detectat suggereix que la pèrdua d'hàbitat natural pot afavorir la introducció i l'expansió d'espècies al·lòctones (Brothers i Spingarn 1992) i remarca la hipòtesi de l'alta resistència a la invasió dels ecosistemes llenyosos mediterranis (di Castri 1989, Casasayas 1990).

Integració i anàlisi del risc d'invasió

Amb la integració de les aproximacions a l'èxit de les espècies i el grau d'invasió hem descobert que, en general, les espècies invasores amb distribucions restringides no tenen requeriments ambientals particulars, sinó que apareixen en hàbitats alterats envaïts per espècies generalistes i àmpliament distribuïdes, i a més a més, són menys tolerants a les condicions de climatologia i del tipus de vegetació. Amb la nostra aproximació a les propietats de nínxol, detectem que les condicions ambientals més comunes i àmpliament distribuïdes a Espanya tenen un grau mitjà de pertorbació, i que les espècies que poden sobreviure i estendre's en aquestes condicions assoleixen distribucions àmplies, encara que no necessàriament tinguin una àmplia tolerància de nínxol (capacitat invasora). Així, proposem que hi ha una relació directa entre la posició de nínxol i l'èxit de les espècies (Figura 7.1), independent de la capacitat invasora, i que aquesta relació està intrínsecament condicionada per les condicions generals de la regió. D'altra banda, una àmplia tolerància climàtica ofereix als invasors una probabilitat més alta d'èxit, perquè tenen un potencial intrínsec per envair (capacitat invasora), i d'aquesta manera, tenen el potencial per expandir-se per Espanya o altres regions.

Com ja hem mencionat, la majoria d'àrees envaïdes a Espanya són costaneres i alterades. No només estan envaïdes per espècies àmpliament distribuïdes, sinó que són punts calents d'espècies invasores de distribució restringida, especialment espècies clonals provinents de regions càlides. Com que en el primer capítol de la tesi també s'ha indicat que les espècies amb rangs de distribució petits són les que s'han introduït més recentment, podem argumentar que els punts calents d'invasió poden ser deguts a un grup de factors majoritàriament relacionats amb els humans, com: (1) gran pressió de propàgul i acumulació de noves introduccions, (2) alta pertorbació antròpica que altera el cicle de nutrients i la riquesa d'espècies natives, (3) l'efecte de la facilitació entre invasions (en anglès: *invasional meltdown)*, que es dóna quan les espècies invasores establertes en un lloc faciliten l'establiment i l'expansió d'altres invasores, i finalment (4) les condicions climàtiques suaus que afavoreixen les espècies amb poca tolerància a les variacions climàtiques.

Després de calcular el rang potencial de cada espècie i projectar-lo a tota la regió amb la mateixa metodologia que en el capítol 2, podem sumar-los tots per dibuixar un mapa de la riquesa potencial de plantes invasores projectat a tot Espanya (Figura 7.2). Aquest mapa ens dóna una idea del grau d'invasió a escala regional que trobaríem a Espanya si totes les plantes invasores que ja estan instal·lades a la regió assolissin les seves distribucions potencials.

Encara que aquest mapa de predicció està restringit per les variables ambientals i els models utilitzats aquí, i no té en compte molts altres factors com els canvis en la pressió de propàgul, les noves introduccions d'espècies, el ritme de l'expansió i la invasió de les plantes al·lòctones ja introduïdes, la capacitat de dispersió de les espècies, ni els canvis climàtics o d'usos del sòl, és el primer intent de fer una aproximació espacial al risc d'invasió a l'Espanya peninsular. Aquest mapa de risc d'invasió, combinat amb una aproximació recent al risc d'invasió dels hàbitats a Europa (Chytrý *et al.* 2008c) i l'aplicació d'un protocol d'avaluació de riscos a nivell d'espècie (ex. WRA), podrien ser bones eines per als gestors a l'hora de decidir el control d'espècies i regions.

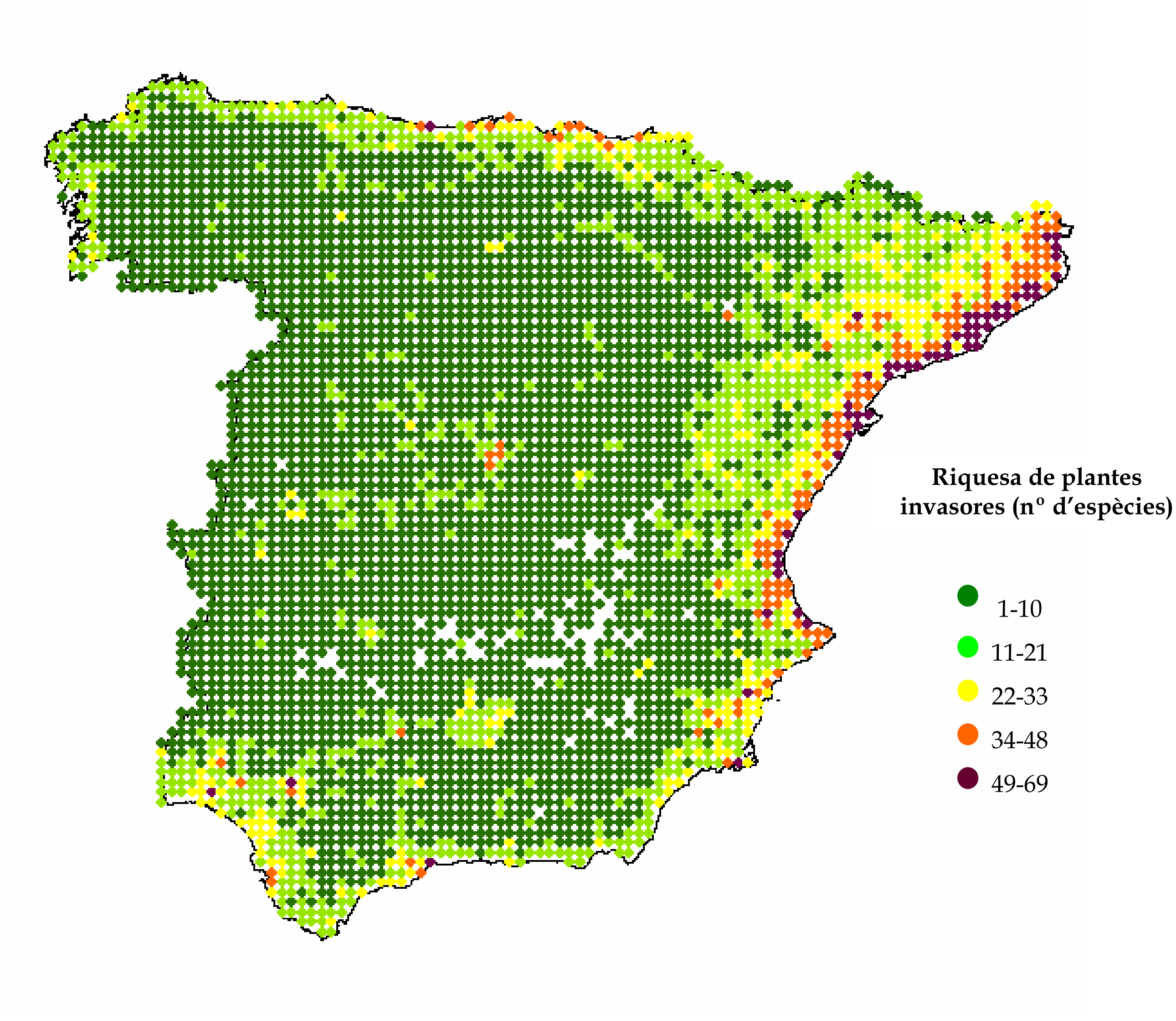

Figure 7.2
Riquesa regional potencial de plantes invasores extesa a tota l'Espanya peninsular. Les àrees costaneres podrien esdevenir molt envaïdes, especialment a la Mediterrània, així com les zones urbanes, agrícoles i de ribera. Els punts blancs representen llocs on cap de les espècies de plantes actualment invasores a Espanya i inclosa en els models podria trobar-s'hi.

Implicacions per la gestió

En general, les plantes invasores a Espanya semblen estar en un estadi inicial de la invasió, perquè la majoria de les espècies no han assolit encara la meitat dels seus rangs potencials. Així, hauríem de fer més atenció a aquelles plantes amb un gran rang potencial però un grau d'ocupació baix, perquè considerem que és només una qüestió de temps que assoleixin la seva màxima extensió de distribució. A més a més, les nostres troballes donen suport a la idea que els esforços de gestió s'haurien de focalitzar en el control de les poblacions d'espècies de vida curta, clonals i dispersades pel vent, tenint en compte que les espècies amb aquestes característiques tenen rangs de distribució més amples i s'expandeixen més de pressa.

Des del punt de vista regional, hauríem de posar més atenció als llocs costaners i antròpics perquè semblen no estar saturats i podrien servir com a àrees focals per a l'expansió d'espècies provinents de regions climàtiques similars cap a àrees naturals no costaneres. Així mateix, els hàbitats antròpics (per exemple les vores de carreteres) contenen més espècies al·lòctones que els naturals. Finalment, creiem que els hàbitats llenyosos mediterranis (boscos i matollars d'espècies perennes) haurien de ser preservats de la fragmentació i la pertorbació perquè la riquesa d'espècies al·lòctones augmenta amb la pèrdua de coberta llenyosa mentre que la riquesa de natives disminueix.

Evitar les introduccions és, de lluny, el mètode menys car i més fiable per lluitar contra les invasions. En l'últim capítol d'aquesta tesi, hem afirmat que el sistema d'avaluació de riscos d'invasores (Australian Weed Risk Assessment, WRA) és extremadament restrictiu quan a la identificació d'espècies al·lòctones amb potencial invasor a Espanya. El WRA és una bona eina per discriminar les espècies invasores, però no les adventícies, i indica que probablement les adventícies podrien esdevenir invasores en el futur. A través de l'exploració d'espècies amb el WRA hem detectat algunes inconsistències entre les qüestions de probabilitat d'invasió i les d'impacte. Suggerim que s'hauria de fer una anàlisi per separat d'aquests dos components del risc, perquè això proporcionaria informació més útil i concreta, especialment per a la gestió.

Perspectives futures

La majoria de la recerca en biologia de les invasions vegetals està enfocada a les espècies invasores i en l'estadi d'expansió, i aquesta tesi reflecteix aquesta tendència. Són necessaris més estudis sobre els diferents estadis del procés d'invasió, especialment del ritme del procés, dels temps de latència i de la dinàmica de les poblacions a escala local. A més a més, com que s'ha demostrat que el tipus d'hàbitat i les condicions de paisatge són molt importants per la presència d'espècies al·lòctones i la seva expansió, s'haurien de fer més esforços per predir com els canvis d'usos del sòl poden afectar la dinàmica de les invasions. En la mateixa direcció, la recerca futura hauria d'estar focalitzada cap a la vinculació del canvi global amb l'expansió d'espècies invasores: per exemple, estimant els rangs de distribució potencials i les taxes d'expansió d'acord amb l'ús que els humans fem de les espècies, i segons futurs escenaris climàtics i d'usos del sòl.

General discussion

Measuring invasion success

Invasion success is a concept with two components: alien species success in the receptor area and the level of invasion of a given site. In this thesis, we integrated these two components by using different approaches at different spatial scales to disentangle which ecological factors affect them and how are they related.

We estimated the level of invasion as the invasive plant richness at the regional scale (i.e. UTM 10x10 km) across Spain and as alien plant richness at the local (i.e. plot) scale in different habitat types in Catalonia. At the regional scale, we found that the areas with the highest level of invasion in Spain are in the NE coast, in accordance with previous findings on Catalonia (Pino *et al.* 2005). At the local scale, previous studies (Vilà *et al.* 2007) already showed that anthropogenic and trampled habitats have the highest alien species richness. At this scale, our study contributed to show that context factors measured at UTM scale can modulate the level of invasion in habitats.

Success of invasive species has been traditionally measured as local or regional abundance or current distribution range in the invaded regions (Mack *et al.* 1996). There is a wide variety of measures to estimate the success of invaders, varying in spatial scale, and the invasion process stage (Pyšek *et al.* 2006). Most of these measures are static, showing a picture of the invasion pattern for a given time step, but they do not inform about the position of this picture within the invasion process in a given region. On this thesis, we used different approaches to estimate species success, from a static to a dynamic point of view, and at different spatial scales. The thesis mainly focused on the last invasion step: species spreading. From a static point of view, we evaluated species success as the current range size, measured as the number of UTMs where the species is currently present in Spain. To increase the reliability and accuracy when measuring species success, we propose using the species occupancy (i.e. the proportion of the potential distribution range currently occupied). From a dynamic point of view, we calculated the spread rate, a measure that integrates the current and potential ranges with residence time. These different descriptors used for measuring species success rank invaders somewhat differently (Table 7.1). These differences show the difficulties of defining invasion success and their dependence from a complex web of factors, which can favour species success by contrasting ways.

Table 7.1 Ranking of the five most and the five less successful invasive plant species in Spain according to the different descriptors of invasion success used on this thesis.

	Current range	Occupancy	Spread rate
Most successful	*Sorghum halepense*	*Robinia pseudoacacia*	*Amaranthus powellii*
	Robinia pseudoacacia	*Sorghum halepense*	*Austrocylindropuntia subulata*
	Amaranthus retroflexus	*Amaranthus retroflexus*	*Fallopia baldschuanica*
	Conyza canadensis	*Eucalyptus globulus*	*Araujia sericifera*
	Amaranthus blitoides	*Amaranthus blitoides*	*Achillea filipendulina*
Least successful	*Baccharis halimifolia*	*Echinochloa oryzoides*	*Lippia filiformis*
	Senecio inaequidens	*Elodea canadensis*	*Tradescantia fluminensis*
	Reynoutria japonica	*Opuntia dillenii*	*Datura innoxia*
	Elodea canadensis	*Tradescantia fluminensis*	*Sophora japonica*
	Sophora japonica	*Senecio inaequidens*	*Tropaeolum majus*

Figure 7.1 illustrates the invasion success components and their driving factors and interactions through an enlarged diagram from Figure 1.1. Some of these interactions were, to our knowledge, analysed here for the first time, such as (1) the relationship between species success and level of invasion, (2) the interaction of species niche breadth and position with species success, and (3) the effect of species traits over species niche breadth and position. According to our findings, human factors are the most important in determining invasion success not only by introducing them but also spreading them through human actions and antropogenic disturbances. Propagule pressure, residence time, and anthropogenic disturbance are, therefore, the factors that mainly drive both species success and the level of invasion in Spain. However, traditionally hypothesized factors such as species traits and environmental conditions (i.e. climate and landscape) have been found to have a secondary but anyway important role in modulating the extent and magnitude of these invasions. On the following sections we will expose the major thesis findings in relation to the connections presented in Figure 7.1 diagram.

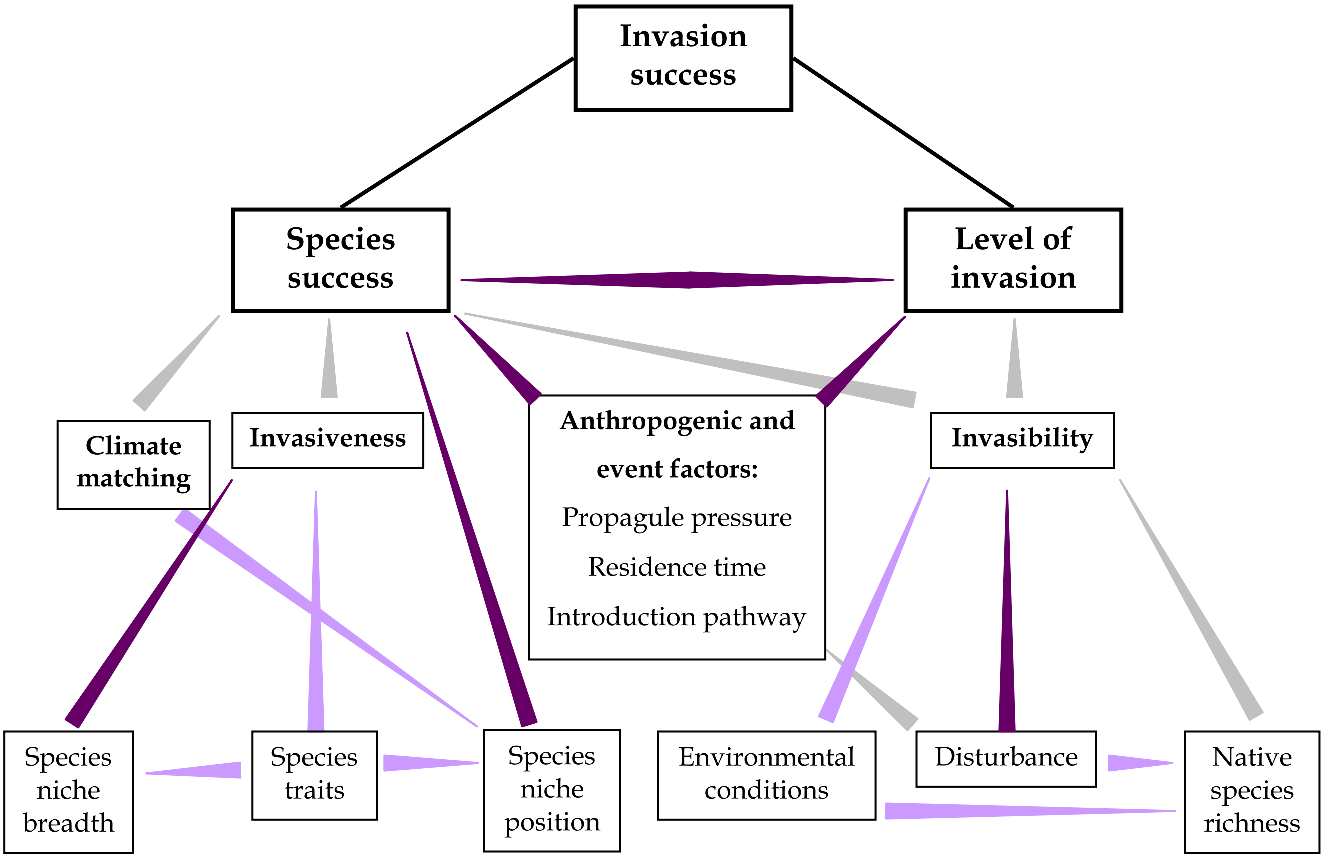

Figure 7.1 Diagram of the invasion success components (i.e. species success and level of invasion) and ecological factors of influence. Grey arrows show hypothetic relationships not tested on this work (or found as not significant in the case of climate matching and species success). Purple arrows show the relationships directly tested. The intensity of purple increases with the importance of each association according to this thesis.

Factors associated to success of invaders

Invasion event factors

Residence time is an historical factor that, according to our results, should be taken into account when evaluating if a species is more invasive than another. Species recently introduced showed more restricted distributions because they have had less opportunity to expand their range. Residence time represents a dimension of propagule pressure: the longer the species is present in the region, the more propagules are spread by human activities and the higher the spatial spread and the probability of founding new populations are (Hamilton *et al.* 2005, Pyšek & Jarosík 2005, Rejmánek *et al.* 2005b). Our analyses revealed that the relationship between residence time and range size disappears when considering species introduced more than 100 years ago (chapter 1). We hypothesised, then, that this result could be due to the fact that these species would have already reached their maximum spreading area in Spain, according to their potential invasiveness and the characteristics of the recipient-area. However, even if the results confirmed our hypothesis that occupancy depended on minimum residence time, still a set of species introduced long time ago (more than 100 years) that have not yet occupied their entire potential suitable habitat. This phenomenon could be due to differences in their spread rates. We found, indeed, that species anciently introduced and with low occupancies spread slowly, what could be related to the history of use of species by humans; a time lag between the date of first introduction and the actual start of the exponential phase of the invasion (Cousens & Mortimer 1995, Crooks *et al.* 2005). The lag phase may depend on the scale of observation. Therefore, although population growth rate may occur in a discrete area, at local scale, this may not correspond to the regional spread rate (Pyšek & Hulme 2005).

From the point of view of the direct effect of propagule pressure, we found that intentional dispersal by humans is related with casual status. Species intentionally introduced in new regions (e.g. for agricultural purposes or as ornamentals) often manage to jump into natural ecosystems and survive; becoming casual species, but their persistence depends on the constant influx of more individuals introduced by humans. Moreover, we found many other factors related to propagule pressure being important for the regional and local level of invasion. They are exposed and discussed in the following sections.

Climate matching: the effect of geographical origin

More than half of the invasive plants in Spain come from Mediterranean, tropical or subtropical regions (Sanz-Elorza *et al.* 2004). On our analyses, geographical origin was highly related with niche position, being species coming from warm regions those present in highly humanized-coastal places with small temperature range between winter and summer. The influence of origin in species niche position supports the theory of climate matching (Brown 1989, Williamson 1996, Panetta & Mitchell 1991, Scott & Panetta 1993) to which species coming from regions with climatic conditions similar to those of the invaded region will be more successful.

Species traits

Only a few traits seem to be consistently associated with invasion success in plants using our different approaches (see chapters 1, 2 and 4) and according to other authors (Pyšek & Richardson 2007). However, we can highlight some found general patterns:

Dispersal syndrome has classically been screened as an important determinant of invasiveness (Vermeij 1996, Richardson *et al.* 2000, Kolar & Lodge 2001). In many regional analyses, wind dispersal (i.e. anemocoria) has been found to be the most effective for invaders to spread (Prinzing *et al.* 2002, Lloret *et al.* 2003). We found, indeed that invasive species dispersed by wind were the most widespread across Spain, and that they had the fastest spread rate. However, we did not find a relationship between dispersal syndrome and invasive species niche breadth.

Clonality was also found to be related to spread rate of invasive species and to climatic tolerance. Clonal growth might have an effect over species success at the local scale, favouring populations to grow and spread at early invasion stages while wind dispersal contributes to create new foci of invasion and spread at regional scale (Pyšek 1997, Lloret *et al.* 2005, Pyšek & Richardson 2007).

Short-lived species have been suggested to be better invaders over longer-lived (Pyšek *et al.* 1995, Cadotte & Lovett-Doust 2001, Pyšek & Richardson 2007) due to the yearly reproduction or survival in adverse conditions as dormant seeds (Crawley 1997). We found that short-lived invasive species occurred in the most widespread environmental conditions and they showed a higher tolerance to climatic and vegetation cover variation.

Nitrogen fixation capacity could be hypothesized as being related to species success because of the competitive advantage that it represents in poor soils (Pyšek & Richardson 2007). However, the cost of this symbiosis cause a severe trade-off problem to nitrogen fixers and species can benefit from this capacity only in nitrogen deficient soils (Fitter 1997), what explain that we found more nitrogen non-fixers in coastal places with high human pressure, where usually the soil is not poor in nitrogen, and that nitrogen non-fixers had wider niche breadths (Fitter 1997) than nitrogen fixers.

Factors associated to level of invasion

Anthropogenic factors

Man-induced disturbances have been traditionally considered a key factor for land cover diversity, and, in turn, for the invasion process (Elton 1958, Kowarik 1990, Jenkins 1996, Pyšek 1998a, Hobbs 2000). In consequence, flora of urban areas and their surroundings is usually richer in alien species than flora of natural areas (Stadler *et al.* 2000, Chocholouškova & Pyšek 2003). Man-modified habitats such as human settlements, old fields, roadsides, rangelands and areas near croplands or plantations are more prone to invasion than natural or seminatural habitats, as found in other studies (Kowarik 1990, Tyser & Worley 1992, Pyšek 1998a, Hobbs 2000, Vilà *et al.* 2003).

We found, indeed, that regional invasive species richness was higher in build-up areas with high density of roads and railways (chapter 1). At the local scale, distance to roads affected both native and alien species richness, being in most of the habitats, higher when closer to the roads (chapter 3). However, the trend is more generalized for alien species richness, as has already been shown in other studies (Tyser & Worley 1992, Lippe & Kowarik 2006). Alien ruderal plants, usually annual or perennial grasses, are typical in disturbed places because they are pioneers in plant succession (Prach *et al.* 2001), and roads and their surrounding habitats are their usual introduction and dispersal vectors (Schmidt 1989, Lippe & Kowarik 2006).

Topography, climate and landscape

Mean altitude and annual rainfall were negatively related with invasive plant richness at the regional scale, as it has also been found in Central Europe (Mihulka 1998, Pyšek et al. 2002), in South Central Chile (Pauchard & Alaback 2004), and in the United States (Stohlgren *et al*. 2005, Chong *et al.* 2006). Low altitudes have been found to have higher propagule pressure than highlands (Becker *et al*. 2005). Mean altitude is also negatively correlated with mean annual temperature, which has also been found to be closely related with invasive plant richness (Pino *et al.* 2005, Chytrý *et al.* 2008a). Therefore, warm and dry climates seem to be advantageous for invasive plants in Spain. Distance to the coastline was negatively related with invasive plant richness. Close to the coastline we find the mildest climates and high human presence, and therefore, a high propagule pressure and disturbance levels.

At the local scale, we found that climate variables were more associated to native than to alien species richness. In most habitats, native species richness increased with annual rainfall and decreased with mean annual temperature. In contrast, temperature and rainfall were only significant for the alien species richness in one and two habitat types, respectively.

In most habitats, native species richness was positively related to the proportion of forest land cover and it was associated to scrubland and cropland cover only in anthropogenic habitats. Changes in native species richness associated to climatic and landscape variables can be determined by complex biogeographic patterns, but also by human effects that might cause the spread of generalist ruderal species and the rarefaction of specialists (McKinney *et al.* 1999, 2006). In contrast, alien species richness was in general negatively associated to forest and shrub cover proportion. Although our study is based on differences on the level of invasion and not on differences in invasibility (Lonsdale 1999), our findings suggest that natural habitat loss can favour the introduction and spreading of alien species (Brothers & Spingarn 1992) and highlight the hypothesis of high resistance to invasion of woody Mediterranean ecosystems (di Castri 1989, Casasayas 1990).

Integration and risk analysis of invasion

From the integration of both species success and level of invasion approaches we learned that in general, invasive species with restricted distribution do not have particular environmental requirements, but that they occur in disturbed places invaded by generalist and widespread species and they are less tolerant to climatic and vegetation cover conditions. With our approach to niche properties, we found that the most common and widespread environmental conditions in Spain have a medium level of disturbance, and that species that can survive and spread in such conditions manage to become widespread themselves, even if they do not have a wide niche breadth (i.e. invasiveness). Thus, we propose that there is a direct relationship between niche position and species success (Figure 7.1), independent of species invasiveness and that this relationship is intrinsically modulated by the general conditions of the given region. From another side, a wide climatic tolerance offer invaders a higher probability of success because they have an intrinsic potential to invade (i.e. invasiveness), and therefore, they have the potential to spread through Spain or through other regions.

The most invaded areas in Spain, as we already mentioned, are coastal and disturbed. We found that they are not only invaded by widespread species but that they are the hot spots of restricted species, especially clonal species coming from warm regions. Because in the first chapter of the thesis we found as well that species with narrow range were those most recently introduced, we can argue that invasion hot spots can be caused by a group of factors mostly related to humans, such as: (1) a high propagule pressure and the accumulation of new introductions, (2) high anthropogenic disturbance that cause the alteration of nutrient cycles and a decrease of native species richness, (3) "invasional meltdown" effect (i.e. invasive species established in a place facilitate the establishment and spread of other invaders), and finally, (4) mild climatic conditions that favour species with low climatic tolerance.

After calculating each species potential range extended to the entire region with the same methodology than in chapter 2, we can add all of them to draw a map of potential invasive plant richness extended to the entire Spain (Figure 7.2). This map gives us an idea of the level of invasion at regional scale that we would find in mainland Spain if all the already installed invasive plants in the region would reach their potential distribution.

Although this prediction map is restricted by the environmental variables and the models used here, and it does not take into account other factors such as changes in propagule pressure, new species introductions, spread and invasion timing of already introduced aliens, species dispersal ability, neither land use or climatic changes, so far it is the first ever spatially-explicit approach of invasion risk in mainland Spain. This invasion risk map, combined with a recent approach of invasion risk of habitat types in Europe (Chytrý *et al.* 2008c) and the application of an accurate species-level risk assessment protocol (e.g. WRA) could be good tools for managers to decide controlling species and regions.

