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Invasive or not - what makes the difference?

A source area approach

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Introduction

The search for determinants of invasions is one of the most urgent agendas in invasion ecology. The issue is complex and there is no single factor driving the invasion process. Therefore, the scientific community has suggested a variety of alternative hypotheses and approaches to this topic so far and tried to find frameworks to arrange the available information and data (Catford, et al., 2009; van Kleunen, et al., 2010a; Gurevitch, et al., 2011; Lockwood, et al., 2005). Whereas some studies concentrate on propagule pressure as a determinant of invasiveness (Lockwood, et al., 2005), others focus on abiotic and biotic factors of the recipient areas and biological communities, or on specific traits of the invading organism (Catford, et al., 2009). However, it has increasingly become clear that multiple factors, together with their interactions, may contribute to invasion success and failure (Dawson, et al., 2009; Krivánek, et al., 2006; Pysek & Richardson, 2007).

There is lot of confusion concerning the terminology in invasion ecology. Here, I follow the standard terminology as proposed by Richardson, et al. (2000). This approach splits the invasion process into several stages and the terminology is closely linked to these stages. In this work, I consider invasive species as that subset of naturalized species that produce offspring in large numbers and at considerable distance from parental plants and which are thus able to invade an extended area (Richardson, et al., 2000; Blackburn, et al., 2011). Although I follow Richardson, et al. (2000) I do not distinguish between invasive species (sensu Richardson, et al. 2000) - see the definition just given - and invasive species according to IUCN (Invasive Alien Species, IAS) - which only refers to species that have a known (negative) impact on native ecosystems (Villà, et al., 2011). While these two species pools overlap to a considerable degree they are not necessarily identical. As a synonym I also use the term environmental weeds which hence comprises all species that invade, harm or impact native ecosystems (Randall, 2012).

Species traits which facilitate successful invasions have been a central topic in invasion ecology and many studies have already addressed this issue, with mixed results (Pysek & Richardson, 2007; van Kleunen, et al., 2010 b; Küster, et al., 2008). This search for traits promoting invasion success is challenging due to the complexity of the invasion processes and the fact that invasiveness is not controlled by one single trait. A common way to detect traits that make species invasive is to compare species groups in the introduced range, e.g.

natives against aliens or invasive aliens against non-invasive aliens. Alternatively, the source area approach focuses on the species pool native to a particular area and compares those species which are invasive elsewhere with those that are not (van Kleunen, et al., 2010a). This source area approach allows to compare the invasion success of a wide range of species native to the study region where the species are integrated and adapted to their respective ecosystem, biotic and abiotic factors. The target area approach however compares species which originate from different source areas or which differ in their residential time in the target area (i.e. when comparing native species with non-natives). This makes a difference as the compared species in the target area hence differ in various important respects like their precedent adaptation to enemies and competitors which are, or are not, shared among native and recipient regions or the time available to evolve the respective traits in the new range. These and other aspects have already been the subject of several hypotheses, for example of the evolution of increased competitive ability (EICA) hypothesis (Blossey & Noetzold, 1995), the enemy release hypothesis (Keane & Crawley, 2002), or the novel weapon hypothesis (Callaway & Ridenour, 2004). When using the source area approach, such differences are minimized at least.

When using a source area approach it is essential that comparisons are restricted to species which are native to the source area in a strict sense (Pysek, et al., 2004), i.e. to those that have evolved in the source area or at least thrived there for a long time. This is obviously not true for neophytes which were introduced to the source area by humans or with human assistance during the last five centuries (post-1500 AD) and thus had a lower chance to establish and spread, to occupy different habitat types or reach their local carrying capacities, and to express their phenotypic plasticity (Pysek, et al., 2004).

The situation is somewhat different for archeophytes which arrived in the source area between the Neolithic revolution and 1500 AD. These species are usually well adapted to the abiotic and biotic conditions in the source area and had more time to fill their ecological niches completely (which increases the chance of getting in touch with humans and hence to be introduced elsewhere). Nevertheless, they are not native to the source area but where introduced by humans or with human help.

In this diploma thesis I have used the source area approach to compare two groups of non woody species native to the Austrian flora: those which have become environmental weeds elsewhere, and those which have not. The comparison is focused on a couple of traits and

attributes including several that have been supposed to foster a species' invasiveness in other work (Pysek, et al., 2004; Prinzing, et al., 2002). Neophytes as well as archeophytes were excluded from the pool of species to be compared. I also refrained from separating species into different biogeographical groups (as suggested by (Pysek, et al., 2004), referring to (Prinzing, et al., 2002). Instead, I collected data that are indicative for the chance of unintentional transportation and considered them explicitly in my comparisons.

Material and Methods

All analyses in this diploma thesis are based on a search for trait data information in several different databases (Kleyer, et al., 2008; Klotz, et al., 2002; Klimesová & Klimes , 2013; Fitter & Peat, 1994). The compiled data set includes trait information for 3,659 vascular plants of the Central and Western European flora. To keep the data source consistent I finally decided to use trait information from (Klotz, et al., 2002), (hereafter referred to as BiolFlor database), only in this work.

Species pool

My analysis focused on the native, non-woody terrestrial vascular plant flora of Austria. From the database I hence excluded (1) all species which are not part of the Austrian flora (according to Fischer et al. 2008); (2) all trees and shrubs; and (3) all neo– and archeophytes (according to BiolFlor database and Fischer et al. (2008)); (4) all hydrophytes, i.e. species growing in more or less permanently inundated habitats. In addition, I eliminated several highly apomictic genera where species definition and identification are contentious or very difficult (e.g. *Alchemilla* spp., *Taraxacum spp*., *Hieracium spp*.) as well as ferns, which have a vastly different life cycle. The final number of species for analysis was 1402 species. A complete overview of the stepwise species selection procedure is given in Table 1.

Table 1: Stepwise reduction of the species pool. The number of species was reduced from 3.659 to 1.402.

Step	Removed species	Reason for exclusion	Number of species left
Remove all non-indigenous species from the species pool	All species with a floristic status different from "indigenous" were removed	When using the source area approach (sensu Pysek et al. 2004), only indigenous species are relevant	2.743
Exclude the following apomictic and / or taxonomically critical genera	*Alchemilla, Festuca, Hieracium, Oenothera, Orobanche, Taraxacum*	These genera are apomictic and species determination is ambiguous.	2.491
Remove all species with not suitable life forms	Chamaephyte, Hydrophyte, Pseudophanaerophyte, Mesophanaerophyte, Macrophanaerophyte, Nanophanaerophte	The species pool should only include the life forms Geophyte, Hemicryptophyte, Hemiphanaerophyte and Therophyte	1.723
Eliminate all species which are not indigenous to Austria. (The source of the database is based on the flora of Germany. Thus the species which are indigenous to Germany but not to Austria had to eliminated)	Elimination of all species which are mentioned in the raw database, but not mentioned in Fischer, et al., 2008 (common field flora for Austria)	No distribution area in Austria and therefore not indigenous	1.463
Eliminate all genera which are ferns	Genera: *Asplenium, Botrychium, Woodsia, Anthyrium, Lastrea, Dryopteris, Ceterach, Pteridium, Ophioglossum, Phegopteris, Blechnum, Polystichum, Phyllitis Thelypteris, Equisetum, Cystopteris, Gymnocarpium, Cryptogramma*	Removal of all ferns in the database to concentrate on spermatophytes	1.409
Last screening of the database	The genus *Willemetia* and *Chondrilla* were removed. *Ceratocephala falcata* *Saxifraga hirculus* *Digitalis purpurea* *Draba muralis*	 Extinct in Austria Extinct in Austria Neophyte or Archeophyte Neophyte in Austria	1.402

Species traits

In the course of this diploma thesis I collected different traits of which fifteen were integrated in the statistical analyses (see Table 2). For fourteen traits a statistical evaluation was done. The traits were grouped into five different trait groups: (1) life history, (2) reproduction, (3) competitiveness, (4) site and (5) human use. Table 2 gives an overview about which trait was assigned to which trait group.

Not all collected traits were available in the BiolFlor database, and trait information included in BiolFlor was not complete. For these reasons several additional sources were used to supplement missing data for the statistical evaluation (see Table 2 for an overview on data sources). However, the vast majority of trait information was derived from only two resources: (1) the BiolFlor database and (2) Fischer, et al. (2008). Furthermore we used mostly only one source per trait or a "main source" and an additional resource to complement the data.

When compiling data from different sources some simplifications were necessary to make information consistent. With respect to breeding systems, it is well-known that most plants are neither strictly allogamous nor strictly autogamous. Nevertheless, I grouped them into three categories "allogamous", "autogamous" and "mixed mating", where the first two categories indicate preferences for one or the other mating system (according to BiolFlor).

Furthermore, if species were split into subspecies or were part of a species aggregate I generalized the available information on the higher taxonomical level. *Angelica sylvestris*, for example, has two different subspecies native in Austria. Subspecies "*sylvestris*" is distributed from the colline to the montane belt whereas subspecies "*montana*" has its distribution range from the montane to the subalpine belt. As all subspecies of a plant species were merged into the parental species, the lower altitudinal limit for *Angelica sylvestris* was given as "colline" and the upper limit as "subalpine". The respective species were accordingly marked in the data base.

In the following an overview on data sampling and data sources for each trait is given.

Family: assignment of species to families mostly follows Fischer et al. (2008). Additional information was extracted from The Plant List, (2010). The information was used as a kind of phylogenetic correction to consider degrees of relationship among species during statistical analyses.

Floristic status: This trait helped to identify the species which are native to the source area. The information was taken from the BiolFlor database. All indigenous species were assigned to the database, and afterwards harmonized with the entries in Fischer et al. (2008) as the native species in the BiolFlor database are not necessarily indigenous to Austria (see Table 1).

Life form: The whole information was taken from the BiolFlor database. All species with life forms "therophyte", "geophyte", hemicryptophyte" and "hemiphanaerophyte" where assigned to the database.

Life span: This trait was used as indicator for generation time. All information was taken from the BiolFlor database. All categories (annual, biennial, perennial-pollakanthic and perennial-hapaxanthic) were added to the species pool.

Breeding system: This trait was used as an indicator for uniparental reproduction. It indicates the preference for one or the other reproductive strategy within generative reproduction. Only the categories "allogamous", "autogamous" and "mixed mating" (see above) were used. The data was extracted from the BiolFlor database.

