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Which species become aliens?

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ABSTRACT

Alien plant species are a potential threat to global biodiversity. However, only a few species in a species pool become aliens. Until now, it was unclear how these alien species differ from non-aliens. We considered central European aliens in two Argentine provinces. We found that these alien species are characterized by: (1) frequency in central Europe and utilization by humans; (2) a preference for warm, dry and nitrogen-rich conditions in central Europe; (3) a native range that covers several floristic zones; and (4) a ruderal life strategy. Aliens are not characterized by wind or vertebrate dispersal. The traits of aliens indicate that they are in frequent contact with humans as their dispersal vector. They are pre-adapted to the abiotic conditions in Argentina. And they are versatile and can colonize disturbed sites. From these traits we were able to predict correctly 81% of alien species. Thus, traits of species may help us to predict future aliens – even across higher plants in total and even based on an incomplete knowledge of the present alien flora. But such a prediction will require extensive knowledge of the species' traits.

Keywords: Argentina, dispersal, ecological versatility, invasive species, life strategy, neophyte, pre-adaptation, species pool.

INTRODUCTION

With the help of humans, some plant species have been able to colonize distant biogeographic regions outside their historical range. Within these target regions, such species are called 'aliens' (e.g. Huston, 1994; Williamson, 1996; Richardson *et al.*, 2000b). Many of these alien species only survive under human cultivation. Those that survive outside cultivation are called 'casual aliens' when they survive occasionally, 'naturalized aliens' when they are able to maintain populations and 'invasive aliens' when they manage to spread over the target region (terminology from Richardson *et al.*, 2000b). Only a small proportion of the alien species manages to become invasive, but these species can exert very negative effects on the local biodiversity (Williamson, 1999). Here, we consider all

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aliens that are casual, naturalized or invasive, but not those that survive only under human cultivation. We refer to all these species simply as 'aliens'. We consider aliens in general for several reasons. First, it may be worthwhile to control them all. Such a strategy of control would prevent invasions at an early stage, which might be much easier than at an advanced stage (Kolar and Lodge, 2001). Second, it is often simply impracticable to further differentiate aliens (e.g. invasive *vs* non-invasive), given that in general only the presence or absence of an alien species in a target region has been recorded. Third, the alien stage is of fundamental importance from a biogeographic point of view; at that stage, a species has managed to survive outside human cultivation in a new biogeographic region.

Interestingly, alien species represent only a minority of the available species pool in a source region (Williamson and Fitter, 1996a; Pyšek, 1998). This begs the question, 'why do some species become aliens whereas most others do not?' Only if we can answer this question can we attempt to predict which species are likely to become aliens in the future (Kolar and Lodge, 2001).

There are two main approaches to the question of why some species become aliens. First, some authors have investigated the biology of individual alien species in detail (for summaries, see Roy, 1990; Williamson, 1996, 1999). The results, however, have proved difficult to generalize from one alien species to another (Rejmánek and Richardson, 1996; Williamson, 1999). Second, others have used a comparative approach to determine whether alien species are characterized by certain traits. Usually, these authors have compared the aliens in a particular target region with the native flora of that region (Thompson *et al.*, 1995; Crawley *et al.*, 1996; Williamson and Fitter, 1996b). These comparisons help us to understand the impact of aliens on natives. But they cannot answer the question of why certain species from a species pool in a source region became aliens in a target region. Aliens may be nothing more than a random sample of their species pool; however, if the whole species pool differs from the natives in the target region, an inevitable difference will be found between aliens and natives.

Thus, for a convincing analysis, aliens in a target region should be compared with the remaining non-aliens in the species pool (Kolar and Lodge, 2001). Such comparisons are rare. Goodwin *et al.* (1999) compared alien species of European origin in human-disturbed habitats in New Brunswick, Canada, with non-alien species in Europe. They considered only a few traits, such as life form, stem height, flowering period and European geographic range size. They found that range sizes were larger in aliens than in non-aliens, but stem height and flowering period did not differ. Scott and Panetta (1993) compared aliens that invaded Australia from southern Africa with non-alien species from southern Africa. They only considered 'weedy aliens', defined as 'species that interfere with human activity or have deleterious effects upon the natural environment'. Scott and Panetta found that the 'weedy aliens' had already been weedy in southern Africa. Finally, some authors have compared invasive aliens with non-invasive aliens (Pyšek *et al.*, 1995; Rejmánek and Richardson, 1996; Reichard and Hamilton, 1997). For example, Rejmánek and Richardson (1996) compared 12 invasive and 12 non-invasive *Pinus* species. The invasive species showed a characteristic life history. Obviously, such comparisons between invasive aliens and non-invasive aliens cannot explain why certain species become aliens. Moreover, to separate invasive from non-invasive aliens, we need very detailed information on the site and the date of introduction (Richardson *et al.*, 2000b). Regrettably for most aliens and most places of the world, we do not have such information. We mostly only have presence/absence lists that indicate which species are aliens and which are not. Overall, the few studies that have taken the species pool of aliens into account have been restricted to very few traits, to small taxa or to a very special subset of the alien species.

In the present study, we considered a large taxon and a set of 11 traits to establish how alien species differ from non-alien species. We focused on higher plant species (Spermatophyta, Pteridophyta) from central Europe and compared those species that have become aliens in two provinces of Argentina – Buenos Aires and Mendoza – with those that have not. Argentina was first colonized by Europeans in the sixteenth century. The first colonists came from Spain. They were followed by colonists from the rest of Europe, particularly from Britain, France, The Netherlands, Germany, Switzerland, Italy, Poland and Russia (Bruns, 1988; Bünstdorf, 1992). Thus, central Europe became a major source pool of aliens to Argentina. In fact, 60% of all alien species in the Buenos Aires province of Argentina occur in central Europe (Söyrinki, 1991).

