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A trait-based approach to disentangle the success of alien weeds in irrigated crops

Alejandro Juárez Escario

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Universitat de Lleida

Tesi Doctoral

A trait-based approach to disentangle the success of alien weeds in irrigated crops

Alejandro Juárez Escario

Memòria presentada per optar al grau de
Doctor per la Universitat de Lleida
(Programa de Doctorat en Ciència i Tecnologia Agroalimentària)

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This PhD has been carried out within the consolidated group of research "Weed Science and Plant Ecology" (2014SGC008) from the Universitat de Lleida. The author was funded by a PhD FI grants from the Generalitat de Catalunya with the collaboration of the EU Social Fund (2009–2011). from Generalitat de Catalunya.

A mi abuelo

Presentación

Esta tesis se ha llevado a cabo bajo la dirección del profesor Dr. Josep Antoni Conesa i Mor dentro del grupo de investigación consolidado de Malherbología y Ecología Vegetal del Departament d´Hortofruticultura, Botànica i Jardineria de l´Escola Tècnica Superior d´Enginyeria Agrària (ETSEA) de la Universitat de Lleida.

Una beca predoctoral FI (BES-2011 047518) fue concedida por l’Agència de Gestió d'Ajuts Universitaris i de Recerca de la Generalitat de Catalunya desde Enero de 2009 a Diciembre de 2011.

A partir de los resultados obtenidos en el desarrollo de esta tesis se han elaborado los siguientes artículos:

-Artículo 1: Changes in alien and native weed communities in irrigated maize crops and fruit tree orchards between 1989-2009. Alejandro Juárez-Escario, Xavier Oriol Solé-Senan, Jordi Recasens, Andreu Taberner y Josep Antoni Conesa. Enviado a la revista *Annals of Applied Biology* en Agosto 2016

-Artículo 2: A plant-traits approach to assessing the success of alien weed species in irrigated Mediterranean orchards. Alejandro Juárez-Escario, Joan Valls, Xavier Oriol Solé-Senan y Josep Antoni Conesa. Publicado en 2013 en la revista *Annals of Applied Biology*, numero 162, páginas 200–213.

-Artículo 3: Management as a driver of functional patterns and alien species prominence in weed communities of irrigated orchards in Mediterranean areas. Alejandro Juárez-Escario, Josep Antoni Conesa y Xavier Oriol Solé-Senan. Enviado a la revista *Agriculture, Ecosystems and Environment* en Agosto 2016.

-Artículo 4: Identifying alien plants linkages between irrigated orchards and adjacent riparian habitats from a trait-based approach. Alejandro Juárez-Escario, Josep Antoni Conesa y Xavier Oriol Solé-Senan. Publicado en 2016 en la revista *Agriculture*, *Ecosystems and Environment*, número 225, páginas 173-183.

Además, durante el transcurso del presente trabajo de ha llevado a cabo la difusión de resultados obtenidos en diversos congresos y grupos de trabajo de ámbito nacional e internacional:

Juárez-Escario A., Solé-Senan XO., Conesa JA. (2014) Are irrigated crops and the surrounding riparian habitats linked by alien weeds? 4th International Symposium on Weeds and Invasive plants, Montpellier (Francia). Presentación oral.

Juárez, A., Solé-Senan XO., Conesa JA., Recasens J. (2011) Are biological traits behind the success of exotic plants in irrigated crops? The case of fruit tree orchards in NE of Spain. 3rd International Symposium on Weeds and Invasive Plants (Agricultural Weeds and Plant Invaders). Ascona (Suiza). Presentación oral.

Juárez A., Solé XO., Conesa JA. (2011) How does irrigation management influence on alien species assemblages? EWRS Joint Workshop. Huesca (España). Presentación oral.

Juárez A., Solé X., Conesa JA. (2010) Diversity and richness of exotic weeds in fruit tree orchards in relation to irrigation management. What makes an alien invasive? Risk and policy responses. The Association of Applied Biologist Conference. Edimburgh (UK). Presentación oral.

Juárez A., Solé XO., Pedrol J., Villena L., Conesa JA. (2010) Flora exòtica, una amenaça per a la conservació dels ecosistemes riparis: El cas del riu Segre. II Jornades Catalanes de Conservació de Flora. Barcelona (España). Poster.

Juárez A., Recasens J., Taberner A., Conesa JA. (2009) Evolución de la flora exótica en frutales de regadío del W de Catalunya (1989-2009). Tercer Congreso Nacional sobre Especies Exóticas Invasoras. Zaragoza (España). Presentación oral.

Conesa JA., Pedrol J., Recasens J., **Juárez A.**, Solé XO., Villena L. (2009) Flora exótica invasora del bosque de ribera en el curso medio-bajo del río Segre (Cataluña). Tercer Congreso Nacional sobre Especies Exóticas Invasoras. Zaragoza (España). Presentación oral.

A lo largo de este periodo también he publicado artículos en revistas de divulgación y en actas de congresos:

Juárez Escario A., Solé-Senan XO., Pedrol, J., Conesa JA., (2016) Estudi de la flora exòtica del riu Segre al seu pas pel Segrià. Origen i potencial invasor. *Shikar: revista del Centre d'Estudis Comarcals del Segrià* 3: 152-155.

Juárez Escario A., Solé-Senan XO., Conesa JA., Recasens J. (2013) Diversidad y riqueza de malas hierbas exóticas en campos de frutales. *Vida rural* 357: 46-49.

Juárez Escario A., Solé-Senan XO., Conesa JA., Recasens J. (2013) Malas hierbas exóticas en cultivos de maíz en Lleida, ¿Qué ha cambiado en veinte años? *Vida rural* 356: 54-58.

Juárez A., Solé X., Conesa JA. (2010) Diversity and richness of exotic weeds in fruit tree orchards in relation to irrigation management. *Aspects of Applied Biology* 104:79-87.

Juárez A., Recasens J., Taberner A., Conesa JA. (2010) Evolución de la flora exótica en frutales de regadío del W de Cataluña (1989-2009) In: Invasiones Biológicas: avances 2009. GEIB Serie Técnica 4: 29-40.

Solé XO.; **Juárez A.**; Pedrol J.; Conesa JA. (2010) Vulnerability of riparian ecosystems in the Mediterranean basin to invasion by exotic plants: the case of middle-low Segre river (Catalonia, NW Iberian peninsula). *Aspects of Applied Biology* 104: 1-9.

Agradecimientos

Al llegar al final de una etapa tan bonita y dura como es la elaboración de la tesis doctoral, miro hacia atrás y veo a toda la gente que me ha acompañado en este camino, que me ha aportado tanto, a nivel profesional y personal, y a la que estoy inmensamente agradecido.

Toda esta historia comenzó un mes de Julio con un e-mail enviado a Jordi Recasens, del grupo de Malherbologia de la Universitat de Lleida. Jordi, muchas gracias por responder ese mail, reunirme en tu despacho y proponerme la idea de pedir una beca para estudiar la flora arvense exótica que está presente en los cultivos de regadío. Esa primera conversación, y muchas otras que vinieron después, se han materializado finalmente en todo este trabajo. Gracias también por animarme a presentar todo este trabajo en los múltiples congresos que hemos compartido y donde he conocido gente tan valiosa.

Aquella beca, y con ella, la posibilidad de realizar todo este estudio, tampoco la hubiese conseguido sin la ayuda de Andreu Taberner, muchas gracias por ofrecerte a ello y por orientarme y ayudarme con la parte más agronómica de este trabajo, que en un principio iba a tener una forma muy diferente a la que finalmente ha adquirido.

La orientación, más ecológica y botánica, debo agradecérsela a mi director de tesis Josep Antoni Conesa. Josep Antoni, muchas gracias por tomar las riendas de la dirección de mi tesis y ayudarme a dirigirla hacia el mundo que realmente me apasiona, el de la botánica y la ecología vegetal, sin poner trabas a las ideas que he ido desarrollando para modelar este trabajo. Gracias por confiar siempre en mí. Siempre me he sentido muy valorado contigo. Muchas gracias además por descubrirnos, junto con Joan Pedrol, otro gran maestro para mí, la gran belleza y diversidad que se esconde en los secanos, en los territorios áridos de esta parte del valle del Ebro, en sitios tan increíbles como los Monegros, y por involucrarnos en tus proyectos de divulgación. Gran parte de mi formación botánica, iniciada en la Universidad Autónoma de Madrid, te la debo a ti, algo que siempre te voy a agradecer.

Finalmente la beca se acabó, demasiado pronto, justo recién acabada la parte experimental de este trabajo, pero con ella llegó la oportunidad de desarrollar mi otra gran pasión, el trabajo de laboratorio, que me ha permitido acabar esta tesis sin presiones económicas, y lo más importante, que me ha ayudado a crecer como persona, a aprender muchísimo a nivel laboral y a conocer gente maravillosa, con la que comparto la rutina diaria en el departamento de Producció Vegetal i Ciència Forestal. Con vosotros me siento valorado, reconocido, cuidado e ir a trabajar cada día se convierte en un placer y en un acto de agradecimiento. Muchísimas gracias a todos, sin excepción. En especial quiero dar las gracias a Tere y a Carmen, mis hadas madrinas en Lleida, con las que comparto cada día risas, confidencias, y que me sostienen en los momentos menos buenos. Gracias por crear ese espacio en el que me siento seguro, tranquilo y feliz. Gracias también a Cristina Chocarro, porque mucho antes de empezar la tesis confió en mí y me regaló esas jornadas maratonianas por los prados del pirineo de Huesca donde tanto aprendí y disfruté.

En todo este tiempo, moviéndome entre Madrid y Lleida, mucha gente ha entrado y salido de mi vida, y todos han dejado su huella…pero hay gente que no se va nunca, aunque ya no esté. Muchas gracias Conchi, por tu inmensa generosidad, por esa risa sonora que nunca se me olvidará, por todo lo que aprendí contigo y porque soy quien soy en parte gracias a ti. Estoy seguro que, de algún modo, y en algún lugar, nos volveremos a encontrar.

Gracias a los colegas de Madrid que me han acompañado en esta etapa, de los que solo quedas en Madrid tú, mi amiga Espe, a la que tanto quiero y tanto extraño. A mi brother topo Blas y a Jana, que son un ejemplo de tantas cosas vividas y por vivir.

Lleida no solo me ha permitido realizarme en lo laboral; lo más importante que me ha regalado es la gente que ha ido apareciendo en mi vida, a la que tanto quiero y que son mi familia aquí.

Muchas gracias Sónia por tantas cosas que no caben en esta tesis, eres un ángel todo de luz que me encontré nada más llegar a esta ciudad y que es ahora como mi hermana en Lleida; y a Arnau, por ser el amigo más generoso y noble que se puede tener.

Ana, encontrarnos en el pasillo de PVCF supuso un antes y un después en mi vida. Solo nosotros sabemos la conexión que nos une. Muchas gracias por estar siempre ahí, con la palabra precisa y la sonrisa perfecta, como dice la canción. Te quiero. También a Matilda, que es toda alegría y que tiene la suerte de tener la mejor madre.
Irene…por las risas descontroladas e incontrolables, por saber lo que piensa el otro sólo con una mirada, por el argot toledano, por ese aire cañí…por todo eso y por mucho más te quiero tanto.
A Tunica, Cesar, Addy, Núria, August, Elsa y el Calamaro, tan especiales que aunque no estén a diario es como si lo estuviesen, que hacen que el sitio de encuentro escogido sea solo un decorado sin importancia. A Natalia, por entenderme tan bien y hacerme la portada más bonita del mundo. A los coperos del dijous, Paulita, Eva, Agnes, Filipe, Blanca, Fran, Diana, Salomé, Carles, Alba, Jonathan, Jordi, Neus, Marina…y todos los que me dejo, que son muchos, por tantos momentos de risas, confidencias, abrazos…que han convertido en días de verano hasta aquellos con más niebla cerrada.
A Xavi, per ser el millor company de tantes i tantes aventures, i, parafrasejant l'Ana, perquè aquesta tesi és tan teva com meva. A l'Ana, el Pepe, la Maria i la padrina per cuidar-me com un membre més de la familia.

Finalmente, sobre todo, a mi familia porque si he llegado hasta aquí ha sido gracias a ellos. A mis abuelos, a los paternos, que se fueron demasiado pronto, y a los maternos, que lo acaban de hacer, porque serán siempre para mí ejemplo de lucha, dulzura y cariño. A mis padres, porque he llegado hasta aquí gracias a vuestro gran esfuerzo y todo el amor que me habéis dado. Por vuestra confianza y apoyo constante, vuestros cuidados, por darme siempre libertad para elegir mi camino con total respeto. Nada de lo que soy seria posible sin vosotros. Mamá y papá, os quiero
A mi hermana, mujer luchadora, amorosa, inteligente, porque es para mi el modelo en el que me inspiro siempre y el faro que me orienta, el refugio y el espacio sin juicios. A mis sobrinos, porque son ángeles que nos ha regalado Dios y por los que doy gracias a diario. A Fabri, por ser ciencia, arte y sensibilidad y ser como el hermano que nunca tuve. Os quiero.

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Summary

Agriculture intensification is driving changes in weed assemblages and enhancing the prominence of alien weeds in crops at a temporal scale. Although irrigation is a major component of agricultural intensification and alien weeds have severe negative economic and ecological impacts in agroecosystems, knowledge of the causes and the processes that lay behind weed assemblies and success of alien weeds in irrigated agricultural crops is currently lacking.

On the one hand, irrigated crops are connected with natural habitats in agricultural landscapes, particularly with riparian habitats. On the other hand, the nature of disturbances operating in both habitats is similar. These facts may favour the establishment of a flow of the most adapted species between crops and natural habitats, which may involve the spread and colonization of those alien plants present in both systems.

In this context, and focusing on irrigated agricultural land in semi-arid north-eastern Iberian peninsula, this study aims at identifying temporal changes in weed community composition as well as unravelling the intrinsic (i.e. functional traits of plant species) and extrinsic (i.e. crop management methods) factors that lay behind the success of alien weeds in irrigated crops (maize and orchards) and their potential capability to spread and colonize surrounding natural habitats. These main goals were addressed using a trait-based approach, since it allows to identify general community assembly rules and their response to management practices as well as to disentangle weed invasion dynamics.

Results showed that at long-term temporal scale, there were changes in diversity, composition and functional structure of weed communities, accompanied by a higher prominence of alien plants within these weed assemblages. These changes were more pronounced in orchards whereas the structure of weed communities in maize crops was more consolidated at a functional scale.

Trait-based approach allowed to identify a suite of traits related to the success of species in these habitats. In orchards, C4 photosynthesis, graminoid and perennial forms, clonal reproduction, hydrochory and seed dispersed by multiple methods were among the most benefited plant traits, which were mainly found in successful alien weeds. This trait selection was mainly driven by flood irrigation, which also modulated the effect of weed control management on functional trait selection. On the other hand, management in drip-irrigated orchards configures a weed community characterized by a lower prominence of alien species and a functional structure that make it less competitive to the trees while enable it to provide pollination services.

Furthermore, the trait syndrome favoured in flood-irrigated orchards was also linked to the capacity of alien species to overcome ecosystems filtering and colonize surrounding natural riparian habitats, thus establishing a flow of alien weeds between crops and natural ecosystems.

In conclusion, this study disentangles for the first time the patterns of functional assembly of weed communities of irrigated crops focusing on alien weed prominence and the role of management practices in the invasibility of orchards, at a temporal and spatial scale. Results provide valuable information that can be addressed to informed management recommendations aimed to establish a proper management intended to prevent the establishment of potentially invasive alien weeds in crops and develop trait-based early detection programs of the problematic alien weeds for establishing effective control and/or eradication measures of those species

Resum

La intensificació agrícola provoca canvis a les comunitats de males herbes als cultius alhora que incrementa la prominència d'espècies exòtiques. Tot i que el regadiu és un dels principals components d'aquesta intensificació, i malgrat els elevats impactes, tant econòmics com ecològics, que produeixen les males herbes exòtiques als agroecosistemes, actualment es desconeixen les causes i els processos que expliquen els patrons florístics de les comunitats de males herbes i l'èxit de les espècies exòtiques als cultius de regadiu.

D'altra banda, en els paisatges agrícoles, els cultius de regadiu es troben en contacte amb els hàbitats naturals, en particular amb els ambients riparis. A més a més, la natura de les pertorbacions que operen tant als cultius de regadiu com als hàbitats riparis és similar. Aquests fets podrien afavorir l'establiment d'un flux entre els cultius i els ambients naturals d'aquelles espècies més adaptades, la qual cosa podria comportar la dispersió i colonització d'espècies exòtiques presents en ambdós ambients.

En aquest context, i particularitzant en les zones de regadiu que ocupen les àrees semiàrides del nord-est de la península Ibèrica, el present estudi es centra a identificar els canvis de la composició florística de les comunitats de males herbes dels cultius de regadiu (panís i fruiterars) al llarg del temps. També vol contribuir a desxifrar els factors intrínsecs (a nivell dels atributs funcionals de les espècies vegetals) i extrínsecs (a nivell de tècniques de maneig) subjacents a l'èxit de les espècies exòtiques en aquests cultius i a la seva potencial capacitat de colonitzar els hàbitats naturals dels voltants. Per assolir

aquests objectius, s’ha utilitzat una aproximació basada en els atributs funcionals de les espècies. Aquesta aproximació permet identificar les regles bàsiques que regeixen l’agrupació d’espècies dins les comunitats vegetals i la seva resposta al maneig, així com també donar resposta a la dinàmica de les invasions biològiques.

Els resultats mostren que a llarg termini, hi ha hagut canvis en la diversitat, la composició i l’estructura funcional de les comunitats de males herbes a més d’un increment del protagonisme de les males herbes exòtiques. Aquests canvis han estat més pronunciats en els fruiterars, mentre que als cultius de panís l’estructura d’aquestes comunitats sembla més consolidada des del punt de vista funcional.

L’aproximació funcional ha permès identificar un conjunt d’atributs relacionats amb l’èxit de determinades espècies dins les comunitats de males herbes. A les comunitats presents als fruiters, entre els atributs funcionals més beneficiats destaquen la via fotosintètica C4, les formes graminoides i perennes i la capacitat de reproducció vegetativa, així com la hidrocòria i les llavors adaptades a més d’un mode de dispersió. Aquests atributs es troben representats principalment a les espècies exòtiques i la seva selecció està dirigida fonamentalment pel sistema de regadiu per inundació, que alhora modula l’efecte que té el mètode de control de les males herbes en la selecció d’atributs funcionals. Per altra banda, el maneig dels cultius regats per degoteig configura una comunitat de males herbes caracteritzada per una menor prominència d’espècies exòtiques i una estructura funcional que la fa menys competitiva envers els arbres fruiters alhora que pot aportar-los recursos ecològics en forma de pol·linitzadors.

D’altra banda, el conjunt d’atributs que es veuen afavorits en els fruiterars irrigats per inundació també es troba relacionat amb la capacitat que tenen les males herbes exòtiques per superar els filtres ambientals dels hàbitats naturals i poder colonitzar els ambients riparis adjacents als cultius, de manera que s’estableix d’aquesta forma un flux d’espècies exòtiques entre els fruiters i els ecosistemes de ribera.

En definitiva, aquest estudi desxifra per primer cop les regles subjacents a la configuració funcional de les comunitats de males herbes dels cultius de regadiu. A més dedica una especial atenció al protagonisme de les espècies exòtiques, així com el paper que tenen les pràctiques agrícoles en la susceptibilitat dels fruiterars a ésser colonitzats per aquestes plantes, tant des d’un punt de vista temporal com espacial. Els resultats obtinguts proporcionen una informació valuosa que pot ser aplicada per formular un seguit de recomanacions dirigides a instaurar unes pràctiques de maneig que permetin prevenir l’establiment als cultius de regadiu d’espècies exòtiques potencialment invasores. També contribueixen a desenvolupar programes de detecció precoç de males herbes problemàtiques fonamentats en una aproximació funcional, de cara a establir mesures efectives de control i/o eradicació d’aquestes espècies.

Resumen

La intensificación agrícola está provocando cambios en las comunidades de malas hierbas presentes en los cultivos a la vez que incrementa la prominencia de especies exóticas en ellos. Aunque el regadío es uno de los principales componentes de esta intensificación, y a pesar de los elevados impactos, tanto económicos como ecológicos que producen las malas hierbas exóticas a los agroecosistemas, actualmente se desconocen las causas y los procesos que explican los patrones florísticos de las comunidades de malas hierbas en los cultivos de regadío y el éxito de las especies exóticas en ellos.

Por otro lado, en los paisajes agrícolas, los cultivos de regadío están en contacto con hábitats naturales, en particular con los ecosistemas riparios. Además, las perturbaciones que operan tanto en los cultivos de regadío como sobre los hábitats riparios son de naturaleza similar. Esta realidad podría favorecer el establecimiento de un flujo entre los cultivos y los ambientes naturales de aquellas especies más adaptadas, lo cual podría comportar la dispersión y colonización de especies exóticas presentes en ambos ambientes.

En este contexto, y particularizando en las zonas de regadío que ocupan las áreas semiáridas del noreste de la península ibérica, el presente estudio se centra en la identificación de los cambios sufridos en la composición florística de las comunidades de malas hierbas de los cultivos de regadío (maíz y frutales) a lo largo del tiempo, así como en descifrar los factores intrínsecos (a nivel de los atributos funcionales de las especies vegetales) y extrínsecos (a nivel de las técnicas de manejo del cultivo) subyacentes al éxito de las especies

exóticas en estos cultivos y a su capacidad potencial de colonizar los hábitats naturales adyacentes. Para lograr estos objetivos, se ha utilizado una aproximación basada en los atributos funcionales de las especies, que permite identificar las reglas básicas que rigen la agrupación de especies dentro de las comunidades y su respuesta al manejo, así como aquellas que explican la dinámica de las invasiones biológicas.

Los resultados muestran que a largo plazo, ha habido cambios en la diversidad, la composición y la estructura funcional de las comunidades de malas hierbas, así como también un incremento del protagonismo de las malas hierbas exóticas. Estos cambios han sido más pronunciados en los frutales, mientras que en los cultivos de maíz la estructura de estas comunidades parece más consolidada desde el punto de vista funcional.

La aproximación funcional ha permitido identificar un conjunto de atributos relacionados con el éxito de determinadas especies dentro de las comunidades de malas hierbas. En las comunidades presentes en los cultivos frutales, entre los atributos funcionales más beneficiados destacan la vía fotosintética C4, las formas graminoides y perennes y la capacidad de reproducción vegetativa, así como la hidrocoria y las semillas adaptadas a más de un modo de dispersión. Estos atributos se encuentran representados principalmente en las especies exóticas y su selección está determinada fundamentalmente por el sistema de riego por inundación, que a su vez modula el efecto que tiene el método de control de las malas hierbas en la selección de atributos funcionales. Por otro lado, el manejo de los cultivos regados por goteo configura una comunidad de malas hierbas caracterizada por una menor prominencia de especies exóticas y una estructura funcional que la hace menos competitiva hacia los árboles frutales, a la vez que puede aportarles recursos ecológicos en forma de polinizadores.

Por otro lado, el conjunto de atributos favorecidos en los cultivos frutales regados por inundación también se encuentra relacionado con la capacidad que tienen las malas hierbas exóticas para superar los filtros ambientales de los hábitats naturales y colonizar los ambientes riparios adyacentes a los cultivos, estableciéndose de esta forma un flujo de especies exóticas entre los cultivos frutales y los ecosistemas de ribera.

En definitiva, este estudio descifra por primera vez las reglas que subyacen en la configuración funcional de las comunidades de malas hierbas de los cultivos de regadío. Presta una especial atención al protagonismo de las especies exóticas, así como al papel que tienen las prácticas agrícolas en la susceptibilidad de los cultivos frutales a ser colonizados por estas especies, tanto desde un punto de vista temporal como espacial. Los resultados obtenidos proporcionan una información valiosa que puede ser aplicada para formular una serie de recomendaciones dirigidas a instaurar unas prácticas de manejo que permitan prevenir el establecimiento en los cultivos de regadío de especies exóticas potencialmente invasoras, así como a desarrollar programas de detección precoz de malas hierbas problemáticas fundamentados en una aproximación funcional, de cara a establecer medidas efectivas de control y/o erradicación de estas especies.

CHAPTER 1

General Introduction

GENERAL INTRODUCTION

Background

Irrigation is a fundamental element of agricultural production in the Mediterranean area due to water scarcity and the high inter-annual and seasonal variability of rainfall typical in this area (Correia, 1999). Irrigation allows crop diversification, helps to increase agricultural production and stabilizes crop yield (Hussain, 2007). For these reasons, irrigation has been encouraged in Mediterranean Southern Europe (González-Estébanez et al., 2011). As a consequence, in the last decades the irrigated area in these European countries has increased by more than 4 million ha. representing nowadays 12% of the total cultivated agricultural land (Plan Bleu, 2008). Amongst all of them, the largest increase of irrigated land has taken place in Spain (Eurostat, 2015), being the European Mediterranean country with the largest irrigated agricultural land; which currently accounts for the 22% of the total Spanish agricultural land (MAGRAMA, 2015) and for the 15% of the total irrigated area of the Mediterranean basin (Daccache et al., 2014).

Conversion from rainfed to irrigated crops is the major driver of agricultural landscape change and makes up one of the principal components of the agriculture intensification. It is widely recognized that agricultural intensification has negative impact on biodiversity (Brotons et al., 2004; Solé-Senan et al., 2014) both at field and at landscape scales (Jose-Maria et al., 2010). Within agroecosystems, weeds are particularly sensitive to this intensification process (Storkey et al., 2012). As a consequence, there has been a general decline of weed diversity in European agroecosystems in the last century (Meyer et al., 2013; Stoate et al., 2001; Van Calster et al., 2008), particularly in Mediterranean areas (Chamorro et al., 2016; Jose-Maria et al., 2010; Solé-Senan et al., 2014) and a change in compositional and functional weed assemblages (Fried et al., 2009; Jose-Maria et al., 2011).

This process has been accompanied by an increase of alien weeds within weed assemblages, since this group is particularly favoured by disturbances and high availability of resources, such as light and nutrients (Pyšek et al., 2005). These are the conditions that take place in irrigated agricultural habitats, particularly in Mediterranean basin, where water availability and high temperatures of summer favour the development of alien flora (Chytrý et al., 2009), specifically those tropical and sub-tropical (Brunel et al., 2010).

The increase of alien species in agricultural lands in the last decades has been reported mainly in the centre and the north of Europe (Lososová and Simonová, 2008; Potts et al., 2010; Šilc and Čarni, 2005). Although the presence of alien weeds has been also described in crops in the Mediterranean area (Casasayas, 1990; Maillet and López-García, 1999; Masalles et al., 1996; Recasens and Conesa, 2003), there is a need of more insight into the long-term temporal changes of the weed assemblages in irrigated agricultural land in Mediterranean areas and the actual prominence of these alien weeds within, since it is expected this process will be enhanced by irrigation.

Moreover, most of the current knowledge at this field has been achieved in annual crops (Fagúndez et al., 2016), whereas perennial crops have been scarcely studied, despite their prominence in irrigated agricultural land in Mediterranean area (perennial crops occupy 42% and 45% of total irrigated area in Spain and in Catalonia, respectively) (IDESCAT, 2013; INE, 2013). Since it has been proved that weed assemblages vary among crop types (Fried et al., 2012) and differences on weed communities between perennial and annual crops have been described (Meiss et al., 2010), a deeper analysis on the structure of weed communities and the prominence of alien weeds in perennial crops is needed.

Impacts of alien plants

It has been widely described how alien plants negatively impact in natural habitats from species (e. g. by decreasing local plant species diversity) (Gaertner et al., 2009; Hejda et al., 2009; Powell et al., 2011) to ecosystem scale (e. g. altering nutrient cycling rates, affecting ecosystem services) (Vilà et al., 2010; Zedler and Kercher; 2004) but they have also taking their toll on agricultural habitats. Alien weeds in crops have a negative economic impact in the form of crop yield loses, weed control costs and impact on the crop price (Vilà et al., 2004). Pimentel et al. (2005) estimated a 12% of crop yield losses in USA due to alien weed impacts, which represents approximately $24 billion in lost crop annually and about 3$ billion in herbicides for invasive alien weed control. At a regional scale, Recasens et al. (2007) estimated in almost €7 million the costs associated to crop losses and control measures of *Abutilon theophrasti* in maize fields in “Pla d’Urgell” county (Lleida). Furthermore, alien weeds not only impact economically in crops, they also cause environmental damages by harming functionality and ecosystem services provided by plant communities in agroecosystems (Crosti et al., 2010). However, despite these impacts, and the fact that irrigated agricultural land in Mediterranean area is among the most invaded habitats in Europe (Chytrý et al., 2009), there is a lack of studies aimed at unravelling the factors laying behind such success.

Overall, among the ecological aspects integrated in the success of an alien plant in colonizing an ecosystem, two factors stand out: the invasiveness of the species and the habitat invasibility (Lonsdale, 1999).

Invasiveness of alien plants

Not all the alien plants that reach a new habitat are able to successfully colonize it and establish permanent reproductive populations (Box 1). It has been estimated that only 1% of the introduced species in a new area will develop invasive behaviour (Williamson, 1996). Possessing a syndrome of traits that benefit these species in the new habitat is a determinant factor that has to be taken into consideration to disentangle their high performance (Thompson et al., 1995; Pyšek and Richardson, 2007). There is a huge amount of scientific literature seeking to identify which traits help to explain plant invasiveness (e.g. Daehler, 2003; Ordonez et al., 2010; van Kleunen et al, 2010). Despite the disparity of approaches and results, traits related to plant height, vegetative growth, specific leaf area and reproductive have been associated to invasiveness (Pyšek and Richardson, 2007). Nevertheless, there is a general consensus that ecological attributes of successful alien invaders are strongly habitat-dependent (Daehler, 2003; Lloret et al., 2005; Thompson et al., 1995). In resource-rich, disturbed habitats alien success is associated with traits that enable high survival rate and fast growth (Dietz and

Edwards, 2006; Funk et al., 2016) whereas in resource-poor habitats, traits related to resource conservation such as high resource-use efficiency are selected (Funk and Vitousek, 2007). Besides, it has been proved that in nutrient-rich habitats alien plants functionally differ from resident plant community, which allow them to colonize empty functional niches, as limiting similarity theory predicts (Abrams, 1983; Hejda and de Bello, 2013; Macarthur and Levins 1967).

BOX 1

Some definitions

It is important to clarify the concepts utilized in this work, taken from Richardson et al. (2000) who described plant invasions as an ecological process, independently from the impacts of this process on the ecosystems.

Alien plant: Plant taxa in a given area whose presence there is due to intentional or accidental introduction as a result of human activity.

Casual alien plants: *Alien plants* that may flourish and reproduce occasionally in an area, but which do not form self-replacing populations, and which rely on repeated introductions for their persistence

Naturalized plants: Alien plants that reproduce consistently and sustain populations over many life cycles without direct intervention by humans (or in spite of human intervention); they often recruit offspring freely, usually close to adult plants, and do not necessarily invade natural, seminatural or human-made ecosystems.

Several studies have described the traits that define successful alien weeds in arable lands in the centre and north of Europe (Jauni and Hyvönen, 2012; Lososová et al., 2006; Lososová et al., 2008), linking weed invasiveness to annual life form and a preference for moisture and nitrogen. Nevertheless, traits favouring alien weeds in irrigated agricultural habitats in Mediterranean area have been scarcely explored so far, focusing only in annual crops (Fagúndez et al., 2016).

Invasibility of habitats

As in the case of alien success, not all the ecosystems are equally susceptible to be invaded. This susceptibility can be interpreted in terms of disturbance regime and resource availability (Pyšek et al., 2010). Successionally advanced plant communities, nutrient-poor habitats or those in extreme terrestrial environments are more resistant to alien plant invasion (Alexander et al., 2011; Rejmánek et al., 2005) whereas disturbed, open, high-resource habitats, such as wetlands, fresh-waters, littoral and man-made habitats exhibit the highest level of invasions (Cadotte and Lovett-Doust, 2001; Chytrý et al., 2008). Disturbances increase the susceptibility of a habitat to be invaded through the generation of empty niches (Shea and Chesson, 2002), reduction of competition from native plants (Catford et al., 2011) and increase of resources availability (Davis and Pelsor, 2001; Maron and Connors, 1996).

In agricultural habitats, disturbances are triggered by management practices (e.g. herbicide application, mowing, ploughing, tilling), which are coupled with pulses of resources increase (e.g. fertilization, increased light availability in summer crops and water supplies by irrigation). These factors make these habitats particularly susceptible to be invaded by alien weeds (Pyšek et al., 2010). On the other hand, it has been proved that the nature of the disturbances modulates invasibility even in a same habitat (Hobbs and Huenneke, 1992; Smith and Knapp, 1999).

These changes in invasibility in response to different disturbances constitute a particular aspect of the overall response of agroecosystems to management practices. Crop management is a major driver of weed composition (e.g., Meiss et al., 2010), diversity (e.g., Légère et al., 2008) and functional assemblages (e.g., Fried et al., 2012) through filtering plant functional traits, and with them, species. This selection also influences the prominence of alien weeds in these communities (Booth and Swanton, 2002). It has been observed that the invasibility of a habitat decreases when resident plant community is highly competitive (Fried et al., 2014). Likewise, functional diverse communities are more resistant to be invaded (Byun et al., 2013) and correlations between richness and diversity of native and alien plants have been described (Levine et al., 2004). Hence, in agricultural systems, disentangling the effect of different management practices on the configuration of weed communities and in the prominence of alien weeds within them by selecting functional traits is crucial to develop measures aimed at configuring weed communities that maximize the provision of ecosystem services to agroecosystems while minimizing invasibility.

The usefulness of the trait-based approach for unraveling general community assembly rules and weed response to management practices has been clearly established in weed science (Booth and Swanton, 2002; Gaba et al., 2014; Navas, 2012). Moreover, it has contributed to predict weed invasion dynamics (Drenovsky et al., 2012). Hitherto, the study of the effects of different management practices on weed community assemblages from a trait-based approach has been intensively explored (e.g. Colbach et al., 2014; Fried et al., 2012; Gaba et al., 2014; McIntyre and Lavorel, 2001;

Trichard et al., 2013) but their influence in the invasibility of crops have been scarcely studied (Vilà and Gimeno, 2007) and to date, there is a lack of studies focusing on this aspect from a trait-based approach (McIntyre et al., 2005).

In the prevention of new invasions of alien weeds, the early recognition of potential invaders is crucial (Simberloff, 2009). This identification can be improved through the trait-based approach, which allows to identify those functional traits related to the invasiveness of the species (Moravcová et al., 2015) and the management practices which enhance the selection of these traits, thus increasing the susceptibility of the habitats to be colonized by these species (Thuiller et al., 2006)

Spatial patterns of alien weeds at regional scale

The invasion process requires an alien species to overcome successive environmental barriers. Primarily, the first environmental barriers are represented by disturbed, human-modified habitats, and after that, species have to cope with the environmental filters of natural or semi-natural vegetation (Richardson et al., 2000). These phases represent a continuum over time or along space and they have been described in urban-natural gradients (Alexander et al., 2011; Burton et al., 2005).

In agricultural landscapes, natural and agricultural elements are adjacent. This is the case of irrigated agricultural land in floodplains, where crops and riparian areas coexist. Plant communities of these ecosystems are subjected to similar disturbances (i.e. periodical flooding, temporary nutrient uptakes) so it is expected that species that compose their plant communities present a similar trait syndrome, which confers them more resistance/resilience to these disturbances. For this same reason, it is feasible that alien species that are able to overcome disturbance constrains of agricultural ecosystems would be equally adapted to disturbances in riparian habitats. These trait similarities and the physical connection between crops and natural areas may trigger the crop-non-crop exchange of plant species (Tscharntke et al., 2005). Moreover, riparian habitats included within agricultural landscapes are negatively affected by intensified farming practices, resulting in higher rates of soil erosion and sedimentation, increased nutrient inputs and physical resources such as light and water table fluctuations (Richardson et al., 2007). This degradation generates favourable conditions for the establishment and spread of alien plants (Liendo et al., 2013; Tabacchi et al., 1996). Invasive species in riparian habitats severely impact on biodiversity, productivity, nutrient cycling and food webs (Richardson et al., 2007). On the other hand, riparian habitats can also act as a source of alien plants, which can invade nearby terrestrial habitats (Pyšek et al., 2007) as well as facilitate dispersion of alien plant propagules through irrigation channels that may subsequently colonize downstream irrigated crops.

Despite these connections, and the fact that irrigated agricultural land and riparian habitats are among the most susceptible ecosystems to plant invasions (Chytrý et al., 2008), particularly in Mediterranean areas (Chytrý et al., 2009; Sanz-Elorza et al., 2006), few attempts have been performed to identify patterns of plant invasion gradients between agricultural and natural ecosystems within agricultural landscape (Ferreira and Moreira, 1995; Liendo et al., 2013), and they have been mainly focused on the level of invasion (Meek et al., 2010) but without take into account the functional aspects that lay behind these processes. This focus is essential to unravel the functional rules that govern mechanisms of plant invasion among habitats in order to develop informed and objective recommendations regarding management, conservation and restoration of these habitats (Catford et al., 2012) aimed to prevent the establishment of alien plants in interconnected agricultural and natural habitats and minimize the exchange of these species between them.

MAIN OBJECTIVES OF THE THESIS

Starting from the study of temporal changes in weed communities in irrigated crops, we apply a functional approach to address the invasiveness of alien weeds and the invasibility of irrigated crops as well as the linkages between those crops and the surrounding natural landscape in terms of alien plants. This framework is specified in these particular objectives:

1. Evaluate long-term temporal changes in the compositional and functional assemblages of weed communities of irrigated annual (maize crops) and perennial crops (fruit tree orchards) focusing particularly on alien weeds.

2. Define a suite of functional traits linked to the success of alien weeds in irrigated orchards

3. Identify how management (i.e. irrigation and weed control methods), affects the compositional and functional structure of weed communities in irrigated orchards.

4. Detect whether the prominence of alien plants in weed communities in irrigated orchards could be the result of particular management practices.

5. Compare the level of invasion of alien weeds in irrigated orchards with that in surrounding natural habitats (i.e. riparian habitats).

6. Determine whether exists a flow of alien plants between irrigated orchards and the surrounding natural habitats and the source of this

exchange, as well as characterizing which functional traits are involved in this process.

These objectives are included in the following chapters of this thesis in the form of scientific papers (i.e., structured in the sections: abstract, introduction, material and methods, results, discussion, conclusions and references), which allow readers to understand each one independently of the others. Finally and to address the main target of the thesis, results from the different chapters are jointly discussed, leading to the main conclusions.

METHODOLOGY AND OUTLINE OF THE THESIS

Field experiments of this work were conducted in the irrigated area included in the Plain of Lleida (Catalonia, NE Spain) (Fig. 1) during summer and autumn seasons between the years 2009 and 2011, coinciding with the irrigation period of the surveyed crops.

Figure 1. Location of study area (green surfaces).

Climate of this area is semiarid Mediterranean, with mean annual temperature ranging from 13.7ºC to 15ºC and annual precipitation of 385 mm, mainly concentrated in spring and autumn (Ninyerola et al., 2005).

To answer objective 1, taking as a reference a group of surveys of weed communities carried out in maize fields and fruit irrigated orchards in 1988-89 (Conesa, 2001; Recasens and Taberner, unpublished), we performed in 2009 new plant inventories in 30m^2 plots (3x10m) in 58 maize fields and 79 orchards located in the same UTM 1km x 1 km squares as in the 1989 surveys, at similar time of the year, following equal methodology. Inventoried weed species were characterized in terms of their origin and by a suite of traits related to crop disturbances. Paired surveys were compared between years for total, alien and native plant species abundance in order to detect increasing, decreasing and stable trajectories. These trajectories were related to functional groups. Results of this study are reported and discussed in Chapter 2.

Objective 2 was addressed by comparing a group of plant attributes between alien and native species identified in 10m^2 plots at random positions in the alleys in 136 flood-irrigated orchards. Concurrently, prominence of alien and native species within weed communities of surveyed orchards was analyzed in terms of species richness and abundance (Chapter 3).

To meet objectives 3 and 4 (Chapter 4), floristic surveys were recorded in 10m^2 plots in 75 flood and 75 drip irrigated orchards, in both alleys, where weeds are controlled mechanically, and in the tree lines, where herbicide is applied. Identified alien and native plants were characterized by those functional traits related to their response to crop disturbances. Species diversity, plant cover, floristic and functional structure were compared among irrigation and weed management methods. Species diversity and cover values were explored for total species and particularly for alien weeds. Functional structure was characterized using the community-weighted means (CWM) of traits (Lavorel et al., 2008), which reflects the average trait value of the most dominant species in a community. This approach was also used for achieving objective 6.

In order to achieve objectives 5 and 6 (Chapter 5), in each kilometre along the 22km that compose the last stretch of the Noguera Ribagorçana river (41º39'-41º51'N; 0º33'-0º43'E), floristic surveys were performed in the three main riparian habitats (i.e. muddy line, reedbed and riparian forest) and in the adjacent irrigated orchards located in a gradient of distance to the stream channel. Within orchards, surveys were carried out both in the alleys and in the tree lines to take into account influence of management in weed composition. Plant diversity, species composition and functional groups were compared within and between orchards and natural habitats both for total, native and alien groups of plants in order to detect similarities among plant communities and identify which functional traits were linked to this exchange. In those habitats where species composition presented similarities, patterns of nestedness between species-rich sites and species-poor sites were sought in order to determine which habitat act as alien species source.

In Chapter 6 results from the preceding chapters are integrated and jointly discussed, leading to the main conclusions.

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CHAPTER 2

Changes in alien and native weed communities in irrigated maize crops and fruit tree orchards between 1989-2009. A functional approach.

Submitted to *Annals of Applied Biology*.

Changes in alien and native weed communities in irrigated maize crops and fruit tree orchards between 1989-2009. A functional approach.

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Abstract

Agricultural intensification in Europe in the last 30 years has led to changes in compositional and functional weed structure in agroecosystems as well as to an increasing in the prominence of alien weeds. Irrigation is one of the major drivers of agricultural intensification, particularly in semi-arid zones of Mediterranean area. In the last decades, irrigated land has been enlarged in the semi-arid agricultural lands in north-eastern Spain, so the aims of this study are to identify in this area long-term temporal changes in compositional and functional weed assemblages in annual (i.e. maize crops) and perennial (i.e. orchards) irrigated crops and unravel whether they affected native and alien plants differently. Changes in diversity, composition and functional groups of the native and alien weed assemblages in fruit tree orchards and maize crops were assessed on plant surveys in 1989 and 2009. In the studied period, in fruit tree orchards it was found a decrease in diversity of native species accompanied by an increase of alien weed diversity and a general decrease in β-diversity in the weed community. In maize crops, diversity values of native and alien plants changed little over 20 years. The identification of functional groups revealed that, in fruit tree orchards, most of the species that increased their cover were graminoid alien species with C4 photosynthesis and water or multiple seed dispersal mode. Changes in mechanical weed control methods may help to explain this trait selection. In maize crops, the identified functional groups did not differ in the proportion of species that changed their cover between 1989 and 2009. In assessing the relationships between changes in weed assemblages and the functional traits of weed species, the multi-trait approach was more explanatory and accurate than was the analysis of single traits.

Keywords

Irrigation, diversity, biological traits, Multiple Correspondence Analysis, management, disturbances.

Introduction

In the last 30 years in the Mediterranean Basin, the amount of irrigated agricultural land has increased by more than 4,000,000 ha, and the largest increase occurred in Spain, where irrigated crops currently accounts for the 22% of the total Spanish agricultural land (MAGRAMA, 2015) and for the 15% of the total irrigated area of the Mediterranean basin (Daccache et al., 2014). The conversion from rainfed to irrigated crops has increased soil moisture and nutrient availability, which has contributed to a change in the weed assemblages' composition (Srivastava and Singh, 2005).

The nature of the selective pressures acting on these weed assemblages is different depending on the type of crop. Among perennial crops, such as fruit tree orchards, weeds are mainly controlled by mechanical and chemical means. In the last 20 years, mechanical weed control in fruit tree orchards has evolved from mowing to a more effective shredding system that improves the precision with which non-beneficial vegetation is eradicated (Taberner, 1999). In annual crops, such as maize, weed control mainly relies on the use of herbicides and crop rotation. In this sense, in the last 20 years the only significant change in chemical weed control has been the specific herbicides used. In 2005, the EU banned the use of atrazine because of its toxic effect in water bodies (European Commission 04/248), and it has been replaced by other active substances, such as terbutilazine, isoxaflutol, and aclonifen (Generalitat de Catalunya 2011). Furthermore, another herbicide, acetochlor, was banned in 2011 (Commission Implementing Regulation 1372/2011). Management filters, as well as plant migration process from surrounding crops, contribute to rapid changes in weed assemblages (Baker, 1974). Moreover, the international seed trade and global markets favour the entrance of alien plants (Recasens and Calvet, 1993; Maillet and Zaragoza, 2002). Crops are suitable habitats for alien plants because periodic disturbances occurring there increase nutrient availability and reduce competition from resident species (Prieur-Richard and Lavorel, 2000). In addition, fertilization and a steady supply of water enhance the growth and spread of the successfully established invaders (Huenneke et al., 1990). Invasive alien weeds can modify the native weed community by competition and dominance changes, which may reduce the richness of native species (Lumaret and Barrientos, 1990; Vilà et al., 2004) leading to biotic homogenization (Olden et al., 2004).

The combined effect of these processes leads to the consolidation of specific plant communities associated to a specific management regime (Lavorel et al., 1997). The biological and ecological traits of alien and native species dictate their ability to adapt themselves to periodic disturbances. Species that have similar attributes will respond in the same way to environmental conditions and disturbances (Weiher and Keddy, 1999). The analysis of single traits or the combined analyses of the suite of traits that identify functional groups are two conceptual approaches to the study of these processes. Plant traits are not independent; thus, a management regime might involve the selection of a particular combination of traits. As such, functional groups approach might be the best means of understanding these processes (Küster et al., 2008). Analyses based on functional groups aid in predicting the way in which a weed community will respond to disturbances and other selection pressures (Leishman and Westoby, 1992). For this reason, to characterize those functional groups, it is essential to focus on the traits affected by those disturbances, e.g., life form, photosynthesis pathway and the capacity for clonal growth (Lavorel et al., 1997).

Several studies have examined temporal changes in weed assemblages within annual crops (Tuesca et al., 2001; Andreasen and Stryhn, 2008; Potts et al., 2010), based on analyses of single attributes of species (Lososová and Simonová, 2008) or functional groups (Fried et al., 2009; Knapp et al., 2010). However, differences between annual and perennial crops in the changes in their associated weed assemblages based on their functional traits and the role of alien species within these groups are poorly documented (Meiss et al., 2010b; Ryan et al., 2010), particularly in the Mediterranean area.

We hypothesized that management of maize crops and fruit tree orchards in the last 20 years have influenced the changes in the composition and functional types of weed assemblages and have benefited alien species at the expense of native weed flora. Furthermore, those changes are reflected in selection for specific combinations of biological traits, which leads to functional groupings of species.

The objectives of this study were to (1) identify changes in the composition and diversity in the weed assemblages in irrigated perennial (fruit tree orchards) and annual (maize) crops over the last 20 years, (2) compare these changes in native and alien plants and (3) assess these changes within the context of species traits, both individually and in functional groups.

Materials and Methods

Study area

Surveys of weed assemblages were conducted in irrigated fruit tree orchards and maize crops in Lleida Province (Catalonia, Spain). The orchards were located in El Segrià county (41º37’N, 0º37’E), where the mean annual temperature is 15º C and total annual rainfall is 385 mm, more of which falls in autumn (Ninyerola et al., 2005). This county has 66% of the irrigated fruit tree orchards (32,626 ha) in the province (IDESCAT, 2010). Maize crops were surveyed in El Segrià, Pla de l’Urgell (41º45’N, 0º36’E), La Noguera (41º54’N, 0º47’E), and Pallars Jussà (42º5’N, 1º05’E) counties, of which the first three have 70% (20,133 ha) of the maize crops in Catalonia (López Querol et al., 2009). Pla de l’Urgell (13.5 º C, 418 mm) and La Noguera (14.9º C, 419 mm) have similar climatic characteristics to El Segrià. The climate is semi-arid Mediterranean, and temperature varies considerably daily and seasonally. Precipitation is higher in Pallars Jussà (13.7º C, 591 mm) (Rivas-Martínez and Rivas-Saenz, 1996-2009).

