

Efectes de la pèrdua i fragmentació de pastures mediterrànies sobre la riquesa, composició i relacions tròfiques de plantes i papallones

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Ph. D. Thesis
Maig 2015



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Ph. D. Thesis

Tesis doctoral

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Programa de Doctorat en Ecologia Terrestre

Centre de recerca Ecològica i Aplicacions Forestals (CREAF)

Universitat Autònoma de Barcelona (UAB)

Bellaterra, maig de 2015



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*A tots els que m'heu ajudat (especialment en Joan, en Ferran i en Constantí),
als que l'heu patit (especialment l'Anna, l'Arlet, la Gemma i en Miquel),
i als qui ja no hi sou (especialment la Francesca).*

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Abstract

Habitat loss and fragmentation are considered the most important causes of biodiversity loss at local, regional and global scales, causing a rarefaction and extinction of some species. However, the importance of these processes remains unclear because frequently there are asynchronies between habitat loss and fragmentation and the subsequent species extinction, causing an extinction debt. Although extinction debt is considered a widespread phenomenon, our understanding of the mechanisms and processes that cause it is still incomplete, as well as the methods to detect it. Moreover, differential extinction and extinction debts in interacting species in fragmented landscapes could cause strong effects on ecological networks. These effects, however, are limited by the slowest responding species group, therefore delayed effects in ecological networks might be expected. The general goal of this thesis is contribute to the knowledge of the effects of habitat loss and fragmentation on species richness, composition and trophic networks in Mediterranean pastures between two trophically related groups (plants and butterflies). First of all (Chapter 2), I explore the methodology to detect extinction debt using plant species richness, focusing on current and past patch and landscape characteristics. To better explain the mechanism causing extinction and extinction debt, I also analyze the differences in species richness at patch scale and species richness of a fixed area within a patch (density), between stable and regressive patches. Secondly (Chapter 3), I explore the effects of current and past patch and landscape properties on species density and richness of plants and butterflies, and their trophic dependence. Finally (Chapter 4), I determine if asynchronies in extinction and extinction debt among plants and butterflies could cause effects their trophic networks, and if current and past patch and landscape properties modulate habitat loss and fragmentation effects on butterfly-plant networks.

Resum

La pèrdua i fragmentació dels hàbitats estan considerades com una de les causes més importants de pèrdua de biodiversitat a escala local, regional i global, causant la rarefacció i extinció d'algunes espècies. Bo i això, no es coneix bé l'abast real que provoca la pèrdua i fragmentació dels hàbitats ja que sovint es donen asincronies entre aquesta pèrdua i la consegüent extinció d'espècies, fet que comporta un deute d'extinció. Tot i que es considera que el deute d'extinció és un fenomen molt estès, el coneixement sobre els mecanismes i processos que el causen encara és molt incomplet, així com les metodologies per a detectar-lo. A més a més, diferències en l'extinció i deute d'extinció entre espècies que interactuen en paisatges fragmentats podrien tenir efectes importants en les xarxes ecològiques. Aquests efectes, però, estarien limitats per l'espècie o el grup que respon més lentament als canvis, pel que es poden esperar efectes retardats en les xarxes d'interaccions ecològiques. La present tesi vol contribuir al coneixement sobre els efectes de la pèrdua i fragmentació de pastures mediterrànies sobre la riquesa, composició i relacions tròfiques entre dos grups d'organismes relacionats tròficament (plantes i papallones). En primer lloc (Capítol 2) s'aprofundeix en els mètodes de detecció de deute d'extinció a partir de la riquesa de plantes vasculars, fent especial èmfasi en les característiques intrínseques de cada clapa a fi de quantificar millor la magnitud del deute d'extinció. S'analitzen, també, les diferències entre la riquesa a escala de tota la clapa i a escala petita d'àrea fixa (densitat), entre clapas estables i clapas en regressió, per intentar explicar els mecanismes d'extinció i de deute d'extinció. En segon lloc (Capítol 3) s'analitzen els efectes de les característiques de la clapa i del paisatge, actuals i pretèrites, sobre la riquesa total i la densitat (escala petita d'àrea fixa) de plantes vasculars i de papallones, així com les dependències tròfiques entre ambdós grups. Finalment (Capítol 4), s'analitza si les possibles asincronies en els fenòmens d'extinció i de deute d'extinció en plantes i papallones afecten les interaccions i les xarxes tròfiques papallona-planta, i si les característiques de la clapa i del paisatge, actuals i pretèrites, poden modular els efectes de la pèrdua d'àrea en les xarxes tròfiques papallona-planta.

Capítol 1

Introducció general



1.1. Efectes de la pèrdua i la fragmentació dels hàbitats sobre la riquesa d'espècies

El canvi en les cobertes i els usos del sòl és un dels principals factors de canvi de la biodiversitat als ecosistemes terrestres (Sala *et al.*, 2000), i és responsable de gran nombre d'extincions i colonitzacions que tenen efectes en la riquesa i la composició d'espècies en els hàbitats (Jackson & Sax, 2010). El canvi en les cobertes i els usos del sòl porta associada la pèrdua i fragmentació d'uns hàbitats determinats, però també l'expansió o aparició d'altres (Vitousek *et al.*, 1997). La pèrdua, degradació i fragmentació dels hàbitats es considera una de les causes principals d'extinció d'espècies a escala global (Fahrig, 2003; Balmford *et al.*, 2005; Lindenmayer & Fischer, 2006; Fischer & Lindenmayer, 2007; Collinge, 2009), juntament amb la invasió d'espècies exòtiques, la sobreexplotació, el canvi climàtic i els processos d'extinció en cascada (Diamond, 1989; Thomas *et al.*, 2004; Brook *et al.*, 2008; Pimm, 2008; Dunn *et al.*, 2009). La fragmentació dels hàbitats és, en tot cas, un procés complex que pot implicar (i) una pèrdua de la superfície total de l'hàbitat –tant o més important que la fragmentació en si–, (ii) una reducció del nombre i la mida dels fragments en què es divideix, i (iii) un increment del grau d'aïllament d'aquells (Fahrig, 2003; Forman, 2005). Aquests processos sovint determinen canvis en les taxes d'extinció i colonització de les espècies que, al seu torn, són deguts a canvis en l'estructura genètica, l'abundància local d'individus, les taxes de natalitat i mortalitat, les taxes de dispersió i les interaccions amb altres organismes (Fahrig, 2003). Tot plegat afecta la persistència de certes espècies i, en conseqüència, es pot reflectir en la riquesa total d'espècies als hàbitats.

La relació entre la riquesa d'espècies i l'àrea dels hàbitats és coneguda des de molt antic (Arrhenius, 1921; Rosenzweig, 1995; Lomolino, 2001). Bona part del marc teòric clàssic que pretén explicar la persistència i la colonització de les espècies en hàbitats fragmentats prové, però, de la teoria de la Biogeografia Insular formulada per MacArthur & Wilson (1963) en illes oceàniques. Segons aquesta teoria, la riquesa total d'espècies a les illes és el resultat d'un equilibri dinàmic entre les taxes d'immigració i d'extinció de cadascuna de les espècies, taxes que presenten una relació positiva i negativa, respectivament, amb el nombre d'espècies presents a l'illa. La teoria dedueix que, en l'equilibri, aquestes dues taxes s'igualaran i el nombre d'espècies romandrà constant. A més, les taxes d'immigració es relacionen positivament amb la proximitat al continent o a altres illes, i les taxes d'extinció són funció de la grandària de l'illa. Això fa que, a igualtat d'altres condicions, el nombre d'espècies augmenti amb la mida de l'illa i amb la seva connectivitat amb altres illes. L'ecologia de metapoblacions va proporcionar posteriorment la base per al tractament quantitatiu d'aquests aspectes teòrics (Hanski 1998; Hanski 1999). Tot i que, com ja s'ha dit, la teoria de la Biogeografia Insular va

ser desenvolupada en illes oceàniques, s'aplica per analogia en hàbitats terrestres fragmentats (Wu & Vankat, 1995). No obstant això, cal tenir present que aquesta aplicació sovint porta implícit un tractament binari del paisatge (hàbitat/no hàbitat) poc adequat per al cas dels hàbitats terrestres. És per això que cada cop sovintegen més treballs que indiquen que les propietats de la matriu del paisatge (l'existència de corredors o d'hàbitats permeables, però també el grau d'antropització, l'efecte barrera de les infraestructures, etc.), modulen de manera molt important els efectes de la mida i del grau d'aïllament dels fragments d'hàbitat (Haila 2002; Ewers & Didham 2006).

1.2. Els patrons temporals d'extinció i el deute d'extinció

Com a conseqüència de l'aplicació de la teoria de la Biogeografia Insular, els efectes de la pèrdua i la fragmentació dels hàbitats sobre la biodiversitat s'han estudiat tradicionalment assumint l'existència d'un equilibri entre la riquesa d'espècies i les propietats dels hàbitats (mida i connectivitat). Diversos treballs posen de manifest, però, que l'assoliment d'aquest equilibri després d'una pertorbació no és immediat, i això porta a l'aparició de decalatges entre la pèrdua i fragmentació dels hàbitats i l'extinció d'espècies resultant (Steffan-Dewenter *et al.*, 2002; Lindborg & Eriksson, 2004; Helm *et al.*, 2006; Öster *et al.*, 2007; Jackson & Sax, 2010; Piqueray *et al.*, 2011b). Piessens & Hermy (2006) estimen que, tot i la reducció del 99% en la superfície de landes al NW de Flandes en els darrers 230 anys, només s'han extingit localment l'11% de les espècies de plantes pròpies d'aquest hàbitat. Larsen (2008), amb dades de papallones diürnes forestals a l'Àfrica occidental, calcula que en els darrers 16 anys només el 3% de les 972 espècies enregistrades històricament a la regió no s'han trobat recentment tot i que la superfície de boscos ha minvat un 87% durant els últims 150 anys. Brooks *et al.* (1999) afirmen que no s'han detectat extincions de cap ocell del bosc plujós atlàntic del sud de Brasil tot i que actualment només resta un 12% de l'extensió original d'aquest bosc. Aquesta escassetat d'extincions en paisatges molt fragmentats podria indicar que la fragmentació i la pèrdua d'hàbitat són forces dèbils en el procés d'extinció de les espècies, però el concepte de deute d'extinció ofereix una alternativa interessant (Jackson & Sax, 2010).

Aquest retard en l'extinció de determinades espècies s'ha anomenat inèrcia biològica en plantes (Summerfield, 1972) o temps de relaxació en animals (Diamond, 1972), mentre que el nombre o proporció d'espècies (en comunitats) o de poblacions (per a una espècie determinada) que s'extingiran quan s'assoleixi un nou equilibri o quasi-equilibri després d'una pertorbació ambiental s'ha anomenat deute d'extinció (Tilman *et al.*, 1994; Kuussaari *et al.*, 2009). Ambdós

conceptes són conseqüència de determinats factors que poden retardar l'extinció local de les espècies després d'una pertorbació, com ara les característiques demogràfiques d'aquestes o les característiques del paisatge (Brooks *et al.*, 1999; Lindborg & Eriksson, 2004; Helm *et al.*, 2006).

Tot i que el deute d'extinció es considera un fenomen molt estès, el coneixement sobre els mecanismes i processos que el causen encara és molt incomplet (Hylander & Ehrlén, 2013). En general es considera que la probabilitat i la magnitud del deute d'extinció depèn principalment de les característiques o trets biològics de les espècies i de les característiques del paisatge (Kuussaari *et al.*, 2009).

Així, en un context de pèrdua i fragmentació d'hàbitats, determinades característiques biològiques ajudarien a causar asincronies entre el canvi en els hàbitats i el recanvi subsegüent d'espècies. Per exemple, les espècies especialistes d'un determinat hàbitat (espècies amb poca amplitud ecològica i fortament associades a un hàbitat concret) són més propenses a processos d'extinció i de deute d'extinció que no pas les espècies generalistes (Helm *et al.*, 2006; Krauss *et al.*, 2010); les espècies més longeves també s'espera que mostrin extincions més retardades i, per tant, deute d'extinció, comparat amb les espècies de vida curta (Lindborg, 2007; Morris *et al.*, 2008); les espècies de nivells tròfics superiors es veuran més afectades per processos d'extinció (*trophic rank hypothesis*; Holt *et al.*, 1999) i mostraran menys deute d'extinció que les espècies de nivells tròfics inferiors, tanmateix, l'extinció de les darreres pot causar extincions ens cascada al llarg de la xarxa tròfica (Haddad *et al.*, 2009). Les característiques del paisatge, com ara l'abundància d'hàbitat en el paisatge circumdant i la seva proximitat, també poden afavorir un efecte de rescat de poblacions reduïdes o en procés d'extinció (Andrén, 1994; Bascompte & Solé 1996; Piessens *et al.*, 2004; Lindborg & Eriksson 2004; Helm *et al.*, 2006).

La detecció del deute d'extinció pot dependre, en tot cas, de les aproximacions metodològiques utilitzades (Piqueray *et al.*, 2011). La metodologia més estesa per determinar l'existència de deute d'extinció es basa en comparar els ajustos de la riquesa actual d'espècies amb l'àrea actual i l'àrea pretèrita de la clapa o de l'hàbitat focal en el paisatge (Kuussaari *et al.*, 2009). Si les característiques pretèrites expliquen millor la riquesa d'espècies que les actuals es pot assumir que hi ha deute d'extinció (Figura 1a). Una metodologia alternativa (Kuussaari *et al.*, 2009) consisteix en calcular els models espècies-àrea amb l'àrea actual i la pretèrita de les clapas estables (les que no han perdut superfície o n'han perdut poca en el període de temps analitzat), i predir amb ells la riquesa d'espècies de les clapas en regressió (les que han perdut força superfície). Llavors, el deute d'extinció en aquestes clapas es pot determinar per un excés d'espècies observades en comparació a les estimades amb els models (Figura 1b).

Aquestes aproximacions consideren, tanmateix, que totes les clapes d'hàbitat estudiat responen per igual a la pèrdua d'àrea i, per tant, hi ha un canvi sistemàtic en la relació espècies-àrea (Ney-Nifle & Mangel 2000; Lewis, 2006), però alguns estudis apunten a que el deute d'extinció pot dependre de les característiques de cada clapa (Piqueray *et al.*, 2011; Guardiola *et al.*, 2013). A més a més, la majoria de treballs es centren a escala de tota la clapa d'hàbitat, tot i que es considera que la detecció del deute d'extinció és més probable si s'utilitzen diferents escales d'anàlisi (Kuussaari *et al.*, 2009) ja que la pèrdua d'àrea incrementa les taxes d'extinció d'espècies i fa decreixer les taxes de colonització, fet que provoca una davallada en la densitat de les espècies (Eriksson *et al.*, 2002; Fahrig, 2003).

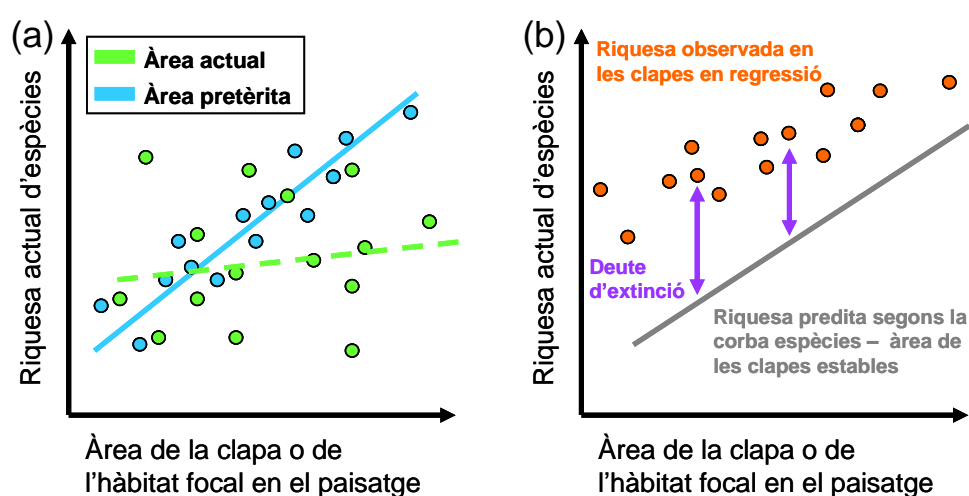


Figura 1 Metodologies proposades per Kuussaari *et al.* (2009) per tal d'avaluar l'existència del deute d'extinció sense haver de disposar de dades pretèrites de riquesa d'espècies: (a) comparació de les relacions espècies-àrea utilitzant l'àrea actual i la pretèrita (de la clapa o del paisatge) i (b) estimació del deute d'extinció a partir de la comparació de la relació espècies-àrea de les clapes estables i les clapes en regressió (redibuixat de Kuussaari *et al.*, 2009).

1.3. Efectes de la pèrdua i la fragmentació dels hàbitats sobre les xarxes ecològiques

Cal esmentar que els efectes de la pèrdua d'àrea i la fragmentació han estat estudiats tradicionalment amb descriptors de comunitat, com la riquesa i diversitat d'espècies, però recentment diversos estudis posen de manifest que aquesta aproximació no permet avaluar els possibles efectes sobre els processos que operen a nivell de comunitat o fins i tot d'ecosistema, com ara els possibles canvis en les interaccions entre espècies (Tylianakis *et al.*, 2007; Villa-Galaviz *et al.*, 2012). Això ha fet que als darrers anys hagi incrementat notablement l'interès per l'estudi de les xarxes ecològiques (Gonzalez *et al.*, 2011). Malgrat tot, encara no estan clars quins efectes tenen la fragmentació i la pèrdua d'àrea sobre les xarxes ecològiques (Gonzalez *et*

al., 2011; Valiente-Banuet *et al.*, 2015). Hi ha estudis que mostren un col·lapse d'aquestes xarxes (Fortuna & Bascompte, 2006; Fortuna *et al.*, 2013) i altres que indiquen que no hi ha cap canvi (Thébaud & Fontaine, 2010; Nielsen & Totland, 2014).

Recentment, s'ha aplicat la teoria de la Biogeografia Insular a l'estudi de les xarxes ecològiques (Sabatino *et al.*, 2010; Sugiura & Taki, 2012), en una aproximació que s'ha anomenat interacció d'espècies-àrea (Sugiura, 2010). Segons aquesta, el nombre d'interaccions entre espècies incrementa amb l'àrea de la clapa, afectant l'estructura de les xarxes ecològiques. També la connectivitat de les clapes tindria un efecte important en les interaccions entre espècies (LeCraw *et al.*, 2014) gràcies a l'efecte rescat de clapes veïnes per la capacitat de dispersió de certes espècies (Brown & Kodric-Brown, 1977). Bo i això, diversos treballs suggereixen que les diferències en l'extinció i deute d'extinció entre espècies que interactuen en paisatges fragmentats podrien tenir efectes importants en les xarxes ecològiques (Gonzalez *et al.*, 2011; Jansen *et al.*, 2012; Bueno *et al.*, 2013; Emer *et al.*, 2013; Spiesman & Inouye, 2013). Aquests canvis, però, estarien limitats per l'espècie o el grup que respon més lentament als canvis, pel que es poden esperar efectes retardats en les xarxes d'interaccions ecològiques (Essl *et al.*, 2015). Tot això ha fet que recentment s'hagi aplicat el concepte de deute d'extinció a les interaccions ecològiques, definit el concepte de deute d'extinció de les interaccions ecològiques com qualsevol pèrdua d'interacció entre espècies deguda a pertorbacions actuals o pretèrites (Valiente-Banuet *et al.*, 2015).

1.4. Causes i conseqüències dels efectes de la pèrdua i la fragmentació sobre el funcionament i els serveis dels ecosistemes

Gerstner *et al.* (2014), en una metanàlisi a nivell mundial, troben que la pèrdua i la fragmentació dels hàbitats causa un descens en la riquesa d'espècies. Qualsevol impacte d'origen antròpic que provoqui una disminució en el nombre d'espècies, pot causar una disminució quantitativament similar sobre l'estabilitat de l'ecosistema (Hautier *et al.*, 2015). Aquests efectes, però, també poden afectar a altres components de la biodiversitat, com les interaccions entre espècies (Valiente-Banuet *et al.*, 2015), les quals, s'han definit com la columna vertebral de la biodiversitat i del funcionament i l'estabilitat dels ecosistemes (Schleuning *et al.*, 2015).

Com ja s'ha comentat, els efectes de la pèrdua i la fragmentació dels hàbitats poden causar l'extinció immediata de moltes espècies, però en d'altres, la resposta pot mostrar-se al cap d'un temps, donant origen als deutes d'extinció esmentats anteriorment. Aquests efectes retardats de

la pèrdua i la fragmentació sobre la biodiversitat es poden acumular i amplificar al llarg del temps. Recentment s'ha proposat el concepte de retards acumulats en la biodiversitat, que integra totes les respostes retardades dels diversos components de la biodiversitat, des de la diversitat genètica de les espècies fins a l'estructura i composició de les comunitats (Essl *et al.*, 2015). A més a més, ja que el funcionament i els serveis ecosistèmics depenen de la biodiversitat, s'espera també un deute en els serveis ecosistèmics, de manera que la pèrdua i la fragmentació dels hàbitats estaria creant una pèrdua retardada dels beneficis que depenen de la biodiversitat i que la humanitat obté dels ecosistemes (Isbell *et al.*, 2015).

Tot això fa que la importància de determinar l'existència de deutes d'extinció i de conèixer els mecanismes que hi estan implicats radiqui especialment en el fet que moltes espècies i poblacions podrien estar amenaçades malgrat que actualment no se'n tingui cap evidència i, a més, perquè encara hi hauria temps per a dur a terme accions per aturar o esmorteir els efectes de la pèrdua d'hàbitat i de canvis en el paisatge (Hanski, 2000).

1.5. Objectius i capítols de la tesi

La present tesi vol contribuir al coneixement sobre la persistència i extinció de les espècies en hàbitats en regressió, i sobre la detecció dels possibles deutes d'extinció i dels factors biològics i ambientals que els determinen. Centra aquests objectius en dos grups d'organismes relacionats tròficament, les plantes vasculares i les papallones, i en un hàbitat especialment sotmès a processos de regressió i fragmentació: les pastures mediterrànies. El treball vol, per tant, donar resposta a les preguntes següents:

1. Les plantes vasculares i les papallones de les pastures mediterrànies mostren patrons de riquesa i deutes d'extinció diferents?
2. El possible deute d'extinció depèn de
 - les característiques, tant actuals com històriques, de la clapa i del paisatge circumdant?
 - l'escala d'anàlisi (àrea fixa *versus* tota la clapa)?
3. La posició tròfica i el grau d'especialisme o generalisme d'hàbitat dels organismes afecta la riquesa d'espècies i la magnitud del deute d'extinció en cada grup?
4. La persistència d'un determinat grup d'espècies és modulada per la d'altres grups tròficament relacionats?
5. Quins efectes tenen les extincions diferencials d'aquests grups d'espècies sobre les xarxes tròfiques corresponents?

Aquestes qüestions són analitzades en capítols diferents. Les preguntes 1 i 2, en el cas de les plantes vasculars, són tractades al **Capítol 2**, on s'aprofundeix en els mètodes de detecció de deute d'extinció a partir de la riquesa de plantes vasculars, fent especial èmfasi en les característiques intrínseques de cada clapa a fi de quantificar millor la magnitud del deute d'extinció. S'analitzen, també, les diferències entre la riquesa a escala de tota la clapa i a escala petita d'àrea fixa, entre clapes estables i clapes en regressió, per veure si els canvis a l'escala petita d'àrea fixa són més ràpids que a l'escala de clapa, i permeten explicar els mecanismes d'extinció i de deute d'extinció.

Les preguntes 1, 2, 3 i 4 són tractades al **Capítol 3**, on s'analitzen els efectes de les característiques de la clapa i del paisatge, actuals i pretèrites, sobre la riquesa total i la densitat d'espècies (escala petita d'àrea fixa) de plantes vasculars i papallones, així com les dependències tròfiques entre ambdós grups.

Finalment, la pregunta 5 és objecte d'estudi al **Capítol 4**, on s'analitza si les possibles asincronies en els fenòmens d'extinció i de deute d'extinció en plantes i papallones afecten les interaccions i les xarxes tròfiques papallona-planta, i si les característiques de la clapa i del paisatge, actuals i pretèrites, poden modular els efectes de la pèrdua d'àrea en les xarxes tròfiques papallona-planta.

1.6. Les espècies d'estudi

Com ja s'ha comentat, aquesta tesi es centra en dos grups d'organismes: les plantes vasculars i les papallones diürnes (incloent ropalòcers i zigènids). Aquests dos grups d'organismes han estat amplament utilitzats com a bioindicadors de l'estat de conservació dels hàbitats (Thomas *et al.*, 2004; Krauss *et al.*, 2010) ja que moltes espècies es troben restringides a determinats tipus d'hàbitats i poden sobreviure en clapes d'hàbitat en paisatges fragmentats (Hanski, 1999; Thomas & Hanski, 2004; Brückmann *et al.*, 2010). Els dos grups difereixen en el seu nivell tròfic i la seva longevitat, ja que moltes plantes són de vida llarga mentre que les papallones són de vida més curta. Estudis previs indiquen, a més, que les característiques de les clapes i del paisatge que les envolta determina en gran mesura la riquesa de plantes (Schmucki *et al.*, 2012) i de papallones (Öckinger *et al.*, 2012). Les característiques del passat (especialment l'àrea i la connectivitat de la clapa; Helm *et al.*, 2006) i el percentatge d'àrea perduda (Piqueray *et al.*, 2011b) també tenen un paper important en determinar la riquesa d'aquests organismes en paisatges fragmentats.

A més a més, plantes i papallones diürnes estan relacionades tròficament ja que les papallones són herbívores durant la fase larvària i pol·linitzadores en la fase adulta. Especialment a la fase larvària, moltes papallones estan força especialitzades tròficament ja que s'alimenten de poques plantes d'una mateixa espècie, d'un gènere o d'una família (Pearse & Altermatt, 2013). Això fa que potencialment puguin estar afectades per extincions en cascada (Krauss *et al.*, 2010).

1.7. El sistema i l'àrea d'estudi

L'estudi es centra en les pastures, un dels hàbitats més interessants per a la conservació de la biodiversitat europea i, alhora, més afectats per processos de pèrdua d'àrea i fragmentació. Es tracta d'hàbitats semi-naturals mantinguts per una pastura secular que, actualment, es troben en regressió accelerada a tot Europa a causa de l'abandonament del seu ús (WallisDeVries *et al.*, 2002). És per això que en els darrers anys han sorgit nombrosos treballs que analitzen les relacions entre la riquesa d'espècies de diversos organismes amb els processos de canvi d'aquests hàbitats a escala de paisatge, alguns dels quals miren d'esbrinar possibles deutes d'extinció. La majoria d'aquests estudis s'han dut a terme en pastures del centre i nord d'Europa i, en canvi, hi ha pocs treballs centrats en la regió mediterrània (vegeu però Pueyo *et al.*, 2008). Aquesta regió es caracteritza per una diversitat i una taxa d'endemicitat elevades, i es considera com un dels hotspots de biodiversitat vegetal del planeta (Médail & Quezel, 1999; Myers *et al.*, 2000) i un dels hotspots d'insectes especialistes (Fonseca, 2009), especialment les àrees muntanyoses (Martínez-Rica, 1998; Lobo *et al.*, 2001). Les pastures mediterrànies però, han sofert un procés d'abandonament de les activitats tradicionals que s'ha traduït en la seva reducció i fragmentació a causa de la colonització d'arbres i arbusts (principalment *Pinus nigra*, *P. sylvestris*, *Juniperus communis*, *J. oxycedrus* i *Buxus sempervirens*), fet que ha tingut un gran impacte sobre la seva biodiversitat (González Bernáldez, 2001; Petit *et al.*, 2001).

En aquesta tesi ens hem centrat en l'estudi de les pastures xerofítiques submediterrànies de les serres del sud de Catalunya (Figura 2). Aquestes pastures corresponen bàsicament a joncedes (incloses dins l'aliança *Aphyllanthion* Br.-Bl. (1931) 1937) corresponents a l'hàbitat CORINE 34.721: Joncedes (prats, sovint emmatats, d'*Aphyllanthes monspeliensis*), calcícoles, de les contrades mediterrànies i de la muntanya mitjana poc plujosa. Són una formació vegetal restringida al nord-oest de la regió mediterrània, des de la meseta castellana fins al nord d'Itàlia. Apareixen en climes submediterranis i mediterranis humits, principalment en el domini de les rouredes seques o dels carrascars. Són pastures baixes (de 30-70 cm), sempre verdes, que solen tenir un recobriment vegetal del 40-90% i estan dominades de manera variable per petites mates

i per plantes junciformes i graminoides. Les joncedes de les serres del sud de Catalunya es caracteritzen per l'abundància de petits camèfits i nanofaneròfits, i un menor recobriment d'hemicriptòfits que les joncedes més septentrionals (Bolòs, 1976; Álvarez de la Campa, 2004; Royo, 2006). Les joncedes comparteixen algunes espècies amb les pastures seques de l'Europa mitjana i dels Pirineus (incloses dins l'aliança *Xerobromion*). Al territori estudiat apareixen majoritàriament en indrets elevats i relativament obacs. En les parts culminals dels massissos estudiats, dins les joncedes sovint s'hi barregen espècies dels matollars oromediterranis (aliança *Ononidion striatae*), mentre que a les zones més seques i de menor altitud hi penetren elements propis de les brolles calcícoles de romaní (aliança *Rosmarino-Ericion*), i de prats secs (aliança *Thero-Brachypodium*) als llocs més secs o pedregosos (Bolòs, 1976; Casas, 2008). En general, l'origen d'aquestes formacions vegetals es troba en l'obertura de pastures en temps molt antics, ja que tradicionalment han estat aprofitades com a pastura de bestiar oví i cabrum, especialment a la primavera. El pasturatge manté i afavoreix la presència d'aquestes joncedes (Bolòs, 1976; Casas, 2008) i l'abandonament de l'activitat ramadera comporta un emmatament i aforestació progressius.