As the central European species pool is well known, we were able to consider a comprehensive list of traits. We considered not only the traits that may favour the introduction of a species to a target region, but also traits that favour the persistence of an alien species within the target region. Persistence is important because it increases the chance of an alien species being discovered. Thus, we considered traits that favour the introduction of species, as well as traits that favour their casual survival outside human cultivation, their naturalization and their ability to invade (Crawley *et al.*, 1996; Williamson, 1996, 1999; Richardson *et al.*, 2000a,b; Kolar and Lodge, 2001) (Table 1).

1. *Frequency within the source region*. This reflects the chance of a species coming into contact with humans, who are the dispersal vectors that can introduce a species to new biogeographic regions. Of course, prevalence may reflect also several other aspects of a species' biology (Hedge and Ellstrand, 1999). Therefore, we also took into account two further traits that increase the chance of coming into contact with humans: the occurrence of species in anthropogenic vegetation and their utilization by humans. While utilization by humans reflects contact with humans as a result of human intention, prevalence and occurrence in anthropogenic vegetation reflect accidental contact with humans.
2. *Niche position along various environmental gradients*. Argentina differs from Central Europe with respect to several abiotic variables (see 'Methods'). Central European species may be more or less pre-adapted to the specific Argentine conditions and pre-adapted species are more likely to survive in Argentina outside human cultivation, at least casually. The extent to which a species is pre-adapted can be inferred from its niche position along abiotic gradients within central Europe, a trait that subsumes many physiological and life-history traits.
3. *Width of the native biogeographic range*. This reflects a species' ecological versatility (Hengeveld, 1990). Versatile species should be more able to survive and even naturalize in a new environment.
4. *Life strategy* (*ruderal vs non-ruderal*). This reflects the ability of a species to colonize disturbed sites (Grime *et al.*, 1988). Such sites may be the gate through which species invade a target region (Crawley, 1986; Rejmánek and Richardson, 1996; Pyšek *et al.*, 1998).
5. *Dispersal vectors*. Species dispersed by vertebrates or wind are able to spread their seeds efficiently in a target region and thereby invade that region (Richardson *et al.*, 2000a).

Table 1. List of species traits considered in the present study

	Scale		Source
1. *Contact with humans as the inter-continental dispersal vector*			
Frequency within Eastern Germany	Number of grids	1–3597	Bernkert *et al.* (1996)
Occurrence in anthropogenic vegetation	Rank scale	1–3	Frank and Klotz (1990)
Use by humans	Rank scale	1–3	Frank and Klotz (1990)
2. *Pre-adaptation to abiotic conditions in Argentina*			
Ellenberg indicator values for temperature, light, soil nitrogen and soil moisture	Rank scale	1–9 or 1–12	Ellenberg (1979) in Frank and Klotz (1990)
3. *Ecological versatility*			
Number of floristic zones in which the species is native	Rank scale	1–8	Schubert *et al.* (1990)
4. *Colonization of disturbed sites*			
Ruderal life strategy (*sensu* Grime *et al.*, 1988)	Rank scale	1–4	Frank and Klotz (1990)
5. *Efficient dispersal*			
Vertebrate dispersal	Rank scale	1–3	Schubert *et al.* (1990)
Wind dispersal	Rank scale	1–3	Schubert *et al.* (1990)

Note: The hypothesized mechanisms by which the traits may increase the chance of a species becoming an alien are listed as points 1–5. Further explanations of the hypotheses are given in the Introduction. A further explanation of our raking of variables is given in the 'Methods' section.

Therefore, Richardson *et al.* (2000a) suggest that potential alien species should be screened for adaptations to vertebrate or wind dispersal.

METHODS

Argentine regions

We considered the provinces of Buenos Aires (307,563 km^2) and Mendoza (excluding the high Andean part, *c.* 100,000 km^2). Within Argentina, the two provinces represent quite different climatic conditions. The Buenos Aires province is characterized by mean annual temperatures of 14.9–17.0°C and a mean precipitation of 306–962 mm. In the city of Mendoza, the mean annual temperature is 15.8°C and the mean annual precipitation is 194 mm (Walter and Lieth, 1960–67; Söyrinki, 1991). However, compared with central Europe, both regions are warm and dry. In central Europe, average annual temperatures range from <5°C to 12.7°C; annual precipitation ranges from 396 to >1650 mm (Walter and Lieth, 1960–67). The combination of higher temperatures and lower precipitation in Argentina results in a distinctly lower soil moisture than in central Europe (Walter and Breckle, 1991). The Argentine provinces also differ from central Europe in that forests are uncommon; thus there are only a few shady habitats (Bruns, 1988; Söyrinki, 1991; Bünstdorf, 1992).

The ecological conditions in the human-made habitats of the Argentine provinces – agricultural areas, parks, gardens – are of particular interest because most of the aliens are found in these habitats (see below). In both provinces, the human-made habitats are nitrogen-rich (Söyrinki, 1991). To some extent, these habitats are also irrigated (Söyrinki, 1991), in particular in the Mendoza province (Bruns, 1988; Bünstdorf, 1992). Thus, human impact reduces the ecological differences between the provinces of Buenos Aires and Mendoza.

Overall in the Argentine provinces, most aliens face conditions that are warmer, dryer, more sunny and richer in nitrogen than most places in central Europe.

Alien status of central European species in Argentina

We considered the 2208 central European species listed in Frank and Klotz (1990), the most comprehensive database of the flora of central Europe. The database covers 90% of the species indigenous or naturalized in Germany (Wisskirchen and Haeupler, 1998). We excluded ‘neophytes’, species introduced to central Europe later than approximately 1500 (Ellenberg, 1996). Such neophytes are essentially from a species pool outside central Europe. Nevertheless, even for the non-neophytes, we cannot rule out the possibility that some of them were introduced to Argentina from species pools outside central Europe.

