Patterns of exotic plant species in the Netherlands: a macroecological perspective

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Patterns of exotic plant species in the Netherlands: a macroecological perspective

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Contents:

1

General introduction

General introduction

Introduced exotic species can become invasive and may have major impacts on economy, ecosystems, or human health (Pimentel et al., 2000, Pimentel et al., 2005). Prevention of introduction is believed to be the most effective management option in combating impacts of exotic species (Keller et al., 2007), especially when compared to eradication. Introduction of most exotic species to a new range is strongly related to human-aided dispersal, either or not deliberately or via introduced species that may act as vectors for dispersal (Hulme et al., 2008, Hulme, 2009). Many of these vectors can be controlled by border authorities, which prevents introduction. However, only a minority of all introduced species will become invasive (Williamson and Fitter, 1996) and many non-invasive species are useful species with economic benefits. Forbidding all introductions would cause substantial economic damage to trade, so that predictions have to be precise enough to discriminate which introduced exotic species will be potential invaders. To be able to prevent introduction of the most likely invasive exotic species, new insights are required in characteristics of potential invaders and characteristics that make plant communities being invaded in order to enable predicting which exotic species will actually become invasive in which part of the new range.

In this thesis I investigated possibilities to predict invasiveness of plant species and invasibility of plant communities. As measurements of invasiveness of exotic species we used information on success of current exotic plant species in the Netherlands regional and the local spatial scales. The unique availability of these data for plant species in the Netherlands provides a novel perspective on the invasion success of exotic plant species at local versus regional spatial scales, which may help to enhance predictability of invasiveness, clarify how invasiveness may change over time, and how the composition of the native community may influence exotic species establishment.

Problems with invasive exotic plant species

The most invasive species on earth can be classified in a large variety of taxonomic groups. Some exotic animals are well known for having severe impacts. For example, the introduction of the brown tree snake on the island Guam has led to the extinction of more than half of the native bird and lizard species (Savidge, 1987, Wiles et al., 2003). Also many exotic plant species are known for their invasive impacts.

Many exotic plant species have been introduced intentionally (REF). They have been transported to new ranges for example to be used as a garden plant, whereas invasive spread has not been foreseen. In the new range, plant species can have unexpected impacts. Some notorious agricultural or forestry weeds are from exotic origin, for example *Cyperus esculentus* and *Prunus serotina*. Economic costs of introduced exotic weeds can increase quickly. Estimated costs of invasive plant species in the USA are 25 billion dollar per year (Pimentel et al., 2005), and 12 billion euro per year in Europe (Kettunen et al., 2008). Other noxious impacts may concern human health. For example, *Heracleum mantegazzianum* causes severe skin burns following contact and exposure to sunlight, and the spread of *Ambrosia artemisiifolia* throughout Europe is problematic because of its strong allergenic properties. Due to its late flowering period, this plant causes prolongation of the hay fever season.

By now, all European ecosystems and all major ecosystem services are known to be affected by invasive plant species (Vilà et al., 2011, Vilà et al., 2010). They affect community diversity and production, soil microbial activity and litter decomposition.

The problem of the invasive species is increasing over time. Increasing trade and transport causes increasing number of exotic species to regions (McNeely, 2006). In the Netherlands numbers of exotic plant species have risen from 29 species in the 18th century to 114 in the 19th century, and even 271 by the end of the 20th century (Tamis et al., 2005).

Awareness of impacts of invasive exotic species in the Netherlands is also increasing. Examples of noxious invaders are the earlier mentioned *Heracleum mantegazzianum* and *Ambrosia artemisiifolia*, but also *Fallopia japonica* and a number of aquatic weeds like *Hydrocotyle ranunculoides*. These issues have resulted in research projects that aim to support the Dutch government in taking decisions on dealing with invasive species. Especially, it was requested to enhance knowledge that enables better predictions on potential invasiveness of introduced exotic plant species. In order to develop such a predictive tool, my research project was proposed in order to find patterns that might help predict which exotic plant species can become invasive in the Netherlands.

Problem solving by prevention

Intentional introductions of most exotic plant species (Keller et al., 2007) make prevention of introduction to be the most logic tool to counteract invasions. However, because many introduced plant species from exotic origin have economic importance, for example ornamental plants or agricultural plants, prevention of introduction of all exotic plant species will receive resistance. Therefore, the aim was to to prevent only introduction of potentially noxious invasive exotic plant species. To achieve this, predictive tools should be available that forecast which species are highly likely to become invasive in a new range. Currently, the usual method to predict which species might become invasive in a new range is considering species that are already invasive elsewhere (Rejmanek, 2000, Hulme, 2012).

Important additional information for prediction may be the preferred climate range of the potential invader. When this species is native to or already invasive in a range with a similar climate as the target region, it is likely to be a successful invader (Rejmánek, 2000). Climate matching tools have proven to be useful for predicting potential invasiveness of introduced exotic plant species (Thuiller, 2005, Richardson and Thuiller, 2007). A drawback of this 'invasiveness elsewhere' method is that species that have not been introduced to new ranges cannot be considered. Also it gives no functional explanation of why some species become invasive and others not. Therefore alternative methods are needed in order to refine predictive capacity.

Trait-based predictions

A possible alternative approach to predict which species might become invasive is based on concepts from functional ecology. Functional ecologists study species in the context of their function in the ecosystem rather than their taxonomic status (Violle et al., 2007, McGill et al., 2006, Lavorel and Garnier, 2002). Irrespective of taxonomy, species can be grouped by functional, morphological, or physiological traits that predict the functioning of species in ecosystems (Diaz et al., 2004). This field in ecology has raised interest in plant traits as tools in predictive ecology, and the trait-based approach also has drawn attention of invasion ecologists. For example, some traits might promote colonization or spread more than others, which could, at least in part explain differences in invasive success of exotic species in their new range. It would be interesting to further explore the use of functional traits in predicting invasiveness.

Specific plant traits correlate to naturalisation or invasion success. Plant species with a high naturalization success appear to have smaller seeds, broader leaves and a higher relative growth rate (Pyšek and Richardson, 2007a, van Kleunen et al., 2009). Addition of other explaining factors like residence time and propagule pressure, will significantly increase the predictive power of plant traits for invasion ecology (Pyšek and Jarošík, 2005, Colautti et al., 2006, Wilson et al., 2007, Lockwood et al., 2009, Lockwood et al., 2005, Williamson et al., 2009).

A next step towards improved prediction is to use plant traits and other factors that might promote invasiveness, to create a scheme that predicts invasive potential of specific plant species. A couple of attempts have been made to work out such schemes. One of the most used schemes is the Australian Weed Risk Assessment (Pheloung et al., 1999). This assessment consists of a questionnaire on topics like naturalization history, biogeography, dispersal and unwanted traits. Answers to the questions result in a final score for a plant species, which results in an advice to consider the species safe or at risk when considering introduction. The assessment has been developed in Australia, but has also been tested on functionality in many other regions like Hawaii (Daehler et al., 2004), Central Europe (Křivánek and Pyšek, 2006), Canada (McClay et al., 2010), Japan (Nishida et al., 2009) and tropical Africa (Dawson et al., 2009b). It would be interesting to know if this scheme is also functional for the Netherlands.

Defining invasiveness

Terminology and definitions complicate prediction of invasiveness. A variety of terms is being used for the same concept and one term may have different meanings. Particularly the term invasive has turned out to be difficult to define adequately and has been used in many different meanings. This makes it difficult to compare studies. For example, some studies use the term invasive species for all species from exotic origin (Müller-Schärer et al., 2004, Leishman et al., 2007, Allison and Vitousek, 2004), whereas others use this term only for the most noxious subgroup of those species of exotic origin (Dawson et al., 2009a, van Kleunen et al., 2009, Pyšek and Richardson, 2007a, Richardson et al., 2000).

The terminology most widely used - and also used in this thesis - is placed within the framework of the invasion process (Richardson et al, 2000, and see Figure 1.1). This is the process where a species passes subsequent phases from initial transport to invasiveness. With each next step in the invasion process, only a subset of all species continues to the next step. After initial transport from the native to a novel range, the species is called an 'exotic species'. Similar terms are 'non-native species', 'introduced species', or 'alien species'. If the species escapes from transport to the (semi)natural area it is called 'casual species'. Most of these casual species fail to form persistent populations in their new range. The species that are able to form self-sustaining populations are called 'naturalised species'. Another term for this group is 'established species'. Finally, some of these naturalised species become invasive. The distinction between 'naturalised invasive' and 'naturalised non-invasive species' is the least clear and most variably described. In general, invasive species are considered exotic species with a negative impact on ecology or economy (Colautti and MacIsaac, 2004, Colautti and Richardson, 2009).

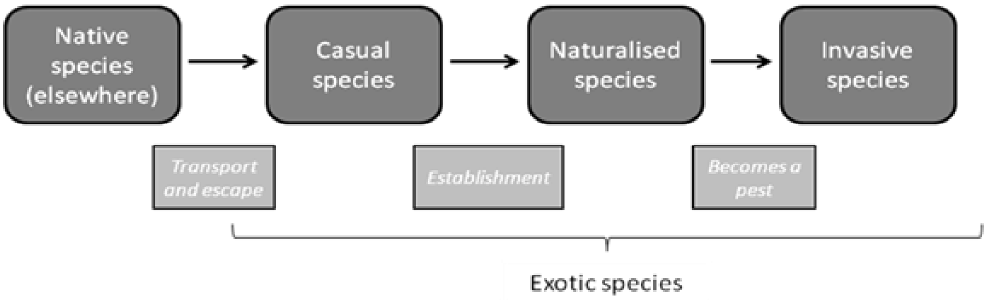

Fig. 1.1 Graphical representation of the invasion process.

A couple of estimates for distinction between invasive and non-invasive exotic species have been most popular: spread, dominance, weediness and expert judgment. One of the most frequently used estimates is spread of the species in the new range. Sometimes a definition with a cut-off score for spread has been used for an exotic species to qualify as invasive or not (Richardson et al., 2000, Dawson et al., 2009a), whereas in other occasions a continuous estimate is used (Küster et al., 2008, Bucharova and van Kleunen, 2009) .

Spread measured as regional performance of a species, however, may not be informative about local performance. In my thesis I added a scale aspect to distinguish invasive from non-invasive plant species, by using data on both regional and local abundance of exotic plant species. I used measurements of spread of the species in the Netherlands to describe the regional abundance and a measurement of local dominance to describe the local abundance. I used them as continuous scales of invasiveness, instead of a dichotomous approach, where species are being characterized as either invasive or non-invasive. Data on local performance of exotic plant species are often lacking and it is not well known how results from regional abundance relate to factors explaining local abundance. Therefore, it is valuable to enhance knowledge on how predicting with traits may vary for these different abundances.

Further, I compared a quantitative approach to defining invasiveness versus a qualitative approach. Quantitative estimates are those like regional frequency and local dominance. Qualitative estimates are mostly based on expert judgment, with experts labelling species as invasive or not. This seems based on impact of species rather than on quantitative estimates. I investigated how these different approaches of defining invasiveness might affect predictions on invasiveness.

Definitions of terms as used in this thesis.

Exotic species: species in a given area that is present due to intentional or accidental introduction by human activity.
Naturalised species: exotic species that reproduces consistently and sustains populations over many life cycles without direct intervention by humans, having at least three generations at three different sites.
Casual species: exotic species that may flourish and even reproduce occasionally in (semi-) natural habitats in a novel area, but which do not form self-replacing populations and persistence depends on repeated introductions.
Invasive species: naturalised exotic species that have a relatively high regional frequency, a relatively high local dominance and/or have a noxious impact.
Invasion process: a temporal process of an exotic species that enters after introduction to a new area: first it becomes a casual species, then a naturalised species and then an invasive species.
Neophytes: exotic plant species naturalised in a new area after 1500 AD
Archeophytes: exotic plant species naturalised in a new area before 1500 AD
Regional frequency: a measurement of invasiveness describing how widespread a species is on a regional scale. In the present study, I quantified it as the promillage of 1x1 km2 grid cells in the Netherlands where that species occurs.
Local dominance: a measurement of invasiveness describing how often a species is dominant at the local scale. In the present study, I quantified it as [the number of vegetation records with that species having > 10 per cent ground cover / the total number of vegetation records with that plant species] x 100 %.

(Van der Meijden et al., 1996, Richardson et al., 2000)

Invasiveness over time

An important factor for prediction of invasiveness in addition to traits and different proxies of invasiveness is the long-term development of invasiveness. For a number of exotic species ‘boom and bust’ patterns have been observed;

after an initial fast increase in population size, the species populations in the new range decreases (Simberloff and Gibbons, 2004, Hawkes, 2007). In order to predict the fate of exotics after introduction to a new range, it is important to investigate how general this boom-bust general pattern is.

A decrease in species populations after an initial increase could be expected within the framework of the enemy release hypothesis. This hypothesis assumes that species are released from the coevolved specialized natural enemies from their native range after introduction to a new range and they will encounter fewer specialized enemies in this new range (Keane and Crawley, 2002, Levine et al., 2006). This provides introduced exotic species with a competitive advantage that may contribute to their invasive success. However, in the novel range local enemies might be able to adapt to the new host, resulting in enhancement of numbers and impacts of enemies on the exotic species, resulting in a decrease of competitive advantage. Evidence for the existence of such a general pattern would be valuable to predict the longer-term fate of an invasive exotic plant species.

Community invasibility

Besides a species perspective, proper prediction of invasiveness also requires a community and habitat perspective. A species may have high invasive potential, but the community needs to be receptive or facilitating as well. Important hypotheses have been formulated, based on niche theory, in order to explain community invasibility. Niche theory states that each species has its own function and resource use in a community, with species-specific needs and impacts (Hutchinson, 1959). The naturalisation hypothesis, which was stated first by Charles Darwin, proposes exotic species that are more likely to naturalise successfully will have few close relatives in their novel range (Darwin, 1859, Diez et al., 2008, Daehler, 2001). This theory assumes that the availability of empty niches will be highest for species that do not have close relatives in the community to be invaded. On the other hand, based on habitat filtering, exotic species are more likely to become naturalised when they have more highly related species present in the novel community (Cornwell et al., 2006, Weiher and Keddy, 2001)). In order to be able to naturalise, the new species need the same adaptations to survive in that specific habitat as are already present in the community to be invaded. A clearer view on how these processes relate to each other might help to predict not only which species are most likely to become invasive, but also in which habitats and communities they are most likely to have the highest impact.

Research questions

The main objective of my thesis was to search for patterns and methods that might help to predict which introduced exotic plant species can become invasive. Major research questions of my thesis are:

1) Can plant traits have enough predictive power to predict which exotic plant species might become invasive?
2) Does the Australian Weed Risk Assessment have enough predictive power to predict which species might become invasive in the Netherlands?
3) Do traits related to the local scale differ from traits related to the regional scale?
4) Does it matter if invasiveness is predicted based on quantitative estimates or on qualitative estimates?
5) Is it likely that invasiveness of introduced exotic plant species changes over long-term evolutionary time scales?
6) Can a community perspective help to predict which exotic plant species can become invasive at which sites?

Macroecology

I addressed most research questions by a macro-ecological approach. Macroecology studies statistical patterns derived from large amounts of data on species distribution, abundance and richness at large spatial and temporal scales (Lawton, 1999, Brown and Maurer, 1989, Smith et al., 2008, Blackburn, 2004, Diniz-Filho and Bini, 2008). This method aims to find more general patterns, opposed to finding specific relations as a result of a reductionist approach as is being applied in experimental ecology.

I used two large Dutch databases on plant species abundance, one with data on regional spread and one with data on local dominance. The great advantage of the availability of both these datasets is the possibility to add a spatial scale dimension to invasion research.

Data from the Netherlands

The natural flora of the Netherlands has a relatively high number of introduced exotic plant species. Exotic plant species comprise 24.4% of all wild vascular plant species in the Netherlands, on a total of 1448 species (Tamis et al., 2005). Most are neophytes, introduced after 1500 (15.3%), whereas the remaining exotics are archeophytes (8.8%). Most exotics originate from other countries in Europe (62.8%), the second largest region of origin is North-America (24.8%).

The two Dutch databases on species abundance used in this thesis are much more detailed than others. The data on the regional frequency of species comes from the Florbase database (Tamis et al., 2004). For this database, the Netherlands are divided into grid cells of 1x1 km^2. Volunteer botanist have visited most of these grid cells and scored the plant species present. Most grid cells have been studied already for many decades, which gives good current and historical insight in the distribution of individual plant species in the Netherlands. Compared to similar databases from other regions, the Florbase database stands out because of the fine scale of the grid cells. For example the British and German datasets use grid cells of 130 km^2.

The data on local dominance have been obtained from the Dutch vegetation database (Hennekens and Schaminée, 2001). This database contains descriptions of co-occurrences of plant species in selected plots at small spatial scales, collected by volunteer and professional botanists. The descriptions inform on which species occur at the plot and at which local abundance. This database currently comprises over 500,000 records (Schaminée et al., 2009).

The great value of combining these two databases for the same region is that they both inform on different aspects of invasiveness. Regional frequency is widely used as an estimate of invasiveness (Küster et al., 2008, Bucharova and van Kleunen, 2009, Gasso et al., 2009), however, interactions between species are local. Availability of such detailed datasets at these two scales, is quite unique worldwide.

Thesis outline

The main objective of my thesis was to search for patterns or methods that might help predicting which exotic plant species can become invasive in the Netherlands. This resulted in the six research questions mentioned above. I based my approach on the invasion process, because possible predictors of invasiveness only become meaningful when applied to the right stage of the invasion process. Figure 1.2 provides an overview of the research chapters, how they relate to the invasion process, as well as to each other.

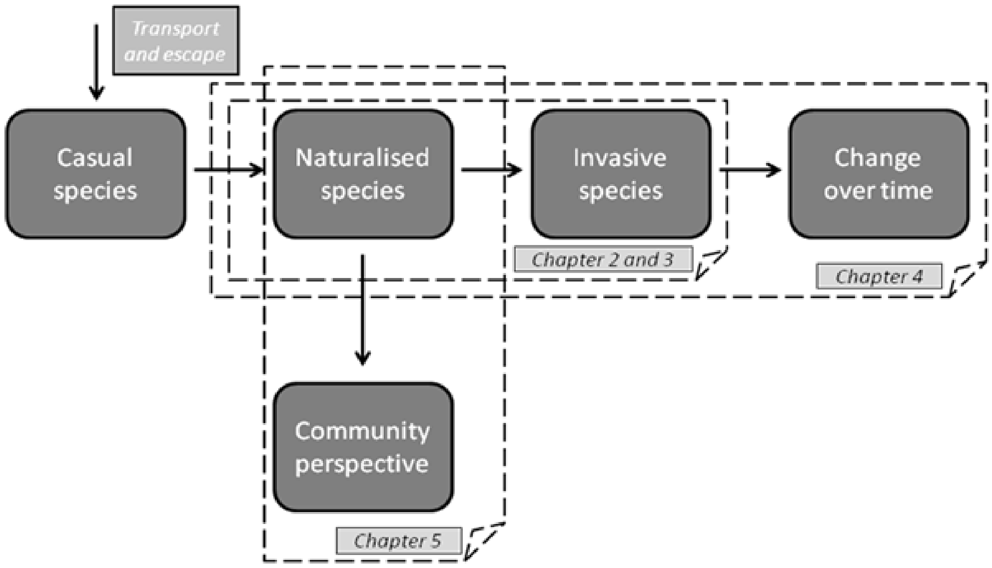

Figure 1.2 Overview scheme of topics under research in this thesis in relation to the invasion process and each other.

Chapter 2:
In this chapter I investigated if plant traits can explain which exotic plant species have been most successful in the Netherlands. I used current naturalised exotic plant species in the Netherlands to find a relationship between invasive success and plant traits, together with other important plant factors like residence time and origin. I used two measures of exotic plant success: abundance at the regional and at the local scale. I compared results from the two scales. I investigated the hypothesis that plant trait and factors that correlate well to invasiveness differs at the local and the regional scale. This chapter aims to find answers to research questions 1 and 3.

Chapter 3:
In this chapter I investigated how scores from the Australian Weed Risk Assessment for exotic plant species in the Netherlands correlated to different proxies of invasiveness. I compared quantitative estimates with a more qualitative estimate. I tested the hypothesis that qualitative estimates relate better to the WRA scores than quantitative estimates. This chapter aims to find answers to research questions 2, 3 and 4.

Chapter 4:
In this chapter I investigated the inverse relationship between residence time and local dominance of exotic plant species in the Netherlands. Such a relationship might indicate the existence of a general pattern of a process of decreased invasiveness over time, for example if enemy numbers and their impact increase over time. I tested the hypothesis that exotic plant species with a longer residence time have a lower local dominance due to increased exposure to soil-borne enemies. I performed a plant-soil feedback experiment to test increase in enemy impact. This chapter aims to find answers to research question 5.

Chapter 5:
Here, I investigated invasibility from a community perspective. I tested the hypothesis that whether the proportion of exotics with a native congener promotes or hampers naturalisation of exotic plant species depends on traits of

the plant community. In order to test this hypothesis, I used information on vegetation types of the Netherlands. I calculated the proportion of exotic species with a native congener and related this to habitat properties like nutrient richness, moisture and light availability. This chapter aims to find answers to research question 6.

Chapter 6:
In the general discussion I reflect on the practicality of the results and conclusions of my thesis for prediction of invasiveness (strength of patterns to predict). I will also discuss how different definitions on invasiveness influence predictability and I will make suggestions on how to define and predict invasiveness. I will discuss the links between the different chapters, discuss the results in a broader context and give recommendations for future research.

