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eman ta zabal zazu

Universidad del País Vasco
Euskal Herriko Unibertsitatea

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Universidad del País Vasco
Euskal Herriko Unibertsitatea

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Plant invasion in Cantabrian rivers: drivers and effects on plant diversity and riparian habitats

Diego Liendo Pérez

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A mis padres

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RESUMEN

Las invasiones biológicas, es decir, el movimiento por parte del hombre de especies fuera de sus límites de distribución natural y su posterior establecimiento en dichas áreas, constituyen uno de los motores principales del denominado cambio global. Si bien este fenómeno se ha producido desde hace milenios, en los últimos siglos se ha acelerado de manera exponencial como resultado de las mejoras en las redes de transporte intercontinental y del marcado incremento del comercio internacional. Como resultado de lo anterior, en prácticamente cualquier hábitat de cualquier región del mundo podemos encontrar especies alóctonas introducidas con el potencial de establecerse y causar problemas ecológicos y/o económicos. En relación a esto, los hábitats riparios están considerados como altamente vulnerables a la invasión por plantas alóctonas y la elevada proporción de este tipo de plantas en estos ambientes parece atestiguarlo.

En este contexto, la presente tesis estudia diferentes aspectos relacionados con la presencia y los efectos de las plantas alóctonas en ríos cantábricos del norte de España. Estos ríos presentan unas características que los hacen muy diferentes de otros tipos de ríos, como por ejemplo los ríos mediterráneos de la Península Ibérica, los cuales están mucho más estudiados en relación a la flora alóctonas y sus efectos. Por esta razón, se estima necesario un estudio detallado de la invasión por plantas alóctonas en los hábitats riparios cantábricos dada, además, la fragilidad de estos hábitats y la diversidad de servicios ecosistémicos que proporcionan.

Tras un primer capítulo introductorio, el segundo capítulo de la tesis contiene los resultados de un estudio piloto en el que se muestrearon tramos de 100 m de longitud correspondientes a los puntos de la Red de Seguimiento del Estado Ecológico de los ríos de la CAPV. En estos puntos se determinó el grado de invasión calculado como la proporción de especies de plantas alóctonas en relación al total de especies de plantas vasculares encontradas en cada punto. Este grado de invasión se relacionó con el estado ecológico, medido a partir del índice químico de calidad general (ICG) y del índice de calidad del bosque de ribera (QBR), así como con la presión antrópica medida a partir de las alteraciones hidrológicas y morfológicas en el río. Mientras que los indicadores del estado ecológico no mostraron apenas relación con el grado de invasión, éste fue significativamente superior en aquellos puntos sometidos a niveles elevados de alteración tanto hidrológica como morfológica. Además, se determinó que las cascajeras fluviales y los taludes creados por el hombre albergaban un número similar de especies alóctonas y superior en ambos casos al de los bosques de ribera.

Con los resultados del segundo capítulo como base, en el capítulo 3 se estudiaron con mayor detalle los factores relacionados con el grado de invasión a escala local (punto

de muestreo) y a escala regional (cuenca hidrográfica). Para ello, se amplió el área geográfica y se muestrearon 80 puntos repartidos al azar por 16 cuencas situadas entre la parte oriental de Cantabria y el norte de Navarra. Entre las variables estudiadas a escala local se incluyeron variables ambientales (climáticas y topográficas) y antrópicas, como los usos del suelo alrededor de cada punto y las distancias a núcleos de población y carreteras. En el caso de las cuencas, se analizó el grado de invasión en relación con su grado de industrialización. El grado de invasión se calculó nuevamente como la proporción de especies alóctonas en relación al número total de especies y, adicionalmente, como el número de especies alóctonas en cada punto. A escala de cuenca se calculó únicamente la proporción de alóctonas utilizando para ello el número acumulado de especies alóctonas y nativas en cada cuenca. Empleando modelos lineales generalizados mixtos (GLMMs), se determinó que el grado de invasión a escala local estaba influido por variables ambientales como el índice de termicidad, la anchura media del cauce y el número de comunidades vegetales presentes en el punto de muestreo, así como por variables antrópicas como la distancia al núcleo de población de más de 5000 habitantes más cercano o la proporción de suelo urbano alrededor de cada punto. A escala de cuenca, las cuencas clasificadas como industrializadas presentaron un grado de invasión significativamente mayor que las no industrializadas. Además, ambos tipos de cuencas diferían marcadamente en la composición de plantas alóctonas. Por último, se determinó qué especies alóctonas eran más frecuentes a ambas escalas.

En el capítulo 4 se estudiaron las diferencias entre dos hábitats riparios cantábricos (bosques y cascajeras fluviales) en el grado de invasión y en la diversidad y estructura filogenéticas de la comunidad nativa, así como el efecto de las especies alóctonas en estos indicadores filogenéticos. Para ello, se utilizaron inventaros de vegetación realizados en ambos hábitats siguiendo el método fitosociológico y se calcularon dos índices filogenéticos, MPD y MNTD, a nivel de inventario. También se calcularon sus valores estandarizados mediante modelos nulos con el fin de determinar si la estructura filogenética era de tipo aleatorio, agrupado o sobredisperso. Confirmando los resultados obtenidos en estudios previos, las cascajeras fluviales estuvieron significativamente más invadidas tanto en términos de riqueza específica como de cobertura. En relación a la diversidad filogenética, las cascajeras fluviales fueron filogenéticamente menos diversas y, además, presentaron una estructura filogenética más agrupada como resultado del mayor nivel de perturbación natural al que están sometidas. No se detectó ninguna relación significativa en ninguno de los hábitats entre la diversidad filogenética del componente nativo de la comunidad y su grado de invasión. Sin embargo, en relación a la estructura filogenética, se observó que cuando se tuvieron en cuenta las especies alóctonas aumentó el grado de dispersión filogenética general (es decir, la diversidad filogenética reflejada por los valores estandarizados del índice MPD) en las cascajeras fluviales. En el caso de los bosques, no se observaron cambios en la diversidad y/o estructura filogenéticas asociados a las especies alóctonas.

Los capítulos 5 y 6 abordan aspectos florísticos. En el capítulo 5 se presentan novedades florísticas a nivel provincial o regional para algunas especies nativas y alóctonas así como nuevas citas de especies que en la actualidad cuentan con escasos registros a dichos niveles. Destaca en este capítulo el descubrimiento de poblaciones naturalizadas de la gramínea de origen norteamericano *Muhlenbergia schreberi*, las cuales constituyen nuevas citas regionales para Navarra y el País Vasco y la segunda referencia para esta especie en la Península Ibérica. Finalmente, el capítulo 6 contiene los resultados de una revisión de material del género *Conyza* en el norte de España. Para ello, se estudiaron ejemplares recolectados por los autores, ejemplares preservados en el herbario BIO de la Universidad del País Vasco (UPV/EHU) y ejemplares prestados por otros herbarios de la CAPV (ARAN, SEST y VIT). La revisión realizada permitió determinar que *C. canadensis*, en el pasado considerada la especie más extendida del género en el área de estudio, en realidad se encuentra prácticamente ausente del mismo. Por el contrario, *C. sumatrensis* y *C. bilbaoana* son las especies más abundantes del género. En relación a *C. bilbaoana*, recolectada por primera vez en Europa en los años 80 del pasado siglo, está escasamente citada en la actualidad en el área de estudio; sin embargo, se encuentra ampliamente extendida, por lo que es posible que se haya confundido con *C. canadensis*, con la que guarda un gran parecido. En este capítulo se incluye una clave de identificación para las cuatro especies de *Conyza* que pueden encontrarse en el norte de España en la que se destacan los principales caracteres que permiten diferenciarlas.

CHAPTER 1

General introduction

The present thesis is the result of an extensive research on the presence of alien plants and their effects on native vegetation in riparian habitats of northern Spain. It falls within a broader research line dealing with alien plant invasion in the Basque Country and neighbouring territories and focuses on riparian habitats given their ecological importance, their profound human-driven alteration and their widely accepted high vulnerability to invasion by alien plants. As a matter of fact, Campos (2010) found that riparian habitats in the Basque Country were second only after ruderal and roadside habitats in relation to alien plant richness (i.e., the most alien-rich natural habitat), highlighting the need for a more thorough assessment of riparian plant invasion. Aspects of alien plant composition, drivers of plant invasion and effects of alien plants on phylogenetic diversity across riparian habitats have been dealt with in this thesis. Additionally, new records of some native and alien plant species at provincial and/or regional scale as well as a revision of the genus *Conyza* in the study area are presented. Some results have already been published in different scientific journals.

Riparian systems: definition, characteristics and importance

Riparian zones are important landscape elements whose spatial extent is not easy to define accurately. They would encompass the stream channel and that portion of the terrestrial landscape between the low and high water mark as well as the floodplain, where vegetation may be influenced by elevated water tables or occasional flooding and by the ability of the soils to hold water (Naiman *et al*. 1993) (Figure 1).

These ecosystems have been described as some of the most dynamic and complex terrestrial habitats (Gregory *et al*. 1991, Naiman *et al*. 1993, Naiman & Décamps 1997) as they are influenced both by non-fluvial disturbances characteristic of adjacent upland ecosystems, such as wind, fire, plant disease or debris flow, and by disturbances associated with aquatic systems, such as lateral channel erosion and flooding (Tang & Montgomery 1995). In addition to natural disturbances, riparian zones are often the focus of intensive human activity (Tockner & Stanford 2002, Richardson *et al*. 2007) due to the presence of human-valued natural resources, and thus these ecosystems are very often shaped by human-mediated disturbances. Anthropogenic activities, such as river regulation, agriculture, industry, urbanisation and the construction of transport networks have resulted in an intense alteration and degradation of the ecological integrity of many riparian environments. Consequently, there is growing awareness of the increased pressure on riparian zones across the world as a result of human activity (Tickner *et al*. 2001).

Riparian zones support distinctive vegetation that differs in structure and function from adjacent upland ecosystems (Naiman & Décamps 1997, Holmes *et al*. 2005). Hydrological processes are the chief determinants of plant community structure and composition in these zones (Hupp & Osterkamp 1996, Holmes *et al*. 2005, Richardson *et al*.

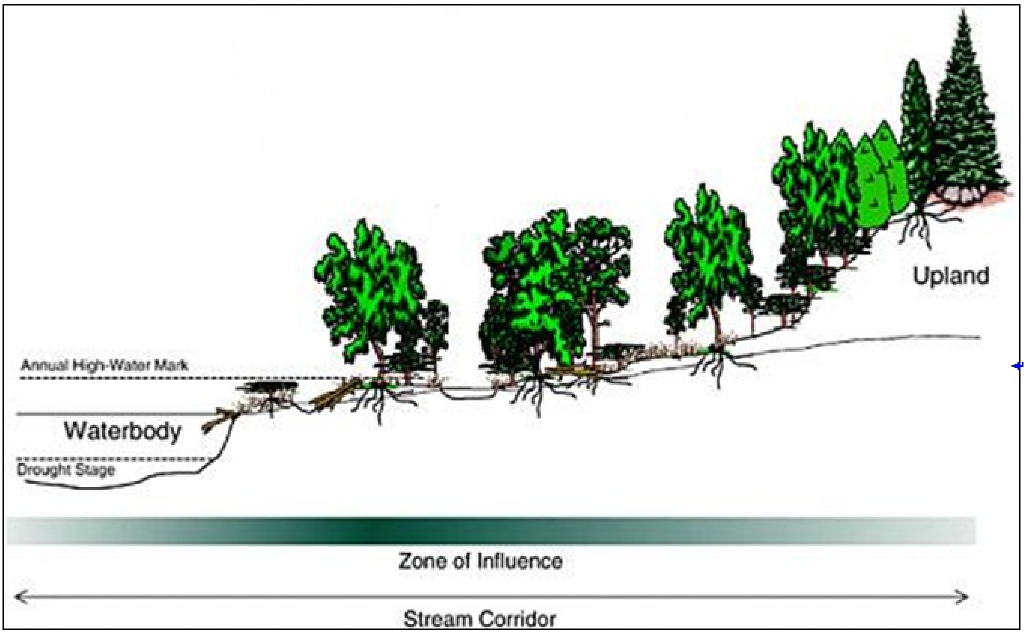

Figure 1. Schematic representation of the riparian zone. Modified from National Research Council (2002): *Riparian areas: functions and strategies for management*. National Academy Press, Washington, D.C.

2007). Riparian plant communities are typically composed of specialised and disturbance-adapted species within a matrix of less-specialised and less disturbance-adapted plant species (Naiman *et al.* 1998, Ward *et al.* 2002, Lyon & Gross 2005) and they exhibit a high degree of structural and compositional diversity (Gregory *et al.* 1991). These communities arrange on the basis of their proximity to running water and, consequently, of flood frequency and duration and soil water content, according to a decreasing disturbance gradient towards the upland. This zonation can be described by means of the concept of fluvial geoseries, which encompasses these plant communities that grow on the riverbed and the perifluvial environment and are subjected to a constant replacement following the patterns of plant succession (Alcaraz 1996, Rivas-Martínez 2007) (Figure 2). Four types of plant communities can be distinguished within a fluvial geoseries: aquatic communities (including helophytes), river bar herbaceous communities, riverbank forests and floodplain forests, as well as shrubby and herbaceous vegetation replacing forests in disturbed riverbanks and floodplains. As a result of the above, riparian zones have been reported as some of the most species rich and most productive systems of temperate regions (e.g. Naiman *et al.* 1993, 1998, Naiman & Décamps 1997, Tockner & Stanford 2002). Several explanations have been proposed for the high plant species richness of riparian zones: regular flood disturbance that periodically destroys vegetation cover, creating bare ground for recolonisation (Naiman *et al.* 1993) and decreasing the strength of competitive interactions (Hood & Naiman 2000); high nutrient availability (Tickner *et al.* 2001); dispersal

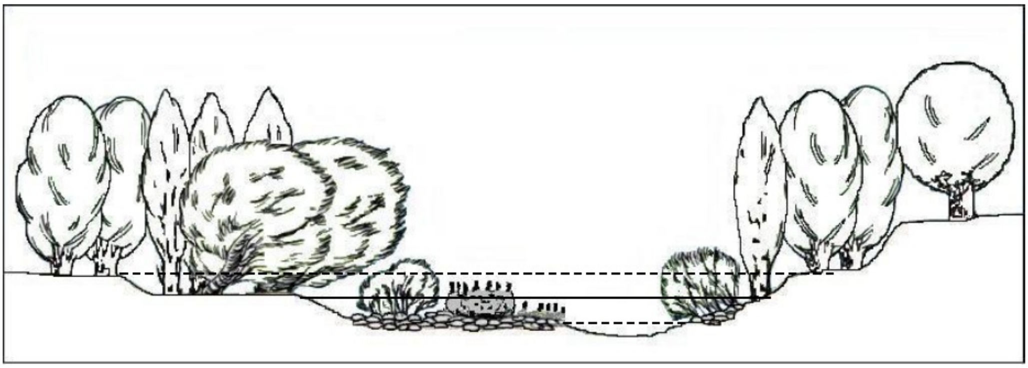

Figure 2. Example of a fluvial geoseries showing different plant communities growing on the riverbed and the perifluvial environment.

of plant propagules by water (i.e., hydrochory) (Nilsson *et al.* 1991, 2010, Johansson *et al.* 1996).

Rivers are important pathways for the flow of energy, matter and organisms through the landscape (Tabacchi *et al.* 1990, 1998, Gregory *et al.* 1991). Furthermore, relative to their minor extent in most landscapes, riparian ecosystems are disproportionately important for the delivery of key services, such as water supply and biodiversity conservation (Naiman & Décamps 1997, Strayer & Findlay 2010). Regarding riparian vegetation, it fulfils or influences various important ecological functions in relation to aquatic habitats (Richardson *et al.* 2007), such as control of the flow of water, nutrients and sediments into streams (Décamps 1993, Barling & Moore 1994, Tabacchi *et al.* 1998), structuring of the physical habitat at several scales (Ward *et al.* 2002), provision of habitat (e.g. Barling & Moore 1994, Ward *et al.* 2002, Holmes *et al.* 2005), moderation of stream water temperature via evapotranspiration and shading (Tabacchi *et al.* 1998, Richardson *et al.* 2007), water filtering (Barling & Moore 1994, Holmes *et al.* 2005) or riverbank stabilisation (e.g. Tang & Montgomery 1995, Tabacchi *et al.* 1998, Tickner *et al.* 2001). Many of these and other conditions created by vegetation-influenced processes contribute directly or indirectly to human welfare, which has been termed ‘ecosystem services’. Any change in the composition of the plant community will entail some change in the ecosystem services that riparian vegetation provides.

Biological invasions

Historical background and current status

In nature, all organisms migrate or disperse to some extent (Shigesada & Kawasaki 1997). The dispersal of organisms is a natural process, important for the distribution of life on earth and for the appearance and expression of biodiversity (Nentwig 2007). Long-distance dispersal of organisms has traditionally been limited by a wide variety of barriers, especially physical and geographical features such as oceans, mountain ranges, deserts, ice sheets or river valleys. These barriers ensured that most species remained localised within their region, resulting in a separate evolution of plant and animal communities in the different continents over time. However, climatic and geological events have sometimes removed these a priori insurmountable barriers and allowed individuals to disperse over relatively long distances, with some species eventually expanding their ranges (Lockwood *et al.* 2007). As soon as humans had the ability to disperse across continents, people have helped to overcome the geographic barriers to species dispersal at global scale. Since the first human migrations and the beginning of agriculture and keeping of livestock, plants and animals have been transported along with other goods as human settlers have moved into novel territories (Crosby 1986, Kowarik & von der Lippe 2007, Lockwood *et al.* 2007), arriving at new locations that they previously could not reach by their own means and colonising in some cases these new environments. These early human movements involved relatively few species. Despite the substantial debate within the scientific community regarding whether range expansions aided by humans are different from range expansions due to paleoclimatic events (Vermeij 2005, Lockwood *et al.* 2007), it is widely accepted that humans have massively increased the rate at which species colonise new areas when compared to natural range expansion, e.g., following deglaciation. This species transfer through human agency is much more frequent, faster, more efficient and occurs from more distant regions than through natural mechanisms and has no parallel in evolutionary history (Elton 1958, Mack *et al.* 2000, Kowarik & von der Lippe 2007).

Despite the fact that humans have moved plant and animal species beyond their ranges for millennia, the majority of alien species have been introduced in the European continent from 1500 AD forward coinciding with the discovery of the Americas by European navigators, which is usually set as the zero point of our current definition of biological invasions (Nentwig 2007). However, it was not until the Industrial Revolution around 1800 AD (Hulme 2009) when a progressive increase in the annual rate of alien species' introductions was observed as a consequence of an increase in international trade. Furthermore, the establishment of European colonies around the world between the 19th and 20th centuries implied that millions of people emigrated to distant places taking with them, whether intentionally or by accident, numerous species (McNeely 2006, Hulme 2009). European settlers often recreated the familiar conditions of their homeland by taking with them species such as wheat, barley, rye and numerous ornamentals (McNeely 2006). Another example of intentional introductions between the second half of the 19th century and the early 20th century is represented by acclimatisation societies. These societies were organisations formed by like-minded citizens whose mutual interest was the introduction of exotic animals and plants in their countries and their adaptation to the conditions provided there (Lever 2011). These alien species were seen as exotic curiosities and, sometimes, as resources. Although these societies introduced plants and insects from time to time, their main focus was on vertebrate animals (Lockwood *et al.* 2007). Documented activities related to acclimatisation of plants date back to the 1780s onwards with the increasing involvement of the *Jardin des Plantes du Roi* in Paris in the introduction of exotic species for commercial and agricultural purposes (Lever 2011). However, the first well-documented acclimatisation society was established in Paris in 1854 (*La Societé Zoologique d'Acclimatation*) for the introduction, acclimatisation and domestication of animals and for the cultivation of plants. Satellite societies were soon formed in several French regions and colonies. Shortly after, in 1860 the British founded the *Society for the Acclimatisation of Animals, Birds, Fishes, Insects and Vegetables* in London, with several regional groups established soon after (Lockwood *et al.* 2007). Important acclimatisation societies were also established between 1860 and the early 1900s in distant territories such as Australia, New Zealand, Hawaii and the USA. Despite the fact that these societies disappeared relatively quickly, they left a profound biological legacy, especially in island countries such as New Zealand.

From the second half of the 20th century onwards the introduction of alien species has increased dramatically in frequency and extent (Andreu & Vilà 2010) as human movements have become more global and international trade has increased (Thuiller *et al.* 2006, Andreu & Vilà 2010). Regarding plants, most of them have been introduced for agricultural, silvicultural, ornamental or medicinal purposes (Reichard & White 2001, Foxcroft *et al.* 2008). For instance, a great deal of human dietary needs in most parts of the world is met by species that have been introduced from elsewhere (McNeely 2006). No areas, however isolated, are totally free from human-assisted introduction, establishment and proliferation of alien species (Foxcroft *et al.* 2007).

Invasions and introductions have fascinated biologists for centuries. Introduced species interested Englishmen and their colonial counterparts by the early 1600s and natural historians, botanists, zoologists and ecologists from many countries have recorded ideas and observations regarding introductions from then on (Chew 2011). For instance, introduced and naturalised species were mentioned in the writings of several 19th century naturalists, such as Charles Darwin, Alphonse de Candolle, Joseph Hooker or Charles Lyell, being these species essentially curiosities at the time and not perceived as a major threat to global biodiversity (Richardson & Pyšek 2008). In the first half of the 20th century, when biological invasions started to become more widespread, Joseph Grinnell, Frank Egler, Herbert Baker, Carl Huffaker and other ecologists also published important contributions on introduced species (Simberloff 2011). However, some authors posit that biologists were slow to focus attention on the phenomenon at that time (Richardson & Pyšek 2007, 2008). It is widely stated that the systematic study of invasions was triggered by Charles Elton's book *The Ecology of Invasions by Animals and Plants* (Elton 1958). In this book Elton summarised a relatively obscure literature on the impact and spread of alien species that, at that time, was largely confined to the disciplines of entomology and plant pathology (Southwood & Clarke 1999). Despite Elton's book being a starting point for the study of biological invasions, research on this subject did not explode after its publication. It was not until the initiation of the SCOPE (Scientific Committee on Problems of the

Environment) programme on the ecology of biological invasions in 1983 when the modern field of invasion biology began to take shape (Drake *et al.* 1989, Richardson & Pyšek 2006, Davis 2011, Simberloff 2011). The SCOPE programme addressed three fundamental questions: which species invade, which habitats are invaded and how can we manage invasions. These three basic questions still form the basis of much of the current research on biological invasions. Research on this topic has grown dramatically over the last few decades since the initiation of this programme, with an increasing number of studies revolving around plant and animal invasions (Pyšek *et al.* 2004) that has resulted in an increasing confusion in terminology both regarding the proliferation of terms and the misuse of existing terminology (Richardson *et al.* 2000, Pyšek *et al.* 2004). For instance, Colautti & MacIsaac (2004) compiled a list of 30 terms used for alien species in the English literature on invasion ecology.

Nowadays, biological invasions are seen as one of the most significant environmental issues of the 21st century (McGeoch *et al.* 2010, Miller *et al.* 2010). They are a worldwide environmental concern as well as an important component of global change (e.g. Vitousek *et al.* 1997, Mack *et al.* 2000, Vilà *et al.* 2006) with serious ecological, economic and human welfare consequences (e.g. Williamson 1996, Pimentel *et al.* 2000, McNeely 2001, Vilà *et al.* 2011). Among the ecological impacts associated to biological invasions are the loss of biodiversity at local and regional scales via competition, predation or hybridisation (Manchester & Bullock 2000, Keane & Crawley 2002, McGeoch *et al.* 2010, Vilà *et al.* 2011), changes in community structure (Hejda *et al.* 2009) and changes in the biogeochemical cycles (Williamson 1996, Liao *et al.* 2008, Ehrenfeld 2010). The direct economic costs of invasive species can be due to losses in production of natural resources, such as crops, grazing areas or fisheries (Pimentel *et al.* 2000, Perrings *et al.* 2005), damage to infrastructures (Pimentel *et al.* 2000, Aguiar & Ferreira 2013) or subsequent costs arising from their control and management (e.g. Sampson 1994, Foxcroft & Richardson 2003, Shaw 2003). However, there is considerable controversy regarding the consideration of invasive species as drivers or as mere passengers of global environmental change (Didham *et al.* 2005, MacDougall & Turkington 2005), with some authors suggesting that they would not be the direct cause of the aforementioned biodiversity loss, but an indirect consequence of habitat modification that would be responsible for biodiversity loss.

Propagule pressure, invasiveness and invasibility

The invasion of an environment by introduced plant species is basically influenced by three factors: propagule pressure, species invasiveness and community/habitat/ecosystem invasibility. Firstly, propagule pressure has emerged as a central theme in invasion ecology. It is a concept that encompasses the variation in the quantity, quality, composition and rate of supply of alien organisms between the donor and recipient regions (Simberloff 2009, Richardson *et al.* 2011). According to Lockwood *et al.* (2005, 2007), propagule pressure incorporates estimates of the absolute number of individuals involved in any one release

Box 1. Terminology for alien plants used throughout this thesis following Pyšek *et al.* (2004).

Native plants (synonym: indigenous): Plants that have evolved in a given area or that arrived there by natural means without human involvement from an area in which they are native.

Alien plants (synonyms: exotic, introduced, non-native, non-indigenous): Plant taxa in a given area whose presence there is due to intentional or accidental introduction as a result of human activity, or which have arrived there without the help of humans from an area in which they are alien.

Casual alien plants (there are not consistently used synonyms in literature): Alien plants that may flourish and even reproduce occasionally in an area, but that eventually die out because they do not form self-replacing populations, and which rely on repeated introductions for their persistence.

Naturalised plants (synonym: established): Alien plants that sustain self-replacing populations over many cycles (for at least 10 years) without direct intervention by humans. They do not necessarily invade natural, semi-natural or human-made ecosystems.

Invasive plants: Subset of naturalised plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants and thus have the potential to spread over a considerable area.

event (propagule size) and the number of discrete release events (propagule number). Despite its importance, propagule pressure is one of the least documented aspects of invasion ecology (Lockwood *et al.* 2007), partly due to the difficulty in gathering information about it especially at the scale of large areas (e.g. habitats, regions). For this purpose, different quantitative surrogates have been used with reasonable success, such as human or road density, distance from human settlements or the proportion of urban, industrial or agricultural land (e.g. Chytrý *et al.* 2008, Gassó *et al.* 2009).

Secondly, species invasiveness refers to the features of an alien organism, such as life-history traits and modes of reproduction, which define their capacity to invade, i.e., to overcome various barriers of invasion (Richardson *et al.* 2011) (Figure 3). Although some studies have identified characteristics associated to plant growth, reproductive potential, ability to reproduce vegetatively or dispersal as important correlates of invasiveness (see Pyšek & Richardson 2007 for a review), these traits need to be related to the features of the invaded communities, geographical conditions, and a set of external factors, including propagule pressure (Pyšek & Richardson 2008). As Richardson & Pyšek (2006) indicate, finding a set of traits associated to invasiveness that would apply to all vascular plants is an unrealistic aim. However, what determines invasiveness of alien organisms is still central in invasion ecology.

Finally, community/habitat/ecosystem invasibility consists of those properties of the system in question that affect exotic species survival and thus determine its inherent vulnerability to invasion (Lonsdale 1999). As Davis *et al.* (2005) point out, this idea dates back to Elton (1958) where the author refers to the ecosystem's "vulnerability to invading species" when talking about natural habitats on small islands (p. 147), although he did not use the term "invasibility". One factor that has been consistently associated to an increased invasibility is the natural and/or human-driven level of disturbance (e.g. Davis *et al.* 2000), which would reduce competition with the resident vegetation and would thus provide more opportunities for alien colonisation and establishment. Invasibility is not a static property, but one that varies in time (Davis *et al.* 2005). At this point, it is important to make the distinction between "invasibility" and "level of invasion", the latter being the actual number or proportion of aliens in a given system (Chytrý *et al.* 2008). Differences in the level of invasion among different systems may be the result of a higher system's invasibility or may simply result from variation in propagule supply among these systems (e.g. Eschtruth & Battles 2011), implying that "more invaded" does not necessarily mean "more invasible".

The invasion process in plant species

The status of a plant species in a given region is determined by three factors (Pyšek & Richardson 2008): (1) whether it is native or alien to that region; (2) when was it introduced and (3) its degree of naturalisation/invasion. On occasions, species of unknown biogeographical history cannot be reliably ascribed as native or alien. Those taxa are termed 'cryptogenic' (Carlton 1996, Richardson *et al.* 2011). For those plants whose alien status is clear, the process of plant invasion has been described as a continuum in which introduced plants have to overcome a series of geographical, environmental and biological barriers in order to invade a new territory (Richardson *et al.* 2000) (Figure 3). The factors allowing plant species to progress along this continuum and their relative importance will vary depending on the barrier in question. Although there are no clearly defined lines separating these barriers, they represent biologically identifiable steps along the process of becoming an invader.

All alien plant species originally begin as individuals (propagules) that are picked up from their native range (donor region), transported to a new area (recipient region) and released into the wild (Lockwood *et al.* 2007). These species can be introduced into a new area intentionally or accidentally, the latter case being more frequent in the past than today as a result of seed cleaning techniques and quarantine inspection services (Mack & Lonsdale 2001). In general, for both types of introductions, higher numbers of propagules increase the likelihood that species will survive transport (Lockwood *et al.* 2005, 2007). Once transport has removed geographical barriers, many of the introduced species that survive transport fail to survive in the recipient region, while some of them manage to deal with local environmental and biotic conditions and even reproduce sexually or vegetatively. These species, called 'casual', rely on repeated introductions (i.e., on propagule pressure) for their persistence in the new region (Richardson & Pyšek 2006) (Box 1). The reason behind this is that initial alien populations are supposed to consist of a small number of

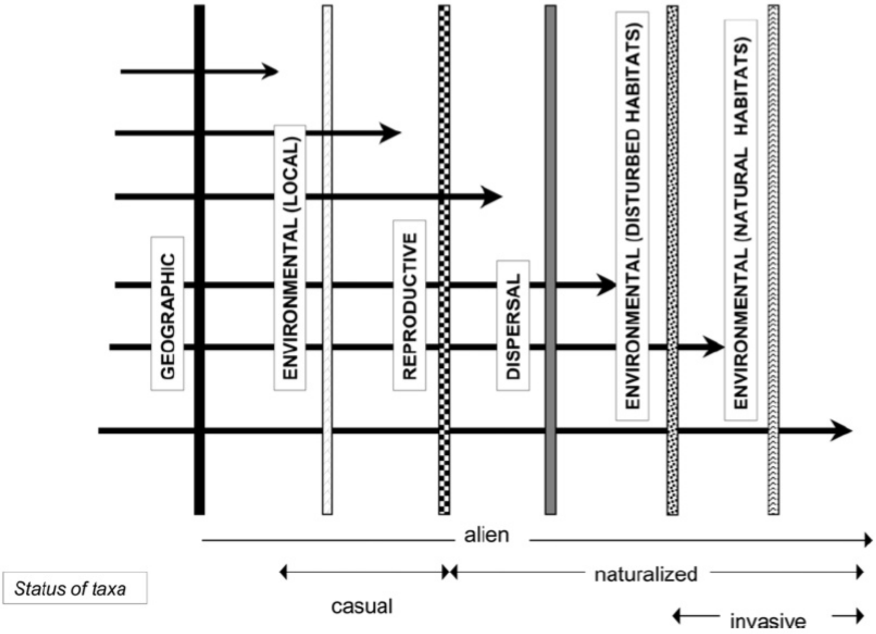

Figure 3. The introduction-naturalisation-invasion continuum in which introduced plant species have to overcome various barriers in order to become casual, naturalised and invasive in the recipient region. [Reprinted from Richardson D.M. & Pyšek P. 2006: Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* **30**: 409-431].

individuals. These small populations, as a result of environmental (e.g. floods, droughts, fires, altered herbivory) or demographic stochasticity (e.g. lack of genetic variability, Allee effects) (Theoharides & Dukes 2007) will die out unless more propagules arrive as they do not achieve a sufficient positive population growth needed to form self-sustaining populations over long periods. Examples of Allee effects include, for outcrossing plant species, the failure to find a mate at low densities or the failure to attract pollinators when there are few conspecifics nearby (Lockwood *et al*. 2007). On the contrary, those plant species that attain sufficient population growth in the recipient region that allows them to form self-sustaining populations and cope with environmental and demographic stochasticity are called 'naturalised'. Thus, at this stage alien plants do not rely on human intervention to persist in the recipient region. During this establishment stage, biotic filters that constrain alien population size, such as competition or interactions with other trophic levels (Theoharides & Dukes 2007), may be more important than environmental conditions and propagule pressure, although they will interact with them. A subset of naturalised plant species will have the ability to expand their geographic range by spreading at considerable distances from the site of introduction. These species, called 'invasive', will thus have the ability to cope with the abiotic environment and the biota in the general area. According to Theoharides & Dukes (2007), the regional spread that convert a naturalised plant species to invasive is influenced by several factors, such as landscape heterogeneity, the size and distribution of suitable habitat patches for the establishment of new populations, the distance between patches or the species' dispersal ability. In relation to the latter, long-distance dispersal (LDD) is of utmost importance at the spread stage (e.g. Nehrbass *et al*. 2007). This LDD may occur by natural means following species ability to disperse over long distances. However, humans play an important role in the movement of alien species within the recipient region, either intentionally (e.g. horticultural and ornamental species) or accidentally (e.g. seeds clung to car tyres or people's clothes and shoes).

It is important to highlight that a lag phase of variable duration (from a few generations to more than 100 years) often takes place between the establishment and the beginning of the phase of exponential increase that characterises the spread (Figure 4). Some reasons have been proposed for explaining the duration of lag phases, such as Allee effects, the existence of a threshold population size for human detection, the time needed for a species to find optimal habitat patches where population growth and spread would trigger, changes in the environment and, again, propagule pressure (Simberloff 2009). Lag phases may lead us to think that some alien species are apparently innocuous when in

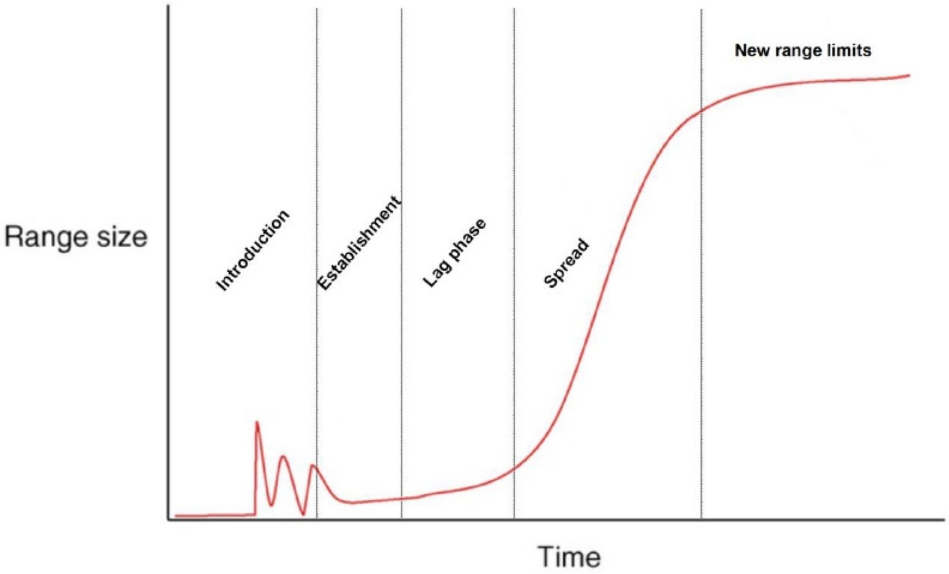

Figure 4. Key stages in the invasion process in relation to the change in range size over time. Initial alien populations in the non-native range are subjected to marked highs and lows as a result of environmental and demographic stochasticity and new introductions. Establishment takes place when these populations achieve a sufficient positive population growth and become self-sustaining without human intervention. A lag phase of variable duration exists between the establishment and the phase of exponential spread that characterises invasive species. Finally, range size stabilises after the phase of exponential spread. [Modified from Prentis *et al*. (2008): Adaptive evolution in invasive species. *Trends in Plant Science* **13**: 288-294].

reality they are on their way to becoming invasive. It has also been suggested that, as a result of lag phases, new invasions would continue to emerge even if introductions ceased because naturalised species that are already present would go a step further entering the invasion stage. This concept has been called 'invasion debt' (Richardson *et al.* 2011, Rouget *et al.* 2016).