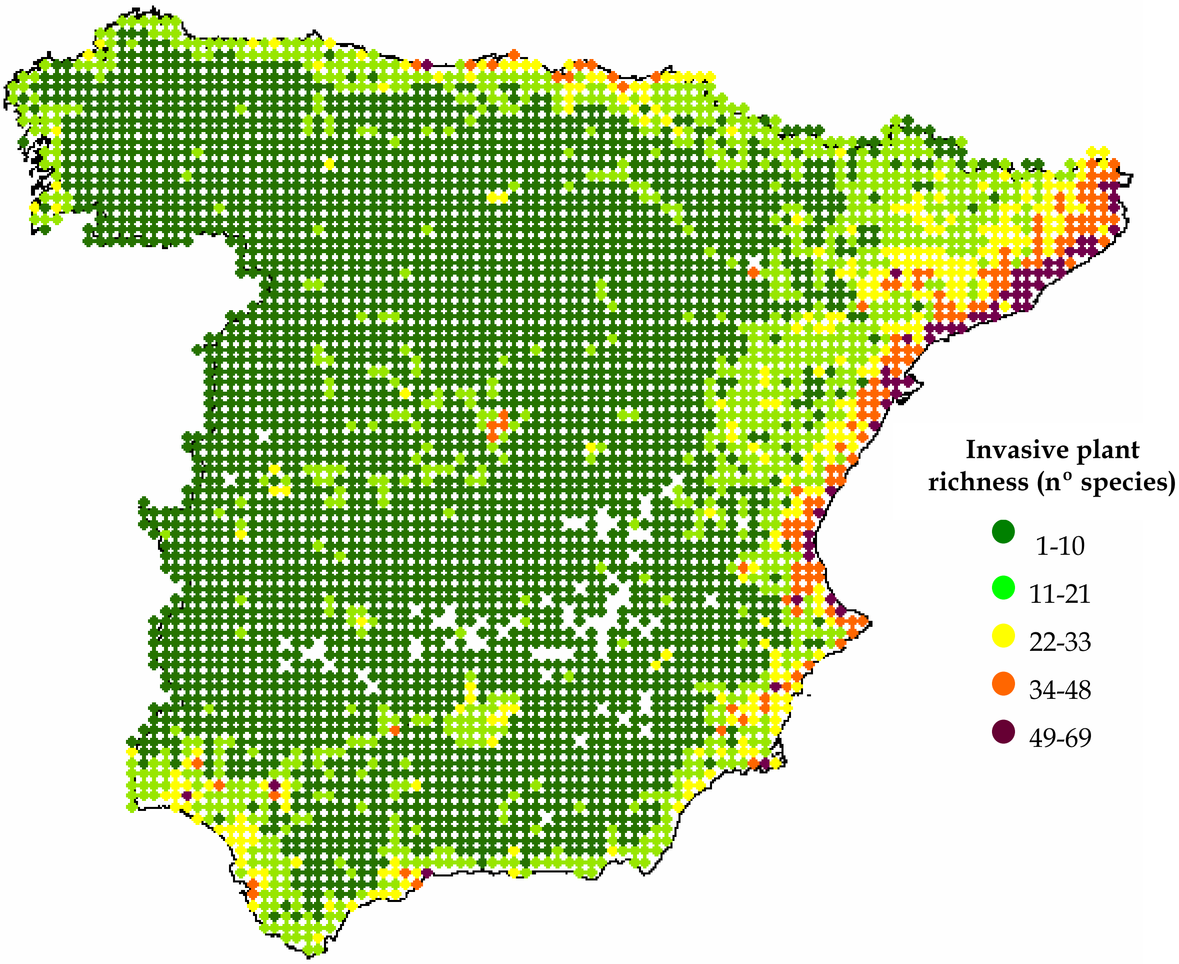

Figure 7.2
Potential regional invasive plant richness extended to the entire mainland Spain. Coastal areas could become very invaded, especially in the Mediterranean, as well as urban, agricultural, and along riverside areas. White points mean that none of the plant species currently invasive in Spain included on the models could spread in these areas.

Management implications

In general, invasive plants in Spain seem to be at an early stage of invasion, because most of the species have not yet reached half of their potential distribution ranges. Therefore, we should pay more attention to those plant species with a large potential distribution range but a low occupancy, because it might be only a matter of time that they reach their maximum area of distribution. Moreover, our findings support that management efforts should focus on controlling the populations of short-lived, clonal, and wind dispersed species taking into account that species with these traits have wider distribution ranges and spread faster in Spain.

From the regional point of view, we should pay more attention to coastal anthropogenic places because they do not seem to be species-saturated and could serve as foci areas of species coming from similar climate regions spreading towards inland natural areas. Moreover, anthropogenic habitats (e.g. roadsides) contain more alien species than natural ones. Finally, we believe that Mediterranean woody habitats (i.e. evergreen forest and scrubland) should be preserved from fragmentation and disturbance because alien species richness increase with woody land cover loss while native species richness decrease.

Avoiding introductions is by far the less expensive and most reliable way to fight against invasions. In the last chapter of this thesis we found that the Australian Weed Risk Assessment (WRA) scheme is extremely restrictive in identifying alien species with invasion potential in Spain. It is a good tool for discriminating invasive species, but not so for casual species, indicating that probably casuals could become invasive in the future. By screening species through the WRA we detected some inconsistencies between invasion likelihood and impact questions. We suggest that a separate analysis should be done to evaluate these two risk components, as this would provide more useful information, especially for management.

Future perspectives

Most research on invasion biology is focussed on invasive species and to the spread stage, and this thesis reflects this bias. More research is needed concerning different stages of the invasion process, especially studying the timing of the process, the time lags and the populations' dynamics at local scale. Moreover, as it has been shown than habitat types and landscape conditions are very important for the presence of alien species and their spread, more efforts should be done in predicting how land-use changes could affect invasion dynamics. On the same direction, future research should be focused on trying to link global change with spreading of invasive species, such as estimating potential distribution ranges and rates of spread according to species human uses and propagule pressure changes, and climatic and land-use future scenarios.

Conclusions

Èxit de les espècies invasores

- L'èxit de les espècies invasores pot ser mesurat de diferents maneres, com les que s'han fet servir aquí: la mida del rang actual, el grau d'ocupació del rang potencial i, des d'un punt de vista dinàmic, la taxa d'expansió. Proposem que el grau d'ocupació del rang potencial i la taxa d'expansió són mesures més acurades que la mida del rang actual perquè tenen en compte el potencial de les espècies per envair una regió determinada i, en el cas de la taxa d'expansió, inclou l'efecte del temps de residència, un paràmetre que pot ser molt útil per a la gestió.

- Les espècies de plantes invasores a Espanya semblen estar en un estadi inicial d'expansió, perquè la majoria d'espècies encara no han assolit la meitat fels seus rangs de distribució potencial.

- El temps des del moment de la introducció és un dels principals agents del rang de distribució actual i el grau d'ocupació del rang potencial. A Espanya, les espècies recentment introduïdes tenen distribucions i graus d'ocupació restringits perquè han tingut menys oportunitats d'expandir els seu rang i menys pressió de propàgul. Aquesta relació desapareix, però, quan es consideren espècies introduïdes fa més de 100 anys. Algunes d'aquestes espècies tenen taxes baixes d'expansió, fet que pot atribuir-se a fases de latència en el procés d'invasió.

- El tipus de dispersió és l'única característica relacionada amb la mida del rang de distribució actual; tenen més èxit les espècies dispersades pel vent. La dispersió pel vent i el creixement clonal també afavoreixen les altes taxes d'expansió. Les espècies clonals, de vida curta i no fixadores de nitrogen tenen amplituds de nínxol més grans pel que fa al clima i una posició de nínxol comuna, i per tant, indirectament, estan àmpliament distribuïdes pel territori.

Grau d'invasió

- Els factors antròpics com la pressió de propàgul i la pertorbació antròpica, i els seus derivats, són els principals agents de l'alt grau d'invasió (la riquesa de plantes invasores), a escala regional i local, ja que afavoreixen punts calents d'invasió no saturats que poden servir com a focus d'invasió de noves espècies al·lòctones que possiblement s'expandeixin cap a àrees naturals.

- Alguns factors topogràfics i climàtics també són importants per determinar el grau d'invasió a Espanya: les zones càlides i seques, costaneres i de baixa altitud estan associades a un grau alt d'invasió regional, mentre que, a escala local, les variables climàtiques estan més associades a la riquesa d'espècies natives que a la d'al·lòctones. En la majoria dels hàbitats, la riquesa d'espècies natives augmenta en llocs plujosos i disminueix en llocs càlids.

- Els hàbitats llenyosos típicament mediterranis (boscos i matollars perennes) tenen la riquesa d'espècies al·lòctones localment més baixa, comparats amb altres hàbitats, d'acord amb la hipòtesi de la seva alta resistència a la invasió.

- A escala local, a Catalunya, el context paisatgístic té una gran influència tant en la riquesa d'espècies natives com en la d'al·lòctones. Una gran proporció de coberta llenyosa incrementa la riquesa d'espècies natives i fa disminuir la riquesa d'al·lòctones, la qual cosa suggereix que la pèrdua d'hàbitat natural pot afavorir la introducció i expansió d'espècies al·lòctones.

Integració i anàlisi del risc d’invasió

- Les espècies de plantes invasores amb distribucions restringides no tenen requeriments ambientals particulars, sinó que es troben en llocs costaners i alterats envaïts per altres espècies invasores generalistes i àmpliament distribuïdes. Aquestes espècies invasores restringides tenen poca tolerància a condicions diferents de clima i de tipus de vegetació (amplitud de nínxol petita).

- L’amplitud i la posició de nínxol de les espècies invasores (calculades a partir d’un conjunt de variables ambientals) estan relacionades amb el seu èxit. Per un costat, les espècies amb una posició de nínxol en condicions ambientals àmpliament distribuïdes a Espanya tenen un rang actual molt ampli i podrien tenir molt d’èxit en regions de clima similar. Per altra banda, hi ha espècies amb un alt potencial d’envair qualsevol regió (capacitat invasora), determinat per la seva amplitud de nínxol. Aquesta diferència pot ser crucial per a la gestió i les prediccions de risc.

- L’origen geogràfic està molt relacionat amb la posició de nínxol, ja que les espècies procedents de regions càlides són presents en llocs costaners i antròpics amb diferències de temperatura moderades entre hivern i estiu. Aquesta troballa reforça la hipòtesi de la concordança climàtica.

- El protocol australià d’avaluació del risc d’invasió (WRA) és molt restrictiu identificant les espècies al·lòctones amb potencial invasor a Espanya. És una bona eina per discriminar espècies invasores però no és acurat per identificar les adventícies, la qual cosa indica que probablement les espècies actualment adventícies podrien ser invasores en el futur.

- Un mapa de risc d’invasió (basat en el rang de distribució potencial de les espècies al·lòctones ja presents a la regió i les espècies invasores en altres regions però amb potencial de ser introduïdes a Espanya), podria ser una bona eina per a la predicció del risc i la gestió de les invasions a escala regional.

Conclusions

Success of invaders

- Invassive species success can be measured in different ways, such the ones used here: current range size, occupancy of potential range and, from a dynamic point of view, the spread rate. We propose that occupancy of potential range and spread rate are more accurate measures than current range size because they account for the species potential to invade a given region and, in the case of spread rate, it includes the effect of residence time, what can be very useful for management.

- Invasive plants in Spain seem to be at an early stage of invasion spreading, because most of the species have not yet reached half of their potential distribution ranges.

- Time since introduction is one of the main drivers of current range size and occupancy of potential range. In Spain, species recently introduced have restricted distributions and occupancies because they have had less opportunity to expand their range and less propagule pressure. This relationship disappears, however, when considering species introduced more than 100 years ago. Some of these species have low spread rates, what can be due to lag phases in the invasion process.

- Dispersal syndrome is the only trait related to current distribution range size, being more successful the species dispersed by wind. Wind dispersal and clonal growth also favour high spread rates. Clonal, short-lived and nitrogen non-fixer species have wider climatic niche breadth and common niche position, and therefore, indirectly, they are widespread.

Level of invasion

- Human-related factors such as propagule pressure and anthropogenic disturbance, and its surrogates, are the main drivers of a high level of invasion (i.e. invasive plant richness), both the regional and at the local scale, inducing invasion non species-saturated hot-spots that can serve as invasion foci de new alien species that can spread towards natural areas.

- Some topographic and climatic factors are also important in determining the level of invasion in Spain: warm, dry and coastal lowlands are associated to a high level of invasion at the regional scale, while, at the local scale, climate variables are more associated to native than to alien species richness. In most habitats, native species richness increase in rainy sites and decrease in hot sites.

- Typical Mediterranean woody habitats (i.e. evergreen forest and scrubland) have the lowest local alien species richness, compared to other habitats, in agreement with the hypothesis of their high resistance to invasion.

- At the local scale, in Catalonia, the landscape context has a high influence on both native and alien species richness. A high site proportion of woody cover increases native species richness and decreases alien species richness, which suggests that natural habitat loss can favour the introduction and spreading of alien species.

Integration and risk analysis of invasion

- Invasive plant species with restricted distribution do not have particular environmental requirements, they occur in coastal disturbed places invaded by other generalist and widespread invasive species. These invasive restricted species have low tolerance to climatic and vegetation cover different conditions (narrow niche breadth).

- Species niche breadth and position (calculated from a set of environmental variables) are highly related to species success. From one side, species with niche position in widespread environmental conditions in Spain have a wide current range, and they could be highly successful in regions with similar climate. From another side, there are species with high success because they have a high potential to invade any region (i.e. invasiveness), given by their niche breadth. This difference can be crucial for management and risk predictions.

- Geographical origin was highly related with niche position, being species coming from warm regions those present in highly humanized-coastal places with small temperature ranges between winter and summer. This finding reinforces the hypothesis of climate matching.

- The Australian Weed Risk Assessment (WRA) scheme is extremely restrictive in identifying alien species with invasion potential in Spain. It is a good tool for discriminating invasive species, but it is not accurate to identify casual species, indicating that probably current casuals could be invasive in the future.

- A risk map of the potential distribution ranges of alien species already present in the region and species invasive in other regions but with potential to be introduced in Spain could be a good tool for invasion risk prediction and management.

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Data appendices

Appendix D.I

List of invasive plant neophytes from the recently published atlas of invasive plant species in Spain (Sanz-Elorza et al. 2004), with indication of their range size (i.e. number of UTM where present).

Family	Species	Range size
Malvaceae	*Abutilon theophrasti*	120
Fabaceae	*Acacia cyanophylla*	34
Fabaceae	*Acacia dealbata*	235
Fabaceae	*Acacia longifolia*	6
Fabaceae	*Acacia melanoxylon*	90
Aceraceae	*Acer negundo*	69
Asteraceae	*Achillea filipendulina*	18
Amaranthaceae	*Achyranthes sicula*	11
Agavaceae	*Agave americana*	284
Asteraceae	*Ageratina adenophora*	6
Simaroubaceae	*Ailanthus altissima*	258
Amaranthaceae	*Amaranthus albus*	501
Amaranthaceae	*Amaranthus blitoides*	525
Amaranthaceae	*Amaranthus hybridus*	440
Amaranthaceae	*Amaranthus muricatus*	251
Amaranthaceae	*Amaranthus powellii*	97
Amaranthaceae	*Amaranthus retroflexus*	673
Amaranthaceae	*Amaranthus viridis*	149
Asteraceae	*Ambrosia artemisiifolia*	5
Asclepiadaceae	*Araujia sericifera*	118
Asteraceae	*Arctotheca calendula*	48
Asteraceae	*Artemisia verlotiorum*	183
Asclepiadaceae	*Asclepias curassavica*	7
Asteraceae	*Aster squamatus*	400
Chenopodiaceae	*Atriplex semibaccata*	12
Cactaceae	*Austrocylindropuntia subulata*	69
Asteraceae	*Baccharis halimifolia*	20
Asteraceae	*Bidens aurea*	88
Asteraceae	*Bidens frondosa*	95
Asteraceae	*Bidens pilosa*	38
Asteraceae	*Bidens subalternans*	155
Poaceae	*Bromus willdenowii*	182
Buddlejaceae	*Buddleja davidii*	108
Aizoaceae	*Carpobrotus acinaciformis*	16
Aizoaceae	*Carpobrotus edulis*	156
Poaceae	*Cenchrus incertus*	8
Poaceae	*Chloris gayana*	30
Asteraceae	*Conyza bonariensis*	428
Asteraceae	*Conyza canadensis*	553
Asteraceae	*Conyza sumatrensis*	329

Poaceae	*Cortaderia selloana*	80
Asteraceae	*Cotula coronopifolia*	59
Crassulaceae	*Crassula lycopodioides*	3
Cactaceae	*Cylindropuntia imbricata*	7
Cactaceae	*Cylindropuntia spinosior*	2
Cyperaceae	*Cyperus alternifolius flabelliformis*	12
Solanaceae	*Datura innoxia*	84
Solanaceae	*Datura stramonium*	461
Poaceae	*Echinochloa hispidula*	44
Poaceae	*Echinochloa oryzicola*	40
Poaceae	*Echinochloa oryzoides*	35
Pontederiaceae	*Eichhornia crassipes*	5
Elaeagnaceae	*Elaeagnus angustifolia*	72
Poaceae	*Eleusine indica*	49
Hydrocharitaceae	*Elodea canadensis*	14
Rosaceae	*Eriobotrya japonica*	4
Myrtaceae	*Eucalyptus camaldulensis*	82
Myrtaceae	*Eucalyptus globulus*	261
Euphorbiaceae	*Euphorbia polygonifolia*	10
Polygonaceae	*Fallopia baldschuanica*	87
Caesalpiniaceae	*Gleditsia triacanthos*	58
Asclepiadaceae	*Gomphocarpus fruticosus*	76
Asteraceae	*Helianthus tuberosus*	199
Boraginaceae	*Heliotropium curassavicum*	64
Convolvulaceae	*Ipomoea indica*	187
Convolvulaceae	*Ipomoea purpurea*	131
Convolvulaceae	*Ipomoea sagittata*	43
Convolvulaceae	*Ipomoea stolonifera*	6
Verbenaceae	*Lantana camara*	7
Fabaceae	*Leucaena leucocephala*	4
Verbenaceae	*Lippia filiformis*	58
Caprifoliaceae	*Lonicera japonica*	94
Nyctaginaceae	*Mirabilis jalapa*	283
Solanaceae	*Nicotiana glauca*	162
Onagraceae	*Oenothera biennis*	125
Onagraceae	*Oenothera glazioviana*	63
Cactaceae	*Opuntia dillenii*	24
Cactaceae	*Opuntia engelmannii*	4
Cactaceae	*Opuntia ficus-indica*	520
Cactaceae	*Opuntia humifusa*	3
Cactaceae	*Opuntia monacantha*	1
Cactaceae	*Opuntia phaeacantha*	1
Cactaceae	*Opuntia stricta*	8
Oxalidaceae	*Oxalis pes-caprae*	401
Caesalpiniaceae	*Parkinsonia aculeata*	9
Poaceae	*Paspalum dilatatum*	221

Poaceae	*Paspalum paspalodes*	265
Poaceae	*Paspalum vaginatum*	61
Poaceae	*Pennisetum setaceum*	5
Polygonaceae	*Reynoutria japonica*	19
Fabaceae	*Robinia pseudoacacia*	646
Anacardiaceae	*Schinus molle*	8
Asteraceae	*Senecio inaequidens*	17
Asteraceae	*Senecio mikanioides*	31
Solanaceae	*Solanum bonariense*	61
Fabaceae	*Sophora japonica*	11
Poaceae	*Sorghum halepense*	824
Poaceae	*Spartina alterniflora*	9
Poaceae	*Spartina patens*	49
Poaceae	*Stenotaphrum secundatum*	47
Commelinaceae	*Tradescantia fluminensis*	23
Iridaceae	*Tritonia x crocosmiiflora*	9
Tropaeolaceae	*Tropaeolum majus*	26
Asteraceae	*Xanthium spinosum*	443
Asteraceae	*Xanthium strumarium strumarium*	307
Zygophyllaceae	*Zygophyllum fabago*	76

Appendix D.II

Minimum residence time (MRT; years), current distribution ranges (CDR; number of UTM 10x10 km), potential distribution ranges (PDR; number of UTM 10x10 km) and occupancy (i.e. proportion of the potential distribution range currently occupied) for 78 invasive plant species in Spain. PDR were calculated according to an average of 4 potential distribution models for each species. The area under the ROC curve (AUC) of this averaged model is also shown on the table. The spread rate (*r* ; UTM/year) of each species is indicated in the last column.

Family	**Species**	**MRT**	**CDR**	**PDR**	**OCCUPANCY**	**AUC**	***r***
Malvaceae	*Abutilon theophrasti*	74	94	680	0.14	0.92	0.065
Fabaceae	*Acacia cyanophylla*	204	20	217	0.09	0.98	0.015
Fabaceae	*Acacia dealbata*	204	204	356	0.57	0.99	0.031
Fabaceae	*Acacia melanoxylon*	204	71	214	0.33	1	0.023
Aceraceae	*Acer negundo*	204	61	393	0.16	0.95	0.021
Asteraceae	*Achillea filipendulina*	22	18	37	0.49	1	0.16
Agavaceae	*Agave americana*	504	217	557	0.39	0.97	0.012
Simaroubaceae	*Ailanthus altissima*	186	210	563	0.37	0.96	0.032
Amaranthaceae	*Amaranthus albus*	143	408	716	0.57	0.95	0.049
Amaranthaceae	*Amaranthus blitoides*	94	445	715	0.62	0.96	0.077
Amaranthaceae	*Amaranthus hybridus*	124	368	718	0.51	0.94	0.055
Amaranthaceae	*Amaranthus muricatus*	96	189	432	0.44	0.97	0.062
Amaranthaceae	*Amaranthus powellii*	21	83	666	0.12	0.93	0.221
Amaranthaceae	*Amaranthus retroflexus*	104	551	854	0.65	0.94	0.073
Amaranthaceae	*Amaranthus viridis*	106	100	444	0.23	0.95	0.047
Asclepiadaceae	*Araujia sericifera*	28	90	311	0.29	0.98	0.174
Asteraceae	*Arctotheca calendula*	88	23	421	0.05	0.97	0.037
Asteraceae	*Artemisia verlotiorum*	91	158	512	0.31	0.97	0.06
Asteraceae	*Aster squamatus*	92	320	641	0.5	0.96	0.072
Cactaceae	*Austrocylindropuntia subulata*	20	48	282	0.17	0.98	0.205
Asteraceae	*Baccharis halimifolia*	55	14	106	0.13	1	0.05
Asteraceae	*Bidens aurea*	41	64	663	0.1	0.91	0.107
Asteraceae	*Bidens frondosa*	60	83	341	0.24	0.97	0.08
Asteraceae	*Bidens pilosa*	91	21	249	0.08	0.98	0.035
Asteraceae	*Bidens subalternans*	69	131	295	0.44	0.99	0.079
Poaceae	*Bromus willdenowii*	100	144	403	0.36	0.97	0.053
Buddlejaceae	*Buddleja davidii*	43	93	305	0.3	0.98	0.116
Aizoaceae	*Carpobrotus edulis*	104	98	441	0.22	0.97	0.047
Poaceae	*Chloris gayana*	102	23	249	0.09	0.99	0.031
Asteraceae	*Conyza bonariensis*	132	348	662	0.53	0.95	0.052
Asteraceae	*Conyza canadensis*	220	456	803	0.57	0.94	0.033
Asteraceae	*Conyza sumatrensis*	100	265	485	0.55	0.96	0.065
Poaceae	*Cortaderia selloana*	35	61	335	0.18	0.98	0.124
Asteraceae	*Cotula coronopifolia*	107	42	361	0.12	0.97	0.036
Solanaceae	*Datura innoxia*	504	62	410	0.15	0.94	0.009
Solanaceae	*Datura stramonium*	504	386	744	0.52	0.95	0.014
Poaceae	*Echinochloa hispidula*	36	37	242	0.15	0.99	0.107
Poaceae	*Echinochloa oryzicola*	104	36	449	0.08	0.98	0.035
Poaceae	*Echinochloa oryzoides*	36	28	629	0.04	0.95	0.096
Elaeagnaceae	*Elaeagnus angustifolia*	204	54	614	0.09	0.92	0.021

Poaceae	*Eleusine indica*	143	43	259	0.17	0.99	0.028
Hydrocharitaceae	*Elodea canadensis*	99	13	362	0.04	0.97	0.027
Myrtaceae	*Eucalyptus camaldulensis*	204	70	578	0.12	0.95	0.022
Myrtaceae	*Eucalyptus globulus*	204	200	317	0.63	0.99	0.031
Polygonaceae	*Fallopia baldschuanica*	26	79	757	0.1	0.94	0.176
Caesalpiniaceae	*Gleditsia triacanthos*	56	51	364	0.14	0.97	0.074
Asclepiadaceae	*Gomphocarpus fruticosus*	242	53	259	0.2	0.99	0.018
Boraginaceae	*Heliotropium curassavicum*	130	36	230	0.16	0.98	0.03
Asteraceae	*Helianthus tuberosus*	304	179	380	0.47	0.98	0.019
Convolvulaceae	*Ipomoea indica*	104	144	381	0.38	0.98	0.053
Convolvulaceae	*Ipomoea purpurea*	104	101	553	0.18	0.94	0.047
Convolvulaceae	*Ipomoea sagittata*	304	36	235	0.15	0.99	0.012
Verbenaceae	*Lippia filiformis*	404	44	490	0.09	0.95	0.01
Caprifoliaceae	*Lonicera japonica*	43	70	303	0.23	0.99	0.105
Nyctaginaceae	*Mirabilis jalapa*	119	223	438	0.51	0.98	0.052
Solanaceae	*Nicotiana glauca*	152	120	425	0.28	0.96	0.034
Onagraceae	*Oenothera biennis*	156	100	451	0.22	0.96	0.032
Onagraceae	*Oenothera glazioviana*	80	50	446	0.11	0.95	0.051
Cactaceae	*Opuntia dillenii*	130	17	421	0.04	0.99	0.022
Cactaceae	*Opuntia ficus-indica*	504	396	728	0.54	0.96	0.014
Oxalidaceae	*Oxalis pes-caprae*	154	199	437	0.46	0.97	0.039
Poaceae	*Paspalum dilatatum*	97	178	441	0.4	0.97	0.06
Poaceae	*Paspalum paspalodes*	180	216	568	0.38	0.97	0.033
Poaceae	*Paspalum vaginatum*	97	38	239	0.16	0.98	0.04
Polygonaceae	*Reynoutria japonica*	30	14	100	0.14	1	0.093
Fabaceae	*Robinia pseudoacacia*	304	559	768	0.73	0.97	0.026
Asteraceae	*Senecio inaequidens*	20	14	609	0.02	0.94	0.133
Asteraceae	*Senecio mikanioides*	71	19	141	0.13	0.96	0.044
Solanaceae	*Solanum bonariense*	121	42	374	0.11	0.97	0.033
Fabaceae	*Sophora japonica*	304	11	97	0.11	1	0.008
Poaceae	*Sorghum halepense*	204	674	935	0.72	0.95	0.04
Poaceae	*Spartina patens*	87	32	186	0.17	1	0.042
Poaceae	*Stenotaphrum secundatum*	101	27	230	0.12	0.97	0.034
Commelinaceae	*Tradescantia fluminensis*	304	17	601	0.03	0.92	0.01
Tropaeolaceae	*Tropaeolum majus*	404	16	315	0.05	0.97	0.007
Asteraceae	*Xanthium spinosum*	304	367	694	0.53	0.95	0.023
Asteraceae	*Xanthium strumarium*	122	262	530	0.49	0.97	0.052
Zygophyllaceae	*Zygophyllum fabago*	143	58	399	0.15	0.96	0.03

Appendix D.III

Correspondence between the 8 EUNIS successfully modelled habitat types and the phytosociological alliances to which the plots were originally ascribed. Syntaxonomical nomenclature follows Bolòs & Vigo (1984) and Rivas-Martínez *et al.* (2001). See table 1 for description of habitat types.

EUNIS	**Alliance**
Anthropogenic	
E5.6	Onopordion acanthii Br.-Bl. 1926
	Sisymbrion officinalis (Br.-Bl.) R. Tx., Lohm. et Preisg. in R. Tx. 1950
	Galio-Alliarion (Oberd.) Lohm. et Oberd. 1967
	Dauco-Melilotion Görs 1966
	Hordeion leporini Br.-Bl. (1931) 1947
	Bromo-Oryzopsion miliaceae O. Bolòs 1970
	Chenopodion muralis Br.-Bl. 1931
	Arction R. Tx. 1937 em. Sissingh 1946
	Rumicion alpini (Rübel) Klika 1944
	Convolvulion sepium R. Tx. 1947
	Bidention tripartitae Nordh. 1940
	Salsolo-Peganion Br.-Bl. et O. Bolòs 1954
	Silybo-Urticion Sissingh 1950
	Carrichtero-Amberboion (Rivas Goday et Rivas Mart.) Rivas Goday 1954
	Onopordion arabici Br.-Bl. et O. Bolòs 1957
	Glaucio-Cakilion R. Tx. 1950 em. nom. O. Bolòs 1967
	Euphorbion peplis R. Tüxen 1950
H5.6	Echio-Galactition O. Bolòs et R. Mol. 1969
	Trifolio-Cynodontion Br.-Bl. et O. Bolòs 1957
	Polygonion avicularis Br.-Bl. 1931 ex Dich. 1933
	Agropyro-Rumicion crispi Nordh. 1940
I1	Diplotaxion erucoidis Br.-Bl. 1931 em. 1936
	Secalion mediterraneum (Br.-Bl.) R. Tx. 1937
	Scleranthion annui (Krusem. et Vlieger) Sissingh 1946
	Panico-Setarion Sissingh 1946
	Caucalidion platycarpae R. Tx. 1950
	Polygono-Chenopodion polyspermi W. Koch 1926 em. Sissingh 1946
Grasslands	
E1	Aphyllanthion Br.-Bl. (1931) 1937
	Thero-Airion R. Tx. 1951
	Mesobromion erecti (Br.-Bl. et Moor) Oberd. 1949
	Thero-Brachypodion Br.-Bl. 1925
	Xerobromion erecti (Br.-Bl. et Moor) R. Tx. et Oberd. 1958
	Phlomidio-Brachypodion retusi G. Mateo inéd.
	Brachypodion phoenicoidis Br.-Bl. 1931
	Saturejo-Hyparrhenion hirtae O. Bolòs 1962
	Agropyro-Lygeion @ Br.-Bl. et O. Bolòs (1954) 1957
	Ononidion striatae Br.-Bl. et Suspl. 1937
	Sedo-Scleranthion Br.-Bl. 1949
	Helianthemion guttati Br.-Bl. 1931
	Alysso-Sedion Oberd. et Th. Müller 1961
	Taeniathero-Aegilopion geniculatae Rivas Mart. et Izco 1977
	Stipion capensis Br.-Bl. in Br.-Bl. et O. Bolòs 1954
	Tuberarion guttatae Br.-Bl. 1931 nom. mut.
	Aegilopion (Rivas Goday et Rivas Mart.) Rivas Goday 1964
	Corynephorion canescentis Klika 1931 em. R. Tx. 1954

E2	Arrhenatherion elatioris Br.-Bl. 1952
	Violion cornutae (Négre) Romo 1986
	Cynosurion cristati R. Tx. 1947
	Deschampsion mediae Br.-Bl. (1947) in Br.-BL. et al 1952
	Agrostion stoloniferae Görs 1966
E3	Isoetion Br.-Bl. 1936
	Juncion acutiflori Br.-Bl. 1947
	Calthion palustris Tüxen 1937
	Molinio-Holoschoenion vulgaris Br.-Bl. (1931) 1947
	Molinion coeruleae Koch 1926
	Paspalo-Polypogonion semiverticillati Br.-Bl. 1952
	Nanocyperion flavescentis W. Koch 1926
	Imperato-Erianthion Br.-Bl. et O. Bolòs 1957
	Lythrion tribracteati Rivas Goday et Rivas Mart. ex Rivas Goday 1970
Woody	
F3	Sarothamnion scoparii R. Tx. ap. Preisg. 1949
	Pruno-Rubion ulmifolii O. Bolòs 1954
	Genistion purgantis R. Tx. in R. Tx. et Oberd. 1958 em.
	Sambuco-Salicion capreae R. Tx. et Neumann 1950
	Rubion subatlanticum R. Tx. 1952
	Ulici-Ericion ciliaris @ Géhu 1973
	Berberidion vulgaris Br.-Bl. (1947) 1950
G1	Quercion pubescenti-petraeae Br -Bl. 1931
	Fagion sylvaticae (Luquet) R. Tx. et Diem. 1936
	Fraxino-Carpinion R. Tx. 1936
	Alno-Padion Knapp 1942
	Quercion robori-petraeae Br.-Bl. 1932
	Tilio-Acerion Kikla 1955
	Populion albae Br.-Bl. 1931
	Alno-Ulmion Br.-Bl. et R. Tx. 1943

Appendix D.IV

List of neophyte species found in 8 EUNIS successfully modelled habitat types classified in anthropogenic, grasslands, and woody habitat types. The number of plots per habitat where each species was found is indicated, as well as ecological category: "w" for "weedy" and "r" for "ruderal" species, according to expertise knowledge (Bolòs *et al.* 2005). See table 4.1 for description of habitat types.

