The role of functional traits across different stages of plant invasion process

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Table of content

Summary

Invasive alien species (IAS) impact ecosystem processes, biodiversity, ecosystem services, and human well-being. Alien plant species were introduced (often deliberately) for food, timber, or ornamental purposes and some of these species spread and became invasive. Many studies highlighted the importance of functional traits in invasion success. Alien species may differ in their traits from natives, and may have characteristics which can be advantageous, e.g. in colonization and competition. Therefore, in my thesis, I focus on the role of functional traits in the invasion process.

My thesis is composed of three main topics where I study the following:

1. Main ecosystem services and disservices provided by invasive plant species and how functional traits link to different socioeconomic and environmental sectors via (dis-) services.
2. Association between functional traits and environmental factors and how does it differ between native and alien plant species.
3. Local changes in functional diversity between native and alien plant species (archaeophytes, non-invasive and invasive neophytes) over three centuries of urbanization.

For my first topic (Chapter 2), I offered a novel conceptual framework, linking functional traits of invasive species with ecosystem services and disservices, that are further associated with six environmental and socioeconomic sectors. The framework thus allows assessing the overall effect of a trait even if the trait benefits one and has a negative impact on another sector. Another advantage of the framework is that, besides displaying the direction of the effect (positive or beneficial and negative or disadvantageous), it exposes the magnitude of the effect by allowing multiple types of categorization (e.g. monetary, according to environmental or socioeconomic effect, etc.). Additionally, the framework is applicable for multiple traits (even if they have contrasting effects) and highlights the main affected sectors.

The second topic (Chapter 3) aims to discuss the trait-environment relationships of native and alien species. I analyzed the relationship between 13 relevant functional traits and 12 environmental factors (climate, land cover types, and soil types). For this, I used 1000 randomly selected grid cells across Germany and 1300 plant species, both native and alien, with different residence time. I found that the relationship between traits and environment was not prominent in native species but it gets more pronounced with the residence time and invasiveness of the species. Thus, invasive neophytes have the largest number of relationships, followed by non-invasive neophytes and finally

archaeophytes. Specifically, I found that non-invasive neophytes mainly differed in traits such as urbanity and self-pollination in response to temperature and precipitation. In addition to these traits, invasive neophytes differ from non-invasive in SLA, storage organs, and beginning of flowering.

In the 4th Chapter of my thesis, I observed how the functional diversity of the above-mentioned species groups changed over 320 years. I asked whether urbanization in the city of Halle (Saale), Germany goes along with altered functional diversity (FD) and in which functional traits. To answer these questions I calculated functional diversity by using Rao's Q index and performed linear regression to examine the change in functional diversity across time, species groups, and traits. I found that overall FD did not change significantly over time. FD increased in invasive and non-invasive compared to native species, and I observed a significant increase in most of the invasive species' traits, except for seed mass. Lastly, besides height, most of the traits showed a decrease in FD over time. I conclude that the homogenization of traits over time is a result of increasing habitat similarity due to urbanization.

This thesis demonstrates the importance of studying functional traits in the invasion process and distinguishing those which promote invasion success. Furthermore, it highlights the importance of linking environmental factors to invasion success. Finally, it offers a comprehensive overview of the positive and negative effects invasive species have on ecosystem functioning and functional diversity.

Zusammenfassung

Invasive Arten beeinflussen Ökosystemprozesse, Biodiversität, Ökosystemleistungen und das Wohlbefinden des Menschen. Studien haben die Bedeutung funktioneller Merkmale für den Invasionserfolg hervorgehoben. Meine Arbeit besteht aus drei Hauptthemen, in denen ich folgendes untersuche:

- Ökosystemleistungen und negative Auswirkungen invasiver Pflanzenarten und wie funktionelle Merkmale über Ökosystemleistungen und negative Auswirkungen mit verschiedenen sozioökonomischen und ökologischen Sektoren verknüpft sind.
- Der Zusammenhang zwischen funktionellen Merkmalen und Umweltfaktoren und wie sie sich zwischen einheimischen und gebietsfremden Pflanzenarten unterscheiden.
- Lokale Veränderungen der funktionellen Vielfalt einheimischer und gebietsfremder Pflanzenarten (Archaeophyten, nicht-invasive und invasive Neophyten) über drei Jahrhunderte der Urbanisierung.

Ich schlage einen neuartigen konzeptionellen Rahmen vor, in dem funktionelle Merkmale invasiver Arten mit Ökosystemleistungen und negativen Auswirkungen verbunden werden, die weiterhin mit sechs Umwelt- und sozioökonomischen Sektoren verknüpft sind. Die Assoziation zwischen funktionellen Merkmalen und Umweltfaktoren ist bei einheimischen Arten nicht besonders ausgeprägt, wird aber mit der Verweilzeit und zunehmendem Invasionsstatus der Art deutlicher. Somit haben invasive Neophyten die größte Anzahl von Assoziationen, gefolgt von nicht-invasiven Neophyten und Archaeophyten. Schließlich stelle ich fest, dass sich die funktionelle Vielfalt im Laufe der Zeit nicht signifikant änderte, die funktionelle Vielfalt der invasiven und nicht invasiven Neophyten aber im Vergleich zu einheimischen Arten zunahm. Ich beobachte einen signifikanten Anstieg der Vielfalt der meisten Merkmale der invasiven Arten, mit Ausnahme der Samenmasse. Schließlich zeigten neben der Wuchshöhe die meisten Merkmale eine Abnahme der funktionellen Vielfalt im Laufe der Zeit. Meine Arbeit zeigt, wie wichtig es ist, funktionelle Merkmale im Invasionsprozess zu untersuchen und diejenigen zu unterscheiden, die den Invasionserfolg fördern.

Kennwörter

Archaeophyten, biologische Invasionen, einheimische Arten, gebietsfremde Arten, funktionelle Merkmale, funktionelle Vielfalt, invasive Arten, konzeptioneller Rahmen, Neophyten, Ökosystemleistungen, negative Auswirkungen, Stadtökologie.

Chapter 1.

General introduction

Plant invasions - definitions and concepts

Alien plant species (also often termed as exotic, non-native or non-indigenous) are those species that did not naturally occur in a region and were deliberately or accidentally introduced by humans (Blackburn et al., 2011; Richardson et al., 2000). This definition excludes natural range expansions as well as species which dispersed due to environmental changes, e.g. climate change or habitat alteration (Essl et al., 2019a). Invasive alien species (IAS) are a subgroup of alien species that have a negative impact, however, many invasive plants are used as food, timber, ornaments, etc. Still, most of the introduced plant species never become invasive (Ricciardi and Cohen, 2007). Pyšek and Richardson (2006) categorized alien species according to their status in the invasion process into casual alien species (which can sporadically spread but do not establish self-replicating populations), naturalized species (species able to establish self-replicating populations), and invasive species. In their classification, IAS are defined as “those naturalized plants with potential for fast spread over large areas” and not because of their impact (Davis and Thompson, 2000), but rather due to biological and ecological properties (propagule pressure).

Further, alien species can be distinguished according to their residence time in the new area (Hoffmann, 1998). In Europe, all alien plants introduced in new regions before 1500 (c. the discovery of America) are classified as archaeophytes (greek, *archaeo*-ancient, early). These plant species are predominately associated with agriculture (Kühn and Klotz, 2003; Preston et al., 2004; Pyšek et al., 2002). The second category of alien species is neophytes, introduced recently (after 1500; greek, *neos*-new). Neophytes are especially common in urban areas, however, especially since the 1950s they are getting increasingly abundant in agricultural landscapes, replacing some native weeds and archaeophytes (Pyšek et al., 2005).

Historical context and drivers of plant invasions

Biological invasions are considered one of the biggest threats to biodiversity, alongside climate change, human population growth, habitat degradation, and urbanization (Brook et al., 2008; Díaz et al., 2019; Pauchard and Shea, 2006; Pyšek et al., 2020). Throughout history, alongside with the development of human communities, plants and animals were considered commodities that were traded, and used as food, medicine, or raw material. As people migrated to other regions they carried useful species with them. With population growth and the "discovery" of ("new") areas and continents, trading of species became the part of the business and introducing species from distant regions became common. One of the examples of species introductions was during the 18th century when many exotic species and seeds were exchanged between plant enthusiasts and horticulturalists in Europe and North America. These exotic species were admired in their new residences because of their ornamental values, and botanical gardens, nurseries, and private collections attracted a lot of attention. The trend of species introduction has not subsided in the following centuries. However, some of these cultivated species did manage to escape and establish, and few of them got so successful that they became invasive. The number of introduced and naturalized plant species around the world currently encompasses almost 14 000 and is expected to increase in the future (van Kleunen et al., 2015). This is particularly pronounced in urbanized habitats where alien species amount up to 28% of the flora (Aronson et al., 2014).

Ecosystem services and disservices provided by IAS

Alien species have a large impact on ecosystem functioning and they provide numerous ecosystem services as well as ecosystem disservices (Vaz et al., 2017). In Europe the taxon with the largest number of introduced species are vascular plants (Hulme, 2007) and most of these species were deliberately introduced (for example, most of the crops were introduced for food). Many alien species were, in fact, introduced for their potential benefits, e.g. food or timber, and since then escaped, established, and spread. DAISIE (Delivering Alien Invasive Species Inventories for Europe) recorded 5789 alien plant species (database includes only neophytes) in Europe, where 326 species (5.6%) have an ecological impact and 315 (5.4%) have an economic impact (Vilà et al., 2010).

Ecosystem services include a positive effect (corresponding to an increase in ES or reduction in EDS) while ecosystem disservices or a reduction in ES bring a negative impact on human well-being (influencing different ecosystem functions and processes; Shackleton et al., 2019). In my thesis, I used the CICES classification (Common International Classification of Ecosystem Services; Haines-Young and Potschin, 2012) which classifies ecosystem services into three categories: “provisioning services” (i.e. food, fiber, pharmaceuticals, water), “regulation and maintenance services” (i.e. climate, water and erosion regulation, nutrient cycling, pollination) and “cultural services” (i.e. recreation, aesthetics, spiritual values). Effects of alien species can be threefold (Charles and Dukes, 2008):

1. Economic (economic losses by estimating costs associated with damage by or eradication of invasive species),
2. Environmental (impact on ecosystem functioning including biodiversity loss),
3. Social (related to loss in cultural services including human health and living standards).

Functional traits and invasiveness

Studies have shown that certain functional traits are associated with invasiveness and are thus of great importance when studying potentially invasive species or the spread of already established invasive species (van Kleunen et al., 2010b). However, despite the benefits of studying plant traits and relating these with invasiveness, it is necessary to compare all relevant traits between native and alien (and ultimately invasive) species (Table 1.1a) under local environmental conditions. Studies often include small sets of species (Van Kleunen et al., 2010b), focus solely on the traits and lack context-dependence, which only offers a very simplified comprehension of the invasiveness. This results in inconsistent or contrasting outcomes, additionally highlighting the importance of including environmental factors when studying invasiveness. In their meta-analysis, van Kleunen et al., (2010b) found that invasive and non-invasive plant species significantly differed in multiple functional traits associated to physiology (e.g. photosynthetic rate, transpiration), leaf and shoot allocation (e.g. specific leaf area, shoot-root ratio), growth rate and size (e.g. biomass, height), and fitness-related traits (e.g. number of seeds, mortality).

The difference in reproductive traits (e.g. production and dispersal of seeds) is particularly pronounced in invasive species (Moravcova et al., 2010). Invasive species are characterized by smaller seeds and higher seed numbers, which enable them to survive in the soil for longer periods. Similarly, Hamilton et al., (2005) showed that smaller seed mass is associated with invasive species, as well as a high specific leaf area (SLA). Other studies as well proved that invasive species have higher SLA compared to non-invasive aliens (Table 1.1b), and they also exhibit dissimilar phenology (longer flowering periods) and higher values for height (Gallagher et al., 2015). When compared to non-invasive alien species, IAS differed in traits related to invasiveness, for example, invasive species showed a decrease in height and leaf area and an increase in SLA (Mathakutha et al., 2019).

(a)

Functional trait	Native	Invasive
Life span	Perennial	Annual and perennial
Life form	Graminoid and herbaceous	Graminoid and herbaceous
Height	Shorter	Shorter
Dispersal mode	Independent or wind	Independent or wind
Leaf area	Bigger	Smaller
SLA	Smaller	Higher
Leaf anatomy	Tougher leaves	Weaker leaves

(b)

Functional trait	Non-invasive alien	Invasive
Life span	Perennial	Annual and perennial
Life form	Graminoid and herbaceous	Graminoid and herbaceous
Height	Shorter	Taller
Dispersal mode	Independent or wind	Independent or wind
Leaf area	Bigger	Smaller
SLA	Smaller	Higher

Table 1.1. The difference in trait values for traits related to morphology, dispersal, and leaves between (a) invasive and native species and (b) invasive and non-invasive species (adapted from Mathakutha et al., 2019).

The meta-analysis by Davidson et al. (2011) showed that phenotypic plasticity under environmental changes (increase in resource availability) is higher for invasive than non-invasive species. However, Matzek (2012) showed that values for many functional traits significantly increased in invasive species compared to non-invasive species, while phenotypic plasticity remained constant across traits, under fluctuating environmental conditions. Further, it has been shown that invasion success depends on the mixture of specific traits and their interaction rather than individual traits (Küster et al., 2008). The authors found interdependency between different traits related to phenology and reproduction, where for example, they recorded relationship between length of flowering and pollination vectors, as well as ploidy and flowering. The invasion success and impact depends on the specific traits (Pyšek and Richardson, 2006) as well as the trait combination. Thus, studying traits and invasiveness is crucial but presents further challenge due to their interaction with environment, where traits of native and invasive species might get more similar, and competition where traits differ at different stages of introduction (Knapp and Kühn, 2012).

Biological invasions and global change

Climate change and land cover present two of the main threats to biodiversity and have a significant impact on native species by altering the conditions of their habitats. Additionally, the impact invasive species have on native flora may vary depending on environmental changes. Studying the responses of native and alien species to climate and land-use change is crucial, because both groups may differ in functional traits and success (e.g. survival, abundance) under new conditions (Hellmann et al., 2008). IAS have larger tolerances to climatic changes (e.g. changes in temperature and precipitation) compared to non-invasive species (Rejmánek, 1995), however, Marini et al., (2012) found that propagule pressure and novel habitats are predominately affecting distribution of aliens. The environment affects alien species at all stages of the introduction process but particularly during colonization and establishment when alien species must overcome environmental filters. Due to their origin, invasive species might be more successful in competition with natives in the future as temperature and precipitation changes (warmer and drier climate; Hulme, 2009). For example, an increase in temperature may affect invasive species introduced from warmer to temperate regions, by prolonging their flowering periods.

Urbanization (increase in human population and infrastructure) presents a particularly important aspect of global change, and it influences biodiversity and the co-occurrence of native and alien species. For example, urbanization affects species diversity (positively or negatively) because it causes loss or gain of different habitats, climate change, and pollution and it is identified as one of the main factors of native species extinction (Czech et al., 2000) especially of rare native species (Kühn and Klotz, 2006). However, an increase in the urban area can have a positive effect on biodiversity. This mainly results from an influx of alien species that are accommodated by highly heterogeneous habitats in the cities or greater resource availability (e.g. water availability or highly fertile soils; McKinney, 2006) which leads to overall higher numbers of native and alien plant species (Kühn et al., 2004). Long term studies, reporting on species occurrences or diversity, over several decades or centuries are available for multiple cities around the world (e.g. Leipzig (Klotz and Gutte, 1992; Scholz, 2008), New York City (DeCandido et al., 2004) or Adelaide (Tait et al., 2005)). Historical data might be valuable for understanding the relationship between species composition, their traits and different aspects of urbanization, as they provide snapshots of flora at different stages of urban developments. As species diversity of aliens increases with human population growth and rise of temperatures, it is crucial to study mechanisms behind their success which explain current state as well as predict future trends (increase in alien species numbers with climate change in urban areas; Marini et al., 2012).

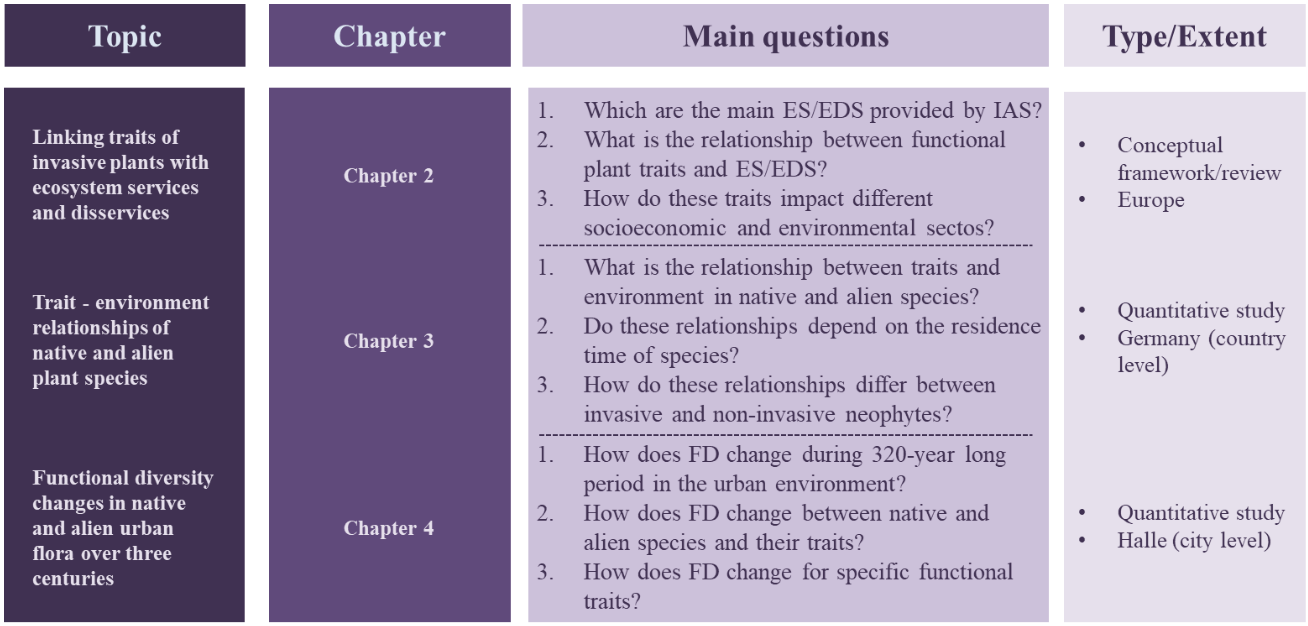
Structure of the thesis

The main aim of this thesis is to evaluate the role of functional traits in the introduction process, by comparing native and alien species at different stages of introduction. I wanted to demonstrate the association of traits with the provision of ecosystem services and disservices as well as to unravel relationships between traits and different climatic and land use conditions. Specifically, I addressed the following topics:

1. Invasive species have positive effects and negative impacts on human well-being. This influence is mediated by species functional traits. In **Chapter 2**, I proposed a conceptual framework, which relates plant traits to ecosystem services and disservices provision. In addition to the identification of functional traits that affect (positively and/or negatively) provision of services, the framework offers a further examination of the relationship between traits, services, and different environmental and socioeconomic sectors of human well-being. Finally, I used all invasive plant species in Europe covered in the DAISIE list “100 of the worst” and reviewed the literature, to assess the effect of these invasive species on ES and EDS (Figure 1.1; published in *Ecosystem Services*, 2020 doi:10.1016/j.ecoser.2020.101072).
2. Invasive species success can be due to the differences in functional traits to native species (or to non-invasive alien species) as IAS may be more successful (widespread occurrence, increase in abundance) under different environmental conditions. In **Chapter 3** I focused on the still pending question: how functional traits of native and alien plant species (at different stages of introduction process) differ in response to environmental predictors. I selected thirteen relevant functional traits and compared how their association with climate (temperature, precipitation), land cover

(different land cover types, number of land cover patches), and geology (soil types, number of geological patches) differs between native species, archaeophytes, and invasive and non-invasive neophytes (Figure 2; published in *NeoBiota*, 2020 doi: 10.3897/neobiota.58.51655).

3. In **Chapter 4** I aim to investigate the changes in the functional diversity of native and alien plant species alongside urbanization. I studied changes in functional diversity for the period from 1687 until 2008 (divided into seven periods spanning over 320 years) in the city of Halle (Saale), Germany. I chose eleven functional traits that are related to competition, reproduction, stress tolerance, and that may promote invasiveness. I tested for the difference in functional diversity between native and alien plant species (alien species divided into archaeophytes, neophytes, and invasive neophytes) over time and for individual traits (Figure 2; submitted to *Biological Invasions*, 2020).
4. Finally, in **Chapter 5**, I review and discuss the main results from chapters 2-4 of this dissertation. Here, I link the main findings from each chapter. In the conclusion section, I discuss the limitations of the studies and I address recommendations for future studies.



Topic	Chapter	Main questions	Type/Extent
Linking traits of invasive plants with ecosystem services and disservices	Chapter 2	1. Which are the main ES/EDS provided by IAS? 2. What is the relationship between functional plant traits and ES/EDS? 3. How do these traits impact different socioeconomic and environmental sectos?	• Conceptual framework/review • Europe
Trait - environment relationships of native and alien plant species	Chapter 3	1. What is the relationship between traits and environment in native and alien species? 2. Do these relationships depend on the residence time of species? 3. How do these relationships differ between invasive and non-invasive neophytes?	• Quantitative study • Germany (country level)
Functional diversity changes in native and alien urban flora over three centuries	Chapter 4	1. How does FD change during 320-year long period in the urban environment? 2. How does FD change between native and alien species and their traits? 3. How does FD change for specific functional traits?	• Quantitative study • Halle (city level)

Figure 1.1. Overview of the main topics and questions for every chapter with the type and extent of the study presented in the final column. ES = ecosystem service, EDS = ecosystem disservice, IAS = invasive alien species, FD = functional diversity

Chapter 2.

Linking traits of invasive plants with ecosystem services and disservices

Introduction

Alien plant species have been introduced by humans all over the globe and many of them have become invasive (i.e. causing impact; see below). They have modified ecosystems for centuries with great effects on the environment and human well-being (Vilà et al., 2010, Vilà and Hulme, 2017). Alien species numbers have increased with the development of agriculture, forestry, and industry (van Kleunen et al., 2015, Pyšek et al., 2017) and this increase is not yet saturated (Seebens et al., 2017). Alien species were reported to have a great effect on agriculture, for instance, in the US introduced species make up 98% of food consumed (Pimentel et al., 2005). Similarly, plant species used in forestry or horticulture are often introduced, e.g. a study in the US showed that 82% of tree species (out of 235) were introduced for landscaping, already in the 17th century, when the first ornamental garden was founded (Reichard and White, 2001). At the same time, there are hundreds of alien woody species (most commonly of the genera *Pinus*, *Eucalyptus* and *Acacia*) commercially planted for timber (Holmes et al. 2009). Herbaceous plant species are introduced as ornamentals in botanical gardens or private gardens because of their exotic appearance (Hulme et al., 2018, van Kleunen et al., 2018) or for the production of pharmaceutical and cosmetic compounds (Scott, 2010). In Europe, the majority of alien plant species were introduced for agriculture, forestry, materials, horticulture or as ornamental species (Lambdon et al., 2008). Further, alien species are used in ecosystem restoration, for soil stabilization, and as phytoremediators or windbreakers (Pejchar and Mooney, 2009).

