

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

Diversity and Distributions

Speek, T.A.A.; Lotz, L.A.P.; Ozinga, W.A.; Tamis, W.L.M.; Schaminée, J.H.J. et al

<https://doi.org/10.1111/j.1472-4642.2011.00759.x>

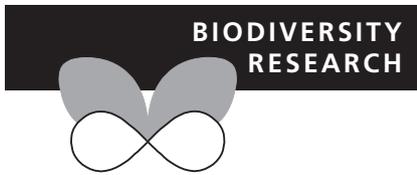
This publication is made publicly available in the institutional repository of Wageningen University and Research, under the terms of article 25fa of the Dutch Copyright Act, also known as the Amendment Taverne.

Article 25fa states that the author of a short scientific work funded either wholly or partially by Dutch public funds is entitled to make that work publicly available for no consideration following a reasonable period of time after the work was first published, provided that clear reference is made to the source of the first publication of the work.

This publication is distributed using the principles as determined in the Association of Universities in the Netherlands (VSNU) 'Article 25fa implementation' project. According to these principles research outputs of researchers employed by Dutch Universities that comply with the legal requirements of Article 25fa of the Dutch Copyright Act are distributed online and free of cost or other barriers in institutional repositories. Research outputs are distributed six months after their first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and / or copyright owner(s) of this work. Any use of the publication or parts of it other than authorised under article 25fa of the Dutch Copyright act is prohibited. Wageningen University & Research and the author(s) of this publication shall not be held responsible or liable for any damages resulting from your (re)use of this publication.

For questions regarding the public availability of this publication please contact [openaccess.library@wur.nl](mailto:openaccess.library@wur.nl)



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

Tanja A. A. Speek<sup>1,2,3\*</sup>, Lambertus A. P. Lotz<sup>1</sup>, Wim A. Ozinga<sup>4</sup>, Wil L. M. Tamis<sup>5</sup>, Joop H. J. Schaminée<sup>4,6</sup> and Wim H. van der Putten<sup>2,3</sup>

<sup>1</sup>Wageningen University Research Centre, Plant Research International, Droevendaalsesteeg 1, 6708 PB, <sup>2</sup>Wageningen University Research Centre, Laboratorium of Nematology, Droevendaalsesteeg 1, 6708 PB, <sup>3</sup>Netherlands Institute of Ecology (NIOO-KNAW), Department of Terrestrial Ecology, Droevendaalsesteeg 10, 6708 PB, <sup>4</sup>Wageningen University and Research Centre, Centre Ecosystem Studies, Droevendaalsesteeg 3a, 6708 PB Wageningen, <sup>5</sup>University Leiden, Institute Environmental Sciences, Einsteinweg 2, 2333 CC Leiden, <sup>6</sup>Radboud University Nijmegen, Department Ecology, Aquatic Ecology and Environmental Biology Research Group, Heyendaalseweg 135, 6525 AJ Nijmegen, the Netherlands

\*Correspondence: Tanja A. A. Speek, Wageningen University & Research Centre, Plant Research International, Droevendaalsesteeg 1, 6708 PB Wageningen, the Netherlands.  
E-mail: tanja.speek@wur.nl

## 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<sup>2</sup> 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. Since the prediction of local impacts is crucial for conservation and risk assessment, our study emphasized the need for better information on the local abundance of exotic invaders.

## Keywords

Biological invasions, database analysis, invasive plants, local dominance, plant traits, regional frequency, spatial scale.

## 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 the 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 whether 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 & Fitter, 1996). The last phase of the invasion process has been described as the spread of exotic species (Richardson *et al.*, 2000; Theoharides & Dukes, 2007), potentially indicating an impact over a large spatial scale (Pyšek & Richardson, 2010). Therefore, regional frequency is often used as an indicator of the invasiveness of exotic plant species (Küster *et al.*, 2008; Bucharova & 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 (Pyšek, 1998; Herron *et al.*, 2007; Pyšek *et al.*, 2009), however, these comparisons may involve subjective measurements (Richardson *et al.*, 2000; Colautti & 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 & 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<sup>2</sup> in Germany (Küster *et al.*, 2008) and 100 km<sup>2</sup> in Spain (Gassó *et al.*, 2009). In some cases, sub-regions are even entire countries (Bucharova & 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 & 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 & Ozinga, 2005). In order to become locally dominant, plants may benefit from enemy release (Keane & 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 1 × 1 km<sup>2</sup>, 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 S1).