Family	Species	Raunkiaer life form	Ecological category	Anthropogenic			Grasslands			Woody		Total nº of plots
				I1	E5.6	H5.6	E3	E2	E1	F3	G1	
Malvaceae	*Abutilon teophrasti*	Therophyte	w	2								2
Aceraceae	*Acer negundo*	Macrophanerophyte	-								3	3
Agavaceae	*Agave Americana*	Chamaephyte	-						1			1
Simaroubaceae	*Ailanthus altissima*	Macrophanerophyte	-						1	1		2
Amaranthaceae	*Amaranthus albus*	Therophyte	w	11	1							12
Amaranthaceae	*Amaranthus blitoides*	Therophyte	w	22	5	1						28
Amaranthaceae	*Amaranthus deflexus*	Chamaephyte	r		1	2						3
Amaranthaceae	*Amaranthus hybridus*	Therophyte	w	12	2		1					15
Amaranthaceae	*Amaranthus muricatus*	Hemicryptophyte	w		2							2
Amaranthaceae	*Amaranthus retroflexus*	Therophyte	w	41	26	4	3		1			75
Asteraceae	*Ambrosia coronopifolia*	Geocryptophyte	r			2						2
Asclepiadaceae	*Araujia sericifera*	Vine	r		1							1
Asteraceae	*Artemisia verlotiorum*	Geocryptophyte	r		9				1		4	14
Asteraceae	*Aster pilosus*	Hemicryptophyte	r	2	6					1		9
Asteraceae	*Aster squamatus*	Therophyte	r	3	37	23	14	5	2	1	2	87
Asteraceae	*Bidens frondosa*	Therophyte	r		8		2					10
Asteraceae	*Bidens pilosa*	Therophyte	r			1						1
Basellaceae	*Boussingaultia cordifolia*	Vine	-		1					1		2
Poaceae	*Bromus catharticus*	Hemicryptophyte	w	16	21	8	2	8	12	1		68
Buddlejaceae	*Buddleja davidii*	Macrophanerophyte	-							1	2	3
Asteraceae	*Calendula officinalis*	Therophyte	r		1							1
Aizoaceae	*Carpobrotus edulis*	Chamaephyte	-		1							1
Solanaceae	*Cestrum parqui*	Nanophanerophyte	-			1						1
Chenopodiaceae	*Chenopodium ambrosioides*	Therophyte	r		11	2					3	16
Asteraceae	*Conyza bonariensis*	Therophyte	r	5	20	2	1		1	2	1	32
Asteraceae	*Conyza Canadensis*	Therophyte	r	3	11	1	5	1				21
Asteraceae	*Conyza sumatrensis*	Therophyte	r	10	8	4			3			25
Brassicaceae	*Coronopus didymus*	Hemicryptophyte	r	1	3	1	2					7
Asteraceae	*Crepis bursifolia*	Hemicryptophyte	r		1	9						10
Asteraceae	*Crepis sancta*	Therophyte	w	9	2	7			14			32
Convolvulaceae	*Cuscuta campestris*	Therophyte	w		2							2
Cyperaceae	*Cyperus eragrostis*	Hemicryptophyte	r	1	7	2	2	1				13
Solanaceae	*Datura stramonium*	Therophyte	w	1	2	1						4
Poaceae	*Echinochloa colonum*	Therophyte	w	10		1						11
Asteraceae	*Eclipta prostrate*	Therophyte	w		1							1
Poaceae	*Eleusine tristachya*	Hemicryptophyte	r			3			6			9
Euphorbiaceae	*Euphorbia lathyris*	Hemicryptophyte	w		1						1	2
Euphorbiaceae	*Euphorbia nutans*	Therophyte	w	3	1		1					5
Euphorbiaceae	*Euphorbia prostrata*	Therophyte	w	4	1	3			2			10
Euphorbiaceae	*Euphorbia serpens*	Therophyte	w			1						1
Asclepiadaceae	*Gomphocarpus fruticosus*	Nanophanerophyte	r						2			2
Asteraceae	*Helianthus tuberosus*	Geocryptophyte	r		5							5
Boraginaceae	*Heliotropium curassavicu*	Geocryptophyte	r			1						1

Convolvulaceae	*Ipomoea indica*	Vine	r		1							1
Convolvulaceae	*Ipomoea purpurea*	Vine	r		1							1
Iridaceae	*Iris germanica*	Geocryptophyte	r						13			13
Juncaceae	*Juncus tenuis*	Hemicryptophyte	-			4						4
Chenopodiaceae	*Kochia scoparia*	Therophyte	r	1	6							7
Caprifoliaceae	*Lonicera japonica*	Vine	-								1	1
Brassicaceae	*Lunaria annua*	Hemicryptophyte	-								1	1
Asteraceae	*Matricaria discoidea*	Therophyte	r			2	5					7
Nyctaginaceae	*Mirabilis jalapa*	Hemicryptophyte	r		1							1
Onagraceae	*Oenothera biennis*	Hemicryptophyte	-		3							3
Cactaceae	*Opuntia ficus-barba*	Mesophanerophyte	-						5			5
Oxalidaceae	*Oxalis debilis*	Geocryptophyte	w	1	1							2
Oxalidaceae	*Oxalis pes-caprae*	Geocryptophyte	w	1								1
Poaceae	*Panicum capillare*	Therophyte	w	1	3	1	1					6
Poaceae	*Paspalum dilatatum*	Hemicryptophyte	r			4	1		1			6
Poaceae	*Pennisetum villosum*	Hemicryptophyte	r		1	1						2
Platanaceae	*Platanus Xhispanica*	Macrophanerophyte	-							2	2	4
Poaceae	*Puccinellia distans*	Therophyte	-		1							1
Fabaceae	*Robinia pseudoacacia*	Macrophanerophyte	-		5					3	6	14
Rubiaceae	*Rubia tinctorum*	Vine	-								2	2
Lamiaceae	*Salvia sclarea*	Hemicryptophyte	r						2			2
Solanaceae	*Solanum chenopodioides*	Therophyte	r		2					2	1	5
Solanaceae	*Solanum lycopersicum*	Vine	r	1	3						1	5
Solanaceae	*Solanum tuberosum*	Geocryptophyte	r	4	1							5
Asteraceae	*Solidago canadensis*	Hemicryptophyte	r		1							1
Poaceae	*Sorghum halepense*	Geocryptophyte	w	36	4	2			3			45
Poaceae	*Sporobolus indicus*	Hemicryptophyte	r		1	14		2	3			20
Asteraceae	*Tanacetum parthenium*	Hemicryptophyte	r		3							3
Asteraceae	*Tapetes minuta*	Therophyte	w	1	1							2
Scrophulariaceae	*Veronica peregrine*	Therophyte	w		5							5
Fabaceae	*Vicia ervilia*	Therophyte	w	1							1	2
Asteraceae	*Xanthium echinatum*	Therophyte	r	3	16	4	8			1		32
Asteraceae	*Xanthium spinosum*	Therophyte	r	1	11							12

Appendix D.V

List of the 74 invader plant species modelled on chapter 4. Distribution range size was measured as the number of UTM 10x10km where the species in present in Spain, and niche position and breadth were extracted from the 2 main axes of the OMI ordination.

Family	Species	Species acronym	Range size (n°UTM)	Axis 1 position	Axis 1 breadth	Axis 2 position	Axis 2 breadth
Malvaceae	*Abutilon theophrasti*	Abu_theop	111	0.76	2.56	0.73	2.58
Fabaceae	*Acacia cyanophylla*	Aca_cyano	21	2.79	3.65	1.85	1.27
Fabaceae	*Acacia dealbata*	Aca_dealb	210	1.50	2.63	-1.85	1.61
Fabaceae	*Acacia melanoxylon*	Aca_melan	71	2.60	1.45	-2.30	0.50
Aceraceae	*Acer negundo*	Ace_negun	66	1.29	6.54	-0.39	2.27
Asteraceae	*Achillea filipendulina*	Ach_filip	18	-0.21	7.00	-0.15	2.58
Agavaceae	*Agave americana*	Aga_ameri	231	0.93	3.23	1.15	1.80
Simaroubaceae	*Ailanthus altissima*	Ail_altis	230	0.61	4.12	-0.09	3.01
Amaranthaceae	*Amaranthus albus*	Ama_albus	467	0.14	3.43	0.02	2.50
Amaranthaceae	*Amaranthus blitoides*	Ama_blito	483	0.55	2.91	0.34	2.51
Amaranthaceae	*Amaranthus hybridus*	Ama_hybri	402	0.49	3.53	-0.46	4.24
Amaranthaceae	*Amaranthus muricatus*	Ama_muric	207	1.49	3.06	1.14	1.84
Amaranthaceae	*Amaranthus powellii*	Ama_powel	90	0.19	4.16	-1.16	5.56
Amaranthaceae	*Amaranthus retroflexus*	Ama_retro	608	0.08	3.19	-0.59	4.20
Amaranthaceae	*Amaranthus viridis*	Ama_virid	116	1.58	3.41	1.27	1.76
Asclepiadaceae	*Araujia sericifera*	Ara_seric	93	2.15	2.99	0.39	1.67
Asteraceae	*Arctotheca calendula*	Arc_calen	24	3.26	2.65	0.41	6.15
Asteraceae	*Artemisia verlotiorum*	Art_verlo	167	1.11	4.02	-0.87	4.24
Asteraceae	*Aster squamatus*	Ast_squam	350	0.92	2.87	0.29	2.60
Cactaceae	*Austrocylindropuntia subulata*	Aus_subul	51	1.22	1.59	1.12	1.31
Asteraceae	*Baccharis halimifolia*	Bac_halim	14	3.98	1.73	-2.32	0.32
Asteraceae	*Bidens aurea*	Bid_aurea	75	1.33	5.50	0.46	2.89
Asteraceae	*Bidens frondosa*	Bid_frond	89	1.13	2.90	-0.72	4.04
Asteraceae	*Bidens pilosa*	Bid_pilos	25	1.97	2.89	1.75	0.93
Asteraceae	*Bidens subalternans*	Bid_subal	134	1.79	2.60	0.22	1.82
Poaceae	*Bromus willdenowii*	Bro_willd	155	1.42	4.94	-0.01	4.90
Buddlejaceae	*Buddleja davidii*	Bud_david	102	1.04	5.09	-2.31	3.98
Aizoaceae	*Carpobrotus edulis*	Car_eduli	105	1.98	3.46	0.27	2.64
Poaceae	*Chloris gayana*	Chl_gayan	24	2.59	2.84	1.45	0.75
Asteraceae	*Conyza bonariensis*	Con_bonar	389	0.66	3.44	0.22	2.79
Asteraceae	*Conyza canadensis*	Con_canad	505	0.15	3.60	-0.75	4.04
Asteraceae	*Conyza sumatrensis*	Con_sumat	289	1.08	3.00	0.17	2.58
Poaceae	*Cortaderia selloana*	Cor_sello	62	3.06	4.42	-1.37	2.45
Asteraceae	*Cotula coronopifolia*	Cot_coron	43	2.81	2.92	-0.26	5.93
Solanaceae	*Datura innoxia*	Dat_innox	71	1.41	3.19	1.25	1.63
Solanaceae	*Datura stramonium*	Dat_stram	421	0.35	3.89	-0.34	4.57
Elaeagnaceae	*Elaeagnus angustifolia*	Ela_angus	63	0.46	5.45	0.82	1.35
Poaceae	*Eleusine indica*	Ele_indic	43	2.50	4.25	0.66	3.60
Myrtaceae	*Eucalyptus camaldulensis*	Euc_camal	75	0.05	1.85	1.32	1.60
Myrtaceae	*Eucalyptus globulus*	Euc_globu	209	2.12	2.60	-2.03	1.42
Polygonaceae	*Fallopia baldschuanica*	Fal_balds	86	-0.76	2.47	-1.23	3.31
Caesalpiniaceae	*Gleditsia triacanthos*	Gle_triac	54	0.42	4.53	0.76	1.05
Asclepiadaceae	*Gomphocarpus fruticosus*	Gom_fruti	55	1.96	2.00	0.63	2.75
Boraginaceae	*Heliotropium curassavicum*	Hel_curas	42	2.84	2.61	2.21	0.50
Asteraceae	*Helianthus tuberosus*	Hel_tuber	184	0.82	4.26	-0.92	4.55
Convolvulaceae	*Ipomoea indica*	Ipo_indic	150	1.71	3.17	0.86	1.44
Convolvulaceae	*Ipomoea purpurea*	Ipo_purpu	129	1.01	4.45	-0.08	3.53
Convolvulaceae	*Ipomoea sagittata*	Ipo_sagit	38	1.84	2.14	1.48	0.87
Verbenaceae	*Lippia filiformis*	Lip_filif	50	1.76	3.89	0.86	3.60
Caprifoliaceae	*Lonicera japonica*	Lon_japon	78	2.09	5.02	-0.38	3.55
Nyctaginaceae	*Mirabilis jalapa*	Mir_jalap	242	1.12	3.32	0.18	2.36

Solanaceae	*Nicotiana glauca*	Nic_glauc	127	1.72	2.50	1.64	1.30
Onagraceae	*Oenothera biennis*	Oen_bienn	112	0.80	4.87	-1.67	4.04
Onagraceae	*Oenothera glazioviana*	Oen_glazi	54	1.04	4.19	-1.26	2.52
Cactaceae	*Opuntia dillenii*	Opu_dille	17	1.81	1.88	1.81	0.60
Cactaceae	*Opuntia ficus-indica*	Opu_ficus	434	0.66	2.15	1.32	2.42
Oxalidaceae	*Oxalis pes-caprae*	Oxa_pes.c	213	1.78	2.55	1.67	1.36
Poaceae	*Paspalum dilatatum*	Pas_dilat	190	2.14	2.89	-0.77	3.67
Poaceae	*Paspalum paspalodes*	Pas_paspa	231	1.22	3.49	0.18	2.77
Poaceae	*Paspalum vaginatum*	Pas_vagin	40	2.97	3.91	-0.32	5.24
Polygonaceae	*Reynoutria japonica*	Rey_japon	14	2.71	4.00	-3.46	2.14
Fabaceae	*Robinia pseudoacacia*	Rob_pseud	594	0.94	3.79	-1.33	3.97
Asteraceae	*Senecio inaequidens*	Sen_inaeq	14	0.95	5.20	-1.37	1.99
Asteraceae	*Senecio mikanioides*	Sen_mikan	20	3.19	3.29	-1.73	1.11
Solanaceae	*Solanum bonariense*	Sol_bonar	48	2.21	3.97	1.66	2.00
Fabaceae	*Sophora japonica*	Sop_japon	11	-0.51	4.35	0.60	1.43
Poaceae	*Sorghum halepense*	Sor_halep	743	0.46	2.47	1.19	2.63
Poaceae	*Spartina patens*	Spa_paten	32	2.91	1.29	-1.41	3.97
Poaceae	*Stenotaphrum secundatum*	Ste_secun	28	3.51	2.32	-0.59	4.23
Commelinaceae	*Tradescantia fluminensis*	Tra_flumi	19	2.78	5.90	-1.21	4.39
Tropaeolaceae	*Tropaeolum majus*	Tro_majus	9	2.58	3.44	-3.35	0.12
Asteraceae	*Xanthium spinosum*	Xan_spino	411	0.02	3.66	-0.09	3.28
Asteraceae	*Xanthium strumarium*	Xan_strum	275	0.72	3.76	0.01	3.25
Zygophyllaceae	*Zygophyllum fabago*	Zyg_fabag	64	1.12	2.55	1.83	1.29

Appendix D.VI

Table of correspondences between questions used in the Australian Weed Risk Assessment system (WRA) of Pheloung et al. (1999) and abbreviations used in our analysis of chapter 5.

Category	WRA code	WRA question	Abbreviation
Domestication/ Cultivation	1.01	Is the species highly domesticated?	Domestication
	1.02	Has the species become naturalized where grown?	Naturalization
	1.03	Does the species have weedy races?	Weedy races
Climate and Distribution	2.01	Species suited to Mediterranean climate	Med climate
	2.02	Quality of climate match data	Quality data
	2.03	Broad climate suitability (environmental versality)	Climate suitability
	2.04	Native or naturalized in regions with extended dry periods	Native med climate
	2.05	Does the species have a history of repeated introductions outside its natural range?	Repeated intro
Weed Elsewhere	3.01	Naturalized beyond native range	Nature native range
	3.02	Garden/amenity/disturbance weed	Garden
	3.03	Weed of agriculture/horticulture/forestry	Agriculture
	3.04	Environmental weed	Environmental
	3.05	Congeneric weed	Congeneric
Undesirable traits	4.01	Produces spines, thorns or burrs	Spines
	4.02	Allelopathic	Allelopathy
	4.03	Parasitic	Parasitic
	4.04	Unpalatable to grazing animals	Unpalatable
	4.05	Toxic to animals	Toxic
	4.06	Host for recognized pests and pathogens	Host pathogens
	4.07	Causes allergies or is otherwise toxic to humans	Allergies
	4.08	Creates a fire hazard in natural ecosystems	Fire hazard
	4.09	Is a shade tolerant plant at some stage of its life cycle	Shade tolerant
	4.10	Grows on infertile soils	Soil
	4.11	Climbing or smothering growth habit	Climbing
	4.12	Forms dense thickets	Dense thickets
Plant type	5.01	Aquatic	Aquatic
	5.02	Grass	Grass
	5.03	Nitrogen fixing plant	Nitrogen
	5.04	Geophyte	Geophyte
Reproduction	6.01	Evidence of substantial reproductive failure in native habitats	Reproductive failure
	6.02	Produces viable seed	Viable seed
	6.03	Hybridizes naturally	Hybridizes
	6.04	Self-compatible or apomictic	Self-compatible
	6.05	Requires specialist pollinators	Specialist pollinators
	6.06	Reproduction by vegetative propagation	Vegetative
	6.07	Minimum generative time	Min time
Dispersal mechanisms	7.01	Propagules likely to be dispersed unintentionally	Unintentionally
	7.02	Propagules dispersed intentionally by people	Intentionally
	7.03	Propagules likely to disperse as a produce contaminant	Contaminant
	7.04	Propagules adapted to wind dispersal	Wind
	7.05	Propagules buoyant	Water
	7.06	Propagules bird dispersed	Bird
	7.07	Propagules dispersed by other animals (externally)	Animals
	7.08	Propagules dispersed by other animals (internally)	Gut
Persistance attributes	8.01	Prolific seed production	Seed production
	8.02	Evidence that a persistent propagule bank is formed	Propagule bank
	8.03	Well controlled by herbicides	Herbicides
	8.04	Tolerates, or benefits from mutilation, cultivation or fire	Tolerates
	8.05	Effective natural enemies present locally	Enemies

Appendix D.VII

Species used to test if the Australian Weed Risk Assessment system (WRA) of Pheloung et al. (1999) was suitable to predict plant invasions in Spain. A) 100 invasive species, and b) 100 casual species.

a)

Family	Species
Malvaceae	*Abutilon theophrasti*
Fabaceae	*Acacia dealbata*
Fabaceae	*Acacia longifolia*
Fabaceae	*Acacia melanoxylon*
Fabaceae	*Acacia saligna*
Aceraceae	*Acer negundo*
Asteraceae	*Achillea filipendulina*
Amaranthaceae	*Achyranthes sicula*
Agavaceae	*Agave americana*
Asteraceae	*Ageratina adenophora*
Simaroubaceae	*Ailanthus altissima*
Amaranthaceae	*Amaranthus albus*
Amaranthaceae	*Amaranthus blitoides*
Amaranthaceae	*Amaranthus hybridus*
Amaranthaceae	*Amaranthus muricatus*
Amaranthaceae	*Amaranthus powelli*
Amaranthaceae	*Amaranthus retroflexus*
Amaranthaceae	*Amaranthus viridis*
Asteraceae	*Ambrosia artemisifolia*
Asclepiadaceae	*Araujia sericifera*
Asteraceae	*Arctotheca calendula*
Asteraceae	*Artemisia verlotiorum*
Asclepiadaceae	*Asclepias curassavica*
Asteraceae	*Aster squamatus*
Chenopodiaceae	*Atriplex semibaccata*
Cactaceae	*Austrocylindropuntia subulata*
Azollaceae	*Azolla filiculoides*
Poaceae	*Bromus willdenowii*
Buddlejaceae	*Buddleja davidii*
Aizoaceae	*Carpobrotus acinaciformis*
Aizoaceae	*Carpobrotus edulis*
Poaceae	*Cenchrus incertus*
Iridaceae	*Chasmanthe aetiopica*
Poaceae	*Chloris gayana*
Asteraceae	*Conyza bonariensis*
Asteraceae	*Conyza canadensis*
Asteraceae	*Conyza sumatrensis*
Poaceae	*Cortaderia selloana*
Asteraceae	*Cotula coronopifolia*
Crassulaceae	*Crassula lycopodioides*
Cactaceae	*Cylindropuntia spinosior*
Cactaceae	*Cylindropuntia imbricata*
Cyperaceae	*Cyperus alterniformis flabelliformis*
Solanaceae	*Datura innoxia*
Solanaceae	*Datura stramonium*
Poaceae	*Echinochloa hispidula*
Poaceae	*Echinochloa oryzicola*
Poaceae	*Echinochloa oryzoides*
Pontederiaceae	*Eichhornia crassipes*
Elaeagnaceae	*Elaeagnus angustifolia*
Poaceae	*Eleusine indica*
Hydrocharitaceae	*Elodea canadensis*
Myrtaceae	*Eucalyptus camaldulensis*
Myrtaceae	*Eucalyptus globulus*

Polygonaceae	*Fallopia baldschuanica*
Polygonaceae	*Fallopia japonica*
Fabaceae	*Gleditsia triacanthos*
Asclepiadaceae	*Gomphocarpus fruticosus*
Asteraceae	*Helianthus tuberosus*
Convolvulaceae	*Ipomoea indica*
Convolvulaceae	*Ipomoea purpurea*
Convolvulaceae	*Ipomoea sagittata*
Convolvulaceae	*Ipomoea stolonifera*
Verbenaceae	*Lantana camara*
Fabaceae	*Leucaena leucocephala*
Verbenaceae	*Lippia filiformis*
Caprifoliaceae	*Lonicera japonica*
Nyctaginaceae	*Mirabilis jalapa*
Solanaceae	*Nicotiana glauca*
Onagraceae	*Oenothera biennis*
Onagraceae	*Oenothera glazioviana*
Cactaceae	*Opuntia dillenii*
Cactaceae	*Opuntia engelmannii*
Cactaceae	*Opuntia ficus-indica*
Cactaceae	*Opuntia humifusa*
Cactaceae	*Opuntia monacantha*
Cactaceae	*Opuntia phaeracantha*
Cactaceae	*Opuntia stricta*
Oxalidaceae	*Oxalis pres-caprae*
Fabaceae	*Parkinsonia aculeata*
Poaceae	*Paspalum dilatatum*
Poaceae	*Paspalum paspalodes*
Poaceae	*Paspalum vaginatum*
Poaceae	*Pennisetum setaceum*
Fabaceae	*Robinia pseudoacacia*
Anacardiaceae	*Schinus molle*
Asteraceae	*Senecio inaequidens*
Asteraceae	*Senecio mikanioides*
Solanaceae	*Solanum bonariense*
Fabaceae	*Sophora japonica*
Poaceae	*Sorghum halepense*
Poaceae	*Spartina alterniflora*
Poaceae	*Spartina patens*
Poaceae	*Stenotaphrum secundatum*
Commelinaceae	*Tradescantia fluminensis*
Iridaceae	*Tritonia crocosmiiflora*
Tropaeolaceae	*Tropaeolum majus*
Asteraceae	*Xanthium spinosum*
Asteraceae	*Xanthium strumarium*
Zygophyllaceae	*Zygophyllum fabago*

b)

Family	**Species**
Fabaceae	*Acacia decurrens*
Fabaceae	*Acacia mearnsii*
Fabaceae	*Acacia pycnantha*
Fabaceae	*Acacia sophorae*
Fabaceae	*Acacia verticilata*
Asteraceae	*Ageratum houstonianum*
Casuarinaceae	*Allocasuarina verticillata*
Liliaceae	*Aloe arborescens*
Liliaceae	*Aloe vera*
Verbenaceae	*Aloysia citrodora*
Amaranthaceae	*Alternanthera sessilis*
Amaranthaceae	*Amaranthus caudatus*
Amaranthaceae	*Amaranthus tricolor*
Poaceae	*Arundo donax*
Liliaceae	*Asparagus setaceus*
Fabaceae	*Bauhimia grandiflora*
Chenopodiaceae	*Beta vulgaris*
Asteraceae	*Calendula officinalis*
Myrtaceae	*Callistemon citrinus*
Sapindaceae	*Cardiospermum halicacabum*
Fabaceae	*Cassia obtusifolia*
Casuarinaceae	*Casuarina cunninghaniana*
Apocynaceae	*Catharanthus roseus*
Cactaceae	*Cereus peruvianus*
Rutaceae	*Citrus limon*
Convolvulaceae	*Convolvulus mauritanicus*
Cupressaceae	*Cupressus macrocarpa*
Rosaceae	*Cydonia oblonga*
Asteraceae	*Cynara scolymus*
Cyperaceae	*Cyperus michelianus*
Solanaceae	*Datura ferox*
Bignoniaceae	*Doxantha unguis-cati*
Myrtaceae	*Eucalyptus gunnii*
Myrtaceae	*Eucalyptus sideroxylon*
Polygonaceae	*Fagopyrum esculentum*
Polygonaceae	*Fagopyrum tataricum*
Asteraceae	*Gamochaeta subfalcata*
Asteraceae	*Gazania rigens*
Malvaceae	*Gossypium arboreum*
Liliaceae	*Hemerocallis lilioasphodelus*
Malvaceae	*Hibiscus rosa-sinensis*
Malvaceae	*Hibiscus syriacus*
Balsaminaceae	*Impatiens glandulifera*
Iridaceae	*Iris albicans*
Bignoniaceae	*Jacaranda mimosifolia*
Oleaceae	*Jasminum nudiflorum*
Cucurbitaceae	*Lagenaria siceraria*
Aizoaceae	*Lampranthus multiradiatus*
Verbenaceae	*Lantana montevidensis*
Pinaceae	*Larix eurolepis*
Fabaceae	*Lathirus odoratus*
Fabaceae	*Lathyrus sativus*
Oleaceae	*Ligustrum lucidum*
Oleaceae	*Ligustrum ovalifolium*

Poaceae	*Lolium multiflorum*
Lamiaceae	*Mentha spicata*
Fabaceae	*Mimosa pudica*
Araceae	*Monstera deliciosa*
Moraceae	*Morus nigra*
Amaryllidaceae	*Narcisus x medioluteus*
Solanaceae	*Nicandra physaloides*
Solanaceae	*Nicotiana tabacum*
Nymphaeaceae	*Nymphaea mexicana*
Onagraceae	*Oenothera laciniata*
Liliaceae	*Ornithogalum arabicum*
Poaceae	*Panicum capillare*
Vitaceae	*Parthenocissus inserta*
Passifloraceae	*Passiflora caerulea*
Scrophulariaceae	*Paulownia tomentosa*
Geraniaceae	*Pelargonium peltatum*
Lamiaceae	*Perilla frutescens*
Fabaceae	*Phaseolus lunatus*
Rosaceae	*Photinia serrulata*
Pinaceae	*Pinus canariensis*
Pinaceae	*Pinus ponderosa*
Pittosporaceae	*Pittosporum tobira*
Salicaceae	*Populus simonii*
Salicaceae	*Populusxcanescens*
Rosaceae	*Prunus persica*
Rosaceae	*Prunus serotina*
Rosaceae	*Pyracantha angustifolia*
Fabaceae	*Robinia hispida*
Rosaceae	*Rosa moschata*
Polygonaceae	*Rumex maritimus*
Polygonaceae	*Rumex patientia*
Lamiaceae	*Salvia microphylla*
Crassulaceae	*Sedum sexangulare*
Asteraceae	*Senecio cineraria*
Asteraceae	*Solidago gigantea*
Rosaceae	*Spiraea cantoniensis*
Oleaceae	*Syringa vulgaris*
Asteraceae	*Tagetes patula*
Commelinaceae	*Tradescantia fluminensis*
Liliaceae	*Tulipa clusiana*
Liliaceae	*Tulipa gesneriana*
Ulmaceae	*Ulmus pumila*
Verbenaceae	*Verbena canadensis*
Vitaceae	*Vitis berlandieri*
Hydrophyllaceae	*Wigandia caracasana*
Agavaceae	*Yucca aloifolia*

Graphic appendices

Appendix G. I

Graphical information for 78 invasive plant species in Spain analyzed on this thesis. We show a picture of the species, a map of the current distribution range (purple; according to the atlas of alien plant species in Spain Sanz-Elorza *et al.* (2004), used in chapter 1) over the potential distribution range (grey; according to the models developed on chapter 2), and finally, the representation of species niche over the environmental axes 1 and 2 of the OMI ordination used on chapter 4. On the OMI graph, the central point of the "star" is the niche position of the species and the lines represent the distance between the environmental conditions of the niche position and each occurrence site. The authors of the pictures are Mario Sanz-Elorza and anonymous authors from several web pages. Hygrophytes (*Echinochloa hispidula, Echinochloa oryzicola, Echinochloa oryzoides, Elodea canadensis*) were excluded on chapter 4, so we do not show their niche graphs.