Plant surveys

Weed flora of fruit tree orchards and maize crops were surveyed firstly in the summer and autumn of 1989 (Conesa, 2001; Recasens and Taberner, unpublished). Weeds were identified within a 30m^2 plot (3x10m) in each field and an abundance-dominance score of between “+” and “5” was assigned to each species based on the Braun-Blanquet scale (1979). The Braun-Blanquet scores were transformed into mean cover percentages (“+”= 0.1%, “1”= 5%, “2”= 17.5%, “3”= 37.5%, “4”= 62.5%, and “5”= 87.5%). All relevés were georeferenced on a 1 km x 1 km UTM grid. In the summer and autumn of 2009, surveys were repeated in fields located in the same UTM 1 x 1 km squares where they had been georeferenced initially, following the same methodology. To avoid biases in the comparisons regarding plant phenology and field location between the two surveys, crops and orchards surveyed in 2009 had similar characteristics that those surveyed in 1989 within the UTM squares and were surveyed at the same time in both years. Vascular plant nomenclature followed Bolòs and Vigo (1984-2001). A total of 79 fruit tree orchards and 58 maize fields were surveyed.

Species traits

Species were classified as either native or alien following Sanz-Elorza et al. (2004), which is the most complete revision of alien flora in Spain so far. Furthermore, each species was categorized based on a set of biological traits related to plant responses to disturbances. For each species, the following traits were collected:

(a) Growth form: annual and perennial graminoids and forbs (Bolòs and Vigo, 1984-2001).

(b) Photosynthetic pathway: C3 or C4 (Pyankov et al., 2010).

(c) Seed dispersal mode: anemochory, barochory, hydrochory, zoochory or combined (more than one dispersal mode) (BIOLFLOR database. Klotz et al., 2002).

(d) Clonal growth: capable or incapable of clonal growth (CLO-PLA3 database. Klimešová and de Bello, 2009).

Data analysis

Changes in richness, diversity, and composition of weed assemblages

Species diversity in orchards and in maize fields in each year were summarised by calculating α- (mean number of species by plot), γ- (total number of species in each year) and β-diversity ([(γ-diversity/mean α-diversity) – 1] (Whittaker, 1960) both for total, for alien and for native weeds. α-and β-diversity values were compared among years using a Wilcoxon signed-rank test, due to the non-normal distribution of the data.

To identify species whose status increased, decreased, or remained stable between 1989 and 2009 in each crop system, mean cover value of species was compared between years using two-part Wilcoxon test, which is the most powerful statistic for analysis of non-normal data with a large proportion of zeros (Taylor and Pollard, 2009).

Single-trait approach

The relationship between species whose status changed and their individual biological traits was analysed by testing the frequency of each attribute in the increasing and decreasing group of species using exact Fisher test.

Multiple-groups approach

To relate changes on species status and specific sets of biological traits, the approach of Fried et al. (2009) was followed. Species were classified into functional groups and the distribution of the species whose status had changed among these groups was evaluated. To define the functional groups, the species/traits matrix was subjected to Multiple Correspondence Analysis (MCA). MCA principal components were used to perform a hierarchical clustering (HCPC) based on Ward's criterion, which indicates the number of optimal non-redundant groups based on the inertia gain. K-means algorithm was used to consolidate partition obtained by the hierarchical tree (Husson et al., 2010). Clusters of individuals were then described from biological traits and percentage of total cover represented by each group was calculated. Fisher's Exact Test was performed to search for significant differences in the distribution of species whose status had changed among the functional groups. All analyses were performed with R software (R Development Core Team, 2011).

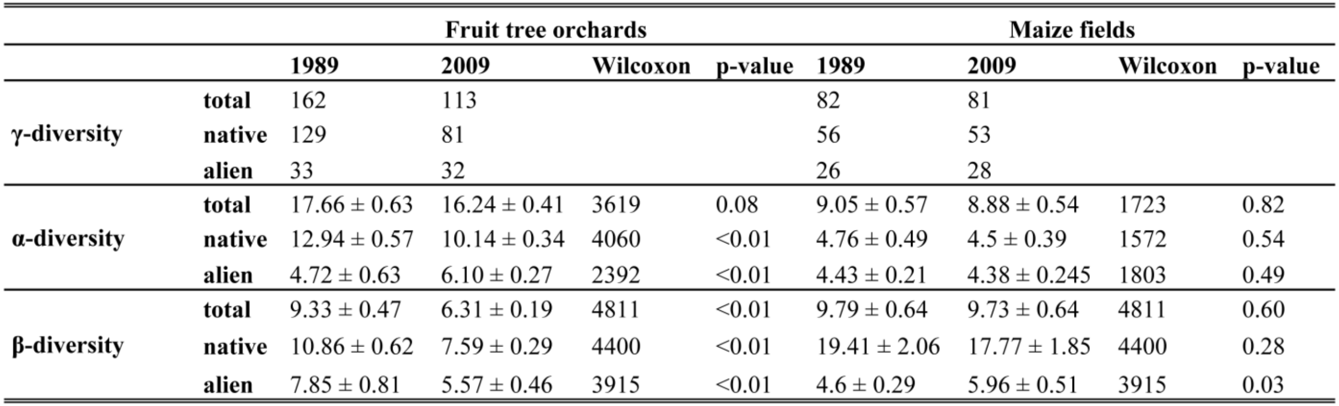
Results

Changes in richness, diversity, and composition of weed assemblages

In the two years, a total of 187 and 110 weed species were recorded in fruit tree orchards and maize crops, respectively. In fruit tree orchards, total γ-diversity was 30% lower in 2009 (113 species) than it was in 1989 (162 species) (Table 1), which was due to a reduction in the number of native weed species (from 129 species in 1989 to 81 species in 2009). The number of alien species did not change (33 species in 1989 and 32 species in 2009). Total α-diversity was slightly, but not significantly, lower in 2009 than it was in 1989, but in the case of alien weeds, its value was significantly higher in 2009 than in 1989. In contrast, α-diversity of native species was significantly lower in 2009 than in 1989. Regarding β-diversity, its value was significantly lower in the second survey in all the groups. In maize crops, neither γ-diversity nor α-diversity changed between 1989 and 2009 in any group of species. Only β-diversity of alien plants increased between the surveys. According to two-part Wilcoxon test results, in fruit tree orchards 22 species decreased their cover in 2009 regarding to 1989 and 15 species increased it. From these, 8 species were not found in 2009 and two species (*Crepis bursifolia* and *Plantago coronopus*) appeared as new in 2009 surveys (Table 2). In this sense, most of those species with a low value of cover in a survey that were not found in the other survey were not confirmed by the test as species whose status significantly changed. *Bromus catharticus, Cynodon dactylon, Cyperus rotundus, Paspalum distichum,* and *Trifolium repens* stood out from the group of species that increased their cover and, by 2009, had become dominant weeds. Some of these species, e.g., *Trifolium repens, Cyperus rotundus*, and *Paspalum distichum*, were already common in 1989. On the contrary, species such as *Amaranthus retroflexus, Poa compressa* and *Portulaca oleracea*, that were prominent species in 1989, became minor species in 2009.

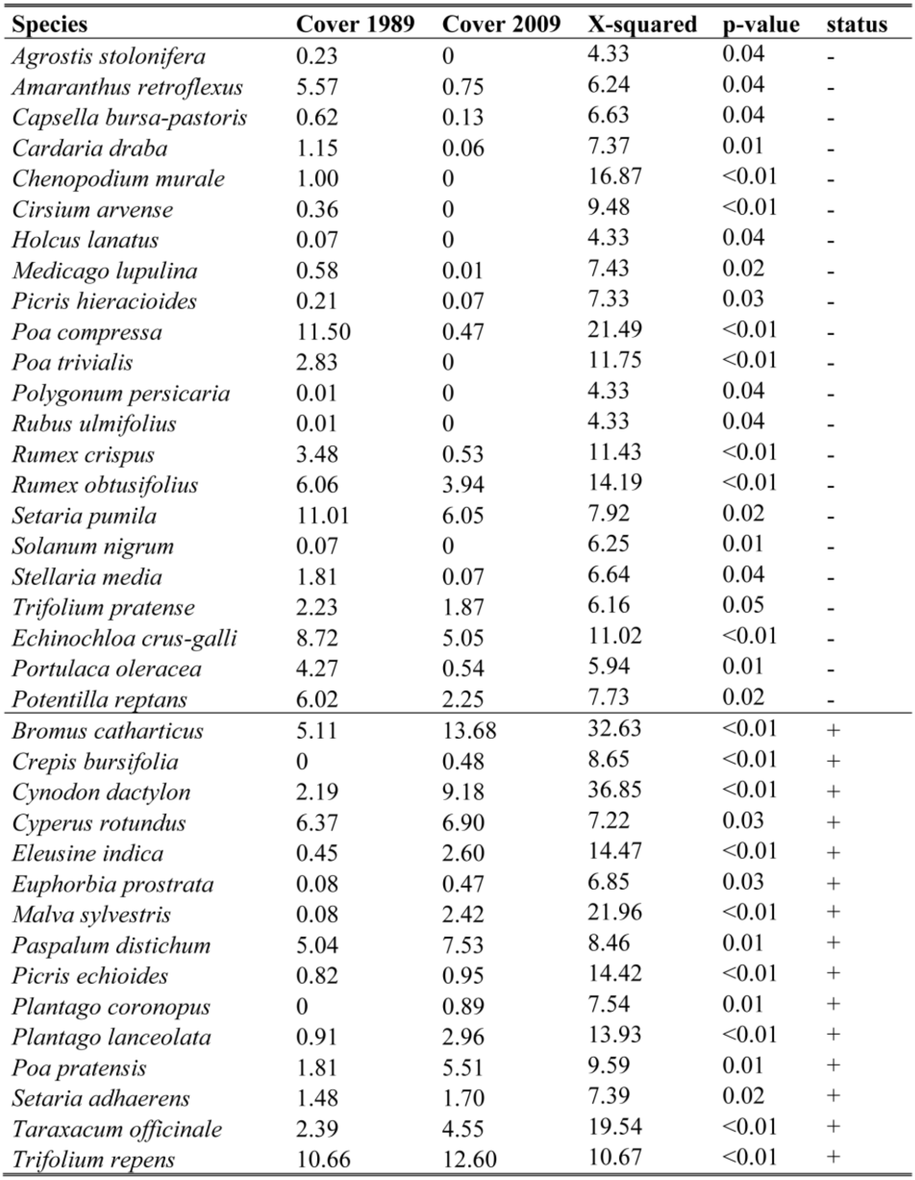
In maize crops, results revealed that 3 species (*Amaranthus hybridus, A. retroflexus* and *Verbena officinalis*) significantly decreased and 14 species increased their cover (Table 3). *Digitaria sanguinalis, Echinochloa crus-galli, Setaria adhaerens* and *Sorghum halepense* were already very common in 1989 but, by 2009, their cover had increased significantly. Some species such as *Abutilon theophrasti, Panicum dichotomiflorum,* and *Xanthium echinatum,* which were minor species in 1989, had increased their cover substantially and were prominent species by 2009. Species that were not found in 1989, such as *Senecio vulgaris* and *Cardamine hirsuta*, were present in small amounts in 2009.

Table 1. γ-, α- and β-diversity of total, native and alien species in fruit tree orchards and maize fields in 1989 and 2009. Total (for γ- diversity) and mean values per field (for α- and β-diversity) are shown (± SE). For α- and β-diversity comparisons, Wilcoxon statistic and p-value are shown.



		Fruit tree orchards				**Maize fields**			
		1989	**2009**	**Wilcoxon**	**p-value**	**1989**	**2009**	**Wilcoxon**	**p-value**
γ-diversity	**total**	162	113			82	81		
	native	129	81			56	53		
	alien	33	32			26	28		
α-diversity	**total**	17.66 ± 0.63	16.24 ± 0.41	3619	0.08	9.05 ± 0.57	8.88 ± 0.54	1723	0.82
	native	12.94 ± 0.57	10.14 ± 0.34	4060	<0.01	4.76 ± 0.49	4.5 ± 0.39	1572	0.54
	alien	4.72 ± 0.63	6.10 ± 0.27	2392	<0.01	4.43 ± 0.21	4.38 ± 0.245	1803	0.49
β-diversity	**total**	9.33 ± 0.47	6.31 ± 0.19	4811	<0.01	9.79 ± 0.64	9.73 ± 0.64	4811	0.60
	native	10.86 ± 0.62	7.59 ± 0.29	4400	<0.01	19.41 ± 2.06	17.77 ± 1.85	4400	0.28
	alien	7.85 ± 0.81	5.57 ± 0.46	3915	<0.01	4.6 ± 0.29	5.96 ± 0.51	3915	0.03

Table 2. Mean cover values of weed species which status changed between 1989 and 2009 in fruit tree orchards according to two-part Wilcoxon test results (test statistic and p-value showed). “-”: decreasing species; “+”= increasing species.



Species	Cover 1989	Cover 2009	X-squared	p-value	status
Agrostis stolonifera	0.23	0	4.33	0.04	-
Amaranthus retroflexus	5.57	0.75	6.24	0.04	-
Capsella bursa-pastoris	0.62	0.13	6.63	0.04	-
Cardaria draba	1.15	0.06	7.37	0.01	-
Chenopodium murale	1.00	0	16.87	<0.01	-
Cirsium arvense	0.36	0	9.48	<0.01	-
Holcus lanatus	0.07	0	4.33	0.04	-
Medicago lupulina	0.58	0.01	7.43	0.02	-
Picris hieracioides	0.21	0.07	7.33	0.03	-
Poa compressa	11.50	0.47	21.49	<0.01	-
Poa trivialis	2.83	0	11.75	<0.01	-
Polygonum persicaria	0.01	0	4.33	0.04	-
Rubus ulmifolius	0.01	0	4.33	0.04	-
Rumex crispus	3.48	0.53	11.43	<0.01	-
Rumex obtusifolius	6.06	3.94	14.19	<0.01	-
Setaria pumila	11.01	6.05	7.92	0.02	-
Solanum nigrum	0.07	0	6.25	0.01	-
Stellaria media	1.81	0.07	6.64	0.04	-
Trifolium pratense	2.23	1.87	6.16	0.05	-
Echinochloa crus-galli	8.72	5.05	11.02	<0.01	-
Portulaca oleracea	4.27	0.54	5.94	0.01	-
Potentilla reptans	6.02	2.25	7.73	0.02	-
Bromus catharticus	5.11	13.68	32.63	<0.01	+
Crepis bursifolia	0	0.48	8.65	<0.01	+
Cynodon dactylon	2.19	9.18	36.85	<0.01	+
Cyperus rotundus	6.37	6.90	7.22	0.03	+
Eleusine indica	0.45	2.60	14.47	<0.01	+
Euphorbia prostrata	0.08	0.47	6.85	0.03	+
Malva sylvestris	0.08	2.42	21.96	<0.01	+
Paspalum distichum	5.04	7.53	8.46	0.01	+
Picris echioides	0.82	0.95	14.42	<0.01	+
Plantago coronopus	0	0.89	7.54	0.01	+
Plantago lanceolata	0.91	2.96	13.93	<0.01	+
Poa pratensis	1.81	5.51	9.59	0.01	+
Setaria adhaerens	1.48	1.70	7.39	0.02	+
Taraxacum officinale	2.39	4.55	19.54	<0.01	+
Trifolium repens	10.66	12.60	10.67	<0.01	+

Table 3. Mean cover values of weed species which status changed between 1989 and 2009 in maize fields according to two-part Wilcoxon test results (test statistic and p-value showed). “-”: decreasing species; “+”= increasing species.

Species	Cover 1989	Cover 2009	X-squared	p-value	status
Amaranthus hybridus	5.72	4.32	15.90	<0.01	-
Amaranthus retroflexus	3.00	0.65	17.90	<0.01	-
Verbena officinalis	0.01	0	4.39	0.04	-
Abutilon theophrasti	1.96	16.71	17.77	<0.01	+
Cardamine hirsuta	0	1.52	4.39	0.04	+
Chenopodium album	0.50	7.94	6.52	0.01	+
Cynodon dactylon	1.79	7.21	8.64	0.01	+
Digitaria sanguinalis	9.89	23.76	10.98	<0.01	+
Echinochloa crus-galli	4.52	21.36	13.00	<0.01	+
Panicum dichotomiflorum	1.08	7.16	11.03	<0.01	+
Senecio vulgaris	0	1.09	4.34	0.04	+
Setaria adhaerens	10.97	14.36	12.55	<0.01	+
Setaria pumila	2.66	9.89	5.23	0.02	+
Sonchus oleraceus	0.73	5.50	8.70	0.01	+
Sorghum halepense	7.14	16.70	6.10	0.05	+
Veronica persica	0.31	5.49	9.01	0.01	+
Xanthium echinatum	0.96	6.43	7.75	0.02	+

Single-trait approach

Results showed that, in fruit tree orchards, only the species origin differed significantly among the species that significantly changed their status between 1989 and 2009 (Table 4). Most of the species that increased their cover in 2009 were alien species (*p*-value= 0.04). In maize crops, no differences were found in the studied traits between increasing and decreasing species.

Multiple-groups approach

In fruit tree orchards, the first two components of MCA explained 41.26% of the total variance in the weed species composition depending on its traits (Fig. 1). Cluster analysis identified three main functional groups (Fig. 1 and Table 4). First group comprised 55 species, mostly native C3 species, perennial forbs with clonal growth and with seeds dispersed by wind. The second group, which included 91 species, was associated with native C3 species, annual forbs, with seeds dispersed by animals or barochory.

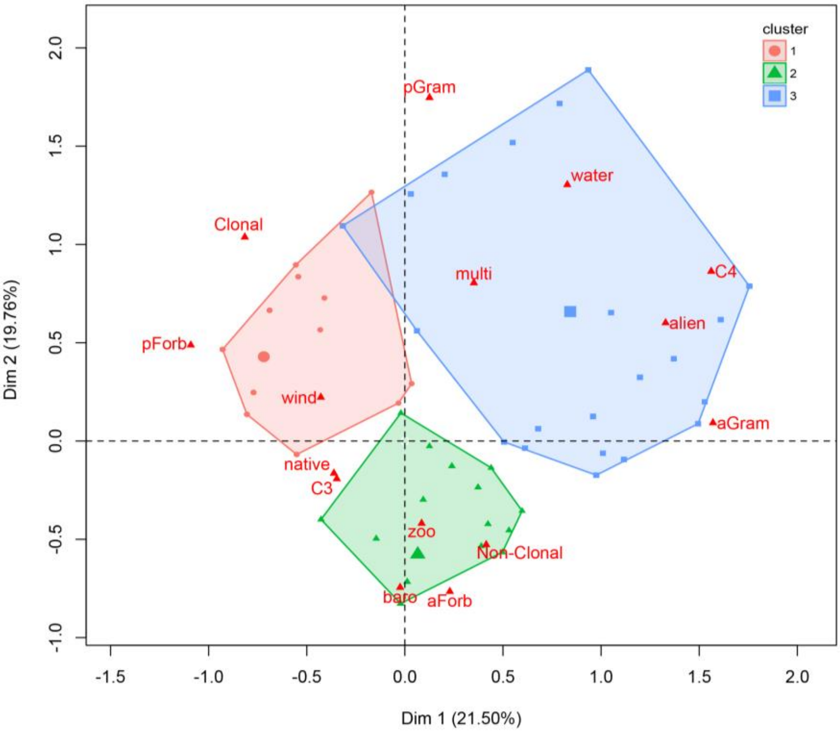


Figure 1. Distribution of the traits of weed species and functional groups in fruit tree orchards in Lleida, Spain, on the first and second axes of the Multiple Correspondence Analysis (MCA). aForb: annual forb, pForb: perennial forb, aGram: annual graminoid, pGram: perennial graminoid, baro: barochory, water: hydrochory, wind: anemochory, zoo: zoochory, multi: more than one seed dispersal method. Small symbols represent species scores on the MCA axes. Big symbols represent centroid of the cluster.

The third group (41 species) was associated with alien C4 species, mostly grasses, with hydrochory or multiple seed dispersal modes. Most of the plant cover (60.3%) in fruit tree orchards was represented by the species included in this group followed by the species of the third group (30.5%) (Table 5).

In maize crops, the first two axes of MCA explained 42.62% of the total variance in the weed species composition (Fig. 2).

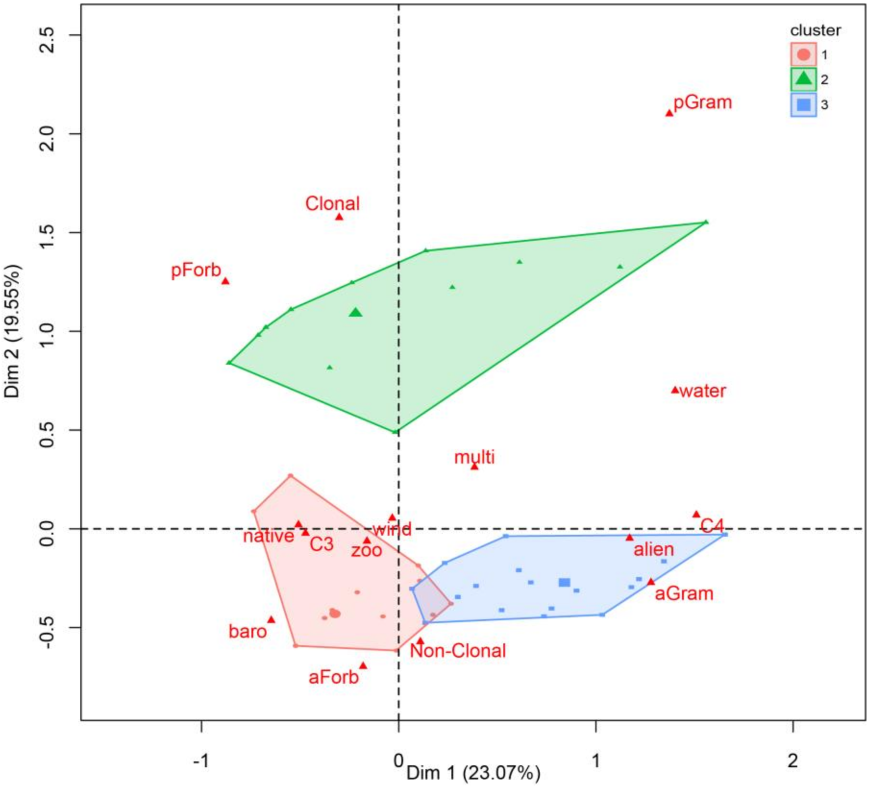


Figure 2. Distribution of the traits of weed species and functional groups in maize fields in Lleida, Spain, on the first and second axes of the Multiple Correspondence Analysis (MCA). aForb: annual forb, pForb: perennial forb, aGram: annual graminoid, pGram: perennial graminoid, baro: barochory, water: hydrochory, wind: anemochory, zoo: zoochory, multi: more than one seed dispersal method. Small symbols represent species scores on the MCA axes. Big symbols represent centroid of the cluster.

The third group (41 species) was associated with alien C4 species, mostly grasses, with hydrochory or multiple seed dispersal modes. Most of the plant cover (60.3%) in fruit tree orchards was represented by the species included in this group followed by the species of the third group (30.5%) (Table 5).

In maize crops, distribution of traits along the two first MCA axes was similar to that of the orchards analysis. Cluster analysis identified three functional groups (Fig 2 and Table 4). Group 1 (53 species) included mainly native C3 plants, annual forbs with barochory. Group 2 (29 species) contained perennial species with clonal growth while group 3 (27 species) was linked mostly with alien C4 species, annual grasses with combined seed dispersal methods. The first and the third groups account for 78.2% of the total cover.

Changes in species status related to functional groups

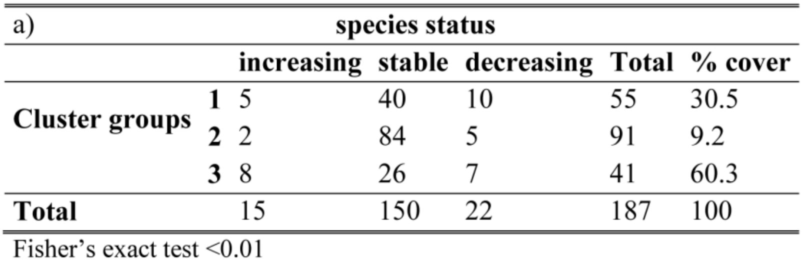
According to Fisher’s exact test, in fruit tree orchards (Table 5a), group 3 included a significantly larger number of species that had increased their cover while group 2 included most of the species whose cover remained stable in both periods.

In maize crops, species that increased, that decreased, or that remained stable in the studied period were distributed randomly among the three functional groups (Table 5b).

Table 4. Relationship between traits and groups of species whose status changed between 1989 and 2009. “Single-trait” column shows p-value of Fisher exact test analysis of the relationship between frequencies of each trait among increasing and decreasing groups of species. “Multi-trait” columns show trait composition of functional groups obtained by MCA-hierarchical clustering analysis on species/trait matrix and their statistical significance of Fisher exact test analysis

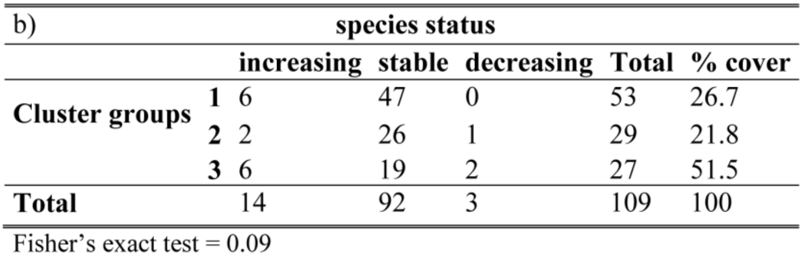
	Orchards					**Maize**				
	Single-trait	**Multi-trait**				**Single-trait**	**Multi-trait**			
		Functional groups					**Functional groups**			
	p-value	**1**	**2**	**3**	**p-value**	**p-value**	**1**	**2**	**3**	**p-value**
life form	0.67				**<0.01**	0.17				**<0.01**
annual forb			+				+			
perennial forb		+						+		
annual grass				+					+	
perennial grass				+				+		
photosynthetic pathway	0.25				**<0.01**	1				**<0.01**
C3		+	+				+			
C4				+					+	
dispersal system	0.84				**<0.01**	0.13				**<0.01**
zoochory			+							
anemochory		+								
hydrochory				+						
barochory			+				+			
combined				+					+	
clonality	0,75				**<0.01**	0.47				**<0.01**
yes		+						+		
no			+				+		+	
origin	0.04				**<0.01**	1				**<0.01**
alien	+			+					+	
native		+	+				+			

Table 5. Contingency tables of functional groups obtained by MCA-hierarchical clustering analysis and the numbers of species whose cover increased, decreased, or remained stable in a) fruit tree orchards and b) maize fields in Lleida, Spain, between 1989 and 2009 and percentage of relative cover of the species included in each group.



a)		species status				
		increasing	**stable**	**decreasing**	**Total**	**% cover**
Cluster groups	**1**	5	40	10	55	30.5
	2	2	84	5	91	9.2
	3	8	26	7	41	60.3
Total		15	150	22	187	100

Fisher's exact test <0.01



b)		species status				
		increasing	**stable**	**decreasing**	**Total**	**% cover**
Cluster groups	**1**	6	47	0	53	26.7
	2	2	26	1	29	21.8
	3	6	19	2	27	51.5
Total		14	92	3	109	100

Fisher's exact test = 0.09

Discussion

Changes in richness and diversity of weed assemblages between 1989 and 2009

Results show that in the studied period the trajectories of the weed communities of orchards and maize crops have a contrasted behaviour. In orchards, there was an increase of alien species' α-diversity as a consequence of the general decline of native α-diversity and at the same time it was a process of homogenization of flora among fields, reflected in a general decrease of β-diversity. However, in maize crops, weed communities seem to be consolidated over time in terms of diversity, with no remarkable changes in diversity values in any group.

Changes observed in weed communities in fruit tree orchards reveals in the irrigated Mediterranean agricultural land the described trend of a general decline in abundance of native species joined by an increase of aliens in agroecosystems in Central Europe (Meyer et al., 2013; Lososová and Simonová, 2008) and in Britain (Preston et al., 2004) as well as in urban flora (Chocholoušková and Pyšek, 2003) and in extensively managed crops (Šilc and Čarny, 2005). In fruit tree orchards, disturbances and increased soil fertility seem to affect more negatively to some native species than to the group of aliens, which has been described to be more adapted to crop disturbances (Prieur-Richard and Lavorel, 2000). This reduction in native species diversity increases empty niches that can be occupied by alien plants, thus increasing their presence in the fields, as it was suggested by MacDougall and Turkington (2005).

In maize crops, lack of rotation and a high homogeneity of crop management, basically driven by herbicides application, promote a less diverse weed community that comprises a few generalist species that are more tolerant to the herbicides used (Grundy et al., 2011). In fact, it has been proved that weed control programs involving regular, repetitive disturbances like chemical weed control foster a balanced weed assemblage (Fried et al., 2006) with a few dominant species. In this sense, in maize crops and in fruit tree orchards, the effects of crop management on weeds assemblages developed over the last 20 years may outweigh the possible effects of the competition between alien and native weeds.

General decrease of β-diversity of weed assemblages in fruit tree orchards between 1989 and 2009 may reflect how selection pressures removed some minor species and balanced the weed assemblages, which led to the homogenization of the flora in a similar way as described by Olden et al. (2004). This pattern is consistent with the ecological assembly theory applied to weed communities (Booth and Swanton, 2002), which suggests how management practices select for specific biological and ecological traits, and, by extension, species, in a similar manner that environmental conditions modify natural systems.

Although diversity values have decreased in fruit tree orchards, their weed communities exhibited greater diversity than did maize crops, both in 1989 and in 2009. Heterogeneity in management systems promotes weed richness and diversity (de la Fuente et al., 2006; Lososová and Cimalová, 2009; Meiss et al., 2010b). In this sense, in maize fields management primarily entails in chemical inputs and there was no crop rotation in the study period. It has been claimed that the absence of crop rotation for many years contributes to the reduction in species richness and the increase in the presence of few adapted species (Colbach et al., 2014). On the other hand, in fruit tree orchards, several methods to control weeds are used in combination; e.g., tilling after the first planting, mowing during the remainder of the trees life and small applications of herbicides along tree lines (Recasens and Taberner, 1988). The use of multiple methods to control weeds benefits groups of species that have different adaptive advantages such as broad-leaved species that have a flat morphology, e.g., *Taraxacum officinale* and *Plantago lanceolata,* which are capable of regrowth after mowing (Meiss et al., 2010b), or graminoid species able to regenerate after disturbances and with highly viable seeds, e.g., *Eleusine indica* (Masin et al., 2006).

Changes in composition of weed assemblages from a functional-groups approach

Results show that in the studied period, the application of the same management methods in each type of crop favours the specialization of weed assemblages filtered by specific traits. This process lay behind the temporal changes found in the composition of weed assemblages (Booth and Swanton, 2002) and the increasing presence of alien species in weed communities (MacDougall and Turkington, 2005).

In fruit tree orchards in 2009, most of the dominant species were mainly included in the third functional group, which contained significant larger number of grasses, C4 species, hydrochorous species and species with more than one mode of seed dispersal. Furthermore, most of those were alien species.

The influence of orchards management in this selection can be detected. It has been shown that annual forbs are more vulnerable to mechanical control than graminoids forms (Meiss et al., 2010a). This kind of management destroys large parts of leaves and meristems needed for resprouting. In graminoids, these structures are located nearer to the soil surface, thus being less affected and in better conditions for resprouting (Meiss et al 2010b). In addition, perennial species can take advantage in pluriannual crops such as fruit trees due to absence of tillage (Albrecht, 2005). In this sense, Recasens and Taberner (1988) showed a positive correlation between the prominence of perennial species in weed communities in orchards and the age of the orchard, which can explain the high cover value of the species included in the first functional group (which are composed mainly by perennial forbs). The greater success of C4 weed species is due to their capacity for high photosynthetic taxes and a more efficient use of nitrogen in environments where there is a CO_2 deficiency and high taxes of photorespiration (Sage and Kubien, 2003). Flooding and high temperatures, as occur in flood irrigated fruit tree orchards in summer, stimulate photorespiration (Sage, 2004), which gives C4 species an advantage over C3 species. The predominance of tropical C4 weed species in irrigated summer crops has been already observed by Recasens and Conesa (2003). Regarding to seed dispersal, hydrochory is favoured by flood irrigation (Merritt and Wohl, 2002). Furthermore, the most successful alien species have seeds that are easily dispersed by more than one seed dispersal method (Moravcová et al., 2010) because it provides a faster expansion capability (Wang et al., 2011).

Annual forbs, species that have seed dispersed by animals and those that have no capacity for clonal growth remained stable between 1989 and 2009 in fruit tree orchards although they represented the lowest value of plant cover. Despite having different traits than those of successful weed species, other traits not evaluated in this study, such as the life cycle duration or seed production, that feed the soil seed bank, might explain their stability within the weed assemblages. For example, in alfalfa crops, annual weed species that have short life cycles are able to produce seeds before mowing time and, therefore, can be maintained in the soil seed bank even though the species are not benefited by management practices (Meiss et al. 2010b).

In maize crops, the three functional groups did not differ significantly in the number of species that increased or decreased their cover between the studied years and most of the cover was represented by annual species. Despite this fact, different traits to those selected in this study appeared to be responsible for the changes in the cover of some species in maize crops in the studied period. The prohibition of atrazine since 2005 appeared to be the factor that led to the increase in the cover of *Panicum dichotomiflorum* (Renoux et al., 2003), while the use of acetochlor appeared to increase the abundance of *Xanthium echinatum* (Marković et al., 2008). The increase in *Sorghum halepense* seems to be influenced by the timing of germination or flowering duration (Maillet and López García, 2000), so as *Abutilon theophrasti* in studied maize crops (Recasens and Calvet, 1993), whose particular success explains the observed high cover value of the first functional group. The first record of *A. theophrasti* in Catalonia was in 1982 (Izquierdo, 1986). In 1991, 44% of the maize crops were infested with this species (Recasens and Calvet, 1993) and in 2009 it was present in almost all of the survey plots. The high production rate of highly viable seeds, which ensures the persistence on the seed bank, its rapid growth after emergence, a high photosynthetic rate and the absence of selective herbicides to control it before 1991 are the main factors that led to the rapid expansion of the species (Recasens et al., 2005).

The biological traits that give alien plants an advantage in fruit tree orchards do not benefit them in maize crops, where the selection pressures are different. Thus, these results support the hypothesis that no single set of traits explains the global success of alien species but, rather, it depends on the host habitat, which in this case is influenced by management practices (Smith and Knapp, 2001; Lloret et al., 2005).

Advantages of a functional-groups approach

This study shows that the multivariate approach in the analysis of the biological traits that have influenced the nature of weed assemblages identified patterns that were not evident in the analysis of the effects of individual traits. The individual analysis of life form, clonality, photosynthesis pathway and mode of seed dispersal did not proved these factors to have a significant effect on the success of weed species but, in combination, these traits provide weeds a better adaptation to weed management in fruit tree orchards. Species that have only one favourable trait might not have success in a community (Fried et al., 2009); rather, having a set of beneficial traits increases the likelihood of the success of weed species (Booth and Larson, 1999). On the other hand, in studies that use a functional approach, the selection of the appropriate plant traits is critical to understand the responses of weed species to specific management practices (Weiher et al., 1999; Violle et al., 2007). Biological traits selected in this study have made possible understand the dynamics of weed assemblages in fruit tree orchards, but they were not useful in the analysis of changes in the species that compose weed communities in maize crops. Traits not analysed in this study like tolerance to herbicides, seed production and flowering phenology may be important traits in annual crops, e.g., maize, where weeds are managed mainly by herbicides (Fried et al., 2009).

The results of this study show that the interpretation of plant shifts driven by weed management improves when species are assigned to functional groups (Lavorel et al., 1997; Pausas and Austin, 2001), which confirms the usefulness of focusing on traits in long-term studies to understand weed assembly rules (Díaz and Cabido, 1997). The identification of functional groups may enable to predict the responses of new weeds to crop management practices and to develop better strategies to control those weed species that are already established (Smith and Knapp, 2001).

Conclusions

This study reveals long-term changes in weed community composition and diversity in irrigated fruit tree orchards in Northeastern Spain as well as a more stability of the weed diversity present in maize crops.

In fruit tree orchards there was a decrease in α-diversity of total and native species and an increase of alien α-diversity whereas β-diversity decreased in all the groups. In maize crops it was detected only a slight increase in alien β-diversity.

The changes observed in weed communities in orchards can be related to the diversity of weed control methods along the studied period while in maize, the more homogeneous management and a lack of crop rotation may explain the lower changes detected in maize crops. In fruit tree orchards, water irrigation and mechanical disturbances help to explain the promotion of alien species, C4 species, perennial graminoids dispersed by water or by combined systems whereas in maize crops, chemical weed control and annual life cycle of the crop configure a weed community dominated by annual weeds.

This study confirms the influence of management in the compositional and functional structure of weed communities as well as the importance of the selection of suitable traits in order to detect patterns of functional composition and influence of crop management in weed community studies.

The study also reveals the advantages of the multivariate approach in identifying the role of functional traits in the weed assemblages, since this approach allows to detect functional patterns that were not evident when traits were analysed individually

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CHAPTER 3

A plant-traits approach to assessing the success of alien weed species in irrigated Mediterranean orchards

Published in *Annals of Applied Biology* 2013, **162**, 200 – 213.

A plant-traits approach to assessing the success of alien weed species in irrigated Mediterranean orchards

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Abstract

In addition to their impact on natural habitats, invasive alien plants can have a significant negative effect on agricultural systems and cause economic losses. Flood-irrigated orchards in the Mediterranean Basin are vulnerable to the invasion of alien weeds, primarily because of the traditional management practices used in the orchards, which are characterized by high soil moisture during the dry summer period, nutrient availability and high levels of disturbance. This study sought to determine whether their biological traits can explain the success of alien weed species. To answer this question, 408 floristic relevés were conducted in 136 flood-irrigated orchards on the Plains of Lleida (Catalonia, NE Spain). Richness and cover of native and alien weeds were compared. Furthermore, a set of biological traits was compared between successful and non-successful weeds for the whole data and separately between native and alien weeds using logistic regression and classification trees. In flood-irrigated orchards, alien species covered most of their area, even though the richness of alien species was lower than that of the native species. The most important species were C4 species with seeds dispersed by water, and on the other hand, rosulate and caespitose-reptant with long flowering period. Most of these traits fitted with those of the invasive alien weeds, which were mostly C4 species that had seeds dispersed by water. Perennial life form characterized successful native weeds.

In this study, we discuss how the traditional management of flood irrigation in fruit tree orchards favours invasive alien weeds that have specific traits, acting as a reservoir for the spread of alien weeds into other crops and surrounding riparian habitats. We also propose changing management practices in order to avoid the selection of alien weeds and to promote native species.

Keywords

Invasive species, traditional management, flood irrigation, logistic regression, classification trees, weediness.

Introduction

Invasion by alien plant species is one of the main threats to biodiversity and a cause of substantial economic losses, particularly, for agriculture (Pimentel et al., 2001). Only in the USA, the economic losses associated with infestations by alien weeds are about 27,000 million dollars per year (including costs of control, harvest losses, and damages to crops) (Pimentel et al., 2005). In Europe, 33.7% of the established alien species (2024 species) was introduced through pathways associated with agriculture (Pyšek et al., 2009b). Alien plants can be introduced into crops either unintentionally, i.e., through contaminated seeds, or intentionally for their use as cover crops, to obtain fibers or food (Sanz-Elorza et al., 2009) and recently for bioenergy production and carbon sequestration (Crosti et al., 2010). Once the alien plants are introduced into a crop, they can become naturalized and, in some cases develop infesting behaviour, which has been described as invasive (Booth et al., 2010; Holt and Boose, 2000). In the Mediterranean region, irrigated crops are suitable habitats for the establishment and expansion of alien flora (Chytrý et al., 2009), particularly those that are tropical or sub-tropical in origin (Brunel et al., 2010) because of the summer irrigation, frequent disturbance, fertilization, and the reduced competition with native species that take place in the crops (Davis et al., 2000).

A useful approach to understand why some species are successful in becoming established and expanding in a given habitat is to identify the differences in the biological and ecological traits between the successful and the non-successful species (Lososová et al., 2008). This approach also allows to check if invasiveness of alien plants is partly consequence of the differences in their attributes with coexisting native plants (Pyšek and Richardson, 2007) and it helps to elucidate the functional keys that underlie the invasion process (Milbau and Stout, 2008).

Most of the studies that have shown that the difference in the traits between invasive alien, non-invasive and native species favoured the former are focused on natural and semi-natural habitats and were conducted at a national scale or over large areas (Sutherland, 2004; Lososová et al., 2008; Küster et al., 2010; Ordonez et al., 2010); however, little is known about the differences in the traits between invasive alien, non-invasive alien and native weeds within agricultural habitats (Daehler, 1998; Maillet and López-García, 2000), where the management practices are crucial in determining the adaptiveness of specific traits (Clements et al., 2004).

Crops can act as reservoir for alien flora which can expand and potentially invade the natural habitats neighbouring (Holt and Boose, 2000). In the Mediterranean region, most of the natural habitats near irrigated agricultural areas are riparian habitats by virtue of the need for accessible irrigation water, with the associated risk that some alien weeds could migrate from the crops into riparian habitats and become invasive there. As has been showed in some studies, Mediterranean riparian habitats are highly vulnerable to invasion by alien species (Aguiar et al., 2006) and the frequency of occurrence of these invasions has been related to the disturbance caused by the intensification of surrounding agricultural systems in Mediterranean areas (Ferreira and Moreira, 1995).

Our study was designed to identify the specific traits that contribute to the success of alien plants in an irrigated agricultural context with the objective of aiding in the development of management practices for the control of biological invasions in irrigated crops.

In this study, we assessed whether flood irrigated perennial crops (i.e., fruit trees) in the Mediterranean region favour the establishment and persistence of alien flora by selecting their biological traits through the management. Specifically we asked (1) Are there differences in richness and cover between native and alien weeds in flood-irrigated fruit tree orchards on the Plains of Lleida (Catalonia, NE of Spain)? (2) What traits differentiate native and alien weeds? (3) Are those traits the most favoured in fruit tree orchards? And moreover, (4) which traits are shared between alien and native successful weeds?

Materials and methods

Study area

The study was conducted in fruit tree orchards in El Segrià county (41º37'N, 0º37'E), Lleida (Catalonia, NE Spain). Mean annual temperature is 15º and annual rainfall is around 385 mm, most of which occurs in autumn. El Segrià has 64% (22,760 ha.) of the irrigated fruit tree orchards in the province (IDESCAT, 2010), and almost all of these orchards are flood-irrigated. The orchards form a mosaic of small fields and depend upon an old extensive irrigation network, portions of which are >100 years old (Dalmau and Iglesias, 1999). Most of the fruit trees are stone and pome fruit (apple, pear, and peach). Apple and pear-tree orchards are irrigated bi-weekly from late March to early September (a total of 10-12 irrigation episodes during this period). The amount of water used in each season is 5,500 m^3/ha. Peach-tree orchards are irrigated in the same way, but total amount of water used is 4,400 m^3/ha. Due to the lack of slope of the ground, water is distributed homogenously, flooding the entire field. Frequently, the crops are subjected to human interventions (e.g., the application of pesticides, lower thinning, and weed control) throughout the lifetime of the crop. Mowing between the rows of trees and application of herbicides (mixed of pendimetalin, oxifluorfen, isoxaben and orizalin in February and gliphosate and fluroxipir between May and June and after September) along the tree line are the primary methods of weed control (Taberner, 2008). Mowing of weeds is carried out with a flail mulcher and it occurs before the fruit harvest, which takes place between late August and September. Shredded weeds remain on the ground acting as mulch material.

Vegetation surveys

In the summer of 2009, a total of 408 floristic surveys were conducted in 136 flood-irrigated fruit tree orchards. In each orchard, three rectangular (2 m x 5 m) plots were surveyed at randomly selected locations, but always in areas between tree rows, where weed diversity is best represented. The management of these plots was the same as the rest of the orchard. Plot size was defined by the minimum area at which the species-area curve became stabilized, following Lacoste et al. (1981). Cover of each species in each plot was recorded using the Sigmatic Method (Braun-Blanquet, 1979), in which the cover-abundance of each species is assigned a value between + (sparse and covering a small area) and 5 (covering more than 75% of the area). Those values were transformed into the mean value of the Braun-Blanquet scale (+=0.01%; 1=5%, 2=17.5%, 3=37.5%, 4=62.5%, 5=87.5%). Vascular plant nomenclature follows local flora (Bolòs and Vigo, 1984-2001).

Plant traits

All the species that were found were categorized as either native or alien plants based on the classification of the Atlas of Invasive Alien Plants in Spain (Sanz-Elorza et al., 2004) that is, up to now, the last and most complete revision of alien flora in Spain. They follow the definition of alien species of Richardson et al. (2000). This publication considers both archaeophytes and neophytes as alien species. For each species, 17 biological and ecological traits associated with colonization capabilities and plant performance were recorded. The attributes selected included vegetative traits, reproductive traits and ecophysiological traits. Raunkiaer's life forms were considered since they has been related to the disturbance response in herbaceous vegetation (McIntyre et al., 1995), the same as photosynthesis pathway, vegetative propagation and lateral spread (Maillet and López-García, 2000; McIntyre et al., 2005; Kühner and Kleyer, 2008). Classical division of weeds into graminoids and forbs was taken into account. Reproductive traits such as seed dispersal, seed size, timing and length of flowering were included as they have been associated with persistence in disturbed habitats (Cornelissen et al., 2003; Gunton et al., 2011) and they have been related with management practices (Fried et al., 2012). As ecophysiological traits, Ellenberg indicator values (Pignatti et al., 2005) representing light, moisture, temperature, pH and nutrient preferences were selected. Ellenberg values are not strictly plant traits but have been commonly used as equivalent for corresponding stress tolerance traits (Gunton et al., 2011). Finally, Grime's strategies are useful to classify the species response to stress, disturbance and competition and have been useful in comparative studies between alien and native plants (Pyšek et al., 2009a) (For list and references of traits see table 1).

Some of the traits selected were highly correlated (e.g. seed length with seed width, vegetative propagation and lateral spread), so lateral spread, seed width and seed length/width were only fitted to an individual logistic regression model and were not included in the multiple statistical analysis.

Statistical analyses

To assess the prominence of native and alien plants in the fruit tree orchards, the mean number and the mean cover values of both groups of species per orchard were compared using the non-parametric Mann-Whitney test since the data were non-normal distributed.

To assess the capacity to discriminate between native and alien plants of the biological and ecological traits, individually and collectively, two approaches were used: logistic regression models and classification trees.

A logistic regression model was fitted to each of the traits, with each trait as single independent variable and origin of the species as the dependent variable. Regarding to the dependent variable, this was coded as binary (1 for natives and 0 for aliens, thus alien as the reference category). Regarding to the independent variables, these were conveniently considered as continuous or nominal. None of them was considered as ordinal, since this was not relevant from the interpretation point of view.

Table 1. Summary of traits used to compare native and alien weeds in flood-irrigated fruit tree orchards in Lleida, Spain.

Attributes	Categories	Reference
Vegetative traits		
Life form (Raunkiaer)	Chamaephytes/phanerophytes, geophytes, hemicryptophytes (caespitoses-reptants, rosulates and scaposes), therophytes (caespitoses-reptants, erects)	Bolòs and Vigo, 1984-2001
Vegetative morphology	Graminoids, forbs	Bolòs and Vigo, 1984-2001
Photosynthesis pathway	C3, C4	Pyankov et al., 2010
Vegetative propagation	Yes, no	Klimešová and de Bello, 2009; Julve, 1998
Lateral spread (m/year)	0, < 0.01, 0.1-0.25, > 0.25	Klimešová and de Bello, 2009
Reproductive traits		
Timing of flowering	Winter, spring, summer, all the year	Bolos and Vigo, 1984-2001
Length of flowering (months)	Continuous	Bolos and Vigo, 1984-2001
Seed length (mm)	Continuous	Klotz et al., 2002; Bolòs and Vigo, 1984-2001
Seed width (mm)	Continuous	Klotz et al., 2002; Bolòs and Vigo, 1984-2001
Seed length/width	Continuous	
Seed dispersal	Barochory, hydrochory, anemochory, zoochory, autochory, multiple systems	Bolòs and Vigo, 1984-2001; SID database, 2008; Julve, 1998
Ecophysiological traits		
Ellenberg index (EI) of light	Continuous (1-9)	Pignatti et al., 2005
EI of temperature	Continuous (1-9)	Pignatti et al., 2005
EI of nitrogen	Continuous (1-9)	Pignatti et al., 2005
EI of pH	Continuous (1-9)	Pignatti et al., 2005
EI of moisture	Continuous (1-12)	Pignatti et al., 2005
Grime strategy	C, S, R and intermediate categories	Klotz et al., 2002; www.wg-ecology.it; Cortina et al., 1998; Pino, 2000; Vicente et al., 2010

To assess the statistical significance of each trait, each model was compared to the null model using a Likelihood Ratio Test. The proportion of the variance explained by each model was evaluated using Nagelkerke's R^2 determination coefficient, which can be seen as the analogous measure of the determination coefficient R^2 in a linear regression, but is appropriate for a logistic regression (Milbau and Stout, 2008).

