Survival rates in the Czech Republic of introduced plants known as wool aliens

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Abstract

The paper analyses an unintentional experiment conducted 40 years ago with species termed wool aliens which were observed in employee garden allotments of a wool-processing factory in Brno, Czech Republic. The waste from processing was used as a garden fertilizer, and alien species were recorded by Dvořák and Kühn (1966) Zavlečené rostliny na pozemcích přádelny vlny 'Mosilana' n.p. v Brně. Preslia 38: 327-332. The survival of these species was assessed by their occurrence in the current alien flora of the Czech Republic. Of the 56 species introduced in the 1960s and classified as wool aliens, 18 are still present in the Czech alien flora. The remaining 38 species are considered extinct, i.e. alien plants not capable of long-term survival in the country. The resulting survival rate of wool aliens is 22.1%. Three species on the list (5.4%) were clearly capable of naturalization. Compared to the other alien flora of the Czech Republic, wool aliens were disproportionally introduced from Australia, Africa and South and Central America. Species from Europe and Africa tended to survive the best. Grasses were most strongly represented, contributing 62.5% to wool alien species but only 7.9% to the total Czech neophyte flora. All surviving species were annuals, whereas none of the perennials survived; the survival rate in annuals was 37.5%. Survival of species introduced with wool was significantly comparable to their performance in the UK and in Central Europe, indicating that survival is not determined by mere chance and that the same species tend to be successful elsewhere in Europe. Maximum height and the month of first flowering were not significantly related to the species survival. The role of specific events in the enrichment of alien floras is discussed.

Introduction

The field of biological invasions is rapidly developing with recently emerged theories being based on standardized comparisons of selected groups of species delimited on taxonomic or life-history bases (Rejmánek 1996, 2000; Rejmánek and Richardson 1996; Grotkopp et al. 2002). Analyses of large species sets, some taking phylogenetic constraints into account (Crawley et al. 1996; Daehler 1998; Pyšek 1998), also provide useful information and if appropriately analysed can contribute to valuable generalizations (Lonsdale 1999). In biological invasions, historical records are of eminent importance; the nature of the field does not permit long-term field experiments, both for technical and ethical reasons. However, time of introduction and time since introduction is a decisive variable in determining the success or failure of particular invasions (Pyšek 2001).

The role of chance and rare events in plant invasions has been stressed and discussed

(Crawley 1989). Building a factory importing disproportionally high numbers of diaspores is such a specific rare introduction event, and similar cases were shown to increase the richness of alien floras (Thellung 1912). Once a species is introduced into previously unexperienced conditions, its fate depends to a large extent on chance. The present paper reports a data set on which role of

chance can be assessed. One of the things complicating research in plant invasions is the lack of information about the source input. Species are usually recorded as they become successful (Pyšek et al. 2002). The present paper makes use of an unintentional experiment initiated 40 years ago with a specific group of species termed wool aliens (Clement and Foster 1994; Ryves et al. 1996). By knowing rather precisely what species had been introduced, it takes into account the potential pool of species transported with wool, and by relying on a four-decade field test by time, it identifies those species that survived this introduction event. Further, it compares this local wool-alien flora with others in Europe and attempts to find determinants of alien species survival under the conditions of the Central-European landscape.

The data

In 1958–1961, Dvořák and Kühn (1966) observed the plants in gardens of employees of the woolprocessing factory Mosilana, located in Brno, S Moravia (Czech Republic, 49.11 N, 16.36 E). The factory processed imported wool, mostly of Australian and South American origin. The workers used the processing refuse to fertilize allotments they had in the area of the factory. The waste was dug into the soil in the late summer and early autumn, before strawberries, the main product of these gardens, were planted. The waste was also used as a fertilizer in other nearby allotments (Brno-Černá pole) where also the occurence of alien species was recorded. In addition, J. Dvořák used the waste to fertilize his own garden in Kuřim in 1962-1963 (49.18 N, 16.32 E) and recorded additional species. In summary, these 5-year observations yielded a reasonably complete knowledge about species introduced with wool and able to germinate under the local conditions.

Herbarium specimens were deposited at BRNU (Dvořák and Kühn 1966).

