Differences in traits between co-occurring alien and native plant species of annual riparian plant communities

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Keywords

alien species, annual plant communities, congeneric species, functional traits, invasive species, phenotypic integration, plant abundance, riparian ecosystems, seed heteromorphism, vegetation survey.

Short abstract

Knowledge about traits driving invasions of alien plants can help to prevent future invasions and inform on interactions between alien and native species. Riparian systems are especially prone to invasions by alien plants due to their high disturbance regime and anthropogenic modifications what makes them valuable study areas. In this thesis I ask:

- How alien riparian species differ in their traits from co-occurring resident native species?
- Can alien species invading riparian ecosystems better adapt to environmental heterogeneity in comparison to co-occurring native species?
- Are abundances of alien and native species co-occurring in riparian plant communities driven by the same traits?

To answer these questions, I conducted three studies comparing trait values, trait variances and relations between traits and plant abundances. I found that alien and native species differ in trait values rather than in trait variances. Moreover, abundances of alien and native species depend on different traits. Observed differences in traits and strategies suggest that investigated alien and native species may coexist in natural ecosystems, like riparian habitats.

Kennwörter

einjährige Pflanzengemeinschaften, funktionelle Merkmale, Gebietsfremde Pflanzen, Integration der Phänotypen, invasive Arten, Pflanzenhäufigkeit, Samenheteromorphismus, Uferökosysteme, Vegetationsaufnahme, verwandte Arten.

Kurze Zusammenfassung

Die Kenntnis der Merkmale, welche Invasionen von gebietsfremden Pflanzen antreiben, kann Informationen über Wirkungen zwischen fremden und einheimischen Arten bereitstellen. Ufersysteme sind, aufgrund der anthropogenen Veränderungen, anfällig für Invasionen. In meiner Doktorarbeit stelle ich die folgenden Fragen:

- Wie unterscheiden sich die gebietsfremden Arten von den einheimischen Uferarten in ihren Merkmalen?
- Können sich gebietsfremde Arten, besser an die Heterogenität der Umwelt anpassen als einheimische Uferarten?
- Hängt die Häufigkeit gebietsfremde und einheimische Uferarten von denselben Merkmalen ab?

Ich habe drei Studien durchgeführt, um die Merkmalswerte, Merkmalsvariabilität und Verbindungen zwischen Merkmalen und Pflanzenhäufigkeiten zu vergleichen. Ich fand heraus, dass gebietsfremde und einheimische Arten sich eher in Merkmalswerten als in Merkmalsvarianzen unterscheiden. Zudem hängt die Häufigkeit gebietsfremder und einheimischer Arten von verschiedenen Merkmalen ab. Die Unterschiede weisen darauf hin, dass die untersuchten gebietsfremden und einheimischen Arten nebeneinander existieren können.

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Summary

Biotic invasions are listed among the most important components of global change. The number of alien plant species introduced worldwide is increasing, and their impact on other species and whole ecosystems is becoming more common. Knowledge about drivers and processes leading to successful invasions can be utilized for prioritization of the most harmful invaders, but can also inform about processes of plant community assembly and between species interactions.

Many studies highlighted the importance of species traits for success of plant invasions. For example, successful alien plants are often characterized by higher biomass and fecundity in comparison to native species. Similarly, they are more efficient in colonization and competition than native plants. Still, defining a precise set of traits that drive success of alien species across a range of environmental conditions is an extremely challenging task. One of the reasons is a large number of environmental variables, which simultaneously filter strategies and traits of species occurring in a given habitat. Therefore, it was suggested, that differences and similarities in species traits between closely related and co-occurring alien and native plant species may determine their success in a plant community and define their reciprocal interactions.

Riparian systems are one of the most commonly invaded habitats. Among the multiple causes leading to this state are common flood disturbances, anthropogenic pressure and presence of untapped ecological niches. Native plants of riparian areas are often characterized by fast growth, high competitive abilities and adaptations to fluctuating environmental conditions. Strategies of alien plants often involve fast development and high competitive abilities, what raises a question, whether successful alien species invading these habitats differ in traits and strategies from successful native riparian species. In this thesis I ask:

- How alien riparian species differ in their traits from co-occurring resident native species?

- Can alien species invading riparian ecosystems better adapt to environmental heterogeneity in comparison to co-occurring native species?
- Are abundances of alien and native species co-occurring in riparian plant communities driven by the same traits?

To answer these questions, I conducted three separate studies comparing different aspects of trait dissimilarities between native and alien plants co-occurring in annual plant communities, located in three big Central European river systems. In the first study I selected three congeneric and alien-native species pairs-common and representative for investigated plant communities. I compared trait means, their correlation patterns and variability across populations of the selected species. I expected alien species to have an advantage over native species in fitness related traits and in trait variability *i.e.* lower phenotypic integration and higher variance across the populations. In the second study I conducted a greenhouse experiment aimed at testing differences in fitness and performance traits between distinct seed morph progenies of selected alien and native species pair, under different competition levels. I expected that both seed morph progenies of alien species will be characterized by a better performance than seed morph progenies produced by native species. In the last study, I tested how particular traits affect abundances of all native and alien plants co-occurring in investigated riparian habitats. I expected that abundances of alien and native species will be driven by different traits.

Investigated alien and native congeners shared some similar characteristics, *e.g.* seed production, or trait variability. Despite it, I found also some differences suggesting a certain degree of divergence in species strategies. The most prominent results include differences in plant height, specific leaf area, and in flowering phenology. These findings concur with conclusions of previously published studies, but also remain relatively consistent across the chapters of this thesis. They implied, that while investigated species share some ecologically relevant traits and adaptations to environmental conditions, some of their traits and consequently strategies differ, potentially facilitating coexistence. Despite I have worked in a single habitat type, I have observed a certain level of context-dependency. For instance, relations between traits and abundances differed between river systems and along the rivers. Although some of the observed patterns, *e.g.* importance of flowering length or vegetative reproductions may be indirectly attributed to frequency of flood events, further studies are needed to associate observed patterns with particular mechanisms.

This thesis demonstrates how similarities and differences in traits can affect success of alien plant species in riparian plant communities. Moreover it discusses, how these differences may affect relations between alien and native plant species and presents the role of context dependency for patterns observed in examined ecosystems. Finally, it provides an insights into the potential avenues of future research, which can further improve our understanding of processes driving biotic invasions in natural ecosystems.

Chapter 1.

General introduction

Biotic invasions as an element of global change

The Anthropocene epoch is defined by the prevailing influence of human activities on ecosystems (Vitousek *et al.* 1997; Crutzen & Stoermer 2000). Human-mediated introductions of organisms outside of their previous geographical range are listed as one of the most distressful anthropogenic agents (Crowl *et al.* 2008; Richardson & Pyšek 2008; Tylianakis *et al.* 2008), and are a serious threat to biodiversity (Sala *et al.* 2000). Species which were intentionally or unintentionally introduced into new regions are defined as alien or exotic (Hulme 2011). Majority of introduced species fail to reproduce or maintain populations over longer periods of time and their occurrence is dependent on repeated introductions (Richardson *et al.* 2000). However, a subset of alien species, can establish self-perpetuating populations in resident assemblages *i.e.* become naturalized (Richardson *et al.* 2011). Naturalized species, that disperse over long distances and spread broadly across various habitats, are called invasive (Richardson *et al.* 2011). While only a relatively small number of introduced alien species becomes invasive (Richardson *et al.* 2000; van Kleunen *et al.* 2015) understanding mechanisms driving this process has been of great interest since Darwin raised this question for the first time in “On the origin of species” (Darwin 1859). Although recent studies greatly advanced our understanding of biotic invasions and its drivers (Pyšek & Richardson 2008), many facets of this phenomenon remain unexplained (Richardson 2011).

One of the major motivations for studying plant invasions is their impact on native species (Vilà *et al.* 2011; Case *et al.* 2016), plant communities (Hejda *et al.* 2009; Lai *et al.* 2015) or even on whole ecosystems (te Beest *et al.* 2015). Considering more than 30 000 plant species introduced worldwide (Pimentel *et al.* 2007) and approximately 3.9% of the global flora recognized as established alien species, invasive plants have a potential to influence most of the terrestrial ecosystems (van Kleunen *et al.* 2015). Although the effects of invasion may vary from negative to neutral or even positive (Keane & Crawley 2002; Vilà *et al.* 2010; Schlaepfer *et al.* 2011), prevailing impacts are considered negative (Pimentel *et al.* 2000; Gaertner *et al.* 2009; Blackburn *et al.* 2014). For example, invasive alien species were shown to affect fitness of native species (Stinson *et al.* 2006) and decrease their ability to sustain or enlarge their populations (Levine *et al.* 2003; Burghardt *et al.* 2010). In some cases invasions may directly lead to extinction of native biota (Gurevitch & Padilla 2004). Conservation and management practices, preventing further invasions or reducing their impact require precise knowledge about mechanisms governing invasion processes as well as their role in natural ecosystems (Rejmánek 2000; Rejmánek *et al.* 2005; Hulme *et al.* 2013).

Biological invasions can also be perceived as an ongoing natural experiment (Daleo *et al.* 2009) that gives us an insight into fundamental evolutionary (Yoshida *et al.* 2007) and ecological mechanisms (Lodge 1993; Sax *et al.* 2007). For instance, studying invasions of introduced species can give us an insight about ecological or even geomorphological disturbances (Vitousek 1990; Mack & D'Antonio 1998; Fei *et al.* 2014). Furthermore, invasions lead to an emergence of novel interactions between taxa, which did not co-occur previously (Callaway & Ridenour 2004; Hobbs *et al.* 2006; Hobbs *et al.* 2009). By identifying mechanisms underpinning invasions we can learn about processes regulating species coexistence, and mechanisms of plant community assembly (Catford & Jansson 2014). Moreover, better understanding of biotic invasions allows us to identify the potential synergies with other global change drivers and thus give us a more complete perspective of the global change (Thuiller *et al*. 2008a).

Drivers of biotic invasions

Irrespective to the motivation which has been weather to reduce ecological and economic losses and management costs (Pimentel *et al.* 2000) or to improve our understanding of ecological processes (Sax *et al.* 2007), identification of processes that facilitate biological invasions has become one of the main objectives of invasion ecology (Rejmánek 2000); reviewed in: (Pyšek & Richardson 2008; Richardson & Pyšek, 2011). Intensive research resulted in multiple hypotheses, which brought various aspects of invasiveness together (see Catford *et al.* 2009) and identified factors promoting invasions such as differences in traits (Funk *et al.* 2008; Leffler *et al.* 2014), high propagule pressure *i.e*. the number of introduced individuals and the frequency of introductions (Lockwood *et al.* 2005), invasion history (Kolar & Lodge 2001; Herron *et al.* 2007), as well as susceptibility of native plant communities (Orians 1986; Alpert *et al.* 2000; Davis *et al.* 2000; Dukes 2002).

Numerous studies highlighted the importance of species traits among other major drivers facilitating invasions. For example, Ideal Weed Hypothesis attributes success of invasive species directly to their ability to outcompete resident species (Rejmánek & Richardson 1996; Elton 2000; Sutherland 2004). Similarly, Global Competition (Alpert 2006; Colautti *et al.* 2006), Sampling (Crawley *et al.* 1999), and EICA Hypotheses (Blossey & Notzold 1995; Joshi & Vrieling 2005) addressed the reasons for trait related competitive advantage of invasive species. Comparative studies demonstrated that reproduction and performance-related traits such as higher specific leaf area (SLA), increased growth rate or reproductive output (Grotkopp *et al.* 2002; Rejmánek *et al.* 2005; Pyšek & Richardson 2008; van Kleunen *et al.* 2010a) were indeed related to success of numerous invasive plants. Nevertheless, contradictory findings such as no association with growth rate (Daehler 2003) or lower reproductive allocation in of invasive plants (Hawkes 2007) are also frequent. Moreover, trait distributions of native, introduced and invasive species often overlap (Ordonez *et al.* 2010). The question whether particular characteristics predispose taxa to become invasive still raises lively debates (compare: Thompson & Davis 2011; van Kleunen *et al.* 2011; Leffler *et al.* 2014; Dawson *et al.* 2015).

One of the potential causes leading to inconsistency of conclusions is the dependency of plant strategies on environmental conditions (Theoharides & Dukes 2007; Pyšek *et al.* 2012; Kueffer *et al.* 2013). For example, high intensity of disturbance (MacDougall & Turkington 2005), environmental fluctuations (Alpert *et al.* 2000; Davis *et al.* 2000; Parepa *et al.* 2013), availability of untapped resources (Davis *et al.* 2000) or low resistance of invaded systems (Levine *et al.* 2004) promote biotic invasions. On the contrary, persisting unfavorable physical conditions e.g. harsh climate, are likely to inhibit invasions (D'Antonio 1993; Rejmánek *et al.* 2005). Environmental filters select for particular combinations of traits advantageous for plants species present in different ecological settings (Daehler 2003; Drenovsky *et al.* 2012; Zefferman *et al.* 2015; Vicente *et al.* 2019). Stronger filtering can increase the competition between functionally similar species occupying given habitat (Gallien & Carboni 2017). This, on the one hand may result in increased suppression of invaders by a plant community, but on the other hand may be a reason for a more severe competitive impact of invading species (Chesson 2000; MacDougall *et al.* 2009). On the contrary, novelty of traits, leading to an ability to use untapped resources, may be an important factor reducing competitive interactions between native and invasive plants, as suggested by limiting similarity theory (Mack 2003; Emery 2007). Studies on divergence or convergence of traits between coexisting alien and native determine which traits or strategies give invasive alien species an advantage over native species (Hamilton *et al.* 2005) and shed light on interactions between them (Gibson *et al.* 2012). Importance of these patterns differs between habitats, across environmental gradients and geographical scales (Cornwell & Ackerly 2009; Price & Pärtel 2013). Therefore, to explore meaningful differences, studies should employ features of investigated ecosystems while addressing success of alien and native species (Lloret *et al.* 2005). Moreover, as in natural ecosystems, multiple abiotic and biotic drivers affect species success simultaneously (Gallien *et al.* 2015), it is important to investigate importance of observed patterns in realistic settings (Florianová & Münzbergová 2018; Vicente *et al.* 2019).

Although local environmental conditions play a substantial role in success of biotic invasions (Theoharides & Dukes 2007; Kueffer *et al.* 2013), majority of invasive plant species are capable of spreading on large geographical areas and across distinct habitats (Lambdon *et al.* 2008). Furthermore, alien species were repeatedly shown to benefit from environmental variability (Alpert *et al.* 2000; Davis *et al.* 2000; Parepa *et al.* 2013). One of the mechanisms, allowing plant species to adapt to wide range of conditions is phenotypic plasticity, *i.e.* the ability of a single genotype to express multiple phenotypes, which can lead to an advantage under particular habitat conditions (West-Eberhard 1989; Sultan 1995). Many studies found that invasive species are more plastic than native species (Daehler 2003; Richards *et al.* 2006). Nevertheless, conclusions of studies comparing phenotypic plasticity in native and alien species do not always support this assumption (Godoy *et al.* 2011; Matzek 2012; Montesinos & Callaway 2018). Moreover, phenotypic plasticity may not always be adaptive (DeWitt *et al.* 1998; Davidson *et al.* 2011) and decrease growth of individual plants and affect population dynamics (Langerhans & DeWitt 2002). Another strategy which share some similar development basis to phenotypic plasticity (Simons & Johnston 1997) is called bet hedging (Childs *et al.* 2010). With bet hedging, single phenotype is neither optimal nor detrimental across given environment conditions (Simons & Johnston 2003; Simons 2011). This strategy develops in more unpredictable environments (Simons 2011), characterized *e.g.* by temporal heterogeneity (Venable 2007), and may affect invasion success or coexistence with native species (Mandák 2003; Fumanal *et al.* 2007; Jiménez *et al.* 2016).

Importance of studying plant invasions in natural plant communities

Conclusions of previous approaches comparing traits of alien and native plant species have drawn attention to the choice of representative species, adequate traits and environmental settings (van Kleunen *et al.* 2010b; Kueffer *et al.* 2013). Numerous studies are limited by use of low species number, misleading comparisons between species (van Kleunen *et al.* 2010b), or unrealistic species combinations (Kuebbing *et al.* 2013; Bernard-Verdier & Hulme 2015).

One of the advised approaches to comparisons between native and alien species uses congeneric species pairs (Harvey & Pagel 1991; Felsenstein 2004; Agrawal *et al.* 2005). Comparing closely related species directly addresses the common problem of phylogenetic independence (Crawley *et al.* 1996), but also ensures that study species are comparable (Muth & Pigliucci 2006). Moreover, closely related invasive-native species pairs are of special interest for conservation biology, due to increased risks of hybridization and extinction of native species (Ayres *et al.* 2004).

Comparisons using invasive-native species pairs may yield valuable information, especially if the species of interest co-occur in the same habitats (Daehler 2003; Ayres *et al.* 2004). For instance, studies conducted in realistic systems allow to compare traits against a common measure of success (Knapp & Kühn 2012), like plant abundances measured in natural plant communities (van Kleunen *et al.* 2010b; Knapp & Kühn 2012). Moreover, studies conducted in natural habitats, can address interactions between biotic and abiotic factors (Thuiller, *et al.*

2008b; Kuebbing *et al.* 2013) and investigate the role of particular mechanisms in natural plant assemblages and under a gradient of natural conditions (Lai *et al.* 2015; Gallien & Carboni 2017). Nevertheless, ecological studies always represent a trade-off between realism, precision, and generality (Morin 1998). Even in a single habitat type, multiple drivers can simultaneously shape success of invasive species (Orrock & Witter 2010). Because of this complexity, it is often difficult to disentangle the role of particular factors (Kueffer *et al.* 2013). Therefore, ideally a thorough research should comprise both manipulative and field approaches, and address as precisely as possible different factors (Kueffer *et al.* 2013).

Plant invasions in riparian plant communities

Riparian ecosystems, located at fringes of rivers, are unique interface zones between terrestrial and aquatic systems (Naiman & Décamps 1997). Major forces shaping vegetation in these habitats are floods and processes associated with them (Bornette & Amoros 1996; Lite *et al.* 2005; Wintle & Kirkpatrick 2007). For instance, disturbances by flooding increase the number of available niches (Henry *et al.* 1996; Hölzel 2005; Pettit & Naiman 2006; Stromberg *et al.* 2011) and reduce competitive pressure of the standing vegetation (Brose & Tielbörger 2005; Jung *et al.* 2009). Prolonged submersion periods, removal and/or deposition of sediments as well as mechanical disturbances caused by floods are the main impacts that floods exert on standing vegetation (Lytle & Poff 2004; Catford & Jansson 2014; Voesenek & Bailey-Serres 2015).

Although riparian habitats are in general rich in species and their assemblages (Naiman *et al.* 1993; Brown & Peet 2003), their community composition often differs from adjacent areas (Sabo *et al.* 2005). Species in riparian habitats have a broad range of strategies which allow them to survive under high disturbance regimes (Bornette *et al.* 2008; Voesenek & Bailey-Serres 2015). These strategies are represented by a variety of physiological, morphological and life history adaptations (see Catford & Jansson 2014 for an overview). Traits can help to withstand detrimental factors *e.g.* presence of aerenchym enables survival under prolonged immersion (Voesenek *et al.* 2006) or recover after their decline *e.g.* fast regrowth after a physical damage (Voesenek & Bailey-Serres 2015). Similarly, adaptations in plant phenology can help plants to avoid unfavorable conditions such as by completing life cycle before the flood occurrence (Catford & Jansson 2014).

Plant communities located in the closest proximity to water edge undergo especially frequent disturbances as an effect of fluctuating water levels. Hence these communities are dominated by annual, fast growing plants, colonizing exposed surfaces and creating dense vegetation patches (Salisbury 1970; Catford & Jansson 2014). One of the adaptations to diverse and unpredictable habitat conditions is seed heteromorphism: a type of bet-hedging strategy based on production of distinct seed types (Venable 1985; Imbert 2002). Seed types may differ in their size, shape and longevity and can facilitate opposing strategies, *e.g.* colonization and maintenance or immediate germination and creation of dormant seed banks (Venable & Brown 1988; Moles & Westoby 2004; Stromberg *et al.* 2011). Some of the adaptations enabling survival under unpredictable disturbance regime, *e.g.* effective colonization, fast growth, vegetative reproduction or ability to adapt to fluctuating conditions, are shared by native and alien plants occupying riparian habitats (Catford & Jansson 2014).

Riparian zones are among the most invaded ecosystems worldwide (Stohlgren *et al.* 1999; Hood & Naiman 2000; Richardson *et al.* 2007), what makes them an invaluable object for studying biotic invasions. High number of invasions can result from spatial and temporal heterogeneity of riparian habitats (Chesson & Huntly 1997; Melbourne *et al.* 2007), complex disturbance regimes and nutrient fluxes (Nilsson & Berggren 2000; Pyšek *et al.* 2010). Furthermore, rivers serve as convenient transport corridors for seeds and vegetative propagules (Nilsson *et al.* 1991; Merritt *et al.* 2010), as well as facilitate spread of invasive plants (Säumel & Kowarik 2010; Zając *et al.* 2011). Increasing anthropogenic pressure is another factor facilitating invasions (Hood & Naiman 2000; Tockner & Stanford 2002). It includes direct modifications of river banks, like river regulations, artificial constructions (Naiman & Décamps 1997; Nilsson & Berggren 2000), as well as eutrophication, pollution and disturbance of adjacent areas (Cooper 1993; Grizzetti *et al.* 2017). All above-listed factors contribute to high susceptibility to invasions (Schooler *et al.* 2010); however artificial structures can impact vegetation structure and composition by dramatically modifying habitat conditions. Changes in length and frequency of floods reduce the abundance of native plants which are adapted to disturbance cycle, and facilitate invasions of species that lack of specific adaptations to environmental conditions (Catford *et al.* 2011; Moles *et al.* 2012; Greet *et al.* 2013). Catford *et al.* (2011) showed that alien species are rarely physiologically or phenologically pre-adapted to flooding, and therefore, can be successfully controlled by natural floods. As a result of ongoing anthropogenic modifications, and alterations of flooding regime, as well as other mechanisms and strategies such as fast growth and competitive ability may increase their importance (Richardson *et al.* 2007). Differences in traits, their variability between native and alien species can thus help to understand how their strategies lead to success in human-modified riparian plant communities.