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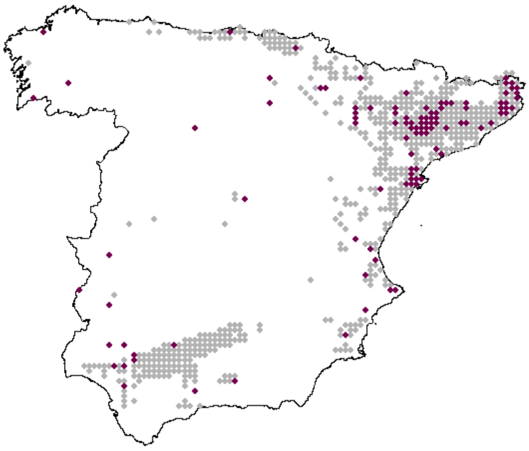
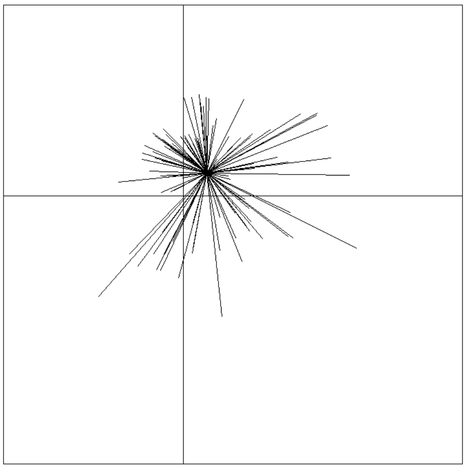
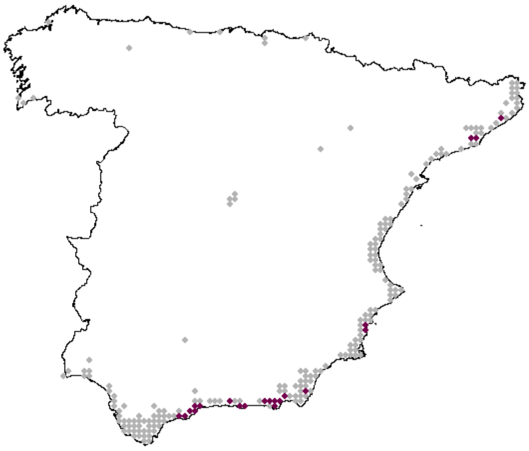
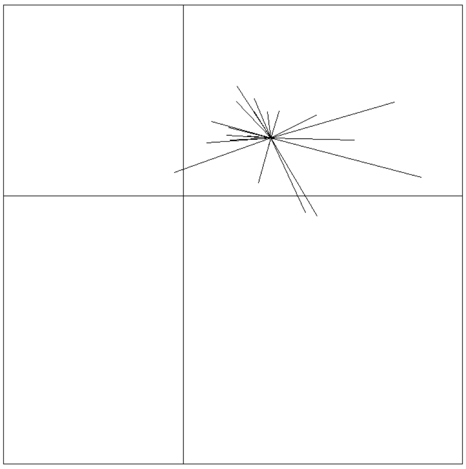




Acacia cyanophylla





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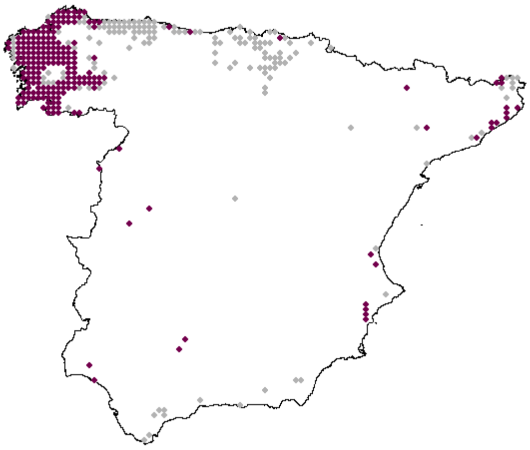
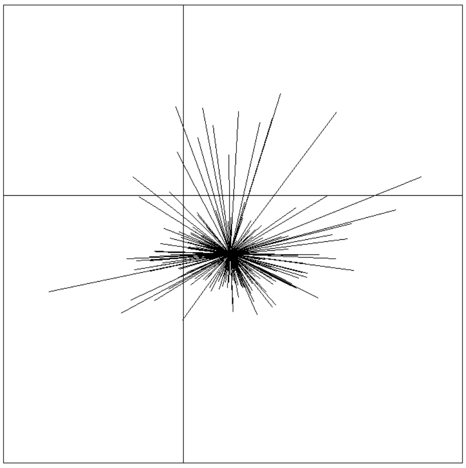
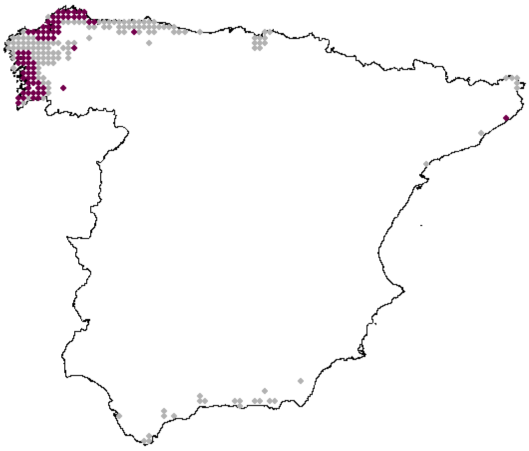
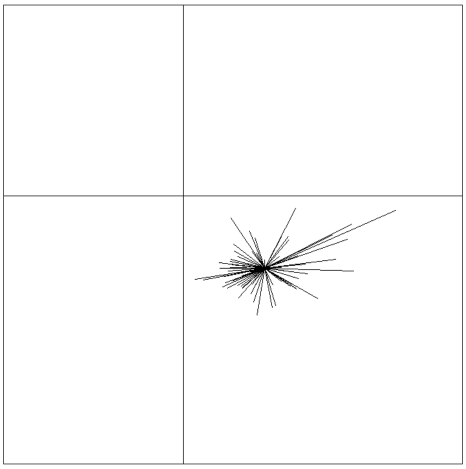


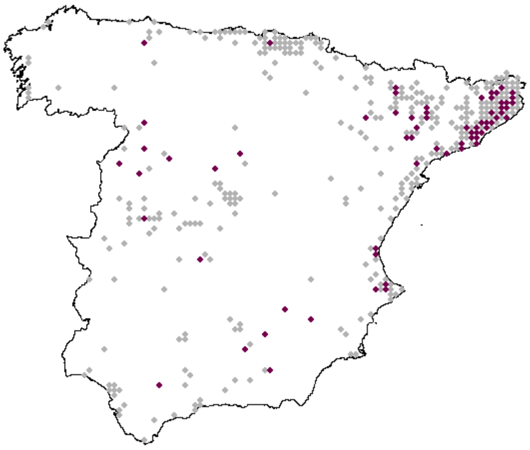


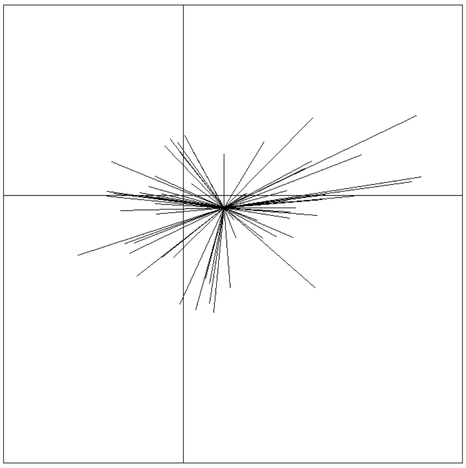
Acacia melanoxylon





Acer negundo





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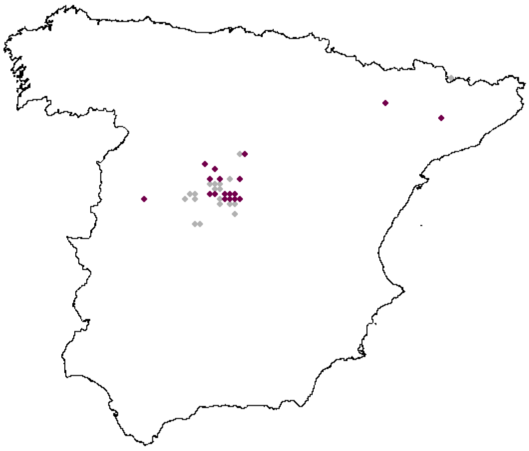
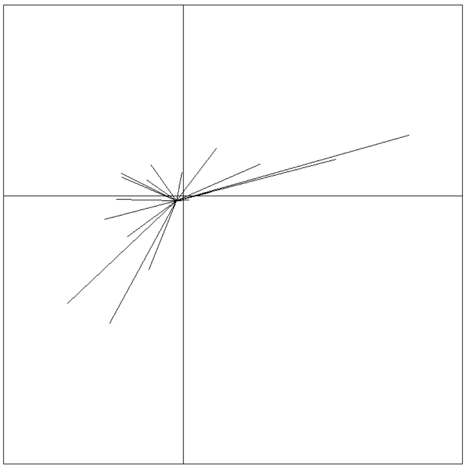
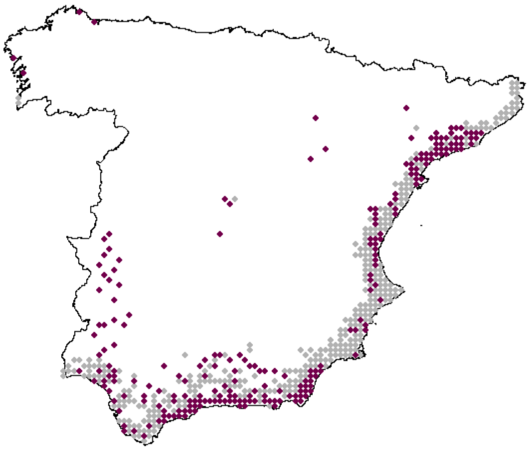
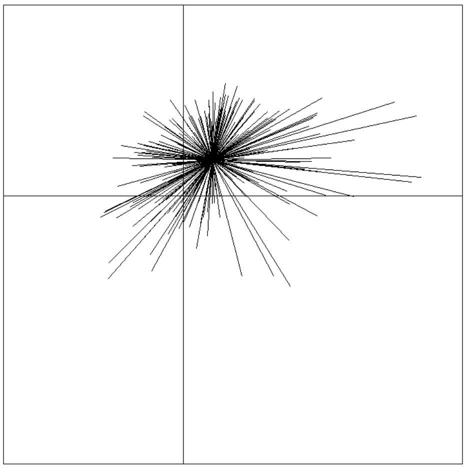


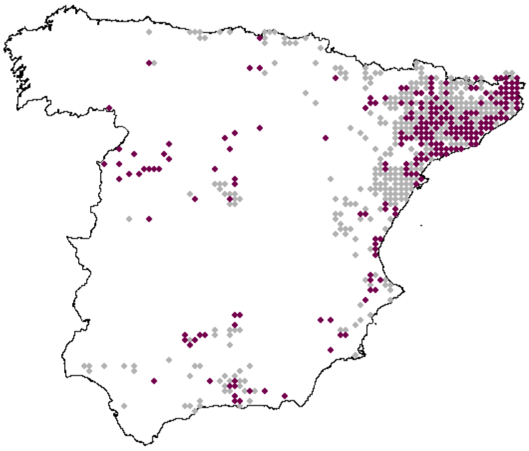


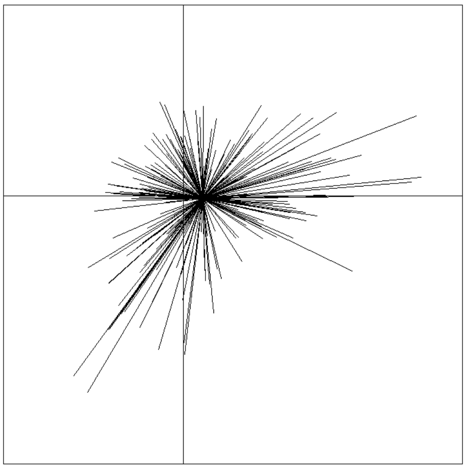
Agave americana





Ailanthus altissima





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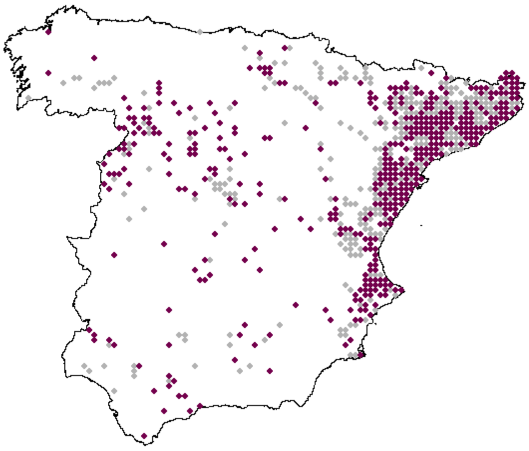

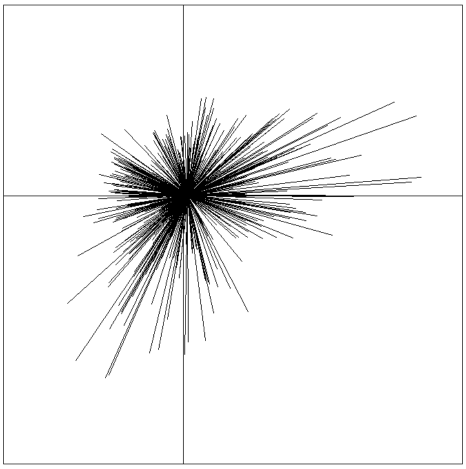

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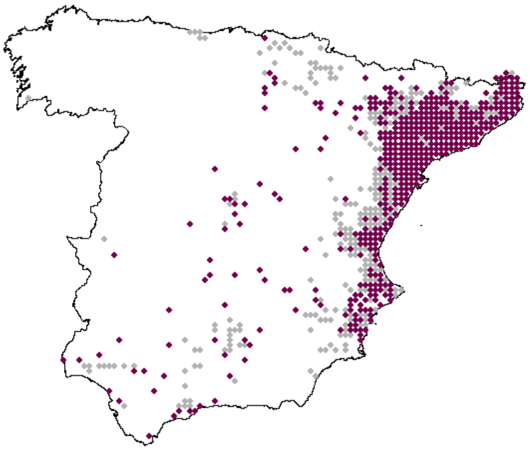

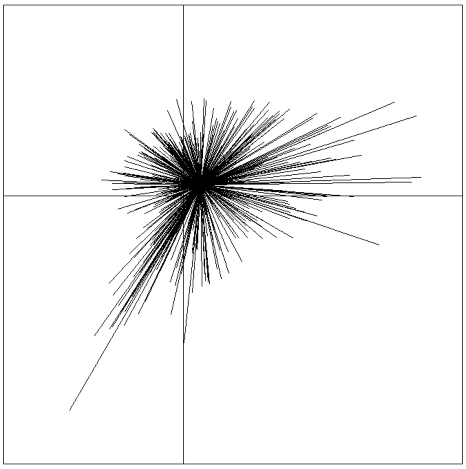

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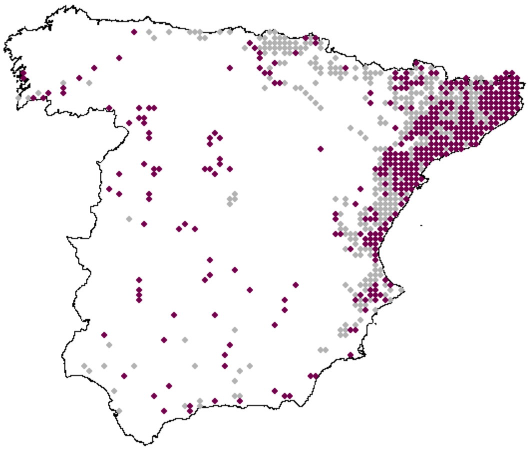

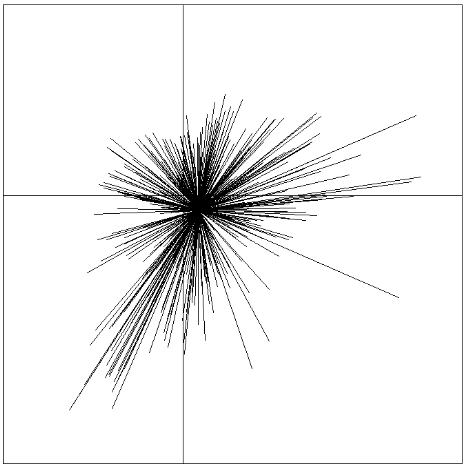

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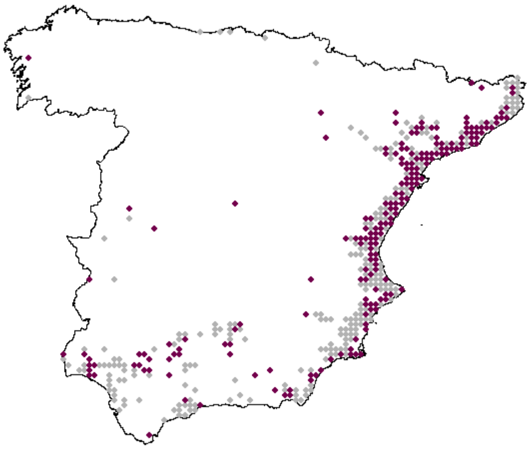

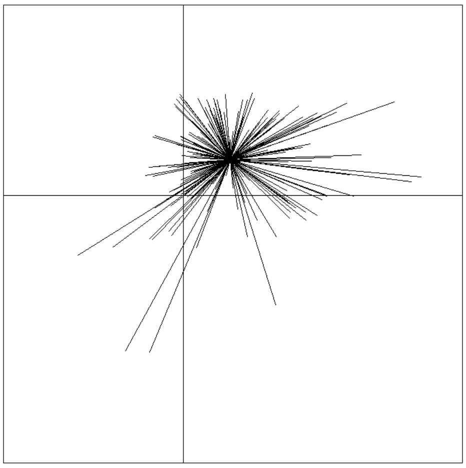

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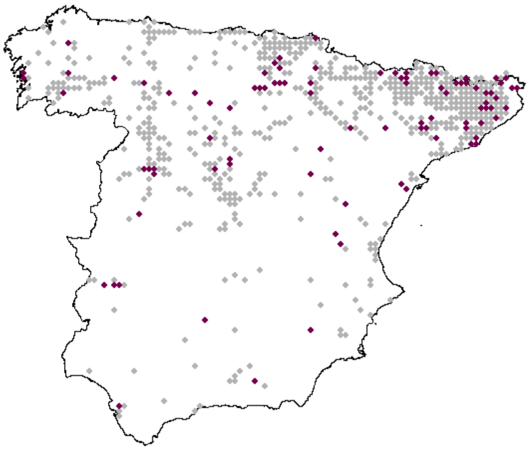

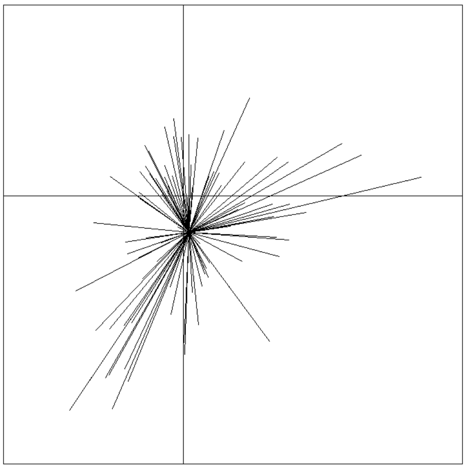

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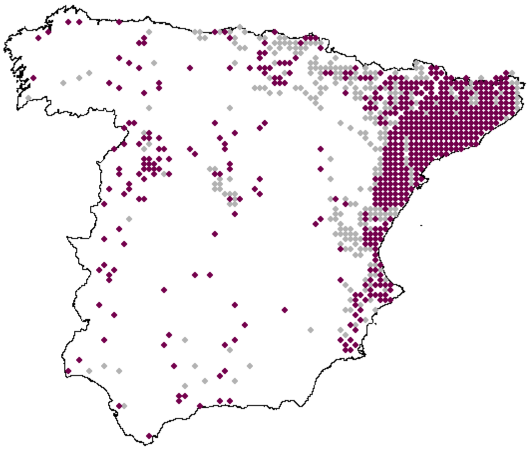

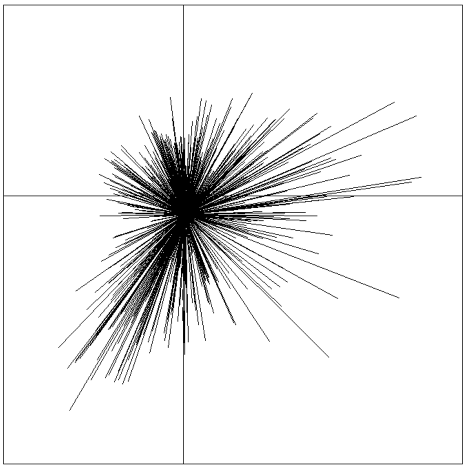

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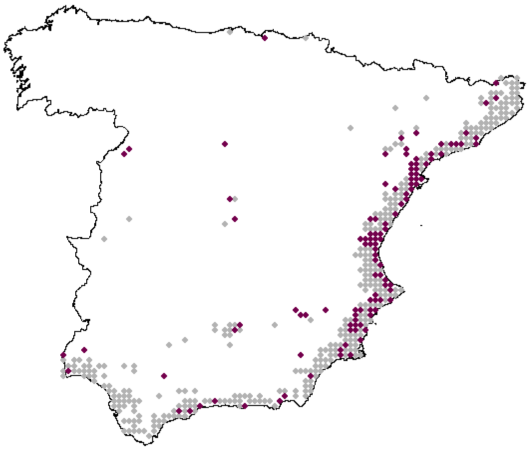

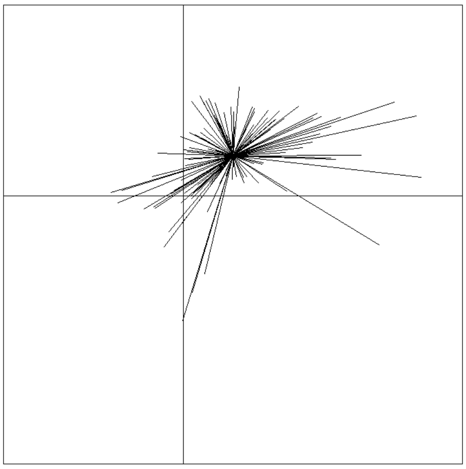

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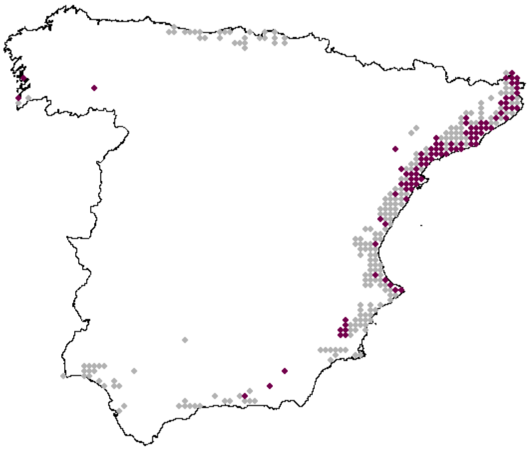

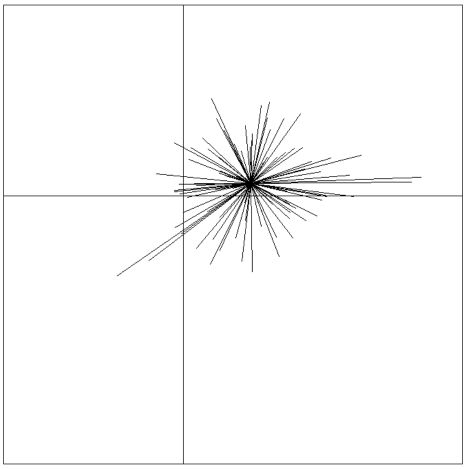

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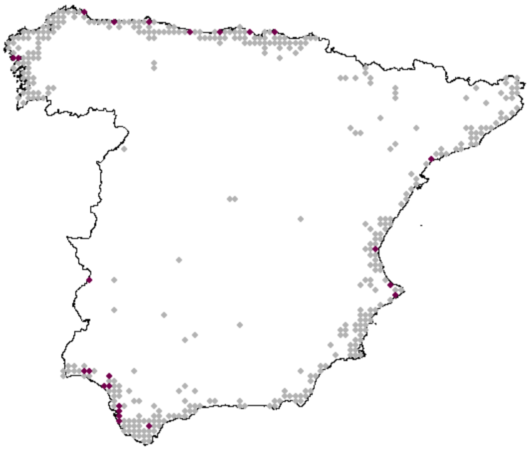

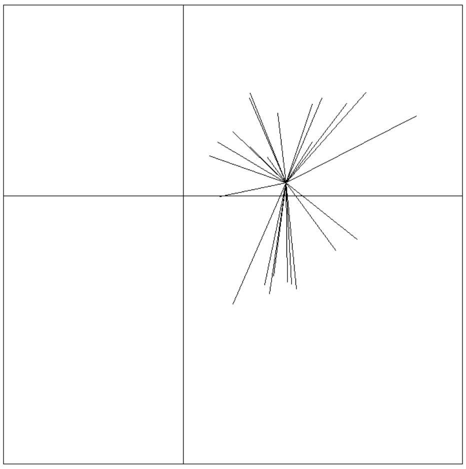

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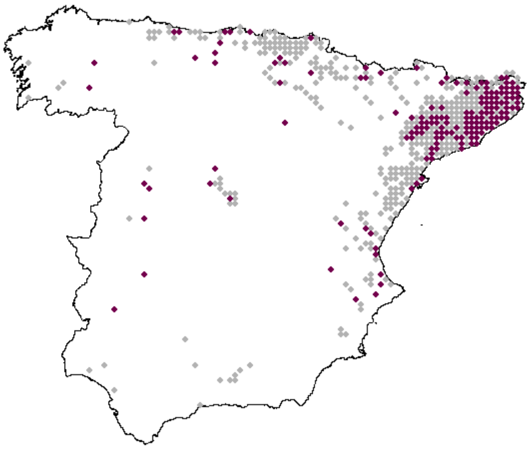

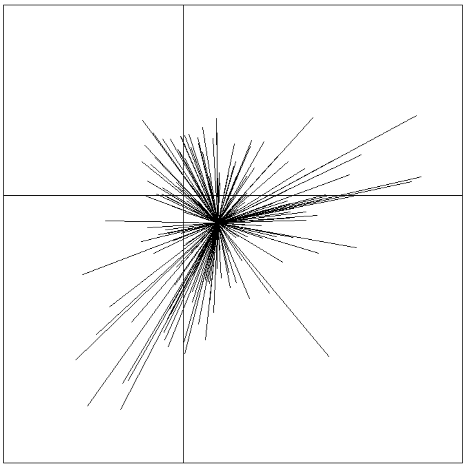

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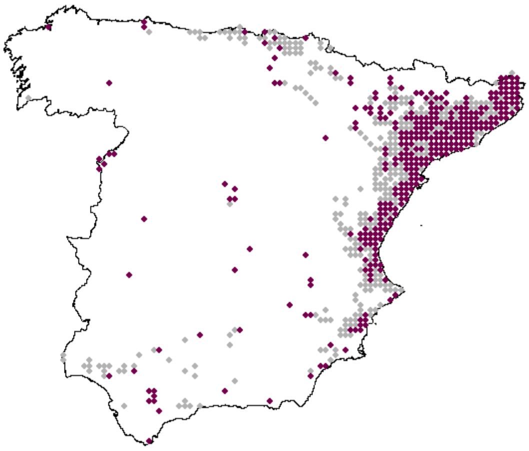

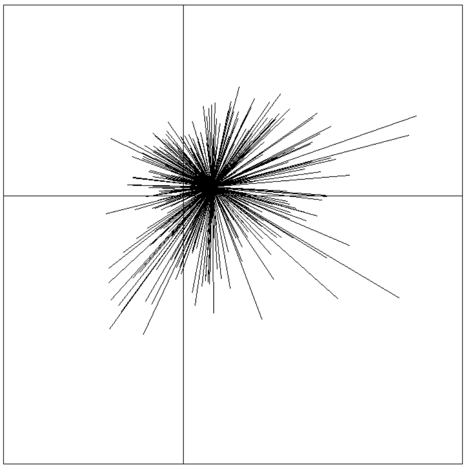

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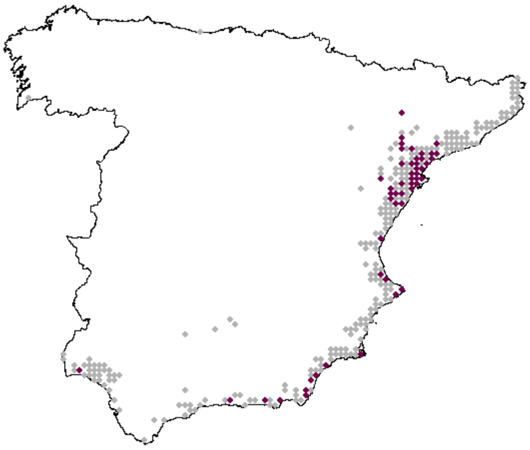