To obtain the list of species specifically introduced with wool, the following groups of species were excluded from the 72 alien species given by Dvořák and Kühn (1966): (a) archaeophytes, i.e. species introduced before 1500, whose occurrence was not associated exclusively with wool import as they have been long present in the Czech landscape (10 species), and (b) those neophytes, i.e. species introduced after 1500 (see Pyšek et al. 2002), that are obviously not associated with wool processing. This group consisted of six species, including the invasive Ambrosia trifida, the naturalized Sisymbrium strictissimum, and others considered casual (definitions of these terms follow Richardson et al. 2000). This screening yielded 56 wool aliens (Table 1) whose occurrence was evidently associated with the wool processing in Brno; the majority of them were also reported in an earlier account of Central-European alien species accompanying wool transport (Probst 1949). For each species, the following characteristics were obtained: area of origin; life form; maximum height; time of flowering in the Czech Republic; number of localities in the Czech Republic (from Kubát et al. 2002; Pyšek et al. 2002) and, for comparative reasons, also in the UK (using ordinal scale of Clement and Foster (1994) and Ryves et al. (1996): 1 = 1-4 localities; 2 = 5-14; 3 = 15-49; 4 = 50-499; 5 = at least 500 localities);and number of localities associated with wool processing in Central Europe (from Probst (1949)).

A recently published detailed account of the current Czech alien flora (Pyšek et al. 2002) made it possible to estimate the fate of the wool aliens reported by Dvořák and Kühn (1966), almost 40 years following their introduction. This source was used because no specific research on the survival of wool aliens from Mosilana wastes has been carried out at Brno. The species were divided into those that clearly have survived and those extinct. A species was considered as surviving if it is currently present in the alien flora of the Czech Republic, and extinct if there is no record of it other than that associated with wool processing in Brno. An analysis was carried out to identify the differences in species traits between these groups.

The species traits were analysed using multiple binary regression (Cox and Snell 1990), with a

Genus	Species	Family	Survival in CR	Number of localities in CR	Origin	LF	Number of localities in Central Europe
Amaranthus	<i>crispus</i> (Lesp. et Thév.) N. Terracc	Ama	r	2	AMS	a	10
Arctotheca	calendula (L.) Levvns	Aster	el	1	AF	p	9
Bassia	tricuspis F. Mueller	Chen	e	1	AU	r a	0
Briza	minor L.	Poac	r	2	Е	a	4
Bromus	lanceolatus Roth	Poac	e1	1	Ē	a	13
Bromus	madritensis L.	Poac	e1	1	Е	a	9
Bromus	rubens L.	Poac	e1	1	Е	a	6
Bromus	scoparius L.	Poac	e1	1	E AS	a	7
Carthamus	lanatus L.	Aster	e1	1	Е	a	9
Centaurea	solstitialis L.	Aster	r	2	E AS	а	14
Chenopodium	microphvllum L.	Chen	e1	1	AU	a	0
Chenopodium	pumilio R. Br.	Chen	sc	4	AU	a	25
Chloris	radiata (L.) Swartz	Poac	el	1	AMC AMS	a	25
Chloris	truncata R. Br.	Poac	e	1	AS AU	a	25
Chloris	virgata Swartz	Poac	e1	1	AMC AMS	a	13
Cotula	<i>australis</i> (Sieb. ex Spreng.) Hook fil.	Aster	el	1	AU	a	7
Cvnosurus	echinatus L.	Poac	r	1	Е	а	7
Cyperus	rotundus L.	Cvp	e	1	Ē	p	2
Dichanthium	<i>sericeum</i> (R. Br.) A. Camus	Poac	el	1	AU	p	6
Ehrharta	longiflora Sw.	Poac	el	1	AF	а	0
Echinochloa	colona (L.) Link	Poac	e	1	Е	а	6
Eleusine	indica (L.) Gaertn.	Poac	r	1	AF	a	0
Eragrostis	<i>cilianensis</i> Vignolo- Lutati ex. Janch.	Poac	e	1	AS AF	a	17
Eragrostis	multicaulis Steud.	Poac	e		AS	а	0
Eragrostis	suaveolens Becher.	Poac	e1	1	E AS	a	0
Eriochloa	<i>procera</i> (Retz.) C. E. Hubb.	Poac	el	1	AS	a	25
Gastridium	<i>ventricosum</i> (Gouan) Schinz et Thell.	Poac	el	1	E AF	a	7
Glyceria	<i>stricta</i> Hook	Poac	el	1	AU	р	0
Hordeum	geniculatum All.	Poac	r	1	E AS	a	25
Hyparrhenia	hirta (L.) Stapf	Poac	el	1	E AS	р	0
Lagurus	ovatus L.	Poac	r	2	Е	a	1
Lawrencia	glomerata Hooker	Mal	el	1	AU	р	0
Leptochloa	filiformis (Lamk.) P. B.	Poac	el	1	AMC AMS	a	0
Lolium	rigidum Gaudin	Poac	el	1	E AS	а	4
Medicago	arabica (L.) Hudson	Fab	r	2	E AF	a	50
Medicago	polymorpha L.	Fab	r	2	Е	а	> 50
Panicum	capillare L.	Poac	sc	2	AMN	a	> 50
Panicum	compressum Bivona	Poac	e1	1	Е	a	1
Panicum	obtusum H., B. et K.	Poac	el	1	AMC AMS	р	0
Papaver	hybridum L.	Pap	e	1	E AS AF	â	2
Phalaris	brachystachys Link	Poac	el	2	E AS	а	4
Phalaris	canariensis L.	Poac	sc	2	Е	a	7
Phalaris	minor Retz.	Poac	el	2	E AS AF	а	17
Phalaris	paradoxa L.	Poac	el	2	E AS AF	a	4
Pholiurus	incurvus Schinz et Thell.	Poac	el	1	E AS	a	3
Polypogon	monspeliensis (L.) Desf.	Poac	r	1	E AS AF	а	25
Schismus	barbatus (L.) Thell.	Poac	el	1	Е	a	6
Silybum	marianum (L.) Gaertner	Aster	r	3	Е	a	8