Pollen vector: Indicator for pollinator dependence. The information was extracted from the BiolFlor database. The trait included the categories wind, insects, selfing, pseudocleistogamy, cleistogamy and geitonogamy. If there was more than one pollen vector specified for the respective species, the vector with the highest abundance mentioned in the BiolFlor database was taken (see Abundance of the pollen vector). If there was more than one pollen vector but no information about the abundance (unknown) given, the information was taken from Jäger & Werner, (2005)

Abundance of pollen vector: This trait is an indicator how prevalent the pollen vector for the respective species is. It was used to get additional information to assign the species to the appropriate classes of the variables "breeding system" and "pollen vector". All data was extracted from BiolFlor database. The classes for the trait were "always", "the rule", "often", "rare" and "unknown".

Type of reproduction: This trait indicates if the respective species favour generative or vegetative reproduction strategies. All data was extracted from the BiolFlor database. The classes for this trait were "by seed and vegetatively", "by seed and by spore", "mostly by seed, rarely vegetatively", "mostly vegetatively, rarely by seed", and "vegetatively".

Strategy type: Indicator of competitive strength. All data was extracted from BiolFlor database. The classification follows the system of Grime strategy types (Grime, 1979). The classes were “competitors”, “competitors/ruderals”, “competitors/stress-tolerators”, “competitors/stress-tolerators/ruderals”, “ruderals”, “stress-tolerators”, and “stress-tolerators/ruderals”.

N-value: Indicator of growth rate according to Ellenberg N-values. Most data was adopted from BiolFlor database. For additional information we used different sources: (1) FloraWeb database and (2) Jäger & Werner (2005), which is a critical field flora for Germany.

Presence in agricultural/ruderal habitat: Indicator of the likelihood of being transported unintentionally. All data was extracted from Fischer, et al. (2008). In this source the term “agricultural/ruderal habitat” comprises almost all ruderal and agricultural types. A list of habitat types included is available in the annex.

Presence around aquatic habitats: This trait was used as indicator of unintentional transportation. All information was extracted from Fischer, et al. (2008). A list of all sites which were considered near to aquatic habitats is available in the annex.

Ornamental use in Austria: Indicator of being transported intentionally. All data was extracted from the PPP-Index (Eugen Ulmer KG, 2006) where I searched for the sale of seeds and/or individuals for each species. Each species name was entered in the search mask, and the search for companies, which are registered in the database and sell seeds or individuals of the respective species was started. Then the list of companies and their addresses were searched for companies in Austrian communities by the four digit postcode of Austrian communities (all other countries had more than four digits in their postcode). If there was at least one company detected, the species was tagged as ornamentally used in the database.

Frequency: Frequency of species within Austria. This trait is also an indicator for unintentional transportation. Frequency was classified in five categories: (1) very rare, (2) rare, (3) dispersed, (4) frequent and (5) very frequent. All information was extracted from Fischer, et al. (2008).

Maximum plant height: Indicator of competitive strength. Almost all data was extracted from Fischer, et al. (2008). As there was only information about the length of creeping plants available, we estimated the height of these plants on basis of the “Illustrierte Flora von Mitteleuropa” (Hegi, 1908-1932).

Altitude lower margin: All data was extracted from Fischer, et al. (2008). Following the classification scheme in the source, the altitudinal levels were classified in “colline”, “submontane”, “lower montane”, “montane”, “upper montane”, “subalpine”, “lower alpine”, “alpine”, “upper alpine” and ”nival”.

Altitude upper margin: All data was extracted from Fischer, et al. (2008). Levels were the same as for the preceding trait.

Presence below the montane belt: Indicator of the likelihood of being transported unintentionally. The data was extracted from Fischer, et al. (2008). All species with occurrences in the colline and/or submontane belt were classified as species with a presence below the montane belt.

Number of altitudinal belts: Indicator of climatic tolerance. I did a simple count of the number of altitudinal belts which were covered by the respective species, following the above mentioned classification scheme and the information in Fischer et al. (2008).

Environmental weed: This trait is used to split the native species pool in two different groups: (1) environmental weed elsewhere (2) not an environmental weed elsewhere. The data were collected from (Randall, 2012) and (Weber, unpublished data)

Table 2: Overview concerning the traits, the trait group to which the trait has been assigned and the main data sources.

Trait	Used for statistic analyses	Trait group	Source
Family	yes	None	(Fischer, et al., 2008) (mainly), (The Plant List, 2010)
Floristic status	no	None	(Klotz, et al., 2002)
Life span	yes	Life history	(Klotz, et al., 2002)
Life form	yes	Life history	(Klotz, et al., 2002)
Breeding system	yes	Reproduction	(Klotz, et al., 2002) (mainly), (Jäger & Werner, 2005)
Pollen vector	yes	Reproduction	(Klotz, et al., 2002)
Abundance of pollen vector	no	None	(Klotz, et al., 2002)
Type of reproduction	yes	Reproduction	(Klotz, et al., 2002)
Strategy type	yes	Competitiveness	(Klotz, et al., 2002)
N-value	yes	Competitiveness	(Klotz, et al., 2002), (Bundesamt für Naturschutz, 2000), (Jäger & Werner, 2005)
Presence in agricultural/ruderal habitats	yes	Site	(Fischer, et al., 2008)
Presence in or around aquatic habitats	yes	Site	(Fischer, et al., 2008)
Ornamental use	yes	Human use	(Eugen Ulmer KG, 2006)
Frequency	yes	Competitiveness	(Fischer, et al., 2008)
Maximum plant height	yes	Competitiveness	(Fischer, et al., 2008) (mainly), own estimation, basis (Hegi, 1908-1932)
Altitude lower margin	no	None	(Fischer, et al., 2008)
Altitude upper margin	no	None	(Fischer, et al., 2008)
Presence below the montane belt	yes	Site	(Fischer, et al., 2008)
Number of altitudinal belts	yes	Site	(Fischer, et al., 2008)
Environmental weed	yes	None	(Randall, 2012), (Weber, unpublished data)

Creating the categories of the species pools

The source area approach requires a division of the native species pool into those that are an environmental weed elsewhere and those that are not. To identify the native plant species of the Austrian flora which are invasive anywhere in the world we used two sources of information. We started with Randall (2012) who gives an excellent worldwide overview about the distribution and status of non-native plants. Supplementarily, we used unpublished data from Ewald Weber who provided us generously with his latest dataset meant to be used in the second edition of his book “Invasive plant species of the world. A reference guide to environmental weeds”.

We screened the above mentioned sources for the 1,402 species in our database. All species which were mentioned in Randall (2012) as environmental weed were assigned to the invasive species pool. All species which were provided by Ewald Weber were also assigned to the "environmental weed pool". All other species represented the non-invasive species pool. Finally the "environmental weed pool" contained 305 species compared to 1,097 non-invasive species.

Statistical evaluation

The statistical analysis was done with the R Software (R Core Team, 2013) using the packages Matrix (Bates & Maechler, 2011) and lattice (Sarkar, 2008). Initially, frequency tables were created for each trait. For visual presentation of the frequency tables, we used the function "barplot" stratified by the weed-status. As we had binomial data (environmental weed yes/no) we used logistic regression techniques to analyze possible differences in trait values among the species groups. And as species are not independent data points but related to each other according to their phylogeny, we used Generalized linear mixed effects models, in the package "lme4" (Bates, et al., 2011) with random effects estimated separately for each family. Significance of the estimated fixed effects was evaluated on the basis of Wald z-values.

Furthermore we calculated Mc Fadden's pseudo-R^2-value as a measure of model goodness-of-fit and the AIC (Akaike Information Criterion) to compare the models among each other.

Results

The results are divided in three different parts. The first section comprises the results of the statistical model of each single trait. In the tables, the levels of each trait and the relevant statistical parameters (i.e. fixed effect, standard error, z-value and p-value) are given. For the p-value the significance level was fixed to 0.05. The standard output of lme4 defines the first (in alphabetical order) level of a categorical variable as the intercept term. Its significance (= difference from 0) indicates that the chance for a species belonging to this class to become invasive anywhere is larger (positive sign) or lower (negative sign) than random. As the non-

invasive group is nearly four times larger than the invasive group, the intercepts are nearly always significantly lower than 0. The coefficients of the other factor levels are meant to be added to the intercept, i.e. they indicate whether the invasiveness of species belonging to these levels is lower or higher than the invasiveness of the species from the 'intercept-class'.

The second part contains the AIC and pseudo R^2 values (Mc Fadden) for each trait and each trait group.

Finally the visualised results of the frequency tables are shown as barplots which have been produced using the function "barplot".

Generalized linear mixed model for the respective traits

With respect to life forms the models indicate that Austrian hemicryptophytes and therophytes do not differ from geophytes in their probability to become invasive anywhere in the world. By contrast, hemiphanaerophytes have a significantly lower chance to become an environmental weed than species of the other three life forms (see Table 3).

The results for the life span of the examined species showed that annual species have a significantly higher chance to become invasive than biennials and perennials. Hapaxantic perennials could not be evaluated separately due to low species numbers and consequent problems with model fitting (see Table 4).

The preferred breeding system does not affect invasion success. Allogamous, autogamous species and those with a mixed mating system have all similar probabilities of becoming invasive (see Table 5).

Similarly, dependence on particular pollen vectors does not appear to be a good predictor of invasiveness. The levels of this variable could either not be evaluated due to low species numbers (geitonogamy, pseudocleistogamy) or did not differ significantly in their probability to become invasive (cleistogamy, insects, selfing and wind) (see Table 6).

A preference for either generative of clonal propagation does not seem to alter the chance of an Austrian plant species to become invasive elsewhere in the world. Mostly vegetatively reproducing species and species which reproduce by seed did not differ in comparison to species which reproduce mostly by seed. Interestingly, species that showed no preference for seed or vegetative reproduction had significantly lower chance to become invasive than

all other species. However, species that reproduce exclusively vegetatively were not evaluated due to low species numbers (Table 7).

With respect to strategy type, our results indicate that invasiveness declines from competitors to ruderals and, finally, stress tolerators. Remarkably, stress-ruderal strategists seem to become environmental weeds rather frequently, too, although stress tolerators are usually not meant to be typical invaders.