Although thousands of plant species have been –and are still- moved across continents, only a small proportion of them become invasive in the introduced range. In relation to this, the Tens Rule (Williamson & Brown 1986, Williamson 1996, Williamson & Fitter 1996, Richardson & Pyšek 2006) predicts that 10 % of imported species become casual, 10 % of casuals become naturalised and 10 % of naturalised plant species become invasive, i.e., only one introduced species in a thousand would become invasive. This rule, however, is potentially misleading since it is usually used as a quantitative tool and it sometimes poorly fits empirical data, especially as we progress through invasion stages (Lockwood *et al.* 2007). Despite the controversy surrounding the Tens Rule, it has been suggested that deviations from this rule would indicate taxa with higher or lower invasiveness and regions/habitats with lower or higher invasibility (Richardson & Pyšek 2006).

Theories and hypotheses in plant invasion

Several theories and hypotheses have emerged in plant invasion biology that can be linked to the aforementioned naturalisation-invasion continuum. Some of these are related to species invasiveness, whilst others focus on community invasibility. At the species level, one of the most robust generalisations is that the probability of invasion increases with residence time, i.e., the time since the introduction of a species into a new region. Because the introduction date is usually not known or inaccurate, the 'minimum residence time' has been proposed (Rejmánek 2000), which is closely associated with the lag phase mentioned above. The 'Baker's rule' (Baker 1955) states that those plant species capable of uniparental reproduction (i.e., self-pollinating species) are more likely to establish populations from a small number of individuals. Self-pollination would allow these species to increase their population size, which would allow them to cope better with environmental and/or demographic stochasticity, but without increasing genetic variability. 'Darwin's naturalisation hypothesis' (DNH), based on the observations of de Candolle (1855), suggests that those alien species with no native congeners in the introduced range are more likely to establish and become invasive (Darwin 1859). He stated that "as species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of different genera". In other words, this increased likelihood of establishment in the absence of closely related taxa would be the result of a more intense competition among congeners given an expected higher similarity among them. The ‘enemy release hypothesis’ (ERH) posits that plant species, when introduced to an exotic region, experience a decrease in regulation by herbivores and other natural enemies that regulate their populations in their native range (Williamson 1996, Keane & Crawley 2002). As a result of this, alien plants would have better chances of establishing and becoming dominant in the introduced range due to an increased competitive ability. A modification of ERH, the ‘resource-ERH’ hypothesis (Blumenthal 2006) suggests that enemy release, in combination with high resource availability, would facilitate the establishment and invasion of fast-growing alien plants adapted to high resource availability. Also closely related to ERH is the ‘evolution of increased competitive ability’ (EICA) hypothesis, which predicts that those plant species introduced to a region that lacks their usual enemies will experience a selection towards individuals that shift resource allocation from enemy defence to faster growth and reproduction (Blossey & Notzold 1995).

Important theories and hypotheses have also emerged at the community level. The ‘theory of fluctuating resources’ (Davis *et al*. 2000, Davis & Pelsor 2001) states that a plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources, such as water, nutrients or light. Increases in resource availability, either by resource enrichment or release, would occur intermittently and should coincide with the availability of invading propagules in order to result in invasion. Disturbance, either natural or human-induced disturbance, would play a central role by reducing the rate of resource use of resident vegetation (e.g. by a partial or total elimination of plant biomass) and/or by increasing the amount of available resource (e.g. increases of N and P associated to fertilisation). The ‘biotic resistance hypothesis’ (also termed the ‘diversity resistance hypothesis’) was first suggested by Elton (1958) and states that a negative relationship exists between native species diversity and community invasibility. This relationship would arise from a more complete use of available resources and stronger intra- and interspecific interactions expected in more diverse communities as less empty niches would be available (Richardson & Pyšek 2006). This hypothesis has been usually tested by exploring the relationship between the number of native and alien species, which has usually been found to be negative at small spatial scales but positive at larger scales. This discrepancy, termed ‘invasion paradox’ (Fridley *et al*. 2007) is mostly due to the spatial scale of observation and would imply that, at large scale, the same abiotic conditions that promote high native diversity would also support high alien plant diversity (Levine 2000, Brown & Peet 2003). In relation to biotic resistance, D’Antonio *et al*. (2001) proposed a model in which they represent resistance as a continuum rather than a static property. Consequently, communities may fluctuate between more or less resistant states through time depending on different external forces (D’Antonio *et al*. 2001, Lockwood *et al*. 2007). Most importantly, where a community lies along this continuum would determine the propagule pressure necessary for a plant species to establish self-sustaining populations. It has also been proposed that the presence of already established alien plant species in a community or ecosystem may facilitate further invasions by other alien species.

This concept, termed 'invasional meltdown' (Simberloff & Von Holle 1999), would be closely linked to the conceptual model of D'Antonio *et al.* (2001) in the sense that the established alien species could weaken community resistance, thus facilitating the invasion by other alien species by lowering the propagule pressure necessary for their invasion.

On the basis of the above, it becomes apparent that the process of plant invasion has an overwhelming theoretical background which aims to shed light to this extremely complex process affected by a myriad of interacting biotic, abiotic and human factors.

Plant invasions in riparian systems

It is widely accepted that there is a considerable variation among habitats/ecosystems in the extent of invasion (i.e. level of invasion) by alien species (e.g. Lonsdale 1999, Chytrý *et al.* 2005, 2008, Vilà *et al.* 2007, Pyšek *et al.* 2010a). Several explanations have been proposed for habitat differences in invasion, such as the availability of resources unexploited by resident species (Davis *et al.* 2000, Davis & Pelsor 2001), differences in propagule pressure of alien species (Lonsdale 1999, Chytrý *et al.* 2008, 2009), and differences in disturbance levels (Chytrý *et al.* 2005, Magee *et al.* 2008). Some clear patterns have emerged: anthropogenic habitats tend to exhibit highest levels of invasion (Chytrý *et al.* 2009, Affre *et al.* 2010, Pyšek *et al.* 2010b), islands are more invaded than continents (Lonsdale 1999, Gimeno *et al.* 2006), temperate mainland regions are more invaded than tropical mainland (Pyšek *et al.* 2010b) and habitats with a higher number of native species harbour a higher number of alien species (Lonsdale 1999, Stohlgren *et al.* 1999). In relation to riparian habitats, these have been found to show high levels of plant invasion (Campos *et al.* 2013).

The level of plant invasion is closely related to habitat invasibility, and riparian habitats have repeatedly been documented as being highly vulnerable to invasion by alien plants (e.g. Planty-Tabacchi *et al.* 1996, Hood & Naiman 2000, Vilà *et al.* 2007, Pyšek *et al.* 2010a). Some authors have pointed out that the same factors that promote high native plant species richness in riparian zones may also increase susceptibility to invasion by alien plants (e.g. Hood & Naiman 2000, Tabacchi & Planty-Tabacchi 2005, Magee *et al.* 2008). This high vulnerability to plant invasions has been linked to high rates of hydrological disturbances that make space and resources available (e.g. Naiman & Décamps 1997, Hood & Naiman 2000, Planty-Tabacchi *et al.* 2001, Tickner *et al.* 2001), high nutrient levels (Tickner *et al.* 2001, Richardson *et al.* 2007, Schnitzler *et al.* 2007), efficient dispersal of plant propagules by water (e.g. Thébaud & Debussche 1991, Johansson *et al.* 1996, Nilsson *et al.* 2010, Jacquemyn *et al.* 2010), or light availability (Parendes & Jones 2000). Besides natural factors, plant invasions in riparian systems are enhanced directly or indirectly by human-mediated activities (Aguiar *et al.* 2001, Richardson *et al.* 2007), such as introduction of alien propagules in catchments (Richardson *et al.* 2007, Walker *et al.* 2009), river regulation (e.g. Aguiar *et al.* 2001, Catford *et al.* 2011; but see Mortenson & Weisberg 2010), urbanisation

(Aguiar *et al*. 2007, Säumel & Kowarik 2010, Sung *et al*. 2011), agriculture (Ferreira & Moreira 1995, Aguiar *et al*. 2007, Meek *et al*. 2010) or livestock grazing (Lunt *et al*. 2012).

River degradation, especially in industrialised countries, is linked to the presence of invasive alien plants, which constitutes a significant threat to the ecological integrity of river ecosystems. Specific impacts of invasive plants in riparian systems include the decrease in native plant richness (e.g. Hulme & Bremner 2006, Maskell *et al*. 2006, Cushman & Gaffney 2010), the alteration of river channel morphology (Rowntree 1991, Tickner *et al*. 2001), stream clogging caused by aquatic species such as *Eichhornia crassipes* (Ruiz Téllez *et al*. 2008, Aguiar & Ferreira 2013) or flow reduction as a consequence of increased transpiration, with several examples such as *Acacia mearnsii* and *Tamarix* spp. (Tickner *et al*. 2001, Dye & Jarmain 2004). Riparian systems can also act as foci of some alien plant species for the subsequent invasion of adjacent terrestrial landscapes (Richardson *et al*. 2007) as well as a conduit for the dispersal of alien plants through otherwise hostile landscapes (Pyšek & Prach 1995, Richardson *et al*. 2007). In addition to the ecological threats to biodiversity, alien plants can reduce key ecosystem services provided by riparian zones (Vilà *et al*. 2009, Meek *et al*. 2010).

Description of the study area

The study area for the present thesis encompasses those river basins between the Nansa and the Bidasoa river basins, which are spread across the autonomous regions of Cantabria, Castile and León, Basque Country and Navarre in northern Spain (Figure 5). This territory is included in the Eurosiberian biogeographic region, which covers a great part of the European continent from Eastern Europe to northern Spain and Portugal, including southern Scandinavia and the British Isles. Within the Eurosiberian region, it belongs to the European Atlantic province and the Basque-Cantabrian sector (Rivas-Martínez 2007). Climate and riparian vegetation in the study area are quite homogeneous (see below).

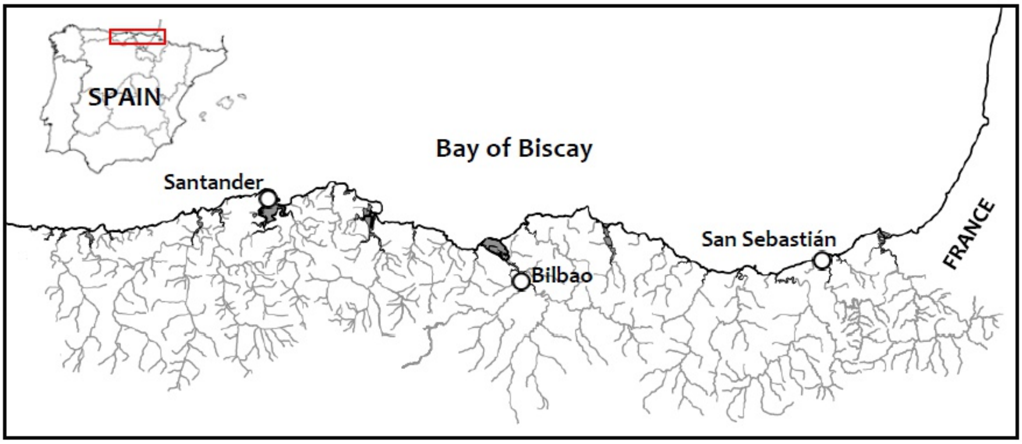

Figure 5. Study area.

Cantabrian river basins show a great variety of lithological substrata and drain areas ranging from 100 to 1000 km². The length of Cantabrian streams ranges from 15 to 70 km as a consequence of their sources in the Cantabrian Mountain Range being in close vicinity to their mouths in the Bay of Biscay (Orive & Rallo 2002), implying that they are rather short in comparison with Mediterranean rivers and streams of the Iberian Peninsula.

An important feature of the study area is the high degree of human-driven disturbance. Human population is especially concentrated around the cities of Santander, Bilbao and Donostia-San Sebastián, though a significant population increase has occurred in the last decades along all coastal areas and the lower sections of many river basins (Figure 6). Besides human population, a remarkable degree of industrial development can be observed once again in coastal areas and the lower sections of the larger streams. Industry, along with farming and forestry, constitute the main land uses of the study area. Additionally, a dense transport network, including high-traffic roads (i.e., highways and national roads) and local and regional roads, has emerged in the last decades (Figure 7). Landscape is thus highly disturbed and riparian areas are heavily modified since many of the aforementioned activities are closely associated to these environments, resulting in many alien plant species reaching and potentially colonising riparian areas.

Climate

Climate in the Cantabrian watershed can be described as temperate oceanic and is mainly determined by its vicinity to the sea, latitude –halfway between the Equator and the North Pole where hot and wet air masses interact resulting in a marked instability- and longitude –its location in the western edge of the European continent results in this territory being highly exposed to western winds from the Atlantic ocean. Mean annual temperature is around 14°C decreasing with altitude and rainfall is spread throughout the year though with lower precipitation in summer months, especially in the western area. Mean annual precipitation ranges from 1000 to ca. 3000 mm (Figure 8). It is important to highlight the considerable local climatic variability resulting from the steep topography (Loidi *et al.* 2005, Durán 2014). With respect to the bioclimatic classification, three belts are distinguished regarding temperature –thermotemperate, mesotemperate and supratemperate-, along with two pluviometric belts –humid and hyperhumid- (Rivas-Martínez 2007, Loidi *et al.* 2011).

Riparian vegetation

Riparian vegetation in all the streams studied corresponds to the Cantabrian-Basque and Oviedese fluvial geoseries (Biurrun 1999, Loidi *et al.* 2011), which characterises the perifluvial and riverbed environments of Cantabrian streams from the sea level to their sources in the Cantabrian Mountain Range. The distribution area of this geoseries covers the territory between central Asturias in northern Spain and the French Basque Country,

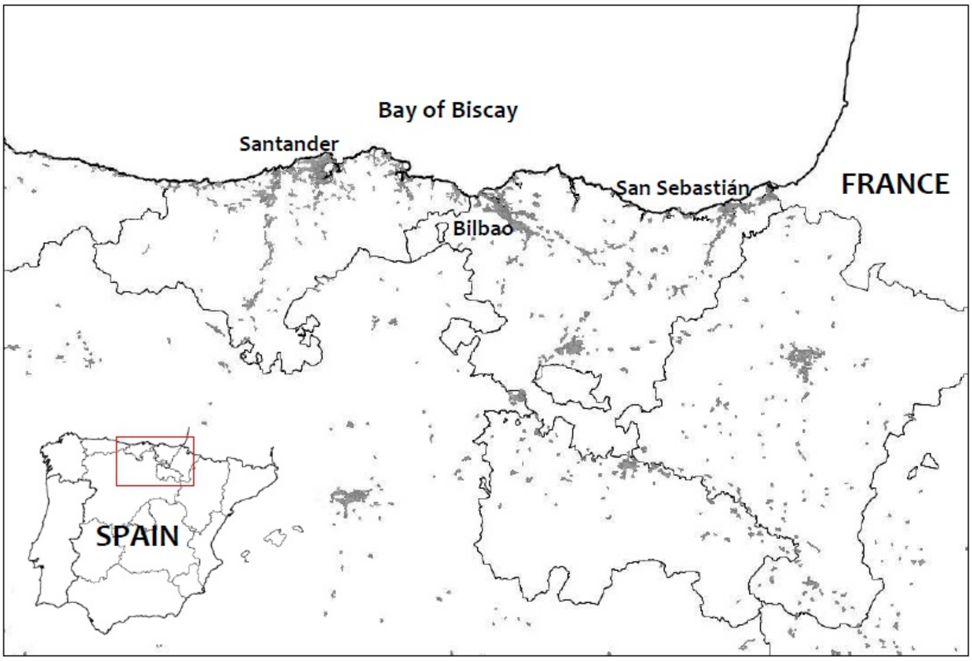

Figure 6. Urban, industrial and commercial areas (grey patches) in the study area based on Spain's CORINE Land Cover Map of the year 2006. Available at: http://centrodedescargas.cnig.es/CentroDescargas.

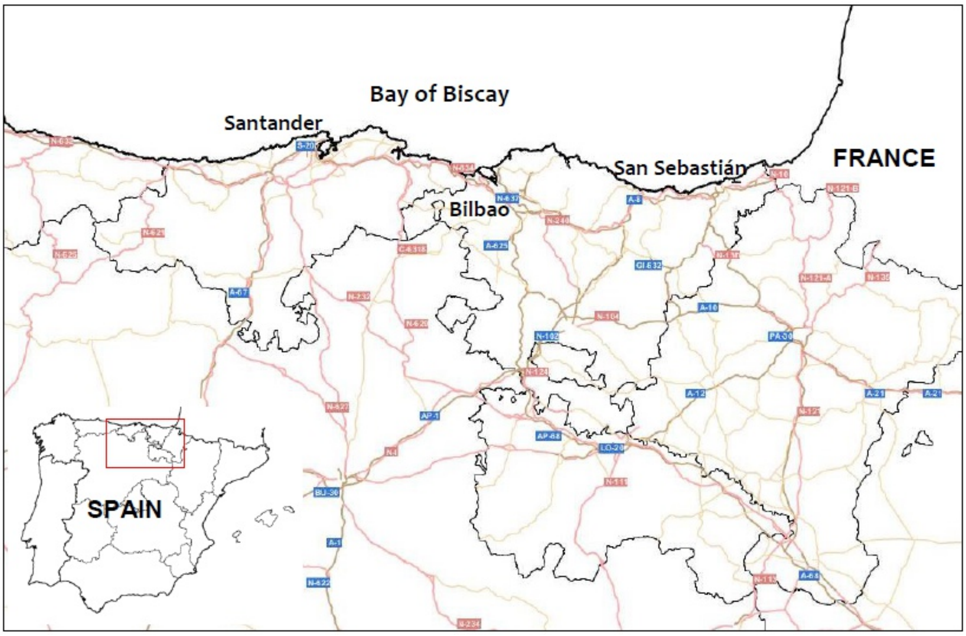

Figure 7. Road network of the study area depicting highways and national roads (i.e., high-traffic roads). Source: Spatial Data infrastructure of Spain (www.idee.es).

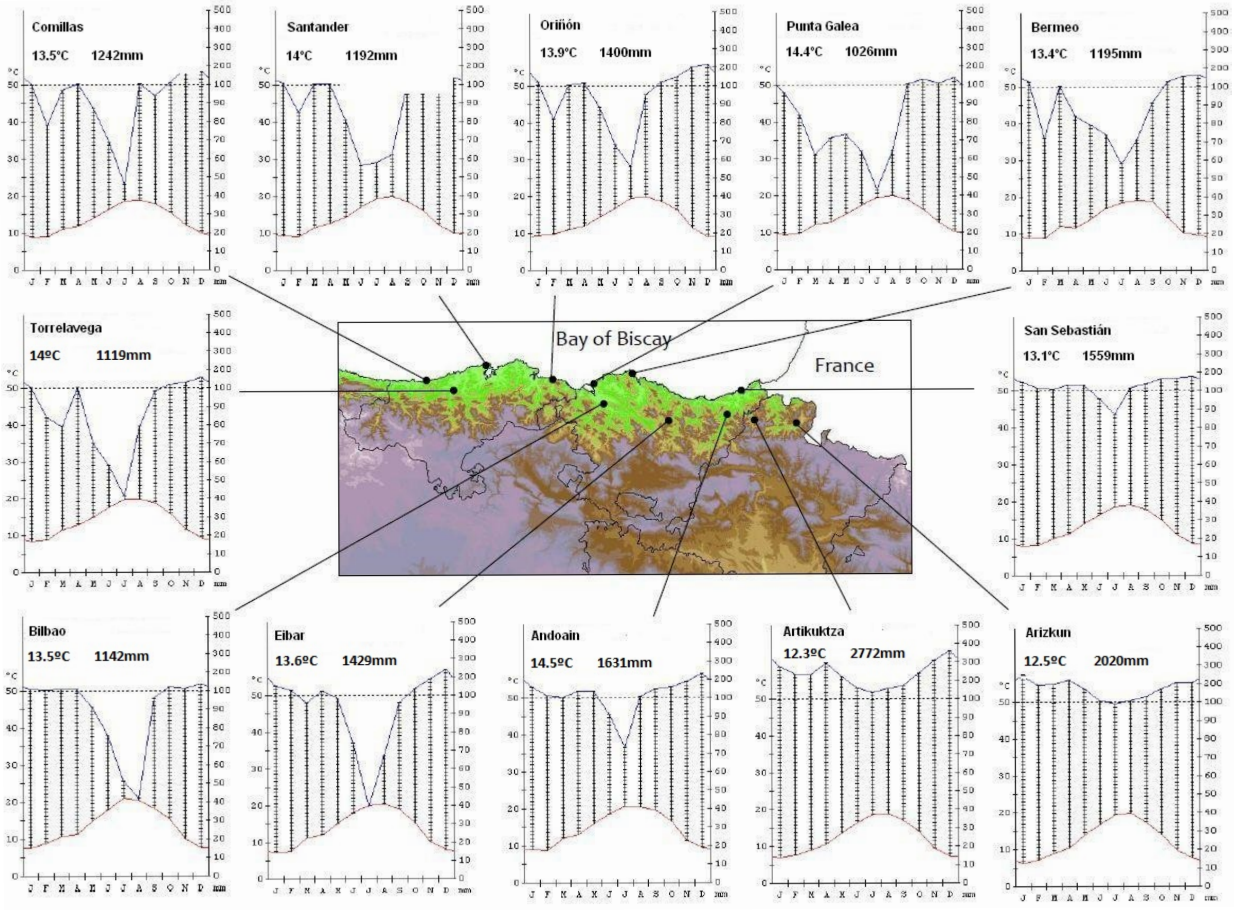

Figure 8. Climate diagrams of some localities within the study area including mean annual temperature and total annual rainfall (source: www.ucm.es/info/cif). The colour map represents elevation above sea level based on a Digital Elevation Model of Spain available at www.idee.es. Green: 0-250 m; beige to dark brown: 250-800 m; lilac/purple: 800-2000 m; white: >2000 m.

and it consists of several plant associations and plant communities that grow on three distinct environments: riverbed, riverbank and floodplain (Figure 9).

1. Riverbed communities

Riverbed vegetation encompasses aquatic (s.s.), helophytic and river bar communities. Aquatic communities are notably scarce and occur almost exclusively on the widest river valleys of the study area and include: (1) communities dominated by *Ranunculus penicillatus* in moderately rapid waters on stony or rocky soils; (2) submerged backwater communities dominated by several species of the *Potamogeton* and *Zannichellia* genera (*Potamogeton perfoliatus*, *P. crispus*, *P. trichoides*, *Zannichellia pedunculata*), with duckweeds (*Lemna minor*, *L. gibba*) occasionally present (Loidi *et al*. 2011).

Helophytic communities, on the other hand, are constituted by plant species that are partly submerged in water and that regrow from buds below the water surface (Hickey & King 2000). Four helophytic associations and communities can be distinguished in the study area: (1) sedge communities of the *Eupatorio cannabini-Caricetum elatae* association, with *Carex elata*, *Lycopus europaeus*, *Lysimachia vulgaris* and *Cyperus longus*, amongst others, are typical of rocky riverbeds with fast growing water; (2) reed beds of the *Typho angustifoliae-Phragmitetum australis* association, which are dominated mainly by *Schoenoplectus lacustris* in running waters on gravel substrate; (3) communities dominated by *Sparganium erectum* ssp. *erectum* growing on clay soils; and (4) small-sized helophyte communities of the *Glycerio declinatae-Apietum nodiflori* association, dominated by *Apium nodiflorum* and *Nasturtium officinale*, with other characteristic species such as *Glyceria fluitans*, *G. declinata*, *Veronica beccabunga* and *V. anagallis-aquatica* (Loidi *et al*. 1997). The latter community is especially associated to nutrient-rich stretches near towns and villages.

Finally, river bar communities are those that grow on elevated areas of sand, gravel or mud built up along the banks of a river or stream (Morris 1992) which are submerged for

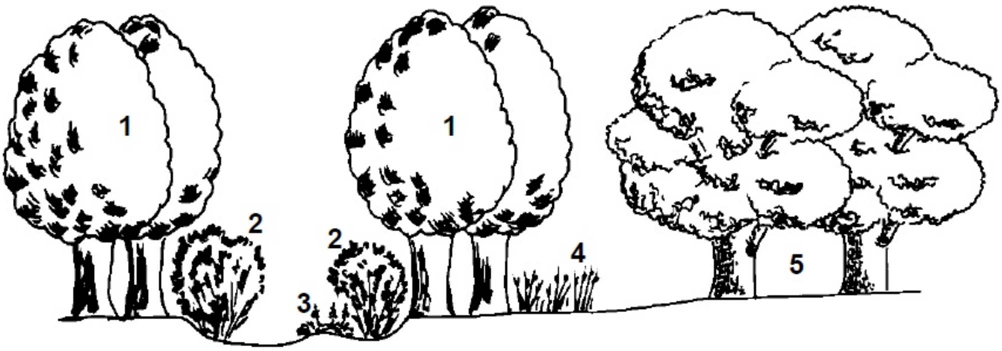

Figure 9. Schematic representation of the Cantabrian-Basque and Oviedese fluvial geoseries. 1: alder forest; 2: river bar willow communities; 3: river bar herbaceous communities; 4: wet meadows; 5: ash forest.

most of the year and emerge during summer until early autumn when rainfall decreases. Two main river bar plant communities can be distinguished in the most flooded part: perennial grasslands dominated by the alien *Paspalum distichum* and nitrophilous communities of macrotherophytes. The former can be found in the lower sections of the Cantabrian streams (thermo- and mesotemperate levels). It occupies muddy to sandy soils that accumulate on the riverbed and which remain flooded for long periods. Noteworthy is the fact that another invasive species, *Cyperus eragrostis*, may attain high abundances in this community. Campos (2010) proposed a new phytosociological association for these Cantabrian riverbed grasslands, *Cypero eragrostidi-Paspaletum distichi*. On the other hand, macrotherophyte communities grow adjacent to the previous perennial grasslands on more sandy and stoney river bars that are water-free for longer periods during the summer. These communities are dominated by species of *Persicaria*, especially *P. lapathifolia* and *P. maculosa*, with *P. mitis* and *P. hydropiper* gaining importance on sandy-muddy soils. *Bidens tripartitus* and the North American neophyte *B. frondosus* can also be important elements (see below). Macrotherophyte communities have been included in the *Xanthio strumarii-Polygonetum persicariae* association in nearby Mediterranean rivers of the Ebro basin. However, Campos (2010) proposed a new association for Cantabrian communities, *Bidenti frondosae-Polygonetum lapathifolii*, which would differ from the Mediterranean one in the relative abundance of the dominant *Persicaria* species, the presence of *B. frondosus* and the absence of some taxa such as *Atriplex prostrata*, *Datura stramonium* and *Cuscuta campestris*. Besides *B. frondosus*, another North American neophyte, *Persicaria pensylvanica*, is currently expanding its range on these communities across the study area. On the other hand, the highest part of the river bars is potentially occupied by riparian willow communities of the *Salicetum angustifolio-albae* association dominated by *Salix alba* and several shrubby willow species such as *S. atrocinerea*, *S. purpurea* subsp. *lambertiana* and *S. triandra* subsp. *discolor*. These willow communities can be colonised by seedlings of alien tree species that grow on nearby alder forests, such as *Platanus hispanica*, *Populus x canadensis* or *Pterocarya stenoptera*, as well as other alien species from adjacent river bar communities, such as *Paspalum distichum* or *Cyperus eragrostis*. Additionally, two types of herbaceous communities can be found occupying the space belonging to these willow communities. First, native megaforb communities with *Mentha aquatica*, *M. suaveolens*, *Epilobium hirsutum*, *Lythrum salicaria* and *Eupatorium cannabinum*, among others, which are sometimes invaded by the North American aster *Helianthus x laetiflorus*. Second, heterogeneous communities with a remarkable presence of species of the *Stellarietea mediae* phytosociological class, where several alien species such as *Amaranthus* spp., *Lycopersicon esculentum*, *Echinochloa crus-galli*, *Dysphania ambrosioides* or *Conyza bilbaoana* may attain high cover values.

2. Riverbank vegetation

Riverbank vegetation in these rivers is potentially formed by alder forests (*Alnus glutinosa*) belonging to the *Hyperico androsaemi-Alnetum glutinosae* association in lowland streams and calcareous ravines and to the *Stegnogrammo pozoi-Alnetum glutinosae* association in siliceous ravines (Biurrun *et al*. 2016). Alder forests grow on permanently wetted soils and show an intricate and dense aspect resulting in these forests being notably dark. Furthermore, as a consequence of the narrowness of many Cantabrian river valleys, alder forests are made up of just one or two lines of trees in many cases. Tree canopy is almost exclusively constituted by alders, with ashes and willows (*Salix atrocinerea*) occasionally present. A remarkable characteristic of alder trees is the establishment of a symbiotic interaction with nitrogen-fixing bacteria of the *Actinomyces* genus, which increases the soil content of this limiting element. Subarboreal strata are profusely developed as a result of the high nutrient availability and water soil content. The shrubby component is abundant and rich in thorny species, such as *Crataegus monogyna*, *Prunus spinosa*, *Rubus ulmifolius*, *R. caesius* and *Rosa* spp. Other important shrubs are *Cornus sanguinea*, *Corylus avellana*, *Euonymus europaeus*, *Ligustrum vulgare*, *Sambucus nigra* and *Frangula alnus*, the latter especially frequent in siliceous basins. The vine component, dominated by *Clematis vitalba*, *Hedera hibernica* and *Tamus communis*, is very important as well. Beneath the subarboreal strata there is a rich and diverse herbaceous stratum with giant sedges and numerous ferns among other species, such as *Carex pendula*, *C. remota*, *Circaea lutetiana*, *Schedonorus giganteus*, *Myosotis martini*, *Primula elatior* and *Silene dioica*. Other typical herbaceous species with a higher ecological breadth are *Ajuga reptans*, *Asplenium scolopendrium*, *Athyrium filix-femina*, *Brachypodium sylvaticum*, *Carex sylvatica*, *Dryopteris affinis*, *D. borreri*, *Euphorbia amygdaloides*, *Geranium robertianum*, *Hypericum androsaemum*, *Lamium galeobdolon*, *Lathraea clandestina*, *Lysimachia nemorum*, *Oxalis acetosella*, *Polystichum setiferum*, *Potentilla sterilis*, *Stellaria holostea* and *Viola reichenbachiana*. Alder forests growing on siliceous ravines are not so diverse, and are defined by the abundance of acidophilous ferns such as *Osmunda regalis* and *Blechnum spicant* and the presence of some thermophilous endangered ferns such as *Stegnogramma pozoi* and *Woodwardia radicans* (Biurrun *et al*. 2016).

Regarding alien plants, several fast-growing tree species cultivated along the riverbanks can be found in Cantabrian alder forests, such as *Platanus hispanica*, *Populus x canadensis*, *Pterocarya stenoptera* or *Acer negundo* (Campos 2010), which can sometimes even replace the native forest. Furthermore, the understory is often invaded by the South African geophyte *Crocosmia x crocosmiiflora*, which creates dense patches through a highly efficient vegetative propagation (Herrera & Campos 2010). Alder forests show a moderate to high degree of human disturbance in the study area and when they are removed due to natural or human-induced disturbances, that space is potentially occupied by two types of plant communities: (1) willow formations (*Salix atrocinerea*) with ashes, elders (*Sambucus nigra*, *S. ebulus*) and numerous blackberries (*Rubus ulmifolius*, *R. caesius*) and (2) a mosaic of herbaceous communities of varying composition depending on local conditions created by human activities (grazing, trampling, etc.): megaforb communities, wet meadows, etc. However, a community dominated by the Asian herbaceous neophyte *Fallopia japonica* frequently replaces alder forests subjected to a high degree of human-driven degradation in low and middle sections of the wider Cantabrian streams, such as Oria, Urola, Deba and Ibaizabal. This community belongs to the *Reynoutrietum japonicae* association and consists of a dense *F. japonica* formation of up to 2.5 m high with some vines occasionally present (Campos 2010). Other herbaceous species are restricted to gaps and edges where light is available.

3. Floodplain forests

Adjacent to alder forests, ash forests of the *Polysticho setiferi-Fraxinetum excelsioris* association constitute the potential vegetation on the floodplains, reaching their optimum in the widest river valleys. Both types of forests are the most complex and species-rich communities of the study area. Ash forests are periodically flooded but only during large floods. The tree canopy consists of several species, such as *Fraxinus excelsior*, *Acer pseudoplatanus*, *A. campestre* and *Ulmus glabra* (Loidi *et al*. 1997), which dominate in these periodically disturbed areas. The shrubby stratum is dense with many thorny Rosaceae species along with *Prunus avium*, *Cornus sanguinea*, *Euonymus europaeus* and *Corylus avellana*, among others. Ivy (*Hedera hibernica*) dominates the vine component and the herbaceous stratum is notably species-rich, with some abundant species such as *Hypericum androsaemum*, *Pulmonaria longifolia*, *Arum italicum*, *Primula acaulis* or *Lamium galeobdolon* as well as some abundant ferns, such as *Polystichum setiferum*, *Dryopteris affinis* and *Athyrium filix-femina*.

Two alien plant species which are becoming increasingly widespread in some Cantabrian river basins, the South American hemicryptophyte *Tradescantia fluminensis* and the Central Asian therophyte *Impatiens balfourii*, can be quite frequent in ash forests. As a result of human activity, ash forests are frequently replaced by two types of plant communities. First, shrubby vegetation consisting of thorny species belonging to the Rosaceae family, such as *Rubus ulmifolius*, *R. caesius*, *Crataegus monogyna*, *Prunus spinosa* and several species of *Rosa* spp. which rapidly spread following tree removal. Second, grasslands dominated by *Brachypodium pinnatum* ssp. *rupestre* and *B. sylvaticum* are created when that shrubby vegetation is removed.

Main objectives of the thesis

The present thesis explores several aspects regarding the invasion by alien plant species in temperate streams of northern Spain. Specific objectives include:

1. Determine which alien plant species can be found in the study system and their biogeographical origin, with a special focus on those widely spread species that could exert a higher ecological and/or economic impact.

2. Detect which factors, both environmental and human-related factors, influence plant invasion at different spatial scales.

3. Test whether differences exist in the level of plant invasion among the different riparian habitats.

4. Assess the effect of alien plant species on the phylogenetic structure and diversity of the two most characteristic riparian habitats, namely riparian forests and river bar communities.

Thesis structure

The first chapter contains the results of a pilot study conducted in Cantabrian streams of Bizkaia and Gipuzkoa at several points included in the Ecological Status Monitoring Network of the Basque Country's rivers. The level of plant invasion at these sites (i.e., the proportion of alien plant species in relation to all plant species) was studied in relation to the ecological status and the anthropogenic pressure. In the second chapter, specific drivers of plant invasion including natural (e.g. climate, stream features) and human-related characteristics (e.g. land use and distance to roads and human settlements) were determined at fine scale (i.e., site scale) and broad scale (i.e., basin scale). For this purpose, 80 sites included in 16 Cantabrian river basins were randomly studied. The third chapter is habitat-focused and deals with the effects of the presence and abundance of alien plants on phylogenetic diversity of river bar communities and riparian forests, as these are the most common habitats in the Cantabrian streams. Finally, chapters 4 and 5 deal with essentially botanical aspects. Chapter 4 contains new records at provincial and/or regional scale of some native and alien species that were recorded during field samplings, whilst chapter 5 includes a review of the genus *Conyza* in north Spain using specimens collected during the conduct of this thesis as well as specimens lent by several herbaria.

