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Is there a taxonomic pattern to plant invasions?

Petr Pyšek

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Alien floras of 26 regions distributed over the globe and covering a variety of habitats were analysed to assess the role of plant families and higher taxonomic units. Alien species were recorded in 164 families. The highest concentration of families containing aliens was recorded in Caryophyllidae (namely Caryophyllales) and Asteridae. The largest families (Gramineae, Compositae, Leguminosae, Cruciferae) contribute most to the total number of alien species in local floras. In relative terms, i.e. related to the species pool available as potential invaders, the best invaders belong to Papaveraceae, Chenopodiaceae, Amaranthaceae, Cruciferae, Polygonaceae and Gramineae. Some families depend largely on deliberate introductions of crops and ornamental species, while the representation of others is enhanced when only accidental introductions are considered. The adventive distribution of families, i.e. the regions into which their members tend to invade, reflects their natural distribution. Particular families tend to invade in the regions with conditions similar to those from their native area. The most successful families possess specific features that could be attributed to their invasiveness. However, there is no simple morphological, physiological or ecological character that could be generally related to the invasiveness of the family.

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Various efforts to generalize the information available on invasive species have been made, mostly concerned with analysing their biological and ecological properties (Newsome and Noble 1986, Noble 1989, Roy 1990, Pyšek et al. 1995, Thompson et al. 1995, Williamson 1996). Attempts have also been carried out to attribute the invasiveness of a species to its taxonomic position, i.e. the higher taxonomical units, and it has been suggested that taxonomic composition of alien floras is a distinctly non-random sample from the pool of available immigrants (Crawley 1987). However, the studies available so far on this issue (Crawley 1987, Rejmánek et al. 1991, Weber 1997) analysed a single data set from one region. Heywood (1989) put the issue into a broader perspective and pointed out that any global survey of the pattern and extent of invasion is bound to be anecdotal to a degree because of the extreme diversity in the sources and unreliability of the available data. Despite special taxonomic problems associated with alien species such as increased possibility of misidentification and the absence of agreed taxonomy between countries (Heywood 1989, Palmer et al. 1995), and difficulties concerning the assessment of species immigration status (Webb 1985, Pyšek 1995a) it seems useful to analyse the available information.

The membership of a particular family reflects a species' evolutionary history and the biological properties that may be expected to affect its performance under particular ecological conditions. The same features that made it possible for evolutionarily advanced families to dominate the present-day world vegetation could be expected to enhance their success as invaders (Heywood 1989). However, quantitative data are needed to test this prediction and a proper relative measure must be applied since a high absolute number of invaders may reflect only a high number of representatives of a given family in the world flora.

The majority of papers on plant invasions focus on the taxonomic level of species; this paper analyses the issue from the viewpoint of higher taxonomical units,

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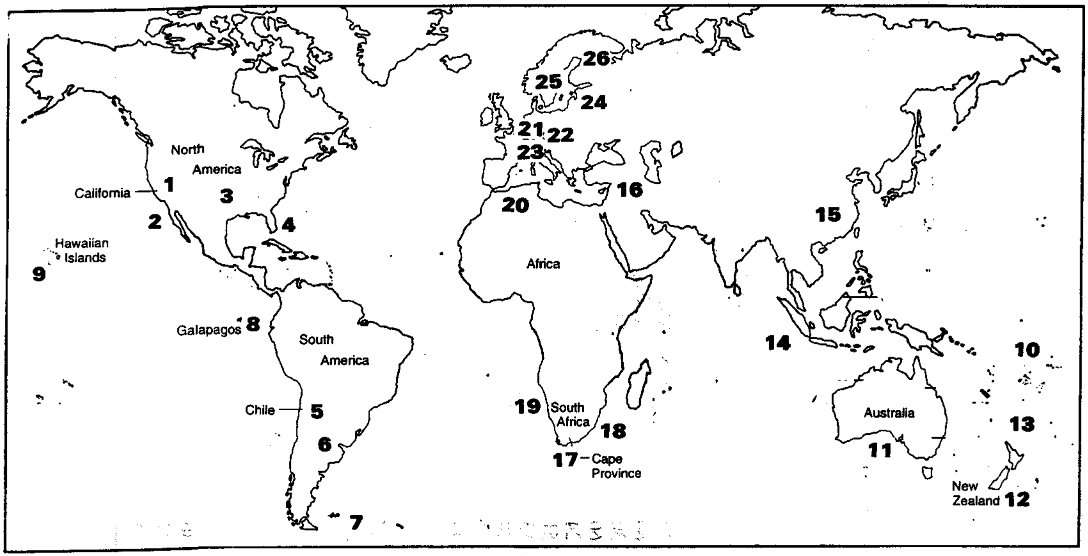

Fig. 1. The world showing geographical locations of alien floras analysed in the present paper. See Table 1 for numbering and characteristics of particular regions.

families in particular (see also Williamson and Brown 1986, Crawley 1987, Heywood 1989, Weber 1997). It aims to (1) gather scattered data on the participation of particular families in the alien floras worldwide, to assess (2) the invasive potential of particular families, and (3) geographical and ecological factors affecting their success in various parts of the globe. Special attention is paid to European species for reasons that are both historical (the most pronounced plant invasions have their roots in Europe, e.g. di Castri 1989) and ecological (European species are considered to have high invasive potential).

Data sources and analysis

I gathered complete lists of alien species from 26 regions (Table 1, Fig. 1). When comparing alien floras, one must cope with the different approach of particular authors to alien species; this is particularly difficult when working with standard floras (Webb 1985, Heywood 1989). For that reason, only studies dealing specifically with alien species and providing their complete lists were considered. The data vary in terms of geographical location and climate, and provide a reasonable global coverage. They include major hot spots of plant invasion in the contemporary world (see Pyšek 1995b). Hence they provide insight into the variety of alien floras all over the world (Table 1). The regions considered also vary remarkably in area (Table 1). This is not a limitation to the purpose of the present study since it is focused on proportions. Further, being aimed at obtaining data from a wide range of environments, the present study considers both data from natural and urban habitats. Nevertheless, the majority of studies represent complete species list from the whole area, thus covering all habitats (Table 1).

In each data set, I classified species into families following Cronquist's system (Mabberley 1987) and calculated the percentage contribution of the family to the total of the respective alien flora. The average value was then calculated for each family and taken as a quantitative measure of its proportional representation in the world's alien floras. Only those families whose proportional representation in alien flora in at least one data set either (a) reached at least 3% and/or (b) were represented by at least 10 alien species were analysed in more detail. This screening yielded 40 families (Table 2).