While ecosystem services (ES) present direct or indirect positive effects, disservices (EDS) generate functions, processes and attributes in ecosystems that result in perceived or actual negative impacts on human well-being (Shackleton et al., 2016). In this chapter, I first introduce invasive alien plant species and their environmental and socioeconomic effects. Further, I present plant functional traits linked with invasiveness and ES / EDS. Additionally, I overviewed main ES/EDS of invasive plant species in Europe as a rationale for a conceptual framework that links IAS, traits and ES/EDS. Here, I used the Common International Classification of Ecosystem Services (CICES; Haines-Young and Potschin, 2012) where ES can be classified as follows: (i) provisioning services (including food, fiber, pharmaceuticals, water and others); (ii) **r**egulation and maintenance services **(**climate, water and erosion regulation, nutrient cycling, pollination etc.); and (iii) cultural services (spiritual and aesthetic values as well as providing foundation for tourism and recreation development).

Background

Invasive plant species

By now, 13,168 alien plant species have been reported as naturalized around the world (GloNAF - Global Naturalized Alien Floras; van Kleunen et al., 2015, Pyšek et al., 2017, van Kleunen et al., 2019), with highest numbers in North America (5958 taxa), Europe (4139) and Australasia (3886; Pyšek et al., 2017). Most alien species that successfully naturalize in a new area (i.e. forming self-sustaining populations by reproducing in the wild without human intervention and thus become permanent parts of the flora; Richardson et al., 2000, Pyšek et al., 2012a), do not necessarily modify their new habitat or cause positive or negative effect on environment or people. Vilà et al. (2010) showed that 5–6 percent of alien plant species in Europe are noted to have an environmental and socioeconomic effect. Estimates of the total numbers of invasive plant species over the globe vary (e.g. 451 in Weber (2003), excluding agricultural weeds, or 672 in the CABI Invasive Species Compendium; www.cabi.org/isc).

In this chapter, I term these “invasive alien species” (IAS), following the IUCN (2000) definition rather than the one commonly used in ecological literature where the criterion for a species to be invasive is rapid spread (Richardson et al., 2000). Therefore, “invasive alien species (IAS) are animals, plants or other organisms that are introduced into places outside their natural range, negatively impacting native biodiversity, ecosystem services or human well-being” (IUCN, 2000). Invasive species are easily transported by people and disperse effectively (Wilson et al., 2016). Additionally, they can rapidly adapt to a range of environmental conditions and therefore, inhabit a variety of ecosystems (Hellmann et al., 2008).

Environmental and socioeconomic effects of IAS

Invasive plant species have negative impacts on the environment, public health, recreation or infrastructure (Pyšek et al., 2012b, Blackburn et al., 2014, Jeschke et al., 2014), related to reduced provision of ES or increased EDS (Vaz et al., 2017, Potgieter et al., 2019). The most frequently documented impacts of invasive species on ecosystems are competition for resources with other plant species (Kumschick et al., 2015) and the spread of diseases and pests (Pimentel et al. 2005, Holmes et al. 2009). Many studies have shown that invasive species impact the diversity of native species in invaded plant communities (Hooper et al., 2005, Hejda et al., 2009, Pyšek et al., 2012b). Biodiversity has an important role in supporting ecosystem functioning and ecosystem services (e.g. food provision, nutrient cycling, microclimate regulation; Altieri, 1999) and according to Millennium Ecosystem Assessment (2005) the maintenance of biodiversity provides significant benefits to humans (although not every ES directly depends on biodiversity; Schwarz et al., 2017). Still, biodiversity is also an important asset (and hence service) in itself. Furthermore, invasive plants can have detrimental effects on ecosystems by altering nutrient and water cycles or facilitating erosion (Kettunen et al., 2008).

Agriculture, forestry and tourism can profit from IAS, however economic costs of losses, damage and control can exceed the profits they provide (Pimentel et al., 2005). For example, in the US, IAS cause the major losses in crop production resulting in 26.4 billion dollar loss per year, including a loss of 21 billion dollars by introduced pests and microbes (Pimentel et al., 2005). Similarly, invasive pathogens result in considerable losses in forestry and recreation sectors – up to 20.3 and 2 billion US dollars annually, respectively (Pimentel et al. 2005, Holmes et al., 2009). Furthermore, there are additional economic and environmental costs resulting from eradication, such as ecosystem recovery from the damages caused by herbicides or other weed removal techniques (Pimentel et al., 2005). In the UK, Japanese knotweed (*Fallopia japonica)* causes significant damages to infrastructure (roads, households, railways), with the costs of vegetation management and eradication totaling 165 million pounds, annually (Williams et al., 2010). Finally, IAS can decrease landscape quality and cause health problems (Kettunen et al., 2008, Pyšek and Richardson, 2010, Sladonja et al., 2015, Lazzaro et al., 2018). Overall, in Europe, terrestrial invasive plants cost 3.74 million euros annually, a third of total economic costs caused by all IAS in Europe (Kettunen et al., 2008).

Nevertheless, some IAS can also have beneficial effects, manifested as increased provision of ES or reduced EDS. They can, consequently, affect environmental and socioeconomic sectors (agriculture, forestry, infrastructure, human health, aesthetics and recreation, environmental effect: sectors adapted from categories by Kumschick et al., 2012) positively and negatively (Table 1). For example, some plant invaders, such as *Ailanthus altissima,* can cause severe allergies in humans, yet, the species is used in the pharmaceutical industry due to its beneficial chemical compounds (Sladonja et al., 2015). Ornamental species can increase the recreational value of the landscape but also have an adverse effect on ecosystems by degrading habitats, reducing biodiversity, causing injuries, and being toxic to humans (Potgieter et al., 2017). Invasive tree species used for timber production can at the same time release chemical compounds via allelopathy (Holmes et al., 2009) thereby inhibiting the growth of surrounding trees (decrease in ES). Many ornamental broad-leaved trees emit biogenic volatile organic compounds, which increase the concentration of ozone and photochemical smog in the atmosphere (Niinemets and Peñuelas, 2008). The complexity of ecosystems and interactions between invasive and native species makes identifying the real effects of invasive species difficult.

Plant traits associated with invasiveness

Many studies showed that certain functional traits of introduced plant species are associated with their ability to become invasive (e.g. flowering period, clonality, height; Pyšek et al., 2015, Pyšek et al., 2009, van Kleunen et al., 2010b). In this chapter, we consider functional traits as “any trait which impacts fitness indirectly via its effects on growth, reproduction and survival” (Violle et al., 2007). Some traits associated with plant invasiveness include: growth rate (IAS grow faster compared with native species), SLA (higher specific leaf area in IAS), flowering phenology (IAS start flowering earlier and have longer flowering periods), higher fecundity and more efficient seed dispersal (Pyšek and Richardson 2007). Given the relationship of plant traits with plants’ invasiveness I argue that plant traits can be an important tool for predicting benefits (ES) or impacts (EDS) for different environmental and socioeconomic sectors (Table 2.1): Traits do affect ecosystem functions (Díaz et al. 2004), which humans might perceive as services or disservices that can translate into societal (monetary or non-monetary) values (cf. ecosystem service cascade; Haines-Young and Potschin 2010).

Thus, it is important to make a distinction (Fig. 2.1) between response and effect traits (Lavorel and Garnier 2002) in different stages of the invasion process, i.e. transport and introduction to a new area, establishment of self-sustaining populations (naturalization), and spread within the new area (Richardson et al., 2000).

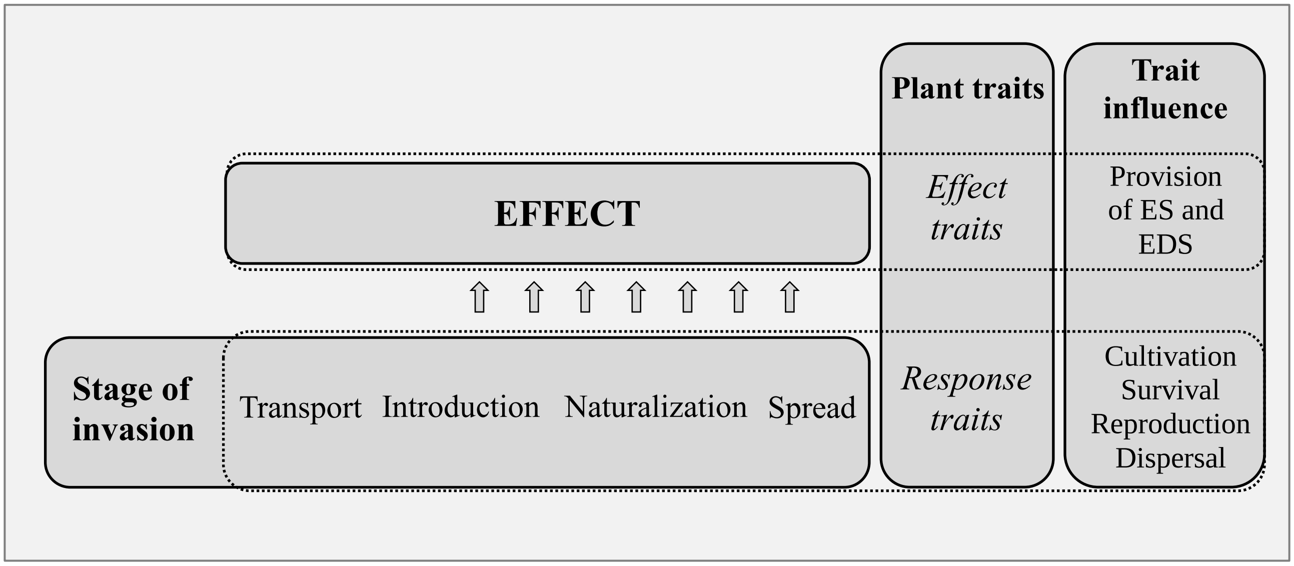


Figure 2.1. Different types of plant traits are important for each stage of invasion; response traits in early stages, while effect traits become more significant when introduced species begin to have an impact. However, the effect can be realized at any stage of the process.

Response traits respond to environmental changes (e.g. life form, SLA, life cycle, relative growth rate, leaf and root morphology and seed mass; Lavorel and Garnier, 2002). Therefore, they are crucial throughout the invasion process, predominantly during the plants' establishment and spread phases when plants need to overcome environmental barriers (Richardson et al., 2000). Different traits may be beneficial in different phases of the invasion process (Richardson and Pyšek, 2012) – such as ornamental traits that might decide which species are transported across countries at all (Reichard and White, 2001). When IAS start to have an impact on ecosystems or economies, effect traits become more relevant since they affect ecosystem functioning and the provision of ES or EDS. These include, among others, plant height and biomass (competitive ability), phenology, mutualism with nitrogen-fixing bacteria, longevity, leaf litter quality or photosynthesis pathway (for example, in South Africa most of the invasive grass species are C3 and can have an advantage over C4 species in disturbed ecosystems or with an increase of CO_2, e.g. more efficient nitrogen use in grasses; Milton, 2004).

Plant traits and ES & EDS

Plants' effects on ES (such as crop yields, cultural services, pollination) are manifested by changing ecosystem functions and related values through the agency of functional traits such as biomass, plant height, canopy and root size/architecture, leaf dry matter content, SLA, soil organic carbon, flowering pattern or leaf P/N concentration (de Bello et al., 2010, Lavorel et al., 2011). Based on the frequency of certain traits, ecosystems may become "hot-spots" of ecosystem services, fostering multiple services provided by some species (Potgieter et al., 2017), or they can exhibit trade-offs between services and disservices as a result of contrasting traits. Some tree species, due to their fast growth contribute carbon sequestration, climate regulation or erosion control (ES), while this trait can lead to increase in fire risk (EDS; Castro-Díez et al., 2019). For example, Millward and Sabir (2011) showed that the effect of maple (*Acer platanoides*) on air quality is two-fold; it sequesters carbon dioxide from the air while emitting biogenic volatile organic compounds, which significantly reduce air quality. Such trade-offs can be expressed as a conflict between service and disservice.

In summary, the extent and direction of IAS' effects on ES and EDS can be ambiguous. Thus, it is necessary to create a framework that provides information on which plant species should be prioritized for management actions in which environmental or socioeconomic sectors, depending on their traits and thus their positive and negative effects. This chapter provides a framework which is an extension of existing frameworks (e.g. Vaz et al., 2017). It examines the relationship of (functional) traits of invasive plants with ecosystem services and disservices, by linking those traits to affected sectors (agriculture, forestry, infrastructure, human health, aesthetics and recreation, and environmental effect).

Hence, I aim to (1) identify the main ES/EDS for a variety of invasive plant species; (2) establish the relationship between functional plant traits with increases or decreases in services and disservices; (3) link these traits to different socioeconomic and environmental sectors and highlight those severely affected by invasive plants.

Main ES and EDS provided by invasive plant species in Europe

In order to identify the benefits (increase in ES/ decrease in EDS) and impacts (increase in EDS/ decrease in ES) of invasive plant species (Table 2.1, Table S2.1), I chose 18 vascular plant species from the list of representative invasive species in Europe provided by DAISIE (2009) and surveyed the literature for information on how these species affect ES/EDS. The main aim was to get an overview of ES and EDS provided by the selected invasive plant species in Europe. The main criterion for a species to be included on the DAISIE list was, besides it being classified as invasive in Europe, to cover a range of representative taxa and their impacts (Pyšek and Richardson, 2012), which makes the selection suitable for the purpose of my study. I listed the ES and EDS mentioned in the investigated literature with the direction of their effects (positive or negative; Table 2.1). For example, for *Fallopia japonica*, the ES reported are the provision of animal food, use in medicine, use as a pesticide and biofuel, and ornamental value (Table 2.1). However, *F. japonica* negatively affects infrastructure, can cause floods (thick plant shoots can block water flow; Palmer 1990, Colleran and Goodall, 2014), produces allelopathic chemicals and changes of habitat (Murrell et al. 2011).

Conceptual Framework

I propose a novel framework (Fig. 2.2) linking invasive plant species via their traits to ES and EDS relevant in different socioeconomic (agriculture, forestry, health) and environmental sector (with ES such as carbon sequestration, erosion control, pollination). The main aim is to link *actors* (IAS and their traits) with *results/effects* (ES and EDS) they generate on different sectors by identifying the impacts and benefits. Thus, the framework comprises three parts: *plant trait*, *ecosystem services* and *disservices*, and *sectors*. It is intended to address the following questions: Which sectors (environmental/socioeconomic) are most impacted by reduced ES/increased EDS contributed by invasive plants; what are the sectors benefiting from different increased ES/reduced EDS provided by invasive plants; which plant traits are predominantly responsible for influencing (positively or negatively via ES or EDS) different sectors; are there trade-offs in the effect caused by the same trait across sectors?

Table 2.1. List of effects on ecosystem services (increase and reduction in ES) and disservices (increase and reduction in EDS) provided by invasive plant species in Europe - (+): Increase in ES or EDS; (-): Decrease in ES or EDS

IAS	Ecosystem service	Ecosystem disservice	References (Table S 2.1)
Acacia dealbata	Used for timber (+) ; Erosion control (+) ; Windbreak (+) ; Ornamental (+) ; Enhancing pollination (+) ; Use in cosmetics (+);	Allelopathy (+) ; Erosion (+) ; Allergies (+) ; Nutrient alteration in soil (+);	Lorenzo et al. 2008; Weber, 2003; Lorenzoni-Chiesura et al. 2000; Chau et al. 1985; Logan, 1987; Le Maitre et al. 2011; Clemson, 1985; Griffin et al. 2011;
Ailanthus altissima	Pesticide (+) ; Use in medicine (+) ; Used for timber and fuel (+) ; Ornamental (+) ; Erosion control (+) ; Soil stabilization (+) ; Animal food (+);	Allelopathy (+) ; Allergies (+) ; Habitat alteration (+) ; Infrastructure damage (+);	Gómez-Aparicio & Canham, 2008; Ding et al. 2005; Ballero et al. 2003; Castro-Diez et al. 2009; Grapow & Blasi, 1998; Sladonja et al. 2015; Kowarik & Säumel, 2007; Lee et al. 1997; Heisey, 1997;
Ambrosia artemisiifolia	Crop yield (-) ; Animal food (+) ; Use in medicine (+) ; Phytoremediation (+); Biodiversity (-);	Pest transmission in crops (+);	Reinhardt et al. 2003; Bohár & Kiss, 1999; Beres et al. 2002; Dechamp, 1999; Stubbendieck et al. 1995; Bassett & Crompton, 1975;
Campylopus introflexus	Ornamental (+) ; Biodiversity (-);	Habitat alteration (+);	Biermann & Daniels, 1997; Daniëls at al. 2008;
Carpobrotus edulis	Ornamental (+) ; Soil stabilization (+) ; Use in traditional medicine (+) ; Used as food (+); Biodiversity (-);	Habitat alteration (+);	Weber, 2017; Moretti, 1939; Ordway et al. 2003; van der Watt & Pretorius, 2001;
Cortaderia selloana	Ornamental (+) ; Erosion control (+) ; Soil stabilization (+) ;	Habitat alteration (+) ; Allergies and injuries (+) ;	Bossard, 2000; DAISIE, 2009; Domènech & Vilà, 2006; Okada et al. 2007;

	Biodiversity (-);	Causes fire (+);	
Echinocystis lobata	Ornamental (+) ; Use in medicine (+); Biodiversity (-);	Toxic (+);	Ielciu et al. 2017; DAISIE, 2009;
Fallopia japonica	Animal food (+) ; Use in medicine (+) ; Pesticide (+) ; Biofuel (+) ; Ornamental (+) ; Biodiversity (-);	Infrastructure damage (+) ; Floods (+) ; Allelopathy (+) ; Habitat alteration (+);	Palmer, 1990; Beerling et al. 1995; Aguilera et al. 2010; DAISIE, 2009; Seiger & Merchant, 1997; Shaw et al. 2011;
Hedychium gardnerianum	Recreation (-) ; Ornamental (+) ; Use in medicine (+); Biodiversity (-);	Erosion (+);	Macdonald et al. 1991; Weyerstahl et al. 1998; Minden at al. 2010;
Heracleum mantegazzianum	Recreation (-); Ornamental (+) ; Use in medicine (+) ; Used as food (+) ; Herbicide (+); Biodiversity (-);	Allergies (+) ; Pathogen transmission (+) ; Habitat alteration (+) ; Erosion (+) ; Allelopathy (+) ;	Tiley et al. 1996; Jandová et al. 2014; Thiele & Otte, 2007; Wille et al. 2013; Nielsen at al. 2007; Chan et al. 2011; Solymosi, 1994; Westbrooks, 1991; Pyšek, 1991;
Impatiens glandulifera	Recreation (-) ; Biodiversity (-) ; Animal food (+) ; Ornamental (+);	Habitat alteration (+) ; Erosion (+) ;	Pattison et al. 2016; Hulme & Bremner, 2006; Beerling & Perrins, 1993; Pyšek & Prach, 1995;
Opuntia ficus-indica	Recreation (-) ; Biodiversity (-) ; Ornamental (+);	Injuries (+); Toxic for people and cattle (+);	Larsson, 2004; Brolin, 2004; Nikodinoska et al. 2014; Griffith, 2004;
Oxalis pes-caprae	Honey production (+) ; Crop yields (-) ; Tourism (+) ; Pollinators (+) ; Biodiversity (-);	Toxic (+);	Marshall, 1987; McLaughlan et al. 2014; DAISIE, 2009;
Paspalum paspaloides	Crop yields (-) ; Preventing floods (+) ; Animal food (+) ; Erosion control (+) ; Phytoremediation (+)	Attractive for mosquitos/disease transmitters (+);	Holm et al. 1979; Lawler et al. 2007; Bernez et al. 2005; Bor, 1960; Rosicky et al. 2006; Shu et al. 2002; Lee et al. 2004;

	; Biodiversity (-);		
Prunus serotina	Forestry (-) ; Agriculture (-) ; Ornamental (+) ; Erosion control (+) ; Used for timber (+) ; Used as food (+) ; Biodiversity (-);	Toxic (+) ; Soil alteration (+);	Verheyen et al. 2007; DAISIE, 2009; Starfinger et al. 2003; Fowells, 1965; Stephens, 1980;
Rhododendron ponticum	Forestry (-) ; Pollination (-) ; Recreation (-) ; Ornamental (+) ; Use in medicine (+) ; Biodiversity (-);	Toxic (+);	Black, 1991; Colak et al. 1998; Milne & Abbott, 2000; Dehnen-Schmutz et al. 2004; Erdemoglu et al. 2003;
Robinia pseudoacacia	used as biofuel (+) ; Forestry (+) ; Ornamental (+) ; Pollination (+) ; Used as food (+) ; Used in cosmetics (+) ; Biodiversity (-);	Habitat alteration (+) ; Toxic (+) ; Infrastructure damage (+);	Sabo, 2000; Benesperi et al. 2012; Rédei et al. 2008; DAISIE, 2009; Rédei et al. 2002; Keresztesi, 1977; Grollier et al. 1986;
Rosa rugosa	Biodiversity (-) ; Recreation (-) ; Tourism (+) ; Erosion control (+) ; Ornamental (+) ; Used as food (+) ; Use in medicine (+) ; Used in cosmetics (+) ; Windbreak (+);	Injuries (+) ; Habitat alteration (+) ; Pest host/transfer (+);	Vanderhoeven et al. 2005; Isermann, 2008; Shorthouse, 1987; Jørgensen & Kollmann, 2009; Weidema, 2006; Dobson et al. 1990; Dubey et al. 2010; Bruun, 2006;

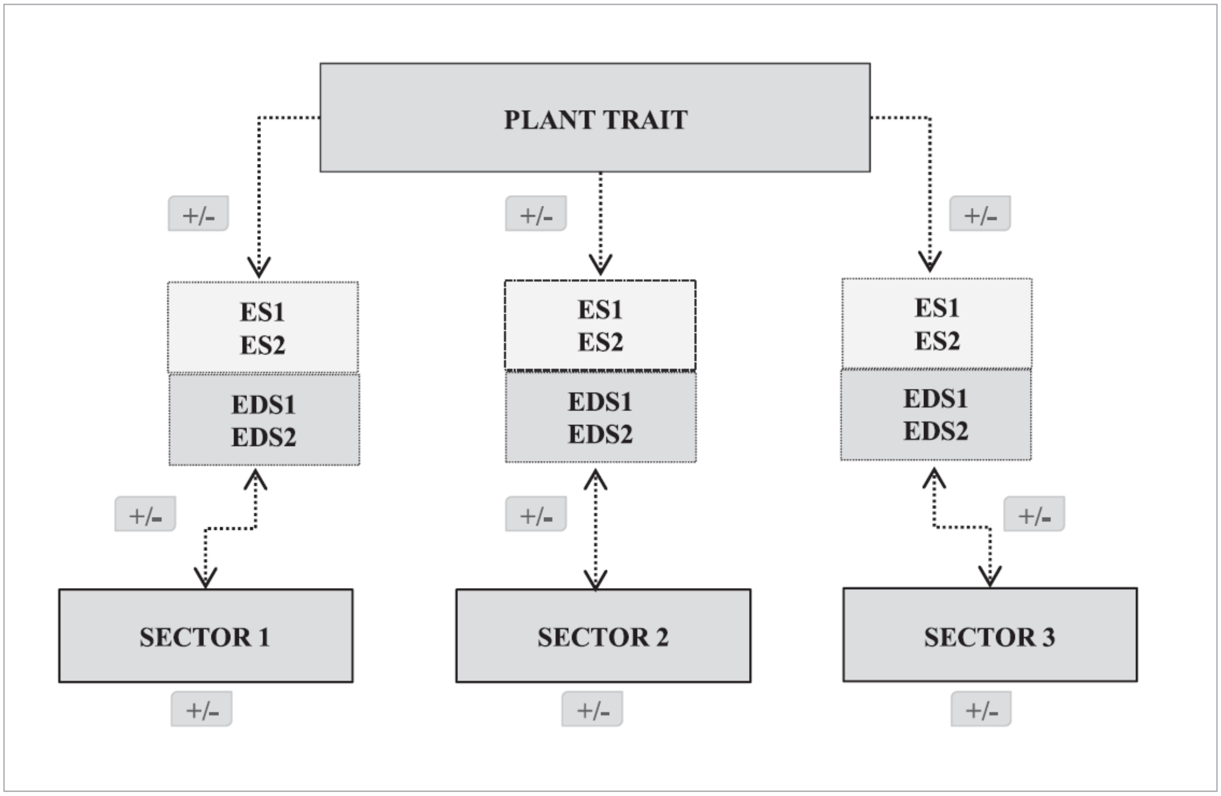


Figure 2.2. Conceptual framework showing the linkage between a plant trait, ecosystem services, ecosystem disservices and different sectors (environmental/ socioeconomic) affected by IAS. Both, ES (light gray box - ES1, ES2) and EDS (dark gray box - EDS1, EDS2) can be increased (“+”) or decreased (“-“) by IAS, resulting in different types of benefits or impacts on sectors. Therefore, benefits are the result of a positive effect on ES or negative effect on EDS and impacts are an outcome of negative influence on ES or positive on EDS. Finally, if the strength of the influence is known (depending on the literature and data availability), it can be presented with the thickness of links between sectors and services (low impact – thin line, medium impact – thicker line, high impact – the thickest line). Moreover, the framework is applicable across all traits and plant species.