Objectives and outline of the thesis

The central aim of this thesis is to assess various aspects of trait divergence between invasive and native species co-occurring in riparian habitats in Central Europe. In details, I follow three lines of inquiry.

1) Successful alien species are often characterized by high values of traits related to competition and performance, as well as high fecundity and effective dispersal. Strategies of annual species that occupy frequently invaded riparian communities often base on fast growth, high reproductive output and fast colonization. Therefore, I ask, whether alien and native riparian species differ in their traits from their native congeners? This overarching question (Q1) was addressed in **Chapter 2**, where I investigate whether alien and native species, co-occurring on natural sites differ in their traits, and in **Chapter 3**, where I test whether alien and native congeneric species differ in response to increased plant intra- and inter-specific plant densities (Fig. 1).

2) Alien species often spread across distinct habitats. Moreover, many of them benefit from environmental disturbances and resource fluctuations. Environmental conditions in riparian habitats are highly variable and native species often possess mechanisms of adaptation to these conditions. I ask whether traits of alien species invading riparian ecosystems are more variable in comparison to their

native congeners? This question (Q2) is addressed in **Chapter 2**, where I examine whether alien and native congeners, co-occurring on natural sites differ in their phenotypic integration and variation of their traits (Fig. 1).

3) Differences in traits between native and alien species may reflect different mechanisms, and their importance for a species success depends on numerous factors. To understand the actual importance of these differences, it is crucial to relate them to species success in natural conditions. I ask (Q3) whether alien and native species co-occurring in riparian plant communities benefit from the same traits in different environmental conditions? This question is addressed in **Chapter 4**, where investigate importance of particular traits and environmental drivers on abundances of alien and native co-occurring species (Fig. 1).

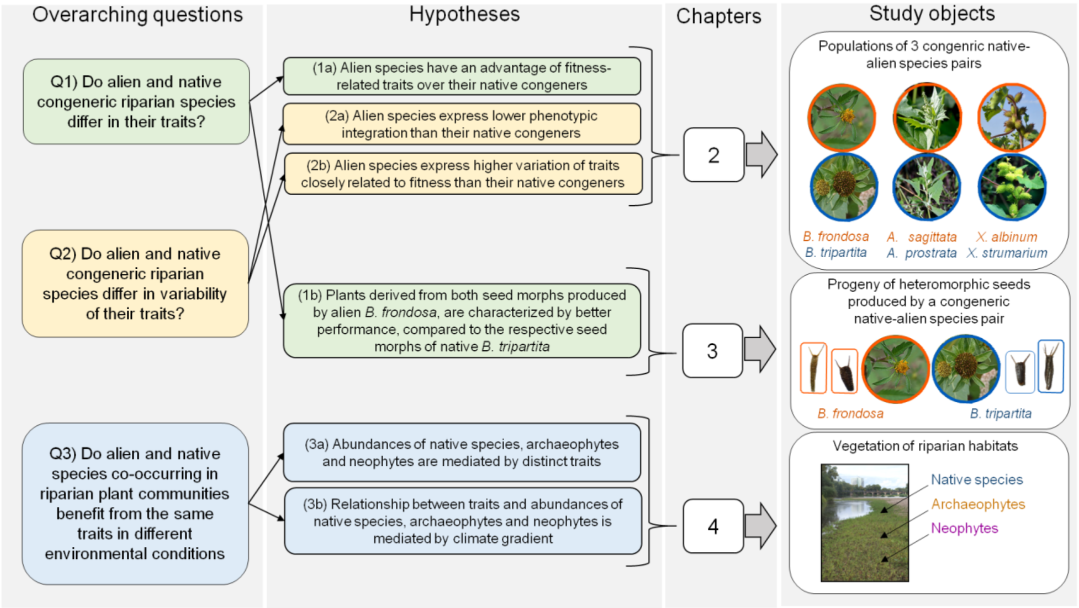

Fig. 1. Short summary of the studies conducted within framework of this thesis. Species status is marked by colors: native-blue, alien-orange. For **Chapter 4**, where alien species were additionally divided into neophytes and archaeophytes the earlier are marked in yellow, while the latter in purple.

This thesis intends to relate the importance of traits to environmental conditions, that shape riparian plant communities. Accordingly, it describes and explains trait values, their variability and role in species abundance across a wide range of habitat conditions. Hence, it contributes to a better understanding of strategies of invasive and native species in riparian communities, and may be utilized by potential management approaches.

In **Chapter 2**, I introduce three pairs of pre-selected congeneric native-alien species pairs later referred as target species, co-occurring in riparian habitats of the three Central-European river systems (Fig. 1). Specifically, I ask whether invasive alien and native species (1a) differ in terms of fitness and niche related traits, (2a) patterns and strength of phenotypic integration and (2b) magnitude of trait variation. This study contributes to a better understanding of mechanisms distinguishing native and alien congeners co-occurring under natural conditions. It addresses three aspects (*i.e*. niche differences, competitive ability, and *inter*-population variability) which are important for the success of invasive species over standing communities.

In **Chapter 3**, I present the results of a greenhouse experiment comparing performance related traits between two distinct seed morph progenies of selected invasive and native species pair (Fig. 1). I ask if (1b) congeneric invasive and native species differ in response to increased plant intra- and inter-specific plant density and if this response depends on the seed morphology, representing a colonization-competition trade-off. This chapter tests, whether performance-related traits give invasive species a constant advantage over its native congener. Moreover, it investigates whether invasive-native congeneric species adopt the same strategy to deal with competition-colonization trade-off. This study not only allowed us to compare direct effect of competition of native and invasive congeneric species, but also gave us an insight into the relevance of seed dimorphism as one of the rarely addressed sources of intraspecific variability.

In **Chapter 4**, I combined a field survey with a database approach in a multispecies study, investigating the importance of species status and traits for realized abundances of riparian plants (Fig. 1). I ask whether the importance of (3a) particular traits and (3b) environmental drivers on species abundances differ between native species and alien species. This broad approach enabled me to relate particular traits to a common measure of success in a standing plant community. Moreover, it demonstrates the importance of environmental drivers that traits-abundance relations.

In **Chapter 5**, I summarize and discuss the main results, presented in this thesis. Particularly, I highlight the links between the different chapters and put the results in the context of an overarching research question. Finally, I discuss the study obstacles and propose directions for future studies.

Study system

The study was conducted on banks of three big Central-European river systems, where all of the plant material and environmental data were collected. Each of the investigated river system comprised a main river and its tributary: Elbe with Saale, Oder with Neisse and Vistula with San (Fig. 2; Table 1). All the main rivers are parallel to each other and are characterized by a similar size and discharge (Table 1; Tockner *et al.* 2009). Although the sampled rivers are at least partly canalized, with the active floodplain limited to the area between the embankments (Fig. 2; Kucharczyk 2003; Kucharczyk & Krawczyk 2004; Tockner *et al.* 2009; Krawczyk 2014), San river is considered a braided river in a part of its course (Kucharczyk 2003; Krawczyk 2014).

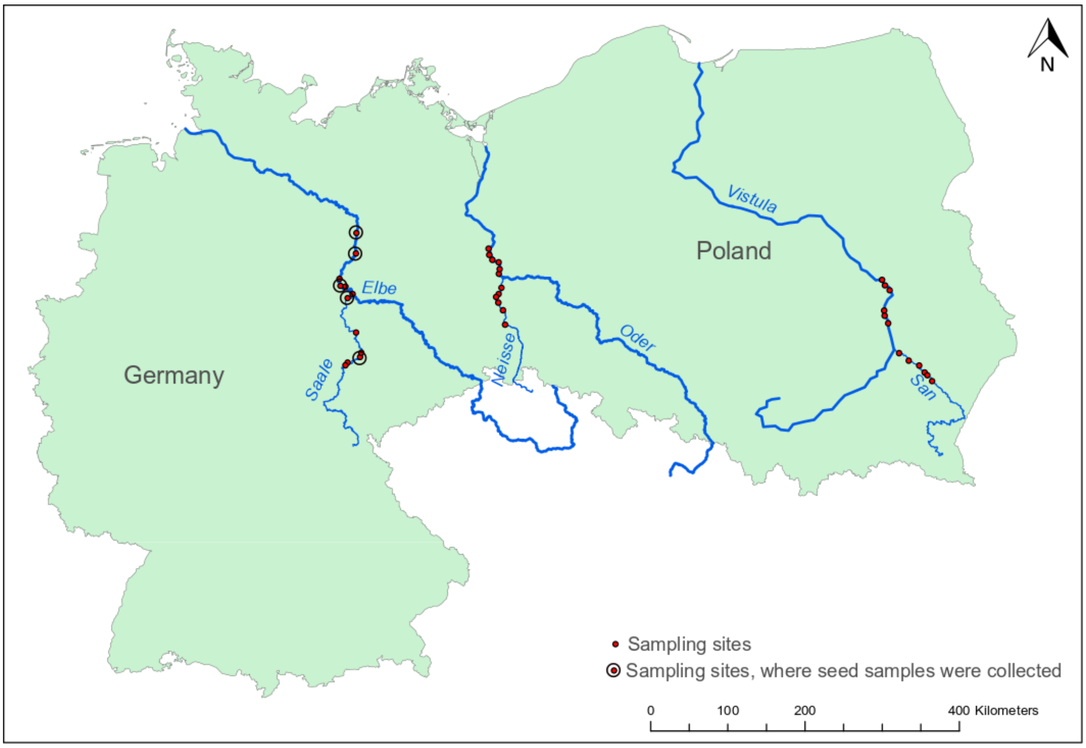

Fig. 2. Location of sampling sites on banks of rivers: Elbe with Saale, Oder with Neisse and Vistula with San. Sampling sites, where I collected vegetation samples (**Chapter 2**) and conducted vegetation survey (**Chapter 4**) are marked in red. Subset of sites, where I additionally collected seed samples (**Chapter 3**) are additionally highlighted with empty circles.

The river systems are located along a climate gradient, varying from sub-oceanic in north-west to sub-continental in south-east (Jäger 1968; Ellenberg & Leuschner 2010).

Table 1. Characteristics of rivers sampled in the study.

River	River system	Type	Length (km)	Basin area (km^2)	Discharge (m^3/s)
Vistula	Vistula-San	Main river	1,047[1]	193,960[1]	1080[1]
San	Vistula-San	Tributary	458[1]	16,877[1]	129[1]
Oder	Oder-Neisse	Main river	840[1]	119,074[1]	567[1]
Neisse	Oder-Neisse	Tributary	252[1]	4,403[1]	31[1]
Elbe	Elbe-Saale	Main river	1,094[2]	148,268[2]	870[2]
Saale	Elbe-Saale	Tributary	413[3]	24,167[3]	115[3]

*Average discharge measured at the river mouth

[1] - Statistical Yearbook of the Republic of Poland 2017, Statistics Poland.

[2] - Elbe River basin. International Commission for the Protection of the Elbe River. Retrieved 2018-03-20.

[3] - Ernst-Otto Luthardt, Reinhard Feldrapp: An der Saale. Vom Fichtelgebirge durch Thüringen bis zur Elbe. Würzburg 1990.

All types of the vegetation and soil samples used in this thesis were collected from 36 study sites, established in 2012. Study sites were evenly distributed among the 6 river systems, resulting in 6 sites on the banks of one river (Fig. 2). All the study sites were located on the river merge, not further than 3 meters from the water edge (Fig. 3). To assure that sampled plant communities are comparable, I have selected sites in areas dominated by early-successional annual plant communities: Cl. *Bidentetea tripartitae* Tx. *et al.* ex von Rochow (Fig. 3; Schubert, Hilbig & Klotz 2001).

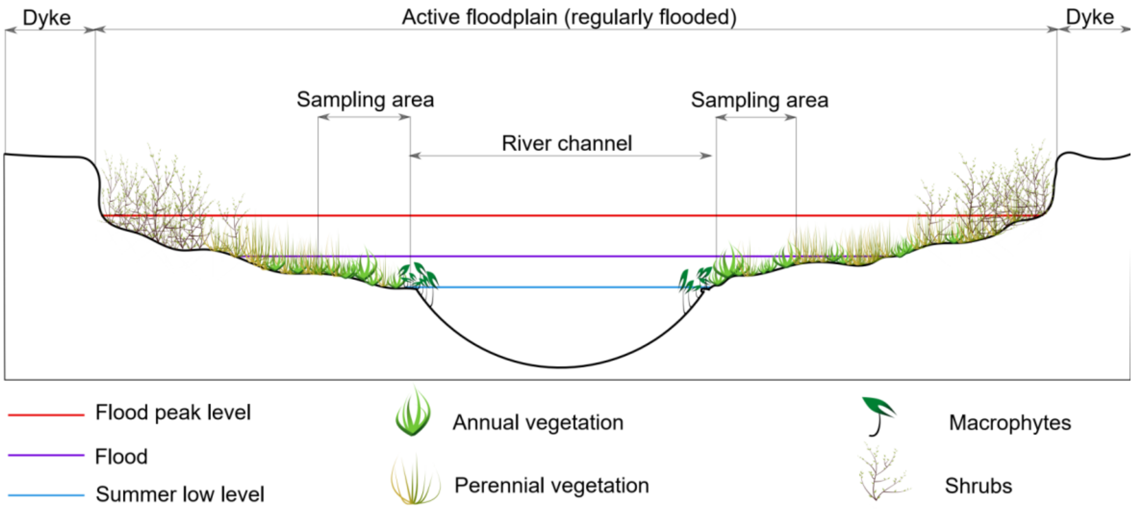

Fig. 3. Schematic representation of an exemplary site, where I collected vegetation samples and conducted a vegetation survey. Representation of riparian vegetation zones follows (Nillson *et al*. 2013).

Study species

This study is focused on native and alien plant species, co-occurring in riparian habitats. As individual chapters address different levels of organization, therefore, they also base on different sets of species.

Full number of vascular plant species occupying study sites is the object of **Chapter 4** , which also presents a full list of species recorded on the study sites (**Chapter 4**). **Chapter 2**, in turn, narrows the scope down to congeneric invasive-native species pairs, selected from species pool of riparian habitats in the study area. These species, henceforth called target species (Table 2), are all summer annuals, common in Central Europe and represent riparian communities (Kucharczyk & Krawczyk 2004; Tokarska-Guzik *et al.* 2012; FLORKART: http://www.floraweb.de/). Moreover, they share similar life strategies and possess traits which may be beneficial in riparian communities. During the establishment of sampling sites, I confirmed the presence of each of the target species in all of the three sampled river systems. Among the target species presented in **Chapter 2**, a single pair: *Bidens frondosa* L.–*Bidens tripartita* L. was used also in **Chapter 3** (compare: Study details).

Table 2. Target species used in this study and chapters in which they were addressed.

Target species	**Status**	**Chapter**
Atriplex sagttata Borkh.	Alien[1]	2,4
Atriplex prostrata Boucher ex DC	Native[1]	2,4
Bidens frondosa L.	Alien[1]	2,3,4
Bidens tripartita L.	Native[1]	2,3,4
Xanthium albinum (Widder) H. Scholz s. l.	Alien[1]	2,4
Xanthium strumarium L. s. str.	Native (a)[1]	2,4

a) Uncertainty of status: species native or archaeophyte
[1]- BiolFlor: BiolFlor plant-trait database (Klotz et al. 2002)

Adopted nomenclature

For transparency, the taxonomic and phytosociological nomenclatures, as well as definitions of floristic statuses used in this thesis follow those presented in BiolFlor (Klotz *et al.* 2002; Kühn, Durka & Klotz 2004; Schubert, Hilbig & Klotz 2001). Species status definition used in **Chapters 2** and **3** is based on the basic division for native and alien species. All the target alien species used in this thesis are naturalized and spreading in the whole study area, as well as often considered as invasive (BIOLFLOR: http://www.ufz.de/biolflor; DAISIE: European Invasive Alien Species Gateway; http://www.europe-aliens.org/, FLORKART: http://www.floraweb.de/; Tokarska-Guzik *et al.* 2012). In this thesis I refer tothem as "alien", as the studies are conducted on a large area, where different nomenclatures are applied. High number of species used in **Chapter 4** enabled me to additionally distinguish two subgroups of alien species: (i) archaeophytes (*i.e.* plants species introduced before 1492 - colonization of the Americas by Europeans) and (ii) neophytes (*i.e.* plants introduced after 1492) (Rejmánek 2000; Brunzel *et al.* 2009; Zając *et al.* 2009). To highlight this difference, **Chapters 2** and **3** I refer to the species status, while **Chapter 4** applies the term 'origin' instead.

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Chapter 2.

Trait means, rather than phenotypic integration or trait variation distinguish annual alien plant species from their native congeners.

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Abstract

Studies investigating traits of alien and native species not only inform about determinants invasion success, but also improve our understanding of species responses to environment. Traits related to superior performance and high plasticity are generally considered to facilitate invasions. However, fitness and niche relations of species can be altered by functional traits and their variability. Correlation patterns among traits, *i.e.* phenotypic integration, in turn, modify species response to environment because they affect trait coherence and plasticity. Comparative studies rarely consider these aspects jointly; although their combined effect can change interactions between invading and resident species.

We compared mean values of traits related to plant performance and biomass allocation, as well as their integration and the partitioning of their variances, using three congeneric alien-native species pairs as study system. These species co-occur in natural riparian ecosystems of three big river systems in Central Europe. We hypothesized that fitness-related traits show consistent differences between alien and native species, while biomass allocation will vary among populations of either native and exotic species in response to environmental conditions. Accordingly, we expected phenotypic traits of alien species to be less integrated then traits of native species.

Alien species showed higher values of plant height, total biomass as well as stem biomass ratio. Native species, in turn, had higher SLA and allocated more biomass to leaves. Although the two species in each congeneric pair differed significantly from each other in phenotypic integration, these differences were not consistent according to native versus alien status. On average, the largest portion of trait variances was attributed to variation among individuals within populations, rather than to variation among river systems, rivers or populations. Still, in contrast to our expectations, within-population variance showed no significant differences between native and alien species.

Taller plant stature and higher biomass can contribute to a competitive advantage of invaders, but differences in SLA as well as in the biomass allocation may mitigate their negative effects on native congeners. Although observed variance patterns could be a result of high environmental heterogeneity and long residence of invaders, differences in phenotypic integration suggest that the species may also vary in strength of responses

to environmental conditions. Yet, trait means were much more important than trait variation in differentiating alien and native species, and are likely to influence interactions among these species in their shared habitat.

Introduction

Biotic invasions represent an important component of global change (Vitousek *et al*. 1997) and a major threat to global biodiversity (Mack *et al*. 2000; Vilà *et al*. 2011). Simultaneously, they provide a rare opportunity to broaden our knowledge of mechanisms shaping interactions between species and their environment (Elton 2000; Sax *et al*. 2007). Knowledge on the processes behind invasions may consequently facilitate predictions of future invasions (Richardson & Pyšek 2008; Kumschick *et al*. 2015). A wide range of factors, like propagule pressure, abiotic conditions or between-species interactions is known to affect invasion success of exotic species in invaded habitats (Alpert *et al*. 2000; Theoharides & Dukes 2007). Still, according to various theories (see MacDougall *et al*. 2009; Catford *et al*. 2009 for a review), biological invasions are at least partly determined by convergence and/or divergence of characteristics between invading and resident native species.

Success of alien species can sometimes be attributed to a set of traits, which, according to modern coexistence theory (Chesson 2000; MacDougall *et al*. 2009), relate either to competitive advantage of successful invaders over native species, to niche differences between them, or to both. Fitness advantages that favor dominance of invaders (Graebner *et al*. 2012; Sendek *et al*. 2015) eventually lead to competitive exclusion of native species (Čuda *et al*. 2015) and prompt the most impactful invasions (MacDougall *et al*. 2009). Consequently, high values of fitness-related traits, like stature, SLA, growth rate and fecundity, are often related to superior performance and competitive success of invasive species (Pyšek & Richardson 2008; van Kleunen *et al*. 2010), but see (Daehler 2003). An ability to utilize previously untapped niche dimensions, in turn, reduces competition for limiting resources and favors establishment of invaders, as well as their coexistence with resident species (Davis *et al*. 2000; Shea & Chesson 2002). Relevance of particular traits is however strongly dependent on environmental conditions (Alpert *et al*. 2000; Chytrý *et al*. 2008) and invasion stage (Dawson *et al*. 2009). Because of spatial variation in environments of the invaded area, an increased ability of species to adjust their responses to a range of conditions, either by phenotypic plasticity and/or by genetic differentiation, can facilitate invasions (Hamilton *et al*. 2005). Attributes, such as biomass allocation, can affect invasiveness indirectly by optimizing resource uptake and compensating for weaker performance in unfavorable conditions (Sultan 2000; Poot & Lambers 2003). For example, altered biomass investment to roots and leafs allows alien species to overcome water or light limitations more efficiently than native plants (Feng *et al*. 2007; Meyer & Hull-Sanders 2008).

In addition, processes resulting from invasion history e.g. hybridization, genetic drift or changes in selection regimes may also affect variability of traits (Amsellem *et al.* 2000; Bossdorf *et al.* 2005; Davidson *et al*. 2011). As a consequence, patterns and sources of trait variability can differ between native and alien species. For instance, it is often suggested that alien species should express higher phenotypic plasticity than native species, while genetic diversity should be in turn higher in native species (Richards *et al*. 2006; Funk *et al.* 2008; Davidson *et al.* 2011). Phenotypic plasticity can promote acclimatization and dominance of alien species by mitigating initial reduction of genetic diversity (Amsellem *et al.* 2000; Sakai *et al.* 2001), expanding ecological niches (Sultan 2001) and maintaining dominance of invaders across multiple habitats (Sultan 2000). According to the concept of the ‘ideal weed’ (Baker 1965), performance of successful invaders should be superior across a wide range of habitats. This fitness homeostasis can be preserved in unfavorable conditions by adjusting niche-related attributes, like biomass allocation (Rejmánek *et al*. 2005; Ruprecht *et al.* 2014). In particular cases plasticity may however turn out to be maladaptive (Valladares *et al.* 2007; Davidson *et al*. 2011) and thus disadvantageous. Accordingly, various studies report lack of differences in trait variability between alien and native species (Godoy *et al*. 2011 and references therein).