The immigration status of the species was taken from the original source (Table 1). Throughout the text, the terms alien and invasive are equivalent (Pyšek 1995a).

Proportional representation of particular families in the world flora was calculated on the basis of species numbers given by Mabberley (1987). For the European flora, the data were obtained by calculating species numbers in Flora Europaea (Tutin et al. 1964–1980); in species-poor families (up to 15 species) introduced species were excluded to obtain exact data on the native species pool whereas in large species-rich families the aliens were regarded as contributing negligibly to the total species number and hence were neglected.

For each data set (region) considered, I gathered information on continent, latitude, mean annual temperature and annual precipitation. The latter two were obtained (if not given in original sources) from climate diagrams (Walter and Lieth 1967) by computing the average values from climate diagrams of all stations located in the area to which the list of aliens was related.

Table 1. Data sets used in the present paper. Number of recorded aliens, and number of families containing alien species are shown (? means that the latter was impossible to infer from the original source). The area covered by the respective study is shown if available (* indicates that it was estimated from a figure provided by the original source). Habitat types to which the particular lists are related: all – data from all habitats encountered in the study region, urban – only urban habitats considered, natural – only natural habitats considered.

No.	Location	Habitats studied	Area (km^2)	No. of alien species	Number of families	Source
1	California (state)	all	411 031	975	?	Rejmánek et al. 1991
2	Hastings Reserve, California	natural	9	143	28	Knops et al. 1995
3	St Louis, Missouri (city)	urban	not given	393	58	Muehlenbach 1979
4	SE Florida	all	170 000*	169	60	Austin 1978
5	Chile (mediterranean zone)	all	not given	128	30	Montenegro et al. 1991
6	Buenos Aires (province)	all	307 563	483	60	Söyrinki 1991
7	Subantarctic Islands	all	276	112	24	Walton 1975, Carcaillet 1993
8	Galapagos	all	8100	126	51	Macdonald et al. 1988
9	Hawaii	all	20 000	813	113	Wester 1992
10	Northern Line Islans	all	413	90	28	Wester 1985
11	South Australia (state)	all	984 000	904	?	Kloot 1991
12	New Zealand, SW South Island	all	150 000*	140	40	Johnson 1982
13	Auckland, New Zealand (city agglomeration)	urban	not given	615	103	Esler 1987
14	Singapore (state)	all	636	136	45	Corlett 1988
15	Hong kong (state)	all	1074	144	44	Corlett 1992
16	Israel (state)	all	20 700	122	25	Dafni and Heller 1990
17	Cape of Good Hope Reserve, South Africa	natural	78	77	28	Macdonald et al. 1987
18	Kruger National Park, South Africa	natural	19 485	113	43	Macdonald and Gertenbach 1988
19	SW Africa/Namibia	natural	800 000*	164	37	Brown and Gubb 1986
20	Africa N of Sahara	all	6 000 000	86	35	Le Floch et al. 1990
21	Germany (state)	all	356 910	595	73	Frank and Klotz 1990
22	Brno, Czech Republic (city)	urban	200	424	45	Grüll 1979
23	Leipzig, Germany (city)	urban	141	583	68	Gutte 1989
24	Riga, Latvia (city)	urban	300	172	30	Schultz 1977
25	Kärsö-Högholmen Island, Sweden	all	2	57	27	Holmberg 1975
26	NE Finland	all	8100	239	35	Ahti and Hämet-Ahti 1971

Table 2. Proportional representation (in %) of particular families in the floras analysed. The proportion of the family in the total world (WorProp) and European (EurProp) floras is also shown; n = total number of species. The mean proportional representation (AliProp) in 26 alien floras is followed by the sign showing the comparison with the family contribution to the total world flora: + over-represented as aliens (i.e. AliProp > WorProp), – under-represented as aliens (i.e. AliProp < WorProp). The last column displays the maximum number of alien species recorded in a single alien flora. Only those families are shown whose contribution to the alien flora in at least one region was at least 3% or were represented by at least 10 alien species in at least one region. Systematic position (D-Dicots, M- Monocots; subclasses and orders abbreviated by the first letters of their Latin names) is indicated.