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CHAPTER 2

Invasion patterns in riparian habitats: the role of anthropogenic pressure in temperate streams

Diego Liendo, Idoia Biurrun, Juan Antonio Campos,
Mercedes Herrera, Javier Loidi & Itziar García-Mijangos

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Abstract

The riparian flora and the level of invasion in streams of the Cantabrian watershed in Spain were studied in relation to the ecological status and the anthropogenic pressure. The level of invasion was also analysed in different riparian habitats: forests, river bars and man-made slopes. For this purpose, 18 sites were sampled and a list of native and alien plant species was made along a 100-m strip at each site. The habitat/s where alien species were found and their abundance per habitat and in the total area were also indicated. Out of 112 alien taxa found, 51 were classified as invasive. Exotic plants native to America were the most common (35 %). The level of invasion was significantly higher in the sampling sites subject to high levels of hydrological and morphological disturbances, proxies of the anthropogenic pressure. River bars and man-made slopes supported similar number of alien plant species, higher than forests. We suggest that disturbance in riverbanks should be minimised as much as possible in order to diminish the risk of invasion.

Key words: alien plants, anthropogenic pressure, habitat, invasion level, river ecosystem, river quality index

Introduction

Biological invasions have been chronicled at least for two last centuries. However, it was not until the initiation of the Scientific Committee on Problems of the Environment (SCOPE) in 1983 that the modern field of invasion biology really began to take shape (Richardson & Pyšek 2006, Davis 2011). There is compelling evidence, based on global trade and movement patterns, that the magnitude of this threat is increasing globally (Hulme 2009, McGeoch *et al.* 2010). Alien or exotic species are often described as one of the primary threats to ecosystems due to their negative impact on native species diversity (Pimm *et al.* 1995, Celesti-Grapow *et al.* 2010) and ecosystem function (Vitousek *et al.* 1997).

Not all regions, biomes, or habitats are invaded to the same extent. In fact, within a particular region the level of invasion usually varies strongly among habitats (Crawley 1987, Chytrý *et al.* 2008b), suggesting that some habitats are more susceptible to invasions than others. Differences in the level of invasion among habitats depend on species traits compared with native species, environmental and biotic characteristics of the recipient habitat and the propagule pressure with which alien species enter into the recipient habitat (Rejmánek *et al.* 2005, Vilà *et al.* 2007, Stanisci *et al.* 2010).

Riparian ecosystems are among the most human-altered ecosystems worldwide (Allan & Flecker 1993). They are considered to be highly prone to invasion by alien plants, largely because of their dynamic hydrology, their role as conduits for efficient propagule dispersal, their human-driven degradation, their nutrient and water conditions and the intense disturbance regimes they experience (Hood & Naiman 2000, Cushman & Gaffney

2010). The expansion of exotic plants in these ecosystems was accelerated when anthropogenic alterations such as channel modifications and flow regulation or drainage were intensified. Moreover, the agricultural wastewaters have increased the eutrophication of these habitats and thus favoured the colonisation by alien species (Celesti-Grapow *et al.* 2010). Some of these alien species may be present in large quantities, so they can cause deep alterations both of floristic composition and of vegetation and soil structure (Urgenson *et al.* 2009, Poldini *et al.* 2011). Riparian areas often show the highest number of neophytes of all natural and semi-natural vegetation types, as some studies conducted in Central Europe states (Pyšek *et al.* 2002, Walter *et al.* 2005, Pyšek *et al.* 2010). This high invasion level is an extremely alarming issue, taking into account that riparian ecosystems are considered of high ecological and economical value. In fact, most riparian habitats have been included in the European Habitat Directive (European Commission DG Environment 2003) due to their priority interest for conservation.

A great progress has been made in the Iberian Peninsula towards the knowledge of the alien flora (Sanz-Elorza *et al.* 2004, Almeida & Freitas 2006, Romero 2007, Campos & Herrera 2009b); however, only a few studies have analysed the plant invasion across habitats (Vilà *et al.* 2007, Campos *et al.* 2013). Some studies have focused on the assessment of plant invasion in particular vegetation types, such as coastal habitats in the North of Spain (Campos *et al.* 2004, Caño *et al.* 2013) and riparian habitats in Portugal (Aguiar *et al.* 2001, 2006, 2007) and southern Spain (Tabacchi *et al.* 1996). Regarding riparian habitats, riverine forests (Biurrun *et al.* 1994, 2014) and herbaceous vegetation of river bars (Amigo 2006, Biurrun *et al.* 2008) have been studied in depth in the North of the Iberian Peninsula; however, the impact of alien species in these riparian habitats has not been analysed yet.

In this study, we have selected riparian ecosystems of a temperate area to test whether the level of invasion is related to human activity and type of habitat. The following objectives were proposed: (1) to identify the alien plants present in streams of the Cantabrian watershed and their categories of invasion; (2) to calculate the level of invasion of these streams; (3) to analyse the level of invasion in relation to the ecological status and anthropogenic pressure of the streams; and (4) to determine which riparian habitats are the most invaded.

Materials and methods

Study area

The study was conducted in river basins of Bizkaia and Gipuzkoa (Basque Country, Spain) (Figure 1), belonging to the Cantabrian–Basque biogeographic sector and the Atlantic European province (Rivas-Martínez 2007). Temperature and rainfall in this territory are homogeneous and highly influenced by its location on the eastern coast of the Bay of Biscay. Overall, the climate is described as temperate oceanic. Mean annual precipitation

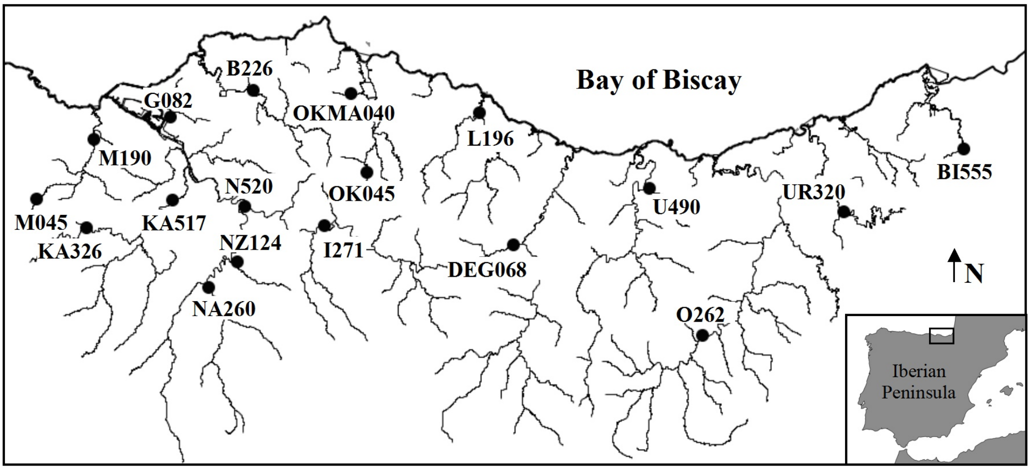

Figure 1. Study area and sampling sites

varies from 1200 to 1700 mm and mean annual temperature varies from 13°C to 14°C. Most sampling points are located in mesotemperate humid areas (Loidi *et al.* 2011).

The studied streams belong to the Cantabrian watershed. All river basins show a great variety of lithological substrata, with areas ranging from 100 to 1800 km^2 (Table I). Stream length varies from 15 to 70 km because their sources in the Cantabrian Mountains and their mouths in the Bay of Biscay are very close. The pronounced slopes they overcome, along with the rainfall pattern, result in these streams showing torrential regimes, except in the final reaches where valleys widen and water velocity decreases. In addition to this, a slight flow reduction occurs during summer due to a decrease in precipitation.

Riparian vegetation in all of the streams studied corresponds to the Cantabrian–Basque fluvial geoseries, which is mainly constituted by alder forests [*Alnus glutinosa* (L.) Gaertn.] (Loidi *et al.* 2011). Ash (*Fraxinus excelsior* L.) and white willow (*Salix alba* L.) forests can sometimes be found in the upper reaches and near the riverbed, respectively. River bars are colonised by several herbaceous communities, such as therophytic hygronitrophilous communities formed by *Polygonum* sp. pl. and *Bidens* sp. pl., flooded grasslands with *Paspalum distichum* and forb communities with *Mentha* sp. pl. Finally, aquatic and helophytic communities may develop associated with riverbeds where water is always available and flow velocity slows down.

Sampling design and data collection

A total of 18 sites corresponding to the Ecological Status Monitoring Network of the Basque Country's Streams were studied (Department of Environment, Basque Government) (Table I). This monitoring network was used because of the availability of data regarding the conservation status and water quality of the streams. Information on different variables was taken from the monitoring network of Basque streams (Gartzia de

Table I. Sampling sites and variables used in the analyses. LI, level of invasion; ICG, general quality index; QBR index, riverbank forest quality index; HD, hydrological disturbances; MD, morphological disturbances.

Site	River	LI	ICG	QBR	HD	MD
B226	Butrón	9.5	69,94	25	No	Medium
BI555	Bidasoa	15.6	80,83	40	Medium	Medium
DEG068	Ego	23.2	56,59	30	Medium	High
G082	Gobelas	29.3	72,26	30	No	High
I271	Ibaizabal	15.5	72,63	15	No	High
KA326	Cadagua	14.8	70,17	25	Medium	High
KA517	Cadagua	25.7	70,56	35	Low	High
L196	Lea	11.6	79,12	65	No	Low
M045	Barbadún	3.8	72,03	100	No	Medium
M190	Barbadún	17.6	78,15	70	No	High
N520	Nervión	41.1	73,89	5	Low	High
NA260	Altube	19.8	78,09	60	Medium	Medium
NZ124	Zeberio	13.1	78,8	30	No	Medium
O262	Oria	22.6	75,85	20	Medium	High
OK045	Oka	9.2	78,12	30	No	Medium
OKMA040	Mape	9.4	82,3	40	No	High
U490	Urola	18.3	70,95	50	Low	Low
UR320	Urumea	8.3	81,93	35	High	Medium

Bikuña *et al*. 2008). Those variables were as follows: chemical status [by means of the general quality index (ICG)] and QBR index (riverbank forest quality index) as proxies for the ecological status, and human-driven hydrological and morphological disturbances as proxies for the anthropogenic pressure.

The ICG index (Gartzia de Bikuña *et al*. 2008) is based on the index of bacteriological and physicochemical quality developed by the Ministry of Environment of Quebec (Canada) (Hébert 1997). The calculation of this index takes into account different parameters, such as pH, conductivity, oxygenation, nutrients and metals. It ranges from 0 (very bad chemical quality) to 100 (excellent chemical quality). The QBR index (Munné *et al*. 2003) is an index used to assess the quality of the riverbank systems which integrates biological and morphological aspects, such as vegetation quality, diversity, structure and cover and stream channel condition. It ranges from 0 (extreme degradation, bad quality) to 100 (riparian habitat in natural condition). Disturbances related to water regulation, extraction and diversion were considered as hydrological disturbances; four categories had been distinguished (Gartzia de Bikuña *et al*. 2008): no disturbance and low, medium and high disturbances. Finally, morphological disturbances included weirs, bridges, breakwaters and other occupations of the Public Hydraulic Domain, with three categories: low, medium and high (Gartzia de Bikuña *et al*. 2008).

Data collection was done from 2008 to 2010 during the period of maximum development of the riparian vegetation (i.e. between June and September). A 100-m strip upstream of each point was sampled (Aguiar *et al*. 2007). The strip's width depended on the perifluvial environment, which was in turn influenced by the geomorphology and the stretch itself. We consider this sampled area to be representative for the study as it usually includes all type of habitats present in the Cantabric streams. A list of native and alien plants present in the area was compiled. The abundance of alien species per habitat and in the total area were quantified by means of a 9- index scale (Braun-Blanquet 1951): r (0.1 %); + (0.5 %); 1 (1–5 %); 2a (5–10 %); 2b (10–20 %); 2c (20–25 %); 3 (25–50 %); 4 (50–75 %); 5 (75– 100 %). Five habitat types were considered: forests, river bars, man-made slopes, terraces and helophytic communities. Forests gather all type of tree formations, provided tree cover is > 50 %. River bars include all type of herbaceous communities developing on sand, mud or gravel bars in riverbeds, e.g. flooded grasslands, nitrophilous therophytic communities and forb communities. Man-made slopes are degraded riverbanks, breakwaters and walls colonised by ruderal communities. Terraces include different kinds of grasslands and forb communities developing in the river terrace, and helophytic communities are those formed by species adapted to the water–land ecotone, such as reed, *Phragmites australis*.

Floristic data

Several sources were used for the identification and nomenclature of native and alien taxa: general floras (Castroviejo *et al.* 1986–2012, Aizpuru *et al.* 1999) and different monographs. Information regarding category of invasion and geographical origin of alien plants was taken from Campos & Herrera (2009b) and Campos (2010). We have considered the categories of invasion proposed by Richardson *et al.* (2000), who recognised four categories: invasive transformer (A), invasive non-transformer (B), naturalised (C) and casual (D). In addition, we have included a new category for those species whose native or alien status is not clear (E) (Campos & Herrera 2009b). The latter were considered as alien species in the analyses. Regarding geographical origin, those plants that were not possible to identify at species level, hybrids and species of unknown geographical origin were included in the category “other” (Table S1).

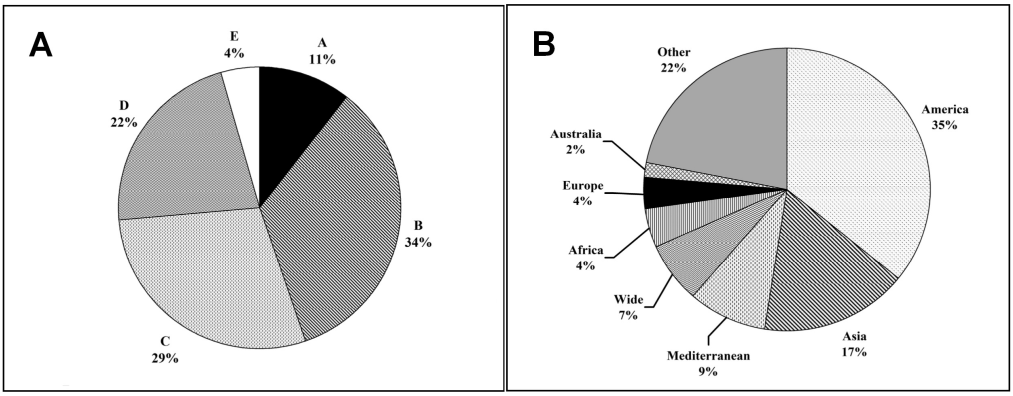

Figure 2. Percentage of alien plants in the Cantabrian streams according to: (A) category of invasion and (B) geographical origin.

Data analyses

The level of invasion was calculated as the proportion of alien plant species in relation to the total number of species (Chytrý *et al.* 2008a). This ratio has been proposed by Catford *et al.* (2011) with the name "relative alien species richness" as a recommended way to calculate the level of invasion, independent of sampling plot size. The original categorical variables for the hydrological and morphological disturbances of the streams were recodified for the statistical analysis due to the low number of cases for some of the variables (see Table I). Two categorical variables were finally established as follows: no disturbance and disturbance (including low, medium and high) for human-driven hydrological disturbances, and high and medium/low for morphological disturbances.

Non-parametrical Mann–Whitney's U-test was used to analyse the level of invasion and the number of alien and native species in relation to the hydrological and morphological disturbances because data were qualitative and did not show a normal distribution. Bivariate correlations were used for the chemical status and the QBR index because quantitative data were available. All statistical analyses were carried out using SPSS statistics 19.0 package.

Results

Categories of invasion and geographical origin of the alien flora

A total of 112 alien plant taxa were found in the sampled streams. These species are listed in Table S1, which includes the family, category of invasion, geographical origin, fluvial habitat/s where the species were found, the number of sites where the species occurred and the mean cover of the species in those sites where they were present. Considering the

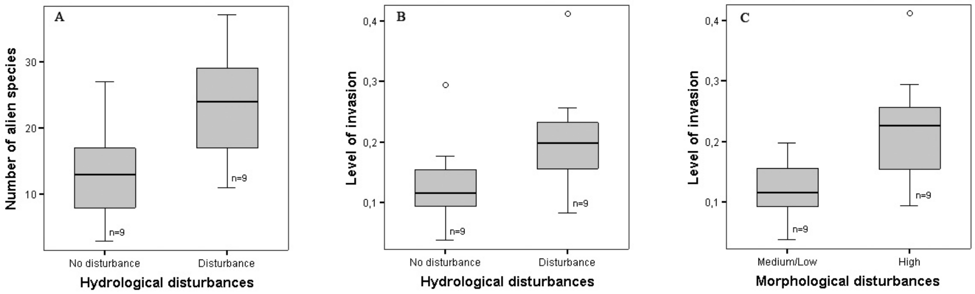

Figure 3. Box-plot diagrams showing the relation between the plant invasion and the anthropogenic disturbance. (A) Relationship between the number of alien species and the hydrological disturbance, (B) relationship between the level of invasion and the hydrological disturbance and (C) relationship between the level of invasion and the morphological disturbance. The boxes represent the interquartile range, the thick line indicates the median, the bars show the values range that accounts for 95 % of the cases and circles represent outliers.

category of invasion (Figure 2A), almost half of the alien species found in the streams of the Cantabrian watershed were invasive (51). Of these, 12 were classified as transformers (11 %), such as *Cyperus eragrostis*, *Fallopia japonica* and *Robinia pseudoacacia*, and 39 as invasive non-transformers (34 %), such as *Crocosmia x crocosmiiflora* and *Platanus hispanica*. In addition, 33 naturalized plants were also found (29 %), such as *Ligustrum ovalifolium*, along with 25 casual species (22 %) and 5 species whose native/alien status is not clear (4 %), such as *Dorycnium rectum*. With regard to the geographical origin (Figure 2B), 41 taxa, such as *Amaranthus* sp. pl., *Conyza* sp. pl., *Cyperus eragrostis*, *Paspalum distichum*, *Robinia pseudoacacia* and *Tradescantia fluminensis*, were native to America, representing the highest proportion (35 %). Asian species, such as *Buddleja davidii*, *Fallopia japonica* and *Ligustrum ovalifolium*, were quite common as well (19 species), representing 17 % of the total, whereas species from Africa, Europe, the Mediterranean basin and Australia were less numerous – 5 (4 %), 4 (4 %), 10 (9 %) and 2 (2 %), respectively. There were also a high number of alien plants belonging to the category “other” (25).

Level of invasion

Overall, the level of invasion was higher in the sites situated on industrial and very populated areas (Table I), with values ranging from 20% to 30% except in the Nervión stream near Bilbao (N520) where the level of invasion was even higher (41 %). Lowest value (4 %) was obtained in the site M045, located in the upper stretch of Barbadún stream that flows through a mountainous valley with low population density. No longitudinal pattern was found along an east–west gradient, but the level of invasion tended to increase downstream.

Level of invasion versus ecological status and anthropogenic pressure

Chemical status (by means of the ICG index) and QBR index as proxies for the ecological status, and hydrological and morphological disturbances (proxies for the anthropogenic pressure) were analysed with regard to the level of invasion and the number of native and alien species in order to find out whether there were any differences among them.

A slight negative correlation was found between the QBR index and the level of invasion ($r = 0.235$; $p < 0.05$). Regarding chemical status, the ICG index is slightly correlated

Table II. Median and interquartile range (IQR) for the number of native and alien species in relation to hydrological and morphological disturbances.

		Native species		Alien species	
		Median	IQR	Median	IQR
Hydrological disturbances	No disturbance	77	65-89	13	8-17
	Disturbance	84	76-122	24	17-29
Morphological disturbances	Medium/Low	113	75-128	13	8-17
	High	77	69-84	23	15-27

with the number of native species (r = 0.241; $p < 0.05$), but not with the level of invasion or the number of alien taxa. With respect to hydrological disturbances, Mann–Whitney's U test revealed that there were significant differences in the number of alien species and the level of invasion ($p < 0.05$, see Figure 3A, B), with higher values in those sites subject to some kind of hydrological disturbance. An increase in the number of native species is also shown, although it is not significant (Table II). Finally, Mann–Whitney's U-test also pointed out that there were significant differences in the level of invasion ($p < 0.05$, see Figure 3C) between both categories of morphological disturbances, with higher values in those sites subject to a high degree of disturbance. In this case, the number of alien species also increases, whereas the number of native taxa decreases (Table II), although not in a significant manner.

Alien plants and riparian habitats

Forests, river bars and man-made slopes are the most common riparian habitats in the streams of the Cantabrian watershed. Terraces and helophytic communities are very scarce due to the geomorphology of these streams, and they were not taken into account because the low number of sites where those habitats occurred did not allow us to carry out an appropriate assessment. River bars and slopes supported a similar number of alien plant species (68 and 65, respectively) and notably more than forests (46). Overall, these differences were due to a higher presence of invasive non-transformer plants (category B, see Figure 4), as the number of species of the remaining categories did not show an important variation.

In riparian forests, *Platanus hispanica* and *Robinia pseudoacacia* were the most remarkable alien species in the tree layer, both of them present in eight sites, with mean cover of 20 % and around 15 %, respectively. In the herb layer, *Tradescantia fluminensis* and *Crocosmia x crocosmiiflora* are also worth mentioning. Although *T. fluminensis* showed a

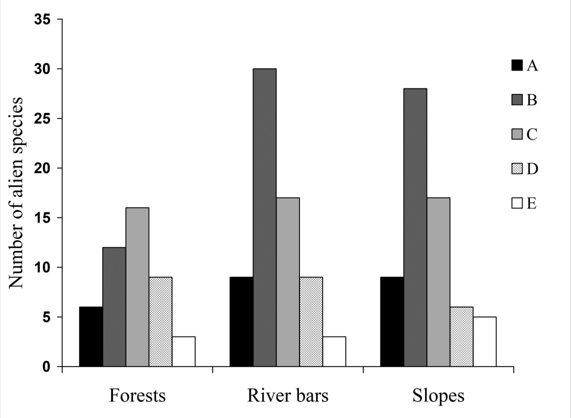

Figure 4. Number of alien plant species in the main riparian habitats regarding their category of invasion. (A) invasive transformer, (B) invasive non-transformer, (C) naturalised, (D) casual and (E) cryptogenic higher mean cover (5 %) than *C. x crocosmiiflora* (3 %), the latter was more frequent, being present in eight sites. On river bars, *Cyperus eragrostis* was the most frequent alien species, being present in 12 sites, with a mean cover around 4 % in this habitat. *Paspalum distichum* showed the highest mean cover (15 %) in the 11 sites where it was present indicating the great invasion success this species has in this habitat. Other species with high frequency on river bars were *Bidens frondosus* (in four sites) and *Amaranthus* sp. pl. (in seven sites); however, the mean cover in both cases was < 1 %. On man-made slopes, *Fallopia japonica* was one of the most prominent species. Even though it was only found in four sites, its mean cover was around 15 % in this man-made habitat, showing therefore a great invasive character that could cause significant problems if spread to other river basins. Other noteworthy species on man-made slopes were *Dorycnium rectum*, present in six sites with a mean cover of 5 %, and *Buddleja davidii*, found in four sites with a mean cover around 4 %.

Discussion

Invasive plants (transformers and non-transformers) represent almost half of the Cantabrian riparian alien flora (44 %, see Figure 2A). This percentage is remarkably higher than that obtained for Bizkaia's riparian habitats (31.2 %) in a study that covered different habitats of this territory (Campos & Herrera 2009a); it is necessary to highlight that the number of invasive non-transformer plant species (B) rises from 16 in the aforementioned study to 38 in this study. This could be due to the fact that this study focused exclusively on riparian systems, with a subsequent more extensive sampling which revealed a major presence of the invasive component of the alien flora. The high proportion of invasive plants could be the outcome of the mild climate of the study area along with the level of disturbance of the streams, which would facilitate the establishment of strong invaders.

An important proportion of the alien plant species found in the studied streams is native to America (39 %), followed by those of Asian origin (16 %). These percentages are similar to those obtained for the province of Bizkaia (Campos & Herrera 2009a), pointing out that the trend would be the same for streams. However, the percentage of Mediterranean species (9 %) has been notably low, probably due to the hygrophilous character of riparian habitats.

The highest level of invasion (around 20–30 %) was found in those river basins subject to the highest level of anthropogenic pressure and in general it coincides with a low QBR index. These river basins are situated in industrialised and densely populated areas, which could facilitate the arrival and subsequent establishment of alien plant species. This level of invasion is similar to that obtained in other studies carried out in rivers and streams of similar climatic and biogeographic conditions, such as the Adour (24 %) and Garonne (21 %) in south-west France (Planty-Tabacchi *et al.* 1996, Tabacchi & Planty-Tabacchi 2005). However, the patterns of invasion of the Cantabrian streams are different to those observed in the French rivers, where the highest proportion of exotic species was found in areas with intermediate disturbance level. Other studies conducted in Mediterranean rivers of Portugal (Aguiar *et al.* 2001) and south-east Spain (Salinas & Casas 2007) showed a similar pattern to our Cantabrian streams, with higher invasion values being found in sites subject to a high level of anthropogenic pressure; although the level of invasion was in general lower in those Mediterranean rivers.

Even though the level of invasion increases with both hydrological and morphological disturbances, only the latter negatively affects native species richness. Should hydrological disturbances occur, the number of native and, more markedly, alien species increases. Thus, many alien plants as well as native ruderals may be favoured by natural and anthropogenic hydrological disturbances (Planty-Tabacchi *et al.* 1996). Nevertheless, further disturbance or stream regulation by higher human pressure could cause the loss of spatial complexity and thus could open the door to some dominant invaders, with drastic consequences on biodiversity (Tabacchi & Planty-Tabacchi 2005). This fits well with our observations in Cantabrian streams, where highly disturbed places, with many morphological alterations, are quite easily colonised by some dominant invaders such as *Fallopia japonica*.

Not only is the invasion level similar in Cantabrian streams and in the Adour and Garonne rivers in southwest France, but they also share many of the alien species, some of which are invasive and very common. Among them, *Acer negundo*, *Robinia pseudoacacia* and *Buddleja davidii* as woody species and *Cyperus eragrostis*, *Bidens frondosus*, *Paspalum distichum* and *Fallopia japonica* as herbaceous taxa are worth highlighting. Nevertheless, some invasive plants in Cantabrian streams such as *Solanum chenopodioides* and *Crocosmia x crocosmiiflora* are not important in the French rivers. The level of invasion in some river basins such as the Barbadún and Ibaizabal tended to increase downstream, a pattern also found in other rivers (Planty-Tabacchi *et al.* 1996, Tabacchi *et al.* 1998) and that has been primarily related to the increasingly mild climate and greater human impact towards the lower valleys.

River bars and man-made slopes are the riparian habitats supporting higher number of alien plant species. Human-driven alterations and frequent natural flood disturbance on man-made slopes and river bars help to create open gaps with light, nutrients and space that can be rapidly colonised by ruderal species, many of them alien plants (Walter *et al.* 2005, Richardson *et al.* 2007).

Further insights

Concerning management of plant invasions, although the level of invasion is the basic issue, it can be complemented with information about alien transformer species (Catford *et al.* 2011). Among the invasive transformers present in Cantabrian streams, one of the most dangerous to be taken into account inthe scope of biological conservation is *Fallopia japonica* (Gerber *et al.* 2008). This Asiatic species has been reported as invasive in Central and Northern Europe since the 19th century, where it has become very dangerous for the fluvial environment (Pyšek 2009). Attempts to control and eradicate *Fallopia japonica* have been carried out in some Cantabrian streams. Mechanical removal and the use of herbicides have been the most widespread treatments to date. However, no results are available at the moment regarding the long-term effectiveness of those treatments.

The high economical costs, lack of public awareness and support and absence of coordination among different public administrations (Andreu *et al*. 2009) difficult the control and eradication of invasive species. In our opinion, the best way to fight against plant invasion is prevention, and the most important actions should be (1) to limit the source of new propagules, (2) to minimise hydrological and morphological disturbances and (3) to maintain and restore riparian forests. Moreover, the first detection is crucial for eradication success because it prevents further population growth and spread (Pluess *et al*. 2012). Thus, this type of survey is very important not only to improve the knowledge about the ecology and distribution of alien species but also to detect new future invasions.

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Table S1. List of alien plants found in the rivers of the Cantabric watershed. Status: A: Transformer; B: Invasive non-transformer; C: Non-invasive naturalized; D: Casual; E: Unclear. Life form: Ph: Phanerophyte; H: Hemicryptophyte; Ch: Chamaephyte; G: Geophyte; Th: Therophyte. Dispersal mode: Ane: Anemochory; Auto: Autochory; Zoo: Zoochory; Hyd: Hydrochory; NS: Not Specified. Habitat: F: Forests; RB: River bars; H: Helophytes; Ter: Terraces; Sl: Slopes.

Alien taxa	Family	Status	Life form	Origin	Dispersal mode	Habitat	N° Sites	Mean cover per site ± SE (%)
Acacia dealbata Link	Fabaceae	B	Ph	Australia	Zoo	F	1	3
Acer negundo L.	Sapindaceae	C	Ph	America	Ane	F, Sl	4	1,6 ± 0,8
Acer saccharinum L.	Sapindaceae	D	Ph	America	Ane	Sl	1	0,1
Ailanthus altissima (Mill.) Swingle	Simaroubaceae	B	Ph	Asia	Ane	Sl	1	3
Albizia julibrissin Durazz.	Fabaceae	D	Ph	Asia	Zoo	RB	1	0,1
Amaranthus blitum L. *s.l.*	Amaranthacae	B	Th	Other	Auto	RB	1	0,1
Amaranthus blitum L. *subsp.* ***blitum***	Amaranthaceae	B	Th	Wide	Auto	RB	2	0,1 ± 0
Amaranthus blitum L. *subsp.* ***emarginatus*** (Moq. Ex Uline & Bray) Carretero, Muñoz Garmendia & Pedrol	Amaranthaceae	C	Th	Wide	Auto	RB	1	0,1
Amaranthus bouchonii Thell.	Amaranthaceae	C	Th	America	Ane	RB	1	0,5
Amaranthus gr. ***hybridus***	Amaranthaceae	B	Th	America	Ane	RB	2	0,3 ± 0,2
Amaranthus hybridus L.	Amaranthaceae	B	Th	America	Ane	RB	2	0,3 ± 0,2
Amaranthus powellii S. Watson	Amaranthaceae	B	Th	America	Ane	RB, Sl	2	0,5 ± 0
Amaranthus *sp.*	Amaranthaceae	B	Th	Other	Ane	Sl	1	0,1
Artemisia verlotiorum Lamotte	Asteraceae	B	H	Asia	Ane	RB, Sl	2	0,3 ± 0,2
Arundo donax L.	Poaceae	B	Ph	Asia	Ane	Sl	2	0,3 ± 0,2
Avena sativa L.	Poaceae	D	Th	Other	Auto	RB	1	0,1
Bidens aureus (Aiton) Sherff	Asteraceae	B	H	America	Zoo	Sl	1	0,1
Bidens frondosus L.	Asteraceae	B	Th	America	Zoo	RB, H, Sl	7	2,8 ± 2,1
Brassica nigra (L.) W.D.J. Koch	Brassicaceae	C	Th	Medit.	Auto	RB	1	0,1
Brassica oleracea L.	Brassicaceae	D	H	Europe	Auto	RB	1	0,1
Brassica rapa L.	Brassicaceae	D	Th	Asia	Auto	Sl	1	0,1
Brassica *sp.*	Brassicaceae	D	Th	Other	Auto	RB	1	0,1
Bromus catharticus Vahl	Poaceae	B	H	America	Ane	Sl	2	0,1 ± 0

Alien taxa	Family	Status	Life form	Origin	Dispersal mode	Habitat	N° Sites	Mean cover per site ± SE (%)
Buddleja davidii Franch.	Buddlejaceae	A	Ph	Asia	Ane	F, RB, Sl	6	3,3 ± 2,4
Calendula officinalis L.	Asteraceae	C	Th	Other	Zoo	RB	1	0,1
Canna indica L.	Cannaceae	D	G	America	NS	F	1	0,1
Centranthus ruber (L.) DC.	Valerianaceae	B	Ch	Medit.	Ane	F, Sl	2	0,1 ± 0
Chamaecyparis lawsoniana (A. Murray bis) Parl. *(planted)*	Cupressaceae	D	Ph	America	Ane	F	1	0,1
Conyza bilbaoana J. Rémy	Asteraceae	C	Th	America	Ane	Sl, RB, F	4	9,7 ± 9,2
Conyza *sp.*	Asteraceae	A	Th	Other	Ane	RB	1	0,5
Conyza sumatrensis (Retz.) E. Walker	Asteraceae	A	Th	America	Ane	RB, Sl, Ter	4	0,2 ± 0,1
Coronopus didymus (L.) Sm.	Brassicaceae	B	Th	Other	Auto	RB, Sl	5	0,8 ± 0,5
Cortaderia selloana (Schult. & Schult. f.) Asch. & Graebn.	Poaceae	A	H	America	Ane	F, Sl	3	0,4 ± 0,1
Crocosmia x crocosmiiflora (Lemoine) N.E.Br.	Iridaceae	B	G	Other	Hyd	F, Sl, RB	9	3,4 ± 1,5
Cucurbita pepo L.	Cucurbitaceae	D	Th	America	Zoo	RB	1	0,1
Cymbalaria muralis P. Gaertner, B. Mey. & Scherb.	Scrophulariaceae	B	Ch	Europe	Auto	F, RB, Sl	4	0,4 ± 0,1
Cyperus eragrostis Lam.	Cyperaceae	A	H	America	Hyd	F, RB, H, Sl	14	1,0 ± 0,3
Cyperus longus L.	Cyperaceae	E	H	Other	Hyd	RB, H, Sl	7	0,6 ± 0,4
Datura stramonium L.	Solanaceae	B	Th	America	Ane	RB, Sl	2	0,1 ± 0
Dittrichia viscosa (L.) W. Greuter	Asteraceae	B	Ph	Medit.	Ane	Sl	1	0,1
Dorycnium rectum (L.) Ser.	Fabaceae	E	Ch	Medit.	Auto	F, RB, Sl	9	2,5 ± 1,6
Dysphania ambrosioides (L.) Mosyakin & Clemants	Amaranthaceae	B	Th	America	Auto	RB	4	0,3 ± 0,1
Echinochloa crus-galli (L.) P.Beauv.	Poaceae	B	Th	Other	Zoo	RB, Sl	8	0,4 ± 0,1
Eragrostis pilosa (L.) P.Beauv.	Poaceae	D	Th	Wide	Ane	RB, Sl	1	0,1
Erigeron karvinskianus DC.	Asteraceae	B	Ch	America	Ane	RB, Sl	6	0,3 ± 0,1
Eucalyptus globulus Labill.	Myrtaceae	C	Ph	Australia	Ane	F	2	1,6 ± 1,5
Euphorbia lathyris L.	Euphorbiaceae	C	H	Medit.	Auto	RB	1	0,1
Fallopia japonica (Houtte) Ronse Decr.	Polygonaceae	A	G	Asia	Hyd	F, Sl	5	7,2 ± 3,2