The inconsistency in results delivered by studies on both trait means and phenotypic plasticity (Daehler 2003; Pyšek & Richardson 2008; van Kleunen *et al*. 2010) indicates that the phenomenon of biotic invasions is much more complex than it was originally assumed (Theoharides & Dukes 2007). As the success of introduced exotic species is strongly dependent on a range of environmental conditions (*e.g*. Molina-Montenegro *et al*. 2012; Franzese & Ghermandi 2014), it is unlikely that a single mechanism underpins invasiveness (Daehler 2003; Theoharides & Dukes 2007). Especially in natural communities, where species responses are driven by numerous selective pressures (Levine *et al.* 2003; Pyšek 2012) complex patterns of traits may underlay invasiveness. For example, it is generally accepted that a species-specific response to the environment often comprises multiple traits rather than a single trait (Reich *et al*. 2003; Pigliucci 2003; Westoby & Wright 2006). Correlations between particular traits are defined as phenotypic integration (Schlichting & Pigliucci 1998; Nash Suding *et al*. 2003; Valladares *et al*. 2007). Stronger correlated phenotypes may more accurately respond to environmental factors (*e.g.* Gianoli & González-Teuber 2005). On the other hand, correlations between particular traits can constrain their plastic responses to environmental changes (Gianoli & Palacio-López 2009) preventing species from a negative effects of maladaptive plasticity. Consequently, a trade-off between integration and plasticity illustrate a compromise between plant flexibility and coherence (Matesanz *et al.* 2010). To date, only few studies investigating biotic invasions have focused on multiple traits (*e.g*. Küster *et al*. 2008), their interactions and link with phenotypic plasticity (*e.g*. Hornoy *et al.* 2011; Godoy *et al.* 2012). As a consequence, their collective effect on performance of alien and native co-occurring species remains unclear (Pigliucci 2003; Gianoli & Palacio-López 2009; Matesanz *et al.* 2010). Furthermore, most of the multispecies, comparative studies published so far were based on literature surveys and trait databases rather than field measurements. Hence, they did not consider intraspecific trait variation in response to realistic environmental conditions which may even obscure interspecific differences (Siebenkäs *et al.* 2015).

Here, we simultaneously examined trait means, phenotypic integration and patterns of trait variation of alien-native congeneric species pairs. As a study system, we used three pairs of species, co-occurring in annual riparian communities of three big European river systems. The present field study is based on a total of 127 local populations embedded in a hierarchical structure of three river systems, located across a broad geographical range and a wide spectrum of field conditions (Fig. 1). Our goal was to test whether alien and native species differ in terms of individual fitness- and niche-related traits as well as in patterns and strength of phenotypic integration. Furthermore, we aimed to assess the magnitude of trait variation and its decomposition between river systems, rivers, populations and individuals. Based on coexistence theory (MacDougall *et al.* 2009) and the concept of the 'ideal weed' (Baker 1974), we hypothesize that while alien species have (a) an advantage in fitness-related traits, they would also express (b) lower phenotypic integration and accordingly (c) higher variation of traits less closely related to fitness, in particular biomass allocation.

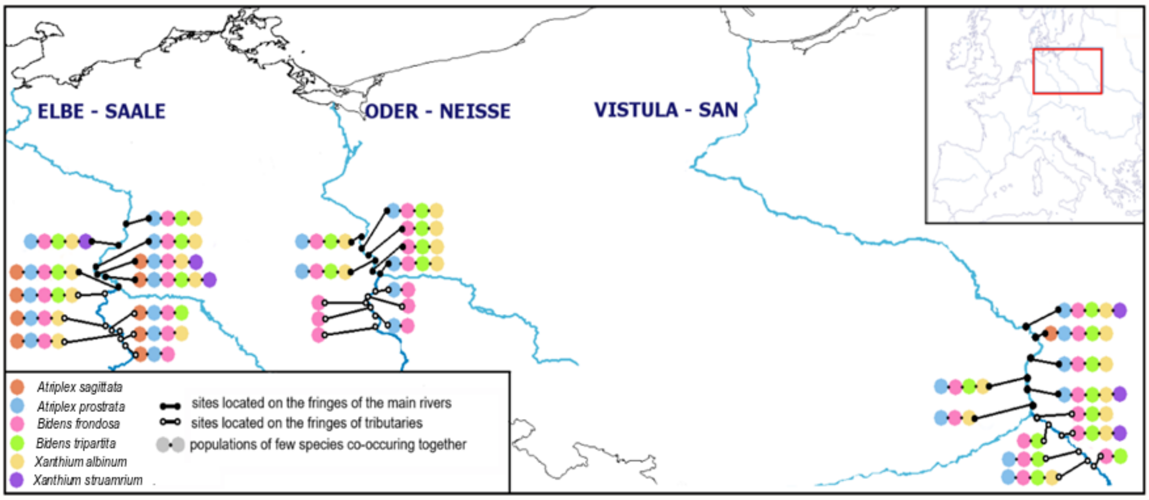

Fig. 1 Locations of study sites on river banks of three big European rivers and their tributaries: Elbe with Saale, Oder with Neisse and Vistula with San. Populations of investigated species occurring on each site are marked with different colours.

Materials and methods

Study species

We selected three congeneric, alien-native pairs of annual species: *Atriplex sagittata* Borkh. (alien) - *Atriplex prostrata* Boucher ex DC. (native), *Bidens frondosa* L. (alien) - *Bidens tripartita* L. (native), and *Xanthium albinum* (Widder) H. Scholz s. l. (alien) - *Xanthium strumarium* L. s. str. (native). We aimed at species pairs which are widespread in Central Europe and common in annual riparian communities (Kucharczyk & Krawczyk 2004; Tokarska-Guzik *et al.* 2012; FLORKART: http://www.floraweb.de/). The investigated species share similar life histories (Kühn *et al.* 2004; BIOLFLOR: http://www.ufz.de/biolflor). Furthermore, they frequently co-occur at the same sites (Fig. 1). All of the selected alien species are furthermore comparable regarding their invasion stage, as they are naturalized and spreading (Gruberová *et al.* 2001; Mandák 2003). Thereby, we avoided confounding effects of life form, adaptations to different habitats, or of different invasion stages (van Kleunen *et al.* 2010).

Selected traits

In this study, we focus on two types of plant characteristics: fitness- and niche-related traits. The first group includes traits often associated with growth and superior performance of alien species, i.e. plant height, plant biomass, specific leaf area (SLA) and propagule mass (Grotkopp & Rejmánek 2007; Graebner *et al.* 2012). The second group comprises biomass allocation to supportive, photosynthetic and reproductive organs, specified here as stem, leaf and reproductive fractions. We consider biomass allocation primarily as niche-related traits, because it represents the ability of plants to capture and utilize available resources (Poorter & Nagel 2000; Poorter *et al.* 2012), and by promoting adaptation to abiotic and biotic conditions it may facilitate spread of alien species (Feng *et al.* 2007). We are aware, however, that the relationship of single functional traits to fitness differences or to stabilizing niche differences is often ambiguous (Kraft *et al.* 2015).

Data collection

The fieldwork was conducted in annual plant communities, located in riparian zones of 3 big central European rivers and their 3 tributaries: Elbe with Saale, Oder with Neisse and Vistula with San (Fig. 1). Each main river with its tributary is further referred to as a river system. On the fringes of each of the 6 rivers, we chose 6 sites (a total of 36 sites) representing the riparian annual plant community (Fig. 1). Minimum distance among two neighboring sites was approximately 2.3 km. Individuals of a given species growing on a particular site are considered a local population. Within each population of every species, we randomly selected 3 to 5 individuals. Before harvesting selected plants, we measured their height and recorded the area of 4 fully expanded leaves, by flattening them in a plastic poach and taking a perpendicular photography (Nikon D90). Thereafter, measured leaves were dried and weighted in the same way as the rest of biomass Total plant biomass was divided into leaf, stem and reproductive fractions, dried at 60^{o}C for 48 hours and weighted. Leaf area was thereafter estimated using ImageJ software (Abramoff *et al.* 2004). Leaf, stem and reproductive ratios were calculated on the basis of dry biomass, as ratios of respective fraction mass to the remaining biomass.

Statistical analysis

All analyses were conducted using the statistical software SAS (ver. 9.4) (Institute 1985) and R (ver. 3.0.2) (Team 2015). In the first step we performed a trait-by-trait analysis using a generalized linear mixed model (SAS, GLIMMIX procedure) with status and species nested within status as fixed effects. As random effects we included in the model: genus, in order to account for the phylogenetic structure of our data; river system, river nested within river system, and site nested within river to account for the geographic structure of the sampling design; and population nested within species to account for the population-level sampling. The significance of fixed factors was tested using type III sum of squares. For total biomass, plant height, SLA and propagule mass we applied a model with lognormal distribution, while for stem, leaf and reproductive ratios, we applied a model with Gaussian distribution to the log transformed data. The natural logarithm of these ratios is identical to a logit transformation of the respective proportions, which is generally recommended to normalize non-binomial proportional data (Warton & Hui 2011).

To compare pattern and strength of phenotypic integration of traits between alien and native congeners, we pooled all individuals across populations, rivers and river systems. Correlations between separate traits were calculated as Pearson product-moment correlation coefficient (SAS, CORR procedure). We applied logarithmic transformation to meet the requirements of normality. To quantify the strength of phenotypic integration, we calculated the geometric mean of squared correlation coefficients (*i.e.* of the coefficients of determination R^2) of all trait combinations for each species (Pigliucci *et al.* 1991). Means and confidence intervals were obtained by bootstrapping (R, boot function) (Canty & Ripley 2008). Because of different sample sizes, caused by unequal occurrences of examined species (compare Fig. 1), we assessed strength of particular correlations using the absolute value of the correlation coefficient rather than by its significances. Additionally, we compared the equality of correlation matrices between congeneric species by fitting a generalized linear model (SAS, GLIMMIX procedure) which modelled the covariance directly from observational data. The unstructured covariance matrix was parametrized in terms of the correlations, and correlations were compared using general contrasts (SAS Institute Inc. (2016) , p. 3541-3548). Test of homogeneity of correlation matrices was based on restricted maximum likelihood.

Next, we explored the structure of trait variation. We estimated variance components attributable to rivers systems, rivers, populations and individuals for each species separately, using a random effects model and the restricted maximum likelihood method (SAS, MIXED procedure). As the final step, we compared intra-population variation of traits between the study species by calculating the coefficient of variation within each population. The coefficients were square-root transformed to obtain normality of residuals and subjected to a generalized linear mixed model (SAS, GLIMMIX procedure), analogue to the model applied to compare trait means.

Results

Traits and their correlations

Among the seven investigated traits, plant height, SLA, and total plant biomass as well as stem and leaf ratio differed significantly between the alien and native status (Table 1a, Fig. 2a,b,e,f,g). Individuals of alien species (*A. sagittata*, *B. frondosa*, *X. albinum*) were on average taller, had higher total biomass, albeit lower SLA in comparison to native species (*A prostrata, B. tripartita*, *X. strumarium*) (Fig. 2a,b,c,d,e). Apart from that, all of the traits with an exception of height differed significantly between particular species (Table 1a, Fig. 2b,c,d,e,f,g,h).

The correlation matrices of traits differed significantly between alien and native species for all of the congeneric pairs (Table 2, Fig. 3). The particular differences were, however, expressed in strength of correlations, rather than in their direction (Fig. 3). According to the absolute value of correlation coefficients, leaf ratio, total biomass and plant height were the strongest integrated traits. On the contrary, SLA was the weakest correlated trait among the examined species.

The overall strength of phenotypic integration among all traits, measured by the mean coefficient of determination (R^2), indicated a slightly lower phenotypic integration of alien species: *A. sagittata* (R^2=0.0189 ± 0.0003) and *B. frondosa* (R^2=0.0414 ± 0.0007) in comparison to their native congeners: *A. prostrata* (R^2=0.0457 ±0.0008) and *B. tripartita* (R^2=0.0487 ± 0.0006). This pattern was reversed in the third pair, comprising alien *X. albinum* (R^2=0.0789 ± 0.0013) and native *X. strumarium* (R^2=0.0622 ±0.0007). In general, differences in phenotypic integration between native species were much smaller than those of alien (Fig. S1).

Table 1. Results of generalized mixed effects models testing for the main effects of status and species (nested within status) on (a) individual plant traits and (b) coefficients of variation of these traits. Bold F values indicate significant effects: * P<0.05, ** P<0.01, *** P<0.001.

a) **trait means**

traits		height		SLA		propagule mass		plant biomass		stem ratio		leaf ratio		rep. ratio	
	df num	*df den*	*F*	*df den*	*F*	*df den*	*F*	*df den*	*F*	*df den*	*F*	*df den*	*F*	*df den*	*F*
status	1	83	**90.55*****	84	**30.59*****	79	2.18	84	**44.41*****	84	**29.72*****	84	**27.64*****	84	1.42
species	4	83	0.90	84	**68.68*****	79	**188.64*****	84	**37.09*****	84	**43.30*****	84	**9.57*****	84	**22.21*****

b) **coefficients of variation**

traits		height		SLA		propagule mass		plant biomass		stem ratio		leaf ratio		rep. ratio	
	df num	*df den*	*F*	*df den*	*F*	*df den*	*F*	*df den*	*F*	*df den*	*F*	*df den*	*F*	*df den*	*F*
status	1	31	0.03	31	0.09	31	0.07	31	1.68	31	0.02	31	0.67	31	0.02
species	4	31	2.02	31	2.69	31	0.71	31	2.71	31	0.81	31	5.21**	31	0.35

Table 2. Results of pairwise comparisons of trait correlation matrices of alien and native congeners.

correlation matrices	**d.f.**	χ^2	**P**
A. sagittata – A. prostrata	21	86.02	**<.0001**
B. frondosa – B. tripartita	21	52.00	**0.0002**
X. albinum – X. struamrium	21	38.45	**0.0114**

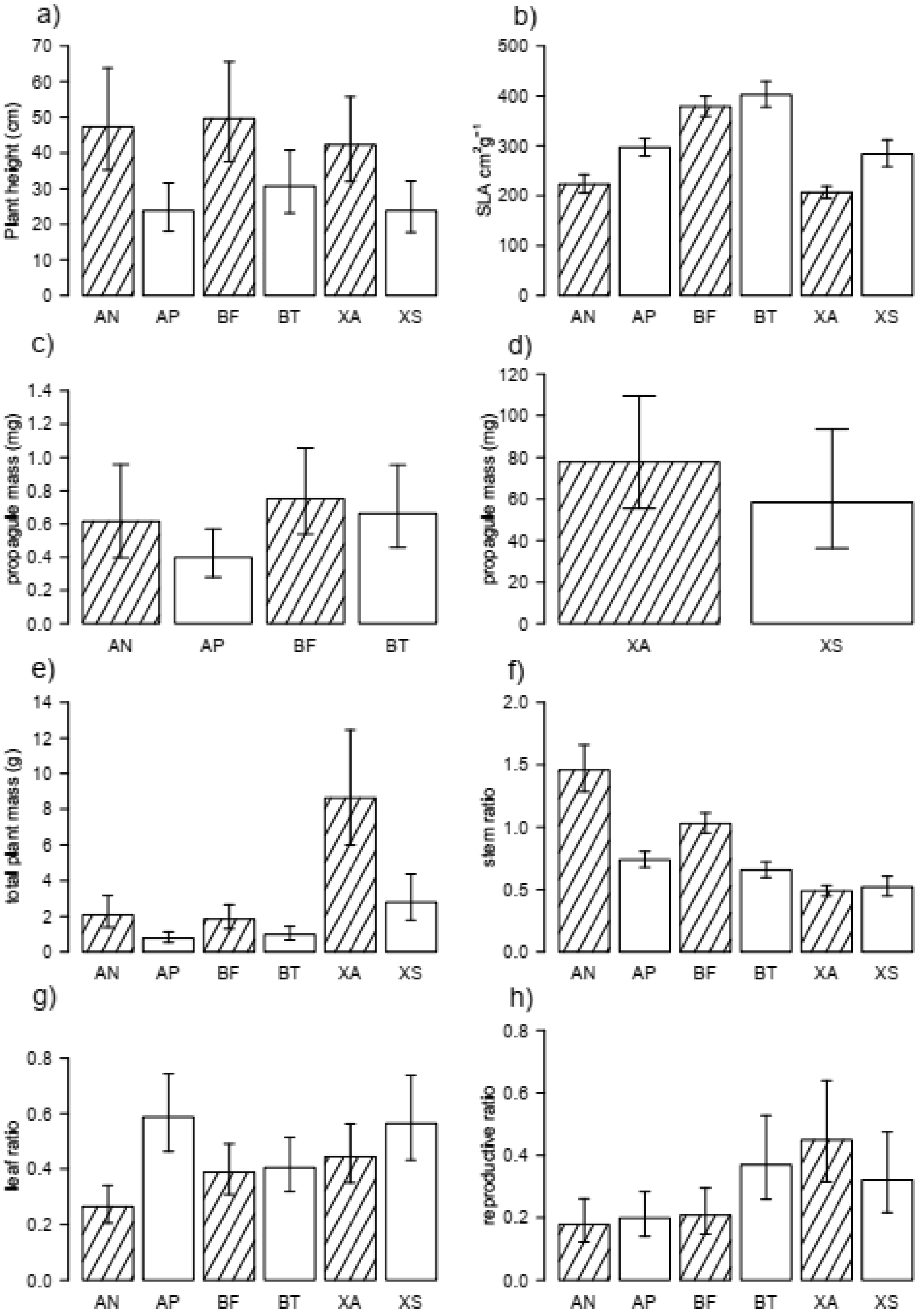

Fig. 2 Average values (means ± SE) of functional traits of alien and native congeneric species pairs: a) plant height, b) specific leaf area (SLA), c) propagule mass of *Atriplex* and *Bidens* species, d) propagule mass of *Xanthium* species, e) total plant mass, f) stem ratio, g) leaf ratio, h) reproductive ratio. Species abbreviations: AN – *Atriplex sagittata*, AP- *Atriplex prostrata*, BF – *Bidens frondosa*, BT – *Bidens tripartita*, XA – *Xanthium albinum*, XS – *Xanthium strumarium*. Alien species are marked by shading.

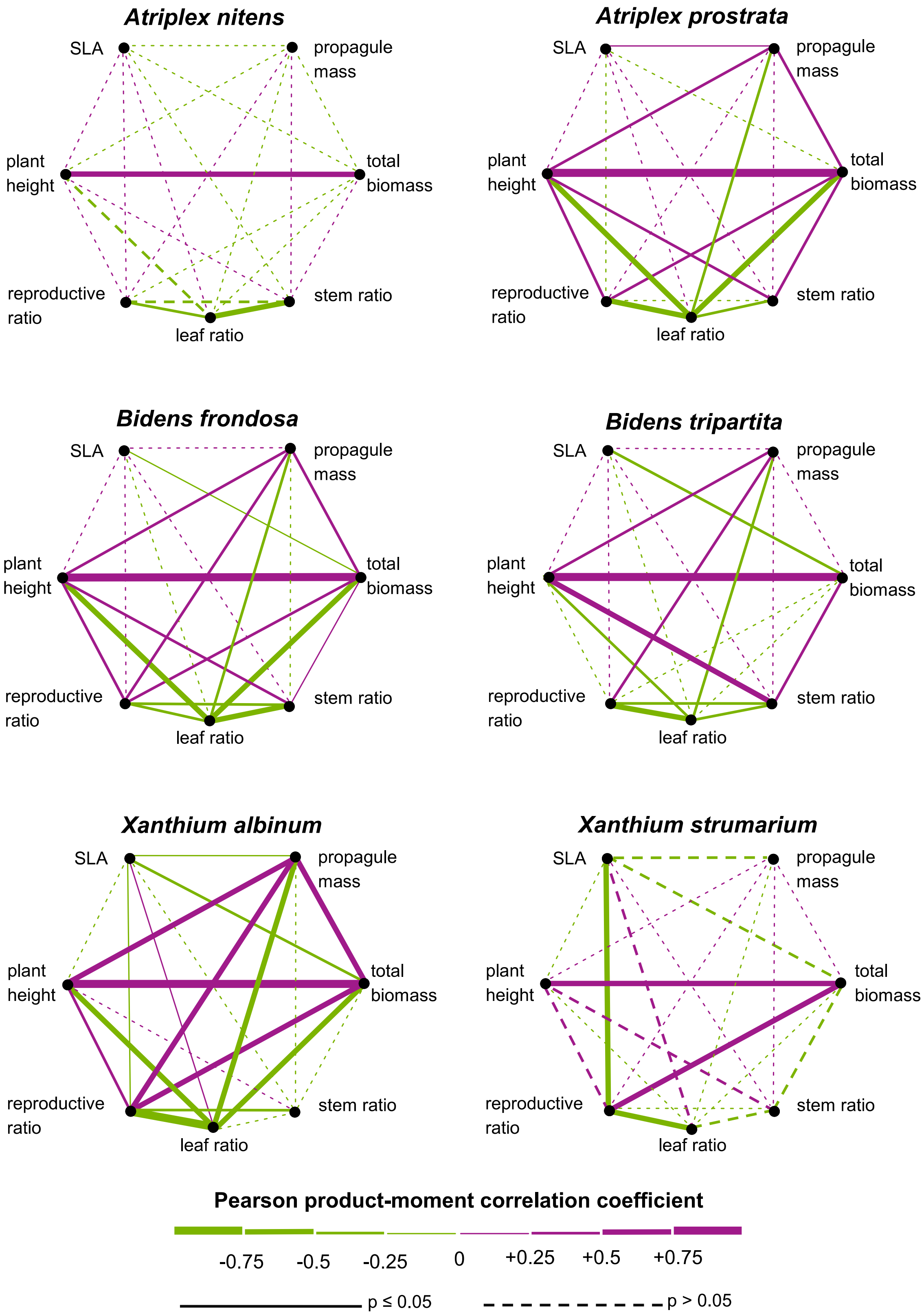

Fig. 3. Patterns of phenotypic integration represented as correlation structures among investigated traits. Strength of correlation is indicated by thickness of the lines. Direction of correlations is depicted by colours: magenta for positive and chartreuse for negative values, while significance (P<0.05) is indicated by solid lines.

Trait variation

Particular species and traits revealed different patterns of variance decomposition among river systems, rivers, populations and individuals (Table S1, Fig. 4). Nevertheless, the contribution of between-individual variation was the highest, averaging at 57% across all species and traits. River systems, followed by populations and rivers explained on average 21%, 12% and 10% of total variation, respectively.