To assess the combined effect of all of the traits, a multiple logistic regression model was obtained using a stepwise procedure. To select the best model (the one that best fitted for the fewest number of explanatory variables), Akaike's Information Criterion (AIC) was used. A deviance table was used to measure the effect of each of the independent variables in the multiple logistic regression model, as well as the measures used for globally assessing the predictive ability of the model by itself.

Classification trees were adjusted to predict origin of species depending on biological and ecological traits. Gini index was used to establish the best binary partitions to discriminate between native or alien plants, considering only those partitions that improved the global Gini index in a percentage, at least, of 1%. Two different classification trees were adjusted: the first one including photosynthetic pathway and the second one excluding this variable, due to the high correlation between origin of species and this variable.

To prove whether traits that differentiated alien from native species are the same that were favoured in the orchards, a classification tree was adjusted to predict the success of species depending on their traits, irrespective of their origin. Species were classified as "high successful" or "low successful" depending on their cover values in the plots. Species with cover values higher that the mean value of cover were included in "high successful" group whereas species with cover values lower than the mean cover value were grouped in "low successful" category. This analysis was also performed for the alien and for the native weeds separately to prove if management filters selected the same traits in alien and native weeds.

In order to test whether alien species grouped into "high successful" category could be considered as invasive, they were compared with DAISIE (Delivering Alien Invasive Species In Europe) classification of invasive plants in natural and semi-natural habitats in Spain (www.europe-aliens.org/) and with a local classification of noxiousness of alien plants in crops made by Recasens and Conesa (2003). For the recorded species that were not present in that catalogue, the original authors of the publication were consulted to classify them.

In the regression logistic models and, more particularly, in the classification trees, the data were assumed to be deterministic, given that there is no random component in either the response or the explanatory variables. Therefore, it was not necessary to perform classical inference from the classification trees or to validate them, in the sense that no random sample can be considered.

Phylogenetic corrections

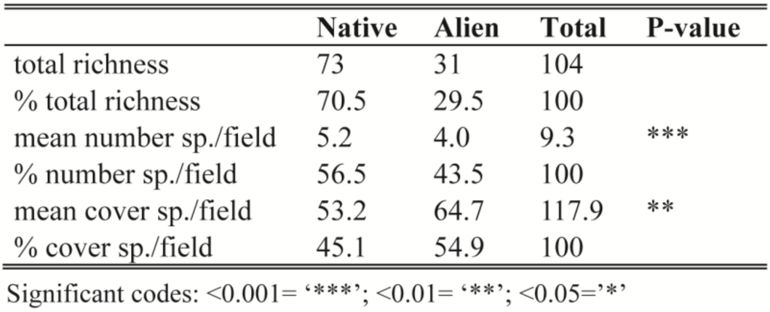
Phylogenetically related species share many traits and tend to occupy similar niches due to common origin rather than independent adaptation (Freckleton et al., 2002). In order to quantify the influence of the phylogeny in the results, variation partitioning method developed by Desdevises et al. (2003) was performed. A phylogenic tree was built using the Phylomatic on-line phylogenetic query tool (Webb and Donoghue, 2005). From the phylogenetic tree, a patristic distance matrix (i.e., a matrix containing distances between species computed from the tree) was built by making each branch length equal to 1 unit. The patristic distance matrix was subjected to principal coordinates analysis (PCoA). Each principal coordinate (PC) of the PCoA represents a certain amount of phylogenetic variation proportional to the associated eigenvalue. In order to select the PCs representing phylogenetic inertia, the broken-stick model was used. This method assumes that the total variance (the sum of eigenvalues) is divided randomly among the eigenvalues, and only the eigenvalues higher than the eigenvalue expected by the broken-stick distribution are considered important (Diniz-Filho et al., 1998).

Through this method, the proportion of variation explained by species traits, phylogeny and the common influence of these two factors were obtained. Further details of the method can be found in Desdevises et al. (2003). SPSS 15 (SPSS, Chicago, Illinois) was used to perform the Mann-Whitney-tests. The logistic regression analyses, classification trees, distance matrix and variation partitioning were performed using vegan package on R (R development Core Team, 2011).

Results

Of the 104 weed species found in the fruit tree orchards, 73 species (70.5%) were native and 31 were alien (29.5%) (Table 2). 8 native species (10.95% of total native species) and 8 alien species (25.81% of total alien) were included into “high successful” category.

Table 2. Summary of richness and cover of native and alien plants in flood-irrigated fruit tree orchards in Lleida, Spain. Mann Withney test was used to evaluate differences in richness and coverage between native and alien plants.



	Native	Alien	Total	P-value
total richness	73	31	104	
% total richness	70.5	29.5	100	
mean number sp./field	5.2	4.0	9.3	***
% number sp./field	56.5	43.5	100	
mean cover sp./field	53.2	64.7	117.9	**
% cover sp./field	45.1	54.9	100	

Significant codes: <0.001= '***'; <0.01= '**'; <0.05='*'

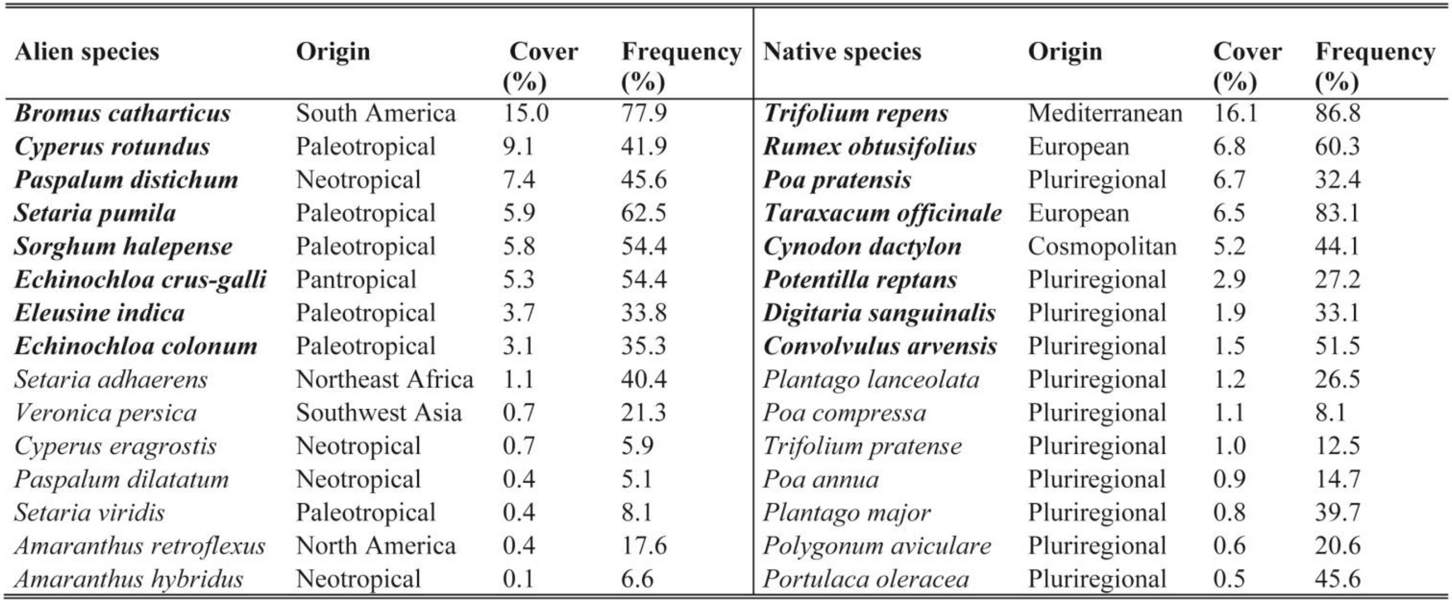
It should be pointed out that 75% of alien species included into "high successful" category were considerate as moderate or severe invasive in crops by Recasens and Conesa (2003) (i.e.: *Bromus catharticus, Cyperus rotundus, Paspalum distichum, Echinochloa crus-galli* and *E. colonum*) and 87.5% of them are considered as invasive established in natural habitats in the Iberian Peninsula by the DAISIE database (all the successful alien species except *E. crus-galli*). The most successful alien species have Paleotropical and Neotropical origin (Table 3). In general, most of the species present in the orchards had higher moisture requirements (higrophylous and mesohygrophylous) (e.g. *Trifolium repens, Rumex obtusifolius, Taraxacum officinale, Potentilla reptans, Sorghum halepense, Setaria pumila, Echinochloa crus-galli*).

The mean number of native species was significantly higher than the mean number of alien species per orchard, and cover of the native and the alien species per orchard differed significantly (Table 2). Alien plants cover represented the 54.90% of the total mean plant cover by plot.

Logistic regression models fitted for each variable (Table 4) showed significant differences between native and alien plants in photosynthetic pathway, timing of flowering, seed dispersal system, Grime's strategy, vegetative morphology, the length of the flowering period, Ellenberg Indices of light and temperature. Photosynthetic pathway, timing of flowering, and mode of seed dispersal had the greatest explanatory power (Nagelkerke R^2 determination coefficient around 44%) and they had the fewest misclassification errors (15%, 19%, and 21%, respectively). Although some of the other traits were statistically significant, they were not useful in discriminating between native and alien plants because their misclassification errors were very high (all around 29%), compared to the theoretical maximum misclassification error which can be priory estimated from the sample as the proportion of plants with the less prevalent category, i.e. alien plants (29.8%) are less frequent than native (70.2%).

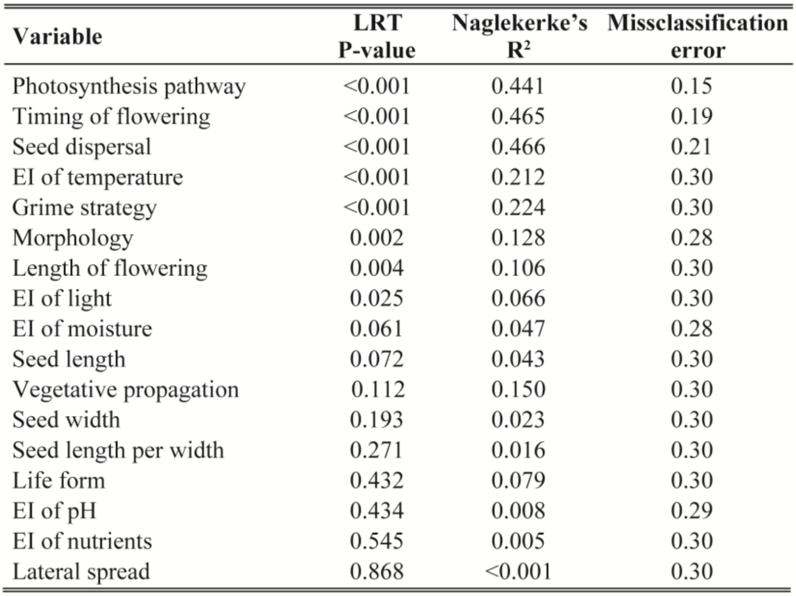
The best multiple logistic regression model included three traits (Table 5): seed dispersal system, flowering period and photosynthetic pathway. The model did not include the rest of the variables that were statistically significant when analyzed individually. The model had a misclassification error of 10.58% and it explained 73.23% of the variability in the response, according to Naglekerke's determination coefficient. The model indicated that most of the alien weeds were C4 species, whose seeds were dispersed by hydrochory. In contrast, most of the native weeds dispersed their seeds by anemochory and barochory. (see supplementary material).

Table 3. Cover (%) and frequency (%) of the 15 dominant alien and native weeds of the fruit tree orchards prospected in decreasing values of cover. Species in bold included in the "high successful" category



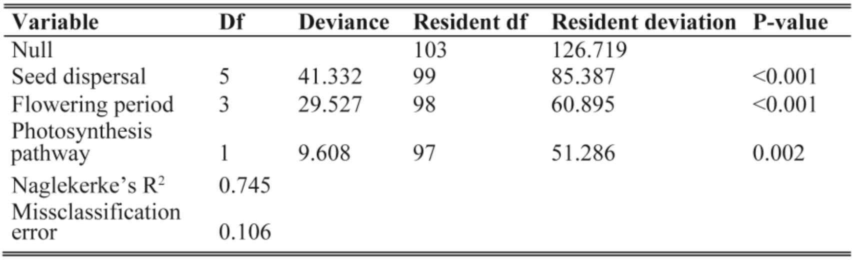
Alien species	Origin	Cover (%)	Frequency (%)	Native species	Origin	Cover (%)	Frequency (%)
Bromus catharticus	South America	15.0	77.9	***Trifolium repens***	Mediterranean	16.1	86.8
Cyperus rotundus	Paleotropical	9.1	41.9	***Rumex obtusifolius***	European	6.8	60.3
Paspalum distichum	Neotropical	7.4	45.6	***Poa pratensis***	Pluriregional	6.7	32.4
Setaria pumila	Paleotropical	5.9	62.5	***Taraxacum officinale***	European	6.5	83.1
Sorghum halepense	Paleotropical	5.8	54.4	***Cynodon dactylon***	Cosmopolitan	5.2	44.1
Echinochloa crus-galli	Pantropical	5.3	54.4	***Potentilla reptans***	Pluriregional	2.9	27.2
Eleusine indica	Paleotropical	3.7	33.8	***Digitaria sanguinalis***	Pluriregional	1.9	33.1
Echinochloa colonum	Paleotropical	3.1	35.3	***Convolvulus arvensis***	Pluriregional	1.5	51.5
Setaria adhaerens	Northeast Africa	1.1	40.4	*Plantago lanceolata*	Pluriregional	1.2	26.5
Veronica persica	Southwest Asia	0.7	21.3	*Poa compressa*	Pluriregional	1.1	8.1
Cyperus eragrostis	Neotropical	0.7	5.9	*Trifolium pratense*	Pluriregional	1.0	12.5
Paspalum dilatatum	Neotropical	0.4	5.1	*Poa annua*	Pluriregional	0.9	14.7
Setaria viridis	Paleotropical	0.4	8.1	*Plantago major*	Pluriregional	0.8	39.7
Amaranthus retroflexus	North America	0.4	17.6	*Polygonum aviculare*	Pluriregional	0.6	20.6
Amaranthus hybridus	Neotropical	0.1	6.6	*Portulaca oleracea*	Pluriregional	0.5	45.6

Table 4. Results from the logistic regression models fitted for each variable separately. Likelihood ratio test (LRT) p-value, Naglekerke's R^2 determination coefficient and misclassification error obtained when using the models for prediction are shown.



Variable	LRT P-value	Naglekerke's R^2	Missclassification error
Photosynthesis pathway	<0.001	0.441	0.15
Timing of flowering	<0.001	0.465	0.19
Seed dispersal	<0.001	0.466	0.21
EI of temperature	<0.001	0.212	0.30
Grime strategy	<0.001	0.224	0.30
Morphology	0.002	0.128	0.28
Length of flowering	0.004	0.106	0.30
EI of light	0.025	0.066	0.30
EI of moisture	0.061	0.047	0.28
Seed length	0.072	0.043	0.30
Vegetative propagation	0.112	0.150	0.30
Seed width	0.193	0.023	0.30
Seed length per width	0.271	0.016	0.30
Life form	0.432	0.079	0.30
EI of pH	0.434	0.008	0.29
EI of nutrients	0.545	0.005	0.30
Lateral spread	0.868	<0.001	0.30

Table 5. Deviance table showing the significance of each of the variables included in the multivariate logistic regression model, fitted with a stepwise method. Naglekerke's R^2 determination coefficient and misclassification error obtained when using the model for prediction are shown.



Variable	Df	Deviance	Resident df	Resident deviation	P-value
Null			103	126.719	
Seed dispersal	5	41.332	99	85.387	<0.001
Flowering period	3	29.527	98	60.895	<0.001
Photosynthesis pathway	1	9.608	97	51.286	0.002
Naglekerke's R^2	0.745				
Missclassification error	0.106				

The optimal classification tree performed for all of the species with all of the variables had six terminal leaves and a discriminant capability of 94.2% i.e., a misclassification error of 5.8%. (Fig 1). Photosynthetic pathway was the main factor (first splitter variable) that differentiated native and alien weeds and, at the second level, seed dispersal and flowering period differentiated native and alien plants. Alien weed species formed two groups: one comprised C4 species that disperse seeds using hydrochory, anemochory or multiple modes of dispersal, which included most (20) of the alien species, and another that included C3 species that flower in summer, use hydrochory or multiple modes of dispersal and have Ellenberg Indices of temperature larger than 5.5. Most of the native weeds were C3 species that flower in winter, spring, or throughout the year. In addition, the native species that flower in summer use anemochory, zoochory, or barochory for seed dispersal.

When photosynthetic pathway was excluded as a potential predictor, the resulting classification tree had seven terminal leaves and could discriminate correctly 97.11% of the species (see supplementary material). In that classification tree, flowering period was the main factor that differentiated native and alien weeds and indicated that most of the alien weeds usually flower in summer and the native weeds do so at other times of the year. Among alien weeds that flower in summer, most of them disperse their seeds by water or use multiple modes of dispersal and have high temperature demands. Among the native plants that flower outside of summer, those that have the highest demand for nutrients and those with a short flowering period were the most abundant.

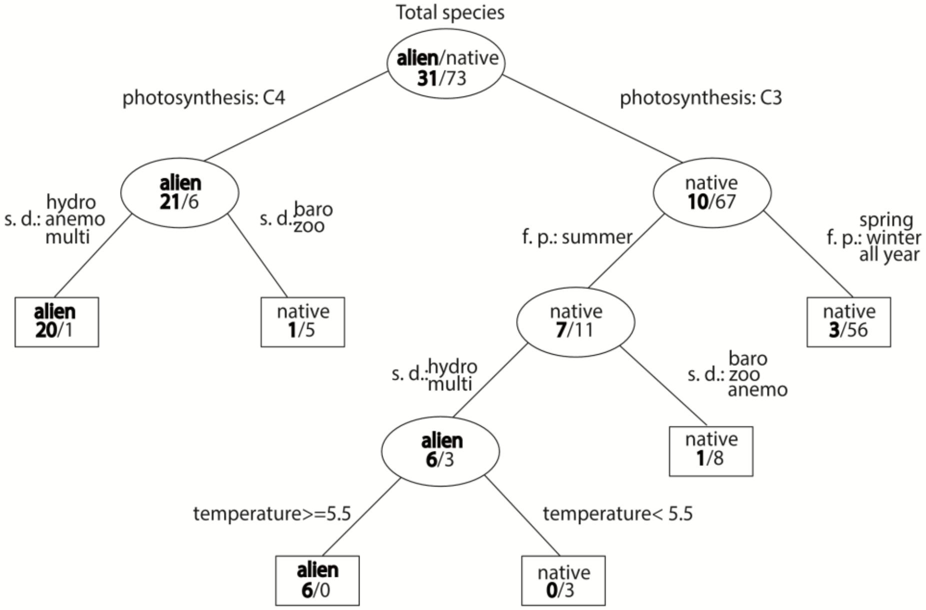


Figure 1. Classification tree to discriminate species origin (native or alien) from biological traits in the flood-irrigated fruit tree orchards in Lleida, Spain. Each node shows the number of alien (bold) and native (light) species and the origin of the majority of the species in this node. Terminal nodes are shown as rectangles. s.d.: seed dispersal, f. p.: flowering period.

The optimal classification tree performed to differentiate successful and non-successful species had six terminal leaves and discriminated correctly 93.26% of the species (Fig. 2). The main split, based on seed dispersal, indicated that successful species disperse their seed by water. Among them, the most abundant species were C4 species. The group of successful species that did not disperse their seeds by water were caespitose-reptant and rosulate hemicryptophytes and geophytes. Among them, the most successful species were those with a long flowering period and with an Ellenberg index of light lower than 7.5

Alien success

The optimal classification tree performed for alien weeds had four terminal leaves. High successful alien species differed from low successful alien species mainly in the seed dispersal system, the photosynthesis pathway and the clonality (Fig. 3). Most of the high successful alien species are C4 species that disperse their seeds by water. Only two species without water seed dispersal and clonal growth showed high cover. The tree classified correctly 93.75% of the species.

Native success

The classification tree that classified successful and non-successful native species had six terminal leaves. It showed that successful native species (Fig 4) were caespitose-reptant and rosulate hemicryptophytes with seeds larger than 1.55 millimetres. Among the group of species with other life forms, those geophytes and reptant therophytes that dispersed their seeds by zoochory and had seeds shorter that 6.4 millimetres were the most abundant, but only represents two species. A total of 95.83% of species were correctly classified.

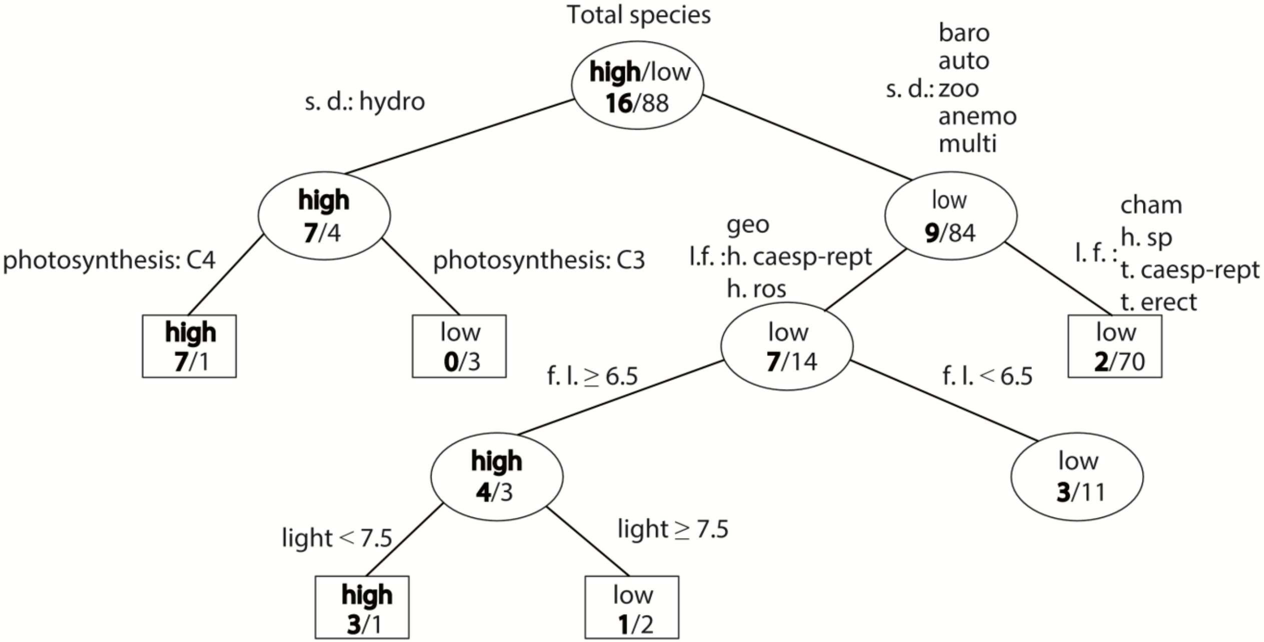


Figure 2. Classification tree to discriminate species success (high or low) from biological traits in flood-irrigated fruit tree orchards in Lleida, Spain. Each node shows the number of high successful (bold) and low successful (light) species and the status of the majority of the species in this node. Terminal nodes are shown as rectangles. s.d.: seed dispersal, l.f.: life form, f.l.: flowering length. Geo: geophytes, h.: hemicryptophytes, cham: chamaephytes, t.: therophytes. caesp-rept, caespitose-reptant, ros: rosulate, sp: scapose, baro: barochory, auto: autochory, zoo: zoochory, anemo: anemochory, multi: combined.

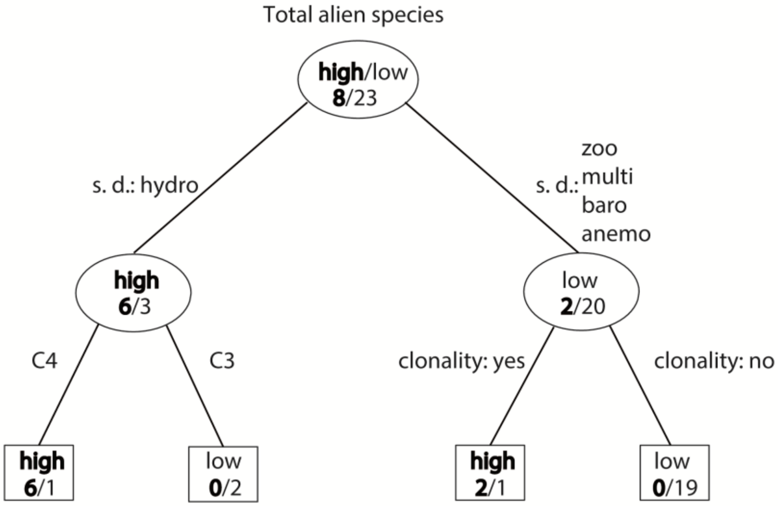


Figure 3. Classification tree to discriminate success of alien plants (high or low) from biological traits in flood-irrigated fruit tree orchards in Lleida, Spain. Each node shows the number of high successful (bold) and low successful (light) alien species and the status of the majority of the species in this node. Terminal nodes are shown as rectangles. s.d.: seed dispersal, zoo: zoochory, multi: combined, baro: barochory, anemo: anemochory.

Phylogenetic corrections

Phylogenetic corrections (Fig. 5) showed that 25.5% of the explained variation was related to biological and ecological traits, whereas 4.6% of the total variation was related to the phylogeny of the species. 14.5% of the total variation was related to the shared effects of species traits and phylogeny. The total amount of variation explained by species traits and phylogeny was 44.6%. The model of variation partitioning was statistically significant (*F*= 7.38; df= 7, 90; *P*<0.005)

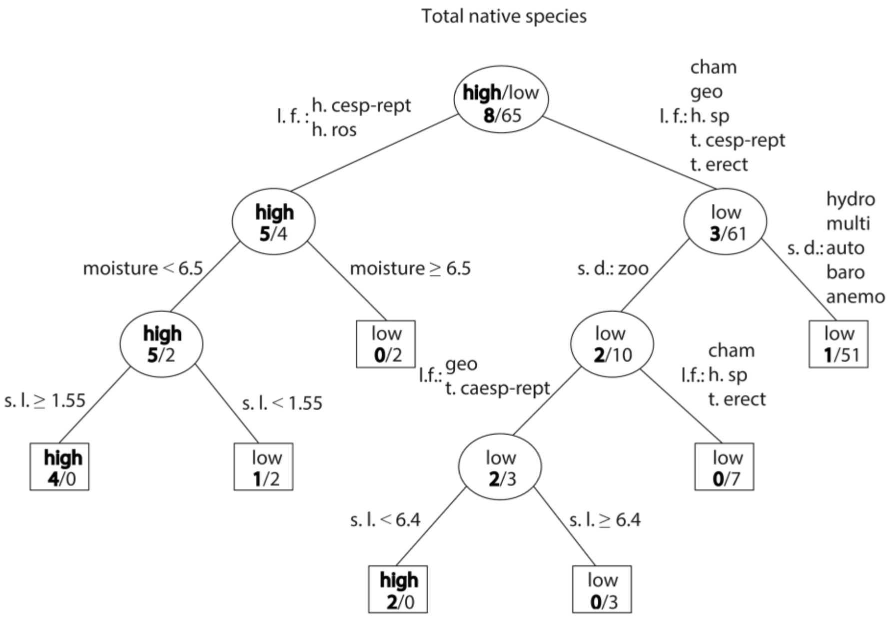


Figure 4. Classification tree to discriminate success of native plants (high or low) from biological traits in flood-irrigated fruit tree orchards in Lleida, Spain. Each node shows the number of high successful (bold) and low successful (light) native species and the status of the majority of the species in this node. Terminal nodes are shown as rectangles. s.d.: seed dispersal, l.f.: life form, s. l.: seed length. Geo: geophytes, h.: hemicryptophytes, cham: chamaephytes, t.: therophytes. caesp-rept, caespitose-reptant, ros: rosulate, sp: scapose.

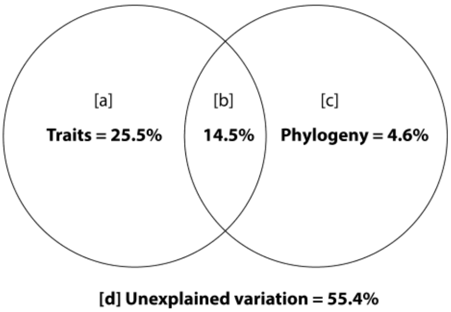


Figure 5 Variation partitioning of the response among biological and ecological traits (a), phylogeny (c) and phylogenetically structured variation of biological and ecological traits (b). The whole rectangle represents 100% of the variation, of which (d) is the unexplained part.

Discussion

Success of alien weeds in fruit tree orchards

This study unravels for the first time the outstanding role of alien species in the weed community of fruit tree orchards. The richness of alien weeds in fruit tree orchards was higher (29.5% of all weed species) than the average richness of alien weeds in other regions in the east and northeast of the Iberian Peninsula (i.e. Huesca and Comunidad Valenciana), where the alien flora does not exceed 20% of the total flora (Sanz Elorza et al., 2006, 2011). The richness of alien weeds in the fruit tree orchards in our study was higher than the richness of alien weeds in other agroecosystems in Catalonia (7.3% in the arable lands and 2.6% in wet grasslands of Catalonia) (Chytrý et al., 2008) and in other regions (e.g., 23.2% in agricultural habitats in Finland) (Hyvönen and Jalli, 2011). Our results reinforce the idea that agricultural habitats, subjected to periodic disturbances, are particularly susceptible to colonization by alien species (Lake and Leishman, 2004).

Role of traits in the success of alien weeds

Most of the biological traits related with the success of the weeds in orchards (i.e. photosynthetic pathway, seed dispersal, life form, flowering length) fit in with those that differentiate alien from native weeds and invasive from non-invasive alien weeds. Therefore, our study provides good evidence that some invasive alien weeds are more successful than most of the native weeds since they possess some traits that are favoured in the orchards.

Traits selected in orchards could be favoured by flood irrigation and mowing. Flooding and high temperatures favour C4 species, since those conditions increase the photorespiration rate (Sage, 2004). In addition, C4 photosynthesis is associated with high rates of productivity over short periods (Pyankov et al., 2010), thereby invasive alien species, which are mostly C4 species, are favoured. The success of alien C4 species in irrigated crops has already been described in other studies (Maillet and López-García, 2000). In general, the traits that promote fast growth rates and the procurement of resources are the most important factors in the establishment of alien flora and the subsequent displacement of native flora (Lavorel and Garnier, 2002; Dietz and Edwards, 2006).

Invasive alien weeds are mainly water dispersed. Surface irrigation is the main way for the input and output of hydrochorous seeds in flood irrigated crops. (Wilson, 1980). Dispersal by water ensures long-distance dispersal, which is advantageous to these alien weeds in plant communities present in open habitats subjected to frequent disturbances (Lake and Leishman, 2004; Gassó et al., 2009; Lososová et al., 2006; Cadotte and Lovett-Doust, 2001). Moreover, weed assemblages in orchards are in the first stage of succession because of the intensive management, which favours hydrochorous alien weeds (Latzel et al., 2011).

In our study, successful weeds had longer flowering periods than did the non-successful weeds, which is also a trait shared by alien weeds. Long flowering period is typical of invasive species (Küster et al., 2010; Pyšek et al., 2009a; Pyšek and Richardson, 2007) in other Mediterranean areas (Celesti-Grapow et al., 2003). Furthermore, long flowering periods are associated with the success of alien species in agricultural habitats (Lloret et al., 2005) because a prolonged flowering period increases the potential for colonization and allows these species to increase the opportunity to produce seeds (Lake and Leishman, 2004). Long flowering period can improve reproductive success and cross-pollination when pollination is seasonal or competition for pollinators is high (Lloret et al., 2005). Although most of alien weeds flower in summer in our study (Fig 1 and supplementay materials), flowering period was not a determinant factor related to the success in the orchards (fig 2). Moreover this trait did not differ between invasive alien and non-invasive alien weeds (fig 3).

Success of native species was defined mainly by their life form (fig 4). Rosulate and caespitose-reptant hemicryptophytes are favoured in the orchards, where weed control consists of mowing with flail mulcher. It has been proved that this practice benefits hemicryptophytes in vineyards (Lososová et al., 2003). In contrast, other studies related the annual species with higher weediness in agricultural habitats. (Pyšek et al., 2009a). In the orchards, annual species are disadvantaged because they are not able to regenerate their structures after mowing disturbance, whereas rosulate and caespitose-reptants hemicryptophytes have more likelihood of surviving due to the possession of perennating buds at ground level (Gago et al., 2007). Our results are consistent with Grubb (1985) that linked meristems close to the ground, a rosette life form and perennial life history with mechanic disturbances, as grazing.

Overall, our results are consistent with the limiting similarity theory, which assumes that alien species should use resources at different times or in different ways in order to avoid the competitive exclusion from the community (Abrams, 1983). Invasive alien species perform better when their traits and their patterns of resource use differ from those of local species (Fargione et al., 2003). Management conditions limit the traits of the species that can persist in a given habitat (in this case the irrigated orchards), which would tend to result in trait similarities between native and alien species (i.e. most of the weeds are mesohygrophilous or hygrophilous). However, individuals compete at the small scale of the orchard. At that scale, trait differences between native and invasive species as a result of limiting similarity can be observed.

Phylogenetic effects

In order to separate ecological and evolutionary responses, comparative studies of alien and native species should take into account the potentially confounding effects of phylogenetic relatedness (Sol et al., 2008). The weak influence of the phylogeny on the results reveals the multiple and independent evolutionary divergences between invasion process and biological traits, as has been demonstrated in others studies (Milbau and Stout, 2008; Lososová et al., 2006). These results reinforce those obtained by Pyšek et al. (2009a) who state that belonging to a particular families does not predispose to be more or less invasive (at least at high taxonomic levels). Nevertheless, the high proportion of variability provided by the phylogenetically structured variation of studied traits shows that the development of shared traits may be related to the colonization of similar niches during evolutionary history (Harvey and Pagel, 1991).

Ecological and agronomical implications

Our study provides good evidence that the flood irrigation system facilitates the success of alien invasive species in the weed community of the fruit tree orchards. We suggest that the combination of the management conditions in fruit tree orchards and the presence of alien plants with a suite of traits that favour high survival rates, rapid growth in response to an infusion of water supply and water seed dispersal may allow successful invasion in flood irrigated orchards communities.

Our study underscores the importance of tree orchards in irrigated agricultural landscapes as local alien weeds reservoirs. The flood irrigation system and the structure of the agricultural landscape as a mosaic of small patches interconnected with each other and with the surrounding natural riparian habitats allow the entry of weeds into the crops. The management practices used in the orchards enhance the establishment and dispersal of that invasive alien flora with traits favoured among the crops and to the surrounding riparian habitats, since the river is used as a drainage channel of the irrigated water. Favouring invasive alien weeds has negative economic and ecological impacts on crops on one hand, and on the other hand with the possibility to develop invasive behaviour in the riparian ecosystems (Miyawaki and Washitani, 2004) that have similar characteristics as the orchards, such as flooding and periodic disturbances. It has been confirmed that favouring invasive species in irrigated crops increases the risk of invasion of these species in the near riparian ecosystems. Ferreira and Moreira (1995) associated sites disturbed by irrigated crops with a high degree of spatial invasiveness of some aliens as *Paspalum distichum, Amaranthus retroflexus* and *Cyperus eragrostis* in southern Iberian river environments. Solé et al. (2010) found similar results in the Segre river on its way through our study area. They showed that the most invasive species were agricultural weeds (i.e. *Paspalum disticum, Cyperus eragrostis, Xanthium echinatum, Amaranthus retroflexus*) reaching the highest invasive degree in the frequently flooded banks. Aguiar et al. (2006) also proved that frequently flooded banks are the most invasible areas of the south Iberian floodplains. It has been suggested that flooding contributes to the invasibility of riparian zones by uncovering flood-prone areas. This process reduces the competitive capability of resident native against colonizing exotic plant species (Hood et al., 2000).

Management implications

Based on the results of the study, some recommendations should be highlighted:

(1) given the clear role of plant traits in promoting the success of invasive alien species, it would be useful to avoid the introduction of alien weeds with traits favoured by flooding irrigation. It is well-documented that most of the alien weeds found in the orchards were unintentionally introduced in Spain, although some of the most invasive have been used as cover plants or as ornamental grasses (i. e. *Bromus catharticus, Paspalum distichum, P. dilatatum*), (Sanz-Elorza et al., 2004); even more, they are recommended as cover plants in organic perennial crops (Domínguez-Gento et al., 2002). Replacing these species for some native, as *Trifolium repens,* that is also successful in orchards (Table 3) can avoid the establishment and spread of those alien species. The use of *T. repens* in cover crops is already well-established in vineyards (Gago et al., 2007) and could be

a good alternative to *Paspalum spp.* and *B. catharticus* (Pardini et al., 2002).

(2) The selection of the appropriate management practices in the agricultural system is crucial to control and prevent the spread of alien flora within the landscape. Thus, changing flood by drip irrigation can limit the entry of seeds dispersed by water and avoid the spread of alien species already presents (Juárez et al., 2010). Moreover, drip irrigation increases the sustainability of the crop, by saving water, which is a key factor in semiarid areas, and improves the crop yield (Bravdo and Proebsting, 1993). In addition, drip irrigation could increase the efficiency of fertilizers use with direct injection. These changes on the current agricultural practices will allow better field access for equipment, reduce humidity associated fungal diseases and decrease the extensiveness of weeds (Fereres et al., 2003).

Conclusions

This study reveals the outstanding role of alien species in weed assemblages in flood irrigated fruit tree orchards, supporting that irrigated agricultural crops in Mediterranean areas undergo high rates of alien plants within the weed community. This prominence of alien weeds is linked to the possession of a suite of traits that are favoured in this habitat, which are also those that differentiate successful alien weeds from non-successful alien and native plants. This selection of traits can be related to the irrigation management of the orchards and the environmental constraints, since flooding and higher temperatures in summer benefit C4 species, dispersed by water, which are mainly alien species. On the other hand, mowing of orchards lay behind the enhancement of perennial caespitose and rosulate forms which are common traits shared by the successful native species.

Our results support the limiting similarity theory acting in flood irrigated orchards by showing that differences in traits between alien and native species enable the success of the former in irrigated fruit tree orchards.

This study highlights on the one hand the role of flood irrigated orchards as reservoir of successful alien weeds, where they are benefited by crop management and from where they can spread and colonize nearby habitats through irrigation water and on the other hand the importance of the trait approach in disentangling the causes of alien plant success in weeds assemblages. Therefore, in order to avoid this invasion process, management should be focused on monitoring traits of new weed species introduced in orchards, for prioritizing control measures on those species which possess the suite of traits known to be favoured there as well as on the selection of potentially successful native species for cover crops, which can prevent the establishment and the expansion of the alien component. In addition, since our results show that successful alien weeds are those that can be spread by flood irrigation, it is strongly recommended to modernize irrigation systems, by changing flooding to other water management, such as drip irrigation.

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Supplementary material 1. Adjusted multiple logistic regresion model, fitted with a stepwise method. Null and residual deviance and Akaike information criterion (AIC) are shown

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.8807  -0.1082   0.1783   0.4103   2.2546

Coefficients:
                         Estimate Std. Error  z value Pr(>|z|)
(Intercept)              -0.2457     1.2910    -0.190  0.84908
seed.dispersal more        2.6783     1.4328     1.869  0.06158
seed.dispersal zoo        22.4724  1952.6065     0.012  0.99082
seed.dispersal unassisted  4.3791     1.7173     2.550  0.01077
seed.dispersal wind        3.0926     1.4789     2.091  0.03651
flowering.period summer   -2.2589     0.7793    -2.898  0.00375
photosynthesis C4         -2.6334     0.9276    -2.839  0.00453
**
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Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 126.719  on 103  degrees of freedom
Residual deviance:  51.286  on  97  degrees of freedom
AIC: 65.286

Number of Fisher Scoring iterations: 18
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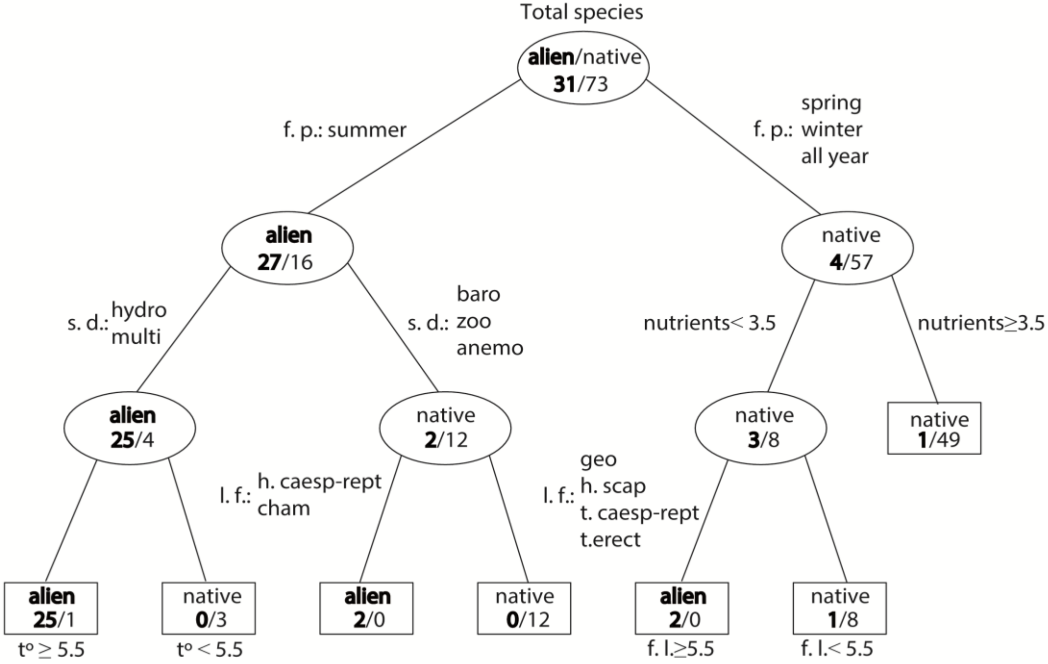

Supplementary material 2. Classification tree to discriminate species origin (alien or native) from biological traits in flood-irrigated fruit tree orchards in Lleida, Spain, excluding photosynthetic pathway. Each node shows the number of alien (bold) and native (light) plants and the origin of the majority of the species in this node. Terminal nodes are shown as rectangles. f. p.: flowering period, s.d.: seed dispersal, l.f.: life form, tº:temperature, f.l.:flowering length. Geo: geophytes, h.: hemicryptophytes, cham: chamaephytes, t.: therophytes. caesp-rept, caespitose-reptant, ros: rosulate, sp: scapose, baro: barochory, auto: autochory, zoo: zoochory, anemo: anemochory, multi: combined.

CHAPTER 4

Management as a driver of functional patterns and alien species prominence in weed communities of irrigated orchards in Mediterranean areas.

Submitted to *Agriculture, Ecosystems and Environment.*

Management as a driver of functional patterns and alien species prominence in weed communities of irrigated orchards in Mediterranean areas.

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Abstract

Weed communities in irrigated orchards configure a spontaneous vegetation cover with a remarkable presence of alien species within. This plant cover can affect negatively orchards by reducing yield but on the other hand it can play a positive role by avoiding soil erosion, increasing biodiversity and providing pollination services. Compositional and functional structure of these weed communities are configured by management practices. Therefore, it is crucial to disentangle which differences in weed communities are mediated by management practices in order to establish a management that promote weed covers which enhance benefits while reducing negative effects on the orchards. In irrigated orchards of the Mediterranean area, management is configured by irrigation (flood/drip) and weed control (mechanical/chemical). To identify how differences in irrigation and weed control modify weed communities in orchards, floristic surveys were carried out in mowed and in herbicide-treated plots on drip and flood irrigated orchards. Weed community structure in each management was evaluated in terms of species cover and diversity and the prominence of alien species from a floristic and a functional approach. Results showed that irrigation system is the main factor influencing weed community structure. Comparing to drip, flood irrigation makes up a denser weed community with larger values of alien weeds. Similarly, irrigation determines taxonomical and functional composition of weed communities and modulates the effect of weed control methods. Flooding favours alien species, C4, perennial grasses, clonal species, zoochorous and hydrochorous and wind-pollinated species whereas drip irrigation selects mostly native C3 forbs, non-clonal, wind-dispersed and insect pollinated species.

Therefore, this study provides insights into how weed management can be adapted to promote a vegetation cover that maximizes benefits to the orchards and the environment while minimizing negative effects of the weeds and prominence of alien species within weed community.

Keywords

Irrigation, weed control, alien plants, biological traits, ecosystem services.

Introduction

Weed communities in perennial crops, such as orchards, play contrasting roles. On the one hand, their presence affects negatively yield (Kaya-Altop et al., 2016) by competing with trees for nutrients and water, especially when trees are young (Travlos, 2013; Oliveira et al., 2016), hosting pests and diseases that can affect the crop and favouring habitats for rodent development that can kill the trees (Lipecki, 2006).

On the other hand it has been proved that weed communities in orchards can have positive effects such as promoting soil enrichment (Travlos, 2013), avoiding soil erosion and mechanical compaction, acting as a source of organic matter and nitrogen (Lipecki, 2006), being natural antagonist of pest and diseases (Cicuzza, 2012) and providing ecosystem services, such as conservation of pollinators (García and Miñarro, 2014). Moreover, weed communities contribute to the increasing of the biodiversity of agroecosystems (Mas et al., 2007).

Weed communities in orchards configure a spontaneous vegetation cover that can play the same role as commercial seeded cover crops. However, spontaneous vegetation is more sustainable at long-term scale due to their self-reseeding capability, their extended germination and their role in the promotion of biodiversity in agroecosystems (Mas et al., 2007). Nevertheless, the overall increase of global trade and the alteration of the environment have boosted the rate of alien plants present in weed communities in crops (Pimentel et al., 2005). These alien weeds have negative effects in terms of crop yield loses and costs of control methods (Recasens et al., 2007) as well as ecological impacts, not only for the agroecosystem (Vilà et al., 2004) but also for the adjacent natural habitats (Juárez-Escario et al., 2016).

For these reasons, in order to maintain an environmental sustainability of orchards while optimizing fruit yield, it is crucial to promote a spontaneous vegetation cover that maximizes the benefits for the orchards and for the environment and minimizes the exposed negative effects of weeds and the prominence of alien species within the weed community.

In this sense, floristic and functional structure of weed communities in crops are determined mainly by management practices (Gago et al., 2007; Mas et al., 2007; Cicuzza et al., 2012). In the case of orchards in Mediterranean areas, management practices include irrigation - traditionally by flooding and more recently by drip irrigation- and weed control management (mechanical and/or chemical) (Mas et al., 2007; Miñarro, 2012).

Several studies focus on analysing weed community structure in irrigated orchards (Mas et al., 2007; Juárez-Escario et al., 2013) and on the influence of management practices such as fertilization and tree-row management (Miñarro, 2012). However, none of them analyzes the effect of the irrigation system on the compositional and functional structure of the weed community, even when the influence of water availability in plant communities subjected to management in Mediterranean areas has been proved (Carmona et al., 2012). Accordingly, it has been showed that flood-irrigated orchards harbour a set of alien weed species that are filtered by possessing some functional traits (Juárez-Escario et al., 2013), but it remains unknown the prominence of alien species in weed communities in drip irrigated orchards and their functional characteristics.

In this sense, clarifying the compositional and functional shifts of weed populations in orchards depending on the irrigation system and the weed control management can facilitate the detection of troublesome species and functional groups under each management system (Gago et al., 2007). This is essential for providing meaningful guidelines for management strategies of weed control in order to maintain a suitable plant cover that improve biodiversity and deliver ecosystem services to the orchards while minimizing competiveness of weeds as well as reducing the presence of alien plants in weed communities.

Consequently, the aims of this work were to (1) compare the effect of both irrigation and weed control systems on the diversity of total and alien weeds present in irrigated orchards on the Plain of Lleida (Catalonia, NE of Spain) (2) identify which management combination is related to the prominence of alien weeds in these communities and (3) determine the compositional and functional structure of these weed communities.