Alien taxa	Family	Status	Life form	Origin	Dispersal mode	Habitat	N° Sites	Mean cover per site ± SE (%)
Ficus carica L.	Moraceae	C	Ph	Medit.	Zoo	F, RB, Sl	10	1,9 ± 1,5
Fraxinus excelsior L. (cultivated var.)	Oleaceae	D	Ph	Other	Ane	Sl	1	0,5
Fraxinus pennsylvanica Marshall	Oleaceae	C	Ph	America	Ane	F	1	0,5
Galinsoga quadriradiata Ruiz & Pavon	Asteraceae	B	Th	America	Ane	RB	2	0,1 ± 0
Gamochaeta coarctata (Willd.) Kerguélen	Asteraceae	B	H	America	Ane	RB	1	0,1
Hedera canariensis Willd.	Araliaceae	D	Ph	Africa	Zoo	F	1	0,1
Helianthus *sp.*	Asteraceae	A	G	Other	Hyd	F, RB, Sl	5	8,3 ± 7,3
Helianthus x laetiflorus Pers.	Asteraceae	B	H	America	Hyd	RB	1	0,1
Hypericum hircinum L. *subsp.* ***majus*** (Aiton) N. Robson	Hypericaceae	E	Ph	Europe	Auto	F, Sl	1	3
Impatiens balfourii Hook. f.	Balsaminaceae	B	Th	Asia	Auto	F, RB, Sl	3	6,0 ± 4,6
Juglans regia L.	Juglandaceae	C	Ph	Wide	Zoo	F, Sl	3	0,2 ± 0,1
Juncus tenuis Willd.	Juncaceae	B	H	America	Zoo	RB	1	0,1
Ligustrum lucidum W.T.Aiton	Oleaceae	D	Ph	Asia	Zoo	Sl	1	0,5
Ligustrum ovalifolium Hassk.	Oleaceae	C	Ph	Asia	Zoo	F, Sl	5	0,3 ± 0,1
Lobularia maritima (L.) Desv.	Brassicaceae	C	Ch	Medit.	Auto	RB, Sl	2	0,1 ± 0
Lonicera japonica Thunb.	Caprifoliaceae	B	Ph	Asia	Zoo	F, Sl	2	7,8 ± 7,3
Lunaria annua L.	Brassicaceae	C	H	Europe	Ane	F	1	0,1
Lycopersicon esculentum Mill.	Solanaceae	C	Th	America	Zoo	RB, Sl	7	0,6 ± 0,4
Morus *sp.*	Moraceae	D	Ph	Other	Zoo	F	1	0,5
Oenothera rosea L'Hér. ex Aiton	Onagraceae	B	H	America	Ane	RB, Sl	5	0,1 ± 0
Oxalis latifolia Kunth	Oxalidaceae	B	G	America	Auto	F, RB, Sl, Ter	8	0,2 ± 0,1
Oxalis pes-caprae L.	Oxalidaceae	D	G	Africa	NS	Sl	1	0,1
Parthenocissus inserta (A.Kern.) Fritsch	Vitaceae	C	Ph	America	Zoo	Sl	2	20,3 ± 17,3
Parthenocissus *sp.*	Vitaceae	C	Ph	Other	Zoo	F, RB	2	1,6 ± 1,5
Paspalum dilatatum Poir.	Poaceae	A	H	America	Zoo	Sl, Ter	1	0,1 ± 0

Alien taxa	Family	Status	Life form	Origin	Dispersal mode	Habitat	N° Sites	Mean cover per site ± SE (%)
Paspalum distichum L.	Poaceae	A	G	America	Hyd	RB, H, Sl	12	2,5 ± 1,2
Persicaria lapathifolia x pensylvanica	Polygonaceae	D	Th	Other	Hyd	Sl	1	0,1
Persicaria pensylvanica (L.) M. Gómez	Polygonaceae	C	Th	America	Hyd	RB, H, Sl	1	15
Phalaris canariensis L.	Poaceae	C	Th	Wide	Zoo	RB	1	0,5
Phyllostachys aurea (Carrière) Rivière & C.Rivière	Poaceae	C	Ph	Asia	NS	Sl	1	0,1
Phyllostachys *sp.*	Poaceae	C	Ph	Asia	NS	F, Sl	3	0,5 ± 0
Pinus radiata D.Don	Pinaceae	C	Ph	America	Ane	F	1	0,5
Piptatherum miliaceum (L.) Coss.	Poaceae	E	H	Other	Ane	F, RB, Sl	4	0,5 ± 0
Platanus hispanica Miller. ex Münchh.	Platanaceae	B	Ph	Other	Ane	F, RB, Sl	10	10,3 ± 6,1
Populus alba L.	Salicaceae	D	Ph	Medit.	Ane	F	1	0,5
Populus x canadensis Moench	Salicaceae	C	Ph	Other	Ane	F, RB, Sl	6	5,7 ± 3,0
Portulaca oleracea L.	Portulacaceae	C	Th	Asia	Auto	RB	1	0,1
Potentilla indica (Jacks.) Th. Wolf	Rosaceae	B	H	Asia	Zoo	F, RB, Sl	1	3
Prunus dulcis (Mill.) D.A.Webb	Rosaceae	D	Ph	Wide	Zoo	F	1	0,1
Prunus laurocerasus L.	Rosaceae	C	Ph	Wide	Zoo	Sl	1	0,1
Prunus *sp.*	Rosaceae	D	Ph	Other	Zoo	F	1	0,1
Robinia pseudoacacia L.	Fabaceae	A	Ph	America	Ane	F, RB, Sl	12	2,0 ± 1,2
Rosa *sp.* (planted)	Rosaceae	C	Ph	Other	Zoo	Sl	1	0,1
Salix alba L. *var.* ***contorta***	Salicaceae	C	Ph	Other	Ane	F	1	0,1
Salix babylonica L.	Salicaceae	D	Ph	Asia	Ane	F	1	3
Sedum sexangulare L.	Crassulaceae	C	Ch	Africa	Ane	Sl	1	0,1
Selaginella kraussiana (Kunze) A.Braun	Selaginellaceae	C	Ch	Africa	Ane	F	1	0,1
Solanum chenopodioides Lam.	Solanaceae	B	Ph	America	Zoo	RB, Sl	8	0,6 ± 0,3
Sonchus tenerrimus L.	Asteraceae	B	Ch	Medit.	Ane	RB	1	0,1
Sporobolus indicus (L.) R.Br.	Poaceae	A	H	America	Zoo	RB	1	0,1

Alien taxa	Family	Status	Life form	Origin	Dispersal mode	Habitat	Nº Sites	Mean cover per site ± SE (%)
Symphyotrichum lanceolatum (Willd.) G. L. Nesom	Asteraceae	C	H	America	Ane	Sl, RB	3	0,2 ± 0,1
Symphyotrichum squamatum (Spreng.) G. L. Nesom	Asteraceae	B	Th	America	Ane	F, RB, Sl	4	0,8 ± 0,7
Trachelium caeruleum L.	Campanulaceae	E	Ch	Medit.	Ane	Sl	1	0,1
Tradescantia fluminensis Vell.	Commelinaceae	B	Ch	America	Auto	F, RB, Sl	6	1,0 ± 0,6
Triticum durum Desf.	Poaceae	D	Th	Asia	Ane	RB	1	0,1
Ulmus pumila L.	Ulmaceae	C	Ph	Asia	Ane	F	1	0,1
Ulmus *sp.*	Ulmaceae	D	Ph	Other	Ane	F	1	0,1
Verbena bonariensis L.	Verbenaceae	B	H	America	Zoo	RB, Sl	3	0,2 ± 0,1
Veronica persica Poir.	Scrophulariaceae	B	Th	Asia	Auto	RB, Sl	7	0,2 ± 0,1
Vicia faba L.	Fabaceae	D	Th	Other	Auto	RB	1	0,1
Vitis vinifera L.	Vitaceae	C	Ph	Wide	Zoo	F, RB, Sl	3	0,1 ± 0
Xanthium strumarium L.subsp. ***italicum*** (Moretti) D. Löve	Asteraceae	B	Th	America	Zoo	RB, Sl	3	0,2 ± 0,1
Zantedeschia aethiopica (L.) Spreng.	Araceae	C	G	Africa	NS	RB	1	0,1

Drivers of plant invasion at broad and fine scale in short temperate streams

CHAPTER 3

Diego Liendo, Itziar García-Mijangos, Juan Antonio Campos, Unai López de Muniain & Idoia Biurrun

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Abstract

Riparian ecosystems have been described as highly prone to alien plant invasions, thus disentangling the contributing factors of the invasion process is of utmost importance to conserving and managing these valuable ecosystems. In this study we examined the drivers of riparian plant invasion in 16 Cantabrian river basins (northern Spain) ranging from 100 to ca. 1050 km^2. A complete flora was determined for 5 randomly selected sites within those basins. One hundred and thirty alien plant species were found across the 80 sampling sites, representing 21 % of the recorded total flora. At site scale, the level of plant invasion, measured as alien richness (AR) and relative alien richness (RAR), was assessed in relation to a set of explanatory variables by means of Generalised Linear Mixed Models. This level of invasion was influenced by environmental variables such as the thermicity index, the average riverbed width and the number of plant communities and by human-related variables such as the distance to the nearest town and the proportion of surrounding urban land. At basin scale, industrialised river basins were more heavily invaded than non-industrialised basins and they both differed in their alien plant composition. Given that some of the alien species occurring in Cantabrian streams are specially abundant (*Crocosmia x crocosmiiflora*) and/or form very dense stands (*Fallopia japonica*, *Paspalum distichum*), future research should focus on the drivers that influence the presence and distribution of these species of special concern.

Key words: alien plant richness, habitat heterogeneity, human impact, level of invasion, northern Spain, riparian, river basin.

Introduction

Riparian ecosystems have repeatedly been reported as highly prone to invasion by alien plants (Planty-Tabacchi *et al.* 1996, Richardson *et al.* 2007). A wide range of biotic and abiotic factors have been proposed for explaining this high susceptibility to invasion, such as the dynamic hydrology (Richardson *et al.* 2007), moisture and nutrient conditions (Foxcroft *et al.* 2008), the ability of rivers and streams to disperse propagules (Pyšek & Prach 1994, Planty-Tabacchi *et al.* 1996), natural and human-mediated disturbances (Hood & Naiman 2000, Aguiar *et al.* 2001) and light availability (Parendes & Jones 2000).

Invasions by non-native plants in riparian communities have altered the structure and function of riparian habitats and threaten biodiversity (Richardson *et al.* 2007). Furthermore, they can reduce ecosystem services provided by riparian zones by affecting flood patterns, water table levels and soil moisture conditions (Tickner *et al.* 2001, Meek *et al.* 2010).

There is growing awareness of the increased pressure on riparian zones worldwide as a result of human activity (Tickner *et al.* 2001). Anthropogenic activities have caused degradation of many riparian environments and have promoted the introduction of alien plants in these systems (Holmes *et al.* 2005, Tabacchi *et al.* 2005). In particular, human settlements and activities around rivers, such as building activities (González-Moreno *et al.* 2013), the construction of dams to regulate water flow (Catford *et al.* 2011, Greet *et al.* 2013), transport networks (Gelbard & Belnap 2003, Marcantonio *et al.* 2013) or agriculture (Chytrý *et al.* 2008), may facilitate the growth of alien plant populations in riparian ecosystems by modifying environmental conditions and establishing new sources of propagules in the vicinity of these systems (Meek *et al.* 2010). This human-induced propagule pressure has therefore been described as a key factor in the process of plant invasions (Lonsdale 1999). Given the difficulties to quantify propagule pressure, different variables related to human activities have been used as surrogates for this phenomenon (e.g. Meek *et al.* 2010, Gassó *et al.* 2012).

The level of plant invasion, i.e., the extent to which a habitat or ecosystem is invaded by plant species (Chytrý *et al.* 2008, Catford *et al.* 2012) can be quantified in different ways. Catford *et al.* (2012) suggest the use of relative alien species richness (RAR) and/or relative alien species abundance (RAA), since these metrics are easy to measure, independent of scale and comparable across regions and ecosystems. Besides RAR, the level of invasion has also been estimated by means of the absolute alien species richness (AR) in some studies dealing with plant invasions (e.g. Pino *et al.* 2005, Ehrenfeld 2008). This metric is easier to obtain than RAR but shows the disadvantage of being dependent of scale, as the number of species in a given site or ecosystem will increase with increasing area (Lonsdale 1999, Catford *et al.* 2012).

Most works dealing with different aspects of riparian plant invasions have been conducted in large Mediterranean (Aguiar *et al.* 2001, 2006, Cushman & Gaffney 2010) or

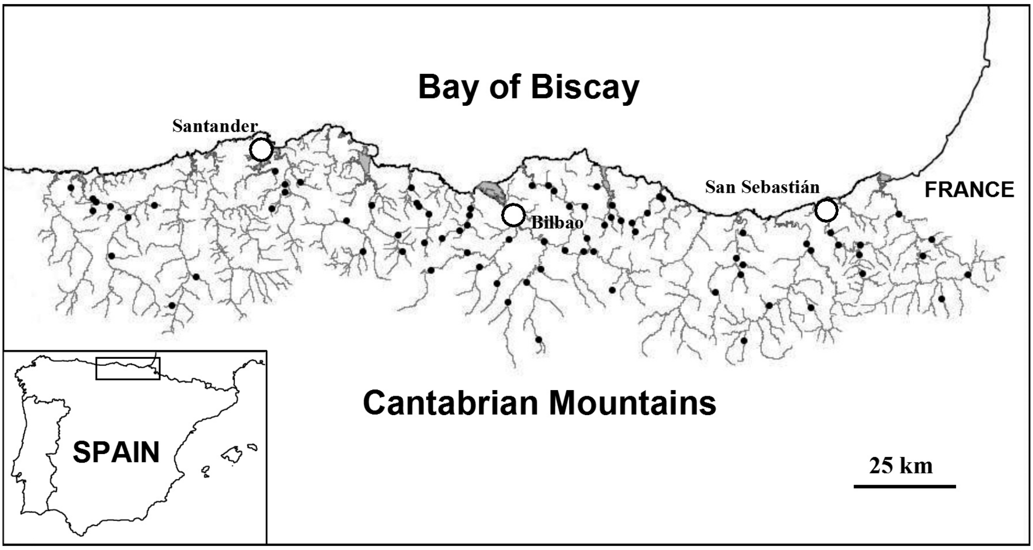

Figure 1. Study area showing the location of the sampling sites.

temperate (Tabacchi *et al*. 2005, Jacquemyn *et al*. 2010) rivers. However, short temperate streams have been scarcely studied (but see Maskell *et al*. 2006, Truscott *et al*. 2008). The present study analyses the level of plant invasion in short temperate streams of northern Spain in relation to environmental and anthropogenic variables at small scale (site scale) and at a larger scale (basin scale). This study includes a number of river basins with varying levels of human occupancy, degree of industrialisation and development of transport networks. Specific goals of the study are to: (1) assess whether the level of plant invasion varies among river basins in relation to their overall degree of human impact; and (2) determine which environmental and/or anthropogenic variables are responsible for explaining the differences in the level of plant invasion at site scale.

Materials and methods

Study area

The present study was conducted in Cantabrian river basins of northern Spain (Figure 1). The main characteristic of Cantabrian streams is their short length (15-70 km long) as a consequence of their sources in the Cantabrian Mountains being in close vicinity to their estuaries in the Bay of Biscay. These streams drain small basins ranging from 100 to ca. 1050 km^2 and flow through narrow valleys. A number of small dams are scattered along Cantabrian streams (URA 2013). These dams were built mainly for irrigation purposes and for small-scale generation of hydroelectric energy and do not significantly alter flow variability.

Climate in the study area is temperate oceanic with relatively mild winters, warm summers and abundant rainfall spread throughout the year (Campos *et al*. 2013). Riparian vegetation in Cantabrian streams is mainly constituted by alder forests (*Alnus glutinosa*) subjected to varying levels of human-driven degradation, with ash (*Fraxinus excelsior*) and white willow (*Salix alba*) forests sometimes found in the upper reaches and near the riverbed, respectively (Loidi *et al*. 2011).

Human influence in the study area is notably high. Human population is mainly concentrated in metropolitan areas around the cities of Santander, Bilbao and San Sebastián, although human settlement has significantly increased in coastal areas in the last years. In addition to human settlements, there is a noteworthy industrial development in coastal areas and in the lower sections of the larger streams. Another important factor of human impact is the construction of high-traffic roads (i.e., highways and national roads) in the last decades. Landscape is thus highly disturbed, especially in the valleys, and floodplain forests are often degraded due to the human-driven alteration.

Sampling design and plant data collection

A total of 16 river basins were randomly chosen out of 28 river basins existing in the study area. Five sampling sites consisting of a 100-m-long stretch were randomly selected within each basin –both main channel and tributaries- using Geographic Information System's software ArcGIS 10.1 (ESRI 2012). Eighty sampling sites were therefore nested within 16 river basins (Figure 1). The chosen length for the sampling sites has proven to be appropriate in other studies conducted in riparian systems (e.g. Aguiar *et al*. 2005, Maskell *et al*. 2006, Liendo *et al*. 2015). The sampling site encompassed the riverbed, the riverbanks and the adjacent floodplain excluding man-made structures and crops. In the field, the limits of the sampling site were established according to the presence of floodplain forests and related hygrophilous herb and rush communities.

Fieldwork was conducted from 2008 to 2013 during the period of peak growth of the riparian vegetation (i.e., between late spring and early autumn) coinciding with the period of relatively low flow. A complete inventory of native and alien plants was compiled at each site by 2-3 experts walking 2-3 hours until no new species were found (larger sites required a bigger effort). Classification of plant taxa as native or alien followed Campos (2010). Species nomenclature follows Aizpuru *et al*. (1999) except for the species not included in it: *Conyza bilbaoana* J. Rémy, *C. sumatrensis* (Retz.) E. Walker, *Muhlenbergia schreberi* J.F. Gmel. and *Pterocarya stenoptera* C. DC.

Basin-scale analyses

In order to analyse the influence of human pressure at the basin scale, the 16 river basins studied were classified as industrialised (7 basins) or non-industrialised (9 basins) (Table I). The former were those basins with urban and/or industrial land adjacent (< 100 m) to the main stream channel in more than 50 % of its length, while this percentage was lower in non-industrial basins. This information was taken from Spain's Land Use Information System of the year 2005 (SIOSE 2005, www.siose.es).

The level of invasion of each basin was calculated as the cumulative number of alien species in that basin divided by the total number of plant species, both alien and native. This metric is analogue to the relative alien richness (RAR) used at site scale (see below). Differences in the overall level of plant invasion between both types of basins were assessed using the Kruskal-Wallis non-parametric test. Additionally, multivariate analyses based on an alien species by basin matrix were carried out to estimate whether both types of basins differed in their alien plant composition. Non-metric multidimensional scaling (hereafter NMDS) based on a Bray-Curtis similarity matrix was performed using PRIMER v.6 (Clarke & Gorley 2006).

Site-scale analyses

The framework of generalised linear mixed modelling (GLMM) was adopted for modelling the variation in the level of plant invasion across Cantabrian streams as a function of a set of explanatory variables. The level of plant invasion was calculated by means of the alien plant richness (AR), i.e., the number of alien plant taxa in each sampling site and the relative alien plant richness (RAR), i.e., the proportion of alien plant species in relation to all

Table I. Descriptive information at basin scale. The "site scale" RAR was calculated averaging the values obtained at the 5 sites sampled in each basin, while the "basin scale" RAR was calculated as the cumulative alien richness at basin scale divided by the total species richness at that scale. NI: non-industrialised basins; I: industrialised basins.

Basin	*Acronym*	*Basin type*	*Main channel (km)*	*Basin area (km^2)*	*Sampled area (Ha)*	***Level of invasion (%)***		***All taxa***		***Native taxa***		***Alien taxa***	
						Site scale (mean and range)	Basin scale	Site scale (mean and range)	Basin scale	Site scale (mean and range)	Basin scale	Site scale (mean and range)	Basin scale
AGÜERA	AGU	NI	26.8	157	0.45	10.76 (6.4-18.3)	14.94	125.8 (90-153)	261	111.8 (81-125)	222	14 (8-28)	39
ASÓN	ASO	NI	37.2	740	0.51	8 (2-17.1)	13.27	105 (84-121)	226	96.4 (77-113)	196	8.6 (2-20)	30
BARBADÚN	BAR	NI	19.2	132	0.87	8.83 (5.1-16.7)	13.16	101.6 (78-109)	228	92.4 (74-102)	198	9.2 (4-18)	30
BIDASOA	BID	I	62.2	700	0.36	8.54 (2.5-15.6)	14.58	101.4 (56-154)	240	91.4 (53-130)	205	10 (2-24)	35
BUTRÓN	BUT	NI	35.1	202	0.86	9.09 (6.7-13.4)	10.86	101.2 (63-125)	221	92.4 (57-116)	197	8.8 (6-11)	24
CADAGUA	CAD	I	57.1	613	0.61	13.93 (8-25.9)	18.87	110.8 (80-125)	265	95.6 (69-115)	215	15.2 (10-29)	50
ESCUDO	ESC	NI	19.2	113	0.37	5.13 (3.2-7.7)	7.32	125.6 (117-146)	246	119.2 (108-139)	228	6.4 (4-9)	18
IBAIZABAL	IBA	I	49.7	452	0.41	11.04 (4.6-15.6)	15.24	85.4 (75-96)	210	76 (63-83)	178	9.4 (4-15)	32
LEA	LEA	NI	21.9	100	0.47	7.38 (5.8-11.2)	9.84	95.4 (69-111)	193	88.6 (61-105)	174	6.8 (4-10)	19
MIERA	MIE	NI	41.7	342	0.55	7.71 (3.3-12.5)	10.59	107.4 (85-129)	236	98.8 (78-119)	211	8.6 (3-16)	25
NERVIÓN	NER	I	58.8	582	0.79	17.84 (3.9-41.2)	21.38	115.8 (85-161)	290	96 (50-129)	228	19.8 (4-35)	62
OKA	OKA	NI	13.6	194	0.41	7.43 (2-10.6)	11.74	109.6 (85-141)	247	101.4 (76-127)	218	8.2 (2-14)	29
ORIA	ORI	I	65.1	882	0.74	13.2 (4.9-22.8)	18.66	108.6 (82-154)	268	92.6 (78-119)	218	16 (4-35)	50
SAJA	SAJ	NI	52.3	1043	1.24	4.34 (1.2-9.7)	8.16	102.4 (72-154)	245	97.4 (68-139)	225	5 (1-15)	20
UROLA	URO	I	54.8	342	0.61	10.74 (8.4-18.5)	14.41	102.4 (77-119)	229	91.6 (70-109)	196	10.8 (7-17)	33
URUMEA	URU	I	43.5	272	0.58	8.43 (2.3-17.4)	12.61	108.2 (87-133)	230	98.2 (83-121)	201	10 (2-23)	29
Mean and range			41.1 (13.6-65.1)	429.1 (100-1043)	0.62 (0.37-1.24)	9.52 (1.2-41.2)	13.54 (7.32-21.38)	106.7 (56-161)	239.7 (193-290)	96.2 (50-139)	206.9 (174-228)	10.4 (1-35)	32.8 (18-62)

plant species occurring in a given sampling site (Catford *et al.* 2012). These metrics were used as response or dependent variables in the subsequent analyses. Additionally, a number of climatic, topographical, landscape and human settlement explanatory or predictor variables were calculated for each sampling site (Table II).

Climatic variables were calculated from the Digital Climatic Atlas of Spain (Ninyerola *et al.* 2005). These variables were the mean annual temperature, mean minimum temperature in January (considered the coldest month in the study area), thermicity index (as an index that accounts for cold intensity, which is a limiting factor for the development of many plants and plant communities), yearly positive temperature, annual rainfall and

Table II. Initial set of potential predictor variables with their corresponding range and mean ± standard deviation. Asterisks indicate those predictor variables which have been removed from further analysis because of their high correlation (Pearson's r > 0.6) with other variables.

Variables	**Range**	**Mean ± SD**
Climate		
Mean annual temperature (°C)*	11.06-14.19	13.44 ± 0.54
Mean minimum temperature in January (°C)*	0.9-5.28	3.77 ± 0.78
Thermicity index	212.13-324.79	289.51 ± 20.19
Yearly positive temperature*	1339-1755	1621 ± 65.8
Annual rainfall (mm)	1135.6-2489.2	1454.9 ± 248.1
Summer rainfall (mm)	151.4-381.7	226.3 ± 45.3
Topography		
Altitude (m)*	7-670	120.61 ± 107.17
Distance to the sea (km)*	4.1-69.7	29.8 ± 16.3
Average width of the stream channel (m)	2-33	10.03 ± 6.34
Landscape (year 2000)		
Proportion of woodlands	0.05-0.71	0.24 ± 0.15
Proportion of tree plantations*	0.0029-0.87	0.35 ± 0.22
Proportion of croplands	0-0.45	0.02 ± 0.06
Proportion of pasture lands	0.03-0.71	0.31 ± 0.18
Proportion of urban land	0-0.63	0.06 ± 0.09
Proportion of roads	0-0.06	0.01 ± 0.01
Human settlement		
Distance to the nearest town of more than 5000 hab. (m)	0-18079	4954 ± 4299.47
Distance to the nearest high-traffic paved roads (m)	10-12294	2722 ± 3082
Other variables		
Number of plant communities	1-9	3.76 ± 1.66
Sampling date (Julian days)	144-279	207 ± 42
Sampled area (m^2)	150-9300	1231.87 ± 1185.15

summer rainfall. Thermicity index is calculated as ten times the sum of the yearly average temperature, the average minimum temperature of the coldest month of the year and the average maximum temperature of the coldest month of the year (Rivas-Martínez 2007). Yearly positive temperature is the sum of the monthly average temperature of those months whose average temperature is higher than 0°C multiplied by ten. Topographical variables included elevation, distance to the sea and the average riverbed width measured in three points along the river stretch. Elevation and riverbed width were calculated in situ with a GPS and a measuring tape, respectively, while distance to the sea was measured as the distance from the sampling site to the outer part of the river estuary using ArcGIS 10.1. Landscape variables included the proportion of land use containing natural forests, tree plantations, agricultural crops, pasture land, urban land (including industrial soil) and roads within a circular buffer zone of 1.5-km diameter around each sampling site. Several cartographic sources in the geographic information software ArcGIS 10.1 were used. Two variables concerning the impact of human settlement on plant invasion were also included in the analyses. Distance to the nearest town of more than 5000 inhabitants was included as towns can act as sources of alien plants for the surrounding landscape. Additionally, distance to the nearest high-traffic paved road (i.e., highways and national roads wider than 6.5 m) was considered as roads can serve as dispersal pathways of alien plant propagules across the landscape. These distances were measured as a straight line from the centroid of the circular buffer zone.

The number of plant communities was defined on the basis of the phytosociological approach, which classifies vegetation in a hierarchical system with the plant association as the basic unit (Weber et al., 2000). Thirty six plant communities were distinguished following Rivas-Martínez *et al.* (2001). The number of plant communities was included as a proxy of the habitat heterogeneity of each sampling site. Sampling date was also considered to account for possible differences in species numbers resulting from sampling being done in late spring, early summer or late summer. Finally, species richness analysis requires area to be consistent across sites or replicates since the number of species increases with increasing area. In our study, the sampled area varied across sites (Table II) depending on the perifluvial environment and the proximity to crops and man-made structures. Consequently, this variable was included in the analysis of AR as an additional explanatory variable to control for the effect of varying area in the number of alien plant species. This variable was not considered in the analysis of RAR as proportions are not area-dependent.

Multicolinearity among the aforementioned explanatory variables was examined prior to modelling using Pearson's correlation coefficient. If two explanatory variables had a correlation coefficient > 0.6, the one less correlated with the response variables was removed from further analysis. The selected explanatory variables were used to model the variation in the level of plant invasion by means of GLMM, which is a useful tool when data are hierarchically structured in some way (sites nested to basins in this case) as it accounts for dependencies within hierarchical groups through the introduction of random effects (Rhodes *et al.* 2009). GLMM with Poisson distribution of errors and logarithmic link function was used for AR, given that this distribution is particularly useful for count data as these tend to be heterogeneous and are always non-negative (Zuur *et al.* 2009). As for RAR, this response variable was modelled by means of a binomial GLMM with logit link function. In both cases the river basin identity was included as a random effect to account for the nested structure of the dataset. In a first step, all selected explanatory variables were included in the model (maximal model). A sequential elimination of non-significant terms was carried out, dropping in each step that non-significant variable with the lowest significance until a minimum adequate model was achieved in which all explanatory variables were significant ($p < 0.05$). Model selection was done by means of Akaike Information Criterion. Finally, model adequacy was assessed by graphical inspection of the residuals. All statistical analyses were performed with the lme4 package in R 3.1.1 (R Development Core Team 2010).

Results

General floristic patterns

Data summarised at basin level are presented in Table I. A total of 627 plant taxa were recorded from the 80 sampling sites, of which 497 were native taxa (79 %) and 130 were alien taxa (21 %). This proportion of alien taxa decreased both at basin scale (13.54 % on average) and at site scale (9.52 % on average) (Figure 2). Total species richness per site averaged 106.7; native species richness per site averaged 96.2, whilst for alien species it averaged 10.4. Alien and native species richness were not significantly correlated (Pearson correlation r = 0.196, p = 0.08). Many native and alien plant species were infrequent, present in only one site (109 and 42, respectively) or in two sites (66 and 22, respectively). At basin scale and with respect to alien plant richness, the Nervión basin was the richest one (62 species) followed by Cadagua and Oria basins with 50 species each. On the other

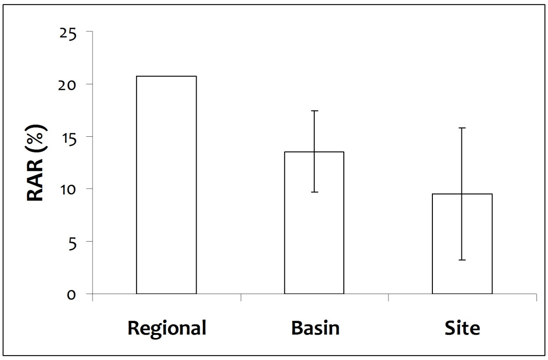

Figure 2. Relative alien richness (RAR, proportion of alien plant species in relation to all plant species) at regional, basin and site scale. The bars represent the standard deviation of the mean values.

hand, the Escudo and Lea basins showed the lowest alien plant richness (18 and 19 species, respectively). The Nervión basin showed the highest level of invasion and the Lea basin the lowest. An important within-basin variability was apparent in all river basins.

The most frequent alien plant in the studied streams was *Crocosmia x crocosmiiflora*, present in 46 sampling sites (Figure 3). Other herbaceous alien plants, such as *Cyperus eragrostis*, *Conyza sumatrensis* and *C. bilbaoana* were quite frequent as well. Regarding woody plants, alien trees intentionally planted in riverbanks for ornamental or timber purposes, such as *Platanus hispanica*, *Robinia pseudoacacia* and *Populus x canadensis*, were widely distributed across Cantabrian streams. Other species, such as *Paspalum distichum*, *Tradescantia fluminensis* and *Fallopia japonica* were less frequent but had the ability of reaching high cover values where present.

Some of the observed alien species are new for the alien flora of the study area. Among them the North American grass *Muhlenbergia schreberi* (nimblewill) emerges as the most important one. It has been localised in three sampling sites of the Urumea basin.

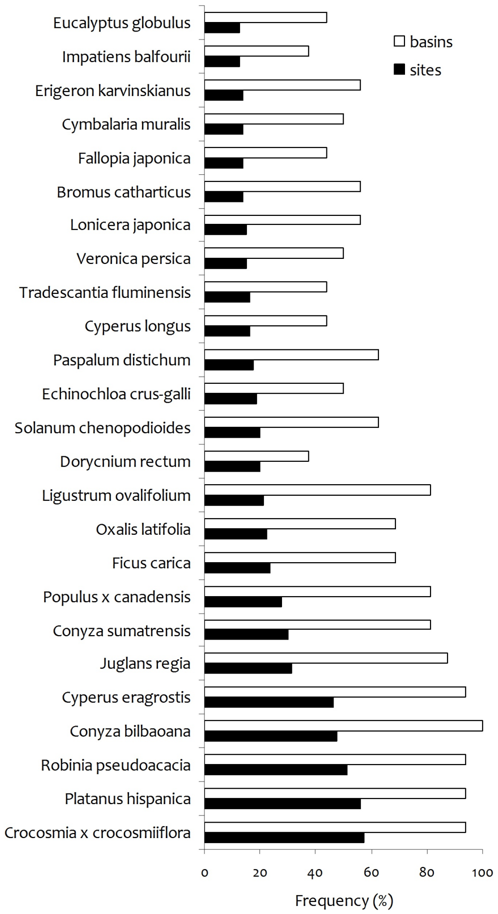

Figure 3. Frequency of sites and river basins where the most frequent alien species were present.

Plant invasion trends across basins

Industrialised river basins showed a significantly higher level of plant invasion than non-industrialised basins (Kruskal-Wallis chi-squared = 7.87, p = 0.005). Multivariate analysis pointed out that differences also existed regarding alien plant composition, with a clear distinction between both types of basins (Figure 4). Some species were associated with industrialised basins, such as *Bidens frondosa*, *Paspalum distichum* and *Acer negundo*. On the other hand, the two most widespread cultivated alien trees, *Eucalyptus globulus* and *Pinus radiata*, were the species with a highest association with non-industrialised river basins.

Plant invasion across sites

Several explanatory variables were highly correlated among them, and thus some of them were excluded from further analyses (see Table II). Generalised linear mixed modelling for RAR yielded a model where thermicity index, riverbed width, number of plant communities, distance to the nearest town and proportion of surrounding urban land were significant predictors ($p < 0.05$). RAR was inversely correlated with the distance to the nearest town, while the remaining significant predictors were directly correlated. The number of plant communities was the most significant predictor (Table III). On the other hand, differences in AR were explained by a model containing thermicity index, riverbed width, number of plant communities and distance to the nearest town, but not the proportion of surrounding urban land (see Table III). The effects of these variables on AR

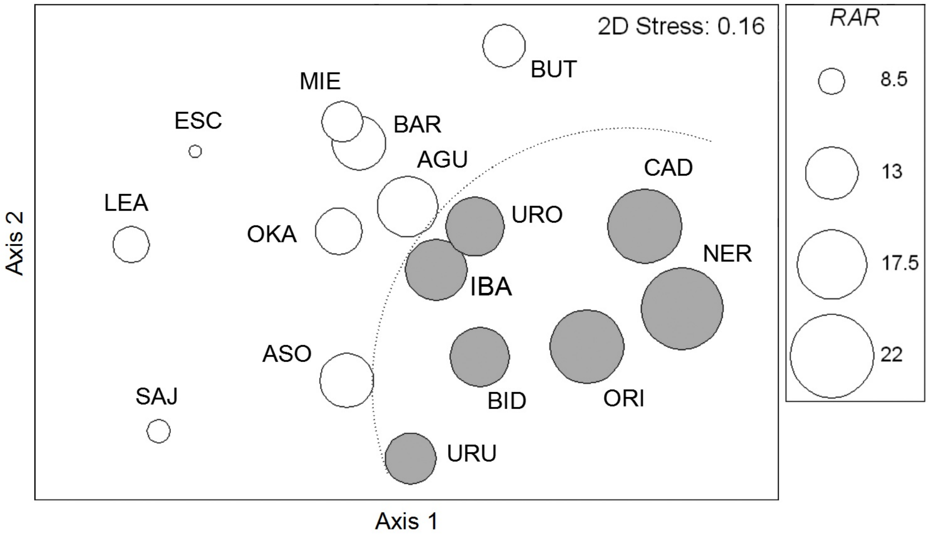

Figure 4. NMDS ordination of the river basins based on their alien species composition. Bubbles represent the relative alien richness (RAR). White bubbles: non-industrialised basins; grey bubbles: industrialised basins.

Table III. Summary statistics of the minimum adequate models for the relative alien richness (RAR) and alien richness (AR) at site scale.

Response variable: **RAR**	**Estimate**	**Std. Error**	**Z value**	**Pr (> |Z|)**
(Intercept)	-5.733	0.8965	-6.395	< 0.0001
Thermicity index	0.0089	0.003	3.009	0.003
Average width of the stream channel	0.023	0.0067	3.353	< 0.001
Number of plant communities	0.1712	0.026	6.509	< 0.0001
Distance to nearest town	-0.00004	0.000015	-2.788	0.005
Proportion of surrounding urban land	1.363	0.4271	3.191	0.001
Response variable: **AR**				
(Intercept)	-1.734	0.7835	-2.214	0.03
Thermicity index	0.01	0.0026	3.959	< 0.0001
Average width of the stream channel	0.028	0.0061	4.674	< 0.0001
Number of plant communities	0.2203	0.025	8.812	< 0.0001
Distance to nearest town	-0.00004	0.000013	-3.226	0.001

were in the same direction as the RAR model. The number of plant communities was again the most significant predictor.