Variance decomposition pattern of *Atriplex sagittata* was strongly uneven and highly variable among the different traits. Averaged across traits, the biggest fractions of variance were explained by river systems (47%) and rivers (14%), with a very low contribution of population component (2%). Furthermore, leaf ratio was the only trait in the whole study exclusively attributed to between-individuals' variation. Variance decomposition pattern of congeneric *A. prostrata* was more balanced, as across the traits, river systems (19%), rivers (9%) and population (12%) were represented more evenly. The contribution of variance components in case of both *Bidens* species was more similar than that observed between other pairs. The most distinctive difference lied in the variation between populations, which played a bigger role in *B. frondosa* (10%) compared to 0.5% in *B. tripartita*. Still, the variance between populations reached the highest values, averaged across traits, in *X. albinum* (32%). In comparison, most of the variation in its native congener *X. strumarium* was allocated to river systems (28%).

Within-population variability of traits, represented by coefficients of variation, did not differ between alien and native species. Moreover, among-species differences within each status were significant only for leaf ratio (Table 1b).

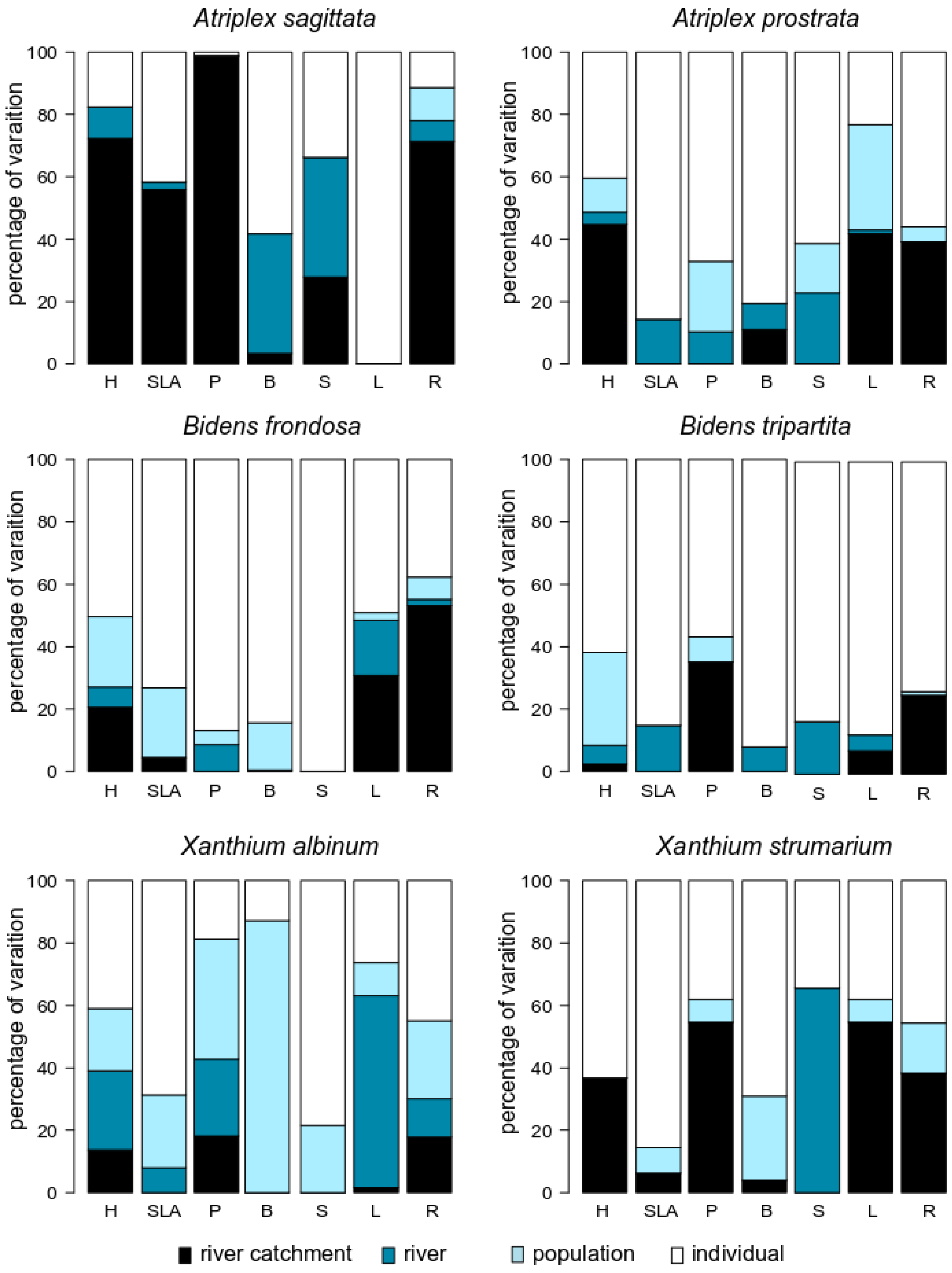

Fig. 4. Proportions of total variance attributed to river systems, rivers, populations and individuals, for all functional traits of alien and native congeneric species pairs. Trait abbreviations: B – total biomass, SLA – specific leaf area, H – plant height, S – stem ratio, L – leaf ratio, R – reproductive ratio, P – propagule mass.

Discussion

We combined three approaches to compare co-occurring alien and native riparian plant species. Firstly, we studied means of individual plant traits. According to our expectations, we found higher mean values of plant height and total biomass in the three alien species compared with their native congeners. Native species were, in turn, characterised by higher SLA. Correspondingly, alien plants allocated more biomass to stems, whereas native plants, to leaves. Second, we focused on phenotypic integration, represented as among-trait correlations. Although coefficient of determination and comparison of correlation matrices indicated differences between species within each congeneric pair, neither the patterns nor the strength of correlations showed consistent patterns with respect to the alien versus native status of species. Third, we compared patterns of variation of traits of alien and native species. Variance components attributable to river systems, rivers, populations and individuals did not express a consistent pattern across species and traits. Surprisingly for us, the degree of within-population variation was similar for alien and native species for all the examined traits.

Traits and their correlations

Congeneric alien and native plant species differed in fitness-related traits: plant height, total biomass and SLA. High mean values of these traits enhance plant growth, competitive ability and fecundity (Grime 1973). In addition, they are essential in riparian communities dominated by fast growing annuals (Pyšek & Prach 1996), where investigated species were sampled. Alien species showed higher values of plant height and total biomass, complying with a rapid growth strategy often attributed to them (Grotkopp *et al.* 2002; Grotkopp & Rejmánek 2007). The main exception from this trend was SLA, which was significantly lower in case of alien species. This unexpected result can, however, be explained by lower stature of native plants compared to invaders (Table 1a, Fig. 2a, field observation), which can lead to an increase of SLA as a response to shading (*e.g.* Sack 2004; Siebenkäs *et al.* 2015). In contrary to other fitness-related traits, propagule mass did not differ between alien and native status, despite big differences between particular species. Seed mass represents a trade-off between dispersal abilities and seedling performance (Jakobsson & Eriksson 2003). For instance, producing heavy seeds can improve seedlings' growth and survival in heterogeneous habitat (Moles & Westoby 2004) or under intense competition (Jakobsson & Eriksson 2003; Coomes & Grubb 2003), while simultaneously reducing seed dispersal (Dubois & Cheptou 2012). Consequently, comparable propagule mass of congeneric species indicates that dominance in stature and biomass of alien species is not underpinned by an advantage at seedling stage provided by higher seed provisioning (Turnbull *et al.* 2004). However, it also indicates a resemblance of colonization-competition strategy between the two species within each genus. Biomass partitioning reveals a higher investment to stems in alien species and to leaves in native ones, a difference which corresponds to the above-mentioned differences in fitness-related traits. Patterns of biomass allocation reflect adaptation of biomass production to environmental conditions (Rubio *et al*. 1995). Shifts in investment between different partitions can therefore affect performance and coexistence of species (Bessler *et al.* 2009), and consequently modulate the outcome of invasions (Pattison *et al.* 1998; Bastlova & Kvet 2002; Zheng *et al.* 2009). Coexistence theory implies a differential but complementary effect of fitness- and niche-related traits on invasion success: higher values of fitness-related traits should lead to competitive dominance of alien species, while differences in niche-related traits between alien and native species should facilitate their coexistence (MacDougall *et al.* 2009). Our findings confirm the superiority of alien over native species in plant height and total biomass, which along with similarities in propagule mass may lead to competitive exclusion of native species. Still, differences in biomass allocation along with higher SLA of native species may also suggest differing strategies of light acquisition, or in other terms niche differentiation with respects to light, which may possibly promote coexistence among examined species (Chesson 2000). However, whether trait differences relate either to fitness differences or stabilizing niche differences is often obscure (Kraft *et al.* 2015). This may also apply to biomass allocation as it may drive competitive dominance as well (*e.g.* Bastlova & Kvet 2002).

Patterns of phenotypic integration did not indicate major changes in direction of trait correlations between the congeneric species. For example, plant height, total biomass and reproductive ratios were generally positively correlated. Similarly, leaf ratio was consistently the most negatively associated trait. It is known that environmental filters may act as drivers of trait convergence between alien and native species (Knapp & Kühn 2012), leading to resemblance of functional traits (Bruno *et al.* 2005; Sax *et al.* 2007). In the same way, selection may favour species with specific relationship between traits (Pigliucci 2003). Consequently, resemblance of correlation pattern as well as propagule mass may suggest a filtering effect of the environment. Alien and native species in all examined pairs, however, differed in strength of phenotypic integration. But in contrary to our expectations, there was no homogenous shift into weaker integration of alien species. Less integrated phenotypes may be more plastic, as the loose relations between traits do not limit variation (Gianoli & Palacio-López 2009). Their adaptive response to changes in environmental conditions may, however, be less efficient (Schlichting 1989; Waitt & Levin 1993; Gianoli 2004). Correspondingly, phenotypic integration is known to increase with environmental stress (Waitt & Levin 1993; Gianoli 2004). (Hornoy *et al.* 2011) showed that in accordance with EICA Hypothesis (Blossey & Notzold 1995), between-trait correlations can be weaker in alien populations as a result of release from natural enemies. However, number of herbivores feeding on alien species may increase in time after introduction (Schultheis *et al.* 2015). Invaders used in this study are long established (Tokarska-Guzik *et al.* 2012), and emerging biotic interactions might strengthen between-trait correlations to a level observed in native species. Nevertheless, consequences of differences in phenotypic integration are still poorly understood and require further studies (Pigliucci 2003).

Trait variation

Patterns of variance decomposition were species and trait specific. Still, a major fraction of variance was explained by within-population differences. This study was focused on quantifying trait differences and total phenotypic variation, as measured in situ. As a consequence, we were unable to distinguish between the two sources of variability, *i.e.* genetic variation and phenotypic plasticity. Phenotypic plasticity is defined as a capacity of a given genotype to render differing phenotypes in response to environmental conditions (Valladares *et al.* 2006) and it may be most prominent where environmental conditions differ the most, i.e. between populations, rivers or river systems. Genetic variance can, in turn, be attributed to all of the hierarchical levels covered by our study. Riparian environments are one of the most heterogeneous habitats, where numerous stressors can affect plants simultaneously (Naiman *et al.* 2005). We therefore suggest that the strong differences between species and traits observed in our study can emerge as a result of joint activity of multiple drivers, affecting plant traits at different scales. Furthermore, it is likely that environmental heterogeneity within sites may have caused the large within-population variation of many traits.

In contrast to our assumptions, within-population trait variation did not consistently differ between alien and native species. Despite their potentially low genetic diversity (Marchini *et al.* 2016), alien species are often characterized by wider niche and higher plasticity (Baker & Stebbins 1965; Funk *et al.* 2008). Although high phenotypic plasticity is hypothesized to enable alien species to colonize novel environments (Schlichting 1986) or outcompete existing vegetation (van Kleunen & Richardson 2007), the generality of this statement is disputable (Daehler 2003). One of the reasons is that importance of plasticity may vary between different stages of the invasion process, being mostly advantageous at early stages of invasion (Richards *et al.* 2006; Theoharides & Dukes 2007). Over time, selection may favour the most adequate phenotype and the initial advantage of plasticity may be lost (Ghalambor *et al.* 2007; Jump *et al.* 2009). Alien species used in our study are naturalized and widespread over a wide geographical range (BIOLFLOR: http://www.ufz.de/biolflor, last accessed on the 21st of May 2016; Tokarska-Guzik *et al.* 2012). Furthermore, all of the investigated species are annuals and may therefore rapidly respond to selection (Jump & Peñuelas 2005; Matesanz *et al.* 2010). In addition, species occupying highly heterogeneous environments tend to express higher levels of plasticity (Donohue *et al.* 2001; Gianoli & González-Teuber 2005). Plasticity may therefore be an important adaptation of both alien and native species to riparian habitats. Hence, the lack of consistent differences in trait variation and phenotypic integration as well as biomass allocation between alien and native species can be explained by exposition to the same set of environmental factors and selection pressures.

Conclusion

In this study, we investigated differences in trait means, their integration and variances between co-occurring alien-native species pairs. Our findings demonstrate that the main factors distinguishing examined alien and native species are trait means. Differences between particular investigated traits may promote dominance of alien species, but also enhance their coexistence with closely related native species. In natural communities, differences in strength of phenotypic integration may affect relations between traits in response to shifts of environmental conditions. Whether this would alter particular traits and consequently between-species interactions require further investigation.

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Supplementary materials

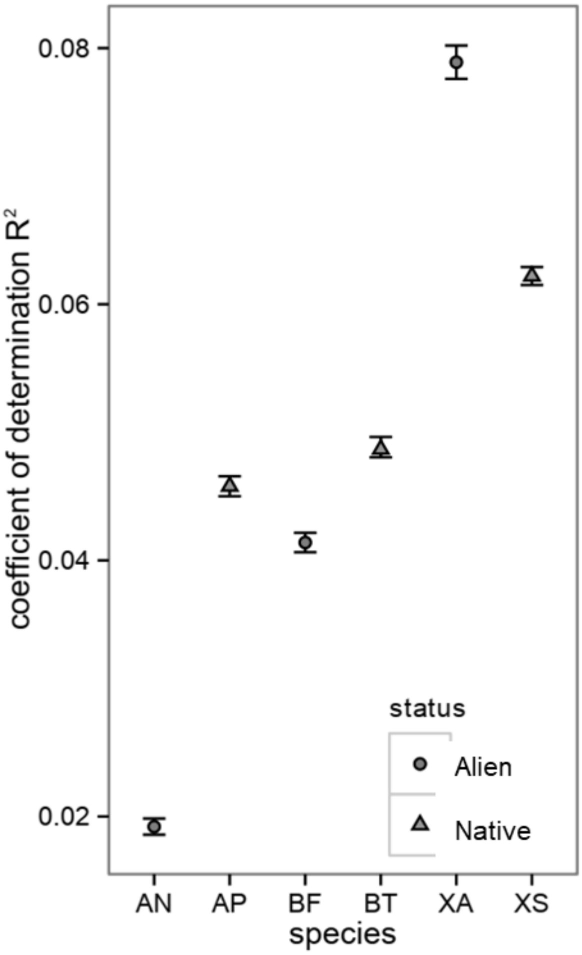

Fig. S1. Coefficients of determination (R^2), calculated for trait correlation matrices of investigated species: AN – *Atriplex sagittata*, AP- *Atriplex prostrata*, BF – *Bidens frondosa*, BT – *Bidens tripartita*, XA – *Xanthium albinum*, XS – *Xanthium strumarium* (Means ± SE of R2 values obtained by bootstrapping – see Materials and Methods).

Table S1. Proportion of variance of examined traits, explained by river catchment (rc), river nested within river catchment (r), population nested within river (pop) and individuals nested within population (ind).

species	**height**				**SLA**				**propagule mass**				**total biomass**			
	rs	**r**	**pop**	**ind**	**rs**	**r**	**pop**	**ind**	**rs**	**r**	**pop**	**ind**	**rs**	**r**	**pop**	**ind**
A. sagittata	72.4	10.0	0.0	17.7	55.9	2.4	0.0	41.7	98.7	0.0	0.2	1.0	3.3	38.4	0.0	58.2
A. prostrata	44.8	3.9	10.9	40.5	0.0	14.4	0.0	85.6	0.0	10.3	22.5	67.1	11.1	8.4	0.0	80.5
B. frondosa	20.5	6.5	22.5	50.4	4.4	0.1	22.2	73.2	0.0	8.7	4.5	86.8	0.0	0.4	15.1	84.5
B. tripartita	2.4	6.1	29.8	61.8	0.0	14.7	0.0	85.3	35.1	0.0	7.9	57.0	0.0	7.9	0.0	92.1
X. albinum	13.7	25.5	19.9	41.0	0.0	8.0	23.3	68.7	18.1	24.7	38.5	18.8	0.0	0.0	87.2	12.8
X. strumarium	36.8	0.0	0.0	63.2	6.3	0.0	8.1	85.6	54.7	0.0	7.3	38.0	4.0	0.0	26.9	69.0

species	**stem ratio**				**leaf ratio**				**reproductive ratio**			
	rs	**r**	**pop**	**ind**	**rs**	**r**	**pop**	**ind**	**rs**	**r**	**pop**	**ind**
A. sagittata	27.9	38.4	0.0	33.7	0.0	0.0	0.0	100	71.4	6.5	10.7	11.4
A. prostrata	0.0	22.7	15.9	61.4	41.8	1.3	33.6	23.3	39.2	0.0	4.8	56.0
B. frondosa	0.0	0.0	0.0	100	30.8	17.6	2.5	49.1	53.1	2.1	7.1	37.7
B. tripartita	0.0	16.8	0.0	83.2	7.5	5.1	0.0	87.4	25.3	0.0	1.2	73.6
X. albinum	0.0	0.0	21.6	78.4	1.6	61.6	10.6	26.3	17.8	12.4	24.9	44.9
X. strumarium	0.0	65.7	0.0	34.3	54.7	0.0	7.3	38.0	38.4	0.0	16.0	45.7

Chapter 3

Performance and responses to competition in two congeneric annual species: does seed heteromorphism matter?

Agnieszka Sendek, Katharina Herz, Harald Auge, Isabell Hensen, Stefan Klotz

Abstract

Variations in seed characteristics observed in heteromorphic species may affect various stages of their life cycles, e.g. seed dormancy, germination characteristics or even adult plant performance. Highly specialized seed morphs - described as colonizers and maintainers - exhibit a trade-off between colonization capacity and competitive traits. The performance of distinct seed morph progenies under competitive conditions, and especially in multi-species arrangements, had previously not been given much attention. In this study, we compared performance and response to competition among distinct seed morph progenies in two congeneric, co-occurring species: the invasive *Bidens frondosa* and the non-invasive *Bidens tripartita*. We hypothesized that maintainer seed morphs of both species would perform better under increased plant densities and within intermorphic mixtures, while colonizer morphs would show stronger responses to increased densities and perform relatively poorly in intermorphic mixtures. We conducted a growth trial and a greenhouse experiment which revealed that seed morph progenies differed significantly in plant height when grown without competition, while under competitive conditions such differences became less apparent. The observed pattern was more strongly pronounced in *B. frondosa*, which showed a general predominance in stature and biomass over its non-invasive congener. Although seed morphs performed equally well under competitive conditions, as reported by previous studies, increased plant height and more rapid germination can favour the maintainer seed morph on sites where vegetation is already present.

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Chapter 4

Species origin determines importance of traits for riparian plants abundance in response to environmental drivers in Central Europe.

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Stefan Klotz, Ingolf Kühn

Abstract

Questions: We ask (1) whether the importance of traits for species abundance depends on the species origin, and (2) whether these relations change across a climatic gradient.

Location: Riparian habitats of Elbe-Saale, Oder-Neisse and Vistula-San river systems, Central Europe.

Methods: We conducted a field survey to estimate identity and abundance of native and alien plants co-occurring on 36 study sites. Conditions of every site were described by climatic conditions (annual mean and range of temperature and precipitation), soil properties (C, N, pH), river system identity and distance from the river source. Each species was characterized by origin (native, archaeophyte and neophyte) and ecologically relevant plant traits (vegetative reproduction, hydrochory, seed mass, specific leaf area, and flowering duration). We used a joint modelling approach, namely multivariate regression to test the interactive effects of origin, species traits and environmental conditions on species abundances.

Results: Relations between abundances and species traits differed among species origins. Their strength and direction varied also among river systems and distance from the river source. Abundances of native species were often positively associated with SLA and with higher seed mass. Neophytes benefited mostly from vegetative reproduction, hydrochory and higher seed mass. Longer flowering period also significantly increased abundances of neophytes, however in the lower river course this pattern was reversed. Abundances of archaeophytes were negatively related to higher SLA and higher seed mass but increased with an ability to spread by hydrochory.

Conclusions: Our findings indicate that different traits are beneficial for abundances of native species, neophytes and archaeophytes. The success of both groups of alien species seems to rely mostly on traits related to dispersal. Furthermore, our findings provide evidence of strong context-dependency of relationships between abundances and traits across all the origins, river systems and along the river course. This implies that explaining success of invasive alien species in natural habitats depends not only on direct, traits-regulated mechanisms but is also modified by broader environmental settings.

Introduction

Biotic invasions are a complex phenomenon associated with numerous factors such as propagule pressure, invader attributes (e.g. range size, traits), composition of recipient community and abiotic conditions (Chytrý *et al.* 2008; Pyšek *et al.* 2015). In natural ecosystems, these drivers jointly affect the success of introduced species (González-Moreno *et al.* 2014). Therefore, a holistic understanding of invasions requires an insight into relationships between multiple mechanisms underlying the success of invasive alien species in standing plant communities (Kuebbing, Nuñez & Simberloff 2013; Kueffer, Pyšek & Richardson 2013; Gallien & Carboni 2017).