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  $1 \times 1 \text{ km}^2$  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  $1 \times 1 \text{ km}^2$  grid cells of The Netherlands (Tamis, 2005). Presence was expressed as the per mille 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 & Schaminée, 2001) was used to collect plant dominance data on the local scale. This database comprises descriptions of approximately 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  $1 \times 1 \text{ m}^2$  for grasslands to  $10 \times 10 \text{ m}^2$  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]  $\times 100\%$ .

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  $> 0$  to 10%, category 15% contained all values from  $> 10$  to 20%, category 25% contained all values from  $> 20$  to 30%, category 35% contained all values from  $> 30$  to 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 (Alberternst & Böhmer, 2006; DAISIE, 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 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 & Richardson, 2007). 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 Research procedure in Genstat (11th edition). From all possible subsets we selected the model with the lowest Akaike Information Criterion. 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.

**Table 1** Explanatory variables used in the model selection analyses, with their sources and attributes.

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

References of the databases: \*(Tamis *et al.*, 2004) †(Klimešová & Klimeš, 2006) ‡(Hill *et al.*, 1999) §(Van der Meijden, 2005), ¶(CBS, 2003), \*\* (Klotz *et al.*, 2002).

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 Desclaves *et al.*, 2003 (also used by Küster *et al.*, 2008; Milbau & Stout, 2008; Dawson *et al.*, 2009; 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 & 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.

## 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, see also Fig. 1). 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 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 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 S2c). 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.

When using the frequency of local dominance data following expert judgement, the minimal adequate model included two plant traits (Table 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.

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  $r = 0.279$ , Fig. 2).

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 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

**Table 2** Factors in the minimal adequate model explaining (a) regional frequency of exotic plant species in the Netherlands (1x1 km<sup>2</sup> 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)

Factor	Before phylogenetic correction				After phylogenetic correction			
	d.f.	Estimate	<i>P</i>	<i>R</i> <sup>2</sup> -adjusted (%)	d.f.	Estimate	<i>P</i>	<i>R</i> <sup>2</sup> -adjusted (%)
<b>(a) Regional frequency*</b>								
Phylogenetic covariate					1	0.01	0.579	-0.4
Life-form	3		0.014	5.3	3		0.024	4.6
<i>Hemicryptophytes</i>		-0.53				-0.53		
<i>Geophytes</i>		-0.52				-0.52		
<i>Phanerophytes</i>		-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
<b>(b) Frequency of local dominance from original data†</b>								
Life-form	3		0.003	9.5				
<i>Hemicryptophytes</i>		-0.43						
<i>Geophytes</i>		-1.41						
<i>Phanerophytes</i>		-0.18						
Vegetative lateral spread	1	0.49	0.025	3.4				
Origin	1	0.36	0.065	2.0				
<b>(c) Frequency of local dominance modified by expert opinion‡</b>								
Vegetative lateral spread	1	0.55	0.005	9.1				
Period of introduction	1	0.23	0.058	2.4				

\*The *R*<sup>2</sup>-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.

†The *R*<sup>2</sup>-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.

‡The *R*<sup>2</sup>-adjusted for the full minimal adequate model is 9.1%. We found no effect of phylogeny.

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.