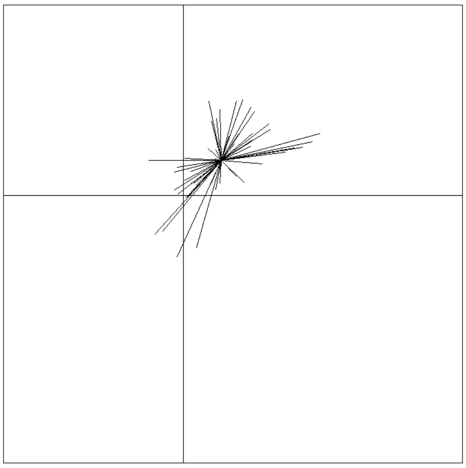

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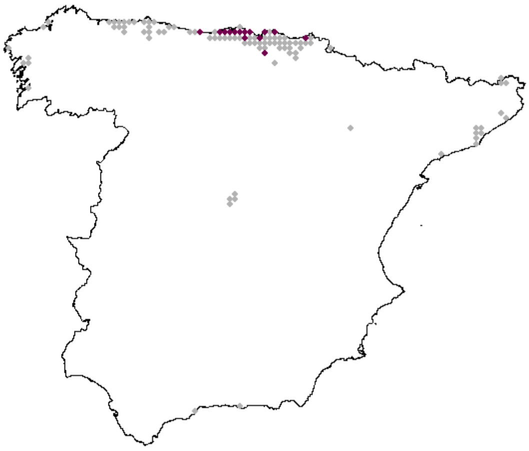
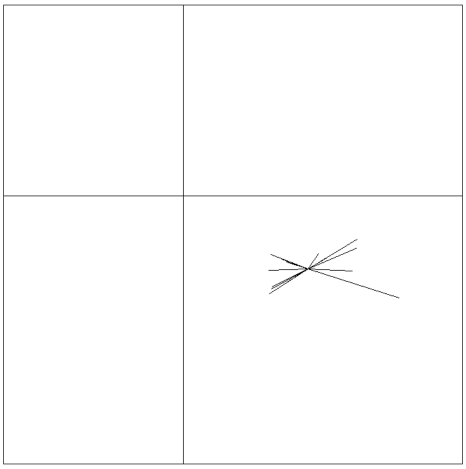
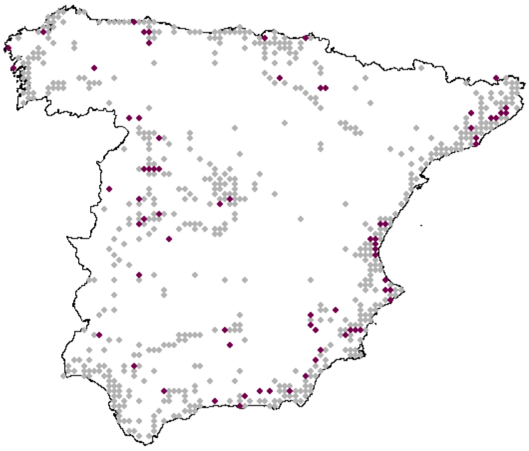
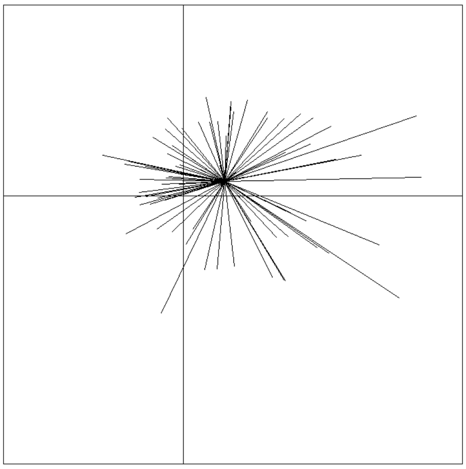


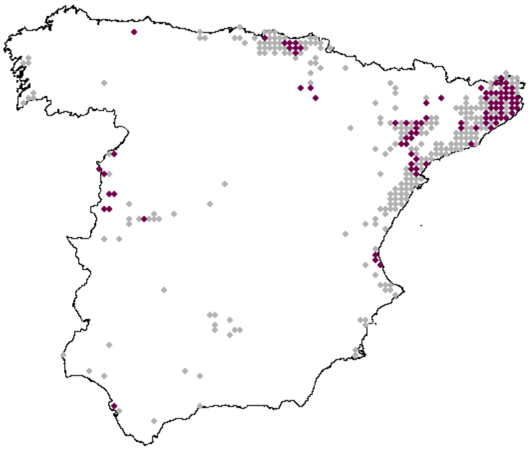


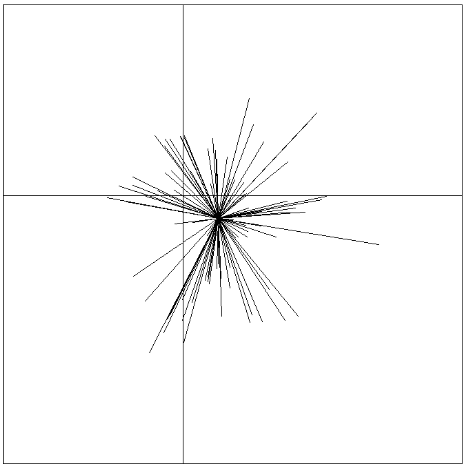
Bidens aurea





Bidens frondosa





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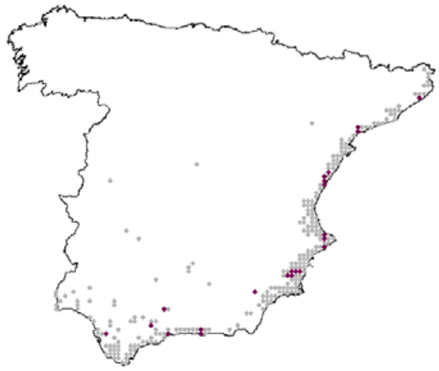

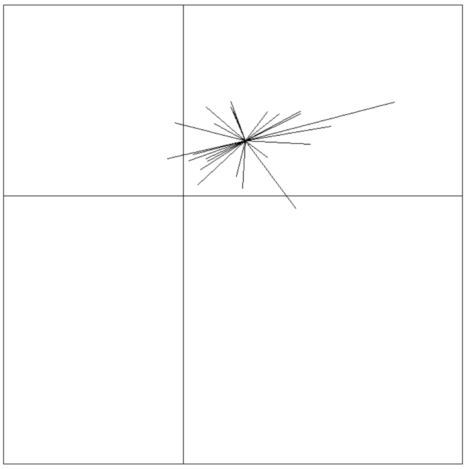

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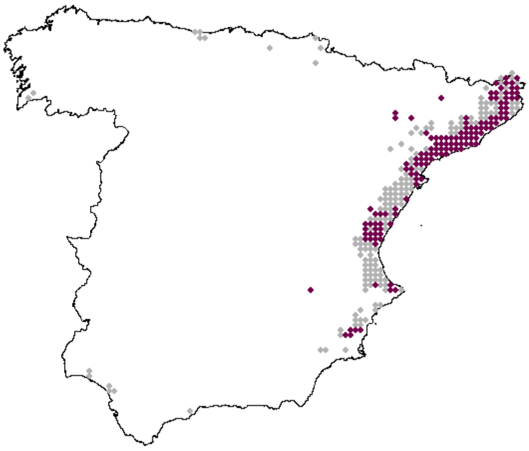

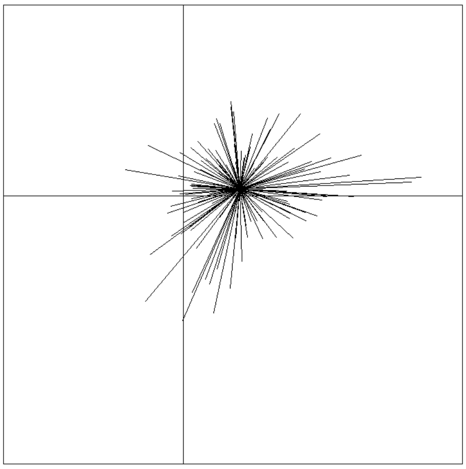

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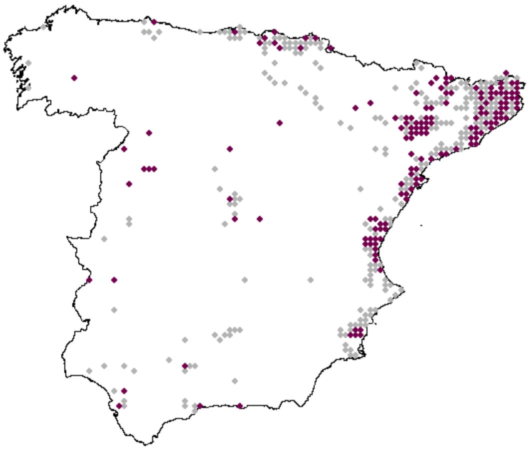
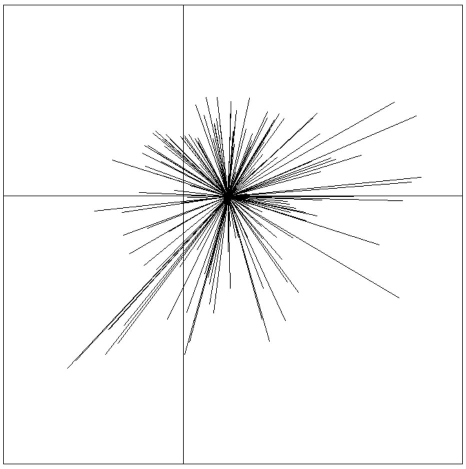
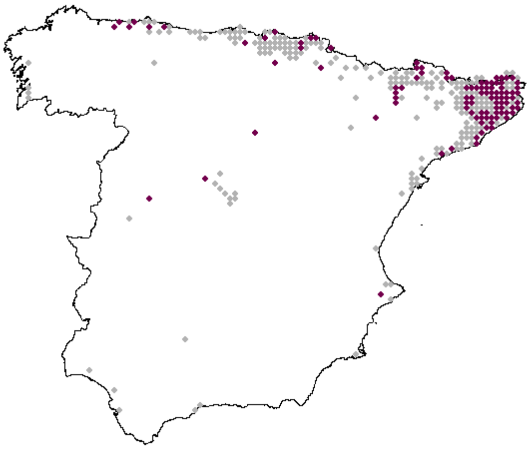
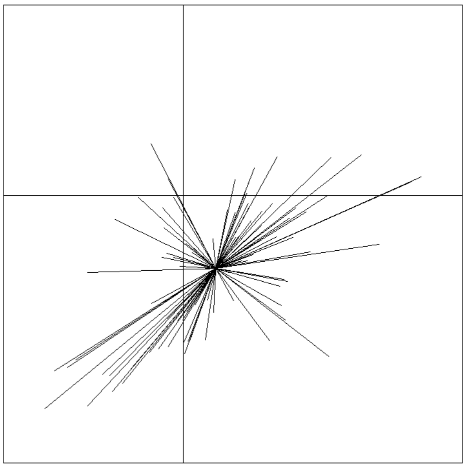




Buddleja davidii





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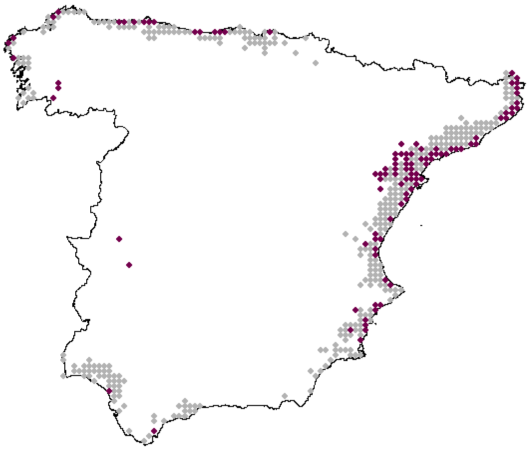
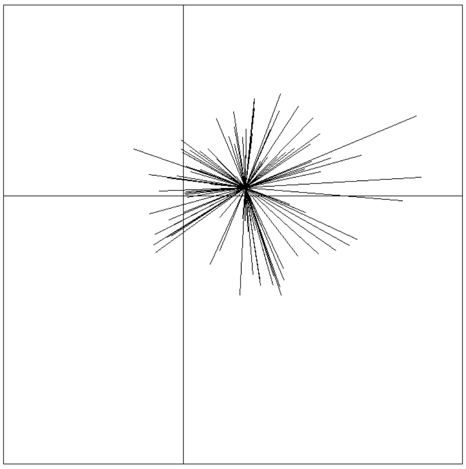
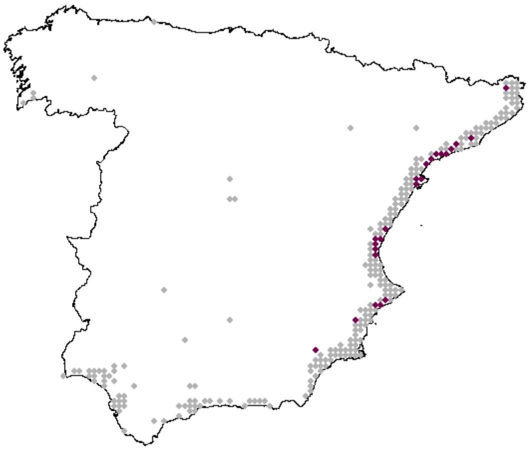
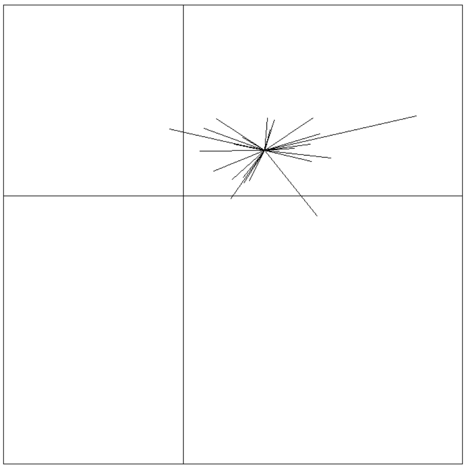


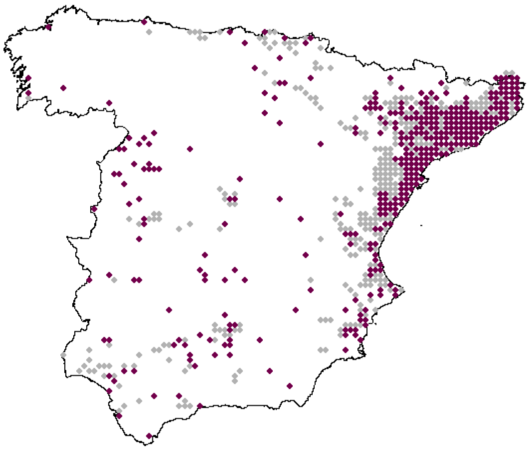


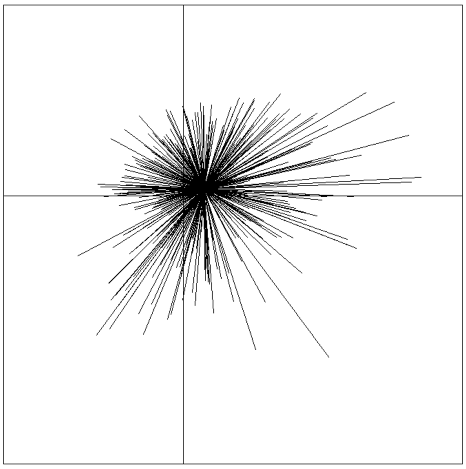
Chloris gayana





Conyza bonariensis





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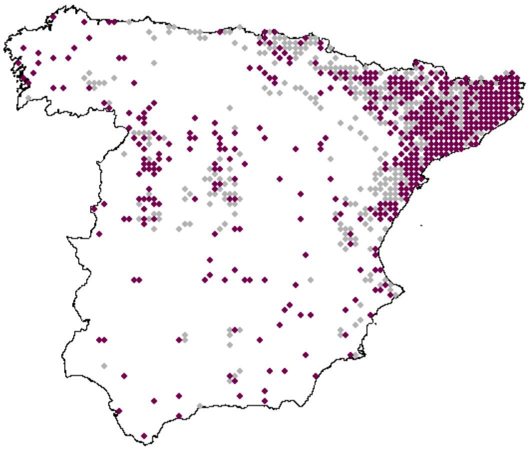
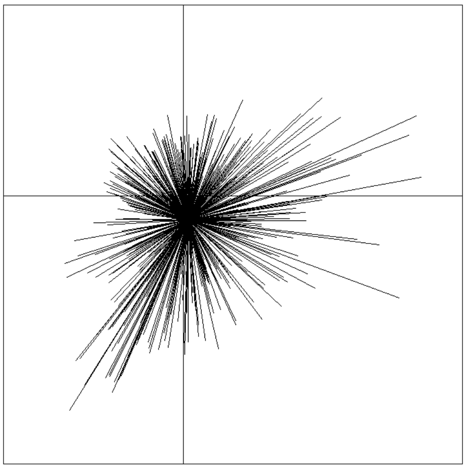
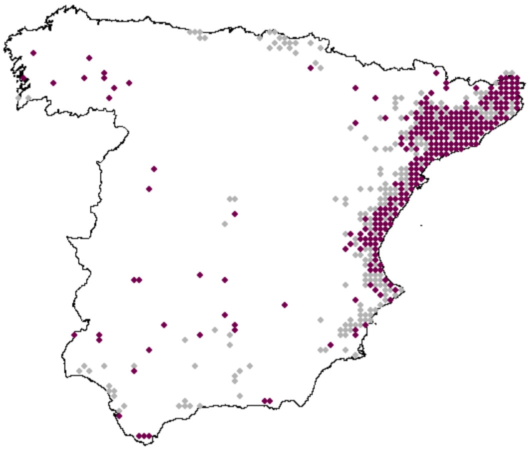
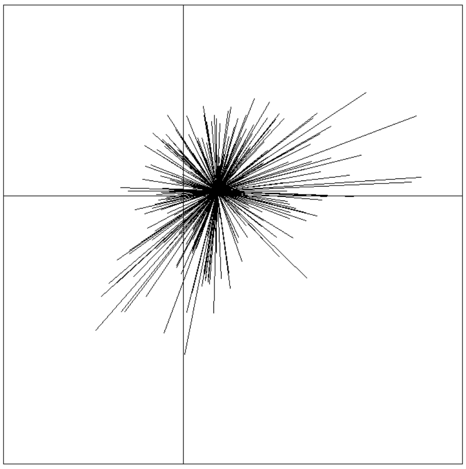


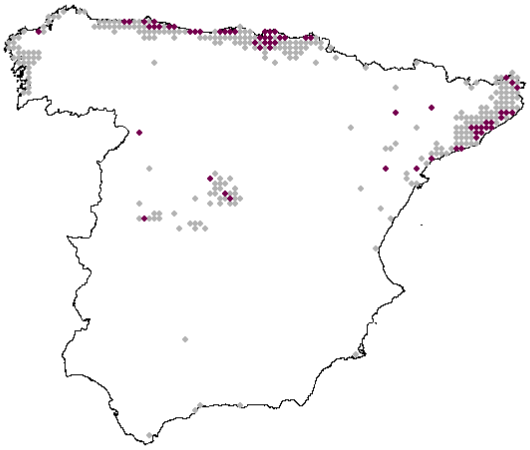


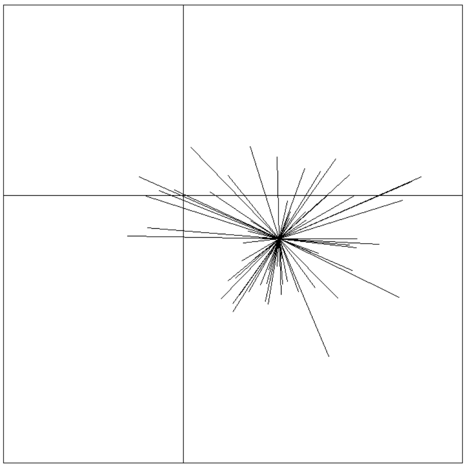
Conyza sumatrensis



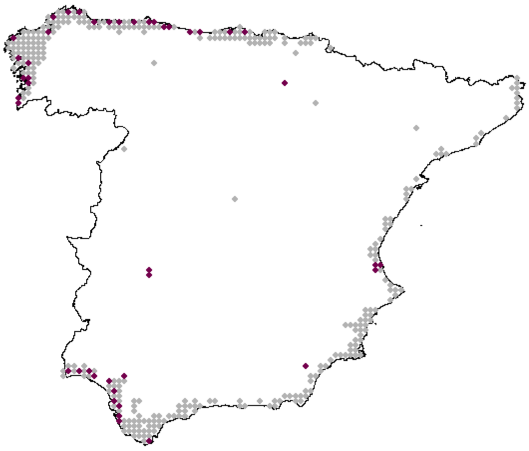


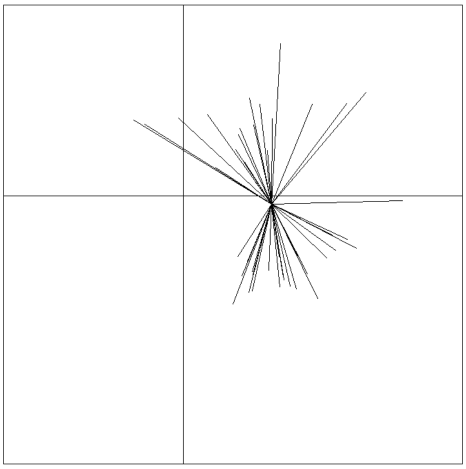
Cortaderia selloana



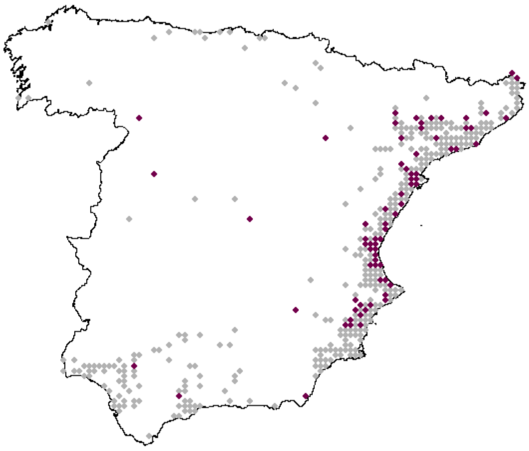


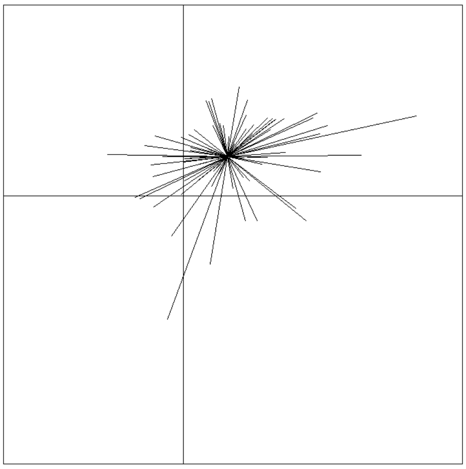
Cotula coronopifolia



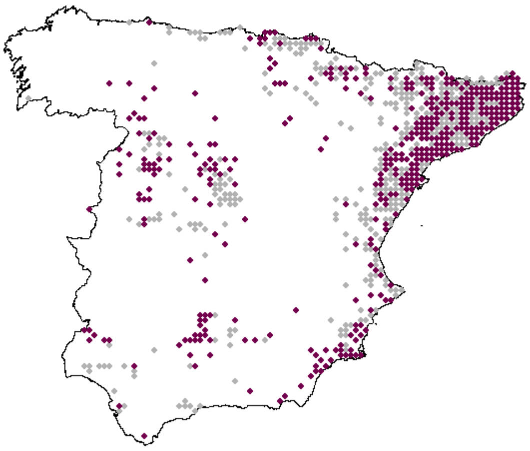


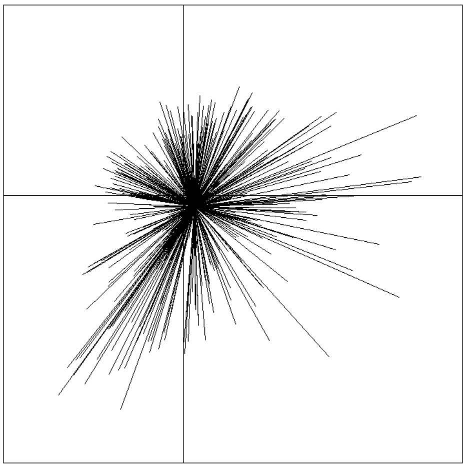
Datura innoxia



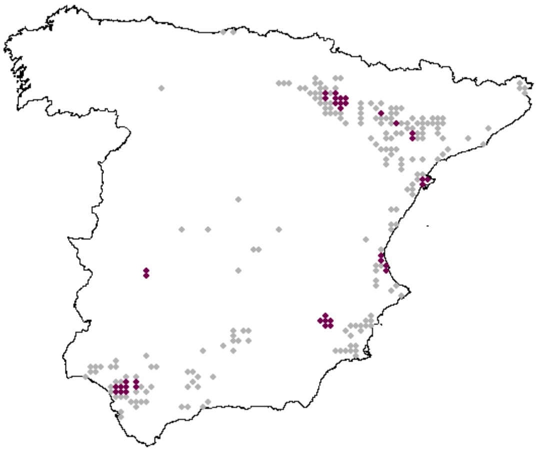


Datura stramonium





Echinochloa hispidula



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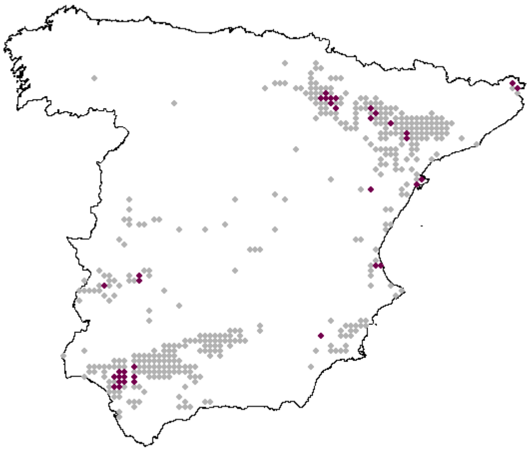

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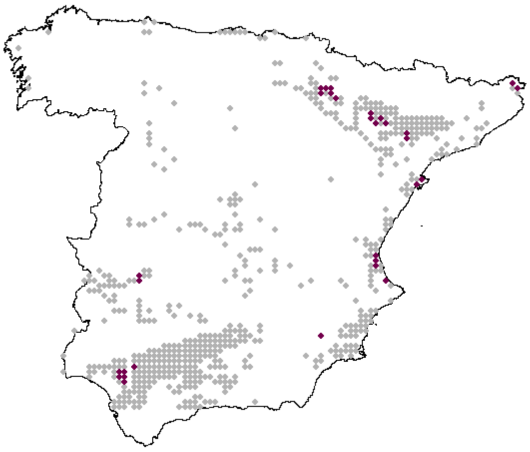
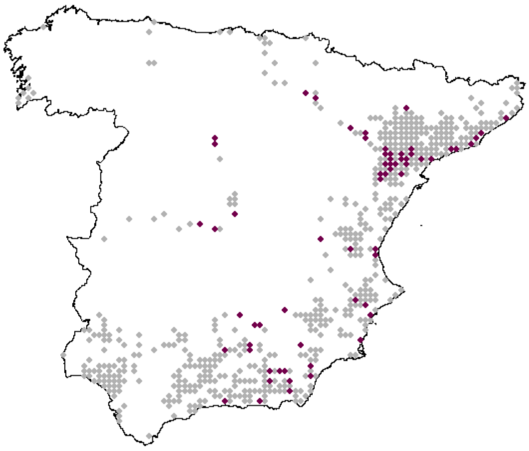
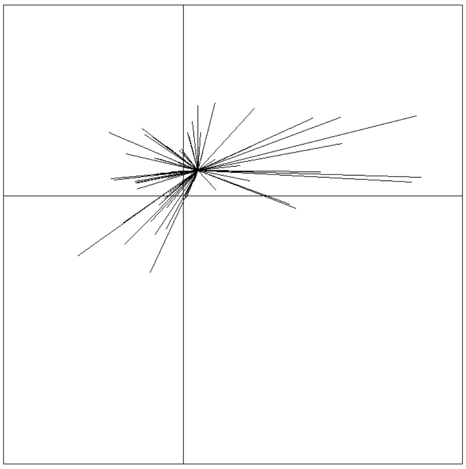
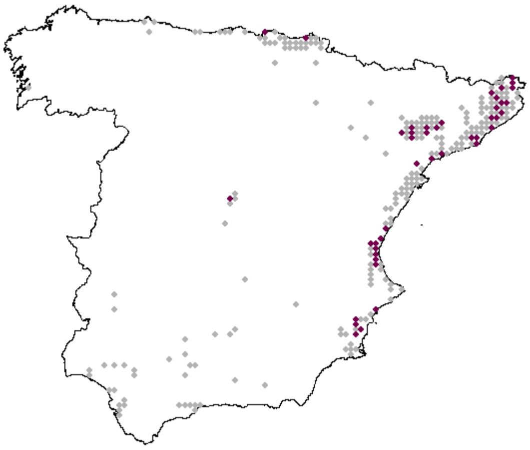