We recorded the central European aliens in the Mendoza province during three visits in November 1993, April 1994 and November 1995, with at least eight excursions per visit. Moreover, we compiled records from the herbarium of the Instituto Argentino de Investigaciones de las Zonas Aridas at Mendoza, which is the most comprehensive herbarium of the Mendoza region. We compiled the central European aliens in the Buenos Aires province using the data of Söyrinki (1991). Söyrinki collected these records during four journeys between 1967 and 1983, which lasted in total approximately 6 months. Söyrinki also lists additional records from earlier researchers that he considered to be incorrect. We did not include these records. The list of alien species is available as Appendix 1 at http://evolutionary-ecology.com/data/PrinzingApp1.pdf.

In the Mendoza province, we sampled all major habitats: arid thorny shrublands, road verges, improved grasslands, parks and other urban habitats. However, we found most of the aliens in urban habitats. In the Buenos Aires province, Söyrinki (1991) apparently also sampled all major habitats, even though he makes no explicit statement of this. Most of his records are from the urban habitats of the city of Buenos Aires; hence, most alien species grew in urban habitats. Nevertheless, the available data did not permit us to take into account the different habitats of the aliens. This is a shortcoming of most published lists of alien species.

The two Argentine provinces share many alien species, on average 57%. Thus, separate analysis of the aliens from the two provinces inevitably yielded very similar results. The parameters of separate logistic regression analyses correlated at $r = 0.78$ and the test statistics correlated at $r = 0.82$. Therefore, we decided to conduct a single analysis in which we defined the alien status of a species across both regions. For logistic regression analyses, we defined alien status as a binary variable: a species does or does not occur in either of the provinces. For sign tests and linear regression analyses, we defined alien status as follows: 0 = a species occurs in neither Argentine province; 1 = a species occurs in one of the two provinces; 2 = a species occurs in both provinces. We treated this parameter as a continuous variable, which permitted us to perform multivariate analyses based on phylogenetically independent contrasts (see below). Treating ranks as continuous variables introduces some error into the statistical analysis. But there was no ambiguity in the results of the analyses – effects were either clearly significant or clearly non-significant.

Species traits

We considered the traits and references listed in Table 1. Most of these traits are measured on a rank scale. More precise data (e.g. on physiological tolerances) will not be available in the near future. We wish to make the following comments on our selection of traits:

1. *Frequency*. To characterize the frequency of a species, we used its grid occupancy in Eastern Germany as one of the core areas of central Europe. The knowledge of the distribution of plant species is much more precise in Eastern Germany than elsewhere in central Europe (the grid size is only 36 km^2). *Occurrence in anthropogenic vegetation*: Frank and Klotz (1990; based on Kunick, 1974; Klotz, 1984) rank the occurrence of species in anthropogenic vegetation as follows: (1) 'oligohemerobous' species occur only in vegetation types with little anthropogenic influence (e.g. forests with no or selective logging); (2) 'mesohemerobous' species also occur in vegetation types with rare and strong, or with continuous and moderate, anthropogenic influence (e.g. forests with clear cuts or meadows with yearly mowing); and (3) 'polyhemerobous' species even occur in vegetation types with continuous and strong anthropogenic influence (e.g. agricultural fields). Various authors have validated these 'Hemerobie' assessments (e.g. Dierschke, 1994; Grabherr *et al.*, 1995). *Use by humans*: Species used by humans are likely to be intentionally introduced into the new colonies of humans. Schlosser *et al.* (1991, in Frank and Klotz, 1990) rank species according to their utilization by humans: 0 = not used; 1 = suitable for very restricted use; 2 = regularly used, or at least suitable for regular use. Schlosser *et al.* only consider native plants, so we included cultivated non-native plants, and assigned them to rank 2.
2. *Pre-adaptation to abiotic conditions*. Argentinean habitats of aliens are in general warmer, drier, more sunny and richer in nitrogen than central European habitats (see above). To characterize a species' pre-adaptation to these conditions, we used the 'Ellenberg indicator values' for temperature, soil moisture, light and soil nitrogen (Ellenberg, 1979; listed in Frank and Klotz, 1990). These values characterize the niche position of plant species in central Europe. Species that occupy the warm, dry, light or nitrogen-rich end of the central European scale use conditions similar to those in Argentina, indicating a pre-adaptation to Argentine conditions. The general correctness of Ellenberg's assessments has been widely validated (e.g. Thompson *et al.*, 1993; Hill and Carey, 1997; Ertsen *et al.*, 1998).
3. *Versatility*. We characterized a species' versatility as the number of floristic zones (arctic, boreal, etc.) covered by the distributional range of a species (Hengeveld, 1990).
4. *Life strategy*. The life strategy of each species was ranked on a scale from 1 (stress tolerant strategy or competitive strategy, without elements of ruderal strategy) to 4 (pure ruderal strategy). The ranking is based on Frank and Klotz (1990), who largely apply the criteria of Grime *et al.* (1988), such as stature, longevity, phenology of flowering or seed dormancy. The ecological significance of the assignments by Frank and Klotz (1990)

has been validated (e.g. Pyšek *et al.*, 1995). Moreover, there is a correlation between assignments by Frank and Klotz (1990) and by Grime *et al.* (1988), despite the different scaling of both assignments: $r_p = 0.62$ ($P < 0.0001$, $n = 418$).

5. *Vertebrate dispersal*. Following Richardson *et al.* (2000b), we scored species with fleshy fruits as 2 (these species profit from the gut passage), species with fruit that attach to the body of vertebrates as 1 and the remaining species as 0 (Frank and Klotz, 1990). The way that we defined the ranks was not crucial. A binary variable, or one that included ant dispersal, led to the same results. *Wind dispersal*: We scored species that are primarily dispersed by wind as 2, species for which wind is of minor importance as 1 and the remaining species as 0 (Frank and Klotz, 1990). Again, the definition of ranks was not crucial: different rankings gave similar results.

Although the above-mentioned traits are obviously intercorrelated, our analyses showed that none of them was redundant (see 'Results').