Family	Abbreviation	Systematic position			Proportion in the flora		Proportion in the alien floras analysed (AliProp)			Presence in the alien floras analysed		Maximum number of alien species
		Cl	Subcl	Order	WorProp (n = 250 948)	EurProp (n = 11 240)	Mean.	S.D.	Max	Number (max. 26)	%	
Gramineae	Gram	M	Com	Cyp	3.2	7.8	15.31+	5.79	28.67	26	100.0	151
Compositae	Comp	D	Ast	Ast	8.4	14.4	13.47+	4.06	19.64	26	100.0	142
Leguminosae	Leg	D	Ros	Fab	6.5	7.5	8.68+	4.39	21.32	25	96.2	83
Cruciferae	Cruc	D	Dil	Cap	1.2	5.7	5.12+	3.84	13.37	23	88.5	60
Solanaceae	Sol	D	Ast	Sol	1.0	0.2	3.34+	2.45	9.76	24	92.3	29
Chenopodiaceae	Chen	D	Car	Car	0.5	1.4	3.02+	3.15	12.79	22	84.6	36
Caryophyllaceae	Car	D	Car	Car	0.8	5.8	2.96+	2.19	7.14	22	84.6	34
Amaranthaceae	Ama	D	Car	Car	0.3	0.2	2.37+	2.77	9.76	17	65.4	13
Labiatae	Lab	D	Ast	Lam	2.2	4.0	2.30	1.43	5.26	23	88.5	25
Scrophulariaceae	Scro	D	Ast	Scro	1.8	4.6	2.21+	1.44	5.26	23	88.5	27
Euphorbiaceae	Euph	D	Ros	Euph	3.1	1.0	2.18–	1.68	6.50	21	80.8	20
Polygonaceae	Pol	D	Car	Pol	0.4	0.9	1.97+	1.44	5.86	22	84.6	21
Rosaceae	Ros	D	Ros	Ros	1.2	4.2	1.93+	2.32	9.21	17	65.4	35
Malvaceae	Mal	D	Dil	Malv	0.6	0.4	1.77+	1.69	7.14	20	76.9	13
Umbelliferae	Umb	D	Ros	Api	1.2	3.8	1.75+	1.40	5.36	20	76.9	21
Liliaceae	Lil	M	Lil	Lil	1.8	3.7	1.58	2.73	14.04	19	76.1	27
Convolvulaceae	Con	D	Ast	Sol	0.7	0.5	1.37+	1.19	4.88	21	80.8	17
Ranunculaceae	Ran	D	Magn	Ran	0.7	2.8	1.31+	1.76	7.02	14	53.8	13
Rubiaceae	Rub	D	Ast	Rub	4.3	2.1	1.27–	1.01	3.68	19	73.1	10
Verbenaceae	Verb	D	Ast	Lam	0.8	0.1	1.20+	1.21	3.97	17	65.4	13
Boraginaceae	Bor	D	Ast	Lam	1.0	2.3	1.14	0.71	2.23	21	80.8	15
Cyperaceae	Cyp	M	Com	Cyp	1.4	2.3	1.04–	1.06	3.33	17	65.4	21
Myrtaceae	Myr	D	Ros	Myrt	1.5	0.0	1.03–	2.18	10.39	9	34.6	11
Geraniaceae	Ger	D	Ros	Ger	0.3	0.7	1.03+	1.25	4.20	14	53.8	23
Papaveraceae	Pap	D	Magn	Pap	0.1	0.4	0.94+	1.38	7.02	17	65.4	7
Oxalidaceae	Oxa	D	Ros	Ger	0.2	0.1	0.91+	0.90	3.49	18	69.2	8
Onagraceae	Ona	D	Ros	Myrt	0.3	0.4	0.71+	0.74	2.44	15	57.5	12
Urticaceae	Urt	D	Ham	Urt	0.4	0.2	0.58	0.71	3.33	15	57.5	7
Juncaceae	Jun	M	Com	Junc	0.1	0.7	0.55+	1.09	4.29	10	38.5	14
Cactaceae	Cac	D	Car	Car	0.7	0.0	0.50	1.14	5.49	8	30.8	9
Crassulaceae	Cras	D	Ros	Ros	0.5	1.0	0.48	0.78	3.51	12	46.2	7
Acanthaceae	Aca	D	Ast	Scro	1.7	0.0	0.48–	0.98	3.68	6	23.1	13
Iridaceae	Iri	M	Lil	Lil	0.7	0.9	0.44–	0.84	3.58	10	38.5	22
Aizoaceae	Aiz	D	Car	Car	1.0	0.0	0.41–	0.74	3.25	11	42.3	14
Passifloraceae	Pass	D	Dil	Viol	0.2	0.0	0.40+	0.68	2.38	8	30.8	10
Pinaceae	Pin	Pinopsida			0.1	0.4	0.39+	1.06	5.19	7	26.9	4
Fumariaceae	Fum	D	Magn	Pap	0.2	0.5	0.38+	0.71	3.13	8	30.8	8
Nyctaginaceae	Nyc	D	Car	Car	0.1	0.0	0.34+	0.75	3.33	8	30.8	3
Tiliaceae	Til	D	Dil	Malv	0.3	0.1	0.31	0.76	3.54	6	23.1	4
Melastomataceae	Mel	D	Ros	Myrt	1.9	0.0	0.10–	0.37	1.72	2	7.7	14

Table 3. Higher systematic units ranked according to the proportion of families containing alien species (based on 26 alien floras analysed). Data for "invasive" families concern the 40 families most represented in alien floras whose contribution to the alien flora in at least one region was at least 3% or which were represented by at least 10 alien species in at least one region. The system of Cronquist (1981) is followed. Only orders and subclasses with more than 5 families are listed.

Order/subclass/class	Total number of families in order/class	Number of families with aliens		Percentage of families with aliens	
		all	invasive	all	invasive
Caryophyllales	12	10	6	83.3	50.0
Urticales	6	5	1	83.3	16.7
Scrophulariales	11	7	2	63.6	18.2
Solanales	7	4	2	57.1	28.6
Myrtales	12	6	3	50.0	25.0
Sapindales	17	8	0	47.1	0.0
Liliales	15	7	2	46.7	13.3
Violales	24	11	1	45.8	4.2
Zingiberales	7	3	0	42.9	0.0
Ranunculales	8	3	1	37.5	12.5
Celastrales	10	3	0	30.0	0.0
Campanulales	7	2	0	28.6	0.0
Rosales	24	6	2	25.0	8.3
Najadales	10	2	0	20.0	0.0
Polygalales	7	1	0	14.3	0.0
Laurales	8	1	0	12.5	0.0
Ericales	8	1	0	12.5	0.0
Theales	18	2	0	11.1	0.0
Magnoliales	10	1	0	10.0	0.0
Santalales	10	0	0	0.0	0.0
Caryophyllidae	14	12	7	85.7	50.0
Asteridae	47	26	9	55.3	19.1
Hamamelidae	24	11	2	45.8	8.3
Liliidae	19	8	2	42.1	10.5
Commelinidae	24	9	3	37.5	12.5
Alismatidae	16	6	0	37.5	0.0
Rosidae	112	40	10	35.7	8.9
Dilleniidae	78	26	4	33.3	5.1
Magnoliidae	38	11	3	28.9	7.9
Dicots	313	126	35	40.3	11.2
Monocots	64	26	5	40.6	7.8

These environmental variables were used as predictors in multiple regression testing the factors affecting the representation of particular families in alien floras. Data were further analysed by means of regression analysis and analysis of variance (Sokal and Rohlf 1981).

The following measures are used for particular families: WorProp (world proportional representation) = number of species in the family worldwide divided by the total number of species in the world's flora; EurProp (European proportional representation) = number of species in the family in Europe divided by the total number of species in the European flora; AliProp (proportional representation in alien flora) = number of family representatives in the alien flora of the region divided by the total number of alien species in the region; AliRat (alien ratio) = number of family representatives in the alien flora of the region divided by the number of species in the family worldwide.

The phylogenetic lineage of families was established according to Chase et al. (1993), using their second search. Families were mapped on the tree (see e.g. van Groenendael et al. 1996) with respect to their invasiveness.