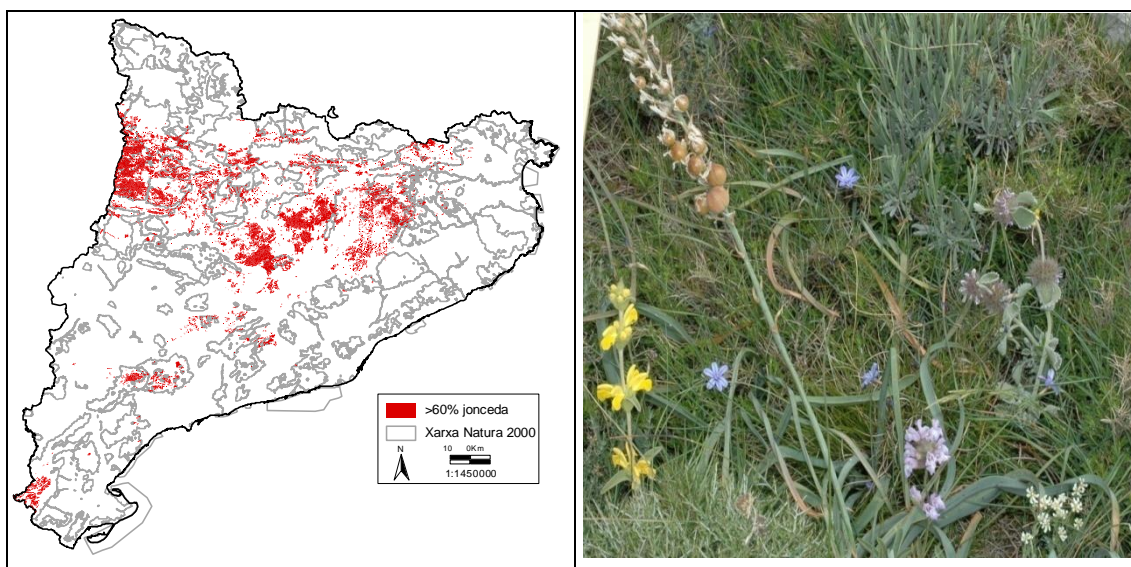


Figura 2. (a) Distribució de les joncedes a Catalunya; el color vermell indica àrees amb recobriments de jonceda superiors al 60%; en color gris s'ha representat els límits dels espais de la xarxa Natura 2000. (b) Detall d'una de les clapes de jonceda estudiades, on es pot veure la diversitat d'espècies.

L'estudi es va dur a terme en diversos altiplans i àrees culminals de quatre massissos calcaris del sud de Catalunya, caracteritzats per un relleu tabular o dissimètric en costes i amb presència abundant de joncedes: les muntanyes de Prades, la serra de Montsant, les serres de Llaberia-Colldejou i el massís dels Ports. A grans trets, el clima general d'aquestes serres és de tipus mediterrani prelitoral sud (Martín-Vide, 1992), amb un índex d'humitat de Thornthwaite

subhúmit (amb valors d'aquest índex que van de 0 a 20) tot i que algunes àrees més continentals (oest de la serra de Montsant i nord del massís dels Ports) presenten un clima sec subhúmit (valors de -20 a 0). Segons l'Atlas Climàtic Digital de Catalunya (Ninyerola *et al.*, 2000), la precipitació mitjana anual en les clapes seleccionades varia entre els 500 i 850 mm, amb màxims a Prades i els Ports. La temperatura mitjana anual oscil·la entre els 13.5 °C i els 11.5 °C, i l'amplitud tèrmica anual entre els 15.5 °C i els 17.5 °C. Val a dir, però, que aquestes variables climàtiques presenten gradients lligats a l'altitud i a l'orientació dins de cada massís.

El paisatge de les serres del sud de Catalunya ha sofert modificacions molt importants en els darrers segles, degut als canvis en el seu aprofitament humà. Des del segle XVII fins al darrer quart del segle XIX van experimentar una expansió del conreu de la vinya (i, en menor grau, de les oliveres i dels ametllers), així com de ramadera extensiva. A finals del segle XIX la fil·loxera va provocar una crisi agrícola que va comportar l'abandonament de conreus i masos. Als anys quaranta del segle passat hi va haver un període de repunt dels aprofitaments dels recursos forestals –fusta i carboneig– coincidint amb el període de postguerra, però al darrer terç del segle van desaparèixer pràcticament les activitats econòmiques tradicionals (Lloret *et al.*, 2002; Pasqual, 2002), amb la desaparició o reducció de l'àrea de moltes pastures.

Inicialment es van seleccionar més d'un centenar de clapes de joncedes a partir de la fotointerpretació en pantalla de les ortofotoimatges de l'ICC de l'any 2003 i de les fotografies de l'anomenat “vol americà”, primer vol fotogramètric realitzat a la península Ibèrica entre els anys 1956 i 1957. Posteriorment, es van superposar aquestes dues fotointerpretacions per poder (i) separar les clapes que ja eren jonceda l'any 1956 de les que eren conreus en actiu o recentment abandonats en aquelles dates i que, en tractar-se d'hàbitats nous, òbviament no són interessants per a un estudi dels efectes de la reducció de l'hàbitat; i (ii) diferenciar les clapes en regressió de les clapes estables i calcular-ne l'àrea perduda en el lapse de temps de 47 anys. Finalment, per a la present tesi es van seleccionar 29 clapes de jonceda a les serralades meridionals catalanes entre Prades i els Ports (Figura 3). De cadascuna d'aquestes clapes es van realitzar dos mostrejors de flora vascular i de papallones, un de proporcional a l'àrea de cada clapa per tal d'obtenir la riquesa total d'espècies, i l'altre mostreig es va realitzar en una àrea fixa per obtenir una densitat d'espècies. De cada clapa també es van calcular un seguit de variables de clapa i de paisatge, actuals i pretèrites.

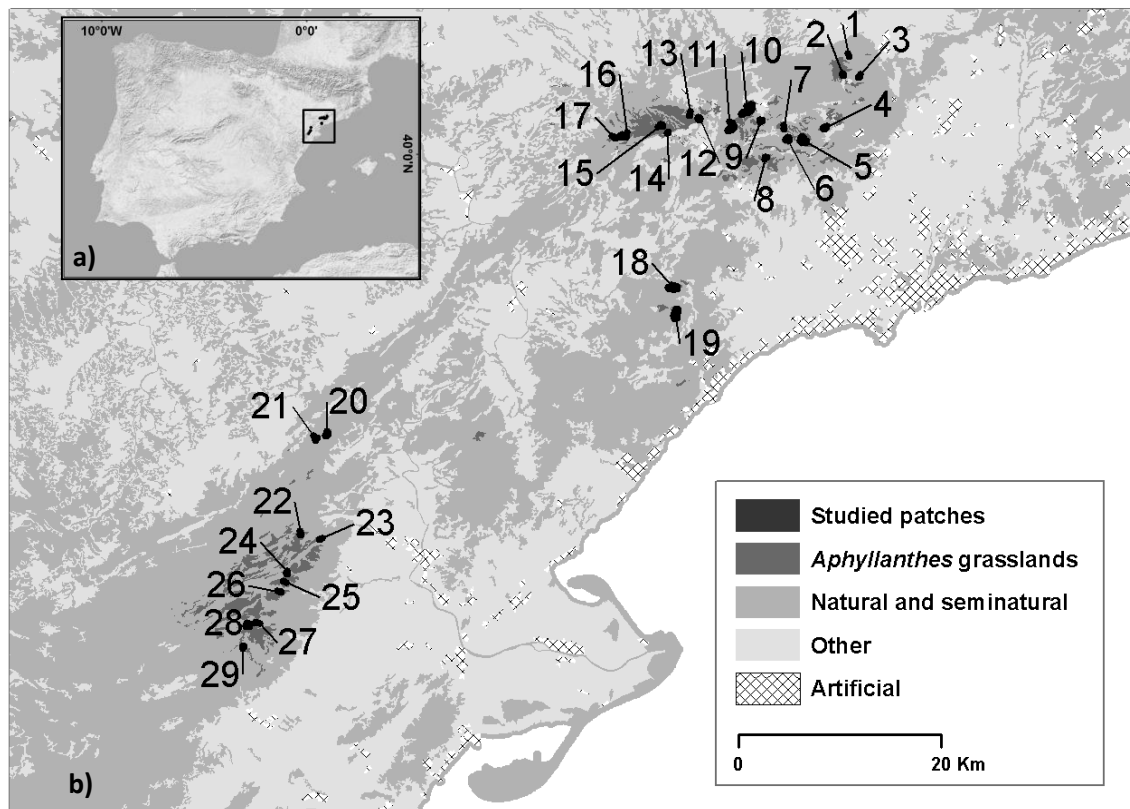


Figura 3 (a) Localització de l'àrea d'estudi (quadrat negre) a la península Ibèrica i de les clapes estudiades (polígons negres); (b) principals cobertes del sòl a l'àrea d'estudi i situació de les clapes estudiades.

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Capítol 2

Patch history and spatial scale modulate local plant extinction and extinction debt in habitat patches



This chapter is published in:

Guardiola, Moisès; Pino, Joan; Rodà, Ferran (2013), Patch history and spatial scale modulate local plant extinction and extinction debt in habitat patches. *Diversity and Distributions*, 19 (7): 825–833. doi: 10.1111/ddi.12045

Abstract

Aim Many species exhibit a time lag between habitat loss and its extinction, resulting in extinction debt. Although extinction debt is considered a widespread phenomenon, differences in methodological approaches can affect its detection. We aim to contribute to this methodological debate by exploring whether extinction debt is either a phenomenon common to all patches or idiosyncratic to the patch and landscape attributes of a given patch. We also aim to determine whether the scale-dependency of species richness might help to explain extinction debt.

Location Southern Catalonia (NE Iberian Peninsula).

Methods We studied the effects of habitat loss on plant species richness (total, specialists and generalists) in stable (habitat loss less than 40% since 1956) and regressive (habitat loss more than 40% since 1956) patches of Mediterranean grasslands at both quadrat and patch scales using general linear models.

Results We detected extinction debt at patch scale but only in regressive patches. The magnitude of extinction debt was not constant but was related to the percentage of patch area reduction. Contrastingly, regressive patches presented fewer species than stable patches at quadrat scale.

Main conclusions Quadrat-scale extinctions in regressive patches lead to rarefaction, but not immediately extinction, of some species at patch-scale and created an extinction debt. Species loss at quadrat scale constitutes an early warning indicator of the effects of habitat loss on biodiversity, while delayed extinctions offer an opportunity for conservation initiatives.

Keywords: extinction debt, habitat loss, landscape change, Mediterranean grasslands, relaxation time, scale-dependence.

2.1. Introduction

Habitat loss is the most important cause of species extinction at local, regional and global scales (Dirzo & Raven 2003). It can also shift the frequency distribution of species toward a higher proportion of rare (and hence extinction-prone) species, with stochastic factors ultimately driving many species extinct (Jackson & Sax 2010). However, there are often much fewer extinctions than predicted, as found in plants (Piessens & Hermy 2006; Vellend *et al.* 2006), butterflies (Larsen 2008) or birds (Brooks *et al.* 1999). This is frequently due to demographic and stochastic processes (Jackson & Sax 2010) that cause a time lag between habitat loss and species extinction (Diamond 1972; Summerfield 1972), and eventually determine the existence of extinction debts. The extinction debt is defined as the number of extant species predicted to become extinct as the species community readjusts after an environmental disturbance (Tilman *et al.* 1994; Kuussaari *et al.* 2009). Habitat-specialist species, i.e. species-dependent or clearly favouring the focal habitat type and with a narrow ecological amplitude, are expected to be most sensitive to these changes in habitat, and thus more prone to exhibit local extinction processes than generalist species (Helm *et al.* 2006; Krauss *et al.* 2010; Cousins & Vanhoenacker 2011).

Although extinction debt is considered a widespread phenomenon (Cousins 2009; Hahs *et al.* 2009; Krauss *et al.* 2010), differences in methodological approaches can affect its detection (Piqueray *et al.* 2011a). There are two major approaches to the evaluation of extinction debt in habitat patches in regression when historical biodiversity data are not available (Kuussaari *et al.* 2009). The first assumes the existence of an extinction debt if current species richness is better described by past patch variables, such as patch size and connectivity, than by present ones (Lindborg & Eriksson 2004; Krauss *et al.* 2010). The second uses the species-area relationships of a subset of patches with little or no habitat loss (stable patches) to predict species richness for patches that have lost a large proportion of their original area (regressive patches); an extinction debt is assumed if there is a surplus of observed species in these regressive patches, compared with the number of species predicted from the species-area relationship of stable patches (Helm *et al.* 2006; Kuussaari *et al.* 2009; Piqueray *et al.* 2011b).

Both approaches to extinction debt are based on the detection of systematic changes in the species-area relationships (Ney-Nifle & Mangel 2000; Lewis 2006), whereby the species richness of all the patches responds in the same direction and intensity to area loss. This might not be the best approach, however, as extinction debt might exhibit an idiosyncratic, patch-dependent pattern (Piqueray *et al.* 2011a). It is known that patch and landscape properties might play a key role in species persistence and colonization, thus affecting patch species richness

(e.g. Pimm & Raven 2000; Krauss *et al.* 2004; Löbel *et al.* 2006) and the subsequent extinction debt.

Moreover, little attention has been focused on spatial scales when exploring extinction debt, even though it is well known that species richness is scale-dependent (Willis & Whittaker 2002; McGill 2010) and extinction debt is more likely to be detected if several spatial scales are used (Kuussaari *et al.* 2009). It has been hypothesized that area loss would increase local extinction rates and decrease colonization rates, thus lowering local species density (Eriksson *et al.* 2002; Fahrig, 2003), and several authors have shown that species loss after a perturbation is first detected in small plots (Galvnek & Lepš 2009), and that vegetation patches that are apparently stable at a larger scale have faster small-scale dynamics (Chytry *et al.* 2001). Nevertheless, the effect of small-scale extinctions on extinction debts has rarely been explored (but see Cousins & Vanhoenacker 2011), and studies on extinction debt continue to focus on the patch scale.

This paper explores the existence of an extinction debt in mountain Mediterranean grasslands through diverse methodological approaches. The Mediterranean region is considered one of the world's biodiversity hotspots (Medail & Quezel 1997; Myers *et al.* 2000), especially its mountain ranges (Martinez-Rica 1988; Lobo *et al.* 2001), which are currently threatened by intense land-use changes resulting in the abandonment of traditional pastures (Petit *et al.* 2001). Our specific objectives were: (i) to investigate whether extinction debt is either a phenomenon common to all patches or idiosyncratic to the patch and landscape attributes of a given patch; and (ii) to determine whether the scale-dependency of species richness could help to explain the phenomenon of extinction debt. We hypothesized that: (i) the idiosyncratic effect of landscape and patch history determines the magnitude of the extinction debt; and (ii) small-scale extinction patterns are crucial for explaining extinction debt at patch scale.

2.2. Methods

2.2.1. Study area

The study was performed in four calcareous massifs (ranging from 860 to 1400 m a.s.l.), along a 150-km, NE-SW gradient in southern Catalonia (NE Iberian Peninsula, 41° N, 0° 30' E). These massifs present a mountain Mediterranean climate with cold winters and dry summers (average temperature, 14.1°C, average annual rainfall 700 mm; Ninyerola *et al.* 2000).

We focused our study on semi-natural Mediterranean mountain grasslands rich in dwarf shrubs, corresponding to the “34.721 *Aphyllanthes* grasslands” of the CORINE habitat classification

(Moss & Wyatt 1994). These grasslands are equally dominated, on average, by hemicryptophytes and chamaephytes of less than 50 cm in height, and they exhibit vegetation cover of between 50% and 80%. In the study area, many of these grasslands, like other low-productivity grasslands in Europe (Kunstler *et al.* 2006), are currently subjected to woody encroachment because livestock grazing (sheep and goat in our study region) has been reduced or discontinued. Woody encroachment in our study area is a slow process due to climatic (hot summer with low precipitation, relative cold winters) and soil (poor, stony, dry...) constraints on woody species establishment and growth; thus specialist species can remain for long in these Mediterranean grasslands. There are no specific data for the study sites about the onset and maximum rate of pasture abandonment, but in general it is assumed that it started in the 1940s (Lloret *et al.* 2002), as in nearby regions such as southern France (Debussche *et al.* 1999). No evidence of human-made afforestation, cultivation or heavy grazing was detected in the field sampling, though Spanish ibex (*Capra pyrenaica hispanica*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) or rabbit (*Oryctolagus cuniculus*) were present. No large fires had occurred during last three decades in the studied patches or in their 1-km buffers (Cartographic Institute of Catalonia; www.icc.cat).

2.2.2. Sampling

We selected 29 grassland patches, immersed in forested landscapes, in relatively similar environmental conditions, between 900 and 1200 m a.s.l. Because of the fragmented distribution of the studied habitat, patches were concentrated in three clumps of less accessible areas in calcareous massifs showing large summit plateaus, traditionally devoted to grazing due to their inaccessibility, where grasslands currently show regression processes due to land abandonment and woody encroachment, and thus were adequate to assess extinction debt in this habitat. No significant differences in woody cover ($F=1.61$, $P=0.22$), patch area ($F=3.19$, $P=0.06$) or patch area loss ($F=1.17$, $P=0.32$) were found between the three clumps of patches. Patches spanned a wide range of patch sizes (0.1 to 26.9 ha in 2003) and intensities of patch area reduction, from stable to high patch regression during the 47-yr period from 1956 to 2003 (see Table S1 in Supporting Information).

Historical (1956) and present-day (2003) grassland patches were digitized by on screen photo-interpretation. The historical aerial photographs were obtained from the archives of the Spanish Army. The scale of the original photos was approximately 1:30000, and the pixel size of the resulting orthophoto-maps was 1 m. Present-day orthoimages, with a pixel size of 0.5 m, were obtained from the Cartographic Institute of Catalonia. The proportion of patch area lost in each

patch was calculated by the difference between past and current patch area divided by the past area. We also estimated the area of grassland habitat in the past and the current surrounding landscape (1-km buffer for each patch including the patch area). We chose this buffer distance because our landscape was too abrupt for wider buffers to be meaningful, and because Lindborg & Eriksson (2004) found that total species richness was positively related to landscape connectivity 50 years ago at a distance of 1 km or less. We estimated woody cover within each patch in 2003 using orthoimages and overlying 50 random points/ha.

In April-May 2007, we conducted two samplings of vascular plant species present in the selected patches. The first was independent of patch area and consisted of recording all species within 25 quadrats of 0.5 x 0.5 m, randomly distributed per patch. All species with any aerial part inside the quadrats were recorded (i.e. the “any-part approach” recommended by Dengler 2008). The second sampling was dependent on patch area and involved an additional time transect proportional to the logarithm of patch area, according to $T = \ln(A+1) \times 30$ (T = time in minutes; A = patch area in ha). In both samplings, plant species were classified as grassland specialists or non-specialists using regional floras (Bolòs *et al.* 1993; Rivas-Martínez *et al.* 2001) and expert advice.

2.2.3. Statistical analyses

We first compared the current species richness of total, specialist and non-specialists plants between stable and regressive patches, at quadrat and patch scales using general linear models (GLM). Quadrat species richness was the mean of the 25 quadrats in each patch, while patch species richness was obtained by counting all the species recorded in the 25 quadrats per patch plus those additionally recorded in the time transect. We included current patch area as an explanative variable in all the models. Also, as species richness is highly influenced by spatial variables (Lobo *et al.* 2001) and in a previous paper (Bagaria *et al.* 2012) we found that the environmental variables that explained more variance of the species frequency in *Aphyllanthes* grasslands were the UTM Y and UTM X coordinates, we included the geographical gradient as follows. Since the sample patches lay broadly along a NE-SW band, their latitude and longitude were highly correlated. We applied a Principal Component Analysis (PCA) to a matrix with the UTM X and UTM Y coordinates of the central point of each patch to obtain a first principal component that explained 98% of the variance of the geographical coordinates of the patches. To detect the influence of this geographical gradient on species richness, we conducted a trend surface analysis (Legendre & Legendre 1998) and we found that geographical variation in species richness (total and specialist, at patch and quadrat scales) was described by a second

order polynomial $PC1-(PC1)^2$, with maximum values to the centre and minimum values to the extremes of the studied area. This polynomial was then included as predictor variable in the GLMs. We have no clear explanations about this pattern but maximum richness values are mainly located in eastern Montsant and western Prades Massifs, two continuous massifs, in one of the plant hotspots in Catalonia (Catalonian Database of Biodiversity, <http://biodiver.bio.ub.es/biocat>) where there is a confluence of chorological elements from three biogeographical regions: Mediterranean, Eurosiberian (from the N), and Continental Iberian (from the SW). Moreover, this geographical gradient is correlated with mean annual precipitation ($r=-0.90$, $P<0.0001$), but not with mean annual temperature ($r=-0.34$, $P=0.07$).

Secondly, we explored the existence of an extinction debt in plant specialists at quadrat and patch scales. Following Kuussaari *et al.* (2009), and since we did not have any historical biodiversity data, we compared the role of past and present patch area in explaining current species richness, in all the study patches, both pooled together and separately, for relatively stable and regressive patches. There is no definitively accepted threshold –if it exists– for classify stable and regressive patches. Several authors proposed a threshold between 10-40% of the original patch size (Fahrig 2003; Cousins *et al.* 2003; Helm *et al.* 2006; Fischer & Lindenmayer 2007). Cousins (2009) pointed out that in studies finding extinction debt, patches still retained more than 10% of the target habitat, and that studies in highly transformed landscapes usually do not find evidence of extinction debt. In our study stable patches had lost less than 40% of their 1956 area (mean percentage of area loss: $10.3 \pm SD 13.7$; $n=16$) while regressive patches had lost more than 40% of their past area (mean percentage of area loss: $79.3 \pm SD 14.6$; $n=13$). There were no differences in environmental conditions (mean annual temperature, elevation, mean annual precipitation, geographical gradient), in initial past area or in past landscape area between stable and regressive patches (Table S3 in Supporting Information). All comparisons were performed using GLMs, including the above-mentioned polynomial of geographical gradient. The Akaike Information Criterion for small sample sizes (AICc) was used to select the best model (Burnham & Anderson 2002). If current species richness was better described by past than by present patch or landscape variables, it could be assumed that extinction debt was present.

Thirdly, we sought to estimate the existence of a systematic extinction debt and assess its magnitude in plant specialists by comparing their present-day species richness in stable and regressive patches. Following Helm *et al.* (2006), the stable patches were used to perform a GLM to predict species richness, using the current patch area and the geographical variation polynomial. Thus, we calculated the extinction debt in each regressive patch as the residual

between the observed and predicted species richness (i.e. using the GLM parameters set for stable patches). The departure from zero (i.e. systematic extinction debt) of the mean of these residuals was then assessed using a Student's t-test, after checking for normality in the residuals.

Finally, for the regressive and for the stable patches, we explored the role of the 1956 patch and landscape properties in extinction debt by using GLMs to assess the relationship of the above-mentioned residuals with three past patch and landscape variables: the percentage of the patch area lost, the past patch area and the past habitat area in the landscape. If residuals were explained by any of these variables, we would assume that extinction debt of each patch depended on its historical patch- or landscape- habitat areas.

All the statistical analyses were performed using the software R 2.11.1 for Windows (R Development Core Team 2010). In all the GLMs, area variables were log 10-transformed, whereas untransformed response variables met the assumptions of normality and homoscedasticity. Because trend surface analysis accounts for trends in data across larger geographical distances but does not address the problem of spatial autocorrelation (Dormann *et al.* 2007), we also tested our GLMs for spatial autocorrelation using Moran's I autocorrelation coefficient. The Moran index did not attain statistical significance in any of the models, indicating that there was no significant spatial autocorrelation in our data. In consequence, we did not include a spatial autoregressive term in the GLMs.

2.3. Results

We recorded 297 vascular plant species on the studied 29 patches. Approximately half of these species were considered grassland specialists using regional floras (Bolòs *et al.* 1993; Rivas-Martínez *et al.* 2001) and expert advice (see Table S4 in Supporting Information). On average, total species richness (mean \pm SD) was 76.1 ± 23.4 species at patch scale and 13.1 ± 2.6 at quadrat scale; specialist species richness averaged 46.7 ± 10.5 species at patch scale and 10.8 ± 2.2 at quadrat scale; generalist species richness averaged 29.4 ± 14.3 species at patch scale and 2.3 ± 1.2 at quadrat scale (see Table S2 in Supporting Information).

At patch scale, total, specialist and generalist species richness were significantly related to patch area and the geographical gradient, but not to patch stability (Table 1). In contrast, at quadrat scale, none of these three types of species richness showed a relationship with patch area, but regressive patches had a significantly lower total and specialist richness than stable ones (Table 1; Fig. 2).

Table 1 Results from GLMs for the effects of patch area, patch stability and geographical variation on total, specialist and non-specialist species richness, at patch and quadrat scales.

	Area	Patch stability	Geographical variation
<i>Patch scale</i>			
Total	F = 39.8 <i>P</i> < 0.00001	F = 0.16 <i>P</i> = 0.69	F = 31.5 <i>P</i> < 0.00001
Specialists	F = 29.2 <i>P</i> < 0.00001	F = 0.01 <i>P</i> = 0.93	F = 24.1 <i>P</i> < 0.00001
Non-specialists	F = 16.9 <i>P</i> < 0.001	F = 0.27 <i>P</i> = 0.61	F = 12.9 <i>P</i> < 0.005
<i>Quadrat scale</i>			
Total	F = 0.04 <i>P</i> = 0.32	F = 12.0 <i>P</i> < 0.005	F = 15.0 <i>P</i> < 0.001
Specialists	F = 1.6 <i>P</i> = 0.22	F = 9.3 <i>P</i> < 0.005	F = 6.7 <i>P</i> < 0.01
Non-specialists	F = 0.08 <i>P</i> = 0.78	F = 0.86 <i>P</i> = 0.36	F = 6.1 <i>P</i> < 0.02

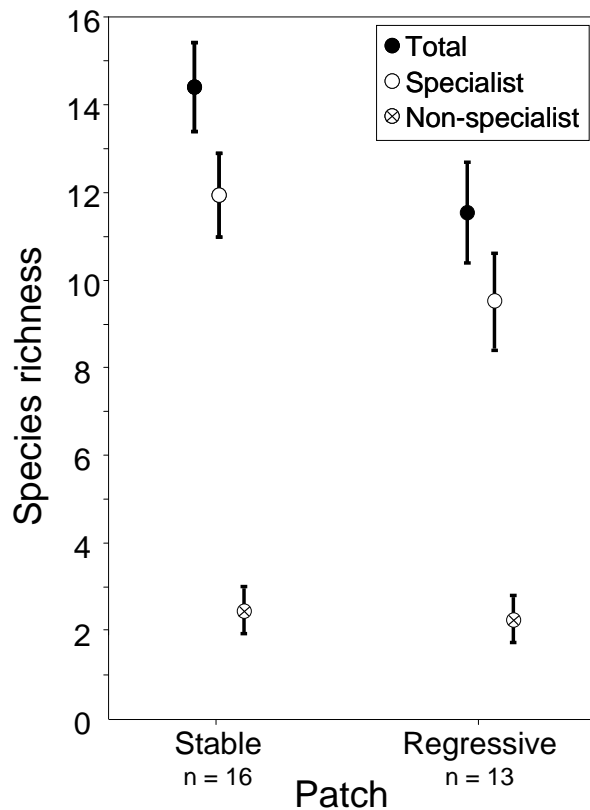


Figure 2 Species richness (total, specialist and non-specialist) at quadrat scale of 0.25 m² in stable and regressive patches (Mean ± SD).

The current richness of plant specialists at patch scale was better explained by current patch area than by past area after pooling together all the 29 studied patches (Table 2). Taking into account stable and regressive patches separately, no differences were found between using current or past area ($\Delta AICc < 2$) in the GLMs of the stable patches, while only past area was significantly related to current specialist species richness in the GLMs of regressive patches (Table 2). Specialist species richness was significantly related to the geographical gradient in all the GLM models.