2

Factors relating to regional and local success of exotic plant species in their new range

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Abstract

Aim

To estimate invasiveness of exotic plant species, many studies have used the frequency of occurrence within a defined region. This measure is informative on how widespread exotics are, however, it does not inform on their local dominance, which is crucial for conservation of biodiversity and ecosystem functioning. The aim of the present study is to determine if regional frequency of occurrence of exotic plant species indeed is indicative of their local dominance. We also determined which plant traits and other factors predict regional and local frequencies best.

Location

The Netherlands

Methods

We used information on exotic plant species established in The Netherlands and compared traits relating to their frequency of occurrence regionally (the entire country) and their frequency of dominance locally (in 1-100 m^2 quadrats). We created minimal adequate models with factors explaining regional frequency and frequency of local dominance of 111 exotic plant species in The Netherlands.

Results

The model that used plant traits to explain regional frequency of exotic plant species differed from the models that best explained their frequency of local dominance. Regionally, the factors that correlated with frequency were: life form, height, polyploidy, length of flowering season, residence time, human use and origin. The factors that correlated to frequency of local dominance were lateral vegetative spread and residence time

Main conclusions

We conclude that plant traits relating to the regional frequency of exotic plant species differ from those that relate to their frequency of local dominance. The implication of our results is that predictive studies on plant invasiveness based on regional frequencies may not be indicative of the local impacts. As the prediction of local impacts is crucial for conservation and risk assessment, our

study points at an increased need of information on local abundance of exotic invaders.

Introduction

Invasive species can have severe and diverse impacts on ecosystems (Vilà et al., 2010). Probably the most cost-effective solution for conservation ecology and risk management is prevention of introduction of noxious invaders (Keller et al., 2007). Prevention requires prediction of which species become invasive. This need to be predictive has led to the search for traits related to invasiveness. In many studies it has been tested if the invasiveness of exotic plant species can be predicted by relating traits of the exotics to their regional frequency of occurrence. However, regional frequency is only one element of invasiveness, and it may not necessarily inform on local dominance, whereas local dominance relates to the ecological effects of plant species on local processes (Grime, 1998, Garnier et al., 2004). Therefore, conservation efforts will be strongly dependent on proper estimates of local dominance of exotic invaders. Therefore, we investigated how traits of exotic plant species relate to their frequency of occurrence at a regional scale, as compared to traits that relate to the dominance of the exotics at local plots within that region.

The process of invasion can be characterized by several phases (Williamson and Fitter, 1996). The last phase of the invasion process has been described as the spreading of exotic species throughout a region (Richardson et al., 2000, Theoharides and Dukes, 2007), indicating an impact on a large spatial scale. Therefore, regional frequency is often used as an indicator of the invasiveness of exotic plant species (Küster et al., 2008, Bucharova and van Kleunen, 2009, Gassó et al., 2009). Other studies use lists of invasive or weedy species to determine whether a species is invasive or not (Herron et al., 2007, Pyšek, 1998, Pyšek et al., 2009), however, these comparisons may involve subjective measurements (Richardson et al., 2000, Colautti and MacIsaac, 2004). A great advantage of considering regional frequency is that it can be quite objective.

Studies that use regional frequency as a measure of invasiveness (Küster et al., 2008, Bucharova and van Kleunen, 2009, Gassó et al., 2009) usually are based on presence/absence data of species in sub-regions of the studied region. These sub-regions are often large grid cells, for example of circa

130 km^2 in Germany (Küster et al., 2008) and 100 km^2 in Spain (Gassó et al., 2009). In some cases, sub-regions are even entire countries (Bucharova and van Kleunen, 2009). These data on large spatial scales are informative on spread, but they do not reveal the impact that widespread species may have on plant communities locally.

A positive correlation between regional frequency of occurrence and local dominance (Collins and Glenn, 1990, Thompson et al., 1998, Gaston et al., 2000), has been named one of the most general patterns in ecology (Holt et al., 2002), although there are also exceptions (Kolb et al., 2006). According to this positive correlation, species that are widespread regionally should also be dominant locally, implying that traits of invasive exotic plant species relating to their regional success also relate to their local success. However, regional and local success of plants is determined in part by different processes. For example regional spread may be facilitated by effective dispersal, whereas local dominance may be facilitated by competitiveness. Regional and local success, therefore, are expected to correlate with different plant traits, which is highly relevant to the search for traits that predict the invasiveness of exotic plant species.

Locally, plant dominance is controlled by bottom-up (resource capture, competition for these resources) and top-down (herbivores or pathogens) factors (Price et al., 1980, Tilman, 1982, Ricklefs, 1987). In order to spread regionally, plants require effective dispersal traits (Kot et al., 1996, Soons and Ozinga, 2005). In order to become locally dominant, plants may benefit from enemy release (Keane and Crawley, 2002). For example, neutral to positive feedback interactions between exotic plants and soil organisms may enhance local plant dominance (Klironomos, 2002), but it may not necessarily influence regional invasive spread (Levine et al., 2006). Therefore, we would expect different traits to relate to invasiveness depending on whether invasiveness is considered at a local or a regional scale. It has already been shown that there are differences between the traits that relate to invasiveness on a continental versus a regional scale. For example, specific leaf area relates to abundance at the continental, but not at the regional scale (Hamilton et al., 2005). However, such tests have not yet been made for regional versus local scales.

We tested the hypothesis that the traits and other factors associated with regional frequency of occurrence of exotic plant species are different from those that are associated with frequency of local dominance. We used two datasets from the Netherlands, one on regional frequency and one on local dominance of plant species. Regional frequency was quantified by the proportion of grid cells across an entire region as large as the Netherlands in which the plant species occur. Local dominance was measured in our study as the frequency of local plots where a plant species reaches a minimum coverage and therefore termed frequency of local dominance. The data used are highly detailed compared to many other datasets that are available for those scales (Schaminée et al., 2009). For the regional scale, during the 20th century in The Netherlands over 10 million records on occurrences of vascular plant species have been collected using grid cells of 1x1 km^2, which is much smaller than the sizes used for such regional datasets in many other countries. In order to quantify frequency of local plant dominance we used data on vegetation descriptions, so-called relevés, which also have been collected during the past century and stored in the Dutch Vegetation Database (Schaminée et al., 2007). This database now comprises around 500,000 relevés.

As most local data have not been collected according to a random, or stratified random pattern, these records were expected to be biased, for example because plant communities highly dominated by exotic species might be underrepresented. Therefore, we used expert judgement of field ecologists with a wide knowledge of the Dutch flora, and analyzed how their estimate of frequency of local abundance of the exotics would influence our conclusions. We discuss our results in relation to the need of conservation biologists and risk managers to obtain accurate predictions on which introduced species have the potential to become invasive and how the pattern of invasiveness in an entire region may relate to the local impacts of the exotic invaders.

Methods

Data collection

We used the Dutch Standard list of vascular plants (Tamis et al., 2004) to select 270 naturalised terrestrial plant species in The Netherlands that are all from exotic origin and that have established after 1500 AD. From this selection, we only included plant species of which suitable data were available on both regional frequency and local dominance and on plant traits. Then, we excluded plant species that were present in less than ten relevés. Exotic plant species that have become naturalised after 1950 were excluded in order to reduce the chance that the exotics have not had the time to occupy all possible regional positions. Moreover, there were hardly any data available on the local dominance of species that naturalized after 1950. Thus we were able to include 111 plant species in our selection and these species were used to test our hypothesis (list in Table S2.1).

For regional frequency we used data from the FLORBASE database. This database contains a huge number of descriptions of occurrences of plants in specified grid cells of 1x1 km^2 covering almost all of the Netherlands, mainly collected by volunteer botanists, from 1975 onwards (Van der Meijden et al., 1996). These data have been used to calculate regional frequency estimates of the 111 exotic plant species by determining their presence in the 1x1 km^2 grid cells of The Netherlands (Tamis, 2005). Presence was expressed as the permillage of the total number of square kilometres of the Netherlands (c. 37,000) in which the species had been observed.

The Dutch Vegetation Database (Hennekens and Schaminée, 2001) was used to collect plant dominance data on the local scale. This database comprises descriptions of appr. 500,000 local plant communities scattered across The Netherlands and is independent of the FLORBASE database on regional frequency. Each record describes the abundance of all plant species in the plant community of the plot expressed as percentage cover per species. The sizes of the plots depend on the type of vegetation and ranges from 1x1 m^2 for grasslands to 10x10 m^2 for forests. To our knowledge, this database is one of the largest in its kind worldwide (Schaminée et al., 2009). There are some biases in the data, which were solved by using only a subset of all descriptions. For example, some plots are monitored every year and many others not. We accounted for this oversampling by randomly selecting one record from re-sampled plots. We selected habitat types according to the frequency in which these habitat types were present in The Netherlands. Selection has been random considering the factor time. However, most records on vegetation relevés are from after 1975, so that only a minority of records originates from earlier time periods. Extremely small and extremely large plots were also removed from the selection. After all these bias-controlling clean-ups, our selection resulted in a subset of approximately 40,000 records.

To calculate local dominance we did not use the average percentage cover per plot, but frequency of local dominance. Using average cover per plot would have underrated exotic plant species that can form dense dominant stands, but that quite often occur as well at very low abundance. For example, seedlings of *Impatiens glandulifera* are often found as a single individual in a community, while this species regularly forms dense stands. With huge numbers of relevés these incidences of low abundance increase in frequency, thereby having strong influence on the average coverage of the species. We believe that for exotic plant species it is more relevant to analyze how often a species becomes dominant to a level that it may influence local processes. Therefore, we assessed how often the exotics reach a minimum threshold of ground cover. We tried several thresholds for the plant species. The threshold of 10% roughly separates subordinate from (co)dominant species (Grime, 1998). Usage of a higher threshold value (50%) resulted in a comparable ranking of species but many species never reach this threshold. Therefore, in order to determine frequency of local dominance for every exotic plant species we determined the percentage plots where that species had a ground cover of > 10 per cent by calculating [the number of vegetation records with that species having > 10 per cent ground cover / the total number of vegetation records with that plant species] x 100 %.

When recording the plant communities in the field, the selection of local plots for vegetation analysis is not always based on completely random sampling. For example, it cannot be excluded that the botanists (often volunteers) recording the vegetation may have avoided plant communities with widespread exotic species, as these plots might be less interesting to botanists. To analyse a possible underrepresentation of these invaders, the correlation between the ratio [number of local vegetation records in which plant species have been recorded]/[grid cell frequency] and the grid cell frequency was calculated. This correlation was significantly negative (Spearman's $r=-0.422$, $p<0.001$), indicating that widespread species might be less often included in vegetation records as one would assume from their regional frequency. However, analysis of a relation between the number of local vegetation records in which plant species have been recorded and the number of grid cells in which the plant species have been detected revealed a strong positive correlation (Spearman's r=0.704, p<0.001). This indicates that, although rare species might be overrepresented to some extent, the number of records including a plant species was in proportion to its regional frequency.

Another problem may be the underrepresentation of relevés that are very densely dominated by exotic plant species, as these plots could be unpopular among botanists. To analyse the influence of this possible bias on the traits related to local dominance we created a modified version of this dataset. In this version we first stratified the data by creating six categories from the unmodified data. Category 0% contained all values of exactly 0%, category 5% contained all values from >0-10%, category 15% contained all values from >10-20%, category 25% contained all values from >20-30%, category 35% contained all values from >30-40%, category 45% contained all values >40% (the highest value of the original data was 56%). Then, we asked three field experts if and how they would change the stratified data of each of the exotic plant species. In some cases the experts considered that the frequency of local dominance values from the database were an under (or over) estimation. In those particular cases we adjusted the data before making further analyses using the averages of the values provided by the three experts as the 'frequency of local dominance modified by experts'. Whenever values were not modified by an expert, the original values were used for calculation of the average. For almost half of the species at least one of the experts proposed higher estimates, among which species like *Fallopia japonica* and *Heracleum mantegazzianum*. These species are among the most invasive plant species and have high potential of forming dense dominant stands according to databases on invasive species like DAISIE, and Nobanis (DAISIE, 2006, Alberternst and Böhmer, 2006, Klingenstein, 2007) This indeed suggests that the original data may under-represent these types of relevés heavily dominated by a single exotic plant species. In our analyses, we included both unmodified and modified databases and discuss the consequences of one versus the other approach for the conclusions of our study.

We used several databases to collect information on plant traits and introduction-related factors that are characteristic for invaders (see Table 2.1). Most of these traits are related to the plant life history and they are relatively insensitive to differences that may appear in the field due to local variation in environmental conditions. We selected traits often found to correlate to one of the steps in the invasion process (Pyšek and Richardson, 2007b). Traits that may have been relevant, but that were not fully available for the exotic plant species in our database were excluded when calculating the final model. Also, traits correlating strongly to other traits that were already in use (for example, growth form strongly correlates to life form and chromosome number correlates with ploidy) were excluded in order to avoid multi-collinearity.

Besides plant traits, a number of introduction-related factors have shown to be important explanatory variables (Wilson et al., 2007), like residence time and propagule pressure. Therefore, we included period of naturalization as a measure for residence time and information on human use as an estimate for propagule pressure. Following the recent observation that both intracontinental range-expanders and species from cross-continental origin can have invasive properties (Engelkes et al., 2008), we also included the origin of species (European vs. non-European) as a factor.

Statistical analyses

In order to analyze which traits are predicting the invasiveness of exotic plant species on regional and local scales, we used generalized linear models. To obtain the best minimal adequate model we performed model selection with the Rsearch procedure in Genstat (11th edition). From all possible subsets we selected the model with the lowest Akaike Information Criterion (AIC). We transformed the data on regional abundance with a base 10 logarithm to obtain a normal error structure. For frequency of local dominance generalized linear models were used with an over-dispersed binomial error structure and logit link, with a maximum value of 100 for the original values and a maximum of 45 for the adjusted values. Of the plant traits plant height was transformed with a base 10 logarithm to improve linearity and reduce outliers. F-values and quasi F-values were calculated for each trait in the final models by removing each variable. Explained variance (R^2-adjusted) for each trait was calculated as the difference between the total R^2-adjusted for the full minimal model and that without the trait. For the binomial model for frequency of local dominance we had to calculate these values by first calculating the R^2 by dividing the deviance of the model by the total deviance. Then, R^2-adjusted values were calculated from these R^2 values. To analyse all pair-wise differences within multilevel factors in the minimal models, accounting for factors that are already in the model, we used the Rpair procedure in Genstat.

Comparative methods with species have to account for a phylogenetic correction, because closely related species share many morphological, physiological and ecological traits due to their common evolutionary history. To deal with this phylogenetic non-independence we used the method following Desdevises and colleagues (Desdevises et al., 2003, Abbott, 1992, Küster et al., 2008, Milbau and Stout, 2008, Dawson et al., 2009a, Pyšek et al., 2009). This method produces a distance matrix from a phylogenetic tree, counting the number of branches between each pair of species. We constructed a phylogenetic tree with the Phylomatic online tool (Webb and Donoghue, 2007), which plots inserted species against a master tree. From this matrix we calculated principal coordinates (PCoA's), to allow their use as covariates in the analysis that account for phylogenetic non-independence The first five PCoA's, which accounted for 98% of the variation in the distance matrix, were tested for significant relations with the regional abundance and local dominance. Only the first PCoA related significantly to regional abundance, whereas no PCoA related to any version of the frequency of local dominance measurement. This first PCoA was introduced into the model for regional frequency as a covariate to investigate how this affected the outcome.

Table 2.1 Explanatory variables used in the model selection analyses, with their sources and attributes.

Trait	***Source***	***Attributes***
Long distance dispersal ability	Standaardlijst[1]	Yes or no
Lateral vegetative spread	CLOPLA3 [2](initial), PLANTATT[3] (additional)	Yes or no
Life form	Heukels flora[4]	Therophytes, hemicryptophytes, geophytes and phanerophytes
Reproduction type	Biobase[5]	Unisexual, bisexual or polygamous (=both unisexual and bisexual flowers on one plant)
Maximum height	Heukels flora[4]	In meters
Onset of flowering	Heukels flora[4]	Month
Length of flowering season	Heukels flora[4]	Number of months
Pollination vector	Biobase[5] (initial) and Biolflor[6] (additional)	Wind or insect
Selfing	Biobase[5] (initial) and Biolflor[6] (additional)	Yes (also species with facultative self-fertilisation)or no (only obligate outcrossing plants)
Polyploidy	Biolflor[6]	Yes or no
Period of naturalisation	Standaardlijst[1]	16 and 17th, 18th, 19th century, 1900-1925, 1925-1950
Origin	Standaardlijst[1]	European or non-European
Human use	Biobase[5]	Yes or no

References of the databases: [1] (Tamis et al., 2004) [2] (Klimešová and Klimeš) [3] (Hill et al., 1999) [4] (Van der Meijden, 2005), [5] (CBS, 2003), [6] (Klotz et al., 2002).

Results

The minimal adequate model for predicting regional frequency of exotic plant species differed substantially from the models that predicted their frequency of local dominance (Table 2.2, see also figure 2.2). Therefore, our hypothesis that regional frequency and frequency of local dominance of exotic plants are predicted best by using different plant traits, still holds. When we used the data on local dominance prior to expert judgement, the model was based on a (to some extent) different set of traits than when accounting for expert judgement.

The minimal adequate model for explaining regional frequency included seven plant traits (Table 2.2a). The plant species that were regionally frequent had a longer flowering period, were used by humans, polyploids, non-European species, species that had naturalised longer ago, and also therophytes (annuals). On the other hand, hemicryptophytes (perennial plants that bear their overwintering buds at soil level) were less often regionally frequent (Table S2a in Supporting Information). This model explained 31.8% of the variation. Height and origin were the most important predictors. When these predictors were deleted, the model lost 8.0% and 7.5% in explained variation, respectively. When comparing this best model to the other top ten models produced by the model selection procedure, we found six out of seven factors in the best model to be incorporated in all other models. The factor human use was not persistently incorporated into the models, however, it was incorporated in seven of the top ten models.

The minimal adequate model for the frequency of local dominance based on the data prior to expert judgement included three plant traits (Table 2.2b) and explained 14.1% of the variation. Similar to regional frequency this model contained life form and origin as predictors. However, these traits explained frequency of local dominance in a different direction, as geophytes (perennial plants that propagate by means of buds below the soil surface) were less often dominant than the other life forms (see Table S2.2c). Moreover, plant species originating from elsewhere in Europe were more often dominant than plant species originating from outside Europe. Lateral vegetative spread was positively related to frequency of local dominance.

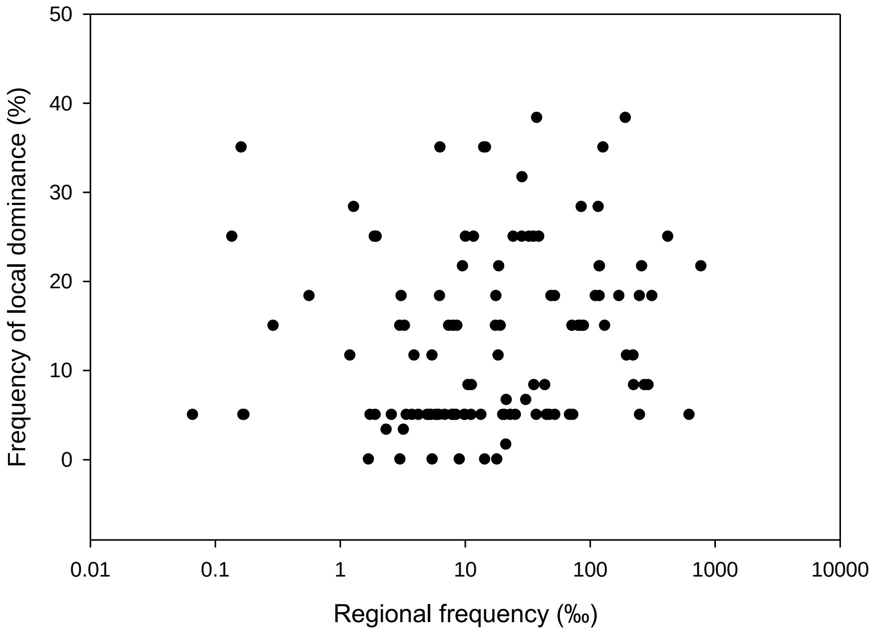

Figure 2.1 Relation between regional frequency of exotic plant species in The Netherlands (1x1 km^2 grid cell frequency) and their frequency of local dominance (based on a frequency of minimum coverage of ten percent when exotic plant species are present in local plots). The data are based on database analyses, following expert judgements of the frequency of local dominance data.

When using the frequency of local dominance data following expert judgement, the minimal adequate model included two plant traits (Table 2.2c) and explained 9.1% of the variation. Similar to regional frequency, this model contained period of naturalisation as a predictor. A longer time present in The Netherlands related to enhanced regional frequency, however, it related to reduced frequency of local dominance. The second trait in this model was lateral vegetative spread. Exotics that exerted lateral vegetative spread were more often dominant than non-vegetative spreading plant species. This conclusion also holds when the model for frequency of local dominance was based on the original data. All top ten models incorporated lateral vegetative spread, whereas eight out of ten models also incorporated period of introduction.