Results

Representation of families in the world's alien floras

In total, 164 families (i.e. 42.3% of the number of families in the world flora) were found to have at least one invasive representative somewhere. Regarding higher taxonomic units, these 164 families are rather unevenly distributed within the system of higher plants. Among Caryophyllales and Urticales, alien species are present in more than 80% of families and in the other 7 orders more than 40% of their families contain aliens. If only "invasive" families (i.e. those 40 with highest representation of aliens) are considered, Caryophyllales again exhibits a remarkable concentration (Table 3). Consequently, Caryophyllidae represents by far the most "invasive" subclass, both in terms of complete data and selected "invasive" families. The proportion of families with invasive species is also high in Asteridae. There is no difference between dicotyledons and monocotyledons in the number of families containing alien species (Table 3).

The distribution of "invasive" families in the phylogenetic tree is illustrated in Fig. 2. Although invasive families are scattered over the tree, some phylogenetic pattern is indicated with the "invasive" families concentrated in Caryophyllidae and in the most advanced groups of Asteridae (in the sense of Chase et al. 1993). Further down the tree, among monocots, invasibility seems to be typical of a group of commelinoid families.

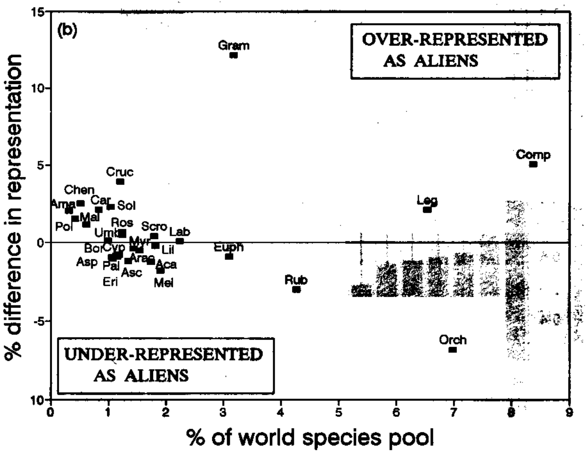

Fig. 3. The difference between the mean proportional representation of the family in alien floras and its representation in the world flora (AliProp-WorProp) is plotted on the y-axis. On the x-axis, families are ranked according to their representation in the world flora (WorProp). Only families contributing at least 1% to the world flora or showing the difference of at least 1% are displayed. Arac – Araceae, Asc – Asclepiadaceae, Asp – Aspleniaceae, Eri – Ericaceae, Orch – Orchidaceae, Pal – Palmae; for abbreviations of names of the other families see Table 2.

The most represented families in the world alien floras are ranked in Table 2, with Gramineae, Compositae, Leguminosae and Cruciferae appearing on top (these appear regularly among the most represented in analyses of alien floras from particular regions, see e.g. Crawley 1987, Weber 1997). The former two are the only families present in each alien flora considered ($n = 26$), with another 13 families occurring in at least 20 data sets, i.e. in more than 75% of alien floras (Table 2). A comparison of the proportional representation among alien floras (AliProp) with its proportion in the world flora (WorProp) (Table 2) reveals the same large families being remarkably over-represented among aliens, whereas others of the world's species-richest families, i.e. Rubiaceae and especially Orchidaceae are strongly under-represented (Fig. 3).

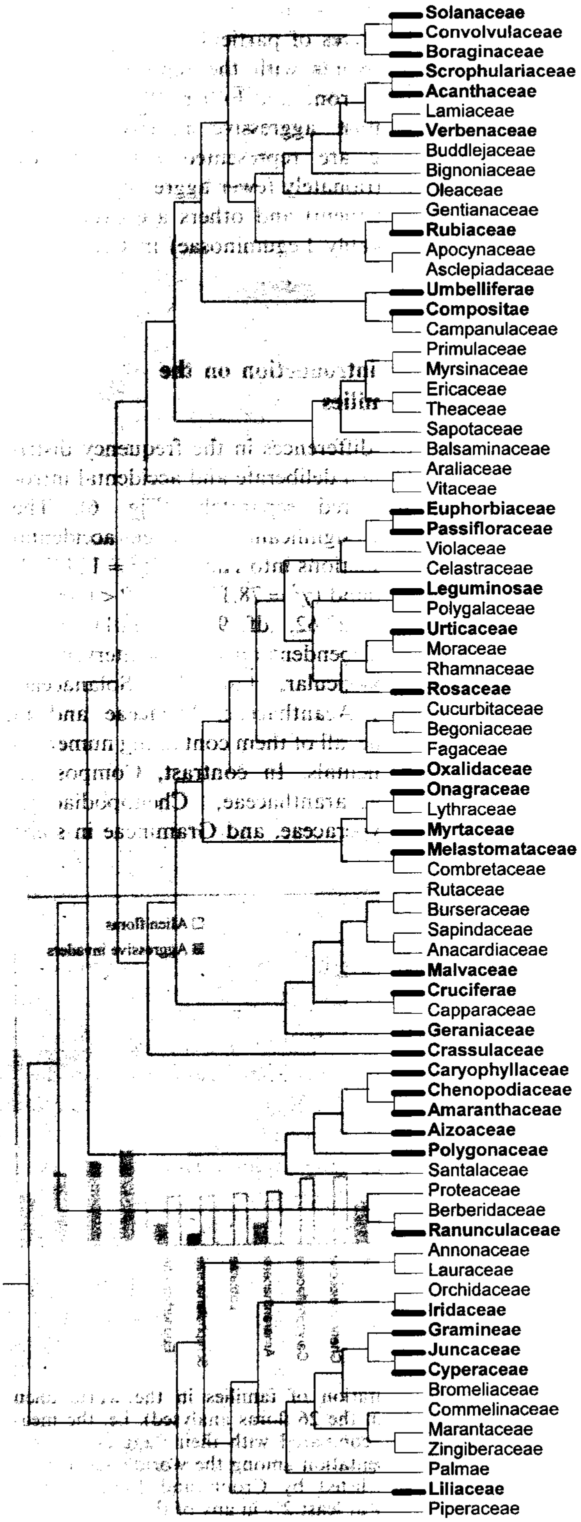

Fig. 2. Phylogenetic tree of angiosperm families, showing their invasiveness. Phylogeny based on Chase et al. (1993). Families that were considered as "invasive" in the context of the present study (i.e. those families whose contribution to the alien flora in at least one of the regions considered was at least 3% or which were represented by at least 10 alien species in at least one region) are distinguished by thick lines and bold type. Only families consisting of at least 500 species are displayed.