Discussion

General floristic patterns

A number of alien species were especially important in relation to their frequency and/or abundance across the study area. Some of these species, such as *Conyza bilbaoana* and *C. sumatrensis*, are ruderal species that reach the riparian environment via human activity and may become quite abundant in highly disturbed sites. Others, such as *Crocosmia x crocosmiiflora* and *Cyperus eragrostis* are typical from wet habitats, in particular riparian ones. Especially important is the former one, *C. x crocosmiiflora*, a geophyte that has the ability of establishing dense stands that can displace native understory herbaceous species in alder forests (Herrera & Campos 2010). This behaviour and the consequent decrease in native diversity have been observed at some sites, in particular along the Lea river basin. Other important riparian alien plant species, such as *Paspalum distichum*, *Fallopia japonica* and *Tradescantia fluminensis* were less widespread than *C. x crocosmiiflora* but did also reach high cover in some sites. *P. distichum* has been found to be one of the most successful invaders in Iberian lowland riparian habitats (Aguiar *et al.* 2005, 2006). This neotropical perennial grass forms dense stands on muddy nitrified river beds all over the Iberian Peninsula. Actually, several plant associations dominated by *P. distichum* have been reported from Mediterranean and Cantabrian rivers (Rivas-Martínez *et al.* 2001). *F. japonica* had its highest cover values in human-disturbed areas, such as ripraps, a trend that has been documented in previous studies (Tiébré *et al*. 2008). Given its successful vegetative propagation, this species can become problematic in riparian zones by affecting the ecosystem dynamics and has been the focus of eradication campaigns in several Basque river basins. Regarding *T. fluminensis*, it has not emerged yet as one of the most frequent alien species in the Cantabrian region. However, this species has the ability to create dense stands in riparian forests that may negatively affect native forest species' seedlings richness and abundance (Standish *et al*. 2001). Finally, alien trees proved to be an important component in Cantabrian streams, with *Platanus hispanica* emerging as the most important one. This species has been traditionally planted along riverbanks in the study area and produces thousands of small fruits that can be easily wind and water dispersed (Campos 2010). As a result of this, *P. hispanica* formations have replaced alder forests in several stream sections and may also hinder both the establishment and regeneration of native species typical of Cantabrian alder forests. Similarly, the Asiatic riparian tree *Pterocarya stenoptera* has invaded and almost completely replaced alder formations along the lowest sections of the industrialised Ibaizabal basin (Herrera & Campos 2010).

Basin-scale patterns of plant invasion

It is widely accepted that the level of plant invasion is dependent on the intensity of anthropogenic development (Vilà & Ibáñez 2011). Our results at basin scale are consistent with this general statement, since those river basins with a higher degree of urbanisation and industrialisation were more invaded than river basins with a lower urban and industrial development. Differences in the level of invasion among both types of basins may arise from the introduction of numerous alien plant species associated with human activities in urban and industrial areas that may eventually establish and proliferate. Furthermore, industrial and urban activities result in an increased traffic intensity that may increase the dispersal rate of alien plant propagules and may also allow these propagules to reach sections of the main corridor and tributaries further away from urban and industrial areas. These new locations can act as foci of new alien plant propagules since the flow-facilitated dispersal can increase the spread of alien plant species downstream (Pyšek & Prach 1993, Johansson *et al*. 1996). An example of this is the grass *Muhlenbergia schreberi*, which has only been previously reported from one locality in the Iberian Peninsula (Catalonia) (Pyke 2008). In the study area, it has only been found along the main corridor in the Urumea basin, where it forms dense stands in the flooded stony river margins.

Site-scale patterns of plant invasion

It has been previously suggested that alien species richness and the fraction of the flora represented by alien species, both used as a measure of the level of invasion, respond to a different set of environmental and human-related factors (Ehrenfeld 2008). In the present study, however, both alien richness (AR) and the relative alien richness (RAR) were driven by a very similar set of explanatory variables. The number of plant communities –a proxy of habitat heterogeneity- emerged as the most significant driver of plant invasion. It is widely assumed that species richness is highly influenced by habitat heterogeneity since this variable is known to promote high plant diversity (Lonsdale 1999, Kumar *et al.* 2006). Alien richness in the present study was highly influenced by habitat heterogeneity. However, the high significance of the number of plant communities in the model for RAR suggests that the increase in alien richness with increasing habitat heterogeneity was higher than the corresponding increase in native richness. A community-level study could help identify those plant communities responsible for this pattern.

Climate has been widely recognised as a key driver of plant invasion (Planty-Tabacchi *et al.* 1996, Pyšek *et al.* 1998). In our study, the thermicity index proved to have a significant influence on plant invasion, which may reflect the small temperature variations that occur along the altitudinal gradient between the sources of the streams and their estuaries. The analysis of species-specific response to climate could allow us to determine which alien species are truly affected by the thermicity index. Riverbed width was another important predictor of the level of plant invasion, a result that is in accordance with previous works conducted in riparian systems (Aguiar *et al.* 2001, Truscott *et al.* 2008). This pattern is probably related to the fact that wider stream sections are found in lowland areas subjected to high levels of human impact (Planty-Tabacchi *et al.* 1996, Truscott *et al.* 2008) which may result in the arrival and establishment of a great number of alien species. Additionally, the probability of finding river bars where many annual alien species such as *Amaranthus hybridus*, *Bidens frondosa* and *Echinochloa crus-galli* may establish increases in wider stream sections.

Among the human-related variables, distance to the nearest town was significant in both models of plant invasion. Urban settlements usually harbour a wide variety of alien plant species since they often contain gardens and parks where many alien species are planted. These areas may therefore act as sources of alien propagules in the surrounding landscape (Duguay *et al.* 2007). As a result of this, those sites closer to towns were more invaded than more distant sites. Although there is ample evidence which suggests that roads facilitate the spread of alien species across the landscape (Parendes & Jones 2000, Gelbard & Belnap 2003), in our study distance to the nearest high-traffic road proved to be a non-significant predictor of plant invasions. This could be due to the fact that the study area is a highly populated territory with a high density of towns and roads, both high-traffic roads and smaller roads. In this context, major roads may play a minor relative role in the dispersal of alien plant species.

Regarding site-specific landscape variables, the proportion of surrounding urban land was the only significant predictor despite the overall low values across sites (see Table II). The positive association between urban land use and the level of plant invasion has already been highlighted in several studies (Borgman & Rodewall 2005, Vilà & Ibáñez 2011). However, in the present study this variable had a significant effect on the relative alien richness (RAR), but not on alien richness (AR). This could suggest that urban land surrounding streams negatively affects native species richness but has a non-significant effect on alien species richness.

The level of invasion, which we have analysed by means of AR and RAR, constitutes the basic knowledge of the invasion features of an ecosystem in a particular region. In order to get a more complete picture of this phenomenon, future research should focus on the drivers that influence the presence and distribution of alien species of special concern, such as *Fallopia japonica*, *Crocosmia x crocosmiiflora* and *Paspalum distichum*. This could allow us to gain some valuable insight that could lead to an improved and more efficient management of these species given the negative effects they may have on riverine plant communities.

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CHAPTER 4

Effect of alien plant invasion on the phylogenetic structure of riverine habitats with different disturbance regime

Diego Liendo, Idoia Biurrun, Juan Antonio Campos &
Itziar García-Mijangos

Abstract

Alien plants can have profound effects on resident vegetation that may go beyond changes in taxonomic diversity. This work explores the differences in the level of invasion and the phylogenetic diversity and structure in two riparian habitats subject to contrasting levels of natural hydrological disturbance, namely riparian forests and river bar communities, along with the effect of alien plant species on these phylogenetic patterns. For this purpose, vegetation plots surveyed following the phytosociological method were used. Phylogenetic diversity was assessed by means of the mean phylogenetic distance (MPD) and the mean nearest taxon distance (MNTD) indices. Additionally, null models were performed to calculate the standardised MPD and MNTD values to determine whether the phylogenetic structure significantly deviated from random expectations. River bar communities were significantly more invaded both in terms of species richness and cover. Additionally, regarding the native component of the community, they were phylogenetically less diverse than riparian forests, which translated into a more clustered phylogenetic structure. No relationship was found between the phylogenetic diversity of the native component and the level of invasion in any of the habitats. Nevertheless, when alien plant species were taken into account, a decrease in the overall level of phylogenetic clustering in river bar communities based on the standardised MPD index was observed, but no effect was found in riparian forests for any index. Further insights into the effect of alien plant species on the phylogenetic diversity and structure could be gained by analysing the effect of specific alien species with a proven invasive behaviour by means of pairwise approaches to identify specific interactions between native riparian species and the invaders.

Key words: alien plants, MPD, MNTD, northern Iberian Peninsula, phylogenetic diversity, phylogenetic structure, riparian forests, river bar communities, vegetation plots.

Introduction

Anthropogenic activities, especially in the last centuries, have helped to breach the biogeographical barriers to species' movement, which has resulted in the global spread and establishment of an increasing number of alien species (Lockwood *et al.* 2007, Ricotta *et al.* 2012) that have been shown to have the potential to cause severe ecological and economic problems (e.g. McNeely 2001, Vilà *et al.* 2011, Simberloff *et al.* 2013, Hoffman & Broadhurst 2016). Consequently, biological invasions are considered among the main components of human-induced global change resulting in biodiversity loss (Vitousek *et al.* 1997, Mack *et al.* 2000, Vilà *et al.* 2006), although controversy exists since it has been suggested that invasive species are not drivers but mere passengers of the aforementioned change (Didham *et al.* 2005, MacDougall & Turkington 2005, HilleRisLambers *et al.* 2010, Bauer 2012). However, invasive alien plant species do not impact all habitats to the same extent (Chytrý *et al.* 2009), with riparian habitats emerging as one of the most invaded worldwide (Richardson *et al.* 2007, Pyšek *et al.* 2010). Moreover, alien plants do not invade the different riparian plant communities equally (Campos *et al.* 2013, Liendo *et al.* 2015).

Biodiversity research on plant communities has traditionally focused on taxonomic diversity by means of different measures of species diversity, especially species richness and other measures taking into account species' relative abundances (Carmona *et al.* 2012, Clark *et al.* 2012), since species are the most readily sampled entities (Kluge & Kessler 2011). This taxonomic diversity has been shown to be negatively affected by the presence of alien plants (e.g. Hejda *et al.* 2009, Vilà *et al.* 2011), though this effect is scale-dependent (Fridley *et al.* 2007). Nevertheless, biodiversity is a multi-faceted concept which includes multiple components beyond species richness (Carmona *et al.* 2012, Dainese *et al.* 2015). Among these, phylogenetic diversity (i.e. the extent of the differences in the evolutionary history of species within floristic assemblages) emerges as a key component of plant community diversity and has been increasingly used in the last years to gain insights into the understanding of the assembly of plant communities and ecological processes (Cadotte *et al.* 2010, Kluge & Kessler 2011, Purschke *et al.* 2013).

In relation to this, co-occurring species in plant communities can be arranged following clustered, random or overdispersed phylogenetic patterns. Phylogenetically clustered communities occur when species are more closely related than expected from random assembly, which has been linked to environmental filtering selecting for species sharing similar traits and ecological requirements (Brunbjerg *et al.* 2014, Lososová *et al.* 2015, Selvi *et al.* 2016). On the other hand, in phylogenetically overdispersed communities species are more distantly related than expected from random assembly (Čeplová *et al.* 2015). Phylogenetic overdispersion has been related to competitive exclusion that limits the coexistence of closely related species (Webb *et al.* 2002) since they would share similar traits and depend on the same resources (but see Bennett *et al.* 2013). Finally, in randomly assembled communities, phylogenetic diversity does not deviate significantly from random expectation (i.e. species composition would consist of a random subset of a reference flora) as a result of stochastic events (Hubbell 2001). As in the case of taxonomic diversity, the introduction of alien species can affect the previous phylogenetic patterns in different ways, with empirical studies providing evidence for phylogenetic clustering (Winter *et al.* 2009, Lososová *et al.* 2015, Selvi *et al.* 2016), overdispersion (Bezeng *et al.* 2016) or no relationship between phylogenetic diversity of native and alien species (Lambdon & Hulme 2006).

The effects of alien plants on the phylogenetic patterns of the invaded communities have been recently assessed using both vegetation plots (e.g. Bezeng *et al.* 2013, Čeplová *et al.* 2015, Selvi *et al.* 2016) and cumulative species pools (e.g. Lososová *et al.* 2016). Here we use vegetation plots in two contrasting riparian habitats in short temperate streams of northern Spain, namely riparian forests and river bar therophyte communities, to explore the phylogenetic diversity and structure of these communities and the effects of alien plant species on them. Previous studies have explored the drivers of plant invasion in this type of streams (Liendo *et al.* 2015, 2016), while in the present work we focus on specific effects of alien plant species on native flora diversity. Riparian forests and river bars are subject to natural flood disturbance but with different intensity and duration. This level of disturbance is high in river bars as a result of their position on the riverbed, implying that they are flooded during long periods, and decreases towards riparian forests given that they occupy a higher position with regard to flowing water and, consequently, are flooded over much shorter periods. As a result of this, we expect that river bar communities will show a more clustered phylogenetic structure than riparian forests. We also expect that this phylogenetic structure will be affected by the alien plant invasion in both habitats. We specifically ask the following questions (1) do riparian forests and river bar communities differ in their diversity patterns? (2) is the phylogenetic diversity of these habitats related to their level of plant invasion? and (3) is there any change in their phylogenetic structure when alien plant species are taken into account?

Methods

Study area and data collection

This study was conducted in riparian forests and river bar therophyte communities of several Cantabrian river basins of northern Spain, between the Nansa river basin on the west and the Bidasoa on the east (Figure 1). Riparian forests included alder forests of the *Hyperico androsaemi-Alnetum glutinosae* and the *Stegnogrammo pozoi-Alnetum glutinosae* associations and ash forests of the *Polysticho setiferi-Fraxinetum excelsioris* association (Loidi *et al.* 1997, Biurrun *et al.* 2016). On the other hand, river bar communities included

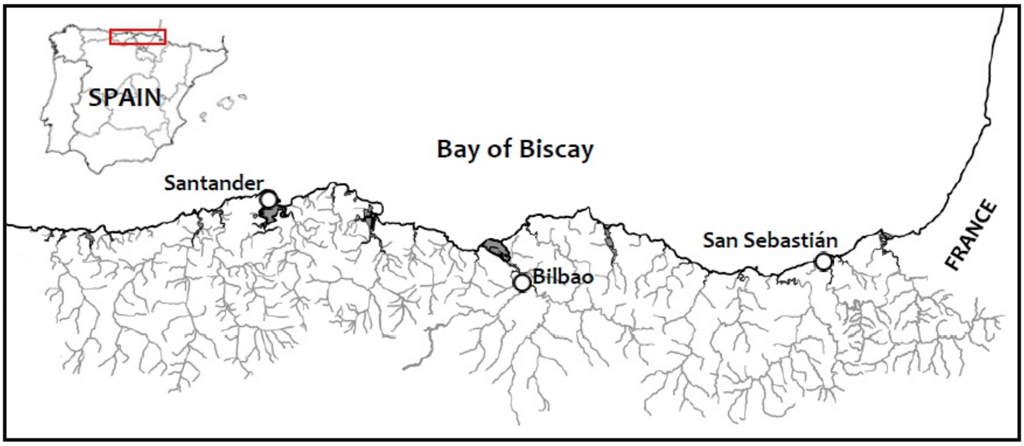

Figure 1. Study area showing the fluvial network and the main cities.

nitrophilous macrotherophyte communities of the *Bidenti frondosae-Polygonetum lapathifolii* association (sensu Campos 2010). These communities were surveyed following the phytosociologial method (Braun-Blanquet 1951). The sampled area of the vegetation plots was 100-200 m^2 for riparian forests and 20-40 m^2 for river bar communities, respectively. All vascular plant species were recorded within these plots and their cover values were estimated by means of a 7-index scale which was subsequently converted to percentage values: r (0.1 %), + (0.5 %), 1 (3 %), 2 (15 %), 3 (37.5 %), 4 (62.5 %) and 5 (87.5 %). Plots surveyed by the authors were used along with plots stored at BIOVEG database (Biurrun *et al.* 2012). A total of 104 forest plots and 49 river bar plots from the period 1985-2015 were used. Species nomenclature follows Euro + Med (2006-2016) except for the *Conyza* and *Persicaria* genera, which follow Aizpuru *et al.* (1999).

Diversity patterns and level of invasion of forests and river bars

The level of plant invasion was estimated by means of three indices (Catford *et al.* 2012, Liendo *et al.* 2016): absolute alien species richness (AR, i.e. the number of alien species in each plot), relative alien richness (RAR, i.e. the proportion of alien species in a plot) and relative alien cover (RAC, i.e. the proportion of alien species cover in relation to the total plant cover in a plot). Differences between diversity measures and the level of plant invasion between riparian forests and river bar communities were analysed using t-tests.

Phylogenetic diversity (PD) and data analyses

A general phylogenetic tree was assembled by pooling all species, native and alien, found in both habitats. Singleton species were excluded along with pteridophytes since the latter branch of very early in the phylogenetic tree and would consequently have too much influence on the values of the PD indices (Van Meerbeek *et al.* 2014). The resulting phylogenetic tree was formed by 329 species. The tree was constructed with the 'phylomatic' function of the R package 'brranching' using the Phylomatic tree R20120829, based on the APG III system (Bremer *et al.* 2009), as the reference tree to which species names were matched. This function created a tree with polytomies that were randomly resolved using the 'multi2di' function of the 'ape' package to get a fully resolved tree. Finally, branch lengths were assigned to the phylogenetic tree using the branch length adjustment algorithm (BLADJ) in Phylocom (Webb *et al.* 2008) and based on estimated family ages from fossil data according to Wikström *et al.* (2001).

PD indices were calculated separately for forests and river bars for the native component and the total communities including native and alien species (four communities in total). For this purpose, the complete phylogenetic tree was used for total communities, whereas for the native component the original tree was pruned with the 'drop.tip' function in 'ape' to obtain a tree including only native species. The same was done to calculate standardised effect sizes (see below). Two complementary PD indices were calculated: mean pairwise distance (MPD) and mean nearest taxon distance (MNTD).

The first of these, MPD, is the average pairwise distance in a plot or community and is a measure of the overall phylogenetic diversity (Swenson 2014). On the other hand, MNTD is the mean distance between one species and its closest relative in a plot or community (Swenson 2014). This measure focuses on 'terminal' diversity (i.e. the tips of the phylogenetic tree) since it is often expected that the strongest interactions will occur between closely related species. Very small MNTD values would indicate the co-occurrence of very closely related species. MPD has been shown to be independent of species richness, whereas MNTD decreases as species are added to a community and consequently can be affected by species richness (Vellend *et al.* 2010).

The relationship between the level of plant invasion (AR, RAR and RAC) and the phylogenetic diversity (MPD and MNTD) of the native communities was calculated by means of linear regressions. Variables were log transformed [$\log_{10}(x + 1)$] when necessary in order to improve the normality of the error distribution, which was assessed by a visual inspection of the residuals. Given that MNTD can be affected by species richness, the standardised MNTD values obtained through randomisation (see below) were used to verify whether the results were consistent after accounting for possible differences in species richness.

To test whether phylogenetic structure of riparian forests and river bar communities was random or deviated from random expectations, the standardised effect sizes (SES.MPD and SES.MNTD) were calculated, which have been shown to be independent of species richness (Pavoine & Bonsall 2011) and equivalent to the NRI and NTI indices (Webb *et al.* 2002) but with opposite sign. This was done by comparing the observed MPD and MNTD values with the values of 999 random communities using the 'taxa.labels' null model in 'picante', which shuffles distance matrix labels across all taxa included in the phylogenetic distance matrix (Kembel *et al.* 2015), thus holding species richness of plots and the species turnover among them constant. SES.MPD (and analogously SES.MNTD) was calculated as:

$$\mathrm{SES.MPD} = (\mathrm{MPD}_{\mathrm{obs}} - \mathrm{MPD}_{\mathrm{rand.mean}})/\mathrm{SD\ MPD}_{\mathrm{rand.mean}}$$

where $\mathrm{MPD}_{\mathrm{obs}}$ is the observed MPD and $\mathrm{MPD}_{\mathrm{rand.mean}}$ and SD $\mathrm{MPD}_{\mathrm{rand.mean}}$ are the mean and standard deviation of the expected MPD values in the 999 randomised communities, respectively. Near-zero values indicate species pools with random phylogenetic assembly, while deviations would indicate phylogenetic clustering ($\mathrm{SES} < 0$) or overdispersion ($\mathrm{SES} > 0$). Values below -1.96 or above 1.96 indicate significant ($p < 0.05$) clustering and overdispersion, respectively (Lososová *et al.* 2015). The four indices, MPD, MNTD, SES.MPD and SES.MNTD, were weighted by species abundances.

Finally, the effect of the presence of alien species on the phylogenetic structure of forest and river bar communities (i.e. alien effect) was estimated, separately for both habitats, as the difference between the SES of the communities containing native and alien species and the SES of the communities containing only native species (modified from Winter *et al.* 2009).

Results

Diversity patterns and level of invasion of forests and river bars

A total of 387 taxa (including subspecies and taxa identified at genus level) were found in the 104 forest plots. Of these, 333 were native and 54 alien. As many as 126 taxa (32.5 %) were present in only one plot, including 98 native and 28 alien taxa. The most frequent native species (occurring in more than 80 plots) were *Alnus glutinosa* (99), *Hypericum androsaemum* (99) *Hedera hibernica* (92), *Carex pendula* (88), *Fraxinus excelsior* (88) and *Brachypodium sylvaticum* (86). In the same way, the most frequent alien species (occurring in more than 20 plots) were *Crocosmia x crocosmiiflora* (24), *Platanus hispanica* (24) and *Robinia pseudoacacia* (24). Information on number of species, cover values and relative alien cover and richness per plot is summarised in Table I. Regarding river bars, 261 taxa (including subspecies and taxa identified at genus level) were found in the 49 river bar plots, including 194 native and 67 alien taxa. As many as 91 taxa (35 %) were found in only one plot, including 64 native and 27 alien taxa. The most frequent native species (occurring in more than 20 plots) were *Persicaria lapathifolia* (34), *P. maculosa* (31), *Calystegia sepium* (27), *Rumex obtusifolius* (27), *Urtica dioica* (27), *Lythrum salicaria* (25), *Apium nodiflorum* (23) and *P. hydropiper* (22). In the same way, the most frequent alien species (occurring in more than 10 plots) were *Cyperus eragrostis* (31), *Paspalum distichum* (31), *Echinochloa crus-*

Table I. Mean plot values and standard deviation (SD) of the level of plant invasion and the floristic and phylogenetic diversity indices (the latter calculated for the native component) in riparian forests and river bar communities. RAC: relative alien cover; RAR: relative alien richness. *** $p < 0.001$; (–) not significant differences.

	FORESTS		**RIVER BARS**		**Forests vs. River bars**
	Mean	**SD**	**Mean**	**SD**	**(t-test)**
Alien cover (%)	11.9	23.55	32.12	28.1	-4.35***
Native cover (%)	246.27	73.69	102.15	46.1	14.72***
Total cover (%)	258.17	71.22	134.3	53.3	12***
RAC (%)	4.74	9.3	22.6	17.8	-8.87***
Alien richness (AR)	1.71	2.2	7.12	5.1	-7.13***
Native richness	41.5	12.75	20.7	14.55	8.57***
Total richness	43.21	13.17	27.8	16.9	5.64***
RAR (%)	3.95	5.15	28.39	14.25	-11.66***
MPDnat	400.33	45.67	280.5	105.1	7.65***
MNTDnat	228.53	40.45	222.14	82.8	—
SES.MPDnat	-0.59	1.02	-1.78	1.78	4.34***
SES.MNTDnat	-0.46	0.77	-1.5	1.2	5.53***

galli (24), *Bidens frondosus* (17), *Conyza bilbaoana* (16), *Digitaria sanguinalis* (14), *Lycopersicon esculentum* (12), *Dysphania ambrosioides* (11) and *Symphyotrichum squamatum* (11). Information on number of species, cover values and relative alien cover and richness per plot is summarised in Table I. There was a positive and significant relationship between the number of native and alien species in river bars ($R^2 = 0.17$; $p < 0.01$ for $\log_{10}$-transformed values), while no relationship was found in riparian forests ($R^2 = 0.01$; $p = 0.28$). River bar communities had significantly higher alien cover and richness and higher values of RAC and RAR than riparian forests. With respect to phylogenetic diversity, the native component of river bar communities had significantly lower MPD values than riparian forests but did not differ significantly in relation to the MNTD index (Table I). Additionally, river bar communities showed significantly lower SES.MNTD and SES.MNTD values, which indicates a more clustered phylogenetic structure of the native component in terms of both indices. This was confirmed by null models which showed that a random phylogenetic structure regarding MPD prevailed over a clustered pattern in the native component of riparian forests, whereas in river bar plant communities almost half of the plots showed a clustered pattern (Figure 2). On the other hand, regarding terminal phylogenetic diversity (MNTD), all forest plots showed a random pattern, while in river bars around 35 % of the plots were significantly clustered. Not a single plot showed an overdispersed phylogenetic pattern in neither of the habitats studied.

Relationship between the level of invasion and the phylogenetic diversity of the native component of riparian forests and river bar communities

The phylogenetic diversity of the native component of riparian forests, both in terms of the MPDnat and MNTDnat indices, was not significantly related to the level of plant invasion. On the contrary, a weak negative but significant relationship was found in river bar communities between AR and MNTDnat ($R^2 = 0.167$, $p < 0.01$) and between RAR and

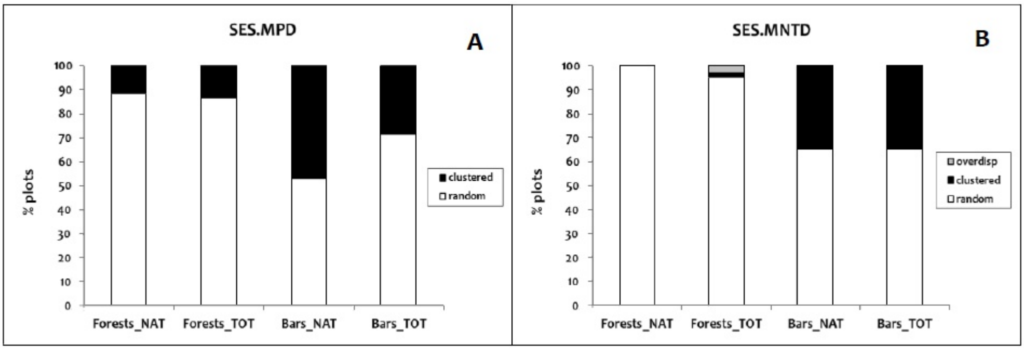

Figure 2. Proportion of plots with random phylogenetic structure (white) or significantly clustered (black) or overdispersed (grey) phylogenetic structure in riparian forests and river bar communities with respect to A) SES of the MPD index and B) SES of the MNTD index. NAT: native component; TOT: total community (native + alien species).

MPDnat ($R^2 = 0.266$, $p < 0.001$). The level of invasion calculated by means of the relative alien cover (RAC) was not significantly related to the phylogenetic diversity of the native component in neither of the habitats. To check for possible bias due to differences in species richness the analyses were repeated for the SES.MNTDnat of native species, resulting in non-significant relationships between SES.MNTDnat and the level of plant invasion for both habitats. Additionally, although the MPDnat index has been shown not to be affected by species richness, we found a positive and significant relationship between this index and the number of native species for both habitats ($R^2 = 0.12$, $p < 0.001$ for forests; $R^2 = 0.44$, $p < 0.001$ for river bars). For this reason, the SES.MPDnat was regressed against the level of invasion yielding non-significant results again.

Effect of alien species on the phylogenetic relatedness

When null models were calculated for the whole community (native and alien species), the level of phylogenetic clustering decreased with respect to the native component in river bars for the MPD index and remained unchanged regarding the MNTD index (Figure 2). Regarding riparian forests, the phylogenetic structure remained almost unchanged in terms of both phylogenetic indices when alien species were taken into account.

These results were confirmed when the alien effect was plotted against the standardized MPDnat and MNTDnat values (Figure 3). This effect was predominantly close to zero in forest plots for both indices and in river bar communities for the MNTD index, implying that alien species had an overall low effect on the phylogenetic pattern. However, alien effect in river bars was positive in most cases for the MPD index, meaning that alien species tended to increase this index and, therefore, to reduce the overall level of clustering. Additionally, this alien effect on MPD was higher when the native community was more strongly clustered.

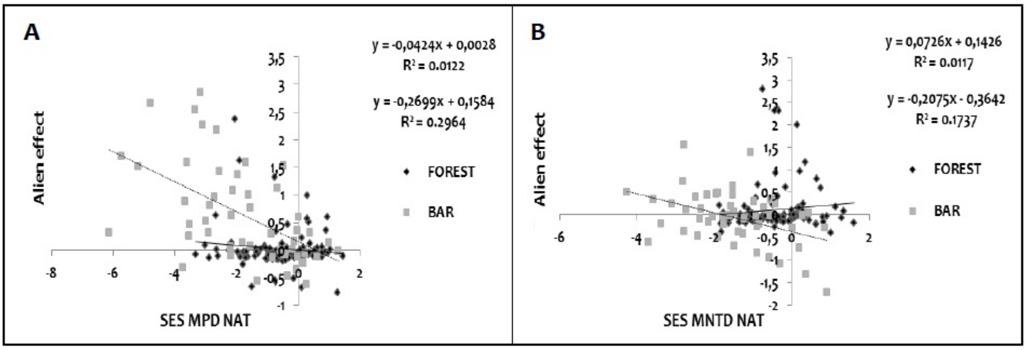

Figure 3. Relationship between the alien effect (SEStotal - SESnative) and the SES values of the MPD (A) and MNTD (B) calculated for the native component in riparian forests and river bar communities. Upper equations correspond to riparian forests and lower equations to river bar communities.

Discussion

Diversity patterns and level of invasion of forests and river bars

Our results confirm previous research showing that river bar communities are notably more invaded than riparian forests (Campos *et al.* 2013), with values of invasiion level similar to those obtained for both habitats in Atlantic rivers (Tabacchi & Planty-Tabacchi 2005, Campos *et al.* 2013). This higher level of invasion in river bar communities is probably the result of the stronger hydrological disturbance they are subject to (Davis *et al.* 2000). River bars emerge seasonally in late spring and are colonised mostly by annual seed-dispersed species (Assini 2001). By late autumn-early winter this vegetation is almost totally removed following an increase in water flow and, consequently, alien species have better chances of establishment in a low-competition environment (Hobbs & Huenneke 1992) due to the absence of native species when water flow decreases again the following year. Additionally, river bars in the study area are concentrated at low elevations near human settlements (Liendo *et al.* 2016). As a result of this, they receive a great deal of nutrients, especially N, allowing for the establishment of many opportunistic and nitrophilous alien therophytes, such as *Amaranthus* spp., *Xanthium strumarium* or *Bidens frondosus* (Campos *et al.* 2013, Bolpagni & Piotti 2015), which can attain very high cover values (Bolpagni & Piotti 2015). Regarding the relationship between native and alien richness, this was not significant in riparian forests, contrary to was previously reported for several types of European riparian forests, where this relationship was significantly positive (Schnitzler *et al.* 2007). The lack of significance in our study may be due to a number of plots containing no alien species or very few compared to the number of native species, which is probably the result of the higher habitat stability which translates into a higher competition with resident species that may hinder alien plant establishment. On the contrary, the number of alien species did have a significant positive relationship with native species richness in river bar communities. This native-alien relationship has been the subject of much controversy, with studies reporting both negative relationships (in line with the 'biotic resistance hypothesis') or positive relationships (in accord with the 'biotic acceptance hypothesis' or 'the rich get richer' concept), though it has been suggested that it depends on the scale of observation (Fridley *et al.* 2007). In our case, the results in river bar communities would concur with 'the rich get richer' concept (Stohlgren *et al.* 2003) in the sense that the aforementioned factors responsible for a high alien plant richness in this habitat (low competition and high availability of bare soil and nutrients due to high levels of disturbance) would also be responsible for a high native species richness.

Riparian forests showed a higher phylogenetic diversity than river bar communities in terms of their native component regarding the observed values of the overall phylogenetic distance between all species in a plot (measured by the MPD index). However, and contrary to expectations, no differences were found at finer phylogenetic scale, measured by the MNTD index. As this index has been shown to be negatively affected by species richness (Vellend *et al.* 2010), and given that riparian forests had significantly more native species than river bar communities (see Table I), we infer that MNTD values calculated on forest plots were low and similar to those of river bar plots as a result of their higher native species richness. When differences in species richness were taken into account by calculating the standardised effect sizes (SES.MPD and SES.MNTD), significant differences emerged between both habitats for both indices. These differences were reflected by more negative values for both indices in river bar communities which indicate that, as expected, the native component in river bar communities showed a more clustered phylogenetic structure than in riparian forests. Phylogenetically clustered patterns have been previously reported both from natural habitats, such as coastal dunes (Brunbjerg *et al.* 2014) and anthropogenic habitats, such as urban plant communities (Čeplová *et al.* 2015). This clustered pattern would be the result of environmental filtering associated to disturbance (Brunbjerg *et al.* 2012, 2014, Lososová *et al.* 2015, Selvi *et al.* 2016) which would select for closely related species sharing similar ecological requirements (Čeplová *et al.* 2015), assuming trait conservatism across the phylogenetic tree (Prinzing *et al.* 2001, Burns & Strauss 2011). In our case, the hydrological disturbance regime river bars are subject to implies that this habitat is chiefly colonised by annual seed-dispersed species, many of them belonging to few families such as Polygonaceae (e.g. *Persicaria* spp.). On the other hand, riparian forests, which are subject to hydrological disturbance to a much lesser extent, showed much lower levels of phylogenetic clustering since the higher habitat stability would allow for the coexistence of species from more distant lineages (Warwick & Clarke 1995).

Relationship between the level of invasion and the phylogenetic diversity

Contrary to expectations, working with vegetation plots and once the differences in the number of species among plots are removed, the phylogenetic diversity of the native component of riparian forests and river bar communities was not significantly related to the number or proportion of alien plant species entering the community. In contrast, previous studies carried out with vegetation plots (Gerhold *et al.* 2011) and cumulative species lists (Lososová *et al.* 2015) have found strong evidence that the phylogenetic diversity of the resident community influences its receptiveness to alien plant species, with the latter increasing with decreasing levels of phylogenetic diversity of the native component. These studies have analysed the relationship between plant invasion and phylogenetic diversity at community level across a wide range of plant community types. However, our study focuses on the comparison of vegetation plots at very fine scale within community types (i.e., riparian forests and river bar communities separately), which may have important consequences on the aforementioned invasion-phylogenetic diversity relationship.

Effect of alien species on the phylogenetic relatedness

Another important finding of the present study is that alien plant species did not affect the phylogenetic structure of riparian forests and river bar communities equally. Firstly, alien plants had a negligible effect on the phylogenetic structure of riparian forests in terms of both SES.MPD and SES.MNTD. Riparian forests had an overall low level of invasion, with a number of plots containing no alien or few alien species. Additionally, they have been shown to be species-rich in terms of native species, with significant higher values than in river bar communities (see Table I). As a result of this, the few alien plants found in forest plots had very little impact on their phylogenetic structure. It has been previously reported that individual species, such as *Crocosmia x crocosmiiflora* and *Tradescantia fluminensis*, can achieve moderate to high cover values in riparian forests of the study area and become locally dominant in the herb layer (Liendo *et al*. 2016), which could have a higher effect on the phylogenetic structure of this habitat. Nevertheless, given that many of the forest plots used in the present study were randomly placed across the study area, these local invasions may not have been well captured. Secondly, alien species decreased the phylogenetic clustering in river bar communities in terms of SES.MPD (i.e. they increased the overall phylogenetic dispersion of river bar plots as a result of the arrival of distantly-related species with respect to native species). Similar results were reported by Gerhold *et al*. (2011) for a number of plant communities assessed by means of vegetation plots at national scale, where they concluded that alien species tended to coexist with rather than replace natives. Additionally, although river bar plots with low phylogenetic diversity were not more invaded than phylogenetically more diverse plots (see above), the decrease in the level of phylogenetic clustering caused by alien plant species was higher in the former. In contrast to this decrease in the overall phylogenetic clustering associated to plant invasion observed in river bar plots, no effect was detected at finer scale as shown by the SES.MNTD. A possible explanation for this is that despite the fact that alien plant species invading river bars are distantly related with respect to native species, these alien species are closely related to each other (e.g. *Amaranthus* spp., *Conyza* spp.). Consequently, the pattern of SES.MPD is not reflected by SES.MNTD, since the former is based on average distances among all species and the latter is based on the nearest distances between species.