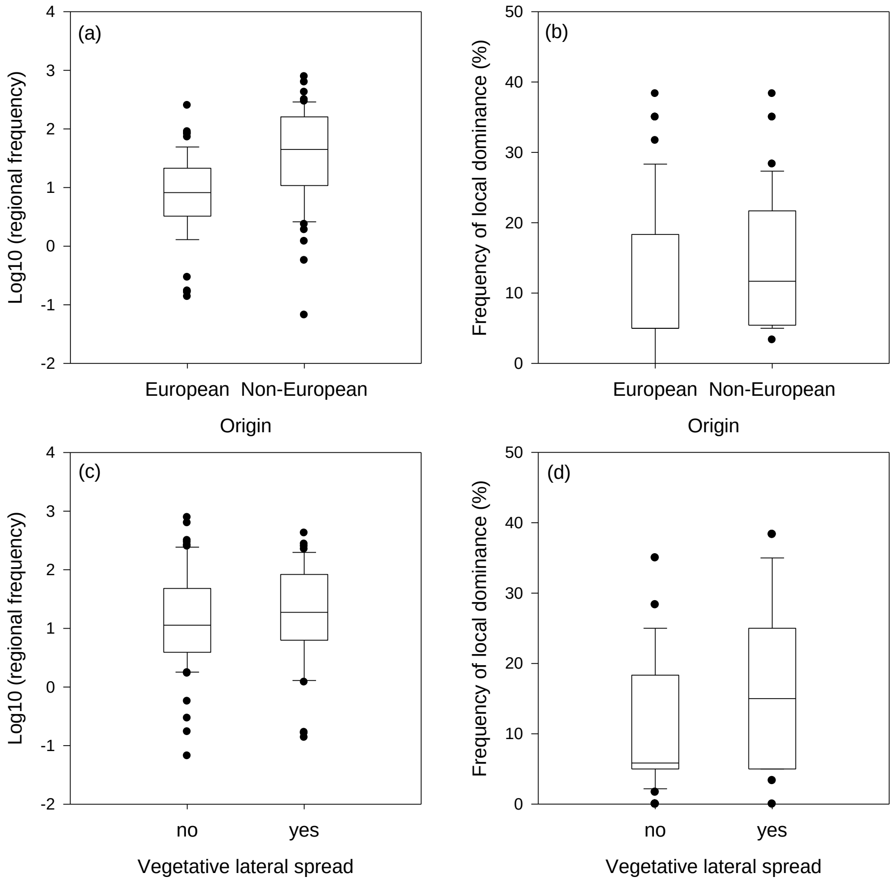

Figure 2.2 Regional frequency (a and c) and frequency of local dominance (b and d) of exotic plant species in The Netherlands for the factors origin (a and b) and vegetative lateral spread (c and d). The lower and upper boundaries of the boxes represent the 25th and 75th percentile respectively, the whiskers represent the 10th and the 90th percentile, the line in the box represents the median, the dots are outliers. The median for the frequency of local dominance of species of European origin falls together with the lower boundary of that box. Frequency of local dominance data are the data after modification by expert judgement. Analysis and graphs show that factors that explain patterns on one scale may not necessarily explain patterns on the other scale.

We found no correlation between the frequency of local dominance and regional frequency (p=0.517, Spearman's r=0.062) when considering the dataset prior to expert judgement. However, when using the dataset according to expert judgement, there was a positive correlation between the frequency of local dominance and regional frequency, although quite a large part of the variation remained unexplained (p=0.005, Spearman's r=0.279, Figure 2.1).

Phylogenetic relatedness had an effect only on the regional frequency. None of the principal coordinates related to frequency of local dominance. For regional frequency, phylogenetic relatedness only had a minor effect on all explanatory variables and most variables decreased in explained variation after correcting for phylogenetic relatedness (Table 2.2a).

Discussion

Our results clearly show that the models explaining regional frequency and the frequency of local dominance varied in the traits that were associated with each scale of observation. There was one factor that contributed to the prediction of both the regional frequency and frequency of local dominance, however, in an opposite direction: period of naturalisation was positively correlated to regional frequency, but negatively correlated to frequency of local dominance. Further, we found only a weak relation between regional frequency and frequency of local dominance. Data show that some species with high frequency of local dominance have low regional frequency and *vice versa*. Therefore, our hypothesis that different factors relate to regional frequency than to local dominance still holds. The implication of these results is that estimates of exotic plant invasiveness based on regional frequency occurrence may not be indicative of their local impact, as not all species that become regionally frequent have the potential to become often locally dominant. This is important information for invasion ecologists, conservation biologists and risk assessors, because it emphasizes the need of data on local dominance of invasive exotic plant species in order to be able to focus conservation and risk control measures.

Local dominance data

A major limitation of many invasiveness studies is that databases, especially on local dominance data are limiting. Our analysis revealed that such data need to be collected and analyzed with care. Even when using a detailed database as available on local plant community composition in The Netherlands, it remained difficult to obtain representative estimates of local dominance of plant species. We showed that using the recorded frequencies of local dominances may be confounded by observer preferences to avoid heavily invaded plots. Such selectivity can affect analysis which plant traits contribute to predicting frequency of local dominance, as the database analysis after expert judgment resulted in slightly different traits predicting frequency of local dominance. Moreover, the relation between the regional frequency and frequency of local dominance was significant only when using the frequency of local dominance data accounting for expert judgement.

Plant traits and scale

The traits that relate to invasiveness at regional and local scales may not typically indicate the processes that are of importance at each scale. We had assumed competition-related traits to be of most importance at the local scale and dispersal-related traits to be of most importance at the regional scale. Height and polyploidy correlate well with regional frequency in our study, as well as in other studies (Lloret et al., 2004, Pyšek et al., 2009, van Kleunen et al., 2009), however, height and polyploidy have been assumed to relate to competitive power (Grime, 2002, Soltis and Soltis, 2000), which is crucial for frequency of local plant dominance. Specifically on the regional scale, we expected a role for long distance dispersal, but did not find it in the final model. These results indicate that there is a need for more information on traits that may help to predict which exotic plants can become invasive at the local scale and at the regional scale in order to facilitate conservation and risk assessment, as well as to better understand which factors promote plant invasion at various spatial scales.

Table 2.2 ab&c Factors in the minimal adequate model explaining (a) regional frequency of exotic plant species in the Netherlands (1x1 km^2 grid cell frequency) , frequency of local dominance (frequency of minimum coverage of ten percent when plant is present in local plot) from original data (b) and frequency of local dominance modified by expert opinions(c).

(a) regional frequency

Factor	***Before phylogenetic correction***				***After phylogenetic correction***			
	d.f.	estimate	p	R^2-adjusted	d.f.	estimate	p	R^2-adjusted
Phylogenetic covariate					1	0.01	0.579	-0.4%
Life form	3		0.014	5.3%	3		0.024	4.6%
Hemicryptophytes		*-0.53*				*-0.53*		
Geophytes		*-0.52*				*-0.52*		
Phanerophytes		*-0.40*				*-0.40*		
Height	1	0.72	<0.001	8.0%	1	0.72	0.001	7.0%
Length flowering season	1	4.48	0.024	2.8%	1	4.48	0.038	2.4%
Polyploidy	1	0.27	0.044	4.8%	1	0.27	0.041	2.2%
Origin	1	-0.49	<0.001	7.5%	1	-0.49	0.001	6.8%
Period of introduction	1	-0.16	0.073	1.5%	1	-0.16	0.106	1.2%
Human use	1	0.22	0.155	0.7%	1	0.22	0.171	0.6%

The R^2-adjusted for the full minimal adequate model is 31.8% before phylogenetic correction and 31.4% after phylogenetic correction.

The estimates of the different attributes of life form are all tested against the life form therophytes.

(b) frequency of local dominance from original data

Factor	***d.f***	***estimate***	***p***	***R^2-adjusted***
Life form	3		0.003	9.5%
Hemicryptophytes		*-0.43*		
Geophytes		*-1.41*		
Phanerophytes		*-0.18*		
Vegetative lateral spread	1	0.49	0.025	3.4%
Origin	1	0.36	0.065	2.0%

The R^2-adjusted for the full minimal adequate model is 14.1%. We found no effect of phylogeny.

The estimates of the different attributes of life form are all tested against the life form therophytes.

(c) frequency of local dominance modified by expert opinion

Factor	***d.f***	***estimate***	***p***	***R^2-adjusted***
Vegetative lateral spread	1	0.55	0.005	9.1%
Period of introduction	1	0.23	0.058	2.4%

The R^2-adjusted for the full minimal adequate model is 9.1%. We found no effect of phylogeny.

Introduction factors and scale

Besides plant traits we also accounted for other factors, including period of naturalisation as an estimate of residence time. As in many other studies (Pyšek et al., 2004, Hamilton et al., 2005, Milbau and Stout, 2008); (Gassó et al., 2009, Bucharova and van Kleunen, 2009) we found that species with a longer residence time are more widespread. Interestingly, in our analysis frequency of local dominance declined with residence time. This might indicate that exotic plants that first gained advantage over their neighbours, for example by enemy release, lose this advantage over time (Lankau et al., 2009, Diez et al., 2010). Otherwise, this observed relationship could be due to other factors confounding with residence time (Pyšek et al., 2003).

Human use is an anthropogenic factor that we included as an estimate of propagule pressure of exotic species. We found human use to be important only in explaining regional frequency and it explained only a minor part, compared to the others factors in our analysis. A number of studies has emphasized the importance of studying propagule pressure in invasion ecology (Lockwood et al., 2005, Lockwood et al., 2009, Colautti et al., 2006, Bucharova and van Kleunen, 2009). Nevertheless, some studies considering propagule pressure found no important effect on invasiveness. This might be explained by the fact that it correlated strongly with other explanatory variables (Hanspach et al., 2008) or because the estimate for propagule pressure might not be an accurate surrogate for propagule pressure (Dawson et al., 2009a).

Non-European exotic plant species had higher regional frequency in the Netherlands than exotics that originate from Europe. The same observation has been made also across Mediterranean islands (Lloret et al., 2004). This might be related, at least to some extent, to more complete enemy release, provided that this enhances regional spread. Intuitively, species that overcome a large barrier might benefit more from the release from enemies than species that move within the same continent, as their enemies may co-migrate. However, previous studies show that both exotic plant species from within and between continents do not differ in their invasive properties (Engelkes et al., 2008) and that exotic species originating from the same continent can escape from soil-borne enemies (van Grunsven et al., 2007, van Grunsven et al., 2010). However, an effect of enemy release was expected to be of importance on frequency of local dominance, instead of on regional frequency. Another explanation may be that species sharing less evolutionary history with native species (which is often assumed for species from other continents) encounter more empty niches, as is suggested by Darwin's naturalisation hypothesis (Thuiller et al., 2010). This might explain why we found an effect of origin on the regional frequency, but not on the frequency of local dominance.

Conclusions

Our conclusion that regional frequency of exotic plant species does not show a strong correlation with their local dominance has important implications for conservation and risk assessment of exotic invaders. As local impacts depend on local dominance (Grime, 1998), conservation efforts based on regional frequencies only will overestimate widespread, but locally non-dominant plant species. On the other hand, conservation efforts might miss those exotic plant species that have regional infrequency, but local dominance. Further, we conclude that this scale issue also matters for predicting which plant species become invasive. Plant traits and other factors that correlate well with regional frequency of exotic plant species differ, at least to some extent, from traits that correlate with local plant dominance. Thus, risk management and prevention based only on traits predicting regional spread will easily overlook traits that are important for predicting invasiveness at the local scale. Therefore, assessing the potential invasiveness of introduced exotic plant species requires multilevel assessments including a variety of plant traits and other factors, such as origin and residence time to be used at datasets on both regional frequency and local dominance.

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Supporting Information

Table S2.1 List of 111 exotic plant species in The Netherlands used in our study.

Table S2.2 Pairwise differences of multilevel factor life form.

Table S2.1
List of 111 exotic plant species in The Netherlands used in our study.

Allium carinatum
Allium paradoxum
Alnus incana
Amaranthus blitoides
Amaranthus retroflexus
Amelanchier lamarckii
Angelica archangelica
Anthemis tinctoria
Anthoxanthum aristatum
Arabis arenosa
Aronia prunifolia (x)
Aster lanceolatus
Berteroa incana
Bidens connata
Bidens frondosa
Buddleja davidii
Bunias orientalis
Ceratochloa carinata
Chenopodium foliosum
Claytonia perfoliata
Claytonia sibirica
Coincya monensis subsp. recurvata
Conyza canadensis
Corispermum intermedium
Coronopus didymus
Cotula coronopifolia
Crambe maritima
Crepis tectorum
Crocus vernus

Cuscuta lupuliformis
Cymbalaria muralis
Cynodon dactylon
Datura stramonium
Diplotaxis muralis
Eragrostis minor
Eragrostis pilosa
Eranthis hyemalis
Erigeron annuus
Erucastrum gallicum
Fallopia japonica
Fallopia sachalinensis
Galanthus nivalis
Galinsoga parviflora
Galinsoga quadriradiata
Geranium phaeum
Geranium pyrenaicum
Heracleum mantegazzianum
Hieracium amplexicaule
Hieracium praealtum
Hordeum jubatum
Hypericum canadense
Impatiens glandulifera
Impatiens parviflora
Juncus tenuis
Lepidium draba
Lepidium virginicum
Leucojum vernum
Lupinus polyphyllus
Lycium barbarum
Mahonia aquifolium
Matricaria discoidea
Medicago sativa
Mibora minima
Muscari botryoides
Muscari comosum

Oenothera parviflora
Ornithogalum nutans
Oxalis corniculata
Oxalis fontana
Oxycoccus macrocarpos
Parentucellia viscosa
Pentaglottis sempervirens
Persicaria wallichii
Poa chaixii
Potentilla intermedia
Potentilla norvegica
Potentilla recta
Prunus serotina
Pseudofumaria lutea
Rapistrum rugosum
Rhododendron ponticum
Ribes alpinum
Robinia pseudoacacia
Rorippa austriaca
Rosa rugosa
Rubus spectabilis
Salix dasyclados
Salvia verticillata
Scilla bifolia
Scilla siberica
Scrophularia vernalis
Senecio inaequidens
Setaria pumila
Setaria verticillata
Sisymbrium altissimum
Sisymbrium austriacum subsp. chrysanthum
Sisymbrium loeselii
Sisymbrium orientale
Solanum triflorum
Solidago canadensis
Solidago gigantea

Spartina anglica
Symphoricarpos albus
Tragopogon porrifolius
Trifolium hybridum
Tulipa sylvestris
Veronica filiformis
Veronica peregrina
Veronica persica
Vicia villosa
Xanthium strumarium

Table S2.2.
Estimates and t-probabilities (in italics, bold when significant) of pairwise differences and estimates of the means on the diagonal for (a) regional abundance, before phylogenetic correction, (b) regional abundance, after phylogentic correction and (c) local dominance, original data.
(a)

	Before phylogenetic correction			
	Therophytes	Hemicrypto	Geophytes	Phanerophytes
Therophytes	1.4553			
Hemicryptophytes	0.4749 ***0.004***	0.9805		
Geophytes	0.4484 *0.064*	-0.0265 *0.911*	1.0070	
Phanerophytes	0.2641 *0.329*	-0.2108 *0.397*	-0.1843 *0.556*	1.1913

(b)

	After phylogenetic correction			
	Therophytes	Hemicrypto	Geophytes	Phanerophytes
Therophytes	1.4401			
Hemicryptophytes	0.4652 ***0.006***	0.9748		
Geophytes	0.3712 *0.167*	-0.0941 *0.718*	1.0689	
Phanerophytes	0.2525 *0.353*	-0.2127 *0.394*	-0.1187 *0.719*	1.1876

(c)

	Therophytes	***Hemicrypto***	***Geophytes***	***Phanerophytes***
Therophytes	-1.720			
Hemicryptophytes	0.428 *0.065*	-2.148		
Geophytes	1.411 ***0.002***	0.983 ***0.034***	-3.131	
Phanerophytes	0.181 *0.549*	-0.247 *0.397*	-1.230 ***0.016***	-1.901

3

Testing the Australian Weed Risk Assessment with different estimates for invasiveness

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Abstract

The Weed Risk Assessment (WRA) has become an effective tool in predicting invasiveness of exotic plant species. In studies testing the WRA, exotic plant species are usually divided into major weeds, minor weeds and non-weeds. However, these divisions are qualitative, as the categories are assigned by experts. Many studies searching for plant traits that are indicative of plant invasiveness use quantitative estimates to measure invasiveness. We compared how quantitative and qualitative estimates of invasiveness may relate to WRA scores. As quantitative estimates we used regional frequency (spread), change in regional frequency and local dominance of naturalized exotic plant species in The Netherlands. To obtain a qualitative estimate we determined if the exotic plant species occurred on a black list in neighbouring regions. We related WRA scores of the exotic plant species to these qualitative and quantitative estimates of invasiveness. Our results reveal that the WRA predicted the qualitative (black list) estimate more accurately than the quantitative (dominance and spread) ones. The black list estimate matches with the overall impact of exotic species, which is assumed to incorporate regional spread, local dominance and noxiousness. Therefore, the WRA predicts the noxiousness component, but to a lesser extent the spatial components of impact of exotic species. On the other hand, studies that use regional spread and other quantitative estimates of invasiveness tend not to include the noxiousness component of impact. We propose that our analyses may also help to further solve the recent debate on whether or not performing research on exotic species.

Introduction

The Weed Risk Assessment (WRA) has been developed in Australia (Pheloung et al., 1999) and has been suggested to be one of the most effective tools to predict which exotic plant species may become invasive. The WRA identifies specific exotic plant species that should be rejected or accepted for import, or when further evaluation is required because a species is categorized as an intermediate risk. The WRA is based on attributes of species that cover biogeography, life history traits and weediness. The WRA has been tested (with some minor modifications) in a number of regions outside of Australia, for example Hawaii (Daehler et al., 2004), Czech Republic (Křivánek and Pyšek, 2006), Italy (Crosti et al., 2010) and Tanzania (Dawson et al., 2009b). In all these regions, the WRA has been shown to effectively predict invasiveness (Gordon et al., 2008). Due to the costs associated with the impacts of problematic weeds, implementing the WRA appears economically prudent, even when some beneficial non-weeds might be rejected for import (Keller et al., 2007). On the other hand, a more recent review is less positive about applying weed risk assessments in general (Hulme, 2012), claiming that issues with objective measures of hazards, with quantifying uncertainty and with biases in expert judgement all limit the utility of weed risk assessments.

In most studies testing WRAs, there is an *a priori* assignment of species to categories of major weeds, minor weeds and non-weeds (Daehler et al., 2004, Gordon et al., 2008, McClay et al., 2010, Nishida et al., 2009, Pheloung et al., 1999). These categories are usually assigned by experts. The question remains how the WRA performs in comparison to other estimates of invasiveness or weediness. Only some studies testing the WRA have used a more quantitative approach to categorise species as major, minor and non-weeds (Křivánek and Pyšek, 2006, Dawson et al., 2009b) These studies used a definition of invasiveness that is based on the concept of the invasion process (Richardson et al., 2000, Blackburn et al., 2011). This more quantitative approach is comparable to the approach mostly used in studies correlating invasion success to ecological or life history factors. A number of quantitative estimates have been used to quantify the last phase of invasiveness in these studies, for example regional frequency (Bucharova and van Kleunen, 2009, Küster et al., 2008, Speek et al., 2011), rate of increase in regional frequency (Thompson et al., 1995), or local dominance (Speek et al., 2011).

The aim of the present study was to compare how qualitative versus quantitative estimates of invasiveness for exotic naturalised species in the Netherlands are predicted by WRA scores. We used three quantitative estimates, including: regional frequency, change in regional frequency over time, and local dominance. The qualitative estimate was perception of invasiveness based on perception of noxiousness in neighbour regions. We have determined these estimates for exotic plant species that have become naturalised in the Netherlands and correlated the estimates with the WRA scores according to Pheloung et al. (1999).

As the estimates may focus on different elements of invasiveness, we expected them to relate to different aspects of the WRA. For example, regional frequency likely reflects how species spread and so may relate to dispersal-related scores in the WRA, rather than to 'undesirable attributes' scores. Therefore, we analysed which of the eight categories of questions in the WRA related best to the different estimates of invasiveness.

Methods

Weed Risk Assessment (WRA)

The WRA consists of 49 questions on biogeography, naturalisation and weediness elsewhere, undesirable traits, and reproduction and dispersal mechanisms (Pheloung et al. 1999). Answers to questions receive a score from -3 to +5. Not all questions need to be answered. The outcome is the sum of all these scores, ranging from -26 to +60. The scores are used to determine whether exotic species that are being considered for introduction, should be rejected (score>6), accepted (score<0) or whether further evaluation is required (0-6 score). We modified a couple of questions to make them suitable for the situation of the Netherlands, as the WRA was originally developed for introduced plants in Australia (Pheloung et al., 1999). The modifications involved question 2.01 'suited to Australian climates', which was changed into 'suited to temperate climates', question 2.04 'regions with extended dry periods', which was changed into 'regions with frost periods', and question 8.05 'enemies present in Australia' was changed into 'enemies present in the Netherlands' (Supplement S3.1). Questions on climate and introduction history were answered as if the species had not yet been naturalised. For that, we did not use information from the Netherlands and Belgium.

The WRA was applied using a well-defined guideline (Gordon et al., 2010). Questions were answered using information from a variety of sources: online factsheets from Nobanis (NOBANIS, 2011), Daisie (DAISIE, 2011) the Global Weed Compendium (GCW, 2011) and CABI Forestry Compendium (CAB International, 2010), books describing plant species, such as the Dutch Flora (Van der Meijden, 2005), and online databases, such as Biolflor (Klotz et al., 2002), and Kew Seed Database (Royal Botanic Gardens Kew, 2008).

Species selection

The Dutch Standard list of vascular plants (Tamis et al., 2004) was used to select naturalised exotic plant species in The Netherlands that have established after 1500 AD. Also, we used only terrestrial plant species, as aquatic species are more difficult to be predicted correctly with the WRA (Gordon and Gantz, 2011). From this selection, we only included plant species of which suitable data were available on both regional frequency and local dominance. Exotic plant species that have become naturalised after 1950 were excluded, because they may not have had time to occupy all suitable positions in the study region (Speek et al., 2011). The selection resulted in 111 exotic plant species (listed in Supplement S3.2).