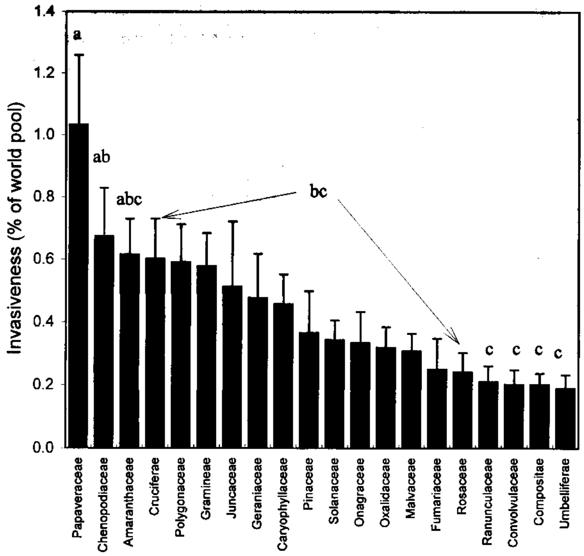

Fig. 4. Families ranked according to their invasiveness on a global scale. The measure used is ratio of aliens to the pool of potential invaders (AliRat); mean values of 26 alien floras analysed are displayed. Only the 20 highest ranked families are shown. Means bearing the same letters were not significantly different in pairwise comparisons (multiple range analysis, Tukey's test, $P < 0.05$).

This measure, however, reflects the absolute number of species in a family because the over- or under-representation is more apparent in large families (simply because their proportional representation in both alien floras and world flora is higher than that of species-poor families and so is the difference between both measures).

Particular families, however, differ in species number and thus the potential size of the pool of alien species is different for each family. To find out whether or not the resulting figures on the proportion of particular families in alien floras (AliProp – Table 2) are only reflecting the fact that species-rich families, in global terms, possess more invaders, the data must be compared with this pool. Hence the best measure of family invasiveness is a ratio (AliRat) of its alien representatives that have naturalized in the given region to the total number of species in the family (Rejmánek et al. 1991), i.e. to the pool of potential invaders. If this measure was used, significant differences between families were revealed by one-way ANOVA ($F_{38,897} = 7.28$, $P < 0.0001$). The most successful family, in global terms, is Papaveraceae; on average more than 1% of the 210 species (Mabberley 1987) appear as aliens and this family differs significantly from all the others but Chenopodiaceae and Amaranthaceae. Cruciferae, Polygonaceae and Gramineae are other families with a value exceeding 0.6% (Fig. 4).

Representation of families among the world's most aggressive invaders

The results presented so far were not taking into account the invasive success, in terms of abundance and spread, of representatives of particular families. Fig. 5 compares the alien floras with the representation of families in the list of Cronk and Fuller (1995), containing the world's most aggressive invasive species. Whereas Gramineae are represented equally, some families have proportionately fewer aggressive invaders (Compositae among them) and others are over-represented (most remarkably Leguminosae) in Cronk and Fuller's list.

Effect of mode of introduction on the performance of families

There are profound differences in the frequency distribution of families when deliberate and accidental introductions are considered separately (Fig. 6). The distributions differed significantly between accidental and deliberate introductions into Hawaii ($\chi^2 = 154.7$, df 9, $P < 0.0001$), Auckland ($\chi^2 = 78.15$, df 9, $P < 0.0001$), and Singapore ($\chi_2 = 22.62$, df 9, $P < 0.01$). Some families are heavily dependent on human intervention, Leguminosae in particular, but also Solanaceae, Rosaceae, Liliaceae, Acanthaceae, Iridaceae and in some areas Gramineae, all of them containing numerous crops and/or ornamentals. In contrast, Compositae, Caryophyllaceae, Amaranthaceae, Chenopodiaceae, Scrophulariaceae, Cyperaceae, and Gramineae in some

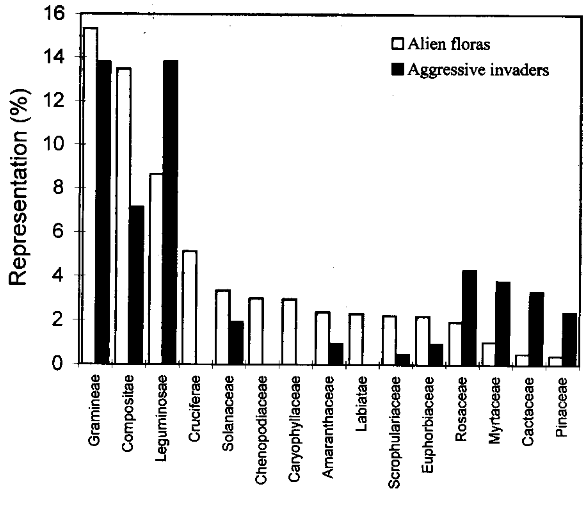

Fig. 5. Total representation of families in the world alien floras (mean value from the 26 floras analysed), i.e. the measure of their richness, compared with their "aggressiveness" expressed as the representation among the world's most invasive aliens, i.e. those listed by Cronk and Fuller (1995). Families represented by at least 2% in any of the two data sets are shown.

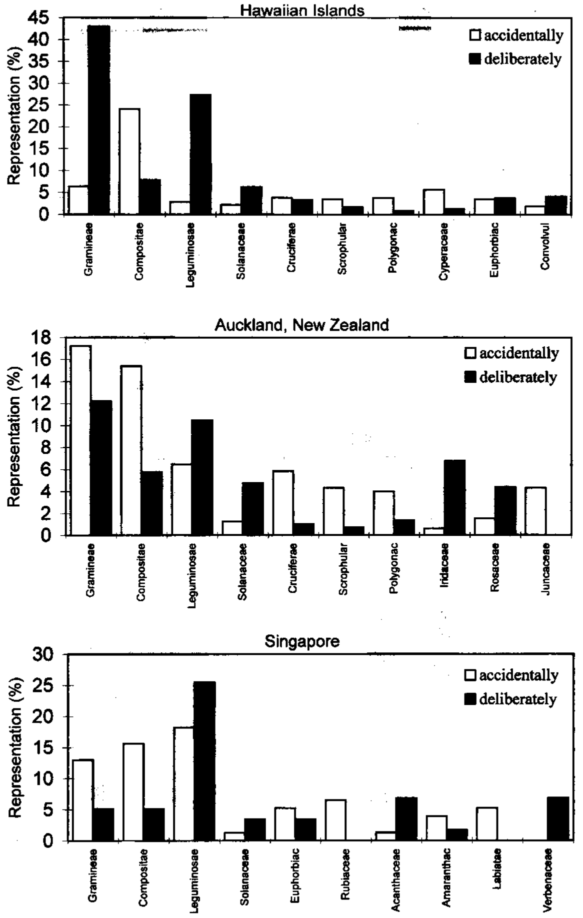

Fig. 6. The proportional representation of families (AliProp) among accidentally vs deliberately introduced alien species expressed for three regions where information on the mode of introduction was available. The first 10 most represented families (regardless of introduction mode) are shown for each region. See text for statistics.

areas are more strongly represented in accidentally introduced alien floras (Table 4).