Concluding remarks

The present study shows that two contrasting riparian habitats, namely riparian forests and river bar communities, differ markedly in their level of plant invasion and in their phylogenetic diversity and structure. However, alien plants had a low overall effect on the phylogenetic diversity and structure of these habitats except for the observed decrease in the level of phylogenetic clustering in river bar communities in terms of the average phylogenetic diversity. Further insights could be gained by analysing the effect of specific alien species with a proven invasive behaviour by means of pairwise approaches to identify specific interactions between native riparian species and the invaders.

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CHAPTER 5

New contributions to the native and alien flora in riparian habitats of the Cantabrian watershed (northern Spain)

Diego Liendo, Juan Antonio Campos, Idoia Biurrun &
Itziar García-Mijangos

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Abstract

As a result of a floristic survey carried out in riparian habitats of northern Spain, new chorological data are provided for 9 alien and 6 native plant species. Some species are reported for the first time at regional scale, such as *Carex strigosa*, *Helianthus x laetiflorus* and *Persicaria pensylvanica* in Cantabria. Also noteworthy is the finding of naturalised populations of the North American grass *Muhlenbergia schreberi* at the Urumea river basin, which represents the second reference for the Iberian Peninsula.

Key words: alien plants, native plants, northern Spain, riparian habitats.

Introduction

Riparian habitats have been repeatedly documented as being highly vulnerable to invasion by alien plants due to natural factors and processes and human-mediated activities. In relation to this, the present work stems from a wider study focused on the analysis of the presence, distribution and impacts of alien plants in riparian habitats of the Cantabrian watershed (northern Spain). Streams in this territory have the distinct characteristic of being notably short in comparison with Mediterranean Iberian rivers since their sources in the Cantabrian Mountains are very close to their mouths in the Bay of Biscay. Additionally, summer low water period is shorter and less intense in Cantabrian streams as a result of a higher summer rainfall. Riparian and adjacent habitats of the Cantabrian watershed have been intensely disturbed in the last decades as a result of human population increase and related anthropogenic activities, such as agriculture, industrial development, urbanisation, and the development of an increasingly dense transport network which, coupled with the benign climate, has resulted in many different alien plant species establishing in these habitats (Campos 2010, Liendo *et al.* 2016).

Fieldwork conducted in 16 randomly selected river basins has allowed the authors to present new chorological data for 9 alien and also 6 native plant taxa, some of which representing new records at provincial and/or regional scale. In this context, it is worth highlighting the finding of naturalised populations of the North American grass *Muhlenbergia schreberi* (nimblewill) along the Urumea stream (Gipuzkoa and Navarra provinces), which represents the second record of this species in the Iberian Peninsula.

Information on species distribution has been gathered from ANTHOS (Information system on vascular plants in Spain), GBIF (Global Biodiversity Information Facility), Flora iberica (Castroviejo 1986-2015) and several bibliographical sources. Species nomenclature follows Euro+Med (www.emplantbase. org, accessed 21-I-2016) except for *Aucuba japonica* Thunb. (*Nov. Gen. Pl.* 3: 62. 1781), *Persicaria pensylvanica* (L) M. Gómez (Anales Inst. Segunda Ensen. 2: 278. 1896), *Pyracantha angustifolia* (Franch.) C. K. Schneid. (Ill. Handb. Laubholzk., 1: 761. 1906), *Verbena brasiliensis* Vell. (Fl. Flumin. 1: Tab. 40. 1827) and *Verbena incompta*

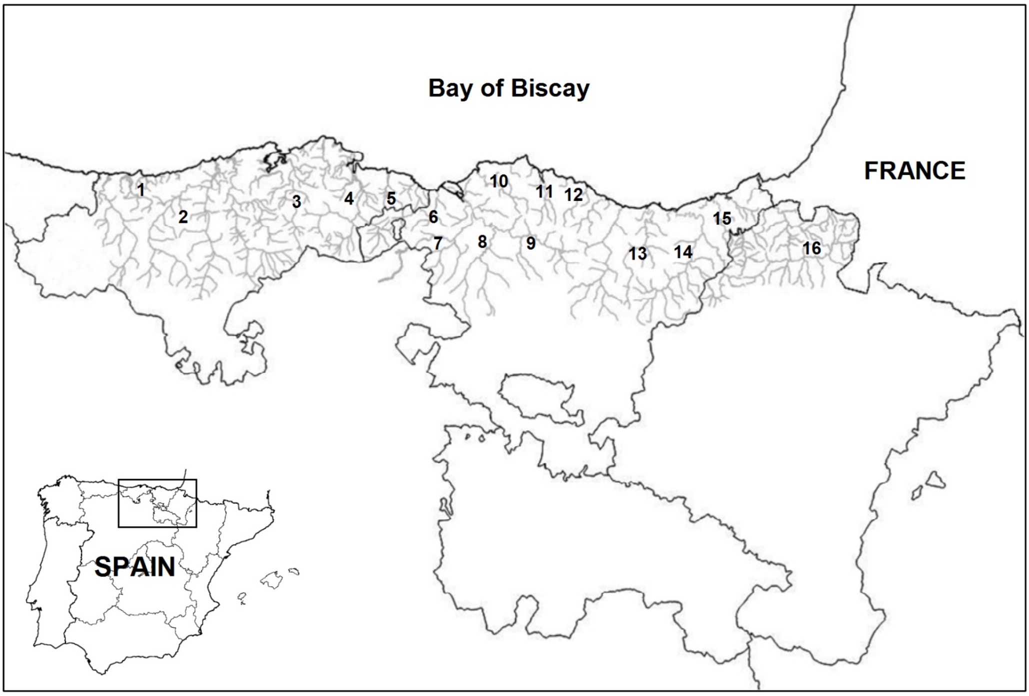

Figure 1. Study area showing the fluvial network and the selected river basins. 1: Escudo; 2: Saja-Besaya; 3: Miera; 4: Asón; 5: Agüera; 6: Barbadún; 7: Cadagua; 8: Nervión; 9: Ibaizabal; 10: Butrón; 11: Oka; 12: Lea; 13: Urola: 14: Oria; 15: Urumea; 16: Bidasoa.

P.W. Michael (Telopea 6: 181-183). For each taxon, the following information is provided: currently accepted name, synonyms, family, type of chorological novelty, locality, province, 1x1 km UTM grid square (ED50 Datum), stream where the specimen was collected, elevation, date and authors of collection and registration code in the BIO Herbarium of the University of the Basque Country (UPV/EHU) where voucher specimens of all taxa are preserved. Additionally, some voucher specimens preserved in the following herbaria have been included in the present work: SEST (Natural Sciences Society of Sestao), VIT (Natural History Museum of Álava), ARAN (Aranzadi Science Society) and MA (Royal Botanical Garden of Madrid).

As mentioned above, the study area encompasses riparian habitats of 16 randomly selected river basins of northern Spain (Figure 1). This area includes partially or totally the provinces of Cantabria, Burgos, Bizkaia, Álava, Gipuzkoa and Navarra. From a biogeographic point of view, the study area is included in the Cantabrian-Atlantic subprovince of the Eurosiberian region (Rivas-Martínez *et al.* 2014). Within this subprovince, most of the river basins belong to the Cantabrian-Basque sector with the exception of the Saja- Besaya and Escudo basins, which are included in the Galician Asturian sector (Berastegi *et al.* 1997, Rivas-Martínez *et al.* 2014).

Riparian vegetation in these river basins corresponds to the Cantabrian-Basque and Oviedese fluvial geoserie *Hyperico androsaemi-Alnetum glutinosae* (Loidi *et al.* 2011), which covers the territory between central Asturias in North Spain and the French Basque Country. This geoserie consists of several plant communities that grow on three distinct environments: riverbed, riverbank and floodplain, with alder forests (*Alnus glutinosa*) associated to the riverbank and river bar plant communities associated to the riverbed being the most widespread ones. Regarding alien plants, some species strongly associated to riparian habitats are commonly found across the study area, such as *Fallopia japonica*, *Crocosmia x crocosmiiflora* and *Cyperus eragrostis* (Liendo *et al*. 2015).

Results and Discussion

Aucuba japonica Thunb. (Garryaceae)

Gipuzkoa: Hernani, Ereñozu, Urumea stream, 30TWN8589, riparian forest, 16 m, 24-IX-2013, *I. Biurrun* & *D. Liendo*, BIO 50909.

Aucuba japonica is a perennial dioecious shrub native to East Asia (China and Japan) which is widely used as ornamental in warm zones of Western Europe and the USA. This shade-tolerant species is valued for its ability to thrive in the most difficult garden environments and numerous cultivars have been obtained. The only previous references of this species in the Basque Country are two herbarium sheets collected in gardens and parks of Vitoria-Gasteiz (Álava, VIT 17944 and VIT 18000). Consequently, our Gipuzkoa locality represents the first record of this species as escaped from cultivation in the Basque Country.

Calamagrostis arundinacea (L.) Roth (Poaceae)

Cantabria: Molledo, Silió, Erecia stream, 30TVN1777, disturbed alder forest, 273 m, 31-VII-2013, *D. Liendo* & *M. Solís*, BIO 50828; Valle de Villaverde, Agüera stream, 30TVN7886, 222 m, alder forest, 22-IX-2011, *I. Biurrun* & *D. Liendo*, BIO 50554.

Indicator species of the *Calamagrostion arundinacea*e alliance, which is the only alliance of the *Calamagrostietalia villosae* order in Spain. This alliance includes acidophilic megaforb communities with a high grass diversity that grow in supra-oro-temperate areas of the Pyrenees (Rivas-Martínez 2011). Both localities included in this work are at a significant lower altitude in mesotemperate areas, as were the records from Liérganes and La Cavada included in Guinea (1953) or those from Ampuero and Soba included in Herrera (1995). Of special relevance is the reference from Silió as it would extend westward the known distribution of the species in the Cantabrian Mountains. It would also indicate that this taxon is probably present at higher elevations in the mountains of the water divide between the Saja-Besaya and the Ebro river basins. The nearest known populations are located in the upper Pas river basin some kilometres eastwards (Aedo *et al*. 1987, Herrera *et al*. 1990).

Carex strigosa Huds. (Cyperaceae)

Cantabria: Valdáliga, Bustriguado, Bustriguado stream, 30TUN9095, alder forest, 105 m, 02-VII-2013, *D. Liendo*, *M. Solís* & *H. Penna*, BIO 50695.

This sedge is found in much of Europe, the Caucasus and northern Iran (Laskurain *et al*. 2003) but it is a very rare plant in the Iberian Peninsula. It is characteristic of the *Alnion incanae* alliance (Rivas-Martínez 2011), though we report it from a Cantabrian alder forest of the *Hyperico androsaemi-Alnetum glutinosae* association included in the *Hyperico-Alnion* alliance (Biurrun *et al*. 2016). Aizpuru *et al*. (2001) reported this species for the first time in the Iberian Peninsula from a mixed-alder forest in Usurbil (Gipuzkoa), which resulted in this taxon being included in the Atlas and Red Book of the Threatened Vascular Flora of Spain (Laskurain *et al*. 2003) as a critically endangered species. Afterwards, Jiménez Mejías *et al*. (2007) provided a new locality from the Bidasoa river basin in Lesaka (Navarra) and pointed out that the localities from Asturias and Gipuzkoa reported in Allorge & Allorge (1941) were not taken into account for the Iberian Peninsula catalogue since no herbarium sheet was found. Finally, Aizpuru *et al*. (2010) included the taxon in the Red List of Vascular Flora of the Basque Country as vulnerable to extinction and provided two new localities: Beluntza (Álava) and Bergara (Gipuzkoa). According to available information, this species has not been reported from Cantabria so far, which means that our voucher specimen from the Bustriguado stream in Valdáliga represents a new addition to the flora of this province.

Helianthus x laetiflorus Pers. (Asteraceae)

Cantabria: Ampuero, Udalla, Asón stream, 30TVN6496, 32 m, river bar, 03-X-2013, *D. Liendo*, *M. Solís* & *M. Torca*, BIO 50886; **Álava**: Llodio, Anuntzibai, Altube stream, 30TWN0576, river bar, 119 m, 29-IX-2008, *I. Biurrun*, *I. García-Mijangos* & *D. García-Magro*, BIO 50844; **Gipuzkoa**: Andoain, Oria stream, 30TWN7986, 40 m, river bar, 25-IX-2013, *I. Biurrun* & *D. Liendo*, BIO 50882.

This North American hybrid and rhizome-forming aster is becoming increasingly widespread along Cantabrian streams. *Helianthus x laetiflorus* can be difficult to distinguish from *H. tuberosus*, though the former presents much narrower leaves and tightly appressed involucral bracts that do not surpass the tubular flowers as the latter do (Aizpuru *et al*. 1999). It has already been cited in the Basque Country (Campos & Herrera 1998, 1999) and Navarre (Catalán & Aizpuru 1985, Biurrun 1999) where it shows similar ecological requirements and distribution than *H. tuberosus*, although the latter is more abundant (Campos 2010). However, it has not been reported from Cantabria so far, implying that our reference from Ampuero would represent a new addition to the flora of this province.

Mentha spicata L. (Lamiaceae)

Bizkaia: Getxo, Algorta, Gobelas stream, 30TVP9900, disturbed shore, 8 m, 29-VII- 2011, *I. García-Mijangos, D. Liendo* & *M. Torca*, BIO 50890.

Despite being native to Europe and Asia, this species of mint is regarded as introduced in Spain (Morales 2010). It is widely cultivated and it frequently escapes from cultivation and establishes next to walls and water courses and on road sides. There is only one previous record of this taxon from Bizkaia in Orduña (herbarium code ARAN 47417). Our reference from Getxo represents therefore the second reference for this province and is located at a considerable lower altitude in a thermotemperate area. Carlón *et al.* (2014) reported this species from a sandy car park of Pedreña (Cantabria), which to date represented the only record in a thermotemperate location of the study area.

Muhlenbergia schreberi J. F. Gmel. (Poaceae)

Gipuzkoa: Hernani, Ereñozu, Urumea stream, 30TWN8589, stony shore with sand accumulation, 16 m, 24-IX-2013, *I. Biurrun* & *D. Liendo*, BIO 50908. **Navarra**: Goizueta, Urumea stream, 30TWN9283, stony shore with sand accumulation, 139 m, 09-IX-2013, *I. Biurrun* & *D. Liendo*, BIO 50904; Goizueta, Urumea stream, 30TWN9378, stony shore with sand accumulation, 201 m, 24-IX-2013, *I. Biurrun* & *D. Liendo*, BIO 50906.

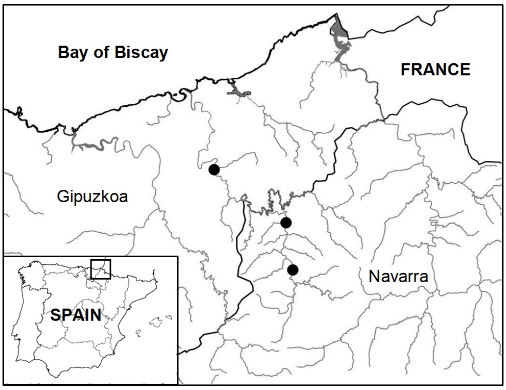

Figure 2. Localities along the Urumea stream where *Muhlenbergia schreberi* was found.

M. schreberi (nimblewill) is a stolon-forming perennial grass native to North America. In its native range it grows in moist to dry woods and prairies on rocky slopes, in ravines, and along sandy riverbanks, at elevations of 60-1600 m (Barkworth *et al.* 2007). It is also common in disturbed sites near cultivated fields, pastures, and roads at those elevations. This species is becoming naturalised in some European countries such as Italy (Pignatti 1982, Aeschimann *et al.*, 2004), Switzerland (Aeschimann & Burdet 1989, Lauber & Wagner 2001), Slovenia (Jogan 1990) and Croatia (Jogan 2014). In the Iberian Peninsula there is only one record for this species from Bordils (Girona) where it was found for the first time in 1932 and was collected again in 2007 in riverine plantations of *Platanus* and *Populus* (Pyke 2008). We report three localities along the Urumea stream in Gipuzkoa and northern Navarra where the species was found growing on stony shores with some accumulation of sand (Figure 2). These populations would therefore represent the second record for the Iberian Peninsula and the first records for the Basque Country and Navarre and should be monitored in order to assess its potential invasive behaviour.

Persicaria pensylvanica (L.) M. Gómez (Synonym: *Polygonum pensylvanicum* L.; Polygonaceae)

Cantabria: Ampuero, Udalla, Asón stream, 30TVN6496, riverbank, 32 m, 03-X-2013, *D. Liendo*, *M. Solís* & *M. Torca*, BIO 50887; **Bizkaia**: Basauri, Nervión stream, 30TWN0987, river bar, 38 m, 18-IX-2008, *I. García-Mijangos* & *M. Herrera*, BIO 50873.

In its native range, this North American neophyte thrives on the reduced competition resulting from disturbance and grows in roadside ditches, waste areas, cultivated fields, riverbanks and shores of ponds, lakes and reservoirs (Flora of North America Editorial Committee 1993+). The presence of this species as naturalised has already been documented for the Basque Country (Patino & Valencia 2000, Campos 2010), where it could expand its range in ruderal and riparian habitats. In relation to the latter, it has been found mainly on river bar therophyte communities of the *Bidenti frondosae- Polygonetum lapathifolii* provisional association (Campos 2010), which are dominated by other *Persicaria* species, especially *P. lapathifolia*, *P. mitis* and *P. hydropiper.* It has not been reported from Cantabria so far, implying that our reference from a river bar community of the Asón stream in Ampuero would represent a new addition to the regional catalogue of vascular plants of this province. The recent naturalisation in the nearby Basque Country suggests that this taxon will probably expand its range in Cantabria in the coming years.

Prunus lusitanica L. (Rosaceae)

Bizkaia: Busturia, Mape stream, 30TWP2301, disturbed alder forest, 40 m, 23-VII-2010, I.García-Mijangos, M. Herrera & D. Liendo, BIO 49929; Amorebieta-Etxano, Ibarra, Ibaizabal stream, 30TWN2284, river embankment with *Platanus hispanica*, 75 m, 12-VII- 2011, I. García-Mijangos, J. Loidi, D. Liendo, M. Solís & M. Torca, BIO 50688.

Diagnostic species of the *Arbuto unedonis-Laurion nobilis* alliance, which encompasses relict small-size forests with abundant lauroid species that grow on siliceous soils in hyperoceanic areas (Rivas-Martínez 2011). This taxon is included in the Red List of Vascular Flora of the Basque Country as critically endangered in this region (Aizpuru *et al.* 2010), given that it is known from only five localities in the Basque Country with less than fifty individuals altogether. In Bizkaia it is known from Ranero Natural Park in Carranza (Pérez de Ana 2004) and from the Leginetxe stream in Amorebieta-Etxano (Calleja 2006, Aizpuru *et al*. 2010). We provide two new records of this endangered species in riparian areas of Amorebieta-Etxano and Busturia municipalities.

Pyracantha angustifolia (Franch.) C.K. Schneid. (Rosaceae)

Cantabria: between La Cavada and Liérganes, Miera stream, 30TVP4100, riverbank, 75 m, 17-VII-2012, *I. Biurrun* & *D. Liendo*, BIO 50866.

This species of firethorn native to SW China is used as an ornamental shrub in Spain. It has been found growing in the wild in Cantabria and the Basque Country in the last decades (Aedo *et al*. 1998) and could also become naturalised elsewhere in Spain given its widespread cultivation. Valdeolivas & Goñi (2011) include this taxon in the Flora of the Dunas de Liencres Natural Park in Cantabria but without geographical references. We provide the first georeferenced locality for this species in Cantabria as escaped from cultivation on the right margin of the Miera stream between La Cavada and Liérganes.

Sison amomum L. (Apiaceae)

Cantabria: Mazcuerras, Cos, Saja stream, 30TUN9993, ash forest, 145 m, 24-VII-2012, *I. Biurrun, D. Liendo* & *J. Rubio*, BIO 50476.

Characteristic species of the *Galio aparines-Alliarion petiolatae* alliance, which includes medium-sized megaforb communities growing in inner forest paths on well developed soils with an input of nitrates and phosphates from human and/or livestock origin (Rivas-Martínez 2011). Not reported from Cantabria by Flora Iberica (Aedo 2003), Alonso Felpete *et al*. (2011) include this taxon in the Floristic Catalogue of the Picos de Europa National Park, where it is reported from one locality in Cantabria (Bejes, Cillorigo de Liébana, herbarium code JBAG 2101). Our reference from Mazcuerras adds a second record for Cantabria at a considerable lower altitude.

Stachys palustris L. (Lamiaceae)

Bizkaia: Trapagaran, Granada stream, 30TVN9993, wall near the bridge, 4 m, 07-VII-2011, *I. García-Mijangos* & *D. Liendo*, BIO 50644; Derio, Asua stream, 30TWN0993, disturbed riverbank, 20 m, 20-VII-2011, *I. Biurrun*, *D. Liendo* & *M. Torca*, BIO 51082.

Characteristic species of the *Filipendulion ulmariae* alliance, which includes Eurosiberian and northern Mediterranean sub-nitrophilous and hygrophilous megaforb associations typical of riverbanks, meadow edges and swamps (Rivas-Martínez 2011). Morales & Pardo de Santayana (2010) indicated that this taxon was scattered across the northern Iberian Peninsula, specifically in Asturias and Gipuzkoa. In the latter province Loidi (1983) reported this species from Endoia and Aseginolaza *et al*. (1985) pointed out that it was scattered across some Gipuzkoan streams. In Bizkaia, Zubía (1921) reported this taxon from Urberuaga and Campos *et al*. (2004) provided a new record from the Zuloko-Ibarreta wetland in Barakaldo. The population from Urberuaga has not been found again, whilst the one from Barakaldo has been confirmed to have gone extinct following the urbanisation of the wetland where it was previously present. As a result of this, and given its limited distribution in the Basque Country, it was included in the Red List of Vascular Flora of the Basque Country (Aizpuru *et al*. 2010) as a near threatened taxon. We provide two riparian records for Bizkaia in Trapagaran and Loiu, which prove that this species is still present in this province.

Symphyotrichum lanceolatum (Willd.) G. L. Nesom (Synonym: *Aster lanceolatus* Willd.; Asteraceae)

Cantabria: Guriezo, Agüera, Agüera stream, 30TVN7994, riverbank, 130 m, 29-IX-2011, *I.Biurrun* & *D. Liendo*, BIO 50853.

This North American aster, widely naturalised in western and central Europe, colonises roads, tips and river margins especially on nitrophilous and moist to humid soils. In Cantabria there is only one previous record of this species from Ribamontán al Mar (herbarium code MA 622465), so that our reference represents the second citation of this species and extends its distribution range eastward in the province. In Bizkaia it has been cited in two localities at relatively short distance from Guriezo: Muskiz (Campos & Herrera 1998; herbarium code BIO 24523) and Arcentales (herbarium code VIT 92102).

Verbena brasiliensis Vell. (Verbenaceae)

Bizkaia: Gatika, near Butrón stream, 30TWP0603, 15 m, roadside, 14-VII-2010, *I. García-Mijangos*, *M. Herrera* & *D. Liendo*, BIO 51083; Bilbao, La Peña, Nervión stream, 30TWN0688, gravel bar, 15 m, 10-X-2012, *I. Biurrun* & *O. Pereda*, BIO 51084; Barakaldo, behind Lasesarre stadium, 30TWN0094, barren vegetation near Nervión estuary, 5 m, 03-VII-1996, *J.A. Campos*, BIO 52085; Güeñes, Arbuio, 30TVN9987, disturbed soil near Cadagua stream, 40 m, 12-X-1995, *S. Patino*, SEST 20277; Güeñes, La Cuadra, 30TVN9785, infill soil near Cadagua stream, 50 m, 21-VI-1996, *S. Patino*, SEST 19498; Galdames, El Cerco, 30TVN8891, disturbed soil, 125 m, 19-X-2014, *S. Patino*, SEST 22041; Sestao, 30TVN9994, disturbed soil near Ballonti stream, 5 m, 05-V-2008, *S. Patino*, SEST 19506; Trapagaran, 30TVN9499, roadside ditch, 5m,

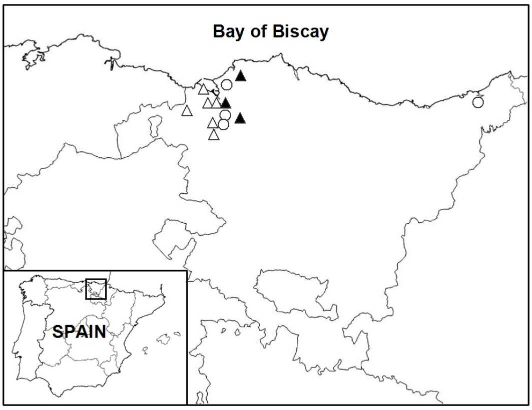

Figure 3. *Verbena brasiliensis* (triangles) and *V. incompta* (circles) in the Basque Country. Empty triangles: unpublished references from the SEST herbarium; Black triangles: records provided by the authors of the present work.

06-VII-1993, *S. Patino*, SEST 745.93 (sub. *Verbena litoralis*); Trapagaran, 30TVN9894, roadside ditch, 10 m, 25-VI-2005, *S. Patino*, SEST 13744 (sub. *Verbena litoralis* var. *brevibracteata*).

This South American vervain is an expanding weed in some parts of Europe (Verloove 2011). The paucity of references for this taxon may be due to the fact that individuals of *V. brasiliensis* have been identified as *V. bonariensis*, a popular ornamental vervain from South America (Campos & Herrera 2009, Campos 2010, Herrera & Campos 2010, Anon. 2014). Controversy has surrounded the taxonomy and nomenclature of this taxon and related species in the last years (O'Leary *et al.* 2007). Verloove (2003) reported *V. brasiliensis* for the first time in the Iberian Peninsula from several localities of Barcelona and Girona as *V. litoralis* and pointed out that those specimens collected in Catalonia belonged to var. *brasiliensis* following Munir (2002). Two years later the same author reported new localities for Barcelona again as *V. litoralis* var. *brasiliensis* (Verloove 2005). In 2008, a new Iberian locality was reported from the province of Huelva but this time as *V. litoralis* var. *brevibracteata* (Verloove & Sánchez Gullón 2008) following O'Leary *et al.* (2007). Finally, Flora Iberica (Pujadas Salvá & Plaza 2010) included the previous references as *V. litoralis* var. *brevibracteata* and also reported this species from Bizkaia on the basis of voucher specimens from this province reviewed by Antonio Pujadas. We provide new references of this species for Bizkaia and present a distribution map including our new references and those localities of voucher specimens preserved at the SEST herbarium under different names (*V. litoralis*, *V. litoralis* var. *brevibracteata* and *V. brasiliensis*) that have not been published so far (Figure 3).

Verbena incompta P.W. Michael (Verbenaceae)

Bizkaia: Getxo, Algorta, 30TWP0000, flooded nitrophilous community behind Fadura, 5 m, 25-IX-1989, *J.M. Olano*, BIO 3831 (sub. *Verbena bonariensis*); Barakaldo, Zubileta, 30TWN0190, waste ground and vegetable gardens, 20 m, 17-IX-1994, *S. Patino* & *J. Valencia*, SEST 1377,94 (sub. *Verbena bonariensis*); Güeñes, Arbuio, 30TVN9987, ruderal land close to Cadagua stream, 40 m, 12-X-1995, *S. Patino*, SEST 20278 (sub. *Verbena bonariensis*); **Gipuzkoa**: Donostia- San Sebastián, highway roadside next to Pasaia exit, 30TWN8795, 17-

VIII-1995, *J. Elorza* & *J. Valencia*, 50 m, SEST 1164,95 (sub. *Verbena bonariensis*).

This species is another South American vervain that, according to Verloove (2011), has been possibly confused with *Verbena bonariensis* in southern Europe where the latter is claimed as a naturalised alien. *V. incompta* is distinguished from *V. bonariensis* by its longer inflorescence spikes, shorter and not showy corolla tubes and shorter mericarps (Verloove 2011). Additionally, *V. bonariensis* has stipitate- glandular leaves and calyces, whilst *V. incompta* is eglandular (Nesom 2010). Verloove (2011) provided the first, and to date the only, bibliographic references of this species in Spain from Gipuzkoa. However, reviewing voucher specimens preserved at the BIO herbarium identified as *V. bonariensis* we found an specimen collected in Algorta (Bizkaia) by J.A. Olano in 1989 that, according to our criteria and following Verloove (2011), would correspond to *V. incompta* (Figure 3). Additionally, some voucher specimens kindly lent by SEST herbarium would also correspond to *V. incompta* (see above). This would indicate that this taxon has been present in Spain for decades, supporting the idea that this species has been largely overlooked in this country.

Veronica ponae Gouan (Scrophulariaceae)

Bizkaia: Munitibar, Lea stream, 30TWN3292, riverbank, 147 m, 11-VI-2013, *D. Liendo* & *M. Solís*, BIO 50757. **Gipuzkoa**: Irún, Endarlaza, Bidasoa stream, 30TXN0394, 30 m, 29- VII-20009, *I. Biurrun* & *M. Herrera*, BIO 50740.

This orophyte is a South Western European endemism native to the mountains of the Iberian Peninsula and the Pyrenees between 800 and 2900 m asl (Martínez Ortega *et al.* 2009), although it can also reach lower elevations through riparian forests. Examples of the latter have been reported from Gipuzkoa and Navarre (Catalán & Aizpuru 1985). In Bizkaia, however, its known distribution is restricted to mountainous areas such as Ordunte (Aseginolaza *et al.* 1985) and Gorbea (Aseginolaza *et al.* 1985, Herrera *et al.* 1991), implying that our reference from the Lea stream in Munitibar would represent a new record at a significant lower elevation.

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Updated taxonomic revision of the genus *Conyza* Less. in the northern Iberian Peninsula

CHAPTER 6

Diego Liendo, Juan Antonio Campos, Itziar García-Mijangos & Idoia Biurrun

Abstract

A revision of the genus *Conyza* in northern Spain is presented. A close examination of numerous *Conyza* specimens collected by the authors as well as voucher specimens preserved at several herbaria has helped clarify several aspects regarding this genus. Four species can be found in the study area: *C. sumatrensis*, *C. bilbaoana*, *C. bonariensis* and *C. canadensis*. *Conyza sumatrensis* and *C. bilbaoana* emerge as the two most abundant and widespread taxa. *C. canadensis*, regarded in the past as the most widespread species of the genus, is almost absent from the study area. Furthermore, as a result of a confusing literature, an important number of specimens previously identified as *C. bonariensis* do actually correspond to *C. sumatrensis*. A detailed identification key highlighting the main features that distinguish the four *Conyza* species is presented.

Key words: *Conyza*, distribution, identification key, nomenclature, northern Spain.

Introduction

The genus *Conyza* Less. (Asteraceae) comprises more than 50 annual and biennial species native to temperate and subtropical regions of North and South America (Noyes 2000, Milovic 2004). According to Thébaud & Abbott (1995), it represents one of the most notable examples of intercontinental plant invasions from the New World to the Old World. This genus is closely related to the genus *Erigeron* L. and their distinction has long been problematic (Nesom 1990), partly due to the dearth of knowledge of the generic boundaries and the biosystematics of *Conyza* (Nesom 1990, Thébaud & Abbott 1995). As a result of this, taxonomic controversy has long existed. *Conyza* and *Erigeron* have been traditionally considered as two separate genera. However, it has been showed that *Conyza* is polyphyletic and nested within *Erigeron* (Noyes 2000) and, thus, some authors merge *Conyza* into a widely delimited genus *Erigeron* (e.g. Greuter 2003 in the Euro+Med treatment of Astereae). We will follow the former criterion and will consider *Conyza* as a separate genus throughout the present work. Several morphologically similar species of *Conyza* (12 according to Euro+Med PlantBase) have been introduced in the last decades and centuries into Europe, where they occur mainly in disturbed habitats, such as wasteland, abandoned fields, cultivated ground, roadsides or railways, although they can also be found in natural and semi-natural habitats such as sand dunes or grasslands (Thébaud & Abbott 1995, Mundell 2001, Campos 2010). Among these, the most widespread ones are *C. canadensis*, *C. bonariensis*, *C. sumatrensis* and *C. bilbaoana* (Mundell 2016).

The first of these, *C. canadensis*, is thought to be native to North America (Cronquist 1976) and was the first species of the genus introduced into Europe at the beginning of the 17th century (Marshall & McClintock 1972, Prieur-Richard *et al*. 2000). It is a highly successful invader which is now widely spread across the globe. Regarding *C. bonariensis*, this species is native to South America and its presence in Europe has been recorded since the 18th century (Prieur-Richard *et al.* 2000) where it has naturalized especially across the Mediterranean basin and Atlantic regions of SW Europe (Milović 2004) given its more thermophilous nature. However, it can also occur, with lower abundance, in northern countries such as the UK (Wurzell 1988, 1994; Rand 2008), Belgium (Verloove & Boullet 2001, Verloove 2006) or Norway (Gederaas *et al.* 2012). The third species of the group, *C. sumatrensis*, is native to South America as well although it was first named from Sumatra (McClintock & Marshall 1988, Mundell 2001) and was introduced into Europe, namely France, during the 19th century (Thébaud *et al.* 1996). At the beginning of the 20th century it was already expanding across France, Spain and Portugal (Milović 2004) and in 1984 it was recorded for the first time in Great Britain (Wurzell 1988). As Milović (2004) pointed out, this species has been widely confused with the aforementioned *C. bonariensis* as a result of their morphological and ecological resemblance and the lack of an appropriate literature (see for example comments in Wurzell 1988, 1994). According to Thébaud & Abbott (1995) *C. sumatrensis*, along with *C. canadensis*, are probably among the most widespread species found throughout the world. Finally, *C. bilbaoana* deserves a more detailed description since it constitutes the core of the present work. It was recorded for the first time in Europe in 1992 in the Woolston area of Southampton (S England), where Paul Stanley found a population of a robust *Conyza* species which was clearly different from *C. canadensis* (Stanley 1996). These specimens were initially identified as *C. sumatrensis* but further investigation in 1994 resulted in them being identified as *C. bilbaoana*. The species was subsequently found at a large number of localities around Southampton (Stanley 1996) and other English counties, such as Surrey (Phillips 1997) and Kent (Philp 2002). It is worth mentioning that also in 1992 Sylvia Reynolds found an unusual *Conyza* in Rosbercon (SE Ireland) which was later confirmed to be *C. bilbaoana* as well following Paul Stanley's finding (Reynolds 1997). In recent years Verloove & Sánchez Gullón (2008) mentioned that this taxon was widely spread in SW France and that, at present, it would be probably the commonest representative of the genus in that territory. They also pointed out that *C. bilbaoana* had been surprisingly overlooked in Spain by some authors such as Campos & Herrera (1997) and Sanz Elorza *et al.* (2004), with just a few references from northern regions (Aedo *et al.* 2001, Verloove & Sánchez Gullón 2008). The paucity of references for this species in Spain may reflect the treatment of the genus in regional floras of this country. Aizpuru *et al.* (1999) in their *Claves ilustradas de la flora del País Vasco y territorios limítrofes* did not include *C. bilbaoana* as it was not known to be present in the territory covered by the flora. Following this flora, some specimens of *C. bilbaoana* could be ascribed to *C. albida* according to Aedo *et al.* (2001). In the same way, Bolòs & Vigo (1996) in their *Flora dels Països Catalans* neither took *C. bilbaoana* into account but did consider another species named *C. blakei*. However, Laínz (2002) stated that the description of *C. blakei* given in the Catalan flora did not match that based on the *Flora de la Provincia de Buenos Aires* (Cabrera 1963-1970) and that the *C. blakei* sensu Bolòs & Vigo (1996) was in

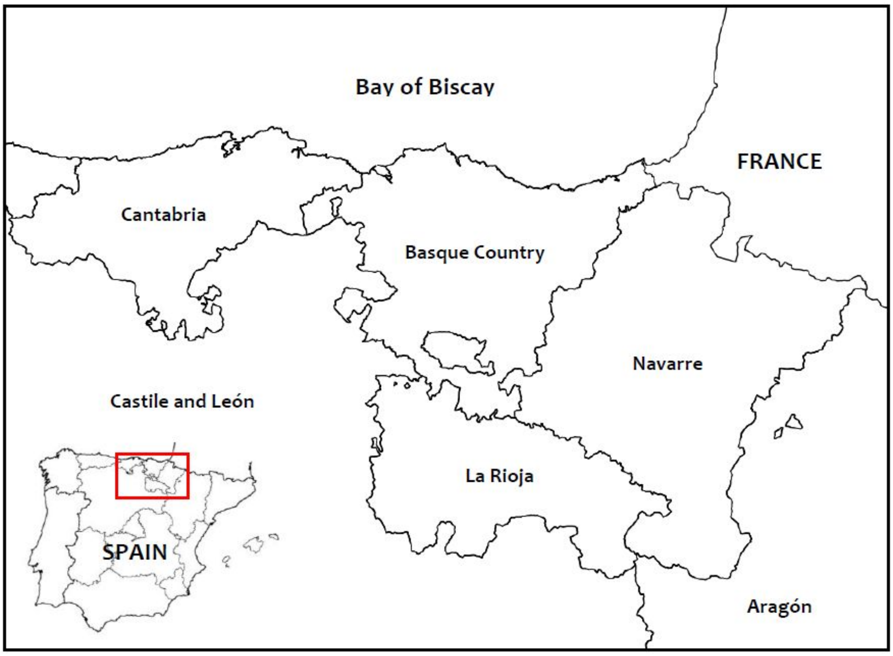

Figure 1. Study area.

fact *C. bilbaoana* (González-Martínez 2015). This taxon would be scattered across northeast Spain (Bolòs & Vigo 1996).