Plant traits

Plant traits were shown to be important for the provision of services and disservices. For example, canopy and root size affect various regulating services (climate and water regulation, soil stability) and the provision of food (de Bello et al., 2010). Leaf traits (leaf dry matter content, SLA and nitrogen content) affect soil fertility but also can be crucial for biocontrol and as a cultural service (ornamental value). For some legume species, traits such as corolla length are valuable for pollination efficiency

(Lavorel et al., 2013). Phenological pattern in flowering (time and duration) is another characteristic affecting the provision of resources for pollinators (Lavorel et al., 2013). In woody plant species, tree height and biomass are principal traits impacting or enhancing provisioning services (timber and biofuel) and cultural services (aesthetic appreciation). Similarly, provisioning services (provision of food for humans or animals) are mainly affected by plant biomass (de Bello et al., 2010), either as the amount of food produced or as decrease in crop yields (via competition or allelopathy). The example of biomass shows that effects of plant traits can be context dependent (can have a positive or negative effect on ES/EDS). However, species with similar life form or habitat might have similar effects on ES/EDS. Provided that the traits show a similar pattern between different IAS, the framework can be used as an efficient way of tackling their impact and can lead to faster interventions.

Sectors, ecosystem services and disservices

I assigned ES and EDS to six main public sectors influenced by invasive plant species: agriculture, forestry, infrastructure, human health, aesthetics and recreation, and environmental effect. Each of these sectors can have numerous services and/or disservices provided by IAS (Fig. 2.3). IAS affect food production, timber, medicine, erosion control, via increasing or reducing these services. Moreover, invasive plants support or diminish disservices, such as pathogen transmission, and damage to infrastructure, human health or fire regimes. However, sometimes apparent disservices (e.g. allelopathy) can be perceived beneficial in specific circumstances or ecosystems (plants can produce and release allelopathic secondary metabolites affecting other plants and ecosystem, while the same chemicals can be used in pharmaceutical industry; Jimenez-Garcia et al., 2013). Identifying cumulative plants' effects (positive or negative) can simplify and improve decision making, particularly when multiple ES and EDS are considered.

Application of the framework

Traits of invasive plant species can affect an array of ES and EDS. Although these effects can be straightforward (e.g. increase in tree biomass provides more timber, pollen of a plant causes allergies etc.) often the effect is ambiguous or even antagonistic (simultaneous provision of both ES and EDS;

Fig. 2.3). Below, I present several examples of plant traits with opposing effects (providing both, ES and EDS), where it can be beneficial to apply the framework for deciding on managing invasive species.

Tree canopy

Plant height and canopy height are traits that can have conflicting effects. For example, tree species can provide shade and climate regulation (ES), however, such shady places can be perceived as unsafe and as cover for burglars or wild animals (Lyytimäki and Sipilä, 2009; Potgieter et al., 2019).

Nitrogen-fixing plants

Black locust (*Robinia pseudoacacia*) is a nitrogen-fixing invasive plant species in Europe. It increases nitrogen in soil and litterfall, which can be a service in nutrient-poor tree plantations (Rice et al., 2004) or a reduced service where it negatively affects the diversity of non-nitrophilous species (Benesperi et al., 2012).

Pollination type

Invasive plant species can be very attractive to pollinators and offer an additional food source. Brown et al. (2002) recorded a decrease in pollination of native *Lythrum alatum* in the presence of invasive *Lythrum salicaria*. Although food availability increased for pollinators (ES), visitation rates decreased for the native species, as well as pollen quality due to heterospecific transfer between the two species (EDS).

Toxicity

Leaves of nettle (*Urtica dioica*) are used as food and herbal medicine in many parts of the world. Yet, when uncooked its stinging leaves are painful in direct contact, and leaf's hairs can cause irritation or even be toxic for humans (Connor, 1977).

Use and data requirements

The conceptual framework has the advantage that it can be applied across multiple invasive species by using species traits as a fundamental unit. Simultaneously, the framework provides an overview of all (selected/observed/interesting/relevant) services and disservices (including whether they are positively or negatively affected, respectively) and highlights main sectors influenced by IAS. It hence brings into focus sectors that urgently need to be addressed and traits most relevant for positive or negative effects in several sectors (Box 2.1).

The application of the conceptual framework requires data on species trait(s) and lists of ES and EDS provided with the effects quantified (or in some cases with qualitative data). Currently, studies quantify effects by (i) numerical scoring (e.g. 1 to 5 or 1 to 3), (ii) description (very high, high, moderate, low, none; Blackburn et al., 2014, Bacher et al., 2018, Nentwig et al., 2016, 2018), (iii) statistical significance (significant or non-significant impact; Pyšek et al., 2012b), (iv) monetization (costs or value; Cook et al., 2007), (v) percentage of increase/decrease (e.g. crop yields; Fried et al., 2017).

IAS have been classified with respect to their environmental impact – EICAT (Blackburn et al., 2014) and socioeconomic impact – SEICAT (Bacher et al., 2018) into several categories: massive, major, moderate, minor and minimal concern. This categorization was developed to help identify the magnitude of negative effects alien species have on the environment and human well-being. Similarly, classification can be established for benefits provided by IAS. Changes caused by IAS can be perceived as beneficial (increased ES/decreased EDS) or harmful (increased EDS/decreased ES) by different people depending on their personal preference, financial status, cultural background or education (Shackleton et al., 2018, Potgieter et al., 2019). Therefore, the main advantage of my framework is that it is suitable for different types of data sets and that it allows flexibility in the choice of scoring systems. It can hence serve as a basis for further meta-analyses. Summarizing, my framework has several advantages: One can use multiple traits and/or multiple species when assessing the effects of IAS. The framework addresses the "bigger picture" by assessing the effect of invasive species on sectors (and not only ES/EDS as in Vaz et al., 2017) and thus "opposing" effects (e.g. positive effect via one ES and impact via another reduced ES /EDS). In this case trait can have predominately negative effect in one sector (e.g. increases in biomass can impact wood production or biodiversity), and mostly positive in another (e.g. increases shade, regulates climate and has ornamental value). Therefore, these species can be considered undesirable in forest but beneficial in urban areas and parks. The framework allows assessing the interplay between different ES/EDS and is adjustable to any type of qualitative and quantitative data. Some traits have multiple services (or disservices) but also there might be interactions among them including the ES/EDS interaction between different sectors.

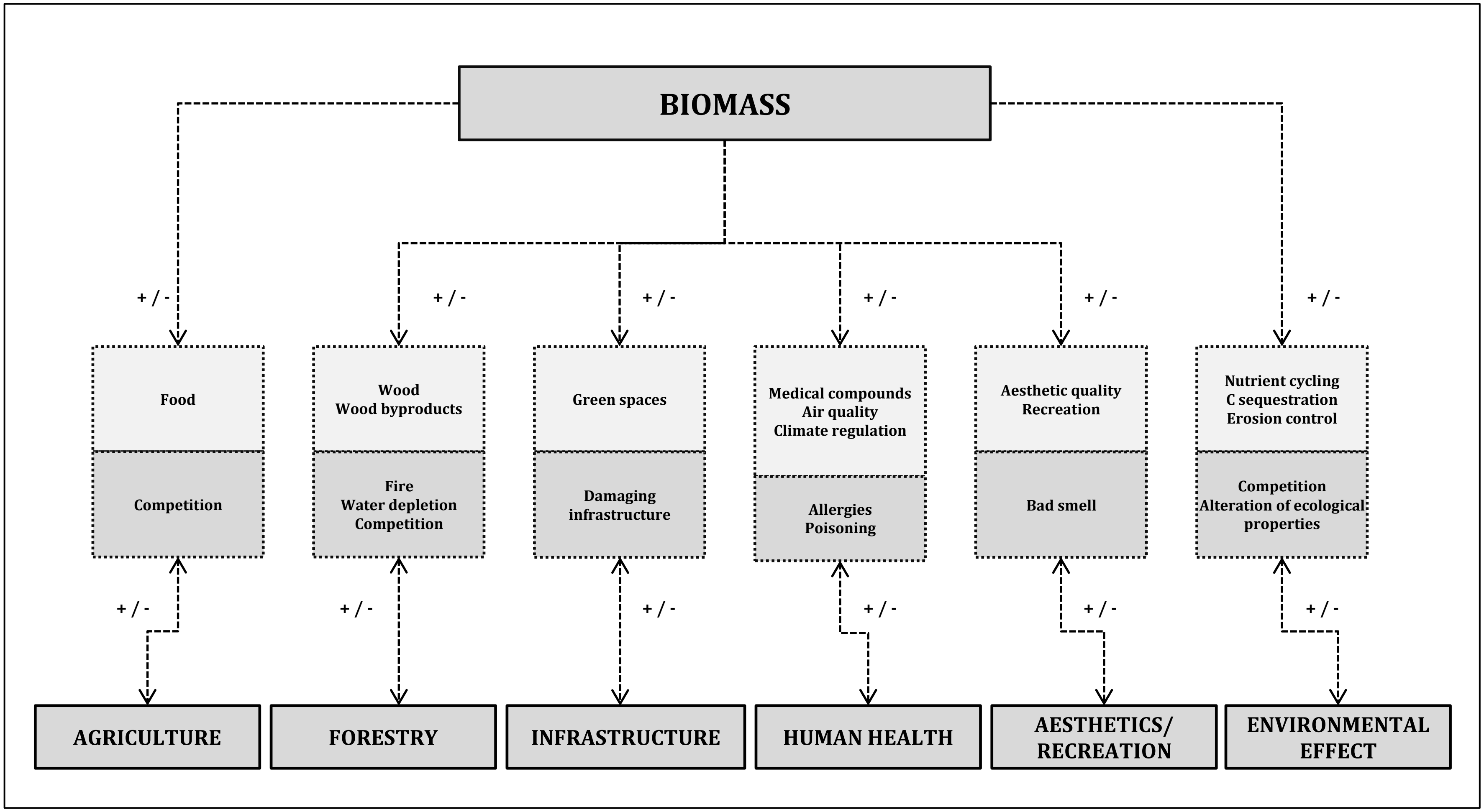
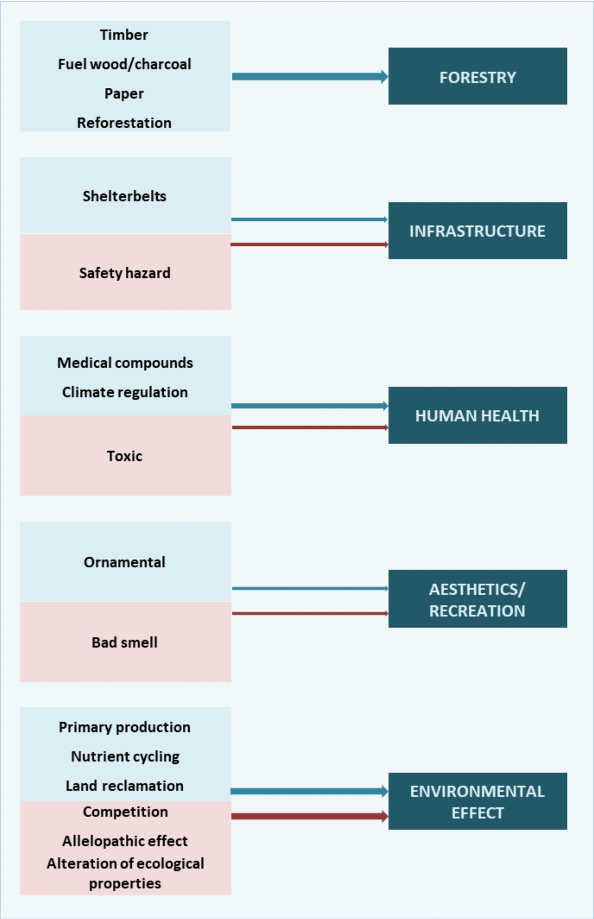


Figure 2.3. Biomass (e. g. increase of biomass) as a trait of invasive species and its benefits (+) or impacts (-) on different sectors and ES (light gray boxes with dotted frame) and EDS (dark grey boxes with dotted frame)

In addition to the framework's advantages, some limitations exist. Due to lack of data, currently, the framework is predominantly applicable using qualitative data since quantitative data are infrequent in the literature. Similarly, it could prove to be difficult to assess if a certain effect is beneficial or disadvantageous. Thus, some traits can be considered ES or EDS depending on the context. Finally, in some cases, it can be challenging to link certain ES/EDS with the specific functional trait (and how much this trait exclusively contributes to ES/EDS). However, the framework can handle the dichotomy of ES and EDS, by allowing the integration of all diverging services and disservices and by focusing on the final outcome within sectors.

Box 2.1. Framework application using invasive species *Ailanthus altissima* (from Sladonja et al., 2015)

Illustrative example of the stem height (biomass) effect as a functional trait of *A. altissima* (tree of heaven) on the (a) ES (left, blue boxes); (b) EDS (left, red boxes); (c) and different sectors (right, dark blue boxes). Benefits of *A. altissima* are presented using blue arrows, and impact via red arrows; the number of different services or disservices is illustrated with different arrow thickness (one ES/EDS - thin line, multiple ES/EDS – thicker line).



An increase in trunk biomass is a benefit for forestry, with the provision of wood and wood by-product and via reforestation. Overall, tree of heaven shows the biggest effect on ecological properties. Due to its very soft, light wood and great resistance property it is a good choice for planting to combat climate change (Enescu, 2014). Since it is often planted at former landfills or mining areas it is useful for restoring derelict land. However, *A. altissima* is a very competitive species and produces allelopathic compounds in the bark. Finally, it affects N, organic C and pH in the soil (Kowarik and Säumel, 2007).

Plantations of *A. altissima* are used as a shelterbelt to control erosion or on sides of the highways, yet they can obstruct the view and therefore present safety hazard. Extracted components from tree of heaven are used in both traditional and conventional medicine. Nevertheless, the sap can be toxic to humans (Nentwig et al., 2017). Trees are suitable for growth in urban areas as they withstand high pollution levels and are valued for their ornamental appearance despite unpleasant odor.

Conclusion

Invasive plant species provide some major services and disservices, directly affecting human well-being. Only recently part of the research agenda on biological invasions shifted toward examining both benefits by providing ecosystem services as well as disservices, e.g. as a direct negative effect of IAS on human well-being (Dobbs et al,. 2014). I classified the main benefits and impacts IAS provide in Europe and disentangled the difference between services and disservices in the context of invasion biology. The conceptual framework uses traits of invasive plant species as a proxy for effects on different services and disservices. The framework provides a simple and comprehensive way of highlighting the main environmental and socioeconomic sectors affected by invasion while enabling the use of multiple (and often conflicting) services and disservices and thus linking plant traits with sectors. This is facilitated by applying the direction (positive/negative) and strength of impact. Clarifying the extent of impact and benefit as well as most affected sectors can help address problems caused by IAS.

Chapter 3.

Trait–environment relationships of plant species at different stages of the introduction process

Introduction

Invasive alien species (IAS) have a large ecological impact on the diversity and abundance of native plant species (Vilà et al., 2010, Pyšek et al., 2012). Worldwide, the number of naturalized vascular plant species reaches almost 14,000 with tendencies for further increase (van Kleunen et al., 2015, 2019, Pyšek et al., 2017; Seebens et al., 2019). Consequently, much effort has been invested to identify the main causes of invasiveness. Multiple studies have shown that certain functional plant traits promote invasiveness (e.g. Pyšek and Richardson, 2007, Küster et al., 2008, van Kleunen et al., 2010b, Tecco et al., 2010, Divíšek et al., 2018). However, a conclusive list of traits that promote successful invasion is lacking mainly due to ambiguous results that can – at least partly – be attributed to the context-dependence of the invasion process (Kueffer et al., 2013). Additionally, propagule pressure and introduction by humans (e.g. cultivation, ornamental purposes) have a great effect on invasiveness (Pyšek et al., 2015).

The distribution of alien species is habitat-dependent (Chytrý et al., 2008a, Chytrý et al., 2008b, Dainese and Bragazza, 2012), thus functional traits relevant in one type of habitat can become unimportant in another (Divíšek et al., 2018). Therefore, within one habitat the set of traits essential for survival and reproduction should be comparable across different groups of plants (native, non-invasive, and invasive alien species). Alien species may thus share some traits with native species which can help them successfully establish under specific environmental conditions (Ordonez et al., 2010), but which may differ among habitats. Yet, alien species exhibit certain dissimilarities to natives, which can be beneficial in the colonization of new environments and reduce competition (Pyšek and Richardson, 2007, Divíšek et al., 2018). A meta-analysis by van Kleunen et al. (2010b) confirmed that invasive species show significantly higher values for all trait categories analyzed (e.g. size, fitness, growth rate) than native and non-invasive species.

To perform comparative studies of the invasiveness of species, several approaches are possible, as conceptualized by van Kleunen et al. (2010a). Of these, the most commonly performed are comparisons of (i) invasive with native species, and (ii) invasive with non-invasive species in the invaded area. However, such comparisons can be performed in both target (introduced) and source area (Parker et al., 2013).

Functional traits can be used to characterize the success of alien species over natives. Alien species (‘exotic’ or ‘non-native’ species) are classified, based on their residence time in the area, into ‘archaeophytes’ (alien species introduced before 1500 CE), and ‘neophytes’ (introduced after 1500 CE). Representatives of both groups can be classified according to the stage they reached in the invasion process into casual, naturalized or invasive; the latter term applies if they spread rapidly, become widely distributed (Richardson et al., 2000, Blackburn et al., 2011) and some have an impact on human well-being, ecosystem functioning, biodiversity, or human infrastrture (Vilà et al., 2010). Comparing traits of invasive and non-invasive plant species in their environmental context can help to elucidate why some alien species become invasive, and others not (van Kleunen et al., 2010b). Considering species at different stages of the invasion process can distinguish between traits that do not confer invasiveness (native vs non-invasive) from those that do (native vs invasive/potential invasive and invasive vs non-invasive) at each stage. The influence of traits on invasiveness can be challenging to interpret since it can differ depending on a species’ residence time (how much time has alien species spent in their introduced area).

A range of environmental variables such as land cover, climate, and geological bedrock, have been shown to affect native and different groups of non-native species differently, and changes in land cover (providing a proxy for habitat) and/or climatic factors (particularly changes in temperature and rainfall amount and range) may particularly benefit invasive species (Hulme, 2009). In Central Europe, both archaeophytes and neophytes prefer similar climatic conditions, reflecting their global environmental preferences, i.e. relatively warm and dry climate possibly due to their origin, i.e. relatively warm and dry climate (Pyšek et al., 2005). Similarly, both groups of alien species are promoted by increasing land-use intensity (Chytrý et al., 2008b, 2012, Polce et al., 2011). Accordingly, alien species can be favored when urban or agricultural land cover increases (neophytes and archaeophytes, respectively; Chytrý et al., 2008a). While geological heterogeneity strongly affects native species, this is not the case for archaeophytes, being mainly abundant on arable fields, i.e. homogenous land with fertile soils, while neophytes are strongly related to urban land cover (Kühn et al., 2003, 2004). Additionally, Tecco et al. (2010) showed that climate (temperature, precipitation, and frost), geological variables and land cover had a negative effect mainly on woody alien species and no significant effect on the herbaceous alien plants. Yet, the success of both native and alien species cannot be assessed in isolation from the environmental determinants of their distribution.

The reason why native and alien species may respond differently to environmental factors is often attributed to their functional traits. Wolf et al. (2020) showed a strong pattern of changes in functional composition concerning the environment in a rural-urban gradient. Traits relevant for the success of alien species are related to stress tolerance (i.e. SLA) or environmental disturbance (height, seed size) (Pyšek and Richardson, 2008, Gallagher et al., 2015). Further, traits related to competitiveness (e.g. height) can prove beneficial for invasive species (Divíšek et al., 2018). For instance, phenology, in terms of earlier or longer flowering duration can be advantageous. Pyšek et al. (2003) showed that IAS might flower earlier or later than native species as a part of a “try harder” hypothesis. Pollination systems do not show significant links to invasion success (Pyšek and Richardson, 2008), but self-pollination tends to support the spread of neophytes more than any other type of pollination (Pyšek et al., 2011). However, the role of pollination in the invasion process is mainly studied without relation to environmental drivers. Kühn et al. (2006), though, showed that pollination types vary spatially and in relation to climatic, geological and land-cover factors.

Evaluating the relationships between the environment and plant functional traits is crucial for understanding the response of species of different origins and different stages in the invasion process to changing environmental conditions (climate change, land-cover change). Here, I quantified the relationships between climate, land cover and bedrocks with relevant plant traits using a dataset with 1,300 plant species in Germany. I examined several groups of plants including natives and different subgroups of alien species across 1,000 randomly selected grid cells in Germany. The following questions are addressed: (i) Is there a relationship between plant traits and the environment in native and alien species? (ii) How do these relationships depend on the residence time of plant species (with archaeophytes being introduced earlier and neophytes more recently)? (iii) How do these relationships differ between non-invasive and invasive neophytes?

Methods

Species occurrence

Species occurrence data were obtained from FLORKART (Federal Agency for Nature Conservation / Network Phytodiversity Germany; http://www.floraweb.de) for the period 1950–2013. FLORKART includes over 14 million records on species occurrences collected by thousands of volunteers. Species were analyzed at a spatial resolution of grid cells with 10' longitude × 6' latitude (~ on average 130 km^2 ranging from 117 to 140 km^2). A presence/absence matrix was generated for a random sample of 1000 grid cells that contained at least 45 (out of 50) species that can be reasonably assumed to occur in every grid cell and serve as a proxy for mapping quality (Kühn et al., 2006). This approach of grid cell selection ensured that chosen grid cells were properly surveyed. Additionally, some grid cells were smaller because they were located at the borders or along the coast. Thus, I excluded cells smaller than 117 km^2 (which is the size of the smallest grid cell that is not truncated by borders or coastlines). Individual matrices were generated for five groups of plants: native (976 species), archaeophytes (168 species) and neophytes (156 species), with 1,300 plant species in total; neophytes were further divided into (i) species featured in the German-Austrian Black List Information System of invasive species (GABLIS; Essl et al., 2011), with 26 species, and (ii) species not included in GABLIS, with 130 plant species. Following GABLIS (Essl et al., 2011), plants were classified into action blacklist (invasive with limited distribution) and management blacklist (invasive and widely distributed species). In this chapter, I will refer to the species from GABLIS blacklist (action and management list) as invasive neophytes and to the ones that are not included in GABLIS as non-invasive neophytes.