Table 1. List of wool aliens recorded in the locality Brno in 1961–1963 as a consequence of wool processing in the Mosilana factory (based on data in Dvořák and Kühn (1966)).

Table 1. Continued.	Table .	1. Con	tinued.
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Genus	Species	Family	Survival in CR	Number of localities in CR	Origin	LF	Number of localities in Central Europe
Sisymbrium	irio L.	Bras	r	2	E AS	а	5
Sporobolus	elongatus (Lam.) R. Br.	Poac	el	1	AS AF	р	25
Trifolium	glomeratum L.	Fab	e	1	E AS	a	9
Trifolium	ornithopodioides L.	Fab	e1	1	Е	a	0
Trifolium	resupinatum L.	Fab	r	3	AS	а	8
Trifolium	subterraneum L.	Fab	r	2	E AS AF	а	6
Trifolium	tomentosum L.	Fab	е	1	E AS	а	4
Xanthium	spinosum L.	Aster	r	2	AMS	а	40

Species are listed alphabetically. Families are indicated by their initial letters, nomenclature follows Kubát et al. (2002). Survival in CR was assessed by the current occurrence in the alien flora of the whole of the Czech Republic (Pyšek et al. 2002): e - extinct; e1 - extinct, with a single locality at Brno in Mosilana wastes; r = rare; sc = scattered. Codes 'e' and 'e1' indicate extinction, 'r' and 'sc' survival in the Czech Republic up to the present times. Number of localities in CR refers to those ever reported from the Czech Republic (Pyšek et al. 2002) expressed by using ordinal scale of Clement and Foster (1994): 1 = 1-4 localities; 2 = 5-14; 3 = 15-49; 4 = 50-499; 5-500 localities and more. The combination of the two measures: e1/1 indicates that a species occurred exclusively in Mosilana and has not been reported from the Czech Republic since then; e/1 that there were other (up to 3) historical localities in the Czech Republic but none of them is currently existing; e/2 indicates up to 14 historical localities with none of them currently existing. Origin: AF – Africa, AU – Australia, AMN – North America, AMC – Central America, AMS – South America, AS – Asia. LF – life form: a - annual, p - perennial. Number of localities in Central Europe as reported by Probst (1949) is given.

species classified as yes (survived) or no (extinct), and with maximum height and the month of first flowering as explanatory variables. Because the explanatory variables may be correlated, model simplifications were made by backward elimination from the maximal model by using step-wise analyses of deviance tables to prevent biases to the model structures caused by the correlation (see Crawley 1993, pp. 192–197). The binary regression procedure was also used to determine whether the species known to be abundant in UK and in Central Europe as a whole, have greater chance to survive than those that are rare. In additional analysis, *G*-test on contingency tables and correlation were used.