Maximum plant height is one of the most tested variables for invasiveness and a lot of works showed varied results. The statistical evaluation in this work is significantly increasing with maximum plant height among the life forms included. (see Table 9).

N-values according to Ellenberg showed a strong and significant correlation between the chance of becoming invasive and higher N-value levels (except for N-value 2) (see Table 10). Remarkable in that context is the relatively clear and constant increase of the estimate values (with the already mentioned exception). That means that the higher the N-value, the higher the chance of becoming invasive. This reflects the common doctrine of the scientific community and is remarkable in this clarity.

The trait frequency showed that very frequent native species of the Austrian flora had a chance of becoming invasive that significantly exceeds 50%. For less frequent species, this chance was significantly lower with little further differences among frequency classes (see Table 11).

In partial agreement with the results for strategy types, species from agricultural or ruderal habitats are more frequently becoming environmental weeds than species that do not occur in such habitats (see Table 12). Similar results were found with respect to species from riverines, floodplains and other sites around aquatic habitats (see Table 13). Species which occur below the montane belt in Austria (see Table 14) and species which cover a large number of altitudinal belts (see Table 15) have a significantly better chance to become invasive elsewhere than species from higher altitudes or those with narrower altitudinal niches. Finally, ornamental use clearly fosters species invasions (see Table 16).

Table 3: Results of a generalized linear mixed effects model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its life form. Given are fixed effects (Estimate), their standard errors (Std error), and the associated z- and p-values. Bold font indicates p-values <0.05.

trait "life form"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept (Geophyte)	-1.36	0.29	-4.70	**<0.001**
Hemicryptophyte	-0.09	0.30	-0.29	0.775
Hemiphanerophyte	-1.53	0.69	-2,23	**0.026**
Therophyte	0.16	0.39	0.41	0.685

Table 4: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elswhere, to its life span. Given are fixed effects (Estimate), their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values < 0.05. Class pluriennial hapaxantic could not be evaluated due to low number of species.

trait "life span"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept (annual)	-0.58	0.20	-2.82	**0.005**
biennial	-0.91	0.40	-2.28	**0.023**
pluriennial hapaxantic	n.e.	n.e.	n.e.	n.e.
pluriennial pollakantic	-1.13	0.20	-5.58	**<0.001**

Table 5: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its breeding system. Given are fixed effects (Estimate), their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05.

trait "breeding system"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept (allogamous)	-1.53	0.14	-10.84	**<0.001**
autogamous	0.23	0.22	1.02	0.309
mixed mating	-0.16	0.53	-0.31	0.760

Table 6: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its pollen vector. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05. The class geitonogamy and pseudocleistogamy could not be evaluated due to low numbers of species.

trait "pollen vector"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept (cleistogamy)	-1.31	0.78	-1.69	0.092
geitonogamy	n.e.	n.e.	n.e.	n.e.
insects	-0.37	0.78	-0.47	0.641
pseudocleistogamy	n.e	n.e.	n.e.	n.e.
selfing	0.05	0.79	0.06	0.949
wind	0.19	0.77	0.25	0.801

Table 7: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its reproduction type. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05. The class for vegetative reproduction “veg” could not be evaluated due to low number of species.

trait "reproduction"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept (most seed rare veg)	-0.90	0.32	-2.78	**0.005**
most_veg_rare_seed	-0.26	0.64	-0.40	0.686
seed_spore	-0.63	0.33	-1.88	0.060
seed_veg	-0.72	0.32	-2.25	**0.025**
veg	n.e.	n.e.	n.e.	n.e.

Table 8: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its strategy type. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05.

trait "strategy"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept (unknown)	-3.62	1.29	-2.81	**0.005**
competitor	2.87	1.29	2.23	**0.026**
competitor-ruderal	3.50	1.38	2.54	**0.011**
competitor-stress	2.00	1.29	1.55	0.121
competitor-stress -ruderal	1.73	1.29	1.34	0.181
ruderal	2.28	1.35	1.69	0.091
stress	0.12	1.46	0.08	0.933
stress-ruderal	2.97	1.32	2.26	**0.024**

Table 9: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its maximum plant height. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05.

trait "maximum plant height"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept	-2.04	0.22	-9.17	**<0.001**
maximum plant height	0.01	0.00	3.94	**<0.001**

Table 10: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its N-value according to Ellenberg. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05.

trait "N-value"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept (unknown)	-3.22	0.52	-6.25	**<0.001**
N-value 1	1.21	0.60	2.03	**0.043**
N-value 2	0.49	0.54	0.91	0.363
N-value 3	1.27	0.54	2.35	**0.019**
N-value 4	1.81	0.53	3.45	**<0.001**
N-value 5	2.14	0.56	3.86	**<0.001**
N-value 6	2.24	0.56	3.98	**<0.001**
N-value 7	2.43	0.56	4.36	**<0.001**
N-value 8	2.82	0.59	4.80	**<0.001**
N-value 9	2.62	0.73	3.61	**<0.001**
N-value x	3.11	0.57	5.45	**<0.001**

Table 11: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its distribution patterns (frequency). Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05. The class for unknown distribution frequency could not be evaluated due to low number of species.

trait "frequency"	**Estimate**	**Std Error**	**z-value**	**p-value**
very frequent	0.77	0,.25	3.02	**0.002**
frequent	-2.06	0.27	-7.65	**<0.001**
dispersed	-2.86	0.29	-9.84	**<0.001**
rare	-2.79	0.36	-7.86	**<0.001**
very rare	-2.33	0.33	-6.97	**<0.001**
unknown	n.e.	n.e.	n.e.	n.e.

Table 12: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its occurrence in agricultural or ruderal habitats. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05.

Trait "agricultural/ruderal habitat"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept	-1.98	0.14	-14.08	**<0.001**
occurrence in agricutural and/or ruderal habitat	1.55	0.20	7.84	**<0.001**

Table 13: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its occurrence around aquatic habitats. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05.

Trait "aquatic habitat"	**Estimate**	**Std Error**	**z-value**	**p-value**
Intercept	-1.68	0.15	-11.15	**<0.001**
occurrence around aquatic habitat	0.75	0.17	4.31	**<0.001**

Table 14: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its occurrence below the montane belt. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05.

trait "below the montane belt"	Estimate	Std Error	z-value	p-value
Intercept	-4.03	0.37	-10.74	**<0.001**
occurrence below the montane belt	2.96	0.35	8.42	**<0.001**

Table 15: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its number of altitudinal belts. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05.

trait "number of altitudinal" belts"	Estimate	Std Error	z-value	p-value
Intercept	-2.18	0.20	-10.76	**<0.001**
number of altitudinal belts	0.20	0.04	5.26	**<0.001**

Table 16: Results of a generalized linear mixed effect model relating the probability of a species of the Austrian flora to become invasive elsewhere, to its ornamental use. Given are fixed effects (Estimates) their standard errors (Std error) and the associated z- and p-values. Bold font indicates p-values <0.05.

trait "ornamental use"	Estimate	Std Error	z-value	p-value
Intercept	-1.96	0.19	-10.30	**<0.001**
ornamental use	0.94	0.17	5.50	**<0.001**

AIC and Mc Fadden´s pseudo-R^2 value

To get an idea how much of the variance was explained by each trait, respectively trait group, McFaddens Pseudo R^2 value was calculated. These R^2 values varied between 0.03 and 0.12 for the single traits and between 0.04 and 0.2 for the trait groups. Hence, explanatory power was generally low to moderate. Most variance was explained by the traits "occurrence below the montane belt" (0.12) and "occurrence in agricultural or ruderal habitats" (0.11). The variables of the reproduction group had on average the lowest explanatory power followed by the human use group, which is remarkable as ornamental use has been shown to be a promising variable to explain biological invasions and invasiveness.

The trait group competitiveness (0.20) and site (0.19) explained variance best, whereas the trait groups human use (0.04), reproduction (0.05) and also life history (0.07) contributed least to the explanation of invasiveness.

Table 17: Pseudo R2 values according to Mc Fadden and Akaike Information criterion (AIC) of the different single-trait and trait-group models to explain invasiveness of the Austrian flora in other parts of the world. All models are generalized linear mixed effects models.

trait group	trait	AIC	pseudo R2 value
life history		1,369.700	0.0717
	life form	1,435.406	0.0348
	life span	1,393.567	0.0635
reproduction group		1,417.822	0.0455
	reproduction	1,430.030	0.0468
	breeding system	1,430.057	0.0317
	pollen vector	1,461.298	0.0349
competitiveness		1,223.721	0.1951
	strategy typ	1,415.324	0.0898
	N-value	1,452.516	0.1095
	maximum plant height	1,376.094	0.0632
	frequency	1,362.986	0.1023
site		1,199.759	0.1855
	occurence in agricutural or ruderal habitats	1,298.422	0.1164
	occurrence around aquatic habitat	1,412.607	0.0381
	occurrence under the montane belt	1,288.731	0.1231
	number of altitudinal belts	1,407.749	0.0415
human use group		1,406.077	0.0399
	ornamental use	1,406.077	0.0399

Visualisation of the frequency tables

Figures 1 to 5 show the visualisation of the frequency table which were calculated with R. The graphs demonstrate the barplots of the two species groups, i.e. being (1) not an environmental weed elsewhere in contrast to (2) being an environmental weed elsewhere.