Analysis

Our first objective was to analyse the relationship between species' traits and alien status. As is now widely accepted, traits of different species are not independent, but are connected by the species' phylogeny, which introduces the risk of phylogenetically induced correlation between traits (Harvey and Pagel, 1991). Such phylogenetic non-independence between species has been demonstrated for several of the traits considered in the present study, such as alien status (Pyšek, 1998), niche position, life strategy (Prinzing *et al.*, 2001 and unpublished) and dispersal modes (Peat and Fitter, 1994). Thus, we performed two types of analyses. First, we used individual species as independent data points. Second, we used phylogenetically independent contrasts to account for the phylogenetic relationships between species (Harvey and Pagel, 1991). Several methods of phylogenetically independent contrasts are available, but there is little agreement about the performance of these methods (Martins, 2000). We applied two methods and checked for the robustness of our results across the methods: (1) the method implemented in the CAIC (Comparative Analysis of Independent Contrasts) program, option 'Crunch' (Purvis and Rambaut, 1995; based on Felsenstein, 1985; Pagel, 1992), and (2) the method suggested by Burt (1989). Burt's method uses the information less efficiently than the CAIC method and does not permit multivariate analysis. On the other hand, Burt's method does not depend on the assumptions underlying the method implemented in CAIC (Purvis and Rambaut, 1995). Nevertheless, both methods led to similar results (see 'Results').

We calculated 'CAIC contrasts' as the differences between sister taxa across a phylogeny. Because there is no hypothesized phylogeny available that covers all our species, we compiled a super-tree from the phylogenies that have been published for individual lineages (see Appendix 2, available at http://evolutionary-ecology.com/data/PrinzingApp2.pdf). There were no branch lengths available for our tree, so we set all branch lengths to the same arbitrary value. Martins and Garland (1991) showed that it is valid to calculate phylogenetically independent contrasts even when branch lengths are arbitrary. We analysed the CAIC contrasts by conventional univariate and multivariate linear regression analyses with an intercept of zero (Purvis and Rambaut, 1995). We confirmed graphically that the regression analyses were not biased by non-linear relationships or outliers.

For technical reasons, we used a taxonomy to calculate contrasts according to Burt (1989). We compiled the taxonomy from the Angiosperm Phylogeny Group (1998) and Schubert *et al.* (1990). For the levels of tribes and sections, we used the references given in Appendix 2. We also tried alternative taxonomies (e.g. Cronquist, 1988; Thorne, 1992), which led to very similar results. Contrasts were calculated as the within-taxon correlation between alien status and independent variables. Species in monotypic taxa were combined across higher taxonomic levels. We analysed the contrasts with a sign test to compare the number of positive and negative correlations (Burt, 1989).

Our second objective was to test whether the traits of central European species permit us to predict their presence or absence in Argentina. For this purpose, we calculated a logistic regression analysis across species with a type III likelihood-ratio test (Statsoft, 1999). We used a cross-validated approach. First, we calculated the logistic regression analysis from a random sample of 50% of the species. Then, we used the resulting logistic regression model to predict the remaining 50% of the species. We repeated this procedure 10 times. We also calculated a logistic regression analysis across all species to determine whether the results agreed with those of the above-mentioned multiple regression analyses.

All analyses were conducted using Statistica software (Statsoft, 1999; procedures ‘multiple regression’ and ‘generalized linear model’).

RESULTS

We recorded 183 alien species of central European origin in the Buenos Aires province and 74 alien species in the Mendoza province. In total, we recorded 197 alien species, representing 11% of the flora indigenous to central Europe. The number of alien species recorded in Argentina that belonged to a particular family reflected the number of species of that family in central Europe: a regression based on the log-transformed numbers for the 20 largest families gave a slope of 1.27. This was not significantly different from 1.00 ($t = 0.79$; FG = 18, $P = 0.22$). However, the dominant families in the alien flora – Poaceae, Asteraceae, Fabaceae, Brassicaceae and Chenopodiaceae – were over-represented compared with the central European flora. In contrast, the species-rich central European Cyperaceae were completely absent from the two Argentine provinces.

Table 2 compares alien status with species traits. In general, the univariate analyses matched the multivariate analyses, and analyses based on species matched analyses based on phylogenetically independent contrasts. We also found general agreement between analyses based on phylogenetically independent contrasts of the ‘CAIC type’ and analyses based on contrasts according to Burt (1989; Table 2). Slightly higher *P*-values in the latter analyses were probably caused by the smaller sample sizes. There was only a clear disparity for niche positions along the light gradient. The analysis by CAIC indicated that aliens prefer very sunny conditions, but the analysis using Burt’s method did not confirm this. Closer inspection of the latter result, however, showed that it was biased. The number of species per contrast varied drastically and more than 60% of the species belonged to contrasts that did confirm the CAIC analysis. Thus, most aliens do prefer sunny conditions.

In the following, we summarize the results of the most informative approach – the multivariate analysis of phylogenetically independent contrasts (Table 2):

1. Aliens are common in central Europe, they are used by humans, but they are not over-represented in anthropogenic vegetation.