Traits

Trait data for all plant species were obtained from the Database on Biological and Ecological Traits of the Flora of Germany, BiolFlor (Klotz et al., 2002; Kühn et al., 2004, http://www2.ufz.de/biolflor/index.jsp), and LEDA (Kleyer et al., 2008, https://uol.de/en/landeco/research/leda/data-files). These traits represent morphology, phenology and habitat preferences of all three groups of plant species: SLA, seed mass, height, storage organs, pollination vector, flowering period, urbanity and hemerobic level (Table 3.1).

Environmental data

Climate data (temperature, precipitation; Table 3.2) was obtained from the ALARM project (Fronzek et al., 2012) for the period 1961–1990, land cover (Table 3.2) data from the CORINE database (Bundesamt für Kartographie und Geodäsie, 2012), and geological data (Table 3.2) from a map of the German Federal Institute for Geosciences and Natural Resources (Bundesanstalt für Geowissenschaften und Rohstoffe, 1993), all scaled to the same resolution as the floristic maps.

Data analysis

I analyzed the relationship between traits and the environment across native and alien plant species. For each group (natives, archaeophytes, neophytes, non-invasive and invasive neophytes) matrices of species presence/absence × grid cells were created (*S*). Correspondingly, environmental matrices (environment × grid cell, *E*) and trait matrices (traits × species, *T*) for every status group were compiled. To directly associate matrices *S* with *E* and *T*, I used a fourth corner approach as implemented in the function *traitglm()*of mvabund in R (Warton et al., 2015). The fourth corner analysis combines *S* (first–upper-left–corner), *E* (second–lower-left–corner) and *T* (third–upper-right–corner). The fourth (missing–lower right) corner is generated as a matrix that describes the trait-environmental relationships. I checked for collinearity among environmental variables and excluded all variables with $r > |0.7|$ (Dormann et al., 2013). The method of *manyglm* presents a multivariate extension of GLM (generalized linear model) and calculates the coefficient estimates of GLMs fitted to all (explanatory) variables simultaneously (Wang et al., 2012). Coefficients describe how environmental predictors can be predicted by changes in traits. Further, I used the function *anova.traitglm()* based on bootstrapping with 99 permutations, to test for the statistical significance of trait–environment relationships in predicting the presence of only non-native species (for computational reasons, see below) on all sites (Appendix S1: Tables S1a–d). Since the response matrix *S* was binary multivariate data, I used binomial distribution. The data analysis was performed using R, version 3.6.1 (R Core Team 2017). The analysis of a larger matrix (e.g. native species) took 19 days on a Dell PowerEdge R930 Server with 4 * CPU E7-8867 v4 2.4 GHz (72 Cores) and 6 TB RAM with Windows 2016.

Table 3.1. Functional traits, environmental associations (hemerobic level and urbanity) and invasiveness data (GABLIS list) and sources used for the analysis

Trait	Values	Units/description	Source
Mean specific leaf area (SLA)	metric	mm^2/mg	LEDA
Seed mass	metric	mg	LEDA
Mean plant height	metric	m	LEDA
Storage organs	yes / no / multiple	Presence Absence Multiple storage organs	BiolFlor
Pollen vector	multiple / insect/ wind / self	Multiple pollination types Wind pollination Self-pollination (including two subgroups: selfing by a neighbouring flower and selfing in an unopened flower) Insect pollination	BiolFlor
Flowering period	months	Beginning of flowering Ending of flowering Duration of flowering period	BiolFlor
Urbanity	1 - 5 values for different states of urbanity	1 – urbanophobic (species grows exclusively outside urban areas) 2 – moderately urbanophobic (species prefers non-urban areas) 3 – urbanoneutral (species has no preference), 4 – moderately urbanophilic (species grows predominantly in urban areas) 5 – urbanophilic (species grow exclusively in human settlements	BiolFlor

Hemerobic level	level of naturalness with values 1 - 9	Polyhemerob and α-euhemerob, values 1-2 (species preference for artificial habitats) β-euhemerob and α-mesohemerob, values 3-4 (species prefers altered habitats) β-mesohemerob and α-oligohemerob, values 5-6 (species preference for moderately altered habitats); β-oligohemerob and γ-oligohemerob, values 7-8 (species prefers semi-natural habitats) Ahemerob, value of 9 (species preference for natural habitats)	BiolFlor
GABLIS sublist	no / ML / AL	Neophytes not present on the list Neophytes on the management Black list (ML) Neophytes on the action Black list (AL)	GABLIS

Table 3.2. Environmental variables and their sources used in the 4th corner analyses of species in Germany

Variable	Abbreviation	Categories	Unit	Source
Temperature	tmn tmx	- mean temperature of the coldest month - mean temperature of the warmest month	°C	Fronzek, Carter & Jylhä, 2012
Precipitation		- mean annual precipitation - precipitation range of the year	mm	Fronzek, Carter & Jylhä, 2012
Land cover	arable land (%) natural cover (%) urban cover (%)	Land cover proportion of: - arable land - natural and semi natural areas - urban areas	proportion	Corine Land Cover (CLC)
Number of CLC patches	CLC patches	Total number of land cover patches per grid cell		Corine Land Cover
Geological types		Proportion of subsoils: - calcareous - loess - sand	proportion	Bundesanstalt für Geowissenschaften und Rohstoffe
Number of geological patches	Geological patches	Total number of geological patches per grid cell (regardless of the number of geological types).		Bundesanstalt für Geowissenschaften und Rohstoffe

Results

Overall, there was an increase in the number of prominent trait–environment relationships from native species to non-invasive archaeophytes, non-invasive and invasive neophytes (Fig. 3.1; Tables S3.1a-e, Tables S3.2a-d).

Native species

Native species in Germany showed high heterogeneity in their functional traits and habitat conditions; thus the relationships between traits and environment were weak (ranging from –0.0003 to 0.01; Table S3.1a).

Archaeophytes

The frequency of archaeophytes well adapted to urban environmental conditions (urbanity; Fig. 3.1a; Table S3.1b) increased with mean temperatures (of both warmest and coldest month), broader precipitation range, across natural and urban areas, and with the number of geological patches. Conversely, their frequency decreased with an increase in annual precipitation, the proportion of calcareous subsoil and the total number of Corine Land Cover (CLC) patches per grid cell.

With higher temperatures of the warmest month, species with high seed mass, wind- or self-pollination, high level of naturalness and those beginning to flower early will increase, while those with a long flowering period will decrease. Increasing amounts of precipitation disadvantaged small species that prefer artificial habitats but promoted species with high SLA, seed mass, presence of storage organs and multiple storage, self-pollination, as well as early beginning and late end of flowering.

Neophytes

Mean annual precipitation and number of CLC patches showed a strong positive relationship with multiple storage organs, yet the mean temperature of the coldest month negatively affected this trait (Fig. 3.1b; Table S3.1c). Both wind- and self-pollination were negatively influenced by mean annual precipitation, and wind pollination was positively related to temperature (of the coldest and warmest month), sandy substrates and number of geological patches. An increase in the temperature of the warmest month promoted urbanophilic species, while the temperature of the coldest month positively affected the duration and end of the flowering period. Mean annual precipitation showed a negative relationship with plant height, but positive effects on SLA and plants with multiple storage organs.

Non-invasive neophytes

Increasing winter temperature positively affected wind- and self-pollination and flowering duration, whereas tall urbanophilic species were negatively affected (Fig. 3.1c; Table S3.1d). Conversely, high summer temperatures was positively correlated with the frequency of tall urbanophilic non-invasive neophytes, and negatively with long flowering duration or larger SLA and seed size. An increase in the number of CLC patches favored insect-pollinated, urbanophilic plant species with higher SLA, while negatively affecting the abundance of long-flowering, self-pollinated species.

Invasive neophytes

The temperature of the warmest month was positively related to SLA, multiple storage organs, self-pollination and negatively to the duration of flowering (Fig. 3.1d; Table S3.1e). In contrast, the temperature of the coldest month was negatively related to SLA and positively to hemeroby. Annual precipitation negatively affected the beginning of flowering, while precipitation range was positively associated with SLA and self-pollination. The number of CLC patches had a positive relationship with multiple storage organs and a negative one with hemeroby.

Differences among invasive neophytes (black list) were positively associated with land cover and mostly negatively with geological predictors. Neophytes with a limited distribution in Germany (action list) had positive relationships with all three types of land cover and with number of CLC patches and negative associations with calcareous, sandy substrates and number of geological patches.

Differences among groups

Archaeophytes and neophytes showed several contrasting trait–environment relationships (Fig. 3.1a & b). Specifically, the frequency of self-pollination in archaeophytes increased with the temperature of the warmest month, mean annual temperature and proportion of loess substrates, while under these conditions the frequency of neophytes diminished. Similarly, in archaeophytes, I observed a positive relationship between urbanity and temperature of the coldest month, the proportion of natural areas and number of geological patches, and a negative relationship with annual precipitation and number of land cover patches. Neophytes showed opposing trends.

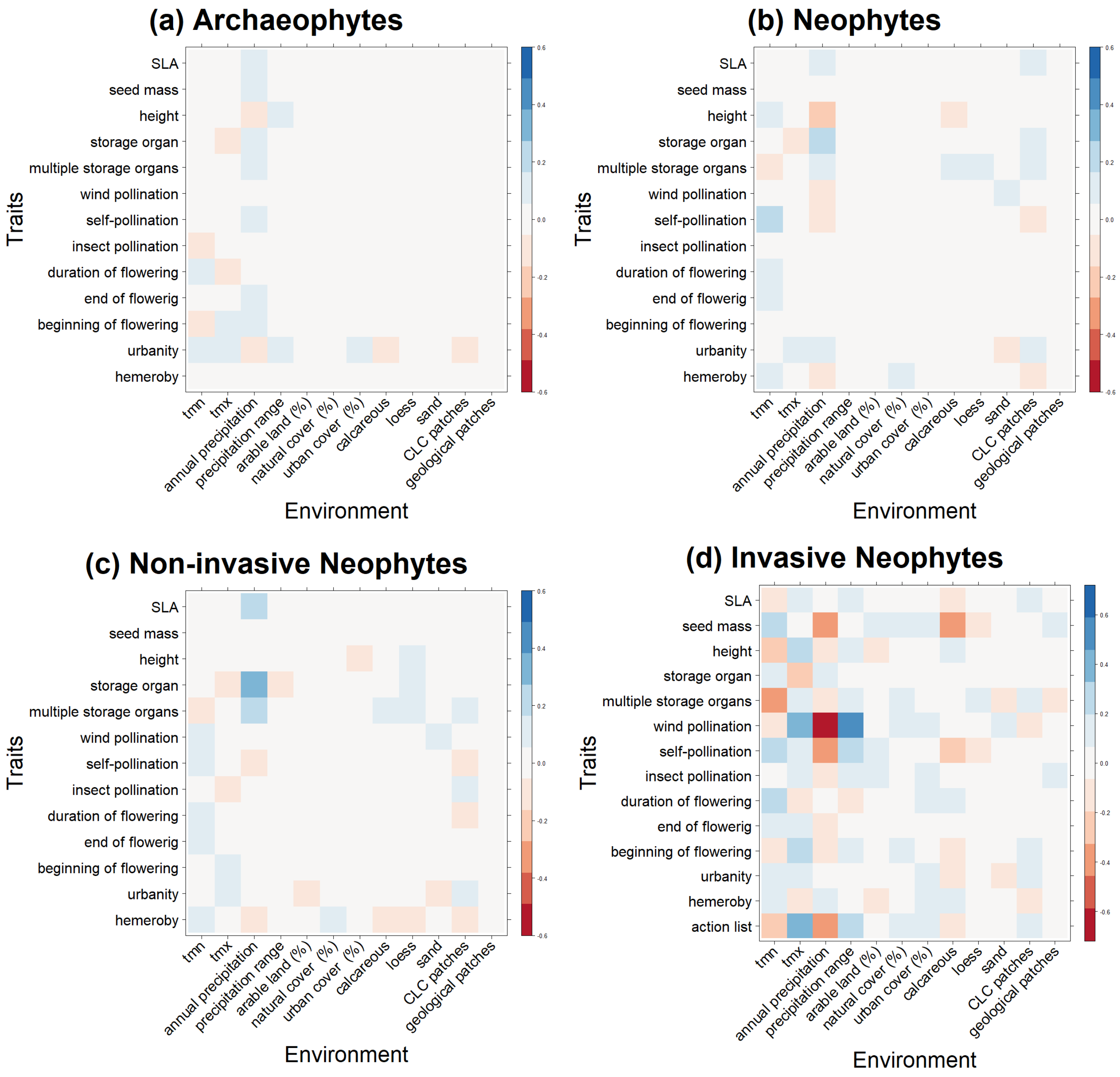


Figure 3.1. Fourth-corner plots for (a) archaeophytes, (b) all neophytes lumped together regardless of status, (c) non-invasive neophytes, and (d) invasive neophytes. Figure shows

standardized interaction coefficients for plant traits (y-axis) and environmental variables (x-axis). Strong relationships are shown in blue (positive) and red (negative) while color intensity shows interaction strength with coefficient values on log scale.

Abbreviations: tmn - mean temperature of the coldest month; tmx - mean temperature of the warmest month; CLC patches - total number of Corine Land Cover patches per grid cell.

Further, I observed differences between non-invasive neophytes and invasive neophytes (Fig. 3.1c & d). While the frequency of invasive neophytes with higher SLA increased with the temperature of the warmest month and precipitation range, non-invasive neophytes displayed reversed trends. Similarly, urbanophilic invasive neophytes were promoted by increasing temperature of the coldest month, and insect-pollinated invasives by the number of geological patches and temperature of the warmest month, with the contrasting tendency in non-invasive neophytes. Finally, insect-pollinated invasive neophytes benefited from increasing annual precipitation and a high number of land-cover patches, although these variables showed to be disadvantageous for non-invasive neophytes.

Discussion

I did not record any strong trait–environment relationships which may be due to the heterogeneity of different ecological groups in native species. Preliminary tests (not shown) indicated that this scarcity of trait–environment relationships was not an artifact of the large sample size of native species. This is because (overall) native species colonize a much wider range of environmental conditions in their native range than species alien to that range. Alien species, for example, are rarely found under extreme environmental conditions such as in mountains, seashores, xeric habitats, bogs or fens (Chytrý et al., 2008, Alexander, 2011). This means that considering only alien plants makes it more likely to find trait–environment relationships than if all native species or random sets of native species (which are not ecologically selected) are taken into account. Therefore, I suggest analyzing trait–environment relationship of ecologically defined groups of native species. This, however, is beyond the scope of this chapter; nevertheless, I report the results of native species to avoid publication bias.

I observed a lower number of strong trait–environment relationships for archaeophytes than neophytes, whereas in invasive neophytes (i.e. those on the GABLIS list) strong relationships were most frequent. Climatic variables had a high explanatory power in all groups. Traits of neophytes were mainly affected by climate and different geological types, and rarely by land cover. Most of the traits of archaeophytes were only affected by climatic conditions, such as temperature and mean annual precipitation (while precipitation range had little effect on their traits) and rarely by other environmental variables. Archaeophytes in Central Europe were predominantly introduced from the Mediterranean and the Middle East (Pyšek et al., 2012b), thus from a smaller range of geographical locations (and hence environmental conditions) than neophytes (introduced from around the globe), and many invasive neophytes originate from different regions and continents, and thus might have adapted to a wider range of environmental factors (Pyšek et al., 2005). This might be the reason why traits of neophytes, in addition to their diverse origin, showed a more pronounced response to climatic and geological factors.

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I observed that relationships between environment and traits for different groups of alien species are more often similar rather than contrasting (e.g. height decreases with annual precipitation for both neophytes and archaeophytes; the beginning of flowering shifts to earlier months with increasing winter temperature and precipitation for invasive and non-invasive neophytes, etc.). Plant growth (e.g. biomass, height, leaf size) and phenology are directly influenced by temperature (Hatfield and Prueger, 2015); for example, extreme temperature (especially summer temperature) can alter the duration and success of the pollination process (Hegland et al., 2009). Furthermore, alien species exhibit traits that allow them to cope better than natives with the recently observed changes in climate or habitats, such as better dispersal ability, higher tolerance to climate change and higher competitiveness (Dukes and Mooney, 1999).

Differences in neophytes vs. archaeophytes

As to the best of my knowledge, no statistical test allows the formal comparison of results across different fourth-corner analyses; I have to interpret differences among the trait-environment responses of different groups qualitatively. Trait-environment relationships were similar (positive or negative, respectively) for archaeophytes and neophytes in 13 cases but differed in seven cases, only. Primarily, urbanity expressed contrasting relationships, suggesting human-induced propagule pressure as an important driver. Neophytes tend to be more urbanophilic, thus the increase in temperature was positively related to this trait (urban heat island effect; Ricotta et al. 2009). Urban areas facilitate neophytes (Kühn et al., 2004, Kühn and Klotz, 2006), and alien species are often associated with cities (Chytrý et al., 2008b, Knapp et al., 2009, Aronson et al., 2014). Some studies showed that neophytes are becoming a dominant group in urban areas (Chocholoušková and Pyšek, 2003, Pyšek et al., 2004), while the association of archaeophytes with this type of environment decreased in recent decades, and they are more common in arable landscapes (Botham et al., 2009). Hence, the increase in the proportion of arable and natural land cover affected urbanophilic neophytes negatively, but the increase in the proportion of urban areas increased their abundance (and resulted in a reversed trend in archaeophytes). Neophytes are cultivated in gardens and public parks (Reichard and White, 2001, Pergl et al., 2016), and their spread is further facilitated by extensive transportation systems (Seebens et al., 2015). Consequently, cities often present harbors for the spread (von der Lippe and Kowarik, 2008) and the establishment of newly introduced species (Kühn et al., 2017).

The majority of neophytes (especially invasive) are pollinated either by insects or wind, whereas archaeophytes are often self-pollinated (Pyšek et al., 2011). Many agricultural weeds are self-pollinated archaeophytes, possibly due to a lack of suitable pollinators or because of abiotic stress. Further, in archaeophytes, self-pollination is more common with increases in the proportion of loess. This can be due to loess being very fertile and suitable for agriculture, so self-pollination can be an alternative (Kühn et al., 2006), especially with the increasing scarcity of insects in regions of intensive agriculture (Hallmann et al., 2017).

Differences in non-invasive vs. invasive neophytes

Flowering phenology is important for the successful spread of invasive species (Knapp and Kühn, 2012). Plant species have evolved in tune to local climatic regimes in their native range or colonized such regions naturally. With increasing temperatures (summer and winter), invasive neophytes finish their flowering period later in the year (with overall shorter duration). However, higher summer temperatures had a negative effect on the duration and higher winter temperatures caused invasive neophytes to start flowering earlier. Many invasive species in Germany originate from warmer climates and as a result, an increase in winter temperature can act as a switch to earlier flowering. Earlier flowering of invasive species compared to non-invasive may ensure their reproductive success, and higher summer temperatures prolong the flowering season to late summer (Knapp and Kühn, 2012). Low precipitation often impedes flowering and the species that flower earlier can avoid summer droughts (Godoy et al., 2009). The increase in precipitation range (usually resulting from wet winters and dry summers) decreases the duration of flowering and plants were flowering later in the year. Depending on the origin of invasive neophytes, I can expect different responses to current or future climatic conditions. Provided that the climate in the introduced area is the same as in the native area, flowering phenology can stay the same. However, if introduced species are subjected to a different climate, the flowering depends on the capability of invasive species to adapt or respond plastically to new conditions.

Alien plants that have often been introduced for their aesthetic features as ornamental plants can attract pollinators (colorful and fragrant flowers) and divert them from native plants (Bjerknes et al., 2007, Muñoz and Cavieres, 2008). The majority of tropical and temperate plants are insect-pollinated (Ollerton et al., 2011), invasive neophytes, though, are primarily insect or self-pollinated. Additionally, many invasive species are annual plants and when suitable pollinators are not available they are able to self-pollinate which can be beneficial for the successful invasion of new areas (van Kleunen et al., 2007).

Climatic factors did not have a different effect on the occurrence of invasive species from the management or action black list. Species on the action list are more likely to be found in all three types of land cover than those from the management list. I can, therefore, expect that species which are invasive but still of limited distribution, will spread especially as habitats become more fragmented (occurrence of action list species shows an increase with CLC number of patches).

General patterns

Geological bedrocks did not have a major effect on most of the traits in different groups, despite explaining roughly a quarter of plant distribution variability in Germany (Pompe et al., 2008). Archaeophytes often occur on loess, which is highly productive and usually used for intense agriculture. However, in calcareous substrates archaeophytes tend to flower later while invasive neophytes flower earlier and are taller. Species-rich calcareous grasslands used to be common in Germany and are now frequently afforested, suffer from shrub encroachment or are surrounded by agricultural fields (Fischer et al., 1996). Sandy substrates can warm up earlier during winter and spring and can be suitable for neophytes introduced from warmer regions. Additionally, due to its low water-retention property, sandy substrates are frequently colonized by species adapted (i.e. having suitable traits) to drought.

Different land-cover types as well as the number of land-cover patches and geological patches had an effect on most of the traits of invasive neophytes, and very little (or no effect) on archaeophytes. Furthermore, landscape transformation and heterogeneity have an effect on invasive species in different stages of invasion and fragmentation of the landscape may facilitate the spread of invasive species (With, 2002). Habitat heterogeneity intensifies invasion and increases dispersal (O'Reilly-Nugent et al., 2016, Dukes and Mooney, 1999), and I have recorded a positive relationship with flowering phenology, SLA, height and seed mass of invasive neophytes. However, invasive neophytes with multiple pollination vectors (i.e. having different pollination types) benefited the most whereas wind-pollinated species colonized the least heterogeneous landscapes. These wind-pollinated invasive species are often dependent on specific habitats, for example, *Fraxinus pennsylvanica* or *Acer negundo* are often abundant in riparian or urban habitats (Burton et al., 2005).

Many studies have shown that functional traits of alien species are associated with invasiveness (Hamilton et al., 2005, Pyšek and Richardson, 2007, Ordoñez et al., 2010, van Kleunen et al., 2010b, Gallagher et al., 2015, Divíšek et al., 2018). However, the results were often ambiguous, possibly due to excluding environmental factors from analyses. In my study, I showed that traits, particularly of invasive neophytes exhibit a strong relationship with the environment. Native species showed fewer associations with environmental factors as their traits may be more conservative in their native habitat and less likely to fluctuate. Yet, we looked at climatic conditions within a limited period (1961–1990) and native species might show significant changes in their functional traits as climate changes. Similar to native species, archaeophytes, the species that have settled in Germany for a long time, showed the least significant trait-environment relationships among alien species, while the traits of invasive neophytes are greatly affected by climate, geology and land cover. As discussed, this might be due to the fact that many invasive species were introduced from areas with different climatic or geological conditions and respond more flexibly to changes in the environment (Hellmann et al., 2008).

Invasive neophytes mainly show positive trait-environment relationships. Since the values for most of the traits increased with the incorporated environmental factors (especially climatic and land cover variables), I can expect future climate and land-cover change to affect invasive neophytes more strongly than other alien groups. I showed that climate may affect in particular SLA, insect pollination and phenology of invasive species, whereas land cover may mainly influence height, seed mass and wind pollination. Climate change could affect archaeophytes as well. They mainly showed positive relationships with climatic variables, and their values increased with the increase in temperature and precipitation. Future studies on the relationship between functional traits and environment of invasive plants are required in order to examine the effects of climate change or land cover changes. There is evidence that climate change may promote invasiveness (Pyšek et al., 2005), thus distinguishing which traits of alien species are benefiting under different climatic scenarios, can be valuable for management implications.

Chapter 4.