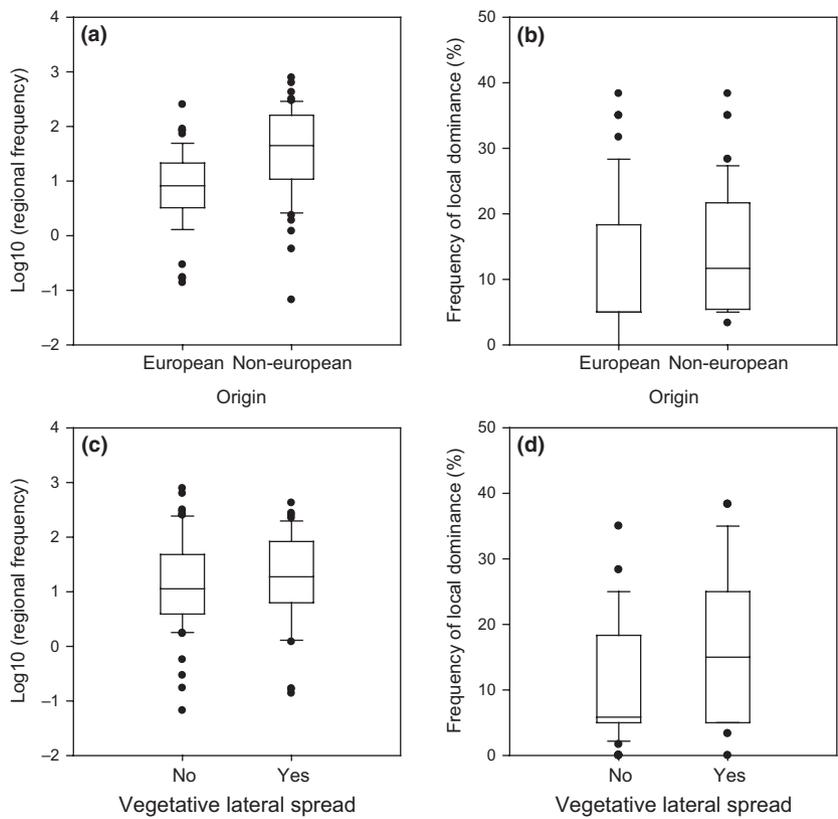
### Local dominance data

A major limitation of many invasiveness studies is that databases, especially there is a shortage of data on local dominance. 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

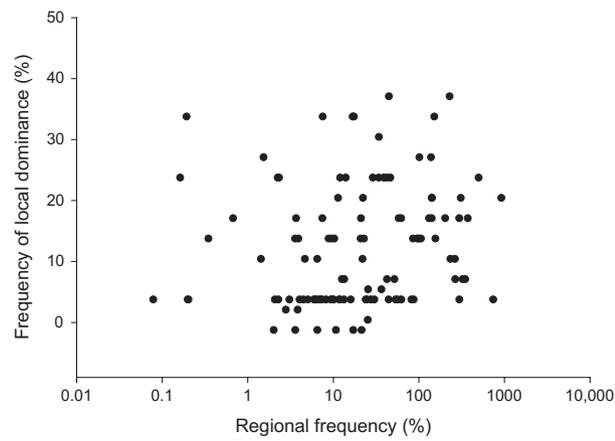
plots. Such selectivity can affect analysis which plant traits contribute to predicting frequency of local dominance, as the database analysis after expert judgment resulted in slightly different traits predicting frequency of local dominance. Moreover, the relation between the regional frequency and 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; van Kleunen *et al.*, 2009; Pyšek *et al.*,



**Figure 1** 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.



**Figure 2** Relation between regional frequency of exotic plant species in The Netherlands ( $1 \times 1 \text{ km}^2$  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.

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.

**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; Wilson *et al.*, 2007; Milbau & Stout, 2008; Bucharova & van Kleunen, 2009; Gassó *et al.*, 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. Several studies have emphasized the importance of studying propagule pressure in invasion ecology (Foxcroft *et al.*, 2004; Lockwood *et al.*, 2005, 2009;

Colautti *et al.*, 2006; Bucharova & 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 this factor (Dawson *et al.*, 2009).

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, 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 occur less frequently regionally, but which can become locally dominant. 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.