Table 2 Comparison of the importance of actual or past patch area in predicting specialist species richness in models considering all patches together, stable patches and regressive patches. Significance codes: *** $P < 0.001$; ** $0.01 > P > 0.001$; * $0.05 > P > 0.01$.

	r^2 adj.	AICc	Log (area)	Geographical variation
<i>a) All patches</i>				
<i>Patch scale</i>				
Area 2003	0.81***	177.1	8.73 (1.3)***	-4.7e-09 (9.4e-10)***
Area 1956	0.72***	188.6	8.29 (1.83)***	-5.2e-09 (1.4e-09)***
<i>Quadrat scale</i>				
Area 2003	0.20 ^{ns}	125.8	0.3 (0.6) ^{ns}	-9.4e-10 (3.9e-10)*
Area 1956	0.21 ^{ns}	125.3	-0.5 (0.6) ^{ns}	-1.2e-09 (3.8e-10)**
<i>b) Stable patches</i>				
<i>Patch scale</i>				
Area 2003	0.87***	96.3	10.8(1.5)***	-3.8e-09 (1.0e-09)**
Area 1956	0.89***	94.3	10.6 (1.4)***	-3.8e-09 (9.4e-10)**
<i>Quadrat scale</i>				
Area 2003	0.22 ^{ns}	69.5	-0.5(0.7) ^{ns}	-1.1e-09 (4.3e-10)*
Area 1956	0.22 ^{ns}	69.6	-0.4 (0.6) ^{ns}	-1.1e-09 (4.4e-10)*
<i>c) Regressive patches</i>				
<i>Patch scale</i>				
Area 2003	0.45**	88.9	2.7 (3.8) ^{ns}	-5.6e-09 (1.7e-09)**
Area 1956	0.60**	84.9	5.5 (2.7)*	-4.1e-09 (1.7e-09)*
<i>Quadrat scale</i>				
Area 2003	0.13 ^{ns}	58.3	-2.2 (1.2) ^{ns}	-4.4e-10 (5.2e-10) ^{ns}
Area 1956	-0.16 ^{ns}	62.1	-0.08 (1.1) ^{ns}	-3.6e-10 (6.9-10) ^{ns}

At quadrat scale, neither current nor past patch area was significantly related to specialist richness, either considering together all the 29 studied patches or separating stable and regressive patches (Table 2). Thus, the number of specialist species per quadrat was only related to the geographical gradient.

The differences between observed and predicted specialist richness in regressive patches were non-significantly different from zero ($t = 0.33$; $df = 12$; $P = 0.75$), indicating that there were no systematic extinction debts in these patches. However, the residuals of this model were correlated with the proportion of area lost in regressive patches ($P = 0.008$; Fig. 3), but not in stable ones ($P = 0.16$) (Table 3). Furthermore, area lost was the only variable that remained significant ($F = 5.12$; $P < 0.05$; $r_{\text{model}} = 0.76$) when applying a GLM on residuals with area lost, past patch area and past landscape area.

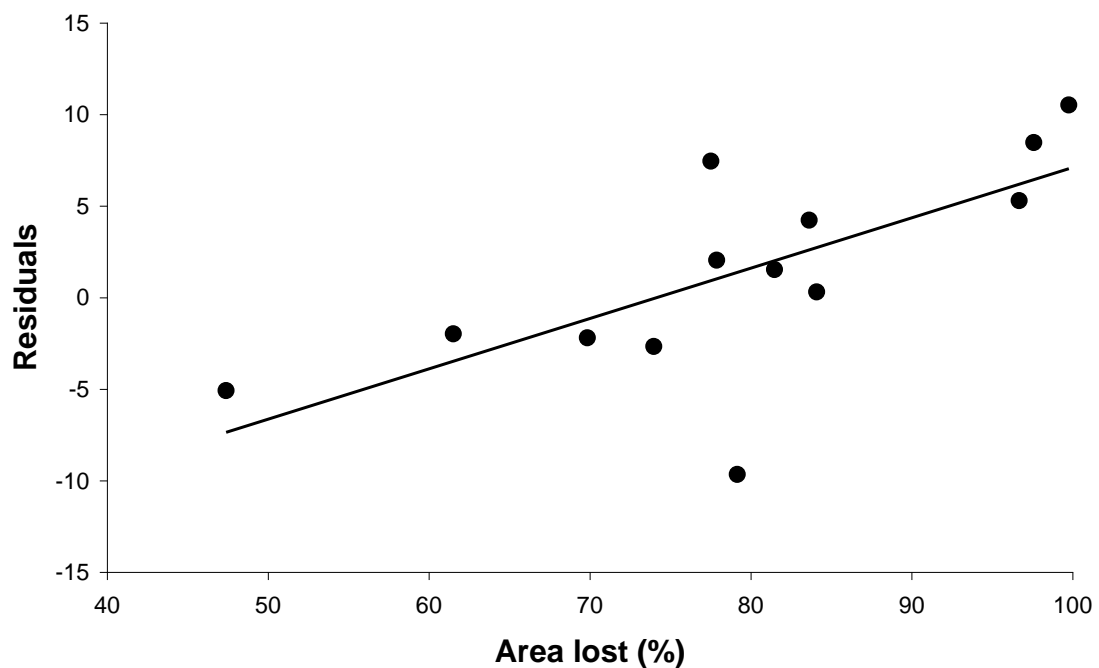


Figure 3 Relationship between the proportion of patch area lost in regressive patches and the residual between observed and predicted specialist species richness, calculated from the current patch area using the species-area relationship of stable patches. The line is the least-squares linear regression. ($r^2 = 0.48$, $P = 0.008$).

Table 3 Correlation between residuals of the observed and predicted specialist species richness (calculated from the current patch area using the species-area relationship of stable patches) with the proportion of area lost, past patch area and past habitat area in the landscape, in stable and regressive patches.

	Area lost (%)	Landscape area in 1956 (log ha)	Patch area in 1956 (log ha)
<i>Residuals stable patches</i>			
r	0.37	0.17	0.04
P	0.16	0.54	0.89
<i>Residuals regressive patches</i>			
r	0.70	0.53	0.48
P	0.008	0.06	0.1

Because the initial patch sizes (in 1956) and size distributions significantly differ between stable and regressive patches and could potentially confound any differences between the patch history groups, we recalculated all analyses minimizing these differences removing from the analyses four stable patches (patches 5, 6, 10 and 11), and two regressive patches (7 and 9) to equalize the initial patch size distribution. Results of this new patch selection (Appendix S5 in Supporting Information) were essentially the same as those obtained including all patches, confirming our results and conclusions.

2.4. Discussion

Our analyses indicate that plant specialists show an extinction debt in Mediterranean grasslands, as already pointed out by Krauss *et al.* (2010) in a cross-European study. However, our study also highlights that this detection is only possible if a set of methodological refinements are performed. In particular, our study highlights the following findings: (i) extinction debt is an idiosyncratic process that depends on patch history, and especially the percentage of area lost in each patch, and (ii) species richness at quadrat scale helps to explain the extinction debt detected at patch scale.

According to Helm *et al.* (2006) and Kuussaari *et al.* (2009), if current species richness is better explained by past rather than current area in habitat patches, this provides preliminary evidence of the existence of an extinction debt in the species under study. We have found that this might depend on patch history, as we found this pattern for regressive patches but the contrary for a mixed set of stable and regressive patches. The magnitude of the extinction debt in these patches

can be assessed by using stable patches to predict the expected species numbers in the regressive ones, as proposed by Helm *et al.* (2006). This helps to remove the artifacts derived from changes in the species-area relationships when assessing the pattern of species richness in mixed sets of stable and regressive patches (Ney-Nifle & Mangel 2000; Lewis 2006). However, all these methodologies considered similar extinction debt in all patches, even though it might be idiosyncratic to a given patch. In our study, the lack of significant differences between observed and predicted specialist species richness in regressive patches indicated an absence of the systematic extinction debt suggested in previous studies (e.g. Helm *et al.* 2006; Kuussaari *et al.* 2009; Krauss *et al.* 2010). Instead, these differences (residuals) were positively associated with the percentage of the patch area lost. This means that regressive patches that had lost the most area had more species than predicted, i.e. higher extinction debt. Though area loss is considered the most important cause of species extinction (Dirzo & Raven 2003), it has been rarely used as a predictive variable to evaluate extinction debt. Piqueray *et al.* (2011a) found that, in Belgian grasslands, plant species richness was significantly related to patch area reduction, despite being mostly determined by current patch area. In any case, patch history includes many factors other than area loss (disturbance regimes, droughts, etc.), which would probably make extinction debt even more idiosyncratic to each patch because patches may differ in the trajectories and timing of their habitat change. However, detailed information on patch history is rarely available (Piqueray *et al.* 2011a).

Our study also highlights the role of spatial scales in detecting extinction debt. Indeed, regressive patches have already lost an average of 2.4 specialist species at quadrat scale compared to stable ones, although this species loss had not yet been detected at patch scale, where a surplus of species (i.e. extinction debt) was found. Similarly, Cousins & Vanhoenacker (2011) found that extinction debt, while still being detected at patch scale, was already being paid at more local scales in Swedish grasslands. In consequence, the evidence of extinction debt at patch scale suggests that species loss at quadrat scale is caused by plant extinctions from quadrats, leading to a rarefaction of some plant species in any given patch; in our study, these processes have not yet caused plant extinctions at patch scale, indicating that some plant species occur as remnant populations (Eriksson 1996). This explanation is congruent with spatially explicit metapopulation models indicating that environmental change and/or habitat loss might shift the distribution frequency of species toward a higher proportion of rare (and hence extinction-prone) species, with stochastic factors ultimately driving many species over their extinction thresholds (Jackson & Sax 2010). Helm *et al.* (2006) pointed out that remnant plant communities in grasslands show a slow response to environmental change, but our results indicated that the response is faster at small scales than at large scales because at small scales

there are fast changes that can affect slower ones at larger scales (Gunderson & Holling 2002). It should be noted that the persistence of grassland plants in regressive patches mainly depends on the rate of encroachment by trees and shrubs (Kunstler *et al.* 2006) but also on the biological and ecological traits of grassland specialists (Bagaria *et al.* 2012; Jacquemyn *et al.* 2012; Saar *et al.* 2012; Marini *et al.* 2012). In our study, we have explored the extinction and extinction debt patterns of grassland plants at community level, without addressing the underlying population processes ultimately determining these patterns. Future research will address the interplay between patch and landscape factors, species composition and plant traits to better explain the idiosyncratic nature of plant extinction and extinction debt in Mediterranean grassland patches.

Finally, it should be mentioned that, as long as extinction after habitat loss is being paid only at quadrat scale, management initiatives to preserve plant biodiversity in these Mediterranean grasslands are still possible because of the slower response of plant populations at patch scale. To prevent grassland impoverishment, conservation measures are required before the extinction debt is paid at patch and landscape scales; thus, species diversity must be considered at multiple spatial scales when decisions are made about grassland management, because species loss at quadrat scale constitutes an early warning indicator of the effects of patch area loss on biodiversity.

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2.6. Supporting information

Table S1. Actual (2003) and past (1956) patch area and area of grassland habitat in the surrounding landscape (landscape area), proportion of patch area lost between 1956 and 2003, mean annual precipitation (mm), mean annual air temperature (°C), and altitude (m a.s.l.).

Patch code	Patch area 2003 (ha)	Patch area 1956 (ha)	Landscape area 2003 (ha)	Landscape area 1956 (ha)	%Patch area lost	Mean annual precipitation (mm)	Mean annual temperature (°C)	Altitude (m a.s.l.)
1	0.101	4.177	0.101	4.857	97.582	744.9	11,5	950
2	0.500	15.038	1.424	15.038	96.675	760.6	11,4	970
3	0.339	1.830	0.339	4.632	81.475	751.8	11,7	920
4	3.105	14.037	3.105	17.985	77.880	764.9	11,8	980
5	19.276	19.276	35.946	95.381	0.000	786.1	11,1	1040
6	7.194	8.785	13.653	93.511	18.110	753.4	11,4	970
7	0.232	94.662	5.210	79.451	99.755	714.1	11,6	960
8	0.677	3.011	1.477	5.595	77.516	742.6	11,4	940
9	1.191	5.713	1.191	5.713	79.153	695.5	11,7	890
10	26.845	35.623	26.845	35.623	24.641	736.3	10,7	1120
11	20.744	33.159	20.744	33.159	37.441	724.6	10,9	1040
12	3.412	4.178	5.805	13.959	18.334	711.9	10,6	1040
13	0.400	2.513	2.739	10.261	84.083	698.0	10,7	1060
14	0.397	0.397	0.608	0.608	0.000	730.4	10,2	1080
15	4.003	4.003	4.142	4.142	0.000	726.6	10,1	1100
16	10.877	10.877	12.184	14.131	0.000	685.7	10,4	960
17	0.629	0.629	8.380	8.380	0.000	669.6	10,6	890
18	15.441	16.875	15.441	16.875	8.498	747.8	11,5	890
19	18.165	18.165	18.165	18.165	0.000	741.1	12,1	840
20	1.336	2.074	8.078	16.352	35.583	798.8	11,7	950
21	4.626	5.927	6.431	13.144	21.950	774.9	12	930
22	0.252	0.968	0.252	0.968	73.967	933.7	11,4	1080
23	0.743	2.463	1.203	5.726	69.834	883.5	12,3	940
24	1.382	2.627	1.660	3.275	47.392	1003.9	11	1160
25	0.278	1.697	1.623	4.260	83.618	1049.6	10,3	1080
26	0.339	0.339	0.764	1.494	0.000	913.5	12,9	930
27	0.214	0.214	4.296	4.296	0.000	1015.1	11,3	1130
28	7.905	7.905	9.648	18.223	0.000	986.6	11,6	1040
29	0.592	1.538	1.075	2.493	61.508	990.7	11,6	1030

Table S2. Plant species richness (total, specialist and non-specialist) at a (1) Quadrat: Individual 0.25 m² quadrats (mean ± standard error of the mean); (2) All quadrats: pooling the 25 quadrats in each patch; (3) Time transect: additional species detected in the time transect; and (4) Patch: Sum of the pooled the quadrats and the additional species from the time transect.

Patch code	Total species richness				Specialist species richness				Non-specialist species richness			
	Quadrat	All quadrats	Time transect	Patch	Quadrat	All quadrats	Time transect	Patch	Quadrat	All quadrats	Time transect	Patch
1	11.9±0.72	50	4	54	10.2±0.73	38	2	40	1.7±0.28	12	2	14
2	12.4±0.44	61	7	68	10.7±0.41	43	2	45	2.2±0.26	18	5	23
3	11.8±0.43	42	12	54	7.4±0.64	34	5	39	1.1±0.15	8	7	15
4	8.1±0.72	49	27	76	7.1±0.67	40	12	52	0.8±0.19	9	15	24
5	13.8±0.60	67	38	105	10.3±0.41	44	14	58	3.4±0.45	23	24	47
6	13.0±0.70	66	38	104	10.2±0.58	43	15	58	2.8±0.38	23	23	46
7	12.9±0.63	60	12	72	11.0±0.63	44	5	49	1.8±0.19	16	7	23
8	13.4±0.70	66	10	76	10.4±0.66	45	7	52	0.9±0.29	21	3	24
9	9.7±0.74	51	22	73	6.4±0.58	27	10	37	3.3±0.36	24	12	36
10	15.3±0.54	65	49	114	12.4±0.60	43	18	61	3.0±0.32	22	31	53
11	13.2±0.67	67	42	109	11.4±0.68	53	13	66	1.7±0.15	14	29	43
12	15.4±0.74	58	31	89	12.8±0.70	42	14	56	2.6±0.16	16	17	33
13	14.6±0.56	58	5	63	13.0±0.48	41	2	43	1.6±0.22	17	3	20
14	17.2±0.67	74	5	79	13.7±0.58	44	1	45	3.5±0.44	30	4	34
15	13.7±0.60	56	17	73	11.3±0.53	39	8	47	2.4±0.35	17	9	26
16	17.6±0.50	62	29	91	16.0±0.49	47	8	55	1.6±0.22	15	21	36
17	14.7±0.60	60	14	74	13.4±0.58	46	2	48	1.2±0.22	14	12	26
18	17.6±0.64	75	31	106	12.6±0.51	48	8	56	5.0±0.56	27	23	50
19	14.7±0.63	66	58	124	11.4±0.51	47	20	67	3.3±0.32	19	38	57
20	18.4±0.89	66	16	82	14.5±0.71	44	2	46	3.9±0.39	22	14	36
21	15.1±0.70	74	29	103	10.6±0.69	39	12	51	4.6±0.71	35	17	52
22	11.5±0.76	56	10	66	8.2±0.47	30	2	32	3.4±0.56	26	8	34
23	10.4±0.58	47	15	62	8.9±0.59	32	6	38	1.6±0.21	15	9	24
24	10.4±0.40	38	15	53	9.8±0.39	31	5	36	0.7±0.15	7	10	17
25	9.9±0.52	44	3	47	9.0±0.51	36	1	37	0.9±0.18	8	2	10
26	10.8±0.41	36	8	44	9.5±0.44	32	2	34	1.2±0.17	4	6	10
27	10.4±0.55	35	1	36	9.2±0.48	28	-1	27	1.1±0.21	7	2	9
28	12.1±0.63	48	20	68	11.2±0.57	39	8	47	1.0±0.19	9	12	21
29	10.8±0.47	34	7	41	9.5±0.42	28	3	31	1.3±0.17	6	4	10

Table S3. Basic statistical description (Mean \pm SD) of the differences between stable and regressive patches with mean annual temperature, elevation, mean annual precipitation, geographical gradient, area 2003, area 1956, landscape area 2003 and landscape area 1956.

	Stable	Regressive	GLM
Mean annual temperature (°C)	11.2 \pm 0.77	11.4 \pm 0.5	F=0.80, P=0.38
Elevation (m)	996.9 \pm 88.9	996.9 \pm 78.5	F=0.00, P=1
Mean annual precipitation (mm)	781.4 \pm 101.8	825.7 \pm 128.0	F=1.08, P=0.31
Geographical gradient	-1,06E+09 \pm 1,07E+09	-1,64E+09 \pm 8,72E+08	F=2.87, P=0.10
Area 2003 (log ha)	0.59 \pm 0.70	-0.29 \pm 0.39	F=16.28, P<0.001
Area 1956 (log ha)	0.64 \pm 0.73	0.62 \pm 0.54	F=0.01, P=0.92
Landscape area 2003 (log ha)	0.89 \pm 0.49	0.04 \pm 0.47	F=22.28, P<0.0001
Landscape area 1956 (log ha)	1.10 \pm 0.58	0.81 \pm 0.46	F=2.12, P=0.16

Table S4. Plant species recorded in this study. Grassland specialists, marked in bold, were selected with the help of regional floras (Bolòs *et al.* 1993; Rivas–Martínez *et al.* 2001) and expert advice.

<i>Acer opalus</i> Mill.	<i>Calicotome spinosa</i> (L.) Link
<i>Achillea ageratum</i> L.	<i>Carduncellus monspeliensis</i> All.
<i>Aegilops geniculata</i> Roth	<i>Carduus nigrescens</i> Vill. subsp. <i>Nigrescens</i>
<i>Aetheorhiza bulbosa</i> (L.) Cass.	<i>Carex flacca</i> Schreber
<i>Aethionema saxatile</i> (L.) R. Br.	<i>Carex halleriana</i> Asso
<i>Allium roseum</i> L.	<i>Carex humilis</i> Leysser
<i>Allium senescens</i> L. subsp. <i>montanum</i> (Fries) Holub	<i>Carthamus lanatus</i> L.
<i>Allium sphaerocephalon</i> L. subsp. <i>sphaerocephalon</i>	<i>Catananche coerulea</i> L.
<i>Althaea hirsuta</i> L.	<i>Catapodium rigidum</i> (L.) C.E. Hubbard
<i>Alyssum spinosum</i> L.	<i>Centaurea linifolia</i> L. subsp. <i>caballeroi</i> (F. Q. et Pau in F. Q.) O. Bolòs et J. Vigo
<i>Amelanchier ovalis</i> Medic.	<i>Centaurea linifolia</i> L. subsp. <i>linifolia</i>
<i>Anagallis arvensis</i> L.	<i>Centaurea montana</i> L. subsp. <i>lingulata</i> (Lag.) O. Bolòs et J. Vigo
<i>Anemone hepatica</i> L.	<i>Centaureum quadrifolium</i> (L.) G. López et Ch. E. Jarvis subsp. <i>barrelieri</i> (Duf.) G. López
<i>Anthemis arvensis</i> L.	<i>Cephalanthera longifolia</i> (L.) Fritsch
<i>Anthericum liliago</i> L.	<i>Cerastium gracile</i> Duf.
<i>Anthyllis montana</i> L.	<i>Cerastium pumilum</i> Curtis
<i>Anthyllis vulneraria</i> L. subsp. <i>fontqueri</i> (Rothm.) A. et O. Bolòs	<i>Chaenorhinum rubrifolium</i> (Robill. et Cast. ex DC.) Fourr. subsp. <i>rubrifolium</i>
<i>Aphyllanthes monspeliensis</i> L.	<i>Cistus albidus</i> L.
Apiaceae 21	<i>Cistus clusii</i> Dunal
<i>Arabis auriculata</i> Lam.	<i>Clematis vitalba</i> L.
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	<i>Colutea arborescens</i> L.
<i>Arenaria conimbricensis</i> Brot. subsp. <i>conimbricensis</i>	Compositae 12
<i>Arenaria serpyllifolia</i> L. subsp. <i>serpyllifolia</i>	Compositae 16
<i>Arenaria tetraqueta</i> L. subsp. <i>condensata</i> Arcang.	Compositae 18
<i>Argyrolobium zanonii</i> (Turra) P. W. Ball	Compositae 19_1
<i>Aristolochia pistolochia</i> L.	Compositae 19_2
<i>Arrhenatherum album</i> (Vahl) W. D. Clayton	Compositae 24
<i>Arrhenatherum elatius</i> (L.) Beauv. ex J. et C. Presl subsp. <i>sardoum</i> (E. Schmid) Gamišans	Compositae 28
<i>Asperula cynanchica</i> L.	Compositae 4
<i>Asphodelus cerasiferus</i> Gay	Compositae 8
<i>Asterolinon linum-stellatum</i> (L.) Duby in DC.	<i>Conopodium majus</i> (Gouan) Loret in Loret et Barr. subsp. <i>ramosum</i> (Costa) Silvestre
<i>Astragalus monspessulanus</i> L. subsp. <i>monspessulanus</i>	<i>Convolvulus arvensis</i> L.
<i>Avenula pratensis</i> L. subsp. <i>iberica</i> St.-Yves.	<i>Convolvulus lanuginosus</i> Desr.
<i>Biscutella laevigata</i> L.	<i>Convolvulus lineatus</i> L.
<i>Blackstonia perfoliata</i> (L.) Huds.	<i>Coris monspeliensis</i> L.
<i>Brachypodium phoenicoides</i> (L.) Roem. et Schultes	<i>Coronilla minima</i> L.
<i>Brachypodium retusum</i> (Pers.) Beauv.	<i>Crataegus monogyna</i> Jacq.
<i>Brimeura amethystina</i> (L.) Chouard subsp. <i>fontqueri</i> (Pau) O. Bolòs & Vigo	<i>Crepis albida</i> Vill.
<i>Briza media</i> L.	<i>Crepis vesicaria</i> L. subsp. <i>taraxacifolia</i> (Thuill) Thell. ex Schinz et Keller
<i>Bromus erectus</i> Huds.	<i>Crucianella angustifolia</i> L.
<i>Bromus squarrosus</i> L.	<i>Cruciata glabra</i> (L.) Ehrend.
<i>Bupleurum baldense</i> Turra subsp. <i>baldense</i>	<i>Crupina vulgaris</i> Cass.
<i>Bupleurum frutescens</i> L.	<i>Cuscuta epithymum</i> (L.) L.
<i>Bupleurum fruticosum</i> L.	<i>Cytisophyllum sessilifolium</i> (L.) O. F. Lang
<i>Bupleurum rigidum</i> L.	
<i>Buxus sempervirens</i> L.	

Dactylis glomerata L. subsp. *hispanica* (Roth) Nyman
Daucus carota L.
Dianthus pungens L. subsp. *tarraconensis* (Costa) O. Bolòs et J. Vigo
Dictamnus hispanicus Webb ex Willk.
Dipcadi serotinum (L.) Medic.
Dorycnium hirsutum (L.) Ser. in DC.
Dorycnium pentaphyllum Scop. subsp. *pentaphyllum*
Echinaria capitata (L.) Desf.
Echinops ritro L.
Echium vulgare L. subsp. *argenteae* (Pau) F. Q.
Epipactis atrorubens (Hoffm.) Bess.
Epipactis helleborine (L.) Crantz
Erica multiflora L.
Erinacea anthyllis Link
Erucastrum nasturtiifolium (Poirlet) O. E. Schulz
Eryngium campestre L.
Erysimum grandiflorum Desf.
Euphorbia characias L.
Euphorbia flavicoma DC. subsp. *mariolensis* (Rouy) O. Bolòs et J. Vigo
Euphorbia nicaeensis All. subsp. *nicaeensis*
Euphorbia serrata L.
Festuca nigrescens Lam.
Festuca ovina L. s.l.
Festuca paniculata (L.) Schinz et Thell. subsp. *spadicea* (L.) Litard.
Fritillaria pyrenaica L.
Fumana ericoides (Cav.) Gandg.
Fumana procumbens (Dunal) Gren. et Godr.
Fumana thymifolia (L.) Spach
Galium lucidum All.
Galium parisiense L.
Galium pumilum Murray
Galium pumilum Murray subsp. *papillosum* (Lap.) Batalla et Masclans ex O. Bolòs
Galium pumilum Murray subsp. *pinetorum* (Ehrend.) J. Vigo
Genista hispanica L.
Genista patens DC.
Genista scorpius (L.) DC. in Lam. et DC.
Geranium columbinum L.
Geranium robertianum L. subsp. *purpureum* (Vill.) Nyman
Geum sylvaticum Pourr.
Gladiolus illyricus Koch
Globularia cordifolia L. subsp. *nana* Lam.
Globularia vulgaris L.
Gymnadenia conopsea (L.) R. Br.
Hedera helix L.
Helianthemum apenninum (L.) Mill.
Helianthemum marifolium (L.) Mill. subsp. *marifolium*
Helianthemum numularium (L.) Mill.
Helianthemum oelandicum (L.) DC. in Lam. et DC. subsp. *italicum* (L.) F.Q. et Rothm.
Helianthemum organifolium (Lam.) Pers. subsp. *molle* (Cav.) F.Q. et Rothm.
Helichrysum stoechas (L.) Moench
Helleborus foetidus L.
Hieracium pilosella L.
Hippocrepis comosa L.
Hornungia petraea (L.) Reichenb.
Hypericum perforatum L.
Hypochoeris radicata L.
Iberis ciliata All. subsp. *ciliata*
Ilex aquifolium L.
Inula helenioides DC. in Lam. et DC.
Inula montana L.
Iris chamaeiris Bertol.
Jasonia tuberosa (L.) DC.
Juniperus communis L.
Juniperus oxycedrus L.
Juniperus phoenicea L.
Knautia arvensis (L.) Coult. subsp. *subscaposa* (Boiss. et Reut.) Maire
Koeleria vallesiana (Honckeny) Gaud.
Lactuca perennis L.
Lactuca tenerrima Pourr.
Laserpitium gallicum L.
Lathyrus filiformis (Lam.) Gay
Lathyrus saxatilis (Vent.) Vis.
Lathyrus setifolius L.
Lavandula angustifolia Mill.
Lavandula latifolia Medic.
Legousia hybrida (L.) Delarbre
Legousia scabra (Lowe) Gamisans
Leontodon taraxacoides (Vill.) Mérat subsp. *hispidus* (Roth) Kerguélen
Leuzea conifera (L.) DC. in Lam. et DC.
Linaria arvensis (L.) Desf. subsp. *simplex* (Willd.) Lange in Willk. et Lange
Linaria supina (L.) Chaz. subsp. *aeruginea* (Gouan) O. Bolòs et J. Vigo
Linum narbonense L.
Linum strictum L. subsp. *strictum*
Linum tenuifolium L. subsp. *suffruticosum* (L.) Litard.
Lithospermum fruticosum L.
Lonicera implexa Ait.
Lonicera pyrenaica L.
Lotus corniculatus L.
Marrubium supinum L.
Medicago minima (L.) L.
Melica ciliata L.
Melica minuta L.
Mercurialis tomentosa L.
Micropus erectus L.
Minuartia hybrida (Vill.) Schischkin in Komarov
Muscari neglectum Guss. ex Ten.
Narcissus assoanus Duf.
Onobrychis supina (Vill.) DC. in Lam. et DC. subsp. *supina*
Ononis minutissima L.