Composition and abundance of plants co-occurring in communities are mediated by functional traits (Westoby & Wright 2006) which define species strategies and reflect their niche requirements. The Habitat Filtering Hypothesis (Keddy 1992) proposes that environmental drivers, such as climatic conditions, select species with favorable trait syndromes (Diaz, Cabido & Casanoves 1998). Simultaneously, trait convergence between co-occurring species can lead to competitive exclusion of either of them (MacArthur& Levins 1967; MacDougall, Gilbert & Levine 2009). These two processes jointly determine coexistence of alien and native species in natural habitats (MacDougall, Gilbert & Levine 2009; Maire *et al.* 2012). Their importance however, varies across spatial scales, dominance structure and environmental gradients (Maire *et al.* 2012; Von Holle 2013; Gallien & Carboni 2017). For instance, under benign environmental conditions competitive interactions should dominate, while under stress facilitation should be more common (Callaway & Walker 1997; Maire *et al.* 2012; Von Holle 2013). The relevance of habitat conditions for trait divergence/convergence makes it crucial to relate observed patterns to particular environmental drivers. Native and alien species co-occurring in standing communities may respond differently to environmental drivers such as climatic or anthropogenic factors e.g. disturbance regime, land use type and intensity or human population density (Polce *et al.* 2011; Greet, Cousens & Webb 2013a; Flanagan, Richardson & Ho 2015; Brummer *et al.* 2016). For instance, alien species seem to benefit from anthropogenic disturbance (Polce *et al.* 2011; Tomasetto, Duncan & Hulme 2013) and suffer from severe climatic conditions more than natives do (Polce *et al.* 2011; Zefferman *et al.* 2015). Making valid inferences about mechanisms regulating coexistence of multiple alien and native species requires a comparison of both of them in one habitat type, against a common measure of success (Knapp & Kühn 2012; Kueffer, Pyšek & Richardson 2013). Furthermore, responses of alien species may depend on residence time (Pyšek & Jarošík 2005). For instance, mechanisms regulating range and abundance differ between archaeophytes (introduced before 1492: colonization of the Americas by Europeans) and neophytes (introduced after 1492) (Brunzel *et al.* 2009; Zając, Zając & Tokarska-Guzik 2009). Consequently, studies should also account for introduction time to assess importance of other ecological factors (Pyšek *et al.* 2005).

Riparian communities are excellent model systems for studying multiple determinants of invasion processes (Pyšek & Prach 1993; Richardson *et al.* 2007; Catford & Jansson 2014). They are not only species rich (Naiman et al. 1993; but see Sabo *et al.* 2005), but are also listed among the most heavily invaded ecosystems (Stohlgren *et al.* 1998; Richardson *et al.* 2007). Their susceptibility to invasions is related to a high level of natural disturbances, resource availability caused by seasonal floods (Richardson *et al.* 2007; Brummer *et al.* 2016), and anthropogenic alterations such as changes of strength and frequency of floods, presence of artificial constructions or intensive exploitation of riparian areas (Nilsson & Berggren 2000; Bunn & Arthington 2002; Poff & Zimmerman 2010). Native riparian plant species developed distinct strategies to survive under natural disturbance regimes (Lytle & Poff 2004; Catford & Jansson 2014). Besides physiological adaptations to inundation and physical damage (see Catford & Jansson 2014 for a review), common strategies involve long-distance water-borne dispersal by seeds (hydrochory) (Jansson *et al.* 2005; Nilsson *et al.* 2010) and by vegetative organs (Riis & Sand-Jensen 2006). Growth and seed production coinciding with flood events are other common adaptations of riparian species (Warwick & Brock 2003; Greet, Cousens & Webb 2013a). For example, fast growth and early flowering may allow species to set seeds before flooding takes place and thus to close their reproductive cycle and to promote seed dispersal (Satake, Sasaki & Iwasa 2001; Lytle & Poff 2004). Similarly, rapid growth enables them to reproduce in a short period of time as well as to quickly regenerate after floods (Lytle & Poff 2004; Catford & Jansson 2014). Fitness-related traits like high specific leaf area (SLA) are related to light acquisition, fast growth and consequently, to competitive and regeneration abilities (Gaudet & Keddy 1988; Tilman 1988). Heavy seeds facilitate seedling growth and survival, thus providing native riparian species with an advantage during the colonization of bare sediments (Willson & Traveset 2000; Xiong *et al.* 2001; Moles & Westoby 2004). As alien plants often lack specific adaptations to disturbance regimes in riparian habitats (Catford & Jansson 2014), they are strongly controlled by natural floods (Greet, Cousens & Webb 2013a; Greet, Webb & Cousens 2015). However, as fast growing generalists (Rejmánek & Richardson

1996; van Kleunen, Weber & Fischer 2010; Graebner, Callaway & Montesinos 2012), they share life-history traits with pioneer riparian vegetation and are adapted to fast recovery after flooding events (Catford & Jansson 2014). Therefore, although most alien species are not specifically adapted to riparian conditions, they are capable to successfully invade riparian communities. This process is especially intense, when effects of the natural disturbance regime are diminished by human activities e.g. river regulation (Greet, Cousens & Webb 2013a).

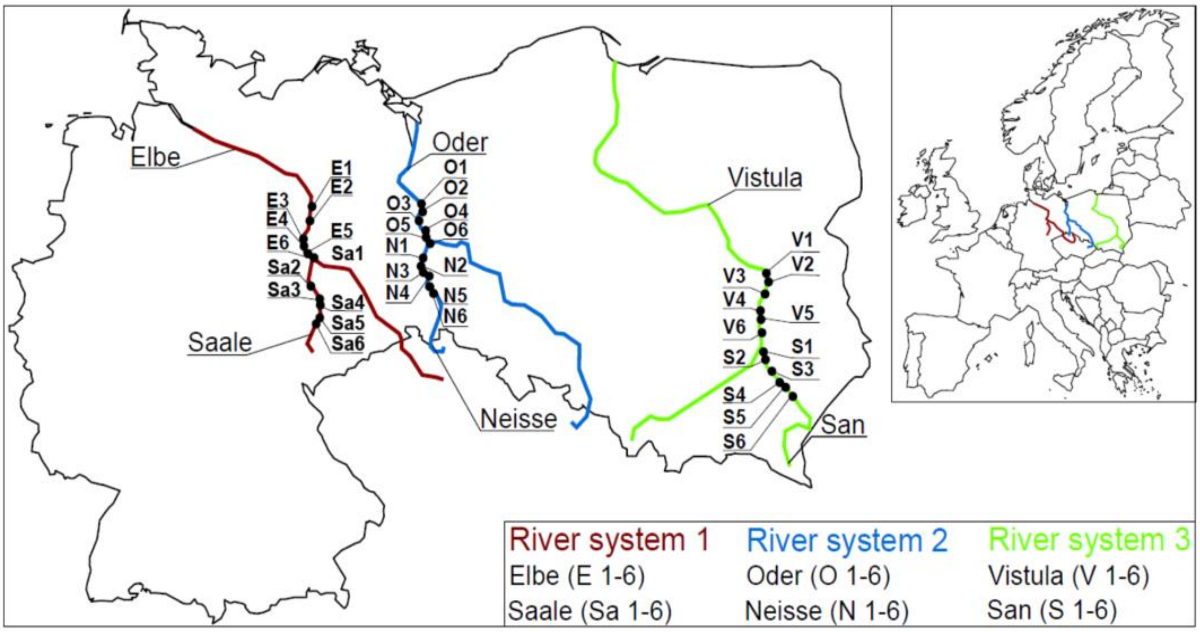
To improve our understanding of mechanisms determining invasions in riparian habitats, we investigated whether the success of alien and native species in natural communities is dependent on different drivers. Our aim was to explain abundances of co-occurring alien and native species using ecologically relevant traits under realistic environmental conditions. A large body of literature is dedicated to investigating trait dissimilarities between invading and resident species and to relating them to the invasion process (Pyšek & Richardson 2008; van Kleunen, Weber & Fischer 2010). However, conclusions are often limited by *a priori* species selection (Kuebbing, Nuñez & Simberloff 2013; Gallien & Carboni 2017), artificial experimental setup (Kuebbing, Nuñez & Simberloff 2013), or the inability to disentangle other mechanisms determining invasiveness, such as time of introduction, or introduction bias (Chrobock *et al.* 2011; Maurel *et al.* 2016). Here, we combine multivariate data of species composition, realized abundance, and traits into a single joint modelling framework (Warton *et al.* 2015; Warton, Shipley & Hastie 2015). This approach allowed us to test whether effects of traits on species abundance differ among species of different origin and residence time. Moreover, we could examine whether observed relations are consistent across riparian systems, located along a climatic gradient expressed in temperature and precipitation differences. Specifically, we ask whether native species, archaeophytes and neophytes are ecologically distinct groups and consequently, whether their respective abundances (1) will be mediated by different traits and (2) will be differently affected by the climatic gradient.

Materials and methods

Study sites and sampling

The study was conducted on the banks of 6 European rivers, grouped in three river systems: Elbe with Saale (river system 1), Oder with Neisse (river system 2), Vistula with San (river system 3) (Fig. 1, Table S1). These three river systems run almost parallel to each other from south to north (Fig. 1), together extending over approximately 280 kilometers from north to south and 750 km from east to west. Climatic conditions in this area vary from sub-oceanic in the north-west to sub-continental in the south-east (Jäger 1968; Ellenberg & Leuschner 2010). While all the examined rivers are controlled by embankments on a large part of their length (Burkart 2001; Kucharczyk & Krawczyk 2004), river San possesses some traits of braided rivers, such as forming sand pools (Krawczyk 2014).

Fig. 1. Location of 36 study sites on the bank of 6 rivers, belonging to 3 river systems in Germany and Poland (Central Europe). Colors identify river system where sampling sites (6 for each river) are located.



In August 2014, on the banks of each of the 6 rivers, we surveyed 6, approximately 800 m^2 large study sites. All of the 36 study sites were established in riparian vegetation bands, not wider than 5 m and adjacent to the riverbed. All sites were dominated by early-successional annual plant communities of the class *Bidentetea tripartitae* TX. et al. ex VON ROCHOW (Schubert, Hilbig & Klotz 2001). Geographical coordinates of the center of each study site were documented with GPS (Table S1). To describe environmental conditions of study sites, we arbitrarily collected 5 soil samples on each site. All samples from a site were mixed, air-dried for 72 hours and subsequently analysed for total soil C and N using elemental analyzer Vario EL III (Elementar Analysen Systeme GmbH, Hanau, Germany) and for pH measured in 1 M KC solution. Furthermore, we obtained information about annual mean values and annual ranges of temperature and precipitation of the study sites from the EU FP5 project ALARM (Fronzek, Carter & Jylhä 2012, Table 1, Fig. S1).

On every site, we arbitrarily selected 10 square plots of $1m^2$ each, in which we recorded the presence and percentage cover of all plant species. Both variables were always estimated by the same observer (A.S.) to the nearest 5%. To avoid pseudo replication, for every species present on a study site, we calculated its mean plant cover across plots. We determined plants to species level (for list of species see Table S2), following the nomenclature used in BiolFlor (Kühn, Klotz 2002). Of all records, 9.7% could be determined only to genus level and were not included in the following analyses.

Table 1. Variables used in the analysis, matrix in which they were implemented in the models, their type, details, sources and amount of missing values. Environmental variables not included in the initial model due to multicollinearity are indicated by (-) in the matrix column.

Variable	Matrix	Type	Details	Source	Missing values
SLA	TRAIT	Num. cont.	Specific leaf area ($mm^2 mg^{-1}$)	LEDA	4.06%
Seed mass	TRAIT	Num. cont.	Seed weight (mg)	LEDA	4.06%
Flowering duration	TRAIT	Num. cont.	Flowering length (months)	BiolFlor	0
Vegetative reproduction	TRAIT	Factor	2 levels (true/false)	BiolFlor	0
Hydrochory	TRAIT	Factor	2 levels (true/false)	BiolFlor	0
Origin	ORIGIN	Factor	3 levels (native, archaeophytes, neophytes)	BiolFlor	0
River system	ENV	Factor	3 levels (1: E+Sa, 2:O+N, 3:V+S)	Map	0
Distance	ENV	Num. cont.	Distance from the river source	GIS	0
N	ENV	Num. cont.	Total soil N	Measurement	0
C	-	Num. cont.	Total soil C	Measurement	0
pH	-	Num. cont.	Soil pH	Measurement	0
Mean temperature	ENV	Num. cont.	Mean annual temperature	ALARM	0
Mean precipitation	ENV	Num. cont.	Mean annual precipitation	ALARM	0
Temperature range	-	Num. cont	Annual temperature range	ALARM	0
Precipitation range	-	Num. cont	Annual precipitation range	ALARM	0

Abbreviations: Num. cont: numeric, continuous variable; E: Elbe, Sa: Saale, O: Oder, N: Neisse, V: Vistula, S: San
LEDA- LEDA Traitbase (Kleyer *et al.* 2008)
BiolFlor - BiolFlor plant-trait database (Klotz *et al.* 2002)
ALARM – EU FP5 project ALARM (Fronzek, Carter & Jylhä 2012)
Map - (www.google.de/maps/)

Data analysis

We investigated whether species abundance is driven by species origin, traits, and environmental variables. Origin, differentiating between native species, archaeophytes and neophytes, was obtained from the BiolFlor database (Klotz *et al.* 2002; Kühn, Durka & Klotz 2004; http://www2.ufz.de/biolflor/index.jsp) and used in the analysis as a single factor: ORIGIN. Species traits (vegetative reproduction, hydrochory, seed mass, flowering duration, SLA), obtained from the BiolFlor and LEDA (Kleyer *et al.* 2008; www.uni-oldenburg.de/en/landeco/research/leda) databases, were compiled as a TRAIT matrix (Table 1). The environmental variables (ENV) describing site conditions consisted of soil nitrogen content, mean temperature and mean annual precipitation (Table 1). To account for spatial variation among sites and the effect of river systems we included identity of river system and distance between centers of each sampling site from the river source (distance from the source). Soil carbon content, pH, temperature and precipitation ranges were strongly correlated to other variables (Fig. S2), and were excluded to avoid collinearity in the statistical model. Spearman's rank correlation coefficients between remaining predictor variables (Table S3) were weak enough $|\rho|<0.7$ to suggest that collinearity among variables does not influence model selection (Dormann *et al.* 2013). After inspecting visual representation of distribution of missing values in the TRAIT matrix (Table 1) we concluded that there was no pattern and applied a single imputation based on 100 iterations and with a predictive mean matching as a selected imputation method (Van Buuren *et al*. 2011).

To analyze abundances of all the species reported on all the study sites we used a joint modelling framework. Our approach was based on fitting a single generalized linear model to each of many response variables with a common set of predictors. Statistical significance was tested by a log-likelihood ratio statistic. The multivariate test was calculated as a sum of univariate test statistics (compare Warton, Wright & Wang 2012). Reported *p*-values were estimated by bootstrapping sites and resampling all observations (999 bootstrap samples) from a site jointly (as in Warton, Wright & Wang 2012). As the most suitable approach we used the pit-trap method, which allows to account for correlation structure among species present within each site (Warton, Thibaut & Wang 2017).

We fitted an initial model, including matrices ENV (environmental traits) and TRAIT (species traits), as well as species origin up to a three-way-interaction ENV: TRAIT: ORIGIN. The model diagnostics indicated that negative binomial error distribution, with a log-link between response and explanatory variables was best suited to our data. However, as this distribution is appropriate for counts (Bliss & Fisher 1953), we rounded up fractions obtained during averaging plant abundances per site, to the nearest integer. We transformed seed mass ($\log_{10}$) in order to linearized its relationship with species abundance

To account for an effect of regional species range size on species abundances, we used the number of grid cells occupied by species in Germany (documented in FLORKART; www.floraweb.de/) as an offset term, i.e. a component of linear predictor, whose coefficient was fixed at 1 instead of being estimated (Venables & Ripley 2002; Crawley 2012). This proxy of species range size was shown to be representative in Germany and adjacent regions (Pyšek *et al.* 2009). We simplified the model with respect to each of the environmental variables and species traits, by a backward selection of single predictors included in the fitted model. To present the effects of predictors and their interactions on abundance, we calculated partial regressions.

The data analysis was conducted in R (R Core Team 2016; R Foundation for Statistical Computing, Vienna, AT). For details of used packages and functions see supplementary materials (S1).

Results

We identified 192 plant species, classified as natives (143 species), archaeophytes (20 species) and neophytes (29 species). Frequency and contribution to the mean plant cover on site was highest for native species (highest abundance: 53% for *Phalaris arundinacea*), followed by neophytes (highest abundance: 39% for *Xanthium albinum*) and archaeophytes (highest abundance: 8% for *Chenopodium album*) (Fig. S3). Abundances of species occurring in riparian habitats were associated with both species traits (TRAITS) and environmental variables (ENV), but strength and direction of associations differed among species origins (ORIGIN) (Table 2, Fig. 2, Fig. 3).

Table 2. Effects of terms of the formula: environmental characteristics (ENV matrix), species traits (TRAITS matrix), species origin (ORIGIN) and their interactions, on species abundance. We applied likelihood ratio test (LR) to assess significance of explanatory variables. Shown-values were obtained by bootstrapping of rows (999 replications). Significant *p*-values ($p<0.05$) are indicated in bold.

Matrices	**Res. df**	**df.diff**	**LR**	***p***
TRAITS	6900	5	229.9	**0.001**
ORIGIN	6898	2	164.5	**0.001**
ENV×TRAITS	6874	24	135.8	**0.001**
ENV×ORIGIN	6862	12	63.16	**0.001**
TRAITS×ORIGIN	6852	10	171	**0.001**
ENV×TRAITS×ORIGIN	6804	48	130.4	**0.001**

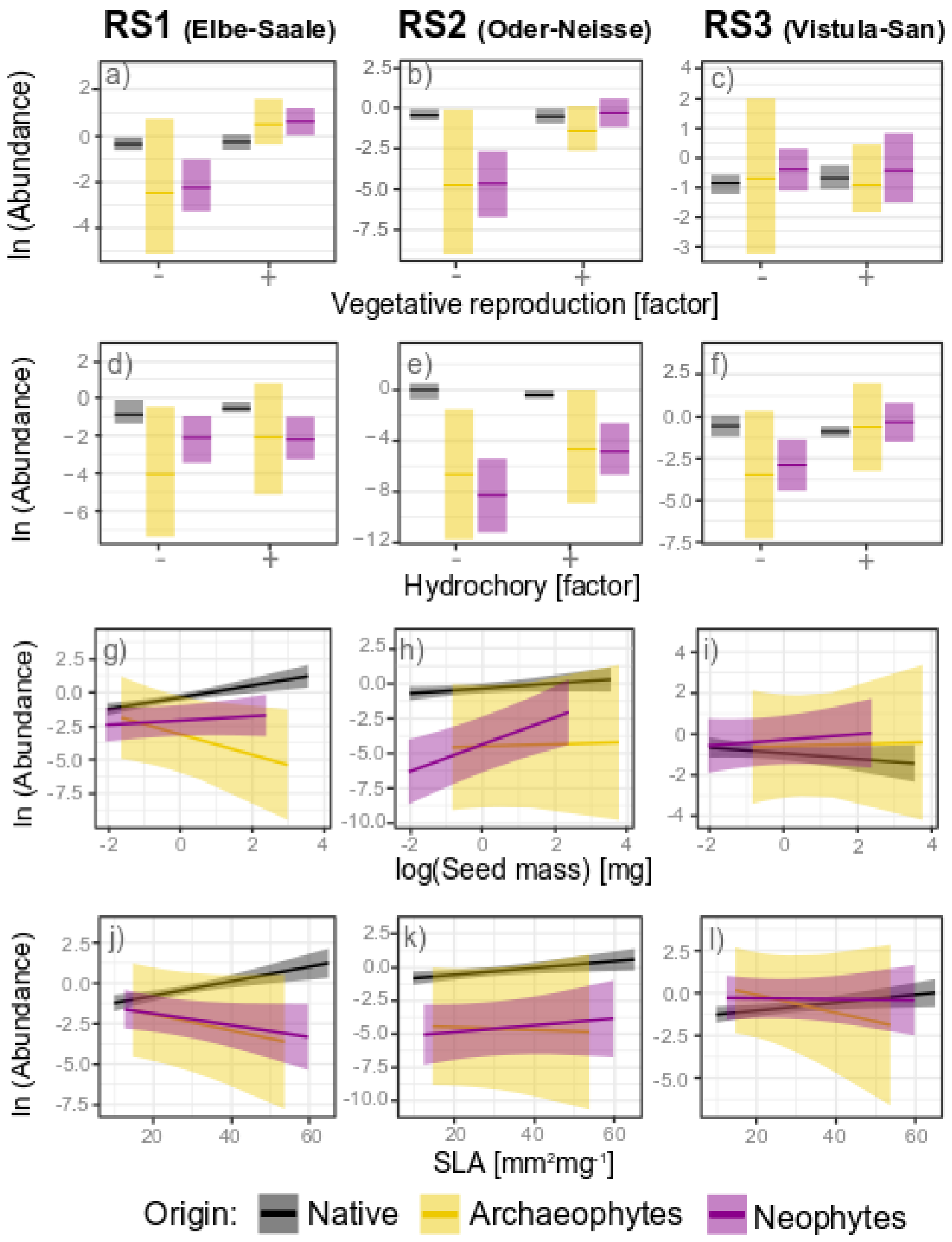


Fig. 2. Effects of vegetative reproduction (a,b,c), hydrochory (d,e,f), seed mass (g,h,i) and SLA (j,k,l) on species abundance across three examined river systems (RS1-3). Colours distinguish three origins: native species, archaeophytes and neophytes. Figures represent fitted values with 95% confidence intervals.