Table 2. Relationship between alien status and species traits (see Table 1)

	Species				Phylogenetically independent contrasts					
	Univariate		Multivariate		Univariate				Multivariate	
					CAIC		Burt		CAIC	
Trait	Beta	*P*	Beta	*P*	Beta	*P*	%	*P*	Beta	*P*
1. *Contact with humans*										
Frequency	0.37	<0.001	0.22	<0.001	0.29	<0.001	78	<0.001	0.20	<0.001
Anthropogenic vegetation	0.31	<0.001	0.02	0.306	0.15	<0.001	90	<0.001	−0.08	0.500
Use by humans	0.18	<0.001	0.07	0.018	0.17	<0.001	75	<0.001	0.14	<0.001
2. *Pre-adaptation to abiotic conditions*										
Temperature	0.11	<0.001	0.09	0.014	0.06	0.065	58	0.111	0.11	0.008
Soil moisture	−0.11	<0.001	−0.11	0.004	−0.07	0.050	55	0.184	−0.12	0.004
Light	0.10	<0.001	0.12	<0.001	0.12	0.002	51	0.500	0.15	<0.001
Soil nitrogen	0.21	<0.001	0.17	<0.001	0.15	<0.001	69	<0.001	0.18	<0.001
3. *Ecological versatility*										
Number of floristic zones	0.22	<0.001	0.14	<0.001	0.27	<0.001	82	<0.001	0.18	<0.001
4. *Colonization of disturbed sites*										
Ruderal life strategy	0.21	<0.001	0.11	0.003	0.15	<0.001	60	0.041	0.10	0.009
5. *Dispersal*										
Vertebrate dispersal	−0.02	0.500	−0.06	0.500	0.03	0.221	54	0.425	−0.02	0.500
Wind dispersal	0.03	0.104	0.00	0.500	−0.06	0.500	50	0.500	−0.07	0.500

Note: Data points were either species or phylogenetically independent contrasts of the 'CAIC' type or of the 'Burt' type (see 'Methods'). Analyses of species were by univariate regression ($n \geq 1018$, depending on availability of information on species traits) and multivariate regression ($n = 748$), respectively. Analyses of CAIC contrasts were by univariate regression and multivariate regression ($n = 563$). Analyses of contrasts according to Burt were by sign test ($n \geq 18$; a multivariate analysis is not possible). Beta = standardized regression coefficient (note that the beta values exactly reflect the t-values); % = percentage of correlation coefficients with a sign in the predicted direction; P = one-tailed P-values associated with hypotheses 1–5. These state that alien species are in frequent contact with humans, are pre-adapted to the abiotic conditions in Argentina, are ecologically versatile, can colonize disturbed sites and can disperse their seeds efficiently (see 'Introduction').

2. In central Europe, the aliens grow in warm, dry, sunny and nitrogen-rich environments.
3. In their native range, the aliens occupy many floristic zones.
4. Aliens are characterized by a ruderal life strategy.
5. Aliens are not characterized by vertebrate or wind dispersal.

There was no single trait of outstanding importance – that is, with an outstanding beta value (Table 2). Frequency in central Europe, occurrence in nitrogen-rich conditions and the size of the native range were almost equally important. Ruderal life strategy, however, was less important than the other significant traits. In total, the traits explained 20–21% of the variance of alien status. The variance explained in univariate regressions was, at most, 9%.

Many of the traits were at least moderately correlated to one another ($r > 0.25$; Table 3). In particular, 'occurrence in anthropogenic vegetation' correlated with 'occurrence in warm and nitrogen-rich conditions', with 'ruderal strategy' and with 'frequency'. However, the correlation between traits never exceeded $r = 0.50$: usually it was much less. Correspondingly, the tolerances of independent variables in the above multiple regression analyses were always greater than 0.53. (Tolerance is the variance of an independent variable that is not explicable by all other independent variables together; Statsoft, 1999.) Overall, none of the traits was redundant.

Finally, we analysed the presence and absence of central European species in Argentina by logistic regression analysis. We found that an analysis across all species led to the same results as the above multiple linear regression analyses. The same traits were significant ($P \leq 0.06$). Only 'use by humans' failed. However, 'use by humans' was significant when we restricted the analysis to aliens in the Mendoza province, which is the more agricultural of the two provinces. More importantly, we found that traits of species truly predict their alien status. A logistic regression model calculated for 50% of the species permitted us to correctly predict the alien status of most of the remaining species (Fig. 1). For instance, if we used a predicted alien status of 0.9 as the cut-off point, we found that the model correctly predicted 81% of the aliens and 70% of the non-aliens. Note that in these logistic regression analyses, it was not possible to take into account the phylogenetic relationship among species. Nevertheless, we were confident of the results given that, in our above analyses, it did not matter whether or not phylogeny was taken into account (Table 2).

DISCUSSION

The present study addressed the following question: 'Which species from a species pool become aliens?' Our analysis was much more comprehensive than in previous studies. First, we considered a larger taxon (higher plants) and, second, we considered all aliens outside human cultivation – casual, naturalized and invasive aliens (Richardson *et al.*, 2000b). We found that, even on such a large scale, aliens differ from non-aliens. Despite much unexplained variance, it was possible to correctly predict most of the alien and non-alien species from their traits. The predictive power of our model was clearly better than that of Goodwin *et al.* (1999). These authors were able to correctly predict only 62% of aliens and non-aliens, even though their analysis was restricted to aliens in disturbed sites. It is probable that Goodwin *et al.* considered too few traits. They considered only the four traits available for each European species: life form, stem height, flowering period and European geographic range size. In contrast, we considered an array of species traits. Not only did we consider traits that increase the chance of being introduced into a target region,

Table 3. Correlations between the traits considered in the present study (see Table 1)