Trait group "competitiveness"

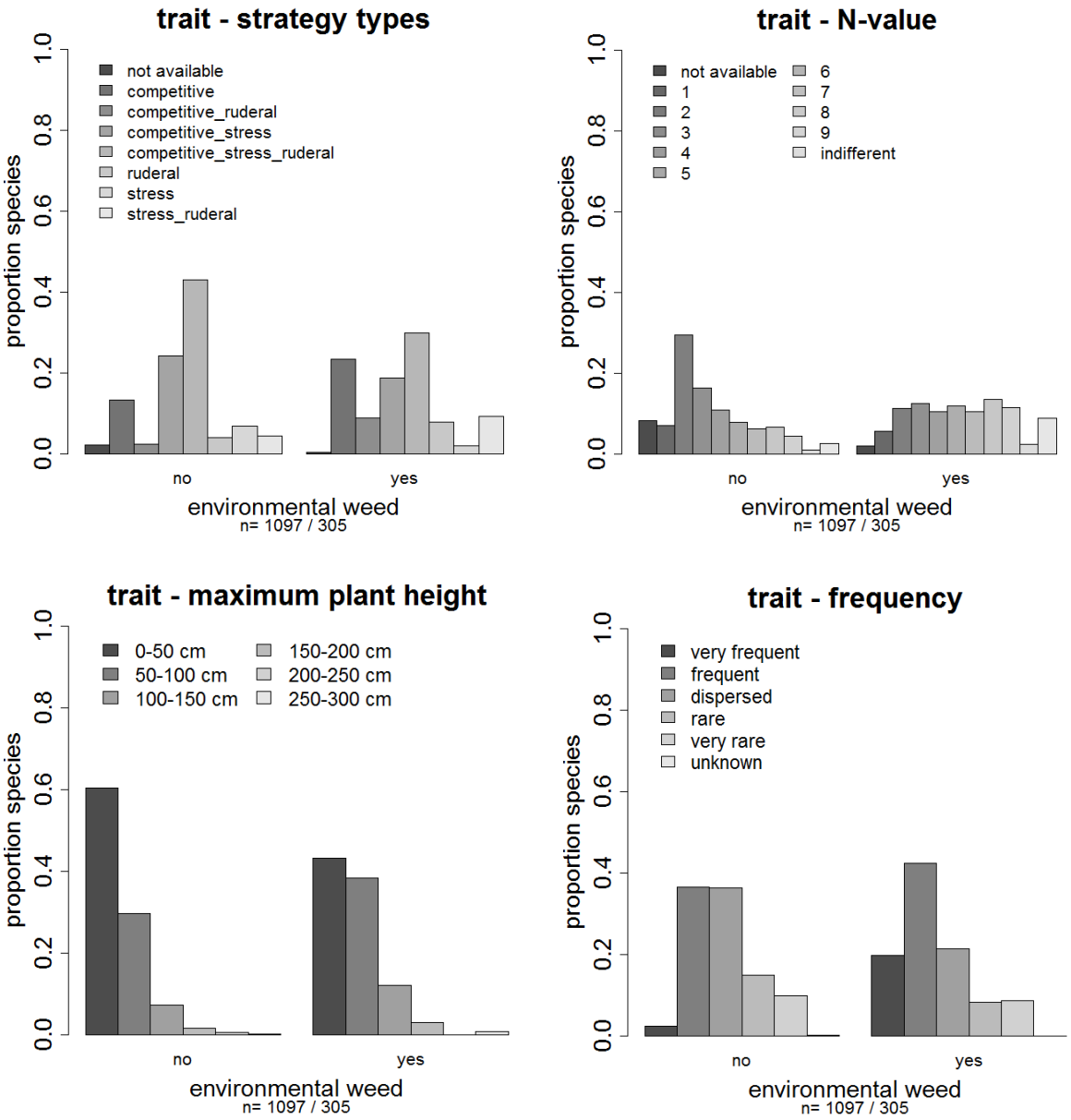

Figure 1: Proportion of species in the classes of the traits belonging to the trait group "competitiveness". The barplot "strategy types" show that the competitive species, stress ruderal strategists and the ruderal strategy type are over represented in the environmental weed species pool. The N-value indicates a shift to higher N-values in the environmental weed pool. The maximum plant height shows also a shift to higher plant heights among the environmental weeds. As expected, the trait frequency shows that frequent and very frequent species are overrepresented in the environmental weed species pool.

Trait group "life history"

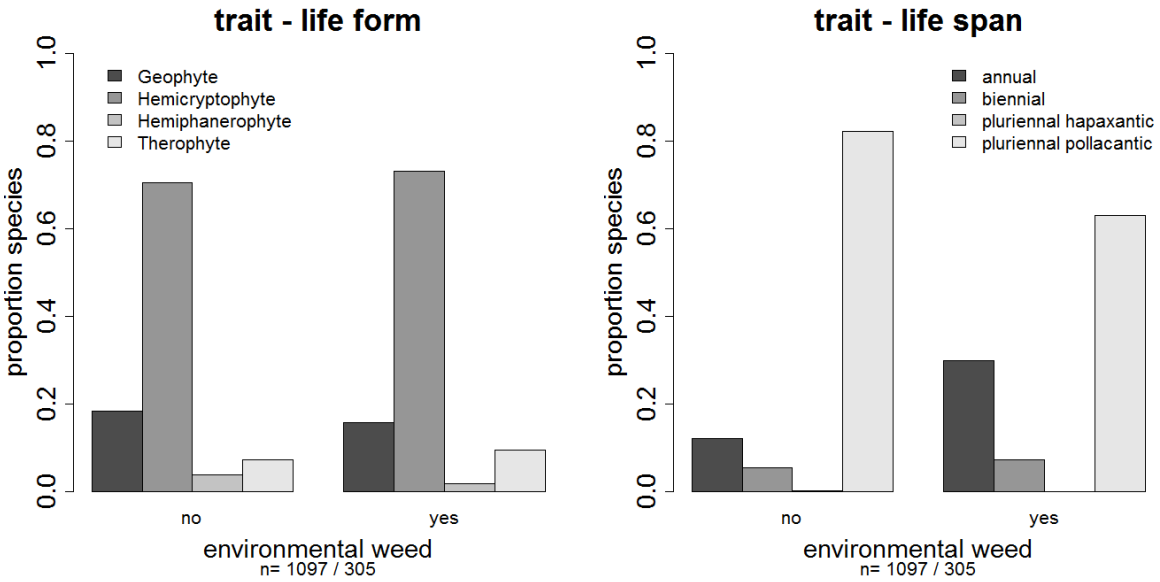

Figure 2: Proportion of species in the classes of the traits belonging to the trait group "life history". The trait life form shows no conspicuous differences between species being environmental weeds and those not being environmental weeds. The trait life span shows a shift within the variable "annual" at the expense of the variable pluriennial pollacantic. Whereas annual species represent about 12% within the non-environmental species pool, the percentage rises up to 28% in the environmental weed species pool. The variable perennial pollacantic however decrease from 82% in the non-environmental weed group to 62% in the environmental weed group.

Trait group "human use"

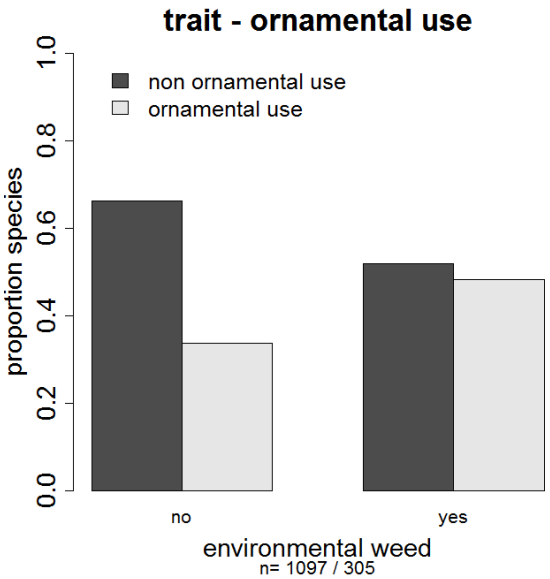

Figure 3: Proportion of species in the classes of the traits belonging to the trait group "human use. The graph shows a substantial change between the non-environmental weed pool (33% are used for ornamental purpose) and the environmental weed pool (48% are used as ornamentals).

Trait group "reproduction"