Materials and methods

Study area

The study was conducted in an irrigated fruit production area included in the Lleida’s Plain (41º25’-41º49’N, 0º20’-1º06’E), which is the main fruit production region in Catalonia (NE Spain) (29,880 ha. of irrigated orchards, 84.24% of the total production area in Catalonia).

Local climate is semiarid continental-Mediterranean with a mean annual temperature of 15ºC and annual rainfall of approximately 385mm, concentrated in spring and autumn (Ninyerola et al., 2005). The soil moisture regime is xeric and the soil temperature is mesic. Land-use is dominated by irrigated crops over shallow chalky-clay soils with presence of calcareous lutites and saline soils (Dalmau and Iglesias, 1999).

In the study area there are established flood and drip irrigated orchards. In the last years, the irrigated area has been enlarged and new drip irrigated orchards have been installed. The expansion of irrigation has been favoured by the peculiar morphological characteristics of the area, which does not present any significant barriers. It is basically configured by a large floodplain surrounded by a series of little high reliefs (Dalmau and Iglesias, 1999).

Selected fruit tree orchards

Selected orchards were stone (pear and apple) and pome (peach and nectarine) orchards, irrigated either by flooding or by drop. Flood irrigated orchards are irrigated bi-weekly from April to early September (a total of 10–12 irrigation episodes during this period) through an extensive old irrigation network that circulates water from large canals originated in the Segre and Noguera Ribagorçana rivers. Drip irrigated orchards are irrigated daily (a minimum of 3-4 l/m^2 weekly) through a complex system that includes artificial ponds, pressure bombs and water distribution pipes. On the other hand, weed control differs between tree rows and under tree lines. Between tree rows, weeds are mainly mechanically controlled to facilitate machinery traffic by using a rotary mower, a flail mower, or a flail crusher before harvesting and in the tree lines weeds are removed by herbicide spraying to reduce competition for water and nutrients (mixed of pendimethalin, oxyfluorfen, isoxaben and oryzalin in February and glyphosate and fluroxypyr between May and June and after September). Shredded weeds and pruning remain on the ground acting as mulch material. At the moment of the surveys all the selected orchards were in production and they were older than 6 years. There were no differences in weed management and fertilization in the age or planting density of both flood and drip irrigated orchards studied.

Vegetation sampling

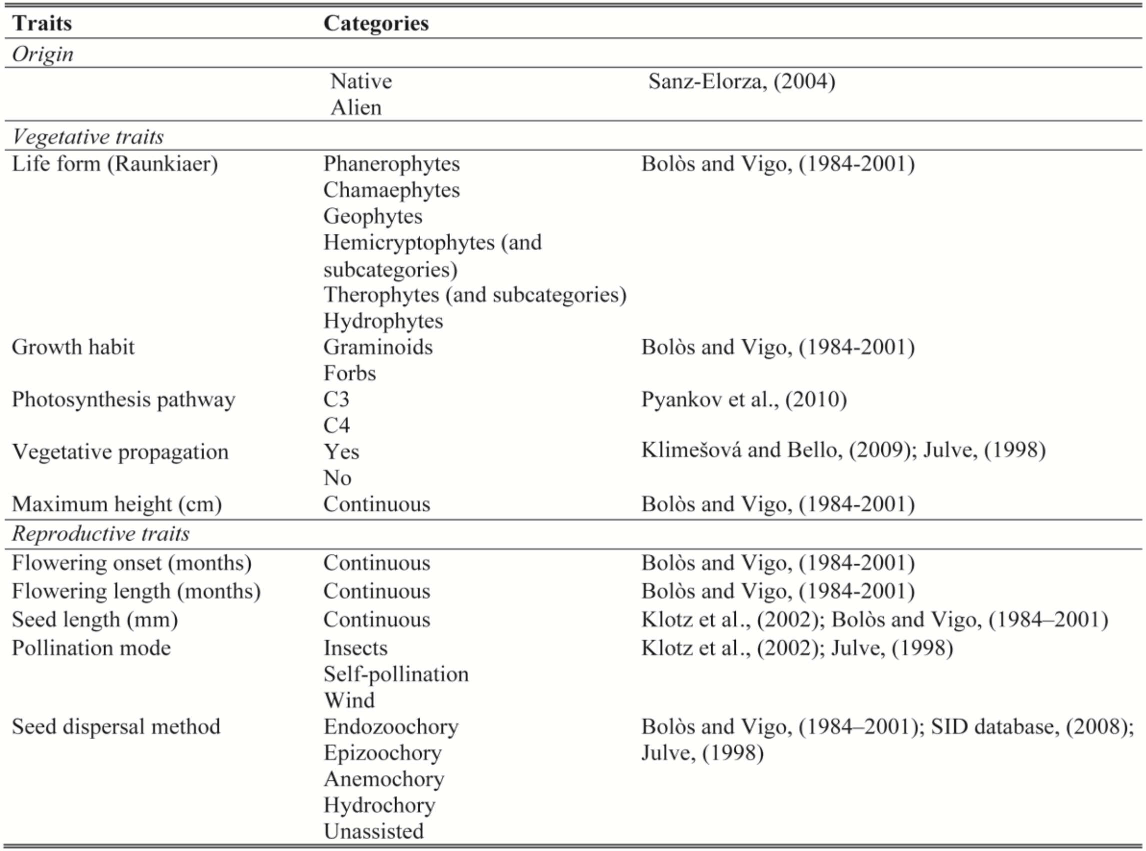
In summer 2011, floristic surveys were recorded on rectangular plots (2m x 5m) in 75 flood and 75 drip irrigated orchards. In each orchard, 6 plots were randomly established, 3 of them in the alleys (mowed areas, codified as FB and DB for flood and drip irrigated orchards respectively) and 3 in the tree rows (herbicide-treated area, codified as FU and DU for flood and drip irrigated orchards respectively). Edges of the fields were avoided in order to avoid ruderal species to be surveyed. Vascular plant nomenclature follows local flora (Bolòs and Vigo, 1984–2001). The Braun-Blanquet (1979) six-point scale was used to quantify species abundance, in which the cover-abundance of each species is assigned a value between + (sparse and covering a small area) and 5 (covering more than 75% of the area). Those values were transformed into the mean value of percent cover range in each cover class (+=0.01%; 1=5%, 2=17.5%, 3=37.5%, 4=62.5%, 5=87.5%). In each orchard, mean cover value of the 3 plots was calculated respectively in each position. Hellinger’s transformation (Rao, 1995) was applied to the species cover matrix to decrease the importance of the most abundant species and avoid problems associated to the Euclidean distance. This transformation is recommended for ordination of species abundance data (Legendre and Gallagher, 2001).

Species traits

Species were classified as alien or native according to Sanz-Elorza et al. (2004), which is the most recent and complete revision of alien flora in Spain up to now. Archaeophytes and neophytes were considered alien species sensu Richardson et al. (2000). Although *Setaria adhaerens* and *Echinochloa crus-galli* are considered cryptogenic plants (i.e. controversial species regarding their origin), in this study they were classified as alien species because of their Paleotropical origin (Campos, 2000; Sanz-Elorza et al., 2011).

Moreover, 10 biological traits regarding growth, reproduction, pollination and dispersal system were recorded (Table 1). The list of selected traits was based on Cornelissen et al. (2003) and Westoby et al. (2002). Selected traits are related to plant response to disturbances and competitive strength as well as to flowering timing and pollination system; this latter is important for this study for providing an ecosystem service to the orchards. Seed dispersal and pollination systems were codified as binomial variables (0/1). For each of these variables, when species presented more than one category, a relative proportion of the total number of categories for each species was assigned to each one (0.5, 0.33 or 0.25 values in case the species has 2, 3 or 4 categories, respectively).

Table 1. Plant species traits selected for the study.



Traits	**Categories**	
Origin		
	Native Alien	Sanz-Elorza, (2004)
Vegetative traits		
Life form (Raunkiaer)	Phanerophytes Chamaephytes Geophytes Hemicryptophytes (and subcategories) Therophytes (and subcategories) Hydrophytes	Bolòs and Vigo, (1984-2001)
Growth habit	Graminoids Forbs	Bolòs and Vigo, (1984-2001)
Photosynthesis pathway	C3 C4	Pyankov et al., (2010)
Vegetative propagation	Yes No	Klimešová and Bello, (2009); Julve, (1998)
Maximum height (cm)	Continuous	Bolòs and Vigo, (1984-2001)
Reproductive traits		
Flowering onset (months)	Continuous	Bolòs and Vigo, (1984-2001)
Flowering length (months)	Continuous	Bolòs and Vigo, (1984-2001)
Seed length (mm)	Continuous	Klotz et al., (2002); Bolòs and Vigo, (1984–2001)
Pollination mode	Insects Self-pollination Wind	Klotz et al., (2002); Julve, (1998)
Seed dispersal method	Endozoochory Epizoochory Anemochory Hydrochory Unassisted	Bolòs and Vigo, (1984–2001); SID database, (2008); Julve, (1998)

Statistical analysis

Weed community structure was analysed in terms of species diversity, cover structure as well as floristic and functional structure for each management system (irrigation and weed control). Species diversity was summarised by calculating α- (mean number of species by plot), γ- (total number of species in each management system) and β-diversity ([γ-diversity/mean α-diversity – 1] (Whittaker, 1960)) both for total and for alien weeds. Total and alien α-and β-diversity were compared among management methods fitting linear mixed-effects models in order to account for nested design, by nesting management factor to the field. Means were compared by using Tukey's Honest Significant Differences (HSD) between groups.

Cover structure was evaluated by comparing cover value of total and alien species among treatments, similarly as for *α*- and β-diversity. Cover values of alien species were squared-root transformed to achieve normality.

In order to analyse how proportional abundances of species varied across management systems, cumulative frequency curves of species were built. In these curves all the species are ranked from the most abundant to the least abundant.

To explore patterns of weed community similarities among management systems, a Bray Curtis similarity hierarchical cluster analysis with Ward distance was performed. Non-metric multidimensional scaling (NMDS) was performed with k=2 number of dimensions and using Bray Curtis' similarity index as the distance measure. Four main cluster groups were selected in order to relate clustered plots with the four different management combinations. The groups obtained in cluster analysis were overlaid on NMDS ordination in order to validate cluster results. Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations was performed on NMDS to evaluate statistical significance of the differences on weed composition among management systems. In order to evaluate which percentage of variability in species composition was due to the differences in each management system, partial Canonical Correspondence Analyses (partial CCA) were performed using either irrigation or weed control methods as explicative variables and the other as covariable, respectively.

Relationships between functional traits and management systems were explored through redundancy analysis on community weighted means values of traits (CWM-RDA). This method is useful to detect changes in average trait expressions of communities along environmental gradients (Kleyer et al., 2012). CWM values were calculated as follows:

$$CWM = \sum_{i=1}^{S} p_i \cdot t_i$$

Where S is the number of species in the community, p_i is the species i abundance proportion and t_i is the trait value of species i (Lavorel et al., 2008).

To identify which traits were present with significant higher values at each management system, linear mixed-effect models, accounting for nested design and post-hoc Tukey HSD comparisons were fitted on CWM values. When normality was not achieved, non-parametric Kruskal-Wallis test, followed by Dunn’s test for multiple pairwise comparisons were carried out.

All analyses were performed with R software (R Development Core Team, 2011), except for partial CCA and CWM-RDA, which were carried out with CANOCO 5 software (Ter Braak and Smilauer, 2012).

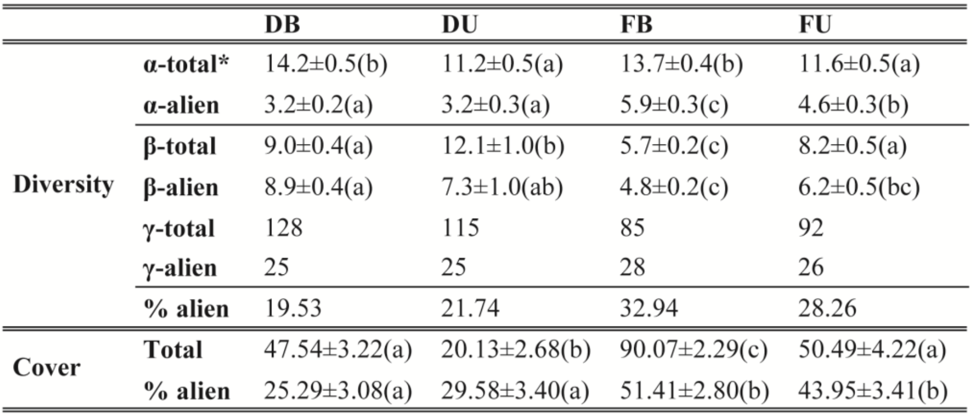
Results

Weed community structure

A total of 173 plant species were recorded in the study, 33 of which were alien weeds. α-diversity of mowed plots was higher than that of herbicide-treated plots (Table 2), regardless of the irrigation system ($F_{3,142}$ = 10.8, p <0.01). This trend was different when focusing on alien species α-diversity, which was higher in flood irrigated orchards, particularly between rows ($F_{3,142}$ = 22.4, p <0.01). Total ($F_{3,142}$ = 18.11, p <0.01) and alien β-diversity ($F_{3,142\,=}$ = 6.73, , p <0.01) were higher in drip irrigated orchards. Likewise, drip irrigated orchards contained a higher γ-diversity than flood irrigated, although proportion of alien plants was higher in flood than in drip irrigated orchards.

Weed cover showed significant differences among treatments, both for total cover ($F_{3,142}$ = 84.7, p <0.01) and for the percentage of alien species represented within ($F_{3,142}$ = 15.4, p <0.01) (Table 2). The highest percentage of plant cover was found in FB and the lowest value was found in DU. Plant cover of flood irrigated orchards included significantly higher percentage of alien plants than that of drip irrigated orchards.

Table 2. α-, β- and γ-diversity of total and alien species (±standard error) and percentage of alien species as well as total and alien cover values (±standard error) in each management type. DB: drip irrigation, between tree rows; DU: drip irrigation, under tree rows; FB: flood irrigation, between tree rows; FU: flood irrigation, under tree rows. Significant differences indicated by different letters within rows based on Tukey HSD tests (p < 0.01). *= squared root-transformed variables



		DB	**DU**	**FB**	**FU**
Diversity	**α-total***	14.2±0.5(b)	11.2±0.5(a)	13.7±0.4(b)	11.6±0.5(a)
	α-alien	3.2±0.2(a)	3.2±0.3(a)	5.9±0.3(c)	4.6±0.3(b)
	β-total	9.0±0.4(a)	12.1±1.0(b)	5.7±0.2(c)	8.2±0.5(a)
	β-alien	8.9±0.4(a)	7.3±1.0(ab)	4.8±0.2(c)	6.2±0.5(bc)
	γ-total	128	115	85	92
	γ-alien	25	25	28	26
	% alien	19.53	21.74	32.94	28.26
Cover	**Total**	47.54±3.22(a)	20.13±2.68(b)	90.07±2.29(c)	50.49±4.22(a)
	% alien	25.29±3.08(a)	29.58±3.40(a)	51.41±2.80(b)	43.95±3.41(b)

Cumulative frequency curves of species showed that in all management types, weed community was dominated by a few number of species (from 6 species in FB and FU to 9 species in DB, accounting for more than 50 % of the total weed cover) (Fig. 1). It is remarkable that the most abundant species in every management systems was an alien species (*Bromus catharticus*, *Echinochloa colonum*, *Crepis bursifolia* and *Setaria adhaeren*s in FB, FU, DB and DU, respectively).

Floristic and functional composition

PERMANOVA analysis on NMDS results showed significant differences among management systems in terms of floristic composition (R^2=0.17; F= 20.06; *p*<0.01) (Fig. 2). The four main cluster groups obtained in cluster analysis separated plots primarily based on irrigation method and were also ordinated in NMDS close to one another, depending on management, confirming that differences in management resulted on differences in plant composition. pCCA results showed that 7.2% of plant composition variability was explained by differences in irrigation system (pseudo-F=22.5, p<0.001), while weed management only accounted for 2.7% of the total variability (pseudo-F=8.1; p=0.001).

Management cobinations explained 17.6% of the total variance in community traits in the CWM-RDA (Fig. 3). First axis (the only one constrained since there is one explanatory variable) separates flood irrigated orchards from those drip irrigated irrespective of weed management, which is in accordance with cluster and pCCA results. Flooding irrigation was related to alien species, caespitose and reptant life forms, grasses, clonality, C4 photosynthesis, wind pollination, zoochory and hydrochory whereas native species, most of the therophytes, non-clonal plants, forbs, C3 photosynthesis, insect and self-pollinated species, barochory and anemochory were associated with drip irrigation.

Linear mixed-effect models and Kruskal-Wallis test fitted on CWM trait values confirmed some of these trends (table 3 and supplementary material). Flood irrigated orchards included significant higher number of alien species, C4 photosynthetic pathway and zoochorous species. Within them, mowing plots contained mainly hemicryptophytes graminoid species, clonal species, wind-pollinated species and species with large seeds dispersed by water whereas in herbicide-treated plots caespitose/reptant annual species stood out. Drip irrigated orchards presented higher number of native plants, non-clonal species, self-pollinated and barochorous. Within them, mowing selected mostly rosulate annual and perennial forbs, C3 species, insect-pollination and wind dispersed seeds. Finally, herbicide application generated a community with erect therophytes with large height and long flowering length.

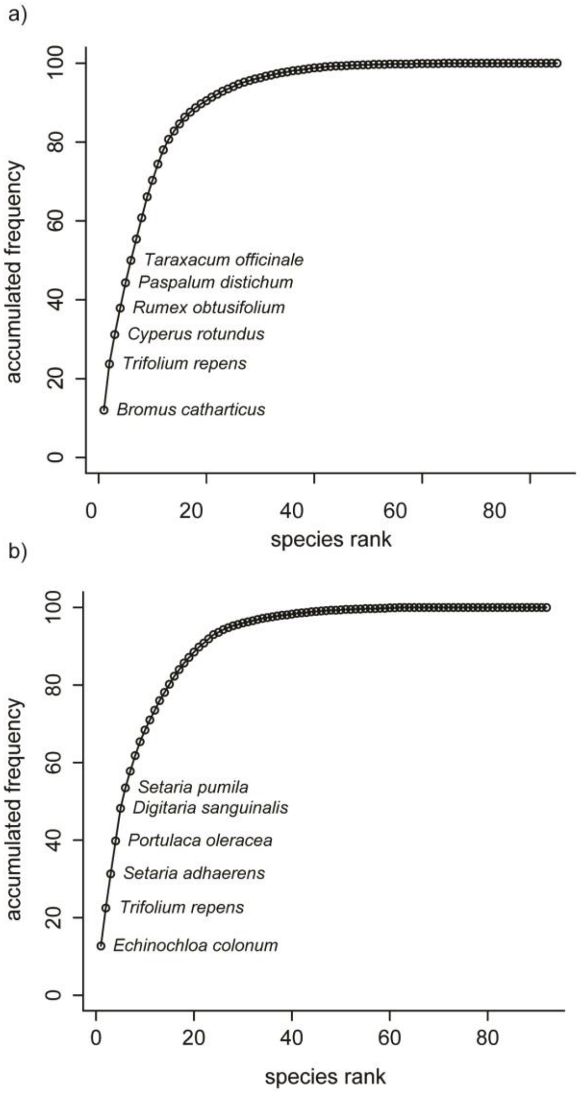


Figure 1 a-b. Cumulative frequency curves of species of a) flood irrigated orchards, plots between the tree lines (FB) b) flood irrigated orchards, plots under tree lines (FU). The name of those species that configure 50% of the total abundance is showed.

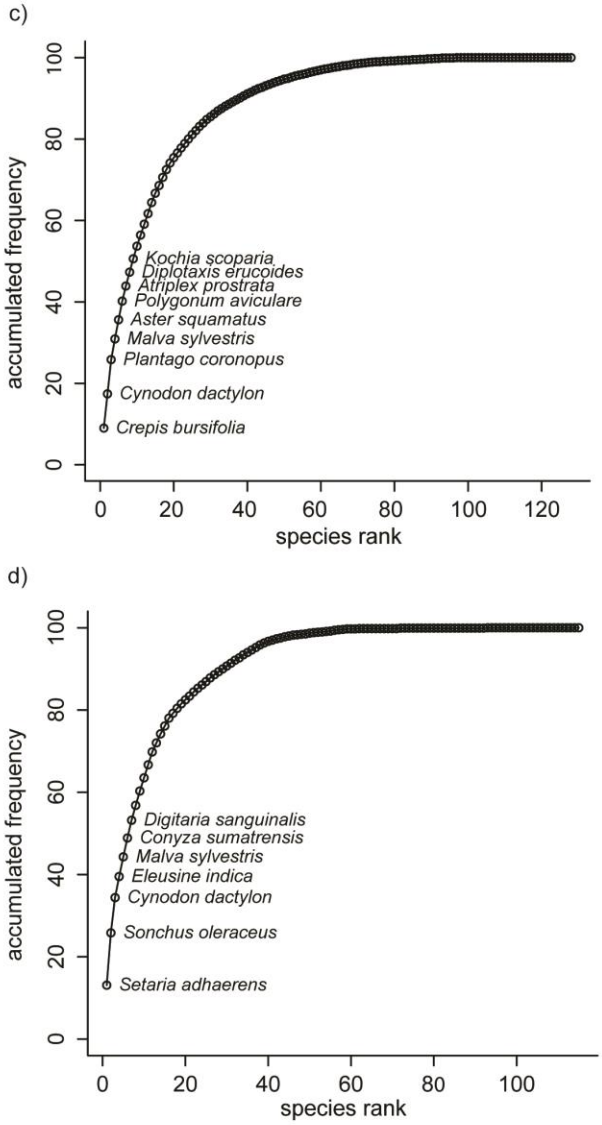


Figure 1 c-d. Cumulative frequency curves of species of c) drip irrigated orchards, plots between the tree lines (DB), d) drip irrigated orchards, plots under tree lines (DU). The name of those species that configure 50% of the total abundance is showed.

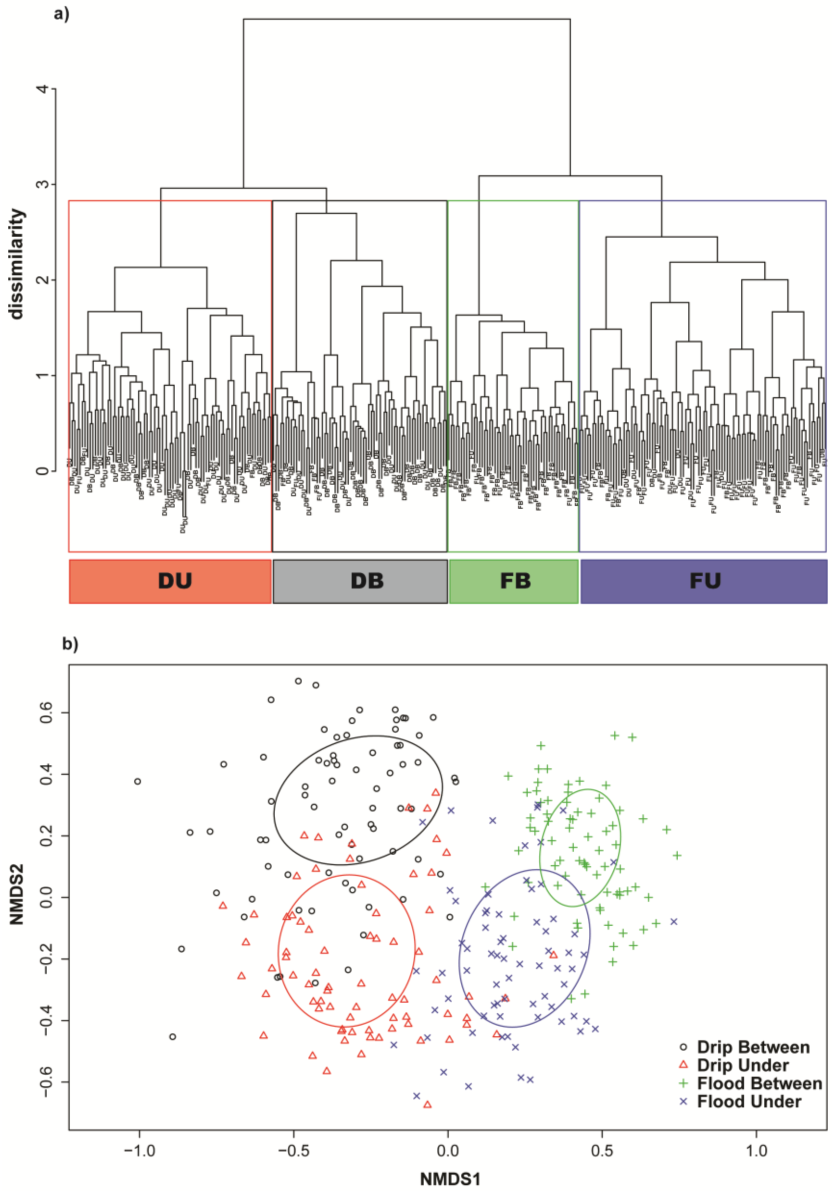


Figure 2. a) Bray Curtis similarity hierarchical cluster analysis with Ward distance and b) Non-metric multidimensional scaling ordination of the study sites based on Bray-Curtis similarities. Circles represent standard deviation of scores based on cluster groups. DU: drip irrigated orchards, plots under tree lines, DB: drip irrigated orchards, plots between the tree lines, FB: flood irrigated orchards, plots between the tree lines, FU: flood irrigated orchards, plots under tree lines.

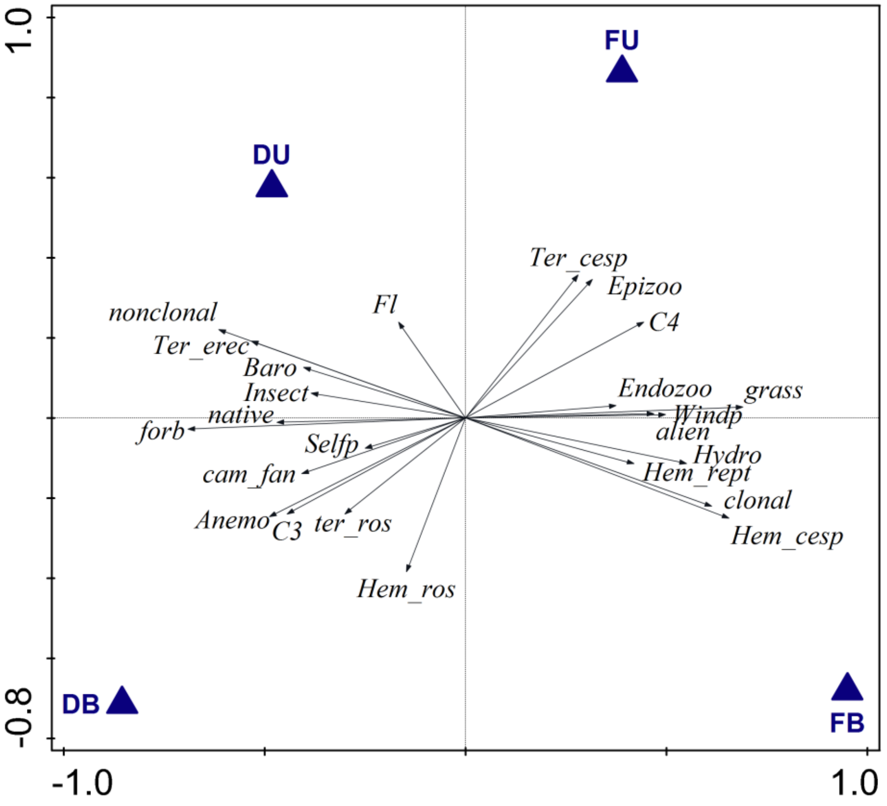
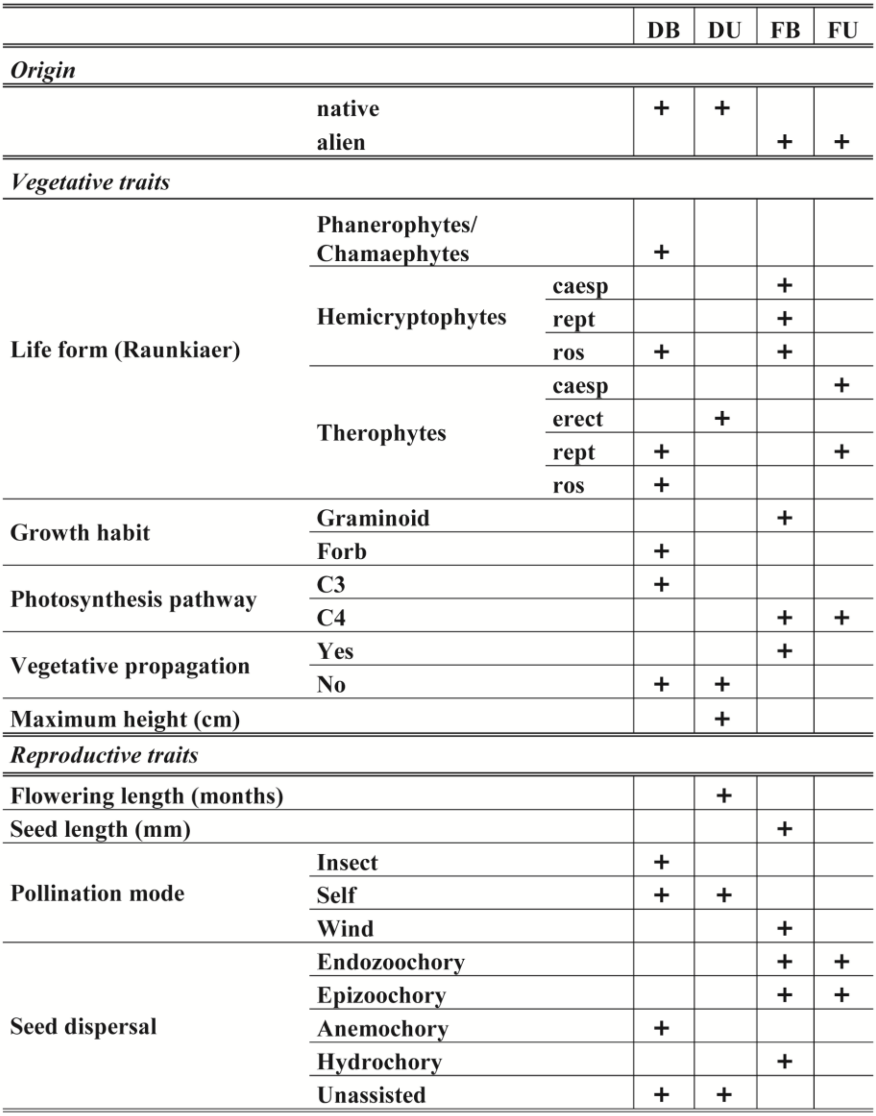


Figure 3. Redundancy Analysis of community-weighted means of trait values (CWM-RDA) of weed species. DU: drip irrigated orchards , plots under tree lines, DB: drip irrigated orchards , plots between the tree lines, FB: flood irrigated orchards , plots between the tree lines, FU: flood irrigated orchards , plots under tree lines. Fl: flowering length, Hem: hemicryptophytes, Ter: terophyte, cam_fan: chamaephyte/phanerophyte, cesp: caespitose, rept: reptant, ros: rosulate, anemo: anemochory, baro: barochory, endozoo: endozoochory, epizoo: epizoochory, hydro: hydrochory, insect: insect-pollinated, selfp: self-pollinated, windp: wind-pollinated.

Table 3. Summary of traits with significantly higher community weighted mean (CWM) values in each habitat ("+" symbol) compared to the rest of the habitats (post-hoc Tukey's test. p<0.05). Caesp: caespitose; rept: reptant; ros: rosulate. DU: drip irrigated orchards, plots under tree lines, DB: drip irrigated orchards, plots between the tree lines, FB: flood irrigated orchards, plots between the tree lines, FU: flood irrigated orchards, plots under tree lines.



			DB	**DU**	**FB**	**FU**
Origin						
	native		+	+		
	alien				+	+
Vegetative traits						
Life form (Raunkiaer)	**Phanerophytes/ Chamaephytes**		+			
	Hemicryptophytes	**caesp**			+	
		rept			+	
		ros	+		+	
	Therophytes	**caesp**				+
		erect		+		
		rept	+			+
		ros	+			
Growth habit	**Graminoid**				+	
	Forb		+			
Photosynthesis pathway	**C3**		+			
	C4				+	+
Vegetative propagation	**Yes**				+	
	No		+	+		
Maximum height (cm)				+		
Reproductive traits						
Flowering length (months)				+		
Seed length (mm)					+	
Pollination mode	**Insect**		+			
	Self		+	+		
	Wind				+	
Seed dispersal	**Endozoochory**				+	+
	Epizoochory				+	+
	Anemochory		+			
	Hydrochory				+	
	Unassisted		+	+		

Discussion

Weed community structure

This study highlights the influence of irrigation and weed management on the structure of spontaneous plant cover in orchards. In flood irrigated orchards, ground was almost entirely covered by weeds, which can be beneficial in the alleys to avoid erosion of soil (Sirrine et al., 2008) and to reduce soil temperature in summer -which is particularly important in Mediterranean areas- since vegetation acts as an insulate layer (Andersen et al., 2013). Yet, a dense cover of weeds competes with trees for nutrients and water, thus negatively impacting on yield (Hipps et al., 2004) particularly in the early ages of plantation, when trees are young and the competition effect is stronger (Cicuzza et al., 2012). On the other hand, weed community in drip irrigated orchards maintained an intermediate level of cover between the rows (aproximately 50%), which can avoid erosion, whereas in the tree line, where herbicides are applied, cover of weeds is minimal, avoiding competition of weeds with tree roots.

Regarding plant diversity, herbicide treatment leads to an effective reduction of the total α-diversity of weeds compared to mowing at both irrigation systems. In orchards, it has been proved that herbicide application is a more effective treatment to hinder weed establishment than mechanical methods (Miñarro, 2012). Conversely, mowing has been related to an increase of weed diversity comparing to herbicide application because it favours seedling recruitment, survival and the reproductive ability of species (Mas et al., 2007 and cites therein).

In drip irrigated orchards, the fact that two contrasted environments (rainfed and irrigated zones) are adjacent explains also the higher values of total γ- and β-diversity as well as alien β-diversity compared to those of flood irrigated orchards. In the former, there is a coexistence of plant species adapted to arid conditions in the inter-rows and others adapted to water in tree lines whereas in the latter, water is homogeneously distributed along the field, thus promoting the dominance of weeds adapted to flooded conditions.

In our study, the prominence of alien weeds in the plant cover stemmed from the irrigation system. Both α-diversity of alien weeds and their proportion in the plant cover were higher in flood than in drip irrigated orchards. It has been proved that in agricultural areas as well as in semiarid regions, such as the study area, an increase of water supply favours habitat invasibility (Dukes and Mooney, 1999), even if this increase is as short as few weeks (Jauni and Hyvönen, 2012; Davis and Pelsor, 2001). Particularly, invasibility is favoured by the alteration of the resident community caused by flood disturbance and by the fluctuating release of unused resources, such as fertilization, that is more efficiently exploited by alien species (Davis et al., 2000). On the other hand, limited water availability has been related to a higher resistance to alien plant invasion (Kreyling et al., 2008), which may explain the lower α-diversity and cover values of alien weeds in drip irrigated orchards, since there, water is only supplied in the area where water drop falls, being the rest of the field a rainfed area.

Floristic and functional composition

This study confirms that is irrigation system, rather than weed management, which mainly determines floristic and functional composition of spontaneous weed cover in orchards. In fact, soil moisture is the main factor affecting weed composition in other irrigated crops, such as rice crops (Bhagat et al., 1999; Towa and Xiangping, 2014) and in Mediterranean grasslands (Carmona et al., 2012). The influence of irrigation system in the structure of the weed cover is not only evident in the selection of different traits, regardless of weed management, but also by modulating the effect of weed management on traits selection, which is in the line of Zheng et al. (2015). Results show that flood irrigation provides suitable conditions for the development of a weed community where alien weeds stand out comparing to drip irrigated orchards, as analyses of diversity and cover also indicate. Not only does flooding favour alien weeds but also a suit of traits that has been previously related to the success of those alien weeds in orchards (Juárez-Escario et al., 2013) such as C4 photosynthetic pathway. C4 species present higher photosynthetic rates - and consequently higher growth rates - than C3 species at higher temperatures and under flooding conditions (Sage, 2004; Sage et al., 2011), that are the conditions occurring in flooded orchards in summer in the Mediterranean area. C4 species fitted better than C3 species in this situation by compensating high photorespiration rates these conditions generate. It has been proved that photorespiration inhibits photosynthetic rate of C3 species up to 30% (Ehleringer et al., 1991) whereas C4 photosynthesis enables to compensate it.

Conversely, drip irrigated orchards -irrespective of the weed management- host a community of weeds where alien plants have a lower prominence. Most of the alien weeds present in irrigated crops in the Mediterranean area come from tropical areas (Brunel et al., 2010; Godoy et al., 2009), and they have high requirements for water and temperature. Limitation of water supply in drip irrigated orchards may prevent the establishment of these species, restricting their presence to the tree lines, where they can be better controlled by herbicide application. Nevertheless, some problematic alien species, such as *Aster squamatus* and *Crepis bursifolia*, presented large cover values in drip irrigated orchards, and control measures should be developed to avoid the expansion of these species.

Influence of irrigation system in the effect of weed management on traits selection can be observed in the presence of a different suite of traits depending on the irrigation system under similar conditions of weed management. In fact, it has been claimed that the effects of mechanical disturbance on the structure and dynamics of plant communities depend largely on water availability (Pérez-Camacho et al., 2012). This fact is consistent with the general hypothesis that the response of plant species and traits to mechanical disturbances (such as grazing or mowing) is largely dependent on resource availability (Zheng et al., 2015 and cites therein), which is represented in Mediterranean areas by water supplies.

In this sense, mowing in flood irrigated orchards favoured hemicryptophytes, graminoids with clonal growth, wind-pollinated species and plants with seeds dispersed by water whereas the same management in drip irrigation selected for annual forb species, C3 species, insect pollinated and with seeds dispersed by wind. It has been proved that moisture favours the emergence of graminoids in agricultural areas (Bhagat et al., 1996) and flooding accompanied by mechanical disturbances selects for clonal plants (Benot et al., 2011). These traits are associated to a fast growth and give advantages for plant survival during the stressful growing conditions while flooded (Benot et al., 2011; Moreno García et al., 2014). Regarding selection of hemicryptophytes, it has been proved that perennial life form is favoured by an increasing of irrigation in Mediterranean grasslands subjected to mechanical disturbances, whereas annual forms have been related to grazing/mowing under typical summer drought conditions of Mediterranean climate both on herbaceous communities (Pérez-Camacho et al., 2012) and on weed community of mandarin orchards (Mas et al., 2007). In addition, under drought conditions perennial grasses are disfavoured and can even disappeared due to desiccation during the summer season (Jackson and Roy, 1986), which results in an increasing of therophytes, which is the life form selected to hold up summer drought (Pérez-Camacho et al., 2012).

The predominance of insect-pollinated plants in mowed plots of drip irrigated orchards highlights how proper management could help to provide benefits in terms of pollination services to the orchards. The presence of insect-pollinated weeds in spontaneous plant cover provides an ecological benefit by increasing floral resources for pollinator communities (García and Miñarro, 2014), which are considered to be in regression (Potts et al., 2010). This is especially important in highly intensified agricultural landscapes, such as the study area, where natural vegetation is scarce and cannot provide this ecosystem service (Miñarro and Prida, 2013).

On the other hand, in the herbicide-treated plots in flooded orchards weed community was dominated by caespitose and reptant therophytes whereas in drip irrigated orchards erect therophytes with long flowering length stood out. Annual life form and longer flowering period have been described as adaptations to chemical disturbances because these traits increase the probability of escaping from herbicide applications (Fried et al., 2012). In addition, the high frequency of herbicide applications (at least three times per year) avoids the establishment of perennial plants, and consequently annual weeds colonize empty niches between herbicide applications.

Management implications

Results of this study show that irrigation is the main factor that configures floristic and functional structure of orchards, even modulating the effect of weed management. This fact has to be taken into account in order to choose the best management system that minimize competition of weeds to the trees and at the same time maximize the potential benefits that plant cover can provide to the orchards.

Moreover, this study highlights the relationship of irrigation management and presence of alien weeds in spontaneous plant cover. In this sense, flood irrigation management not only favours both the richness and cover of alien species but also play a predominant role in their dispersion, since species composing weed cover in flood orchards have seeds mainly water-dispersed. It has been proved that flooding irrigation mediates the presence of alien weeds in natural ecosystems near orchards whereas alien species present in drip irrigated orchards are better confined to these crops (Juárez-Escario et al., 2016).

In addition, drip irrigation combined with mowing in the inter-rows and herbicide application under tree lines, is much more beneficial than flood irrigation in maintaining a proper weed cover in the inter-rows for avoiding soil erosion and providing pollination services to the agroecosystem while minimizing the presence of weeds in the tree lines where they would effectively compete with trees and consequently reducing yield.

The benefits of drip irrigation in terms of water resources protection, avoiding nutrient lixiviation and soil erosion have been already described (Coolong, 2013) but this is the first study that provides further ecological arguments related to alien plant invasion from a trait-based approach to support the selection of this irrigation system in order to increase sustainability of the crops.

In those cases where it is not possible to change the irrigation system, an alternative method to avoid the large presence of alien species in weed cover is to sow a selected plant cover mixture of native species which be functionally similar to those more successful aliens with the objective of displacing alien species from the cover while maintaining functionality of the cover. Besides avoiding establishment of alien species, cover crops provides other benefits to the orchards, such as reduced soil erosion, improve water infiltration, soil moisture retention, organic matter, organic carbon and nitrogen (Mennan et al., 2006 and references therein). Alternatively, changing the time of flooding may be an option to try to reduce the dominance of some alien weeds in the plant cover. In this sense, it has been proved that changes in flooding time can effectively suppress germination of alien grasses, such as *Echinochloa* spp. (Kent et al., 2001).

Conclusions

This study reveals that irrigation management is the main factor that explains the compositional and functional structure of weed assemblages in irrigated fruit tree orchards in Mediterranean areas and also modulates the effect of weed management on these aspects. Flood irrigation configures a weed community with a dense cover in the inter-rows where there is a high prominence of alien species characterized by a suite of traits linked to their success in these habitats, such as perennial form, graminoids, C4 species, clonality, zoochory and hydrochory. On the contrary, drip irrigated orchards favours weed communities less dense but more rich and diverse than that of flood irrigated orchards where the alien component is more reduced. Moreover, from a functional point of view, weed communities of drip irrigated orchards can deliver ecosystem services to the orchards in the form of pollination resources. Therefore, our results provide new original arguments to the well-known benefits of drip irrigation (i.e. more sustainability of water use, decreased lixiviation) in terms of the configuration of a weed cover that can benefit the crop by avoiding soil erosion and favouring pollination while reducing the presence of alien weeds, particularly those with high capability to colonize and spread both irrigated crops and the surrounding natural habitats.

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Supplementary Material 1. Mean values (± standard errors) of CWM values of traits in each management and results of Linear Mixed-effects models and Kruskall Wallis test on CWM values. Ter: therophyte, Hemi: hemicrytophyte, Cham/Phan: camephyte/phanerophyte.*=squared root-transformed variables, **=log-transformed variables.

					LINEAR MIXED-EFFECTS MODEL			KRUSKAL-WALLIS		
	DB	**DU**	**FB**	**FU**	**F**	**DF**	**p-value**	**Chi-squared**	**DF**	**p-value**
Native	0.76±0.02 (a)	0.71±0.02 (a)	0.50±0.02 (b)	0.57±0.02 (b)	22.65	3.14	<0.01			
Alien	0.24±0.02 (a)	0.29±0.02 (a)	0.50±0.02 (b)	0.43±0.02 (b)	22.65	3.14	<0.01			
Cham./Phan.	0.10±0.02 (a)	0.07±0.01(b)	0.01±0.002 (c)	0.004±0.001 (c)				90.63	3	<0.01
Geophyte	0.05±0.01	0.08±0.01	0.05±0.01	0.06±0.01				2.26	3	<0.01
Hemi. caespitose	0.01±0.003 (a)	0.02±0.005 (a)	0.24±0.02 (b)	0.08±0.01 (c)				154.91	3	<0.01
Hemi. reptant	0.08±0.01(a)	0.06±0.01(a)	0.23±0.02 (b)	0.05±0.01(c)				77.69	3	<0.01
Hemi. rosulate	015±0.02 (a)	0.02±0.005 (b)	0.08±0.01 (a)	0.03±0.01(b)				73.47	3	<0.01
Hemi. scapose	0.09±0.01	0.08±0.01	0.09±0.01	0.05±0.01	2.58	3.14	0.06			
Ter. caespitose	0.04±0.01(a)	0.17±0.02 (b)	0.16±0.02 (b)	0.27±0.02 (c)				82.46	3	<0.01
Ter. erect **	0.33±0.02 (c)	0.44±0.02 (d)	0.11±0.01 (a)	0.21±0.01 (b)	58.28	3.14	<0.01			
Ter. reptant	0.09±0.01 (b)	0.06±0.01 (a)	0.04±0.01 (a)	0.14±0.01 (b)				38.22	3	<0.01
Ter. rosulate	0.04±0.01(a)	0.001±0.001(b)	0	0				76.32	3	<0.01
C3	0.81±0.02 (c)	0.68±0.03 (b)	0.54±0.02 (a)	0.46±0.03 (a)	33.99	3.14	<0.01			
C4	0.18±0.02 (a)	0.32±0.03 (b)	0.46±0.02 (c)	0.54±0.03 (c)	33.99	3.14	<0.01			
Forb	0.87±0.02 (a)	0.73±0.03 (b)	0.39±0.01 (c)	0.55±0.02 (d)				141.41	3	<0.01
Graminoid	0.13±0.02 (a)	0.27±0.03 (b)	0.6±0.02 (c)	0.45±0.02 (d)				141.41	3	<0.01
Epizoochory *	0.08±0.01(a)	0.19±0.01(b)	0.19±0.01(bc)	0.26±0.02 (c)	29.4	3.14	<0.01			
Endozoochory *	0.03±0.004 (a)	0.04±0.01 (a)	0.09±0.01 (b)	0.07±0.01 (b)	22.04	3.14	<0.01			
Anemochory	0.51±0.02 (a)	0.41±0.02 (b)	0.28±0.01 (c)	0.22±0.02 (c)	42.8	3.14	<0.01			
Hydrochory	0.10±0.01 (a)	0.09±0.01 (a)	0.34±0.02 (b)	0.24±0.02 (c)				100.97	3	<0.01
Barochory	0.27±0.02 (a)	0.27±0.02 (a)	0.09±0.01 (b)	0.2±0.02 (c)				58.6	3	<0.01
Flowering period	4.73±0.11	4.67±0.12	4.88±0.06	4.88±0.10	1.1	3.14	0.35			
Flowering length	6.03±0.13 (a)	6.75±0.13 (b)	5.81±0.07 (a)	6.21±0.12 (c)				29.22	3	<0.01
Maximum height	78.11±2.9 (a)	100.00±4.47 (b)	76.66±1.79 (a)	77.12±2.7 (a)				40.79	3	<0.01
Non-clonal	0.79±0.02 (a)	0.76±0.02 (a)	0.37±0.02 (b)	0.65±0.02 (c)				120.48	3	<0.01
Clonal	0.21±0.02 (a)	0.24±0.02 (a)	0.63±0.02 (b)	0.35±0.02 (c)				120.48	3	<0.01
Seed length	3.19±0.18 (a)	3.21±0.22 (a)	3.74±0.12 (b)	2.92±0.16 (a)				33.19	3	
Self-pollinated	0.43±0.02 (b)	0.44±0.02 (b)	0.36±0.01 (a)	0.33±0.02 (a)	9.22	3.14	<0.01			
Wind-pollinated	0.20±0.028 (a)	0.27±0.02 (a)	0.46±0.02 (b)	0.38±0.02 (c)				74.51	3	
Insect-pollinated	0.35±0.01 (a)	0.29±0.02 (b)	0.17±0.01 (c)	0.28±0.02 (b)				60.5	3	

CHAPTER 5

Identifying alien plants linkages between irrigated orchards and adjacent riparian habitats from a trait-based approach

Published in *Agriculture, Ecosystems and Environment*
2016, 225, 173-183.