Results

Of the 56 species classified as wool aliens from the data set of Dvořák and Kühn (1966), 18 have lasted well in the alien flora of the Czech Republic. Most of these survivors are casuals with the number of localities not exceeding 14 (abundance 1 or 2 on the scale of Clement and Foster 1994; see Table 1). Only three species are naturalized (*Chenopodium pumilio, Panicum capillare* and *Xanthium spinosum*; Pyšek et al. 2002). Most of these species are being repeatedly introduced to other localities in the country, and their occurrence need not strictly be associated with wool import. However, this mode of introduction is typical of them (Probst 1949), so they can be considered as introduced by this mode to Brno, and capable of survival under local conditions of the Czech Republic (Pyšek et al. 2002).

Thirty-eight species are considered extinct at Brno, because they are not capable of long-term survival in the Czech Republic. Of these, nine were reported at another locality, outside Brno, in the past (Table 1) but they did not survive there either, which justifies their inclusion among the extinct. The resulting survival rate is therefore 18/56 = 22.1%, and the extinction rate is 77.9%. The three species on the list which are capable of naturalization, make it possible to express the naturalization rate which is 3/56 = 5.4%.

Compared to the other alien flora of the Czech Republic (defined as total neophytes with wool aliens excluded, Pyšek et al. 2002), wool aliens were disproportionally introduced more from Australia, Africa and South and Central America. There is a remarkable under-representation of North America among wool aliens, and these results were highly significant (Figure 1a). Species from Europe and Africa tend to exhibit higher survival rates than those from other continents (12/33 = 36.4% and 4/12 = 33.3%, respectively) while species from Australia were especially poor survivors (1/8 = 12.5%). However, the differences in the place of origin between surviving and extinct wool aliens were not significant (Figure 1b).

Grasses are most strongly represented; they contributed 62.5% to wool aliens but only 7.9% to the other neophytes reported from the Czech Republic. Legumes are also in greater proportion in this data set (12.5% vs 7.0%); representation of the only two other families with at least three species among wool aliens corresponds to that in all other neophytes: Asteraceae 10.7% vs 13.0%, Chenopodiaceae 5.4% vs 3.0% (Table 2). Some other families which are highly represented among Czech neophytes (Pyšek et al. 2002) were represented by only one species or not all. Some differences, though non-significant, were also found in survival rate, which was high in Fabaceae and Asteraceae but low in Chenopodiaceae and Poaceae. However, because of the high number of representatives of the latter family, it is most abundant among survivors (Table 2).

The wool-alien flora contained 72.7% annuals and 27.3% perennials, and survival differed significantly between both groups. All surviving species were annuals, with the survival rate 18/48 = 37.5%. There were eight perennials in the species set, all among the extinct species (Figure 3). No woody life form (i.e. shrub, tree or climber) was present among wool aliens; they were significantly different from the other neophytes in this respect (Figure 2).

To obtain an indication of the role of chance in the fate of wool aliens, their survival was compared with their performance elsewhere in Europe. Binary regression performed with a number of localities in the UK used as the predictor, revealed that species with higher abundance in the UK had significantly higher likelihood of surviving after their introduction into the Brno locality reported in the present paper (Figure 3). The same statistics using the number of localities in Probst (1949) was also significant (probability of survivorship = $-1.61 \pm 0.44 + 0.075 \pm 0.028$ number of localities; $\chi^2 = 60.46$; df = 54, P < 0.005). These results indicate that survival monitored in the present study is not determined by mere chance, but the same species tend to be successful in different geographical locations. In the next step, survival or extinction of species in the locality studied was related to biological features known to affect invasive success, i.e. maximum height and the month of the first flowering. Both factors were found to be non-significant.

Discussion

The 1966 data set of Dvořák and Kühn is remarkable because some of the biases usually beyond the control of a researcher were filtered out by the 'design' of this unintentional experiment. By essentially sowing the seeds when using the waste from wool-processing factory as a fertilizer, variation in diaspore input was much reduced. Of course, we only know about diaspores that were able to germinate, with the list being more complete because J. Dvořák purposely made further observations in his own garden. Unfortunately, we do not know about introduced diaspores that were not able to germinate. Introductions that fail after the diaspore reaches the new region and before it germinates represent the largest knowledge-gap in the transition rates between particular stages of naturalization (Richardson et al. 2000). Non-germinating diaspores were present in the refuse from wool processing; for example, 15-cm size fruits of Proboscidea jussieui from tropical North America were observed in the waste after processing (Dvořák and Kühn 1966).