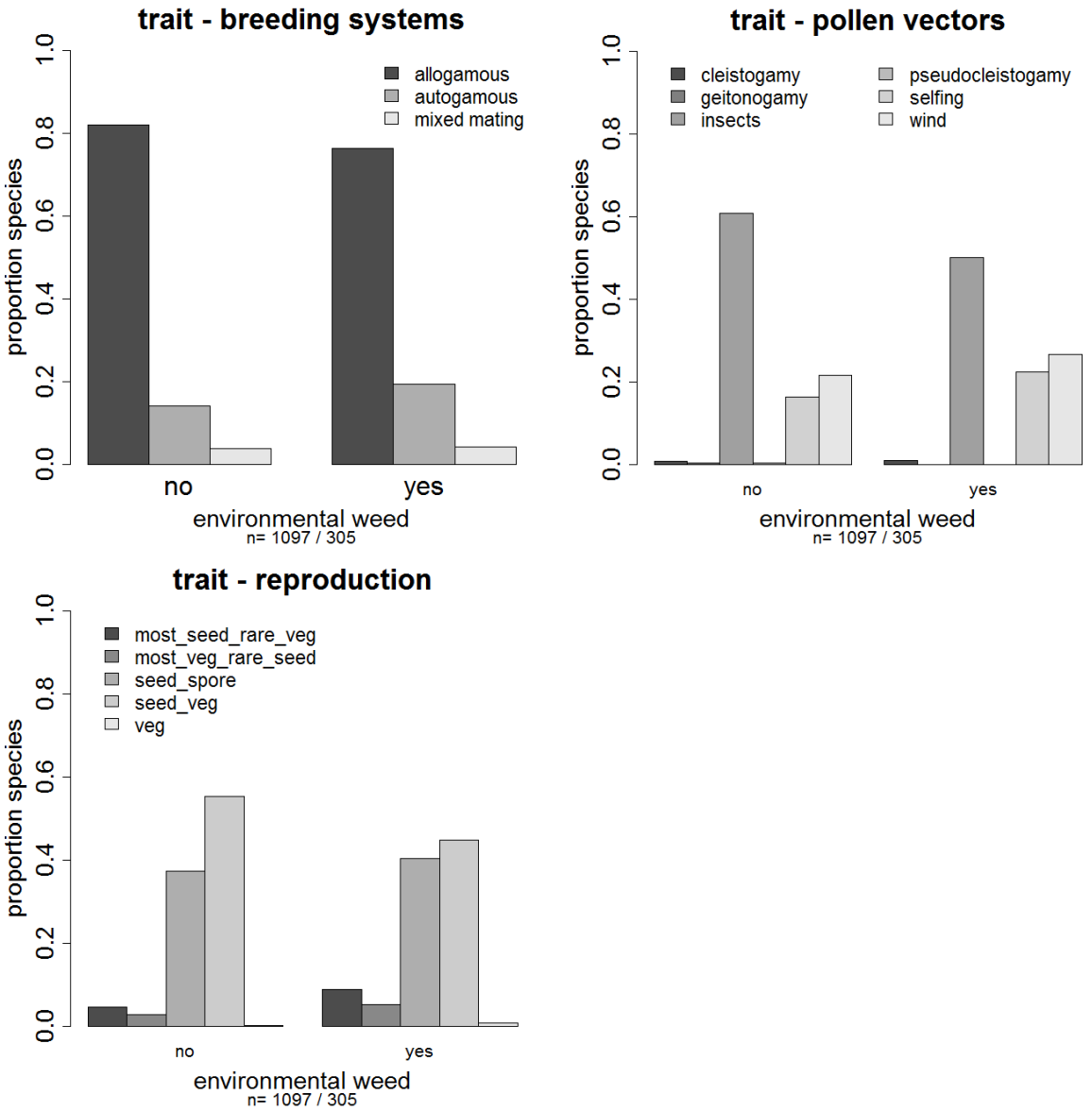

Figure 4: Proportion of species in the classes of the traits belonging to the trait group "reproduction". The trait breeding system displays a slight shift from the variable allogamous (82% non-environmental weeds versus 76% environmental weeds) to autogamous (14% non-environmental weeds to 19% environmental weeds). The results for the trait pollen vectors confirm this finding. The proportion of the variable "insects" decreased from 60% (non-environmental weeds) to 50% (environmental weeds), whereas the variables selfing (16% non-environmental weeds to 22% environmental weeds) and wind (21.5% non-environmental weeds to 26.5% environmental weeds) increased. The trait reproduction shows a light shift for the variables "most seed rare veg" and "most veg rare seed" and "seed spore". These variables increased slightly in the environmental weed pool at the expense of the variable "seed veg".

Trait group "site"

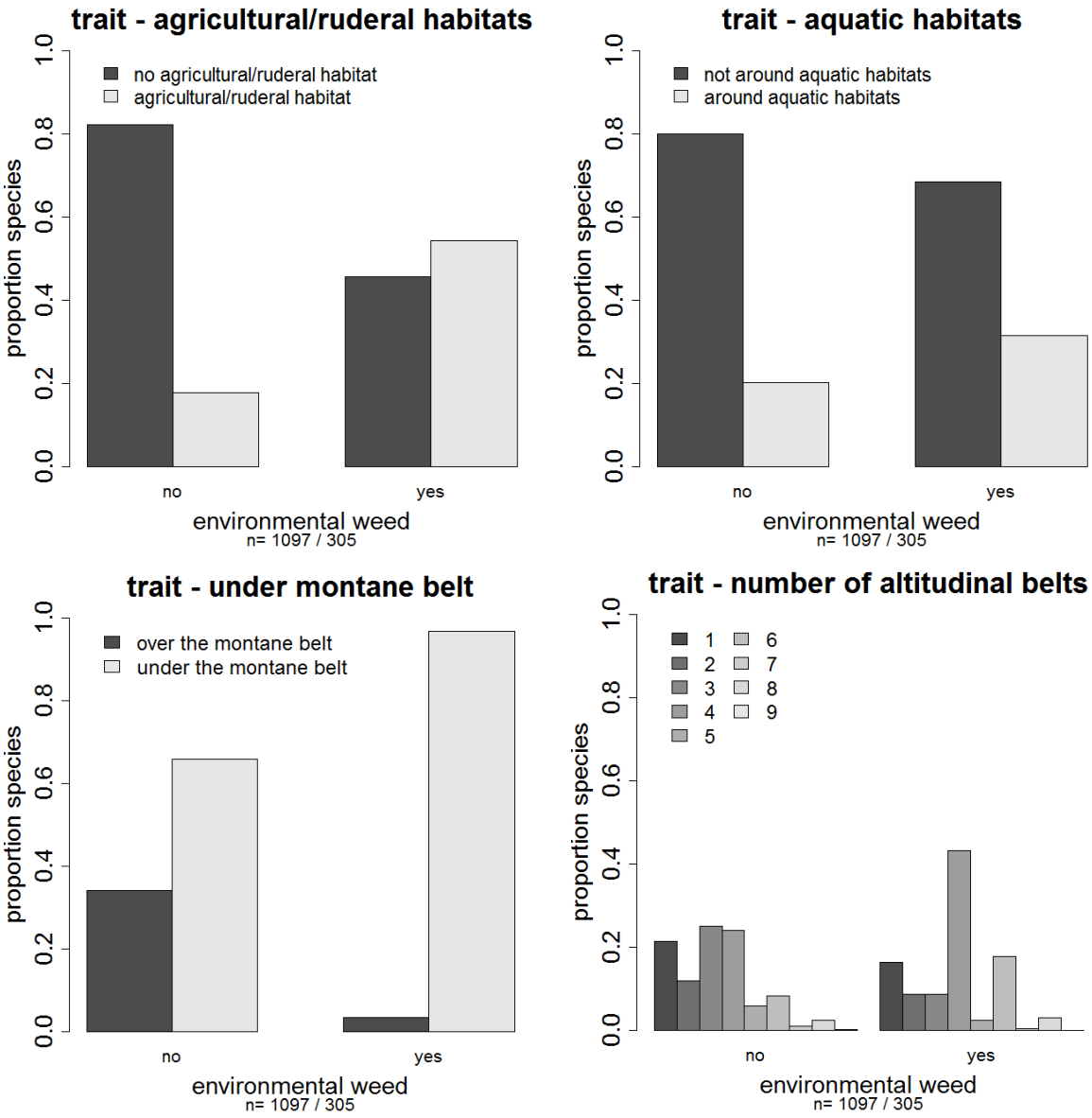

Figure 5: Proportion of species in the classes of the traits belonging to the trait group "site". The trait agricultural and ruderal habitats show an unambiguously result. The percentage of species which are occurring in agricultural or ruderal habitats increased strongly from 18% (non-environmental weed pool) to about 55% (environmental weed pool). The same correlation (but not that strong) holds for the trait "aquatic habitats" where 20% of the non-environmental weeds have their distribution around aquatic habitats compared to 31% in the environmental weeds pool. An extreme result indicates the trait "distribution below the montane belt". About 66% of the species in the non-environmental weed pool have an occurrence below the montane belt. This number increases strongly to 97% in the environmental weed pool. The trait "number of altitudinal belts" indicates a tendency to a higher amount of altitudinal belt in the environmental weed group.

Discussion

The main purpose of this diploma thesis was to identify traits which facilitate the invasion of plants into new ecosystems. The results were partly expected and partly unexpected.

Which traits make a species a successful alien elsewhere?

Life form is one of the most tested traits with respect to invasiveness. However, the scientific community had provided various findings so far. In their review, Pysek & Richardson, (2007) concluded that life form and life span of alien species vary considerably but that long-lived life forms tend to be more closely associated with invasiveness (Pysek & Richardson, 2007). The results of my diploma thesis do not corroborate this suggestion as I found no difference among Austrian theorphytes, geophytes and hemicryptophytes with respect to their probability to become invasive elsewhere in the world. For hemiphanaerophytes (similar to chamaephytes - for exact information see Klotz, et al. 2002) which are as a general rule long-lived, the chance was even significantly lower.

Another tested trait was life span. I detected a significantly higher chance for annuals compared to biennials and pollakanthic species to become invasive. Pysek & Richardson, (2007) suggested that life form is a stage specific trait within aliens and that annual species are promoted in earlier invasion stages. They also refer to Crawley, et al., (1996) who suggested that within native-alien comparisons there are - among the alien species - c-strategists (which are mostly perennial species, and long-lived) on the one side and r-strategist (which are often short lived) on the other side. These two groups of species have different sets of traits and occupy different ends of the niche axes. Following this argumentation, it is less life span per se but the match between the characteristics of the recipient habitat and the trait-syndrome associated with life spans that determine whether a species becomes invasive. However, annual species of the native flora of Austria have a higher chance to become invasive probably because they are well adapted to disturbed habitats - which are often colonized by alien species particularly during early invasion stages (Chytrý, et al., 2005), due to their fast life cycle which helps them to establish and build self-sustaining populations, as well as due to the lack of competition in such habitats.

During the statistical evaluation I tested also whether there is a difference between allogamous species, autogamous species and species which do not have a preference for one

of these mating systems. The findings did not yield significant differences between mating systems. This is not what was expected as autogamous species, which are not, or less dependent on pollinators, should have a better chance to settle down in a new area. However, this is probably only an advantage during early stages of the invasion process when only small populations are present and autogamous species are thus promoted (Harmon-Threatt, et al., 2009) and does not seem play a crucial role in later stages of the invasion. Harmon-Threatt, et al. (2009) moreover suggested in their study on 10 closely related pairs of native and introduced plants that successfully introduced species are either autogamous or have a similar pollinator visitation rate as their native relatives.

As there was a slight shift to wind and self-pollination among the environmental weeds in the visualized frequency tables, I would have expected that self-fertilisation or abiotic pollen vectors (wind) foster invasiveness, but statistical models do not suggest any relationship between pollen vector and the probability of a species to become invasive. However, Pysek & Richardson, (2007) have already suggested that pollen vectors have only little explanatory power for invasion success. They further refer to Crawley, et al. (1996) who has drawn similar conclusions.

With respect to reproduction modes, I had expected to find vegetatively reproducing species to be more likely to become invasive as (Kolar & Lodge, 2001), in their review, had found that vegetative reproduction correlates with invasiveness. However, these results could not be confirmed by my findings as they showed that preference of generative or vegetative reproduction modes does not alter the probability of Austrian plants to become invasive weeds. However, this result might not necessarily hold if the group of taxonomically problematic apomictic species could be properly integrated into the analysis.

A competitive life history strategy (C and CR strategists) is usually meant to foster invasiveness and my findings confirm this conjecture. Surprising at the first glance was the fact that a ruderal strategy did not alter the chance of becoming invasive. However, as written above, we suppose that a ruderal strategy is advantageous for invasiveness in early stages of the invasion process, but less so during the establishment phase. (Crawley, et al., 1996; Sutherland, 2004). As our classification of invasive weeds is based on data sources which focus on species already established in some parts of the world, competitive species might be more likely to have become listed than ruderals.