Regarding nomenclature, some *Conyza* species, in particular *C. sumatrensis* and *C. bilbaoana*, have been given different specific epithets in the last decades, which has hindered the comparison among different floras and, thus, their identification. For instance, *C. floribunda* has been given as a synonym for both *C. sumatrensis* and *C. bilbaoana* and vice versa (*C. sumatrensis* and *C. bilbaoana* as synonyms for *C. floribunda*).

In the course of several research works carried out by the Flora and Vegetation Research Group of the University of the Basque Country (UPV/EHU), important doubts emerged regarding the identification of numerous *Conyza* specimens collected in northern Spain, especially those glabrescent plants that did not match the well-known *C. canadensis*. Therefore, in the present work we have examined specimens of the genus collected in this territory in order to (1) determine which species of *Conyza* are currently present, (2) estimate which of them are the most abundant and (3) check whether *Conyza* specimens preserved in different herbaria of northern Spain are correctly identified on the basis of recent developments in the genus, which could contribute to (1) and (2).

Methods

The study area for the present work corresponds to the regions of Cantabria, Basque Country and Navarre and neighbouring territories in northern Spain (Figure 1). Within this area, the vast majority of the specimens were collected between Cantabria in the west and

Box 1. Synonyms for the different *Conyza* species identified in northern Spain.

***Conyza canadensis* (L.) Cronq.**
Erigeron canadensis L.

***Conyza bonariensis* (L.) Cronq.**
Erigeron bonariensis L.
E. crispus Pourr.
E. linifolius Willd.
C. ambigua DC

***Conyza sumatrensis* (Retz.) E. Walker**
Erigeron sumatrensis Retz.
E. naudinii (Bonnet)
E. daveauanus (Sennen) Greuter
E. floribundus (Kunth) Schultz-Bip.
C. floribunda Kunth
C. erigeroides DC.
C. albida Willd. ex Sprengel
C. floribunda Kunth var. *subleiotheca* (Cuatrec.) J.B. Marshall

***Conyza bilbaoana* J. Rémy**
Erigeron bilbaoanus (J. Rémy) Cabrera
E. floribundus (Kunth) Schultz-Bip.
C. floribunda Kunth
C. floribunda Kunth var. *floribunda*
C. sumatrensis var. *leiotheca* (S.F. Blake) Pruski & G. Sancho

northern Navarre in the east. Initially, we focused on specimens collected by the authors and other members of the Flora and Vegetation Research Group along with voucher specimens preserved at the BIO herbarium of the University of the Basque Country (UPV/EHU). Subsequently, in order to study as many *Conyza* specimens from the study area as possible, we did also examine voucher specimens borrowed from the following Basque herbaria: ARAN (Aranzadi Society of Sciences), SEST (Natural Sciences Society of Sestao) and VIT (Natural History Museum of Álava). These herbaria did also contain voucher specimens from SW France (Atlantic Pyrenees department) and nearby Mediterranean localities that were also examined (Annex 1). A total of 261 voucher specimes were examined.

As a result of the revision, we provide an identification key based on own observations, measurements made by the authors in a number of *Conyza* specimens and previous works (Campos 2010) for the different *Conyza* species identified in the study area in a similar way than Alves & Aguiar (2012) did for Portugal. Additionally, distribution maps of the most abundant species based on the examined specimens are presented. For this purpose, bibliographical references were not taken into account since we cannot confirm whether the identification is correct on the basis of recent developments in the genus.

Results and discussion

Four species of *Conyza* have been identified in northern Spain: *C. sumatrensis*, *C. bonariensis*, *C. bilbaoana* and *C. canadensis* (see Box 1 for synonyms). Of these, *C. sumatrensis* and *C. bilbaoana* are the most abundant and widespread taxa of the genus (Figure 2). In our study area they occupy riparian zones, especially elevated parts of river

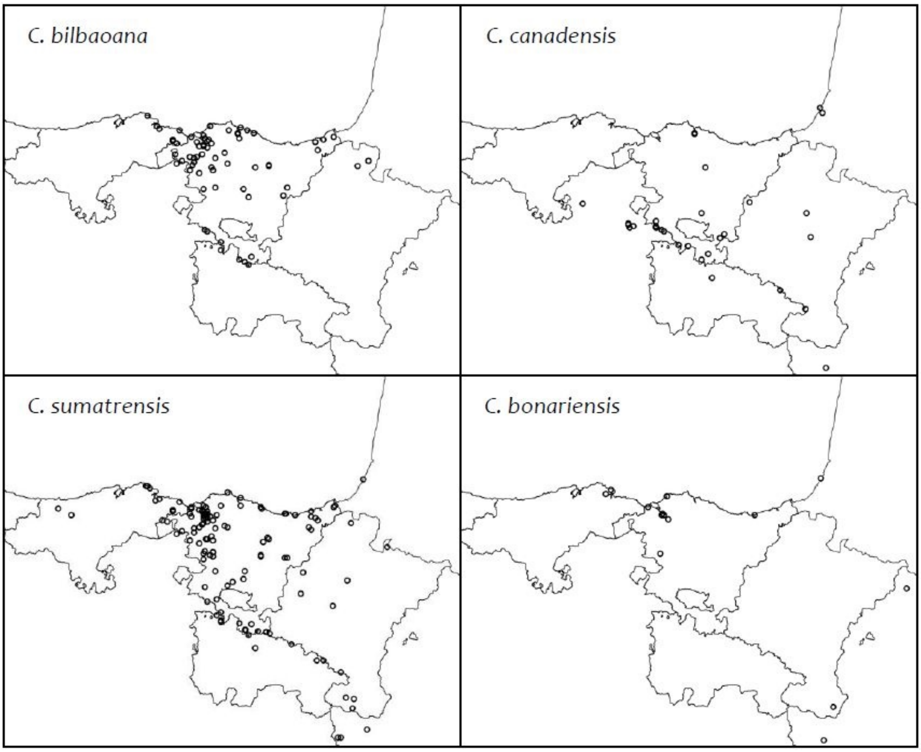

Figure 2. Known distribution of *Conyza bilbaoana*, *C. canadensis*, *C. sumatrensis* and *C. bonariensis* in the study area based on the examined voucher specimens (see Annex 1).

bars, coastal dunes and a wide range of anthropogenic habitats, such as road edges, abandoned fields, crops and waste ground.

Regarding glabrescent taxa (see key below), *C. canadensis* was thought to be much more widespread than *C. bilbaoana* across the study area. In fact, it was regarded in the past as the most widespread species of the genus. However, a close examination of numerous glabrescent specimens determined that almost half of the voucher specimens previously identified as *C. canadensis* were in fact *C. bilbaoana* (Table I), many of them from tha Atlantic watershed. This suggests that *C. bilbaoana* is actually the species which is widely spread across this region, which is in accordance with the aforementioned statement that *C. bilbaoana* is probably the commonest representative of the genus in SW France and that it has been surprisingly overlooked in Spain (Verloove & Sánchez Gullón 2008). Additionally, and according to several voucher specimens examined, *C. bilbaoana* would have been present, though wrongly identified, in inland and coastal areas of the study area since the early 1980s, a decade before its discovery in southern England (Stanley 1996), which to date constitutes the first reference for this species in Europe. *C. canadensis*, on the other hand, would be almost absent from the Atlantic watershed since only a few specimens collected in the 80s and 90s in Bizkaia and SW France, respectively, were confirmed as such. A similar pattern has been reported from another oceanic

Table I. Correspondence (number of voucher specimens) between the original identification of the *Conyza* specimens used in the present study and the correct determination based on the identification key proposed in the present work. Bold: cases where a high number of voucher specimens were wrongly identified.

		Correct determination			
		C. canadensis	*C. bilbaoana*	*C. sumatrensis*	*C. bonariensis*
Original identification	*C. canadensis*	30	**29**	5	–
	C. bilbaoana	–	31	–	–
	C. sumatrensis	–	–	91	–
	C. bonariensis	–	2	**47**	13
	C. albida x *bonariensis*	–	1	1	–
	C. albida x *canadensis*	1	4	–	–
	Conyza sp.	2	2	2	–

territory such as New Zealand, where true *C. canadensis* is a rare plant and it is the widespread *C. bilbaoana* which is known there as 'Canadian fleabane' due to an early identification error (Kent 1991, Stanley 1996, Mundell 2001). In the words of Kent (1991), in New Zealand *C. canadensis* would be 'part of a complex, the true species being rare, and the most widespread being the South American *C. bilbaoana*'.

With respect to the pubescent taxa, our examination revealed that a significant number of specimens currently identified as *C. bonariensis* are in fact *C. sumatrensis* (Table I). A possible explanation for this is that the aforementioned key in Aizpuru *et al.* (1999) does not include *C. sumatrensis* and considers *C. bonariensis* as the only pubescent taxa of the genus. This, along with the great amount of *C. sumatrensis* recently recorded in the study area, suggests that the latter is much more abundant than *C. bonariensis*, which is in accordance with previous works (e.g. Campos 2010).

Below we provide an identification key for mature individuals of the four *Conyza* species identified in northern Spain. It is worth highlighting the differences in the involucral bracts between *C. bilbaoana* and *C. canadensis* that have not been pointed out in previous keys. We consider that this feature could allow a quick and robust separation of these taxa.

<u>Identification key</u>

1. Leaves glabrous or nearly glabrous with scattered hairs along the underside midrib, margins ciliate (ciliae often 1 mm long). Capitulae ca. 2-3 mm wide at anthesis. Involucral bracts glabrous or nearly glabrous. Tubular florets 4-5 lobed. Inflorescence columnar or pyramidal..2

1. Leaves pubescent. Leaf margins densely appressed pubescent, hardly ciliated towards the base. Capitulae with parallel sides, ca. 5-10 mm wide at anthesis.

Involucral bracts softly pubescent. Tubular florets 5-lobed Inflorescence pyramidal or subcorymbous...3

2. Inner involucral bracts 3-3.5 (3.8) mm long x 0.3-0.4 (0.5) mm wide. Inner tubular florets mostly 4-lobed, not becoming wider towards the apex, ca. 12-15 (20) per capitulum. Ligules always present, > 0.7 mm long, white, distinctly exceeding involucre. Inflorescence narrowly cylindrical or columnar, much longer than wide. Middle and lower stem leaves entire or softly toothed. Plant annual, yellowish-green, stem not hirsute with hairs < 1.2 mm long.....................................***C. canadensis***

2. Inner involucral bracts 3.5-4.1 (4.5) mm long x 0.6-0.7 (0.8) mm wide. Inner tubular florets mostly 5-lobed, becoming wider towards the apex, ca. 4-6 (8) per capitulum. Ligules absent or rudimentary, < 0.4 mm long, not exceeding involucre. Inflorescence much broader, sometimes rhomboid, only slightly longer than wide. Middle and lower stem leaves deeply lobed, lobes > 1.5 mm long. Plant mostly biennial, dull greyish-green, stem densely hirsute with hairs usually > 1.8 mm long..***C. bilbaoana***

3. Robust plant, ca. 30-200 cm. Inflorescence grey-pubescent, not glandular, broad and profusely ramified, pyramidal or rhomboid, side branches not overtopping the main axis. Apex of involucral bracts not purplish. Tubular florets 5 lobed, ca. 7-10 per capitulum. Middle stem leaves narrowly lanceolate, usually toothed, ca. 5-20 mm wide, side veins conspicuous. Capitulae ca. (4) 5-7 mm wide at anthesis..***C. sumatrensis***

3. Plant hardly exceeding 60 cm. Inflorescence glandular, sticky, branches less numerous with side branches overtopping the main axis. Apex of involucral bracts often purplish. Tubular florets 5 lobed, ca. 13-16 per capitulum. Stem leaves sublinear, entire or minutely toothed, less than 4 mm wide. Capitulae ca. 6-10 mm wide at anthesis...***C. bonariensis***

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Annex 1

Voucher specimens of *Conyza* included in the present work. For each specimen, the following information is provided: province, locality, 1x1 km UTM grid square (ED50 Datum), elevation, habitat, date of collection, collerctor/s and herbarium code. Additionally, when voucher specimens were originally wrongly identified the original name is included as (*sub*. 'original identification').

Conyza bilbaoana J. Rémy

SPAIN. ÁLAVA: Arceniega, 30TVN8974, 192 m, terrenos removidos, salida pueblo, 30/10/2012, J.A. Campos *et al.*, BIO-50923; Ayala, de Respaldiza a Okondo, 30TVN9672, 250 m, ruderal, 11/09/2012, J.A. Campos *et al.*, BIO-50929; Llodio, Anuntzibai, río Altube, 30TWN0576, 119 m, cascajera fluvial, 29/09/2008, I. Biurrun, I. García-Mijangos & D. García-Magro, BIO-50514; Zuia, Ziorraga, río Altube, 30TWN0861, 357 m, cascajera fluvial, 23/09/2008, I. Biurrun, I. García-Mijangos & D. García-Magro, BIO-50499; Salinillas de Buradón, hacia Zambrana, 30TWN1220, 443 m, cuneta húmeda, 26/10/2012, J.A. Campos *et al.*, BIO-50914; Baños de Ebro, 30TWN2607, 07/10/1980, P.M. Uribe-Echebarría, VIT-12432, (sub. *C. albida x canadensis*); Villarreal de Álava, 30TWN2960, 550 m, orilla del pantano, 26/09/1983, J.A. Alejandre & G. Morante, VIT-12426, (sub. *C. canadensis*); Elciego, 30TWN3005, 400 m, estercoleros, 13/03/1982, J.A. Alejandre & P.M. Uribe-Echebarría, VIT-12418, (sub. *C. albida x bonariensis*); Lapuebla de Labarca, 30TWN3303, 440 m, talud sobre el río Ebro, 30/03/1984, G. Morante, VIT-12413, (sub. *C. bonariensis*); Arrazua-Ubarrundia, Isla de los Conejos, 30TWN3354, 550 m, banda sumergida en invierno, 26/11/1982, P. Heras & P.M. Uribe-Echebarría, VIT-12430, (sub. *C. canadensis*); Laguardia, 30TWN3509, 29/10/1980, P.M. Uribe-Echebarría, VIT-12417, (sub. *C. albida x canadensis*). **BIZKAIA**: Balmaseda, 30TVN8381, 145 m, herbazal nitrófilo, descampado junto a carretera, 30/10/2012, J.A. Campos *et al.*, BIO-50919; Zalla, 30TVN8984, 97 m, herbazal nitrófilo, junto a las vías del tren, 30/10/2012, J.A. Campos *et al.*, BIO-50920; Muskiz, playa de La Arena, 30TVN9099, 8 m, dunas, 10/05/2012, J.A. Campos, BIO-50732; Gordexola, 30TVN9178, 160 m, pinar, 27/09/1983, C. Aseginolaza, ARAN-3115, (sub. *C. canadensis*); Gordexola, barrio Mazukera, 30TVN9178, 112 m, huerto abandonado, 30/10/2012, J.A. Campos *et al.*, BIO-50528; Gordexola, barrio El Pontón-Urarte, 30TVN9280, 95 m, herbazal nitrófilo, 30/10/2012, J.A. Campos *et al.*, BIO-50615; Güeñes, barrio Sologutxi, 30TVN9283, 83 m, terrenos removidos en zona abandonada, 30/10/2012, J.A. Campos *et al.*, BIO-50922; Güeñes, 30TVN9484, 100 m, ambiente ruderalizado junto a una casa, 18/02/1982, C. Aseginolaza, C. Aseginolaza-11082, (sub. *C. canadensis*); Abanto y Ciérvana, Gallarta, junto a la mina Concha-2, 30TVN9495, 220 m, terreno baldío pedregoso, 10/06/2012, M. Herrera, BIO-50727; Valle de Trápaga, La Arboleda, 30TVN9692, 400 m, mina abandonada, 09/02/1982, C. Aseginolaza, C. Aseginolaza-320482, (sub. *C. canadensis*); Güeñes, Zaramillo, 30TVN9886, 73 m, junto a la carretera, 30/10/2012, J.A. Campos *et al.*, BIO-50926; Orduña, 30TVN9960, 288 m, junto a la carretera, 11/09/2012, J.A. Campos *et al.*, BIO-50932; Valle de Trápaga, 30TVN9992, 10 m, terrenos ruderales junto a la autovía, 35374, S. Patino & J. Valencia, SEST-260.96; Valle de Trápaga, 30TVN9993, 5 m, matorral ruderal nitrófilo de *Dittrichia viscosa*, 10/11/2012, J.A. Campos, BIO-50534; Getxo, Algorta, río Gobelas, 30TVP9900, 8 m, aliseda degradada, 29/07/2011, I. García-Mijangos, D. Liendo & M. Torca, BIO-50682; Leioa, 30TWN0098, 30 m, borde de prado de siega abandonado en suelo removido, 27/09/2009, M. Herrera, BIO-49918; Bilbao, Zorroza, 30TWN0291, 10 m, terrenos ruderales, 09/06/1994, J. Elorza & J. Valencia, SEST-1303.94, (sub. *C. bonariensis*); Erandio, 30TWN0296, 15 m, herbazal higronitrófilo de *Convolvulion sepium* en terreno abandonado, 10/05/2012, J.A. Campos, BIO-50706; Leioa, 30TWN0397, 80 m, barbecho de habas, 11/03/1996, J.A. Campos, BIO-51021; Derio, 30TWN0594, 15 m, escombrera, 29/09/1983, C. Aseginolaza, ARAN-3114, (sub. *C. canadensis*); Orozko, hacia Llodio, 30TWN0674, 132 m, ruderal, junto a cantera, 11/09/2012, J.A. Campos *et al.*, BIO-50933; Arrigorriaga, 30TWN0883, 86 m, ruderal, 11/09/2012, J.A. Campos *et al.*, BIO-50928; Galdakano, 30TWN1587, 150 m, borde de camino, 03/05/1982, C. Aseginolaza, C. Aseginolaza-17782, (sub. *C. canadensis*); Igorre, 30TWN1779, 100 m, cuneta, 10/08/1995, J.A. Campos, BIO-51009; Forua, 30TWN2698, 20 m, muro de roca caliza, 16/08/1995, J.A. Campos, BIO-51020; Elorrio, 30TWN3876, 350 m, escombrera, 19/08/1982, C. Aseginolaza, C. Aseginolaza-296982, (sub. *C. canadensis*); Gorliz, 30TWP0407, dunas, 08/05/1982, C. Aseginolaza, C. Aseginolaza-261382, (sub. *C. canadensis*); Bermeo, carretera Bermeo-Sollube, 30TWP1804, 300 m, zona de surgencia de aguas, 21/10/1981, C. Aseginolaza, C. Aseginolaza-62381, (sub. *C. canadensis*); Busturia, ría de Gernika, 30TWP2501, arenal de las marismas, 21/10/1981, C. Aseginolaza, C. Aseginolaza-57281, (sub. *C. canadensis*); Busturia, ría de Gernika, 30TWP2502, playa, 23/06/1982, C. Aseginolaza, C. Aseginolaza-155282, (sub. *C. canadensis*); Ibarrangelu, Laga, 30TWP2706, playa, 03/08/1982, C. Aseginolaza, C. Aseginolaza-281882, (sub. *C. canadensis*); Ea, Natxitua, 30TWP3204, itsas ertz-ertza, Natxituko Lapatzean, 20/09/1983, C. Aseginolaza, BIO-660, (sub. *C. canadensis*); Ispaster, Ogella, 30TWP3702, borde inferior de encinar que llega prácticamente al mar, 23/08/1981, C. Aseginolaza, C. Aseginolaza-33781, (sub. *C. canadensis*). **BURGOS**: Valle de Mena, Nocedal, río Cadagua, 30TVN7979, 213 m, cascajera fluvial, 10/10/2012, I. Biurrun & D. Liendo, BIO-50604; Miranda de Ebro, Suzana, 30TWN0029, 09/05/1980, J.A. Alejandre & P.M. Uribe-Echebarría, VIT-12433, (sub. *C. canadensis*); Miranda de Ebro, 30TWN0228, 500 m, rastrojos y campos incultos, cantos rodados y arenas, 16/09/1983, C. Aseginolaza & P.M. Uribe-Echebarría, ARAN-3110, (sub. *C. albida x canadensis*). **CANTABRIA**: Guriezo, río Agüera, 30TVN7696, 81 m, cascajera fluvial, 09/09/2011, I. Biurrun & D. Liendo, BIO-50660; Guriezo, Trebuesto, río Agüera, 30TVN7697, 65 m, cascajera fluvial, 31/08/2011, I. García-Mijangos, D. Liendo & M. Torca, BIO-50637; Valle de Villaverde, río Agüera, 30TVN7886, 222 m, cascajera fluvial, 22/09/2011, I. Biurrun & D. Liendo, BIO-50657; Guriezo, Agüera, río Agüera, 30TVN7994, 130 m, cascajera fluvial, 29/09/2011, I. Biurrun & D. Liendo, BIO-50645; Bareyo, Ajo, 30TVP51, 1 m, dunas fijas, 29/08/1984, M. Herrera, BIO-7379, (sub. *C. canadensis*); Noja, 30TVP5715, 32 m, ruderal, solar abandonado, 11/11/2012, J.A. Campos et al., BIO-50937; Laredo, 30TVP6407, 5 m, dunas fijas, 02/09/1986, M. Herrera, BIO-6697, (sub. *C. canadensis*); Laredo, 30TVP6407, 10 m, dunas fijas con nitrofilia, 03/01/1987, M. Herrera, BIO-6696, (sub. *C. canadensis*); Limpias, Seña, 30TVP6605, 105 m, cuneta de carretera, 11/11/2012, J.A. Campos, BIO-50940; Castro Urdiales, 30TVP8104, 35 m, terreno degradado junto a *Cortaderia selloana*, 20/10/2012, D. Liendo, BIO-50502. **GIPUZKOA**: Bergara, del puente del polígono de Osintxu hacia el sur antes del viaducto de la GI-627 que cruza el Deba, 30TWN4877, 93 m, ribera del río, 31/10/2006, A. Agut, BIO-49261, (sub. *C. canadensis*); Bergara, río Deba, 30TWN4878, 118 m, playa fluvial de cantos rodados, 17/10/2006, A. Agut, BIO-49241, (sub. *C. canadensis*); Zegama, hacia Otzaurte, 30TWN5955, 500-540 m, trampal, 10/20/1982, X. Lizaur, ARAN-3113, (sub. *C. canadensis*); Idiazabal, río Urtsuaran, 30TWN6261, 263 m, herbazal junto al río, 25/09/2013, I. Biurrun & D. Liendo, BIO-50525; Donostia-San Sebastián, barrio de Amara, 30TWN8395, 10 m, terreno ruderalizado de relleno en zona de carrizales, 09/08/1983, M. Salaverría, ARAN-3112, (sub. *C. albida x canadensis*); Hernani, Ereñozu, río Urumea, 30TWN8589, 16 m, comunidad nitrófila junto al río, 10/09/2013, I. Biurrun & D. Liendo, BIO-50807; Valle de Leizaran, 30TWN87, 30/07/1988, A. Cervello, BIO-9995, (sub. *C. canadensis*); Lezo, 30TWN8997, 10 m, borde de carretera, 25/09/1980, I. Aizpuru & P. Catalán, ARAN-20159, (sub. *C. canadensis*); Irún, 30TWN9799, 10 m, zonas ruderalizadas junto al parking de camiones, 13/09/1996, S. Patino & J. Valencia, SEST-942.96. **LA RIOJA**: Haro, 30TWN1214, 455 m, herbazal hipernitrófilo de *Chenopodion muralis* junto al río, 26/10/2012, J.A. Campos et al., BIO-50915. **NAVARRA**: Baztán, Mardea de Arrayoz, 30TXN1577, 160 m, pradera al borde de la carretera, 18/08/1988, A. Aldezabal, ARAN-15283, (sub. *C. canadensis*); Baztán, Ordoki de Arizkun, 30TXN2381, 260 m, borde de carretera, 18/08/1988, A. Aldezabal, ARAN-15285, (sub. *C. canadensis*).

Conyza canadensis (L.) Cronq.

SPAIN. ÁLAVA: Lantarón, Fontecha, 30TVN93, 500 m, camino cerca del pueblo, 13/09/1983, P. Urrutia, P. Urrutia-885; Lantarón, Fontecha, Los Cañales, 30TVN9631, 472 m, tierra de cultivo en barbecho sobre suelos arenosos, 25/08/2015, J. Garmendia, M. Arrieta, M. Etxeberria & L. Zabala, VIT-95017; Lantarón, Fontecha, 30TVN9632, 500 m, carrascal arenoso en terraza del Ebro, 23/08/1982, J.A. Alejandre, J. Loidi & P.M. Uribe-Echebarría, VIT-12429; Lantarón, Fontecha, 30TVN9632, 500 m, carrascal arenoso en terraza del Ebro, 16/09/1983, C. Aseginolaza & P.M. Uribe-Echebarría, VIT-12424; Lantarón, Bergüenda, 30TVN9636, 500 m, terrenos baldíos a la salida del pueblo, 30/08/1978, P.M. Uribe-Echebarría, VIT-12435; Conchas de Haro, 30TWN1318, 500 m, cunetas, espacios abiertos, zona de viñas descuidadas, 19/05/1978, P.M. Uribe-Echebarría, VIT-12436; Elciego, Regoyos, 30TWN3007, 450 m, viñedos, 19/09/1983, P.M. Uribe-Echebarría, VIT-12425; Vitoria-Gasteiz, Otazu, 30TWN3042, 530m, barbechos de 2 años, 25/08/1991, J.M. Aparicio, VIT-7459; Laguardia, balsa El Prado, 30TWN3511, 570m, cunetas y márgenes de cultivos, 10/01/1993, J.M. Aparicio & Txema Pérez, VIT-17689; Bernedo, San Román de Campezo, 30TWN4423, 750 m, cunetas de carretera recientemente arreglada, 23/08/2000, P.M. Uribe-Echebarría, VIT-64885; Arraia-Maeztu, monte Soila, 30TWN4726, 800 m, pista en carrascal con grava caliza, 08/10/1985, P. Urrutia, VIT-12422. **BIZKAIA**: Abadiño, 30TWN3376, 150 m, escombrera de fundición, 13/09/1982, C. Aseginolaza, C. Aseginolaza-328682; Busturia, ría de Gernika, 30TWP2501, arenal de las marismas, 21/10/1981, C. Aseginolaza, C. Aseginolaza-57981; Gernika, San Cristóbal, 30TWP2502, 03/05/1982, C. Aseginolaza, C. Aseginolaza-255582. **BURGOS**: Tubilleja, 30TVN4149, 600 m, alrededores del pueblo, 23/05/1998, S. Patino & J. Valencia, VIT-57659; Frías, 30TVN7533, 560 m, finca de cereal, 09/09/1990, I. García-Mijangos, BIO-12417; Frías, 30TVN7534, 540 m, cultivos, 21/10/1984, I. García-Mijangos, BIO-12422; Frías, monte Santa Lucía, 30TVN7534, 600 m, baldío, 08/09/1984, I. García-Mijangos, BIO-12423; Frías, Tobera, monte Valdemoro, 30TVN7631, 650 m, camino en pinar, 06/08/1987, I. García-Mijangos, BIO-12421; Valderrama, camino a monte Hurmión, 30TVN7932, 620 m, cultivo de cereal abandonado, 01/07/1989, I. García-Mijangos, BIO-12419; Miranda de Ebro, Suzana, 30TWN0029, 09/05/1980, J.A. Alejandre & P.M. Uribe-Echebarría, VIT-12433; Miranda de Ebro, Los Mojones, 30TWN0228, 500 m, rastrojos y campos incultos, 16/09/1983, C. Aseginolaza & P.M. Uribe-Echebarría, VIT-12423. **LA RIOJA**: Entrena, 30TWM3893, 565 m, herbazales y orillas entre cultivos, 25/09/1996, M.A. Domingo, VIT-39111; San Vicente de la Sonsierra, Rivas de Tereso, 30TWN2017, 650 m, borde de carretera en la cara sur del puerto de Rivas, 30/10/1978, J.A. Alejandre & P.M. Uribe-Echebarría, VIT-12435. **NAVARRA**: Azagra, La Barca, 30TWM8984, 300 m, cascajera del Ebro, 24/09/1987, P.M. Uribe-Echebarría, VIT-12421; Alsasua, polígono industrial del río Alzania, 30TWN6650, 510 m, baldíos industriales, 29/06/1994, J.M. Aparicio & J.M. Pérez Dacosta, VIT-19098; Castejón, río Ebro, 30TXM0870, 250 m, cascajeras del río, 24/09/1987, C. Aseginolaza, C. Aseginolaza-224687; Pamplona, barrio de San Jorge, 30TXN0942, 410 m, borde de camino, 20/10/1987, I. Aizpuru & P. Catalán, ARAN-20160; Unzué, estribaciones de la Sierra de Alaiz, 30TXN1224, 760 m, borde de cultivo, 24/09/1988, I. Aizpuru & P. Catalán, ARAN-20161. **ZARAGOZA:** Calcena, Collado del Campo, 30TXM0718, 1250-1350 m, pastos y matorrales venteados sobre calizas, 27/08/1999, P.M. Uribe-Echebarría, MONCAYO-2079. **FRANCE. PYRÉNÉES-ATLANTIQUES**: Bayonne, Blancpignon, 30TXP1921, 8 m, terrenos ruderales arenosos junto a la desembocadura del Adour, 14/09/1996, S. Patino & J. Valencia, SEST-986.96; Bayonne, zona industrial de St.Étienne, 30TXP21, 50 m, terrenos removidos, escombrera, 17/09/1994, P. Urrutia, VIT-19508, (sub. *C. albida x canadensis*); Bayonne, 30TXP2117, 10 m, terrenos arenosos junto al Adour, 35620, S. Patino & J. Valencia, SEST-1127.97.