Estimates of invasiveness

We used three quantitative estimates of invasiveness: regional frequency, change in regional frequency, and local dominance. For regional frequency we used data from the FLORBASE database containing approximately 8 million descriptions of occurrences of plants in specified grid cells of 1 x 1 km^2 covering almost all of the Netherlands. These data have been collected predominantly by volunteer botanists from 1975 onwards (Van der Meijden et al., 1996). Regional frequency estimates of the 111 exotic plant species were calculated by enumerating their presence in all 1 x 1 km² grid cells of The Netherlands (Tamis, 2005, Tamis and van't Zelfde et al., 2005). Presence was expressed as the permillage (/1000) of the total number of square kilometres of the Netherlands (c. 37,000) in which the species had been observed.

Data on change in regional frequency were based FLORBASE, supplemented with information from another database, FLORIVON. The latter contains information on plant occurrences from 1900-1950 (Kloosterman and Van der Meijden, 1994). Change represents the increase in regional frequency from the period 1900-1950 to the last decade of the 20th century expressed as: change = log10(regional frequency last period) – log10 (regional frequency first period) . The numbers of recordings of grid cells vary considerably. For comparison in time, the most recent observations of each period have been used. The data have been corrected for temporal and geographic differences in sampling intensity (Tamis, 2005, Tamis and van't Zelfde et al., 2005).

The Dutch Vegetation Database (Hennekens and Schaminée, 2001) was used to collect local plant dominance data. This database comprises descriptions of approximately 500,000 local plant communities scattered across The Netherlands and is independent of the FLORBASE and FLORIVON databases. Each record in the Dutch Vegetation Database describes the abundance of all plant species in the plant community of the plot expressed as percentage cover per species. The sizes of the plots depend on the type of vegetation and ranges from 1 x 1 m² for grasslands to 10 x 10 m² for forests.

To calculate local dominance we divided the number of vegetation records with that species having > 10 per cent ground cover by the total number of vegetation records with that plant species and multiplied this number by 100 to obtain a percentage (Speek et al., 2011). This results in frequency of local dominance, which will be named 'local dominance' throughout this paper. To reduce bias from non-random sampling we checked the data of all exotic plant species and modified the local dominance of some species according to expert opinion (Speek et al., 2011).

As a fourth and qualitative estimate, we used information on species from our selection that were on lists of the most invasive species in surrounding regions. We used data from EPPO, the European phytosanitairy service (EPPO, 2011), the '100 of the Worst' by DAISIE, the European network for invasive species (DAISIE, 2011), the NOBANIS system from North and Central Europe (NOBANIS, 2011) and Harmonia from Belgium (Branquart, 2011). This resulted in 19 species that were identified as noxious invaders (Supplement S3.2). These lists are collections of exotics that are perceived as some of the worst in that region; they do not claim to be complete overviews of all noxious invaders. We termed this the 'black list estimate, with the most noxious species as the black list species and the others the non-black list species. It is comparable to the a priori distinction between minor and major weeds. According to our data, these black list species are on average more widespread (t_{109}=-3.54; $p<0.001$), spread faster (t_{109}= -4.66; $p<0.001$) and have a higher local dominance (t_{109}=-3.46; $p<0.001$) than selected species that are not on a black list (Figure 3.1).

Statistics

We used linear regression models to analyse relationships between the WRA-score and the different estimates for invasiveness. These estimates were considered as the outcome variables and the WRA scores were considered as the predictors. Regional frequency was log-transformed to obtain a normal error structure. Outcomes for local dominance were analysed using a generalized linear model with a binomial error structure and a logit link. Binomial totals were set at 50, because 50% was the maximum value of dominance achieved and expert opinion was used to modify the data with this maximum as a boundary. Outcomes for the black list estimate were analysed by a logistic regression.

We used the sequential Bonferroni correction procedure (Holm, 1979) to account for multiple testing of each WRA-score against the variety of estimates, which is less conservative than the normal Bonferroni correction . This procedure adjusts the significance level at which hypotheses are tested. It first ranks p-values from largest to smallest. The smallest p-value is tested against α/c, the next at α /(c-1), the next at α /(c-2), etc, with c being the number of p-values tested (4 in our study) and α being 0.05.

R-square values of different statistical models are difficult to compare. Therefore we performed additional analyses on the data. We compared how well WRA-scores predicted the different proxies for invasiveness with Receiver Operating Characteristics (ROC) (Fawcett, 2006, Delong et al., 1988), as has become custom when testing WRA outcomes (Gordon et al., 2008, Dawson et al., 2009b, McClay et al., 2010). However, the method requires that a continuous predictor is tested against an outcome variable with two categories. This could be done for the black list proxy, with 19 species on a European black list and the other 92 species not. We categorised the quantitative proxies for invasiveness, based on continuous values, in a similar way, with the 19 highest values classified as invaders and the 92 lowest values classified as non-invaders in order to stay in line with the black list proxy.

ROC-curves are used to analyse the true positive rate versus the false positive rate. Each data point in the graph represents the true positive and false positive rate at different possible cut-off points. To analyse how well outcomes are predicted the Area Under the Curve (AUC) is calculated (Fawcett, 2006, Youden, 1950). If the AUC is close to 0.5 the method is not a better predictor than a random guess, if the AUC is 1.0 it is a perfect predictor. We used Sigmaplot to create graphs and perform basic analyses. We used the R package pROC (Robin et al., 2011) to compare the different AUC's and to calculate the optimal cut-off point for each proxy, using Youdens' Index (Youden, 1950). Again, we corrected for multiple testing with the sequential Bonferroni method.

To analyse which part of the WRA relates best to each estimate for invasiveness, we have summed the WRA scores per category, resulting in eight partial scores (Appendix 1). We used model selection procedures to obtain the minimum adequate model for each estimate. To choose this model from all possible subsets, we used Schwartz Information Criterion (SIC). This criterion is more conservative and also more robust than the more often used Akaike Information Criterion (Murtaugh, 2009). Scores from all eight categories of question were used as predictors in the full model. We also included residence time as a predictor, because it has been shown that measurements like regional frequency and local dominance are dynamic in time (Bucharova and van Kleunen, 2009, Dawson et al., 2009a, Hamilton et al., 2005, Speek et al., 2011). This might explain why certain species with a high WRA score are not invasive yet (Gasso et al., 2010). These analyses were done in Genstat version 11.

Questions or answers in the WRA may be interpreted in different ways. We made a quality assessment of our scoring by comparing with a study from Japan (Nishida et al, 2009). Fourteen species evaluated by us also have been evaluated in Japan under similar climate conditions. We used Wilcoxon matched pair test to investigate whether the studies from Japan and the Netherlands have a different mean score.

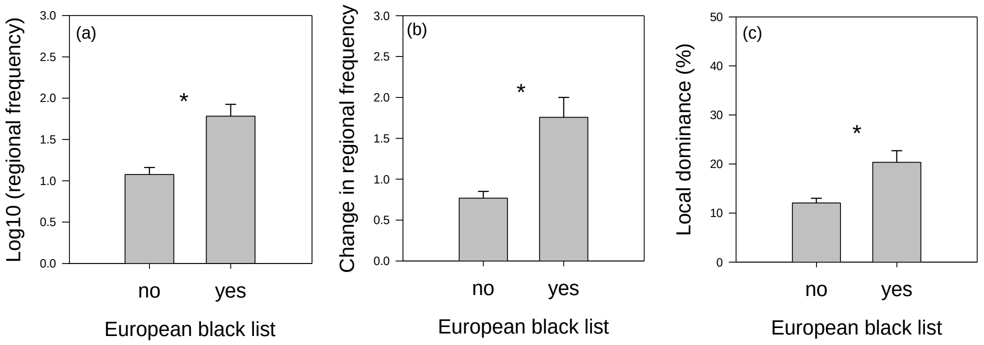

Figure 3.1 Differences in regional frequency (a), change in regional frequency from 1900-1950 to 1990-2000 (b) and local dominance (c) for exotic plant species in the Netherlands that are on black lists in neighbouring regions or not. Asterisks indicate significant differences at $p<0.05$. Error bars are standard errors of the mean.

Results

Total WRA-scores ranged from 3 to 32. Only one species (*Salix dasyclados*), was not immediately rejected (score<6), but had a score that would require further evaluation. Number of questions answered varied from 17 to 39. Comparison with the Japanese study showed that outcomes of the WRA for the same species were not significantly different (t(13)=36.00, p=0.515).

Relationships between the WRA score and the different estimates of invasiveness showed that the WRA correlated best with the black list estimate (Figure 3.2, Table 3.1). Regional frequency was also significantly correlated to the WRA-score, but explained variation was relatively low ($r^2 = 0.045$). Change in regional frequency and local dominance were marginally significantly (p=0.081 and p=0.070 respectively) correlated to the WRA-score.

Results from ROC analyses confirmed that the WRA is significantly better at predicting the black list estimate and the regional frequency estimate than a random guess (Figure 3.3, Table 3.2). Moreover, the black list estimate is significantly better predicted by WRA than the change in regional frequency and the local dominance (Table 3.2). The optimal cut-off score for the black list estimate was at WRA-score 18.

Categories of questions in the minimal adequate model varied per estimate of invasiveness (Table 3.3). Regional frequency correlated positively to the climate and distribution scores of the WRA. None of the other WRA categories of questions were included as predictors in the minimal adequate model. Change in regional frequency was only predicted by residence time; plant species with a shorter residence time increased more in regional frequency than species with a longer residence time. High local dominance was best predicted by a high score for weediness elsewhere. Being a black list species was best predicted by a longer residence time, a high score for weediness elsewhere and a high score on undesirable attributes.

Table 3.1 P-values and R^2 –adjusted values of the relationships between the different estimates of invasiveness and the WRA-scores. In bold are the results that remained significant after sequential Bonferroni correction.

Estimate of invasiveness	***Estimate***	***p-value***	***Adj-R^2***
Regional frequency	**0.036**	**0.014**	**0.045**
Change in regional frequency	0.029	0.081	0.019
Local dominance	0.034	0.070	0.021
European black list	**0.271**	**0.001**	**0.240**

Table 3.2 Test-values for ROC-curves using WRA scores to test different estimates of invasiveness. Letters in the last column show which AUC values were significantly different from each other after sequential Bonferroni correction.

Estimate	***AUC***	***S.E.***	***CI***	***p-values***	***Compare AUC's***
Regional frequency	0.6891	0.0641	0.563-0.815	0.0097	ab

Change in regional frequency	0.5363	0.0738	0.392-0.681	0.6191	a
Local dominance	0.5850	0.0871	0.414-0.756	0.2450	a
European black list	0.8587	0.0392	0.782-0.936	<0.0001	b

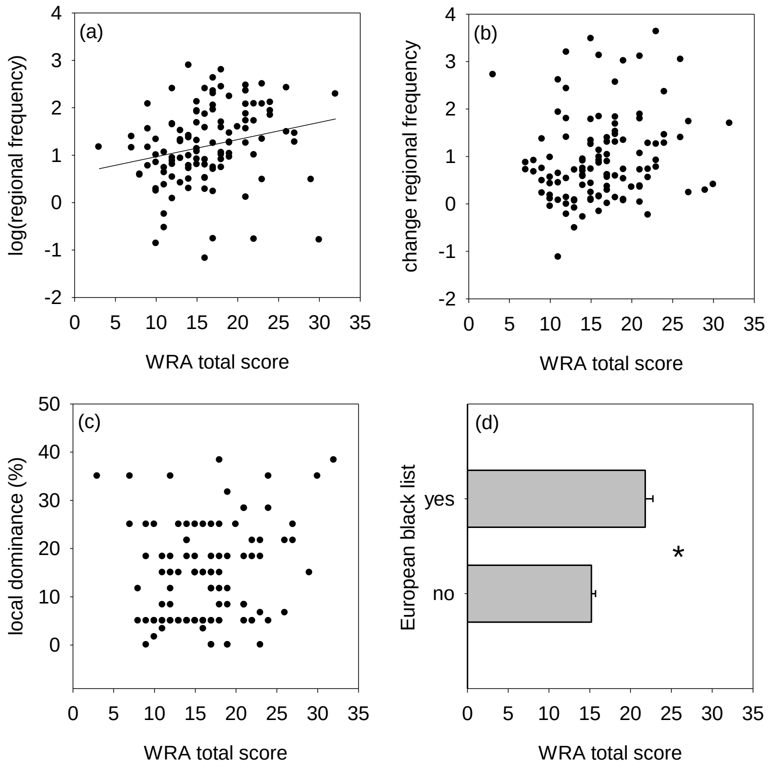

Figure 3.2 Relationships between different estimates of invasiveness of exotic plant species in the Netherlands and WRA-scores. The estimates are regional frequency (a), change in regional frequency from 1900-1950 to 1990-2000 (b), local dominance (c) and being on a black list or not in a neighbouring region (d) of exotic plant species in the Netherlands. A line indicates a significant correlation. Asterisks indicate significant differences between categories. Error bars are standard errors of the mean.

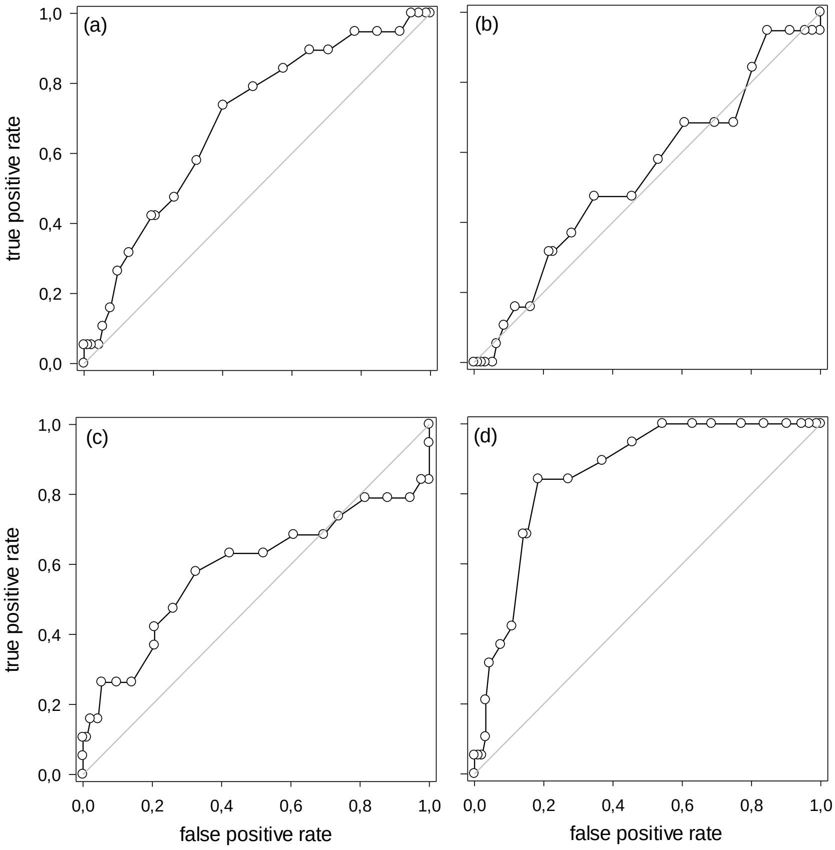

Figure 3.3 ROC graphs of the performance of the WRA to predict whether species are defined as invasive or non-invasive, for the estimates of invasiveness regional frequency (a), change in regional frequency (b), local dominance (c) and being on a black list or not (d). We categorised the continuous proxies for invasiveness into dichotomous factors, with the top 19 species as invasive and the others as non-invasive (in line with the 19 species that are European black list species). Each data point in the graph represents a different cut-off point for the WRA score that defines species as invasive or non-invasive. False positive rate is the proportion of species that are incorrectly classified as invasive at each cut-off score. True positive is the proportion of species that is correctly classified as invasive at each cut-off score.

Table 3.3 Results of minimal adequate model after model selection for four different estimates of invasiveness of exotic plant species in the Netherlands. Predictors are partial scores of the WRA, per category of questions and residence time.

Proxy for invasiveness	*WRA predictors*	*estimate*	*p-value*	*R^2-adj*
Regional frequency	Climate and distribution	0.561	<0.001	0.112
Change of regional frequency	Residence time	-0.004	<0.001	0.127
Local dominance	Weed elsewhere	0.085	0.022	0.039
Black list*	Residence time	-0.014	<0.001	0.082
	Weed elsewhere	0.372	<0.001	0.075
	Undesirable traits	0.499	<0.001	0.081

*total R^2-adjusted for this model is 34.5%

Discussion

Estimates of invasiveness and WRA

The qualitative estimate of invasiveness, occurrence on a black list in surrounding countries, was best predicted by the WRA-score. The WRA did not predict the quantitative estimates of invasiveness (regional spread, change in regional spread, and local dominance) very well. Interestingly, the quantitative estimates related well to the qualitative estimate, which begs the question why the WRA predicts the black listing better than regional spread or local dominance. In order to better understand the predictions of the WRA, we further examined the impact of exotic species. We assume it is this impact that the WRA strives to predict. Impact can be considered as: $I = R \times A \times E$; where I is the overall impact of a species, R is the range size (or regional frequency), A is the average abundance (comparable to local dominance) and E is the noxious impact effect per individual (Parker et al., 1999). What this ‘noxious effect per individual’ comprises, is highly variable. Studies on invasive species have shown many different types of noxious impacts. Exotics can become noxious weeds in croplands, with large economic impacts due to expensive control measures and reduced crop yields (Pimentel et al., 2005). Another example of a noxious effect is impact on human health such as the allergenic properties of *Ambrosia artemisiifolia* pollen (Taramarcaz et al., 2005). Ecosystem impacts of exotic species include altered nutrient cycling, microbial activity and community composition as exotics replace natives (Vilà et al., 2011). All these factors can contribute to the noxiousness of exotic plants.

Black list species in our study appear to have all the impact elements; they have greater regional frequency (R) and an increase in regional frequency, they have greater local dominance (A) and are also perceived as noxious invaders (E). The black list proxy, therefore, seems an appropriate proxy for the impact, which may explain why it is so well predicted by the WRA.

’Weed elsewhere and undesirable traits’ are the categories of questions that relate strongest to the species placement on the black list. This is quite different from the results for the quantitative estimates, which appeared unrelated to ‘undesirable traits’, except that local dominance was related to ‘weed elsewhere’. Regional frequency related to WRA climate and distribution questions, whereas change in regional frequency related most to residence time. Clearly, these factors are not typical indicators of noxious effects. Therefore, our results suggest that black list species are so well predicted by the WRA, because it includes their individual noxious effects.

Our results seem to indicate that although the quantitative estimates include an important part of the impact of invasive species, they exclude the noxious impact per individual, which can be important as well. For example, *Matricaria discoidea* is one of the most widespread exotic plant species in the Netherlands and in Europe more generally (Lambdon et al., 2008). It has a higher than average local dominance, but has not been considered to have noxious impacts.

Recently, proponents have argued that decisions to implement species control measures should be based on impact and not origin (Thompson and Davis, 2011, Davis et al., 2011). Our study indicates that the WRA already focuses strongly on the noxiousness of exotic species, which is an important aspect of their impact. Thus, the WRA does not promote combatting exotic species because of their origin, but for their impacts. This has been shown as well in a study on native weeds, which have a WRA score similar to exotic weeds (Nishida et al., 2009). Our study also shows that quantitative estimates of invasiveness miss out on the noxious part of impact.

On the other hand, our results suggest that the WRA has a stronger focus on the noxiousness component of impact than on spread and dominance components of impact. This is evidenced by our results showing that the black list estimate relates strongly to the WRA, but the quantitative estimates do not, even though they relate strongly to the black list. This is further supported by our analyses of which categories of questions are most related to the black list, including the presence of undesirable traits and weediness elsewhere, which are questions about noxiousness. Further, species that are weedy elsewhere are perceived as noxious or weedy in one region and therefore are likely to be perceived as noxious or weedy in another region.

Species selection bias

Data on regional frequency and local dominance are only available for naturalised species. This causes a bias in our species selection. Usually the WRA is tested with species from the entire range of the invasion process, including casuals and even non-escaping exotic plant species (Dawson et al., 2009b, Gordon et al., 2008, Křivánek and Pyšek, 2006, McClay et al., 2010), but our analysis includes only exotic species at the last phase of the invasion process, and therefore only species at the high end of the WRA scores. Our species selection does not enable us to compare the WRA between non-naturalised versus naturalised exotic species. It needs to be confirmed if our conclusions may be extrapolated to species with lower WRA scores as well.

Performance of WRA in the Netherlands

Applying the WRA to data from naturalized exotic plant species in the Netherlands resulted in quite high scores and all species but one were categorized as ‘rejected’, which means that they should be prevented from entering this region. Our results showed no higher average scores than the same species in a Japanese study, so the relatively high WRA scores do not seem to be caused by a tendency of us to answer questions differently (Nishida et al., 2009). Our WRA scores might be explained partially by our species selection of only naturalised species. However, studies testing naturalised non-invasive species (Dawson et al., 2009b; Křivánek and Pyšek, 2006) found scores low enough to have these non-invaders accepted, that is having scores below zero. Possibly, the increased availability of data on exotic species increases the WRA scores. Availability of factsheets on weedy species is increasing. Moreover, factsheets on weedy species typically describe species in relation to the most severe impact (Hulme, 2012), and so the increased availability of these data should result in higher WRA scores. Other studies also resulted in a relatively high scores and a higher a cut-off point for the 'reject' category, for example a score of 10 (Nishida et al., 2009) or even a score of 14 (McClay et al., 2010) compared to a score of 6 as used in the Australian WRA. For our study, a cut-off score of 18 is calculated to give the best result for black list species. This cut-off score, therefore, might be more appropriate when using the WRA to predict which new exotic plant species could become invasive in the Netherlands.