European species as aliens elsewhere

In those data sets where region of origin was indicated, European species constitute on average 58.9% of the aliens present which is in sharp contrast to the 4.4% contribution of European species to the world flora.

At the family level, the preponderance of European species among world aliens is reflected in a much closer correlation between representation of families in alien floras (AliProp) and that in the European flora (EurProp) ($F_{1,162} = 494.7$, $P < 0.0001$, $r = 0.87$, i.e. 75.3% of variance explained) than in the world's flora (WorProp) ($F_{1,162} = 138.34$, $P < 0.0001$, $r = 0.68$, 46.1%). This indicates that families typical of European flora contribute to the global invasive pool disproportionately more than expected from the proportion of particular families in the world's flora.

Using the relative measure, i.e. the percentage of the total number of European species recorded in the area as aliens, yielded much higher values than comparing the total list of aliens in the given area with the world pool (AliRat) (Fig. 7). With some exceptions, however, the ranking of families is similar regardless of whether expressed in European or global terms; both measures were significantly correlated (Kendall rank correlation coefficient) in Auckland ($P < 0.01$), Buenos Aires ($P < 0.01$), and California ($P < 0.05$). The correlation was marginally significant in Hawaii ($P = 0.063$) and non-significant for Chile ($P = 0.267$).

Table 4. Comparison of families with respect to the mode of introduction. A relative measure (in %) is given showing whether the representation of the family among accidental introductions considered separately is higher (positive values) or lower (negative values) if compared to the representation of the family in the total alien flora of the region (= 100%). The value −100% means that all representatives of a given family were introduced deliberately. Families showing inconsistent trend are not displayed.

Auckland	Hawaii	Singapore	
Alien species number	615	813*	136
Introduced accidentally	325	316	77
Introduced deliberately	295	481	59
Families supported by accidental introductions:			
Amaranthaceae	+89.2	+114.4	+32.5
Caryophyllaceae	+89.2	+157.3	+76.6
Compositae	+41.2	+105.8	+41.3
Cyperaceae	+74.7	+120.5	+76.6
Euphorbiaceae	+5.1	+41.5	+17.7
Rubiaceae	+89.2	+105.8	+76.6
Scrophulariaceae	+65.6	+76.9	+76.6
Urticaceae	+89.2	+28.6	+76.6
Cruciferae	+63.4	+54.4	
Geraniaceae	+89.2	+114.4	
Chenopodiaceae	+89.2	+63.7	
Juncaceae	+26.2	+157.3	
Malvaceae	+41.9	+63.7	
Onagraceae	+41.9	+14.3	
Polygonaceae	+44.7	+105.8	
Ranunculaceae	+26.2	+105.8	
Families supported by deliberate introductions:			
Aizoaceae	−100.0	−100.0	
Crassulaceae	−52.7	−100.0	
Liliaceae	−100.0	−100.0	
Myrtaceae	−100.0	−100.0	
Papaveraceae	−100.0	−100.0	
Passifloraceae	−100.0	−100.0	
Pinaceae	−100.0	−100.0	
Acanthaceae	−100.0	−100.0	−64.7
Leguminosae	−23.6	−69.9	−14.7
Rosaceae	−47.4	−100.0	−100.0
Solanaceae	−57.9	−28.0	−41.1

* Mode of introduction is not known for some Hawaiian aliens so the sum of accidentally and deliberately introduced species is not equal to the total number of aliens.