***Ononis pusilla* L.**
Ononis spinosa L.
Ononis viscosa L.
Ophrys apifera Huds.
***Ophrys fusca* Link**
 Orchidaceae
Orchis maculata L.
***Orchis mascula* (L.) L.**
Orchis ustulata L.
***Orobanche caryophyllacea* Sm.**
Orobanche sp.
Paeonia officinalis L.
Petrorhagia prolifera (L.) P. W. Ball et Heyw.
***Peucedanum officinale* L. subsp. *stenocarpum* (Boiss. et Reut.) F. Q.**
***Phleum phleoides* (L.) Karsten**
***Phlomis lychnitis* L.**
***Phyteuma orbiculare* L. subsp. *ibericum* (R. Schulz) P. Fourn.**
Pinus halepensis Mill.
Pinus nigra Arnold
Pinus sylvestris L.
Pistacia lentiscus L.
Plantago lanceolata L.
Plantago sempervirens Crantz
Platanthera bifolia (L.) L. C. M. Richard
Poa bulbosa L.
***Polygala calcarea* F.W. Schultz**
***Polygala monspeliaca* L.**
Polygala rupestris* Pourr. subsp. *rupestris
Polygala vulgaris L.
***Potentilla neumanniana* Reichenb.**
Potentilla reptans L.
Primula veris L. subsp. *columnae* (Ten.) Maire et Petitmengin
***Prunella laciniata* (L.) L.**
Prunus spinosa L.
Psoralea bituminosa L.
Quercus cerrioides Willk. et Costa
Quercus coccifera L.
Quercus faginea Lam.
Quercus humilis Mill.
Quercus ilex L.
***Ranunculus bulbosus* L.**
***Ranunculus gramineus* L.**
Reseda luteola L. subsp. *luteola*
Rhamnus alaternus L. var. *balearicus* DC.
Rhamnus saxatilis Jacq.
Rosa pimpinellifolia L. subsp. *myriacantha* (DC.) O. Bolòs et J. Vigo
Rosa sicula Tratt.
Rosa sp.
***Rosmarinus officinalis* L.**
Rubia peregrina L.
Rubus ulmifolius Schott
Rumex intermedius DC. in Lam. et DC.
Ruscus aculeatus L.
***Salvia officinalis* L. subsp. *lavandulifolia* (Vahl) Gams**
***Sanguisorba minor* Scop.**
***Santolina chamaecyparissus* L.**
Saponaria ocymoides L.
***Satureja montana* L.**
Schoenus nigricans L.
Scirpus holoschoenus L.
***Scorzonera angustifolia* L.**
***Scorzonera hirsuta* L.**
***Scorzonera hispanica* L. subsp. *crispata* (Boiss.) Nyman**
Sedum acre L.
Sedum sediforme (Jacq.) Pau
Senecio vulgaris L.
***Serratula nudicaulis* (L.) DC. in Lam. et DC.**
Seseli montanum* L. subsp. *montanum
Sherardia arvensis L.
Sideritis hirsuta L. subsp. *hirsuta*
***Sideritis spinulosa* Barnades ex Asso subsp. *ilicifolia* (Willd.) O. Bolòs et J. Vigo**
Silene conica L. subsp. *conica*
Silene gallica L.
***Silene italica* (L.) Pers. subsp. *nevadensis* (Boiss.) F. Q.**
Silene nutans L. subsp. *brachypoda* (Rouy) Asch. et Graebn.
Silene vulgaris (Moench) Garcke subsp. *prostrata* (Gaud.) Schinz et Thell.
Silene vulgaris (Moench) Garcke subsp. *vulgaris*
Sonchus tenerrimus L.
Sorbus aria (L.) Crantz
Sorbus domestica L.
***Stachys heraclea* All.**
***Staehelina dubia* L.**
***Stipa offneri* Breistr.**
***Stipa pennata* L. subsp. *iberica* (Martinovsky) O. Bolòs, R. M. Masalles et J. Vigo**
Tanacetum corymbosum (L.) Schultz Bip. subsp. *corymbosum*
Taraxacum obovatum (Willd.) DC.
Taraxacum officinale Weber in Wiggers
Teucrium botrys L.
Teucrium chamaedrys L.
***Teucrium polium* L.**
***Thalictrum tuberosum* L.**
***Thesium humifusum* DC.**
Thlaspi perfoliatum L. subsp. *perfoliatum*
***Thymelaea tinctoria* (Pourr.) Endl.**
***Thymus serpyllum* L. subsp. *fontqueri* (Jalas) O. Bolòs et J. Vigo**
***Thymus vulgaris* L.**
***Tragopogon porrifolius* L. subsp. *australis* (Jord.) Nyman**
Trifolium campestre Schreb. in Sturm
Trifolium stellatum L.
Trigonella monspeliaca L.
***Trinia glauca* (L.) Dumort.**

Tulipa sylvestris L. subsp. *australis* (Link) Pamp.

Valeriana tuberosa L.

Veronica austriaca L. subsp. *tenuifolia* (Asso) O. Bolòs et J.

Vigo

Vicia peregrina L.

Vicia sativa L. subsp. *nigra* (L.) Ehrh.

Viola rupestris F.W. Schmidt

Xeranthemum inapertum (L.) Mill.

Appendix S5. Results removing from the analyses a set of stable (patches 5, 6, 10 and 11) and regressive (7 and 9) patches to minimize differences in patch size distributions between the two considered groups (stable and regressive).

Table S5.1 Results from GLMs for the effects of patch area, patch stability and geographical variation on total, specialist and non-specialist species richness, at patch and quadrat scales.

	Area	Patch stability	Geographical variation
<i>Patch scale</i>			
Total	F = 22.4 <i>P</i> < 0.0002	F = 0.20 <i>P</i> = 0.66	F = 27.4 <i>P</i> < 0.0001
Specialists	F = 19.2 <i>P</i> < 0.0002	F = 0.004 <i>P</i> = 0.95	F = 21.6 <i>P</i> < 0.0002
Non-specialists	F = 8.4 <i>P</i> < 0.01	F = 0.22 <i>P</i> = 0.65	F = 11.0 <i>P</i> < 0.005
<i>Quadrat scale</i>			
Total	F = 0.21 <i>P</i> = 0.65	F = 11.1 <i>P</i> < 0.005	F = 12.2 <i>P</i> < 0.005
Specialists	F = 0.44 <i>P</i> = 0.51	F = 9.0 <i>P</i> < 0.01	F = 5.1 <i>P</i> = 0.03
Non-specialists	F = 0.09 <i>P</i> = 0.77	F = 0.67 <i>P</i> = 0.42	F = 5.1 <i>P</i> = 0.03

Table S5.2 Comparison of the importance of actual or past patch area in predicting specialist species richness in models considering all patches together, stable patches and regressive patches. Significance codes: *** $P < 0.001$; ** $0.01 > P > 0.001$; * $0.05 > P > 0.01$.

	r^2 adj.	AICc	Log (area)	Geographical variation
<i>a) All patches</i>				
<i>Patch scale</i>				
Area 2003	0.81***	1125.8	8.7.1 (1.4)***	-4.5e-09 (7.9e-10)***
Area 1956	0.78***	152.2128.9	8.7.5 (1.7)***	-4.8e-09 (8.3e-10)***
<i>Quadrat scale</i>				
Area 2003	0.35**	193.6	0.6 (0.7) ^{ns}	-1.1e-9 (3.8e-10)**
Area 1956	0.34*	108.394.0	-0.5 (0.8) ^{ns}	-1.3e-09 (3.7e-10)**
<i>b) Stable patches</i>				
<i>Patch scale</i>				
Area 2003	0.86***	74.566.3	98.7(1.7)**	-3.7e-09 (9.3e-10)**
Area 1956	0.87***	74.265.2	9.8.7 (1.7)***	-3.6e-09 (8.8e-10)**
<i>Quadrat scale</i>				
Area 2003	0.36	5550.7	-0.3(0.9) ^{ns}	-1.1e-09 (4.6e-10)*
Area 1956	0.36	550.6	-0.4 (0.8) ^{ns}	-1.1e-09 (4.6e-10)*
<i>c) Regressive patches</i>				
<i>Patch scale</i>				
Area 2003	0.69*	869.1	46.0 (3.1)	-6.2e-09 (1.4e-09)**
Area 1956	0.78**	77.465.1	8.9 (3.0)*	-4.8e-09 (1.3e-09)**
<i>Quadrat scale</i>				
Area 2003	0.14 ^{ns}	53.745.9	-1.5 (1.1) ^{ns}	-7.2e-10 (4.9e-10) ^{ns}
Area 1956	-0.005 ^{ns}	55.647.0	-1.3 (1.3) ^{ns}	-8.9e-10 (5.7e-10) ^{ns}

Table S5.3 Correlation between residuals of the observed and predicted specialist species richness (calculated from the current patch area using the species-area relationship of stable patches) with the proportion of area lost, past patch area and past habitat area in the landscape, in stable and regressive patches.

	Area lost (%)	Landscape area in 1956 (log ha)	Patch area in 1956 (log ha)
<i>Residuals stable patches</i>			
<i>r</i>	0.37	0.19	0.04
<i>P</i>	0.26	0.58	0.92
<i>Residuals regressive patches</i>			
<i>r</i>	0.76	0.54	0.55
<i>P</i>	0.007	0.07	0.08

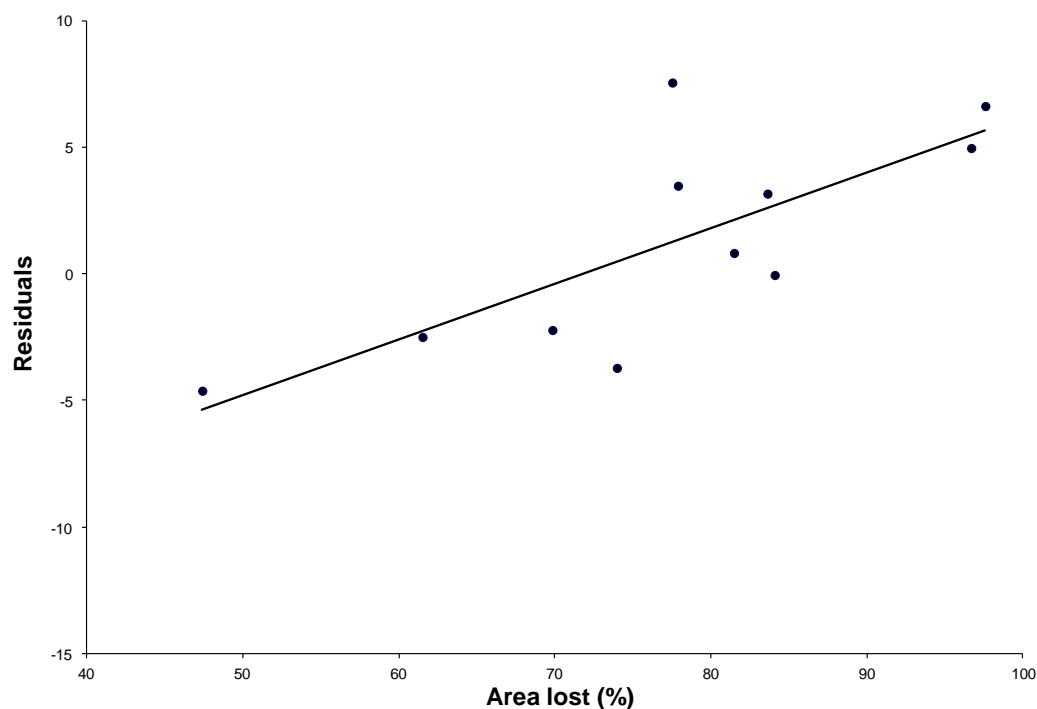


Figure S5.1 Relationship between the proportion of patch area lost in regressive patches and the residual between observed and predicted specialist species richness, calculated from the current patch area using the species-area relationship of stable patches. The line is the least-squares linear regression. ($r^2 = 0.57$, $P = 0.007$).

Capítol 3

Extinction patterns of plants and butterflies in Mediterranean grasslands: direct and indirect effects of landscape, patch area and trophic relationships



This chapter is submitted:

Guardiola, Moisès; Stefanescu, Constantí; Rodà, Ferran & Pino, Joan (2015). Extinction patterns of plants and butterflies in Mediterranean grasslands: direct and indirect effects of landscape, patch area and trophic relationships.

Abstract

Both past and present landscape configurations affect the species richness in fragmented habitat patches, but their effects depend on spatial scale and species types and interactions, and remain largely unknown. We assessed the direct and indirect effects of historical and current patch and landscape areas, patch area loss and patch quality on species density (fixed-area sampling) and richness (area-proportional sampling) in declining Mediterranean grasslands. The study focused on total species and habitat specialists of two trophically-related species groups: vascular plants and butterflies. Current patch area had strong effects on plant and butterfly species richness, directly in plants but indirectly in butterflies via its effects on plant richness, revealing a trophically-mediated effect. Past surrounding grassland area also explained specialist plant species richness, suggesting an extinction debt. On the contrary, patch isolation and patch area loss were the main variables explaining plant species density, plus plant species richness for explaining butterfly species density. Contrasting landscape effects on the species density and richness of plants and butterflies suggest a complex extinction pattern following habitat loss. Patch isolation and area loss might cause a decrease in plant species density, thus favouring the extinction of the rarest species. Effects were stronger on specialist plants, which already show an extinction debt. In contrast, butterfly species density increased in patches with higher area loss suggesting a generalized crowding effect in grassland patches. Because most butterfly species depend trophically on plants, we expect cascade-amplified effects of habitat loss on butterflies.

Keywords: Conservation; extinction debt; habitat loss; isolation; patch history.

3.1. Introduction

Habitat loss is one of the main threat to biodiversity at local, regional and global scales (Dirzo and Raven 2003; Didham *et al.* 2012), increasing the rarity of species and ultimately driving many species to extinction (Jackson and Sax 2010). Species richness is predicted to decrease with area loss and with increasing isolation of habitat patches (MacArthur and Wilson 1963). However, these effects can be modulated by landscape properties, which determine changes in population, community and ecosystem processes (Tschardt *et al.* 2012). Furthermore, the quality of local habitat patches can also play an important role in shaping species distribution in fragmented landscapes (Mortelliti *et al.* 2010; Zulka *et al.* 2014).

Time-lags between habitat loss and subsequent species extinction (Diamond 1972; Summerfield 1972; Tilman *et al.* 1994) are responsible for extinction debts that have been found in many organisms across diverse habitats (see Kuussaari *et al.* 2009 for a review). Extinction debts are commonly assumed when species richness is better explained by past than by present landscape variables like habitat area and connectivity. At the same time, delayed extinctions due to trophic dependencies are expected when the increased mortality rate and decreased abundance of a given species in the food web lead to other species being no longer viable; the former species can thus be considered ecologically or functionally extinct (Säterberg *et al.* 2013). However, the importance of these processes for the species extinction pattern in shrinking habitats remains unclear because assessing it is complex for many reasons, namely the scale dependency of species richness, the within-patch characteristics, the contrasting responses of different organisms and the types and strength of trophic interactions.

Landscape-change effects on species richness might be highly idiosyncratic to each habitat patch (Piqueray *et al.* 2011a) as recently shown by Guardiola *et al.* (2013), who found that extinction debt depends on the area loss of a given patch. Although area loss is considered the most important cause of species extinction (Dirzo and Raven 2003), it has been rarely included as an explicit variable in models of patch-scale species richness (Cousins, 2009; but see Piqueray *et al.*, 2011b). Moreover, although species richness is scale dependent, little attention has been paid to spatial scales when exploring effects of area loss on species richness (McGill 2010). Indeed, species density (species richness of a fixed area within a patch) and species richness (the number of species in the entire habitat patch) are influenced by different patch and landscape characteristics (Reitalu *et al.*, 2012) and ignoring multiple scales can lead to incorrect generalizations (Turtureanu *et al.*, 2014). Species richness in patches is associated with patch area and within-patch environmental heterogeneity (Krauss *et al.*, 2004; Cousins *et al.*, 2007). Species density is related with present and/or past habitat connectivity (Lindborg and Eriksson,

2004), management regime (Cousins et al 2007) or landscape properties (Reitalu et al 2009). A common pitfall in some studies is not differentiating between species richness and species density, and few studies explore changes in species richness at multiple spatial scales in fragmented habitats. It should be noted that effects of area loss are detected earlier in species density than in species richness (Galvnek and Lepš 2008). However, while several organisms show a decrease in their density before their extinction in patches (Berglund and Jonsson 2005; Guardiola et al 2013), others show no decrease in their density, or even an increase (Ewers and Didham 2006).

It is already known that extinction debts are more likely to be more pronounced and/or to persist longer in long-lived or low-trophic level species than in short-lived or high-trophic level ones, because the latter respond faster to habitat changes (Morris et al 2008; Kuussaari et al 2009; Krauss et al 2010). Besides, at all trophic levels, habitat specialists are more prone to exhibit delayed extinctions than generalists (Kuussaari et al 2009; Krauss et al 2010). Moreover, the trophic rank hypothesis holds that habitat loss and fragmentation effects are larger at higher rank along the food chain because consumers are affected by the direct effects of fragmentation on their populations but also by spatial constraints influencing their food sources (Holt et al 1999). Thus, the diversity of herbivores and predators is predicted to be positively linked to plant diversity, thus determining cascade effects on species extinctions across food webs (Haddad et al 2009). As long-lived vascular plants show time-delayed extinctions across European grasslands whereas short-lived butterflies do not (Krauss et al 2010), interacting species at different trophic levels might have different extinction debts, so co-extinctions involving long-lived taxa might amplify future biodiversity loss even without any further habitat fragmentation (Hagen et al 2012).

Vascular plants and butterflies have been widely used as indicators of the conservation status of grasslands (Thomas et al 2004; Krauss et al 2010), because many species are restricted to specific habitat types and can persist in habitat remnants in increasingly fragmented landscapes (Hanski 1999; Thomas and Hanski 2004; Brückmann *et al.* 2010). Both groups differ in their trophic level and longevity, as most grassland plants are long-lived perennials while butterflies are short-lived and, in addition, they are herbivores in the larval stage and pollinators in the adult stage, thus directly depending on their food plants. It is well established that patch and landscape characteristics determine species richness for plants (Schmucki *et al.* 2012) and butterflies (Öckinger et al 2012a). But the legacy of past patch structure (specially past area and connectivity; Helm *et al.*, 2006) and the percentage of area lost in each patch (Piqueray *et al.*,

2011b; Guardiola *et al.*, 2013) also play an important role on plant species richness in fragmented landscapes.

This paper aims to explore direct and indirect effects of patch and landscape characteristics and trophic dependencies on grassland plant and butterfly species density and richness in Mediterranean mountain grasslands. Grasslands are globally threatened due to conversion into arable or urban land and to cessation of traditional extensive grazing regimes in recent decades (WallisDeVries *et al* 2002), the Mediterranean basin is not an exception to this trend (Debussche *et al* 1999). Moreover, the Mediterranean basin is one of the world's biodiversity hotspots (Myers *et al* 2000), especially its mountain ranges (Martínez-Rica 1988), and this poses a serious problem for biodiversity conservation because an important species pool is becoming endangered (Myers *et al* 2000).

Our specific questions are: (i) Do plants and butterfly species respond differently to patch and landscape changes? (ii) Is there a different response due to habitat specialization (specialist and generalists)? (iii) Do species richness and species density respond differently to patch and landscape changes? And (iv) are patch and landscape effects on butterfly species density and richness affected by trophic relationships with plant species?

We address these questions through multi-model selection and structural equation modelling aimed at examining direct and indirect effects of historical and current patch and landscape properties and patch area loss on species density and richness of vascular plants and butterflies, separately for grassland specialists and for all species of each group.

3.2. Materials and methods

3.2.1. Study area and sites

The study was located in the southern Prelitoral mountain range of Catalonia (NE Iberian Peninsula, 41° N, 0° 30' E), in calcareous massifs (ranging from 860 to 1400 m a.s.l.) along a 150-km NE-SW gradient (see Guardiola *et al.*, 2013 for further details), all included in the European Union Nature 2000 network and catalogued as both Special Conservation Area and Special Protection Area for Birds. The focus of this study was on semi-natural Mediterranean mountain grasslands, corresponding to habitat “34.721 *Aphyllanthes* grasslands” of the CORINE habitat classification (Moss and Wyatt 1994). In the study area, like many other low-productivity grasslands in Europe (Kunstler *et al* 2006), there is a slow process of woody encroachment (mainly by *Pinus nigra*, *P. sylvestris*, *Juniperus communis*, *J. oxycedrus* and

Buxus sempervirens) due to abandonment of livestock grazing (sheep and goats) and to climatic and soil constraints on woody species establishment and growth.

3.2.2. Sampling

We selected 29 patches of *Aphyllanthes* grasslands in large summit plateaus, immersed in forested landscapes, with a wide range of patch sizes and intensities of patch area reduction, from stable to high patch regression during the 47-yr period from 1956 to 2003 (see details in Guardiola *et al.*, 2013 and Table S1 in Supplementary material).

3.2.2.1. Patch and landscape variables

For each selected patch, past (1956) and current (2003) patch area and past (1956) and current (2003) surrounding landscape area (1-km buffer for each patch, including the patch area) were calculated by on screen photo-interpretation, while patch area lost was determined as the difference between past and current patch area divided by the past area. Current patch woody cover, a measure of woody encroachment within each patch, was assessed through the percent cover of trees and large shrubs, estimated using orthoimages and overlying 50 random points/ha; this is a proxy of habitat quality for grassland plants and butterflies, with habitat quality decreasing with increasing woody cover. We also used plant species richness and plant species density as a measure of patch quality for butterfly species. Finally, as an indirect measure of grassland patch isolation we included the cover percentage of woody habitats (forest and scrub) in the surrounding landscape, obtained from the Land Cover Map of Catalonia (<http://www.creaf.uab.cat/mcsc/>).

3.2.2.2. Butterfly sampling

In five occasions from May to September 2007, we recorded butterflies (including burnet moths) in each selected patch using fixed-area sampling and area-proportional sampling. Fixed-area sampling was independent of patch area and consisted in walking a fixed 350-m transect identifying and counting all butterflies within a 5-m corridor along the transect line. Proportional sampling was proportional to patch area and involved a time transect adjusted to patch area according to: $T = \ln(A + 0.75) \times 15$, (T = searching time in minutes; A = patch area in ha). Species density and richness were estimated from these samplings as explained for plants.

Butterfly species were classified as grassland specialists or non-specialists based on habitat preference data from the Catalan Butterfly Monitoring Scheme (www.catalanbms.org). We considered a butterfly species to be a specialist if it is mainly restricted to grassland habitats, forms “closed” populations in the classical sense of Thomas and Hanski (2004), or is likely to form “metapopulations”, and behaves as a montane species or, at least, cannot be considered as a lowland species in our study area. We considered as non-specialists some species that are typically found in open habitats but are so common in the region that show an almost ubiquitous distribution, encompassing a wide range of habitats (e.g. *Pyronia cecilia*, *P. bathseba*, *Coenonympha dorus*).

3.2.2.3. Plant sampling

We used the same plant data collected by Guardiola *et al.* (2013) from two simultaneous samplings of vascular plant species: a fixed-area sampling and area-proportional sampling. The latter was independent of patch area and consisted of recording all species within 25 randomly distributed quadrats of 0.5 x 0.5 m per patch. Proportional sampling was dependent on patch area and involved a time transect throughout each patch of a duration proportional to the logarithm of patch area, according to $T = \ln(A+1) \times 30$ (T = searching time in minutes; A = patch area in ha).

Fixed sampling allows estimating plant species densities as the mean of the recorded species within the 25 quadrats. We estimated plant species richness in each patch by pooling the data from fixed and proportional samplings. Hence, species density was obtained from fixed sampling, and species richness from proportional and fixed sampling. Plant species were classified as grassland specialists using regional floras (Bolòs *et al.* 1993; Rivas–Martínez *et al.* 2001) and expert advice.

3.2.3. Statistical analyses

We first log 10-transformed area variables (patch- and landscape area) to linearize relationships and to meet the assumptions of normality and homoscedasticity. As species richness in these grassland patches were in part related to the patch geographical gradient (Bagaria *et al.* 2012), we included this effect by applying a trend surface analysis (Legendre and Legendre 1998) with the first principal component extracted from the principal component analysis of the UTM-X and UTM-Y coordinates of the central point of each patch. The geographical gradient in species density and richness (for both total and specialist species) was best described by a second order

polynomial of the first principal component (PC1) scores, $PC1-(PC1)^2$, with maximum values to the centre and minimum values to the extremes of the studied area (for more details see Guardiola *et al.*, 2013). This geographical gradient was then included as a predictor variable in the analysis for both plants and butterflies.

Then, we compared the effects of patch and landscape area in 1956 and 2003, patch area loss between these dates, patch isolation and patch quality on vascular plants and butterflies, separately for species richness (patch level) and species density (fixed areas within patches) of both total and specialist species. We performed GLMs with all combinations of these variables and including the above-mentioned geographical gradient. The effect of these variables was assessed through multi-model selection based on the Akaike Information Criterion for small sample sizes (AICc) to select the best model (Burnham and Anderson 2002): all possible models were ranked by its delta AICc value ($AICc(i) - AICc(\min)$) and we selected as the best models those who had a delta AICc ≤ 2 (Burnham and Anderson 2002).

Finally, although it is possible to use Akaike's model weights to evaluate the relative importance of variables, this approach has been criticized in cases of collinearity between predictor variables (Murray and Conner 2009), as is the case of our data (Table S2). Therefore, to estimate the relative contributions of the variables included in the best models selected by AICc, we used structural equation modelling (SEM; Grace, 2006). We constructed a model that incorporates all response variables in the models selected by AICc criterion and we analyzed which variables had significant direct and indirect effects on plant and butterfly species density and richness. We started with the 'saturated model' including all possible directional relationships between plant and butterfly species density and richness and patch and landscape variables, plus all possible covariations among patch and landscape variables. This model was simplified by stepwise removing the least significant path until the fit of the model did not increase further. SEM enables the examination of direct and indirect effects of predictors on response variables, taking into account the possible collinearity among predictors. Direct effects are measured by standardized partial regression coefficients between a predictor and a response variable, whereas indirect effects are calculated as the sum of the products of all standardized partial regression coefficients over all paths between a predictor and a response variable. These coefficients were estimated by maximum likelihood procedures, as recommended for small sample sizes (Iriondo et al 2003). Parameter significance was accepted at $\alpha = 0.05$. The overall fit of the model was assessed using the Chi-square statistic and the Bentler comparative fit index (CFI). The lack of significance of the probability associated to the Chi-square ($P > 0.05$) and CFI > 0.90 indicate a good fit of the model.

Statistical analyses of multi-model selection were performed using the software R 2.15.1 for Windows (RCoreTeam 2012) and the MuMIn package version 1.9.0 (Barton 2012). SEM analyses were performed using the AMOS.18.0 software (Arbuckle 2009).

3.3. Results

We recorded 297 vascular plant and 85 butterfly species in the 29 studied patches, with 42% of plants and 40% of butterflies being considered grassland specialists. Detailed data of species richness and density is given in Table S3 for plants and Table S4 for butterflies, and the complete list of species in Table S5 for plants and Table S6 for butterflies.

For plants, three models were selected at the patch scale to explain total plant species richness (models with $\Delta AICc \leq 2$; Table S7); predictor variables included in these models were current patch area, current patch woody cover, patch isolation and geographical gradient variables. For total plant species richness, the model built with all these variables using SEM showed direct positive effects only of current patch area and the geographical gradient (Table 1; Fig. 2). For specialist plants richness, a model with current patch area, past surrounding grassland area and geographical gradient was selected (Table S7); SEM analysis yielded positive direct effects of current patch area and past surrounding grassland area and negative direct effects of the geographical gradient on specialist plant species richness (Table 1; Fig. 2). At the quadrat scale, total plant species density was related to the geographical gradient, to percentage of patch area lost and to patch isolation (i.e., the proportion of forest and scrub in the landscape); SEM analysis showed that total plant species density was directly and negatively related to these three variables. Four models were selected to explain specialist plant species density; these models incorporated patch isolation, patch area loss and geographical gradient (Table S7) and with SEM analysis we found negative direct effects of patch isolation and area loss on specialist plant species density (Table 1; Fig. 2).

Table 1 Total, direct and indirect effects of patch and landscape variables on total and specialist plant species richness, and on total and specialist plant species density derived from the structural equation modelling. Total model variation explained (R^2) is shown. The path diagram is shown in Fig. 2.

	Current patch area	Current surrounding grassland area	Past patch area	Past surrounding grassland area	Current patch woody cover	Patch isolation	Patch area loss	Geographical variation	Total model variation explained
<i>Total plant species richness</i>									87%
Total	0.64	-	-	-	-	-	-	-0.46	
Direct	0.64	-	-	-	-	-	-	-0.46	
Indirect	-	-	-	-	-	-	-	-	
<i>Specialist plant species richness</i>									87%
Total	0.44	-	-	0.29	-	-	-	-0.43	
Direct	0.44	-	-	0.29	-	-	-	-0.43	
Indirect	-	-	-	-	-	-	-	-	
<i>Total plant species density</i>									58%
Total	-	-	-	-	-	-0.34	-0.41	-0.38	
Direct	-	-	-	-	-	-0.34	-0.41	-0.38	
Indirect	-	-	-	-	-	-	-	-	
<i>Specialist plant species density</i>									39%
Total	-	-	-	-	-	-0.45	-0.43	-	
Direct	-	-	-	-	-	-0.45	-0.43	-	
Indirect	-	-	-	-	-	-	-	-	

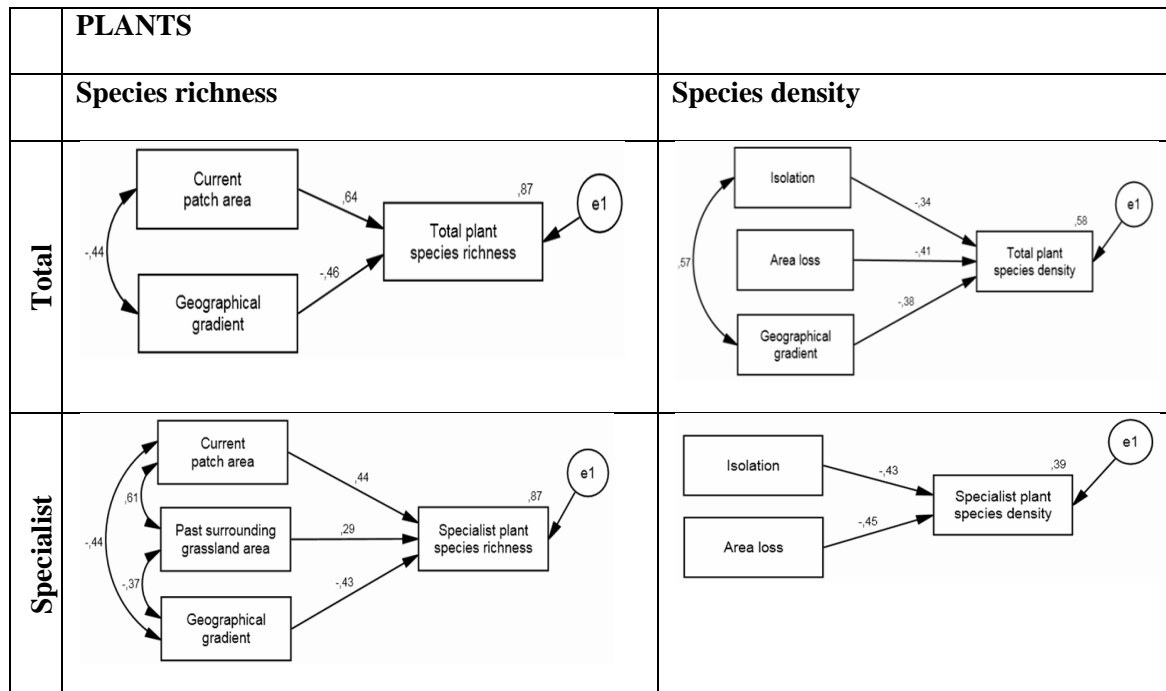


Fig. 2. Path diagrams of the SEMs relating patch and landscape variables to total and specialist plant species richness and species density. Standardized partial regression coefficients between predictors and response variables are shown only for the significant relationships. Estimated squared multiple correlation (R^2) of the response variable in each model is shown. Single-headed arrows indicate direct causal effects and double-headed ones indicate partial correlations. e1 = error variable not directly observed or proportion of the variance not accounted by all other variables in the model.