Plant height is often used as indicator for invasiveness, as it is a good indicator for competitive strength (Pysek & Richardson, 2007). A lot of papers have shown a correlation between plant height and invasiveness e.g. (Goodwin, et al., 1999; Crawley, et al., 1996) and so does this work. Goodwin, et al., (1999) is a good example relating to this diploma thesis, as they also used the "source area approach" for detecting determinants of invasion and came to the result, that invasive species were 16 cm taller on average, than congeneric non-invasive species. It seems to be logical that plants which achieve large plant heights have an advantage in competition as they can overshadow their competitors. This result is moreover in perfect agreement with the detected advantage of competitive strategists in becoming invasive.

The barplot for the ecological trait "N-value" shows that there is a shift to higher N-values - in the species pool containing the environmental weeds. This preference for nitrogen rich conditions among alien species was already pointed out in previous work (Prinzing, et al., 2002; Pysek, et al., 1995) and was fully corroborated in my paper. The clarity of the nearly linear correlation between invasiveness and N-values was particularly remarkable.

There are some studies which associate a wider distribution in the native range of a species with a higher chance of becoming an alien or a weed anywhere else, as the species with large range sizes have a higher chance of getting in touch with humans as their dispersal vector or have other traits which facilitate the spread over large geographical areas (Pysek, et al., 2009; Pysek, et al., 2004). My "frequency" variable refers to abundance, but indirectly also to range size, as "frequent" species are meant to be those that grow at many sites in the country and frequency and range size are hence closely correlated. My results are therefore in line with those of Pysek, et al., (2009), who also found that the distribution range in the source area plays an important role for the probability of becoming an alien or weed. Agricultural and ruderal ecosystems are habitats which have been created de novo by mankind and are therefore massively transformed by humans. The flora of these ecosystems has a high share of species adapted to frequent disturbances and high nutrient availability (Chytrý, et al., 2005). Kalusová, et al. (2013) demonstrated that species which occur in such habitats within their natural ranges are also more often invasive outside their native range. Furthermore (Essl & Rabitsch, 2002) suggested that there are characteristics of ecosystems which facilitate a successful invasion, like high natural or anthropogenic disturbance intensity and that the trait set of plants which occur in such habitats often favours

competitiveness and therefore also invasiveness. Summing it up, there is evidence for a strong correlation between invasiveness and (human) transformed habitats (e.g. agricultural and ruderal habitats) which is also confirmed by this diploma thesis.

One of the differences between alluvial forests and other European habitats is a high disturbance frequency through periodical flooding (which also guarantees abundant nutrient input to the system) that facilitates the transport of propagules over long distances (Kalusová, et al., 2013). These characteristics make floodplain ecosystems particularly prone to invasions but might also foster the invasiveness of species adapted to this ecosystem in their native range. This is the reason why we examined if there is a higher chance that native Austrian species from ecosystems which are located around aquatic habitats have a higher chance of becoming environmental weeds. The results in my work support this hypothesis and the findings of Kalusová, et al. (2013).

I found that Austrian plant species which have at least parts of their ranges below the montane altitudinal vegetation belt have a higher chance of becoming invasive elsewhere in the world. This is what I had expected as the chance of unintentional transportation by humans is higher and anthropogenic alteration of ecosystems (e.g. nitrogen deposition), which favors traits which are often associated with invasiveness, is more severe at lower altitudes. I also found a strong relationship between the chance of becoming an environmental weed and the number of altitudinal belts covered by the respective species. These results are the same (for native species) as shown by Alexander, et al. (2011) who describe alien floras along elevation gradients by directional ecological filtering. They suggest that alien plants in high elevations have a broad ecological tolerance which allows them to survive. The species are introduced to low elevations and have a unidirectional expansion from lower altitudes to higher elevation. During this process species with narrow elevation amplitudes drop out, a phenomenon they call directional ecological filtering (Alexander, et al., 2011).

Out of the 305 environmental weeds in our statistical analyses only 10 species did not occur below the montane belt (figure 5, trait – below montane belt). That means that 295 out of 305 environmental weed species have their lower elevation level in the colline or submontane belt (294 colline belt, 1 submontane belt). Figure 5 essentially illustrates the same gradient as described in Alexander, et al. (2011), i.e. a gradual decline of non-native species with elevation, for natives which are environmental weeds outside their native

range. The right barplot group of Fig. 5 shows the coverage of altitudinal belts for native species which are environmental weeds and have their lower distribution limits in the colline belt (this is, as mentioned above, valid for 294 of 305 species in this graph). One can see a gradient beginning at the montane belt and declining up to higher elevation levels. The reason for having peaks at the coverage of 4, 6 and 8 belts is due to data sampling as most authors in Fischer, et al. (2008) used a rough classification of the elevation levels and only some authors a more sensitive classification. We followed the more sensitive classification to capture all data in this source. For more detail, have a look to the trait description above in the chapter “Material and Methods”. In summary, this study demonstrates that the findings from (Alexander, et al., 2011) are also valid for environmental weeds within their source area.

It is well known that ornamental use of plants has a long tradition in Europe, but is becoming more and more a threat to biodiversity (Hulme, 2011). More than 50% of all invasive species were introduced for ornamental purpose (Li, et al., 2004). For Austria the percentage is even 57% (Essl & Rabitsch, 2002). There is a huge research interest in this sector and a lot of information and proposals were given (Li, et al., 2004; Dehnen-Schmutz, et al., 2007). In the work of Li, et al., (2004) for example the authors proposed to use sterile cultivars to avoid spread of ornamentals. An interesting insight to horticultural trade and ornamental plant usage was given by Dehnen-Schmutz, et al. (2007). They linked propagule pressure which is facilitated by ornamental plant trade, with the ability to escape and build sustainable populations in the wild. They found a difference between escaping and non-escaping species according to their traded volume in the nineteenth century as well as today and showed that propagule pressure enhance the chance of a species to build sustainable populations. Although propagule pressure is not one of the examined traits in this work, such considerations show the importance of horticulture in connection with invasiveness. This work provides evidence from a source area perspective in that it demonstrates that species used for ornamental purpose in their native range also have a higher chance to become invasive elsewhere in the world.

Explanatory power

For computing the explanatory part of each trait respective to the total variance, we used McFaddens pseudo R^2 value. As can be seen in Table 17 the explanatory power for the single traits as well as the trait groups was not particularly high. This is what I had expected, as there is not "the only reason" which explains invasion processes. Biological invasions are very complex and versatile and therefore not dependent on a single trait.

Noticeable is the fact, that the trait group competitiveness (20%) and site (19%) have the highest explanatory power. This indicates that traits which are related to competition and the characteristics of native habitats of a species could be more predictive than other traits. Especially the fact that reproduction and life history traits have only very limited support as predictors of invasiveness is salient and worth considering in any screening or black-listing approach.

Conclusio

A huge number of species have been transported to new environments by human activities, and the rate of introductions is steadily increasing (Lambdon, et al., 2008). Some of them become invasive in the recipient areas and represent a threat to native species whereas others fail to establish or become naturalized without causing any discernible impact (Villà, et al., 2011). The aim of this diploma thesis was to determine traits which explain why some species become invasive in their new range whereas others are not. I examined a suite of traits related to life history, human use, reproduction and competitiveness as well as site specific traits. I found that site specific traits as well as competitiveness traits contribute most to predict invasiveness in the new range. However, the poor to moderate explanatory power of individual traits and also the clustered trait groups in explaining invasion success elsewhere provide evidence that successful invasions depend also on other factors including introduction effort, pathways, residence time and the climatic matching of the old and new environments (Krivánek, et al., 2006; Pysek & Richardson, 2007). These results were not surprising as biological invasions are complex phenomena which depend on the interplay of many factors. Thus, combining source area-approach studies with additional information relevant in shaping invasion success are an important way forward to provide a more comprehensive understanding of biological invasions.

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References

Alexander, J. M. et al., 2011. Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *PNAS*, 11 January, pp. 656 - 661.

Bates, D. & Maechler, M., 2011. *Matrix: Sparse and Dense Matrix Classes and Methods. R package version 0.999375-50.*. [Online] Available at: http://CRAN.R-project.org/package=Matrix [Accessed June 2013].

Bates, D., Maechler, M. & Bolker, B., 2011. *lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39.*. [Online] Available at: http://CRAN.R-project.org/package=lme4 [Accessed 02 06 2013].

Blackburn, T. M. et al., 2011. A proposed unified framework for biological invasions. *Trends in Ecology & evolotion*, Issue 7, Volume 26, pp. 333 - 339.

Blossey, B. & Noetzold, R., 1995. Evolution of Increased Competitive Ability in Invasive nonindigenous Plants: A Hypothesis. *The Journal of Ecology*, Vol. 83 No. 5 October, pp. 887 -889.

Bundesamt für Naturschutz, 2000. *FloraWeb.* [Online] Available at: http://www.floraweb.de/ [Accessed 18 10 2012].

Callaway, R. M. & Ridenour, W. M., 2004. Novel weapons: invasive succsess and the evolution of increased competitive ability. *Frontiers in Ecology and Environment*, Volume 2, Issue 8 October, pp. 436 - 443.

Catford, J. A., Jansson, R. & Nilsson, C., 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distribution*, 15, pp. 22 - 40.

Chytrý, M. et al., 2005. Invasion by alien plants in the Czech Republic: a quantitative assesment across habitats. *Preslia, Praha*, 77:, pp. 339-354.

Crawley, M. J., Harvey, P. H. & Purvis, A., 1996. Compararive ecology of the native and alien floras of the British Isles. *Phil. Trans. R. Soc. Lond. B*, 351, pp. 1251 - 1259.

Dawson, W., Burslem, D. F. R. P. & Hulme, P. E., 2009. Factors explaining alien plant invasion success in a tropical ecosystem differat each stage of invasion. *Journal of ecology*, 97, pp. 657 - 665.

Dehnen-Schmutz, K., Touza, J., Perrings, C. & Williamson, M., 2007. The Horticultural Trade and Ornamental Plant Invasions in Britain. *Conservation Biology*, Volume 21, pp. 224-231.

Essl, F. & Rabitsch, W., 2002. *Neobiota in Österreich.* Wien: Umweltbundesamt.