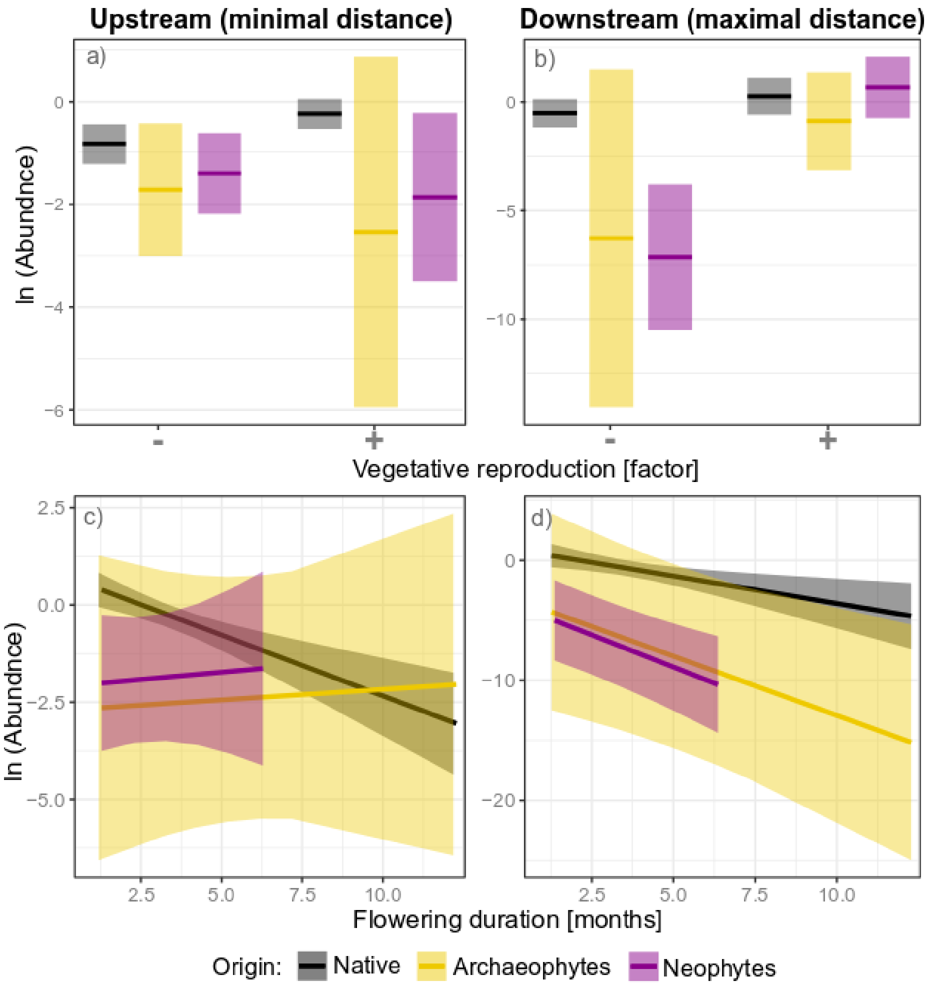


Fig. 3. Effects of vegetative reproduction (a,b) and flowering duration (c,d) on species abundance in relation to distance from the river source. Colors distinguish three origins: native species, archaeophytes and neophytes. Figures represent fitted values with 95% confidence intervals.

From the five environmental variables included in the initial model of species abundance, only river system, distance from the river source and mean annual precipitation were retained in the minimum adequate model. All of the investigated species traits remained in the minimal adequate model and interacted significantly with species origin (Table 3): Effects of vegetative reproduction, hydrochory, seed mass and SLA on species abundances varied among river systems. The ability to reproduce vegetatively was advantageous for neophytes in river systems 1 and 2 only (Table 3, Fig. 2a,b,c). The pattern was similar for archaeophytes but effects were not significant in any river system (Table 3, Fig. 2a,b,c).

Table 3. Summary of the minimal adequate model, explaining abundances of species with species origin, species traits and environmental characteristics. Values representing significance of each of multivariate terms specified in the model are based on Wald statistic (W). Presented *p*-values are obtained by bootstrapping (999 replications). For clarity, only significant terms are presented. For all results, compare with table S4.

Matrices	**Variables**	**W**	***p***
ENV	River system 2	2.866	0.018
TRAIT	Seed mass	5.05	0.001
	SLA	2.512	0.033
ENV×TRAIT	River system 2: Flowering duration	2.909	0.012
	River system 3: Seed mass	4.617	0.001
	Distance: Vegetative reproduction	2.817	0.022
	Mean precipitation: SLA	2.791	0.022
ENV×ORIGINS	River system 2: Archaeophytes	2.538	0.019
	River system 2: Neophytes	4.254	0.002
	River system 3: Neophytes	4.175	0.001
	Distance: Neophytes	2.723	0.021
TRAIT×ORIGIN	Hydrochory: Archaeophytes	2.526	0.022
	Seed mass: Archaeophytes	3.144	0.005
	SLA: Archaeophytes	2.729	0.017
	SLA: Neophytes	4.108	0.001
ENV×TRAIT×ORIGIN	RS3: Vegetative reproduction: Neophytes	3.426	0.003
	RS2: Hydrochory: Neophytes	4.025	0.001
	RS3: Hydrochory: Neophytes	4.092	0.001
	RS2: Seed mass: Archaeophytes	1.982	0.039
	RS3: Seed mass: Archaeophytes	2.812	0.002
	RS2: Seed mass: Neophytes	3.675	0.001
	RS3: SLA: Neophytes	2.356	0.050
	Distance: Vegetative reproduction: Neophytes	3.557	0.002
	Distance: Flowering duration: Neophytes	3.557	0.002

There was no overall effect of vegetative reproduction on abundance of native species. Hydrochory was, in turn, significantly beneficial for neophytes in river systems 2 and 3, while a weak positive effect on abundances of archaeophytes remained across all the river systems (Table 3, Fig. 2d,e,f). Again, the abundance of native species seemed in general unaffected by hydrochory. The effects of seed mass on the abundance of neophytes and native species were similar in river systems 1 and 3. In river system 2, however, the abundance of neophytes increased with seed mass more so than the abundance of native species (Table 3, Fig. 2g,h,i). Higher SLA was beneficial for native species, but not for archaeophytes and neophytes in river systems 1 and 3 (Fig. 2j,k,l). In addition, the effect of SLA on species abundance was positively related to an increase of mean annual precipitation (Table 3).

Distance from the river source modified the relationships of species abundances with vegetative reproduction and flowering duration. Neophytes reproducing vegetatively obtained higher abundances on sites located downstream (maximal distance), while for native species this pattern was reversed (Table 3, Fig. 3a,b). Abundances of archaeophytes behaved similarly to neophytes, however in their case the difference to native species remained not significant (Table 3, Fig. 3a,b). On downstream sites longer flowering duration was disadvantageous for all species independent of their origin (Table 3, Fig. 3c). This relation was reversed for both groups of alien species in the upstream sites (short distance) (Fig. 3c), but the difference was significant only for neophytes (Table 3).

Discussion

Our results indicate that relationships between traits and plant abundances in riparian ecosystems depend on species origin. These findings support our assumption that native species, neophytes and archaeophytes constitute ecologically distinct groups (van Kleunen, Dawson & Dostal 2011). As such, they should respond differently to environmental drivers in natural ecosystems (Knapp & Kühn 2012; Brummer *et al.* 2016). Strength and direction of observed interactions in our study were also modified by site conditions. This demonstrates the importance of context-dependency of mechanisms shaping abundances of alien species in natural ecosystems (González-Moreno *et al.* 2014). Furthermore it suggests that other aspects of biotic invasions such as propagule pressure or residence time can be similarly important for the success of invasive alien species (Pyšek *et al.* 2015).

Although our study was conducted across an apparent climatic gradient, identity of river system and distance from the river source had stronger effects on species abundances and their relation with traits than climate. In contrast to our expectations, we did not observe an adverse effect of severe continental conditions on abundances of alien species. It may be related to the fact that identity of river systems comprised additional environmental drivers (e.g. flow regime, substrate texture, catchment size), or anthropogenic disturbances (e.g. river control structures), as well as local conditions, such as land use type or local species pools (Tabacchi *et al.* 1996; Naiman and & Decamps 1997; Nilsson & Berggren 2000) in addition to differences in climatic conditions. Similarly, distance from the river source is related to river discharge, size and duration of flood, floodplain characteristics as well as type and intensity of anthropogenic disturbances (Harding *et al.* 1999; Inoue & Nakagoshi 2001). Hence, river system identity and distance from the river source contained more information than any single environmental predictor and consequently effects of the investigated climatic drivers might be marginalized. Interactions between hydrological and geomorphological factors in riparian systems are very complex (Naiman & Decamps 1997) and their detailed investigation exceeds the scope of this study. Nevertheless, divergence of results across examined river systems demonstrates the role of context-dependency in the success of native and alien species in natural ecosystems.

Effects of vegetative reproduction and hydrochory on the abundance of neophytes varied from strongly positive to neutral across river systems. It has been shown that neophytes benefit from both of these traits as they spread along river corridors (Pyšek & Prach 1993; Richardson *et al.* 2007; Nilsson *et al.* 2010). As abundances of native species did not follow a similar pattern, these two dispersal-related traits may promote invasiveness in the examined riparian systems. Vegetative reproduction was most beneficial in river systems 1 and 2. Both of these river systems are areas known to be highly invaded (Tokarska-Guzik 2005; Kleinbauer et al. 2010; www.floraweb.de; www.bfn.de). In contrast, sampling sites for river system 3 are located in regions where neophytes are less common (Zając 1978; Tokarska-Guzik 2005). Osawa *et al.* (2013) demonstrated that dispersal from neighboring farmlands or urbanized areas may be more important for spread of neophytes than transport along the river flow. Therefore, in areas where neophytes are abundant, vegetative reproduction may not only promote their spread along the river, but also facilitate colonization of river banks from neighboring sites.

Abundance of neophytes spreading by hydrochory increased in river systems 2 and 3. This finding can also be related to distribution patterns of neophytes, as Oder and even more so Vistula river catchments (incorporating both Vistula and San) are considered centers of distribution for neophytes that are strongly affiliated with rivers (Tokarska-Guzik 2005; Tokarska-Guzik, Zając & Zając 2008) and thus likely dependent on hydrochory.

Our results indicate that neophytes producing lighter seeds were less abundant than native species producing light weighted seeds, especially in river system 2. We expected that fitness-related traits, like SLA or seed mass will have a positive effect on abundances, especially for neophytes. Heavier seeds improve seedling survival and growth in unfavorable conditions, which in turn strengthen competitive abilities in early stages of plant growth (Jakobsson & Eriksson 2003; Turnbull *et al.* 2004). The fact that native species also seem to benefit from increased seed mass in river systems 1 and 2 proves that their environmental drivers disfavor small seeds. In contrast to other groups, abundances of archaeophytes were negatively related to seed mass, especially in river system 1. Low seed mass is related to a ruderal strategy *sensu* Grime (1979). Archaeophytes are often distinguished as an ecologically and historically distinct group, consisting mainly of arable or ruderal weeds (Pyšek & Jarošík 2005; Pyšek *et al.* 2005). Many of these plants do not propagate vegetatively, but rather spread by zoochory, anthropochory or anemochory and as such, benefit from lighter seeds (Lososová *et al.* 2006; Zając, Zając & Tokarska-Guzik 2009). Archaeophytes with light weighted seeds were most successful in river system 1. It emphasizes the role of disturbed adjacent areas in the spread of alien species, which lack specialist adaptations to river transport.

In contrast to our expectations, the effect of SLA on abundances was positive for native species across all the examined river systems. This trait was advantageous for neophytes only in river system 2 and was disadvantageous for archaeophytes across all the river systems. Alien species are often characterized by higher SLA, which allows them to grow rapidly and outcompete co-occurring native plants (Grotkopp & Rejmánek 2007). Nevertheless, pioneer species, which often dominate annual riparian communities, are also adapted to fast growth (Salisbury 1970; Burkart 2001). Previous studies revealed that neither SLA nor relative growth rate differ between native and alien congeneric species pairs, co-occurring at the examined sites (Sendek *et a*l. in preparation; Sendek *et al.* 2015). Here, we show that, in contrast to native species, neither neophytes nor archaeophytes benefit from this strategy overlap, what is consistent with the theory of limiting similarity (MacArthur & Levins 1967).

The effects of vegetative reproduction and flowering duration on abundance differed among species origins and along the rivers course. Abundances of vegetatively reproducing neophytes were higher downstream. This can be explained by the role of vegetative reproduction in re-colonization after disturbances. Magnitude and duration of floods can increase in the lower river course as more tributaries participate in the flood-wave accumulation (Dubicki *et al.* 2005). Species that lack physiological adaptation to physical damage or inundation may rely on the recolonization of flooded areas (Catford & Jansson 2014). Propagules transported by the river, local propagule banks as well as adjacent vegetation participate in this process (

Although some traits had similar effects on abundances of native and alien species, differences between origins were more evident. For instance, both groups of aliens benefited mostly from dispersal-related traits, whereas for native species especially SLA was advantageous. Although we have observed strong evidence of context-dependency, due to a complex character of river system and distance from the source, our conclusions concerning the role of environmental factors are limited. Differences between examined river systems and distance from the source can be related to river characteristics and surrounding vegetation, as well as their specific conditions. Further studies, aimed at mechanistic approaches are needed to fully explain ecological mechanisms behind the observed patterns.

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Supplementary materials

S1. Libraries and functions used for the analysis and graphical representation of results.

Spearman correlations between variables were calculated with the ‘rcorr’ function of the ‘Hmisc’ package. Relations between variables were further explored using the PCA, ‘prcomp’ function from the ‘stats’ package and visualized with the ‘fviz_pca_biplot’ function from the ‘factorextra’ package. Patterns of missing values were visualized by ‘marginplot’ and ‘aggr_plot’ from the package ‘VIM’. To impute missing species traits, we used the ‘mice’ function of the ‘mice’ package. Multivariate generalized linear models of species abundance were fitted using the ‘mvabund’ package. We applied the ‘manyglm’ function to fit the models, ’anova.manyglm’ to perform log-likelihood ratio tests, ‘summary.manyglm’ for backward selection and ‘predict.manyglm’ to present results. Graphical representation of effects as a partial regression was constructed in the ‘ggplot2’ package. Radar plots used to demonstrate the range of environmental variables were created using ‘fmsb’ library.

Table S1. GPS coordinates of the 36 study sites.

No.	Site	Latitude	Longitude
1	Elbe_1	52°66'58.0"N	12°00'96.7"E
2	Elbe_2	52°43'56.6"N	11°99'18.7"E
3	Elbe_3	52°13'97.3"N	11°66'34.2"E
4	Elbe_4	52°06'11.7"N	11°68'26.9"E
5	Elbe_5	52°02'73.5"N	11°73'41.7"E
6	Elbe_6	51°96'19.8"N	11°90'44.5"E
7	Saale_1	51°91'65.1"N	11°81'22.8"E
8	Saale_2	51°51'30.6"N	11°95'31.6"E
9	Saale_3	51°20'96.4"N	11°97'18.9"E
10	Saale_4	51°20'29.3"N	11°96'39.9"E
11	Saale_5	51°09'46.3"N	11°49'42.5"E
12	Saale_6	51°09'53.7"N	11°46'56.9"E
13	Oder_1	52°28'88.6"N	14°57'79.4"E
14	Oder_2	52°25'42.5"N	14°69'26.9"E
15	Oder_3	52°16'94.5"N	14°70'68.1"E
16	Oder_4	52°13'70.9"N	14°68'25.6"E
17	Oder_5	52°11'98.3"N	14°68'39.9"E
18	Oder_6	52°07'19.7"N	14°75'46.3"E
19	Neisse_1	51°95'65.9"N	14°71'59.9"E
20	Neisse_2	51°88'52.1"N	14°65'73.2"E
21	Neisse_3	51°85'57.2"N	14°60'28.2"E
22	Neisse_4	51°81'16.1"N	14°60'20.3"E
23	Neisse_5	51°69'58.5"N	14°71'63.6"E
24	Neisse_6	51°52'57.7"N	14°73'90.7"E
25	Vistula_1	51°54'12.4"N	21°83'49.8"E
26	Vistula_2	51°47'71.2"N	21°87'35.5"E
27	Vistula_3	51°42'02.6"N	21°94'88.1"E
28	Vistula_4	51°16'03.4"N	21°78'67.3"E
29	Vistula_5	51°12'62.2"N	21°78'92.8"E
30	Vistula_6	51°03'84.1"N	21°82'31.2"E
31	San_1	50°67'35.3"N	21°93'13.7"E
32	San_2	50°56'84.6"N	22°08'16.1"E
33	San_3	50°38'17.4"N	22°26'24.3"E
34	San_4	50°40'30.3"N	22°34'70.1"E
35	San_5	50°36'38.8"N	22°32'34.9"E
36	San_6	50°24'62.2"N	22°50'30.2"E

Table S2. List of species recorded at the study sites. Scientific names and species origin follow nomenclature of BiolFlor (Klotz, Kühn, Durka 2002).

No.	**Origin**	**Species name**
1	Neo	*Acer negundo L.*
2	Nat	*Achillea millefolium L.*
3	Nat	*Agrostis capillaris L.*
4	Nat	*Agrostis stolonifera L.*
5	Nat	*Aira caryophyllea L. s. str.*
6	Nat	*Alisma plantago-aquatica L. s. str.*
7	Nat	*Alliaria petiolata (M. Bieb.) Cavara & Grande*
8	Nat	*Allium schoenoprasum L.*
9	Nat	*Alnus incana (L.) Moench*
10	Nat	*Alopecurus aequalis Sobol.*
11	Nat	*Alopecurus geniculatus L.*
12	Neo	*Amaranthus albus L.*
13	Neo	*Amaranthus retroflexus L.*
14	Neo	*Ambrosia trifida L.*
15	Nat	*Arctium lappa L.*
16	Neo	*Armoracia rusticana G. Gaertn., B. Mey. & Scherb.*
17	Neo	*Artemisia annua L.*
18	Nat	*Artemisia vulgaris L.*
19	Nat	*Atriplex patula L.*
20	Nat	*Atriplex prostrata Boucher ex DC.*
21	Arc	*Atriplex sagittata Borkh.*
22	Arc	*Ballota nigra L. s. l.*
23	Nat	*Barbarea stricta Andrz.*
24	Nat	*Barbarea vulgaris R. Br. s. str.*
25	Nat	*Bidens cernua L.*
26	Neo	*Bidens connata Muhl. ex Willd.*
27	Neo	*Bidens frondosa L.*
28	Nat	*Bidens tripartita L.*
29	Nat	*Bolboschoenus maritimus (L.) Palla*
30	Neo	*Brassica nigra (L.) W. D. J. Koch*
31	Nat	*Calystegia sepium (L.) R. Br.*
32	Neo	*Cannabis sativa L. s. l.*
33	Nat	*Capsella bursa-pastoris (L.) Med.*
34	Nat	*Carex acutiformis Ehrh.*
35	Nat	*Cardamine amara L.*
36	Nat	*Carduus crispus L.*
37	Nat	*Cardamine pratensis L.*
38	Nat	*Chaerophyllum bulbosum L.*
39	Arc	*Chenopodium album L.*
40	Nat	*Chenopodium ficifolium Sm.*
41	Nat	*Chenopodium glaucum L.*
42	Arc	*Chenopodium hybridum L.*

43	Nat	*Chelidonium majus L.*
44	Nat	*Chenopodium polyspermum L.*
45	Nat	*Chenopodium rubrum L.*
46	Neo	*Chenopodium strictum Roth*
47	Nat	*Cirsium arvense (L.) Scop.*
48	Nat	*Cirsium palustre (L.) Scop.*
49	Nat	*Cirsium vulgare (Savi) Ten.*
50	Nat	*Convolvulus arvensis L.*
51	Nat	*Corrigiola litoralis L.*
52	Nat	*Crepis capillaris (L.) Wallr.*
53	Nat	*Cuscuta europaea L.*
54	Nat	*Cyperus fuscus L.*
55	Nat	*Daucus carota L.*
56	Nat	*Deschampsia cespitosa (L.) P. Beauv. s. str.*
57	Arc	*Digitaria sanguinalis (L.) Scop.*
58	Arc	*Echinochloa crus-galli (L.) P. Beauv.*
59	Neo	*Echinocystis lobata (Michx.) Torr. & A. Gray*
60	Nat	*Eleocharis palustris (L.) Roem. & Schult.*
61	Nat	*Elymus repens (L.) Gould s. str.*
62	Neo	*Epilobium ciliatum Raf.*
63	Nat	*Epilobium lanceolatum Sebast. & Mauri*
64	Nat	*Epilobium parviflorum Schreb.*
65	Neo	*Eragrostis pilosa (L.) P. Beauv.*
66	Nat	*Erigeron acris L. s. l.*
67	Neo	*Erigeron annuus (L.) Pers.*
68	Neo	*Erigeron canadensis L.*
69	Arc	*Erucastrum gallicum (Willd.) O. E. Schulz*
70	Nat	*Erysimum cheiranthoides L.*
71	Arc	*Euphorbia peplus L.*
72	Nat	*Festuca rubra L.*
73	Nat	*Galium boreale L.*
74	Neo	*Galium mollugo L. s. str.*
75	Nat	*Galium palustre L. s. str.*
76	Neo	*Galinsoga parviflora Cav.*
77	Neo	*Galinsoga quadriradiata Ruiz & Pav. s. str.*
78	Nat	*Glechoma hederacea L.*
79	Nat	*Gnaphalium uliginosum L.*
80	Nat	*Holcus mollis L.*
81	Nat	*Humulus lupulus L.*
82	Nat	*Hypericum maculatum Crantz s. str.*
83	Neo	*Impatiens glandulifera Royle*
84	Nat	*Inula britannica L.*
85	Nat	*Iris pseudacorus L.*
86	Arc	*Juglans regia L.*
87	Nat	*Juncus bufonius L.*
88	Nat	*Juncus compressus Jacq.*

89	Nat	*Juncus effusus L.*
90	Neo	*Juncus tenuis Willd.*
91	Neo	*Lepidium draba L. s. l.*
92	Nat	*Limosella aquatica L.*
93	Nat	*Linaria vulgaris Mill.*
94	Nat	*Lolium perenne L.*
95	Nat	*Lycopus europaeus L.*
96	Nat	*Lysimachia vulgaris L.*
97	Nat	*Lythrum salicaria L.*
98	Arc	*Malva neglecta Wallr.*
99	Nat	*Medicago lupulina L.*
100	Nat	*Mentha aquatica L.*
101	Nat	*Mentha arvensis L.*
102	Nat	*Mentha longifolia (L.) Huds.*
103	Nat	*Mentha pulegium L.*
104	Nat	*Myosotis arvensis (L.) Hill*
105	Nat	*Myosotis scorpioides L.*
106	Nat	*Oenanthe aquatica (L.) Poir.*
107	Neo	*Oxalis corniculata L.*
108	Neo	*Oxalis stricta L.*
109	Arc	*Panicum miliaceum L.*
110	Nat	*Persicaria amphibia (L.) Delarbre*
111	Nat	*Persicaria hydropiper (L.) Delarbre*
112	Nat	*Persicaria lapathifolia (L.) Delarbre s. l.*
113	Nat	*Persicaria maculosa Gray*
114	Nat	*Peucedanum officinale L.*
115	Nat	*Phalaris arundinacea L.*
116	Nat	*Phragmites australis (Cav.) Trin. ex Steud.*
117	Nat	*Picris hieracioides L. s. l.*
118	Nat	*Pimpinella major (L.) Huds.*
119	Neo	*Pisum sativum L.*
120	Arc	*Plantago lanceolata L.*
121	Nat	*Plantago major L. s. str.*
122	Nat	*Poa annua L.*
123	Nat	*Poa compressa L.*
124	Nat	*Poa nemoralis L.*
125	Nat	*Poa palustris L.*
126	Nat	*Poa pratensis L. s. str.*
127	Nat	*Poa trivialis L. s. l.*
128	Nat	*Polygonum aviculare L. s. l.*
129	Neo	*Populus canadensis Moench*
130	Nat	*Potentilla anserina L.*
131	Nat	*Potentilla erecta (L.) Raeusch.*
132	Nat	*Potentilla reptans L.*
133	Nat	*Potentilla supina L.*
134	Nat	*Prunus avium L.*