Identifying alien plants linkages between irrigated orchards and adjacent riparian habitats from a trait-based approach

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Abstract

Floodplains and crops are particularly susceptible to alien plant invasion, often leading to negative ecologic and economic impacts. As irrigated crops and riparian habitats are interconnected at landscape scale, plant species of each habitat may be susceptible to colonize the other. In order to avoid alien plant invasions of natural habitats and surrounding crops and to develop management practices to face this problem, it is not only essential to understand which traits favour the success of alien plants in irrigated crops and floodplains, but also whether a flow of species between these two habitats actually exists. With this aim, floristic surveys were carried out on riparian habitats (riparian forest, reedbed and muddy line) and on irrigated orchards at a gradient of distance from the river. Differences in weed management techniques applied in orchards were taken into account during the surveys. Plant diversity, composition and invasion levels were evaluated for each habitat and differences in floristic composition were interpreted in terms of functional traits. Natural habitats were well differentiated from crops in terms of native plants, but when considering alien plants, muddy line and flood irrigated orchards showed similar floristic composition. Alien plant community in the muddy line was a subset of that of flooded orchards and it was composed by C4 species, with clonal growth, perennial graminoids and water seed dispersal. This work proves that, unlike native species, alien species are shared between irrigated orchards and adjacent floodplains, which is favoured by a set of traits that allows them to colonize and establish new populations there. These results can help to develop strategies for preventing the establishment of alien plants in these habitats and to manage already present populations.

Keywords

Floodplain; irrigation system; weed management; exotic weeds; biological attributes.

Introduction

Invasive species have taken their toll on natural habitats by reducing both their biodiversity and the ecosystem services provided (Fried et al., 2014; Hejda and de Bello, 2013; Hejda et al., 2009; Vilà et al., 2010). Despite causing yield losses, crop damage and heightened control costs in agriculture (Baker et al., 2005; Pimentel et al., 2005; Vilà et al., 2004), alien invasions have mostly been studied in natural habitats. Furthermore, few previous studies have included research on biological invasions simultaneously affecting natural and agricultural habitats (Galatowitsch et al., 1999; Liendo et al., 2013) although they are interconnected at landscape scale. Irrigated agricultural lands in floodplains are an example of this connection. Crops are established close to floodplains because fertile alluvial soils allow for increased crop yields and rivers provide water for irrigation.

Invasion success of alien species is largely due to species invasiveness and habitat invasibility (Milbau et al., 2003). Those habitats subjected to frequent disturbances are prone to be invaded (Burke and Grime, 1996) because disturbances increase availability of resources and open new colonisable niches where competition for those resources is low (Davis et al., 2000). This is the case of irrigated croplands and floodplains that are highly vulnerable to alien plant colonization, especially in the Mediterranean area (Chytrý et al., 2009).

Regarding species invasiveness, some biological attributes favour the success of an alien plant in establishing populations in the host habitat. They include suitable seed dispersal systems for reaching new habitats, as well as higher photosynthetic rates, clonal growth, small seeds and long-distance seed dispersal which allow the plant to successfully overcome the ecological filters of the host habitat, giving it advantages to compete with the native (Pyšek and Richardson, 2007; Pyšek et al., 1995). Thus, in order to understand the processes that lay behind the ecology of invasive species, studies should include both diversity aspects and a trait-based approach.

This study makes an original and significant contribution to knowledge of the connection between natural and agricultural habitats in terms of alien plant species from a trait-based approach, by focusing on an irrigated agricultural area on a floodplain in the Mediterranean zone. Specifically, we selected a landscape of irrigated orchards arranged at a gradient of distance from a riparian corridor because both systems are subjected to similar disturbances (i.e. water logging, fluctuating water levels, high nutrient levels and physical disturbances) (Catford and Jansson, 2014; Juárez-Escario et al., 2013), which increase their susceptibility to be colonized by alien plants. Riparian habitats provide important ecosystem services such as improving water quality, increasing biodiversity or stability of the riverbanks. In these habitats, alien plants negatively impact biodiversity, productivity, nutrient cycling and even the food web (Richardson et al., 2007). Moreover, human-mediated disturbances, such as water regulation (Catford et al., 2011; Jansson et al., 2000), channel management (Tabacchi et al., 2005) and close proximity to human activities can increase riparian invasion (Catford and Jansson, 2014; Liendo et al., 2013).

In the case of riparian habitats in an agricultural matrix, it has been claimed that alien species present in the riverbanks might have been first introduced in nearby agricultural fields (Ferreira and Moreira, 1995; Meek et al., 2010) by human-mediated dispersal. But at a finer landscape scale, it could be also plausible that agricultural sites downstream would be contaminated through water irrigation by alien weeds previously established on upstream riverbanks. Detecting nestedness in species richness patterns is therefore a useful tool to determine which habitats act as a source of alien species along invaded landscapes (Alexander et al., 2011). Conversely, the different ecological conditions of riparian habitats and irrigated orchards as well as the differences in some physical disturbances to which they are subjected (mainly flooding in riparian habitats and trampling and weed control besides flooding in orchards) may suppose a filter for the alien plant flow from one zone to the other (Tabacchi et al., 2005). Likewise, it has been proved that higher diversity in riparian habitats may reduce the susceptibility to be invaded by reducing the effective number of ecological niches suitable for invasion (Loreau and Hector, 2001). Nevertheless, other studies in this field have sown contradictory results (Gilbert and Lechowicz, 2005).

Disentangling the causes that lay behind the success of colonization of alien plants in irrigated crops and floodplains and the connection between these two areas in terms of these species is key in developing suitable management and conservation projects aimed to prevent the establishment of alien plants in interconnected agricultural and natural areas and minimize the exchange of alien plants between those habitats.

For these reasons, we consider it essential to focus the present study on evaluating whether alien plants present in irrigated fruit tree orchards are also established in nearby riparian habitats and identifying which functional traits are related to this process.

In this study we expect that highly perturbed habitats shelter a rich community of alien plants with a set of traits that let them to spread and colonize surrounding habitats, thus establishing an exchange of those species among them.

The main study objectives were: (1) to evaluate native and alien plant diversity at different spatial scales and to analyse the invasion level of each habitat through the analysis of the total richness and the richness and abundance of alien species, (2) to determine whether exists an exchange of alien species between riparian habitats and orchards located in a gradient of distance from the river as well as detecting nestedness patterns in this process, and (3) to identify which functional traits are involved in this exchange.

Material and methods

Study area

The study was conducted in a floodplain located along the last 22 km of the Noguera Ribagorçana River in Western Catalonia, NE Iberian Peninsula (41º39'-41º51'N; 0º33'-0º43'E), a tributary of the Segre river (i.e. the main tributary of the Ebro river, which is the large-flowing river in the Iberian Peninsula). The river has a total length of 136.9 km and water flow is regulated through 3 main dams. The study was conducted in the lowland river segment, which ranges from 305 m a.s.l in the Santa Ana dam to 172 m a.s.l. in the confluence with the Segre river (mean slope: 0.58%). This is an edaphological and structural homogeneous area largely made up of Tertiary detrital and alluvial deposits (mostly clay, sand and graves) and terraces, which are consequence of sedimentary processes along the floodplain. Dominant land-use in the floodplain is for irrigated agriculture. Wetted channel width ranges approximately from 20 to 35m. The average annual evapotranspiration is 750mm and the average annual flow is $17.9\text{m}^3\ \text{s}^{-1}$ (Ministerio de Medio Ambiente, 2007). The climate is Continental-Mediterranean, with a mean annual temperature of 13.5ºC and annual rainfall of 390mm (Ninyerola et al., 2005).

Natural habitats

Within the riparian habitats, three plant communities stem from the gradient of distance and moisture in the stream channel: 1) the frequently flooded bank, referred to as the “muddy line” in this study, 2) the reedbed and 3) the riparian forest. The muddy line corresponds to clay soils with high content in organic matter provided by the water. Muddy line vegetation is composed of hygronitrophylous communities and grasslands developed on mud bars. The reedbed is dominated by perennial graminoids mainly represented by common red (*Phragmites australis*). Finally, riparian forests are wet deciduous woodland composed of a variety of Eurosiberian and Mediterranean trees, typical to Mediterranean rich soils with slow flowing eutrophic water.

Irrigated orchards

Flood irrigated fruit tree orchards are located close to the river (Dalmau and Iglesias, 1999) Irrigation is performed via an extensive irrigation network, which takes the water from the river and later returns the excess irrigation water again to the river. In the last decades, the area occupied by irrigated orchards has been increased and drip irrigated orchards have been established farther from the river. The surveyed crops were stone and pome fruit tree orchards (apple, pear and peach). Flood irrigated orchards are irrigated bi-weekly from April to early September (a total of 10–12 irrigation episodes during this period). Drip irrigation systems need a complex infrastructure of artificial ponds, pressure bombs and water distribution pipes and orchards are typically irrigated daily (a minimum of 3-4 l/m^2 weekly). Weed control of orchards differs between tree rows and under tree lines. In the inter-row space, weeds are mechanically controlled by mowing or shredding and under the tree lines herbicide is sprayed (a mix of pendimethalin, oxyfluorfen, isoxaben and oryzalin in February and glyphosate and fluroxypyr between May and June and after September)

Floristic surveys

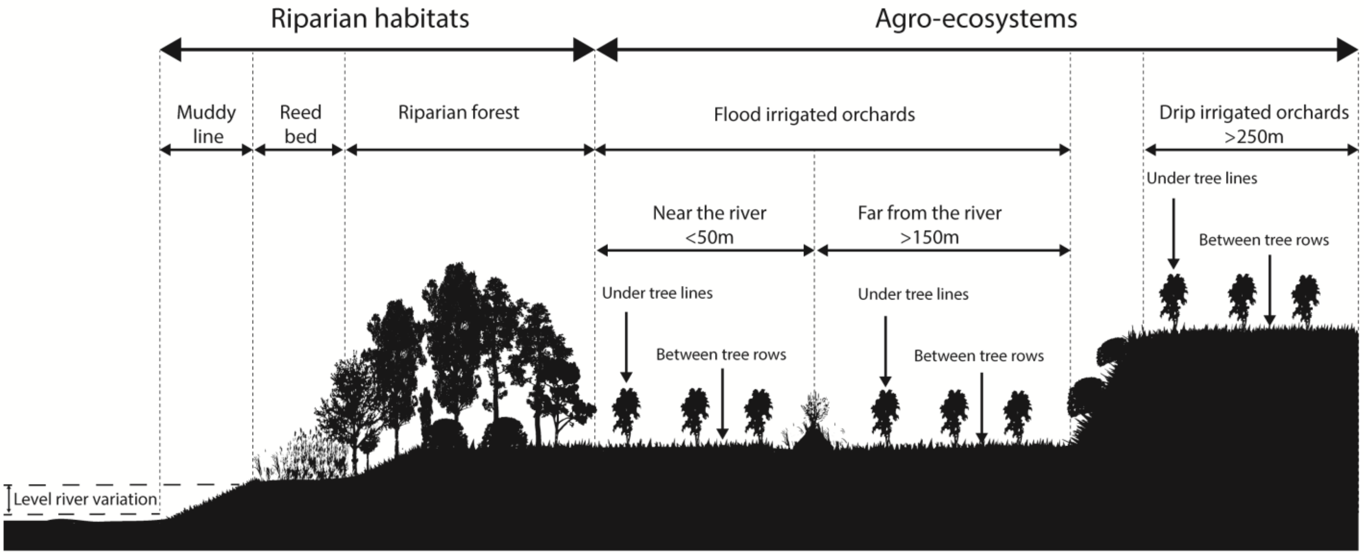
In summer of 2011, along the last 22 km of the Noguera Ribagorçana river, floristic surveys were performed at each kilometre in the three main riparian habitats (muddy line, reedbed and riparian forest) (Fig. 1), as well as in the nearby orchards, following a gradient of distance from the river. In each riparian habitat, 3 rectangular plots were randomly established (10m^2 in the muddy line and reedbed, but 200m^2 in the riparian forest). In the orchards, weed control differs between the inter-rows and under-tree lines, so floristic surveys were carried out in 3 randomly established rectangular plots of 10m^2 at two positions, namely: “between tree-lines” (B) and “under tree-lines” (U). The surveys were performed in flood irrigated orchards located at less than 50 meters from the riparian forest (NOB and NOU), in flood irrigated orchards located at more than 150 meters from the riparian forest (FOB and FOU) and in drip irrigated orchards located at more than 250 m from the riparian forest (DOB and DOU).

The Braun-Blanquet (1979) six-point scale was used to quantify species' abundance, in which the cover-abundance of each species is assigned a value between + (sparse and covering a small area) and 5 (covering more than 75% of the area). Those values were transformed into the mean value of percent cover range in each cover class (+=0.01%; 1=5%, 2=17.5%, 3=37.5%, 4=62.5%, 5=87.5%). Since the 3 plots for each habitat in each transect cannot be considered as completely independent, mean cover values of species for each habitat in each transect were calculated from the 3 plots. Plant nomenclature followed Bolòs and Vigo (1984-2001).

Plant traits

Each recorded species was classified as alien or native according to Sanz-Elorza et al., 2004, that is, the most recent and complete revision of alien flora in Spain up to now. This work considers both archaeophytes and neophytes as alien species sensu Richardson et al. (2000). *Setaria adhaerens* and *Echinochloa crus-galli* are cryptogenic plants (i.e. controversial species regarding their origin) but in this study were classified as alien species because of their Paleotropical origin (Campos, 2010; Sanz-Elorza et al., 2011). A total of 8 traits were recorded for each species (Table 1).

Among vegetative traits, growth form, photosynthesis pathway, vegetative propagation and plant height were selected since they are involved in the response of vegetation to disturbances (Cornelissen et al., 2003), whereas reproductive traits such as seed dispersal, seed



Abbreviature	MUD	RB	RIPFOR	NOU	NOB	FOU	FOB	DOU	DOB
Number of plots	3	3	3	3	3	3	3	3	3
Plot size	$10m^2$	$10m^2$	$200m^2$	$10m^2$	$10m^2$	$10m^2$	$10m^2$	$10m^2$	$10m^2$

Figure 1. Scheme of the experimental design.

Table 1. Plant species traits selected for the study.

Traits	**Categories**	**Reference**
1. Vegetative traits		
1.1 Whole-plant traits		
Growth habit	Annual graminoid Perennial graminoid Annual forb Perennial forb Liana Shrub Tree	Bolòs and Vigo (1984-2001); NRCS (2014)
Plant height (cm)	Continuous	Bolòs and Vigo (1984-2001)
Vegetative propagation	Yes No	Klimešová and Bello (2009); Julve (1998)
1.2 Leaf traits		
Photosynthesis pathway	C3 C4	Pyankov et al. (2010)
2. Reproductive traits		
Flowering onset (months)	Continuous	Bolòs and Vigo (1984-2001)
Flowering length (months)	Continuous	Bolòs and Vigo (1984-2001)
Seed length (mm)	Continuous	Bolòs and Vigo (1984-2001); Klotz et al. (2002)
Seed dispersal method	Zoochory Anemochory Hydrochory Unassisted	Bolòs and Vigo (1984-2001); Julve (1998); SID database (2008)

length, flowering onset and flowering length have been associated with persistence in disturbed habitats (Gunton et al., 2011).

Each seed dispersal mode was codified as a binomial variable (0/1) except for the species that presented more than one. In those cases, 0.5, 0.33 or 0.25 values were assigned to each dispersal mode in case the species has 2, 3 or 4, respectively.

Data analysis

Plant diversity and abundance among habitats

α- (mean species richness per site) and γ- (total richness per habitat) diversity were calculated for total species, and separately for native and alien species for each habitat. Since size plots were larger in riparian forests, γ-diversity cannot be directly compared among habitats. Rarefaction curves allow for meaningful standardization and comparison of richness data for datasets obtained by different sampling effort (Gotelli and Colwell, 2001). Therefore, γ-diversity was estimated by constructing rarefaction curves based on 999 random replicates, using First-order Jackknife richness estimator, which is one of the most accurate index in determining species richness comparing to other estimators (Hortal et al., 2006)

In order to compare levels of invasion among habitats and to identify patterns of dominant alien species, relative richness and abundance of alien plants for each habitat were calculated, since they are the most suitable and meaningful indicators of invasion level (Catford et al., 2012b). Changes in α-diversity for all the groups of species as well as in relative richness and abundance of alien species among habitats were fitted using generalised least squared models (GLS) with Tukey's posthoc test for multiple pairwise comparisons. To normalize data, relative cover values of alien plants were logit-transformed (Warton and Hui, 2011). In order to correct for spatial autocorrelation, exponential correlation structure function with latitude and longitude coordinates of each site was added to each model as recommended by Dormann et al. (2007). To check whether spatial autocorrelation was corrected in the obtained models, Moran's I autocorrelation coefficient of normalized residuals was calculated following Gittleman and Kot (1990).

The strength of the relationship between native and alien richness was evaluated by comparing α-diversity of native and alien plant species within each habitat, using linear regression analysis.

Compositional dissimilarity among habitats

In order to determine differences in floristic composition among the habitats, Nonmetric Multidimensional Scaling ordination (NMDS) was performed on Hellinger-transformed species data (Legendre and Gallagher, 2001), separately for native and alien species, with Bray-Curtis dissimilarity distance. Permutational Multivariate Analysis of Variance (PERMANOVA) was performed on NMDS to evaluate statistical significance of the differences on floristic composition among habitats. Likewise, ANOVA and Tukey's post-hoc test were used to find differences among habitat types in the NMDS first axis since this axis accumulates the greatest variance of NMDS points, taking into account that NMDS axes are an approximation of the rank ordering of the original distances.

To assess the importance of nestedness in determining the distribution patterns of alien plants among habitats, "nestedness metric based on overlap and decreasing fill" (NODF) values for rows (NODFsites)

(Almeida-Neto et al., 2008) was calculated among those habitats where alien plant composition did not show significant differences. This index is robust for testing whether the composition of species-poor sites is nested within the composition of species-rich sites (Alexander et al., 2011; Marini et al., 2013) and it is relatively independent of matrix size and shape (Almeida-Neto et al., 2008).

In order to detect the direction of the nestedness patterns, NODF was calculated on matrices with the rows (sites) ordered by an agricultural-natural gradient and vice versa and columns (alien species) ordered by decreasing abundances. Statistical significance of the nestedness patterns was tested using a null model (999 replicates) that maintains both row and column frequencies using the quasi-swap method. This method randomizes species composition keeping the number of species per row in the randomized data fixed.

Trait patterns among habitats

In order to test whether average trait expressions of native and alien plants respond differently in each habitat, a redundancy analysis (RDA) was performed on centred and standardized community weighted means of trait values (CWM) for each site, separately for native and for alien plants. CWM values were calculated as:

$$CWM = \sum_{i=1}^{S} p_i \cdot t_i$$

where S is the number of species in the community, pi is the species i abundance proportion and ti is the trait value of species i (Lavorel et al., 2008).

To assess statistical significance differences of CWM values among habitats generalised least squared models (GLS) with Tukey's posthoc test for multiple pairwise comparisons were fitted on the CWM values, also accounting for spatial autocorrelation. CWM values were squared root/log transformed when normality was not achieved (supplementary material). Alien plant CWM values of reedbed habitat were not included in the models because the low number of alien species per plot rendered few analysed traits, thus giving inconsistent and meaningless parameters for this habitat in fitted models.

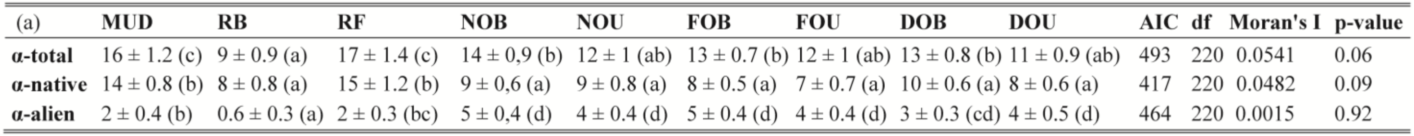
All analyses were performed with R software (R Development Core Team, 2011), except for the CWM-RDA analyses, which were carried out with CANOCO 5 software (Ter Braak and Smilauer, 2012).

Results

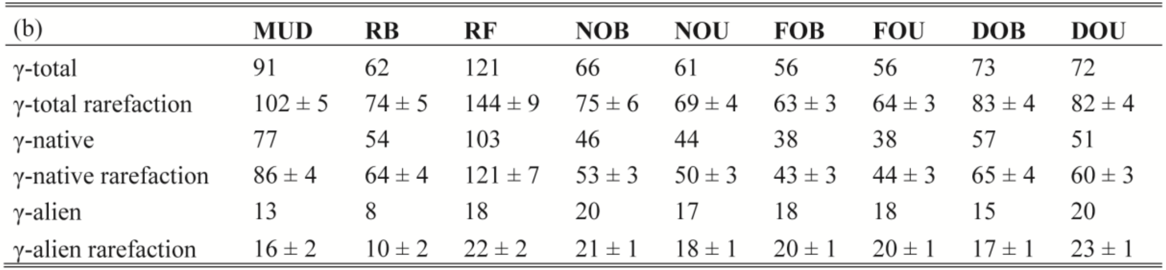
Richness and abundance of species

A total of 231 plant species were recorded throughout the study area, 37 of which were alien. Among natural habitats, riparian forest and the muddy line contained the highest number of total and native plant species both at local scale (α-diversity; table 2a) and at habitat scale (γ-diversity, table 2b). Among orchards, total and native α-diversity were similar irrespective of the distance from river and the management, while total and native γ-diversity were slightly higher in drip irrigated orchards. For alien species, α-diversity was significantly higher in orchards than in natural habitats. Among all the habitats, reedbed harboured the lowest value of alien α-diversity. Although γ-diversity of alien species was rather similar in all the habitats (apart from reedbed), relative percentage of alien richness per plot was significantly higher in orchards than in riparian habitats (Fig. 2).

Table 2. Total, native and alien plant α- (a) and γ- (b) diversity (±standard error) found in the studied habitats and results of GLS on α-diversity.MUD: Muddy line, RB: reed bed, RF: riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree lines.



(a)	**MUD**	**RB**	**RF**	**NOB**	**NOU**	**FOB**	**FOU**	**DOB**	**DOU**	**AIC**	**df**	**Moran's I**	**p-value**
α-total	16 ± 1.2 (c)	9 ± 0.9 (a)	17 ± 1.4 (c)	14 ± 0,9 (b)	12 ± 1 (ab)	13 ± 0.7 (b)	12 ± 1 (ab)	13 ± 0.8 (b)	11 ± 0.9 (ab)	493	220	0.0541	0.06
α-native	14 ± 0.8 (b)	8 ± 0.8 (a)	15 ± 1.2 (b)	9 ± 0,6 (a)	9 ± 0.8 (a)	8 ± 0.5 (a)	7 ± 0.7 (a)	10 ± 0.6 (a)	8 ± 0.6 (a)	417	220	0.0482	0.09
α-alien	2 ± 0.4 (b)	0.6 ± 0.3 (a)	2 ± 0.3 (bc)	5 ± 0,4 (d)	4 ± 0.4 (d)	5 ± 0.4 (d)	4 ± 0.4 (d)	3 ± 0.3 (cd)	4 ± 0.5 (d)	464	220	0.0015	0.92



(b)	**MUD**	**RB**	**RF**	**NOB**	**NOU**	**FOB**	**FOU**	**DOB**	**DOU**
γ-total	91	62	121	66	61	56	56	73	72
γ-total rarefaction	102 ± 5	74 ± 5	144 ± 9	75 ± 6	69 ± 4	63 ± 3	64 ± 3	83 ± 4	82 ± 4
γ-native	77	54	103	46	44	38	38	57	51
γ-native rarefaction	86 ± 4	64 ± 4	121 ± 7	53 ± 3	50 ± 3	43 ± 3	44 ± 3	65 ± 4	60 ± 3
γ-alien	13	8	18	20	17	18	18	15	20
γ-alien rarefaction	16 ± 2	10 ± 2	22 ± 2	21 ± 1	18 ± 1	20 ± 1	20 ± 1	17 ± 1	23 ± 1

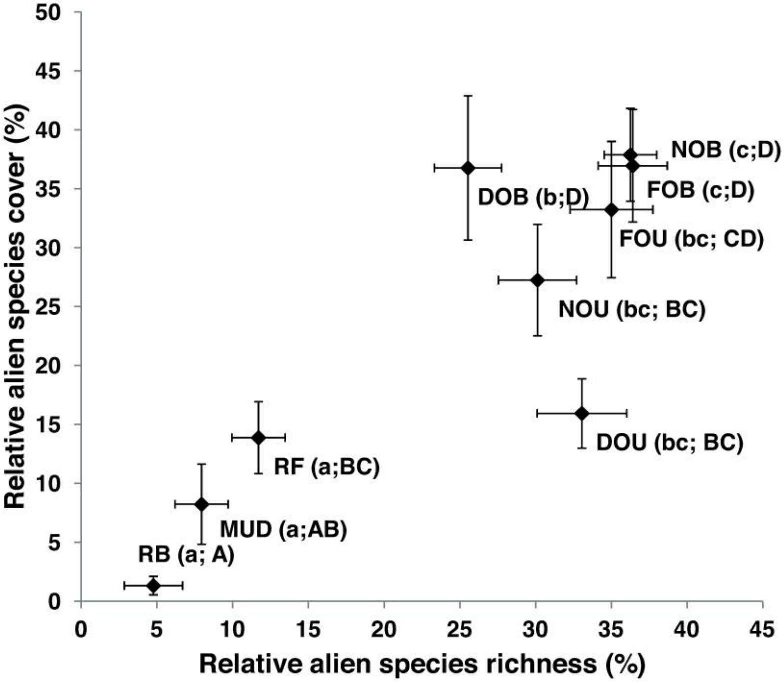


Figure 2. Plot of percentage of relative alien plant richness versus percentage of relative alien plant cover. Different letters represent significant differences in GLS analysis (Tukey's test, p<0.05) both for richness values (lower case) and for cover values (upper case).

Regarding relative alien species cover per plot, it was significantly higher in DOB, FOB and NOB. The relationship between relative richness and cover of alien species showed that orchards sustained comparatively higher levels of invasion than natural habitats. Overall, relative alien species richness and cover presented similar values in each habitat except for DOU, where richness of alien plants was higher than cover and for DOB, where cover value of aliens was higher than richness.

A significant positive relationship between native and alien species α-diversity was found in the riparian forest, muddy line, FOB, NOB and NOU (Fig. 3), although the strongest correlation occurred in the muddy line.

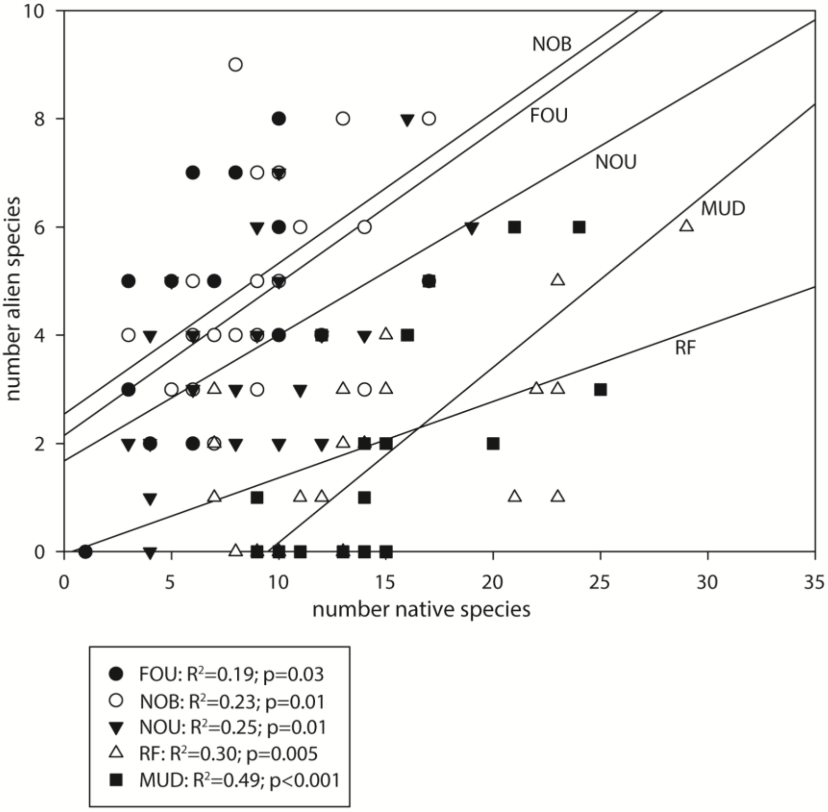
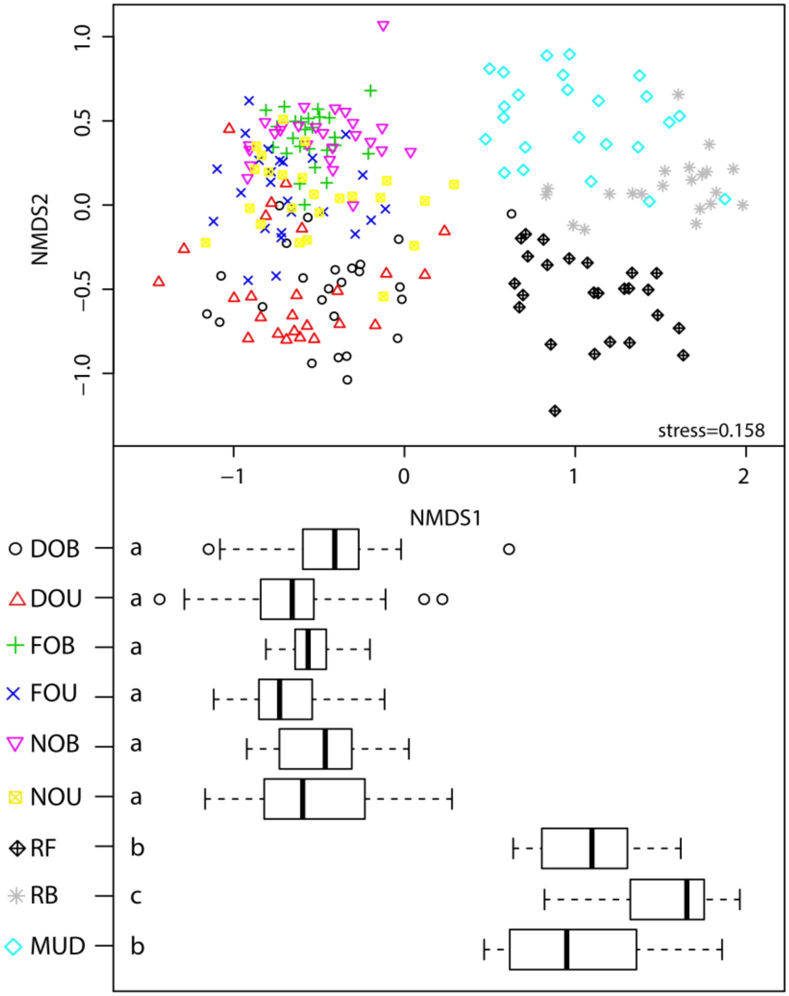


Figure 3. Plot of linear regression of α-diversity (number of species) of alien and native species in the habitats where linear regression is statistically significant. MUD: muddy line, RF: Riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOU: flood irrigated orchards far from the river.

Plant community composition and nestedness patterns

NMDS and PERMANOVA showed significant differences on floristic composition among habitats, both for native (R^2 = 0.38, F = 16.4, $p < 0.001$) (Fig. 4a) and for alien species (R^2 = 0.31, F = 9.9, $p < 0.001$) (Fig. 4b). Native species in the riparian habitats differed significantly from those in the orchards (df=8, F=169.5, $p<0.001$). Within the riparian habitats, reedbed plant communities differed the most from those of muddy line and riparian forest, whereas there were not such pronounced differences among orchards. Regarding alien species, the floristic composition of muddy line was similar to flood irrigated orchards and DOU, but different from that of reedbed and riparian forest (df=8, F=49.43, $p <0.001$). Composition of flood irrigated orchards was similar irrespective to the distance from the river or the weed management. Finally, DOB composition was different from the rest of the habitats.

The analysis of nestedness indicated that alien plant community of muddy line was a subset of the alien plant community of flood irrigated orchards (table 3) whereas no pattern of nestedness was found neither in the gradient from muddy line to orchards, from flood irrigated orchards to DOU nor from DOU to flooded orchards.



a) Native species

Figure 4a. NMDS ordination plot of the study sites based on Bray-Curtis similarities on native species composition. Boxplots show the results of the ANOVA of plot scores on the first axis. Boxes and whiskers plots include 25–75% and min/ max values, respectively. Vertical lines within boxes indicate medians. Open circles represent outliers. Different letters represent statistically significant differences.

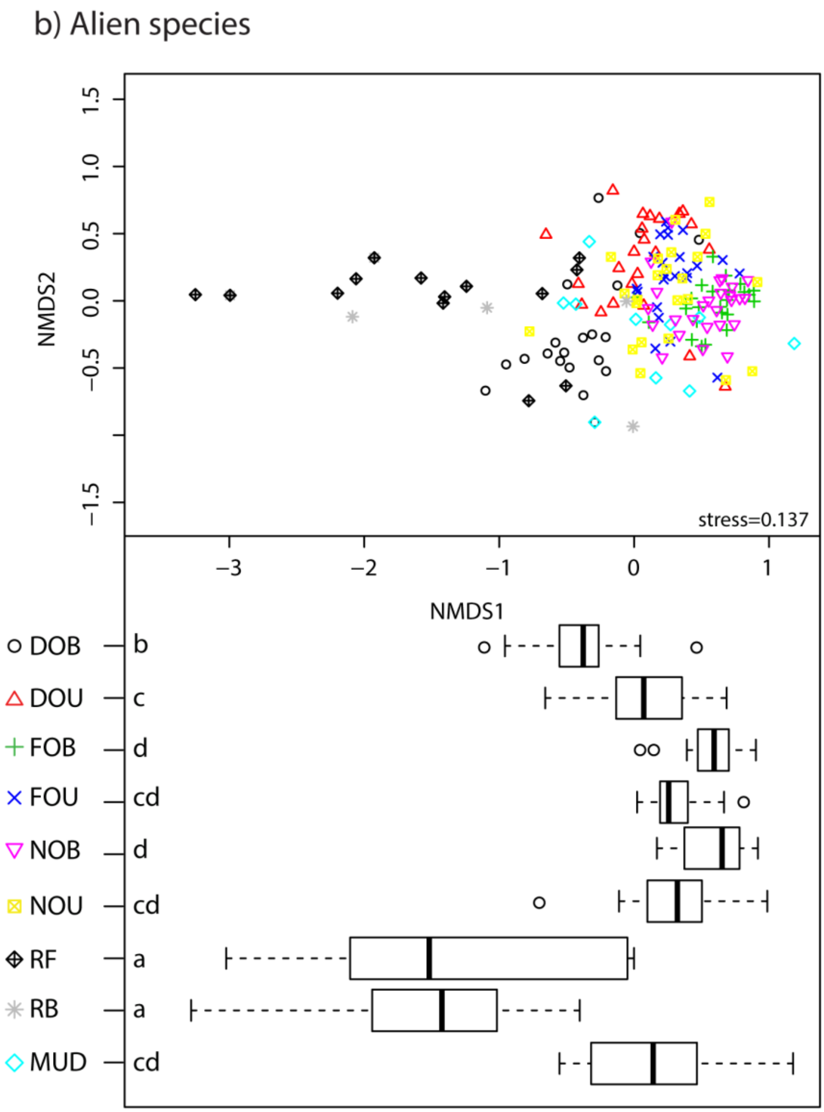
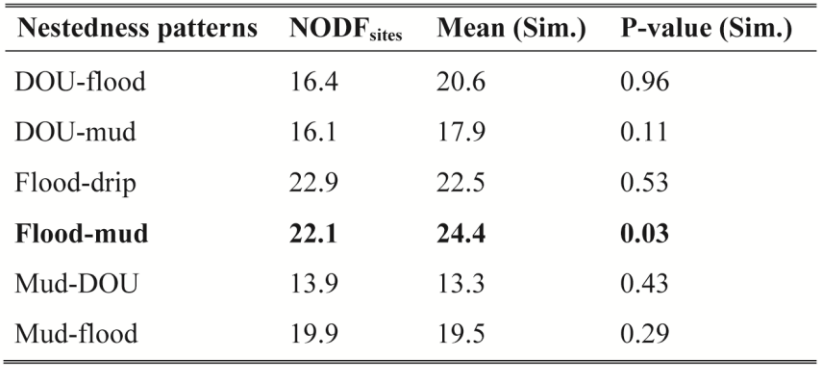


Figure 4b. NMDS ordination plot of the study sites based on Bray-Curtis similarities on alien species composition. Boxplots show the results of the ANOVA of plot scores on the first axis. Boxes and whiskers plots include 25–75% and min/ max values, respectively. Vertical lines within boxes indicate medians. Open circles represent outliers. Different letters represent statistically significant differences.

Table 3. Null model test for significant metacommunity nestedness for alien plant communities among those habitats that presented significantly similar alien plant composition. 3 possible nestedness patterns were evaluated: from DOU (drip irrigated orchards under tree lines), from flood irrigated orchards (flood) and from muddy line (mud) to the rest of the habitats. The metacommunities in different habitats are significantly nested under the constrained null model at $p < 0.05$ (bold text)



Nestedness patterns	$\text{NODF}_{\text{sites}}$	Mean (Sim.)	P-value (Sim.)
DOU-flood	16.4	20.6	0.96
DOU-mud	16.1	17.9	0.11
Flood-drip	22.9	22.5	0.53
Flood-mud	**22.1**	**24.4**	**0.03**
Mud-DOU	13.9	13.3	0.43
Mud-flood	19.9	19.5	0.29

Trait correlations and relationship with habitats

CWM values significantly varied among habitats, both for native (pseudo-F=24.1; p<0.05) (Fig. 5a) and for alien plants (pseudo-F=14; p<0.05) (Fig. 5b). Variance in community traits explained by habitats for native species was 47.7%, (22.2% and 14.5% by the first and second axes) and 39.4% for alien species, (18.9% and 12.1% by the first and second axes).

For native species analysis (Fig. 5a) ,the first axis clearly separated the riparian habitats from the orchards. Within orchards, flood irrigated orchards were separated depending on the position of the plots, while drip orchards were clustered together. Maximum height, photosynthetic pathway, most of the growth forms and flowering length were related to first axis whereas second axis was related to perennial grasses and forbs, clonality and hydrochory.

CWM-RDA on alien plants (Fig. 5b) positioned riparian forest, reedbed and DOB on the positive side of the axis and muddy line and the rest of the orchards on the negative side. Muddy line was clustered together with FOB and NOB. First axis was mostly related to maximum height, photosynthetic pathway, trees and annual grasses and zoochory whereas forbs, perennial graminoids, clonality and hydrochory were mostly associated to the second axis.

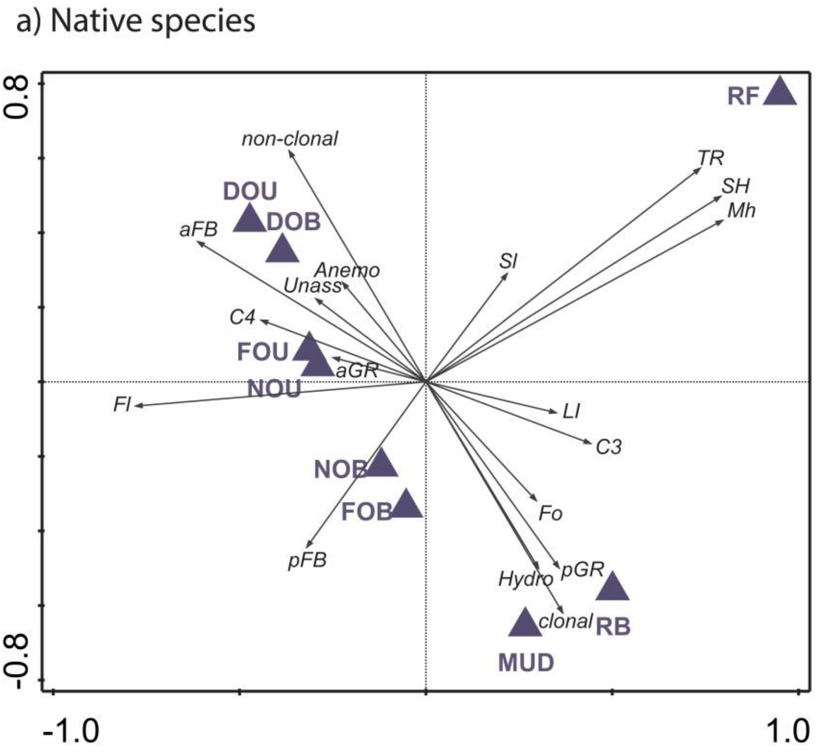
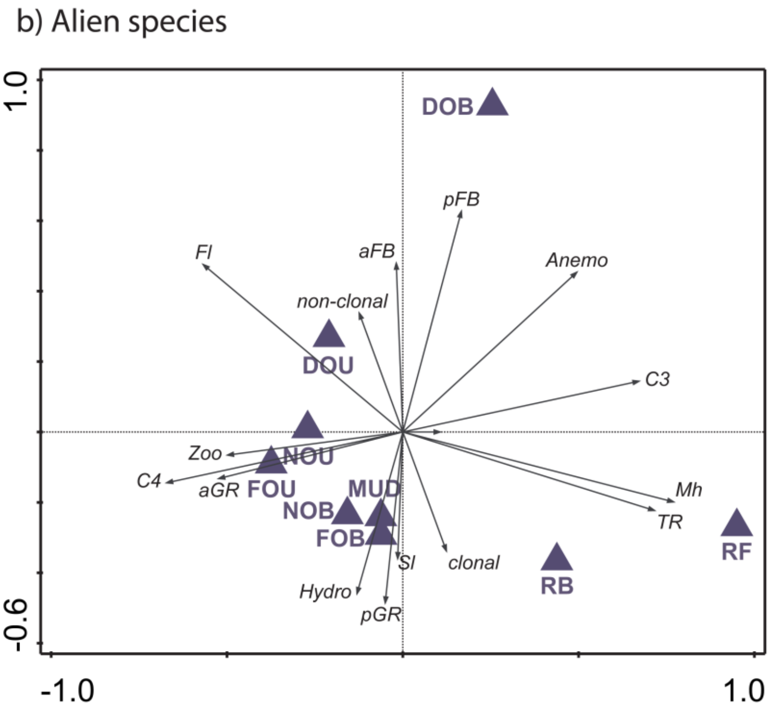


Figure 5a. Redundancy Analysis of CWM trait values (CWM-RDA) of native species. LI: lianas, TR: tree, SH: shrubs, FB: forb, GR: graminoid, a: annual, p: perennial. Mh: maximum height, Fl: flowering length, Fo: flowering onset, Sl: seed length. Anemo: anemochory, Hydro: hydrochory, Unass: unassisted.



b) Alien species

Figure 5b. Redundancy Analysis of CWM trait values (CWM-RDA) of alien species. TR: tree, FB: forb, GR: graminoid, a: annual, p: perennial. Mh: maximum height, Fl: flowering length, Sl: seed length. Anemo: anemochory, Hydro: hydrochory, Zoo: zoochory.

Generalized least squared models (Table 4 and Supplementary material) confirmed some of the trends observed in the ordination of traits in the CWM-RDA analyses. Regarding native species, riparian forests presented significantly higher values of trees and shrubs, larger height values, C3 species, short flowering length and larger zoochorous seeds. Muddy line and reedbed included larger number of C3 species with clonal reproduction, a late summer flowering period and hydrochory. Flood irrigated orchards, on the other hand, were mainly composed of species with long flowering length and zoochorous seeds. NOB and FOB presented dominance of perennial forbs, whereas NOU and FOU included significant larger values of annual grasses. DOB and DOU included annual species, with seeds dispersed by wind or barochory. However, results showed some different trends for alien plants. Alien species in riparian forest shared similar traits to native species, but were also clonal species with small seeds dispersed by wind. Muddy line, as well as flooded orchards, contained mainly graminoids, clonal, and C4 species dispersed by water. Perennial graminoids were better represented in both muddy line and NOB and FOB, whereas NOU and FOU included significantly higher proportions of annual graminoids. DOU included annual forbs, C4 zoochorous species, whereas alien plants in DOB were mainly C3, anemochorous forbs. Regarding reedbeds, CWM-RDA showed that alien species were mostly tall perennial C3 species with clonal reproduction.

Table 4. Summary of traits with significantly higher community weighted mean values in each habitat compared to the rest of the habitats for native and alien species (post-hoc Tukey's test. p<0.05).

		MUD	RB	RF	NOB	NOU	FOB	FOU	DOB	DOU
NATIVE	**GROWTH FORM**	pFORB	pGRASS	TREE SHRUB	pFORB aGRASS	aGRASS	pFORB	aGRASS	aFORB	aFORB aGRASS
	MAXIMUM HEIGHT			MAX. HEIGHT						
	PHOTOSYNTHESIS	C3	C3	C3	C4	C4	C3	C4	C4	C4
	FLOWERING ONSET	LATE	LATE							
	FLOWERING LENGTH			SHORT	LONG	LONG	LONG	LONG		LONG
	CLONALITY	YES	YES		YES		YES		NO	NO
	SEED LENGTH	SHORT	LONG	LONG			LONG			
	DISPERSAL	HYDRO.	HYDRO.	ZOO.	ZOO.	ZOO.	ZOO. ANEMO.	ZOO.	ANEMO. UNASS.	ANEMO. UNASS.
ALIEN	**GROWTH FORM**	pGRASS		TREE	aGRASS pGRASS	aGRASS	pGRASS	aGRASS	aFORB pFORB	aFORB
	MAXIMUM HEIGHT			MAX. HEIGHT						
	PHOTOSYNTHESIS	C4		C3	C4	C4	C4	C4	C3	C4
	FLOWERING ONSET	LATE							LATE	LATE
	FLOWERING LENGTH			SHORT				LONG	LONG	LONG
	CLONALITY	YES		YES	YES		YES		NO	NO
	SEED LENGTH	SHORT		SHORT	LONG	SHORT	LONG	SHORT	SHORT	SHORT
	DISPERSAL	HYDRO		ANEMO	ZOO HYDRO	ZOO HYDRO	ZOO HYDRO	ZOO HYDRO	ANEMO	ZOO

Discussion

Richness and abundance patterns

Results showed that γ-diversity was higher in natural habitats than in orchards, apart from reedbed, which harbours the lowest number of species among natural habitats. It is assumed that riparian habitats include more species than surrounding ecosystems (Brown and Peet, 2003), especially in Mediterranean areas (Stella et al., 2013). Reedbed communities were almost totally represented by common reed (*Phragmites australis*). Although it is native in the study area, it tends to form dense monotypes, impeding the development of other species (Zedler and Kercher, 2004). Besides, inflow of returned irrigation flow from agricultural areas increases rates of nutrient concentration of lowland streams (Baattrup-Pedersen et al., 2013), which has been related to the decrease in plant diversity in reedbeds (Kovács et al., 1995). Regarding the origin of the species most of them were native in riparian habitats, while the percentage of alien species as well as their relative cover values were significantly higher in orchards, as found in previous studies (Juárez-Escario et al., 2013). This confirms the susceptibility of irrigated crops to alien plant invasions already described in the Mediterranean region (Chytrý et al., 2009). The fluctuating resources theory (Davis et al., 2000) affirms that those communities affected by an increase in the amount of unused resources are more prone to be invaded. Irrigated orchards show this effect, as management includes periodic increases of resources (i.e. summer irrigation, nutrient uptake). Besides, weed management reduces competition with local species for those resources. This trend was already observed in drip irrigated orchards by Juárez-Escario et al. (2010) and in non-irrigated arable land in Catalonia by Chytrý et al. (2009). Nevertheless, alien γ-diversity was lower in DOB than in the rest of the orchards. The inter-row area in drip irrigated orchards is actually a rainfed area, and it contains typical rainfed-crop weeds adapted to the semiarid Mediterranean climate of the region that are mostly native. Nevertheless, relative alien cover was higher than expected based on relative richness. It could be explained by the dominance of species such as *Crepis bursifolia* and *Aster squamatus* in the alien community (see frequency and cover values of alien plants in supplementary material). To avoid these species to reach later stages of invasion, its abundance should be monitored and the causes of their expansion should be analyzed. Anemochory and mowing management of the inter-rows –since both species are able to resprout- may favour their increase.

On the other hand, the largest positive relationship between native and alien plant richness found in the muddy line has been previously described for communities that are not species saturated (Gilbert and Lechowicz, 2005; Moore et al., 2001) and also for riparian habitats (Tabacchi et al., 2005). The muddy line is subject to periodic flooding episodes that open new niches susceptible to colonization; therefore plant communities in this habitat remain in a primary or intermediate stage of succession. In this situation, alien species can settle in this habitat and increase the local diversity without implying loss of native species (Gilbert and Lechowicz, 2005). Similar patterns have been observed in other semi-arid Iberian rivers (Aguiar et al., 2006).