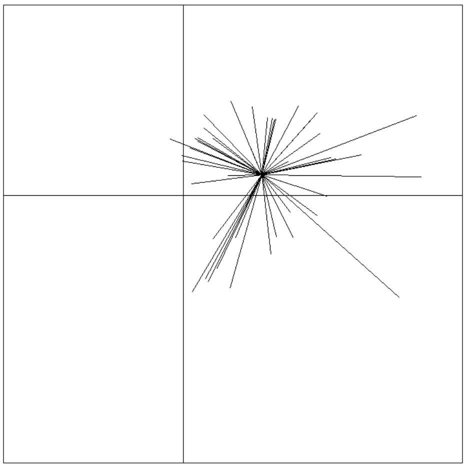
Elaeagnus angustifolia





Eleusine indica





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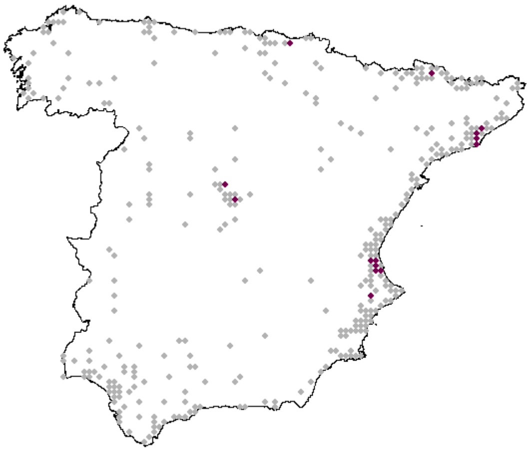
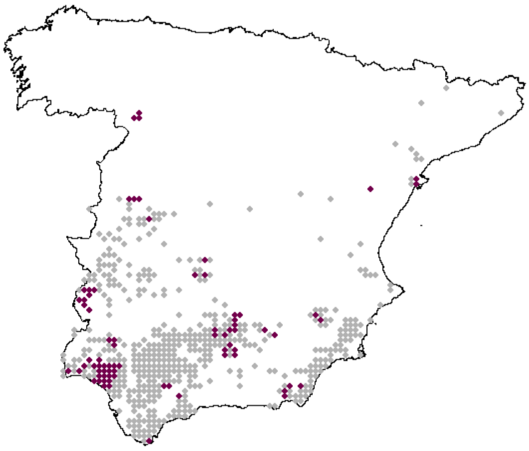
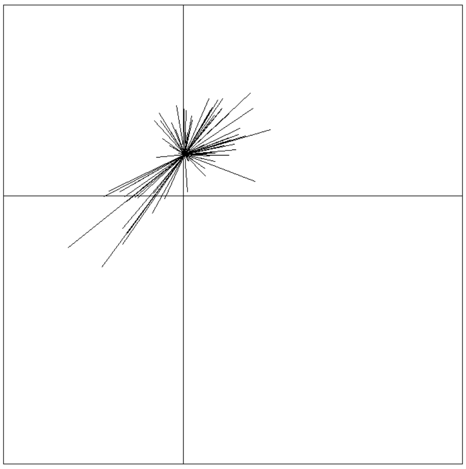


Eucalyptus camaldulensis





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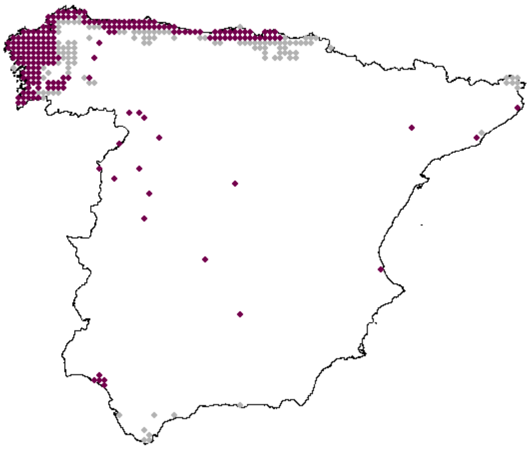
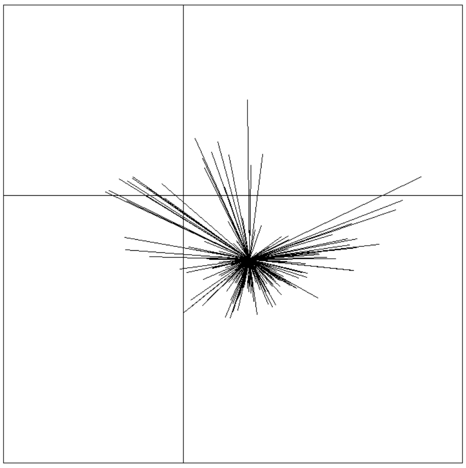
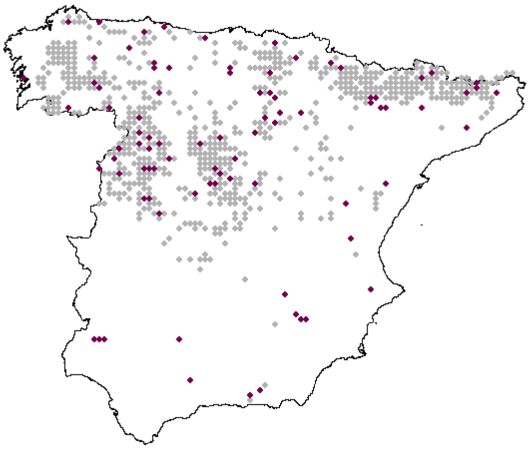
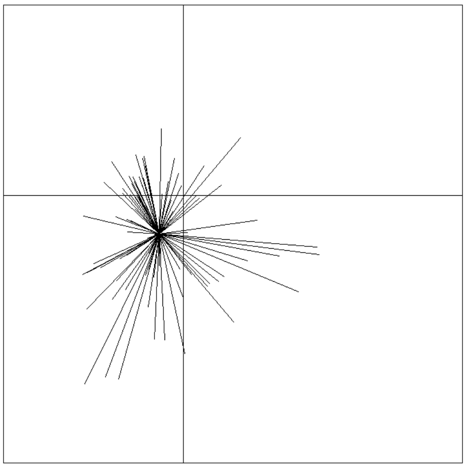


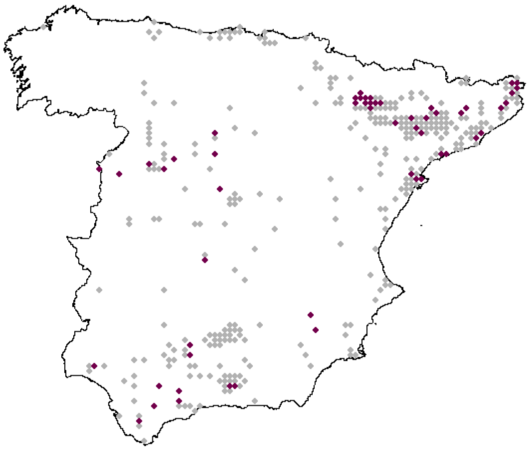


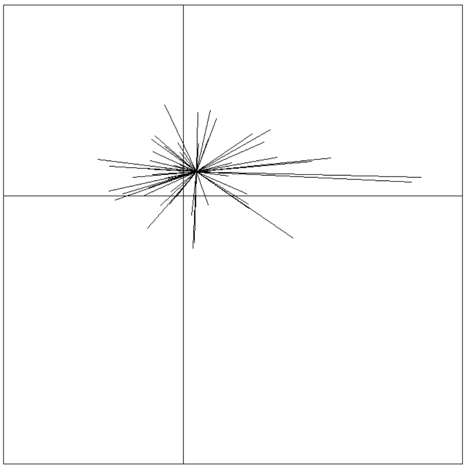
Fallopia baldschuanica



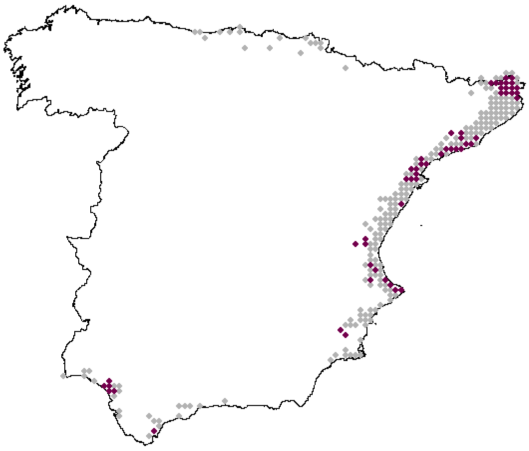


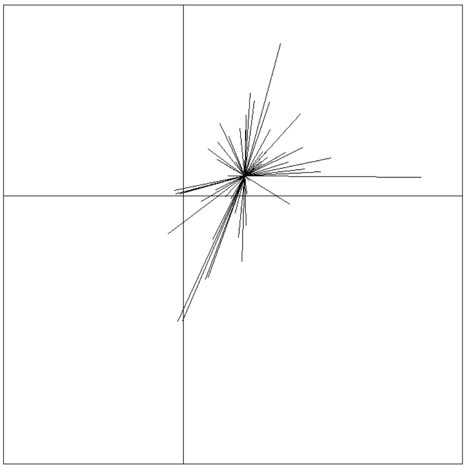
Gleditsia triacanthos





Gomphocarpus fruticosus





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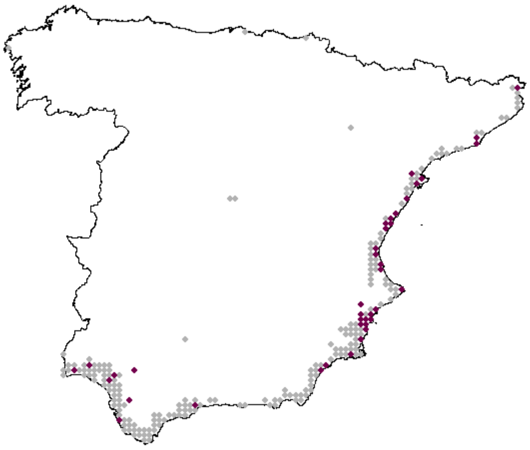

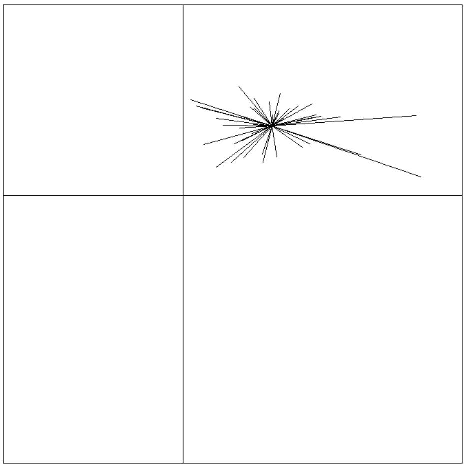

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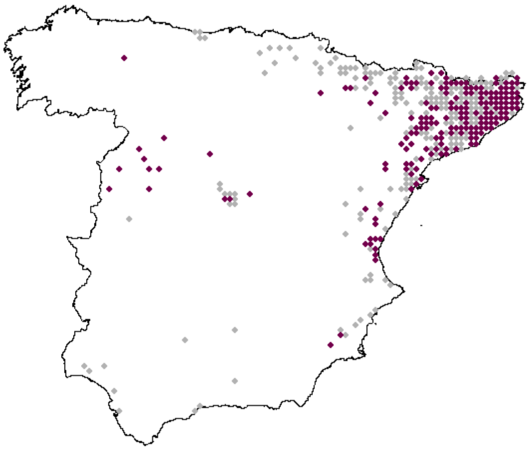
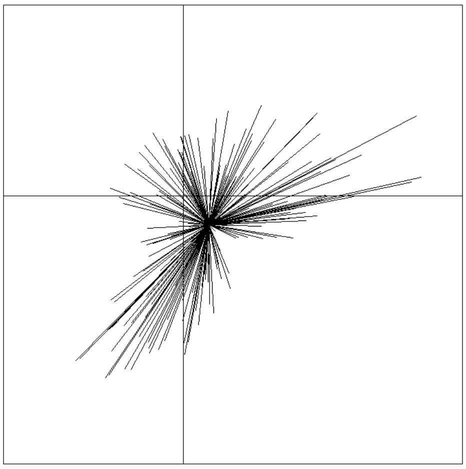
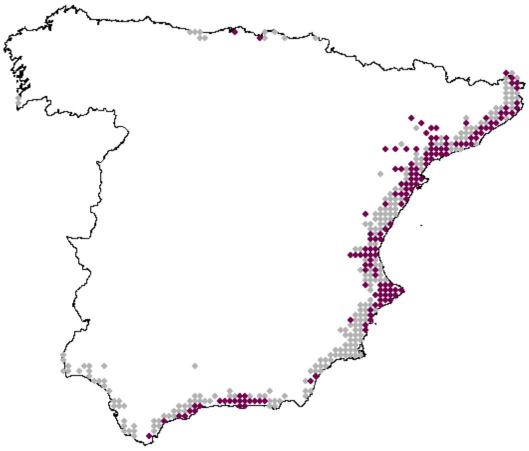
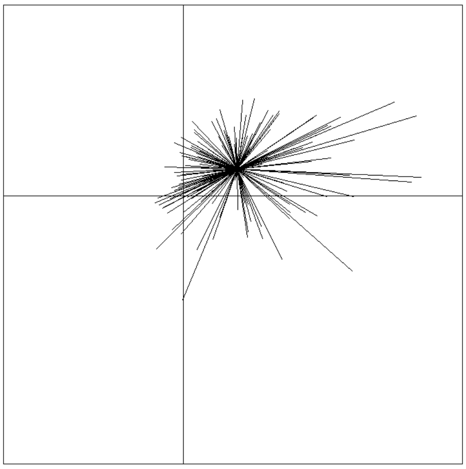




Ipomoea indica





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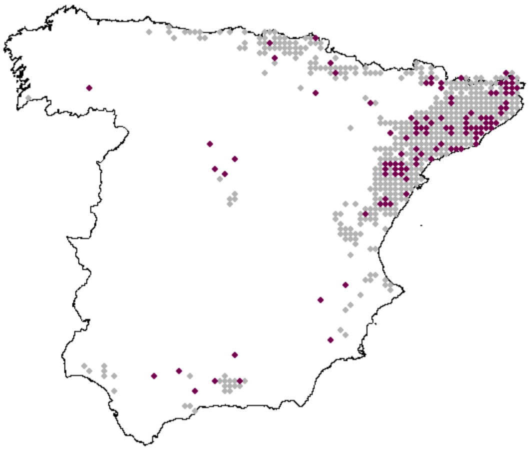

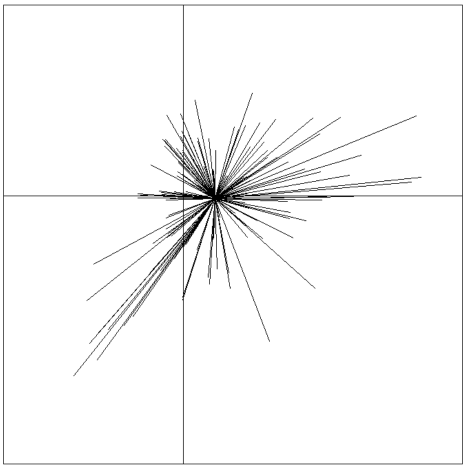

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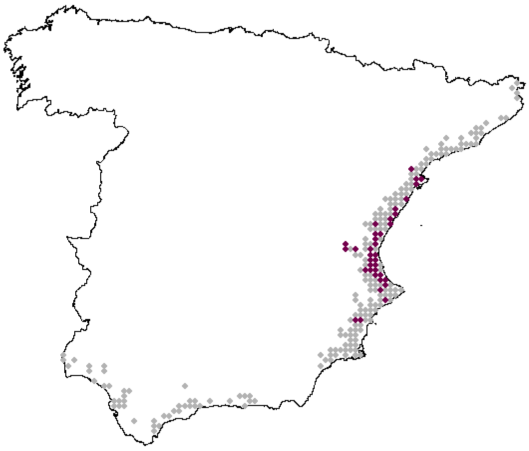
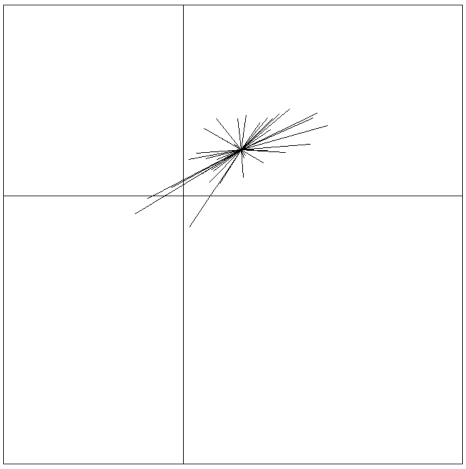
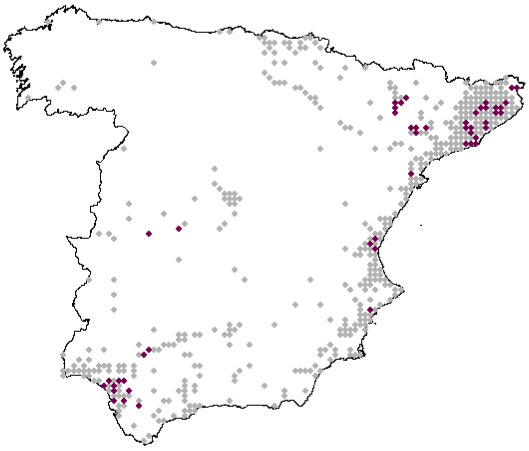
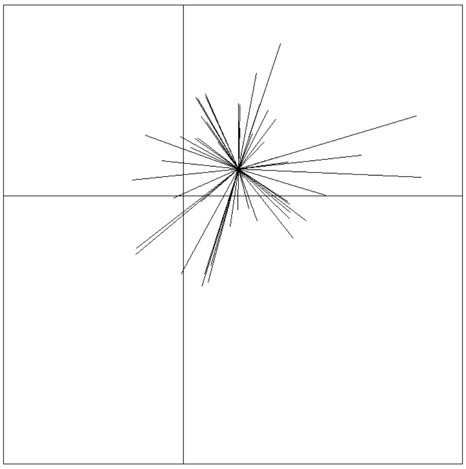