## ACKNOWLEDGEMENTS

The authors would like to thank Cajo Ter Braak for statistical advice for this paper, and Baudewijn Odé, Eddy Weeda and Roy van Grunsven for their expert judgment on the local dominance data, and three anonymous referees for constructive comments on an earlier draft of this paper. The research was funded by the Dutch Ministry of Agriculture, Nature and Food Quality, FES-programme 'Versterking Infrastructuur Plantgezondheid'. WvdP was supported by ALW-Vici grant.

## REFERENCES

- Alberternst, B. & Böhmer, H.J. (2006) NOBANIS – invasive alien species fact sheet – *fallopia japonica*. In: *Online database of the north european and baltic network on invasive alien species – NOBANIS*. Available at: <http://www.nobanis.org>.
- Bucharova, A. & van Kleunen, M. (2009) Introduction history and species characteristics partly explain naturalization success of North American woody species in Europe. *Journal of Ecology*, **97**, 230–238.
- CBS (2003) *Biobase 2003. Register biodiversiteit*. CBS, Voorburg/Heerlen.
- Colautti, R.I. & MacIsaac, H.J. (2004) A neutral terminology to define 'invasive' species. *Diversity and Distributions*, **10**, 135–141.
- Colautti, R.I., Grigorovich, I.A. & MacIsaac, H.J. (2006) Propagule pressure: A null model for biological invasions. *Biological Invasions*, **8**, 1023–1037.
- Collins, S.L. & Glenn, S.M. (1990) A hierarchical analysis of species abundance patterns in grassland vegetation. *The American Naturalist*, **135**, 633–648.
- DAISIE (2006) *Heracleum mantegazzianum*. In: *DAISIE, European invasive alien species gateway*. Available at: [http://www.europe-aliens.org/pdf/Heracleum\\_mantegazzianum.pdf](http://www.europe-aliens.org/pdf/Heracleum_mantegazzianum.pdf) (accessed January 2010).
- Dawson, W., Burslem, D. & Hulme, P.E. (2009) Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. *Journal of Ecology*, **97**, 657–665.
- Desdevises, Y., Legendre, P., Azouzi, L. & Morand, S. (2003) Quantifying phylogenetically structured environmental variation. *Evolution*, **57**, 2647–2652.
- Diez, J.M., Dickie, I., Edwards, G., Hulme, P.E., Sullivan, J.J. & Duncan, R.P. (2010) Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, **13**, 803–809.
- Engelkes, T., Morriën, E., Verhoeven, K.J.F., Bezemer, T.M., Biere, A., Harvey, J.A., McIntyre, L.M., Tamis, W.L.M. & van der Putten, W.H. (2008) Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature*, **456**, 946–948.
- Foxcroft, L.C., Rouget, M., Richardson, D.M. & MacFadyen, S. (2004) Reconstructing fifty years of *Opuntia stricta* invasion in the Kruger National Park: environmental determinants