	Contact with humans			Pre-adaptation to abiotic conditions						Dispersal	
	Fre-quency	Anthropo-genic vegetation	Use by humans	Tempera-ture	Soil moisture	Light	Soil nitrogen	Eco-logical versatility	Ruderal life strategy	Vertebrate dispersal	Wind dispersal
Frequency	—	0.33	0.12	−0.15	0.12	−0.05	0.27	0.31	0.06	0.03	−0.02
Anthropogenic vegetation	*0.31*	—	0.07	0.40	−0.15	0.17	0.36	0.11	0.40	0.03	−0.02
Use by humans	*0.20*	*0.10*	—	0.00	−0.10	−0.01	0.09	−0.03	−0.19	0.18	−0.10
Temperature	*−0.16*	*0.25*	*−0.11*	—	−0.35	0.24	0.04	−0.17	0.30	−0.01	0.00
Soil moisture	*0.01*	*−0.02*	*−0.06*	*−0.13*	—	−0.10	0.31	0.22	−0.23	−0.07	−0.02
Light	*−0.06*	*0.09*	*−0.03*	*0.19*	*−0.02*	—	−0.22	0.02	0.12	−0.06	0.22
Soil nitrogen	*0.29*	*0.25*	*0.10*	*−0.06*	*0.23*	*−0.28*	—	0.09	0.07	0.11	−0.13
Ecological versatility	*0.38*	*0.22*	*0.02*	*−0.14*	*0.08*	*0.08*	*0.14*	—	0.13	−0.02	−0.05
Ruderal life strategy	*0.09*	*0.30*	*−0.10*	*0.15*	*−0.12*	*0.10*	*−0.02*	*0.14*	—	−0.05	−0.02
Vertebrate dispersal	*0.03*	*0.00*	*0.07*	*−0.04*	*0.00*	*−0.11*	*0.11*	*0.03*	*0.01*	—	−0.50
Wind dispersal	*−0.04*	*−0.02*	*0.00*	*0.01*	*−0.01*	*0.19*	*−0.08*	*−0.04*	*−0.06*	*−0.43*	—

Note: Correlations were calculated either across species as data points ($n \geq 862$, normal font) or across phylogenetically independent contrasts of the CAIC type ($n = 563$, *italics*). For consistency, we only present Pearson correlation coefficients. Analysis by Spearman coefficient would be more appropriate when species were used as data points, but it gave almost identical results.

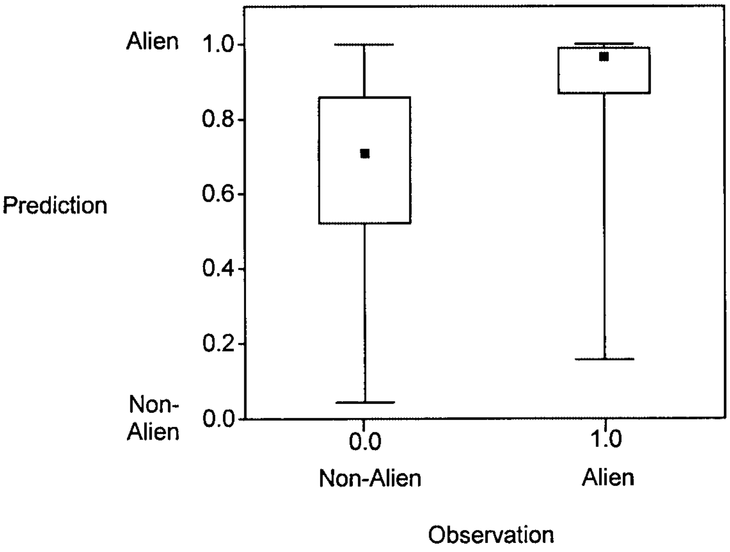

Fig. 1. Observed versus predicted presence of species as aliens in Argentina. Prediction was by logistic regression analysis with cross-validation. The figure summarizes 10 runs of the cross-validation ($n = 10 \times 374$ species). Solid squares are medians; boxes are 25% to 75% percentiles; whiskers are min–max ranges.

we also considered traits that increase the chance of persisting in the target region: to survive casually without human cultivation or even to naturalize and to invade (Richardson *et al.*, 2000b).

It is important to note that the scope of our analysis was biased towards urban habitats. As in most other parts of the world, most of our records of aliens were from urban habitats (Williamson, 1996). We took this 'urban bias' into account when we described the living conditions in Argentina (see 'Methods'). We did not try to restrict our analysis to the few aliens in non-urban habitats. Rather, our intention was to characterize the majority of alien species in a given geographic region and to understand why they became aliens.

Species that come into frequent contact with humans have more chance of being introduced to an alien continent than other species. Indeed, we found that alien species may frequently come into contact with humans, both by chance (common species) and because of human intention (species utilized by humans). 'Occurrence in anthropogenic vegetation', however, did not foster the chance of a species becoming an alien. One possible explanation is multicollinearity. 'Occurrence in anthropogenic vegetation' was correlated with several other relevant traits (Table 3). Such multicollinearity reduces the signal of 'occurrence in anthropogenic vegetation' in multivariate analysis. A variable that is more linearly related to alien status than 'occurrence in anthropogenic vegetation' can have a better fit in the linear regression analysis, even though the effect of 'occurrence in anthropogenic vegetation' may be more directly causal. Another possible explanation is that our definition of 'occurrence in anthropogenic vegetation' may be incorrect. Our definition was based on the central European distribution of species in recent times. This definition may be incorrect for the many species that were introduced more than a 100 years ago, during the main period of colonization from central Europe (Bünstdorf, 1992). At that time, anthropogenic impact on vegetation was much less intense than today (Ellenberg, 1996). Thus, at that time, even species that only tolerate little or moderate anthropogenic impact were abundant in anthropogenic vegetation (Ellenberg, 1996). Even these species came into frequent contact with humans.

Our finding that species utilized by humans had an increased chance of becoming an alien may be case-specific. In our study, many of the aliens were introduced by colonists. Colonists often try to re-establish their original way of life. Therefore, colonists import the plant species they used in their homeland. In other cases, introduction of species by colonists may be much less important. For instance, it may be unimportant for the current introduction of plants species from Argentina to the USA. Overall, the cultural background of species introductions has to be taken into account.

After a species has become successfully introduced to an alien region, it may manage to survive at least casually without human cultivation. Species that are pre-adapted to the abiotic conditions in the alien region have a better chance of survival than other species (Richardson *et al.*, 2000b). Indeed, we found that the central European aliens in Argentina appear to be pre-adapted to the warm, dry, sunny and nitrogen-rich conditions in this country. Several earlier studies demonstrated the climatic match between a species' native range and the alien range (Jäger, 1988; Crawley *et al.*, 1996; Pyšek, 1998). We have additionally shown that the species' niche position within the native range matches the abiotic conditions in the alien range. This contradicts the notion of niche position as primarily a regional phenomenon (Pianka, 1988, Walter and Breckle, 1991).