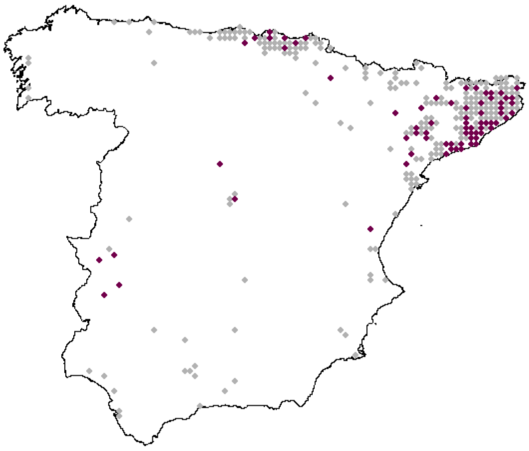


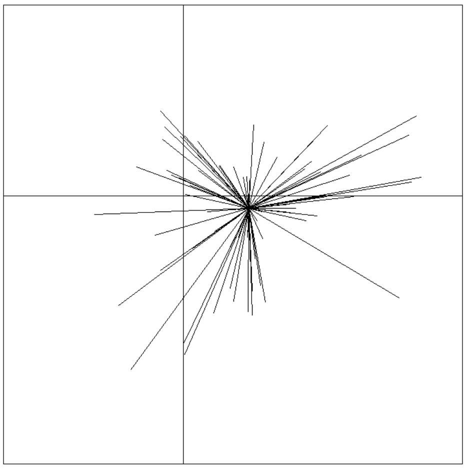
Lippia filiformis



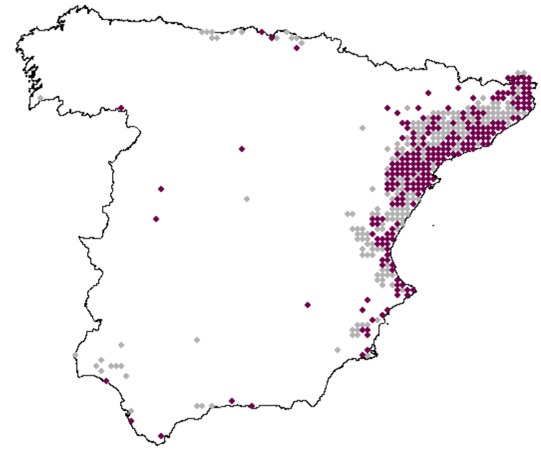


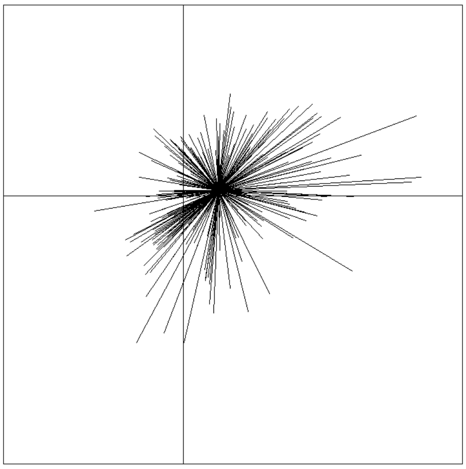
Lonicera japonica



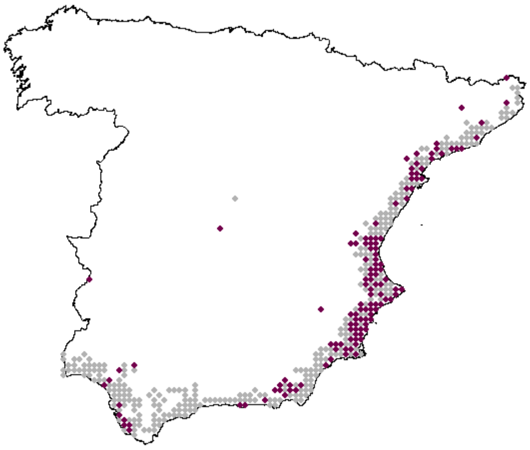


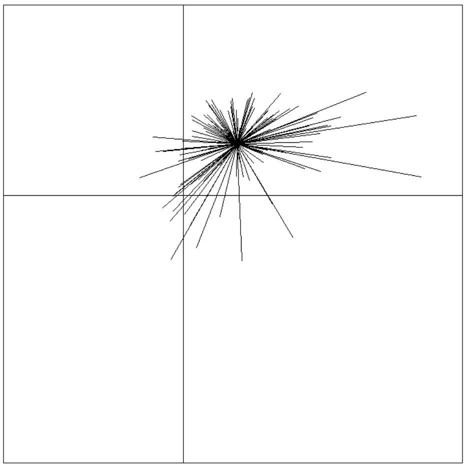
Mirabilis jalapa



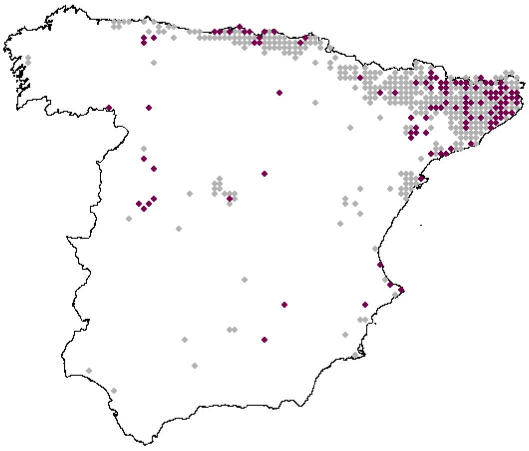


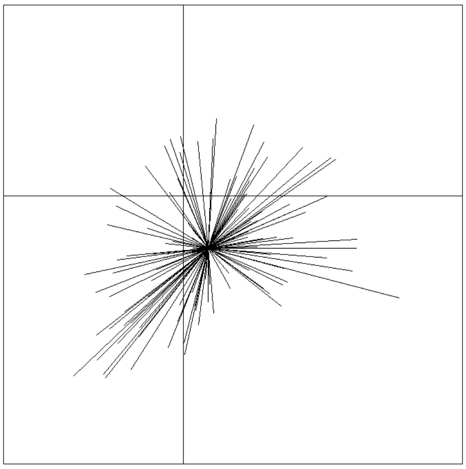
Nicotiana glauca



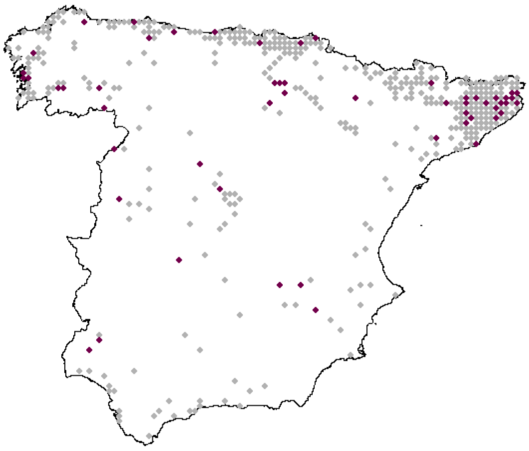


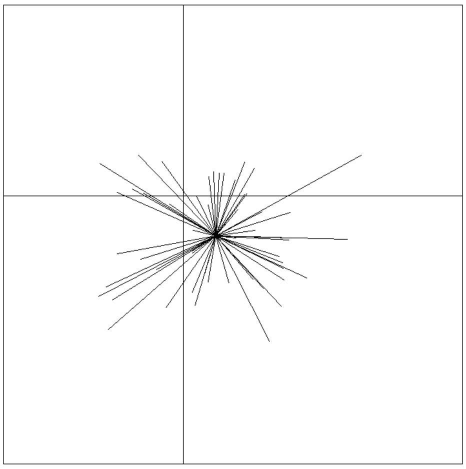
Oenothera biennis



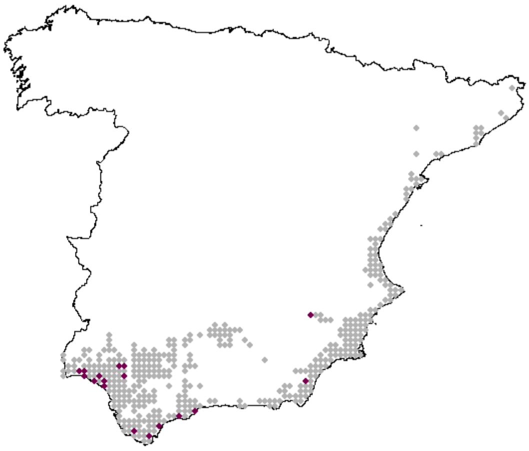


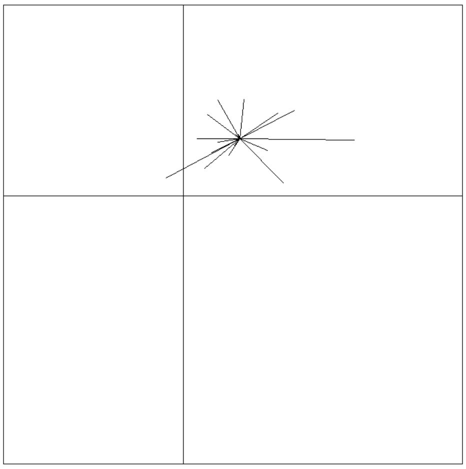
Oenothera glazioviana



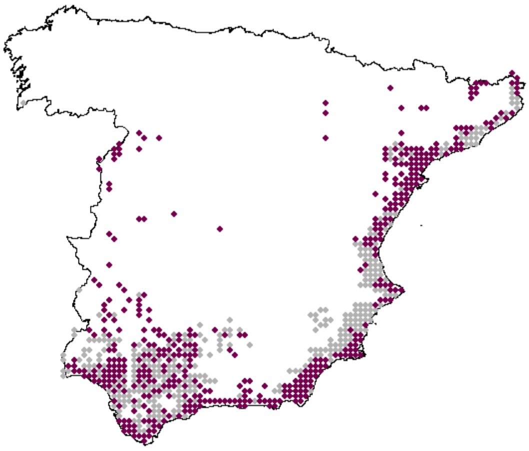


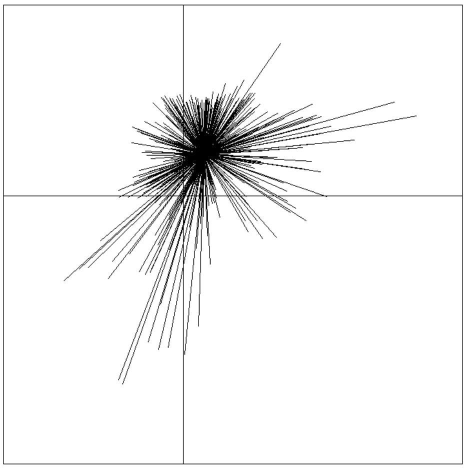
Opuntia dillenii



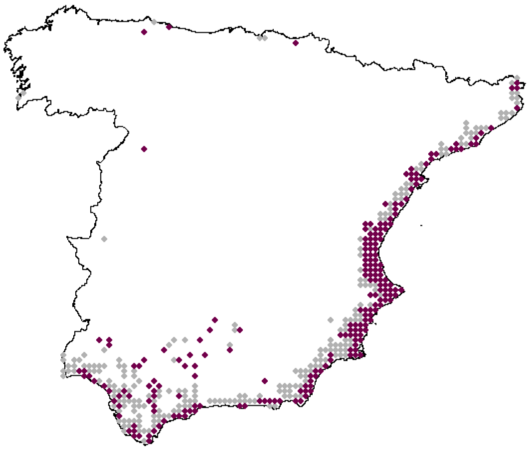


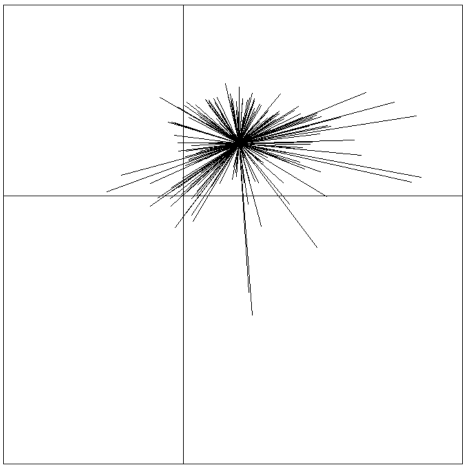
Opuntia ficus-indica



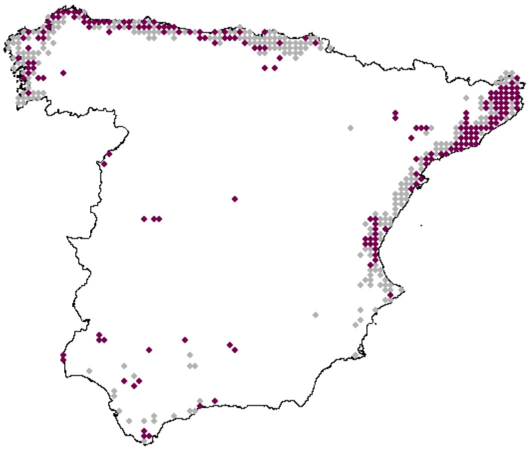


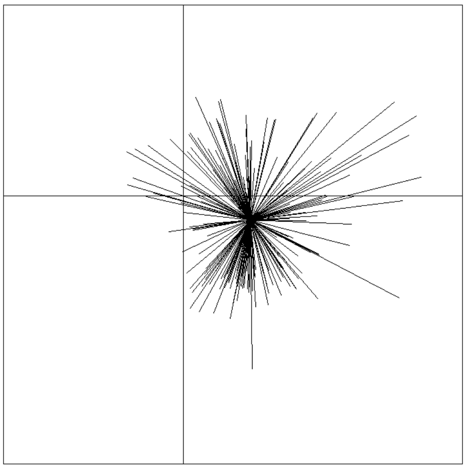
Oxalis pes-caprae



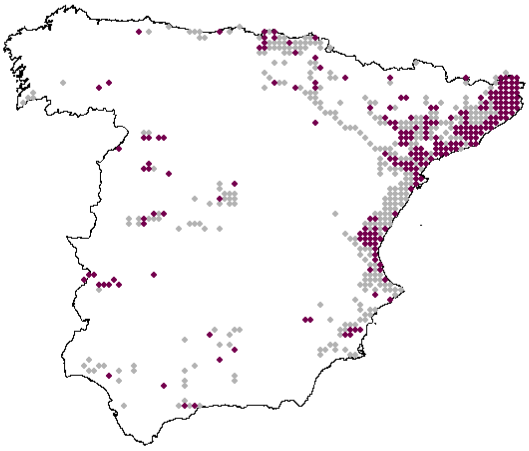


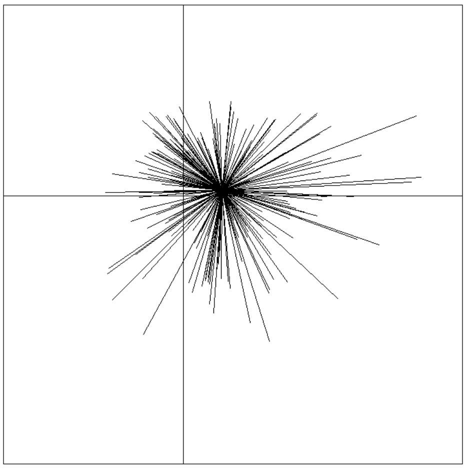
Paspalum dilatatum



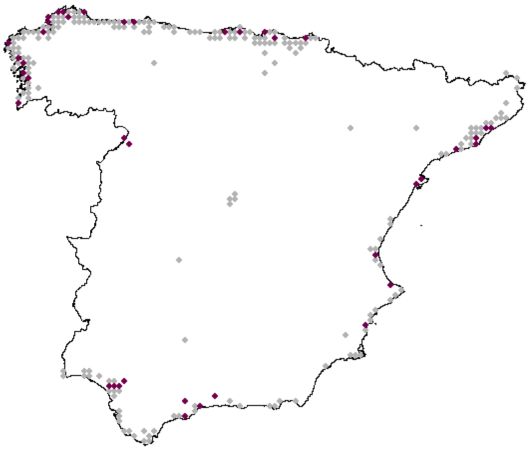


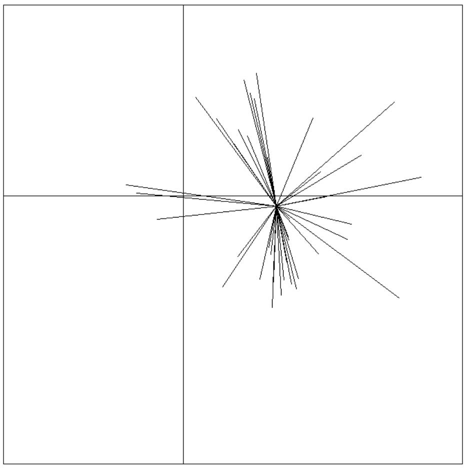
Paspalum paspalodes



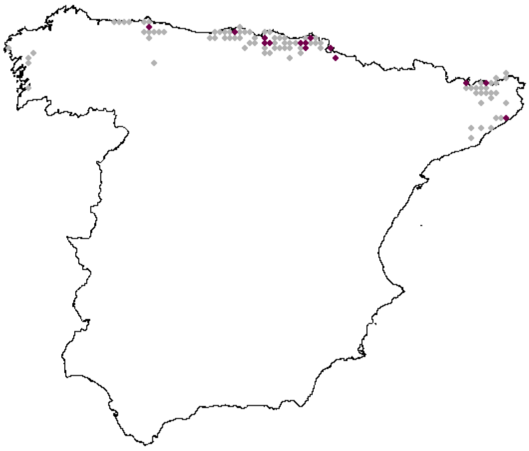


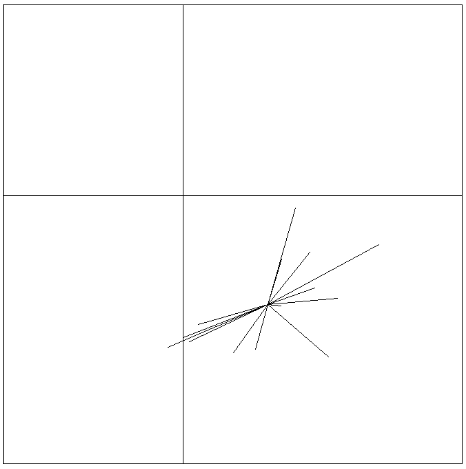
Paspalum vaginatum



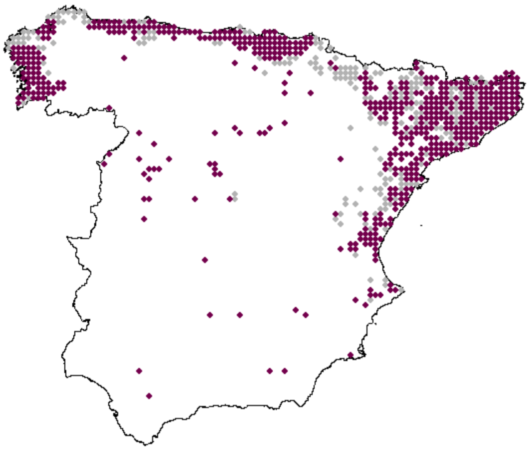


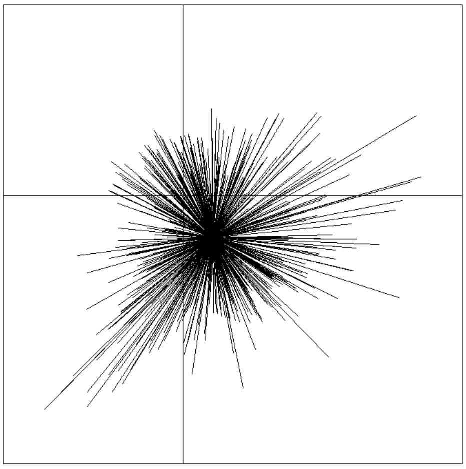
Reynoutria japonica



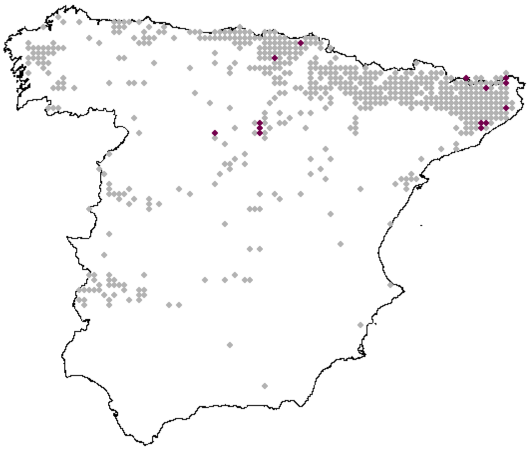


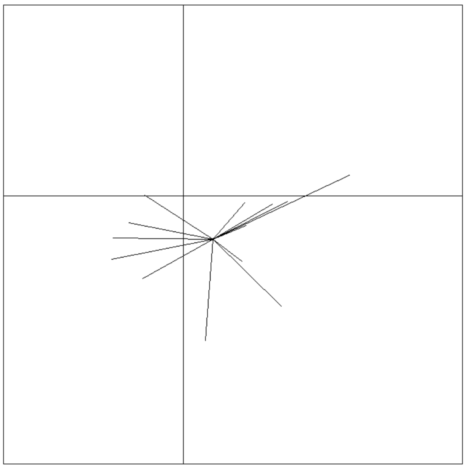
Robinia pseudoacacia



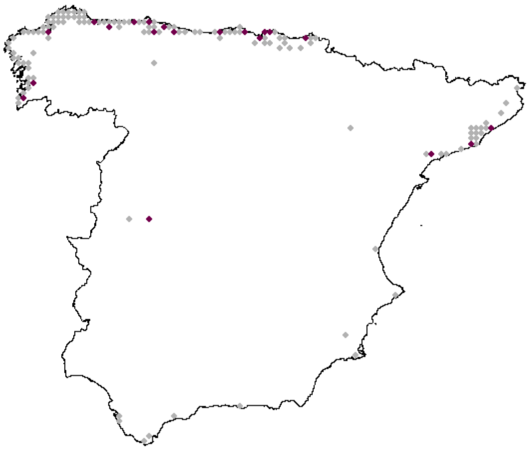


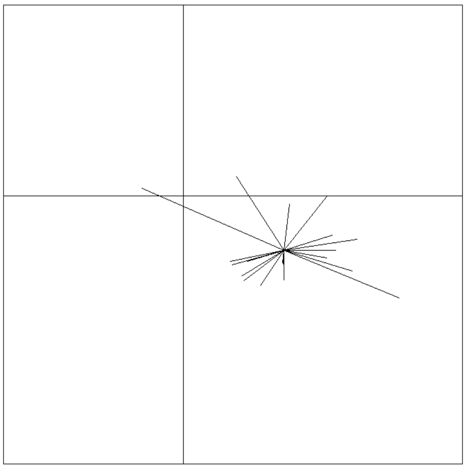
Senecio inaequidens



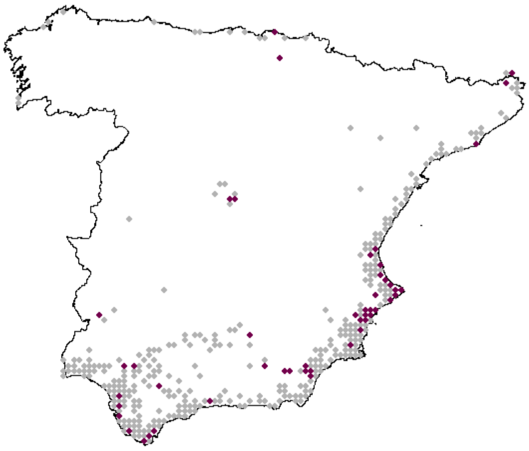


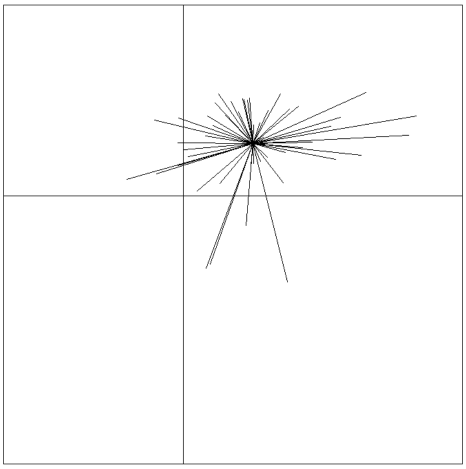
Senecio mikanioides



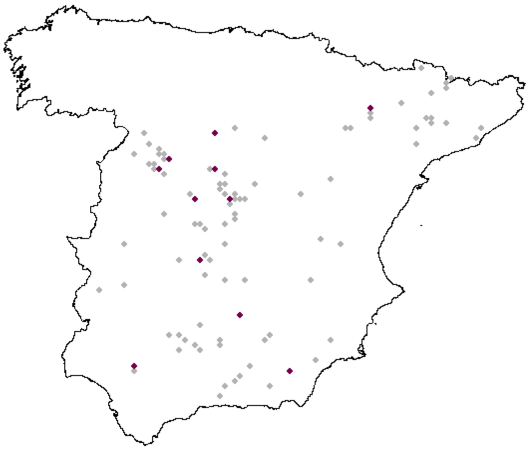


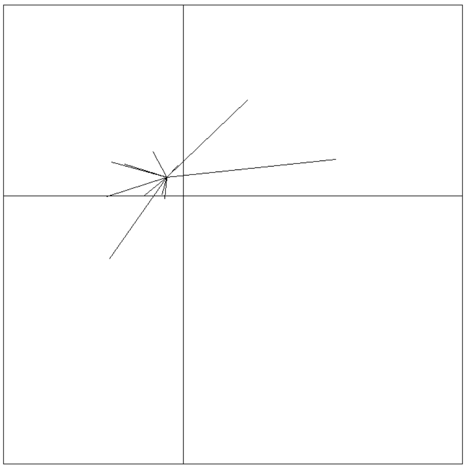
Solanum bonariense



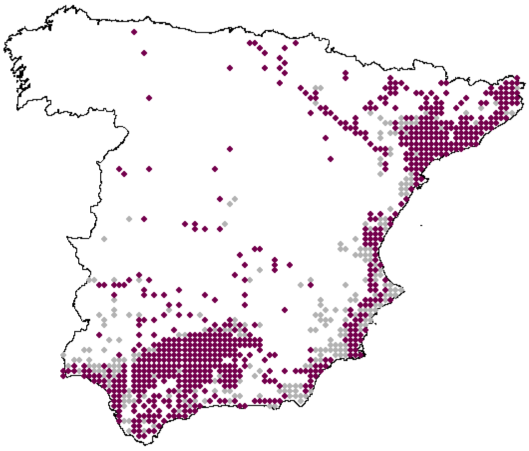


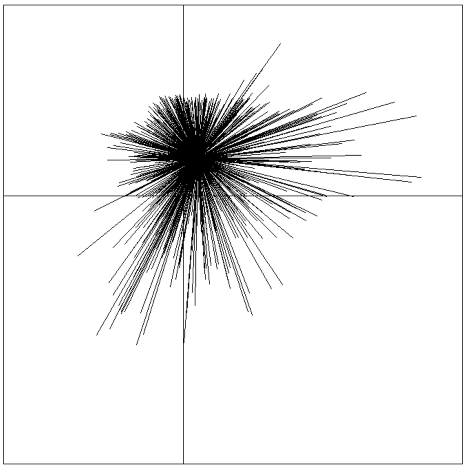
Sophora japonica



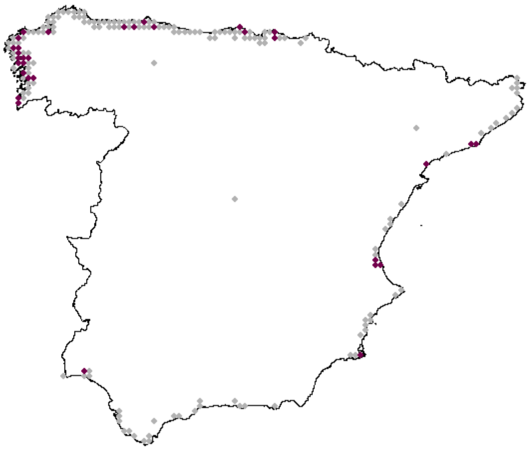


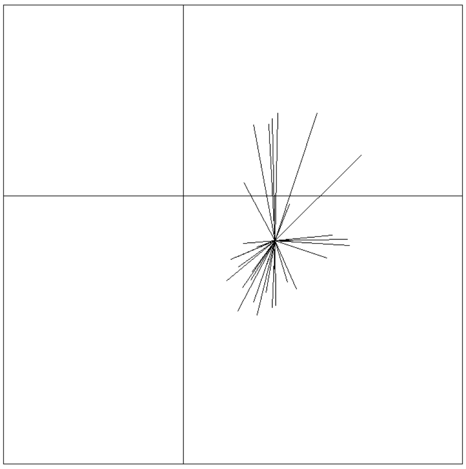
Sorghum halepense



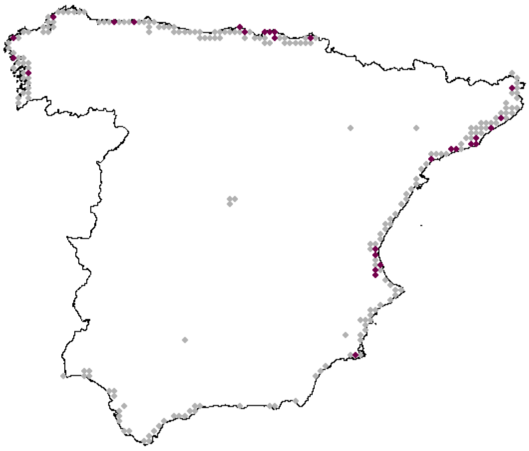


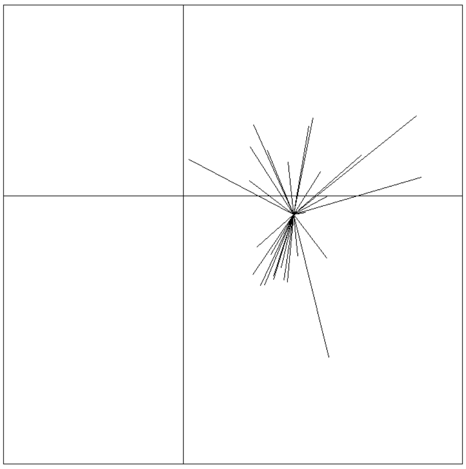
Spartina patens



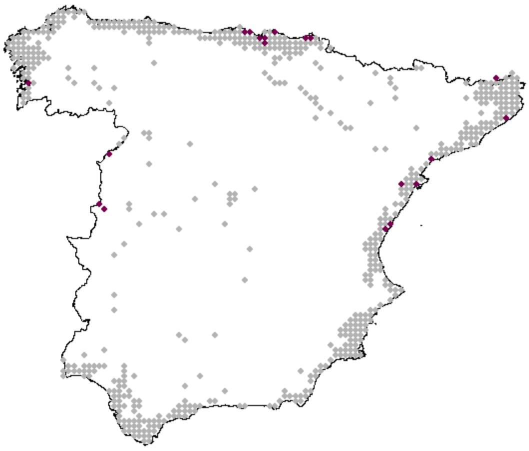


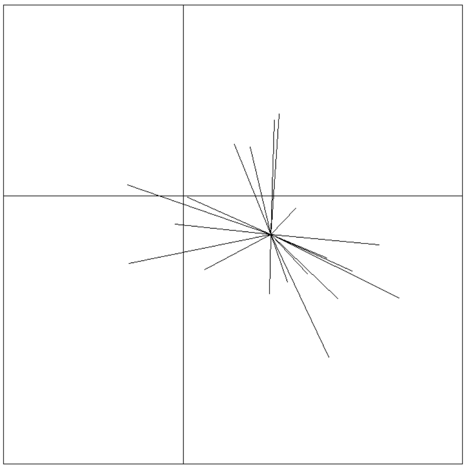
Stenotaphrum secundatum



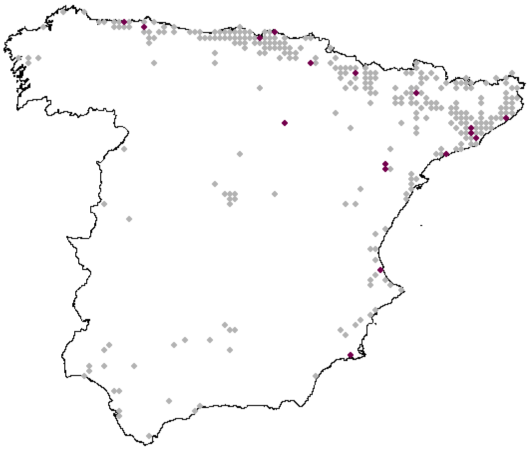


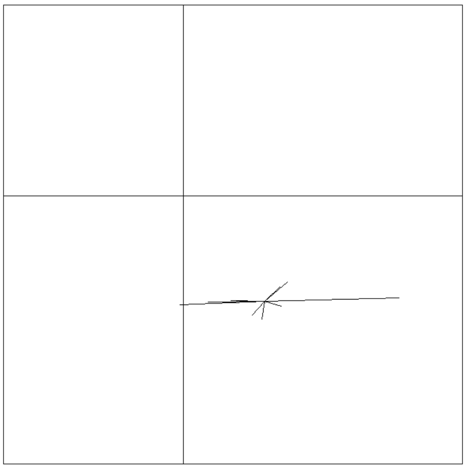
Tradescantia fluminensis



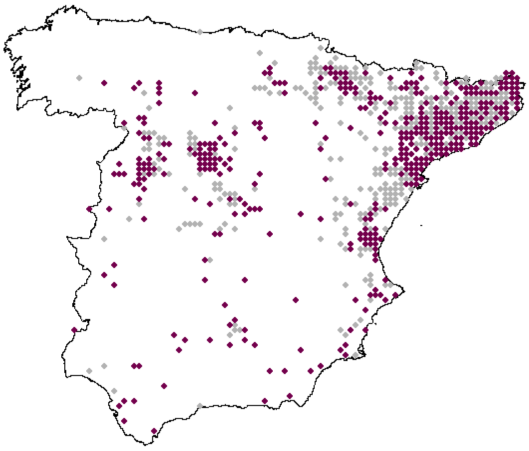


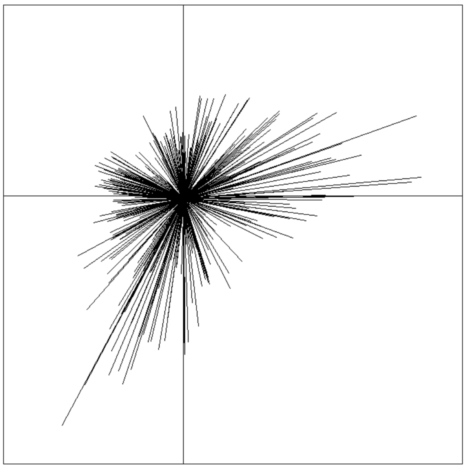
Tropaeolum majus



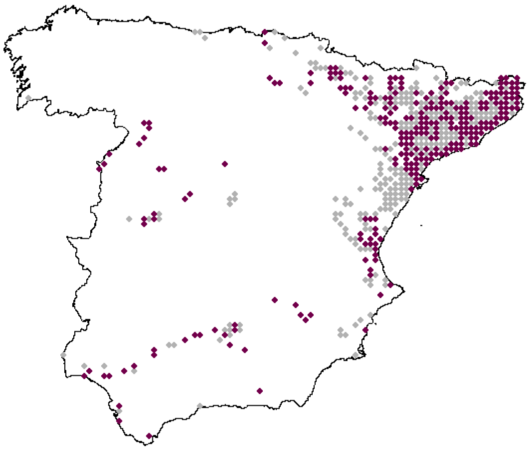


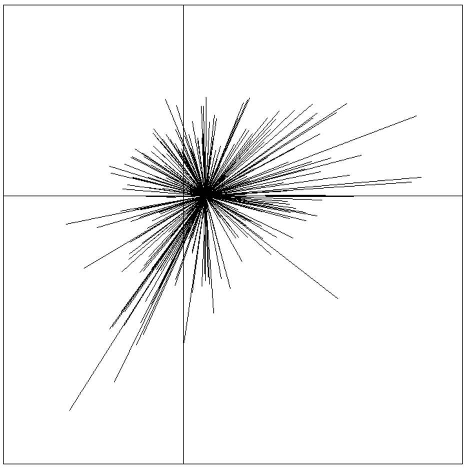