Conclusion

In our study, the WRA predicted quantitative estimates of invasiveness, like regional spread and local dominance, less well than the more qualitative proxy of occurring on a blacklist in the surrounding region. Quantitative estimates of invasiveness apparently do not include the noxiousness of species, which is generally believed to be an important component of invasiveness. Whereas the WRA is heavily weighted by the noxious aspects of invasive species, it only weakly predicts the dominance and spread of these species. This shows an important gap between studies testing the WRA, using more qualitative proxies of invasiveness and studies searching for traits related to invasiveness, mostly using quantitative estimates like spread and dominance. We conclude that it may be valuable in future studies to use different estimates of invasiveness for both type of studies, in order to bridge this gap. This may also help to further research and management priorities.

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Supplemental information S3.1

Questions in the WRA. Parts of the questions that are in bold, are the parts where the questions have been adapted to the Dutch situation.

			History/Biogeography
1	*Domestication/ cultivation*	1.01	Is the species highly domesticated. If answer is 'no' got to question 2.01
		1.02	Has the species become naturalised where grown
		1.03	Does the species have weedy races
2	*Climate and Distribution*	2.01	Species suited to **temperate** climates
		2.02	Quality of climate match data
		2.03	Broad climate suitability (environmental versatility)
		2.04	Native or naturalised in regions with **frost** periods
		2.05	Does the species have a history of repeated introductions outside its natural range
3	*Weed elsewhere*	3.01	Naturalised beyond native range
		3.02	Garden/amenity/disturbance weed
		3.03	Weed of agriculture/horticulture/forestry
		3.04	Environmental weed
		3.05	Congeneric weed
			Biology/Ecology
4	*Undesirable traits*	4.01	Produces spines, thorns or burrs
		4.02	Allelopathic
		4.03	Parasitic
		4.04	Unpalatable to grazing animals
		4.05	Toxic to animals
		4.06	Host for recognised pests and pathogens
		4.07	Causes allergies or is otherwise toxic to humans
		4.08	Creates a fire hazard in natural ecosystems
		4.09	Is a shade tolerant plant at some stage of its life cycle
		4.10	Grows on infertile soils
		4.11	Climbing or smothering growth habit
		4.12	Forms dense thickets

5	*Plant type*	5.01	Aquatic
		5.02	Grass
		5.03	Nitrogen fixing woody plant
		5.04	Geophyte
6	*Reproduction*	6.01	Evidence of substantial reproductive failure in native habitat
		6.02	Produces viable seed
		6.03	Hybridises naturally
		6.04	Self-fertilisation
		6.05	Requires specialist pollinators
		6.06	Reproduction by vegetative propagation
		6.07	Minimum generative time (years)
7	*Dispersal mechanisms*	7.01	Propagules likely to be dispersed unintentionally
		7.02	Propagules dispersed intentionally by people
		7.03	Propagules likely to disperse as a produce contaminant
		7.04	Propagules adapted to wind dispersal
		7.05	Propagules buoyant
		7.06	Propagules bird dispersed
		7.07	Propagules dispersed by other animals (externally)
		7.08	Propagules dispersed by other animals (internally)
8	*Persistence attributes*	8.01	Prolific seed production
		8.02	Evidence that a persistent propagule bank is formed (>1 yr)
		8.03	Well controlled by herbicides
		8.04	Tolerates or benefits from mutilation, cultivation
		8.05	Effective natural enemies present in **the Netherlands**

Supplemental information S3.2

Species in bold are species that were identified as being on a black list in a neighboring region

Species	***WRA-score***	***Species***	***WRA-score***
Allium carinatum	17	*Leucojum vernum*	17
Allium paradoxum	11	***Lupinus polyphyllus***	16
Alnus incana	16	*Lycium barbarum*	18
Amaranthus blitoides	16	***Mahonia aquifolium***	26
Amaranthus retroflexus	21	*Matricaria discoidea*	14
Amelanchier lamarckii	18	*Medicago sativa*	15
Angelica archangelica	18	*Mibora minima*	10
Anthemis tinctoria	8	*Muscari botryoides*	9
Anthoxanthum aristatum	13	*Muscari comosum*	13
Arabis arenosa	10	*Oenothera parviflora*	14
Aronia prunifolia (x)	11	*Ornithogalum nutans*	17
Aster lanceolatus	19	*Oxalis corniculata*	19
Berteroa incana	9	*Oxalis fontana*	16
Bidens connata	12	*Oxycoccus macrocarpos*	12
Bidens frondosa	21	*Parentucellia viscosa*	14
Buddleja davidii	21	*Pentaglottis sempervirens*	12
Bunias orientalis	21	*Persicaria wallichii*	11
Ceratochloa carinata	18	*Poa chaixii*	22
Chenopodium foliosum	14	*Potentilla intermedia*	10
Claytonia perfoliata	17	*Potentilla norvegica*	19
Claytonia sibirica	12	*Potentilla recta*	22
Coincya monensis subsp. recurvata	9	***Prunus serotina***	17
Conyza canadensis	18	*Pseudofumaria lutea*	7
Corispermum intermedium	7	*Rapistrum rugosum*	10

Coronopus didymus	15	***Rhododendron ponticum***	19
Cotula coronopifolia	16	*Ribes alpinum*	16
Crambe maritima	12	***Robinia pseudoacacia***	19
Crepis tectorum	13	*Rorippa austriaca*	17
Crocus vernus	8	***Rosa rugosa***	24
Cuscuta lupuliformis	15	*Rubus spectabilis*	18
Cymbalaria muralis	20	*Salix dasyclados*	3
Cynodon dactylon	21	*Salvia verticillata*	11
Datura stramonium	21	*Scilla bifolia*	23
Diplotaxis muralis	15	*Scilla siberica*	15
Eragrostis minor	12	*Scrophularia vernalis*	10
Eragrostis pilosa	15	***Senecio inaequidens***	23
Eranthis hyemalis	17	*Setaria pumila*	19
Erigeron annuus	18	*Setaria verticillata*	18
Erucastrum gallicum	13	*Sisymbrium altissimum*	17
Fallopia japonica	24	*Sisymbrium austriacum subsp. chrysanthum*	16
Fallopia sachalinensis	27	*Sisymbrium loeselii*	14
Galanthus nivalis	15	*Sisymbrium orientale*	16
Galinsoga parviflora	23	*Solanum triflorum*	14
Galinsoga quadriradiata	21	***Solidago canadensis***	22
Geranium phaeum	11	***Solidago gigantea***	32
Geranium pyrenaicum	14	***Spartina anglica***	15
Heracleum mantegazzianum	26	*Symphoricarpos albus*	24
Hieracium amplexicaule	30	*Tragopogon porrifolius*	11
Hieracium praealtum	29	*Trifolium hybridum*	12
Hordeum jubatum	12	*Tulipa sylvestris*	10

Hypericum canadense	16	*Veronica filiformis*	9
Impatiens glandulifera	21	*Veronica peregrina*	14
Impatiens parviflora	22	*Veronica persica*	17
Juncus tenuis	17	*Vicia villosa*	13
Lepidium draba	27	*Xanthium strumarium*	23
Lepidium virginicum	15		

4

Local dominance of exotic plants declines with residence time: a role for plant soil feedback?

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Abstract

Recent studies have shown that introduced exotic plant species may escape from their native soil-borne pathogens, but that they become exposed to increased soil pathogen activity in the new range when time since introduction increases. Other studies have shown that introduced exotic plant species become less dominant when time since introduction increases, and that plant abundance may be controlled by soil-borne pathogens, however, no study yet has tested if these soil effects might explain the decline in dominance of exotic plant species following their initial invasiveness. Here we determine plant-soil feedback of 20 plant species that have been introduced into The Netherlands. We tested the hypotheses that (1) exotic plant species with a longer residence time have a more negative soil feedback, and (2) greater local dominance of the introduced exotic plant species correlates with less negative, or more positive plant-soil feedback. Although the local dominance of exotic plant species decreased with time since introduction, there was no relationship of local dominance with plant-soil feedback. Plant-soil feedback also did not become more negative with increasing time since introduction. We discuss why our results may deviate from some earlier published studies and why plant-soil feedback may not in all cases, or not in all comparisons explain patterns of local dominance of introduced exotic plant species.

Introduction

An important challenge for invasion ecologists is to predict the course of invasions of introduced exotic species. This requires insight in the factors that may control the abundance and dominance of species in both their native and new ranges. It has been well established that regional distribution of exotic plant species increases with residence time (Pyšek et al., 2004, Hamilton et al., 2005, Wilson et al., 2007, Milbau and Stout, 2008, Bucharova and van Kleunen, 2009, Gassó et al., 2009). It has also been argued that increased residence time may result in lower local dominance and invasiveness (Carpenter and Cappuccino, 2005, Hawkes, 2007, Speek et al., 2011). Local dominance of introduced exotic plant species may be, at least in part, driven by interactions with soil biota, including effects of soil-borne enemies and symbionts (Inderjit and Van der Putten 2011). The question that we address in the present study is how residence time and local dominance of exotic plant species may relate to enemy impact of the soil biota. Ultimately, this information may be used to enhance predictions on the course of invasiveness of introduced exotic plant species.

A possible explanation for lower local dominance of introduced exotic plant species with a long residence time is that enemy species may increasingly adapt and accumulate when time of exposure to the new hosts increases (Diez et al., 2010, Hawkes, 2007). Both aboveground (Bentley and Whittaker, 1979, Gange and Brown, 1989) and belowground (Klironomos, 2002, Johnson et al., 2012, Mangan et al., 2010, van der Putten et al., 1993) enemies may control local plant dominance. Release from natural enemies by introduction to a new range has been proposed to enhance the performance of species and, therefore, their invasiveness (Elton, 1958, Keane and Crawley, 2002). This 'enemy release hypothesis' (Keane and Crawley, 2002) has been supported by surveys showing that introduced plant species have fewer enemies in their novel than native range (e.g. Mitchell and Power, 2003).

Thus far, the majority of research on enemy release of exotic plant species has been dedicated to aboveground enemies. However, an increasing amount of studies is showing that introduced exotic plant species can be released from native soil-borne enemies as well (van Grunsven et al., 2010, Reinhart et al., 2003, Reinhart et al., 2010, Callaway et al., 2004). Introduced exotic plant species suffer less from soil-enemies of the invaded range than congeners that are native in that range (Maron and Vilà, 2001, Agrawal et al., 2005, van Grunsven et al., 2007, Engelkes et al., 2008).

The change in performance of exotic species with progressing residence time has been described for several invaders (Simberloff and Gibbons, 2004). Loss of exotic dominance might be caused by evolutionary adaptation of enemies in the new range to the introduced plant species (Müller-Schärer et al., 2004). Such adaptive potential may be deduced from reported higher frequencies of specialist compared to generalist herbivores (Andow and Imura, 1994), higher exposure (Mitchell et al., 2010), and higher impact (Hawkes, 2007) of enemies on crop and exotic plant species in relation to increasing residence time. Similarly, in New Zealand plant-soil feedback of 12 exotic plant species related negatively to their residence time (Diez et al., 2010) and in the Czech Republic giant hogweed (*Heracleum mantegazzianum*) developed negative feedback effects from the soil biota in fields that had been colonized for some decades (Dostál *et al.*, 2013). However, in these latter studies, increased enemy exposure has not yet been related to local dominance of the exotic plant species, which is the key aim of the present study.

A recent analysis established that exotic plant species with a long residence time in the Netherlands have lower local dominance than recently introduced species (Speek et al., 2011). Until now, no study has related such patterns in local dominance to plant-soil feedback effects. Therefore, in the present study, we determine how residence time, local dominance and soil pathogen effects to exotic species may relate to each other. We tested soil pathogen effects by plant-soil feedback approach (Bever et al., 1997), which is a way to experimentally integrate all positive and negative interactions between plants and the soil biota. We first tested the hypothesis that species with a longer residence time have a more negative plant-soil feedback (Diez et al., 2010). Then, we tested the hypothesis that species with a more positive plant soil feedback have a higher local dominance (Klironomos, 2002).

Methods

Data on plants, their residence time and local dominance

Data on residence time were derived from information on period of naturalization according to the standard list of the Dutch flora (Tamis et al., 2004). Data on local dominance were derived from the Dutch Vegetation Database (Schaminée et al., 2007), containing over 500,000 vegetation records including data on local species cover in plots varying from 1 by 1 m^2 to 10 by 10 m^2. Plot sizes used for recording depended on the characteristics of vegetation, for example largest plot sizes were used for forests. Data on plant species cover were used to calculate local dominance as [the number of vegetation records with that species having > 10 per cent ground cover / the total number of vegetation records with that plant species] x 100 % (Speek et al., 2011). Therefore, local dominance expresses the frequency of how often a plant species has a minimum cover of ten percent, when present in the vegetation record. In order to exclude recorder bias, for example due to avoiding taking records of vegetation heavily invaded by exotic plant species, we used expert judgment to check and where necessary adjust the cover data (Speek et al., 2011).

Soil feedback experiment

We used a selection of 20 introduced exotic plant species in the Netherlands for a plant-soil feedback experiment (supplement S4.1). The selection of 20 plant species was based on a number of criteria. First, we excluded woody species, because the length of the plant-soil feedback is too limited for capturing a substantial part of the life cycle of trees. We then selected as many as possible plant species from riverine areas in order to be able to use the same soil origin for all plant species. Finally, the selection was limited as the seeds of some plant species did not germinate. Seeds had been collected by specialized seed companies that collect seeds locally, or by ourselves or colleagues.

Of the 20 plants species, 14 occur in the Millingerwaard (Dirkse et al., 2007), a riverine floodplain area of 700 hectares. Millingerwaard is a nature reserve in the riverine floodplain of the river Waal, which is the southern branch of the Rhine river in the Netherlands (51°87’ N, 6°01’ E). Three other species occur near or in other riverine areas in the Netherlands and the remaining three occur outside riverine areas. We collected soil from the Millingerwaard area, instead of from a larger variety of sites, as soil from a variety of sites would have introduced additional variation due to soil type, fertility, pH etc. All plant species were forbs that varied in local dominance from 5 - 38 per cent and in residence time from 75 to 400 years.

Seeds were germinated on glass beads placed in demineralised water. Germination was carried out in transparent plastic containers of 17 x 12 x 5 cm that were placed under conditions of 16 hrs 22 °C in the light (day) and 8 hrs 10 °C in the dark (night). *Xanthium strumarium* seeds were germinated at a higher temperature: 16 hrs 32 °C and 8 hrs 20 °C. Germinated seedlings were stored at 4 °C and 10/14 hrs light/dark until transplantation in soil, to ensure equal sizes at start of the experiment. Soil was collected from five random locations in Millingerwaard. Soil to be used as inoculum was collected in October 2010, prior to the first phase of the experiment. Soil from the five sampling locations was sieved (mesh size 5 mm) to remove coarse roots, stones and other large particles, and subsequently homogenized. The bulk soil was collected in January 2010, sterilized by gamma irradiation (25 KGray) and stored in sealed plastic bags at 4 °C until use.

The sensitivity of exotic plant species to soil-borne enemies was determined in a so-called two phase plant-soil feedback experiment (Bever et al., 1997). In the first phase, which started from one pooled sample, the seedlings were grown to condition the field soil. In that phase, soil biota that can grow on resources provided by that particular plant species are enumerated (Grayston et al., 1998, Kowalchuk et al., 2002). In the second phase, we kept all replicates of own soil separate. In order to do so, the soil of each pot was split in two halves: one half was used as own soil, whereas the other half was mixed with the halves of all other replications and species, to be used as away soils. The replicates of the mixed soil were not kept intact, because there was no relationship between replicate 1 conditioned by species A or B. Comparing plant performances in own and mixed soils enabled us to make a home (own) versus away (mixed) comparison, which is a less sensitive and ecologically more realistic method of detecting plant-soil feedback effects than a comparison of non-sterilized versus sterilized soil (Kulmatiski et al., 2008). In the final analysis, plant species was the unit of replication.

For the first –conditioning– phase, bulk soil and inoculum were mixed at a ratio of 4:1, with a total of 1200 gram soil per pot on a dry weight basis. Pots of 1.3 L were used. For the second –feedback– phase, 'own soil' and 'mixed soil' were homogenized with sterilised bulk soil at a ratio of 1:1 in order to keep pot volumes equal between the two feedback phases. For each plant species, we had five independent replicates with own and five with mixed soil. Every pot contained three seedlings, except *Amaranthus retroflexus* that was planted as two seedlings per pot due to poor germination of the seeds. Dead seedlings were replaced until the first week after transplanting. Greenhouse conditions were maintained at 60% RH, day temperature 21 °C, night temperature 16 °C. Daylight was supplemented with lamps (SON-T Agro, 225 μmol^{-1} m^{-2}), to ensure a minimum of 16 hours light per day.

Before planting, the water content in each pot was set at 20% (w/w). Plants were supplied with water three times a week and once a week the water content was re-set to 20% by weighing. Plants received 10 ml 0.5 strength Hoagland per pot in weeks two, three and four, and 20 ml in weeks five and six after transplanting in order to meet increasing demand. Plants were harvested six weeks after planting. The length of growth was the same for both phases, which is relatively short, but ample for testing feedback responses (Van der Putten *et al.* 1988). When harvesting, shoots of the three (or two) plants per pot were clipped at ground level, pooled, dried in paper bags at 75 °C until constant weight and weighed, so that biomass data per pot were obtained.

Statistical analysis

The effect of soil feedback on shoot and root biomass was calculated as ln[(biomass in own soil)/(biomass in mix soil)] (Brinkman et al., 2010). We assigned pairs of own soil with mixed soil randomly. To analyze if residence time or local dominance could explain mean shoot and root feedback responses we used linear models. The unit of replication was the plant species. For residence time we used models with a normal distribution, for local dominance we used models with a binomial distribution and a logit link, with binomial totals set to 50% (the highest value in our dataset).

We analyzed which traits and other factors related best to residence time by a model selection procedure within a linear model with a normal distribution. Thus, we selected the best minimal adequate model with the lowest Akaike Information Criterion value from all possible subsets. Although time and dominance were related, the relation of a trait or other factor to residence time may not necessarily imply that there is a relation with local dominance as well. Therefore, the factors in the best minimal adequate model were added to a generalized linear model with residence time explaining local dominance. By adding each factor separately, we analyzed which one significantly changed the model. Factors that affected the model were likely to be a better explanation for variation in local dominance than residence time. For explaining local dominance we used a binomial distribution with a logit link, binomial totals set at 50 and accounting for overdispersion. All analysis were done in Genstat version 14.

Results

Opposite to our hypothesis, we found neither a significant relationship between residence time and plant-soil feedback of the exotic plant species, nor for shoots (F=0.10, t_{18}=-0.32, p=0.751, Fig. 4.1) nor roots (F=0.41, t_{18}=-0.64, p=0.529). Local plant dominance also did not relate to the feedback effect on shoots (F=0.09, t_{18}=-0.31, p=0.763) or roots (F=0.73, t_{18}=-0.85, p=0.404). Excluding species from riverine habitats, which may not be responsive to soil biota from that habitat, or Fabaceae species, which may have a different feedback due to symbiosis with rhizobia did not alter the significance of the results (data not shown). Therefore, our hypotheses that species with a longer residence time have a more negative plant-soil feedback, and that species with a less negative or more positive plant-soil feedback have a higher local dominance were not supported.

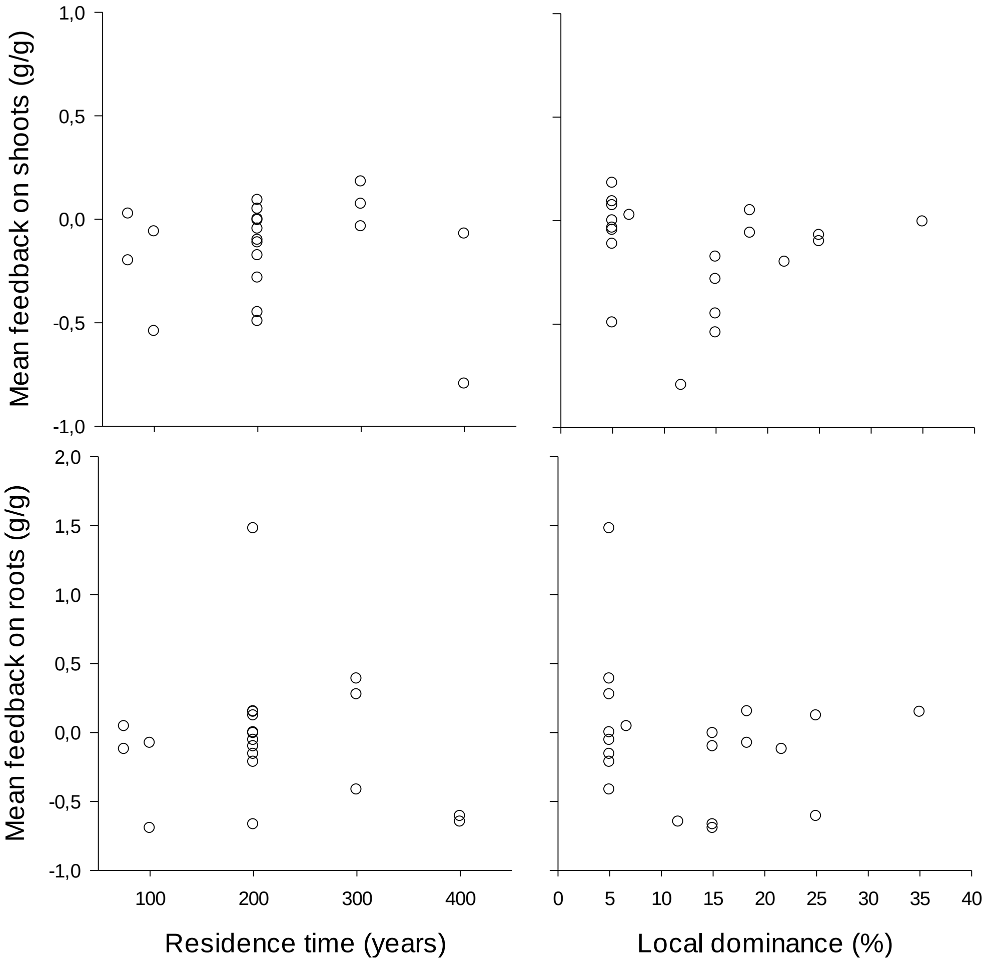

Figure 4.1. Mean soil feedback effect on the biomass of shoots and roots in relation to the residence time or the local dominance of naturalized exotic plant species in the Netherlands. Each circle represents a different plant species.