Similarly, lower positive correlation found in flood irrigated orchards might be explained because this process was overshadowed by the strong effect of crop management. As Davis et al. (2000) and Wardle (2001) described, disturbances such as fertilization trigger an increase in net resource availability that facilitate invasion, independent of the species diversity.

Composition, nestedness and dominant traits of native and alien plants

This study shows the importance of identifying differences in some traits between native and alien species for understanding differenced distribution of those communities among habitats.

Differences in floristic composition among habitats are mediated by ecological and management-related constraints (Götzenberger et al., 2012). Regarding native species, floristic composition of natural habitats was different from orchards. Within natural habitats, forest, reedbed and muddy line plant communities were well delineated as a result of the adaptation of the species to the multiple abiotic constraints that impact each habitat with various intensities; i.e. periodic flooding, sediment regimes and seasonal water shortage (Stella et al., 2013). Traits favoured at each habitat indeed reflect these adaptations. Hence, reedbeds and muddy line habitats, which are periodically flooded, have species whose seeds are dispersed by water and flower in late summer, when the level of water decreases in Mediterranean floodplains. In the riparian forest, however, which is established on infrequently flooded surfaces, communities can achieve a more advanced stage of plant succession (Tabacchi et al., 1998) and are dominated by trees and shrubs. As Catford and Jansson (2014) pointed out, such a variety of attributes proves that there are many possible combinations of successful adaptations to the diversity of environmental conditions in riparian habitats, which sustain the well-described high riparian biodiversity.

On the other hand, irrigation and weed management of orchards configure common compositional patterns, independently of the distance to the river. Flood irrigated orchards contain a weed community composed of zoochorous species with a long flowering period. Long flowering has been related to increased chances of colonization and better reproductive success (Lake and Leishman, 2004; Lloret et al., 2005). Regarding seed dispersal, most of the weeds present, like *Bromus diandrus*, *Hordeum murinum, Setaria verticillata, Torilis spp.* and *Tribulus terrestris* have seeds with adherent structures that enable their attachment to animal fur, which also facilitates human-mediated dispersion. On the other hand, mowing in the inter-row spaces favours the establishment of perennial forbs (Juárez-Escario et al., 2013; Lososová et al., 2003) whereas under tree rows where herbicides are applied, perennial form is not benefited and the well-described dominance of annual species in crops arises (Lososová et al., 2006).

In drip irrigated orchards, differences in the weed management between positions lead to the establishment of compositionally different but functionally similar weed communities, dominated by annual anemochorous forbs. Under the trees, therophytes that can escape from herbicide drift are able to establish, as well as individuals which are favoured by intense disturbances occurring in the inter rows (i.e. shredding and water shortage). These disturbances maintain the weed community in a primary stage of succession where vegetation cover is low and sparse and where wind dispersed annual plants dominate (Bonet, 2004).

Regarding alien species, data showed the composition of riparian forest, reedbed and DOB to be clearly differentiated whereas high similarities were found between muddy line and flood irrigated orchards. From a trait-based approach, alien plants in flood irrigated orchards-particularly between the rows- and the muddy line were mainly C4 species, perennial graminoids, with clonal growth and with water-dispersed seeds. This set of attributes facilitates alien species to colonize those habitats (via water dispersal) and to resist and recover from ecophysiological stress caused by inundation and physical disturbances from floods that characterize both orchards and the muddy line (Catford and Jansson, 2014).

Large nestedness from flood irrigated orchards to muddy line in terms of alien plants indicates that most of the shared alien species were introduced in the flooded orchards, and that only a subset of this community reaches the muddy line. This is consistent with the hypothesis of Clark and Johnston (2011) who argue that alien species establish in high disturbance areas first and, from there, they can adapt to and colonise sites with different environmental conditions. Influence of alien plants of agricultural uplands in the composition of alien communities in riparian habitats has been already showed (Ferreira and Moreira, 1995; Miyawaki and Washitani, 2004), and is enhanced in regulated rivers (Jansson et al., 2000) such as the studied river.

Lack of nested patters between DOU and flood orchards' alien weed community suggests that alien weeds were introduced independently in those habitats, probably by human-mediated pathways, establishing a similar community of weeds selected and maintained by a similar management (water supplies). A plausible hypothesis to explain the spread of alien plants from flooded orchards to muddy line is through irrigation water corridors (Benvenuti, 2007), after which it is presumed that a bidirectional flow of alien species was established, since propagules of alien plants settled in muddy line can also reach flooded orchards downstream through irrigation water.

This scenario is also supported by the evidence that alien plants present both in flood irrigated orchards and in the muddy line have water-dispersed seeds. In fact, the importance of hydrochory in riparian plants' distribution patterns has been previously described (Burkart, 2000) since it enables long-distance seed dispersal and effective colonization of riparian zones (Nilsson et al., 2010). Furthermore, success of invasive species in riparian habitats has also been related to hydrochory (Tabacchi et al., 2005). On the other hand, alien weeds of flood irrigated orchards are not only hydrochorous, but also zoochorous, which can increase the capability of colonization of new habitats. In fact, having more than one dispersal mechanism confers advantage in terms of undergoing rapid expansion (Wang et al., 2011).

The role of seed dispersal systems in colonizing both riparian habitats and nearby agricultural habitats is also reflected in the fact that some traits that confer adaptation to riparian disturbances are also present in alien species of drip irrigated orchards (i.e. C4, small seeds or late flowering onset); lack of hydrochory, however, may prevent these species from reaching the muddy line, as lack of nestedness patterns between those two habitats confirms. Some native and alien weeds present in orchards with traits adapted to riparian disturbances actually have the potential to establish populations in riparian zones, but their seed dispersal system does not facilitate the colonization of these habitats. This study thus reveals the role of the dispersal system as a key for species to overcome the filter of new habitats, and potentially become invasive, as was previously described by Richardson et al. (2000).

In terms of persistence and competitive capabilities, photosynthetic pathway, clonality and graminoid form confer advantages to alien weeds both in muddy line and in flooded orchards. Under flooding and high temperature conditions, C4 physiology allows plants to concentrate CO2 and enables carbon uptake from sediments, thus facilitating survival during water submergence. Moreover, in flood conditions, C4 species present a faster growth rate and higher photosynthetic productivity than C3 species due to a greater net assimilation rate (Sage, 2004). In fact, previous studies have shown that C4 photosynthesis is related to the selection of alien weeds in flood irrigated orchards (Juárez-Escario et al., 2013) and in riverbanks (Schmitz, 2006).

Two explanations may be responsible for the fact that alien species in muddy line and in flood irrigated orchards are mainly graminoids. For one, it is probable that photosynthetic pathways and life forms are phylogenetically related. In fact, a link between Poaceae and Cyperaceae perennial grasses and C4 photosynthesis has been observed in agricultural weeds (Haakansson, 1995). Alternately, grasses selected by the management of flood irrigated orchards can benefit in the muddy line, since flooding has been found to increase the overall productivity of graminoids (Insausti et al., 1999).

After disturbance episodes, vegetative reproduction benefits plants so they quickly (re)colonize areas (resilience) during terms without mechanical intervention or at inter-flooding periods (Gaba et al., 2014). This mechanism also allows them to survive disturbance events (resistance), despite losing some biomass, as occurs in the mowing of the inter-rows or after flooding episodes, since floods do not destroy entire clones (Catford and Jansson, 2014). Moreover, these clones can be water dispersed, therefore acting as propagules benefiting establishment and colonization of new areas.

Agro-ecological implications for conservation

This study highlights the role of irrigated orchards surrounding riparian habitats as alien weed reservoirs; permitting certain species to overcome the ecological filters of floodplains, and establish populations in the muddy line. Muddy line can also act as a source of propagules of those species to the orchards via irrigation water. On the other hand, the study reveals the role of the irrigation management of these orchards in configuring a community of alien weeds able to overcome invasion constraints of riparian habitats. For these reasons, both agronomic and ecological approaches are proposed to deal with this scenario.

From an agronomic point of view, since flood irrigated orchards appear to be the first receptor of alien plants, preventing the introduction and establishment of invasive alien species in flood orchards should be the first direct management strategy. Early detection measures based on weed risk assessment approaches and monitoring established aliens plant populations, focusing the eradication measures on those species whose traits have been related to the success in natural habitats have been proved effective at controlling other alien weeds invasions in the study area (i.e. *Sicyos angulatus* in maize fields or *Leersia oryzoides*, *Leptochloa* spp. and *Sagittaria* spp. in rice fields) (Brunel et al., 2013). In this sense, improving weed control techniques may be effective to control the most problematic species. Increasing the frequency of mechanical weed control may help to prevent plants to achieve phenological stages that involve seed production, hence breaking the spread of alien propagules by running water.

On the other hand, it has been widely proved that cover crops can effectively reduce or even suppress weed presence on crops providing at the same time ecosystem services (see Lemessa and Wakjira (2015) and the references therein). Thus, using cover crops mixture of native plants which present traits similar to successful alien plants can on the one hand reduce the cover of alien weeds and on the other hand increase the propagules supply of native species. Native plants should be selected based on their traits and ability to establish and persist under the environmental conditions of the host habitat, as Catford et al. (2012a) pointed out.

From an ecological point of view, disturbance regimes are a key in maximizing the total biodiversity across a floodplain (Ward et al., 1999). In this sense, flooding is possibly the most important factor in the maintenance of a temporal and spatial heterogeneity of riparian habitats that sustain a high diversity of biotic communities (Ward, 1998). Reduction of flood episodes in regulated rivers has been related to an increase in the establishment of alien plant communities by providing drier conditions (Catford et al., 2011), which could be related to the success of perennial life forms observed in the muddy line against more typical therophytes of this habitat. On the other hand, increasing flooding episodes has been accepted as an effective measure to control the establishment and development of alien plant communities in riparian habitats (Catford et al., 2011). Baattrup-Pedersen et al. (2013) found that low frequency flooding can increase richness of native vegetation within riparian areas in streams draining catchments dominated by agriculture, coinciding with the characteristics of our study area.

Hence, using environmental flows can be an effective way to avoid the establishment of alien plants in muddy line, therefore breaking the flow of alien plants between riparian habitats and agricultural areas nearby and confining alien plants in the orchards.

Conclusions

This study confirmed that riparian habitats in contact with irrigated orchards harboured rich and diverse plant communities at an habitat scale compared to the less diverse weed communities of the orchards, which were well-represented by alien species. Regarding native species, plant communities in riparian habitats were well differentiated from those of orchards, and within orchards, two different weed communities were found, depending on the irrigation system. In terms of alien plants, similar composition was found between the muddy line and the flood irrigated orchards and a nested pattern was detected from flood orchards' alien community to that of the muddy line. These results revealed that alien plants are shared between flood irrigated orchards and the muddy line. This connection is mediated by a group of traits adapted to disturbances and flood, such as the C4 photosynthetic pathway, clonal growth, graminoid form and water seed dispersal. Some of these traits were also present in native weed communities but lack of hydrochorous seeds prevents the establishment of those species in the muddy line.

This study revealed the role of flood irrigation in maintaining an alien weed community both in orchards and in nearby natural riparian habitats. This finding has important agronomic and ecological implications, and some management measures are proposed in order to reduce the flow of alien species between flood irrigated orchards and riparian habitats, thus maintaining these species confined to agricultural areas.

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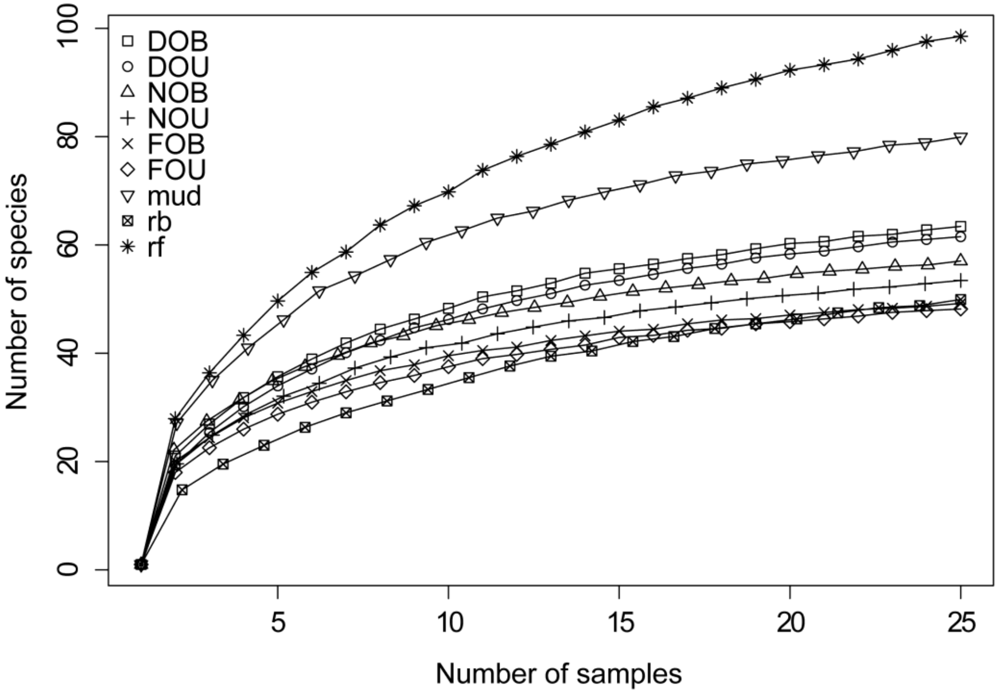
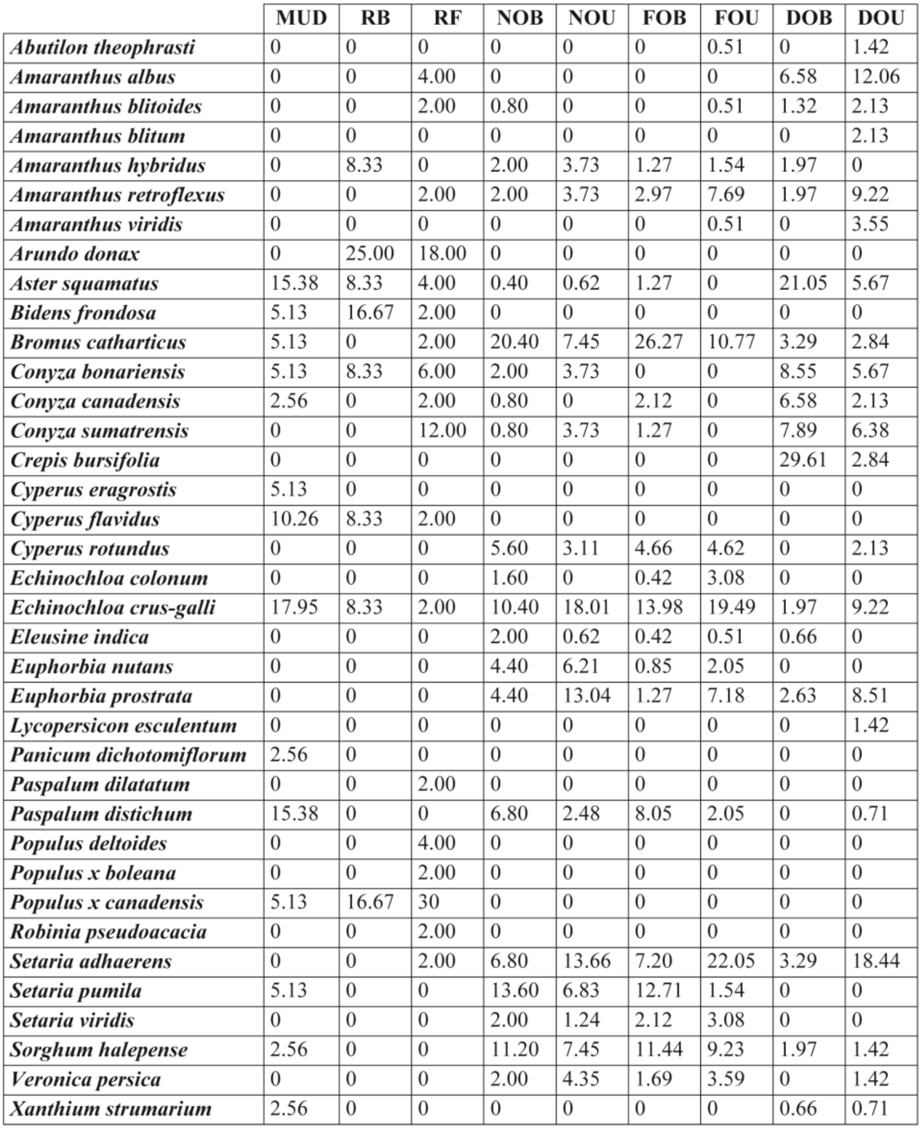


Supplementary material 1. Sampled-based rarefaction curves on each habitat based on 999 random replicates. mud: Muddy line, rb: reed bed, rf: riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree lines.

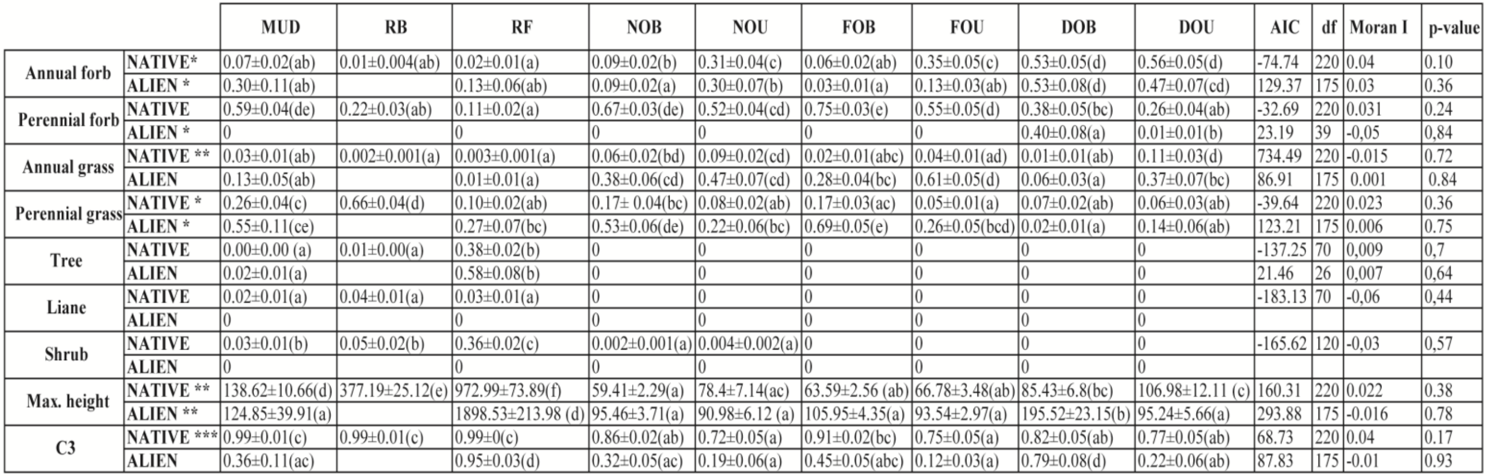
Supplementary material 2. Relative frequency in % of alien species in each habitat. MUD: Muddy line, RB: reed bed, RF: riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree-lines.



	MUD	RB	RF	NOB	NOU	FOB	FOU	DOB	DOU
Abutilon theophrasti	0	0	0	0	0	0	0.51	0	1.42
Amaranthus albus	0	0	4.00	0	0	0	0	6.58	12.06
Amaranthus blitoides	0	0	2.00	0.80	0	0	0.51	1.32	2.13
Amaranthus blitum	0	0	0	0	0	0	0	0	2.13
Amaranthus hybridus	0	8.33	0	2.00	3.73	1.27	1.54	1.97	0
Amaranthus retroflexus	0	0	2.00	2.00	3.73	2.97	7.69	1.97	9.22
Amaranthus viridis	0	0	0	0	0	0	0.51	0	3.55
Arundo donax	0	25.00	18.00	0	0	0	0	0	0
Aster squamatus	15.38	8.33	4.00	0.40	0.62	1.27	0	21.05	5.67
Bidens frondosa	5.13	16.67	2.00	0	0	0	0	0	0
Bromus catharticus	5.13	0	2.00	20.40	7.45	26.27	10.77	3.29	2.84
Conyza bonariensis	5.13	8.33	6.00	2.00	3.73	0	0	8.55	5.67
Conyza canadensis	2.56	0	2.00	0.80	0	2.12	0	6.58	2.13
Conyza sumatrensis	0	0	12.00	0.80	3.73	1.27	0	7.89	6.38
Crepis bursifolia	0	0	0	0	0	0	0	29.61	2.84
Cyperus eragrostis	5.13	0	0	0	0	0	0	0	0
Cyperus flavidus	10.26	8.33	2.00	0	0	0	0	0	0
Cyperus rotundus	0	0	0	5.60	3.11	4.66	4.62	0	2.13
Echinochloa colonum	0	0	0	1.60	0	0.42	3.08	0	0
Echinochloa crus-galli	17.95	8.33	2.00	10.40	18.01	13.98	19.49	1.97	9.22
Eleusine indica	0	0	0	2.00	0.62	0.42	0.51	0.66	0
Euphorbia nutans	0	0	0	4.40	6.21	0.85	2.05	0	0
Euphorbia prostrata	0	0	0	4.40	13.04	1.27	7.18	2.63	8.51
Lycopersicon esculentum	0	0	0	0	0	0	0	0	1.42
Panicum dichotomiflorum	2.56	0	0	0	0	0	0	0	0
Paspalum dilatatum	0	0	2.00	0	0	0	0	0	0
Paspalum distichum	15.38	0	0	6.80	2.48	8.05	2.05	0	0.71
Populus deltoides	0	0	4.00	0	0	0	0	0	0
Populus x boleana	0	0	2.00	0	0	0	0	0	0
Populus x canadensis	5.13	16.67	30	0	0	0	0	0	0
Robinia pseudoacacia	0	0	2.00	0	0	0	0	0	0
Setaria adhaerens	0	0	2.00	6.80	13.66	7.20	22.05	3.29	18.44
Setaria pumila	5.13	0	0	13.60	6.83	12.71	1.54	0	0
Setaria viridis	0	0	0	2.00	1.24	2.12	3.08	0	0
Sorghum halepense	2.56	0	0	11.20	7.45	11.44	9.23	1.97	1.42
Veronica persica	0	0	0	2.00	4.35	1.69	3.59	0	1.42
Xanthium strumarium	2.56	0	0	0	0	0	0	0.66	0.71

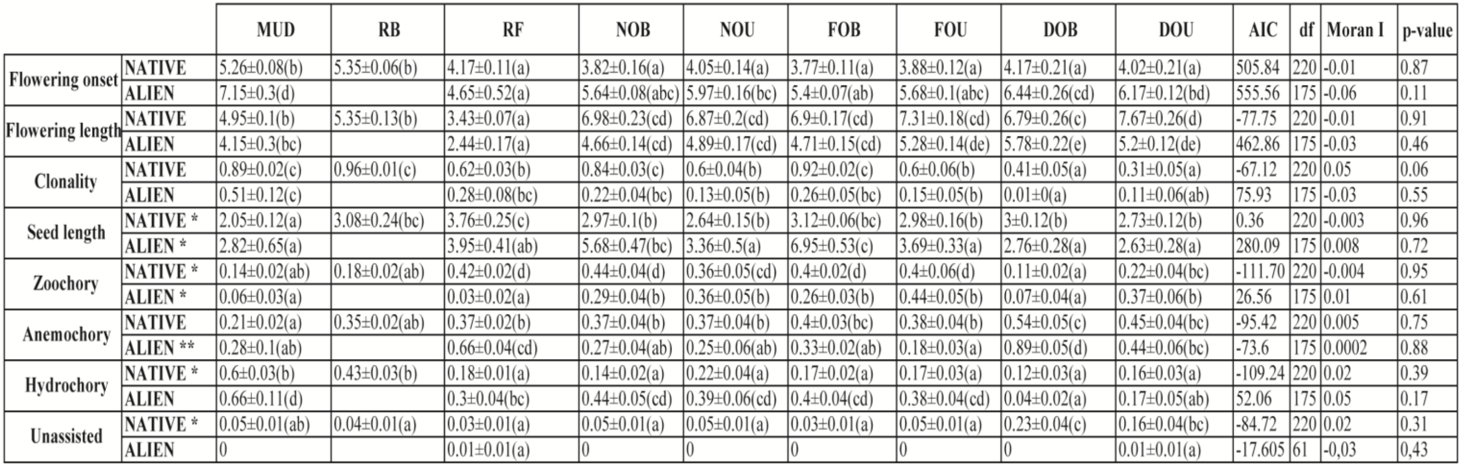
Supplementary material 3. Average cover in % of alien species in each habitat. MUD: Muddy line, RB: reed bed, RF: riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree-lines.

	MUD	**RB**	**RF**	**NOB**	**NOU**	**FOB**	**FOU**	**DOB**	**DOU**
Abutilon theophrasti	0	0	0	0	0	0	0	0	0.10
Amaranthus albus	0	0	0.03	0	0	0	0	6.31	21.66
Amaranthus blitoides	0	0	0.02	0.01	0	0	0	0.02	0.15
Amaranthus blitum	0	0	0	0	0	0	0	0	13.66
Amaranthus hybridus	0	0.30	0	0.32	1.63	0.01	0.25	0.52	0
Amaranthus retroflexus	0	0	0.02	0.02	0.59	0.16	4.31	0.03	0.65
Amaranthus viridis	0	0	0	0	0	0	0	0	0.25
Arundo donax	0	67.87	34.20	0	0	0	0	0	0
Aster squamatus	0.37	0.30	0.03	0	0.01	0.28	0	14.97	0.40
Bidens frondosa	3.13	0.60	0.02	0	0	0	0	0	0
Bromus catharticus	0.12	0	0.02	42.03	1.70	37.87	9.85	4.03	0.20
Conyza bonariensis	0.12	0.30	0.05	0.17	2.45	0	0	4.11	7.70
Conyza canadensis	0.06	0	0.02	0.16	0	2.58	0	6.58	0.15
Conyza sumatrensis	0	0	0.10	0.16	0.59	0.01	0	3.34	0.45
Crepis bursifolia	0	0	0	0	0	0	0	56.98	0.20
Cyperus eragrostis	0.12	0	0	0	0	0	0	0	0
Cyperus flavidus	24.60	15.02	0.02	0	0	0	0	0	0
Cyperus rotundus	0	0	0	4.56	1.10	12.46	1.25	0	2.58
Echinochloa colonum	0	0	0	1.86	0	0	1.36	0	0
Echinochloa crus-galli	3.44	15.02	0.02	9.75	35.90	14.42	21.30	0.52	25.24
Eleusine indica	0	0	0	3.17	0.01	0	0	0.01	0
Euphorbia nutans	0	0	0	2.80	5.92	0.14	0.50	0	0
Euphorbia prostrata	0	0	0	0.03	2.84	0.01	1.27	1.02	0.60
Lycopersicon esculentum	0	0	0	0	0	0	0	0	0.10
Panicum dichotomiflorum	0.06	0	0	0	0	0	0	0	0
Paspalum dilatatum	0	0	0.02	0	0	0	0	0	0
Paspalum distichum	67.61	0	0	11.75	2.95	11.84	0.50	0	0.05
Populus deltoides	0	0	11.39	0	0	0	0	0	0
Populus x boleana	0	0	0.02	0	0	0	0	0	0
Populus x canadensis	0.12	0.60	54.01	0	0	0	0	0	0
Robinia pseudoacacia	0	0	0.02	0	0	0	0	0	0
Setaria adhaerens	0	0	0.02	1.88	25.97	1.29	48.45	1.52	25.63
Setaria pumila	0.12	0	0	10.16	11.53	6.03	0.50	0	0
Setaria viridis	0	0	0	0.70	4.01	0.42	2.70	0	0
Sorghum halepense	0.06	0	0	10.47	2.22	12.47	6.76	0.03	0.10
Veronica persica	0	0	0	0.02	0.60	0.01	1.00	0	0.10
Xanthium strumarium	0.06	0	0	0	0	0	0	0.01	0.05



		MUD	RB	RF	NOB	NOU	FOB	FOU	DOB	DOU	AIC	df	Moran I	p-value
Annual forb	**NATIVE***	0.07±0.02(ab)	0.01±0.004(ab)	0.02±0.01(a)	0.09±0.02(b)	0.31±0.04(c)	0.06±0.02(ab)	0.35±0.05(c)	0.53±0.05(d)	0.56±0.05(d)	-74.74	220	0.04	0.10
	ALIEN *	0.30±0.11(ab)		0.13±0.06(ab)	0.09±0.02(a)	0.30±0.07(b)	0.03±0.01(a)	0.13±0.03(ab)	0.53±0.08(d)	0.47±0.07(cd)	129.37	175	0.03	0.36
Perennial forb	**NATIVE**	0.59±0.04(de)	0.22±0.03(ab)	0.11±0.02(a)	0.67±0.03(de)	0.52±0.04(cd)	0.75±0.03(e)	0.55±0.05(d)	0.38±0.05(bc)	0.26±0.04(ab)	-32.69	220	0.031	0.24
	ALIEN *	0		0	0	0	0	0	0.40±0.08(a)	0.01±0.01(b)	23.19	39	-0,05	0,84
Annual grass	**NATIVE ****	0.03±0.01(ab)	0.002±0.001(a)	0.003±0.001(a)	0.06±0.02(bd)	0.09±0.02(cd)	0.02±0.01(abc)	0.04±0.01(ad)	0.01±0.01(ab)	0.11±0.03(d)	734.49	220	-0.015	0.72
	ALIEN	0.13±0.05(ab)		0.01±0.01(a)	0.38±0.06(cd)	0.47±0.07(cd)	0.28±0.04(bc)	0.61±0.05(d)	0.06±0.03(a)	0.37±0.07(bc)	86.91	175	0.001	0.84
Perennial grass	**NATIVE ***	0.26±0.04(c)	0.66±0.04(d)	0.10±0.02(ab)	0.17± 0.04(bc)	0.08±0.02(ab)	0.17±0.03(ac)	0.05±0.01(a)	0.07±0.02(ab)	0.06±0.03(ab)	-39.64	220	0.023	0.36
	ALIEN *	0.55±0.11(ce)		0.27±0.07(bc)	0.53±0.06(de)	0.22±0.06(bc)	0.69±0.05(e)	0.26±0.05(bcd)	0.02±0.01(a)	0.14±0.06(ab)	123.21	175	0.006	0.75
Tree	**NATIVE**	0.00±0.00 (a)	0.01±0.00(a)	0.38±0.02(b)	0	0	0	0	0	0	-137.25	70	0,009	0,7
	ALIEN	0.02±0.01(a)		0.58±0.08(b)	0	0	0	0	0	0	21.46	26	0,007	0,64
Liane	**NATIVE**	0.02±0.01(a)	0.04±0.01(a)	0.03±0.01(a)	0	0	0	0	0	0	-183.13	70	-0,06	0,44
	ALIEN	0		0	0	0	0	0	0	0				
Shrub	**NATIVE**	0.03±0.01(b)	0.05±0.02(b)	0.36±0.02(c)	0.002±0.001(a)	0.004±0.002(a)	0	0	0	0	-165.62	120	-0,03	0,57
	ALIEN	0		0	0	0	0	0	0	0				
Max. height	**NATIVE ****	138.62±10.66(d)	377.19±25.12(e)	972.99±73.89(f)	59.41±2.29(a)	78.4±7.14(ac)	63.59±2.56 (ab)	66.78±3.48(ab)	85.43±6.8(bc)	106.98±12.11 (c)	160.31	220	0.022	0.38
	ALIEN **	124.85±39.91(a)		1898.53±213.98 (d)	95.46±3.71(a)	90.98±6.12 (a)	105.95±4.35(a)	93.54±2.97(a)	195.52±23.15(b)	95.24±5.66(a)	293.88	175	-0.016	0.78
C3	**NATIVE *****	0.99±0.01(c)	0.99±0.01(c)	0.99±0(c)	0.86±0.02(ab)	0.72±0.05(a)	0.91±0.02(bc)	0.75±0.05(a)	0.82±0.05(ab)	0.77±0.05(ab)	68.73	220	0.04	0.17
	ALIEN	0.36±0.11(ac)		0.95±0.03(d)	0.32±0.05(ac)	0.19±0.06(a)	0.45±0.05(abc)	0.12±0.03(a)	0.79±0.08(d)	0.22±0.06(ab)	87.83	175	-0.01	0.93

Supplementary material 4. Mean values and standard errors of CWM values of traits for native and alien plants in each habitat and results of GLS models on CWM values. MUD: Muddy line, RB: reed bed, RF: riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree-lines.*=squared root-transformed variables, **=log-transformed variables, ***arcsinus-squared root-transformed variables



		MUD	RB	RF	NOB	NOU	FOB	FOU	DOB	DOU	AIC	df	Moran I	p-value
Flowering onset	**NATIVE**	5.26±0.08(b)	5.35±0.06(b)	4.17±0.11(a)	3.82±0.16(a)	4.05±0.14(a)	3.77±0.11(a)	3.88±0.12(a)	4.17±0.21(a)	4.02±0.21(a)	505.84	220	-0.01	0.87
	ALIEN	7.15±0.3(d)		4.65±0.52(a)	5.64±0.08(abc)	5.97±0.16(bc)	5.4±0.07(ab)	5.68±0.1(abc)	6.44±0.26(cd)	6.17±0.12(bd)	555.56	175	-0.06	0.11
Flowering length	**NATIVE**	4.95±0.1(b)	5.35±0.13(b)	3.43±0.07(a)	6.98±0.23(cd)	6.87±0.2(cd)	6.9±0.17(cd)	7.31±0.18(cd)	6.79±0.26(c)	7.67±0.26(d)	-77.75	220	-0.01	0.91
	ALIEN	4.15±0.3(bc)		2.44±0.17(a)	4.66±0.14(cd)	4.89±0.17(cd)	4.71±0.15(cd)	5.28±0.14(de)	5.78±0.22(e)	5.2±0.12(de)	462.86	175	-0.03	0.46
Clonality	**NATIVE**	0.89±0.02(c)	0.96±0.01(c)	0.62±0.03(b)	0.84±0.03(c)	0.6±0.04(b)	0.92±0.02(c)	0.6±0.06(b)	0.41±0.05(a)	0.31±0.05(a)	-67.12	220	0.05	0.06
	ALIEN	0.51±0.12(c)		0.28±0.08(bc)	0.22±0.04(bc)	0.13±0.05(b)	0.26±0.05(bc)	0.15±0.05(b)	0.01±0(a)	0.11±0.06(ab)	75.93	175	-0.03	0.55
Seed length	**NATIVE ***	2.05±0.12(a)	3.08±0.24(bc)	3.76±0.25(c)	2.97±0.1(b)	2.64±0.15(b)	3.12±0.06(bc)	2.98±0.16(b)	3±0.12(b)	2.73±0.12(b)	0.36	220	-0.003	0.96
	ALIEN *	2.82±0.65(a)		3.95±0.41(ab)	5.68±0.47(bc)	3.36±0.5(a)	6.95±0.53(c)	3.69±0.33(a)	2.76±0.28(a)	2.63±0.28(a)	280.09	175	0.008	0.72
Zoochory	**NATIVE ***	0.14±0.02(ab)	0.18±0.02(ab)	0.42±0.02(d)	0.44±0.04(d)	0.36±0.05(cd)	0.4±0.02(d)	0.4±0.06(d)	0.11±0.02(a)	0.22±0.04(bc)	-111.70	220	-0.004	0.95
	ALIEN *	0.06±0.03(a)		0.03±0.02(a)	0.29±0.04(b)	0.36±0.05(b)	0.26±0.03(b)	0.44±0.05(b)	0.07±0.04(a)	0.37±0.06(b)	26.56	175	0.01	0.61
Anemochory	**NATIVE**	0.21±0.02(a)	0.35±0.02(ab)	0.37±0.02(b)	0.37±0.04(b)	0.37±0.04(b)	0.4±0.03(bc)	0.38±0.04(b)	0.54±0.05(c)	0.45±0.04(bc)	-95.42	220	0.005	0.75
	ALIEN **	0.28±0.1(ab)		0.66±0.04(cd)	0.27±0.04(ab)	0.25±0.06(ab)	0.33±0.02(ab)	0.18±0.03(a)	0.89±0.05(d)	0.44±0.06(bc)	-73.6	175	0.0002	0.88
Hydrochory	**NATIVE ***	0.6±0.03(b)	0.43±0.03(b)	0.18±0.01(a)	0.14±0.02(a)	0.22±0.04(a)	0.17±0.02(a)	0.17±0.03(a)	0.12±0.03(a)	0.16±0.03(a)	-109.24	220	0.02	0.39
	ALIEN	0.66±0.11(d)		0.3±0.04(bc)	0.44±0.05(cd)	0.39±0.06(cd)	0.4±0.04(cd)	0.38±0.04(cd)	0.04±0.02(a)	0.17±0.05(ab)	52.06	175	0.05	0.17
Unassisted	**NATIVE ***	0.05±0.01(ab)	0.04±0.01(a)	0.03±0.01(a)	0.05±0.01(a)	0.05±0.01(a)	0.03±0.01(a)	0.05±0.01(a)	0.23±0.04(c)	0.16±0.04(bc)	-84.72	220	0.02	0.31
	ALIEN	0		0.01±0.01(a)	0	0	0	0	0	0.01±0.01(a)	-17.605	61	-0,03	0,43

Supplementary material 4 (cont.). Mean values and standard errors of CWM values of traits for native and alien plants in each habitat and results of GLS models on CWM values. MUD: Muddy line, RB: reed bed, RF: riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree-lines.*=squared root-transformed variables, **=log-transformed variables, ***arcsinus-squared root-transformed variables

CHAPTER 6

General discussion and main conclusions

General discussion

The experimental work presented in this thesis allows to improve insights into the long-term temporal trajectories of weed communities in irrigated crops and the intrinsic (in terms of functional traits) and extrinsic (in terms of crop management) factors linked to the expansion of alien plants, both within weed communities of irrigated orchards and between these orchards and the surrounding natural habitats. These results can be applied to develop further management practices aimed at preventing and controlling this process.

Our results point up that ecological dynamics of weed communities show independent trajectories in perennial and in annual crops, thus confirming that different management practices associated to each crop create particular conditions that provide specific ecological niches for weeds (Meiss et al., 2010). At long-term scale, we prove that weed communities associated to irrigated orchards are involved in a process of homogenization of flora as well as in a functional specialization whereas in maize field these processes seem to be more consolidated (Chapter 1). These results support that the specialization of flora is higher in monocultures with no crop rotation (Fried et al., 2010). In annual crops, such as studied maize fields with a minimal rotation rate, the total removal of weed community at harvest time and the chemical weed control configure a weed community mostly composed by annual plants with a synchronized life cycle with the crop, which can escape form herbicides or are less sensitive to them, as has been showed in other annual crops in Europe (Fried et al., 2009). In this sense, the observed changes in maize fields were more species-related than traits-related, since the proportion of species in functional groups did not significantly change.

In flood-irrigated orchards, weed control methods are more heterogeneous than in maize fields, involving mowing, shredding as well as located herbicide applications, and they do not imply total removal of weeds but only destruction of the aerial part. It promotes higher α- (local) and γ- (regional) diversity of weed communities than in maize fields confirming that diversification of management practices in crops promotes higher values of weed richness and diversity (de la Fuente et al., 2006; Lososová and Cimalová, 2009; Meiss et al., 2010; Colbach et al., 2014)

This thesis also highlights how the homogenization of weed communities in flood-irrigated orchards is giving rise to specific plant assemblages where the alien component is increasing its prominence (chapters 1 and 2). Alien weeds represented less of 30% of total species in weeds assemblages (chapter 1 and 2) although they occupy over half of the total weed cover in flood irrigated orchards (chapter 2 and 4). The prominence of alien weeds is linked to the possession of a group of traits that benefit them against most of the native species. Thereby, we have proved that in flood irrigated orchards successful alien weeds are mostly C4 species, with clonal reproduction and seeds dispersed by water or by multiple methods as well as graminoids and perennial growth forms. Perennial form is also related to the most successful native species, particularly those rosulate, caespitose and reptant forms. Particularly, C4 photosynthesis ensures high photosynthetic rates and a more efficient use of nitrogen in environments with high photorespiration rates such as flooded orchards in summer (Sage and Kubien, 2003) increasing growth rates over short periods (Pyankov et al., 2010). Clonality is involved in the resistance of plants to flooding and mechanical disturbances (Benot et al., 2011 and references therein). Graminoids and perennial forms are favoured against annual forbs in perennial crops since their leaves and resprouting structures are located near soil surface, hence being less damaged by mowing (Albrecht, 2005; Gago et al., 2007; Meiss et al., 2010). Hydrochory and the capacity of disperse seeds by multiple methods favour long-distance dispersal and a faster expansion capacity (Moravcová et al., 2010; Wang et al., 2011). Therefore, our results point in the same direction that in resource-rich, disturbed habitats those traits related to fast growth rates, rapid resource capture as well as resistance to/ resilience from disturbances are selected (Dietz and Edwards, 2006) which also benefit invasiveness (Van Kleunen et al., 2010a).

At this point, it is important to underscore that the functional approach of our study not only allows to distinguish between successful alien species from natives but also from those aliens that do not succeed, which is crucial to properly disentangle the role of traits associated to invasiveness (Moravcová et al., 2010).

The fact that benefited alien species own a group of traits that differs to those of the native species support limiting similarity theory (Macarthur and Levins, 1967), which predicts that successful invaders should differ functionally from species already present in the community. Our results confirm that this process operate in high-resources habitats, whereas native and invasive species occurring in low- resource environments in Mediterranean areas are functionally similar, as environmental factors constrain the range of beneficial physiological and morphological traits (Funk et al., 2016).

Regarding invasibility of the irrigated orchards, our study shows for the first time that the irrigation method has a more relevant role in favouring alien weeds than weed management (chapter 3), hence confirming that in Mediterranean areas such habitats with higher water disponibility are more prone to be invaded (Arianoutsou et al., 2010).

Irrigation method configures compositional and functionally differentiated weed assemblages in orchards as well as modulates the effect of weed management in those communities. Even though weed management has been widely considered as a strong factor in configuring weed assemblages in perennial crops (Fracchiolla et al., 2016; Cicuzza et al., 2012; Mas et al., 2007), in Mediterranean areas, where the most limiting factor is water disponibility, is this element and the way it is supplied to the orchards which mainly determines both compositional and functional structure of weed communities (Carmona et al., 2012) and its susceptibility to be invaded (Dukes and Mooney, 1999; Arianoutsou et al., 2010; Fagúndez et al., 2016).Furthermore, this work corroborates that the effects of mechanical disturbances on the structure and the dynamic of plant communities strongly depend on water availability (Perez-Camacho et al., 2012). In this sense the increase of alien weeds that are graminoids, C4 species, clonal species dispersed by water or by multiple systems is driven more by flood irrigation than for weed management, being the latter more related to the selection of perennial life form in the interrows, where weeds are mowed, and annual weeds under tree, where herbicide is applied, regardless the origin of the species (chapter 3 and 4).

This study unravels that the described traits of successful alien weeds in the orchards not only lay behind the increase of their prominence there, but also allow them to colonize riparian habitats that surround these orchards (chapter 4). Although our results show that riparian habitats closed to irrigated orchards present a low invasion degree compared to irrigated orchards nearby, we have been able to identify the establishment of a flow of the alien weeds between the irrigated orchards and the muddy line. This process is favoured by the similarity of the nature of disturbances operating in flooded orchards and in muddy line, where periodical inundation plays a key role in trait selection (Chapter 2, 3 and 4) and the connection of those habitats by irrigation channels, through which hydrochorous propagules can effectively disperse (chapter 4).

It is assumed that this flow is bidirectional, from orchards to the riparian habitats through irrigation channels and from upstream riparian areas to downstream flooded orchards through irrigation water but our study shows for the first time that most of the shared alien plants come from flood irrigated orchards. Conversely, the presence of some similar alien species in drip and in flood irrigated orchards is the result of independent introductions (chapter 4), probably human-mediated. From these results, the evidence of the influence of flood irrigation in the success of colonization and dispersal of alien weeds in crops and in the surrounding natural habitats is reinforced.

In addition, this study shows how mechanisms of limiting similarity operate both a local (field) and a regional (landscape) scale, thus helping to explain the success of alien plants at different spatial scales as well as providing additional support to that regional processes influence on local species assemblages (Catford and Jansson, 2014; Ordonez et al., 2010). However, an analysis of functional diversity at different spatial scales would complement the unravelling of the mechanisms driving trait convergence and divergence of alien and native weed assemblages in agricultural areas (Bello et al., 2009).

Implications for management and control

Drip irrigated orchards not only host less richness and diversity of alien weeds than flood-irrigated orchards (chapter 3 and 4), but also the alien weeds present in weed assemblages in drip-irrigated orchards showed lower chances of colonizing riparian habitats nearby (chapter 4). On the one hand, drip irrigation system avoids direct connection between these habitats through water channels and, on the other hand, the suite of traits favoured in drip irrigation is different to those selected in the muddy line.

From these results, our work offers new and original arguments supporting drip irrigation against traditional flood irrigation. It is well-know that drip irrigation is highly efficient in terms of saving water, reducing soil erosion and crop diseases, increasing the efficiency of fertilizers and reducing weed growth (Coolong, 2013 and references therein) but hitherto any study has shown the benefits of drip irrigation in terms of limiting the prominence of alien species in weed assemblages (chapter 3) and avoiding the flow of successful alien weeds between orchards and riparian habitats (chapter 4).

Moreover we show that drip irrigation configures a weed cover that can provide ecological services to the crop in the form of pollinator resources (chapter 3), which corroborates that ecological services of weeds may be enhanced by crop management (Fracchiolla et al., 2016; Gerowitt et al., 2003).

In this sense, this thesis demonstrates that irrigation system becomes an essential aspect for configuring weed assemblages that provide ecological services, reducing competence with crops and minimizing the prominence of alien weeds within.

However, it is important to remark that the presence of some problematic alien species in drip irrigated orchards (i.e. *Aster squamatus*, *Conyza* spp.), makes appealing to perform further studies regarding the selection of these species since they are naturalized in agricultural and natural habitats (Carretero, 1994), and biotypes resistant to herbicides have been already described (Okada et al., 2015; Osuna et al., 2003).

From our results, monitoring measures of alien weeds based on their functional traits can be developed. This may help to establish priorities and optimize efforts in terms of control, quarantine and early eradication measures on those weed species whose suite of traits favour them in agricultural habitats, as it has been applied on other species based on its potential negative impact in the agriculture (DOGC, 2005; 2006), allowing to strongly reduce the economic losses caused by a late intervention protocol (Recasens et al., 2007).

On the other hand, links of biological traits and the success of alien weeds in irrigated crops corroborated by this work make it advisable the inclusion of questions regarding functional traits in the current weed risk assessment protocols as well as developing new protocols focused on agricultural habitats. This is necessary since most of the elements configuring weed risk assessment protocols are more aimed at evaluating species invasiveness and their impacts into natural habitats rather than in agricultural areas, since the latter are supposed to be highly and homogeneously susceptible to invasive species. This assumption could provide biased results since it has been proved that rainfed crops in dryland areas are more resistant to invasive weeds than irrigated crops (Chytrý et al., 2008) and our work shows that within them, drip-irrigated are more resistant to alien weed colonization than flooded ones.

Metodological remarks

The trait-based approach applied in this work has allowed us to identify functional weed assemblages in irrigated crops and the attributes that make some of those groups successful at different space-temporal scales. It provides additional support to the usefulness of the functional traits perspective in the identification of the assembly rules of plant communities in long-term plant survey data (Fried et al., 2009) and the intrinsic factors linked to invasiveness of alien plants (Drenovsky et al., 2012).

At this point, many studies have identified traits related to the success of alien plants at different spatial scales (e.g. Funk et al., 2016; Ordonez et al., 2013; Moravcová et al., 2010; Godoy el al., 2009).