For butterflies, seven models were selected at the patch scale to explain total butterfly species richness; these models were composed by patch isolation, patch area loss, geographical gradient, total plant species richness and total plant species density variables (Table S8). Analyzing a model with these variables using SEM, we only found a direct effect of plant species richness, and indirect effects of patch area (positive) and geographical gradient (negative) via its effects on plant species richness. For specialist butterfly species richness, five models composed by current surrounding grassland area, patch isolation, patch area loss and total plant species richness variables were selected (Table S8); essentially the same results as for total species richness were obtained when a SEM analysis was conducted (Table 2; Fig. 3). At fixed scale, nine models composed by current patch area, current surrounding grassland area, past patch area, patch isolation, patch area loss, geographical gradient and total plant species density and richness variables were selected to explain total butterfly species density (Table S8); SEM analysis showed that butterfly species density was only positively influenced by plant species density and richness and by area loss, and indirectly by current patch area (positive) and geographical gradient (negative) through plant species density and richness (Table 2; Fig. 3). Four models composed by current patch area, past patch area, patch isolation, patch area loss, and total plant species density and richness variables were selected to explain specialist butterfly species density (Table S8); SEM analysis showed that specialist butterfly species density was only positively influenced by plant species richness and patch area loss, negatively by isolation and past patch area, and indirectly by current patch area and geographical gradient (through plant species richness; Table 2; Fig. 3).

Table 2 Total, direct and indirect effects of patch and landscape variables on total and specialist butterfly species richness and on total and specialist butterfly species density derived from the structural equation modelling. Total model variation explained (R^2) is shown. The path diagram is shown in Fig. 3.

	Current patch area	Current surrounding grassland area	Past patch area	Past surrounding grassland area	Current patch woody cover	Patch isolation	Patch area loss	Geographical variation	Total plant species richness	Total plant species density	Total model variation explained
<i>Total butterfly species richness</i>											
Total	0.48	-	-	-	-	-	-	-0.34	0.75	-	56%
Direct	-	-	-	-	-	-	-	-	0.75	-	
Indirect	0.48	-	-	-	-	-	-	-0.34	-	-	
<i>Specialist butterfly species richness</i>											
Total	0.42	-	-	-	-	-	-	-0.30	0.66	-	43%
Direct	-	-	-	-	-	-	-	-	0.66	-	
Indirect	0.42	-	-	-	-	-	-	-0.30	-	-	
<i>Total butterfly species density</i>											
Total	0.25	-	-	-	-	-	0.50	-0.40	0.38	0.37	50%
Direct	-	-	-	-	-	-	0.64	-	0.38	0.37	
Indirect	0.25	-	-	-	-	-	-0.14	-0.40	-	-	
<i>Specialist butterfly species density</i>											
Total	0.56	-	-0.56	-	-	-0.28	0.59	-0.38	0.74	-	57%
Direct	-	-	-0.56	-	-	-0.28	0.59	-	0.74	-	
Indirect	0.56	-	-	-	-	-	-0.38	-	-	-	

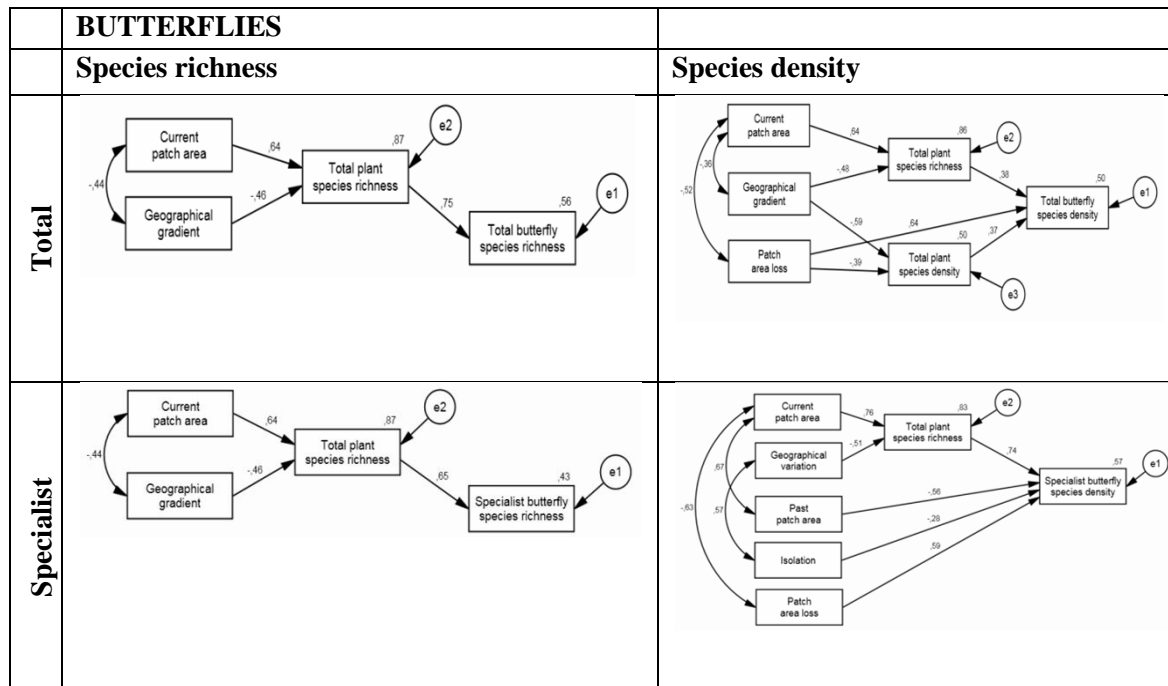


Fig. 3. Path diagrams of the SEMs relating patch and landscape variables to total and specialist butterfly species richness and species density. Standardized partial regression coefficients between predictors and response variables are shown only for the significant relationships. Estimated squared multiple correlation (R^2) of the response variable in each model is shown. Single-headed arrows indicate direct causal effects and double-headed ones indicate partial correlations. e1-3 = error variables not directly observed or proportion of the variance not accounted by all other variables in the model.

3.4. Discussion

In accordance with previous studies in temperate grasslands (Kuussaari et al 2009; Krauss et al 2010) plant and butterfly species richness in Mediterranean *Aphyllanthes* grasslands respond differently to present and past landscape variables. New in our study are the findings that these responses differ between species density and richness, reflecting contrasting spatial scales (patch versus within-patch fixed area), and that they are modulated by trophic relationships between the studied groups.

Species richness (patch scale)

In general, species richness at patch scale was predicted by current patch area, directly in plants but indirectly in butterflies through its relationship with plant species richness. Interestingly, effects of patch and landscape histories on plant species richness were limited to plant specialists, suggesting an extinction debt in these species as already indicated by Guardiola *et al.* (2013) and in accordance with previous studies (Helm et al 2006; Kuussaari et al 2009). In our case, patches with more grassland area in their surrounding past landscape have presently more specialist plant species, suggesting a rescue effect from nearby habitat patches (Fischer and Stöcklin 1997; Piessens et al 2004). In contrast, no effect of past landscape was found on butterfly specialists, as also found Krauss *et al.* (2010) across Europe. These authors suggested that contrasting effects of past landscape on plants and butterflies are due to the differences in their life-cycle length: butterflies, as short-lived organisms, seem to respond more rapidly to environmental changes than plants.

Species density (fixed area, within-patch scale)

In our study, species density of plants and butterflies were determined by other variables than those driving species richness at the patch scale. Samples of equal fixed area within habitat patches could in principle have the same number of species (i.e. the same species density), independently of patch size, if species were distributed at random in the habitat. However, there can also be an influence of patch area and patch isolation on species density because when a species becomes extinct in a given sampling unit the chance of recolonising that unit likely decreases with decreasing patch area and increasing isolation (MacArthur and Wilson 1963; Fischer and Stöcklin 1997; Köchy and Rydin 1997). Contrarily to patch species richness, our study did not detect any significant effect of patch area on species density of both plants and

butterflies, in accordance with previous studies (Köchy and Rydin 1997; Krauss et al 2004; Helm et al 2006). However, our results highlight the importance of direct negative effects of patch isolation on species density for total and specialist plant species but not for non-specialist butterflies (Figs. 2, 3). Habitat specialist and dispersal-limited species are expected to be especially sensitive to isolation (Kuussaari et al 2009). Specialist butterflies are less mobile than non-specialists (Stefanescu et al 2011), and thus more sensitive to isolation (Öckinger et al 2010; Öckinger et al 2012b). Our results also suggest that specialists would particularly rely on dispersal from neighbouring patches (a rescue effect) to prevent their rarefaction (Piessens et al 2004). Interestingly, more isolated patches had lower species densities but not lower species richness. Therefore, patch isolation would have caused a decrease in many plant and butterfly species density through small-scale extinctions within patches, causing their rarefaction but not yet their extinction at the patch scale, thus some plant and butterfly species occurred as remnant populations (Eriksson, 1996).

Our study emphasizes the contrasting association of patch dynamics with species density and richness of plant and butterflies, suggesting a distinct effect on the extinction pattern of these species groups at the patch- and within-patch scales. Area loss effects on plants and butterflies were only detectable for species density but not for species richness. However, area loss showed opposed relationships with plant and butterfly species densities, being negative in the first case but positive in the last. In highly fragmented landscapes, most patches are small and thus contain small populations; a positive feed-back toward local extinction can then occur when, as in many organisms, a further decrease of fragment area causes a decrease in population density (Ewers and Didham 2006). In our study, the negative direct effects of area loss on total and specialist plant species density suggest that, as for isolation, area loss would have caused a rarefaction of some plant species but not yet their extinction at the patch scale. However, this is not the case for many invertebrate populations for which the literature results are less consistent (Ewers and Didham 2006). The positive effect of area loss on population density of mobile organisms has been called “crowding effect”: when habitat is removed, surviving individuals will move into the remaining habitat fragments thus increasing their population density (Debinski and Holt 2000; Grez et al 2004). Grassland remnants represent the last food sources for many invertebrates in woody-encroached landscapes and they tend to accumulate individuals from the surroundings (Steffan-Dewenter and Tschardt 2000), though this effect might be transient. For example, Hambäck *et al.* (2007) found that current patch area was negatively related to butterfly density. Although this behaviour has been reported at the population level, a similar response at the whole community level might be expected, being an expression of extinction debt or delayed community response to habitat loss (Metcalf et al

2007). As community response is supposed to be slower than that of particular species, this might explain why in our study past patch area had direct negative effects on specialist butterfly species density. Moreover, as area loss of our habitat patches started more than 70 years ago and it is still ongoing, the effect we detected of area loss on species density is probably not a short-duration transient response.

Woody-encroachment, due to reduced extensive livestock grazing, is also responsible for a diffuse habitat loss within our study patches, but we failed to detect any effect of woody cover within grassland patches either on plant or butterfly species density or richness. Mean percentage of woody cover in our patches was 30%, and some studies point out that there is a threshold of 70-80% shrub cover to detect a clear decrease in species richness (Rejmének and Rosén 1992; Bartolomé et al 2000). Moreover, in the case of butterflies, some specialist species tend to be more abundant where there is a relative abundance of shrubs because they provide refuge against predators and under unfavourable weather conditions (Dover et al 1997; Dennis and Sparks 2006).

Trophic dependencies

Our study shows the importance of trophic dependencies (i.e. direct effects of plant species on butterfly species) to account for butterfly species density and richness in habitat patch remnants. Although patch area and connectivity have been shown to increase butterfly species richness (Öckinger et al 2010; Sang et al 2010; Brückmann et al 2010; Öckinger et al 2012a), a number of studies suggest that plant richness and/or nectar availability is the main driver of butterfly species richness in habitat patches (Menéndez et al 2007; Pöyry et al 2009; Rosin et al 2012). We have found that plant species richness is a major determinant of butterfly (total, specialist and non-specialist) species density and richness in our study system, and that current patch area only had an indirect effect through plant species richness (Figs. 2, 3; Tables 3, 4). This suggests that patches with higher plant richness might have more potential host plants for butterfly larvae and higher quantity and diversity of nectar sources for adults, thus favouring butterfly species persistence. Krämer *et al.* (2012) also found that plant species richness might be used as a surrogate of available resources (both larval host plants and nectar sources) for butterflies in a patch, as it positively affects butterfly species richness in German grasslands.

3.5. Conclusions, implications for conservation and future research

Our results show that plant and butterfly species richness depend, directly or indirectly, on the area of habitat patches. Hence, preventing patch area loss in fragmented landscapes is the first step towards retaining the patch-habitat specialists. But our results also demonstrate that patch isolation and patch area loss cause a decrease in plant species density that reveals a rarefaction of some plant species, making them more prone to extinction and eventually causing cascading extinctions or co-extinctions in butterflies (and other obligate herbivores) likely associated to trophic effects. We also found that plant specialist species richness showed extinction debt, so as the extinction debt is paid for, a proportion of specialist butterfly species might be on a deterministic path to extinction even without any further habitat loss occurring. Moreover, we found that butterfly species density increases in patches with higher area loss, while plant species density decreases. But although we have not addressed them in this paper, responses among plant and butterfly species should differ according to their ecological traits, the plant-butterfly trophic interactions and the effects of area loss on the trophic network. To improve our knowledge on the existence and magnitude of future extinctions, future research will address these issues. Meanwhile, management initiatives to preserve biodiversity in grasslands should consider species richness and species density, because species density loss due to patch area loss and isolation constitutes an early warning indicator of the effects of habitat fragmentation on biodiversity. Then, policies should strive not only to conserve the area of grasslands patches, but to promote restoration and connectivity of habitat patches. Otherwise, the continued area loss of grassland patches will result in the local extinction of many specialist plants and butterflies.

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3.7. Supplementary material

Table S1. Current patch area, current grassland area in the surrounding patch landscape, past patch area, past grassland area in the surrounding patch landscape, current tree and scrub cover in the patch, current tree and scrub cover surrounding patch landscape, proportion of patch area lost between 1956 and 2003, mean annual precipitation (mm), mean annual air temperature (°C), and altitude (m a.s.l.) of studied patches.

Patch code	Current patch area (ha)	Past patch area (ha)	Current surrounding grassland area (ha)	Past surrounding grassland area (ha)	Patch area loss (%)	Patch isolation	Current patch woody cover	Mean annual precipitation (mm)	Mean annual temperature (°C)	Altitude (m a.s.l.)
1	0.101	4.177	0.101	4.857	97.582	97,4	40,0	744.9	11,5	950
2	0.500	15.038	1.424	15.038	96.675	86,1	29,2	760.6	11,4	970
3	0.339	1.830	0.339	4.632	81.475	89,2	41,2	751.8	11,7	920
4	3.105	14.037	3.105	17.985	77.880	86,1	26,3	764.9	11,8	980
5	19.276	19.276	35.946	95.381	0.000	96,2	31,6	786.1	11,1	1040
6	7.194	8.785	13.653	93.511	18.110	91,9	41,7	753.4	11,4	970
7	0.232	94.662	5.210	79.451	99.755	78,5	41,7	714.1	11,6	960
8	0.677	3.011	1.477	5.595	77.516	95,6	23,5	742.6	11,4	940
9	1.191	5.713	1.191	5.713	79.153	91,8	33,3	695.5	11,7	890
10	26.845	35.623	26.845	35.623	24.641	76,5	21,8	736.3	10,7	1120
11	20.744	33.159	20.744	33.159	37.441	88,4	42,8	724.6	10,9	1040
12	3.412	4.178	5.805	13.959	18.334	83,1	33,1	711.9	10,6	1040
13	0.400	2.513	2.739	10.261	84.083	87,9	31,8	698.0	10,7	1060
14	0.397	0.397	0.608	0.608	0.000	84,4	28,6	730.4	10,2	1080
15	4.003	4.003	4.142	4.142	0.000	91,5	29,1	726.6	10,1	1100
16	10.877	10.877	12.184	14.131	0.000	87,8	24,7	685.7	10,4	960
17	0.629	0.629	8.380	8.380	0.000	88,4	19,4	669.6	10,6	890
18	15.441	16.875	15.441	16.875	8.498	85,5	16,3	747.8	11,5	890
19	18.165	18.165	18.165	18.165	0.000	86,7	25,8	741.1	12,1	840
20	1.336	2.074	8.078	16.352	35.583	81,8	10,5	798.8	11,7	950
21	4.626	5.927	6.431	13.144	21.950	77,3	25,3	774.9	12	930
22	0.252	0.968	0.252	0.968	73.967	94,5	41,7	933.7	11,4	1080
23	0.743	2.463	1.203	5.726	69.834	88,2	18,9	883.5	12,3	940
24	1.382	2.627	1.660	3.275	47.392	99,0	18,8	1003.9	11	1160
25	0.278	1.697	1.623	4.260	83.618	94,9	35,7	1049.6	10,3	1080
26	0.339	0.339	0.764	1.494	0.000	95,4	29,4	913.5	12,9	930
27	0.214	0.214	4.296	4.296	0.000	98,6	27,3	1015.1	11,3	1130
28	7.905	7.905	9.648	18.223	0.000	94,5	19,8	986.6	11,6	1040
29	0.592	1.538	1.075	2.493	61.508	98,1	48,3	990.7	11,6	1030

Table S2. Pearson correlations between predictor variables.

	Current surrounding grassland area	Past patch area	Past surrounding grassland area	Current patch woody cover	Patch isolation	Patch area loss
Current patch area	0,9247***	0,7169***	0,5008**	-0,1242 ^{ns}	-0,2311 ^{ns}	-0,3288 ^{ns}
Current surrounding grassland area		0,6406***	0,6280***	-0,0188 ^{ns}	-0,1690 ^{ns}	-0,3915*
Past patch area			0,4369*	0,0246 ^{ns}	-0,4517*	-0,0504 ^{ns}
Past surrounding grassland area				-0,1262 ^{ns}	-0,3604 ^{ns}	-0,3710*
Current patch woody cover					0,2504 ^{ns}	0,4008*
Patch isolation						0,1117 ^{ns}

(*** p < 0.001; ** p < 0.01; * p < 0.05; ns p > 0.05)

Table S3. Total, specialist and non-specialist plant species richness at a (1) Quadrat (species density): Individual 0.25 m² quadrats (mean ± standard error of the mean); (2) All quadrats: pooling the 25 quadrats in each patch; (3) Time transect: additional species detected in the time transect; and (4) Patch (species richness): Sum of the pooled quadrats and the additional species from the time transect.

Patch code	Total species				Specialist species				Non-specialist species			
	Quadrat	All quadrats	Time transect	Patch	Quadrat	All quadrats	Time transect	Patch	Quadrat	All quadrats	Time transect	Patch
1	11.9±0.72	50	4	54	10.2±0.73	38	2	40	1.7±0.28	12	2	14
2	12.4±0.44	61	7	68	10.7±0.41	43	2	45	2.2±0.26	18	5	23
3	11.8±0.43	42	12	54	7.4±0.64	34	5	39	1.1±0.15	8	7	15
4	8.1±0.72	49	27	76	7.1±0.67	40	12	52	0.8±0.19	9	15	24
5	13.8±0.60	67	38	105	10.3±0.41	44	14	58	3.4±0.45	23	24	47
6	13.0±0.70	66	38	104	10.2±0.58	43	15	58	2.8±0.38	23	23	46
7	12.9±0.63	60	12	72	11.0±0.63	44	5	49	1.8±0.19	16	7	23
8	13.4±0.70	66	10	76	10.4±0.66	45	7	52	0.9±0.29	21	3	24
9	9.7±0.74	51	22	73	6.4±0.58	27	10	37	3.3±0.36	24	12	36
10	15.3±0.54	65	49	114	12.4±0.60	43	18	61	3.0±0.32	22	31	53
11	13.2±0.67	67	42	109	11.4±0.68	53	13	66	1.7±0.15	14	29	43
12	15.4±0.74	58	31	89	12.8±0.70	42	14	56	2.6±0.16	16	17	33
13	14.6±0.56	58	5	63	13.0±0.48	41	2	43	1.6±0.22	17	3	20
14	17.2±0.67	74	5	79	13.7±0.58	44	1	45	3.5±0.44	30	4	34
15	13.7±0.60	56	17	73	11.3±0.53	39	8	47	2.4±0.35	17	9	26
16	17.6±0.50	62	29	91	16.0±0.49	47	8	55	1.6±0.22	15	21	36
17	14.7±0.60	60	14	74	13.4±0.58	46	2	48	1.2±0.22	14	12	26
18	17.6±0.64	75	31	106	12.6±0.51	48	8	56	5.0±0.56	27	23	50
19	14.7±0.63	66	58	124	11.4±0.51	47	20	67	3.3±0.32	19	38	57
20	18.4±0.89	66	16	82	14.5±0.71	44	2	46	3.9±0.39	22	14	36
21	15.1±0.70	74	29	103	10.6±0.69	39	12	51	4.6±0.71	35	17	52
22	11.5±0.76	56	10	66	8.2±0.47	30	2	32	3.4±0.56	26	8	34
23	10.4±0.58	47	15	62	8.9±0.59	32	6	38	1.6±0.21	15	9	24
24	10.4±0.40	38	15	53	9.8±0.39	31	5	36	0.7±0.15	7	10	17
25	9.9±0.52	44	3	47	9.0±0.51	36	1	37	0.9±0.18	8	2	10
26	10.8±0.41	36	8	44	9.5±0.44	32	2	34	1.2±0.17	4	6	10
27	10.4±0.55	35	1	36	9.2±0.48	28	-1	27	1.1±0.21	7	2	9
28	12.1±0.63	48	20	68	11.2±0.57	39	8	47	1.0±0.19	9	12	21
29	10.8±0.47	34	7	41	9.5±0.42	28	3	31	1.3±0.17	6	4	10

Table S4. Butterfly total and specialist species density (fixed transect of 350 m), total and specialist species richness (time transect proportional to the logarithm of patch area (time), and species richness per patch (patch).

Patch code	Total species			Specialist species			Non-specialist species		
	Density	Time	Patch	Density	Time	Patch	Density	Time	Patch
1	17	0	17	3	0	3	14	0	14
2	29	14	32	8	4	9	21	10	23
3	18	5	19	5	1	6	13	4	13
4	10	14	16	2	5	5	8	9	11
5	14	31	34	5	10	10	9	21	24
6	13	23	25	3	5	6	10	18	19
7	13	0	13	4	0	4	9	0	9
8	15	10	17	3	3	4	12	7	13
9	21	26	32	8	13	14	13	13	18
10	22	37	37	6	9	9	16	28	28
11	24	33	37	8	10	11	16	23	26
12	16	37	37	5	13	13	11	24	24
13	15	9	16	4	3	4	11	6	12
14	18	12	21	6	4	7	12	8	14
15	10	19	20	2	5	5	8	14	15
16	13	22	23	4	8	8	9	14	15
17	13	6	13	5	2	5	8	4	8
18	12	28	28	4	9	9	8	19	19
19	10	22	22	4	7	7	6	15	15
20	21	29	31	9	10	11	12	19	20
21	20	34	35	7	14	14	13	20	21
22	18	0	18	8	0	8	10	0	10
23	10	14	16	3	4	4	7	10	12
24	6	7	7	1	1	1	5	6	6
25	12	0	12	5	0	5	7	0	7
26	6	7	8	1	2	2	5	5	6
27	6	2	7	1	0	1	5	2	6
28	10	24	26	2	6	6	8	18	20
29	6	8	10	1	2	2	5	6	8

Table S5. Plant species recorded in this study. Grassland specialists, marked in bold, were selected with the help of regional floras (Bolòs *et al.* 1993; Rivas–Martínez *et al.* 2001) and expert advice.

<i>Acer opalus</i> Mill.	<i>Carduncellus monspelliensis</i> All.
<i>Achillea ageratum</i> L.	<i>Carduus nigrescens</i> Vill. subsp. <i>Nigrescens</i>
<i>Aegilops geniculata</i> Roth	<i>Carex flacca</i> Schreber
<i>Aetheorhiza bulbosa</i> (L.) Cass.	<i>Carex halleriana</i> Asso
<i>Aethionema saxatile</i> (L.) R. Br.	<i>Carex humilis</i> Leysser
<i>Allium roseum</i> L.	<i>Carthamus lanatus</i> L.
<i>Allium senescens</i> L. subsp. <i>montanum</i> (Fries) Holub	<i>Catananche coerulea</i> L.
<i>Allium sphaerocephalon</i> L. subsp. <i>sphaerocephalon</i>	<i>Catapodium rigidum</i> (L.) C.E. Hubbard
<i>Althaea hirsuta</i> L.	<i>Centaurea linifolia</i> L. subsp. <i>caballeroi</i> (F. Q. et Pau in F. Q.) O. Bolòs et J. Vigo
<i>Alyssum spinosum</i> L.	<i>Centaurea linifolia</i> L. subsp. <i>linifolia</i>
<i>Amelanchier ovalis</i> Medic.	<i>Centaurea montana</i> L. subsp. <i>lingulata</i> (Lag.) O. Bolòs et J. Vigo
<i>Anagallis arvensis</i> L.	<i>Centaureum quadrifolium</i> (L.) G. López et Ch. E. Jarvis subsp. <i>barrelieri</i> (Duf.) G. López
<i>Anemone hepatica</i> L.	<i>Cephalanthera longifolia</i> (L.) Fritsch
<i>Anthemis arvensis</i> L.	<i>Cerastium gracile</i> Duf.
<i>Anthericum liliago</i> L.	<i>Cerastium pumilum</i> Curtis
<i>Anthyllis montana</i> L.	<i>Chaenorhinum rubrifolium</i> (Robill. et Cast. ex DC.) Fourr. subsp. <i>rubrifolium</i>
<i>Anthyllis vulneraria</i> L. subsp. <i>fontqueri</i> (Rothm.) A. et O. Bolòs	<i>Cistus albidus</i> L.
<i>Aphyllanthes monspeliensis</i> L.	<i>Cistus clusii</i> Dunal
Apiaceae 21	<i>Clematis vitalba</i> L.
<i>Arabis auriculata</i> Lam.	<i>Colutea arborescens</i> L.
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	Compositae 12
<i>Arenaria conimbricensis</i> Brot. subsp. <i>conimbricensis</i>	Compositae 16
<i>Arenaria serpyllifolia</i> L. subsp. <i>serpyllifolia</i>	Compositae 18
<i>Arenaria tetraqueta</i> L. subsp. <i>condensata</i> Arcang.	Compositae 19_1
<i>Argyrolobium zanonii</i> (Turra) P. W. Ball	Compositae 19_2
<i>Aristolochia pistolochia</i> L.	Compositae 24
<i>Arrhenatherum album</i> (Vahl) W. D. Clayton	Compositae 28
<i>Arrhenatherum elatius</i> (L.) Beauv. ex J. et C. Presl subsp. <i>sardoum</i> (E. Schmid) Gamisans	Compositae 4
<i>Asperula cynanchica</i> L.	Compositae 8
<i>Asphodelus cerasiferus</i> Gay	<i>Conopodium majus</i> (Gouan) Loret in Loret et Barr. subsp. <i>ramosum</i> (Costa) Silvestre
<i>Asterolinon linum-stellatum</i> (L.) Duby in DC.	<i>Convolvulus arvensis</i> L.
<i>Astragalus monspessulanus</i> L. subsp. <i>monspessulanus</i>	<i>Convolvulus lanuginosus</i> Desr.
<i>Avenula pratensis</i> L. subsp. <i>iberica</i> St.-Yves.	<i>Convolvulus lineatus</i> L.
<i>Biscutella laevigata</i> L.	<i>Coris monspeliensis</i> L.
<i>Blackstonia perfoliata</i> (L.) Huds.	<i>Coronilla minima</i> L.
<i>Brachypodium phoenicoides</i> (L.) Roem. et Schultes	<i>Crataegus monogyna</i> Jacq.
<i>Brachypodium retusum</i> (Pers.) Beauv.	<i>Crepis albida</i> Vill.
<i>Brimeura amethystina</i> (L.) Chouard subsp. <i>fontqueri</i> (Pau) O. Bolòs & Vigo	<i>Crepis vesicaria</i> L. subsp. <i>taraxacifolia</i> (Thuill) Thell. ex Schinz et Keller
<i>Briza media</i> L.	<i>Crucianella angustifolia</i> L.
<i>Bromus erectus</i> Huds.	<i>Cruciata glabra</i> (L.) Ehrend.
<i>Bromus squarrosus</i> L.	<i>Crupina vulgaris</i> Cass.
<i>Bupleurum baldense</i> Turra subsp. <i>baldense</i>	<i>Cuscuta epithymum</i> (L.) L.
<i>Bupleurum fruticosens</i> L.	<i>Cytisophyllum sessilifolium</i> (L.) O. F. Lang
<i>Bupleurum fruticosum</i> L.	<i>Dactylis glomerata</i> L. subsp. <i>hispanica</i> (Roth) Nyman
<i>Bupleurum rigidum</i> L.	<i>Daucus carota</i> L.
<i>Buxus sempervirens</i> L.	<i>Dianthus pungens</i> L. subsp. <i>tarraconensis</i> (Costa) O. Bolòs
<i>Calicotome spinosa</i> (L.) Link	

et J. Vigo

***Dictamnus hispanicus* Webb ex Willk.**

Dipcadi serotinum (L.) Medic.