Discussion

In our study we tested the hypotheses that species with a longer residence time have a more negative plant-soil feedback and that species with a less negative, or more positive plant soil feedback have a higher local dominance. We used an experimental approach to measure soil-borne enemy impact by plant-soil feedback approach. However, opposite to a study from New Zealand (Diez et al., 2010), and to a study on introduced *H. mantegazzianum* in the Czech Republic (Dostál *et al.*, 2013) we did not find such a relationship between time since introduction of 20 exotic plant species in the Dutch flora and plant-soil feedback.

There are several possible explanations for these results. Our results could indicate that not all introduced exotic plant species develop negative plant-soil feedback when time since introduction increases. In the field, other ecological processes may be influencing community composition and aboveground interactions can either increase or decrease with the strength of the belowground interactions. Another possible explanation concerns the choice of soils for the plant-soil feedback experiment. We have chosen soils from areas where most exotic plant species may occur, but we did not use soils from the root zone of particular populations. This approach has led to marked differences in plant-soil feedback between natives and exotics (Van Grunsven et al., 2007, Engelkes et al., 2008), however, it has resulted in scattered results when testing soil responses across an entire native range (Van Grunsven et al., 2010).

The results may also depend on the relatively short conditioning and testing phases of 6 weeks each. Test phases of 6 weeks can detect feedback effects (Van der Putten et al., 1988). Longer test periods may even result in pot limitations, which may obfuscate results. Conditioning for 6 weeks will have been relatively short, but to our experience this is possible when adding soil inocula to sterilized soil, as has been done in the present study.

Our use of pooled soils as ‘ away’ treatment may have provided a conservative estimate of plant-soil feedback effects, because of reducing variances. Nevertheless, since we did not find significant relationships with time since abandonment, or local dominance, our results show that even with a highly sensitive test still no relationship could be detected between time since introduction, or local dominance, and plant-soil feedback. Mixing soils from all plant species to produce ‘away’ soils could theoretically have led to single pathogens dominating the entire away soil community. However, a previous addition study using a variety of amounts of soil inocula showed that soil feedback effects increased gradually with the amount of inoculum added (Van der Putten et al., 1988), which does not point at a disproportional role of pathogens from single plant species in the away soil mixtures.

Plant-soil biota interactions are highly local (Levine et al., 2006, Bezemer et al., 2010, Genung et al., 2012), and adaptation of soil organisms to new plant species does not take place at a national, but at a local scale through direct interactions between plant roots and the soil biota (Schweitzer et al. 2008, Lankau et al., 2009, Lau and Lennon, 2012, Lau and Lennon, 2011). As the feedback was estimated at a regional scale, also the local dominance was measured at a regional scale (first occurrence in the Netherlands). Using first occurrence in a larger region as estimate of residence time could result in an over-estimation of the local residence time. On the other hand, the study from New Zealand (Diez et al., 2010) also used data on residence time for the entire country and not specifically for the sites from which the soil has been collected.

We expected plant-soil feedback to be negatively related to local dominance (Klironomos, 2002, Mangan et al., 2010). However, in our study we did not observe such an inverse relationship. A possible explanation is that the previous studies by Klironomos (2002) and Mangan et al. (2010) on dominance-feedback relationships have been based on native species, and that these relations may differ when considering exotic species. Moreover, we used dominance estimates averaged across the entire Netherlands (Speek et al., 2011), which differs from the local dominance estimates as used in other studies (e.g. Klironomos 2002). National estimates (in the case of the Netherlands concerning an area of appr. 150 x 300 km) will not provide accurate information about the local dominance of exotics in the riverine ecosystem where the soil for testing plant-soil feedback originated from. Therefore, it is possible that soil origin and plant dominance data were not well linked to each other, or that a relationship between plant-soil feedback and dominance works out differently for exotic plant species than for natives. Alternatively, our study may add to other examples where plant dominance does not relate to plant-soil feedback (Reinhart, 2012).

An alternative explanation for the rejection of our hypotheses could be that the evolutionary dynamics leading to increased enemy pressure on exotic plant species is not strong enough to result in a change in mean local dominance. Meta-analyses have shown that a general pattern of decreased enemy numbers on exotic species in the novel range was not reflected in a general pattern of higher plant performance (Chun et al., 2010). Adaptation can occur both at the soil species level but also at the plant species level. This adaptation at two fronts is likely to result in a mixed general outcome. Moreover, while local dominance has been assumed to increase after introduction to a new range (Keane and Crawley, 2002), recent work has shown that most species have the same dominance in both their introduced and native ranges (Firn et al., 2011). Clearly, local dominance is a complex trait, with a high variation both between and within species that can be influenced by a large number of ecological processes.

Conclusions

We found no support for the hypothesis that the negative relationship between residence time and local dominance of exotic species in The Netherlands is caused by an increase in negative plant soil feedback. It may be that data on residence time, dominance, enemy exposure and impact need to be collected all from the same area, or that different choices in plant-soil feedback approach need to be made (e.g. longer conditioning and/or feedback phases, a more sensitive ‘ away’ soil treatment). Alternatively, it might be better to track single species across an introduction gradient (Lankau et al., 2009, Lankau, 2011). It could also mean that not all introduced exotic plant species develop negative plant-soil feedback when time since introduction increases or that the hypothesized effect of increasing enemy pressure on dominance of introduced exotic plant species might not be strong enough to emerge from examining a large diversity of species across a variation of locations. Therefore even though we are aware of weaknesses of our paper (aspects of the experimental design that were not ideal, for example sampling of soil from one location that did not include all of the study species, pooling "away" soils, method of pairing of home and away pots to calculate response ratios), our results may add to the debate on change in invasiveness of exotic plant species after introduction.

Acknowledgements

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Supporting Information S4.1

Plant species naturalized in the Netherlands that were used in soil-plant feedback experiments

Occurrence in Millingerwaard (area where soil was collected) is based on maps in Dirkse et al. 2007. + does occur in Millingerwaard; 0 does not occur in Millingerwaard but does occur in other floodplains in the Netherlands; - does not occur in Millingerwaard or other floodplains in the Netherlands.

Plant species	***Family***	***Local dominance (%)***	***Residence time (year)***	***Occurs in Millinger-waard***
Allium carinatum	Liliaceae	5.00	200	-
Amaranthus blitoides	Amaranthaceae	15.00	100	+
Angelica archangelica	Apiaceae	18.33	100	+
Anthemis tinctoria	Asteraceae	11.67	400	0
Berteroa incana	Brassicaceae	25.00	200	+
Cymbalaria muralis	Scrophulariaceae	25.00	400	+
Datura stramonium	Solanaceae	5.00	300	+
Geranium pyrenaicum	Geraniaceae	5.00	200	+
Hieracium amplexicaule	Asteraceae	35.00	200	0
Medicago sativa	Fabaceae	15.00	200	+
Potentilla recta	Rosaceae	5.00	200	+
Salvia verticillata	Lamiaceae	15.00	200	0
Scrophularia vernalis	Scrophulariaceae	5.00	300	0
Senecio inaequidens	Asteraceae	21.67	75	+
Sisymbrium altissimum	Brassicaceae	15.00	200	+
Sisymbrium orientale	Brassicaceae	5.00	200	+
Solidago canadensis	Asteraceae	18.33	200	+
Tragopogon porrifolius	Asteraceae	5.00	300	+
Vicia villosa	Fabaceae	5.00	200	+
Xanthium strumarium	Asteraceae	6.67	75	-

5

Habitat properties help resolve Darwin's naturalization conundrum

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Abstract

Darwin's naturalisation conundrum includes two opposite hypotheses about how naturalization success of exotic species is linked to the degree of relatedness of the exotics with plant species in the native community. One hypothesis assumes that when exotic species are less similar to natives they are more likely to fill empty niches in a novel habitat, because of the novel trait combinations and ecological requirements. The other hypothesis is based on habitat filtering theory and predicts that exotic species should be similar to natives in order to successfully establish. Here, we aim to explore whether habitat properties may explain similarity between exotic species and species that are native in the new range. We assumed habitats with extreme abiotic conditions to be more challenging for species to cope with than habitats with more intermediate abiotic conditions. In extreme habitats, habitat filtering has been assumed to be more important for species establishment than competition

For habitats, we used data on vegetation types in the Netherlands. These are local-scale data on plant community composition. Plant communities have been classified according to main vegetation types. For habitat properties, we used Ellenberg indicator values on light, moisture and nutrient richness of these vegetation types. Classification of vegetation types into main habitat types was used as a cue for the degree of disturbance.

We show that relatedness of exotic to native plant species is selected for in habitats where competition for niche space is important. When competition is less important, species are less often closely related to native species. We conclude that relatedness of exotic to native plant species is selected for in habitats where competition for niche space is important. When competition is less important, species are less often closely related to native species. This may be an effect specific for exotics compared to natives, because of differences in enemy pressure, when competing for the same niche. If valid, this has large implications for using knowledge on community assembly in predicting which exotic species might be able to naturalise in a new range.

Introduction

Darwin's naturalisation conundrum includes two opposite hypotheses about how naturalization success of exotic species is linked to the degree of relatedness of the exotics with the native community of invaded habitats. Darwin already pointed out that floras gain relatively more naturalized species from new genera (Darwin, 1859), which suggests that naturalisation of exotic plant species could be hampered by similarity with natives. Theory underpinning this statement comes from classical niche theory (Hutchinson, 1959, MacDougall et al., 2009), which predicts that exotic species less similar to natives are likely to fill the empty niches in a novel range, because of their novel trait combinations and ecological requirements. On the other hand, habitat filtering theory (Cornwell et al., 2006, Weiher and Keddy, 2001) predicts that exotic species should be similar to natives in order to establish (Daehler, 2001, Diez et al., 2009), because specific habitat properties select for specific adaptations of species (Cornwell et al., 2006).

Theories on similarity between exotic and native plant species have been tested in a wide variety of areas with different species groups. Outcomes are strongly mixed (Mitchell et al., 2006, Thuiller et al., 2010). Hampering of naturalisation by similarity has been shown for plant species in California (Rejmanek, 1996), aquatic species around the globe (Ricciardi and Atkinson, 2004), and grass species in California (Strauss et al., 2006). Promotion of naturalisation by similarity has been shown for plant species in Hawaii (Daehler, 2001), plant species in New Zealand (Duncan and Williams, 2002), and Australia (Diez et al., 2009). Some studies showed no specific pattern for either promotion or hampering by similarity (Lambdon and Hulme, 2006) or mixed results within one study (Diez et al., 2008).

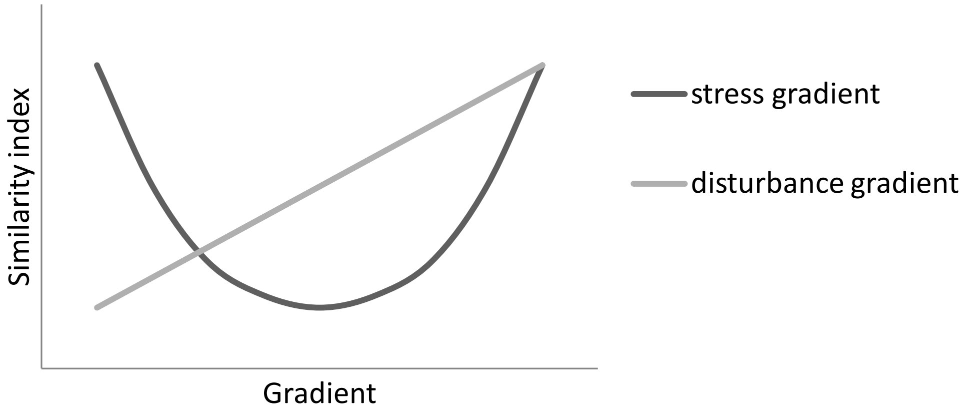
A number of explanations have been proposed to understand the variety of outcomes. One of the most important explanations is the spatial scale at which the naturalisation hypothesis has been tested . A number of studies have tested the naturalisation hypothesis at the scale of an entire region, or even at the scale of a continent (Daehler, 2001, Rejmánek and Richardson, 1996, Diez et al., 2008). However, niche overlap is a process operating on very small spatial scales (Scheffer and van Nes, 2006). Indeed, scale has been demonstrated to influence outcomes of testing the naturalization hypothesis (Diez et al., 2008). Another explanation has focused on how to express relatedness (Thuiller et al., 2010). Several studies have used different approaches to measure similarity by phylogenetic relatedness, for example by focusing on the presence of native congeners to the exotic species, or by measuring the phylogenetic distance, to either the nearest native or to the entire community (Thuiller et al., 2010, Strauss et al., 2006). In another approach functional similarity was used instead of phylogenetic similarity (Ordonez, 2014). These differences are also likely to explain variation in outcomes. Furthermore, the stage of the invasion process that is being investigated has varied. Many studies have looked at the stage of naturalization (Rejmanek, 1996, Daehler, 2001, Diez et al., 2009), posing the question whether naturalized species are more often similar or dissimilar to native species. Other studies investigated patterns of 'pest' versus 'non-pest' naturalized species (Strauss et al., 2006), investigating the question whether invasive exotics are more often similar or dissimilar to native species, compared to non-invasive exotics. Possibly, it is easier to naturalise when being similar and easier to become a pest when being dissimilar.

In spite of the many studies on this controversy, very few, if any have considered that the importance of niche space versus habitat filtering may depend on habitat properties. This is remarkable, because many studies have shown that habitat properties influence the relative numbers of exotic species in a new range. Resource-rich habitats are known to host relatively more exotic species than resource-poor habitats (Davis et al., 2000). If species numbers depend on habitat properties, selection of types of species likely will also depend on habitat properties.

In the present study, we aim to explore whether habitat properties may relate to the level of similarity between exotic and native species. We assumed habitats with extreme abiotic conditions to be more challenging for species to cope with than habitats with more intermediate abiotic conditions. In extreme habitats, habitat filtering has been assumed to be more important for species establishment than competition (Kraft et al., 2007) . Therefore, we expected habitat filtering to be more important in extreme conditions than competition for niche space. As a result, we expect that in extreme habitats more exotics will be similar to natives than in habitats with moderate abiotic conditions. For example in severely nutrient limited habitats, only few species can cope with the local conditions (Northup et al., 1995, Northup et al., 1998). In such extreme habitats, plant species need to have specific life history traits to deal with low nutrient availabilities, or they depend on specific symbioses, for example ericoid mycorrhizal fungi (Northup et al., 1995, Northup et al., 1998) . On the other hand, in habitats with moderate, or intermediate environmental conditions, less specific adaptations are required and competition is expected to play a more important role in structuring plant community composition (Brooker et al., 2006).

We tested the hypothesis that extreme habitats will host relatively more exotic plant species that are related to natives than intermediate habitats. As gradients for level of extremity, we used information on the level of stress and disturbance of the habitats. Stress and disturbance are the two main categories that together select for three main plant strategies: stress-tolerators, competitors and ruderals (Grime, 2002, Grime, 1977). Stress limits the production of plant biomass by restricting photosynthesis, for example by shortages of light, water, nutrients or sub-optimal temperatures . Disturbance removes plant biomass, for example by fire, soil erosion, human activities, or severe drought . Based on our hypothesis, we expected that in habitats with low stress and low disturbance, established exotic species will be more dissimilar to the natives because of the need to compete for open niches.

In order to test our general hypothesis, we used data from a large number of vegetation plots, summarized into vegetation types covering all habitat types across the Netherlands (Schaminée et al., 1995-1999). A strong advantage of using these records is that they originate from a spatial scale that accounts for local interactions among individuals (Schaminée et al., 2009). To our knowledge using data from this fine spatial scale scale has not yet been done for this type of question. This could be a very important advantage over other studies, as the processes underlying our hypothetic outcome are very local. In order to obtain an estimate of similarity or relatedness of exotics to the native species we determined whether or not exotic species had a native congener in that specific vegetation type.



Graph 5.1. Hypothesized results of relation between habitat properties and a similarity index.

Methods

Vegetation type data

To discriminate between different habitat types, we used the hierarchical classification of vegetation types across the Netherlands originating from the Dutch vegetation database (Schaminée et al., 2007). The Dutch vegetation database contains descriptions of the species composition of small plots, i.e. local co-occurrences. Vegetation types are descriptions of plant species that can potentially co-occur under specific environmental conditions, i.e. representing the 'habitat species pool'. The Dutch vegetation classification was based on a stratified selection of about 20,000 plots (from a total of over 500,000 plots, (Ozinga et al., 2005). On the lowest hierarchical level 264 vegetation types ('associations') have been described in the Netherlands (Schaminée et al., 1995-1999). Lists of species occurring in the vegetation types (with their frequency of occurrence) arise from aggregating all the co-occurrence descriptions that have been specified in the selection as being typical of that vegetation type. This means that really not all plant species from the same vegetation type may co-occur in practice. Nonetheless these data are a substantial improvement compared to other studies where the flora's of entire regions or continents have been investigated. Vegetation type data are much closer to actual descriptions of plant communities. The large advantage of using vegetation types over single descriptions of plant communities is the availability of quantitative information on properties of the vegetation types, like nutrient availability, light availability and moisture (Schaminée et al., 2007).

Some plant species have a very low frequency of occurrence within a given vegetation type. We wanted to exclude species with such a very low frequency, but while doing that we did not want to lose specialized species that are very typical for that association, even though they may not be included in a large proportion of the descriptions. Therefore, we used a conservative cut-off score for the frequency of occurrence of 1%. Numbers of plant species found in the selected vegetation types ranged from 10 to 85 plant species.

To determine the degree of similarity between exotic and native species in the plant communities we chose a taxonomic approach based on whether or not the exotic species in a specific vegetation type had native relatives in the same genus (Diez et al., 2009). As a measurement of similarity we used the percentage exotics in a vegetation type that have a native congener in that same vegetation type. A high percentage similarity means that many exotic species have a native congener, suggesting that similarity promotes naturalisation of exotics; a low percentage means few exotics have a native congener, suggesting that similarity hampers naturalisation of exotics. We termed this measurement the 'similarity index'. Taxonomic classification into genera was based on the 23d edition of the Dutch flora (Van der Meijden, 2005). The assignment of species to the genus level in this flora is based on phylogenetic information from the Angiosperm Phylogeny Group as incorporated in (Mabberley, 2008).

Data on origin of species were gathered from the Dutch standard list (Tamis et al., 2004). We divided species as being natives or exotics (n.b.: exotics defined as plant species naturalized in the Netherlands after 1500 AD). In the Netherlands we often also distinguish a group of plants as archeophytes (naturalized before 1500 AD). Archaeophytes are an intermediate group of plant species, from the perspective of their time of origin. The Dutch landscape has changed drastically since these species were naturalised. Current vegetation types are a product of these changes. Archaeophytes, therefore, might be considered native species rather than exotics when investigating current plant communities, which is what we did in the present analyses. A number of vegetation types did not contain any neophytes, resulting in no value for these types, because one cannot calculate with a percentage of zero. Therefore, these vegetation types were not used for further analyses. Our selection resulted in 160 vegetation types.

Data on light, moisture and nutrient availability of the vegetation types were used as parameters that inform on variation in the amount of stress between the vegetation types (Grime, 1977, Grime, 2002). We assumed high stress with low or high nutrients, with low or high moisture and low or high light conditions and hence we assumed low stress with more intermediate nutrients, moisture or light conditions.

We used Ellenberg indicator values from the SynBioSys datasystem (Schaminée et al., 2007) in order to calculate mean nutrient richness, light and moisture. These data on the vegetation type level have been estimated using Ellenberg values of plant species of those vegetation types (weighted by their frequency of occurrence). We excluded completely aquatic and saline vegetation types, as they are much more distinct from the other vegetation types (Ozinga et al., 2005). A good amount of wet vegetation types - with a high Ellenberg value for water – remained.

In addition, an aggregation of the 264 specific vegetation types into main habitat types (e.g. swamps, grasslands, forests) was used to test our hypothesis on disturbance. Some habitat types typically vary in the levels of disturbance. For example, habitat types like peatland, swamps and aquatic systems have low disturbance, whereas high-disturbance habitat types were pioneer and ruderal systems.

Analyses and statistics

We used a model selection approach as is common for data from non-experimental studies. For these types of data there is not simply one correct statistical model, so that many candidate models need to be compared. We used Ellenberg indicator values on light, moisture and nutrients as predictors. We also added data on the number of native species and the number of archaeophytes as explanatory variables in the model. We did this because a higher number of native species will increase the chance that an exotic species can be matched to a native species from the same genus.