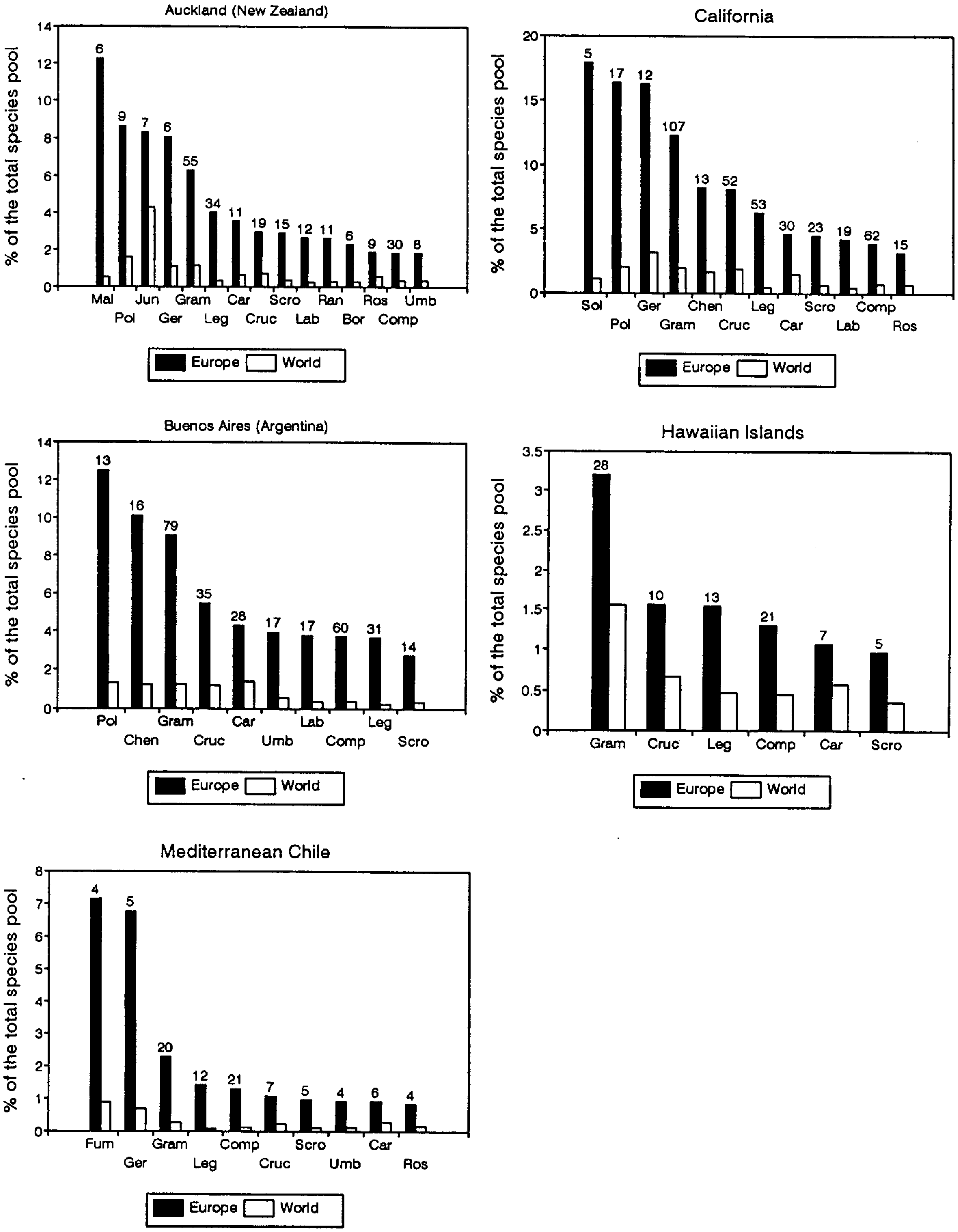

Fig. 7. Invasive potential of European representatives of particular families. Representation of European species in each of the five alien floras is expressed as the ratio to the total number of the family representatives in European flora and compared with the ratio of aliens to the world pool of potential invaders (AliRat). Correlation between both measures (European and global) using Kendall rank correlation coefficient was: Auckland $r = 0.62$, $P < 0.01$, $n = 15$, Buenos Aires $r = 0.71$, $P < 0.01$, $n = 10$, Chile $r = 0.36$, $P > 0.05$, $n = 10$, California $r = 0.69$, $P < 0.05$, $n = 12$, Hawaii $r = 0.82$, $P < 0.1$, $n = 6$. Only those families are shown which had at least 4 (Chile), 5 (Hawaii, Auckland, California) or 10 (Buenos Aires) aliens of European origin. Number of European aliens are given on top of the bars for each family. Note the different scales on the y-axis. See Table 2 for abbreviations of names of families.

Table 5. Factors affecting the representation of particular families in 26 alien floras analysed (see Fig. 1). The data were analysed using stepwise multiple regression (forward selection) with mean annual temperature, sum of annual precipitation, and the latitude of a given region used as predictors. Significant predictors ($P < 0.05$) are indicated: POS means that the family representation in alien floras is positively correlated with the factor, NEG means negative relationship. Asterisk indicates log-transformed data. Percentage of variability explained by the significant predictors is shown (% var). The effect of continent on the family representation in alien floras was tested using ANOVA (df 6) and the results are displayed in the last column. If ANOVA was significant ($P < 0.05$), the continents on which the family is over-represented in alien floras are listed (between brackets if the effect of continent was only marginally significant, $P < 0.1$). Families whose performance in alien floras cannot be related to any of the factors analysed are not shown in the Table but listed below.

	Temperature	Precipitation	Latitude	% var	Continent
Acanthaceae	—	POS	NEG	72.1	(Asia)
Amaranthaceae	—	—	—	—	(Africa, Asia)
Boraginaceae	NEG	—	—	21.7	
Cactaceae	—	—	—	—	Africa
Caryophyllaceae	NEG	—	—	49.7	
Chenopodiaceae	—	NEG*	—	27.2	
Convolvulaceae	POS	—	—	20.8	Asia, South America, Africa
Cruciferae	NEG	—	—	64.8	Europe, South & North America
Cyperaceae	—	POS	—	30.2	
Euphorbiaceae	POS	—	—	26.8	Asia
Geraniaceae	—	—	POS*	16.9	South & North America, Europe
Juncaceae	NEG*	POS*	—	40.8	Australasia
Labiatae	—	—	POS	17.1	Europe
Leguminosae	—	—	NEG	29.4	
Malvaceae	—	—	NEG	19.1	
Melastomataceae	—	POS*	—	27.3	
Nyctaginaceae	[illegible]	—	NEG*	34.2	
Onagraceae	[illegible]	—	POS*	26.2	
Oxalidaceae	—	—	—	—	Asia, Africa
Papaveraceae	—	NEG*	—	20.7	Europe, South America
Passifloraceae	—	—	NEG	61.1	Asia, Oceania
Polygonaceae	NEG	[illegible]	—	29.2	(Australasia, Europe, America)
Ranunculaceae	NEG*	—	—	45.7	
Rosaceae	NEG	—	—	24.6	(Australasia, Europe, South America)
Rubiaceae	—	POS	—	17.5	
Scrophulariaceae	—	—	POS	30.4	Europe, S America, Australasia
Solanaceae	POS*	NEG*	—	55.0	Africa, Asia
Tiliaceae	—	—	NEG*	25.7	
Umbelliferae	NEG	—	—	34.7	
Urticaceae	—	—	NEG	18.8	
Verbenaceae	—	—	NEG	64.8	Oceania, Asia, Africa

No significant effect was found for the following families: Aizoaceae, Amaranthaceae, Compositae, Crassulaceae, Fumariaceae, Gramineae, Iridaceae, Liliaceae, Myrtaceae, and Pinaceae.

Geographical and ecological factors affecting the success of families

Climatic data and the geographical position (latitude, continent) were used to explain the performance of families in alien floras (Table 5). In 30 families (of 40), their representation in alien floras can be related to some of the factors considered (Table 5). The performance of families with temperate affiliations (e.g. Cruciferae, Juncaceae, Polygonaceae, Ranunculaceae, Umbelliferae) is negatively correlated with increasing temperatures, while some of the rather tropical families (e.g. Melastomataceae, Acanthaceae) are positively correlated with increasing temperatures and/or precipitation, or negatively with latitude (e.g. Leguminosae). The abundance of the largest families (Compositae, Gramineae), extremely successful in terms of percentage contribution to local alien floras, does not seem to be related to any of the predictors used (Table 5).