Functional diversity changes in native and alien species over 3 centuries

Introduction

“There was no doubt about it: the City was the culmination of man’s mastery over the environment”, Isaac Asimov wrote in his 1953 novel *The Caves of Steel*. The major factors behind the changes in species composition are human activities, particularly as their settlements expand and many habitats change or disappear. Processes associated with urbanization are mainly related to human population growth and an increase in built infrastructure for living, industry, and traffic (Sukopp, 2002; (Hua et al., 2017) which lead to habitat loss and fragmentation (Kowarik, 1995a; (Syphard et al., 2011), pollution, changes in climate (temperature, moisture), hydrological systems (Paul and Meyer, 2001), and soil (Kalnay and Cai, 2003; Song et al., 2014; Trusilova et al., 2008). Humans benefit from urban plant species as they provide multiple ecosystem services in cities, in terms of air quality improvement, noise reduction (Bolund and Hunhammar, 1999), climate regulation, water regulation and storage, aesthetics and recreation (Gómez-Baggethun and Barton, 2013; Potgieter et al., 2017) or food provision (via urban gardening; Barthel, Parker, Folke, & Colding, 2014). Urbanization leads to habitats becoming more homogenized and thus many specialist species get lost (loss of natural or specific anthropogenic habitats) to the benefit of generalists and species adapted to urban conditions (Williams et al., 2015). In parallel, species mobility (dispersal ability) plays an important factor in colonizing new urban habitats (Concepción et al., 2015), where those species that are highly mobile respond positively to increases in the proportion of urban habitats. Additionally, alien species are very abundant in cities, to which they were mostly deliberately introduced, and these urban and suburban areas provide a range of different local conditions suitable for a variety of species (Lippe & Kowarik, 2008; Pyšek, 1998).

Further, those alien species that become invasive can impact ecosystem services and disservices by affecting local diversity, causing health issues (i.e. allergic reactions) or damaging infrastructure. Biodiversity has been widely studied using many different indices, such as species abundance, diversity, and distribution (Díaz et al., 2006). However, species diversity might not be the most appropriate proxy to determine the effect of biodiversity on ecosystem processes (and vice versa). To this end, taking into account species' functional traits via calculating functional diversity (FD) is considered to be more appropriate (Mcgill et al., 2006; Villéger et al., 2008). Functional diversity accounts for "the range and value of those species and organismal traits that influence ecosystem functioning" (Tilman, 2001) and several FD indices relate this to the distribution of species in niche space (e.g. functional richness, evenness, divergence; Mason, Mouillot, Lee, & Wilson, 2005). Additionally, specific functional traits of plant species can explain different ecosystem processes. For example, leaf traits can be related to drought tolerance and competition, seed traits to life strategies, dispersal and establishment, and root traits or species height help in understanding invasibility and community competitiveness (Funk et al., 2017; Laughlin, 2014). Further, SLA (specific leaf area) underlines strategies of nutrient acquisition and competition, while pollination type and flowering period relate to species dispersal. Using functional traits (rather than only species diversity) is therefore particularly important in communities with an abundance of alien and invasive species because higher FD indicates higher resistance to invasiveness (Funk et al., 2008).

The numbers of alien plant species introduction in Europe steadily rose from the 15th century with a more intensive increase since the 19th century (Pyšek et al., 2009). Additionally, it is expected that alien plant invasions will intensify in the future depending on socioeconomic scenarios (particularly in arable and urban landscapes; (Chytrý et al., 2012), and due to the phenomenon of invasion debt (Essl et al., 2011). Thus, having a record of invasive species through time (decades or centuries) presents a unique opportunity and may be important for studying invasiveness and assessing future trends. So far, comparisons of historical urban floras with present state were made for Leipzig (1867-1989, (Klotz and Gutte, 1992; Scholz, 2008), Halle/ Saale (1848-1983, Klotz 1987; 1687-2005, (Knapp et al., 2010), Zürich (1839-1998, (Landolt, 2000), Plzeň (1880–1990s, (Chocholoušková and Pyšek, 2003; Pyšek et al., 2004a), Brussels (Godefroid, 2001), Turnhout (Van der Veken et al., 2004), Bologna (1894-2018, (Salinitro et al., 2019), New York City (DeCandido et al., 2004), Indianapolis (Dolan et al., 2011), and Adelaide (Tait et al., 2005), as well as for selected parts of a city (e.g., Pelham Bay Park, New York

City, (DeCandido, 2004); Central Park New York City, (DeCandido et al., 2007). Still, none of these studies focused on functional diversity.

In our paper, I followed the classification of alien species based on their residence time in Germany, including archaeophytes (alien species introduced before 1500 CE), and neophytes (introduced after 1500 CE) with the addition of invasive species (invasive neophytes; see (Pyšek et al., 2004b; Richardson et al., 2000) for definitions). I studied how functional diversity changes in the city of Halle (Saale), Germany. Relevant functional traits were selected to examine the difference in functional diversity for native and alien plant species. Specifically, I studied: (i) functional diversity changes occurring during a 320-year period in the urban setting; (ii) differences in the trajectories of functional diversity between native species and the three groups of alien species defined above, representing different stages of the invasion process, and their functional traits; (iii) functional diversity changes for specific functional traits related to urbanization processes (e.g. stress, competitiveness, and ecophysiology). Determining which plant groups (natives and alien) and functional traits benefit and which ones are disadvantaged by urbanization-related processes is important for understanding the mechanisms shaping the composition of urban floras, and for predicting trends in the future as the human population continues to move from rural to urban areas (DESA, 2019).

Materials and methods

Study area

The city of Halle (Saale) is located in central Germany (state of Saxony-Anhalt; Fig. 4.1b), east of the Harz Mountains (latitude of 51° 28' N; longitude 11° 58' E) with a mean elevation of 87 m a.s.l. (range 70-140 m; (Stolle and Klotz, 2004).

Halle (Saale) covers an area of about 135 km^2 and a population of 240 900 inhabitants (in 2019, Fig. 4.1a). There was a steady increase (since the beginning of recording in 1871) in population until the late 1980ies and a pronounced drop in the 1990ies due to the political changes in Germany. In recent years, population numbers stabilized.

The city is located in the rain shadow of the Harz Mountains, with mean annual precipitation of only 497mm and a mean annual temperature of 9.1°C. Halle is traversed by the river Saale (for 27 km) which divides into several branches, forming small islets. Soils are highly heterogeneous, and the non-residential areas within the city predominantly consist of agricultural/horticultural land (~21%), forests (~10%), industrial and commercial areas (~9%), herbaceous flora/grasslands (~8%) and green urban areas (3%; Arnold et al., 2018). The original natural vegetation types in the area today covered by Halle (Saale) were mainly forests: alder, alder-ash, ash-elm, willow-poplar, oak-hornbeam, dry forests (Stolle and Klotz, 2004). The current vascular flora comprises c. 1400 species (Stolle and Klotz, 2004). Areas for nature conservation mainly comprise alluvial forests and meadows as well as dry lawns on porphyritic rock (rhyolite).

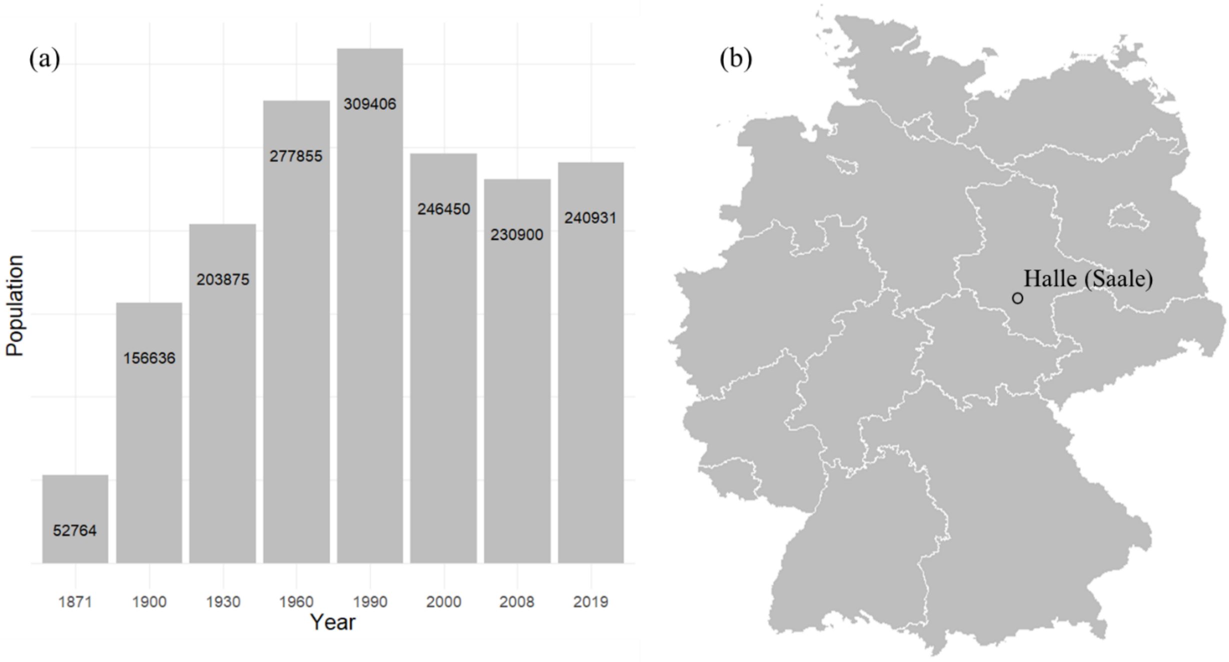

Figure 4.1. Population development in Halle (Saale) for the period of 1871-2019 (a); Location of Halle (Saale) in Germany (b).

Historical data

First known records of Halle date from 806. The city started to extensively develop during the 12th century. During the 20th century, Halle expanded by incorporating several municipalities. In our analysis, I used historical floristic data on vascular plant species occurrences for the period 1687-2008.

Historical records were related to the area within the present administrative borders of Halle with the help of site references given in historical publications. Historical data was composed of published species records performed by over 20 botanists since the late 17th century, as well as manuscripts and herbarium records (Table 4.1). The accuracy of species occurrences was evaluated by Jens Stolle, a competent local botanist and the following modifications were made. Species were excluded if (a) it is unlikely that the species occurred in the study area; (b) they occurred casually for a very short period; (c) they were merged into "superspecies". Further, I included rare species with low dispersal capacity if they occur in Halle today but were not recorded by earlier botanists, assuming that these species must have been overlooked in former times (for further details see Knapp, Kühn, Stolle, & Klotz, 2010).

I determined the total number of species and the number of unique species of every status group per time step (species numbers across time steps: native 833, archaeophytes 141, neophytes 136; status groups categorized according to BiolFlor database, (Klotz et al., 2002), where time steps were distinguished based on publication dates of historical records (Fig. 4.2). I further distinguished invasive neophytes according to their negative impact, following the KORINA (The Coordination Centre for Invasive Plants in protected areas of Saxony-Anhalt) blacklist of neophytes in Saxony-Anhalt (http://www.korina.info).

Trait data

The traits were obtained from the BiolFlor and LEDA databases (Table 4.2; Kleyer et al., 2008; Klotz et al., 2002). Regarding alien status, plant species were divided into native, archaeophytes, and neophytes (Kühn, Durka, & Klotz, 2004; http://www.ufz.de/biolflor).

Table 4.1. Data sources of seven-time periods (1687-2008) for the study area (Halle (Saale), Germany) including published and unpublished inventories and herbariums (detailed information in S4.1)

Timestep	**Data source**
1687–1689	Knauth (1687); improved edition 1989
1721–1783	Buxbaum (1721); Senckenberg (1731); Leysser (1761); Leysser (1783); Roth (1783)
1806–1856	Luyken (1806); Sprengel (1806); Wallroth (1815); Wallroth (1822); Garcke (1848); Garcke (1856)
1857–1901	Fitting et al. (1899); Fitting et al. (1901)
1902–1949	Fitting et al. (1903); Schulz & Wüst (1906); Schulz & Wüst (1907); Wangerin & Ule (1909); Schulze (1936; 1938); Knapp (1944a,1944b); Knapp (1945)
1950–1999	Rauschert (1966a, 1966b, 1967, 1972, 1973, 1975, 1977a, 1977b, 1979, 1980, 1982); Grosse (1978, 1979, 1981, 1983, 1985, 1987); Grosse & John (1987); Grosse & John (1989); Grosse & John (1991); Klotz & Stolle (1998)
2000–2008	Stolle & Klotz (2005); unpublished data Stolle & Klotz (2005–2008)

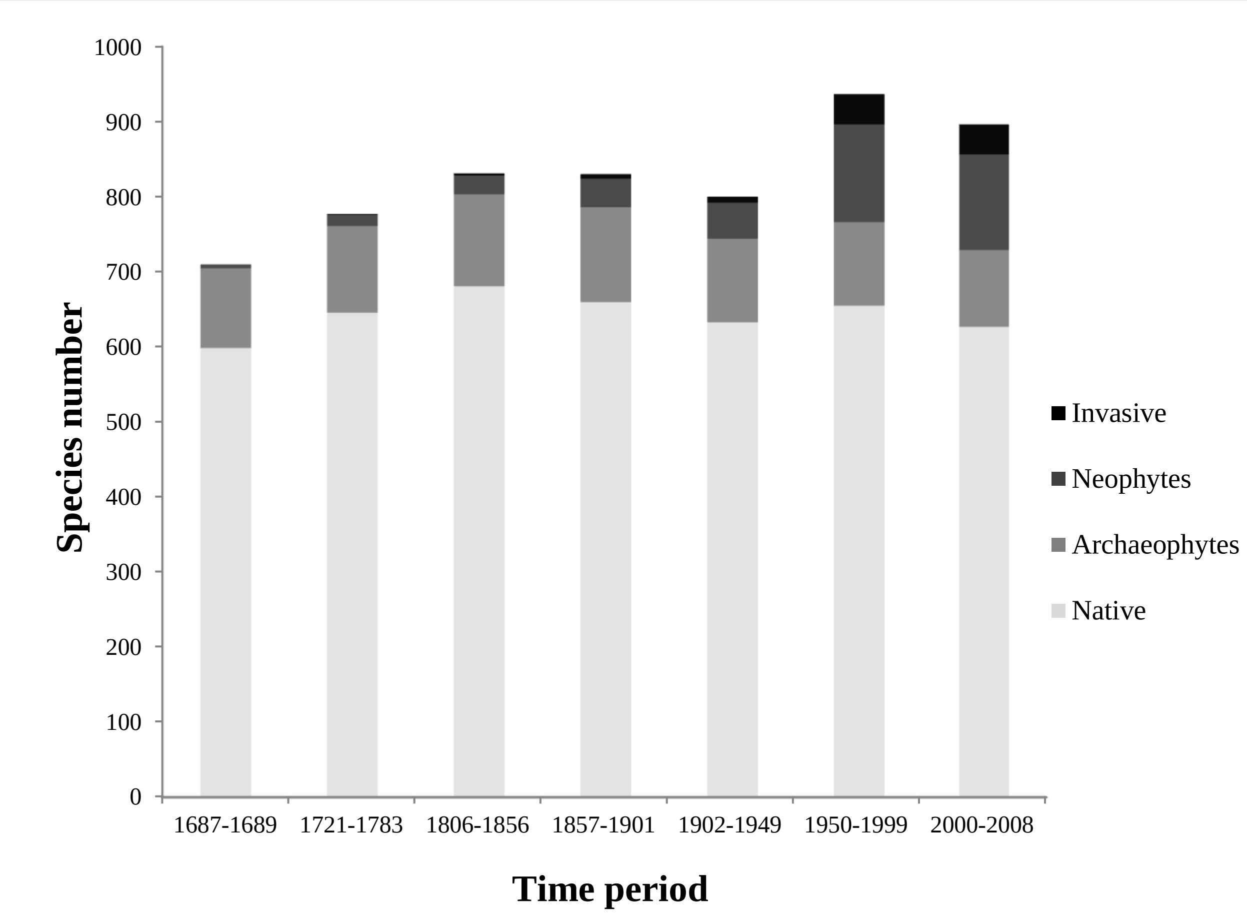

Figure 4.2. Species number for seven-time periods (1687-2008) in Halle (Saale), Germany for the status groups native, archaeophytes, non-invasive neophytes, and invasive neophytes.

Table 4.2. Functional trait data and their source

Trait	**Trait states**	**Values**	**Source**
Mean vegetative plant height	m	metric	LEDA
Mean specific leaf area (SLA)	mm^2/mg	metric	LEDA

Mean seed mass	mg	metric	LEDA
Flowering period	Beginning of flowering End of flowering Duration of flowering period	months	BiolFlor
Storage organs	Presence Absence Multiple storage organs	Yes / No / Multiple	BiolFlor
Life form	Hydrophyte (A) Chamaephyte (C) Geophyte (G) Hemicryptophyte (H) Phanerophyte (P; including macrophanerophyte, nanophanerophyte, and hemiphanerophyte) Therophyte (T) Multiple life forms	A / C / G / H / P / T / Multiple	BiolFlor
Clonal growth organs	Presence Absence Multiple clonal growth organs	Yes / No / Multiple	LEDA
Pollination vector	Multiple pollination types Wind pollination Self-pollination (including two subgroups: selfing by a neighboring flower and selfing in an unopened flower) Insect pollination Pollination by water	Insect/ Wind / Self / Water / Multiple	BiolFlor
Ploidy	Diploid with haploid basic number Polyploid with haploid basic number Multiple	D / P / Multiple	BiolFlor
Leaf anatomy	Hydromorphic (A) Succulent (C) Helomorphic (E) Scleromorphic (S) Mesomorphic (M) Hygromorphic (Y)	A / C / E / S / M / Y	BiolFlor
Life span	Annual Pluriennial (including biennial) Multiple	A / P / Multiple	BiolFlor

Note. **Life form**: *Hydrophyte* (survival buds submerged or floating on the water); *Chamaephyte* (a herbaceous or woody plant with buds on or few centimeters above the surface); *Geophyte* (species with storage organs protected underground); *Hemicryptophyte* (herbaceous species with buds lying on the ground protected by litter, leaves or stem); *Phanerophyte* (shrubs and trees, i.e. with buds located above the ground); *Therophyte* (short-lived annual herbs). **Leaf anatomy**: *Hydromorphic* (small number or lack of stomata, adapted to aquatic conditions); *Succulent* (drought-resistant species with water reservoirs in the leaves and restricted respiration); *Helomorphic* (many stomata and aeration tissue in the root to compensate for the lack of oxygen in the soil e.g. marshes, bogs); *Scleromorphic* (hard leaves with thick cuticle and epidermis); *Mesomorphic* (between scleromorphic and hygromorphic); *Hygromorphic* (thin cuticle and epidermis, species require relatively high humidity).

Data analysis

All data analysis was performed using R, version 3.6.1 (R Core Team 2017). Functional diversity was calculated for all selected functional traits (listed in Table 4.2) using the occurrences of every species. Occurrence matrices included the presence and absence of every species for each time step, while functional trait matrices included the categorical and standardized (zero mean, unit standard deviation) numerical trait values for every species. Among the various indices for calculating FD, I chose RaoQ (Rao's quadratic entropy; (Botta-Dukát, 2005) as one of the most versatile and unbiased metrics for each trait per time step and status (Ricotta and Moretti, 2011), using function *dbFD()* in the FD package (Laliberté and Shipley, 2011). I selected multivariate RaoQ because it is suitable for multiple traits and it allows a mixture of categorical and continuous variables (Schleuter et al., 2010). RaoQ accounts for both functional richness and divergence (Mason and Bello, 2013) as it includes species occurrences and the pairwise functional differences between species (Botta-Dukát, 2005). RaoQ values increase with dissimilarity between traits of species and present abundance-weighted differences between species using their functional traits (Pavoine, 2020.). I checked for the independence of RaoQ among periods (temporal autocorrelation) using the *correlog()* function (ncf package, Bjornstad & Cai, 2019). FD indices were not significantly autocorrelated and thus I did not need to account for temporal autocorrelation in the model. To test whether FD significantly changes over time for each status group and for which functional traits, I used linear regression with RaoQ as a response and status, time, all of the traits and interactions of the previous three groups as predictors. I also performed a test for normality for the transformed and untransformed dependent variable. Untransformed RaoQ values yielded the best model fits and were used in the analysis. For model selection, I used a multi-model inference approach (Burnham and Anderson, 2002), employing the function *dredge* (package MuMIn, Barton, 2015). For multiple posthoc comparisons between status groups, Iused estimated marginal mean of linear trends (function *emtrends* from the package emmeans; Lenth, Singmann, Love, Buerkner, & Herve, 2018), where all possible pairwise contrasts were tested. For graphical visualization, I used packages ggplot2 (Wickham et al., 2016) and maps (Becker et al., 2018).

Results

Functional diversity for different status groups

RaoQ values range from 4×10^{-7} to 3.104. Average values of RaoQ (Fig. 4.3) were highest for native species, followed by archaeophytes, neophytes, with the lowest average RaoQ for invasive neophytes. The best model included RaoQ ~ Status + Time + Trait + Status:Time + Status:Trait + Time:Trait, and AICc weight of 0.963 which means that it is the most likely model of the ones tested; see S4.2). The second-best model had AICc weight 0.019 (with a delta AICc of 7.81). The best linear model had a high proportion of variation explained (78%), with FD of non-invasive and invasive neophytes differing significantly from native species (Table 4.3).

Functional diversity changes over time for different status groups

The functional diversity of native species did not significantly change over the seven time periods (Table 4.3b). Compared to native species, FD of neophytes and invasive neophytes increased significantly over time (Table 4.3d, Fig. 4.4). Pairwise comparisons showed that there was no significant difference between native species and archaeophytes or between alien groups (Table 4.4).

Changes in FD for different traits for different status groups and over time

Except for the negative relationship of FD with height, there were no significant relationships for other functional traits (Table 4.3c). Compared to native species, archaeophytes did not show any significant difference in FD related to traits. FD values differed for two traits when I compared neophytes and native species, with height and seed mass significantly decreasing (Table 4.3e). However, invasive neophytes showed a significant increase in FD, compared to natives, for the duration of flowering, life form, life span, pollination vector, SLA, and storage organs, and a significant decrease for seed mass (Table 4.3e).

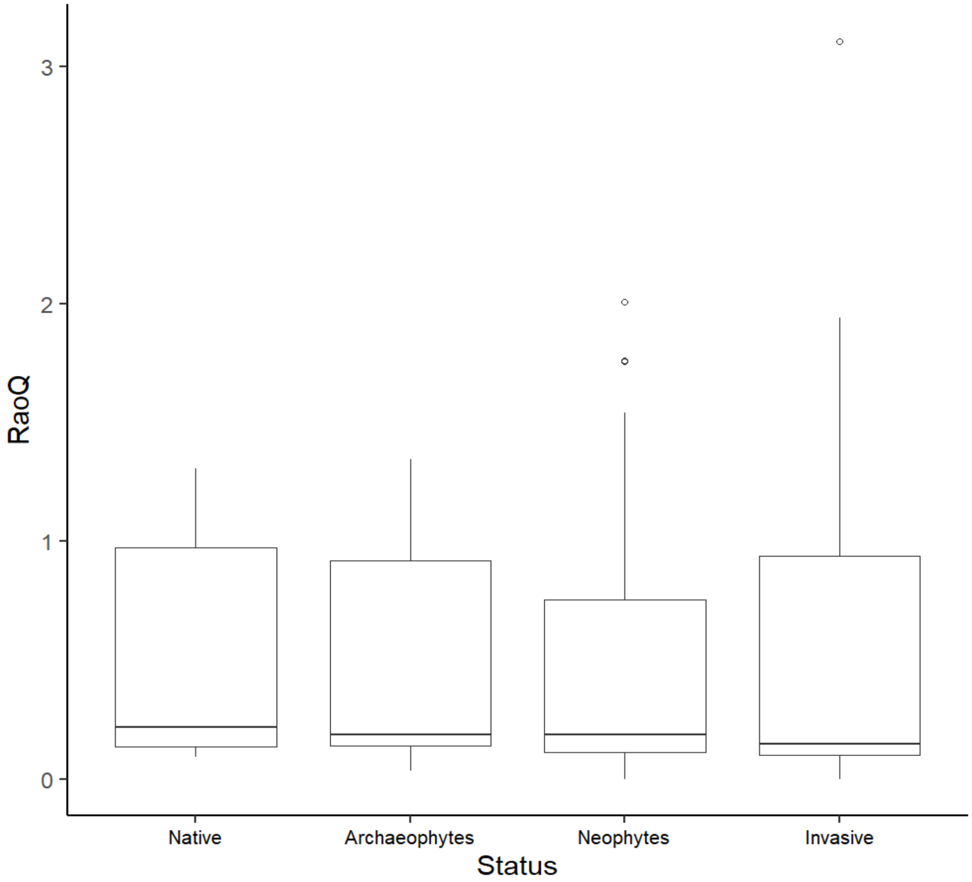

Figure 4.3. Comparison of RaoQ values for native and non-native plant species

Table 4.3. Multiple linear regression coefficients for predicting RaoQ as an index of functional diversity from explanatory variables (status, time and traits, a-c) and all two-way interactions (d-f) with significant differences in bold.