The 67.9% extinction rate reported in this paper is a minimum value. The real figure could be even higher because data are not available to assess whether the 18 aliens considered as survivors actually survived in the given locality, i.e. whether their later occurrence in the region was associated with this event or was supported by other independent introductions. They were labelled as survivors here because they still occur in the country (Pyšek et al. 2002) and have thus a potential to survive in the Czech Republic.

This data set makes it possible to evaluate how important a specific event, such as building a wool-processing factory and use of the processing waste as a fertilizer, can be in terms of the enrichment of alien flora of a given region. The



Figure 1. Comparison with respect to the area of origin of (a) wool aliens with other neophytes of the Czech flora, and (b) those wool aliens that survived with those that were only reported once in the 1960s and are therefore considered extinct. Species having their primary distribution range on more than one continent were included in each. *G*-test on contingency tables: extinct vs survived: $\chi^2 = 8.86$, df = 6, NS; wool aliens vs neophytes: $\chi^2 = 50.87$, df = 6, P < 0.001.

29 species which were only found once in the whole territory of the country here and went extinct probably immediately after the 5-year study period in the 1960s, represent 2.8% of the Czech neophytes (Pyšek et al. 2002). Twelve species on the list have never been reported before from Central Europe (they are not given in Probst 1949); none of these species survived. This illustrates the high level of uncertainty in plant-invasion research. Had the authors of the original paper (Dvořák and Kühn 1966) not been given a note from an employee of the factory, these species might have disappeared unnoticed. Similarly, the balance between the disappearance and survival of plants here must be viewed in the context of employees preparing suitable conditions for seed germination by cultivation practices such as tilling and watering.

Table 2.	Taxonomic structure of	f the wool alien	flora and its comparisor	n with the situation in oth	er Czech neophytes.

	Extinct	Survived	Survival (%)	Wool aliens total	Other neophytes
Poaceae	27	8	22.9	35	78
Fabaceae	3	4	57.1	7	69
Asteraceae	3	3	50.0	6	129
Chenopodiaceae	2	1	33.3	3	30
Total	38	18	32.1	56	990

G-test on contingency tables: extinct vs survived: $\chi^2 = 4.12$, df = 3, NS; wool aliens vs neophytes: $\chi^2 = 37.05$, df = 3, P < 0.001.



Figure 2. Proportional representation of life forms among wool aliens that survived (n = 18), went extinct (n = 38), and among other Czech neophytes (n = 990, wool aliens excluded). G-test on contingency tables: extinct vs survived: $\chi^2 = 6.82$, df = 1, P < 0.05; wool aliens vs neophytes total: $\chi^2 = 41.16$, df = 2, P < 0.001.

In the literature of countries with a long tradition in alien-plant research there are valuable data sets which, if appropriately analysed, can provide interesting insights into various aspects of plant invasions. Pyšek (2001) reported on data sets from the Czech flora that allowed testing the success of predictions of invasiveness for a number of agricultural weeds. The data analysed in the present paper are rather unique, but too small (though long enough in terms of duration, spanning over 40 years) to allow robust generalizations, but they show that the predictions such as the 'tens rule' (Williamson 1996; Williamson and Fitter 1996) do have a reasonable base. The 'tens rule' predicts that 10% of casual species become naturalized, with confidence limits between 5% and 20% (Williamson 1996); the naturalization rate of 5.4% estimated in the present paper thus fits this prediction. There is one data set which can be used for comparison. This is the intriguing record of the alien flora of Montpellier (Thellung 1912) which includes 800 alien species that had at least one generation of offspring following introduction. Kowarik (2003) pointed out that a large majority (77.6%) were introduced accidentally. The naturalization success of these species was 7.4%. This value corresponds well to the naturalization rate of 5.4% found for the wool aliens of Brno. The data set assessed in the present paper is much smaller but it was 'standardized' to some degree by the seeds being given suitable conditions for germination over several years, with purposeful observations of new or repeated occurrences.