Dorycnium hirsutum (L.) Ser. in DC.

Dorycnium pentaphyllum* Scop. subsp. *pentaphyllum

Echinaria capitata (L.) Desf.

***Echinops ritro* L.**

Echium vulgare L. subsp. *argentae* (Pau) F. Q.

Epipactis atrorubens (Hoffm.) Bess.

Epipactis helleborine (L.) Crantz

***Erica multiflora* L.**

***Erinacea anthyllis* Link**

Erucastrum nasturtiifolium (Poiret) O. E. Schulz

Eryngium campestre L.

Erysimum grandiflorum Desf.

Euphorbia characias L.

***Euphorbia flavicoma* DC. subsp. *mariolensis* (Rouy) O. Bolòs et J. Vigo**

Euphorbia nicaeensis* All. subsp. *nicaeensis

Euphorbia serrata L.

***Festuca nigrescens* Lam.**

***Festuca ovina* L. s.l.**

***Festuca paniculata* (L.) Schinz et Thell. subsp. *spadicea* (L.) Litard.**

***Fritillaria pyrenaica* L.**

***Fumana ericoides* (Cav.) Gandg.**

***Fumana procumbens* (Dunal) Gren. et Godr.**

***Fumana thymifolia* (L.) Spach**

Galium lucidum All.

Galium parisiense L.

Galium pumilum Murray

Galium pumilum Murray subsp. *papillosum* (Lap.) Batalla et Masclans ex O. Bolòs

***Galium pumilum* Murray subsp. *pinetorum* (Ehrend.) J. Vigo**

***Genista hispanica* L.**

Genista patens DC.

Genista scorpius (L.) DC. in Lam. et DC.

Geranium columbinum L.

Geranium robertianum L. subsp. *purpureum* (Vill.) Nyman

Geum sylvaticum Pourr.

***Gladiolus illyricus* Koch**

Globularia cordifolia L. subsp. *nana* Lam.

***Globularia vulgaris* L.**

***Gymnadenia conopsea* (L.) R. Br.**

Hedera helix L.

***Helianthemum apenninum* (L.) Mill.**

Helianthemum marifolium* (L.) Mill. subsp. *marifolium

***Helianthemum numularium* (L.) Mill.**

***Helianthemum oelandicum* (L.) DC. in Lam. et DC. subsp. *italicum* (L.) F.Q. et Rothm.**

***Helianthemum organifolium* (Lam.) Pers. subsp. *molle* (Cav.) F.Q. et Rothm.**

Helichrysum stoechas (L.) Moench

Helleborus foetidus L.

***Hieracium pilosella* L.**

***Hippocrepis comosa* L.**

Hornungia petraea (L.) Reichenb.

Hypericum perforatum L.

***Hypochoeris radicata* L.**

Iberis ciliata All. subsp. *ciliata*

Ilex aquifolium L.

Inula helenioides DC. in Lam. et DC.

***Inula montana* L.**

***Iris chamaeiris* Bertol.**

Jasonia tuberosa (L.) DC.

Juniperus communis L.

Juniperus oxycedrus L.

Juniperus phoenicea L.

***Knautia arvensis* (L.) Coult. subsp. *subscaposa* (Boiss. et Reut.) Maire**

***Koeleria vallesiana* (Honckeny) Gaud.**

Lactuca perennis L.

Lactuca tenerrima Pourr.

Laserpitium gallicum L.

***Lathyrus filiformis* (Lam.) Gay**

***Lathyrus saxatilis* (Vent.) Vis.**

Lathyrus setifolius L.

***Lavandula angustifolia* Mill.**

***Lavandula latifolia* Medic.**

Legousia hybrida (L.) Delarbre

Legousia scabra (Lowe) Gamisans

Leontodon taraxacoides (Vill.) Mérat subsp. *hispidus* (Roth) Kerguélen

***Leuzea conifera* (L.) DC. in Lam. et DC.**

Linaria arvensis (L.) Desf. subsp. *simplex* (Willd.) Lange in Willk. et Lange

Linaria supina (L.) Chaz. subsp. *aeruginea* (Gouan) O. Bolòs et J. Vigo

***Linum narbonense* L.**

Linum strictum L. subsp. *strictum*

***Linum tenuifolium* L. subsp. *suffruticosum* (L.) Litard.**

***Lithospermum fruticosum* L.**

Lonicera implexa Ait.

Lonicera pyrenaica L.

***Lotus corniculatus* L.**

Marrubium supinum L.

Medicago minima (L.) L.

Melica ciliata L.

Melica minuta L.

Mercurialis tomentosa L.

Micropus erectus L.

Minuartia hybrida (Vill.) Schischkin in Komarov

Muscari neglectum Guss. ex Ten.

***Narcissus assoanus* Duf.**

Onobrychis supina* (Vill.) DC. in Lam. et DC. subsp. *supina

***Ononis minutissima* L.**

***Ononis pusilla* L.**

Ononis spinosa L.

Ononis viscosa L.

Ophrys apifera Huds.
***Ophrys fusca* Link**
 Orchidaceae
Orchis maculata L.
***Orchis mascula* (L.) L.**
Orchis ustulata L.
***Orobanche caryophyllacea* Sm.**
Orobanche sp.
Paeonia officinalis L.
Petrorhagia prolifera (L.) P. W. Ball et Heyw.
***Peucedanum officinale* L. subsp. *stenocarpum* (Boiss. et Reut.) F. Q.**
***Phleum phleoides* (L.) Karsten**
***Phlomis lychnitis* L.**
***Phyteuma orbiculare* L. subsp. *ibericum* (R. Schulz) P. Fourn.**
Pinus halepensis Mill.
Pinus nigra Arnold
Pinus sylvestris L.
Pistacia lentiscus L.
Plantago lanceolata L.
Plantago sempervirens Crantz
Platanthera bifolia (L.) L. C. M. Richard
Poa bulbosa L.
***Polygala calcarea* F.W. Schultz**
***Polygala monspeliaca* L.**
Polygala rupestris* Pourr. subsp. *rupestris
Polygala vulgaris L.
***Potentilla neumanniana* Reichenb.**
Potentilla reptans L.
Primula veris L. subsp. *columnae* (Ten.) Maire et Petitmengin
***Prunella laciniata* (L.) L.**
Prunus spinosa L.
Psoralea bituminosa L.
Quercus cerrroides Willk. et Costa
Quercus coccifera L.
Quercus faginea Lam.
Quercus humilis Mill.
Quercus ilex L.
***Ranunculus bulbosus* L.**
***Ranunculus gramineus* L.**
Reseda luteola L. subsp. *luteola*
Rhamnus alaternus L. var. *balearicus* DC.
Rhamnus saxatilis Jacq.
Rosa pimpinellifolia L. subsp. *myriacantha* (DC.) O. Bolòs et J. Vigo
Rosa sicula Tratt.
Rosa sp.
***Rosmarinus officinalis* L.**
Rubia peregrina L.
Rubus ulmifolius Schott
Rumex intermedius DC. in Lam. et DC.
Ruscus aculeatus L.
***Salvia officinalis* L. subsp. *lavandulifolia* (Vahl) Gams**

***Sanguisorba minor* Scop.**
***Santolina chamaecyparissus* L.**
Saponaria ocymoides L.
***Satureja montana* L.**
Schoenus nigricans L.
Scirpus holoschoenus L.
***Scorzonera angustifolia* L.**
***Scorzonera hirsuta* L.**
***Scorzonera hispanica* L. subsp. *crispatula* (Boiss.) Nyman**
Sedum acre L.
Sedum sediforme (Jacq.) Pau
Senecio vulgaris L.
***Serratula nudicaulis* (L.) DC. in Lam. et DC.**
Seseli montanum* L. subsp. *montanum
Sherardia arvensis L.
Sideritis hirsuta L. subsp. *hirsuta*
***Sideritis spinulosa* Barnades ex Asso subsp. *ilicifolia* (Willd.) O. Bolòs et J. Vigo**
Silene conica L. subsp. *conica*
Silene gallica L.
***Silene italica* (L.) Pers. subsp. *nevadensis* (Boiss.) F. Q.**
Silene nutans L. subsp. *brachypoda* (Rouy) Asch. et Graebn.
Silene vulgaris (Moench) Garcke subsp. *prostrata* (Gaud.) Schinz et Thell.
Silene vulgaris (Moench) Garcke subsp. *vulgaris*
Sonchus tenerrimus L.
Sorbus aria (L.) Crantz
Sorbus domestica L.
***Stachys heraclea* All.**
***Staelina dubia* L.**
***Stipa offneri* Breistr.**
***Stipa pennata* L. subsp. *iberica* (Martinovsky) O. Bolòs, R. M. Masalles et J. Vigo**
Tanacetum corymbosum (L.) Schultz Bip. subsp. *corymbosum*
Taraxacum obovatum (Willd.) DC.
Taraxacum officinale Weber in Wiggers
Teucrium botrys L.
Teucrium chamaedrys L.
***Teucrium polium* L.**
***Thalictrum tuberosum* L.**
***Thesium humifusum* DC.**
Thlaspi perfoliatum L. subsp. *perfoliatum*
***Thymelaea tinctoria* (Pourr.) Endl.**
***Thymus serpyllum* L. subsp. *fontqueri* (Jalas) O. Bolòs et J. Vigo**
***Thymus vulgaris* L.**
***Tragopogon porrifolius* L. subsp. *australis* (Jord.) Nyman**
Trifolium campestre Schreb. in Sturm
Trifolium stellatum L.
Trigonella monspeliaca L.
***Trinia glauca* (L.) Dumort.**
***Tulipa sylvestris* L. subsp. *australis* (Link) Pamp.**
***Valeriana tuberosa* L.**
***Veronica austriaca* L. subsp. *tenuifolia* (Asso) O. Bolòs et J. Vigo**

Vicia peregrina L.

Vicia sativa L. subsp. *nigra* (L.) Ehrh.

Viola rupestris F.W. Schmidt

Xeranthemum inapertum (L.) Mill.

Table S6. Butterfly species recorded in this study. Butterfly specialists, marked in bold, were selected based on habitat preference data from the Catalan Butterfly Monitoring Scheme (www.catalanbms.org).

<i>Anthocharis cardamines</i> (Linnaeus, 1758)	<i>Leptotes pirithous</i> (Linnaeus, 1767)
<i>Anthocharis euphenoides</i> Staudinger, 1869	<i>Libythea celtis</i> (Laicharting, 1782)
<i>Aporia crataegi</i> (Linnaeus, 1758)	<i>Limenitis reducta</i> (Staudinger, 1901)
<i>Arethusana arethusa</i> (Denis y Schiffermüller, 1775)	<i>Lycaena alciphron</i> (Rottemburg, 1775)
<i>Argynnis aglaja</i> (Linnaeus, 1758)	<i>Lycaena phlaeas</i> (Linnaeus, 1761)
<i>Argynnis niobe</i> (Linnaeus, 1758)	<i>Maniola jurtina</i> (Linnaeus, 1758)
<i>Argynnis pandora</i> (Denis y Schiffermüller, 1775)	<i>Melanargia lachesis</i> (Hübner, 1790)
<i>Argynnis paphia</i> (Linnaeus, 1758)	<i>Melanargia occitanica</i> (Esper, 1789)
<i>Argynnis sp.</i> Fabricius, 1807	<i>Melitaea cinxia</i> (Linnaeus, 1758)
<i>Aricia cramera</i> (Eschscholtz, 1821)	<i>Melitaea didyma</i> (Esper, 1778)
<i>Boloria dia</i> (Linnaeus, 1767)	<i>Melitaea phoebe</i> (Denis y Schiffermüller, 1775)
<i>Brintesia circe</i> (Fabricius, 1775)	<i>Muschampia proto</i> (Ochsenheimer, 1808)
<i>Carcharodus alceae</i> (Esper, 1780)	<i>Favonius quercus</i> (Linnaeus, 1758)
<i>Carcharodus baeticus</i> (Rambur, 1839)	<i>Ochlodes venatus</i> (Bremer y Grey, 1852)
<i>Carcharodus lavatherae</i> (Esper, 1780)	<i>Papilio machaon</i> Linnaeus, 1758
<i>Celastrina argiolus</i> (Linnaeus, 1758)	<i>Pararge aegeria</i> (Linnaeus, 1758)
<i>Coenonympha arcania</i> (Linnaeus, 1761)	<i>Pieris brassicae</i> (Linnaeus, 1758)
<i>Coenonympha dorus</i> (Esper, 1782)	<i>Pieris rapae</i> (Linnaeus, 1758)
<i>Coenonympha pamphilus</i> (Linnaeus, 1758)	<i>Plebejus argus</i> (Linnaeus, 1758)
<i>Colias alfacariensis</i> Ribbe, 1905	<i>Polyommatus coridon</i> (Poda, 1761)
<i>Colias crocea</i> (Geoffroy, 1785)	<i>Polyommatus daphnis</i> (Denis y Schiffermüller, 1775)
<i>Cupido minimus</i> (Fuessly, 1775)	<i>Polyommatus escheri</i> (Hübner, 1823)
<i>Cupido osiris</i> (Meigen, 1829)	<i>Polyommatus icarus</i> (Rottemburg, 1775)
<i>Erebia triaria</i> (Prunner, 1798)	<i>Polyommatus nivescens</i> (Keferstejn, 1851)
<i>Erynnis tages</i> (Linnaeus, 1758)	<i>Polyommatus ripartii</i> (Freyer, 1830)
<i>Euphydryas aurinia</i> (Rottemburg, 1775)	<i>Pontia daplidice</i> (Linnaeus, 1758)
<i>Gonepteryx cleopatra</i> (Linnaeus, 1767)	<i>Scolitantides panoptes</i> (Hübner, 1813)
<i>Gonepteryx rhamni</i> (Linnaeus, 1758)	<i>Pyrgus alveus</i> (Hübner, 1803)
<i>Gonepteryx sp.</i> Leach, 1815	<i>Pyrgus malvoides</i> (Elwes y Edwards, 1897)
<i>Hesperia comma</i> (Linnaeus, 1758)	<i>Pyronia bathseba</i> (Fabricius, 1793)
<i>Hipparchia alcyone</i> (Denis y Schiffermüller, 1775)	<i>Pyronia Cecilia</i> (Vallantin, 1894)
<i>Hipparchia fidia</i> (Linnaeus, 1767)	<i>Pyronia tithonus</i> (Linnaeus, 1771)
<i>Hipparchia semele</i> (Linnaeus, 1758)	<i>Satyrium acacia</i> (Fabricius, 1787)
<i>Hipparchia statilinus</i> (Hufnagel, 1766)	<i>Satyrium esculi</i> (Hübner, 1804)
<i>Hyponephele lycaon</i> (Kühn, 1774)	<i>Satyrium ilicis</i> (Esper, 1778)
<i>Iphiclides podalirius</i> (Linnaeus, 1758)	<i>Satyrium spini</i> (Denis y Schiffermüller, 1775)
<i>Issoria lathonia</i> (Linnaeus, 1758)	<i>Satyrus actaea</i> (Esper, 1781)
<i>Lampides boeticus</i> (Linnaeus, 1767)	<i>Spialia sertorius</i> (Hoffmannsegg, 1804)
<i>Lasiommata maera</i> (Linnaeus, 1758)	<i>Thymelicus acteon</i> (Rottemburg, 1775)
<i>Lasiommata megera</i> (Linnaeus, 1767)	<i>Thymelicus sylvestris</i> (Poda, 1761)
<i>Leptidea sinapis</i> (Linnaeus, 1758)	<i>Vanessa atalanta</i> (Linnaeus, 1758)

Vanessa cardui (Linnaeus, 1758)

***Zygaena lavandulae* (Esper, 1783)**

***Zygaena sarpedon* (Hubner, 1790)**

Table S7 Models selected (with a delta AICc ≤ 2) predicting total and specialist plant species richness and total and specialist plant species density. Models' coefficients are shown for each variable included in the model. For each model, we show number of parameters (k), adjusted R² (R²adj.), second order information criterion value (AICc), delta AICc (Δ_i) and Akaike weight (w_i). Models are ordered by increasing values of the information criterion.

Current patch area	Current surrounding grassland area	Past patch area	Past surrounding grassland area	Current patch woody cover	Patch isolation	Patch area loss	Geographical variation	k	R ² adj.	AICc	Δ_i	w_i
<i>Total plant species richness</i>												
20.0					-0.64		-8.3E-09	5	0.88	213.3	0.00	0.50
20.8				0.24	-0.71		-8.2E-09	6	0.88	214.3	1.02	0.30
20.5							-1.0E-08	4	0.86	215.2	1.93	0.20
<i>Specialist plant species richness</i>												
6.41			5.57				-4.4E-09	5	0.86	170.1	0.00	1.00
<i>Generalist plant species richness</i>												
11.43					-0.46		-4.196E-09	5	0.77	205.5	0.00	0.34
11.76							-5.712E-09	4	0.74	205.9	0.39	0.287
11.08							-8.144E-09	5	0.76	206.6	1.05	0.20
10.86					-0.42		-6.457E-09	6	0.78	206.8	1.26	0.18
<i>Total plant species density</i>												
					-0.14	-0.03	-9.5E-10	5	0.56	122.6	0.00	1.00
<i>Specialist plant species density</i>												
					-0.14	-0.02		4	0.35	119.7	0.00	0.35
						-0.02	-8.7E-10	4	0.34	120.2	0.50	0.27
					-0.09	-0.02	-2.8E-10	5	0.37	120.4	0.77	0.24
					-0.12	-0.03		5	0.35	121.5	1.85	0.14
<i>Generalist plant species density</i>												
							-9.933E-10	4	0.39	87.1	0.00	0.64

Table S8. Models selected ($\Delta AICc \leq 2$) predicting total and specialist butterfly species richness and total and specialist butterfly species density. Models' coefficients are shown for each statistically significant ($P < 0.05$) variable included in the model. For each model, we show number of parameters (k), adjusted R^2 (R^2_{adj}), second order information criterion value (AICc), delta AICC (Δ_i) and Akaike weight (w_i). Models are ordered by increasing values of the AICc.

Current patch area	Current surrounding grassland area	Past patch area	Past surrounding grassland area	Current patch woody cover	Patch isolation	Patch area loss	Geographical variation	Total plant species richness	Total plant species density	k	R^2_{adj}	AICc	Δ_i	w_i
<i>Total butterfly species richness</i>														
								0,31		3	0,56	195,6	0,00	0,28
							4,32E-09	0,38		5	0,62	197,1	1,48	0,13
					-0,25			0,27		4	0,58	197,1	1,48	0,13
						0,03	6,51E-09	0,36	1,04	6	0,66	197,3	1,63	0,12
								0,33		4	0,57	197,4	1,77	0,11
							1,57E-09	0,36		4	0,57	197,5	1,84	0,11
					-0,35		5,19E-09	0,35		6	0,65	197,6	1,93	0,11
<i>Specialist butterfly species richness</i>														
								0,10		3	0,43	147,5	0,00	0,31
								0,08		4	0,48	147,7	0,15	0,29
	-1,26							0,13		4	0,45	149,0	1,52	0,15
						0,01		0,11		4	0,45	149,3	1,76	0,13
	-1,16				-0,15			0,10		5	0,50	149,5	2,00	0,12
<i>Generalist butterfly species richness</i>														
							6,118E-09	0,26	0,87	6	0,74	166,3	0	1
<i>Total butterfly species density</i>														
								0,10		5	0,48	176,6	0,00	0,22
		-4,84					4,46E-09	0,12		8	0,63	177,5	0,88	0,14
		-2,62						0,12		6	0,51	178,2	1,54	0,10
								0,08		4	0,39	178,2	1,57	0,10
		-3,53						0,11		5	0,45	178,3	1,69	0,09
								0,07	1,05	5	0,45	178,4	1,74	0,09
	-2,30							0,09	0,80	6	0,50	178,5	1,84	0,09
-3,72								0,06		5	0,44	178,6	1,91	0,08
					-0,26			0,07		5	0,44	178,6	1,92	0,08
<i>Specialist butterfly species density</i>														
		-2,28						0,11		5	0,45	127,1	0,00	0,31
		-2,24				-0,11		0,09		6	0,51	127,2	0,12	0,29
		-1,94						0,09	0,27	6	0,50	127,7	0,62	0,22
-2,62								0,11		4	0,37	128,1	1,05	0,18
<i>Generalist butterfly species density</i>														
		-2,63					0,07	3,74E-09	0,14	8	0,68	149,73	0,00	0,23
			-2,47				0,05	3,78E-09	0,12	8	0,67	149,83	0,09	0,22
							0,05	2,89E-09	0,07	7	0,62	150,53	0,80	0,15
					-0,27			1,96E-09		5	0,51	151,20	1,47	0,11
	-2,92				-0,15	0,06	3,99E-09	0,14	0,60	9	0,71	151,26	1,52	0,11
			-2,73		-0,15	0,04	4,02E-09	0,11	0,64	9	0,70	151,45	1,72	0,10
						0,04	1,90E-09	0,83	0,55	6	0,55	151,72	1,99	0,08

Capítol 4

Do asynchronies in extinction debt affect food network structure? A case study in plant-butterfly networks



This chapter is submitted:

Guardiola, Moisès; Stefanescu, Constantí; Rodà, Ferran & Pino, Joan (2015). Do asynchronies in extinction debt affect food network structure? A case study in plant-butterfly networks

Abstract

Habitat loss and fragmentation affect species richness in fragmented habitat patches, causing immediate but also time-delayed extinctions. Asynchronies in extinction and extinction debt among interacting species could cause strong effects on ecological networks but they remain largely unknown. We evaluated the effects of habitat loss and fragmentation on butterfly-plant trophic networks in Mediterranean grasslands. We sampled current species richness of all species and habitat specialists of vascular plants and butterflies in 26 grassland fragments of various size and degree of connectivity. We assessed the direct effects of historical and current patch and landscape characteristics on species richness and on food network metrics. Our results show that butterfly-plant networks in fragmented landscapes are subjected not only to changes in species richness and network links but also to changes in network architecture, and that both current and past patch and landscape configuration modulate ecological networks. Network links followed the interactions–area relationship but the more isolated patches had fewer total links in networks than more connected ones, indicating a rescue effect. Most network indices were also related to current patch area, in a way that the larger patches had more network stability: more compartments and lower connectance. We have also detected a past patch and landscape effect on network asymmetry indicating both different extinction rates and extinction debts of butterflies and plants, and an extinction debt of ecological networks.

Keywords: biotic interactions; diversity; ecological network; extinction debt of ecological networks; habitat loss; isolation.

4.1. Introduction

Habitat loss and fragmentation have been identified as the most important environmental cause of biodiversity loss (Dirzo & Raven, 2003), determining a general decrease of species richness in habitat patches (Fahrig, 2003; Tschardt et al., 2012) as predicted by the species-area relationship (Rosenzweig, 1995; Rybicki & Hanski, 2013), but also determining strong changes in species composition through contrasting processes (Olden, 2006; Arroyo-Rodríguez et al., 2013; Püttker et al., 2015). However, a growing number of studies show that extinctions often occur less frequently than expected due to extinction debts. These are defined as the number of extant species predicted to become extinct as the species community readjusts after an environmental disturbance (Tilman et al., 1994; Kuussaari et al., 2009), and are the outcome of diverse demographic and stochastic processes (Jackson & Sax, 2010). Extinction debt is usually assumed when species richness is better explained by past than by present landscape variables like habitat area and connectivity (Kuussaari et al., 2009).

Although extinction debts are widespread (Cousins, 2009; Hahs et al., 2009; Krauss et al., 2010), our understanding of their occurrence and ubiquity across species groups is still incomplete. Extinction debts seem to differentially affect species as a result of differences in species attributes such as habitat specialization, longevity, dispersal ability or resource specialisation (Kuussaari et al., 2009; Jackson & Sax, 2010; Krauss et al., 2010), but also differences in patch and landscape structure and legacy account for extinction and extinction debts (Piqueray et al., 2011; Guardiola et al., 2013). Thus, habitat-specialist species, i.e. species with a narrow ecological amplitude strongly associated with a focal habitat type, are more prone to exhibit local extinction processes and extinction debts than generalist species when changes in the focal habitat occur (Helm et al., 2006; Krauss et al., 2010). Moreover, according to the trophic rank hypothesis (Holt et al., 1999), habitat loss and fragmentation effects are larger at higher rank along the food chain because consumers are affected by both the direct effects of fragmentation on their populations and by the spatial constraints influencing their food sources. Furthermore, the extinction of a species of the lower trophic level could cause cascade effects on species extinctions across food webs (Haddad et al., 2009). As a result, species from higher trophic levels show lower population sizes and higher population variability than species from lower trophic levels (Morris et al., 2008; Krauss et al., 2010; Guardiola et al., submitted/Chapter 3), and the former species group are more prone to exhibit extinction debts than the latter (Didham et al., 1998; Komonen et al., 2000).

Differential extinction debts in interacting species could cause strong effects on ecological networks, as recently suggested by a number of works (Gonzalez et al., 2011; Jansen et al.,

2012; Bueno et al., 2013; Emer et al., 2013; Spiesman & Inouye, 2013). However, some authors suggest that network architecture might buffer the effects of species loss on ecological interactions (Thébault & Fontaine, 2010), with either the food web network metrics being unchanged (resistance) or recovering after a disturbance (resilience). While presumed to be especially important (Hagen et al., 2012), the effects of habitat loss and fragmentation on species interactions remain largely unknown (Gonzalez et al., 2011; Valiente-Banuet et al., 2015), with examples showing either a collapse of trophic networks above a critical value of habitat destruction in theoretical studies (Fortuna & Bascompte, 2006; Fortuna et al., 2013) or no changes in their structural properties because of their high resistance or resilience in empirical studies (Thébault & Fontaine, 2010; Nielsen & Totland, 2014).

Recently, the theory of Island Biogeography has been applied to study ecological networks (Sabatino et al., 2010; Sugiura & Taki, 2012) in a new approach: species interactions–area relationships (Sugiura, 2010). According to this, the number of species interactions increases with area and this affects the structure of species interaction networks. However, these also are determined by landscape properties. In their review, LeCraw et al. (2014) concluded that patch connectivity mostly determines positive effects on species richness and on the links per species due to rescue effects, because of the ability of some species to disperse from neighbouring patches (Brown & Kodric-Brown, 1977). However, in fragmented landscapes, differential extinction and extinction debts among interacting species could cause a mismatch between species and interaction losses. Valiente-Banuet et al. (2015) recently defined the extinction debt of ecological interactions as any future interaction loss (i.e. when its ecological outcomes are no longer functional) that has to be realized due to a current or past environmental disturbance. Using a modelling approach, they explored the potential decoupling in species and interaction losses (namely interaction balance) following habitat alteration (i.e. patch area, habitat loss or isolation), which might result in surpluses or deficits of species interactions. The former case occurs when species are lost at higher rates than interactions and thus the community is resistant to interaction losses, while the latter when interactions are lost at higher rate than species and the community is prone to cascading interaction losses. Valiente-Banuet et al. (2015) also reported three possible types of response to link richness to habitat loss: additive or gradual, keystone or disproportionately high, and redundant or replaceable.

In any case, it remains largely unknown how losses in species interactions affect other structural properties of ecological networks besides the number of interactions, namely connectance, nestedness, number of compartments or asymmetry. There is a debate of which network architecture confers more stability and resilience to species loss in ecological networks

(Thébaud & Fontaine, 2010). There are two major categories of ecological networks (Hagen et al., 2012): mutualistic (e.g. pollination, seed dispersal networks) and antagonistic (e.g. food webs, host–parasitoid networks), which differ in their structure and in their response to disturbances (Thébaud & Fontaine, 2008; Hagen et al., 2012; Morris et al., 2014). Connectance, nestedness and number of compartments are considered the most important factors that give robustness to ecological networks against species loss (Fortuna & Bascompte, 2006; Thébaud & Fontaine, 2010; Hagen et al., 2012; Valladares et al., 2012). However, stability of mutualistic networks is promoted by highly connected and nested architecture networks whereas stability of antagonistic networks is improved by more compartmented and less connected architectures (Thébaud & Fontaine, 2010). Furthermore, differential extinction rates between trophic levels can cause asymmetries in networks (Schleuning et al., 2014).

In this study we investigated the effects of patch and landscape changes on butterfly-plant food networks in Mediterranean grasslands, taking plant species and their associated butterfly herbivores as a case study. While considered a biodiversity hot-spot (Myers et al., 2000), traditional seminatural grasslands in the Mediterranean are threatened because of land use change involving the cessation of extensive grazing (Debussche et al., 1999; Feranec et al., 2010). Furthermore, the Mediterranean basin is one of the World hotspots of specialists insects, many of them being likely to become extinct in the short term due to direct and indirect (i.e. through cascading effects in trophic networks) habitat effects (Fonseca, 2009). Extinction debts of grassland plants and butterflies have been analyzed (Helm et al., 2006; Krauss et al., 2010; Sang et al., 2010; Guardiola et al. 2013; submitted/Chapter 3; Bommarco et al., 2014), with a number of studies showing extinction debts in long-lived grassland-specialist plants (Lindborg & Eriksson, 2004; Helm et al., 2006; Guardiola et al., 2013), but not in butterflies that typically have shorter life-cycles (Krauss et al., 2010). Moreover, since many of these butterfly and plant species are trophically related through pollination and herbivory, these species groups are potentially affected by cascade extinctions due to host fidelity of butterflies (Krauss et al., 2010). However, it remains unclear what happens in butterfly-plant interaction networks subjected to habitat loss.