- and propagule pressure. *Diversity and Distributions*, **10**, 427–437.
- Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Gassó, N., Sol, D., Pino, J., Dana, E.D., Lloret, F., Sanz-Elorza, M., Sobrino, E. & Vilà, M. (2009) Exploring species attributes and site characteristics to assess plant invasions in Spain. *Diversity and Distributions*, **15**, 50–58.
- Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M. & Lawton, J.H. (2000) Abundance-occupancy relationships. *Journal of Applied Ecology*, **37**, 39–59.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.
- Grime, J.P. (2002) *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley & Sons, Ltd., Chichester.
- van Grunsven, R.H.A., van der Putten, W.H., Bezemer, T.M., Tamis, W.L.M., Berendse, F. & Veenendaal, E.M. (2007) Reduced plant-soil feedback of plant species expanding their range as compared to natives. *Journal of Ecology*, **95**, 1050–1057.
- van Grunsven, R.H.A., van der Putten, W.H., Bezemer, T.M., Berendse, F. & Veenendaal, E.M. (2010) Plant-soil interactions in the expansion and native range of a poleward shifting plant species. *Global Change Biology*, **16**, 380–385.
- Hamilton, M.A., Murray, B.R., Cadotte, M.W., Hose, G.C., Baker, A.C., Harris, C.J. & Licari, D. (2005) Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters*, **8**, 1066–1074.
- Hanspach, J., Kühn, I., Pyšek, P., Boos, E. & Klotz, S. (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 241–250.
- Hennekens, S.M. & Schaminée, J.H.J. (2001) TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science*, **12**, 589–591.
- Herron, P.M., Martine, C.T., Latimer, A.M. & Leicht-Young, S.A. (2007) Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England. *Diversity and Distributions*, **13**, 633–644.
- Hill, M.O., Preston, C.D. & Roy, D.B. (1999) *Plantatt: attributes of British and Irish plants*. DETR/C.E.H., Cambridgeshire.
- Holt, A.R., Gaston, K.J. & He, F.L. (2002) Occupancy-abundance relationships and spatial distribution: a review. *Basic and Applied Ecology*, **3**, 1–13.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.
- Keller, R.P., Lodge, D.M. & Finnoff, D.C. (2007) Risk assessment for invasive species produces net bioeconomic benefits. *Proceedings of the National Academy of Sciences USA*, **104**, 203–207.
- van Kleunen, M., Weber, E. & Fischer, M. (2009) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235–245.
- Klimešová, J. & Klimeš, L. (2006) Clo-Pla3 – database of clonal growth of plants from Central Europe. Available at: <http://clopla.butbn.cas.cz/> (accessed November 2008).
- Klingenstein, F. (2007) NOBANIS – Invasive alien species fact sheet – *heracleum mantegazzianum*. In: *Online database of the North European and Baltic network on invasive alien species – NOBANIS*. Available at: <http://www.nobanis.org>.
- Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67–70.
- Klotz, S., Kühn, I. & Durka, W. (2002) *BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland*. Bundesamt für Naturschutz, Bonn.
- Kolb, A., Barsch, F. & Diekmann, M. (2006) Determinants of local abundance and range size in forest vascular plants. *Global Ecology and Biogeography*, **15**, 237–247.
- Kot, M., Lewis, M.A. & vandenDriessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77**, 2027–2042.
- Küster, E.C., Kühn, I., Bruelheide, H. & Klotz, S. (2008) Trait interactions help explain plant invasion success in the German flora. *Journal of Ecology*, **96**, 860–868.
- Lankau, R.A., Nuzzo, V., Spyreas, G. & Davis, A.S. (2009) Evolutionary limits ameliorate the negative impact of an invasive plant. *Proceedings of the National Academy of Sciences USA*, **106**, 15362–15367.
- Levine, J.M., Pachepsky, E., Kendall, B.E., Yelenik, S.G. & Hille Ris Lambers, J. (2006) Plant-soil feedbacks and invasive spread. *Ecology Letters*, **9**, 1005–1014.
- Lloret, F., Médail, F., Brundu, G. & Hulme, P.E. (2004) Local and regional abundance of exotic plant species on Mediterranean islands: are species traits important? *Global Ecology and Biogeography*, **13**, 37–45.
- Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.
- Lockwood, J.L., Cassey, P. & Blackburn, T.M. (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions*, **15**, 904–910.
- Milbau, A. & Stout, J.C. (2008) Factors associated with alien plants transitioning from casual, to naturalized, to invasive. *Conservation Biology*, **22**, 308–317.
- Price, P.W., Bouton, C.E., Gross, P., McPherson, B.A., Thompson, J.N. & Weis, A.E. (1980) Interactions among 3 trophic levels - Influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11**, 41–65.
- Pyšek, P. (1998) Is there a taxonomic pattern to plant invasions? *Oikos*, **82**, 282–294.