Even though several attempts have been conducted to describe the suite of traits which explain the global invasiveness of alien plants (Pyšek and Richardson, 2007; Van Kleunen et al., 2010b), it is widely accepted that there is not a universal profile of traits that define the global success of alien plants, but rather it depends on the ecological constraints and characteristics of each habitat (Jauni and Hyvönen, 2012; Lloret el at., 2005), as we have also proved (chapter 1). For this reason, the selection of the correct candidate traits in the study of the success of alien plants in a particular habitat is crucial to avoid biased conclusions. In our work, we have selected those traits related to the disturbances and constraints that filter species in the agricultural habitats (Fried et al., 2009). The robustness of the traits selected for achieving the foreseen objectives of our study relies on the fact that similar results have been obtained in independent analyses at different spatial scales along the different chapters of this thesis. Nevertheless, it would be also of interest analysing those traits related to other aspects such as the response of the seed bank and emergence processes to crop management (Recasens et al., 2005) or the role of invasion history and habitat preferences of alien weeds in their success in agricultural habitats (Jauni and Hyvönen, 2012)

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Main conclusions

The characterization of weed assemblages of the irrigated crops in Northeastern Spain highlights the prominence of alien plants in these communities. Particular management practices of annual and perennial crops help to explain the different trajectories of the associated weed communities of each system at long-term temporal scale. In irrigated orchards, flood irrigation system has proved to be the main factor to trigger the recruitment of a set of alien weeds with a syndrome of traits that enable them not only to succeed in the orchards, but also to spread and colonize the surrounding natural habitats. The results obtained in this thesis provide new and original reasons for supporting drip irrigation against flooding in irrigated orchards in the Mediterranean area and illustrate the usefulness of functional trait approach in unravelling weed assemblage rules in crops and in developing measures for preventing and controlling alien plant invasions.

The main conclusions of this study are:

Temporal changes of weed communities

1. On a long-term scale, it has been detected a process of compositional and functional homogenization of the weed assemblages of irrigated fruit tree orchards, which implies an increase of the prominence of alien weeds within them. This process seems to be more consolidated in maize crops.

2. The higher heterogeneity in the management practices in orchards comparing to those in maize fields results in higher diversity values in the weed community of the former both at local and at regional scale.

3. As the ecological assembly theory applied to weed communities affirms, differences in crop management between maize crops and orchards results on the selection of specific functional groups of weeds in each case. Thereby, chemical weed control and lack of crop rotation favour annual weeds in maize crops whereas mechanical weed control allows perennial forms to stand out in orchards.

Invasiveness of alien weeds

4. The resistance and resilience to flooding and to mechanical management through the possession of a suite of traits adapted to these disturbances explains the success of alien weeds in flood irrigated orchards, where they represent more than a half of the total plant cover. These selected traits include C4 photosynthesis, clonality, water seed dispersal and seeds dispersed by more than one method as well as perennial forms and graminoid growth forms.

5. Successful native and alien weeds in flood irrigated orchards differ in most of their traits, which support limiting similarity theory to explain the ecological processes that regulate the assembly of the weed communities in orchards and the success of alien weeds there.

Invasibility of irrigated orchards

6. Irrigation management is the main factor configuring the compositional and functional structure of weed communities in orchards and modulates the effect of weed management on weed assemblages.

7. Flood irrigation is linked to the maintenance of a dense weed cover in the alleys of the orchards as well as to the promotion of a group of alien weeds that possess the suite of traits that enables them to succeed in orchards and in the surrounding natural habitats.

8. Weed communities favoured in drip irrigated orchards not only possess a cover structure less competitive with the crop and a low prominence of alien plants than in flood irrigated orchards, but also present higher diversity values and can deliver ecosystem services in form of pollination resources, which results in an agronomic benefit.

9. The effect of weed management in the functional structure of weed assemblages is restricted to the selection of perennial species in the alleys of the orchards and annual species in the tree lines.

Alien weeds of irrigated orchards in the context of agricultural landscape

10. Riparian habitats that surround irrigated orchards harbour a lower level of alien plants, which indicates more resistance of natural habitats to plant invasion, even in the case of riparian habitats, which are among the most susceptible habitats to plant invasion.

11. In the agricultural landscape, flood irrigated orchards act as a source of alien weeds that can reach the muddy line of the river due to the possession of seeds adapted to water dispersal and the connection between those habitats through irrigation canals. Those traits related to resistance to flooding and to mechanical disturbances allow these species to successfully colonize both habitats, which are subjected to similar disturbances, thus creating a flow of these alien species between them.

12. Links between alien weeds populations of flood and drip irrigated orchards in terms of nestedness patterns have not been found, which suggests independent introductions of those species in those habitats.

Agronomic and ecological implications

13. The trait-based approach proved to be an useful tool to disentangle the success of alien weeds in weed communities of irrigated crops, which allows to establish some recommendations about monitoring weed species from the analysis of their attributes in order to establish priorities in control measures and to insightfully predict the competitive behaviour of new alien weeds detected in these habitats.

14. Modernization of irrigation in North-eastern Spain by changing flood to drip irrigation should be a priority in order to prevent the increasing prominence of successful alien weeds in weed communities as well as to avoid their spread to surrounding riparian habitats where they can successfully develop.

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APPENDIX

Published papers

Annals of Applied Biology ISSN 0003-4746

RESEARCH ARTICLE

A plant-traits approach to assessing the success of alien weed species in irrigated Mediterranean orchards

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Keywords
Classification trees; flood irrigation; invasive species; logistic regression; traditional management; weediness.

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Received: 8 August 2012; revised version accepted: 4 December 2012.

doi:10.1111/aab.12012

Abstract

In addition to their impact on natural habitats, invasive alien plants can have a significant negative effect on agricultural systems and cause economic losses. Flood-irrigated orchards in the Mediterranean Basin are vulnerable to the invasion of alien weeds, primarily because of the traditional management practices used in the orchards, which are characterized by high soil moisture during the dry summer period, nutrient availability and high levels of disturbance. This study sought to determine whether their biological traits can explain the success of alien weed species. To answer this question, 408 floristic relevés were conducted in 136 flood-irrigated orchards on the Plains of Lleida (Catalonia, NE of Spain). Richness and cover of native and alien weeds were compared. Furthermore, a set of biological traits were compared between successful and non-successful weeds for the whole data and separately between native and alien weeds using logistic regression and classification trees. In flood-irrigated orchards, alien species covered most of their area, even though the richness of alien species was lower than that of the native species. The most important species were C4 species with seeds dispersed by water, and on the other hand, rosulate and caespitose-reptant hemicryptophytes with long flowering period. Most of these traits fitted with those of the invasive alien weeds, which were mostly C4 species with seeds dispersed by water. Perennial life form characterized successful native weeds. In this study, we discuss how the traditional management of flood irrigation in fruit-tree orchards favours invasive alien weeds that have specific traits, acting as a reservoir for the spread of alien weeds into other crops and surrounding riparian habitats. We also propose changing management practices in order to avoid the selection of alien weeds and to promote native species.

Introduction

Invasion by alien plant species is one of the main threats to biodiversity and a cause of substantial economic losses, particularly, for agriculture (Pimentel *et al.*, 2001). Only in the USA, the economic losses associated with infestations by alien weeds are about 27 000 million dollars per year (including costs of control, harvest losses and damages to crops) (Pimentel *et al.*, 2005). In Europe, 33.7% of the established alien species (2024 species) was introduced through pathways associated with agriculture (Pyšek *et al.*, 2009a). Alien plants can be introduced into crops either unintentionally, i.e. through contaminated seeds, or intentionally for their use as cover crops, to obtain fibres or food (Sanz-Elorza *et al.*, 2009) and recently to bioenergy production and carbon sequestration (Crosti *et al.*, 2010). Once the alien plants are introduced into a crop, they can become naturalized and, in some cases develop infesting behaviour, which has been described as invasive (Holt & Boose, 2000; Booth *et al.*, 2010). In the Mediterranean region, irrigated crops are suitable habitats for the establishment and expansion of alien flora (Chytrý *et al.*, 2009), particularly those that are tropical or sub-tropical in origin (Brunel *et al*., 2010), because of the summer irrigation, frequent disturbance, fertilization and the reduced competition with native species that take place in the crops (Davis *et al*., 2000).

A useful approach to understand why some species are successful in becoming established and expanding in a given habitat is to identify the differences in the biological and ecological traits between the successful and the non-successful species (Lososová *et al*., 2008). This approach also allows to check if invasiveness of alien plants is partly consequence of the differences in their attributes with coexisting native plants (see review by Pyšek & Richardson, 2007) and it helps to elucidate the functional keys that underlie the invasion process (Milbau & Stout, 2008).

Most of the studies that have shown that the difference in the traits between invasive alien, non-invasive alien and native species favoured the former are focused on natural and semi-natural habitats and were conducted at a national scale or over large areas (Sutherland, 2004; Lososová *et al*., 2008; Küster *et al*., 2010; Ordonez *et al*., 2010); however, little is known about the differences in the traits between invasive alien, non-invasive alien and native weeds within agricultural habitats (Daehler, 1998; Maillet & Lopez-Garcia, 2000), where the management practices are crucial in determining the adaptiveness of specific traits (Clements *et al*., 2004).

Crops can act as reservoir for alien flora which can expand and potentially invade the natural habitats neighbouring (Holt & Boose, 2000). In the Mediterranean region, most of the natural habitats near irrigated agricultural areas are riparian habitats by virtue of the need for accessible irrigation water, with the associated risk that some alien weeds could migrate from the crops into riparian habitats and become invasive there. As has been showed in some studies, Mediterranean riparian habitats are highly vulnerable to invasion by alien species (Aguiar *et al*., 2006) and the frequency of occurrence of these invasions has been related to the disturbance caused by the intensification of surrounding agricultural systems in Mediterranean areas (Ferreira & Moreira, 1995).

Our study was designed to identify the specific traits that contribute to the success of alien plants in an irrigated agricultural context with the objective of aiding in the development of management practices for the control of biological invasions in irrigated crops.

In this study, we assessed whether flood-irrigated perennial crops (i.e. fruit trees) in the Mediterranean region favour the establishment and persistence of alien flora by selecting their biological traits through the management. Specifically we asked: (a) Are there differences in richness and cover between native and alien weeds in flood-irrigated fruit-tree orchards on the Plains of Lleida (Catalonia, NE of Spain)? (b) What traits differentiate native and alien weeds? (c) Are those traits the most favoured in fruit-tree orchards? and moreover (d) Are those traits shared by alien and native successful weeds?

Materials and methods

Study area

The study was conducted in fruit-tree orchards in El Segrià county (41°37′N, 0°37′E), Lleida (Catalonia, NE of Spain). Mean annual temperature is 15°C and annual rainfall is around 385 mm, most of which occurs in autumn. El Segrià has 64% (22 760 ha) of the irrigated fruit-tree orchards in the province (Idescat, 2010), and almost all of these orchards are flood-irrigated. The orchards form a mosaic of small fields and depend upon an old extensive irrigation network, portions of which are >100 years old (Dalmau & Iglesias, 1999). Most of the fruit trees are stone and pome fruit (apple, pear and peach). Apple and pear-tree orchards are irrigated bi-weekly from late March to early September (a total of 10–12 irrigation episodes during this period). The amount of water used in each season is 5500 $m^3\ ha^{-1}$. Peach-tree orchards are irrigated in the same way, but total amount of water used is 4400 $m^3\ ha^{-1}$. Due to the lack of slope of the ground, water is distributed homogenously, flooding the entire field. Frequently, the crops are subjected to human interventions (e.g. the application of pesticides, lower thinning and weed control) throughout the lifetime of the crop. Mowing between the rows of trees and application of herbicides (mixed of Pendimethalin, Oxyfluorfen, Isoxaben and Oryzalin in February and glyphosate and fluroxypyr between May and June and after September) along the tree line are the primary methods of weed control (Taberner, 2008). Mowing of weeds is carried out with a flail mulcher and it occurs before the fruit harvest, which takes place between late August and September. Shredded weeds remain on the ground acting as mulch material.

Vegetation surveys

In the summer of 2009, a total of 408 floristic surveys were conducted in 136 flood-irrigated fruit-tree orchards. In each orchard, three rectangular (2 × 5 m) plots were surveyed at randomly selected locations, but always in areas between tree rows, where weed diversity is best represented. The management of these plots was the same as the rest of the orchard. Plot size was defined by the minimum area at which the species-area curve became stabilized, following Lacoste & Salanon (1981). Cover of each species in each plot was recorded using

Table 1 Summary of traits used to compare native and alien weeds in flood-irrigated fruit-tree orchards in Lleida, Spain

Attributes	Categories	Reference
Vegetative traits		
Life form (Raunkiaer)	Chamaephytes/phanerophytes, geophytes, hemicryptophytes (caespitoses-reptants, rosulates and scaposes), therophytes (caespitoses-reptants, erects)	Bolòs & Vigo (1984–2001)
Vegetative morphology	Graminoids, forbs	Bolòs & Vigo (1984–2001)
Photosynthesis pathway	C3, C4	Pyankov *et al*. (2010)
Vegetative propagation	Yes, no	Klimešová & Bello (2009); Julve (1998)
Lateral spread (m/year)	0, <0.01, 0.1–0.25, >0.25	Klimešová & Bello (2009)
Reproductive traits		
Timing of flowering	Winter, spring, summer, all the year	Bolòs & Vigo (1984–2001)
Length of flowering (months)	Continuous	Bolòs & Vigo (1984–2001)
Seed length (mm)	Continuous	Klotz *et al*. (2002); Bolòs & Vigo (1984–2001)
Seed width (mm)	Continuous	Klotz *et al*. (2002); Bolòs & Vigo (1984–2001)
Seed length/width	Continuous	
Seed dispersal	Barochory, hydrochory, anemochory, zoochory, autochory, multiple systems	Bolòs & Vigo (1984–2001); SID database (2008); Julve (1998)
Ecophysiological traits		
Ellenberg index (EI) of light	Continuous (1–9)	Pignatti *et al*. (2005)
EI of temperature	Continuous (1–9)	Pignatti *et al*. (2005)
EI of nitrogen	Continuous (1–9)	Pignatti *et al*. (2005)
EI of pH	Continuous (1–9)	Pignatti *et al*. (2005)
EI of moisture	Continuous (1–12)	Pignatti *et al*. (2005)
Grime strategy	C, S, R and intermediate categories	Klotz *et al*. (2002); www.wg-ecology.it; Cortina *et al*. (1988); Pino (2000); Vicente *et al*. (2010)

the Sigmatic Method (Braun-Blanquet, 1979), in which the cover-abundance of each species is assigned a value between + (sparse and covering a small area) and 5 (covering more than 75% of the area). Those values were transformed into the mean value of the Braun-Blanquet scale (+ = 0.01%; 1 = 5%, 2 = 17.5%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%). Vascular plant nomenclature follows local flora (Bolòs and Vigo, 1984–2001).

Plant traits

All the species that were found were categorized as either native or alien plants based on the classification of the Atlas of Invasive Alien Plants in Spain (Sanz-Elorza *et al*., 2004) that is, up to now, the last and most complete revision of alien flora in Spain. They follow the definition of alien species of Richardson *et al*. (2000). This publication considers both archaeophytes and neophytes as alien species. For each species, 17 biological and ecological traits associated with colonization capabilities and plant performance were recorded. The attributes selected included vegetative traits, reproductive traits and ecophysiological traits. Raunkiaer's life forms were considered, because that has been related to the disturbance response in herbaceous vegetation (McIntyre *et al*., 1995), the same as photosynthesis pathway, vegetative propagation and lateral spread (Maillet & Lopez-Garcia, 2000; McIntyre *et al*, 2005; Kühner & Kleyer, 2008). Classical division of weeds into graminoids and forbs was taken into account. Reproductive traits such as seed dispersal, seed size, timing and length of flowering were included as they have been associated with persistence in disturbed habitats (Cornelissen *et al*., 2003; Gunton *et al*., 2011) and they have been related with management practices (Fried *et al*., 2012). As ecophysiological traits, Ellenberg indicator values (Pignatti *et al*., 2005) representing light, moisture, temperature, pH and nutrient preferences were selected. Ellenberg values are not strictly plant traits but have been commonly used as equivalent for corresponding stress tolerance traits (Gunton *et al*., 2011). Finally, Grime's strategies are useful to classify the species response to stress, disturbance and competition and have been useful in comparative studies between alien and native plants (Pyšek *et al*., 2009b) (For list and references of traits see Table 1).

Some of the traits selected were highly correlated (e.g. seed length with seed width, vegetative propagation and lateral spread), so lateral spread, seed width and seed length/width were only fitted to an individual logistic regression model and were not included in the multiple statistical analysis.

Statistical analyses

To assess the prominence of native and alien plants in the fruit-tree orchards, the mean number and the mean cover values of both groups of species per orchard were compared using the non-parametric Mann-Whitney test since the data were non-normal distributed.

To assess the capacity to discriminate between native and alien plants of the biological and ecological traits, individually and collectively, two approaches were used: logistic regression models and classification trees.

A logistic regression model was fitted to each of the traits, with each trait as single independent variable and origin of the species as the dependent variable. Regarding to the dependent variable, this was coded as binary (1 for natives and 0 for aliens, thus alien as the reference category). Regarding to the independent variables, these were conveniently considered as continuous or nominal. None of them was considered as ordinal, because this was not relevant from the interpretation point of view. To assess the statistical significance of each trait, each model was compared to the null model using a Likelihood Ratio Test. The proportion of the variance explained by each model was evaluated using Nagelkerke's R^2 determination coefficient, which can be seen as the analogous measure of the determination coefficient R^2 in a linear regression, but is appropriate for a logistic regression (Milbau & Stout, 2008).

To assess the combined effect of all of the traits, a multiple logistic regression model was obtained using a stepwise procedure. To select the best model (the one that best fitted for the fewest number of explanatory variables), Akaike's Information Criterion (AIC) was used. A deviance table was used to measure the effect of each of the independent variables in the multiple logistic regression model, as well as the measures used for globally assessing the predictive ability of the model by itself.

Classification trees were adjusted to predict origin of species depending on biological and ecological traits. Gini index was used to establish the best binary partitions to discriminate between native or alien plants, considering only those partitions that improved the global Gini index in a percentage, at least, of 1%. Two different classification trees were adjusted: the first one including photosynthetic pathway and the second one excluding this variable, due to the high correlation between origin of species and this variable.

To prove whether traits that differentiated alien from native species are the same that were favoured in the orchards, a classification tree was adjusted to predict the success of species depending on their traits, irrespective of their origin. Species were classified as 'high successful' or 'low successful' depending on their cover values in the plots. Species with cover values higher that the mean value of cover were included in 'high successful' group whereas species with cover values lower than the mean cover value were grouped in 'low successful' category. This analysis was also performed for the alien and for the native weeds separately to prove if management filters selected the same traits in alien and native weeds.

In order to test whether alien species grouped into 'high successful' category could be considered as invasive, they were compared with DAISIE (Delivering Alien Invasive Species In Europe) classification of invasive plants in natural and semi-natural habitats in Spain (www.europe-aliens.org/) and with a local classification of noxiousness of alien plants in crops made by Recasens & Conesa (2003). For the recorded species that were not present in that catalogue, the original authors of the publication were consulted to classify them.

In the regression logistic models and, more particularly, in the classification trees, the data were assumed to be deterministic, given that there is no random component in either the response or the explanatory variables. Therefore, it was not necessary to perform classical inference from the classification trees or to validate them, in the sense that no random sample can be considered.

Phylogenetic corrections

Phylogenetically related species share many traits and tend to occupy similar niches due to common origin rather than independent adaptation (Freckleton *et al.*, 2002). In order to quantify the influence of the phylogeny in the results, variation partitioning method developed by Desdevises *et al.* (2003) was performed. A phylogenetic tree was built using the Phylomatic online phylogenetic query tool (Webb & Donoghue, 2005). From the phylogenetic tree, a patristic distance matrix (i.e. a matrix containing distances between species computed from the tree) was built by making each branch length equal to 1 unit. The patristic distance matrix was subjected to principal coordinates analysis (PCoA). Each principal coordinate (PC) of the PCoA represents a certain amount of phylogenetic variation proportional to the associated eigenvalue. In order to select the PCs representing phylogenetic inertia, the broken-stick model was used. This method assumes that the total variance (the sum of eigenvalues) is divided randomly among the eigenvalues, and only the eigenvalues higher than the eigenvalue expected by the broken-stick distribution are considered important (Diniz-Filho *et al.*, 1998).

Through this method, the proportion of variation explained by species traits, phylogeny and the common influence of these two factors was obtained. Further details of the method can be found in Desdevises *et al.*

(2003). SPSS 15 (SPSS, Chicago, IL, USA) was used to perform the Mann–Whitney-tests. The logistic regression analyses, classification trees, distance matrix and variation partitioning were performed using vegan and rpart packages on R (R development Core Team, 2009).

Results

Of the 104 weed species found in the fruit-tree orchards in El Segrià county, Catalonia, Spain, 73 species (70.5%) were native and 31 were alien (29.5%; Table 2). Eight native species (10.95% of total native species) and eight alien species (25.81% of total alien) were included into 'high successful' category. It should be pointed out that 75% of alien species included into 'high successful' category were considerate as moderate or severe invasive in crops by Recasens & Conesa (2003) (i.e.: *Bromus catharticus*, *Cyperus rotundus*, *Paspalum distichum*, *Echinochloa crus-galli* and *Echinochloa colona*) and 87.5% of them are considered as invasive established in natural habitats in Spain by the DAISIE database (all the successful alien species except *E. crus-galli*). The most successful alien species have Paleotropical and Neotropical origin (Table 3). In general, most of the species present in the orchards had higher moisture requirements (higrophylous and mesohygrophylous) (e.g. *Trifolium repens*, *Rumex obtusifolius*, *Taraxacum officinale*, *Potentilla reptans*, *Sorghum halepense*, *Setaria pumila*, *E. crus-galli*).

The mean number of native species was significantly higher than the mean number of alien species per orchard, and cover of the native and the alien species per orchard differed significantly (Table 2). Alien plants cover represented the 54.90% of the total mean plant cover by plot.

Logistic regression models fitted for each variable (Table 4) showed significant differences between native and alien plants in photosynthetic pathway, timing of flowering, seed dispersal system, Grime's strategy, vegetative morphology, the length of the flowering period and Ellenberg Indices of light and temperature. Photosynthetic pathway, timing of flowering and mode of seed dispersal had the greatest explanatory power (Nagelkerke R^2 determination coefficient around 44%) and they had the fewest misclassification errors (15%, 19% and 21%, respectively). Although some of the other traits were statistically significant, they were not useful in discriminating between native and alien plants because their misclassification errors were very high (all around 29%), compared to the theoretical maximum misclassification error which can be a priori estimated from the sample as the proportion of plants with the less prevalent category, i.e. alien plants (29.8%) are less frequent than native (70.2%).

Table 2 Summary of richness and cover of native and alien plants in flood-irrigated fruit-tree orchards in Lleida, Spain. Mann–Whitney test was used to evaluate differences in richness and coverage between native and alien plants

	Native	Alien	Total	*P*-value
Total richness	73	31	104	
% total richness	70.5	29.5	100	
Mean number sp./field	5.2	4.0	9.3	***
% number sp./field	56.5	43.5	100	
Mean cover sp./field	53.2	64.7	117.9	**
% cover sp./field	45.1	54.9	100	

Significant codes: <0.001 = '***'; <0.01 = '**'; <0.05 = '*'.

The best multiple logistic regression model included three traits (Table 5): seed dispersal system, flowering period and photosynthetic pathway. The model did not include the rest of the variables that were statistically significant when analyzed individually. The model had a misclassification error of 10.58% and it explained 73.23% of the variability in the response, according to Naglekerke's determination coefficient. The model indicated that most of the alien weeds were C4 species, whose seeds were dispersed by hydrochory. In contrast, most of the native weeds dispersed their seeds by anemochory and barochory (see Supporting Information).

The optimal classification tree performed for all of the species with all of the variables had six terminal leaves and a discriminant capability of 94.2% (Fig. 1); i.e. a misclassification error of 5.8%. Photosynthetic pathway was the main factor (first splitter variable) that differentiated native and alien weeds and, at the second level, seed dispersal and flowering period differentiated native and alien plants. Alien weed species formed two groups: one comprised C4 species that disperse seeds using hydrochory, anemochory or multiple modes of dispersal, which included most (20) of the alien species, and another that included C3 species that flower in summer, use hydrochory or multiple modes of dispersal and have Ellenberg Indices of temperature larger than 5.5. Most of the native weeds were C3 species that flower in winter, spring or throughout the year. In addition, the native species that flower in summer use anemochory, zoochory or barochory for seed dispersal.

When photosynthetic pathway was excluded as a potential predictor, the resulting classification tree had seven terminal leaves and could discriminate correctly 97.11% of the species (see Supporting Information). In that classification tree, flowering period was the main factor that differentiated native and alien weeds and indicated that most of the alien weeds usually flower in summer and the native weeds do so at other times of the year. Among alien weeds that flower in summer, most of them disperse their seeds by water or use multiple

Table 3 Cover (%) and frequency (%) of the 15 dominant alien and native weeds of the fruit-tree orchards prospected in decreasing values of cover

Alien species	Origin	Cover (%)	Frequency (%)	Native species	Origin	Cover (%)	Frequency (%)
Bromus catharticus	South America	15.0	77.9	***Trifolium repens***	Mediterranean	16.1	86.8
Cyperus rotundus	Paleotropical	9.1	41.9	***Rumex obtusifolius***	European	6.8	60.3
Paspalum distichum	Neotropical	7.4	45.6	***Poa pratensis***	Pluriregional	6.7	32.4
Setaria pumila	Paleotropical	5.9	62.5	***Taraxacum officinale***	European	6.5	83.1
Sorghum halepense	Paleotropical	5.8	54.4	***Cynodon dactylon***	Cosmopolitan	5.2	44.1
Echinochloa crus-galli	Pantropical	5.3	54.4	***Potentilla reptans***	Pluriregional	2.9	27.2
Eleusine indica	Paleotropical	3.7	33.8	***Digitaria sanguinalis***	Pluriregional	1.9	33.1
Echinochloa colona	Paleotropical	3.1	35.3	***Convolvulus arvensis***	Pluriregional	1.5	51.5
Setaria adhaerens	Northeast Africa	1.1	40.4	*Plantago lanceolata*	Pluriregional	1.2	26.5
Veronica persica	Southwest Asia	0.7	21.3	*Poa compressa*	Pluriregional	1.1	8.1
Cyperus eragrostis	Neotropical	0.7	5.9	*Trifolium pratense*	Pluriregional	1.0	12.5
Paspalum dilatatum	Neotropical	0.4	5.1	*Poa annua*	Pluriregional	0.9	14.7
Setaria viridis	Paleotropical	0.4	8.1	*Plantago major*	Pluriregional	0.8	39.7
Amaranthus retroflexus	North America	0.4	17.6	*Polygonum aviculare*	Pluriregional	0.6	20.6
Amaranthus hybridus	Neotropical	0.1	6.6	*Portulaca oleracea*	Pluriregional	0.5	45.6

Species in bold included in the 'high successful' category.

Table 4 Results from the logistic regression models fitted for each variable separately. Likelihood ratio test (LRT) *P*-value, Naglekerke's R^2 determination coefficient and misclassification error obtained when using the models for prediction are shown

Variable	LRT *P*-value	Naglekerke's R^2	Misclassification error
Photosynthesis pathway	<0.001	0.441	0.15
Timing of flowering	<0.001	0.465	0.19
Seed dispersal	<0.001	0.466	0.21
EI of temperature	<0.001	0.212	0.30
Grime strategy	<0.001	0.224	0.30
Morphology	0.002	0.128	0.28
Length of flowering	0.004	0.106	0.30
EI of light	0.025	0.066	0.30
EI of moisture	0.061	0.047	0.28
Seed length	0.072	0.043	0.30
Vegetative propagation	0.112	0.150	0.30
Seed width	0.193	0.023	0.30
Seed length per width	0.271	0.016	0.30
Life form	0.432	0.079	0.30
EI of pH	0.434	0.008	0.29
EI of nutrients	0.545	0.005	0.30
Lateral spread	0.868	<0.001	0.30

modes of dispersal and have high temperature demands. Among the native plants that flower outside of summer, those that have the highest demand for nutrients and those with a short flowering period were the most abundant.

The optimal classification tree performed to differentiate successful and non-successful species had six terminal leaves and discriminated correctly 93.26% of the species (Fig. 2). The main split, based on seed dispersal, indicated that successful species disperse their seed by water. Among them, the most abundant species were C4 species. The group of successful species that did not disperse their seeds by water were caespitose-reptant and rosulate hemicryptophytes and geophytes. Among them, the most successful species were those with a long flowering period and with a Ellenberg index of light lower than 7.5

Alien success

The optimal classification tree performed for alien weeds had four terminal leaves. High successful alien species differed from low successful alien species mainly in the seed dispersal system, the photosynthesis pathway and the clonality (Fig. 3). Most of the high successful alien species are C4 species that disperse their seeds by water. Only two species without water seed dispersal and clonal growth showed high cover. The tree classified correctly 93.75% of the species.

Native success

The classification tree that classified successful and non-successful native species had six terminal leaves. It showed that successful native species (Fig. 4) were caespitose-reptant and rosulate hemicryptophytes with seeds larger than 1.55 mm. Among the group of species with other life forms, those geophytes and reptant therophytes that dispersed their seeds by zoochory and had seeds shorter than 6.4 mm were the most abundant, but only represent two species. A total of 95.83% of species were correctly classified.

Phylogenetic corrections

Phylogenetic corrections (Fig. 5) showed that 25.5% of the explained variation was related to biological and

Table 5 Deviance table showing the significance of each of the variables included in the multivariate logistic regression model, fitted with a stepwise method. Naglekerke's R^2 determination coefficient and misclassification error obtained when using the model for prediction are shown

Variable	*Df*	Deviance	Resident *Df*	Resident deviation	*P*-value
Null			103	126.719	
Seed dispersal	5	41.332	99	85.387	<0.001
Flowering period	3	29.527	98	60.895	<0.001
Photosynthesis pathway	1	9.608	97	51.286	0.002
Naglekerke's R^2	0.745				
Misclassification error	0.106				

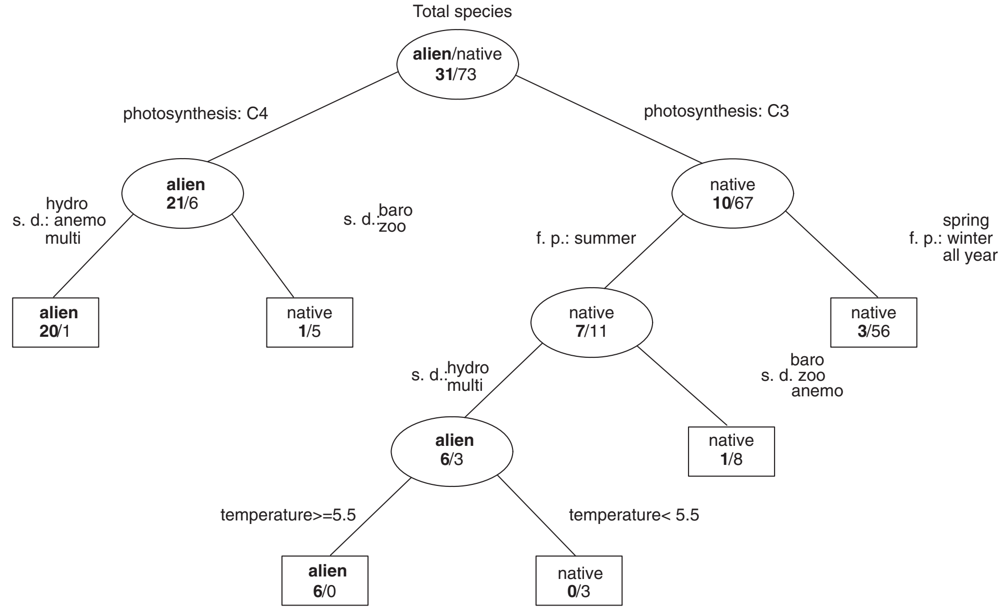

Figure 1 Classification tree to discriminate species origin (native or alien) from biological traits in the flood-irrigated fruit-tree orchards in Lleida, Spain. Each node shows the number of alien and native species and the origin of the majority of the species in this node. Terminal nodes are shown as rectangles. s.d: seed dispersal, f.p.: flowering period.

ecological traits, whereas 4.6% of the total variation was related to the phylogeny of the species; 14.5% of the total variation was related to the shared effects of species traits and phylogeny. The total amount of variation explained by species traits and phylogeny was 44.6%. The model of variation partitioning was statistically significant ($F = 7.38$; $df = 7, 90$; $P < 0.005$).

Discussion

Success of alien weeds in fruit-tree orchards

This study unravels for the first time the outstanding role of alien species in the weed community of fruit-tree orchards. The richness of alien weeds in fruit-tree orchards was higher (29.5% of all weed species) than the average richness of alien weeds in other regions in the east and northeast of the Iberian Peninsula (i.e. Huesca and Comunidad Valenciana), where the alien flora does not exceed 20% of the total flora (Sanz-Elorza *et al.*, 2006, 2011). The richness of alien weeds in the fruit-tree orchards in our study was higher than the richness of alien weeds in other agroecosystems in Catalonia (7.3% in the arable lands and 2.6% in wet grasslands of Catalonia; Chytrý *et al.*, 2008) and in other regions (e.g. 23.2% in agricultural habitats in Finland; Hyvönen & Jalli, 2011). Our results reinforce the idea that

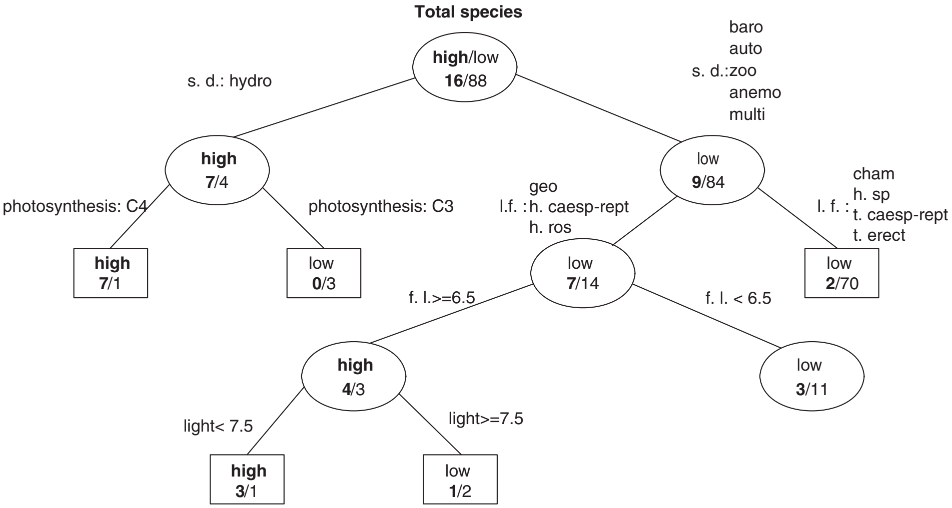

Figure 2 Classification tree to discriminate species success (high or low) from biological traits in flood-irrigated fruit-tree orchards in Lleida, Spain. Each node shows the number of high successful and low successful species and the status of the majority of the species in this node. Terminal nodes are shown as rectangles. s.d.: seed dispersal, l.f.: life form, f.l.: flowering length, Geo: geophytes, h.: hemicryptophytes, cham: chamaephytes, t.: therophytes. caesp-rept: caespitose-reptant, ros: rosulate, sp: scapose.

agricultural habitats, subjected to periodic disturbances, are particularly susceptible to colonization by alien species (Lake & Leishman, 2004).

Role of traits in the success of alien weeds

Most of the biological traits related with the success of the weeds in orchards (i.e. photosynthetical pathway, seed dispersal, life form, flowering length) fit in with those that differentiate alien from native weeds and invasive from non-invasive alien weeds. Therefore, our study provides good evidence that some invasive alien weeds are more successful than most of the native weeds because they possess some traits that are favoured in the orchards.

Traits selected in orchards could be favoured by flood irrigation and mowing. Flooding and high temperatures favour C4 species, because those conditions increase the photorespiration rate (Sage, 2004). In addition, C4 photosynthesis is associated with high rates of productivity over short periods (Pyankov *et al*., 2010), thereby invasive alien species, that are mostly C4 species, are favoured. The success of alien C4 species in irrigated crops has already been described in other studies (Maillet & Lopez-Garcia, 2000). In general, the traits that promote fast growth rates and the procurement of resources are the most important factors in the establishment of alien flora and the subsequent displacement of native flora (Lavorel & Garnier, 2002; Dietz & Edwards, 2006).

Invasive alien weeds are mainly water dispersed. Surface irrigation is the main way for the input and output of hydrochorous seeds in flood irrigated crops (Wilson, 1980). Dispersal by water ensures long-distance dispersal, which is advantageous to these alien weeds in plant communities present in open habitats subjected to frequent disturbances (Cadotte & Lovett-Doust, 2001; Lake & Leishman, 2004; Lososová *et al*., 2006; Gassó *et al*., 2009). Moreover, weed assemblages in orchards are in the first stage of succession because of the intensive management, which favours hydrochorous alien weeds (Latzel *et al*., 2011).

In our study, successful weeds had longer flowering periods than did the non-successful weeds, which is also a trait shared by alien weeds. Long flowering period is typical of invasive species (Küster *et al*., 2010; Pyšek *et al*., 2009b; Pyšek & Richardson, 2007) in other Mediterranean areas (Celesti-Grapow *et al*., 2003). Furthermore, long flowering periods are associated with the success of alien species in agricultural habitats (Lloret *et al*., 2005) because a prolonged flowering period increases the potential for colonization and allows these species to increase the opportunity to produce seeds (Lake & Leishman, 2004). Long flowering period can improve reproductive success and cross-pollination when

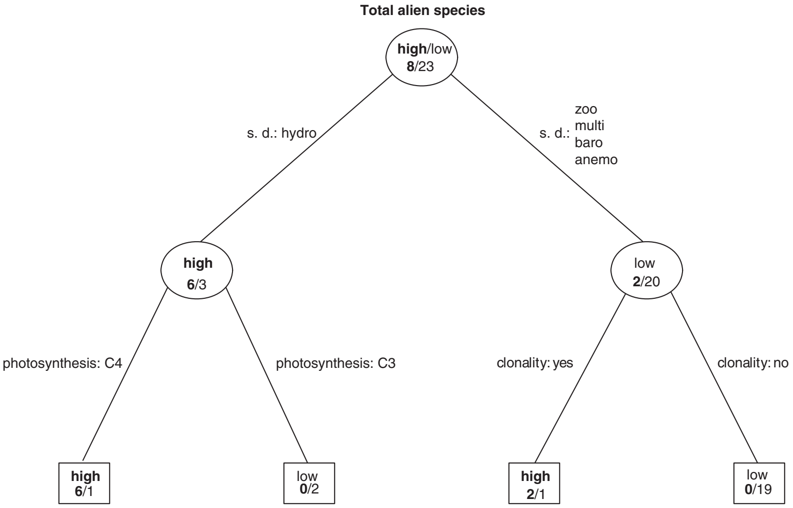

Figure 3 Classification tree to discriminate success of alien plants (high or low) from biological traits in flood-irrigated fruit-tree orchards in Lleida, Spain. Each node shows the number of high successful and low successful alien species and the status of the majority of the species in this node. Terminal nodes are shown as rectangles. s.d.: seed dispersal.

pollination is seasonal or competition for pollinators is high (Lloret *et al*., 2005). Although most of alien weeds flower in summer in our study (Fig. 1 and Supporting Information), flowering period was not a determinant factor related to the success in the orchards (Fig. 2). Moreover this trait did not differ between invasive alien and non-invasive alien weeds (Fig. 4).

Success of native species was defined mainly by their life form (Fig. 5). Rosulate and caespitose-reptant hemicryptophytes are favoured in the orchards, where weed control consists of mowing with flail mulcher. It has been proved that this practice benefits hemicryptophytes in vineyards (Lososová *et al*., 2003). In contrast, other studies related the annual species with higher weediness in agricultural habitats (Pyšek *et al*., 2009b). In the orchards, annual species are disadvantaged because they are not able to regenerate their structures after mowing disturbance, whereas rosulate and caespitose-reptant hemicryptophytes have more likelihood of surviving due to the possession of perennating buds at ground level (Gago *et al*., 2007). Our results are consistent with Grubb (1985) that linked meristems close to the ground, a rosette life-form and perennial life history with mechanical disturbances, as grazing.

Overall, our results are consistent with the limiting similarity theory, which assumes that alien species should use resources at different times or in different ways in order to avoid the competitive exclusion from the community (Abrams, 1983). Invasive alien species perform better when their traits and their patterns of resource use differ from those of local species (Fargione *et al*., 2003). Management conditions limit the traits of species which can persist in a given habitat (in this case irrigated orchards), which would tend to result in trait similarities between native and alien species (i.e. most of the weeds are mesohygrophilous or hygrophilous). However, individuals compete at the small scale of the orchard. At that scale, trait differences between native and invasive species as a result of limiting similarity can be observed.

Phylogenetic effects

In order to separate ecological and evolutionary responses, comparative studies of alien and native species should take into account the potentially confounding effects of phylogenetic relatedness (Sol *et al*., 2008). The weak influence of the phylogeny on the results reveals the multiple and independent evolutionary divergences between invasion process and biological traits, as has been demonstrated in other studies (Lososová *et al*., 2006; Milbau & Stout, 2008). These results reinforce those obtained by Pyšek *et al*. (2009) who state that belonging to a particular family does not predispose to be more or less invasive (at least at high taxonomic levels). Nevertheless, the high proportion of variability provided by the

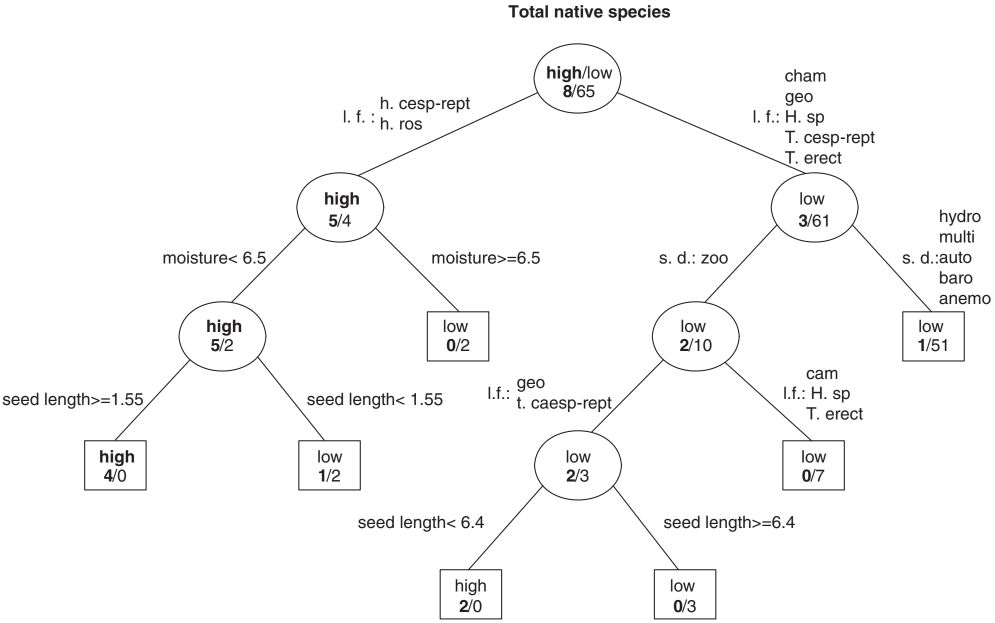

Figure 4 Classification tree to discriminate success of native plants (high or low) from biological traits in flood-irrigated fruit-tree orchards in Lleida, Spain. Each node shows the number of high successful and low successful native species and the status of the majority of the species in this node. Terminal nodes are shown as rectangles. s.d.: seed dispersal, l.f.: life form, Geo: geophytes, h.: hemicryptophytes, cham: chamaephytes, t.: therophytes, caesp-rept: caespitose-reptant, ros: rosulate, sp: scapose.

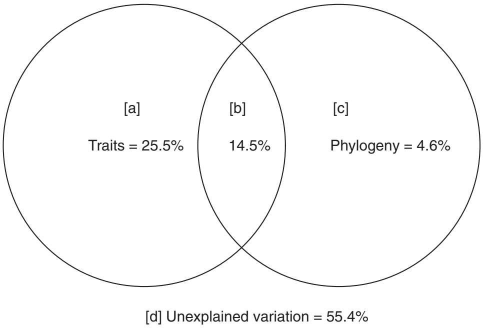

Figure 5 Variation partitioning of the response among biological and ecological traits (a), phylogeny (b) and phylogenetically structured variation of biological and ecological traits (b). The whole rectangle represents 100% of the variation, of which (d) is the unexplained part.

phylogenetically structured variation of traits study shows that the development of shared traits may be related to the colonization of similar niches during evolutionary history (Harvey & Pagel, 1991).

Ecological and agronomical implications

Our study provides good evidence that the flood irrigation system facilitates the success of alien invasive species in the weed community of the fruit-tree orchards. We suggest that the combination of the management conditions in fruit-tree orchards and the presence of alien plants with a suite of traits that favour high survival rates, rapid growth in response to an infusion of water supply and water seed dispersal may allow successful invasion in flood irrigated orchard communities.

Our study underscores the importance of tree orchards in irrigated agricultural landscapes as local alien weeds reservoirs. The flood irrigation system and the structure of the agricultural landscape as a mosaic of small patches interconnected with each other and with the surrounding natural riparian habitats allow the entry of weeds into the crops. The management practices used in the orchards favour the establishment and dispersal of that invasive alien flora with traits favoured among the crops and to the surrounding riparian habitats, because the river is used as a drainage channel of the irrigated water. Favouring invasive alien weeds has negative economic and ecological impacts on crops on one hand, and on the other hand with the possibility to develop invasive behaviour in the riparian ecosystems (Miyawaki & Washitani, 2004) that have similar characteristics as the orchards, such as flooding and periodic disturbances. It has been confirmed that favouring invasive species in irrigated crops increases the risk of invasion of these species in the near riparian ecosystems. Ferreira & Moreira (1995) associated sites disturbed by irrigated crops with a high degree of spatial invasiveness of some aliens as *Paspalum distichum*, *Amaranthus retroflexus* and *Cyperus eragrostis* in southern Iberian river environments. Solé *et al*. (2010) found similar results in the Segre river on its way through our study area. They showed that the most invasive species were agricultural weeds (i.e. *Paspalum distichum*, *Cyperus eragrostis*, *Xanthium echinatum*, *Amaranthus retroflexus*) reaching highest invasive degree in the frequently flooded banks. Aguiar *et al*. (2006) also proved that frequently flooded banks are the most invasible areas of the south Iberian floodplains. It has been suggested that flooding contributes to the invasibility of riparian zones by uncovering flood-prone areas. This process reduces the competitive capability of resident native against colonizing exotic plant species (Hood & Naiman, 2000).

Management implications

Based on the results of the study, some recommendations should be highlighted: (1) given the clear role of plant traits in promoting the success of invasive alien species, it would be useful to avoid the introduction of alien weeds with traits favoured by flooding irrigation. It is well-documented that most of the alien weeds found in the orchards were unintentionally introduced in Spain, although some of the most invasive have been used as cover plants or as ornamental grasses (i.e. *B. catharticus*, *P. distichum*, *P. dilatatum*; Sanz-Elorza *et al*., 2004); even they are recommended as cover plants in organic perennial crops (Domínguez-Gento *et al*., 2002). Replacing these species for some native, as *T. repens*, which is also successful in orchards (Table 3), can avoid the establishment and spread of those alien species. The use of *T. repens* in cover crops is already well-established in vineyards (Gago *et al*., 2007) and could be a good alternative to *Paspalum* spp. and *B. catharticus* (Pardini *et al*., 2002). The selection of the appropriate management practices in the agricultural system is crucial to control and prevent the spread of alien flora within the landscape. Thus, changing flood by drip irrigation can limit the entry of seeds dispersed by water and avoid the spread of alien species already present (Juárez *et al*., 2010). Moreover, drip irrigation increases the sustainability of the crop, by saving water, which is a key factor in semiarid areas, and improves the crop yield (Bravdo & Proebsting, 1993). In addition, drip irrigation could increase the efficiency of fertilizers use with direct injection. These changes on the current agricultural practices will allow better field access for equipment, reduce humidity associated fungal diseases and decrease the extensiveness of weeds (Fereres *et al*, 2003).

Acknowledgements

The authors acknowledge Andreu Taberner (Departament d’Agricultura, Alimentació i Acció Rural, Generalitat de Catalunya) for providing orchards management information and Jordi Tunica for his help in collecting field data. In addition, the authors gratefully acknowledge two anonymous reviewers for their comments and suggestions for manuscript improvement. Financial support was provided by Generalitat de Catalunya (FI PhD grants).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Adjusted multiple logistic regression model, fitted with a stepwise method. Null and residual deviance and Akaike information criterion (AIC) are shown.