In previous studies in these Mediterranean mountain grasslands (Bagaria et al., 2012; Guardiola et al., 2013; submitted/Chapter 3) we found that plants and butterflies showed a complex pattern of current and past patch- and landscape-effects on species richness, a high degree of plant-dependence of butterfly species richness due to trophic dependence, and an extinction debt on grassland-specialist plants. In this paper, we address the following questions: (i) Do asynchronies in extinction and extinction debt between butterflies and plants affect food

network structure, thus determining changes in the species interactions–area relationships? (ii) Do these changes affect other butterfly-plant network metrics? (iii) Do landscape properties, either current or historical, modulate the effects of area loss and fragmentation on network metrics?

We hypothesize that asynchronies in extinction and extinction debt between specialist butterflies and plants will cause an interaction surplus (higher average number of interactions per species) because generalist species survive better and are more connected than specialist ones. In consequence, there will be an extinction debt of ecological interactions and the species interactions–current area relationship will be weakened. We also hypothesize that other network metrics (i.e. connectance, number of compartments or web asymmetry) will be affected by differential extinction, potentially affecting network stability. Finally, we expect that past landscape properties will explain some network metrics, indicating the existence of extinction debt in the structure of butterfly-plant ecological networks.

We address these questions through hierarchical partitioning analysis with the aim to examine the effects of landscape structure, both historical and current, and recent landscape dynamics on bipartite networks indices of vascular butterfly-plant food webs, separately for butterfly specialists and for all butterfly species in habitat patches.

4.2. Methods

4.2.1. Study area

The study was conducted in calcareous grasslands in Catalonia (NE Iberian Peninsula, 41° N, 0° 30' E; for more details see Guardiola et al., 2013). The focus of this study were butterflies and vascular plants of the semi-natural Mediterranean mountain grasslands, corresponding to habitat “34.721 *Aphyllanthes* grasslands” of the CORINE habitat classification (Moss & Wyatt, 1994). Like many other low-productivity grasslands in Europe (Kunstler et al., 2006), these grasslands have been subjected to a slow woody encroachment (trees and shrubs) in the last half century, because of livestock grazing (sheep and goats) cessation.

4.2.2. Sampling

We selected 26 patches of *Aphyllanthes* grasslands in calcareous massifs (ranging from 860 to 1400 m a.s.l.), immersed in forested landscapes, with a wide range of patch sizes (from 0.1 to

26.9 ha in 2003) and intensities of patch area reduction, from stable to high patch regression during the last half century (from 0 to more than 95% of area reduction). In each selected patch we sampled all vascular plants and butterflies (including burnet moths) and determined a set of patch and landscape metrics (see details in Guardiola et al., 2013; submitted/Chapter 3): past (1956) and current (2003) patch area, patch area loss between these dates, past and current patch connectivity (area of focal habitat in a 1-km buffer for each patch, including the patch area), patch isolation (as the cover percentage of woody habitats in the surrounding landscape). Because species richness in these grassland patches was in part related to the geographical gradient (Bagaria et al., 2012), and because geographical variation can modulate interaction patterns along a gradient (Dáttilo et al., 2013; Trøjelsgaard et al., 2015), we included this effect by applying a trend surface analysis (see details in Guardiola et al., 2013; submitted/Chapter 3) and included this geographical gradient as a predictor variable in all statistical analyses.

4.2.3. Measuring butterfly-plant food networks

Butterfly species have in general high resource specialization in the larval stage (Pearse & Altermatt, 2013), being monophagous (butterflies feeding on plants of a single genus or a single species), oligophagous (butterflies feeding on plants of various genera but belonging to the same family), or polyphagous species (butterflies feeding on a diversity of plants belonging to various families). In this study, we used the comprehensive compilation provided by García-Barros et al. (2013) of the food plants used by larvae of butterfly species in the Papilionoidea superfamily (including Papilionidae, Hesperidae, Pieridae, Riodinidae, Lycaenidae and Nymphalidae) in the Iberian Peninsula, plus unpublished data by one of the authors (CS), to construct a bipartite interaction matrix with our data of plants and butterflies sampled in the 26 habitat patches and their food interactions (Figure S1).

Network metrics are highly influenced by the sampling completeness of network interactions (Rivera-Hutinel et al., 2012). But limitation of sampling effort is a common problem and there are several ways to deal with this bias, like using additional information sources as evidence of links that may exist but have not detected (Blüthgen, 2010). In plant–pollinator networks, Bosch et al. (2009) demonstrated that traditional pollination network surveys, i.e. plant-centred visual surveys of plant–pollinator contacts, caused a very significant decrease in the number of interactions detected through other data sources as pollen analysis. Likewise, Gibson et al. (2011) found that transects and timed observation methods affected the number of unique interactions and the web asymmetry. In our case, because of the methodological difficulties to

perform complete sampling of caterpillars in the field, we constructed our butterfly-plant food networks linking our plant and adult butterfly data sampled in the same patch with the most reliable information on host-plant requirements of butterfly larvae for the study region. Although it cannot be assured that all the interactions assembled in networks are actually occurring in a specific patch, this is the approximation generally followed when no specific patch data are available (Pearse & Altermatt, 2013; Pellissier et al., 2013a, 2013b). In this sense, Gilarranz et al. (2014) pointed out that sampling all interactions is up to five times more time-consuming than sampling all species.

For each sampled grassland patch we calculated several qualitative network metrics of the total and specialist butterfly-plant bipartite networks (Dormann et al., 2009):

- Plant species richness (I): number of plant species (low trophic level) involved in the network (i.e. richness of food plants).
- Butterfly species richness (J): number of butterfly species (high trophic level) involved in the network.
- Total links (L): number of realized links in a network.
- Links per species (L_s): mean number of links per species, $L_s = L/(I+J)$
- Connectance (C): realized proportion of possible links in the network, $C = L/(IJ)$
- Nestedness: measure of the deviation from systematic arrangement of species by niche width. High nestedness occurs when rows and columns in the matrix of trophic interactions are ordered by decreasing number of links, and links of each row and column match the previous ones or represent a subset of them. Low nestedness indicated a random arrangement. Nestedness index values ranged from 0 (high nested pattern) to 100 (not nested pattern, chaos).
- Web asymmetry (W): balance between numbers in the two trophic levels $W = (J-I)/(I+J)$. Positive values indicate more higher-trophic level species (butterflies), negative more lower-trophic level species (plants).
- Number of compartments: number of subwebs not connected to other subwebs (through either higher or lower trophic levels).

4.2.4. Statistical analyses

Independent and conjoint contributions of each response variable (network metrics) with patch and landscape metrics were assessed through hierarchical partitioning analysis (Chevan & Sutherland, 1991; Mac Nally, 2000), which was conducted using linear regression and R-

squared as goodness-of-fit measures. This statistical procedure allowed us to identify those predictors with an important independent –non partial– correlation with species richness (Heikkinen et al., 2005) and network metrics. Statistical significances of the independent contributions of selected predictors were tested by a randomization procedure of 100 randomizations (Mac Nally & Horrocks, 2002), which yielded Z-scores for the generated distribution of randomized independent contributions and an indication of statistical significance ($P < 0.05$) based on an upper 0.95 confidence limit ($Z \geq 1.65$). Variables of current and past patch and landscape area were log 10-transformed to meet the assumptions of normality and homoscedasticity.

All the statistical analyses were performed using the software R 2.15.1 for Windows (RCoreTeam, 2012). We used the hier.part package (Nally & Walsh, 2004) Version 1.0-3 for the hierarchical partitioning analyses and all network metrics were calculated using the package Bipartite (Dormann et al., 2008, 2009).

4.3. Results

We recorded 85 butterfly species in the 26 studied patches with 40% being considered grassland specialists, and 297 vascular plant species in the 26 studied patches. According to known food-plants requirements for butterfly larvae (see Methods), only 101 plants were hosts for the 85 butterflies recorded in our patches (see Table S1 and S2 for species list), and involved a total of 319 links between butterflies and plants (Figure S1; detailed network metrics of each patch analysed are shown in Table S3 for all butterfly-plant networks and Table S4 for specialist butterfly-plant networks). For only two highly-mobile butterflies we found no host plant in our surveys: the regular long-distance migrant *Vanessa atalanta* (Stefanescu, 2001), whose larvae consume *Parietaria officinalis* or *Urtica* spp.; and the summer-altitudinal migrant *Libythea celtis*, whose larvae feed on *Celtis australis* in the spring (García-Barros et al., 2013). In consequence, these two species were not considered in butterfly-plant food networks. In all the butterfly-plant networks analysed here, plant richness refers to the species richness of plants that are food plants for at least one of the caterpillar butterfly species recorded in the studied patches.

All butterflies-all plants species networks

Current patch area was the main variable explaining species richness and food network architecture. Larger patches had more plants and butterflies, involving higher total links and compartments (Figure 1). Species richness of butterflies in networks was positively related to current patch area while plant species richness and total links in networks were positively related to current patch area and negatively to patch isolation (Table 1a). Connectance was negatively related to current patch area and to the geographical gradient. Nestedness was negatively related to current surrounding grassland area. Links per species was not related to any of the response variables analyzed. Web asymmetry was negatively related to both past patch area and past surrounding grassland area, while the number of compartments was positively related to current patch area.

Specialist butterflies-all plants species networks

Current patch area also was the main variable explaining species richness and food network architecture in the same way of all butterflies-all plants networks, but with less species interacting and with simplest networks (Figure 2). Species richness of butterfly specialists in networks was positively related to current patch area while plant species richness was positively related to current patch area and to the current surrounding grassland (Table 1b). Total links in networks were positively related to current patch area and negatively to patch isolation. Connectance was negatively related to current patch area, while nestedness was positively related to current patch area and to the geographical gradient. Links per species were negatively related to patch isolation. Web asymmetry was not related to any of the patch and landscape variables analyzed. Number of compartments was positively related to current patch area and to the geographical gradient.

Table 1 Results (Z-score) of the randomization tests for the independent contributions of separate predictor variables (current and past patch area, current and past connectivity, patch isolation, proportion of patch area lost, and geographical variation) in hierarchical partitioning analysis to explain network metrics (butterfly and plant species, connectance, nestedness, total links, links per species, web asymmetry and compartments) of (a) all butterfly-plant networks and (b) specialist butterfly-plant networks. Bold numbers indicate variables with a significant ($P < 0.05$) independent contribution.

	Current patch area	Past patch area	Current connectivity	Past connectivity	Patch isolation	Patch area lost	Geographical variation	R ² of the selected model
<i>(a) All butterfly-plant</i>								
Butterfly species	(+)3.57	-0.01	1.04	-0.16	0.87	0.52	0.70	0.41
Plant species	(+)2.78	0.30	1.35	0.31	(-)2.26	0.74	0.50	0.66
Connectance	(-)1.91	0.25	0.99	0.37	1.06	0.66	(-)2.30	0.52
Nestedness	0.94	-0.32	(-)1.87	-0.01	0.37	0.10	-0.54	0.27
Total links	(+)3.40	-0.02	1.32	-0.04	(-)1.94	0.36	0.26	0.53
Links per species	0.27	-0.54	-0.54	-0.61	-0.45	-0.26	-0.58	-
Web asymmetry	0.39	(-)2.48	0.96	(-)1.71	1.33	-0.42	-0.44	0.38
Compartments	(+)2.99	0.11	1.39	0.19	0.79	0.77	1.11	0.47
<i>(b) Specialist butterfly-plant</i>								
Butterfly species	(+)1.80	-0.45	0.51	-0.44	1.27	0.72	-0.38	0.29
Plant species	(+)2.64	-0.21	(+)1.77	-0.09	1.33	0.70	0.21	0.39
Connectance	(-)2.88	0.77	0.00	-0.47	-0.77	1.02	0.79	0.20
Nestedness	1.43	-0.14	0.32	-0.39	-0.44	-0.19	(+)6.06	0.30
Total links	(+)1.81	-0.27	1.27	-0.21	(-)2.38	0.35	-0.48	0.41
Links per species	-0.12	0.43	0.98	-0.02	(-)2.94	-0.65	0.22	0.23
Web asymmetry	0.00	-0.33	-0.15	1.21	-0.36	0.23	-0.29	-
Compartments	(+)2.65	-0.24	0.35	-0.19	-0.29	1.05	(+)1.75	0.42

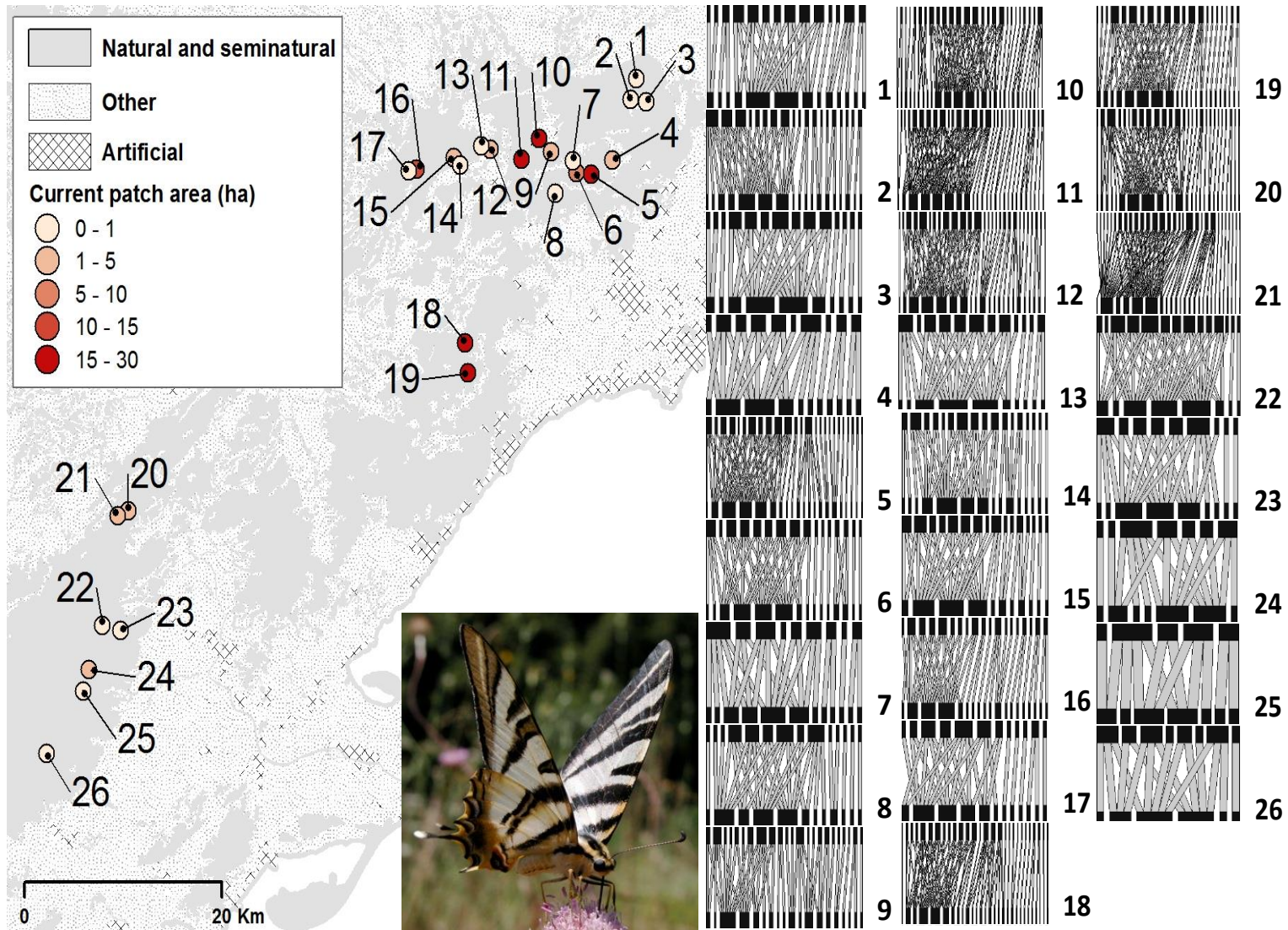


Figure 1 Study region and distribution of the selected patches indicating their patch area and bipartite graphs of the all butterfly-plant interaction networks: lower bands represents plant species and upper bands butterfly species, the width of the bands reflects the number of interactions for each species; grey lines connecting the bands represent a trophic interaction. *Iphiclides podalirius* is a non-specialist species in our study (Photo: J. Corbera).

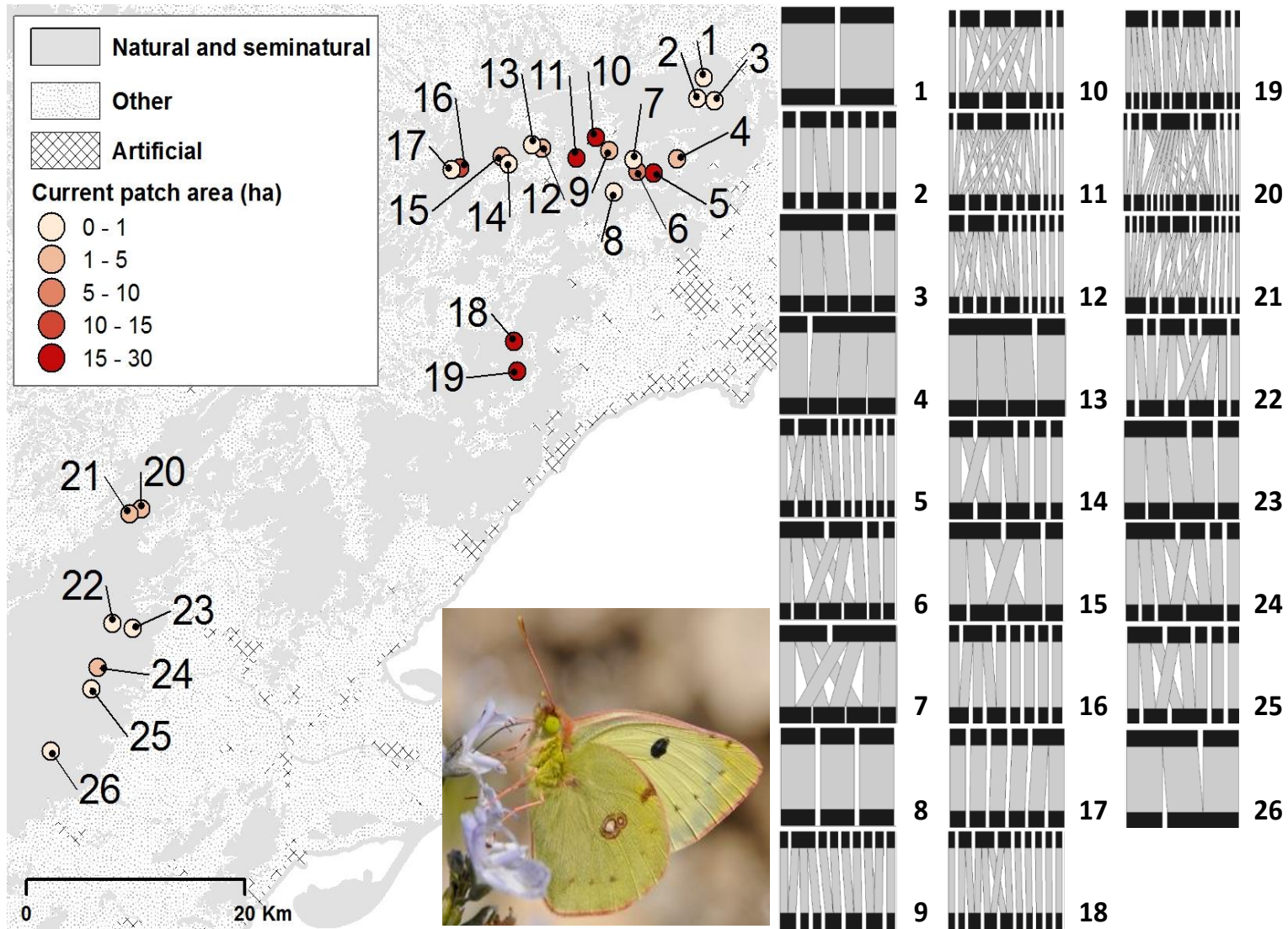


Figure 2 Study region and distribution of the selected patches indicating their patch area and bipartite graphs of the specialist butterfly-plant interaction networks: lower bands represents plant species and upper bands butterfly species, the width of the bands reflects the number of interactions for each species; grey lines connecting the bands represent a trophic interaction. *Colias alfacariensis* is a specialist species in our study (Photo: J. Corbera).

4.4. Discussion

Despite the well studied effects of habitat loss on plants and butterflies, to our knowledge this is the first study assessing the effects of patch and landscape changes on butterfly-plant networks. We have found neither collapse nor resilience in butterfly-plant networks after habitat loss but patch and landscape metrics influencing both species richness and network structure and stability.

Contrary to our expectations derived from the detection of extinction debt in plants in a previous study (Guardiola et al., 2013), the positive association of current patch area with species richness of plants and butterflies and with network links was strong, as supported by the interactions–area relationship hypothesis (Sugiura, 2010). Patch area loss did not explain any of our indices of network structure, indicating no extinction debt in ecological interactions (Valiente-Banuet et al., 2015).

However, total links of both all butterfly-plant and specialist butterfly-plant networks were related positively to current patch area but also negatively to patch isolation. Therefore, the more isolated patches had fewer total links in networks than more connected ones, indicating respectively an interaction deficit or surplus due to a rescue effect from nearby habitat patches (as suggested by LeCraw et al. 2014). As a consequence, interaction balance (average number of interactions per species) might be idiosyncratic to each habitat patch, as reported for species extinction debt (Piqueray et al., 2011; Guardiola et al., 2013).

Interestingly, mean links per species in all butterfly-plant networks was not related to any of the response variables analyzed, but was negatively related to patch isolation in specialist butterfly-plant networks. Isolation did not cause a decrease in both specialist plant and butterfly species richness but patches more isolated had fewer links per specialist species (Table 1b), causing an interaction deficit. This suggests that some links in specialists specialist butterfly-plant networks are promoted by the rescue effect from populations inhabiting in nearby patches.

Contrary to our expectations we could not find any effect of patch area loss on all butterfly-plant and specialist butterfly-plant network indices. An explanation for this result is that effects of patch area loss could be fast and, hence, undetected using the analysed 47-yr period (from 1956 to 2003). On the other hand, despite our patches spanned a wide range of patch area reduction, some studies claim that there is a sudden collapse of networks at higher habitat destruction thresholds (Fortuna & Bascompte, 2006), and most of our networks probably did not reach this threshold.

In this sense, it is important to remark that few specialist plant species in our grasslands are abundant in all patches sampled, and these plant specialists are hosts of a higher number of caterpillar butterflies (i.e. up to fourteen butterflies recorded in our study feed on *Brachypodium retusum* or *Festuca ovina*; or up to five on *Anthyllis vulneraria* subsp. *fontqueri* or *Viola rupestris*). A more severe patch area loss in our grasslands could affect these specialist plant species causing their extinction and causing a severe effect on butterfly-plant networks.

Besides these changes in links between butterflies and plants, we also focused our analysis in other network metrics to reveal butterfly-plant network changes. We found that the positive association of network indices with current patch area is strongly modulated by the known area effects on plant and butterfly species richness. The larger the patch area, the more species (butterflies and plants) were involved in networks, thus determining a higher number of total links, but forming new compartments that decreased network connectance. Because of these changes in network indices, our butterfly-plant networks show neither resilience nor stability, nor collapse, but moderate changes in their structure. In contrast, Villa-Galaviz et al. (2012) found resilience in caterpillar-plant networks but analyzing networks of a very contrasted habitats in a secondary succession from pasture to mature Mexican tropical dry forest. Passmore et al. (2012) also found resilience but in ant-plant mutualistic networks in Amazonian forest fragments.

The increase of number of compartments with patch area has been also reported in other studies (Valladares et al., 2012; Emer et al., 2013). It is supposed to increase network persistence in trophic networks (Thébault & Fontaine, 2010) because compartments isolate the effects of disturbances and buffers the propagation of species extinction (Stouffer & Bascompte, 2011). But it has been also hypothesized that the extinction of some species might disconnect interaction networks increasing the number of compartments (Gonzalez et al., 2011). Interestingly, we found that all butterfly-plant networks had more compartments than specialist butterfly-plant networks, hence the latter were likely less stable.

On the other hand, we have found that connectance was negatively related to current patch area in both specialist and all butterfly-plant networks, as also reported in forest plant-herbivore and host-parasitoid trophic networks (Valladares et al., 2012) and in plant-pollinator networks (Spiesman & Inouye, 2013). Lower connectance is predicted to stabilize trophic networks by reducing the propagation of the negative effects of species loss throughout the network (Thébault & Fontaine, 2010; Villa-Galaviz et al., 2012). Thus our study networks were presumably more stable in large patches than in small ones. On the other hand, some studies pointed out that patch reduction affects more intensely specialized consumers (less connected).

Hence, and as found in our study, smaller patches might have more interactive food networks with highly connected species (Morris et al., 2014) because species number decreases and high-trophic-level generalists are expected to survive better than specialists (Hagen et al., 2012).

Nestedness is assumed to have no major effect on the stability of antagonistic networks, but it is thought to enhance the stability of mutualistic networks (Thébault & Fontaine, 2010). We found that nestedness of specialist butterfly-plant networks was not related to any patch or landscape metric but to the geographical gradient. However, patch connectivity has a significant negative effect on nestedness in all-butterfly-plant networks. Nested networks are highly cohesive because species interacting with specialists are a subset of species interacting with generalists (Bascompte et al., 2003). Thus, networks in patches with high patch connectivity are less cohesive in that some species interact with few species of the other level. However, these species are more sensitive to habitat fragmentation (Bascompte et al., 2003; Fortuna & Bascompte, 2006) because they are more specialized (as we argue below).

In addition to current patch and landscape effects on network indices, we found that web asymmetry (balance between numbers of butterflies and plants) in all butterfly-plant networks was negatively related not to current but past patch and landscape habitat areas, indicating both differential extinctions and extinction debt (Kuussaari et al., 2009). The larger the past patch and landscape habitat areas, the less asymmetry in all butterfly-plant networks: i.e., the balance between butterflies and plants shifted towards more plants and less butterflies. Asymmetries in ecological networks are caused by different extinction rates of the species in the different trophic levels (Schleuning et al., 2014) or reflect the interaction strength between trophic levels (Blüthgen, 2010) in a way that the more species in the high trophic level, the lower degree of specialization of the high trophic level and vice versa (Blüthgen et al., 2007). In accordance, our results suggest either that extinction is biased towards specialists because they did not show asymmetry or that patches with more past patch and landscape area had more richness of (host) plant species, hence butterflies were more specialized than in patches with less past patch and landscape area. This is congruent with Krauss et al. (2010) who found that specialists are more prone to extinction effects and that long-lived vascular plants show time-delayed extinctions whereas short-lived butterflies do not; therefore more plants still persist in those patches that had more past patch and landscape area.

Furthermore, because web asymmetry is better explained by past than current landscape characteristics, an extinction debt can be assumed in ecological networks, as stated for species richness (Kuussaari et al., 2009). This finding allows us to extend the concept of extinction debt of ecological interactions by Valiente-Banuet et al. (2015) to a wider concept of extinction debt

of ecological networks. Thus, the presence of extinction debt of ecological networks can be assumed not only through the balance between number of interactions and habitat loss as stated by Valiente-Banuet et al. (2015), but it also can be assumed if current network metrics are better explained by past than by present patch or landscape characteristics. Our concept includes any present or future change in network structure due to a current or past environmental disturbance. This is congruent with studies pointing out that some network indices (as connectance, nestedness or number of compartments, but not number of links) give robustness to ecological networks against species loss (Fortuna & Bascompte, 2006; Thébault & Fontaine, 2010; Hagen et al., 2012; Valladares et al., 2012).

Finally, as stated in Methods, one caveat of the assumptions we have made in our study is that we related our data of plants and adult butterflies sampled in the 26 habitat patches with data of caterpillar plant-resources recently compiled in the Iberian Peninsula (García-Barros et al., 2013) plus our unpublished data, using data of butterfly adults as a proxy of its larvae. However, in our study system, with large patches, this is the most feasible approximation (as in other studies: Pearse & Altermatt, 2013; Pellissier et al., 2013a, 2013b) because (i) most caterpillars are cryptic and difficult to detect in the field, (ii) caterpillars are difficult to identify at species level, (iii) there are not standardized methods to sample caterpillars (iv) and caterpillar sampling is high time-consuming. Although we cannot be sure that all interactions assembled in our networks are occurring in a specific patch, at least there is a great possibility of this interaction. However, because of the difficulties in caterpillar sampling, the reverse problem would arise only sampling caterpillars, because if we found a host plant species but no caterpillar on it in a given patch, we would never be sure if this missing link is real or due to undersampling. Moreover, especially in the case of specialist butterfly-plant networks, we should bear in mind that butterfly habitat-specialist species in general occupy the same habitat throughout their entire life cycle because they have low dispersal abilities (Sekar, 2012; Stevens et al., 2012), and are less prone to use matrix habitats (Hambäck et al., 2007). Hence, it is highly probable that if we detect a specialist butterfly, there will be its caterpillars in the same grassland patch.