We used a generalized linear model with a binomial error structure, because our data are proportions. A logit link was used. The binomial totals are the total number of exotic plant species in a vegetation type. In our dataset the number of neophyte exotics per vegetation type varied from 1 to 27. This value was weighted in the binomial model, so that more weight was given to values with higher total numbers of exotics.

We predicted a polynomial shape for the relation between nutrients, light and moisture and percentage neophytes with a native congener. We tested for quadratic shapes in light, nutrient or moisture values of the vegetation types in univariate models. We only included the quadratic term in the model selection procedure when adding this term to the linear term resulted in a significant improvement of the model. This was only the case for the data on moisture. Models with the linear and the quadratic term might suffer from high collinearity, because the terms are highly correlated. We checked whether this might affect our model by checking the Variance Inflation Factor (Quinn and Keough, 2002). As this check resulted in low values, we concluded that our models were not influenced by high collinearity.

As a selection criterion we used both the Akaike Information Criterion (AIC) and the Schwartz Information Criterion (SIC). The AIC is used more frequently and originates from classic information theory, however, it often includes a relatively high number of predictors. SIC is more robust and includes relatively fewer predictors in the best models (Murtaugh, 2009) . Therefore, all analyses were done with both the AIC and the SIC.

Rather than presenting only the data of the best model, we presented data on all models. We calculated Akaike weights for all models and summarized them for each parameter in the model separately. This enabled us to identify which parameters were most important in explaining the percentage of neophytes with a native congener (Mitchell et al., 2010).

The main vegetation types were not included in the model selection together with the Ellenberg values, as it would result in too many variables for proper analyses. Therefore, we analysed the main types separately. The model had the same GLM with binomial error construction as in the model selection procedure, including a logit link and number of neophytes as the binomial totals. For three habitat types we had only data on one vegetation type, so we excluded these main types from the analyses. All analyses were done in Genstat version 14.

Results

Our results reveal that moisture and nutrients have an important role in explaining variation in the relatedness index of exotic plant species over all vegetation types (see Table 5.1). From both the top 5 AIC and SIC selected models it became clear that moisture and its quadratic term are important explanatory variables in all those models. Nutrients are important model variables in most of them, mainly the AIC selected models. The role of light availability was relatively small. Also the numbers of natives and of archaeophytes are important predictors in most models. We added these factors, because we expected that with more natives (and archaeophytes), chances of encountering a native congener would increase. All these results are also reflected in the relative Akaike weights (Figure 5.3). For the best models a maximum of 17,6% for the R^2-adjusted is calculated.

All habitat gradients show a different relation with the relatedness index (Figure 5.2a), whereas we predicted one pattern for all gradients – a concave hull (Figure 5.1). For moisture, the relation with the relatedness index was a convex hump shape, which was opposite to our expectations. For nutrients the relation was a positive linear relation. For moisture, results showed a negative linear relation.

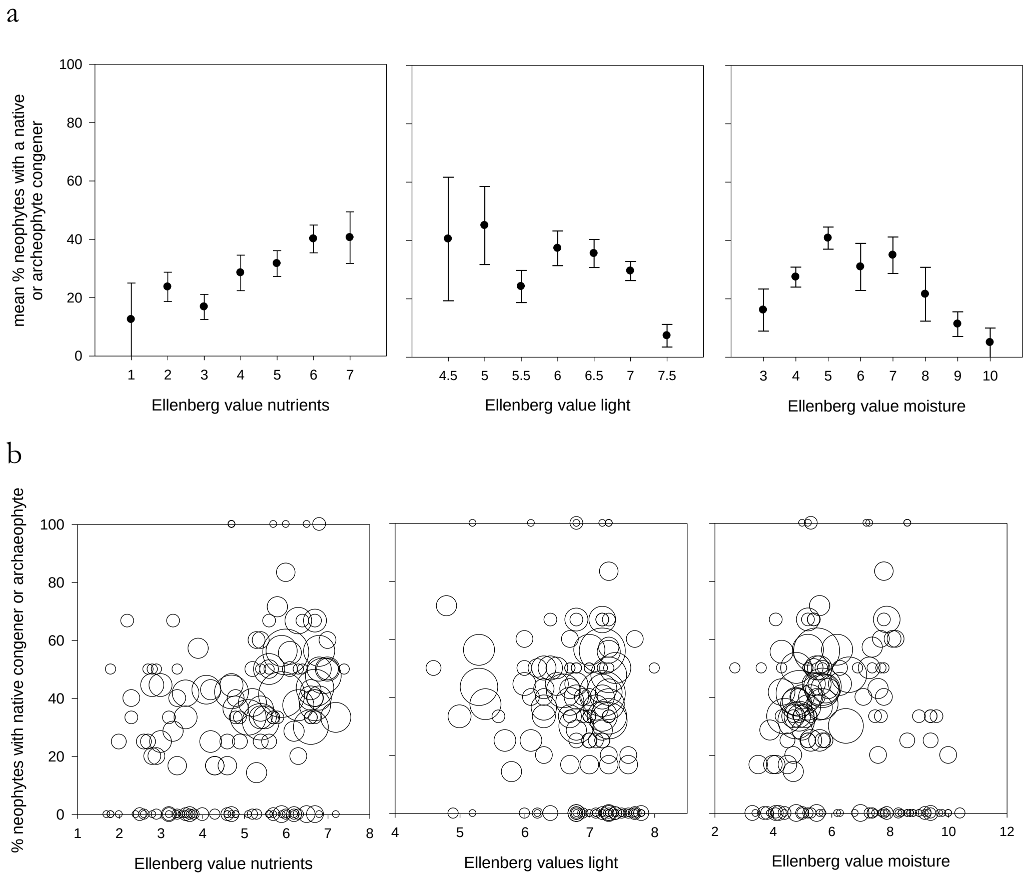


Figure 5.2. Relation between the position of vegetation types along environmental gradients (based on Ellenberg values for nutrients, moisture or light of the component species) and the percentage neophytes that has a native congener in the vegetation types. Each circle represents a vegetation type. Data are based on vegetation records from the Netherlands. The original data on Ellenberg values of the vegetation types were continuous, on one decimal. In panel a, we grouped the Ellenberg values according to a decimal scale (see supplements S6). In panel b every vegetation type is represented by a circle. The size of the circle represents the total number of neophytes in that vegetation type, the smallest circle representing 1 neophyte.

Table 5.1. Top 5 models of the model selection procedures for the models that were best at predicting which properties of vegetation types explain the percentage neophytes having a native congener. Values for parameters are p-values in that model. A hyphen indicates that the parameter was not incorporated into that model.

AIC/SIC	*Akaike weight*	*Adj* R^2	*Df*	*nutrients*	*light*	*moisture*	*moisture*^{2}	*natives*	*archaeos*
AIC									
156.42	0.177	17.6	5	0.033	-	0.001	0.001	0.054	-
157.78	0.090	17.4	6	0.12	-	0.001	0.001	0.149	0.425
157.88	0.085	16.78	5	0.136	-	0	0	-	0.133
158.13	0.075	16.08	4	-	-	0	0	-	0.014
158.17	0.074	16.07	4	0.014	-	0	0	-	-
SIC									
170.23	0.189	16.08	4	-	-	0	0	-	0.014
170.26	0.186	16.07	4	0.014	-	0	0	-	-
171.13	0.120	15.58	4	-	-	0	0	0.023	-
171.50	0.100	13.15	3	-	-	0	0	-	-
171.54	0.098	17.6	5	0.033	-	0.001	0.001	0.054	-

We grouped vegetation types with continuous Ellenberg values into categories of Ellenberg values (see supplements S5.1) and presented only the mean relatedness index per category (Figure 5.2a). However, the data analysed are scattered with Ellenberg values in decimals. Also, in the analyses, the number of neophytes was used to weigh the data, because with proportional data, a percentage derived from 20 vegetation types should be given more weight than a percentage from 1 vegetation type. This factor is visualized in Figure 5.2b: the size of the circles indicates the number of exotic plant species in that vegetation type. Compared to Figure 5.2a, Figure 5.2b provides more information about the variation and weighing of the individual data points. The smallest circles represent vegetation types with only one exotic, a circle twice that surface represents vegetation types of only two exotics, and to the largest circle represents vegetation types with 27 exotic plant species.

Results in the model selection procedure using AIC or SIC were highly similar, although the importance of nutrients was relatively smaller for SIC selected models than for AIC selected models (see Table 5.1 and Figure 5.3).

In Figure 5.4, habitat types on the x-axis have been ranked according to the relatedness index of the vegetation types (Figure 5.4). We could not simply rank vegetation types according to a disturbance gradient. However, pioneer and ruderal vegetation types exemplify high disturbance, and these are ranked towards the right of the x-axis having a relatively high relatedness index. Therefore, this ranking tends to be in support of our hypothesis that in highly disturbed habitats exotic species are more likely to establish in habitats with congeneric natives.

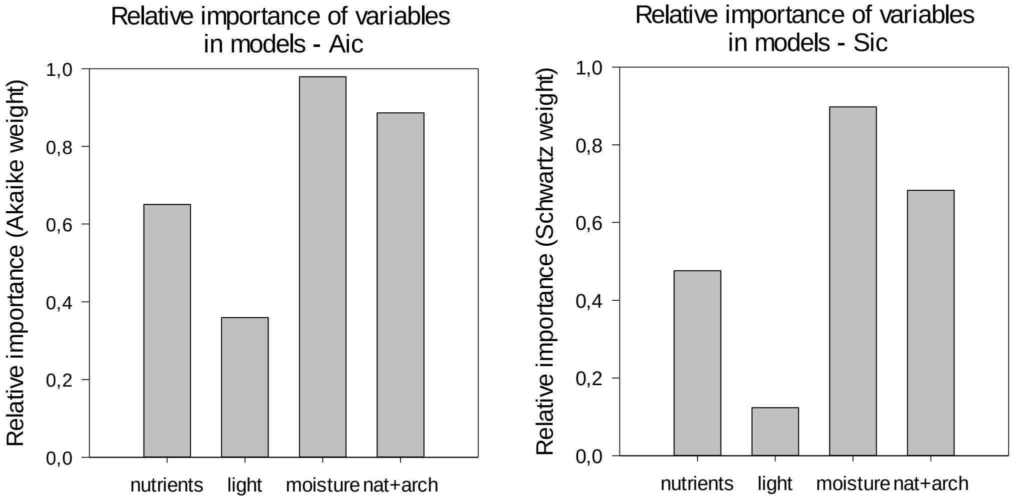


Figure 5.3. Relative importance of nutrients, light, moisture, and the number of native plant species in the vegetation types as explanation of the percentage neophytes having a native congener. Nutrients, light and moisture are based on Ellenberg values. Relative importance is the sum of the Akaike weights for all the models that included that factor. Maximum value is 1.0. For moisture we grouped the linear and quadratic term together.

Discussion

We investigated whether Darwin's' naturalisation conundrum might be solved by accounting for variation in habitat properties. Two main processes that are involved in structuring plant communities are habitat filtering and competition for niche space. We hypothesized that in naturalisation processes habitat filtering might be most important in extreme habitats, favoring exotic species that are similar to the natives, and that competition is important in habitats with intermediate environmental conditions, favoring exotic species that are strong competitors for niche spaces. We tested this hypothesis by analyzing the amount of exotic plant species with a congener in relation to Ellenberg values for nutrients, moisture, and light.

Our results support the expectation that not under all habitat conditions the proportion of exotics that would have a native congeneric is the same. Indeed, percentages of exotics having a congeneric native varied among habitats. Habitat properties such as nutrient availability, moisture and degree of disturbance explained part of this variation. However, we did not observe concave hump-shaped relationships between the similarity index and Ellenberg values, as we hypothesized.

The result for the relation between the relatedness index and the moisture gradient is opposite to what we hypothesized. A possible explanation for this pattern may be that habitat filtering is not the most important process determining whether exotics are more or less related to the resident native plant species. These challenging habitats are actually very limited in the number of available niches, and only a limited number of species is able to cope with these circumstances. Competition is probably the more important process, selecting for species that differ only slightly.

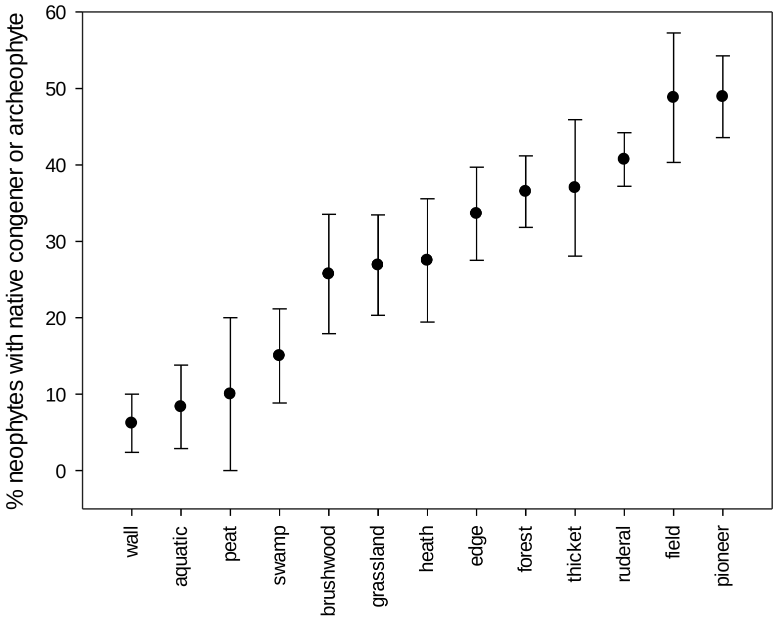


Figure 5.4. Habitat types in the Netherlands and their mean percentage exotics having a native congener, ranked from low to high mean percentage.

In nutrient-rich habitats, the relatedness index was highest in the high productive habitats, where we expected most competition for niche space (Hutchinson, 1959, MacDougall et al., 2009). However, as in the case of moisture, nutrient-rich habitats seem to select for relatedness of exotic species. Typically, in nutrient-rich habitats species are strongly controlled by their enemies in their native range (Blumenthal, 2006, Blumenthal et al., 2009). When these species are establishing in a new range, they have a competitive advantage over the native species by being released from their native enemies. This gives exotics an advantage over highly related natives in competition for niches.

The result for the relation between the relatedness index and the light gradient also did not support our hypothesis. The habitats with the highest relatedness index were typically half-shaded. However, this gradient explained little variation in our models.

When ranking the habitat types based on their relatedness index (Figure 5.4), results showed that exotics in habitats with a high level of disturbance have a relatively high relatedness index. This is in support of our hypothesis. Moreover, these are also habitats with species that are typically highly controlled by enemies (Blumenthal, 2006, Blumenthal et al., 2009, Blumenthal, 2005). In a new range, these species would profit from enemy release. Again, competing for niche space with strongly related species gives exotics an advantage over natives, promoting their establishment.

Another alternative explanation of rejecting our hypothesis could be due to the number of species that can be used in the comparison (Daehler, 1998). The most extreme habitats typically host fewest species, both natives and exotics. The chance of encountering a congeneric native plant species will be lower when there are only few native species.

A number of studies have used phylogenetic distance to quantify relatedness between exotics and natives (Strauss et al., 2006, Thuiller et al., 2010, Ordonez, 2014). However, a number of these studies are based on phylogenetic distance between an exotic species and all native co-occurring species in the new habitat. The advantage of our approach is that we compare an exotic species with single congeneric native species instead of all other species. That such a native congener persists in that habitat, is very relevant, meaning that it is suited for the habitat, just like the related exotic. This may be more relevant than an average distance to all natives.

We did not, however, look at the functional traits of the species considered. Niches are not created by relatedness, but by the functional traits of the species in interaction with available resources of the habitat (Duckworth et al., 2000). Using our method for relatedness, we assume that species from the same genus also share most functional traits. This does not have to be true. It has been suggested and shown (Ordonez, 2014, Thuiller et al., 2010) that relatedness from an exotic compared to the native community may differ for a phylogenetic analyses versus a trait-based analyses. Future studies might take, or include, a trait-based approach.

Conclusions

We conclude that relatedness of exotic to native plant species is selected for in habitats where competition for niche space is important. When competition is less important, species are less often closely related to native species. This may be an effect specific for exotics compared to natives, because of differences in enemy pressure, when competing for the same niche. If this explanation is valid, this has large implications for using knowledge on community assembly in predicting which exotic species might be able to naturalise in a new range. Possibly patterns that predict assembly of native species might not be predictive for exotic plant species.

Supplements S5.1

Table S5.1 Grouping of Ellenberg values of vegetation types into categories for graphical use (see Figure 5.2a).

Nutrients	***Light***	***Moisture***
1 = 1,7-1,9	4,5 = 4,5-4,9	3= 2,7-3,9
2 = 2,0-2,9	5,0 = 5,0-5,4	4 = 4,0-4,9
3 = 3,0-3,9	5,5 = 5,5-5,9	5 = 5,0-5,9
4 = 4,0-4,9	6,0 = 6,0-6,5	6 = 6,0-6,9
5 =5,0-5,9	6,5 = 6,6-6,9	7= 7,0-7,9
6 =6,0-6,9	7,0 = 7,0-7,5	8 = 8,0-8,9
7 = 7,0-7,4	7,5 = 7,5-8,0	9 = 9,0-9,9
		10=10,0-11,0

6

General discussion and synthesis

General discussion and synthesis

The main objective of my thesis was to search for patterns that enable predicting which exotic plant species have the potential to become invasive in the Netherlands. To search for such patterns, I examined which plant traits and other plant factors relate to invasiveness of current exotic plant species in the Netherlands. I elucidated how different scales and proxies of invasiveness influence these outcomes, I explored how the temporal dynamics of invasiveness may or may not influence the level of invasiveness, and how the composition of the native community may influence naturalisation of the exotic species. In this chapter I will discuss the main findings and synthesize the results. I will also suggest advices for invasive species management and propose some directions for future research.

Plant traits and scale-dependent plant abundance dynamics in relation to invasiveness

Plant traits and other factors concerning the introduction events of exotic plant species, have shown to be related to invasiveness of these plant species. For example, specific traits like height and level of ploïdy are positively related to measurements of invasiveness (Chapter 2). Clearly, traits are relevant when considering correlates of invasiveness. In my study, I have shown that these correlations are scale-dependent (Chapter 2). For example, life form, height, length of flowering season, polyploidy, origin, residence time and human use related to regional frequency and residence time and vegetative lateral spread related to local dominance. This was not unexpected, because the most relevant ecological processes differ greatly at each scale. Invasiveness at the regional scale and possible predictors thereof have been studied more intensively than invasiveness at the local scale. Other studies have shown that also at regional and continental scales, differences will be found in related traits (Hamilton et al., 2005).

Another aspect that makes prediction challenging is the temporal dynamics of invasiveness. Other studies have shown temporal variation in invasiveness of introduced plant species after residence time passes; both increases and decreases in invasiveness have been observed (Simberloff and Gibbons, 2004, Hawkes, 2007, Wilson et al., 2007, Pyšek and Jarošík, 2005, Hamilton et al., 2005). As my results in Chapter 2 have shown, this even may be different between regional and local scales. I showed that regional invasiveness increased with residence time, whereas local invasiveness decreased with residence time. The pattern for the locally decreasing invasiveness when time passes on is usually explained by increasing enemy pressure in the new range over an evolutionary time scale (Bardgett and van der Putten, 2014).

When I investigated enemy pressure of introduced exotic plant species in the Netherlands using a plant-soil-feedback experimental approach, we did not find any evidence for differences in enemy pressure explaining this pattern (Chapter 4). These results oppose earlier findings by Diez et al. (2010) and Dostal et al. (2013), but are in line with McGinn (McGinn, in preparation). Possibly these patterns are not as uniform as suggested by the earlier findings, perhaps because they may differ greatly between ecosystems and plant species. In my study, I could explain the temporal pattern in declining local abundance with time since introduction by an overrepresentation of plants with bulbs, which also typically had a lower local dominance. This, rather than changing plant-enemy dynamics seemed to explain our pattern (Speek unpublished results).

Predictions using plant traits might also depend on community-specific traits. Not all plant communities have shown to be equally receptive to plant introductions and plant invasions and the characteristics of the plant communities or the habitat might be responsible for whether communities are, or are not easily invaded. This is also likely to interact with the plants and their traits that are being introduced (Richardson, 2006). Therefore I investigated how plant community properties may predict which exotic plant species are most likely to be introduced in specific habitats. I have shown that community traits influence whether exotic plants are more or less likely to establish in a community with mostly related plant species (Chapter 5). It seems that habitats where competition is high rather promote similar species.

Invasive species management

Can traits predict enough?

Although we did find plant traits and other factors, such as residence time and origin, to relate to plant invasiveness, the power of using these factors and traits to predict which species might become invasive, seems too low to be used by border authorities in preventing plant species with high risk profiles to be imported into the Netherlands. Explained variation of my statistical models was only 15 to 30 %. This means that many species that fit the profile, because they have many of the traits that should result in high invasiveness, may not become invaders (these are so-called false positives). It also means that there will be exotic species that do not fit the profile, but will become invaders (so-called false negatives). This implies that using the models based on my results as predictive models, will on the one hand unnecessary harm economical values, but on the other hand still pose too much of a risk to allow potential invaders to become introduced. Even when using data from a much finer grid scale than in comparable studies, and even when using data on local plant communities, the models did not result in more explained variation. Therefore, I conclude that using my trait model as main predictor does not seem to provide further advantages over using the classification 'invasiveness elsewhere' combined with a good climate match as a predictor.