Species that are ecologically versatile have a better chance of survival and even naturalization in an alien region. We inferred a species' ecological versatility from the width of its biogeographic range across floristic zones (Hengeveld, 1990) and found that species with a wide range were more common among aliens than expected by chance. However, there are three alternative explanations for this observation. First, the wide range of aliens may indicate that they grow in vegetation types with an azonal distribution. That is, the aliens may be restricted to certain ecological conditions that occur throughout a wide biogeographic range, such as wetlands or cold mountain tops (Walter and Breckle, 1991). However, most aliens did not grow under such conditions. Only very few aliens used wet or cold conditions. Second, the wide range of aliens may indicate that they are 'experienced competitors' rather than being ecologically versatile (Huston, 1994). The idea is that species with a wide range encounter many competitor species and adapt to most of them. However, potential competitiveness (C-strategy *sensu* Grime *et al.*, 1988; taken from Frank and Klotz, 1990) proved to be of no importance in characterizing the aliens in Argentina (linear regression analysis based on phylogenetically independent contrasts of the CAIC-type: $R^2 < 0.001$; $n = 563$; $P > 0.40$). Third, a wide biogeographic range may indicate a high abundance (Gaston, 1994). High abundance, in turn, may foster the chance of a species having frequent contact with their inter-continental dispersal vector – that is, humans. Yet, in our multivariate analyses, abundance was already covered by frequency in Eastern Germany. Nevertheless, there is a possibility that a species' prevalence in Eastern Germany is not correlated with the species' abundance across its entire distributional range.

After a species has successfully been introduced to a target region, to survive and to naturalize outside human cultivation, it may invade the target region (Richardson *et al.*, 2000b). Often such invasions start from disturbed sites (Crawley, 1986; Pyšek *et al.*, 1998; Richardson *et al.*, 2000b). Species with a ruderal life strategy thrive at such sites (Rejmánek and Richardson, 1996). Indeed, species with a ruderal strategy were over-represented among the aliens in the two Argentine regions. This indicates that even the invasion stage was important for a species persisting as an alien.

Species that are dispersed by vertebrates or wind may be more efficient at spreading their seeds and thereby invading a target region (Richardson *et al.*, 2000a). However, we found no relationship between dispersal mode and alien status, even though many of the aliens did manage to invade the two Argentine provinces (Söyrinki, 1991). It is possible that these invasive species were dispersed by vectors other than vertebrates or wind. Cars or agricultural machinery, for example, can be important dispersal vectors in anthropogenic landscapes (Strykstra *et al.*, 1997). Moreover, even poor dispersers may have had a chance to invade our study areas. These areas are close to the putative sites of introduction; these introductions mostly took place several decades or even centuries ago (Söyrinki, 1991). Since then, even poor dispersers may have been able to reach our study areas.

In conclusion, we have shown that aliens differ from non-aliens in their species pool. Aliens were common within their source region, utilized by humans, pre-adapted to the abiotic conditions in the target region, ecologically versatile and able to colonize disturbed sites. These traits permitted us to correctly predict 81% of our alien species. Our results suggest that a species' ability to become an alien, and to persist as an alien, does not only depend on its chance of being introduced to the target region; the chances of naturalization and of becoming invasive in the target region are also important.

It was promising to see that the differences between traits of aliens and non-aliens were distinct, even across a large taxon such as higher plants. And the differences were distinct, even when nothing more than the presence or absence of aliens in the target region was known. For many potential target regions, such 'presence/absence' lists of aliens are now available (Daehler, 1998; Pyšek, 1998). However, for many of the potential source regions of the aliens, we still lack information on species traits – the information we need to predict future aliens. There are very few regions in the world where the database on native species is as good as that for central Europe. And even for central Europe, we lack information for a number of species. This is an important message: we first need to improve our knowledge of the attributes of species within their source region if we wish to improve our ability to predict future aliens.

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APPENDIX 1

List of central European plant species found in the provinces of Buenos Aires and Mendoza (1 = found; 0 = not found). Species that were introduced to Europe after 1500 were omitted

Species	Buenos Aires	Mendoza	Species	Buenos Aires	Mendoza
Achillea millefolium	1	0	*Centaurium pulchellum*	1	0
Agrostemma githago	1	0	*Centunculus minimus*	1	0
Agrostis stolonifera	1	1	*Cerastium arvense*	1	0
Aira caryophyllea	1	0	*Cerastium glomeratum*	1	0
Alchemilla vulgaris	1	0	*Chamomilla recutita*	1	0
Alyssum alyssoides	1	0	*Chenopodium album*	1	1
Amaranthus blitum	1	0	*Chenopodium murale*	1	1
Anagallis arvensis	1	0	*Cichorium intybus*	1	1
Anchusa officinalis	1	0	*Cirsium vulgare*	1	1
Anthemis cotula	1	1	*Conium maculatum*	1	1
Anthoxanthum odoratum	1	0	*Convolvulus arvensis*	1	1
Apium graveolens	1	1	*Coronilla varia*	1	0
Apium nodiflorum	1	0	*Crataegus laevigata*	0	1
Arctium minus	1	0	*Crepis capillaris*	1	1
Arenaria serpyllifolia	1	0	*Dactylis glomerata*	1	1
Arrhenatherum elatius	1	1	*Daucus carota*	0	1
Artemisia absinthium	1	0	*Digitaria sanguinalis*	1	1
Asparagus officinalis	0	1	*Dipsacus sylvestris*	0	1
Atriplex patula	1	0	*Echinochloa crus-galli*	1	1
Atriplex prostrata	1	0	*Elytrigia repens*	1	0
Atriplex rosea	1	1	*Erodium cicutarium*	1	1
Avena fatua	1	0	*Erysimum repandum*	1	0
Avena sativa	1	0	*Euphorbia helioscopia*	1	0
Ballota nigra	1	0	*Euphorbia peplus*	1	1
Bellis perennis	0	1	*Euphorbia platyphyllos*	1	0
Bromus arvensis	1	0	*Fallopia convolvulus*	1	1
Bromus commutatus	1	0	*Fallopia dumetorum*	1	0
Bromus hordeaceus	1	1	*Festuca arundinacea*	1	1
Bromus racemosus	1	0	*Festuca pratensis*	0	1
Buglossoides arvensis	1	0	*Fumaria officinalis*	1	0
Bupleurum tenuissimum	1	0	*Fumaria parviflora*	1	0
Cakile maritima	1	0	*Galium aparine*	1	0
Calendula arvensis	1	0	*Galium mollugo*	1	0
Camelina alyssum	1	0	*Galium palustre*	1	0
Camelina microcarpa	1	0	*Geranium dissectum*	1	0
Camelina sativa	1	0	*Geranium molle*	1	0
Capsella bursa-pastoris	1	1	*Geranium robertianum*	1	0
Cardamine hirsuta	1	1	*Gypsophila muralis*	1	0
Carduus acanthoides	1	0	*Hedera helix*	1	0
Carduus nutans	1	1	*Holcus lanatus*	1	0
Centaurea cyanus	1	0	*Holosteum umbellatum*	1	0
Centaurea jacea	1	0	*Hordeum murinum*	1	1
Centaurium erythraea	1	0	*Hypericum perforatum*	1	0