Comparison with other regions shows that neither survival nor further fate of wool aliens in the adventive territory is a matter of complete



Figure 3. The effect of the number of localities in the UK (= LocNo) on observed (1 = survived, 0 = extinct) and expected data of species survival after introduction to Brno. The expected data are fitted by binary regression logit of probability of survivorship = $-4.584 \pm 1.482 + 1.487 \pm 0.5121$ Loc-No ($\chi^2 = 39.64$; df = 38, P < 0.001).

chance. Species that are abundant elsewhere in Europe appeared more likely to survive. There is also a significant relationship between the abundance of wool alien survivors in the Czech Republic and elsewhere in Europe; the number of wool aliens in Czech localities was significantly correlated with the abundance of the same species in UK (Spearman's rank correlation coefficient = 0.58, P < 0.001, n = 40) and with the number of wool aliens in localities in Central Europe as listed by Probst (1949) (Spearman's rank correlation = 0.32, P < 0.01). For the two countries with most detailed records on their alien floras, i.e. UK (Clement and Foster 1994, Ryves et al. 1996) and Czech Republic (Pyšek et al. 2002), the species spectra of wool aliens are fairly similar. Of the 56 wool aliens of Brno, 40 are reported from UK (although not necessarily currently present); of the 38 extinct at Brno, 25 (65.8%) were recorded in UK, while of the 18 that survived, 15 (83.3%) are known from the UK. It appears that for such a specialized mode of introduction, it also holds that the introduced species will tend to establish if introduced and established elsewhere (Scott and Panetta 1993; Reichard and Hamilton 1997; Lockwood et al. 2001).

With such a limited species number, it is difficult to evaluate factors that determine which species survive and which do not. Only annuals were found to survive; this can be associated with the habitat in which the species grew, i.e. garden allotments. Herbarium specimens indicate that the majority of species set seed, but it is not known if these seeds were viable. Some of the annuals might have profited from better adaptation to the disturbance regime associated with such habitat.

Species from Europe and Africa, its northern part in most cases, exhibited a disproportionally higher survival rate than those from Australia and the Central and South Americas (but note that the three species considered naturalized, i.e. C. pumilio, P. capillare and X. spinosum are from Australia, North America and South America, respectively). This result was non-significant, probably due to low species number, but still it indicates the importance of climatic match for the success of alien plants (Panetta and Dodd 1987). Species from areas with climate dramatically different from Central Europe were obviously less successful. Some species must have been introduced into Brno not directly from the region of primary distribution but from another secondary area, which is a quite common feature of plant introductions (di Castri 1989) and has been recently proved for some species by using genetic methods (Novak and Mack 2001). It could be the case of widespread invaders, such as Oxalis pes-caprae, a species that was also present at Brno but excluded from the list of the 56 wool aliens because it is being introduced by other means (Clement and Foster 1994) and not given in Probst (1949). There was no trade between South Africa and the former Czechoslovakia at that time, and the species was probably introduced from Australia, where also it is invasive (Michael 1964).

The two biological features which were previously shown to affect invasion success, i.e. height and flowering time (Pyšek et al. 1995, 2003; Celesti-Grapow et al. 2003) failed to distinguish between survivors and losers. One reason for this could be the limited number of species, but more probably, their survival is determined by more subtle factors such as germination requirements, dormancy, early population dynamics and pattern of fecundity, i.e. features on which information is not generally available for many species.

Unusual and opportunistic data sources, such as the one reported in this paper, can provide insights into how rare alien species are recorded in national or regional species list. Wastes from factories processing wool, soy beans or oil plants, i.e. commodities which are often accompanied by alien species introduced from distant regions, are normally deposited in rubbish dumps where alien species are often found by botanists (Pyšek et al. 2002; Mihulka et al. 2003). The situation described here was rather special in that how the wastes from wool processing were used. This lead to an unintentional experiment which allowed to obtain an information on the initial composition of the wool-alien flora at Brno, and compare its survival rates after several decades. On the other hand, it must be borne in mind that the evidence of survival rates reported here is indirect; there was no later systematic research on the fate of these introduced species in the locality reported by Dvořák and Kühn (1966), and nothing has been known about repeated introductions and propagule pressure. However, the fact that some species were not recorded in the whole territory of the country since then, provides a reasonable basis for considering them extinct.

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