Appendix S2 Classification tree to discriminate species origin (alien or native) from biological traits in flood-irrigated fruit-tree orchards in Lleida, Spain, excluding photosynthetic pathway. Each node shows the number of alien and native plants and the origin of the majority of the species in this node. Terminal nodes are shown as rectangles. s.d.: seed dispersal, f.p.: flowering period, l.f.: life form, geo: geophytes, h.: hemicryptophytes, cham: chamaephytes, t.: therophytes. caesp-rept: caespitose-reptant, ros: rosulate, sp: scapose.

Agriculture, Ecosystems and Environment 225 (2016) 173–183

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Identifying alien plants linkages between irrigated orchards and adjacent riparian habitats from a trait-based approach

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ARTICLE INFO

Article history:
Received 29 November 2015
Received in revised form 19 April 2016
Accepted 20 April 2016
Available online 28 April 2016

Keywords:
Floodplain
Irrigation system
Weed management
Exotic weeds
Biological attributes

ABSTRACT

Floodplains and crops are particularly susceptible to alien plant invasion, often leading to negative ecologic and economic impacts. As irrigated crops and riparian habitats are interconnected at the landscape scale, plant species of each habitat may be susceptible to colonizing the other. In order to avoid alien plant invasions of natural habitats and surrounding crops and to develop management practices to face this problem, it is not only essential to understand which traits favour the success of alien plants in irrigated crops and floodplains, but also whether a flow of species between these two habitats actually exists. With this aim, floristic surveys were carried out on riparian habitats (riparian forest, reedbed and muddy line) and on irrigated orchards at a gradient of distance from the river. Differences in weed management techniques applied in orchards were taken into account during the surveys. Plant diversity, composition and invasion levels were evaluated for each habitat and differences in floristic composition were interpreted in terms of functional traits. Natural habitats were well differentiated from crops in terms of native plants, but when considering alien plants, muddy line and flood irrigated orchards showed similar floristic composition. Alien plant community in the muddy line was a subset of that of flooded orchards and it was composed by C4 species, with clonal growth, perennial graminoids and water seed dispersal. This work proves that, unlike native species, alien species are shared between irrigated orchards and adjacent floodplains, which is favoured by a set of traits that allows them to colonize and establish new populations there. These results can help to develop strategies for preventing the establishment of alien plants in these habitats and to manage already present populations.

1. Introduction

Invasive species have taken their toll on natural habitats by reducing both their biodiversity and the ecosystem services provided (Fried et al., 2014; Hejda and de Bello, 2013; Hejda et al., 2009; Vilà et al., 2010). Despite causing yield losses, crop damage and heightened control costs in agriculture (Baker et al., 2005; Pimentel et al., 2005; Vilà et al., 2004), alien invasions have mostly been studied in natural habitats. Furthermore, few previous studies have included research on biological invasions simultaneously affecting natural and agricultural habitats (Galatowitsch et al., 1999; Liendo et al., 2013) although they are interconnected at landscape scale. Irrigated agricultural lands in floodplains are an example of this connection. Crops are established close to floodplains because fertile alluvial soils allow for increased crop yields and rivers provide water for irrigation.

Invasion success of alien species is largely due to species invasiveness and habitat invasibility (Milbau et al., 2003). Those habitats subjected to frequent disturbances are prone to be invaded (Burke and Grime, 1996) because disturbances increase availability of resources and open new colonisable niches where competition for those resources is low (Davis et al., 2000). This is the case of irrigated croplands and floodplains that are highly vulnerable to alien plant colonization, especially in the Mediterranean area (Chytrý et al., 2009).

Regarding species invasiveness, some biological attributes favour the success of an alien plant in establishing populations in the host habitat. They include suitable seed dispersal systems for reaching new habitats, as well as higher photosynthetic rates, clonal growth, small seeds and long-distance seed dispersal which allow the plant to successfully overcome the ecological filters of the host habitat, giving it advantages to compete with the native

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http://dx.doi.org/10.1016/j.agee.2016.04.015
0167-8809/

(Pysek and Richardson, 2007; Pysek et al., 1995). Thus, in order to understand the processes that lay behind the ecology of invasive species, studies should include both diversity aspects and a trait-based approach.

This study makes an original and significant contribution to knowledge of the connection between natural and agricultural habitats in terms of alien plant species from a trait-based approach, by focusing on an irrigated agricultural area on a floodplain in the Mediterranean zone. Specifically, we selected a landscape of irrigated orchards arranged at a gradient of distance from a riparian corridor because both systems are subjected to similar disturbances (i.e. water logging, fluctuating water levels, high nutrient levels and physical disturbances) (Catford and Jansson, 2014; Juárez-Escario et al., 2013) which increase their susceptibility to be colonized by alien plants. Riparian habitats provide important ecosystem services such as improving water quality, increasing biodiversity or stability of the riverbanks. In these habitats, alien plants negatively impact biodiversity, productivity, nutrient cycling and even the food web (Richardson et al., 2007). Moreover, human-mediated disturbances, such as water regulation (Catford et al., 2011; Jansson et al., 2000), channel management (Tabacchi et al., 2005) and close proximity to human activities can increase riparian invasion (Catford and Jansson, 2014; Liendo et al., 2013).

In the case of riparian habitats in an agricultural matrix, it has been claimed that alien species present in the riverbanks might have been first introduced in nearby agricultural fields (Ferreira and Moreira, 1995; Meek et al., 2010) by human-mediated dispersal. But at a finer landscape scale, it could be also plausible that agricultural sites downstream would be contaminated through water irrigation by alien weeds previously established on upstream riverbanks. Detecting nestedness in species richness patterns is therefore a useful tool to determine which habitats act as a source of alien species along invaded landscapes (Alexander et al., 2011). Conversely, the different ecological conditions of riparian habitats and irrigated orchards as well as the differences in some physical disturbances to which they are subjected (mainly flooding in riparian habitats and trampling and weed control besides flooding in orchards) may suppose a filter for the alien plant flow from one zone to the other (Tabacchi et al., 2005). Likewise, it has been proved that higher diversity in riparian habitats may reduce the susceptibility to be invaded by reducing the effective number of ecological niches suitable for invasion (Loreau and Hector, 2001). Nevertheless, other studies in this field have sown contradictory results (Gilbert and Lechowicz, 2005).

Disentangling the causes that lay behind the success of colonization of alien plants in irrigated crops and floodplains and the connection between these two areas in terms of these species is key in developing suitable management and conservation projects aimed to prevent the establishment of alien plants in interconnected agricultural and natural areas and minimize the exchange of alien plants between those habitats.

For these reasons, we consider it essential to focus the present study on evaluating whether alien plants present in irrigated fruit tree orchards are also established in nearby riparian habitats and identifying which functional traits are related to this process.

In this study we expect that highly perturbed habitats shelter a rich community of alien plants with a set of traits that let them to spread and colonize surrounding habitats, thus establishing an exchange of those species among them.

The main study objectives were: (1) to evaluate native and alien plant diversity at different spatial scales and to analyse the invasion level of each habitat through the analysis of the total richness and the richness and abundance of alien species, (2) to determine whether exists an exchange of alien species between riparian habitats and orchards located in a gradient of distance from the river as well as detecting nestedness patterns in this process, and (3) to identify which functional traits are involved in this exchange.

2. Material and methods

2.1. Study area

The study was conducted in a floodplain located along the last 22 kms of the Noguera Ribagorçana River in Western Catalonia, NE Iberian Peninsula (41°39′–41°51′N;0°33′–0°43′E), a tributary of the Segre river (i.e. the main tributary of the Ebro river, which is the large-flowing river in the Iberian Peninsula). The river has a total length of 136.9 km and water flow is regulated through 3 main dams. The study was conducted in the lowland river segment, which ranges from 305 m a.s.l in the Santa Ana dam to 172 m a.s.l. in the confluence with the Segre river (mean slope: 0.58%). This is an edaphological and structural homogeneous area largely made up of Tertiary detrital and alluvial deposits (mostly clay, sand and graves) and terraces, which are consequence of sedimentary processes along the floodplain. Dominant land-use in the floodplain is for irrigated agriculture. Wetted channel width ranges approximately from 20 to 35 m. The average annual evapotranspiration is 750 mm and the average annual flow is 17.9 $m^3 s^{-1}$ (Ministerio de Medio Ambiente, 2007). The climate is Continental-Mediterranean, with a mean annual temperature of 13.5 °C and annual rainfall of 390 mm (Ninyerola et al., 2005).

2.1.1. Natural habitats

Within the riparian habitats, three plant communities stem from the gradient of distance and moisture in the stream channel: (1) the frequently flooded bank, referred to as the “muddy line” in this study, (2) the reedbed and (3) the riparian forest. The muddy line corresponds to clay soils with high content in organic matter provided by the water. Muddy line vegetation is composed of hygronitrophylous communities and grasslands developed on mud bars. The reedbed is dominated by perennial graminoids mainly represented by common red (*Phragmites australis*). Finally, riparian forests are wet deciduous woodland composed of a variety of Eurosiberian and Mediterranean trees, typical to Mediterranean rich soils with slow flowing eutrophic water.

2.1.2. Irrigated orchards

Flood irrigated fruit tree orchards are located close to the river (Dalmau and Iglesias, 1999) Irrigation is performed via an extensive irrigation network which took the water from the river and later returned the excess irrigation water again to the river. The area occupied by irrigated orchards has increased and drip irrigated orchards have been established farther from the river. The surveyed crops were stone and pome fruit tree orchards (apple, pear and peach). Flood irrigated orchards are irrigated bi-weekly from April to early September (a total of 10–12 irrigation episodes during this period). Drip irrigation systems need a complex infrastructure of artificial ponds, pressure bombs and water distribution pipes and orchards are typically drip irrigated daily (a minimum of 3–4 l/m^2 weekly). Weed control of orchards differs between tree rows and under tree lines. In the inter-row space, weeds are mechanically controlled by mowing or shredding and under the tree lines, herbicide is sprayed (a mix of pendimethalin, oxyfluorfen, isoxaben and oryzalin in February and glyphosate and fluroxypyr between May and June and after September).

2.2. Floristic surveys

In summer of 2011, along the last 22 kms of the Noguera Ribagorçana river, floristic surveys were performed at each kilometre in the three main riparian habitats (muddy line, reedbed and riparian forest) (Fig. 1), as well as in the nearby orchards, following a gradient of distance from the river. In each riparian habitat, 3 rectangular plots were randomly established ($10\,m^2$ in the muddy line and reedbed, but $200\,m^2$ in the riparian forest). In the orchards, weed control differs between the inter-rows and under-tree lines, so floristic surveys were carried out in 3 randomly established rectangular plots of $10\,m^2$ at two positions, namely: "between tree-lines" (B) and "under tree-lines" (U). The surveys were performed in flood irrigated orchards located at less than 50 m from the riparian forest (NOB and NOU), in flood irrigated orchards located at more than 150 m from the riparian forest (FOB and FOU) and in drip irrigated orchards located at more than 250 m from the riparian forest (DOB and DOU).

The Braun-Blanquet (1979) six-point scale was used to quantify species' abundance, in which the cover-abundance of each species is assigned a value between + (sparse and covering a small area) and 5 (covering more than 75% of the area). Those values were transformed into the median value of percent cover range in each cover class (+ = 0.01%; 1 = 5%, 2 = 17.5%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%). Since the 3 plots for each habitat in each transect cannot be considered as completely independent, mean cover values of species for each habitat in each transect were calculated from the 3 plots. Plant nomenclature followed Bolòs and Vigo (1984–2001).

2.3. Plant traits

Each recorded species was classified as *alien* or *native* according to Sanz-Elorza et al. (2004), that is, the most recent and complete revision of alien flora in Spain up to now. This work considers both archaeophytes and neophytes as alien species *sensu* Richardson et al. (2000). *Setaria adhaerens* and *Echinochloa crus-galli* are cryptogenic plants (i.e. controversial species regarding their origin) but in this study were classified as alien species because of their Paleotropical origin (Campos, 2010; Sanz-Elorza et al., 2011). A total of 8 traits were recorded for each species (Table 1). Among vegetative traits, growth form, photosynthesis pathway, vegetative propagation and plant height were selected since they are involved in the response of vegetation to disturbances (Cornelissen et al., 2003), whereas reproductive traits such as seed dispersal, seed length, flowering onset and flowering length have been associated with persistence in disturbed habitats (Gunton et al., 2011).

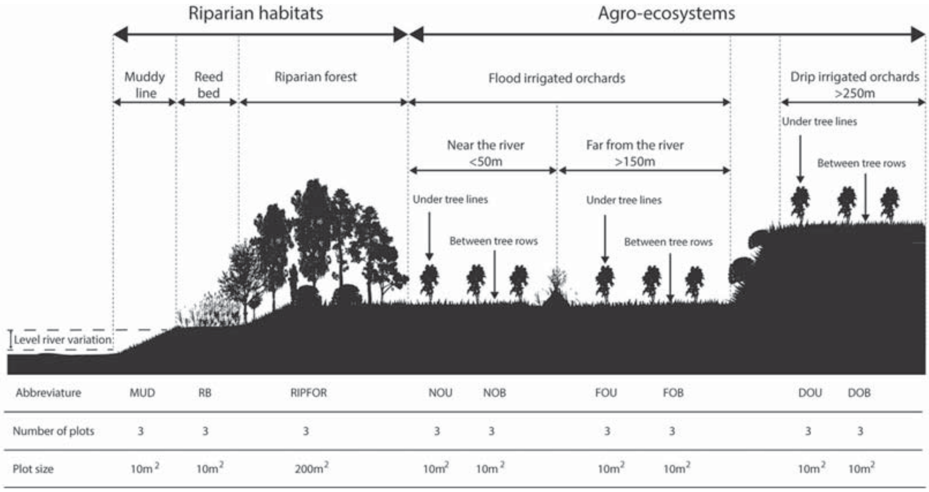
Each seed dispersal mode was codified as a binomial variable (0/1) except for the species that presented more than one. In those cases, 0.5, 0.33 or 0.25 values were assigned to each dispersal mode in case the species has 2, 3 or 4, respectively.

2.4. Data analysis

2.4.1. Plant diversity and abundance among habitats

α-(mean species richness per site) and γ- (total richness per habitat) diversity were calculated for total species, and separately for native and alien species for each habitat. Since size plots were larger in riparian forests, γ-diversity cannot be directly compared among habitats. Rarefaction curves allow for meaningful standardization and comparison of richness data for datasets obtained by different sampling effort (Gotelli and Colwell, 2001). Therefore, γ-diversity was estimated by constructing rarefaction curves based on 999 random replicates, using First-order Jackknife richness estimator, which is one of the most accurate index in determining species richness comparing to other estimators (Hortal et al., 2006).

In order to compare levels of invasion among habitats and to identify patterns of dominant alien species, relative richness and abundance of alien plants for each habitat were calculated, since they are the most suitable and meaningful indicators of invasion level (Catford et al., 2012b). Changes in α-diversity for all the groups of species as well as in relative richness and abundance of alien species among habitats were fitted using generalised least squared models (GLS) with Tukey's posthoc test for multiple pairwise comparisons. To normalize data, relative cover values of alien plants were logit-transformed (Warton and Hui, 2011). In order to correct for spatial autocorrelation, exponential correlation structure function with latitude and longitude coordinates of each site was added to each model as recommended by Dormann et al. (2007). To check whether spatial autocorrelation was corrected in the obtained models, Moran's I autocorrelation coefficient of



Abbreviature	MUD	RB	RIPFOR	NOU	NOB	FOU	FOB	DOU	DOB
Number of plots	3	3	3	3	3	3	3	3	3
Plot size	$10m^2$	$10m^2$	$200m^2$	$10m^2$	$10m^2$	$10m^2$	$10m^2$	$10m^2$	$10m^2$

Fig. 1. Scheme of the experimental design.

Table 1
Plant species traits selected for the study.

Traits	Categories	Reference
1. Vegetative traits		
1.1 Whole-plant traits		
Growth habit	Annual graminoid Perennial graminoid Annual forb Perennial forb Liana Shrub Tree	Bolòs and Vigo (1984–2001); NRCS (2014)
Plant height (cm)	Continuous	Bolòs and Vigo (1984–2001)
Vegetative propagation	Yes No	Klimešová et al. (2008); Julve (1998)
1.2 Leaf traits		
Photosynthesis pathway	C3 C4	Pyankov et al. (2010)
2. *Reproductive traits*		
Flowering onset (months)	Continuous	Bolòs and Vigo (1984–2001)
Flowering length (months)	Continuous	Bolòs and Vigo (1984–2001)
Seed length (mm)	Continuous	Klotz et al. (2002); Bolòs and Vigo (1984–2001)
Seed dispersal method	Zoochory Anemochory Hydrochory Unassisted	Bolòs and Vigo (1984–2001); SID Database (2015); Julve (1998)

normalized residuals was calculated following Gittleman and Kot (1990).

The strength of the relationship between native and alien richness was evaluated by comparing α-diversity of native and alien plant species within each habitat using linear regression analysis.

2.4.2. Compositional dissimilarity among habitats

In order to determine differences in floristic composition among the habitats, Nonmetric Multidimensional Scaling ordination (NMDS) was performed on Hellinger-transformed species data (Legendre and Gallagher, 2001), separately for native and alien species, with Bray-Curtis dissimilarity distance. Permutational Multivariate Analysis of Variance (PERMANOVA) was performed on NMDS to evaluate statistical significance of the differences on floristic composition among habitats. Likewise, ANOVA and Tukey's post-hoc test were used to find differences among habitat types in the NMDS first axis since this axis accumulates the greatest variance of NMDS points, taking into account that NMDS axes are an approximation of the rank ordering of the original distances.

To assess the importance of nestedness in determining the distribution patterns of alien plants among habitats, "nestedness metric based on overlap and decreasing fill" (NODF) values for rows ($NODF_{sites}$) (Almeida-Neto et al., 2008) was calculated among those habitats where alien plant composition did not show significant differences. This index is robust for testing whether the composition of species-poor sites is nested within the composition of species-rich sites (Alexander et al., 2011; Marini et al., 2013) and it is relatively independent of matrix size and shape (Almeida-Neto et al., 2008).

In order to detect the direction of the nestedness patterns, NODF was calculated on matrices with the rows (sites) ordered by an agricultural-natural gradient and vice versa and columns (alien species) ordered by decreasing abundances. Statistical significance of the nestedness patterns was tested using a null model (999 replicates) that maintains both row and column frequencies using the quasi-swap method. This method randomizes species

Table 2
Total, native and alien plant α- (a) and γ-diversity (b) (±standard error) found in the studied habitats and results of GLS on α-diversity. Different letters represent significant differences in GLS analysis (Tukey's test, $p < 0.05$). MUD: Muddy line, RB: reedbed, RF: riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree lines.

(a)	MUD	RB	RF	NOB	NOU	FOB	FOU	DOB	DOU	AIC	df	Moran's I	p-value Moran's I
α-total	16 ± 1,2 (c)	9 ± 0,9 (a)	17 ± 1,4 (c)	14 ± 0,9 (b)	12 ± 1 (ab)	13 ± 0,7 (b)	12 ± 1 (ab)	13 ± 0,8 (b)	11 ± 0,9 (ab)	493	220	0.0541	0.06
α-native	14 ± 0,8 (b)	8 ± 0,8 (a)	15 ± 1,2 (b)	9 ± 0,6 (a)	9 ± 0,8 (a)	8 ± 0,5 (a)	7 ± 0,7 (a)	10 ± 0,6 (a)	8 ± 0,6 (a)	417	220	0.0482	0.09
α-alien	2 ± 0,4 (b)	0,6 ± 0,3 (a)	2 ± 0,3 (bc)	5 ± 0,4 (d)	4 ± 0,4 (d)	5 ± 0,4 (d)	4 ± 0,4 (d)	3 ± 0,3 (cd)	4 ± 0,5 (d)	464	220	−0.00146	0.92

(b)	MUD	RB	RF	NOB	NOU	FOB	FOU	DOB	DOU
γ-total	91	62	121	66	61	56	56	73	72
γ-total rarefaction	102 ± 5	74 ± 5	144 ± 9	75 ± 6	69 ± 4	63 ± 3	64 ± 3	83 ± 4	82 ± 4
γ-native	77	54	103	46	44	38	38	57	51
γ-native rarefaction	86 ± 4	64 ± 4	121 ± 7	53 ± 3	50 ± 3	43 ± 3	44 ± 3	65 ± 4	60 ± 3
γ-alien	13	8	18	20	17	18	18	15	20
γ-alien rarefaction	16 ± 2	10 ± 2	22 ± 2	21 ± 1	18 ± 1	20 ± 1	20 ± 1	17 ± 1	23 ± 1

composition keeping the number of species per row in the randomized data fixed.

2.4.3. Trait patterns among habitats

In order to test whether average trait expressions of native and alien plants respond differently in each habitat, a redundancy analysis (RDA) was performed on centred and standardized community weighted means of trait values (CWM) for each site, separately for native and for alien plants. CWM values were calculated as:

$$CWM = \sum_{i=1}^{S} p_i \cdot t_i$$

where S is the number of species in the community, p_i is the species i abundance proportion and t_i is the trait value of species i (Lavorel et al., 2008).

To assess statistical significance differences of CWM values among habitats generalised least squared models (GLS) with Tukey's posthoc test for multiple pairwise comparisons were fitted on the CWM values, also accounting for spatial autocorrelation. CWM values were squared root/log transformed when normality was not achieved (supplementary material). Alien plant CWM values of reedbed habitat were not included in the models because the low number of alien species per plot rendered few analysed traits, thus giving inconsistent and meaningless parameters for this habitat in fitted models.

All analyses were performed with R software (R Development Core Team, 2011), except for the CWM-RDA analyses, which were carried out with CANOCO 5 software (Ter Braak and Smilauer, 2012).

3. Results

3.1. Richness and abundance of species

A total of 231 plant species were recorded throughout the study area, 37 of which were alien. Among natural habitats, riparian forest and the muddy line contained the highest number of total and native plant species both at local scale (α-diversity; Table 2a) and at habitat scale (γ-diversity, Table 2b). Among orchards, total and native α-diversity were similar irrespective of the distance from river and the management, while total and native γ-diversity were slightly higher in drip irrigated orchards. In terms of alien species, α-diversity was significantly higher in orchards than in natural habitats. Among all the habitats, reedbed harboured the lowest value of alien α-diversity. Although γ-diversity of alien species was rather similar in all the habitats (apart from reedbed), relative percentage of alien richness per plot was significantly higher in orchards than in riparian habitats (Fig. 2). Regarding relative alien species cover per plot, it was significantly higher in DOB, FOB and NOB. The relationship between relative richness and abundance of alien species showed that orchards sustained comparatively higher levels of invasion than natural habitats. Overall, relative alien species richness and cover presented similar values in each habitat except for DOU, where richness of alien plants was higher than cover and for DOB, where cover value of aliens was higher than richness.

A significant positive relationship between native and alien species α-diversity was found in the riparian forest, muddy line, FOB, NOB and NOU (Fig. 3), although the strongest correlation occurred in the muddy line.

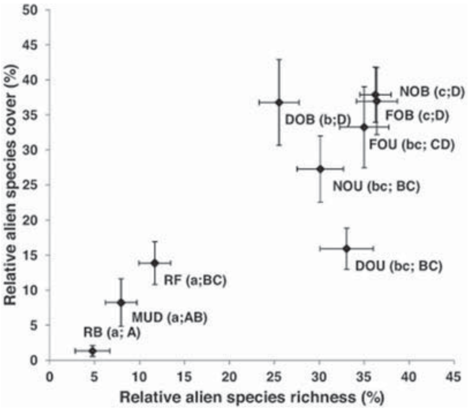


Fig. 2. Plot of percentage of relative alien plant richness versus percentage of relative alien plant cover. Different letters represent significant differences in GLS analysis (Tukey's test, $p < 0.05$) both for richness values (lower case) and for cover values (upper case). MUD: muddy line, RB:reedbed, RF: Riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree lines.

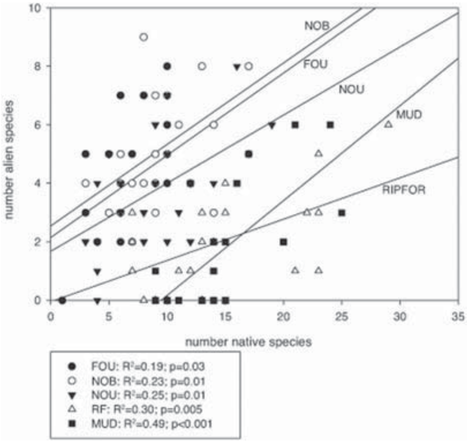


Fig. 3. Plot of linear regression of α-diversity (number of species) of alien and native species in the habitats where linear regression is statistically significant. MUD: muddy line, RF: Riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOU: flood irrigated orchards far from the river.

3.2. Plant community composition and nestedness patterns

NMDS and PERMANOVA showed significant differences on floristic composition among habitats, both for native species ($R^2 = 0.38$, $F = 16.4$, $p < 0.001$) and for alien species ($R^2 = 0.31$, $F = 9.9$, $p < 0.001$) (Fig. 4). Native species in the riparian habitats differed significantly from those in the orchards ($df = 8$, $F = 169.5$, $p < 0.001$).

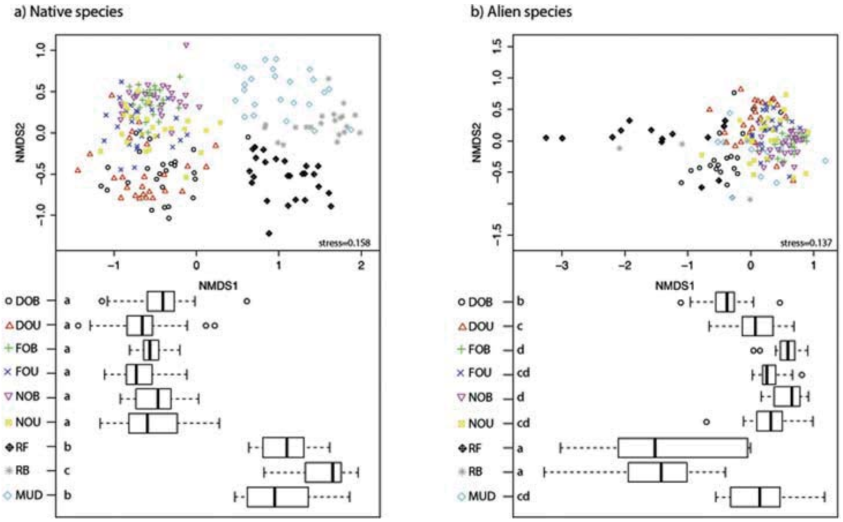


Fig. 4. NMDS ordination plot of the study sites based on Bray-Curtis similarities on native (a) and alien (b) species composition. Boxplots show the results of the ANOVA of plot scores on the first axis. Boxes and whiskers plots include 25–75% and min/max values, respectively. Vertical lines within boxes indicate medians. Open circles represent outliers. Different letters represent statistically significant differences. MUD: muddy line, RB:reedbed, RF: Riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree lines.

Within the riparian habitats, reedbed plant communities differed the most from those of muddy line and riparian forest, whereas there were not such pronounced differences among orchards. Regarding alien species (df = 8, F = 49.43, $p < 0.001$), the floristic composition of muddy line was similar to flood irrigated orchards and DOU, but different from that of reedbed and riparian forest. Composition of flood irrigated orchards was similar irrespective to the distance from the river or the weed management. Finally, DOB composition was different from the rest of the habitats.

The analysis of nestedness indicated that alien plant community of muddy line was a subset of the alien plant community of flood irrigated orchards (Table 3) whereas no pattern of nestedness was found neither in the gradient from muddy line to orchards, from flood irrigated orchards to DOU nor from DOU to flooded orchards.

Table 3
Null model test for significant metacommunity nestedness for alien plant communities among those habitats which presented significantly similar alien plant composition. 3 possible nestedness patterns were evaluated: from DOU (drip irrigated orchards under tree lines), from flood irrigated orchards (flood) and from muddy line (mud) to the rest of the habitats. The metacommunities in different habitats are significantly nested under the constrained null model at $p < 0.05$ (bold text).

Nestedness patterns	$NODF_{sites}$	Mean (Sim.)	P value (Sim.)
DOU-Flood	16.4	20.6	0.96
DOU-mud	16.1	17.9	0.11
Flood-drip	22.9	22.5	0.53
Flood-mud	**22.1**	**24.4**	**0.03**
Mud-DOU	13.9	13.3	0.43
Mud-flood	19.9	19.5	0.29

3.3. Trait correlations and relationship with habitats

CWM values significantly varied among habitats, both for native (pseudo-F = 24.1; $p < 0.05$) and for alien plants (pseudo-F = 14; $p < 0.05$).Variance in community traits explained by habitats for native species was 47.7%, (22.2% and 14.5% by the first and second axes) and 39.4% for alien species, (18.9% and 12.1% by the first and second axes) (Fig. 5). For native species analysis, the first axis clearly separated the riparian habitats from the orchards. Within orchards, flood irrigated orchards were separated depending on the position of the plots, while drip orchards were clustered together. Maximum height, photosynthetic pathway, most of the growth forms and flowering length were related to first axis whereas second axis was related to perennial grasses and forbs, clonality and hydrochory. CWM-RDA on alien plants positioned riparian forest, reedbed and DOB on the positive side of the axis and muddy line and the rest of the orchards on the negative side. Muddy line was clustered together with FOB and NOB. First axis was mostly related to maximum height, photosynthetic pathway, trees and annual grasses and zoochory whereas forbs, perennial graminoids, clonality and hydrochory were mostly associated to the second axis.

Generalized least squared models (Table 4 and Supplementary material) confirmed some of the trends observed in the ordination of traits in the CWM-RDA analyses. Regarding native species, riparian forests presented significantly higher values of trees and shrubs, larger height values, C3 species, short flowering length and larger zoochorous seeds. Muddy line and reedbed included larger number of C3 species with clonal reproduction, a late summer flowering period and hydrochory. Flood irrigated orchards, on the other hand, were mainly composed of species with long flowering length and zoochorous seeds. NOB and FOB presented dominance of perennial forbs, whereas NOU and FOU included significant larger values of annual grasses. DOB and DOU included annual

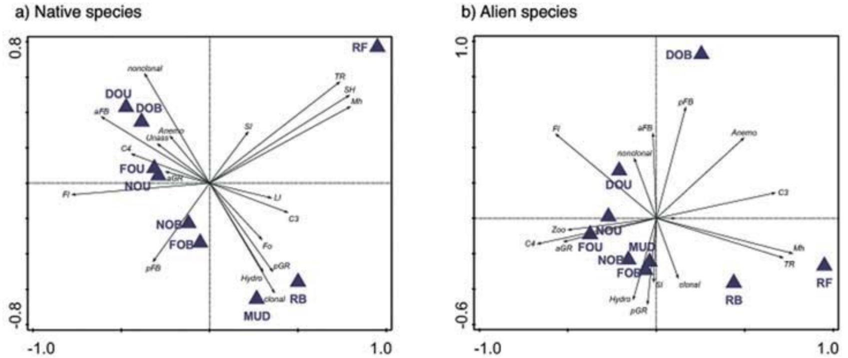


Fig. 5. Redundancy Analysis of community-weighted means of trait values (CWM-RDA) of native (a) and alien (b) plant species. MUD: muddy line, RB:reedbed, RF: Riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree lines. aFB: annual forbs, pFB: perennial forbs, aGR: annual grasses, pGR: perennial grasses, TR: trees, SH: shrubs, LI: lianas, anemo: anemochory, hydro: hydrochory, zoo: zoochory; unass: unassisted, Sl: seed length, Mh: maximum height, Fl: flowering length, Fo: flowering onset. Only those traits more correlated with the plotted ordination axes (i.e. those with vectors longer than the radius of the Equilibrium Contribution circle) are represented.

Table 4
Summary of traits with significantly higher community weighted mean values in each habitat compared to the rest of the habitats for native and alien species (post-hoc Tukey's test. $p < 0.05$). MUD: Muddy line, RB: reedbed, RF: riparian forest, NOB: flood irrigated orchards near the river, plots between tree rows, NOU: flood irrigated orchards near the river, plots under tree lines, FOB: flood irrigated orchards far from the river, plots between tree rows, FOU: flood irrigated orchards far from the river, plots under tree lines, DOB: drip irrigated orchards, plots between tree rows, DOU: drip irrigated orchards, plots under tree lines.

		MUD	RB.	RF	NOB	NOU	FOB	FOU	DOB	DOU
NATIVE	GROWTH FORM								aFORB	aFORB
		pFORB			pFORB		pFORB			
					aGRASS	aGRASS		aGRASS		aGRASS
			pGRASS							
				TREE/SHRUB						
	MAXIMUM HEIGHT			MAX. HEIGHT						
	PHOTOSYNTHESIS	C3	C3	C3	C4	C4	C3	C4	C4	C4
	FLOWERING ONSET	LATE	LATE							
	FLOWERING LENGTH			SHORT	LONG	LONG	LONG	LONG		LONG
	CLONALITY	YES	YES		YES		YES		NO	NO
	SEED LENGTH	SHORT	LONG	LONG			LONG			
	DISPERSAL			ZOO.	ZOO.	ZOO.	ZOO.	ZOO.		
							ANEMO.		ANEMO.	ANEMO.
		HYDRO.	HYDRO..							
									UNNASS.	UNNASS.
ALIEN	GROWTH FORM								aFORB	aFORB
									pFORB	
					aGRASS	aGRASS		aGRASS		
		pGRASS			pGRASS		pGRASS			
				TREE						
	MAXIMUM HEIGHT			MAX. HEIGHT						
	PHOTOSYNTHESIS	C4		C3	C4	C4	C4	C4	C3	C4
	FLOWERING ONSET	LATE							LATE	LATE
	FLOWERING LENGTH			SHORT				LONG	LONG	LONG
	CLONALITY	YES		YES	YES		YES		NO	NO
	SEED LENGTH	SHORT		SHORT	LONG	SHORT	LONG	SHORT	SHORT	SHORT
	DISPERSAL			ANEMO					ANEMO	
					ZOO	ZOO	ZOO	ZOO		ZOO
		HYDRO			HYDRO	HYDRO	HYDRO	HYDRO		

species, with seeds dispersed by wind or barochory. However, results showed some different trends for alien plants. Alien species in riparian forest shared similar traits to native species, but were also clonal species with small seeds dispersed by wind. Muddy line, as well as flooded orchards, contained mainly graminoids, clonal, and C4 species dispersed by water. Perennial graminoids were better represented in both muddy line and NOB and FOB, whereas NOU and FOU included significantly higher proportions of annual graminoids. DOU included annual forbs, C4 zoochorous species, whereas alien plants in DOB were mainly C3, anemochorous forbs. Regarding reedbeds, CWM-RDA showed that alien species were mostly tall perennial C3 species with clonal reproduction.

4. Discussion

4.1. Richness and abundance patterns

Results showed that γ-diversity was higher in natural habitats than in orchards, apart from reedbed, which harbours the lowest number of species among natural habitats. It is assumed that riparian habitats include more species than surrounding ecosystems (Brown and Peet, 2003), especially in Mediterranean areas (Stella et al., 2013). Reedbed communities were almost totally represented by common reed (*Phragmites australis*). Although it is native in the study area, it tends to form dense monotypes, impeding the development of other species (Zedler and Kercher, 2004). Besides, inflow of returned irrigation flow from agricultural areas increases rates of nutrient concentration of lowland streams (Baattrup-Pedersen et al., 2013), which has been related to the decrease in plant diversity in reedbeds (Kovács et al., 1995). Regarding the origin of the species most of them were native in riparian habitats, while the percentage of alien species as well as their relative cover values were significantly higher in orchards, as found in previous studies (Juárez-Escario et al., 2013).This confirms the susceptibility of irrigated crops to alien plant invasions already described in the Mediterranean region (Chytrý et al., 2009). The fluctuating resources theory (Davis et al., 2000) affirms that those communities affected by an increase in the amount of unused resources are more prone to be invaded. Irrigated orchards show this effect, as management includes periodic increases of resources (i.e. summer irrigation, nutrient uptake). Besides, weed management reduces competition with local species for those resources. This trend was already observed in drip irrigated orchards by Juárez-Escario et al. (2010) and in non-irrigated arable land in Catalonia by Chytrý et al. (2009). Nevertheless, alien γ-diversity was lower in DOB than in the rest of the orchards. The inter-row area in drip irrigated orchards is actually a rainfed area, and it contains typical rainfed-crop weeds adapted to the semiarid Mediterranean climate of the region that are mostly native. Nevertheless, relative alien cover was higher than expected based on relative richness. It could be explained by the dominance of species such as *Crepis bursifolia* and *Aster squamatus* in the alien community (see frequency and cover values of alien plants in supplementary material). To avoid these species to reach later stages of invasion, its abundance should be monitored and the causes of their expansion should be analyzed. Anemochory and mowing management of the inter-rows −since both species are able to resprout- may favour their increase.

On the other hand, the largest positive relationship between native and alien plant richness found in the muddy line has been previously described for communities that are not species saturated (Gilbert and Lechowicz, 2005; Moore et al., 2001) and also for riparian habitats (Tabacchi et al., 2005). The muddy line is subject to periodic flooding episodes that open new niches susceptible to colonization; therefore plant communities in this habitat remain in a primary or intermediate stage of succession. In this situation, alien species can settle in this habitat and increase the local diversity without implying loss of native species (Gilbert and Lechowicz, 2005). Similar patterns have been observed in other semi-arid Iberian rivers (Aguiar et al., 2006).

Similarly, lower positive correlation found in flood irrigated orchards might be explained because this process was overshadowed by the strong effect of crop management. As Davis et al. (2000) and Wardle (2001) described, disturbances such as fertilization trigger an increase in net resource availability that facilitate invasion, independent of the species diversity.

4.2. Composition, nestedness and dominant traits of native and alien plants

This study shows the importance of identifying differences in some traits between native and alien species for understanding differenced distribution of those communities among habitats.

Differences in floristic composition among habitats are mediated by ecological and management-related constraints (Götzenberger et al., 2012). Regarding native species, floristic composition of natural habitats was different from orchards. Within natural habitats, forest, reedbed and muddy line plant communities were well delineated as a result of the adaptation of the species to the multiple abiotic constraints that impact each habitat with various intensities; i.e. periodic flooding, sediment regimes and seasonal water shortage (Stella et al., 2013). Traits favoured at each habitat indeed reflect these adaptations. Hence, reedbeds and muddy line habitats, which are periodically flooded, have species whose seeds are dispersed by water and flower in late summer, when the level of water decreases in Mediterranean floodplains. In the riparian forest, however, which is established on infrequently flooded surfaces, communities can achieve a more advanced stage of plant succession (Tabacchi et al., 1998) and are dominated by trees and shrubs. As Catford and Jansson (2014) pointed out, such a variety of attributes proves that there are many possible combinations of successful adaptations to the diversity of environmental conditions in riparian habitats, which sustains the well-described high riparian biodiversity.

On the other hand, irrigation and weed management of orchards configure common compositional patterns, independently of the distance to the river. Flood irrigated orchards contain a weed community composed of zoochorous species with a long flowering period. Long flowering has been related to increased chances of colonization and better reproductive success (Lake and Leishman, 2004; Lloret et al., 2005). Regarding seed dispersal, most of the weeds present, like *Bromus diandrus, Hordeum murinum, Setaria verticillata, Torilis* spp. and *Tribulus terrestris* have seeds with adherent structures that enable their attachment to animal fur which also facilitates human-mediated dispersion. On the other hand, mowing in the inter-row spaces favours the establishment of perennial forbs (Juárez-Escario et al., 2013; Lososová et al., 2003) whereas under tree rows where herbicides are applied, perennial form is not benefited and the well-described dominance of annual species in crops arises (Lososová et al., 2006).

In drip irrigated orchards, differences in the weed management between positions lead to the establishment of compositionally different but functionally similar weed communities, dominated by annual anemochorous forbs. Under the trees, therophytes that can escape from herbicide drift are able to establish, as well as individuals which are favoured by intense disturbances occurring in the inter rows (i.e. shredding and water shortage). These disturbances maintain the weed community in a primary stage of succession where vegetation cover is low and sparse and where wind dispersed annual plants dominate (Bonet, 2004).

Regarding alien species, data showed the composition of riparian forest, reedbed and DOB to be clearly differentiated whereas high similarities were found between muddy line and flood irrigated orchards.

From a trait-based approach, alien plants in flood irrigated orchards-particularly between the rows- and the muddy line were mainly C4 species, perennial graminoids, with clonal growth and with water-dispersed seeds. This set of attributes facilitates alien species to colonize those habitats (via water dispersal) and to resist and recover from ecophysiological stress caused by inundation and physical disturbances from floods that characterize both orchards and the muddy line (Catford and Jansson, 2014).

Large nestedness from flood irrigated orchards to muddy line in terms of alien plants indicates that most of the shared alien species were introduced in the flooded orchards, and that only a subset of this community reaches the muddy line. This is consistent with the hypothesis of Clark and Johnston (2011) who argue that alien species establish in high disturbance areas first and, from there, they can adapt to and colonise sites with different environmental conditions. Influence of alien plants of agricultural uplands in the composition of alien communities in riparian habitats has been already showed (Ferreira and Moreira, 1995; Miyawaki and Washitani, 2004), and is enhanced in regulated rivers (Jansson et al., 2000) such as the studied river.

Lack of nested patters between DOU and flood orchards' alien weed community suggests that alien weeds were introduced independently in those habitats, probably by human-mediated pathways, establishing a similar community of weeds selected and maintained by a similar management (water supplies). A plausible hypothesis to explain the spread of alien plants from flooded orchards to muddy line is through irrigation water corridors (Benvenuti, 2007), after which it is presumed that a bidirectional flow of alien species was established, since propagules of alien plants settled in muddy line can also reach flooded orchards downstream through irrigation water.

This scenario is also supported by the evidence that alien plants present both in flood irrigated orchards and in the muddy line have water-dispersed seeds. In fact, the importance of hydrochory in riparian plants' distribution patterns has been previously described (Burkart, 2000) since it enables long-distance seed dispersal and effective colonization of riparian zones (Nilsson et al., 2010). Furthermore, success of invasive species in riparian habitats has also been related to hydrochory (Tabacchi et al., 2005). On the other hand, alien weeds of flood irrigated orchards are not only hydrochorous, but also zoochorous, which can increase the capability of colonization of new habitats. In fact, having more than one dispersal mechanism confers advantage in terms of undergoing rapid expansion (Wang et al., 2011).

The role of seed dispersal systems in colonizing both riparian habitats and nearby agricultural habitats is also reflected in the fact that some traits that confer adaptation to riparian disturbances are also present in alien species of drip irrigated orchards (i.e. C4, small seeds or late flowering onset); lack of hydrochory, however, may prevent these species from reaching the muddy line, as lack of nestedness patterns between those two habitats confirms. Some native and alien weeds present in orchards with traits adapted to riparian disturbances actually have the potential to establish populations in riparian zones, but their seed dispersal system does not facilitate the colonization of these habitats. This study thus reveals the role of the dispersal system as a key for species to overcome the filter of new habitats, and potentially become invasive, as was previously described by Richardson et al. (2000).

In terms of persistence and competitive capabilities, photosynthetic pathway, clonality and graminoid form confer advantages to alien weeds both in muddy line and in flooded orchards. Under flooding and high temperature conditions, C4 physiology allows plants to concentrate CO_2 and enables carbon uptake from sediments, thus facilitating survival during water submergence. Moreover, in flood conditions, C4 species present a faster growth rate and higher photosynthetic productivity than C3 species due to a greater net assimilation rate (Sage, 2004). In fact, previous studies have shown that C4 photosynthesis is related to the selection of alien weeds in flood irrigated orchards (Juárez-Escario et al., 2013) and in riverbanks (Schmitz, 2006).

Two explanations may be responsible for the fact that alien species in muddy line and in flood irrigated orchards are mainly graminoids. For one, it is probable that photosynthetic pathways and life forms are phylogenetically related. In fact, a link between Poaceae and Cyperaceae perennial grasses and C4 photosynthesis has been observed in agricultural weeds (Haakansson, 1995). Alternately, grasses selected by the management of flood irrigated orchards can benefit in the muddy line, since flooding has been found to increase the overall productivity of graminoids (Insausti et al., 1999).

After disturbance episodes, vegetative reproduction benefits plants so they quickly (re)colonize areas (resilience) during terms without mechanical intervention or at inter-flooding periods (Gaba et al., 2014). This mechanism also allows them to survive disturbance events (resistance), despite losing some biomass, as occurs in the mowing of the inter-rows of after flooding episodes, since floods do not destroy entire clones (Catford and Jansson, 2014). Moreover, these clones can be water dispersed, therefore acting as propagules benefiting establishment and colonization of new areas.

4.3. Agro-ecological implications for conservation

This study highlights the role of irrigated orchards surrounding riparian habitats as alien weed reservoirs; permitting certain species to overcome the ecological filters of floodplains, and establish populations in the muddy line. Muddy line can also act as a source of propagules of those species to the orchards via irrigation water. On the other hand, the study reveals the role of the irrigation management of these orchards in configuring a community of alien weeds able to overcome invasion constraints of riparian habitats. For these reasons, both agronomic and ecological approaches are proposed to deal with this scenario.

From an agronomic point of view, since flood irrigated orchards appear to be the first receptor of alien plants, preventing the introduction and establishment of invasive alien species in flood orchards should be the first direct management strategy. Early detection measures based on weed risk assessment approaches and monitoring established aliens plant populations, focusing the eradication measures on those species whose traits have been related to the success in natural habitats have been proved effective at controlling other alien weeds invasions in the study area (i.e. *Sicyos angulatus* in maize fields or *Leersia oryzoides*, *Leptochloa* spp. and *Sagittaria* spp. in rice fields) (Brunel et al., 2013). In this sense, improving weed control techniques may be effective to control the most problematic species. Increasing the frequency of mechanical weed control may help to prevent plants to achieve phenological stages that involve seed production, hence breaking the spread of alien propagules by running water.

On the other hand, it has been widely proved that cover crops can effectively reduce or even suppress weed presence on crops providing at the same time ecosystem services (see Lemessa and Wakjira (2015) and the references therein). Thus, using cover crops mixture of native plants which present traits similar to those of successful alien plants can on the one hand reduce the cover of alien weeds and on the other hand increase the propagules supply of native species. Native plants should be selected based on their traits and ability to establish and persist under the environmental conditions of the host habitat, as Catford et al. (2012a) pointed out.

From an ecological point of view, disturbance regimes are a key in maximizing the total biodiversity across a floodplain (Ward et al., 1999). In this sense, flooding is possibly the most important factor in the maintenance of a temporal and spatial heterogeneity of riparian habitats that sustain a high diversity of biotic communities (Ward, 1998). Reduction of flood episodes in regulated rivers has been related to an increase in the establishment of alien plant communities by providing drier conditions (Catford et al., 2011), which could be related to the success of perennial life forms observed in the muddy line against more typical therophytes of this habitat. On the other hand, increasing flooding episodes has been accepted as an effective measure to control the establishment and development of alien plant communities in riparian habitats (Catford et al., 2011). Baattrup-Pedersen et al. (2013) found that low frequency flooding can increase richness of native vegetation within riparian areas in streams draining catchments dominated by agriculture, coinciding with the characteristics of our study area.

Hence, using environmental flows can be an effective way to avoid the establishment of alien plants in muddy line, therefore breaking the flow of alien plants between riparian habitats and agricultural areas nearby and confining alien plants in the orchards.

5. Conclusions

This study confirmed that riparian habitats in contact with irrigated orchards harboured rich and diverse plant communities at an habitat scale compared to the less diverse weed communities of the orchards, which were well-represented by alien species. Regarding native species, plant communities in riparian habitats were well-differentiated from those of orchards, and within orchards, two different weed communities were found, depending on the irrigation system. In terms of alien plants, similar composition was found between the muddy line and the flood irrigated orchards and a nested pattern was detected from flood orchards' alien community to that of the muddy line. These results revealed that alien plants are shared between flood irrigated orchards and the muddy line. This connection is mediated by a group of traits adapted to disturbances and flood, such as the C4 photosynthetic pathway, clonal growth, graminoid form and water seed dispersal. Some of these traits were also present in native weed communities but lack of hydrochorous seeds prevents the establishment of those species in the muddy line.

This study revealed the role of flood irrigation in maintaining an alien weed community both in orchards and in nearby natural riparian habitats. This finding has important agronomic and ecological implications, and some management measures are proposed in order to reduce the flow of alien species between flood irrigated orchards and riparian habitats, thus maintaining these species confined to agricultural areas.

Acknowledgements

Financial support was provided by the Generalitat de Catalunya (FI PhD grants). We would like to acknowledge the farm owners for allowing them to conduct the study in their orchards, as well as Jordi Tunica for their help in collecting field data and Sarah Lade for improving the English in this paper. We also thank the anonymous reviewers for the insightful comments that improved early drafts of the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.04.015.

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