Species	Buenos Aires	Mendoza	Species	Buenos Aires	Mendoza
Hypochoeris glabra	1	0	*Populus nigra*	0	1
Hypochoeris radicata	1	1	*Portulaca oleracea*	1	1
Iris pseudacorus	1	0	*Prunella vulgaris*	1	0
Juncus balticus	0	1	*Quercus pubescens*	0	1
Juncus bufonius	1	0	*Quercus robur*	0	1
Lactuca saligna	1	0	*Ranunculus bulbosus*	1	0
Lactuca serriola	1	1	*Ranunculus repens*	1	1
Lamium amplexicaule	1	1	*Raphanus raphanistrum*	1	0
Lapsana communis	1	0	*Rapistrum rugosum*	1	1
Leontodon hispidus	0	1	*Reseda luteola*	1	0
Leontodon taraxacoides	1	1	*Rhamnus cathartica*	1	0
Leucanthemum vulgare	1	0	*Rorippa palustris*	1	0
Lolium perenne	1	1	*Rubus plicatus*	1	0
Lolium temulentum	1	0	*Rumex acetosella*	1	1
Lotus corniculatus	1	0	*Rumex conglomeratus*	1	1
Lotus tenuis	1	0	*Rumex crispus*	1	1
Lychnis flos-cuculi	1	0	*Rumex obtusifolius*	1	0
Lythrum hyssopifolia	1	0	*Sagina ciliata*	1	0
Malva neglecta	1	0	*Sagina procumbens*	1	0
Malva sylvestris	1	0	*Salsola kali*	1	0
Marrubium vulgare	1	1	*Salsola ruthenica*	0	1
Medicago lupulina	1	1	*Saponaria officinalis*	1	0
Medicago minima	1	0	*Sarothamnus scoparius*	1	0
Melilotus alba	1	1	*Scleranthus annuus*	1	0
Melilotus officinalis	1	1	*Senecio vulgaris*	1	0
Mentha aquatica	1	1	*Setaria italica*	1	0
Mentha pulegium	1	0	*Setaria verticillata*	1	1
Mentha suaveolens	1	1	*Setaria viridis*	1	1
Myosotis caespitosa	1	0	*Sherardia arvensis*	1	0
Nasturtium officinale	1	1	*Silene dioica*	1	0
Neslia paniculata	1	0	*Silene pratensis*	1	0
Onopordum acanthium	1	1	*Silene vulgaris*	1	0
Papaver dubium	1	0	*Sinapis arvensis*	1	0
Papaver rhoeas	1	0	*Sisymbrium officinale*	1	1
Parietaria officinalis	1	0	*Sonchus asper*	1	1
Pastinaca sativa	1	1	*Sonchus oleraceus*	1	1
Phalaris arundinacea	1	0	*Spergula arvensis*	1	0
Phleum pratense	1	0	*Spergularia maritima*	1	0
Plantago lanceolata	1	1	*Spergularia rubra*	1	0
Plantago major	1	1	*Stachys arvensis*	1	0
Poa annua	1	1	*Stellaria media*	1	1
Poa compressa	1	0	*Tanacetum vulgare*	1	0
Poa pratensis	1	1	*Taraxacum laevigatum*	1	0
Poa trivialis	1	0	*Taraxacum officinale*	1	1
Polygonum aviculare	1	1	*Tragopogon dubius*	1	0
Polygonum persicaria	1	0	*Tragopogon pratensis*	1	1
Populus alba	0	1	*Trifolium dubium*	1	0

Species	Buenos Aires	Mendoza	Species	Buenos Aires	Mendoza
Trifolium pratense	1	1	*Veronica polita*	1	0
Trifolium repens	1	1	*Veronica scutellata*	1	0
Urtica dioica	1	0	*Veronica serpyllifolia*	1	0
Urtica urens	1	1	*Vicia angustifolia*	1	0
Vaccaria hispanica	1	0	*Vinca minor*	1	0
Valerianella locusta	1	0	*Viola arvensis*	1	0
Verbascum thapsus	1	1	*Vulpia bromoides*	1	0
Veronica anagallis-aquatica	1	0	*Vulpia myuros*	1	0
Veronica arvensis	1	0			

APPENDIX 2

References from which we compiled the phylogeny used to calculate phylogenetically independent contrasts.

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