β: standardized coefficient; S.E.: standard error of estimate; p: level of significance, *****p<0.05; ******p<0.01; *******p<0.001

Variable	**β**	**S. E.**	**t value**	**p**
Intercept	0.00	0.97	-0.43	0.67
(a) Status				
Archaeophytes	-1.07	0.64	-1.75	0.08
Neophytes	**-2.15**	**0.64**	**-3.53**	*******
Invasives	**-2.82**	**1.10**	**-3.09**	******
(b) Time	0.16	0.00	1.44	0.15
(c) Trait				
Clonal growth organs	0.97	1.28	1.35	0.18
Duration of flowering	0.98	1.27	1.36	0.18
End of flowering	0.76	1.27	1.04	0.30

Height	**-1.79**	**1.27**	**-2.47**	*****
Leaf anatomy	0.96	1.28	1.33	0.18
Life form	0.93	1.27	1.29	0.20
Life span	0.98	1.27	1.35	0.18
Ploidy	0.96	1.28	1.34	0.18
Pollination vector	0.96	1.27	1.33	0.19
Seed mass	0.24	1.27	0.34	0.74
SLA	-0.40	1.27	-0.55	0.58
Storage organs	0.99	1.27	1.36	0.17
(d) Status × Time interaction				
Archaeophytes:Time	1.05	0.00	1.75	0.08
Neophytes: Time	**1.99**	**0.00**	**3.33**	******
Invasives: Time	**2.49**	**0.00**	**2.73**	******
(e) Status × Trait interaction				
Archaeophytes: Clonal growth organs	0.00	0.18	-0.06	0.95
Invasives: Clonal growth organs	0.09	0.21	1.78	0.08
Neophytes: Clonal growth organs	0.05	0.18	0.87	0.38
Archaeophytes: Duration of flowering	-0.03	0.18	-0.52	0.61
Invasives: Duration of flowering	**0.13**	**0.21**	**2.47**	******
Neophytes: Duration of flowering	0.11	0.18	1.91	0.06
Archaeophytes: End of flowering	0.00	0.18	0.06	0.95
Invasives: End of flowering	0.07	0.21	1.24	0.22
Neophytes: End of flowering	0.03	0.18	0.56	0.58
Archaeophytes: Height	-0.11	0.18	-1.96	0.05
Invasives: Height	-0.06	0.21	-1.20	0.23
Neophytes: Height	**-0.13**	**0.18**	**-2.36**	*****
Archaeophytes: Leaf anatomy	0.00	0.18	-0.05	0.96
Invasives: Leaf anatomy	0.09	0.21	1.90	0.06
Neophytes: Leaf anatomy	0.05	0.18	0.82	0.41
Archaeophytes: Life form	0.01	0.18	0.20	0.85
Invasives: Life form	**0.12**	**0.21**	**2.17**	*****
Neophytes: Life form	0.06	0.18	1.03	0.31
Archaeophytes: Life span	0.02	0.18	0.37	0.71
Invasives: Life span	**0.12**	**0.21**	**2.26**	*****
Neophytes: Life span	0.08	0.18	1.36	0.17
Archaeophytes: Ploidy	0.01	0.18	0.24	0.81
Invasives: Ploidy	0.08	0.21	1.68	0.09
Neophytes: Ploidy	0.06	0.18	0.99	0.32
Archaeophytes: Pollination vector	0.01	0.18	0.25	0.80
Invasives: Pollination vector	**0.11**	**0.21**	**2.10**	*****
Neophytes: Pollination vector	0.05	0.18	0.90	0.37
Archaeophytes: Seed mass	-0.10	0.18	-1.73	0.08
Invasives: Seed mass	**-0.12**	**0.21**	**-2.32**	*****
Neophytes: Seed mass	**-0.23**	**0.18**	**-4.12**	*******
Archaeophytes: SLA	0.03	0.18	0.62	0.54
Invasives: SLA	**0.14**	**0.21**	**2.59**	*****
Neophytes: SLA	-0.02	0.18	-0.34	0.73
Archaeophytes: Storage organs	-0.01	0.18	-0.25	0.80
Invasives: Storage organs	**0.11**	**0.21**	**2.06**	*****

Neophytes: Storage organs	0.04	0.18	0.79	0.43
(f) Time × Trait interaction				
Time: Clonal growth organs	-1.41	0.00	-1.95	0.05
Time: Duration of flowering	-0.93	0.00	-1.28	0.20
Time: End of flowering	-0.74	0.00	-1.03	0.31
Time: Height	**1.79**	**0.00**	**2.46**	*****
Time: Leaf anatomy	**-1.46**	**0.00**	**-2.02**	*****
Time: Life form	**-1.45**	**0.00**	**-2.00**	*****
Time: Life span	**-1.48**	**0.00**	**-2.05**	*****
Time: Ploidy	**-1.43**	**0.00**	**-1.98**	*****
Time: Pollination vector	**-1.45**	**0.00**	**-2.00**	*****
Time: Seed mass	-0.10	0.00	-0.13	0.89
Time: SLA	0.33	0.00	0.46	0.64
Time: Storage organs	**-1.43**	**0.00**	**-1.98**	*****
Number of observations	**335**			
R^2	**0.78**			
Adj. R^2	**0.73**			
Residual Std. Error	**0.24 (df = 267)**			
F Statistic	**14.45*** (df = 67, 267)**			
p-value	**$<2e^{-16}$**			

Table 4.4. Pairwise comparison of estimated marginal means of linear trends between native species and alien plant species at different stages of introduction. Estimate presents the difference between the groups (corresponds to the difference in slope coefficients for the given comparison) with significant values in bold.

Status	**Estimate**	**S.E.**	**t-ratio**	**p-value**
native × archaeophyte	-0.0005	0.0003	-1.751	0.29
native × neophyte	-0.0011	0.0003	-3.326	**0.00**
native × invasive	-0.0015	0.0005	-2.730	**0.03**
archaeophyte × neophyte	-0.0005	0.0003	-1.575	0.39
archaeophyte × invasive	-0.0009	0.0005	-1.693	0.39
neophyte × invasive	0.0004	0.0005	0.760	0.87

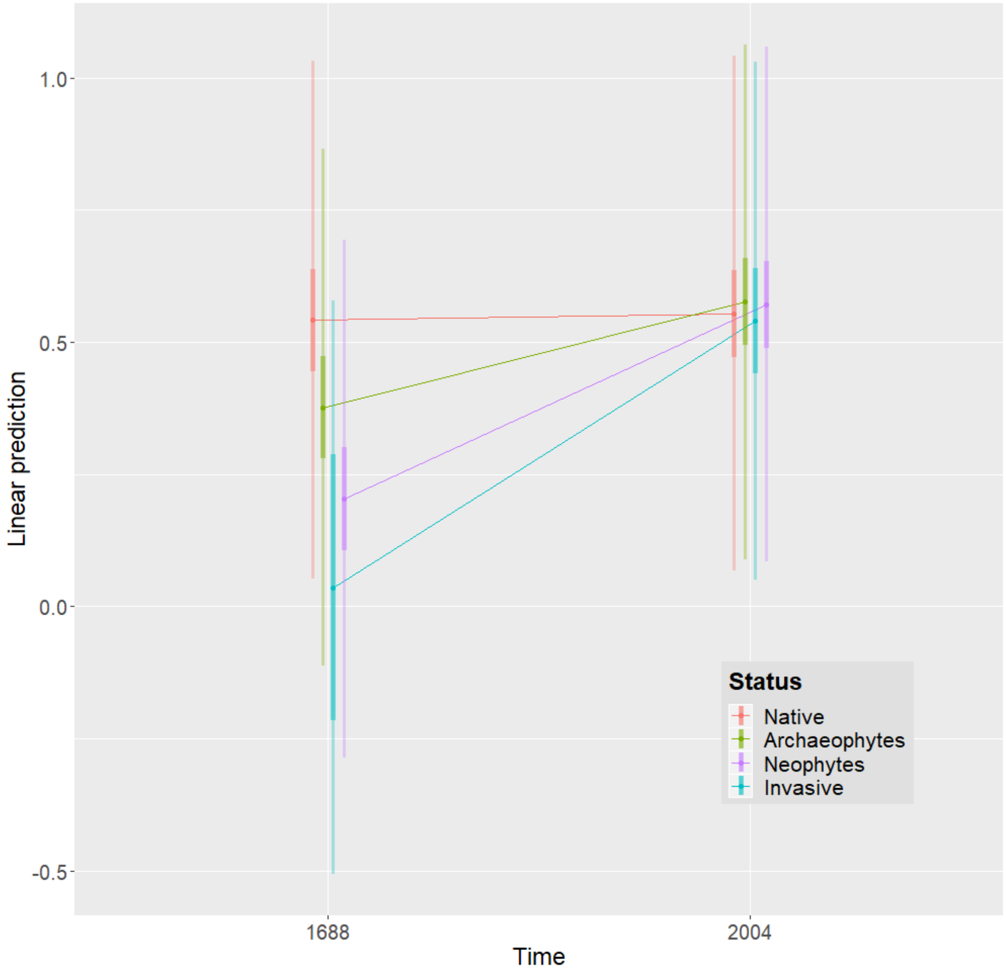

Figure 4.4. Pairwise interaction plot (based on the fitted model) for the estimated marginal means of linear trends. The figure shows linear predictions of the response variable (RaoQ) depending on the predictor variable (time) for native species and alien plant species at different stages of the invasion process with the 95% confidence interval.

Height was the only functional trait significantly increasing over time compared to the reference trait (beginning of flowering), while leaf anatomy, life form, life span, ploidy, pollination vector, and storage organs significantly decreased over time (Table 4.3f, Fig. 4.5).

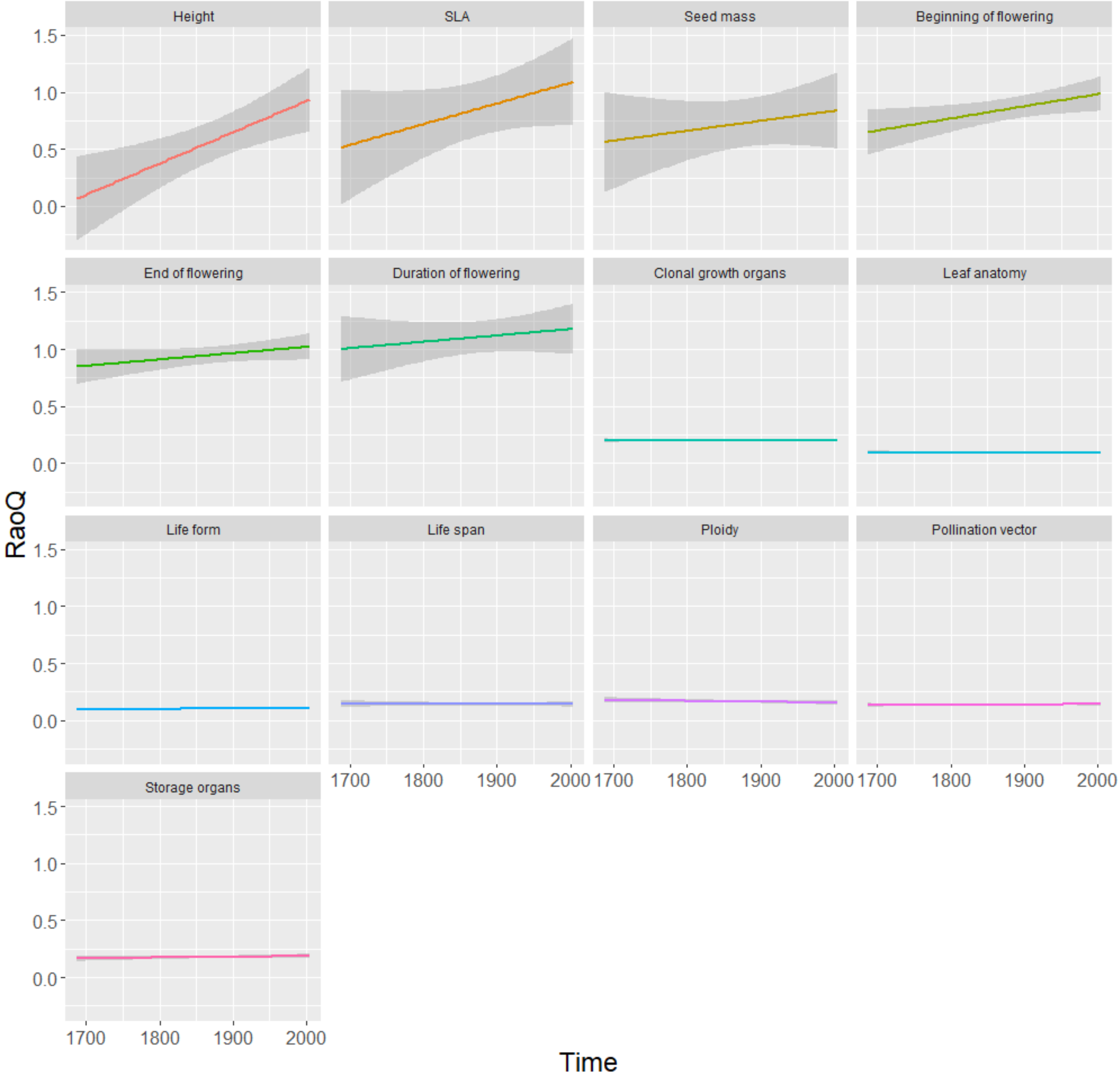

Figure 4.5. Changes in predicted RaoQ (response variable) over time (predictor variable) for each functional trait (predictor variables). Colored lines represent the linear regression line, and grey shading shows the 95% confidence interval of the fit.

Discussion

The species diversity of the urban flora of Halle (Saale) increased over three centuries, however FD did not significantly change over time. This suggests that on average species that colonized urban habitats as newcomers and those that went extinct were neither more nor less similar to the resident species. Urban areas are often hotspots of a high plant diversity and particularly alien plant species (Haeupler 1974, Pyšek 1998, Kühn et al. 2004, Kowarik, 2011). I recorded an increase in native species (that are most likely locally introduced from surrounding regions) and an influx of neophytes, while there was a decrease in archaeophytes, probably as a result of arable land reduction on the account of urbanization (Jarošik et al., 2011). The disappearance of distinctive types of habitats resulted in the loss of some native species, while others might have been introduced or immigrated into the city because of novel environmental conditions. Incoming native and alien species, as well as species remaining present across all time steps, possess traits that make them well adapted to these conditions (the strong filtering effect of urban environmental conditions; (Aronson et al., 2016; Williams et al., 2009). For example, under an environmental gradient (e.g. temperature, precipitation, soil characteristics) species occupying a habitat will have a suite of functional traits that allow them to exist along the whole gradient represented in that habitat. In the case of environmental changes associated with urbanization, functional trait values might shift along the corresponding environmental gradient and thus some trait states can be lost or gained (Williams et al., 2015). As the proportion of urban areas increased over time, semi-natural, nutrient-poor, and wet habitats were replaced by those habitats that were dry and nutrient-rich (typical for urban conditions; Pyšek et al., 2004b, Kowarik, 2011). These novel habitats still foster a similar amount of variation of functional trait states as before, however, trait values or trait states change due to the presence of new species with different trait values. Accordingly, despite species turnover, overall FD does not change because new traits (which replaced previous traits) occupy a different part of the environmental gradient. (Knapp et al., 2010) showed that trait composition in Halle shifted while here I show that variation stayed the same because of losing and gaining environmental conditions at different ends of the cline. The results hence show that urbanization processes do not directly lead to a decrease in FD but rather a functional shift, by providing conditions for the same amount of functional variation as previous habitats.

Worldwide, 55% of people live in urban areas (DESA, 2019). The level and rate of urbanization might influence species and functional diversity. Studies so far showed that moderate urbanization promotes species diversity (McKinney, 2008), yet across the globe urban floras tend to share species, making urbanization a driver of biotic homogenization (Kühn and Klotz, 2006; McKinney, 2006). Williams et al., (2009) developed a framework specifying several filters that limit or promote species survival in urban conditions. The urbanization process begins with habitat transformation via loss and gain of novel habitats. Compared to rural areas, cities contain higher diversity of habitats, communities, and species (Sukopp, 1998). For example, in Germany, novel ecosystems emerging from urbanization proved to be beneficial for alien plants (such as neophytes) but lead to homogenization in natives and archaeophytes (Kühn and Klotz, 2006). Novel ecosystems are those ecosystems which are originally modified by humans and exhibit historically different abiotic and biotic properties (Hobbs et al., 2006). These novel environments influence interaction between species (or individuals) or directly affect organisms (Heger et al., 2019). Following transformation, habitats get more fragmented and this phase is characterized by species extinction and introduction (emerging of new habitats and edge effect instigate introduction of new species; Fahrig, 2003), as well as narrow functional trait range. For example, the increase in species diversity recorded in Halle can be attributed to an increase in the number of native species (immigrating from the regional species pool to Halle) and alien species (mainly neophytes) which were able to establish and spread after introduction (e.g. to abandoned urban areas; Bello et al., 2006). For the city of Plzeň, Czech Republic, there was a decline in native species and an increase in neophytes over 120 years, but the total species number declined, and the dynamics differed between the city and its surroundings (Chocholoušková and Pyšek, 2003). Finally, environmental changes and human preferences are shaping urban flora (Williams et al., 2009), where functional traits either get confined or shift. As the human population continues to rise, I can expect that the preference for certain species (Marco et al., 2008) will become more pronounced (e.g. preference for woody and ornamental species) and functionally more similar communities will appear. For example, the size and colour of flowers and leaves as well as the selection of traits for ecological reasons such as tolerance to drought or "exoticness" of cultivated floras were shown to be important in urban landscapes (Kendal et al., 2012). In the urban areas of the United States, (Dolan et al., 2011) found species turnover (loss of species preferring natural habitat, i.e. wetlands) to correlate with a decrease in native and an increase in alien species during the last 70 years.

Changes in functional diversity for different status groups

The increase in overall neophyte species richness and in that of invasive neophytes parallels a significant increase in their FD between 1687 and 2008, although FD for both groups remains significantly lower compared to native species. Across all time steps, native species have both the highest species numbers and FDs while for invasive neophytes I recorded an increase in FD for multiple traits. Archaeophytes and non-invasive neophytes showed no difference or decrease in FD compared to the native group. The reasons for this may be threefold.

First, alien species responded, unlike native species, with an increase in FD to urbanization, as they may be less limited by fragmented urban habitats – many of them posses high dispersal ability or are very fecund (Williams et al., 2009). The loss of natural habitats such as bogs, the gain of typical urban habitats (e.g. roadside vegetation, parks, modern residential areas, industrial estates) and competition between native and alien species over the last three centuries is likely to be the driver behind 22% species turnover in Halle (presence/absence of species between different time periods, previously reported by Knapp et al., (2010) as well as changes in FD.

Second, functional trait values for both continuous and categorical traits are getting similar over time which can be associated with environmental filtering (due to fragmentation or destruction of habitats, pollution, environmental stressors) and the limited number of potential niches. For example, land-use changes (e.g. transformation of natural or agricultural areas to urban) may promote the expansion of previously non-dominant native or alien species (e.g. woody species; (Díaz et al., 2007).

Third, because of the marked increase in the number of established neophytes in Halle during the last centuries (and especially during the 1900s, where neophytes increased from 38 to 127 species, Fig. 4.2) there is a tendency for trait homogenization and communities are getting more functionally similar.

Alien species were shown to promote the homogenization of native floras as themselves, being the drivers of change, or they adapt to and benefit from novel conditions and thus indicate habitat homogenization resulting from a process in which they act as passengers (HilleRisLambers et al., 2010; MacDougall and Turkington, 2005). Species as drivers can become dominant (successful alien and native generalists) and alter environmental conditions. However, if the habitat conditions get more homogenized, species that introduced and naturalized have more similar functional traits, contrary to invasive species tend to be successful due to their dissimilarities (e.g. greater height compared to natives and non-invasive aliens; (Divíšek et al., 2018). In Halle, both overall FD and trait FD remained constant over time for natives and species introduced more than five centuries ago (i.e. archaeophytes). Due to their long residence time, these alien species tend to stay functionally similar and thrive in homogenous habitats such as arable fields (Kühn and Klotz, 2006).

Functional diversity of individual functional traits

As I observed a decrease in FD for many of the traits investigated, I can expect further filtering of species in the future and uniformity for traits such as life form, pollination vector, or life span. Our analysis demonstrated shifts in certain traits over time, such as phenology expressed as the beginning of flowering. However, focusing on the FD for specific groups, only invasive neophytes showed an increase in half of the studied traits, while archaeophytes and non-invasive neophytes did not differ significantly from natives. As population growth and urbanization intensified in Halle from the 17th century onward, these developments affected species richness, composition, and functional traits. These effects are significant mainly because the changes due to urbanization are dramatic (great changes in the relatively short period) and usually encompass large areas (McKinney, 2006). For most of the traits a meta-analysis by (Williams et al., 2015) did not find consistent responses to disturbances in urban areas, with the exceptions of increasing values of plant height and seed mass. However, I found that height was the only trait showing an increase in FD over time and this might be because urban areas can promote a wide range of different plant heights. Over the last 5000 years, forest cover decreased, and forests were particularly reduced in the 18th century (at the beginning of our study period). Prussians started reforestation of the area in the late 19th century (Albrecht et al., n.d.). This indicates that during the first time steps only species with specific heights were dominant (either tall or shorter species) and in proceeding periods (following replanting of the forest) I can observe an increase in height heterogeneity. Additionally, a wide range of heights in the urban area can be attributed to habitat transformations where smaller and short-lived ruderal species (growing along roads, railway or on brownfields) can increase in abundance, and to competition as taller species can be successful in competing with shorter species and human preference and cultivation. Taller species (trees and shrubs) are introduced to parks and gardens, and some of these species escape and establish – this process takes decades to centuries, depending on species (Ingo Kowarik, 1995). Since cities provide different types of habitats many species can grow spontaneously and colonize these areas.

Further, I found a decrease in FD for life form and life span over time, related to habitat loss and environmental changes as a result of urbanization. Extinction of many species which leads to homogenization of functional traits is associated with the disappearance of specific habitats (Pykälä, 2019) and conditions which lead to loss of respective traits (e.g. bogs, wet meadows; (Knapp et al., 2010). Furthermore, many phanerophytes (Table 4.2) are successful in urban areas since they are favoured for their ornamental value and often cultivated in parks and gardens. Certain life forms i.e. geophytes and therophytes (abundant in the cities due to high soil fertility and habitats with high disturbance, Table 4.2) often compete with other groups.