Conyza sumatrensis (Retz.) *E. Walker*

SPAIN. ÁLAVA: Arceniega, 30TVN8974, 192 m, terrenos removidos, salida pueblo, 30/10/2012, J.A. Campos *et al.*, BIO-50924; Ayala, de Respaldiza a Okondo, 30TVN9672, 250 m, ruderal, 11/09/2012, J.A. Campos *et al.*, BIO-50930; Amurrio, 30TVN9964, 265 m, cuneta junto al maizal, 03/09/1997, J.A. Campos, BIO-51071; Salinas de Añana, río Omecillo, 30TWN0039, 568 m, aliseda degradada, 30/09/2010, I. Biurrun, M. Herrera & D. Liendo, BIO-51022; Amurrio, 30TWN0066, 214 m, ruderal, 11/09/2012, J.A. Campos *et al*., BIO-50935; Amurrio, salida hacia Orduña, 30TWN0066, 200 m, ruderal, viario, 30/09/1997, J.A. Campos, BIO-50936; Llodio, polígono industrial de Acenor, 30TWN0275, 130 m, huertas abandonadas, 30/09/1992, J.M. Aparicio & T. Pérez, VIT-10538, (sub. *C. bonariensis*); Amurrio, 30TWN0463, 350 m, brezal sobre el talud de la carretera, 13/08/1997, J.A. Campos, BIO-51044; Amurrio, 30TWN0662, 350 m, parte superior de talud, 13/08/1997, J.A. Campos, BIO-51045; Amurrio, 30TWN0665, 310 m, cuneta de carretera al pie de tapia, 04/09/1997, J.A. Campos, BIO-51068; Kuartango, Anda, antes de Subijana, 30TWN0851, 588 m, terraplén al borde de la carretera, 26/10/2012, J.A. Campos *et al*., BIO-50918; Armiñón, bajo el cerro Quintanilla, 30TWN0930, 505-525 m, cunetas de pista de parcelaria, 10/02/2004, P.M. & X. Uribe-Echebarría, VIT-75502, (sub. *C. bonariensis*); Salinillas de Buradón, hacia Zambrana, 30TWN1220, 443 m, cuneta húmeda, 26/10/2012, J.A. Campos *et al*., BIO-50546; Iruña de Oca, Nanclares de la Oca, 30TWN1740, 509 m, intersticios del suelo al lado de gasolinera abandonada, 26/10/2012, J.A. Campos *et al*., BIO-50917; Vitoria-Gasteiz, polígono industrial de Júndiz, 30TWN2143, 500 m, suelos removidos, 15/10/1992, J. Aparicio & T. Pérez, VIT-10627, (sub. *C. bonariensis*); Samaniego, 30TWN2612, 560 m, talud nitrófilo, 11/06/1997, J.A. Campos, BIO-51038; Arrazua-Ubarrundia, Salburua, entre arroyo Errekabarri y canal del río Alegría, 30TWN2945, 510 m, margen de chopera, campo de cultivo y taludes con tierra suelta, 08/04/2003, P.M. Uribe-Echebarría, VIT-70057, (sub. *C. bonariensis*); Vitoria-Gasteiz, Salburua, Elorriaga, al oeste del río Errekaleor, 30TWN2945, 510 m, tierra removida por obras recientes, entre rastrojeras de cereal, 22/08/2003, P.M. Uribe-Echebarría, VIT-70096, (sub. *C. bonariensis*); Lapuebla de Labarca, 30TWN30, 400 m, viñedo abandonado, 28/09/1983, J.A. Alejandre & G. Morante, ARAN-3099, (sub. *C. bonariensis*); Elciego, Regoyos, 30TWN3007, 450 m, viñedos, 19/09/1983, P.M. Uribe-Echebarría, VIT-12420, (sub. *C. bonariensis*); Vitoria-Gasteiz, Amárita, 30TWN3051, 715 m, acequias entre cultivos, 19/10/1978, P.M. Uribe-Echebarría, VIT-12419, (sub. *C. bonariensis*); Elciego, 30TWN3107, 19/08/1980, P.M. Uribe-Echebarría, VIT-12416, (sub. *C. bonariensis*); Lapuebla de Labarca, 30TWN3303, 440 m, talud sobre el río Ebro, 30/03/1984, G. Morante, VIT-12413, (sub. *C. bonariensis*); Laguardia, balsa El Prado, 30TWN3511, 570 m, taludes y cunetas de caminos, 13/08/1993, J.M. Aparicio & T. Pérez, VIT-17240, (sub. *C. bonariensis*); Laguardia, Laserna, 30TWN4006, 400 m, calles del pueblo, 08/10/1982, P.M. Uribe-Echebarría, ARAN-3098, (sub. *C. bonariensis*); Laguardia, Laserna, 30TWN4006, 400 m, calles del pueblo, 19/08/1982, P.M. Uribe-Echebarría, VIT-12415, (sub. *C. bonariensis*); Oyón, polígono industrial, 30TWN4605, 400 m, baldíos recientes con cascajos, 16/09/1992, J. Aparicio & T. Pérez, VIT-10477, (sub. *C. bonariensis*). **BIZKAIA**: Valle de Carranza, 30TVN6889, 100 m, roca caliza, 28/09/1983, C. Aseginolaza, C. Aseginolaza-1946, (sub. *C. bonariensis*); Valle de Carranza, 30TVN7288, 300 m, borde de camino asfaltado, 14/08/1997, J.A. Campos, BIO-51046; Balmaseda, 30TVN8381, 145 m, herbazal nitrófilo, descampado junto a carretera, 30/10/2012, J.A. Campos *et al*., BIO-50422; Muskiz, Covarón-Pobeña, 30TVN89, borde de carretera, 15/10/1988, A. Cervello, BIO-7105, (sub. *C. canadensis*); Muskiz, 30TVN8994, 15 m, camino forestal, 13/11/1996, J.A. Campos, BIO-51036; Muskiz, playa de La Arena, 30TVN9092, 12 m, terrenos ruderalizados junto a la playa, 16/09/1992, S. Patino, SEST-919.92; Muskiz, Pobeña, 30TVN9098, 10 m, talud de margocalizas, 19/08/1996, J.A. Campos, BIO-51049; Muskiz, Pobeña, 30TVN9099, 0 m, zona elevada en la marisma, 19/08/1996, J.A. Campos, BIO-51050; Muskiz, playa de La Arena, 30TVN9099, 0 m, dunas fijas cerca de la marisma, 21/08/1996, J.A. Campos, BIO-51051; Muskiz, playa de La Arena, 30TVN9099, dunas fijas en talud más húmedo (con *Dorycnium rectum*), 23/05/1999, J.A. Campos, BIO-51030; Muskiz, playa de La Arena, 30TVN9099, 8 m, dunas, 10/05/2012, J.A. Campos, BIO-50734; Gordexola, barrio El Pontón-Urarte, 30TVN9280, 95 m, herbazal nitrófilo, 30/10/2012, J.A. Campos *et al.*, BIO-50423; Güeñes, barrio Sologutxi, 30TVN9283, 83 m, terrenos removidos en zona abandonada, 30/10/2012, J.A. Campos *et al.*, BIO-50921; Güeñes, Sodupe, 30TVN9684, 50 m, terreno rellenado cerca del río, 12/09/1996, J.A. Campos, BIO-51034; Santurce, barrio de El Bullón, 30TVN9697, 40 m, camino, 21/09/1986, I. Zorrakin, VIT-12411, (sub. *C. bonariensis*); Güeñes, Zaramillo, 30TVN9886, 73 m, junto a la carretera, 30/10/2012, J.A. Campos *et al.*, BIO-50925; Portugalete, 30TVN9896, 40 m, ruderal, 10/07/2012, M. Torca, BIO-50685; Santurce, 30TVN99, tiesto en el balcón de casa, 16/08/1985, I. Zorrakin, VIT-12410, (sub. *C. albida x bonariensis*); Orduña, 30TVN9960, 288 m, junto a la carretera, 11/09/2012, J.A. Campos *et al.*, BIO-50931; Alonsotegui, barrio de Arbuyo, 30TVN9987, 29 m, junto a la carretera, 30/10/2012, J.A. Campos *et al.*, BIO-50417; Barakaldo, El Regato, 30TVN9990, 21 m, orilla elevada en cola de embalse, 04/10/1995, J.A. Campos, BIO-51033; Valle de Trápaga, 30TVN9992, 10 m, terrenos ruderales junto a la autovía, 05/11/1996, S. Patino & J. Valencia, SEST-263.96, (sub. *C. bonariensis*); Valle de Trápaga, río Granada, 30TVN9993, 4 m, cascajera fluvial, 07/07/2011, I. García-Mijangos & D. Liendo, BIO-50787; Sestao, barrio de Galindo, 30TVN9994, 19 m, terreno baldío junto a las vías de tren, 10/09/2012, E. Miguel, BIO-50711; Getxo, Algorta, río Gobelas, 30TVP9900, 8 m, aliseda degradada, 29/07/2011, I. García-Mijangos, D. Liendo & M. Torca, BIO-50553; Barakaldo, 30TWN0093, 10 m, isleta-jardincillo, 23/07/1996, J.A. Campos, BIO-51040; Barakaldo, 30TWN0094, 15 m, pared natural margosa, 18/08/1995, J.A. Campos, BIO-51060; Llodio, 30TWN0175, 145 m, cuneta de carretera, 03/09/1997, J.A. Campos, BIO-51065; Barakaldo, 30TWN0193, 18 m, solar en ladera aterrazada, 13/11/1995, J.A. Campos, BIO-51043; Barakaldo, 30TWN0194, 5 m, protosuelos con escorias de la fundición, 18/08/1995, J.A. Campos, BIO-51059; Barakaldo, 30TWN0194, 5 m, comunidad en protosuelos de escorias mineras, 03/07/1996, J.A. Campos, BIO-51031; Barakaldo, 30TWN0194, 5 m, herbazal-baldío, 27/08/1996, J.A. Campos, BIO-51053; Barakaldo, 30TWN0194, 5 m, herbazal-matorral pie de muro, 27/08/1996, J.A. Campos, BIO-51052; Barakaldo, 30TWN0194, 20 m, montón de tierra, 11/09/1997, J.A. Campos, BIO-51074; Berango, 30TWN0199, 5 m, herbazal húmedo cerca del río, 28/08/1996, J.A. Campos, BIO-51057; Berango, 30TWN0199, 20 m, bosquete de *Robinia pseudoacacia*, 28/08/1996, J.A. Campos, BIO-51055; Berango, 30TWN0199, 10 m, herbazal hipernitrófilo, 28/08/1996, J.A. Campos, BIO-51056; Llodio, 30TWN0275, 130 m, arriete de *Catalpa bignonioides*, 03/09/1997, J.A. Campos, BIO-51066; Bilbao, de Zorroza a Alonsotegui, 30TWN0288, 5 m, herbazal junto al río, 23/09/1996, J.A. Campos, BIO-51035; Bilbao, Zorroza, 30TWN0291, 10 m, terrenos ruderales, 09/06/1994, J. Elorza & J. Valencia, SEST-1303.94, (sub. *C. bonariensis*); Barakaldo, 30TWN0293, 12 m, borde de solar removido, 27/10/1995, J.A. Campos, BIO-51032; Barakaldo, Lutxana, 30TWN0293, 5 m, cuneta al pie de tapia, 27/08/1996, J.A. Campos, BIO-51054; Erandio, hacia Asua, 30TWN0294, 5 m, herbazal húmedo con *Cortaderia selloana*, 30/08/1996, J.A. Campos, BIO-51062; Erandio, 30TWN0296, 10 m, matorral-baldío, 27/08/1996, J.A. Campos, BIO-51063; Leioa, 30TWN0296, 12 m, cuneta, 02/10/2012, M. Herrera, BIO-50698; Bilbao, 30TWN0492, 120 m, cortafuegos entre robiniales, 24/07/1996, J.A. Campos, BIO-51041; Arakaldo, 30TWN0577, 130 m, borde de la autopista, junto a área de descanso, dirección Vitoria, 23/09/1995, J. Valencia, SEST-1302.95, (sub. *C. bonariensis*); Orozko, hacia Llodio, 30TWN0674, 132 m, ruderal, junto a cantera, 11/09/2012, J.A. Campos *et al.*, BIO-50934; Bilbao, 30TWN0689, 3 m, muro de contención sobre la ría, 23/07/1996, J.A. Campos, BIO-51039; Arrigorriaga, 30TWN0883, 86 m, ruderal, 11/09/2012, J.A. Campos *et al.*, BIO-50927; Derio, Río Asua, 30TWN0993, 20 m, margen del río, 20/07/2011, I. Biurrun, D. Liendo & M. Torca, BIO-50748; Galdakano, 30TWN1585, 50 m, cuneta al pie de muro en protosuelos, 02/09/1997, J.A. Campos, BIO-51067; Lemona, 30TWN1784, 60 m, cuneta en talud descendente, 02/09/1997, J.A. Campos, BIO-51072; Lemona, 30TWN1784, 60 m, bianuales sobre suelos removidos, 02/09/1997, J.A. Campos, BIO-51070; carretera de Ondarroa a Lekeitio, 30TWN4299, 03/08/1982, C. Aseginolaza, D. Gómez & G. Morante, PV-14; Ondarroa, 30TWN4398, 10 m, 28/04/1982, C. Aseginolaza, C. Aseginolaza-41582, (sub. *C. canadensis*); Mungia, 30TWP1200, 40 m, borde de herbazal de *Dauco-Melilotion*, 17/06/1997, J.A. Campos, BIO-51037; Bermeo, San Juan de Gaztelugatxe, 30TWP1710, 75 m, ruderales, 19/10/2012, M. Solís & M. Torca, BIO-50686; Gernika, 30TWP2700, parte derecha de las marismas, 13/09/1983, C. Aseginolaza, C. Aseginolaza-1741, (sub. *C. canadensis*); Ibarrangelu, Laga, 30TWP2706, arenas de la playa, 10/11/1981, C. Aseginolaza, C. Aseginolaza-50381, (sub. *C. bonariensis*). **BURGOS**: Valle de Mena, Nocedal, río Cadagua, 30TVN7979, 213 m, cascajera fluvial, 10/10/2012, I. Biurrun & D. Liendo, BIO-50448; Miranda de Ebro, 30TWN0228, 470 m, baldíos removidos con escombreras, 09/12/1992, J. Aparicio & T. Pérez, VIT-10430, (sub. *C. bonariensis*). **CANTABRIA**: Valdáliga, Roiz, río del Escudo, 30TUN9098, 41 m, cascajera fluvial, 25/05/2011, I. García-Mijangos & D. Liendo, BIO-50847; Mazcuerras, Cos, 30TVN0093, 150 m, prado de siega, 26/09/2012, I. Biurrun, I. García-Mijangos & D. Liendo, ARAN-80091; Guriezo, río Agüera, 30TVN7696, 81 m, cascajera fluvial, 09/08/2011, I. Biurrun & D. Liendo, BIO-50633; Guriezo, Trebuesto, río Agüera, 30TVN7697, 65 m, cascajera fluvial, 31/08/2011, I. García-Mijangos, D. Liendo & M. Torca, BIO-50640; Noja, 30TVP5615, 1 m, marisma, 15/10/2012, M. Herrera *et al.*, BIO-50493; Noja, 30TVP5715, 32 m, ruderal, solar abandonado, 11/11/2012, J.A. Campos *et al.*, BIO-50938; Noja, 30TVP5913, 3m, duna terciaria a sotavento, 08/09/1995, J.A. Campos, BIO-51061; Colindres, 30TVP6304, 0m, prado húmedo en la marisma, 18/09/1996, J.A. Campos, BIO-51058; Colindres, 30TVP6304, 5 m, zona de relleno en salida de autovía, 29/09/1997, J.A. Campos, BIO-51080; Limpias, Seña, 30TVP6605, 105 m, cuneta de carretera, 11/11/2011, J.A. Campos, BIO-50941; Castro Urdiales, 30TVP8103, 35 m, borde de camino, 20/10/2012, D. Liendo, BIO-50510. **GIPUZKOA**: Aretxabaleta, Goroeta, 30TWN4262, 335 m, orilla elevada del embalse, 10/09/1997, J.A. Campos, BIO-51075; Aretxabaleta, Goroeta, 30TWN4263, 335 m, 3ª línea de la orilla, contacto con prado, 10/09/1997, J.A. Campos, BIO-51076; Bergara, entre caserío Aldai y caserío Meltxorena, 30TWN4473, 341 m, plantación joven de *Pinus radiata*, 11/07/2007, A. Agut, BIO-48223, (sub. *C. bonariensis*); Bergara, hacia Placencia, 30TWN4776, 130 m, talud derecho del río Deba, 06/09/1996, J.A. Campos, BIO-51081; Bergara, Abrain erreka ascendiendo junto al cauce, 30TWN4875, 227 m, pequeño hayedo, 05/10/2006, A. Agut, BIO-49212; Segura, 30TWN6061, 210 m, cultivo de pequeñas píceas abandonado, 23/09/1997, J.A. Campos, BIO-51079; Zumaia, 30TWN6094, 0 m, postduna nitrificada, 16/06/1998, J.A. Campos, BIO-51048; Zumaia, 30TWN6194, 0 m, dunas fijas, 13/07/1995, J.A. Campos, BIO-51064; Idiazabal, río Urtsuaran, 30TWN6261, 263 m, herbazal junto al río, 25/09/2013, I. Biurrun & D. Liendo, BIO-50468; Zarautz, 30TWN6893, 0 m, herbazal en borde de camino, 16/06/1998, J.A. Campos, BIO-51047; Andoain, 30TWN7884, 50 m, orilla del río, 03/10/1997, J.A. Campos, BIO-51077; Valle de Leizaran, 30TWN8082, 125 m, taludes herbosos, 13/03/1982, M. Salaverría, ARAN-3100, (sub. *C. bonariensis*); Donostia-San Sebastián, 30TWN8092, 50 m, cultivo de vainas en descanso, 03/10/1997, J.A. Campos, BIO-51078; Donostia-San Sebastián, 30TWN8096, 5 m, herbazal en escombros de obras, 08/09/1997, J.A. Campos, BIO-51073; Hernani, 30TWN8391, 10 m, depresión húmeda en baldío, 03/10/1997, J.A. Campos, BIO-51042;

Hernani, Ereñozu, río Urumea, 30TWN8589, 16 m, comunidad nitrófila junto al río, 10/09/2013, I. Biurrun & D. Liendo, BIO-50798; Irún, 30TWN9799, 10 m, zonas ruderalizadas junto al parking de camiones, 13/09/1996, S. Patino & J. Valencia, SEST-946.96, (sub. *C. bonariensis*); Irún, 30TWP9800, 5 m, escombrera, 19/09/1981, I. Aizpuru & P. Catalán, ARAN-20154, (sub. *C. bonariensis*). **LA RIOJA**: Entrena, 30TWM3893, 565 m, herbazales y orillas entre cultivos, 25/09/1996, M.A. Domingo, VIT-39112, (sub. *C. bonariensis*); Calahorra, cementerio, 30TWM8484, 330 m, baldíos urbanos secos, 07/06/1993, J.M. Aparicio & Txema Pérez, VIT-16832, (sub. *C. bonariensis*); Villalba de Rioja, 30TWN0918, 620 m, cuneta del camino, 26/10/2012, J.A. Campos *et al.*, BIO-50598; Haro, 30TWN1213, 469 m, descampado, 26/10/2012, J.A. Campos *et al.*, BIO-50592; Haro, 30TWN1214, 455 m, herbazal hipernitrófilo de *Chenopodion muralis* junto al río, 26/10/2012, J.A. Campos *et al.*, BIO-50916. **NAVARRA**: Mendavia, 30TWM6596, 320 m, choperas y graveras, 27/09/1986, I. Aizpuru & P. Catalán, ARAN-20156, (sub. *C. bonariensis*); Azagra, La Barca, 30TWM8984, 300 m, cascajeras del río Ebro, 24/09/1987, P.M. Uribe-Echebarría, VIT-12408, (sub. *C. bonariensis*); Viana, laguna de Las Cañas, 30TWN4904, 380 m, orillas (no encharcadas) de la laguna sobre terreno arcilloso, 20/09/1984, G. Morante, VIT-12412, (sub. *C. bonariensis*); Viana, 30TWN50, 450 m, ruderal, 11/04/1980, P. Isaba, ARAN-49099, (sub. *C. canadensis*); Améscoa Baja, 30TWN7234, 500 m, chopera con suelo removido, 13/10/1987, C. Aseginolaza, C. Aseginolaza-237387, (sub. *C. bonariensis*); Etxarri-Aranatz, río Burunda, 30TWN7450, 490 m, acequias de prado, junto al río, 09/10/1987, C. Aseginolaza, C. Aseginolaza-194887, (sub. *C. bonariensis*); Puente la Reina, 30TWN9625, 340 m, cascajeras del río Arga, 14/10/1987, C. Aseginolaza, C. Aseginolaza-246187, (sub. *C. bonariensis*); Milagro, 30TXM0275, 300 m, huertas en la confluencia de los ríos Aragón y Ebro, 23/09/1987, P.M. Uribe-Echebarría, VIT-124098, (sub. *C. bonariensis*); Tudela, balsa de Purguel, 30TXM0656, 320 m, cubeta endorreica, zona húmeda, 23/09/1987, C. Aseginolaza, C. Aseginolaza-197887, (sub. *C. bonariensis*); Ablitas, laguna de Lor, 30TXM1148, ribazos de la laguna, 06/02/1987, ARAN-20157, (sub. *C. bonariensis*); Tudela, carretera de Murchante, 30TXM1255, 290 m, acequias de regadío, 23/09/1987, C. Aseginolaza, C. Aseginolaza-206787, (sub. *C. bonariensis*); Pamplona, polígono industrial del Soto, 30TXN0744, 430 m, baldíos industriales, 10/12/1994, J.M. Aparicio & J.M. Pérez Dacosta, VIT-19889, (sub. *C. bonariensis*); Etxalar, 30TXN1087, 100 m, herbazal nitrófilo, borde del juncal, 27/08/1992, I. Biurrun, BIO-21221, (sub. *C. canadensis*); Valcarlos, 30TXN3769, 480 m, cuneta, robledal-castañar, 30/09/1987, I. Aizpuru & P. Catalán, ARAN-20158, (sub. *C. bonariensis*). **ZARAGOZA**: Añón de Moncayo, Barranco de Morca, 30TXM0026, 1200-1250 m, orillas de pistas, en pinares con haya sobre sustrato silíceo, 23/09/1999, P.M. Uribe-Echebarría, MONCAYO-2216, (sub. *C. bonariensis*); Purujosa, 30TXM0215, 880-950 m, terreno calizo nitrogenado, 20/08/1999, D. & D. Gómez & P.M. Uribe-Echebarría, MONCAYO-2059, (sub. *C. bonariensis*); Añón de Moncayo, Barranco de Morca, cerca de la central de Morca, 30TXM0226, 950 m, orla de rebollar y cunetas de carretera sobre sustrato silíceo, 10/04/1999, C. Aseginolaza, D. Gómez & P.M. Uribe-Echebarría, MONCAYO-2280, (sub. *C. bonariensis*); Borja, 30TXM2232, 440 m, baldíos industriales, 19/10/1994, J.M. Pérez Dacosta, VIT-20227, (sub. *C. bonariensis*); Borja, polígono industrial, 30TXM23, 420-440 m, baldíos, 26/05/1994, J.M. Pérez Dacosta, VIT-18611, (sub. *C. bonariensis*). **FRANCE. PYRÉNÉES-ATLANTIQUES**: Bayonne, La Barre, 30TXP1920, 13 m, arenales ruderalizados junto a los lagos de La Barre, 14/09/1996, S. Patino & J. Valencia, SEST-972.96, (sub. *C. bonariensis*); Mouguerre, zona industrial de Mouguerre-Port, 30TXP21, terrenos ruderalizados arenosos, 18/09/1994, P. Urrutia, VIT-19601, (sub. *C. bonariensis*); Bayonne, La Barre, 30TXP22, arenales removidos, 24/05/1994, P. Urrutia, VIT-18542, (sub. *C. bonariensis*).

Conyza bonariensis (L.) Cronq.

SPAIN. ÁLAVA: Amurrio, 30TVN9964, 265 m, cuneta junto al maizal, 03/09/1997, J.A. Campos, BIO-51024. **BIZKAIA**: Muskiz, 30TVN9099, 5 m, pastizal pisoteado en la postduna, 07/10/1997, J.A. Campos, BIO-51028; Barakaldo, 30TWN0093, 25 m, protosuelos sobre el asfalto, 11/09/1997, J.A. Campos, BIO-51023; Barakaldo, 30TWN0093, 10 m, herbazal higrófilo en baldío, 07/10/1997, J.A. Campos, BIO-51027; Barakaldo, Lutxana, 30TWN0293, 5 m, cuneta, 27/08/1996, J.A. Campos, BIO-51026; Bilbao, 30TWN0590, 7 m, borde de camino sombrío y pisoteado, 23/07/1996, J.A. Campos, BIO-51025; Gorliz, 30TWP0407, dunas, 08/05/1982, C. Aseginolaza, ARAN-3102. **CANTABRIA**: Escalante, 30TVP5809, 0 m, pastizal pisoteado, 13/09/1996, J.A. Campos, BIO-51029. **GIPUZKOA**: Orio, 30TWN7093, 10 m, arenales en la parte trasera de la playa, ruderalizado, 16/09/1983, M. Salaverría & X. Lizaur, ARAN-3101. **HUESCA**: Valle de Hecho, Santidero, 30TXN8438, 775 m, cascajeras del río Aragón Subordán, sauceda de *S. eleagnos*, 15/08/1995, I. Aizpuru, ARAN-52576. **NAVARRA**: Buñuel, 30TXM2949, 240 m, cascajeras y soto a orillas del Ebro, 10/06/1996, I. Aizpuru & P. Catalán, ARAN-54969. **ZARAGOZA**: Purujosa, 30TXM0215, 880-950 m, terreno calizo nitrogenado, 20/08/1999, D. & D. Gómez & P.M. Uribe-Echebarría, MONCAYO-2059. **FRANCE. PYRÉNÉES-ATLANTIQUES**: Bayonne, St. Bernard, 30TXP21, 15 m, ruderales entre vías de ferrocarril, 07/02/1995, I. Aizpuru, ARAN-52759.

GENERAL CONCLUSIONS

The present thesis has allowed gaining important insights in relation to alien plant invasion in riparian habitats of northern Spain, such as alien plant composition, drivers of plant invasion, differences in invasion among riparian habitats and effects of alien species on the phylogenetic diversity.

Alien flora

A total of 156 alien taxa, mainly from America and Asia, have been found during the development of the present thesis. Around 40% of these taxa were singleton species that were found only once. Alien plant composition was remarkably different in the two most characteristic riparian habitats: riparian forests and river bar communities. Firstly, the most frequent alien species in riparian forests were *Crocosmia x crocosmiiflora* and several trees, namely *Platanus hispanica*, *Robinia pseudoacacia* and *Populus x canadensis*. Other species, such as *Fallopia japonica*, *Tradescantia fluminensis*, *Impatiens balfourii*, *Pterocarya stenoptera* and *Selaginella kraussiana* were less frequent but can achieve moderate to high cover values. Among them, *Fallopia japonica* has emerged as the most problematic species despite not being the most frequent. This species becomes especially dominant in man-made slopes and in highly disrupted alder forests. Secondly, the most frequent alien species in river bar communities were *Paspalum distichum*, *Cyperus eragrostis* and a wide range of nitrophilous species, such as *Bidens frondosus*, *Echinochloa crus-galli*, *Conyza bilbaoana*, *Dysphania ambrosioides*, *Symphyotrichum squamatum*, *Digitaria sanguinalis*, *Lycopersicon esculentum* and several species of *Amaranthus*. Some of them, such as *P. distichum*, *B. frondosus* and *E. crus-galli* can achieve moderate to high cover values, especially *P. distichum*, which can form almost monospecific communities on sandy-muddy substrates.

Some alien species were found for the first time at provincial and/or regional scale, such as *Helianthus x laetiflorus* and *Persicaria pensylvanica* in Cantabria and *Muhlenbergia schreberi* in the Basque Country and Navarra. The latter represents the second reference for this species in the Iberian Peninsula and is becoming increasingly widespread in river bars at the Urumea river basin. For this reason, it should be monitored in the forthcoming years given its potential invasive behaviour.

In the study area the genus *Conyza* is becoming increasingly abundant in natural habitats, such as coastal dunes, and especially in anthropogenic habitats, such as road edges, abandoned fields and waste ground. Moreover, it has been found in number of river bar communities sampled for the present thesis, indicating that it is increasingly colonising this riparian habitat. Important doubts emerged regarding the identification of the *Conyza* specimens collected. This, along with the previous long-standing confusion regarding the identification of the different *Conyza* species, largely as a result of the erroneous or incomplete treatment of the genus in different floras, inspired the revision of the genus in northern Spain. This revision has helped set the fundamental differences important for the identification of the four *Conyza* species that have been identified in this territory and, additionally, it has allowed getting a more accurate picture of their current distribution.

Drivers of plant invasion

One of the aims of the present thesis was to determine whether environmental and/or human-related factors were related to the level of plant invasion in Cantabrian streams. Once the level of invasion was seen to be related to hydrological and morphological disturbances, a more detailed analysis showed that at local scale (sampling point), the level of plant invasion was influenced both by environmental and anthropogenic factors. Environmental factors included climate features (thermicity index), stream morphology (average riverbed width) and habitat heterogeneity (number of plant communities present at the sampling point). On the other hand, anthropogenic variables included the distance to the nearest town and the proportion of surrounding urban land as sources of alien plant propagules.

At regional scale (river basin), we found that industrialised river basins were significantly more invaded than non-industrialised ones and that both types of basins differed in their alien plant composition. Some alien species, such as *Bidens frondosus*, *Paspalum distichum* and *Acer negundo* were associated to industrialised basins, whilst two of the most cultivated alien trees (*Eucalyptus globulus* and *Pinus radiata*) were associated to non-industrialised ones.

Plant invasion in riparian habitats

Significant differences have been observed among the different riparian habitats in relation to their level of plant invasion. The pilot study (Chapter 2) showed that river bar communities and man-made slopes contained a similar number of alien species and higher than riparian forests. These differences were due to a major presence of species categorised as invasive in river bar communities and man-made slopes. Given than the latter encompassed a heterogeneous range of plant communities resulting from human activities, further analysis were conducted by means of vegetation plots in the most characteristic natural riparian habitats (i.e., riparian forests and river bar communities).

This plot-based analysis confirmed that river bar communities of the *Bidenti frondosae-Polygonetum lapathifolii* association (sensu Campos 2010) were significantly more invaded in terms of absolute and relative alien species richness and cover than riparian forests, which included alder forests of the *Hyperico androsaemi-Alnetum glutinosae* and *Stegnogrammo pozoi-Alnetum glutinosae* associations and ash forests of the *Polysticho setiferi-Fraxinetum excelsioris* association. The higher level of invasion in river bar communities has been linked to the higher level of hydrological disturbance these communities are subjected to, which creates bare ground that can be rapidly colonised by a great number of opportunistic alien species in a low-competition environment. Additionally, river bars in the study area are concentrated in the lower sections of the streams close to urban settlements and industrial areas that serve as sources for alien plant species.

Alien plants and phylogenetic diversity and structure in riparian habitats

Before testing whether alien plants had an effect on the phylogenetic diversity and structure of riparian habitats, we detected that, on the basis of the native component and using vegetation plots, river bar communities were phylogenetically less diverse than riparian forests, which translated into a more clustered phylogenetic structure (i.e., native species in river bar communities tended to be phylogenetically closer than random) in terms of both MPD and MNTD phylogenetic indices. Again, this higher level of phylogenetic clustering in river bar communities would be the result of a higher disturbance regime that would select for phylogenetically close species sharing ecological adaptations, in this case nitrophilous annual seed-dispersed species (assuming trait conservatism across the phylogenetic tree).

No significant relationship was detected between the phylogenetic diversity of the native component of both habitats (in terms of MPD and MNTD indices) and the level of plant invasion. Regarding river bar communities, this lack of significance was due to the differences in the number of native species among plots as shown by the standardised MPD and MNTD values. Notwithstanding the above, alien plants did cause a decrease in the overall level of phylogenetic clustering in river bar communities in terms of the MPD index but not of the MNTD index, implying that alien plants entering river bar communities were less closely related than expected to native species but, at the same time, were closely related among them. In riparian forests no effect of alien plant species on the phylogenetic diversity and structure was detected.

CONCLUSIONES ABREVIADAS

1. Se han encontrado un total de 156 taxones de flora alóctona en los ríos cantábricos estudiados, la mayoría originarios de América y Asia. Un 40 % de estos taxones aparecieron en una única localidad. Además, se ha determinado cuáles son las especies de flora alóctona más frecuentes y/o abundantes en los principales hábitats riparios.

2. Se han aportado nuevas citas de especies nativas y alóctonas a escala provincial y/o regional, destacando en este apartado el descubrimiento de poblaciones naturalizadas de *Muhlenbergia schreberi*, gramínea norteamericana encontrada en el río Urumea en Gipuzkoa y Navarra y que representa la segunda referencia de esta especie en la Península Ibérica.

3. La revisión taxonómica del género *Conyza* en el norte de España ha permitido establecer las principales diferencias entre las cuatro especies presentes en el territorio, lo que supone un importante avance en su identificación. Asimismo, esta revisión ha ayudado a obtener una imagen más detallada de la distribución de estas cuatro especies en el norte de España.

4. Se ha determinado un conjunto de variables ambientales y antrópicas relacionadas con el grado de invasión por plantas alóctonas a escala local (punto de muestreo) y a escala regional (cuenca hidrográfica). El índice de termicidad, la anchura media del cauce, el número de comunidades vegetales, la distancia a núcleos urbanos y la proporción de suelo urbano circundante afectaron al grado de invasión a escala local, mientras que el grado de industrialización influyó a escala regional.

5. A nivel de hábitat, se ha comprobado que las cascajeras fluviales están más invadidas que los bosques riparios en relación tanto a la riqueza de especies alóctonas como a la cobertura de las mismas. Los taludes creados por el hombre presentaron unos niveles de invasión similares a los de las cascajeras fluviales.

6. A escala de inventarios de vegetación, las cascajeras fluviales son filogenéticamente menos diversas que los bosques riparios como consecuencia del mayor nivel de perturbación natural al que están sometidas. Además, como resultado de lo anterior, las cascajeras fluviales presentan un patrón filogenético agrupado en mayor medida que los bosques riparios, en los que el patrón predominante es de tipo aleatorio.

7. La entrada de especies alóctonas trajo consigo una disminución en el grado de agrupamiento filogenético en las cascajeras fluviales, mientras que no produjo ningún cambio significativo en la diversidad y estructura filogenéticas de los bosques riparios.

APPENDIX 1. List of alien plant species found in Cantabrian streams and number of sites where these species occurred. Asterisks indicate species included in vegetation plots from the BIOVEG database (ssee Chapter 4) but not found during the field sampling carried out for the present thesis.

Alien species	No sites	Alien species	No sites
Acacia dealbata	3	*Coronopus didymus*	6
Acacia melanoxylon	1	*Cortaderia selloana*	8
Acanthus mollis	2	*Cotoneaster* sp.	1
Acer negundo	5	*Crataegus germanica*	2
Acer platanoides	1*	*Crocosmia x crocosmiiflora*	46
Acer saccharinum	1	*Cucurbita pepo*	1
Actinidia chinensis	1*	*Cymbalaria muralis*	11
Aesculus hippocastanum	1	*Cyperus eragrostis*	37
Ailanthus altissima	2	*Cyperus glomeratus*	1
Albizia julibrissin	1	*Cyperus longus*	13
Amaranthus albus	1*	*Datura stramonium*	3
Amaranthus blitum	6	*Delairea odorata*	2
Amaranthus bouchonii	2	*Digitaria ischaemum*	1
Amaranthus deflexus	1*	*Digitaria sanguinalis*	6
Amaranthus emarginatus	4	*Dittrichia viscosa*	1
Amaranthus hybridus	5	*Dorycnium rectum*	16
Amaranthus hypochondriacus	1*	*Dysphania ambrosioides*	5
Amaranthus powellii	5	*Echinochloa crus-galli*	15
Amaranthus retroflexus	1*	*Eragrostis pectinacea*	2*
Artemisia verlotiorum	3	*Eragrostis pilosa*	1
Arundo donax	4	*Eragrostis virescens*	1*
Aucuba japonica	1	*Erigeron karvinskianus*	11
Avena sativa	1	*Eucalyptus globulus*	10
Baccharis halimifolia	1*	*Euonymus japonicus*	2
Begonia sp.	1	*Euphorbia lathyris*	1
Bidens aureus	1	*Fallopia japonica*	11
Bidens frondosus	7	*Ficus carica*	19
Brassica napus	3*	*Fraxinus pennsylvanica*	1
Brassica nigra	1	*Galinsoga quadriradiata*	6
Brassica oleracea	1	*Gamochaeta coarctata*	1
Brassica rapa	5	*Hedera canariensis*	1
Bromus catharticus	11	*Helianthus tuberosus*	3*
Buddleja davidii	9	*Helianthus x laetiflorus*	7
Calendula officinalis	1	*Hydrangea macrophylla*	1
Canna indica	1	*Hypericum hircinum* subsp. *majus*	2
Catalpa bignonioides	1*	*Impatiens balfourii*	10
Centranthus ruber	2	*Ipomoea indica*	1
Chamaecyparis lawsoniana	5	*Juglans nigra*	1
Citrullus lanatus	2*	*Juglans regia*	25
Conyza bilbaoana	38	*Juncus tenuis*	4
Conyza sumatrensis	24	*Larix kaempferi*	1

Alien species	No sites	Alien species	No sites
Leersia oryzoides	10	*Prunus serotina*	1
Ligustrum japonicum	1	*Pterocarya stenoptera*	1
Ligustrum lucidum	2	*Pyracantha angustifolia*	2
Ligustrum ovalifolium	17	*Pyrus communis*	2
Lobularia maritima	2	*Quercus rubra*	3
Lonicera japonica	12	*Robinia pseudoacacia*	41
Lunaria annua	1	*Rosa* 'cultivar'	2
Lycopersicon esculentum	8	*Salix alba* var. *contorta*	1
Mentha spicata	1	*Salix babylonica*	1
Mirabilis jalapa	1	*Sedum sexangulare*	1
Morus sp.	1	*Selaginella kraussiana*	3
Muhlenbergia schreberi	3	*Solanum chenopodioides*	16
Myrtus communis	2	*Solanum villosum* subsp. *villosum*	1*
Oenothera biennis	1*	*Sonchus tenerrimus*	1*
Oenothera glazioviana	2	*Sporobolus indicus*	1
Oenothera rosea	8	*Symphyotrichum lanceolatum*	7
Oxalis latifolia	18	*Symphyotrichum squamatum*	3
Oxalis pes-caprae	2	*Symphytum x uplandicum*	1
Parthenocissus inserta	3	*Syringa vulgaris*	1
Paspalum dilatatum	5	*Tanacetum parthenium*	1
Paspalum distichum	14	*Trachelium caeruleum*	1
Passiflora caerulea	1	*Trachycarpus* sp.	1
Pelargonium zonale agg.	1*	*Tradescantia fluminensis*	13
Persicaria pensylvanica	2	*Triticum durum*	1
Phalaris canariensis	1*	*Ulmus pumila*	2
Phoenix sp.	1	*Verbena bonariensis*	2
Phyllostachys sp.	12	*Verbena brasiliensis*	2
Pinus radiata	9	*Veronica persica*	12
Platanus hispanica	45	*Vicia faba*	1
Populus alba	1	*Vinca difformis*	1
Populus nigra var. *italica*	7	*Vinca major*	1
Populus x canadensis	22	*Vitis vinifera*	6
Portulaca oleracea	3	*Xanthium strumarium*	4
Potentilla indica	2	*Yucca* sp.	5
Prunus domestica	8	*Zantedeschia aethiopica*	4
Prunus laurocerasus	3	*Zea mays*	1*
Prunus persica	1		