Eugen Ulmer KG, 2006. *PPP-Index Pflanzeneinkaufsführer für Europa.* [Online] Available at: http://www.ppp-index.de/pppindex.dll?MID=2756 [Accessed 07. - 17. 02 2013].

Fischer, M. A., Oswald, K. & Adler, W., 2008. *Exkursionsflora für Österreich, Liechtenstein, Südtirol.* 3. Auflage ed. Linz: Biologiezentrum der Oberösterreichischen Landesmuseen.

Fitter, A. H. & Peat, H. J., 1994. The Ecological Flora Database. *J. Ecol.*, pp. 415-425.

Goodwin, B. J., McAllister, A. J. & Fahrig, L., 1999. Predicting Invasiveness of Plant Species Based on Biological Information. *Conservation Biology*, Vol. 13 April, pp. 422 - 426.

Grime, J. P., 1979. *Plant strategies and vegetation processes.* 222 S ed. Chichester: Wiley.
Gurevitch, J. et al., 2011. Emergent insight from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters*, 14:, pp. 407-418.

Harmon-Threatt, A., Burns, J. H., Shemyakina, L. A. & Knight, T. M., 2009. Breeding system and pollination ecology of introduced plants compared to their native relatives. *American Journal of Botany*, 96 (8), pp. 1544-1550.

Hegi, G., 1908-1932. *Illustrierte Flora von Mitteleuropa.* München: J. F. Lehmann Verlag.

Hulme, P. E., 2011. Adressing the threat to biodiversity from botanic gardens. *Trends in Ecology and Evolution*, Vol. 26 No. 4 April, pp. 168-174.

Jäger, E. J. & Werner, K., 2005. *Rothmaler, Exkursionsflora von Deutschland, Gefäßpflanzen: Kritischer Band.* 10. Auflage ed. München: Elsevier.

Kalusová, V. et al., 2013. Where do they come from and where do they go? European natural habitats as donors if invasive alien plants globally. *Diversity and Distribution*, 19, pp. 199 - 214.

Keane, R. M. & Crawley, M. J., 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, Vol. 17 April, pp. 164 -170.

Kleyer, M. et al., 2008. The LEDA Traitbase: A database of life-history traits of Northwestern European flora.. *Journal of Ecology*, 96:, pp. 1266-1274.

Klimesová, J. & Klimes , L., 2013. *Clo-Pla3 - database of clonal growth of plants from Central Europe.*. [Online] Available at: http://clopla.butbn.cas.cz/ [Accessed 21 07 2013].

Klotz, S., Kühn, I. & Durka, W., 2002. *BiolFlor Datenbank biologisch-ökologischer Merkmale der Flora von Deutschland.* [Online] Available at: http://www2.ufz.de/biolflor/index.jsp [Accessed 14 11 2012].

Kolar, C. S. & Lodge, D. M., 2001. Progress in invasion biology: predicting invaders. *TRENDS in Ecology & Evolution*, Vol. 16 No. 4, pp. 199-204.

Kriványek, M., Pysek, P. & Jarosík, V., 2006. Planting History and Propagule Pressure as Predictors of Invasion by Woody Species in an Temperate Region. *Conservation Biology*, Issue 5 Vol. 20, pp. 1487 - 1498.

Küster, E. C., Kühn, I., Bruelheide, H. & Klotz, S., 2008. Trait interactions help explain plant invasion sucess in the German flora. *Journal of Ecology*, 96, pp. 860 - 868.

Lambdon, P. W. et al., 2008. Alien flora of Europe: species diversit, temporal trends, geographical patterns and research needs. *Preslia*, 80, pp. 101-149.

Li, Y. et al., 2004. Invasive Ornamental Plants: Problems, Challenges and Molecular Tools to Neutralize Their Invasiveness. *Critical Reviews in Plant Sciences*, 23:5, pp. 381 - 389.

Lockwood, J. L., Casey, P. & Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, 5 May, pp. 223 - 228.

Prinzing, A., Durka , W., Klotz, S. & Brandl, R., 2002. Which species become aliens. *Evolutionary Ecology Research*, 4:, pp. 385 - 405.

Prinzing, A., Durka, W., Klotz, S. & Brandl, R., 2005. How to characterize and predict alien species? A response to Pysek et. al. 2004. *Diversity and distribution* , 11, pp. 121 - 123.

Pysek, P. et al., 2009. The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distibution*, 15, pp. 891 - 903.

Pysek, P., Prach, K. & Smilauer, P., 1995. Relating invasion success to plant traits: an analysis of the Czech alien flora.. In: P. K. R. M. M. (. Pysek P, ed. *Plant invasions: general aspects and specific problems.* Amsterdam: SPB Acad. Publishing, pp. 39 - 60.

Pysek, P. & Richardson, D. M., 2007. Traits associated with invasiveness in alien plants: Where do we stand?. In: W. Nentwig, ed. *Ecological Studies.* Vol. 193 ed. Heidelberg: Springer Verlag, pp. 97-122.

Pysek, P., Richardson, D. M. & Williamson, M., 2004. Predicting and explaining plant invasions through analysis of source area floras: some critical consideration. *Diverity and Distribution*, Vol. 10, pp. 179-187.

R Core Team, 2013. *R: A Language and Environment for Statistical Computing.* [Online] Available at: http://www.R-project.org

Randall, R. P., 2012. *A Global Compendium of Weeds.* 2nd Edition ed. Department of Agriculture and Food: Western Australia.

Richardson, D. M. et al., 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distribution*, 6, pp. 93 - 107.

Sarkar, D., 2008. *Lattice: Multivariate Data Visualization with R.*. ISBN 978-0-387-75969-2 ed. New York: Springer.

Sutherland, S., 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologica*, 141, pp. 24-39.

The Plant List, 2010. *The plant list.* [Online]
Available at: http://www.theplantlist.org/
[Accessed 25 01 2013].

van Kleunen, M. et al., 2010a. Are invaders different? A conceptual framework of comperative approaches for assessing determinants of invasiveness. *Ecology Letters*, Vol. 13, pp. 947-958.

van Kleunen, M., Weber, E. & Fischer, M., 2010 b. A meta-analysis between invasive and non-invasive plant species. *Ecological Letters*, Vol 13, pp. 235-245.

Villà, M. et al., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14:, pp. 702-708.

Weber, E., unpublished data. s.l.:s.n.

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Appendix

Appendix 1: List of agricultural and ruderal habitats from Fischer, et al. (2008)

List of agricultural and ruderal habitats which were extracted from Fischer et al. (2008)	
(Halb)-ruderalstellen	Gärten
Äcker	Gärtnereien
Ackerbrachen	Getreideäcker
Ackerraine	Getreideäcker (bodensauer, sandig)
Ackerränder	Gleisschotter
alte Gärten	grasreiche Obstgärten
alte Parkanlagen	Hackfruchtäcker
Autobahnen	halbruderal
Autobahnränder	halbruderale Halbtrockenrasen
Bahnanlagen	halbruderale Trockenrasen
Bahnböschungen	Halbruderale Trockenwiesen
Bahndämme	halbruderale Wiesen
Bahngelände	Halbruderalfluren
Bahngleisschotter	Halbruderalstellen
Bahnhöfe	halbsegetal
Bahnschotter	Kalkarme, bodensaure, lehmig-tonige Äcker
Baumschulen	Karrenwege
Begrünungssaaten	Kartoffeläcker
bodensaure Äcker	Kiesgruben
Burgen und Burgruinen	kiesige Wegränder
Dämme	lehmige Äcker
extensiv genutzte Äcker	lehmige bis tonige Äcker
Fahrrillen auf Wegen	Lehmige, meist stickstoffreichere Äcker
Feldwege	Maisäcker
feuchte Äcker	mäßig trockene Halbruderalstellen
feuchte Forststrassen	Mauern
feuchte Forststrassenränder	Mauerspalten
feuchte Forstwege	nährstoffreiche Äcker
feuchte kalkarme Äcker	nährstoffreiche Getreideäcker
feuchte Ruderalfluren	nährstoffreiche Ruderalfluren
feuchte Ruderalstellen	nasse Äcker
feuchte Sandgruben	nasse Feldwege
feuchte Waldwege	nasse Mulden auf Forstwegen
feuchte Wege	nasse Waldwege
feuchte, tonige, wechselnasse Äcker	nasse Wege
Fichtenforste	Obstgärten
Forststraßenränder	offene wechselfeuchte Ruderalfluren
Forstweg	offene Wegböschungen
Forstwegböschungen	Parkanlagen

Fortststrassen	Parkrasen
Fortstwegböschungen	Pflasterritzen
Friedhöfe	quellige Wegränder
Frische, halbruderale Gebüsche	Robinienforste
frische lehmreiche Äcker	ruderal
frische nährstoffreiche Äcker	ruderal beeinflusste Halbtrockenrasen
frische ruderale Gebüsche	ruderal beeinflusste Rasen
frische Ruderalstellen	ruderale Gebüsche
ruderale Gebüschsäume	Tonböden in Schottergruben
ruderale Rasen	tonreiche Äcker
ruderale Säume	Trittrasen
ruderale Wald- und Gebüschsäume	trockene Halbruderalfluren
Ruderalfluren	trockene Ruderalstellen
Ruderalsstellen	trockene Wegränder
Ruderalstellen in siedlungsnähe	trocken-warme Ruderalstellen
salzhältige Ruderalfluren	überschwemmt gewesene Äcker
Sandgruben	überschwemmte Äcker
sandige Äcker	vernässte Karrenwege
Schipisten	versalzene Straßen
Schlossparks	verwachsene Forstwege
Schottergruben	Waldwege
Schottergrubentümpel	Waldwegmulden
Schuttplätze	warme, trockene Ruderalfluren
Schuttstellen	Wassergräben
selten ruderal	wechsel(grund)feuchte, nährstoffreiche Bahndämme
Sommergetreideäcker	wechselfeuchte Ruderalfluren
Spurrillen in sumpfigen Wegen	wechselnasse Äcker
stark gedüngte Äcker	Wegböschungen
staudenreiche Ruderalgesellschaften	Wege
staunasse Waldwege	Wege und Böschungen
Steinbrüche	Wegmulden
steinige Ruderalstellen	Wegraine
steinige Straßenböschungen	Wegränder
Stoppeläcker	Wegränder in sonniger warmen Lage
Straßenböschungen	Wegrinnen
Straßengräben	Weinberge
Straßenränder	Weinbergränder
streugesalzene Straßenränder	Weingärten
subruderale Halbtrockenrasen	Weingartenränder
subruderale Rasen	Wirtschaftswiesen
Subruderalfluren	