In my study, I also used plant traits in the predictive framework of the Australian Weed Risk Assessment (WRA). I have shown that this approach has great potential for predicting invasiveness of new exotic plant species in the Netherlands (Chapter 3). In the WRA most plant traits were directly related to dispersal abilities, climate-pre-adaptation, and traits related to noxiousness. Traits that I used to predict regional spread and local dominance are more indirectly related to invasiveness, for example plant height and self compatibility; these traits are more related to competitive potential of plants. Possibly, these competition-related traits could be a valuable addition to the WRA.

Moreover, in the WRA, plant traits are an addition to questions on invasiveness elsewhere and climate matching. An exotic plant species that is already invasive elsewhere and has a good climate match with the region under investigation, will already result in a high enough score to be categorized as a potential invader. This shows that such plant traits are not necessarily better predictors than information on invasiveness elsewhere in combination with climate matching, but that they may provide an important addition that can further improve the quality of assessing invasive potential (Pheloung et al., 1999, Hulme, 2012).

Besides predicting invasive potential, it would also be valuable if we could predict which species have variable invasiveness over time, and how invasiveness may vary with time. However, although a number of studies have shown enemy exposure and enemy effects to increase when time since introduction increases (Diez et al., 2010, Dostál et al., 2013), I did not find such a pattern in an experimental plant-soil feedback study. As there are only two such studies published that do not agree with my results (Diez et al., 2010, Dostál et al., 2013), and one in prep that confirms my results (McGinn, in preparation). Therefore, I propose that more studies are needed in order to determine if general patterns indeed may occur, or not. As far as concerning effects of soil-borne pathogens. Therefore, I conclude that more such studies are needed under a variety of environmental conditions before the results may be included into predictions on the temporal development of plant invasions.

Similarly I tried out the use of plant community properties to predict which exotic plant species may naturalise. I concluded that this research is promising, but still contains many unanswered questions. Community ecology has invested many efforts in research that questions which species may establish in which communities (Hutchinson, 1961, MacArthur, 1967, Hubbell, 1997). A relevant question about using previous community composition research is whether research on native plants can be used to predict outcomes for exotic plant species. My results showed that possibly communities may select differently against plants that are normally strongly controlled by enemies compared to plants that are normally not strongly controlled by enemies. This may mean that results for native or exotic species may strongly differ.

What other information do we need to enhance predictive capacity?

Functional ecology is an exciting field, where plant traits are being used to understand and predict ecological processes and principles. Many plant traits might have been relevant for my research, but I was limited by the availability of traits for the selection of plant species that I could use. Other interesting traits could be e.g. more specific ones on seed dispersal, specific leaf area or competition-, stress- or ruderal strategy types (CSR-strategy) (Ozinga et al., 2009, Westoby, 1998, Grime, 1977).

What also would have been interesting is to use data on regional spread per ecosystem. When regional spread of a species is measured across all different ecosystems the species from more widespread ecosystems will have a higher regional spread than species from very specific ecosystems, while the impact may actually be higher at a less common but more valuable ecosystem. Further, higher quality data on propagule pressure will improve predictability (Wilson et al., 2009, Lockwood et al., 2009, Lockwood et al., 2005, Křivánek et al., 2006). Finally, more information on human aided dispersal in the Netherlands might have been valuable as well to enhance predictive capacity of trait models (Hulme et al., 2008, Hulme, 2009).

Could we use the WRA, how could it be improved?

Results showed that the only proxy that is properly predicted by the WRA is whether or not a species was found on a black list in our region. This is the most qualitative and subjective of all four proxies of invasiveness. Although subjectivity often has a bad taste in science, a more qualitative approach to the proxy of invasiveness might be most valuable for policy concerning invasive species. From this perspective the WRA turns out to be a valuable tool for prediction. When using more qualitative proxies to define invasiveness, I would recommend to continue discussions on which elements are relevant and what types of invaders can be distinguished. I will suggest some important elements for defining invasiveness in the next part.

Defining invasiveness

As argued in Chapter 2 and 3 it matters for predictors how invasiveness is defined. Consequently, the question arises how definition of invasiveness could be further improved. An interesting aspect of this question is that focus may differ depending on the user of the term. It seems that science and policy use different elements of the terminology of invasiveness . Science prefers to use more quantitative proxies, whereas policy prefers to use more qualitative proxies (IUCN/SSC, 2000, Hulme et al., 2009). For science, to be of value for policy issues, it would be preferable to use the same proxies for invasiveness. My recommendation on how to define invasiveness is the following:

*Invasiveness=Range*local dominance*impact*

which is the definition mentioned in Chapter 3, adapted from (Parker et al., 1999). Range should be included in the definition, because the more widespread a species, the more spots were it might have an impact. Local dominance is included because a larger dominance will more likely affect the plant community. Impact is the most difficult part. It is already used in factsheets in databases on invasive species, like Daisie, Harmonia, Eppo, Gisd and Nobanis. The meaning of impact is often not clarified, but it is mostly similar to how the definition of a weed is used: a species at an unwanted place at an unwanted time (Holzner, 1982). Examples of impacts of invasive exotic plant species are weeds in agriculture (Randall, 2012, Holzner, 1982), weeds in parks and gardens (Randall, 2012, Pimentel et al., 2005), smothering growth (e.g. *Pueraria Montana,* (Forseth and Innis, 2004), allergenic properties (e.g. *Ambrosia artemisiifolia,* (Laaidi et al., 2003), toxicity to animals (e.g. *Giant hogweed,* Pysek, 2007), hybridisation with a native species (Bleeker et al., 2007, Fitzpatrick et al., 2010), establishment in valuable habitats (e.g. Natura 2000 areas), ecosystem disrupters (e.g. *Eichhornia crassipes,* (Masifwa et al., 2001) and alterations of soil nutrient cycling (Ehrenfeld, 2003).

When considering the predictability of these different examples of impact, it becomes clear that they will strongly differ. Whereas toxicity to animals is easy to predict, ecosystem disruption is much more difficult to predict. Predictability of the other elements of invasiveness, range and local dominance, have shown to be more challenging to be predicted (Chapter 2 and 3). From the literature, it appears that, like invasiveness elsewhere, also range elsewhere and local dominance elsewhere might be strong predictors for range and dominance in yet another new range: Native range and native local dominance even seem predictive of non-native range and local dominance (Firn et al., 2011, Pyšek et al., 2009).

Future research

Although for some exotic species boom and bust patterns have been observed, most exotic species are not known to show such temporal dynamics. If these patterns are caused by changing relations with enemies and mutualist, they are likely to change over relatively long temporal scales, which might be stretching beyond the recent history of invasion biology research. Therefore, monitoring the fate of current exotic plant species is just as important as monitoring introductions of new exotics. But besides monitoring, also more research on the possible changing relationships of exotic plant species and their enemies and mutualists with changing residence time, will be necessary.

Another line of research that will help advancing the prediction of plant invasiveness, is to investigate what is going on for the species that are invasive in one exotic range but not in the other. How many of the current noxious invaders are invasive in one range but not in the other? Is this mainly due to novel relations with enemies and mutualists (Reinhart and Callaway, 2006), have they established in other ecosystems (Broennimann et al., 2007), or have these plant species become incorporated into other vectors causing different patterns of spread (Hulme et al., 2008, Hulme, 2009). This knowledge might help us clarify how relevant it is to develop other methods than invasiveness elsewhere to predict potential invaders and what are the most important routes for future research to help predict invasive potential across the globe.

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Summary

Summary

Introduced exotic species can become invasive and may have major impacts on economy, ecosystems, or human health. Prevention of introduction is believed to be the most effective management option in combatting impacts of exotic species. In this thesis I investigated possibilities to predict invasive potential of introduced plant species and invasibility of plant communities in the Netherlands. I based my research on exotic plant species that had already been introduced, as those could be evaluated on invasion success. In order to quantify invasiveness of exotic species I used information on regional and local spread of current exotic plant species in the Netherlands. The unique availability of these data for plant species in the Netherlands provides a novel perspective on the invasion success of exotic plant species at local versus regional spatial scales, which may help to enhance predictability of invasiveness, clarify how invasiveness may change over time, and how the composition of the native community may influence exotic species establishment.

To compare exotic success on regional versus local scales, I investigated which plant traits correlated to each scale (Chapter 2). I concluded that plant traits relating to the regional frequency of exotic plant species differ from those that relate to their local dominance. The factors that correlated with regional occurrence were: life form, height, polyploidy, length of flowering season, residence time, human use, and origin. The factors that correlated to local dominance were lateral vegetative spread and residence time. The implication of my results is that predictive studies on plant invasiveness based on regional occurrence may not be indicative of the local performance. As the prediction of local performance is crucial for conservation and risk assessment, my study points out that more information is needed on local abundance of exotic invaders.

The Weed Risk Assessment (WRA) has become a popular tool in predicting invasiveness of exotic plant species. I compared how quantitative and qualitative estimates of invasiveness may relate to WRA scores (Chapter 3). As quantitative estimates I used regional spread, change in regional spread and local dominance of naturalized exotic plant species in The Netherlands. To obtain a qualitative estimate I determined if the exotic plant species occurred

on a black list in neighbouring regions. My results revealed that the WRA predicted the qualitative (black list) estimate more accurately than the quantitative (dominance and spread) ones. It seems the WRA predicts the noxiousness component better than the spatial components of impact of exotic species.

In Chapter 2 I found that exotic species with a longer residence time had a lower local dominance. I performed a plant-soil feedback experiment to investigate whether increased accumulation of belowground plant enemies over time might explain this relationship (Chapter 4). There was no relationship of local dominance with plant-soil feedback. Plant-soil feedback also did not become more negative with increasing time since introduction. Plant-soil feedback may not in all cases, or not in all comparisons explain patterns of local dominance of introduced exotic plant species. This conclusion might need more verification, as it contradicts results from two studies in New Zealand and the Czech Republic. However it shows that those results may not apply to just any other case.

Darwin's naturalisation conundrum includes two opposite hypotheses about how naturalization success of exotic species is linked to the degree of relatedness of the exotics with plant species in the native community. One hypothesis assumes that when exotic species are less similar to natives they are more likely to fill empty niches in a novel habitat, because of the novel trait combinations and ecological requirements. The other hypothesis is based on habitat filtering theory and predicts that exotic species should be similar to natives in order to successfully establish. I explored whether habitat properties may explain similarity between exotic species and species that are native in the new range (Chapter 5). For habitats, I used data on vegetation types in the Netherlands. For habitat properties, I used Ellenberg indicator values on light, moisture and nutrient richness of these vegetation types. I showed that relatedness of exotic to native plant species appears to be selected for in habitats where competition for niche space is important. When competition seemed less important, in more stressful habitats, exotic plant species were less often closely related to native plant species. I concluded that relatedness of exotic to native plant species is selected for in habitats where competition for niche space was important, but not so much in stressed habitats.

When placing my results in the context of usability, I concluded that the traits related to the local and regional scale of invasiveness do not have enough predictive power to be used by phytosanitary authorities to distinguish between plant species that may become invaders and non-invaders. This implies that using the models based on my results as predictive models, will on the one hand unnecessary harm economical values, but on the other hand still pose too much of a risk to allow potential invaders to become introduced.

My research showed that the Australian weed risk assessment (WRA) turns out to be a valuable tool for prediction of invasive potential in the Netherlands. The WRA predicts invasiveness -based on being on a black list or not in the Western European region- very well, which proofs it to be a useful tool. As the WRA is more predictive for invasiveness defined in a qualitative than a quantitative way, this may have implications for how invasiveness should be defined.

I suggested to define invasiveness as the product of regional occurrence, local dominance and noxiousness. This will enhance usability of predictive schemes like the WRA, but also help to close the gap between science and policy in the ongoing debate on invasive plant species.

Nederlandse samenvatting (Dutch summary)

Exoten kunnen na introductie zich invasief gaan gedragen en grote gevolgen hebben voor economie, ecosystemen of volksgezondheid. Het voorkomen van introductie wordt beschouwd als de meest effectieve manier om dit brede probleem aan te pakken. In dit proefschrift heb ik onderzocht wat mogelijkheden zijn om het invasief potentieel van geïntroduceerde plantensoorten en de invasibiliteit van plantengemeenschappen in Nederland te voorspellen. Ik heb voor mijn onderzoek soorten gebruikt die hier al geïntroduceerd zijn, omdat van deze hun invasief succes bekend is. Om hun invasiviteit te kwantificeren heb ik informatie gebruikt over de regionale en lokale verspreiding van de soorten. De unieke beschikbaarheid van deze datasets voor plantensoorten in Nederland bieden nieuwe kansen, die mogelijk helpen de voorspelbaarheid van invasiviteit te verhogen, uit te leggen hoe invasiviteit van een soort kan veranderen in de tijd en hoe de samenstelling van de plantengemeenschap kan bepalen welke geïntroduceerde soorten zich kunnen vestigen.

Om het succes van exoten te vergelijken op een lokale versus een regionale schaal heb ik onderzocht welke planteigenschappen correleren aan elke schaal (Hoofdstuk 2). Mijn conclusies waren dat de planteigenschappen die samenhangen met regionaal succes van exoten andere zijn dan de eigenschappen die samenhangen met lokaal succes van exoten. De factoren die correleren aan regionale verspreiding zijn levensvorm, lengte, polyploidy, lengte van het groeiseizoen, hoe lang de soort hier al is, of deze door mensen nuttig wordt gebruikt of niet en uit welke werelddeel ze oorspronkelijk komen. De factoren die correleren aan lokale dominantie zijn het beschikken over laterale vegetatieve groei, en hoe lang de soort hier al is. Dit betekent dus dat resultaten voor het voorspellen van invasiviteit op de regionale schaal waarschijnlijk niet voorspellende zijn voor invasiviteit op de lokale schaal. Omdat de invasiviteit op lokale schaal van groot belang is voor natuurbeheer en risico-inschattingen toont mijn onderzoek aan dat er meer onderzoek nodig is naar de lokale dominantie van soorten.

De 'Weed Risk Assessment (WRA)' is een populaire assessment geworden om de invasiviteit van uitheemse plantensoorten te voorspellen. Ik heb vergeleken hoe kwantitatieve versus kwalitatieve maten van invasiviteit samenhangen met de scores die voortkomen uit de WRA (Hoofdstuk 3). Als kwantitatieve maten gebruikte ik regionale verspreiding, verandering in regionale verspreiding in de tijd en lokale dominantie van genaturaliseerde uitheemse plantensoorten in Nederland. Als kwalitatieve maat gebruikte ik het wel of niet voorkomen van een plantensoort op een 'zwarte lijst' in naburige regio's. Mijn resultaten onthullen dat de WRA de kwalitatieve maat voor invasiviteit ('zwarte lijst') beter voorspelt dan de kwantitatieve maten (dominantie en vespreiding). Het lijkt erop dat de WRA de schadelijkheidscomponent van de impact van exoten beter voorspelt dan de ruimtelijke componenten.

In hoofdstuk 2 heb ik gevonden dat uitheemse plantensoorten met een langere tijd sinds introductie een lagere lokale dominantie hadden.Ik heb een plant-soil feedback experiment opgezet om te onderzoeken of toenemende ophoping van ondergrondse vijanden dit verband kan verklaren (Hoofdstuk 4). Ik vond geen verband tussen lokale dominantie en plant-soil feedback effect en geen verband tussen tijd sinds introductie en plant-soil feedback effect. Dus, plant-soil feedback kan niet altijd patronen van lokale dominantie van uitheemse planten verklaren. Deze conclusie behoeft nog verdere bevestiging, omdat het in tegenstelling si tot resultaten van twee studies uit Nieuw-Zeeland en Tsjechië. Echter toont het al wel aan dat die resultaten niet in elk geval lijken op te gaan.

Darwin's naturalisation conundrum omvat twee tegengestelde hypotheses over hoe naturalisatie succes van uitheemse soorten gekoppeld is aan de mate van verwantheid van die uitheemse soorten met de inheemse gemeenschap. De ene hypothese stelt dat als exoten minder op de natives lijken het waarschijnlijk is dat ze de lege niches van een nieuwe habitat zullen opvullen vanwege de nieuwe combinatie van kenmerken en ecologische behoefte. De andere hypothese stelt vanuit het idee van 'habitat filtering' dat exoten meer gelijk zullen zijn aan de inheemse soorten in een gemeenschap om zich succesvol te vestigen. Ik heb onderzocht of habitat eigenschappen de mate van gelijkheid kunnen voorspellen tussen exoten en de inheemse gemeenschap

(Hoofdstuk 5). Als habitat gebruikte ik vegetatietypes in Nederland. Als habitateigenschappen gebruikte ik Ellenberg waarden voor licht, vocht en nutriënten rijkheid van deze vegetatietypes. Ik toonde aan dat hogere verwantheid van exoten aan inheemsen samenhangt met habitats waar competitie voor niche ruimte belangrijk is. Als competitie minder belangrijk leek, in meer stressvolle habitats, waren exoten minder verwant aan de inheemse planten.

Als ik mijn resultaten plaats in het licht van hun gebruikswaarde, trek ik de conclusie dat eigenschappen die correleren aan de lokale en de regionale schaal van invasiviteit niet genoeg voorspellende kracht hebben om gebruikt te worden door fytosanitaire instanties om een onderscheid te maken tussen exoten die invasief of niet-invasief kunnen worden. Dit betekent dat het gebruiken van de modellen uit mijn resultaten als voorspellende modellen, aan de ene kant onnodig schade zal doen aan economische belangen en aan de andere kant nog steeds een te groot risico zal geven op introductie van invasieve exoten.

Mijn onderzoek heeft aangetoond dat de WRA een waardevol instrument kan zijn voor het voorspellen van invasief potentieel in Nederland. De WRA voorspelt invasiviteit – gebaseerd op wel of niet op een zwarte lijst staan in West-Europa – goed, wat bewijst dat het waardevol kan zijn. Omdat de WRA kwalitatieve maten voor invasiviteit beter voorspelt dan kwantitatieve maten, kan dit gevolgen hebben voor hoe we invasiviteit het beste kunnen definiëren.

Ik heb voorgesteld om invasiviteit te definiëren als het produkt van regionale verspreiding, lokale dominantie en schadelijkheid. Dit zal de gebruikswaarde van voorspellende schema's als de WRA verhogen, maar zal ook helpen om het gat te sluiten tussen wetenschap en beleid in het doorgaande debat over invasieve plantensoorten.

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Curriculum vitae

Tanja Anna Antoinette Speek was born in Breda on the 7th of August, 1979. In 1999 she started her study Biology at the Radboud University in Nijmegen. She fulfilled her M.Sc. theses at the department of Experimental Plant Ecology, the department of Molecular Ecology at the Radboud University and at the editorial office of the magazine 'Bionieuws' in Utrecht.

After graduation in September 2005 she worked as a student-supervisor for first year students Biology. In February 2006 she started to work as a biology teacher at the Kandinsky College in Nijmegen, partly in supervision by the postdoctoral institute for teachers.

In 2008 she started the PhD research that resulted in this thesis. She performed her research at the department of Agrosystems at Plant Research International (PRI), as part of Wageningen University and Research together with the Department of Terrestrial Ecology at the Netherlands Institute of Ecology (NIOO).

In 2013 she started as a scientific assessor Efficacy at the Dutch board for authorisation of plant protection products (Ctgb) in Wageningen.

List of publications

International peer-reviewed journals:

Lenssen, J.P.M., Hershock, C., **Speek , T.A.A.**, During, H.J. and Kroon, H. de (2005). Experimental ramet aggregation in the clonal plant *Agrostis stolonifera* reduces its competitive ability. Ecology 86, 1358-1365.

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Other:

Duistermaat, L., Valkenburg, J. van, **Speek, T.A.A.**, Wiel, C.C.M. van de, Smulders, M.J.M., Moorsel, R. van & Lotz, B. (2011). De ontwikkeling van een informatiesysteem voor invasieve plantensoorten. Gewasbescherming, 42(2), 53-57.

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (4.5 ECTS)

- Predicting invasive behaviour of alien plants (2007)

Writing of project proposal (3 ECTS)

- Project proposal invasive plants

Post-graduate courses (7.4 ECTS)

- Multivariate analysis; PE&RC (2008)
- Linear models; PE&RC (2009)
- Understanding global environmental change: processes, compartments and interactions; Sense (2009)
- Soil ecology: taking global issues underground; PE&RC, Sense & RSEE (2010)

Competence strengthening / skills courses (4.5 ECTS)

- PhD Competence assessment; WGS (2008)
- Project & time management; WGS (2009)
- Effective behaviour in your professional surroundings; WGS (2009)
- Techniques for writing and presenting scientific papers; WGS (2009)
- Career orientation; WGS (2010)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- PE&RC Weekend (2008)
- PERC Day (2008)
- PERC Day (2009)

Discussion groups / local seminars / other scientific meetings (6.2 ECTS)

- NIOO PhD Discussion group (2007-2011)
- Netherlands Annual Ecology Meeting; oral presentation; Lunteren, the Netherlands (2009)
- Netherlands Annual Ecology Meeting; poster presentation; Lunteren, the Netherlands (2010)

International symposia, workshops and conferences (9 ECTS)

- Neobiota; poster presentation; Prague, Czech Republic (2008)
- GFO Annual meeting; oral presentation; Bayreuth, Germany (2009)
- Workshop on biological invasions – towards general rules across taxa; oral presentation; Murren, Switserland (2010)
- Neobiota; poster presentation; Copenhagen, Denmark (2010)
- Popbio conference; oral presentation; Nijmegen, the Netherlands (2010)

Lecturing / supervision of practical's / tutorials (1.2 ECTS)

- Conservation biology; Leiden (2008-2010)
- Agrodiversiteit; WUR (2010)

Supervision of MSc student (1.5 ECTS)

- Soil-feedback experiment phase 1; time and dominance of exotic plant species in the Netherlands