Xanthium spinosum



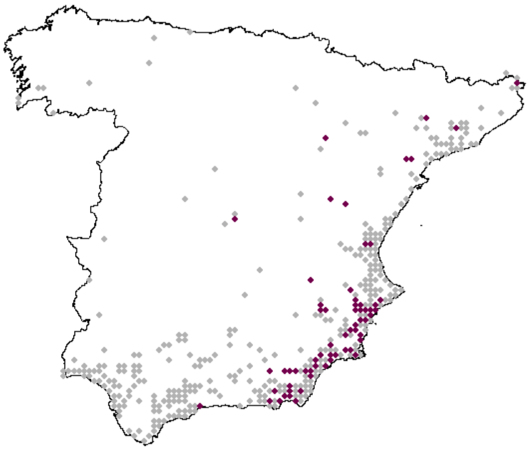


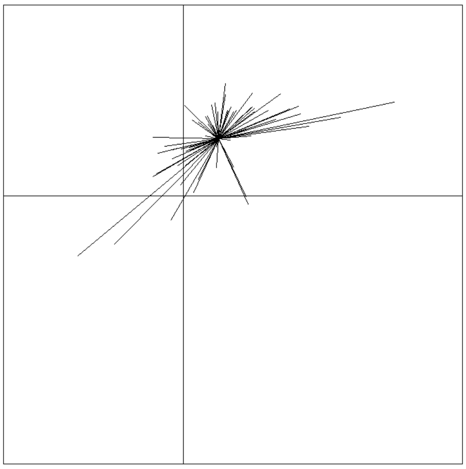
Xanthium strumarium





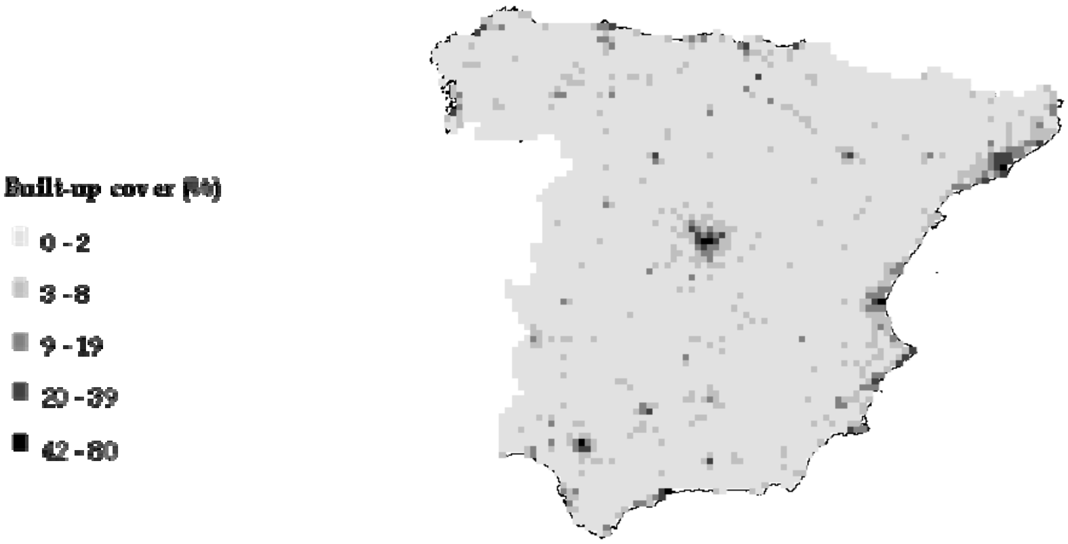
Zygophyllum fabago

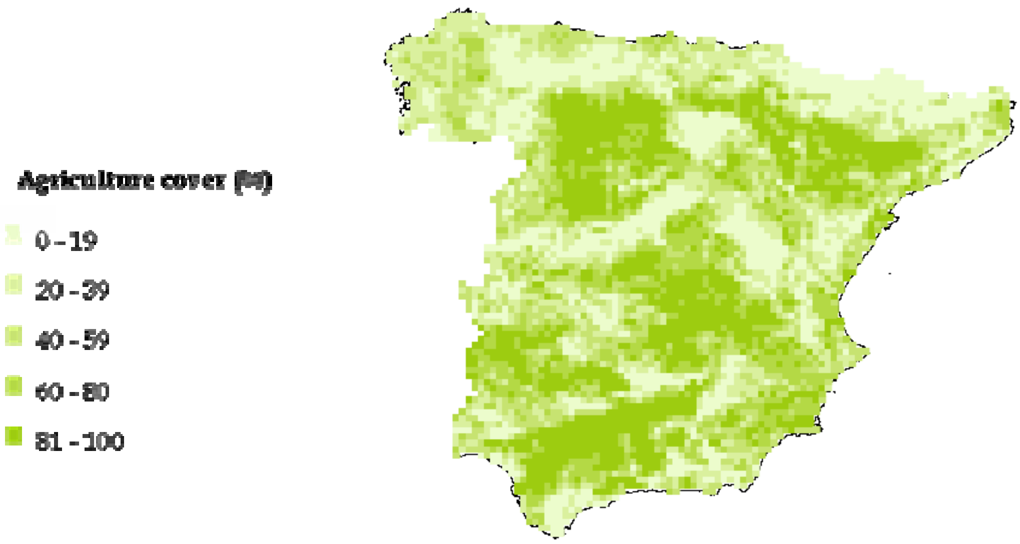


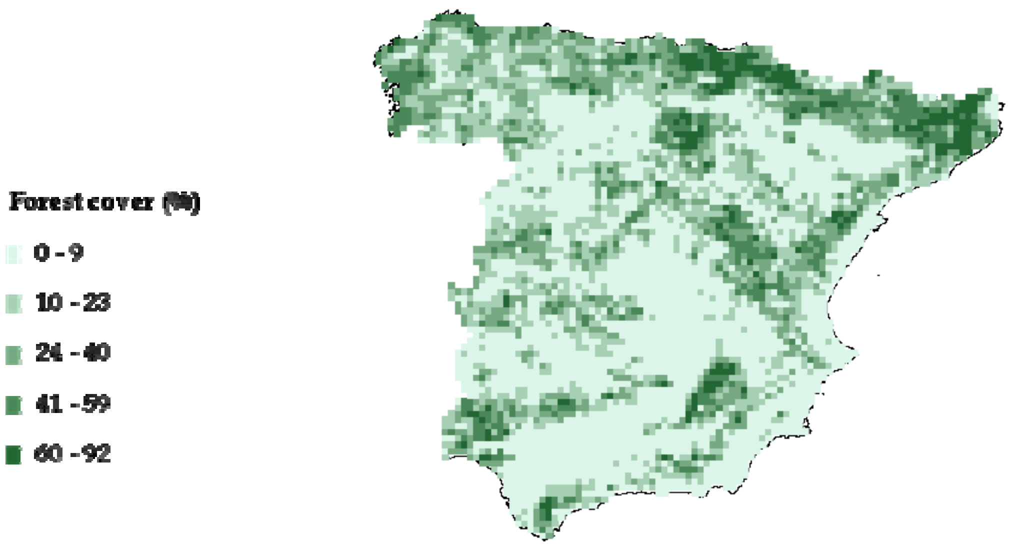


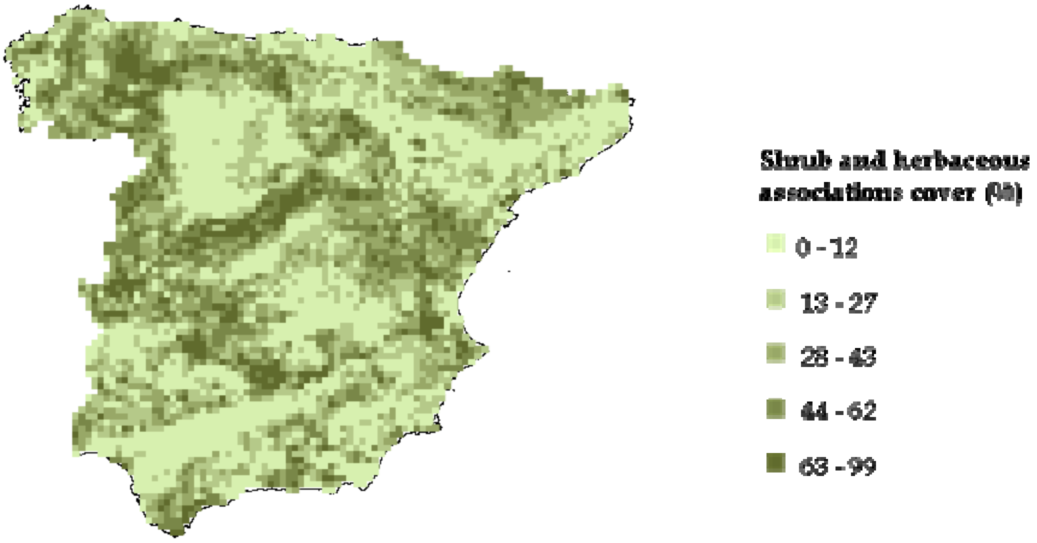
Appendix G. II

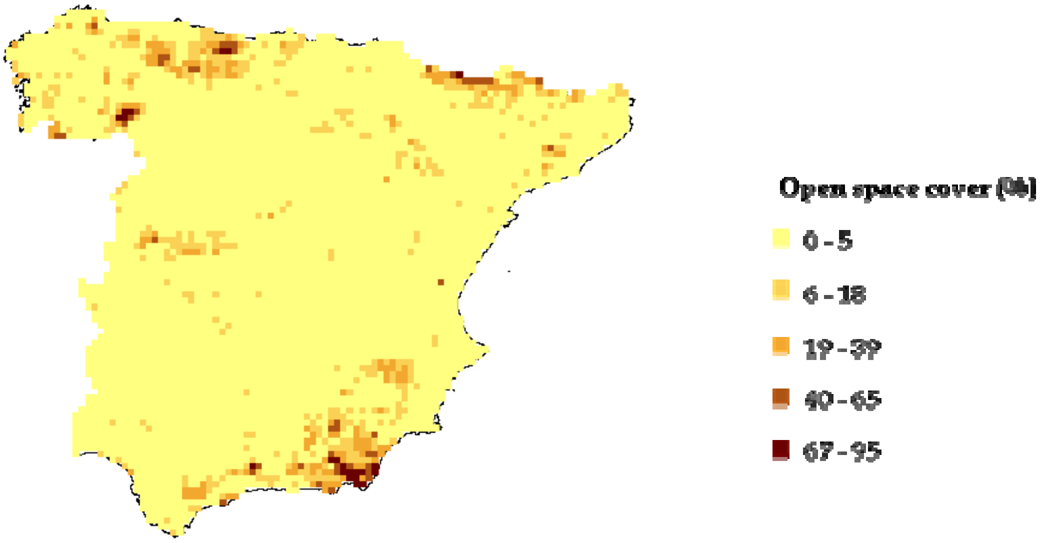
Graphical information on environmental data used on this thesis. All the variable values are shown at UTM 10x10 km scale. Not all the variables were included in each chapter (see chapters).

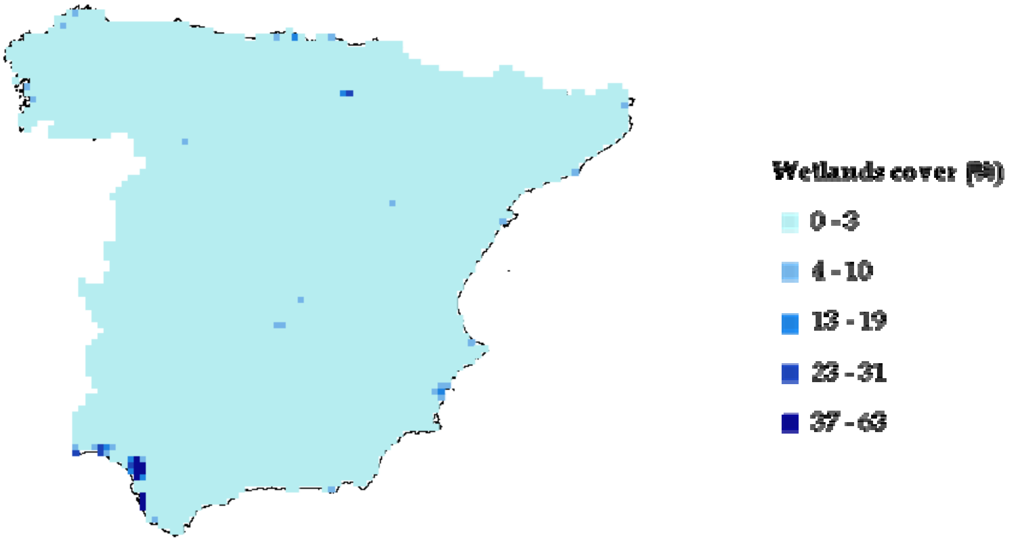


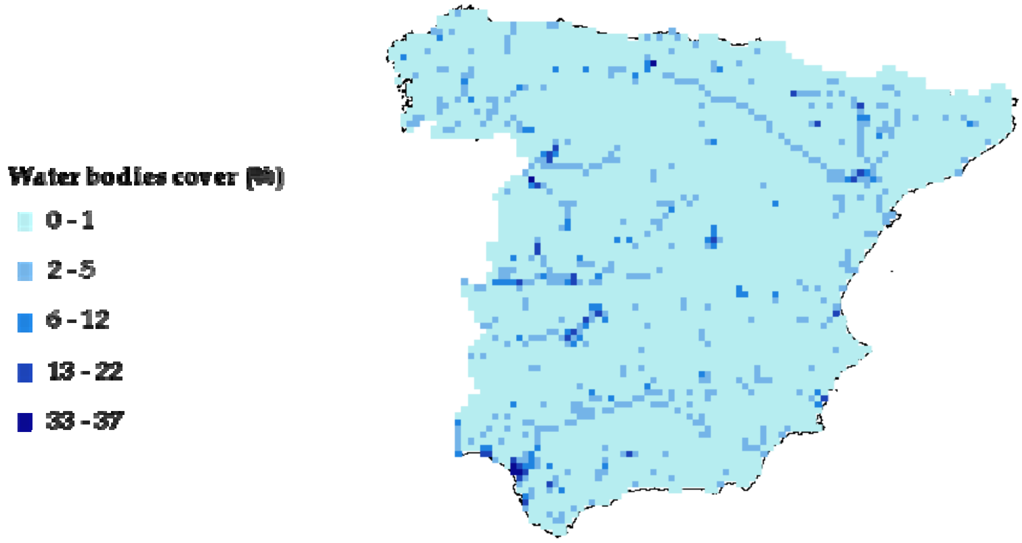


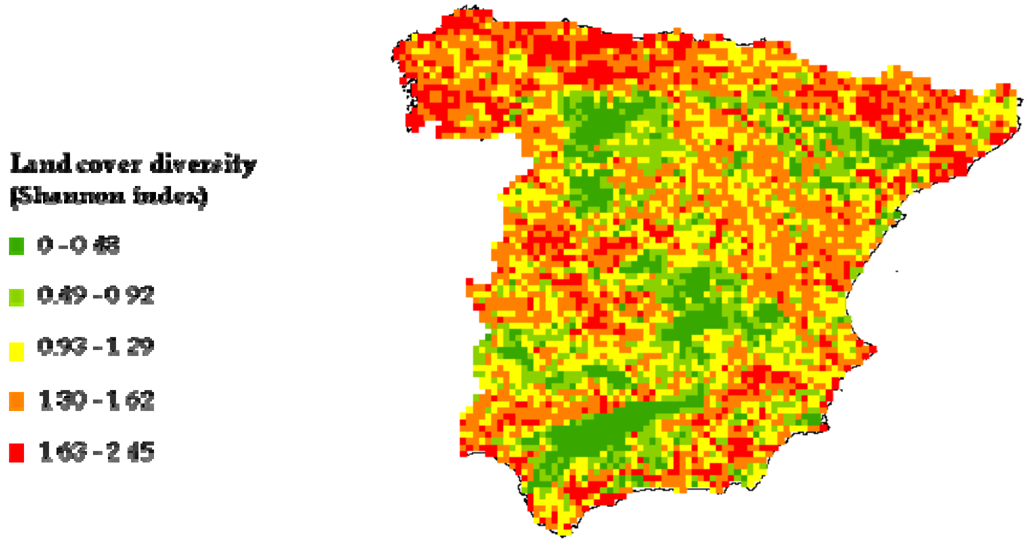



Shrub and herbaceous associations cover (%)
0 - 12
13 - 27
28 - 43
44 - 62
63 - 99

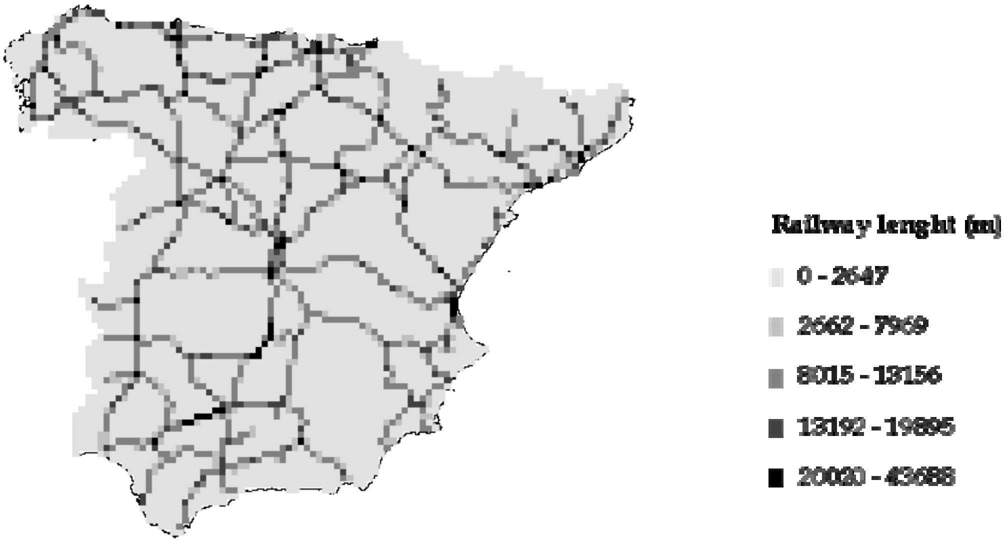

Open space cover (%)
0 - 5
6 - 18
19 - 39
40 - 65
67 - 95

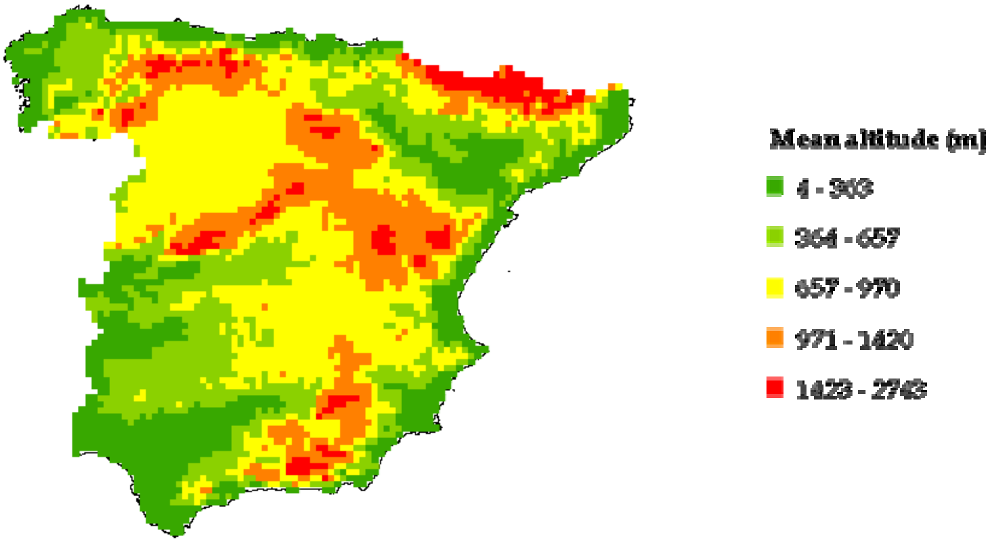

Wetlands cover (%)
0 - 3
4 - 10
13 - 19
23 - 31
37 - 63

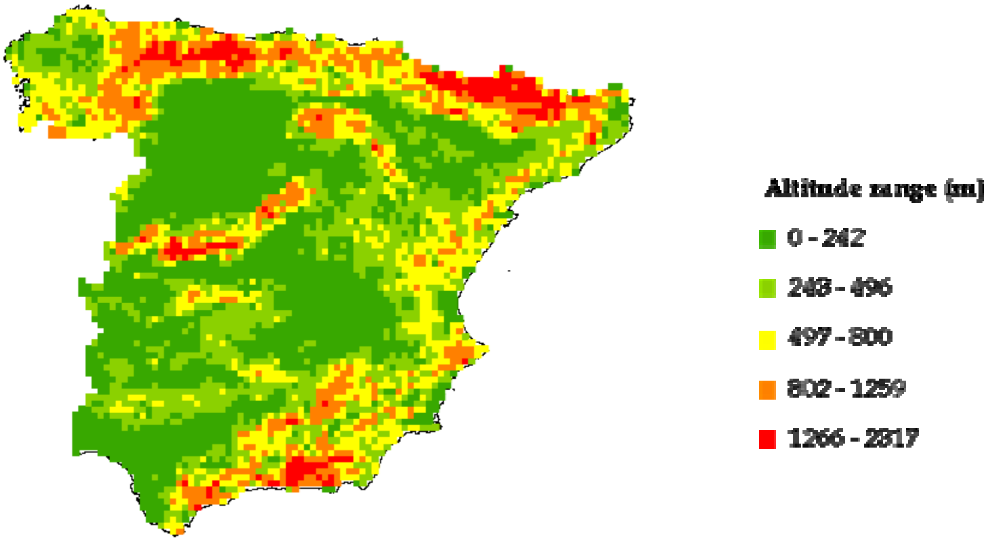

Water bodies cover (%)
0 - 1
2 - 5
6 - 12
13 - 22
33 - 37

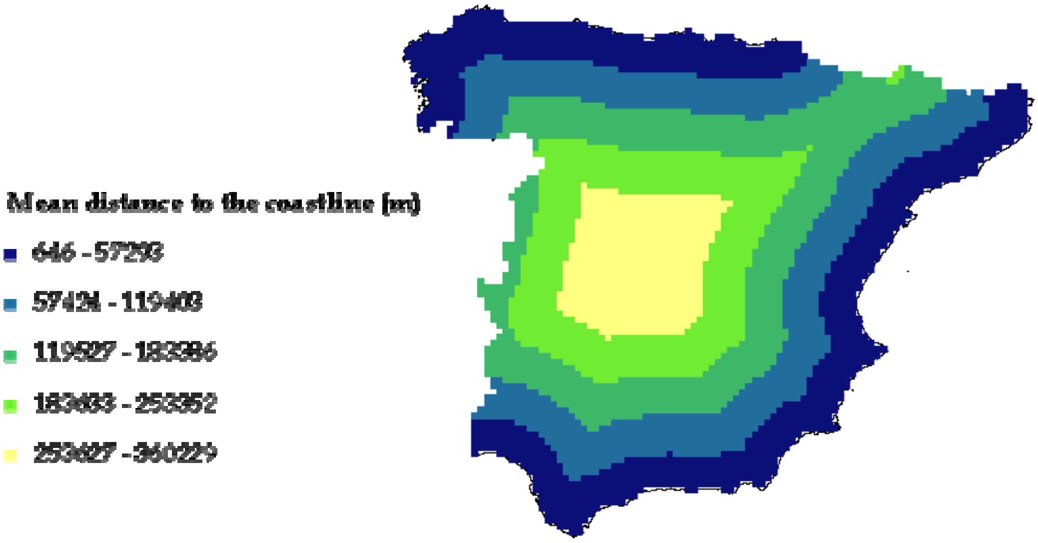

Land cover diversity (Shannon index)
0 - 0.48
0.49 - 0.92
0.93 - 1.29
1.30 - 1.62
1.63 - 2.45

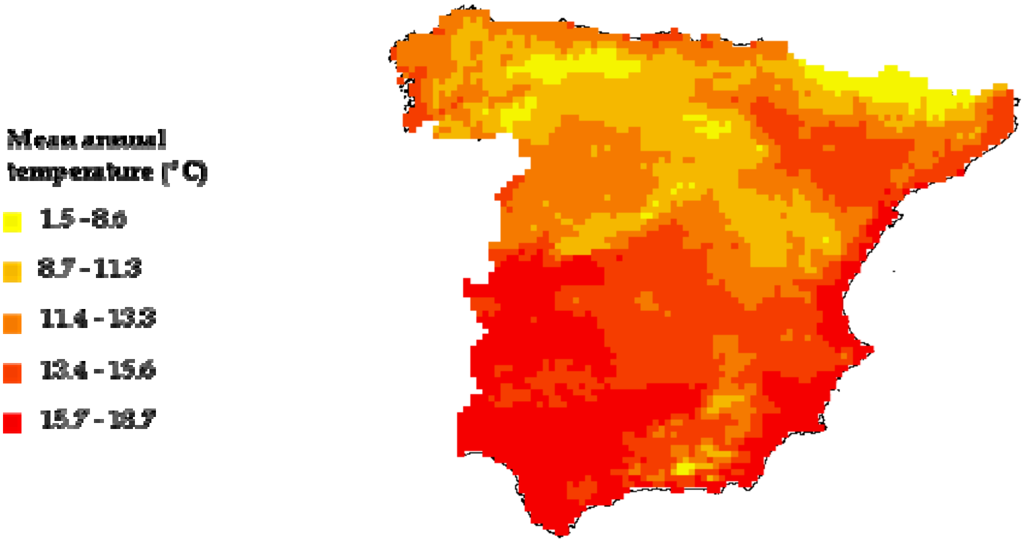

Road lenght (m)
0 - 3230
3236 - 9080
9098 - 16110
16120 - 26319
26414 - 46908

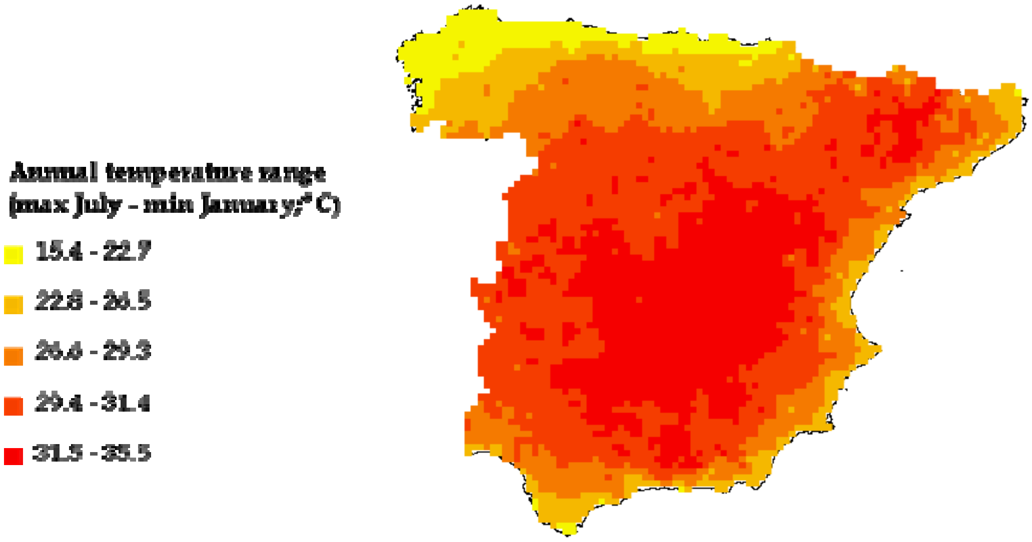

Railway lenght (m)
0 - 2647
2662 - 7969
8015 - 13156
13192 - 19895
20020 - 43688

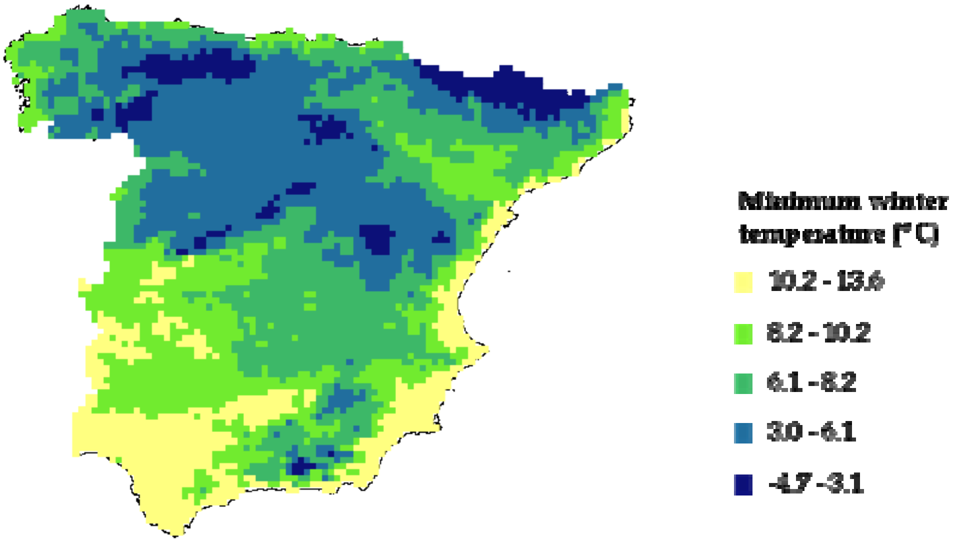

Mean altitude (m)
4 - 363
364 - 657
657 - 970
971 - 1420
1423 - 2743

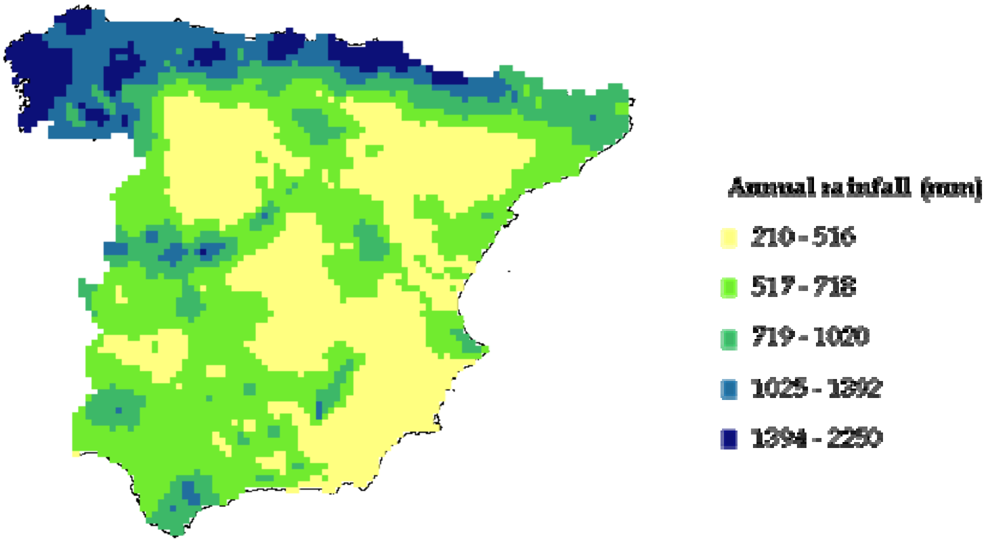

Altitude range (m)
0 - 242
243 - 496
497 - 800
802 - 1259
1266 - 2817

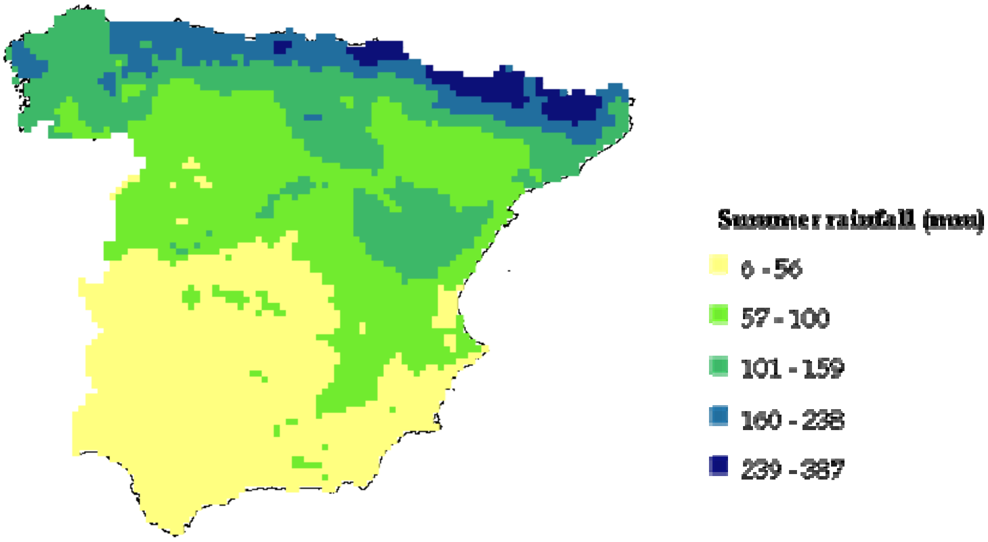

Mean distance to the coastline (m)
646 - 57293
57424 - 119403
119527 - 183986
183483 - 253352
253627 - 360229

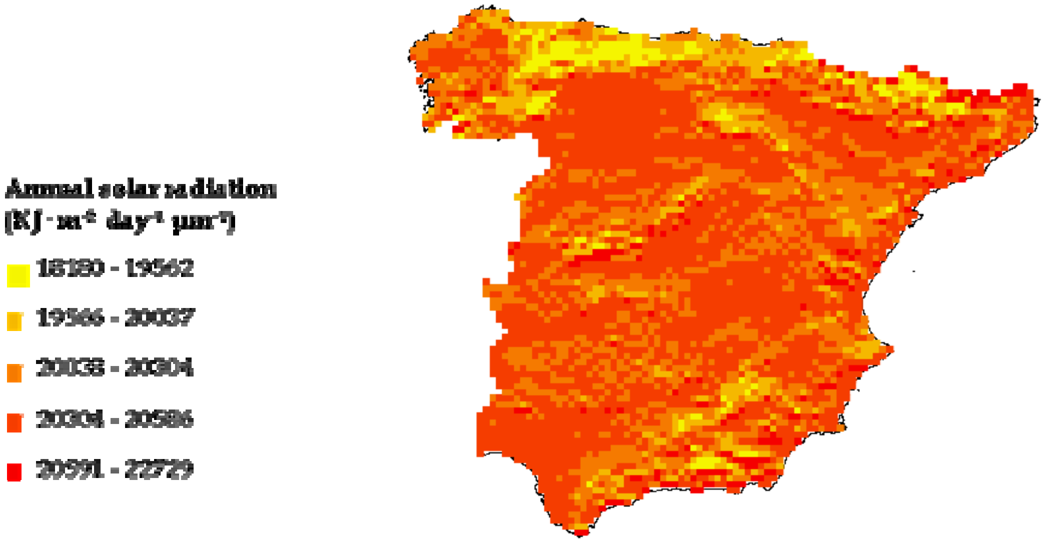

Mean annual temperature (° C)
1.5 - 8.6
8.7 - 11.3
11.4 - 13.3
13.4 - 15.6
15.7 - 18.7


Annual temperature range (max July - min January;° C)
15.4 - 22.7
22.8 - 26.5
26.6 - 29.3
29.4 - 31.4
31.5 - 35.5


Minimum winter temperature (° C)
10.2 - 13.6
8.2 - 10.2
6.1 - 8.2
3.0 - 6.1
-4.7 -3.1


Annual rainfall (mm)
210 - 516
517 - 718
719 - 1020
1025 - 1392
1394 - 2250


Summer rainfall (mm)
6 - 56
57 - 100
101 - 159
160 - 238
239 - 387


Annual solar radiation
(KJ · m-2 day-1 µm-1)
18180 - 19562
19566 - 20037
20038 - 20304
20304 - 20586
20591 - 22729

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