Appendix 2: List of habitats in or around aquatic habitats from Fischer, et al. (2008)

List of habitats which occur near aquatic habitats which were extracted from Fischer et al. (2008)	
Fluss- und Bachalluvionen	nährstoffreiche Verlandungsgesellschaften
Alluvionen	nährstoffreiche, kalkarme Ufer
Altwässer	nährstoffreiches Röhricht
am Rand stehender oder langsam fließenden Gewässern	nasse Uferstaudenfluren
an und in fließenden und stehenden Seichtgewässern	offene, zeitweise überschwemmte Ufer
an und in stehenden Gewässern	oft bei Wasserfällen
an und in stehenden und träg fließenden Gewässern	Quellfluren
Anlandungen in Stauseen	Ränder stehender nährstoffreicher Gewässer
Au- und Bruchwälder	Röhrichte
Auen	Sandbänke grösserer Flüsse
Auen Altwässer	sandige Ufer
Augebüsch	Säume von Auwaldgebüschen
Augebüsch-Säume	Säume von Bächen
Auwälder	Säume von Flüssen
Auwaldränder	Schilfbestände
Auwaldsäume	schilfreiche Seeufer
Auwiesen	Schilfröhricht
Bachalluvionen	schlammige Ufer
Bachauen	Schlammufer
Bachauwälder	Schotteralluvionen
Bachauwiesen	Schotterfluren
Bäche	schottrige Ufer
Bachgeröll	schwach salzige Schilfbestände
Bachkies	Seeufer
Bachränder	Staudenfluren an Bächen
Bachufer	Staudenfluren an Flüssen
erdige Ufer	Staudenfluren an Ufern
Erlen-Auwald	Stauden- und Weidengebüsche der Auen
feuchte, nährstoffreiche Uferstaudenfluren	stehende Gewässer
feuchte, sandige Teichufer	stehende Gewässer in Auen
Fischteiche	stehende und träg fließende Gewässer
flache Badeseeufer	steinige Quellfluren
Flussalluvionen	Teiche
Flussauen	Teichränder
Flussdämme	trockenfallende Uferrasen
Flüsse	überschwemmte Flussufer
Flussgeschiebe	überschwemmte Teichufer
Flusskies	überschwemmte Wiesen
Flussnahe, wechselfeuchte Auwiesen	Überschwemmungsbereiche größerer Flüsse
Flussschotter	Ufer
Flussstandorte	Ufer der Gebirgsflüsse

Flussufer	Ufer fließender und stehender Gewässer
Gebüsche an Bachrändern	Ufer träg fließender Gewässer
gewässerbegleitend	Ufer von Seen
Grauerlen-Auwald	Ufer von Tümpeln und Teichen
Harte Auwälder	Uferböschungen
in und an fließenden Gewässern	Ufergebüsch
kalkarme Flussufersäume	Ufergehölze
kalkarme Sand- und Lehmböden an Ufern	Ufergesellschaften
kalkreiche Schotteralluvionen	Ufersäume
Kiesbänke der Alpenflüsse	Verlandungsgesellschaften
kiesige bis sandige Ufer	Verlichtungen von Auwäldern
kiesige Ufer	Waldbachfluren
Krautfluren an Teichrändern	Weichholzau
nährstoffreiche Bachufer	zeitweise überflutete Flussufer
nährstoffreiche schlammige Ufer	zeitweise überflutete, sandige Ufer
nährstoffreiche Teichufer	zeitweise überschwemmte Ufersäume

Appendix 3: Abstract

Biological invasions are versatile and complex processes which are controlled by multiple, potentially interacting factors. Therefore it is not easy to find an answer to the question: "What determines a species to become invasive"? Many species of the Austrian flora have become invasive elsewhere whereas others have not. The aim of this diploma thesis is to search for physiological and ecological traits which could increase the chance of becoming an environmental weed. Using the so-called source area approach I examined 1,402 native species of the Austrian flora and compared those which are invasive elsewhere (so called environmental weeds) against those which are not with respect to these traits.

The statistical evaluation of fourteen different traits showed various outcomes. While often examined "classical" traits like life form or pollen vector showed ambiguous results, ecological traits or related to the species native range characteristics (e.g. occurrence in agricultural or ruderal habitats, occurrence under the montane belt, N-value according to Ellenberg) or its competitiveness (strategy type, plant height) were more clearly related to invasiveness. Overall, goodness-of-model fit was low to moderate for all traits, however, suggesting that, as expected, invasions are processes that defy simple uni-causal explanations. Interactions among the tested traits, as well as with traits not accounted for in my study, might deliver a more comprehensive picture of successful invaders. However, random processes will likely always play a role in invasions making every attempt to predict them an informed guess at best.

Appendix 4: Kurzfassung

Biologische Invasionen sind komplexe Prozesse, die verschiedene Gründe haben können. Da einige Arten der einheimischen österreichischen Flora in anderen Regionen invasiv sind (sogenannte „environmental weeds“), während andere einheimische Arten in neuen Lebensräumen nicht invasiv werden, drängt sich folgende Frage auf: „Welche Eigenschaften machen Arten invasiv“?

Diese Diplomarbeit untersucht 1.402 Arten der einheimischen österreichischen Flora hinsichtlich physiologischer und ökologischer Merkmale, die die Chance erhöhen könnten, dass Arten in anderen Teilen der Welt invasiv werden. Die statistische Auswertung von 14 verschiedenen Pflanzeneigenschaften zeigte, dass „klassische“, oft analysierte Eigenschaften wie z. B. „Lebensform“ oder „Pollenvektor“ Invasivität kaum erklären, während Standortmerkmale (z.B. Auftreten in landwirtschaftlichen oder ruderalen Habitaten, Vorkommen unterhalb der Montanstufe, Stickstoffwerte nach Ellenberg) oder solche, die sich auf die Konkurrenzkraft der Arten beziehen (Strategietyp nach Grime, Höhe der Pflanzen) relativ eng mit der Chance invasiv zu werden korreliert sind. Im Zuge der statistischen Auswertung wurde auch der Erklärungswert, sowohl der einzelnen Variablen, als auch der aus ähnlichen Merkmalen zusammengestellten Eigenschaftengruppen untersucht. Diese Erklärungswerte waren insgesamt gering bis durchschnittlich und bestätigen damit die Einschätzung, dass Invasionen komplexe Prozesse sind, die sich monokausalen Erklärungsversuchen entziehen. Interaktionen zwischen den untersuchten Traits, sowie mit nicht untersuchten andern Eigenschaften, mögen es erlauben, den Typ des erfolgreichen Neophyten noch etwas schärfer zu charakterisieren. Trotzdem werden Zufallsereignisse in jedem Invasionsprozess eine Rolle spielen und Versuche, dieselben zu prognostizieren daher immer an Grenzen stoßen.

Appendix 5: Curriculum vitae

Lebenslauf

Persönliche Daten

Name:	Stefan Fischer
Geburtsdatum:	21.03.1977
Wohnort:	1180 Wien, Erndtgasse 9-11/9
Telefon:	+43 650/522 69 79
E-mail:	stefan.fischer1@gmx.at
Familienstand:	ledig

Ausbildung

seit WS 2006	Biologiestudium(Spezialisierung auf Ökologie mit Schwerpunkt Natur- und Landschaftsschutz – Diplomarbeitsthema: ➢ Invasive or not – What makes the difference? A source area approach ➢
1999	Ableistung des Präsenzdienstes
1993 – 1998	Höhere Bundeslehranstalt für wirtschaftliche Berufe, 1190 Wien
1992 – 1993	Marianum, Oberstufenrealgymnasium, 1180 Wien
1987 – 1992	Bundesgymnasium und Bundesrealgymnasium, 1170 Wien
1983 – 1987	Volksschule der Schulbrüder, 1180 Wien

Beruflicher Werdegang

24.01.2013 – heute	Beschäftigt als Bürohilfskraft bei Top consult (Geringfügig)
20.01.2011 – 24.01.2013	Beschäftigt bei INF Networks GmbH.
10.08.2009 − 11.07.2011	Beschäftigt als Lagerarbeiter bei Logistikpark 19 (Geringfügig)
01.01.2007 – 31.12.2008	Beschäftigt als Bürohilfskraft bei Anaxo AG (Geringfügig)
01.04.2003 – 31.12.2006	Gefahrgutbeauftragter bei Borealis Polyolefine GmbH am Standort Schwechat
01.12.1999 – 31.03.2003	Gefahrgutbeauftragter beiPolydan GmbH (100%ige Tochter der Borealis Polyolefine GmbH.)
01.07.1997 – 31.07.1997	Bank Austria Handelsbank AG (Ferialpraxis)
01.06.1996 – 31.08.1996	Hotel Europa (Ferialpraxis)

Berufliche Fort- und Weiterbildung

11/2009	Verlängerung Gefahrgutbeauftragtennachweis(Straße/Schiene)
06/2005	Ausbildung zum Abfallbeauftragten gem. § 11 Abfallwirtschaftsgesetz
10/2004	Verlängerung Gefahrgutbeauftragtennachweis (Straße/Schiene)

05/2003	Ausbildung zum Gefahrgutbeauftragten (Schienenverkehr) gem. § 11 Gefahrgutbeförderungsgesetz
09/2000	Fortschreibung und Optimierung des Abfallwirtschaftskonzepts
01/2000	Ausbildung zum Gefahrgutbeauftragten (Straßenverkehr)gem. § 11 Gefahrgutbeförderungsgesetz
2001 – 2006	laufende Schulungen (jährlich) über Änderungen im Gefahrgutrecht

Besondere Kenntnisse

MS Office (Word, Excel, Power Point, Access)

Geographische Informationssysteme: (Arc Gis)

Statistikprogramme: R, SPSS(Grundkenntnisse)

Turboveg 2.0

Englisch (sehr gut in Wort und Schrift)

Französisch (Schulkenntnisse)

Führerschein Klasse B

Wien am 22.07.2013 Unterschrift