135	Nat	*Pulicaria dysenterica (L.) Bernh.*
136	Nat	*Pulicaria vulgaris Gaertn.*
137	Nat	*Quercus robur L.*
138	Nat	*Ranunculus repens L.*
139	Nat	*Ranunculus sceleratus L.*
140	Arc	*Raphanus raphanistrum L.*
141	Nat	*Rorippa amphibia (L.) Besser*
142	Nat	*Rorippa palustris (L.) Besser*
143	Nat	*Rorippa sylvestris (L.) Besser*
144	Nat	*Rubus caesius L.*
145	Nat	*Rumex acetosa L.*
146	Nat	*Rumex acetosella subsp. acetosella L.*
147	Nat	*Rumex conglomeratus Murray*
148	Nat	*Rumex crispus L.*
149	Nat	*Rumex maritimus L.*
150	Nat	*Rumex obtusifolius L.*
151	Nat	*Rumex palustris Sm.*
152	Nat	*Sagina procumbens L.*
153	Nat	*Salix alba L.*
154	Nat	*Salix fragilis L.*
155	Nat	*Salix purpurea L.*
156	Nat	*Salix viminalis L.*
157	Nat	*Sambucus nigra L.*
158	Nat	*Schoenoplectus x carinatus agg.*
159	Nat	*Scorzoneroides autumnalis (L.) Moench*
160	Nat	*Scrophularia nodosa L.*
161	Nat	*Senecio vulgaris L.*
162	Arc	*Setaria pumila (Poir.) Roem. & Schult.*
163	Arc	*Setaria viridis (L.) P. Beauv.*
164	Neo	*Solidago canadensis L.*
165	Nat	*Solanum dulcamara L.*
166	Neo	*Solanum lycopersicum L.*
167	Arc	*Solanum nigrum L.*
168	Nat	*Sonchus arvensis L.*
169	Nat	*Sonchus asper (L.) Hill*
170	Nat	*Sonchus oleraceus L.*
171	Nat	*Spergularia rubra (L.) J. Presl & C. Presl*
172	Nat	*Stachys palustris L.*
173	Nat	*Stellaria aquatica (L.) Scop.*
174	Arc	*Stellaria media (L.) Vill. s. str.*
175	Nat	*Stellaria nemorum L. s. l.*
176	Nat	*Symphytum officinale L. s. str.*
177	Nat	*Tanacetum vulgare L.*
178	Nat	*Taraxacum sect. Ruderalia Kirschner, H. Øllg. & Štěpánek*
179	Nat	*Thalictrum flavum L.*
180	Arc	*Thlaspi arvense L.*

181	Nat	*Tripleurospermum maritimum (L.) W. D. J. Koch*
182	Nat	*Trifolium repens L.*
183	Nat	*Tussilago farfara L.*
184	Nat	*Ulmus minor Mill.*
185	Nat	*Urtica dioica L. s. l.*
186	Nat	*Veronica anagallis-aquatica L.*
187	Nat	*Veronica beccabunga L.*
188	Nat	*Veronica catenata Pennell*
189	Nat	*Veronica maritima L.*
190	Nat	*Vicia cracca L. s. str.*
191	Arc	*Viola arvensis Murray*
192	Neo	*Xanthium albinum (Widder) H. Scholz s. l.*
193	Nat	*Xanthium strumarium L. s. str.*

Abbreviations: Nat-native, Arc-archaeophytes, Neo-neophytes.

Table S3. Spearman rank correlation coefficients between the predictor variables used in the model. Significant correlations ($p<0.05$) are indicated in bold. Abbreviations: Ori: Species origin, Fl_d: flowering duration, S_m: seed mass, SLA: Specific leaf area, Hydrochory: Hydrochory, Veg: Vegetative reproduction, Dist: Distance from the river source, Soil N: Soil nitrogen, Temp: Mean annual temperature, Prec: Mean annual precipitation, RS: River system identity.

	Ori	**Fl_d**	**S_m**	**SLA**	**Hyd**	**Veg**	**Dist**	**Soil N**	**Temp**	**Prec**	**RS**
Ori	1										
Fl_d	**0.08**	1									
S_m	**0.13**	**-0.18**	1								
SLA	**0.11**	**0.26**	**-0.19**	1							
Hyd	**-0.38**	**-0.08**	**-0.19**	**-0.04**	1						
Veg	**-0.29**	**-0.15**	**-0.16**	0.00	**0.17**	1					
Dist	0	0	0	0	0	0	1				
Soil N	0	0	0	0	0	0	-0.09	1			
Temp	0	0	0	0	0	0	**-0.51**	-0.20	1		
Prec	0	0	0	0	0	0	**-0.36**	-0.27	-0.30	1	
RS	0	0	0	0	0	0	0.27	**-0.34**	**-0.63**	**-0.62**	1

Table S4. Summary of the minimal adequate model, explaining abundances of species with species origin, species traits and environmental characteristics. Values representing significance of each of multivariate terms specified in the model are based on Wald statistic (W). *p*-values are obtained by bootstrapping (999 replications). Significant *p* values ($p<0.05$) are indicated in bold.

Matrices	Variables	W	*p*
	Intercept	0.986	0.415
ENV	River system 2	2.866	**0.018**
	River system 3	0.564	0.637
	Distance	2.197	0.066
	Mean precipitation	1.794	0.134
TRAITS	Vegetative reproduction	2.128	0.071
	Flowering duration	0.016	0.984
	Hydrochory	1.110	0.332
	Seed mass	5.05	**0.001**
	SLA	2.512	**0.033**
ORIGIN	Archaeophytes	0.359	0.737
	Neophytes	0.268	0.806
ENV x TRAITS	River system 2: Vegetative reproduction	0.452	0.701
	River system 3: Vegetative reproduction	0.101	0.927
	River system 2: Flowering duration	2.909	**0.012**
	River system 3: Flowering duration	1.108	0.335
	River system 2: Hydrochory	1.590	0.186
	River system 3: Hydrochory	1.748	0.124
	River system 2: Seed mass	2.132	0.059
	River system 3: Seed mass	4.617	**0.001**
	River system 2: SLA	1.358	0.266
	River system 3: SLA	1.532	0.203
	Distance: Vegetative reproduction	2.817	**0.022**
	Distance: Flowering duration	1.007	0.392
	Mean precipitation: SLA	2.791	**0.022**
ENV x ORIGIN	River system 2: Archaeophytes	2.538	**0.019**
	River system 3: Archaeophytes	1.722	0.130
	River system 2: Neophytes	4.254	**0.002**
	River system 3: Neophytes	4.175	**0.001**
	Distance: Archaeophytes	1.120	0.321
	Distance: Neophytes	2.723	**0.021**
TRAITS x ORIGIN	Vegetative reproduction: Archaeophytes	0.173	0.730
	Vegetative reproduction: Neophytes	2.130	0.051
	Flowering duration: Archaeophytes	1.955	0.091
	Flowering duration: Neophytes	2.186	0.059
	Hydrochory: Archaeophytes	2.526	**0.022**
	Hydrochory: Neophytes	0.360	0.742
	Seed mass: Archaeophytes	3.144	**0.005**
	Seed mass: Neophytes	1.611	0.153

Matrices	Variables	W	*p*
	SLA: Archaeophytes	2.729	**0.017**
	SLA: Neophytes	4.108	**0.001**
ENV x TRAITS x ORIGIN	RS2: Vegetative reproduction: Archaeophytes	0.294	0.337
	RS3: Vegetative reproduction: Archaeophytes	1.580	0.076
	RS2: Vegetative reproduction: Neophytes	1.800	0.112
	RS3: Vegetative reproduction: Neophytes	3.426	**0.003**
	RS2: Hydrochory: Archaeophytes	0.717	0.512
	RS3: Hydrochory: Archaeophytes	1.483	0.134
	RS2: Hydrochory: Neophytes	4.025	**0.001**
	RS3: Hydrochory: Neophytes	4.092	**0.001**
	RS2: Seed mass: Archaeophytes	1.982	**0.039**
	RS3: Seed mass: Archaeophytes	2.812	**0.002**
	RS2: Seed mass: Neophytes	3.675	**0.001**
	RS3: Seed mass: Neophytes	2.190	0.071
	RS2: SLA: Archaeophytes	1.123	0.307
	RS3: SLA: Archaeophytes	0.350	0.773
	RS3: SLA: Neophytes	2.356	**0.050**
	RS3: SLA: Neophytes	1.895	0.104
	Distance: Vegetative reproduction: Archaeophytes	0.894	0.399
	Distance:Vegetative reproduction: Neophytes	3.557	**0.002**
	Distance: Flowering duration: Archaeophytes	1.950	0.085
	Distance: Flowering duration: Neophytes	3.557	**0.002**

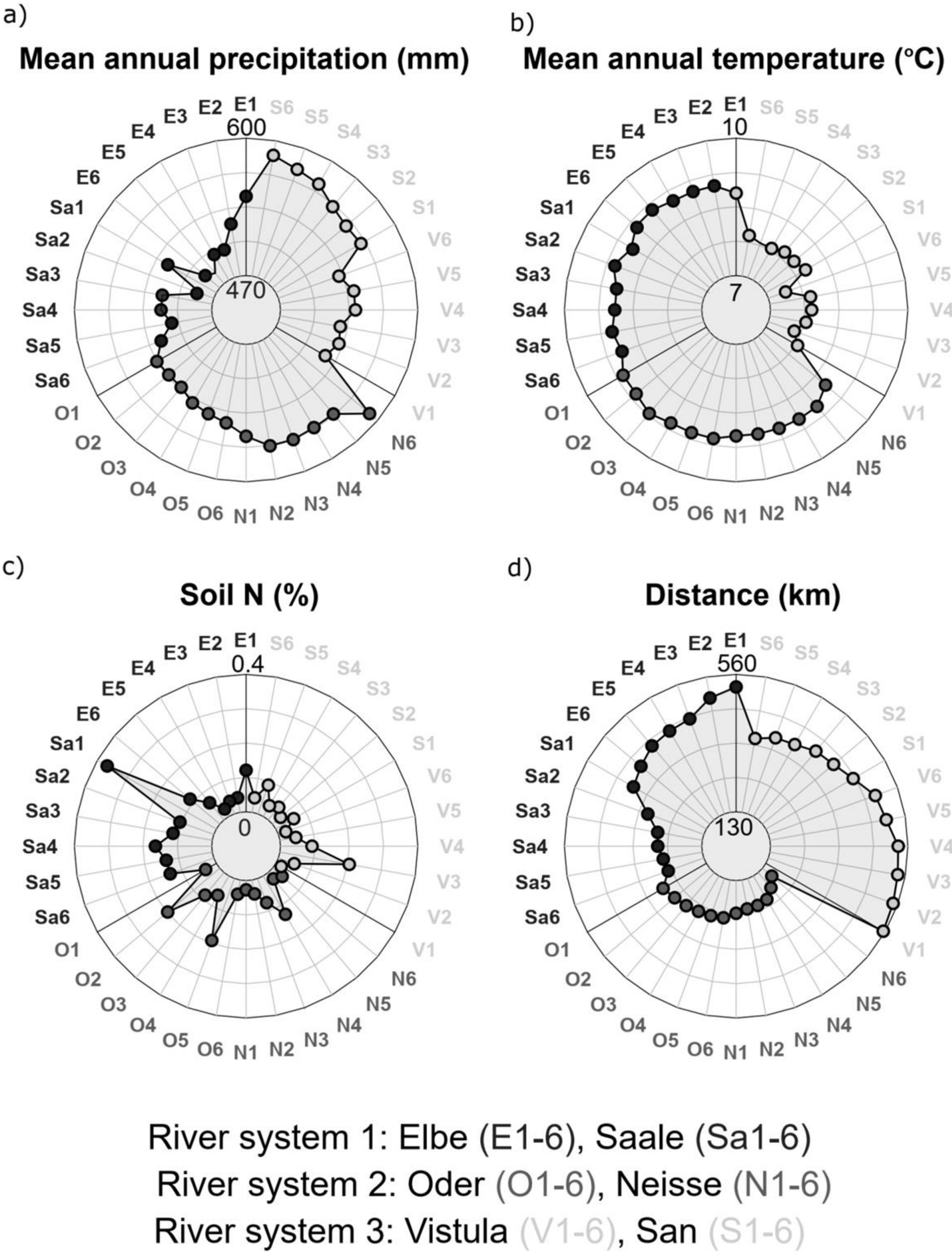

Fig. S1. Range of environmental variables included in the model. Values of (a) mean annual precipitation, (b) mean annual temperature, (c) soil nitrogen and (d) distance from the river source are presented for each of the 6 study sites, sampled on banks of 6 rivers (in total 36 sites). Identity of the river system is determined by colors and rivers by letters.

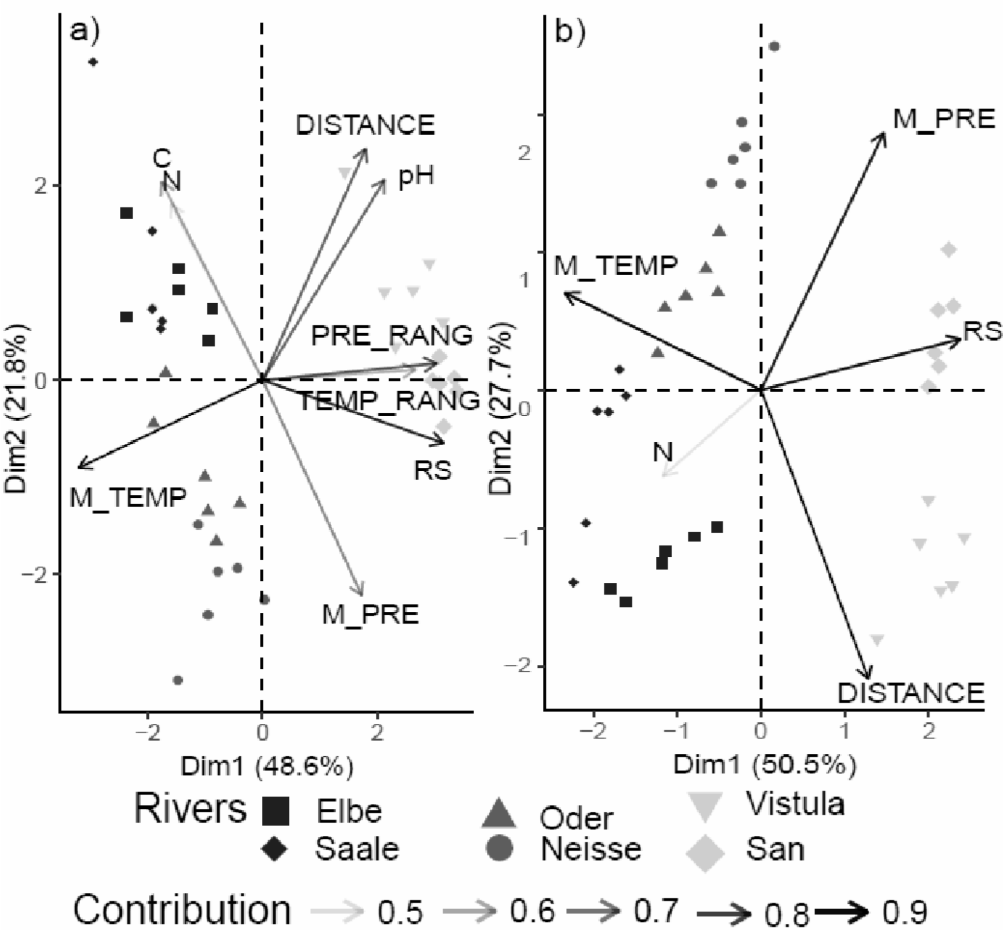

Fig S2. Principal component analysis (PCA) of (a) all measured environmental factors characterizing study sites, and (b) environmental factors included in the model. Axes 1 and 2 account for (a) 48.6% and 21.8% and (b) 50.5% and 27.2% of the variation respectively. Identity of river systems is distinguished by different colours and rivers by shapes. Transparency of arrows representing environmental variables is determined by their contributions to presented axes.

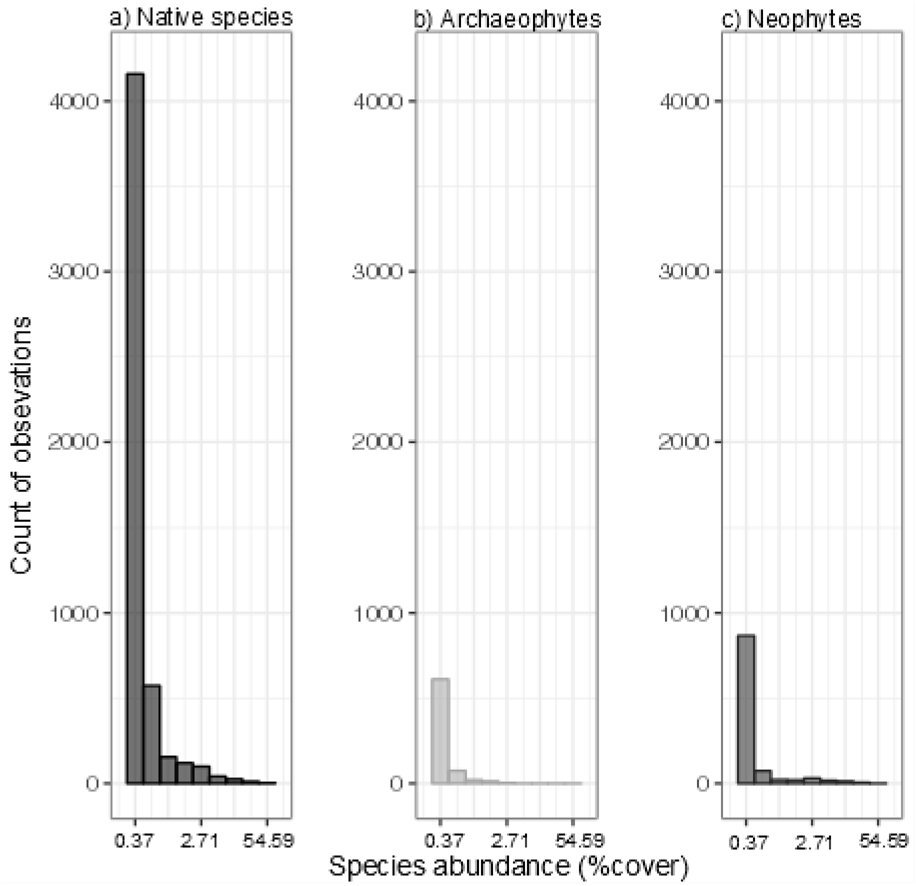

Fig. S3. Distribution of abundances across taxa belonging to three origin groups: a) native species, b) archaeophytes and c) neophytes. We present data transformed by a natural logarithm, as it was applied in the analysis, on the back-transformed x axis.

Chapter 5

Synthesis

General discussion

Determining whether distinct features of alien species facilitate their success in recipient communities is one of the fundamental questions of invasion ecology (Pyšek *et al.* 2015). I addressed it by exploring differences in traits between co-occurring alien and native species and by relating them to plant success in riparian communities of Central Europe. To obtain a broad context on between species differences I not only compared trait values **(Chapters 2; 3)**, but also examined their variability within and across plants populations **(Chapter 2)**. Moreover, I investigated how particular traits affect abundance of native and alien species across an environmental gradient (**Chapter 4**). This thesis contributes to a better understanding of plant strategies that allow co-existence of alien and native species. In particular it sheds light on differences between co-occurring alien and native plants in respect to growth, competition, and adaptation to fluctuating conditions.

In this thesis I made an attempt to address several obstacles, which may affect inferences of comparative studies. One of the problems, obstructing broad comparisons of traits and strategies between native and alien species is their context dependency (Kueffer *et al.* 2013). It not only hiders disentangling the key drivers and mechanisms, but also reduces the possibility to generalize obtained findings (Thuiller *et al.* 2006; Kuebbing *et al.* 2013; compare: Study limitations). To decrease complexity caused by number and heterogeneity of abiotic drivers, I focused on a single plant community type: annual communities growing in a close proximity to the water edge (**Chapter 1**). In order to maintain an ability to draw more general conclusions, I studied these communities across a range of abiotic conditions in a natural settings of three parallel river systems of Central Europe (**Chapter 1**).

A common concern of studies comparing native and alien plants is the correct choice of investigated species. For instance, not accounting for phylogenetic patterns or comparing rare, native plant with an abundant alien may lead to unreliable conclusions (Pyšek & Richardson 2008; van Kleunen *et al.* 2010). To avoid these problems, studies should be based on species equally successful in a given habitat and apply phylogenetically independent comparisons (Pyšek & Richardson 2008; van Kleunen *et al.* 2010; Gallagher *et al.* 2015). In **Chapters 2** and **3** I used native and alien species that are not only common in investigated habitats, but also belong to the same genus. Use of congeneric species pairs allows to substantially reduce phylogenetic bias (Felsenstein 1985; van Kleunen *et al*. 2008). Nevertheless, it was not possible to profoundly solve this problem (**Chapter 4**; compare: Study limitations).