Discussion

The results concerning representation of families in the world's alien floras are difficult to interpret unequivocally. The concentration of aliens in Caryophyllales (and Caryophyllidae) is striking, and moreover, the order contains four of the highest ranking families when the ratio of aliens to the pool of potential invaders (AliRat) is used (Fig. 4). Of the features characteristic for this group, i.e. unusually high proportion of succulents and halophytes, anomalous secondary thickening, presence of betalains (Cronquist 1970), the former seem to be ecologically most relevant by providing its members with the ability to survive in adverse and disturbed conditions (which alien species must often face, e.g. when transported). However, the ecological interpretation of these results remains on a speculative basis. Obviously, there is no clear link between evolutionary advancement and the number of families with invasive species within a group. Although Asteridae does exhibit a slight concentration of "invasive" families, and the opposite holds for evolutionarily primitive Magnoliidae, the by far highest figure was found in Caryophyllidae, a class on the intermediate level of evolution. Even within the class, the most "invasive" order of Caryophyllales is clearly the most primitive of the four (Cronquist 1970).

Unfortunately, the global floristic information is fairly scattered and uneven and the data are not easily available (Heywood 1989), for which reason any attempt to give a reliable estimate of the number of world invaders is necessarily biased. The data presented here must therefore be considered a preliminary conservative estimate. However, the ranking of the taxonomic units most successful in terms of alien numbers can be explained, at least to some extent, by their biological features. The Compositae is one of the evolutionarily most advanced families (Cronquist 1981), possessing a number of features advantageous in the invasion process, e.g. high reproductive rate, specialized dispersal structures, diversity of metabolic products providing protection from grazing, high level of apomixis, etc. (Heywood 1989, Pyšek 1997). Similarly, successful dispersal mechanisms in Gramineae and Leguminosae together with a highly evolved inflorescence in the former, and an ability to fix atmospheric nitrogen as well as remarkably successful pollination systems in the latter may serve to explain why these families are among the world's leading invaders. Extreme diversity of habits and ecological adaptations is typical of all these families and probably also contributes to their invasion success (Heywood 1989). Considering other successful families (if relative measures are used) the clue for success of some of them may be in their high reproductive rate, long viability of seed or in the C4 photosynthetic pathways in some members of Amaranthaceae and Chenopodiaceae (Cronquist 1970, 1981, Heywood 1989). Papaveraceae exhibits no particular ecological unity but all species have a latex system of alkaloids and include a number of showy garden ornamentals (Cronquist 1970); the latter factor certainly could have played a significant role in the translocation of them throughout the world.

Although at the global level it is difficult to adopt a convenient measure of invasive behaviour which would make it possible to compare invaders in particular regions by using the same criteria, comparison with the list of Cronk and Fuller can be taken as an indication. Some of the families that are most successful in terms of relative species numbers (e.g. Papaveraceae, Chenopodiaceae, Cruciferae) are completely absent from the list of the world's most invasive species, and others (Amaranthaceae, Polygonaceae, Juncaceae) are poorly represented. Obviously, the capability of successfully accompanying humans and becoming an alien is, at the level of families, only weakly related to the ability to become abundant and penetrate massively into native vegetation.

To assess the capability of particular families to become part of alien floras, the mode of introduction should be taken into account (Crawley 1987, Crawley et al. 1996). Deliberate introductions bias our knowledge of the ability of particular species to spread into adventive areas by their own means which could be supposed to reflect better their biological and ecological properties. Clearly, the phase of introduction (i.e. dispersal of a propagule into the new area) is critical for the outcome of the invasion process and being artificially taken through this phase constitutes an advantage for a species. On the other hand, some families (e.g. Compositae, Caryophyllaceae, Amaranthaceae, Chenopodiaceae, Scrophulariaceae, Cyperaceae) appear to be relatively independent of deliberate spread by humans. Some of them possess features that may constitute an advantage for spontaneous spread without human interventions, e.g. dispersal structures, apomictic breeding system, specialized products of secondary metabolism, and adaptation to disturbances (Cronquist 1981).

Species of European origin are considered to have higher invasive potential than aliens from other parts of the world, this phenomenon being explained by the long-lasting common history with humans (di Castri 1989). Results of the present analysis further support this statement about enhanced invasive potential of European species (di Castri 1989). However, one must bear in mind that available data come largely outside the tropics, so that the families with temperate affiliations can be over-represented in the present data set.

The same geographical and climatic factors that affect principally the distribution of plant families on the globe (i.e. temperature, precipitation, latitude, and continent) explain, at least to some extent, the performance of the majority of families in alien floras. The results indicate that particular families hardly overcome their evolutionary and ecological limitations in that they tend to invade in the regions with conditions similar to those in their native area. It appears that the homoclimatic hypothesis formulated at the species level (Panetta and Mitchell 1991, Chicoine et al. 1985) is also valid at the level of higher taxonomic units. In large families that are rather successful as invaders, it is often difficult to predict their invasion success. Their representatives are being widely introduced worldwide (Compositae, Gramineae), some of them are widely planted (e.g. Pinaceae – Richardson and Bond 1991) so that the factors underlying the adventive distribution may be hidden.

Conclusions

1. In total, 164 families (i.e. over 40% of the world total) were recorded to supply alien species to local floras in at least one region worldwide. Invasive families

are unevenly distributed in higher taxonomic units, with a remarkable concentration found in Caryophyllidae (namely Caryophyllales) and Asteridae. In quantitative terms, the "invasiveness" of higher units does not seem to be related to the degree of their evolution.

2. The largest families (Gramineae, Compositae, Leguminosae, Cruciferae) contribute most to the total number of alien species in local floras. If the success is expressed in relative terms, i.e. related to the species pool available as potential invaders, the most invasive species are from Papaveraceae, Chenopodiaceae, Amaranthaceae, Cruciferae, Polygonaceae and Gramineae. The most successful families possess some features that could be attributed to their invasiveness, but these are rather complex and there is no simple morphological, physiological or ecological character that could be related to the invasiveness of a particular family.

3. The families having their evolutionary centre in temperate regions and native to Europe are disproportionally more frequent among the highly invasive families. The world invasive pool, viewed at the family level, corresponds closely to the European pool.

4. The ability to accompany humans and become introduced into an adventive region is, at the family level, poorly correlated with the ability of its representatives to penetrate massively into local vegetation.

5. The frequency distribution of aliens in their families is strongly biased by deliberate introductions. Some families depend largely on purposeful introductions as crops or ornamentals, while the representation of others dramatically increases when only accidental introductions are considered.

6. The natural distribution of families on the globe is reflected in their adventive distributions. Particular families tend to invade in the regions with conditions similar to those from their native area.

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