On the other hand, butterflies interact with plants in antinomic ways because they are herbivores in the larval stage (antagonistic interaction) and pollinators in the adult stage (mutualistic interaction). These could affect our results as we only analyzed trophic interactions; however, our results show that our network's structure and their response to disturbances behave as expected in antagonistic networks: decreasing the number of compartments and increasing connectance, an opposite pattern of mutualistic networks.

4.5. Conclusions

Our results show that the number of network links follows the interactions–area relationship. However, patch and landscape metrics modulate both species richness and network links in a way that the interaction balance (*sensu* Valiente-Banuet et al., 2015) might be idiosyncratic to each habitat patch, causing a deficit of interactions in the more isolated patches but a surplus of interactions in the less isolated patches.

Moreover, the decrease of species richness and network links with decreasing patch area is accompanied by changes in network architecture that imply a reduction of network stability: fewer compartments and higher connectance. But we also detected a past patch and landscape effect on network asymmetry indicating both different extinction rates and extinction debts of butterflies and plants.

Our results suggest that butterfly-plant networks in fragmented landscapes are subjected not only to changes in species richness and network links but also to changes in network architecture, and that both current and past patch and landscape configuration modulate ecological networks. Therefore we define extinction debt of ecological networks as any present or future change in the network metrics due to a current or past environmental disturbance.

Further studies of butterfly-plant –and other groups– networks in fragmented landscapes are needed to corroborate our findings and determine whether habitat loss affect species links and network structure, and which role plays current and past landscape configuration.

Moreover, future research is needed to understand and predict how network metrics respond to current and past patch and landscape changes, especially at high levels of habitat loss; to investigate if there are some species traits that enhance network persistence; to determine if species phylogeny plays a role on network interactions; and to compare our results based on binary interaction matrices (qualitative metrics) with matrices considering species abundance and interaction intensity between species (quantitative metrics).

Finally, our results have implications for conservation of plants and butterflies in Mediterranean grasslands. It is known that small and isolated patches have less plant and butterfly species, but our results show that small patches also have food networks that are likely to be less stable, thus more prone to decline or collapse in front of further impacts. Moreover, we have found that few specialist plant species are abundant in all patches sampled and they are hosts of a higher number of caterpillar butterflies. Although the intensity of area loss in our grasslands is not so high to affect these specialist plant species, a more severe area loss causing the extinction of

these plants, would affect keystone interactions and could cause a network collapse. However, as far as we did not yet find any collapse of species interaction networks, conservation and management initiatives are needed before the continued area loss and fragmentation of grassland patches will cause a network collapse.

4.6. References

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4.7. Supporting information

Figure S1. Overall butterfly (upper) plant (bottom) interaction network including all plants and butterflies recorded in 26 patches analyzed. Each line between butterfly and plant corresponds to a trophic interaction between butterfly larvae and their food plants.

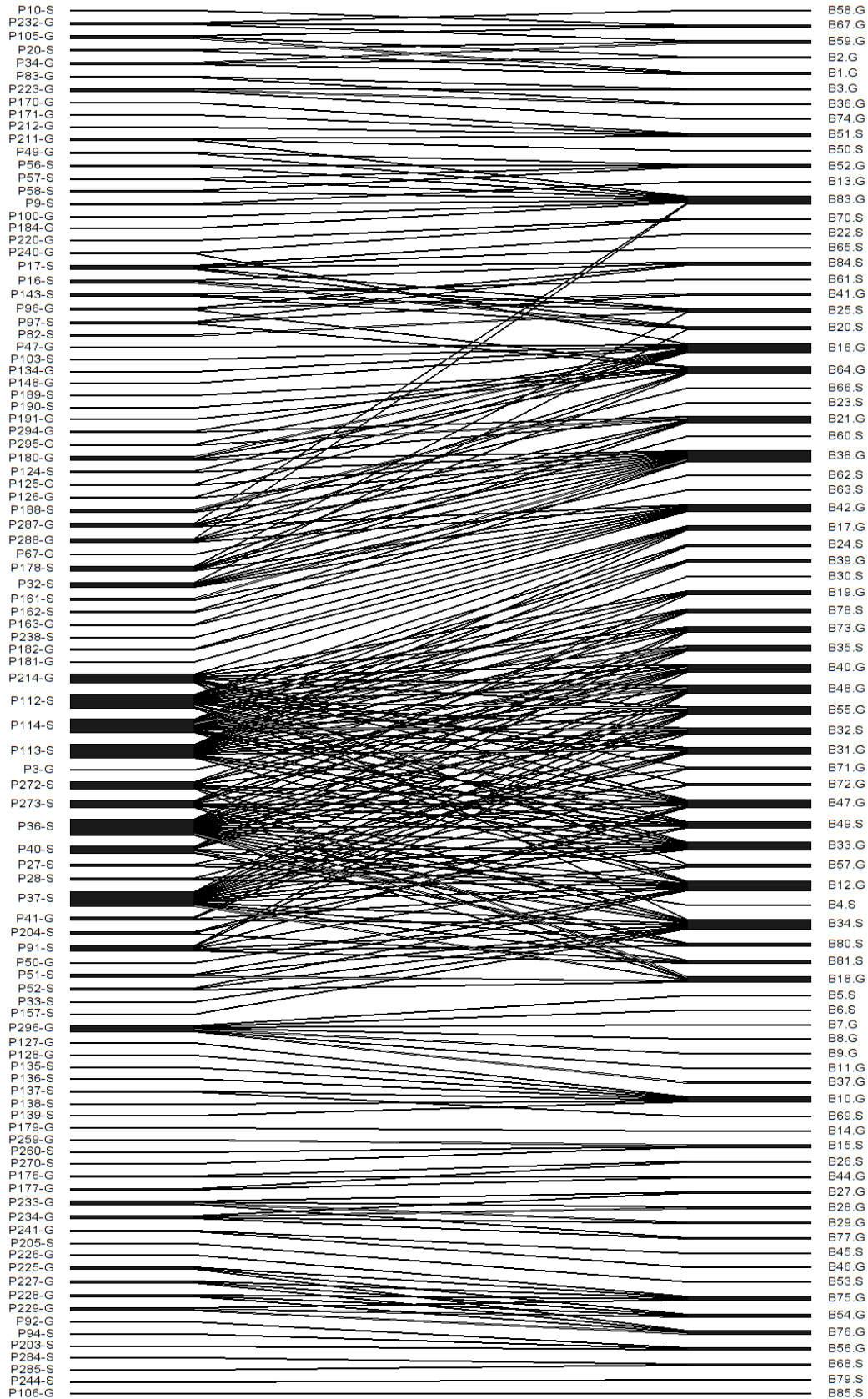


Table S1. Butterfly species recorded in this study with the code used in the analysis. Grassland specialists, marked with S at the end of the code, were selected based on habitat preference data from the Catalan Butterfly Monitoring Scheme (www.catalanbms.org).

Code	Butterfly species	B41-G	<i>Leptidea sinapis</i>
B1-G	<i>Anthocharis cardamines</i>	B42-G	<i>Leptotes pirithous</i>
B2-G	<i>Anthocharis euphenoides</i>	B43-G	<i>Libythea celtis</i>
B3-G	<i>Aporia crataegi</i>	B44-G	<i>Limenitis reducta</i>
B4-S	<i>Arethusana arethusana</i>	B45-S	<i>Lycaena alciphron</i>
B5-S	<i>Argynnis aglaja</i>	B46-G	<i>Lycaena phlaeas</i>
B6-S	<i>Argynnis niobe</i>	B47-G	<i>Maniola jurtina</i>
B7-G	<i>Argynnis pandora</i>	B48-G	<i>Melanargia lachesis</i>
B8-G	<i>Argynnis paphia</i>	B49-S	<i>Melanargia occitanica</i>
B9-G	<i>Argynnis sp.</i>	B50-S	<i>Melitaea cinxia</i>
B10-G	<i>Aricia cramera</i>	B51-S	<i>Melitaea didyma</i>
B11-G	<i>Boloria dia</i>	B52-G	<i>Melitaea phoebé</i>
B12-G	<i>Brintesia circe</i>	B53-S	<i>Muschampia proto</i>
B13-G	<i>Carcharodus alceae</i>	B54-G	<i>Neozephyrus quercus</i>
B14-G	<i>Carcharodus boeticus</i>	B55-G	<i>Ochlodes venata</i>
B15-S	<i>Carcharodus lavatherae</i>	B56-G	<i>Papilio machaon</i>
B16-G	<i>Celastrina argiolus</i>	B57-G	<i>Pararge aegeria</i>
B17-G	<i>Coenonympha arcania</i>	B58-G	<i>Pieris brassicae</i>
B18-G	<i>Coenonympha dorus</i>	B59-G	<i>Pieris rapae</i>
B19-G	<i>Coenonympha pamphilus</i>	B60-S	<i>Plebejus argus</i>
B20-S	<i>Colias alfacariensis</i>	B61-S	<i>Polyommatus coridon</i>
B21-G	<i>Colias crocea</i>	B62-S	<i>Polyommatus daphnis</i>
B22-S	<i>Cupido minimus</i>	B63-S	<i>Polyommatus escheri</i>
B23-S	<i>Cupido osiris</i>	B64-G	<i>Polyommatus icarus</i>
B24-S	<i>Erebia triaria</i>	B65-S	<i>Polyommatus nivescens</i>
B25-S	<i>Erynnis tages</i>	B66-S	<i>Polyommatus ripartii</i>
B26-S	<i>Euphydryas aurinia</i>	B67-G	<i>Pontia daplidice</i>
B27-G	<i>Gonepteryx cleopatra</i>	B68-S	<i>Pseudophilotes panoptes</i>
B28-G	<i>Gonepteryx rhamni</i>	B69-S	<i>Pyrgus alveus</i>
B29-G	<i>Gonepteryx sp.</i>	B70-S	<i>Pyrgus malvoides</i>
B30-S	<i>Hesperia comma</i>	B71-G	<i>Pyronia bathseba</i>
B31-G	<i>Hipparchia alcyone</i>	B72-G	<i>Pyronia cecilia</i>
B32-S	<i>Hipparchia fidia</i>	B73-G	<i>Pyronia tithonus</i>
B33-G	<i>Hipparchia semele</i>	B74-G	<i>Satyrrium acaciae</i>
B34-S	<i>Hipparchia statilinus</i>	B75-G	<i>Satyrrium esculi</i>
B35-S	<i>Hyponephele lycaon</i>	B76-G	<i>Satyrrium ilicis</i>
B36-G	<i>Iphiclides podalirius</i>	B77-G	<i>Satyrrium spini</i>
B37-G	<i>Issoria lathonia</i>	B78-S	<i>Satyrus actaea</i>
B38-G	<i>Lampides boeticus</i>	B79-S	<i>Spialia sertorius</i>
B39-G	<i>Lasiommata maera</i>	B80-S	<i>Thymelicus acteon</i>
B40-G	<i>Lasiommata megera</i>	B81-S	<i>Thymelicus sylvestris</i>

B82-G *Vanessa atalanta*

B83-G *Vanessa cardui*

B84-S *Zygaena lavandulae*

B85-S *Zygaena sarpedon*

Table S2. Plant species recorded in this study with the code used in the analysis. Grassland specialists, marked with S at the end of the code, were selected with the help of regional floras (Bolòs *et al.* 1993; Rivas–Martínez *et al.* 2001) and expert advice.

Code	Plant species	P126-G	<i>Genista scorpius</i>
P3-G	<i>Aegilops geniculata</i>	P127-G	<i>Geranium columbinum</i>
P9-S	<i>Althaea hirsuta</i>	P128-G	<i>Geranium robertianum purpureum</i>
P10-S	<i>Alyssum spinosum</i>	P134-G	<i>Hedera helix</i>
P16-S	<i>Anthyllis montana</i>	P135-S	<i>Helianthemum appeninum</i>
P17-S	<i>Anthyllis vulneraria fontqueri</i>	P136-S	<i>Helianthemum marifolium marifolium</i>
P20-S	<i>Arabis auriculata</i>	P137-S	<i>Helianthemum numularium</i>
P27-S	<i>Arrhenatherum album</i>	P138-S	<i>Helianthemum oelandicum italicum</i>
P28-S	<i>Arrhenatherum elatius sardoum</i>	P139-S	<i>Helianthemum origanifolium molle</i>
P32-S	<i>Astragalus monspessulanus monspessulanus</i>	P143-S	<i>Hippocrepis comosa</i>
P33-S	<i>Avenula pratensis iberica</i>	P148-G	<i>Ilex aquifolium</i>
P34-G	<i>Biscutella laevigata</i>	P157-S	<i>Koeleria vallesiana</i>
P36-S	<i>Brachypodium phoenicoides</i>	P161-S	<i>Lathyrus filiformis</i>
P37-S	<i>Brachypodium retusum</i>	P162-S	<i>Lathyrus saxatilis</i>
P40-S	<i>Bromus erectus</i>	P163-G	<i>Lathyrus setifolius</i>
P41-G	<i>Bromus squarrosus</i>	P170-G	<i>Linaria arvensis simplex</i>
P47-G	<i>Calicotome spinosa</i>	P171-G	<i>Linaria supina aeruginea</i>
P49-G	<i>Carduus nigrescens nigrescens</i>	P176-G	<i>Lonicera implexa</i>
P50-G	<i>Carex flacca</i>	P177-G	<i>Lonicera pyrenaica</i>
P51-S	<i>Carex halleriana</i>	P178-S	<i>Lotus corniculatus</i>
P52-S	<i>Carex humilis</i>	P179-G	<i>Marrubium supinum</i>
P56-S	<i>Centaurea linifolia caballeroi</i>	P180-G	<i>Medicago minima</i>
P57-S	<i>Centaurea linifolia linifolia</i>	P181-G	<i>Melica ciliata</i>
P58-S	<i>Centaurea montana lingulata</i>	P182-G	<i>Melica minuta</i>
P67-G	<i>Colutea arborescens</i>	P184-G	<i>Micropus erectus</i>
P82-S	<i>Coronilla minima</i>	P188-S	<i>Onobrychis supina supina</i>
P83-G	<i>Crataegus monogyna</i>	P189-S	<i>Ononis minutissima</i>
P91-S	<i>Dactylis glomerata hispanica</i>	P190-S	<i>Ononis pusilla</i>
P92-G	<i>Daucus carota</i>	P191-G	<i>Ononis spinosa</i>
P94-S	<i>Dictamnus hispanicus</i>	P203-S	<i>Peucedanum officinale stenocarpum</i>
P96-G	<i>Dorycnium hirsutum</i>	P204-S	<i>Phleum phleoides</i>
P97-S	<i>Dorycnium pentaphyllum pentaphyllum</i>	P205-S	<i>Phlomis lychnitis</i>
P100-G	<i>Echium vulgare argentae</i>	P211-G	<i>Plantago lanceolata</i>
P103-S	<i>Erica multiflora</i>	P212-G	<i>Plantago sempervirens</i>
P105-G	<i>Erucastrum nasturtiifolium</i>	P214-G	<i>Poa bulbosa</i>
P106-G	<i>Eryngium campestre</i>	P220-G	<i>Potentilla reptans</i>
P112-S	<i>Festuca nigrescens</i>	P223-G	<i>Prunus spinosa</i>
P113-S	<i>Festuca ovina</i>	P225-G	<i>Quercus cerrioides</i>
P114-S	<i>Festuca paniculata spadicea</i>	P226-G	<i>Quercus coccifera</i>
P124-S	<i>Genista hispanica</i>	P227-G	<i>Quercus faginea</i>
P125-G	<i>Genista patens</i>	P228-G	<i>Quercus humilis</i>

P229-G	<i>Quercus ilex</i>	P270-S	<i>Stachys heraclea</i>
P232-G	<i>Reseda luteola</i>	P272-S	<i>Stipa offneri</i>
P233-G	<i>Rhamnus alaternus var balearicus</i>	P273-S	<i>Stipa pennata iberica</i>
P234-G	<i>Rhamnus saxatilis</i>	P284-S	<i>Thymus serpyllum fontqueri</i>
P238-S	<i>Rosmarinus officinalis</i>	P285-S	<i>Thymus vulgaris</i>
P240-G	<i>Rubus ulmifolius</i>	P287-G	<i>Trifolium campestre</i>
P241-G	<i>Rumex intermedius</i>	P288-G	<i>Trifolium stellatum</i>
P244-S	<i>Sanguisorba minor</i>	P294-G	<i>Vicia peregrina</i>
P259-G	<i>Sideritis hirsuta hirsuta</i>	P295-G	<i>Vicia sativa nigra</i>
P260-S	<i>Sideritis spinulosa ilicifolia</i>	P296-G	<i>Viola rupestris</i>

Table S3. Values of the all butterfly-plant network metrics of each patch analysed.

<i>All butterfly-All plant</i>	Butterfly species	Plant species	Connectance	Nestedness	Total links	Links per species	Web asymmetry	Compartments
1	14	13	0,165	32,955	30	1,111	0,037	6
2	19	18	0,126	17,789	43	1,162	0,027	7
3	14	10	0,193	50,301	27	1,125	0,167	7
4	10	11	0,200	24,935	22	1,048	-0,048	4
5	25	21	0,110	17,704	58	1,261	0,087	10
6	16	15	0,163	29,651	39	1,258	0,032	7
7	9	12	0,213	28,087	23	1,095	-0,143	4
8	14	12	0,185	23,602	31	1,192	0,077	6
9	23	19	0,098	16,696	43	1,024	0,095	7
10	26	28	0,099	18,619	72	1,333	-0,037	11
11	29	25	0,112	15,904	81	1,500	0,074	12
12	28	22	0,104	12,705	64	1,280	0,120	10
13	12	10	0,233	23,217	28	1,273	0,091	4
14	17	15	0,133	24,949	34	1,063	0,063	7
15	16	11	0,182	32,878	32	1,185	0,185	6
16	19	19	0,108	18,001	39	1,026	0,000	9
17	12	12	0,188	30,690	27	1,125	0,000	6
18	28	29	0,083	16,211	67	1,175	-0,018	12
19	21	22	0,126	21,100	58	1,349	-0,023	9
20	27	25	0,098	13,510	66	1,269	0,038	12
21	30	25	0,108	8,262	81	1,473	0,091	10
22	14	8	0,339	24,857	38	1,727	0,273	3
23	9	9	0,284	31,498	23	1,278	0,000	3
24	10	8	0,263	26,691	21	1,167	0,111	3
25	14	14	0,158	20,202	31	1,107	0,000	6
26	8	6	0,333	25,643	16	1,143	0,143	2

Table S4. Values of the specialist butterfly-plant network metrics of each patch analysed.

<i>Specialist butterfly-All plant</i>	Butterfly species	Plant species	Connectance	Nestedness	Total links	Links per species	Web asymmetry	Compartments
1	2	2	0,500	37,696	2	0,500	0,000	2
2	6	6	0,194	55,201	7	0,583	0,000	5
3	3	5	0,333	44,897	5	0,625	-0,250	3
4	2	4	0,500	46,842	4	0,667	-0,333	2
5	8	9	0,167	45,512	12	0,706	-0,059	6
6	4	6	0,375	42,319	9	0,900	-0,200	3
7	2	4	0,875	0,000	7	1,167	-0,333	1
8	3	3	0,333	47,215	3	0,500	0,000	3
9	9	7	0,175	34,275	11	0,688	0,125	5
10	6	7	0,333	54,500	14	1,077	-0,077	4
11	8	9	0,292	39,459	21	1,235	-0,059	4
12	9	10	0,178	52,482	16	0,842	-0,053	6
13	2	4	0,500	46,842	4	0,667	-0,333	2
14	5	5	0,320	52,449	8	0,800	0,000	3
15	3	4	0,500	28,385	6	0,857	-0,143	2
16	7	7	0,184	49,032	9	0,643	0,000	5
17	5	6	0,200	51,763	6	0,545	-0,091	5
18	9	10	0,144	53,768	13	0,684	-0,053	7
19	7	11	0,208	42,334	16	0,889	-0,222	4
20	9	13	0,197	22,333	23	1,045	-0,182	4
21	12	9	0,185	39,229	20	0,952	0,143	5
22	6	6	0,306	32,930	11	0,917	0,000	2
23	3	4	0,417	26,769	5	0,714	-0,143	2
24	4	5	0,400	20,162	8	0,889	-0,111	2
25	5	5	0,320	33,112	8	0,800	0,000	3
26	2	2	0,750	0,000	3	0,750	0,000	1

Capítol 5

Conclusions generals



La present tesi doctoral és un dels primers treballs que analitza els patrons de riquesa d'espècies i de deute d'extinció de dos grups d'organismes tròficament relacionats (les plantes vasculares i les papallones diürnes) en un hàbitat (les pastures mediterrànies) en procés de regressió i fragmentació, i en relació amb diversos factors ambientals i del paisatge actual i històric. També estudia, per primer cop, els efectes dels patrons de deute d'extinció i dels seus factors associats sobre l'estructura de les xarxes tròfiques entre aquests organismes.

Aquests aspectes són desenvolupats en tres capítols que combinen objectius diversos. Seguidament es llisten les principals conclusions del conjunt del treball, fent referència al capítol corresponent on s'analitzen.

- La detecció del deute d'extinció dels organismes que viuen en pastures mediterrànies en regressió depèn de diversos factors com ara el grup estudiat, les característiques biològiques i ecològiques de les espècies, les característiques de la clapa i del paisatge, actuals i pretèrites, i també de les aproximacions metodològiques utilitzades per al seu estudi (**capítols 2 i 3**).
- La riquesa total de plantes vasculares depèn de l'àrea actual de la clapa d'hàbitat, però en el cas de les especialistes de pastures també hem detectat un efecte significatiu de l'àrea pretèrita sobre la riquesa d'aquestes, cosa que indica l'existència d'un deute d'extinció (**capítol 3**). Per tant, bona part d'aquests especialistes poden estar immersos en un procés d'extinció que encara no ha acabat per la pròpia demografia de les espècies i pel possible efecte de rescat de poblacions veïnes.
- Per contra, la riquesa de papallones (totals i especialistes) depèn de forma directa només de la riquesa de plantes vasculares, i de forma indirecta (a través de la seva relació amb la riquesa de plantes) de l'àrea actual de la clapa (**capítol 3**). Les papallones, per tant, no mostren cap deute d'extinció, cosa que indica que la seva extinció es pot haver produït poc després de la pèrdua i fragmentació dels hàbitats. Amb tot, la seva dependència de les plantes vasculares fa preveure futures extincions locals quan aquestes s'extingeixin.
- Tot i ser aspectes poc o gens considerats en treballs empírics, la incorporació de les característiques de cada clapa i del seu paisatge circumdant permet millorar la detecció del deute d'extinció i dels mecanismes involucrats (**capítol 2**).
- Analitzant per separat les clapas que mostren una pèrdua i fragmentació de la seva superfície (clapas en regressió) els darrers cinquanta anys respecte de les que no (clapas estables), s'ha observat que el deute d'extinció de plantes vasculares és un procés idiosincràtic, que depèn especialment de l'àrea que ha perdut cada clapa i de l'estructura històrica del seu paisatge circumdant.
- D'altra banda, l'estudi del deute d'extinció a diverses escales permet una visió complementària d'aquest (**capítol 2**). En el cas de les plantes vasculares, això ha permès detectar una pèrdua d'espècies a escala d'àrea fixa (una mitjana de 2.4 espècies en clapas en regressió, comparat amb les clapas estables) que no es detecta a escala de clapa. Això indica que a les clapas en regressió es produeix una rarefacció –però encara no l'extinció–

d'algunes espècies a la clapa, cosa que evidencia l'existència del deute d'extinció abans esmentat.

- A escala d'àrea fixa, la densitat d'espècies de plantes i papallones no depèn de forma directa de l'àrea de la clapa, sinó de l'aïllament, de l'àrea perduda i de la l'àrea pretèrita de la clapa (**capítol 3**).
- Les clapas més aïllades i les que han perdut més superfície tenen menor densitat d'espècies de plantes totals i d'especialistes. Les clapas que han perdut més superfície tenen major densitat d'espècies de papallones totals i d'especialistes; i les clapas més isolades i amb més àrea en el passat tenen menor densitat de papallones especialistes (**capítol 3**).
- L'aïllament de les clapas dificulta l'efecte rescat de clapas veïnes i, per tant, provoca una rarefacció de plantes i papallones especialistes, que sovint són menys mòbils que les generalistes (**capítol 3**). La pèrdua d'àrea fa decreixer la densitat d'espècies de plantes (rarefacció) però fa incrementar la de papallones, segurament per l'atracció dels pocs fragments de pastures que queden, causant un agrupament o "*crowding effect*".
- La riquesa i densitat d'espècies de papallones està modulada tròficament per la riquesa de plantes a la clapa, i l'àrea de la clapa ho fa de manera indirecta a través de la seva relació amb la riquesa de plantes (**capítol 3**). Les clapas amb més espècies de plantes, tenen potencialment més disponibilitat de plantes hostes per les larves de papallones i més diversitat de nèctar per les papallones adultes.
- La pèrdua i fragmentació de l'hàbitat i les extincions diferencials entre papallones i plantes ni provoquen el col·lapse ni disminueixen previsiblement la resiliència de les xarxes tròfiques que integren aquests organismes, però sí ocasionen un seguit de canvis en l'estructura d'aquelles (**capítol 4**).
- Les clapas més grans tenen major nombre d'espècies de papallones i de plantes hostes involucrades a les xarxes tròfiques (**capítol 4**). Aquesta major riquesa d'espècies determina un major nombre d'interaccions entre espècies, però aquestes xarxes tròfiques tenen també més compartiments i menor connectància, fet que les fa en principi més estables respecte les clapas més petites.
- L'aïllament i la connectivitat actuals també determinen certs aspectes de les xarxes tròfiques entre papallones i plantes (**capítol 4**). Les clapas més aïllades tenen menor riquesa de plantes hostes i de nombre d'interaccions a les xarxes tròfiques quan es consideren totes les papallones; per a les xarxes de les papallones especialistes l'aïllament causa un decrement del nombre d'interaccions i del nombre mitjà d'interaccions per espècie.
- Finalment, el balanç entre el nombre d'espècies de papallones i plantes (asimetria) a les xarxes tròfiques amb totes les papallones depèn de l'àrea pretèrita de la clapa i del paisatge (**capítol 4**). Les clapas que eren més grans en el passat actualment tenen major proporció de plantes. Això indicaria o bé extincions diferencials entre els dos grups (més extincions de papallones) o bé que les papallones d'aquestes clapas que eren més grans en el passat són tròficament més especialistes.

En resum, l'estudi detecta un deute d'extinció en plantes vasculars pròpies de les pastures estudiades, però no en les papallones. Aquest deute d'extinció depèn, però, de l'escala d'anàlisi i de diverses característiques pròpies de cada clapa i del paisatge històric circumdant. Amb tot, l'estudi també posa de manifest la importància de les relacions tròfiques entre plantes i papallones per determinar la riquesa d'aquestes darreres, cosa que pot afectar els futurs patrons d'extinció de les espècies d'aquest grup, un cop les plantes hagin pagat el seu deute d'extinció. Per tant, les papallones també es poden veure afectades per un deute d'extinció indirecte, fruit dels efectes en cascada que pot comportar l'extinció de les seves plantes nutrícies. L'estudi indica, d'altra banda, que la pèrdua d'àrea no sembla afectar algunes propietats bàsiques de l'estructura de les xarxes tròfiques papallona-planta, tot i que això pot estar condicionat pel pagament del deute d'extinció de les plantes. Com que en general els canvis en les interaccions entre espècies estan força determinats pel nivell tròfic que respon més lentament, és a dir les plantes, l'extinció futura d'aquestes –i els efectes en cascada sobre les papallones– poden determinar canvis importants en les xarxes tròfiques.

La realització d'aquest treball ens ha portat a noves preguntes que caldrà respondre en un futur. N'apuntem algunes que ja hem començat a treballar o que ho farem properament:

- Quins efectes tenen la pèrdua i la fragmentació dels hàbitats sobre la diversitat beta dins les clapas? Hi ha homogeneïtzació biòtica a les clapas més petites o a les que han perdut més superfície?
- Quins efectes tenen la pèrdua i la fragmentació dels hàbitats sobre les corbes de rang-freqüència? Disminueix la freqüència de les espècies més abundants i/o de les més rares?
- Hi ha alguns trets biològics que facin a les espècies més sensibles als efectes de la pèrdua i la fragmentació dels hàbitats?
- Hi ha senyal filogenètic en les interaccions papallona-planta (*cophylogenetic analysis*)? Quines implicacions té?
- Què passa quan a una clapa hi ha la planta nutrícia però no la papallona que s'alimenta d'ella? Quines característiques tenen aquestes plantes i papallones?

Finalment, cal assenyalar que el treball realitzat es centra en la detecció de *patrons*, corresponents a la riquesa d'espècies dels grups estudiats i als deutes d'extinció associats a aquests, i també a l'estructura de les xarxes tròfiques que integren. Resta pendent l'estudi dels *processos* que determinen aquests patrons a nivells de metapoblació (dinàmica de les diverses poblacions, dispersió entre poblacions, etc.), metacomunitat (conjunt de comunitats locals connectades a través de processos de dispersió de múltiples espècies que interactuen entre si) o

fins i tot de metaecosistema (canvis en les relacions tròfiques entre els diversos organismes en l'espai i el temps). L'estudi d'aquests processos en pastures mediterrànies pot contribuir de manera decisiva a la comprensió dels patrons espaciotemporals d'extinció d'espècies en aquests hàbitats en regressió importants per a la conservació de la biodiversitat. Amb tot, però, caldrà posar a punt aproximacions metodològiques específiques que depassen sobradament les dimensions del present treball.