A potential source of bias lies in the low resemblance of artificial plant assemblages, often used in experimental studies, to natural plant communities (compare: Study limitations). Artificial systems may poorly reflect interactions between environmental drivers and between-species relations of natural communities, what can undermine conclusions of comparative studies (van Kleunen *et al*. 2010; Chrobock *et al*. 2011) and decrease their value for *e.g.* conservation (Kuebbing *et al*. 2013). Moreover, species composition of a given plant communicity is shaped by a range of environmental drivers, that affect their abundance in given conditions (Daehler 2003; Drenovsky *et al.* 2012; Zefferman *et al.* 2015; Vicente *et al.* 2019). Plants randomly selected from the pool of introduced species may not reflect these mechanisms. For example, species with certain traits, may have been introduced earlier or more frequently than others and as a consequence can be overrepresented in the full species pool (van Kleunen *et al*. 2015; Maurel *et al*. 2016). One way of addressing this introduction bias involves testing importance of traits for species success in a given habitat (Knapp & Kühn 2012). I focus on these issues in **Chapter 4**, where I estimate if traits affect success of alien and native species in riparian plant communities.

Trait values and their role for species abundance

In this thesis I investigated differences in performance- and reproduction-related traits of co-occurring native and alien species in natural habitats (**Chapter 2**) and under different levels of competition (**Chapter 3**). Besides that, I tested importance of performance-, reproduction- and dispersal-related traits for abundance in standing plant communities (**Chapter 4**). Species traits play a substantial role in explaining biotic invasions and predicting invaders (Rejmánek & Richardson 1996). Although finding traits consistently associated with invasiveness may be challenging (Alpert *et al*. 2000), some characteristics, like high SLA and growth rate, high reproductive output and high colonization ability seem to be shared by many successful invaders (Ordonez *et al*. 2010; van Kleunen *et al*. 2010). Many of these traits are often associated with superior performance and a competitive advantage over co-occurring native species (Reichmann *et al*. 2016). Conversely, if alien species are able to occupy empty ecological niches, they may face reduced competitive pressure in recipient plant communities (Ordonez *et al*. 2010; van Kleunen *et al*. 2015). In accordance with Darwin's Naturalization Hypothesis (Darwin 1859), dissimilarity of traits between alien and native species may not only promote invasions, but also may be more important than traits *per se* (Funk *et al*. 2008; Leffler *et al*. 2014).

Both field (**Chapter 2**) and experimental (**Chapter 3**) comparisons of traits delivered consistent results. In particular, the larger stature and biomass of the investigated alien species may provide them an advantage over their native congeners. For instance, alien *Bidens frondosa* showed larger plant biomass and height than native *Bidens tripartita* in the growth trial as well as in the competition experiment (**Chapter 3**). Although the study did not reveal significant differences in relative growth rate between these two species, superior height of *B. frondosa* was followed by a biomass increase in my competition experiment. The field study, (**Chapter 2**), confirmed that under natural conditions, investigated alien plants are higher and invest more biomass in supportive structures *e.g.* stem compared to co-occurring native species (**Chapter 2**). Native species, in turn, were characterized by higher SLA (**Chapter 2**). SLA was also positively related to abundance of native species in all of the investigated river systems (**Chapter 4**). Contrastingly, in both investigated groups of alien species (neophytes and archaeophytes), the association between abundance and SLA varied across the sites (**Chapter 4**). These findings may be surprising, as high SLA as well as high RGR are commonly associated with invasiveness (Baruch & Goldstein 1999; Burns 2006; Leishman *et al*. 2007). To better understand this findings, it is important to consider that investigated native species are also fast-growing annuals (**Chapter 1**), which share similar adaptations beneficial in riparian habitats (Garnier & Laurent 1994). Additionally, rapid growth and competitive ability are especially important in investigated early-successional plant communities (Levine & Rees 2002). Alternatively, observed increase of SLA can be perceived as a reaction to shading (Gommers *et al*. 2013), what may suggest a potential divergence in light acquisition strategies between native and alien species. While superior height grants better access to light, supporting organs like stems or branches require large biomass investments (Falster & Westoby 2003), as it was presented in a form of a biomass allocation pattern in **Chapter 2**. Increasing of SLA can be interpreted as a contrasting strategy, adopted by plants when overgrowned by a competitor (Gommers *et al*. 2013). Higher leaf biomass and higher SLA of native species (**Chapter 2**) may imply that they depend on this light-acquisition strategy more than on a height. I investigated plant growth under different levels of intraspecific competition only for *Bidens* (**Chapter 3**). Native *B. tripartita* was less affected by competition for light and higher plant density than its alien congener – *B. frondosa*. These findings may imply that differences in traits between native and alien plants may allow co-occurrence of both groups by allowing native plants to better withstand competition for light, however further comparative studies are needed to address this issue more directly.

Reproductive traits, like high fecundity or long flowering period, often contribute to invasion success (Rejmánek 2000; Kolar & Lodge 2001; Lloret *et al.* 2005; Pyšek & Richardson 2008). Higher reproductive output along with production of numerous, light seeds increase species dispersal and colonization abilities (Coomes & Grubb 2003), but see (Thomson *et al.* 2011) and often characterize successful alien species (Mason *et al.* 2008; Correia *et al.* 2016). Heavier seeds, in turn, promote seedlings survival and growth in unfavorable environments and may improve their tolerance to competition (Geritz *et al.* 1999; Coomes & Grubb 2003; Turnbull *et al.* 2004). Fast growth in early stages of development was suggested to be one of the key traits leading to competitive superiority (Ni *et al.* 2018).

Co-occurring alien and native target species investigated in this thesis did differ neither in their investment in the reproductive structures nor in the propagule mass (**Chapter 2**; **Chapter 3**). These findings can be also attributed to similarities in their life histories, as annual plants are particularly dependent on their reproductive output and seed characteristics (Rees 1995; Levine & Rees 2002). Regarding the whole plant community (**Chapter 4**), seed mass often affected species abundance, even though direction of relationships differed across river systems and origins. For example, in one of the examined river systems, heavier seed mass was negatively related to abundance of archaeophytes. Archaeophytes are distinguished from neophytes on the basis of their long residence time in the non-native range (Pokorna *et al.* 2018) and are often considered an ecologically distinct group (Jehlík *et al.* 2016; Vaz *et al.* 2018; Menzel *et al.* 2018). Majority of archaeophytes are listed among ruderal or segetal species and are particularly common in disturbed and cultivated areas (Celka 2007; Pokorna *et al.* 2018). These species disperse mostly by zoochory, anthropochory or anemochory, and may benefit from lighter seeds (Lososova *et al.* 2006; Zając *et al.* 2009). Contrastingly, species benefiting mostly from hydrochory may take an advantage of heavier seeds (Jager *et al.* 2019); what can partially explain patterns observed in **Chapter 4**.

Similarly to seed mass, importance of flowering period is dependent on multiple environmental factors. Although some authors argue that this trait does not play an important role in invasiveness (Thompson *et al*. 1995; Reichard & Hamilton 1997), other studies show that longer flowering period may be beneficial for alien species (Lloret *et al*. 2005; Küster *et al*. 2008; Pyšek & Richardson 2008). In riparian systems phenology is critically important due to temporal occurrence of flood events (Catford & Jansson 2014). Observations discussed in **Chapter 3**, demonstrates that even in controlled conditions, alien *B. frondosa* flowers later than *B. tripartita*. Postponed flowering may allow species to gather more resources or use an empty temporal niche (Godoy *et al*. 2009). Still, in regularly flooded, riparian habitats prolonged flowering may lead to failure in producing ripe seeds. Results presented in **Chapter 4** show that in lower part of the river, longer flowering period is not advantageous for all species groups. Although flood wave of examined rivers is flattened in lowlands, the floods occur more often in lower river courses (Kundzewicz *et al*. 2005). Since investigated plant communities were located close to the water edges, they were affected even by the minor floods. Therefore, it can be assumed that a main difference between downstream and upstream river course lies in flood frequency. Consequently, on sites which due to their location in upper river course were less frequently disturbed, prolonged flowering duration was beneficial for both groups of alien species. This conclusion is in agreement with other studies that investigated effects of disturbances on alien species in riparian systems (Stromberg *et al*. 2007; Catford *et al*. 2011). For example, (Catford *et al*. 2011) demonstrated that smaller or less common floods favor invasions in riparian habitats. Still, a more complete explanation of the complex relationships between flooding intensity and phenology requires further attention. Gathered evidence, however, suggests that timing of life cycle events may be especially important for alien species in temporally disturbed habitats, like river systems, (compare: Boedeltje *et al*. 2004). Moreover, as other studies suggest, this importance may increase under changing climatic conditions (Godoy *et al*. 2009; Hulme 2011).

Although floods may have detrimental effects on riparian vegetation (Catford & Jansson 2014), their role also involves propagation of seeds and vegetative propagules (Boedeltje *et al*. 2004; Nathan *et al*. 2008). Because of the efficiency of water transport, rivers are considered important dispersal corridors for both native and alien species (Johansson *et al*. 1996; Andersson *et al*. 2000; Jansson *et al*. 2005; Richardson *et al*. 2007). In this thesis, I treat the ability to spread by hydrochory as a proxy for a long-distance dispersal in the river corridors (Nilsson *et al*. 1991; Jansson *et al*. 2005). Nevertheless, transport of vegetative organs by water may be equally relevant for plant composition and abundance in riparian communities (Boedeltje *et al*. 2004; Catford & Jansson 2014). This issue was not directly tackled in this thesis, however, other obtained results suggest that mode of dispersal may be especially important for abundances of riparian species. In **Chapter 4**, neophytes most predominantly benefited from hydrochory. This should not be surprising, considering a huge role of rivers in spread of alien species (Richardson *et al*. 2007; Tokarska-Guzik *et al*. 2012). Still, depending on origin, river system identity or distance from the river source, other means of dispersal were favorealso d. For instance, input of diaspores from other habitats might play a role for abundances of neophytes, especially in highly invaded areas (**Chapter 4**). Correspondingly, species abundances depended also on light seeds dispersed mostly by anemochory, as discussed in case of archaeophytes, or on vegetative spread from adjacent areas (**Chapter 4**). Although target species were not reported to propagate vegetatively, and consequently vegetative reproduction was not addressed in **Chapters 2** and **3**, this trait affected abundance of neophytes (**Chapter 4**). Particular mechanisms behind observed effect are difficult to pinpoint because of sheer number of processes affected by vegetative spread (Johansson *et al*. 1996; Andersson *et al*. 2000; Jansson *et al*. 2005; Richardson *et al.* 2007). Still, described positive relation was mostly pronounced downstream, where flood disturbances were especially common, suggesting that vegetative reproduction plays an important role in recovery after a disturbance. Nevertheless, these conclusions remain hypothetical and should serve as a challenge for future studies, focusing on more specific effects (compare: **Conclusions and future implications**).

Adaptations to environmental heterogenity

In this thesis I focused on a single habitat type, however riparian habitats are among the most heterogeneous ones (Naiman *et al*. 2005; Lite *et al*. 2005; Wintle & Kirkpatrick 2007; Stella & Bendix 2019). The environmental variability of the investigated river systems modified relations between species traits and abundance, as featured in **Chapter 4**. Species present in such diverse habitats can be expected to possess a strategy allowing them to adapt to temporal and spatial heterogenity of the environment (Pan *et al*. 2006; Stella & Bendix 2019). Alien species are often shown to benefit from environmental fluctuations (Davis *et al*. 2000). Furthermore, they are capable of spreading over large spatial distances and invading distinct habitats (Richardson *et al*. 2000). Finally, they may reach high average fitness across many environments (van Kleunen & Fischer 2005). Phenotypic plasticity allows to express different phenotypes in different conditions, what is often highlighted as a mechanism underlying the success of alien invasive species (Schlichting 1986; Pigliucci 2001; Pigliucci 2005). The theory of 'general purpose phenotype' (Baker 1965; Richards *et al*. 2006) propose that phenotypic plasticity is one of the traits characterising 'ideal weeds'. Empirical evidences show that plasticity may indeed enhance breadth of ecological niche and allow organisms to adjust their phenotypes to a broad range of habitats (Sultan *et al*. 1998; Sultan 2001; Richards *et al*. 2005; Davidson *et al*. 2011). Still some authors argue that importance of this characteristic is narrowed down to certain stages of invasion, traits or scales of comparison (Palacio-López & Gianoli 2011).

Although in this thesis I was not able to distinguish between the two sources of variability, *i.e*. phenotypic plasticity and genetic variation (compare: Study limitations), I quantified differences in trait variation between alien and native congeneric species. In **Chapter 2**, besides investigating mean trait values I compared variability of particular traits, expressed as their coefficients of variation. Moreover, I studied patterns of phenotypic integration and variance allocation to river systems, rivers, populations and individuals. None of the conducted comparisons provided consistent findings, which could confirm a systematic difference in trait variability between native and alien species. One of the potential reasons is the above mentioned, lack of ability to distinguish between distinct mechanisms that may affect trait variation (Hamilton *et al*. 2005). Some of them *e.g*. hybridization, genetic drift or a bottleneck effect result from invasion history (Amsellem *et al*. 2000; Bossdorf *et al*. 2005; Davidson, Jennions & Nicotra 2011). All of the alien target species have already long residence history in Central Europe (**Chapter 1**) while phenotypic plasticity may be the most important in the early stages of invasion, when genetic diversity of alien species tends to be the lowest (Thuiller *et al*. 2006; Theoharides & Dukes 2007). This conclusion is in accordance with the results of variance partitioning, which show that across all the traits, within-population variability is relatively high for both alien and native species (**Chapter 2**). As plasticity increases trait variability in response to environmental conditions (Valladares *et al*. 2006), it should be rather pronounced across rivers or river systems, especially as differences in environmental conditions between them are apparent (**Chapter 4**).

Heterogeneity of environmental conditions in riparian habitats may also partially explain the inconsistence of results regarding phenotypic integration (**Chapter 2**) and seed heteromorphism (**Chapter 3**). Patterns and strength of correlations between particular traits determines coherence in responses to environmental factors (Gianoli 2004) and constrains responses to environmental changes (Gianoli & Palacio-López 2009), compare **Chapter 1**. Although strength of integration differed significantly in each of the target species pairs, alien species were not consistently less integrated (*i.e.* more variable) than their native congeners (**Chapter 2**). Although I expected higher trait variability of alien species, native plants occurring in heterogenic habitats should also remain flexible in their responses to environmental factors. The second potential restriction of these results is relatively low number of traits and species used. More accurate information on this topic can be delivered by a comparison using a higher number of traits, which would better reflect species strategies (Pigliucci *et al.* 1991; Pigliucci & Preston 2004).

Another adaptation to changing environmental condition, which I addressed in this thesis, is the bet-hedging strategy (Venable 2007). In case of all native and alien target species, this strategy is expressed in ability to produce distinct seed morphs (**Chapter 1**). Seed morphs can be distinguished on the basis of differences in seed size, seed mass, dormancy and dispersal-related structures (Mandák 2003). Similarly, progenies of distinct seed morphs can be expected to be better adapted to particular functions *e.g.* dispersal (colonizer seed type) or competition (maintainer seed type) (Imbert 2002). Differences between seed morphs may be weaker or stronger depending on species and habitat type (Imbert 2002). Nevertheless, seed heteromorphism may be exceptionally beneficial for plants growing under unpredictable environmental conditions (Venable 1985; Imbert 2002; Dubois & Cheptou 2012) as well for alien species (Mandák 2003; Fumanal *et al.* 2007; Vitalos & Karrer 2009). In riparian habitats, patches of bare sand are mixed with dense vegetation stands, what favours both efficient colonization and competitive strength (Naiman *et al.* 2005). An ability to produce distinct seed morphs may, to some extent, compromise these two distinct strategies (Imbert 2002). In this thesis I have explored seed heteromorphism only in the *Bidens* species pair (**Chapter 3**). Although seed morphs produced by *Bidens* are expected to play roles of colonizers and maintainers (Brandel 2004), the only differences in growth of respective seed morph progenies occurred in the early stage of plant development and dimnished in following weeks (**Chapter 3**). Alien species may be expected to exceptionally benefit from variability provided by seed hetermorphism (Fumanal *et al*. 2007; Vitalos & Karrer 2009), however my experiment does not confirm this assumption (**Chapter 3**). Closely related species, occupying identical habitats may depend on identical strategies, especially under strong environmental filters (Ordonez 2014), what could explain lack of differences between seed morph progenies of investigated species. Moreover, I did not observe differences in seed mass of distinct seed morphs (**Chapter 3**). This suggests, that potential differences between *Bidens* seed morphs, may be expressed rather in other traits, not addressed by my study, *e.g.* in dispersal ability or in seed longevity. Although in this thesis I focused solely on effects of seed heteromorphism on seedling performance, it is well known that different seed morphs may differ in dormancy and germination time (Imbert 2002). Therefore, these relations may be especially interesting for future studies (*e.g*. Fenesi *et al.* 2019).

Effects of adaptations to environmental variability are less unambiguous than previously described comparisons of trait values and their importance. This may have resulted from difficulties in separating particular mechanisms affecting traits (compare: **Study limitations**) or from specific, fluctuating conditions of riparian systems (Naiman *et al*. 2005; Lite *et al*. 2005; Wintle & Kirkpatrick 2007; Stella & Bendix 2019). Moreover, a more diverse set of compared species, *e.g.* representing different stages of invasion, can give us a meaningful perspective on the role of adaptations to environmental heterogeneity for plant invasions (Thuiller *et al*. 2006; Theoharides & Dukes 2007).

Study Limitations

From a methodological point of view, every study addressing ecological problems, has to face a complex trade-off between realism, precision, and generality (Morin 1998). **Chapters 2** and **4** describe field studies, representing high level of realism, however simultaneously suffering from a lower level of precision and reduced ability to provide mechanistic explanation. Contrastingly, **Chapter 3** is dedicated to precision, while simultaneously lessening the aspect of realism. This trade-off was especially pronounced in **Chapter 4**, which was aimed at relating particular traits with plant abundance. While this study provided important findings, which can help to understand relations between traits and success (Kuebbing *et al*. 2013), it could not isolate single mechanisms explaining observed patterns, as *e.g*. in the case of vegetative reproduction (**Chapter 4**). Although this trait was an important driver of abundance, on the basis of obtained results, it was not possible to determine, whether observed positive effect was more related to regeneration ability, dispersal or colonization strength (Johansson *et al*. 1996; Andersson *et al*. 2000; Jansson *et al*. 2005; Richardson *et al*. 2007). Similarly, in field settings it was not possible to distinguish different sources of trait variability *i.e.* phenotypic plasticity and genetic variability (**Chapter 2**).

A limitation of studies conducted in the natural systems is the complexity of methodology, which has to respond to different field conditions. For example, correctly analyzing data originating from different populations, located in distinct river systems, may require sophisticated statistical approaches (*e.g.* **Chapter 2**). Similarly, accounting for geographical localization might potentially affect importance of other, environmental factors *e.g.* climatic variables (**Chapter 4**). Restriction originating from filed conditions can also hamper gathering additional environmental data. For instance, localization of suitable study sites in reference to gauging stations (outside of the sampling areas), precluded the use of hydrological data *e.g.* river discharge (**Chapter 4**). Similarly, other factors *e.g.* species composition on adjacent areas could improve understanding of processes occurring on the study sites. For instance, it could improve our understanding of spread from adjacent areas and consequently help to explain importance of vegetative reproduction for investigated species (**Chapter 4**).

One of the commonly highlighted complications concerning multispecies studies is the importance of phylogenetic relationships between species (Pyšek & Richardson 2008; Gallagher *et al*. 2015). This problem was resolved in **Chapters 2** and **3** by comparing closely related pairs (Felsenstein 1985; van Kleunen *et al*. 2008), however on the cost of generality of delivered results. Still in **Chapter 4** due to the problems with model convergence, it was not possible to include phylogenetic information.

Difficulties with maintaining uniformity of approaches can be problematic for studies using various methodological approaches. Here one of the encountered problems was a difficulty with applying identical sets of traits across all the chapters. For instance, **Chapter 4** did not use trait values measured *in situ*, but rather information collected from databases. This resulted in a potential bias *e.g.* related to intraspecific variability or presence of juvenile forms of plants on the sites.

Conclusions and future implications

In this thesis I investigated traits of alien and native riparian plant species and their relation to plant success in riparian plant communities. Obtained results demonstrate that despite general similarities of strategies, alien and native plants differ in *e.g.* light acquisition strategy, biomass, type of spread or flowering duration. Observed differences, despite differences across sampled sites, contribute in explaining success of alien species in riparian habitats. Moreover, they shed light on mechanisms allowing coexistence of alien and native plants occupying riparian habitats.

It is rather unlikely to find a single set of attributes that can explain success of invasions across different conditions (Thompson *et al*. 1995; Alpert *et al*. 2000; Rejmánek 2000). **Chapter 4** demonstrated, that relations between traits and species abundances are highly dependent on environmental settings. As environmental variables considered in this thesis *e.g.* climae gradient were not of the main importance for relationship between traits and abundance, future studies could focus on different environmental drivers. For instance, differences observed in this thesis between river systems or along the river run, may be explained by flow characteristics *e.g.* mean annual river discharge, flooding length and frequency. These factors were previously showed to have different effects on native and alien plants species (Catford *et al*. 2011; Catford & Jansson 2014). Moreover, importance of some of the traits which affected abundance of investigated species *e.g.* beginning and length of flowering period (**Chapters 3**, **4**) can be driven by length and frequency of floods. This temporal perspective may be also related to observed differences in dispersal mode (**Chapter 4**) and may rise new questions related to colonization aspects of seed heteromorphism (**Chapter 3**). Importance of particular traits may differ not only across environmental conditions, but also between plants differing in life history or ecological strategies (Westoby *et al.* 2002). This possibility was indicated in **Chapter 4**. The main focus of this thesis was on annual plants, especially on congeneric pairs of species compared in **Chapters 2** and **3.** Similarly, alien species used for detailed comparisons were on identical invasion stage and shared similar residence time. This, may be one of the possible reasons for the lack of differences in trait variability described in **Chapter 2**. Results delivered by comparisons of alien species not as broadly established may differ from those delivered by my studies. To conclude, a comparison of patterns across other plant groups of plants differing in life histories, strategies or invasion stage and history is an interesting challenge for future studies that will further enhance our understanding of biotic invasions in riparian habitats.

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Appendix

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Publications of this thesis

Agnieszka Sendek, Katharina Herz, Harald Auge, Isabell Hensen, Steffan Klotz. (2015) Growth, reproduction and competitive ability of congeneric Native and invasive plant species. Does seed heteromorphism matter? Plant Biology 17(6). DOI: 10.1111/plb.12372.

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Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „*Differences in traits between co-ocurring alien and native plant species of annual riparian plant communities”* bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde. Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), 01.04.2019

Agnieszka Sendek