Functional diversity of SLA (specific leaf area) did not significantly change over time, possibly because extreme values (both low and high) of SLA may prove to be beneficial in cities (Thompson and McCarthy, 2008). For example, higher temperature and aridity (characteristic for urban areas and aridity particularly prominent in Halle) lead to very low SLA, while high nutrient availability in the soil promotes higher SLA values. Changes in precipitation primarily affect species with different leaf types. Halle's dry climate promotes plant species adapted to drought, i.e. species with scleromorphic or mesomorphic leaf types are prevailing over other types. Further, urban areas with lower air moisture are advantageous for wind-pollinated species, considering that under these conditions chances of pollen reaching flower stigma are higher (Knapp, 2010). Genetic traits (i.e. ploidy level) may have the potential in explaining species establishment and colonization of new habitats. Polyploidy (high ploidy levels) is an important trait of alien and invasive species, affecting the probability of invasion success (Te Beest et al., 2012) and they might be more flexible and able to grow in different habitats (genetic variability leads to adaptation under new environmental conditions; (Pandit et al., 2014; Winter et al., 2008). Thus, climatic limitations are particularly favourable for plant species characterized by idiosyncratic trait states (or extreme values) rather than facilitating heterogeneity for the majority of the functional traits. Winter et al., (2009) showed that homogenization resulted from losing native species with unique traits and gaining alien and native generalist species. Functional homogenization can be further promoted in disturbed urban areas, as generalist species increase in numbers and potentially replace specialist species.

Chapter 5.

General discussion

Main findings

Defining the key plant functional traits associated with the invasion success presents a challenge, mainly due to the context-dependence of the invasion process and link between traits and environment. The role of plant traits is reciprocal, where a trait might respond to environmental changes as well as influence ecosystem functioning and eventually ecosystem services (Lavorel and Garnier, 2002). Thus, the main theme of my thesis is the effect of alien species traits on ecosystems and their relationship with environmental factors (Figure 5.1).

In my thesis, I addressed the effect of invasive species on ecosystem services (ES) and ecosystem disservices (EDS) using their functional traits (**Chapter 2**, Milanović et al., 2020a). The proposed conceptual framework includes ecosystem services, disservices and their relations to environmental and socio-economic sectors, allowing for a more comprehensive understanding of invasive species impact. In the associated literature overview, I found that the most common invasive plant species in Europe (DAISIE, 2009) provide a variety of both, benefits and impacts. This indicates the complexity of the relationship between traits and their function in ecosystems as well as their relations in services to humans, and thus, requires studying ES/EDS via functional traits. Therefore, the basis of the framework are functional traits and not individual species, which enables the inclusion of multiple species and their effect on the observed sector. Additionally, invasive species traits often have a contrasting effect on the ecosystem (e.g. beneficial for one service/sector and disadvantageous for others). The use of this framework can overcome this issue by highlighting their impact on sectors and specific services and disservices. Shifting the perspective from single invasive species to the affected sector is crucial for identifying main traits impacting ecosystem functioning and human well-being and instigates faster management actions. Recently, a new concept - NCP (nature's contribution to people), shifts from

ES/EDS and focuses on contributions provided by nature (Díaz et al., 2018). The main advantage of NCP is including the cultural aspect in the relationship between people and nature, as well as the interdisciplinary approach (incorporates social science, local knowledge and indigenous people, in contrast to ES which place emphasis on economics).

Studying how traits respond to environmental changes is equally important because it can help in understanding species distributions under different environmental conditions. For this reason, I studied the relationship between traits and the environment (**Chapter 3** and **4**; Milanović et al., 2020b). I found that traits of invasive species have the most pronounced association with climate, land use and geological predictors, while other groups of alien species (i.e. archaeophytes and non-invasive and invasive neophytes) show fewer trait-environmental interactions (**Chapter 3**). Due to the (functional) heterogeneity of the group of native species, I did not find a prominent set of relationships of traits with environmental factors. Further, comparing alien species with different residence time, I found that aliens more often share the same trait-environment relationship (same direction, e.g. different alien groups showing a positive relationship between specific trait-environmental predictor) than contrasting relationships. This implies that all alien groups foster trait-environmental relationships which might lead to successful naturalization, while the highest number of trait-environmental associations recorded for invasive species may be an indication of their success over naturalized aliens under different environmental conditions and disturbances.

Aronson et al. (2014) showed that environmental changes associated with the development of urban areas are particularly affecting species and functional diversity, where almost a third of the urban flora consists of alien species. The majority of the alien species have been introduced into the cities where they provide multiple ecosystem services (**Chapter 2**). In **Chapter 4** I showed that overall functional diversity did not change over three centuries in a central European urban area, however, I found that for invasive and non-invasive neophytes, functional diversity increased over time. I recorded a significant decrease in functional diversity for the majority of traits, which suggest functional homogenization as an outcome of environmental filtering.

In the following sections, I will discuss the role of traits during the invasion process, their impact on ES/EDS and interconnection with the environment. Finally, I will discuss some limitations of the thesis and propose future research directions.

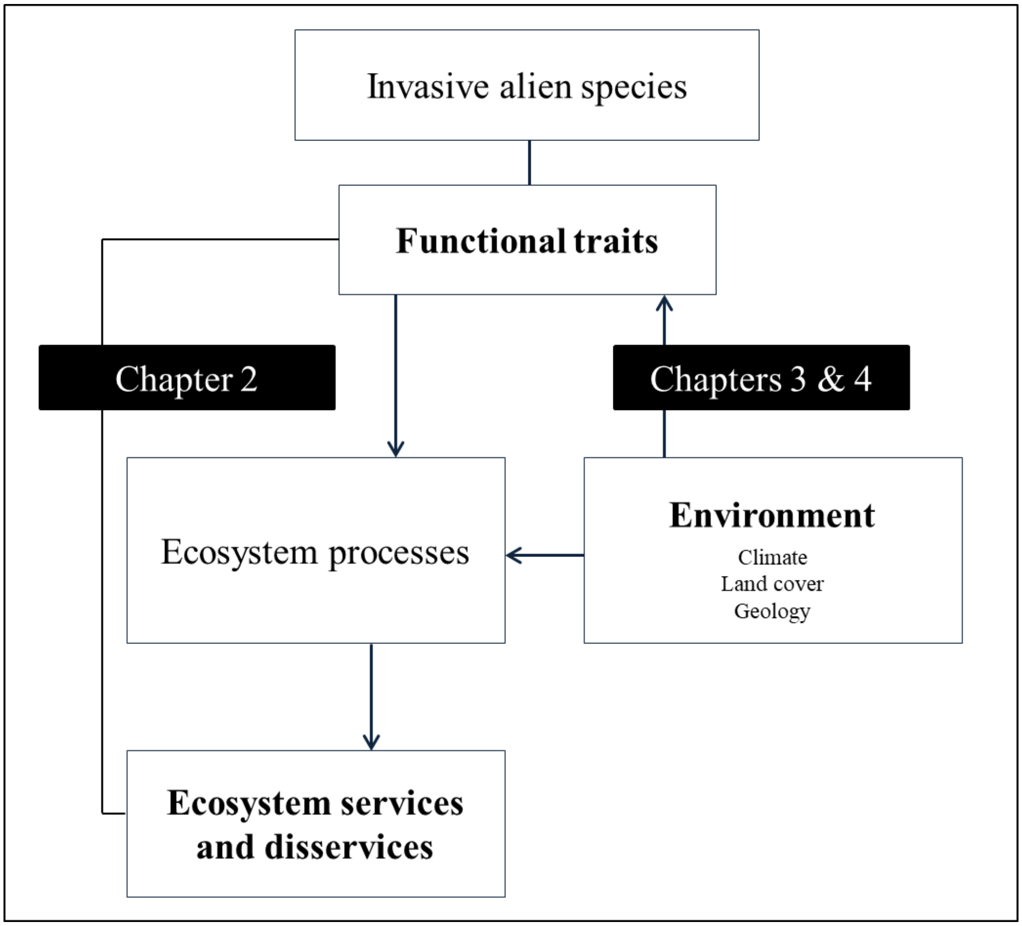

Figure 5.1. Context-dependence between functional traits, environment and ecosystem services/disservices, and overview of these aspects in different thesis chapters. Chapter 2 focuses on distinguishing the relationship between traits and ES/EDS; Chapters 3 focuses explicitly on the relationship between environment and functional traits, while chapter 4 uses time series to implicitly deduce patterns resulting from such changes.

Role of traits in invasion ecology

A number of studies found correlations between functional traits of alien plant species and their ability to become invasive (Cadotte et al., 2006; Knapp and Kühn, 2012; Küster et al., 2008; Ordonez et al., 2010; Pyšek and Richardson, 2006; van Kleunen et al., 2010b). Traits related to plant growth rate (fast-growing aliens), higher SLA, flowering phenology (longer and earlier flowering periods) and greater seed dispersal are found to be important for the success of alien species (Milanović et al., 2020b; Pyšek and Richardson, 2006). Additionally, I found that seed mass, presence of storage organs and pollination (especially wind and self-pollination) of invasive species showed strong relationships with multiple environmental conditions (**Chapter 3**). Additionally, in urban areas, not only trait values but also functional diversity for multiple traits proved to be associated to invasiveness (**Chapter 4**). For example, the diversity of traits related to phenology, pollination, or species growth (life span and form) increased over time. Considering that functional traits of invasive species impact ecosystem functions (e.g. increase in nitrogen availability in the soil due to nitrogen-fixing species; Díaz et al., 2004), we can use this information to predict if a species is beneficial or harmful (by providing ES/EDS; **Chapter 2**) under different environmental conditions. For instance, the same trait in different land cover can provide services and disservices simultaneously. For example, we can observe an increase in species biomass (Fig. 2.3) in urban areas as a disservice, where it may damage infrastructure or compete with native species but as a service in natural or agricultural landscapes (e.g. related to production of wood or erosion control). Furthermore, individuals of the same species may be susceptible to eco-evolutionary changes under different environmental conditions and therefore their effect on ecosystem processes may vary (e.g. the weed *Crepis sancta* with altered dispersal in urban compared to non-urban areas; Alberti, 2015; Cheptou et al., 2008). While some functional traits can be significant at earlier stages of invasion (e.g. during establishing and naturalization of aliens), studying traits may be particularly relevant for invasive species since they have an impact on ecosystem processes and services. However, the effect or impact of traits may be perceived during every stage of the introduction process. In **Chapters 3** and **4**, I focused on functional traits (1) to observe trait changes at a different stage of invasion (native compared with archaeophytes, neophytes and invasives) and (2) because these traits respond to environmental changes (Lavorel and Garnier, 2002). For example, I found a higher number and stronger associations between traits and climate for invasive neophytes compared to other alien groups (**Chapter 3**). I recorded a stronger relationship with traits as temperature increases (both, summer and winter temperature) for invasive species, which can be related to their origin since many invasive species in Germany were introduced from warmer regions. This is particularly pronounced in the urban areas, which on average have a higher temperature (urban heat island effect; Oke, 1982) and where I recorded an increase in functional diversity for invasive species and a further increase in FD for individual traits (**Chapter 4)**.

Taking advantage of historical botanical data is greatly beneficial as these data often attest to the transformation from rural (e.g. sparingly inhabited) to an urban area (densely populated with developed infrastructure). Environmental conditions in cities likely change over long periods, and the current environmental setting differs from the original conditions, with both past and present land use reflected in present urban floras (Salinitro et al., 2019). For example, Williams et al., (2005) showed urbanization results in a higher probability of species extinction compared to rural areas, particularly of those species with certain functional traits such as life form (geophytes or hemicryptophytes) and seed dispersal (wind or insect). Further, urban conditions (e.g., higher temperature or nutrient availability) drive an increase in species with large seed mass and height (Duncan et al., 2011; Williams et al., 2015). Traits differ between specific habitats along the urban-rural gradient. In this context, Song et al., (2019) demonstrated that in forested areas within the city, species had higher SLA, leaf nitrogen content, and lower C:N ratio, compared to species in rural forested areas, which indicates that those species are more adapted to urban conditions. Therefore, certain trait values (or states) along with high functional diversity result in alien species becoming the dominant group in cities.

Besides climatic factors, land cover and land cover changes are associated with functional traits. In **Chapter 3**, I showed that traits of invasive neophytes had multiple positive relationships with an increase in urban areas (e.g. seed mass, wind and insect pollination, flowering duration, etc.), while non-invasive neophytes and archaeophytes did not show a prominent relationship with urban or any other type of land cover. This can be a result of higher urbanity levels in invasive neophytes as they are introduced from warmer regions and thus facilitated in urban areas characterized by higher temperatures than surrounding rural areas (Kühn and Klotz, 2006). Similarly, functional diversity remained constant over time for most of the plant groups (native and non-native; **Chapter 4**). Due to urbanization many habitats, such as bogs or agricultural fields (Knapp et al., 2010) formerly occupied by native species or archaeophytes, changed or disappeared. Novel environmental conditions, particularly those associated with urban landscapes, facilitate the establishment and spread of alien species and alter their functional diversity. Since there was an increase in species diversity (Knapp et al., 2010) while overall functional diversity did not change, we can hypothesize that urban areas promote a shift in functional diversity, where some trait values get replaced but the overall variation in functional traits remains the same. Thus, despite the influx of species (either natives from surrounding areas or aliens), we can expect that climate and land cover changes have led to trait homogenization. Invasive species might further impact these novel habitats (as driver or passenger of change; MacDougall and Turkington, 2005), altering ecosystem processes and providing a new set of ecosystem services and disservices. Novel ecosystems present transformed habitats that differ in composition or function compared to the former ones (Hobbs et al., 2006). Generally, the changes in these habitats are the result of disturbances caused mainly by invasive species or climate change, which alter species richness, ecosystem functioning (e.g. nutrient cycling) and resilience. A novel ecosystem may benefit from invasive species (providing a new positive effect on processes and services), and Ewel and Putz (2004) showed that IAS can be effective in habitat restoration and phytoremediation. Further, human selection of certain species might affect trait composition and diversity. For example, alien tree species planted in parks and gardens (as ornamental species) might shape future trait distribution by replacing smaller herbaceous species and thus increasing trait values for e.g. SLA or height. Williams et al., (2009) discussed these novel habitats will promote traits shifts, among others to wind-dispersed alien species, tolerant to stress and generalists in terms of pollination vector. Similarly, invasive species with certain flowering duration or pollination vectors are often introduced in cities because of the aesthetic quality or to enhance pollination. Thus, traits related to phenology (flowering periods) and pollination are positively associated with climate (temperature) and urban land cover (**Chapter 3**, **Chapter 4**).

Alien species in Germany are introduced from regions with varying environmental conditions and are adaptable to environmental changes. For that reason, functional traits of alien species (especially invasive neophytes) display a strong relationship with climate and land cover.

Study limitations

Macroecological studies are often based on extensive data types including: large spatial and temporal extent with coarse resolution as well as the inclusion of a large number of species (McGill, 2019). However, studies rarely incorporate all three. For example, in **Chapter 3**, I analyzed trait-environmental relationships using a large number of taxa and a large spatial extent (1000 cells for the whole of Germany) at coarse resolution (c. 130km^2) – but with no temporal aspect. Therefore, my results might have missed those signals which would be observed on a finer resolution or over longer time periods. This is because large grid cells may contain habitats with a variety of climatic conditions and different land cover and soil types, and these can change over time.

Further, in my thesis, a potential limitation arises from using databases for trait values. Ideally, traits and environmental predictors should be measured on individual plants/sites and in situ, which would allow for assessing intraspecific variation and the relationship between traits and local conditions. However, according to Funk et al., (2017), the interspecific variation is larger than the variation between individuals of the same species and may sufficiently explain ecological and evolutionary processes (interspecific variation explaining ~70% of processes). Potentially, assessing intraspecific variability for historical data would be possible using specimens from herbariums and applying non-destructive measurements of some traits.

Furthermore, working with databases inevitably leads to a lot of missing data (NAs). The statistical approach in **Chapter 3** required the absolute absence of NAs and I needed to exclude all species with missing trait values or traits which were available only for a smaller number of taxa, which had the potential to influence final results (predominately by excluding a large number of native species). This was not a major issue in **Chapter 4**, since the calculation of functional diversity did not require a consistent number of species across selected functional traits.

In **Chapter 3**, I used a novel approach to study the relationship between 13 traits and 12 environmental predictors, using all plant species occurring in the whole of Germany. This method combines multivariate analysis and generalized linear model and relies on very time consuming computation. Thus, it was necessary to adjust the size of the data, and I randomly selected only 1000 grid cells (out of total 2995 cells), potentially excluding some types of habitat. Finally, the *trait.glm* method allows only statistical testing (*anova.traitglm*) for trait-environmental relationships for each model individually (e.g. archaeophytes, neophytes, invasive neophytes) while the formal test of significance between groups was not possible. Alternatively, I compare them qualitatively.

In **Chapter 4** I focused solely on temporal data collected over three centuries, using a single spatial point (city of Halle). Understanding the relationship between species (and their response) and the environment is affected by spatial extent (possibly concealing the effect of traits; Jackson and Fahrig, 2015). Focusing on one spatial extent and resolution may lead to uncertainty in understanding ecological processes, as this setup may disclose crucial patterns (particularly in dynamic and rapidly changing ecosystems; Estes et al., 2018). Working with historical data provides a unique opportunity because it allows an assessment of ecological changes and patterns over a long period, but also presents a challenge. For example, the main challenge is using the data recordings (for both historical data and

FLORKART; **Chapters 3** and **4**) from multiple authors or the possibility that some taxa were overlooked. Uncertainty regarding the quality of surveys, variety of methodologies and different sampling intensity, characteristic for many macroecological studies may be overcome by standardizing survey activities or applying appropriate statistical approaches (simulation approach i.e. Beals' index for estimating species occurrence probability; Bruelheide et al., 2020).

Conclusions and future directions

One of the biggest challenges in invasion ecology is assigning a certain functional trait or set of traits relevant for invasion success. Studies often overlook the fact that traits of invasive and native species vary under different environmental conditions. Thus in this thesis (**Chapter 3**), I incorporated the aspect of the environment, as in climate, land cover, or geology, to assess which traits are crucial at different stages of invasion and how do they depend on the environment. Future research should focus its efforts on further disentangling the relationship between functional traits of invasive species and the environment. To develop more in-depth results on the trait-environmental relationship, it would be valuable to study it in finer resolution (information on environmental conditions on a more local scale), across a broader spatial extent and to include habitat information. Some habitats are more susceptible to invasion (e.g. habitats with distinctive resource availability or ecological disturbance), which is particularly pronounced if invasive species share similar habitats in their native and invaded areas (Hejda et al., 2009). Identifying the importance of certain invasive species' functional traits in specific habitats (e.g. grasslands) would be useful for distinguishing which traits make the biggest impact on ecosystem functioning and processes, as well as which species are most likely to invade certain habitats. Those traits can be further applied in the framework from **Chapter 2**. Assessing the total impact of invasive species (via their traits) requires effort in creating a unified classification of the possible effects, which in the current literature are reported in various ways (descriptively, monetary, percentage, etc.). The main outcome of the framework is to highlight the final impact of traits on different sectors and then prioritizing the management actions on the sectors of most concern. Finally, using different climate and land cover scenarios the framework would show which alien species might spread and cause an impact in the future, (by developing scenarios for biological invasions and their impact; Essl et al., 2019b).

The main focus of the thesis was to contribute to the knowledge on the role of functional traits in the invasion process and to provide a framework which would use traits as a proxy in studying the impact of invasive species. I found that invasive species show a more pronounced association between their traits and environment, both, on the large scale (**Chapter 3**) and over long periods (**Chapter 4**). IAS exhibit higher adaptation to local conditions compared to natives and their success may be contributed to higher tolerance to a wide range of climatic and land cover factors, resulting in traits becoming context-specific (Higgins and Richardson, 2014). Future studies should take advantage of emerging databases, such as, for example, a new trait database, focusing on root traits – GRoot developed (Guerrero-Ramírez et al., n.d.). Implementing root traits (e.g. specific root length), which are severely understudied in invasion ecology but known to be related to species growth and tolerance to environmental changes (Funk, 2013; Grotkopp and Rejmánek, 2007; Mathakutha et al., 2019) can help in understanding the co-occurrence of native and alien species in the same habitat. Finally, performing in-situ measurements of plant traits (and environmental conditions) would be favorable to identify which traits of invasive species determine their success under local conditions. The success of IAS depends on a mixture of factors, with climate only partially explaining the distribution of IAS, while the context of landscape and habitat may provide a comprehensive understanding of the invasion process. For example, local climatic conditions (physiological tolerance of plants in dry vs wet and warm vs colder areas), the structure of landscape (patchiness, connectedness) and the presence of suitable habitat (forest vs open area) affect the spread and establishment of invasive species (Ibáñez et al., 2009).

In conclusion, to comprehensively evaluate the effect of invasive species or to predict the future spread or impact of alien species, it is necessary to understand the relationship between traits and the environment. Evidence suggests that climate change will further promote the spread of invasive species (Allen and Bradley, 2016; Bellard et al., 2018; Liu et al., 2017; Pyšek et al., 2005; Rockwell-Postel et al., 2020). The results in this thesis identify which traits are associated with environmental conditions, as well as how they might affect ecosystem processes and services. Understanding the role of functional traits in invasion under climate change is crucial and would facilitate suitable management actions (Beaury et al., 2020).

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Appendices

Table S2.1 References from the species classification table (Table 2.1)

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Table S3.1: Coefficient values from *traitglm* model for (a) native species, (b) archaeophytes, (c) neophytes, (d) non-invasive neophytes, (e) invasive neophytes in Germany. Coefficients describe how traits are related environmental conditions; values show strength of interaction and direction (positive/negative).