- Pyšek, P. & Richardson, D.M. (2007) Traits associated with invasiveness in alien plants: where do we stand? *Biological Invasions* (ed. by W. Nentwig), pp. 97–126, Springer-Verlag, Berlin & Heidelberg.
- Pyšek, P. & Richardson, D.M. (2010) Invasive species, environmental change and management, and ecosystem health. *Annual Review of Environment and Resources*, **35**, 25–55.
- Pyšek, P., Sadlo, J., Mandak, B. & Jarošík, V. (2003) Czech alien flora and the historical pattern of its formation: what came first to Central Europe? *Oecologia*, **135**, 122–130.
- Pyšek, P., Richardson, D.M. & Williamson, M. (2004) Predicting and explaining plant invasions through analysis of source area floras: some critical considerations. *Diversity and Distributions*, **10**, 179–187.
- Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I., Tichý, L., Danihelka, J., Chrtek, J.J. & Sádlo, J. (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions*, **15**, 891–903.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.
- Ricklefs, R.E. (1987) Community diversity - relative roles of local and regional processes. *Science*, **235**, 167–171.
- Schaminée, J.H.J., Hennekens, S.M. & Ozinga, W.A. (2007) Use of the ecological information system SynBioSys for the analysis of large datasets. *Journal of Vegetation Science*, **18**, 463–470.
- Schaminée, J.H.J., Hennekens, S.M., Chytrý, M. & Rodwell, J.S. (2009) Vegetation-plot data and databases in Europe: an overview. *Preslia*, **81**, 173–185.
- Soltis, P.S. & Soltis, D.E. (2000) The role of genetic and genomic attributes in the success of polyploids. *Proceedings of the National Academy of Sciences USA*, **97**, 7051–7057.
- Soons, M.B. & Ozinga, W.A. (2005) How important is long-distance seed dispersal for the regional survival of plant species? *Diversity and Distributions*, **11**, 165–172.
- Tamis, W.L.M. (2005) Coping with recording bias. *Gorteria*, **6**(Suppl.), 17–52.
- Tamis, W.L.M., van der Meijden, R., Runhaar, J., Bekker, R.M., Ozinga, W.A., Odé, B. & Hoste, I. (2004) Standaardlijst van de Nederlandse flora 2003. *Gorteria*, **30**, 101–195.
- Theoharides, K.A. & Dukes, J.S. (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256–273.
- Thompson, K., Hodgson, J.G. & Gaston, K.J. (1998) Abundance-range size relationships in the herbaceous flora of central England. *Journal of Ecology*, **86**, 439–448.
- Thuiller, W., Gallien, L., Boulangéat, I., de Bello, F., Münkemüller, T., Roquet, C. & Lavergne, S. (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions*, **16**, 461–475.
- Tilman, D. (1982) *Resource competition and community structure*. Princeton University Press, New Jersey.
- Van der Meijden, R. (2005) *Heukels' Flora van Nederland*, 23rd edn. Wolters-Noordhoff, Groningen.
- Van der Meijden, R., Groen, C.L.G., Vermeulen, J.J., Peterbroers, T., Van 't Zelfde, M. & Witte, J.P.M. (1996) De landelijke floradatabank FLORBASE-1; eindrapport. In: RHHB/CML/UL-WHH.
- Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E. & DAISIE partners (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment *Frontiers in Ecology and the Environment*, **8**, 135–144.
- Webb, C.O. & Donoghue, M.J. (2007) Phylomatic: a database for applied phylogenetics. Available at: <http://www.phylodiversity.net/phyloomatic> (accessed July 2009).
- Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661–1666.
- Wilson, J.R.U., Richardson, D.M., Rouget, M., Procheş, S., Amis, M.A., Henderson, L. & Thuiller, W. (2007) Residence time and potential range: crucial considerations in modelling plant invasions. *Diversity and Distributions*, **13**, 11–22.

## SUPPORTING INFORMATION

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

**Table S1** List of 111 exotic plant species in The Netherlands used in our study.

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

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

## BIOSKETCH

This work is part of **Tanja Speek's** PhD thesis under the supervision of **Bert Lotz** and **Wim van der Putten**. Tanja Speek is interested in the possibility to predict which exotic plant species may become invasive in The Netherlands.

Author contributions: All authors contributed to developing the ideas. T.A.A.S., W.A.O. and W.L.M.T. collected the data, T.A.A.S. analyzed all data, all authors contributed to the writing of the manuscript which was led by T.A.A.S. and W.v.d.P.

Editor: Ingolf Kühn