(a) Native species

Trait	**tmn**	**tmx**	**annual precipitation**	**precipitation range**	**arable land (%)**	**natural cover (%)**	**urban cover (%)**	**calcareous**	**loess**	**sand**	**CLC patches**	**geological patches**
Urbanity	0,015	-0,011	-0,007	0,0007	0,000	0,003	0,003	-0,001	-0,0006	0,009	0,000	0,000
Beginning of flowering	0,012	-0,007	0,011	-0,013	0,000	0,002	0,002	0,001	0,0003	0,001	0,000	0,000
End of flowering	0,006	-0,001	0.010	-0.008	0,000	0.005	0.004	0.0003	0.001	-0.0002	0,000	0,000
Duration of flowering	-0,002	0,005	0.002	0.002	0,000	0.004	0.003	-0.001	0.001	-0.000	-0,001	0,000
Hemeroby	0,015	-0,014	0.013	-0.011	0,000	0.006	0.013	-0.002	0.006	-0.0006	0,000	0,000
Insect pollination	-0,010	0,004	-0.001	0.003	0,000	-0.0007	0.001	-0.003	0.001	0.010	0,000	0,000
Self-pollination	0,015	0,001	0.013	0.003	0,000	-0.0008	-0.002	0.005	0.002	0.003	0,000	0,000
Wind pollination	0,008	-0,05	0.006	-0.001	0,000	0.004	-0.001	0.003	0.002	-0.008	0,000	0,000
Multiple storage organs	-0,024	0,011	-0.014	0.012	0,000	-0.004	-0.007	-0.011	-0.002	**-0.0003**	0,000	0,000
Storage organ	-0,024	0,007	-0.027	0.025	0,000	-0.005	-0.003	-0.012	0.0002	-0.008	0,000	0,000
Height	-0,007	0,004	0.001	-0.001	0,000	-0.004	0.002	-0.005	-0.003	-0.002	0,000	0,000
Seed mass	-0,015	0,007	-0.003	0.0005	0,000	0.007	0.009	-0.006	0.003	0.005	0,000	0,000
SLA	-0,005	0,0003	-0.009	0.005	0.000	-0.0001	-0.004	0.007	-0.005	-0.002	0,000	0,000

(b) Archaeophytes

Trait	tmn	tmx	annual precipitation	precipitation range	arable land (%)	natural cover (%)	urban cover (%)	calcareous	loess	sand	CLC patches	geological patches
Urbanity	0,082	0,080	-0,134	0,061	-0,021	0,029	0,060	-0,088	-0,001	0,015	-0,101	0,031
Beginning of flowering	-0,073	0,116	0,085	0,004	0,014	0,014	0,011	0,045	0,018	-0,011	0,016	-0,021
End of flowering	0,027	-0,010	0,073	-0,009	0,015	0,001	0,003	0,001	0,014	-0,009	0,011	-0,005
Duration of flowering	0,074	-0,087	0,009	-0,011	0,004	-0,008	-0,004	-0,030	0,000	-0,001	-0,001	0,010
Hemeroby	0,014	0,045	-0,034	0,013	-0,011	0,034	0,008	-0,016	0,012	0,009	0,002	-0,002
Insect pollination	-0,076	-0,008	-0,022	0,013	-0,003	-0,003	-0,011	0,012	-0,005	0,007	-0,003	-0,003
Self-pollination	0,020	0,037	0,066	0,011	-0,015	-0,002	0,022	-0,005	0,030	0,002	0,012	0,002
Wind pollination	-0,006	0,034	-0,008	-0,018	0,013	-0,030	0,019	-0,015	-0,016	0,015	-0,048	0,020
Multiple storage organs	-0,050	0,034	0,057	-0,008	-0,004	-0,016	0,043	0,025	-0,009	-0,005	0,007	0,000
Storage organ	0,047	-0,079	0,068	-0,018	-0,010	0,004	0,035	-0,003	0,018	-0,028	-0,001	0,006
Height	-0,022	-0,008	-0,122	0,055	-0,011	0,016	-0,028	-0,039	0,019	0,000	0,021	0,025
Seed mass	0,022	0,029	0,096	-0,005	0,009	0,010	0,014	0,022	-0,001	-0,009	0,044	0,007
SLA	-0,015	0,018	0,063	0,016	-0,001	-0,010	0,016	0,015	-0,014	-0,017	0,000	-0,009

(c) Neophytes

Trait	tmn	tmx	annual precipitation	precipitation range	arable land (%)	natural cover (%)	urban cover (%)	calcareous	loess	sand	CLC patches	geological patches
Urbanity	-0,043	0,162	0,065	-0,012	-0,045	-0,048	0,039	-0,015	0,048	-0,079	0,078	-0,052
Beginning of flowering	0,023	0,025	0,014	0,008	-0,004	0,017	0,010	0,007	0,015	0,019	0,043	0,020
End of flowering	0,096	-0,014	-0,009	0,009	0,002	0,016	0,029	0,013	-0,011	0,021	-0,018	0,024
Duration of flowering	0,087	-0,034	-0,020	0,004	0,005	0,004	0,024	0,009	-0,024	0,008	-0,053	0,011
Hemeroby	0,083	0,004	-0,080	0,013	-0,022	0,073	0,024	-0,055	-0,053	-0,012	-0,073	-0,001
Insect pollination	-0,007	-0,027	0,028	0,001	0,022	0,011	0,028	0,040	0,002	-0,021	0,022	-0,002
Self-pollination	0,231	-0,032	-0,139	0,049	0,019	-0,015	0,018	-0,003	-0,048	0,024	-0,061	0,036

Wind pollination	0,041	0,051	-0,106	0,052	0,015	0,023	0,023	0,000	-0,022	0,058	-0,046	0,044
Multiple storage organs	-0,138	0,008	0,101	0,009	-0,012	0,006	-0,006	0,101	0,070	-0,035	0,128	-0,040
Storage organ	0,003	-0,079	0,207	-0,035	-0,007	-0,019	0,001	0,023	0,054	0,005	0,059	-0,025
Height	0,074	-0,018	-0,192	0,010	-0,035	0,023	0,001	-0,087	0,016	0,008	0,011	0,022
Seed mass	-0,049	-0,006	-0,020	-0,007	0,014	0,001	-0,024	0,044	0,009	0,035	-0,013	-0,005
SLA	-0,009	0,002	0,115	0,032	0,002	0,007	0,010	-0,015	0,008	0,027	0,063	0,016

(d) Non-invasive Neophytes

Trait	**tmn**	**tmx**	**annual precipitation**	**precipitation range**	**arable land (%)**	**natural cover (%)**	**urban cover (%)**	**calcareous**	**loess**	**sand**	**CLC patches**	**geological patches**
Urbanity	-0,051	0,161	-0,025	0,017	-0,055	-0,054	0,039	-0,012	0,054	-0,061	0,084	-0,043
Beginning of flowering	-0,031	0,068	-0,043	0,031	-0,010	0,010	0,014	-0,005	-0,002	0,003	0,013	0,019
End of flowering	0,063	0,005	-0,026	0,015	-0,004	0,029	0,039	-0,007	-0,026	0,014	-0,045	0,025
Duration of flowering	0,085	-0,044	0,004	-0,007	0,003	0,022	0,029	-0,004	-0,025	0,012	-0,055	0,012
Hemeroby	0,059	0,008	-0,101	-0,022	-0,025	0,071	0,017	-0,087	-0,060	-0,012	-0,073	0,002
Insect pollination	0,011	-0,083	0,031	-0,017	0,012	0,024	0,030	0,034	0,013	-0,034	0,064	-0,032
Self-pollination	0,152	-0,026	-0,070	0,017	-0,003	0,017	0,024	0,009	-0,029	0,027	-0,055	0,014
Wind pollination	0,076	0,002	-0,007	-0,002	0,014	0,022	0,029	-0,008	-0,023	0,058	-0,010	0,045
Multiple storage organs	-0,139	0,018	0,201	-0,016	-0,025	-0,010	-0,015	0,111	0,074	-0,025	0,126	-0,034
Storage organ	-0,027	-0,055	0,292	-0,067	-0,011	-0,016	0,003	0,025	0,061	0,000	0,052	-0,036
Height	-0,033	0,054	-0,012	0,043	-0,050	0,020	-0,063	-0,005	0,063	0,009	-0,006	-0,026
Seed mass	-0,017	-0,038	-0,039	-0,032	0,028	0,005	0,009	0,015	-0,020	0,033	-0,020	0,017
SLA	-0,004	-0,046	0,182	-0,032	0,003	0,029	0,003	-0,042	0,011	0,001	0,036	0,000

(e) Invasive Neophytes

Trait	tmn	tmx	annual precipitation	precipitation range	arable land (%)	natural cover (%)	urban cover (%)	calcareous	loess	sand	CLC patches	geological patches
Action list	-0,211	0,436	-0,332	0,236	0,034	0,104	0,081	-0,188	-0,011	-0,038	0,101	-0,032
Urbanity	0,090	0,132	0,058	-0,044	0,016	-0,021	0,083	-0,139	-0,012	-0,136	0,117	-0,050
Beginning of flowering	-0,077	0,319	-0,166	0,136	0,057	0,100	0,023	-0,130	0,024	0,011	0,108	0,000
End of flowering	0,075	0,142	-0,101	0,061	0,045	0,045	0,057	-0,026	0,019	0,019	0,051	0,000
Duration of flowering	0,234	-0,172	0,042	-0,072	0,004	-0,053	0,069	0,125	0,002	0,018	-0,052	0,001
Hemeroby	0,146	-0,071	0,137	0,007	-0,068	0,049	0,080	0,151	-0,035	0,029	-0,149	0,049
Insect pollination	0,008	0,128	-0,094	0,082	0,093	0,002	0,080	-0,008	-0,032	0,003	-0,043	0,077
Self-pollination	0,294	0,186	-0,359	0,200	0,092	-0,025	0,003	-0,206	-0,080	0,006	-0,031	0,052
Wind pollination	-0,108	0,410	-0,712	0,460	0,044	0,087	0,071	0,043	0,033	0,087	-0,098	0,006
Multiple storage organs	-0,349	0,151	-0,146	0,128	0,021	0,067	-0,036	0,058	0,077	-0,094	0,160	-0,085
Storage organ	0,086	-0,246	0,155	-0,017	-0,032	-0,008	0,034	0,062	0,021	0,022	0,063	0,020
Height	-0,304	0,223	-0,128	0,096	-0,080	-0,035	-0,052	0,127	0,054	-0,044	0,037	-0,025
Seed mass	0,310	-0,009	-0,338	0,028	0,124	0,114	0,118	-0,337	-0,114	0,042	0,055	0,113
SLA	-0,169	0,193	-0,050	0,156	0,009	0,021	0,057	-0,079	-0,014	0,048	0,129	0,021

Table S3.2. Results of *anova.traitglm* for different groups of non-native species with 99 permutations (probability integral transform residual bootstrap (PIT-trap) block resampling which accounts for correlation in testing).

(a) Archaeophytes

Archaeophytes	**Res.Df**	**Df.diff**	**Dev**	**Pr**
env:trait (fourth corner)	167664	144	2737	0.01 **

(b) Neophytes

Neophytes	**Res.Df**	**Df.diff**	**Dev**	**Pr**
env:trait (fourth corner)	155676	144	3210	0.01 **

(c) Non-invasive neophytes

Non-invasive neophytes	**Res.Df**	**Df.diff**	**Dev**	**Pr**
env:trait (fourth corner)	129702	144	2615	0.01 **

(d) Invasive neophytes

Invasive neophytes	**Res.Df**	**Df.diff**	**Dev**	**Pr**
env:trait (fourth corner)	25794	156	2615	0.01 **

S4.1. Data sources of seven time periods (1687-2008) for the study area, Halle (Saale), Germany

1. **Time period 1687 – 1689**
    - Knauth, C. (1687) Enumeratio plantarum circa Halam Saxonum et in ejus vicinia, ad trium fere miliarium serptium, sponte provenientium. Lipsiae. – improved edition 1689
2. **Time period 1721-1783**

- Buxbaum, J.C. (1721) Enumeratio plantarum accuratior in agro Hallensi locisque vicinis crescentium una cum aerum characteribus et viribus qua variae quam ante descriptae exhibentur. Halae Magdeburgicae.
- Senckenberg, J.C. (1731), published in Spilger, L. (1937) Aus Senckenbergs botanischen Aufzeichnungen (1730/31) über Halle. Hercynia, 1, 166-173.
- Leysser, F.W. (1761) Flora Halensis exhibens plantas circa Halam Salicam tes secundum systema sexuale Linnaeanum distributas. Ed. I. Halle (Saale).
- Leysser, F.W. (1783) Flora Halensis exhibens plantas circa Halam Salicam tes secundum systema sexuale Linnaeanum distributas. Ed. II. Halle (Saale).
- Roth, A. (1783) Additamenta ad Floram Halensam (edita a J.J. Reichhard). Nova Acta Leopoldina, 7, 201.

3. Time period 1806-1858

- Luyken, J.A. (1806) – not published but documented in the herbarium of the Westphalian Museum of Natural History in Münster)
- Sprengel, C. (1806) Florae, Halensis tentamen novum. Halle (Saale).
- Wallroth, C.F.W. (1815) Annus botanicus sive supplementum tertium ad Curtii Sprenglii Floram Halensem. Halle (Saale).
- Wallroth, C.F.W. (1822) Schedulae criticae de plantis florae Halensis selectis. Corollarium novum ad C.Sprengelii floram Halensem. Accedunt generum quorumdam specierumque omnium definitiones novae, excursus in stirpes difficiliores et icones V. Tom. I. Phanerogamia. Halle (Saale).
- Garcke, A. (1848) Flora von Halle mit näherer Berücksichtigung der Umgegend von Weissenfels, Naumburg, Freiburg, Bibra, Nebra, Querfurt, Allstedt, Artern, Eisleben, Hettstedt, Sandersleben, Aschersleben, Stassfurt, Bernburg, Köthen, Dessau, Oranienbaum, Bitterfeld und Delitzsch. Erster Theil. Halle (Saale).
- Garcke, A. (1856) Flora von Halle mit näherer Berücksichtigung der Umgegend von Weissenfels, Naumburg, Freiburg, Bibra, Nebra, Querfurt, Allstedt, Artern, Eisleben, Hettstedt, Sandersleben, Aschersleben, Stassfurt, Bernburg, Köthen, Dessau, Oranienbaum, Bitterfeld und Delitzsch. Zweiter Theil. Kryptogamen nebst einem Nachtrage zu den Phanerogamen. Halle (Saale).

4. **Time period 1857-1901**

   Herbarium of the University of Halle

   - Fitting, H., Schulz, A. & Wüst, E. (1899) Nachtrag zu August Garckes Flora von Halle. Verhandlungen des Botanischen Vereins der Provinz Brandenburg, 41, 118-165.
   - Fitting, H., Schulz, A. & Wüst, E. (1901) Nachtrag zu August Garckes Flora von Halle. Verhandlungen des Botanischen Vereins der Provinz Brandenburg, 43, 34-53.

5. **Time period 1902-1949**

   Herbarium of the University of Halle

   - Fitting, H., Schulz, A. & Wüst, E. (1903) Beiträge zur Kenntnis der Flora der Umgebung von Halle a. S. Zeitschrift für Naturwissenschaften, 76, 110-113.
   - Schulz, A. & Wüst, E. (1906) Beiträge zur Kenntnis der Flora der Umgegend von Halle a. S. II. Zeitschrift für Naturwissenschaften, 78, 166-171.
   - Schulz, A. & Wüst, E. (1907) Beiträge zur Kenntnis der Flora der Umgegend von Halle a. S. III. Zeitschrift für Naturwissenschaften, 79, 267-271.
   - Wangerin, W. & Ule, W. (1909) Die Vegetationsverhältnisse. Heimatkunde des Saalkreises einschließlich des Stadtkreises Halle und des Mansfelder Seekreises. Verlag der Buchhandlung des Waisenhauses, Halle (Saale).
   - Schulze (1936; 1938) – unpublished manuscripts stored in the archive of the “working group of hercynian florists”
   - Knapp, R. (1944) Über Zwergstrauch-Heiden im Mitteldeutschen Trocken-Gebiet. Halle (Saale).
   - Knapp, R. (1944) Vegetationsaufnahmen von Trockenrasen und Felsfluren Mitteldeutschlands, Teil 2: Atlantisch-Submediterrane und Dealpine Trockenrasen (Bromion erecti). Halle (Saale).
   - Knapp, R. (1945) Die Ruderalgesellschaften in Halle an der Saale und seiner Umgebung. Halle (Saale).

6. **Time period 1950-1999**

   Herbarium of the University of Halle

   - Rauschert, S. (1959-1982) – unpublished manuscripts

- Rauschert, S. (1966) Aufruf zur Neubestätigung verschollener und zweifelhafter Pflanzenfundorte im Bezirk Halle. Wissenschaftliche Zeitschrift der Universität Halle, 15, 774-778.
- Rauschert, S. (1966) Zur Flora des Bezirkes Halle. Wissenschaftliche Zeitschrift der Universität Halle, 15, 737-750.
- Rauschert, S. (1967) Zur Flora des Bezirkes Halle (2. Beitrag). Wissenschaftliche Zeitschrift der Universität Halle, 16, 867-868.
- Rauschert, S. (1972) Zur Flora des Bezirkes Halle (4. Beitrag). Wissenschaftliche Zeitschrift der Universität Halle, 21, 63-65.
- Rauschert, S. (1973) Zur Flora des Bezirkes Halle (5. Beitrag). Wissenschaftliche Zeitschrift der Universität Halle, 22, 32-33.
- Rauschert, S. (1975) Zur Flora des Bezirkes Halle (6. Beitrag). Wissenschaftliche Zeitschrift der Universität Halle, 24, 84-91.
- Rauschert, S. (1977) Zur Flora des Bezirkes Halle (7. Beitrag). Mitteilungen zur floristischen Kartierung, 3, 50-56.
- Grosse, E. (1978) Neufunde und Bestätigungen aus dem Gebiet nördlich von Halle (Saale). Mitteilungen zur floristischen Kartierung, 4, 50-52.
- Grosse, E. (1979) Neufunde und Bestätigungen aus dem Gebiet nördlich von Halle (Saale) 2. Beitrag. Mitteilungen zur floristischen Kartierung, 5, 75-81.
- Rauschert, S. (1979) Zur Flora des Bezirkes Halle (8. Beitrag). Mitteilungen zur floristischen Kartierung, 5, 57-73.
- Rauschert, S. (1980) Zur Flora des Bezirkes Halle (9. Beitrag). Mitteilungen zur floristischen Kartierung, 6, 30-36.
- Grosse, E. (1981) Neufunde und Bestätigungen aus dem Gebiet nördlich von Halle (Saale) 3. Beitrag. Mitteilungen zur floristischen Kartierung, 7, 101-111.
- Rauschert, S. (1982) Zur Flora des Bezirkes Halle (10. Beitrag). Mitteilungen zur floristischen Kartierung, 8, 55-59.
- Grosse, E. (1983) Anthropogene Florenveränderungen in der Agrarlandschaft nördlich von Halle (S.). Martin-Luther-University Halle-Wittenberg, Halle (Saale).

- Klotz, S. (1984) Phytoökologische Beiträge zur Charakterisierung und Gliederung urbaner Ökosysteme, dargestellt am Beispiel der Städte Halle und Halle-Neustadt. PhD thesis, Martin-Luther-University Halle-Wittenberg.
- Grosse, E. (1985) Beiträge zur Geschichte der Wälder des Stadtkreises Halle und des nördlichen Saalkreises. Hercynia N.F., 22, 37-52.
- Grosse, E. (1987) Anthropogene Florenveränderungen in der Agrarlandschaft nördlich von Halle (Saale). 2. Folge: Arten naturnaher Wälder. Hercynia N.F., 24, 179-209.
- Grosse, E. & John, H. (1987) Zur Flora von Halle und Umgebung. 1. Beitrag. Mitteilungen zur floristischen Kartierung, 13, 85-112.
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- Klotz, S. & Stolle, J. (1998) Farn- und Blütenpflanzen. Arten- und Biotopschutzprogramm Sachsen-Anhalt. Berichte des Landesamtes für Umweltschutz, special edition 4/1998, Halle (Saale).

7. Time period 2000-2008

- Stolle, J. & Klotz, S. (2005) Flora der Stadt Halle (Saale). Calendula, hallesche Umweltblätter, Halle (Saale). – with updates covering 2005 to 2008

Model	Log(L)	df	AICc	Delta AICc	AICc weight
RaoQ ~ Status + Time + Trait + Status:Time + Status:Trait + Time:Trait	**35.562**	**69**	**103.3**	**0.00**	**0.963**
RaoQ ~ Status + Time + Trait + Status:Time + Time:Trait	-18.842	33	111.1	7.81	0.019
RaoQ ~ Status + Time + Trait + Status:Trait + Time:Trait	26.733	66	111.5	8.20	0.016
RaoQ ~ Status + Time + Trait + Time:Trait	-25.498	30	117.1	13.78	0.001
RaoQ ~ Status + Time + Trait + Status:Time	-36.229	21	117.4	14.08	0.001

S4.2. Comparison of multiple linear models using the *MuMIn*::*dredge* function. The response variable is RaoQ value for each time period per trait for species at different stages of introduction. Log(L) is the log-likelihood, df is degrees of freedom in each model. AICc is the Akaike Information Criterion, and Delta AICc shows the difference between the model AICc and the lowest AICc for the model set. AICc weights are the relative likelihood of each model: the bigger the Delta AICc, the smaller the weight and thus the model has lower explanation power.

Curriculum vitae

CONTACT

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ACADEMIC PROFILE

2017 - present Doctoral Researcher at Helmholtz-Centre for Environmental Research - UFZ, Department Community Ecology & Martin Luther University Halle-Wittenberg (Institute for Biology, Geobotany)

2014 - 2016 International Master in Applied Ecology MSc. Candidate with 100% Scholarship on tuition, living & travel

Jan-Sept. 2016 Christian-Albrechts University of Kiel, Germany Institute for Natural Resource Conservation, Department for Landscape Ecology Master thesis & internship Title: Wild bee diversity on wild flower areas in relation to landscape composition

Sept-Jan. 2015/16 University of Poitiers, Faculty of Fundamental and Applied Science, France Module: Evolutionary Ecology (Research stream)

April-July 2015 University of Coimbra, Portugal

Ecosystems and Environmental Quality Assessment, including laboratory studies

Feb-March 2015 University San Francisco de Quito, Ecuador

- Ecosystem Services and Conservation in Andean Watersheds

- Indigenous Groups, Oil Industry and Ecosystem Conservation in Biodiversity Hotspots

- Natural Resource Use and Tourism in Fragile Ecosystems of the Galapagos Islands

Sept-Feb. 2014/15

University of Poitiers, France

2012 - 2013 University of Belgrade, Faculty of Biology, Serbia MSc. in Biology, specialization in Experimental and Applied Botany with 100% scholarship on tuition Title: Antioxidative potential of different extracts Stachys iva Griseb. (Lamiaceae)

2007-2012 University of Belgrade, Faculty of Biology, Serbia BSc. in Biology, with 100% scholarship on tuition

CONFERENCES & TALKS

September 15th to 18th 2020

11th International Conference on Biological Invasions NEOBIOTA, Vodice, Croatia “Changes in functional diversity of native and alien urban flora over three centuries” (Standard talk)

9th to 13th September 2019

EMAPi 15th International Conference on Ecology and Management of Alien Plant invasions, Prague, Czech Republic

“Trait – environment relationships in native vs. non-native plant species” (Standard talk)

May 8th 2019

HIGRADE conference, Leipzig, Germany Best poster prize “Trait – environment relationships in native vs. non-native plant species”

September 4th to 7th 2018

10th International Conference on Biological Invasions NEOBIOTA, Dun Laoghaire, Dublin, Ireland

“Linking traits of invasive plants with ecosystem services and disservices” (Poster)

May 9th 2017

IP11 plenary meeting, Leipzig, Germany “An integrated assessment of effects of plant invasions on ecosystem services” (Pitch talk & poster)

20th April 2017

ESCALATE conference, Leipzig, Germany “An integrated assessment of effects of plant invasions on ecosystem services” (Poster)

June 13th to 16th 2013

Symposium on the Flora of Southeastern Serbia and Neighboring Regions, Vlasina Lake, Serbia

- Rubus caesius L. var. arvalis Rchb.: Antioxidative capacity of leaf extracts (Poster)
- Antioxidative potential of different extracts Stachys iva Griseb. (Lamiaceae) (Poster)

WORKSHOPS

October 2017

Fawkes III workshop “Conservation of birds and land-use”

The first meeting at University of Leeds, UK April 2018 Second meeting in Leipzig, Germany

PUBLICATIONS

Milanović M., Knapp S., Pyšek P., Kühn I. (2020) Linking traits of invasive plants with ecosystem services and disservices. Ecosystem Services. doi:10.1016/j.ecoser.2020.101072

Milanović M., Knapp S., Pyšek P., Kühn I. (2020) Trait–environment relationships of plant species at different stages of the introduction process. NeoBiota 58:55-74 doi:10.3897/neobiota.58.51655

Milanović M., Kühn, I., Pyšek P., Knapp S. (submitted to Biol Invasions) Functional diversity changes in native and alien urban flora over three centuries

Beckmann M., Ziv G., Gavish Y., Hölting L., Langer L., **Milanović M.**, Osterman J., Preidl S., Richter R., Wang Y., Václavík T. (in prep.) How birds in Europe see land-use change across Natura 2000 sites protected areas?

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „The role of functional traits across different stages of plant invasion process” 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), ________________

Marija Milanović

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