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The importance of human mediation in species establishment: analysis of the alien flora of Estonia

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In order to analyse the mechanisms of the crossing of invasion phases by alien species, a comprehensive 787-species database of all alien neophytes ever recorded in the Estonian flora was compiled. The invasiveness (invasive status, abundance type, introduction mode, residence time, etc.) of each species was estimated and analysed. Our analysis shows that humans have played a more profound role in fostering plant naturalisations than by acting simply as dispersers — the percentage of naturalisation among the deliberately introduced species is considerably higher than among the accidentally introduced taxa. Cultivation has preferred long-lived species that have advantages for reaching greater abundance and naturalised status in the area, especially in (semi-)natural communities. Invasion success also increases with alien species residence time in the study area. There is definitely a need, in the future, to regulate introductions, especially to control the ornamental plant trade.

Introduction

Ground and approaches

The global increase in trade and travel has enhanced the frequency of human-mediated intentional or accidental introductions of alien species resulting in their subsequent establishment. Consequently, within less than the last 500 years, alien (non-indigenous) species have become components of the flora of most regions of the world (Weber 1997). Biological invasions have increasingly been recognized as a key problem in the conservation of biological diversity (Cronk and Fuller 1995, Reichard and White 2003), and have also attracted extensive attention due to economic costs worldwide (Naylor 2000, Perrings *et al*. 2005). In addition, invasions are also the key object of a young and rapidly emerging research area — the study of biotic homogenisation (Qian and Ricklefs 2006, Olden 2006, La Sorte *et al*. 2007).

There are various approaches for explaining the mechanisms of biological invasions, mostly for the purposes of predicting the processes of ecosystem dynamics. As it was pointed out by Williamson (2006), looking for universal attributes and causes of invasions through a series of stages is not profitable and prediction is far harder than explanation. However, in recent research, four approaches have been prevailing: (1) to focus on the characteristics of invading species (e.g. Goodwin *et al*. 1999, Prinzing *et al*. 2002, Lloret *et al*. 2005), (2) to identify the characteristics of the communities and/or whole ecosystems which have been invaded (Shea and

Chesson 2002, Rejmánek *et al*. 2005, Stachowicz and Tilman 2005), (3) to investigate the relationship between the invading species and the invaded community — the key–lock approach (e.g. Davis *et al*. 2000, Alpert *et al*. 2000, Davis *et al*. 2005, Vilà *et al*. 2006), or (4) to differentiate the invasion process in time models of steps and stages (Williamson 1996, Richardson *et al*. 2000, Kowarik 2003, Coulatti and McIsaac 2004; for all four *see* additional earlier references, and also discussion about usefulness and limitations of these approaches in Heger and Trepl [2003]).

Recent efforts in invasion biology show, in addition to the analysis of problems posed by non-native species, a re-focusing of attention on basic research questions and general principles concerning species invasions (Mooney and Cleland 2001, Sax *et al*. 2005, Lockwood *et al*. 2005, Coulatti *et al*. 2006, Pyšek and Richardson 2006, Richardson and Pyšek 2006).

Databases of alien species

An inevitable task is the continual compilation of reliable databases of alien species of a certain territory (e.g., Turner 1997, Weber 1997, Arroyo *et al*. 2000, Wu *et al*. 2004) or certain species groups (Binggeli 1996, Clout and Lowe 2000, Liu *et al*. 2005), for the comparative understanding of plant invasions in different locations around the world. Studies of the characteristics that make some alien species invasive in the recipient region are essential for understanding the processes and patterns of plant invasion generally (Vermeij 1996, Rejmánek and Richardson 1996, Pyšek *et al*. 2004a). Comparative studies of floras provide a useful tool for generating hypotheses that can be tested using other approaches (Daehler 2001, Duncan and Williams 2002).

Complete catalogues of alien species with adequate information on origin, invasion status, introduction mode, etc., are rare throughout the world. For the majority of the European countries the specialized lists of aliens are almost nonexistent; studies of that kind must rely on standard floras for comparisons. Exceptions include the studies from British Isles (Clement and Foster 1994), the Czech Republic (Pyšek *et al*. 2002), Germany (Kühn and Klotz 2003), Switzerland (Gassmann and Weber 2005), and the Azores archipelago (Silva and Smith 2004). The main data source for northern and eastern Europe, where there is also a lack of uniform scientific data (cf. Fremstad and Elven 1997), is a report on alien species introduced and established in the Nordic area (Weidema 2000) and a regional portal on invasive alien species (North European and Baltic Network on Invasive Alien Species at www.nobanis.org).

Aims of the present study

A widely appreciated approach for explaining the mechanisms of the crossing of invasion phases is the compilation and analysis of reliable alien species databases of a certain recipient territory.

In light of the lack of good reviews from the northern part of Europe, we decided to compile a comprehensive alien neophyte’s flora database of Estonia using all available data sources. We aimed to understand better the overall structure and composition of this part of the flora, analysing the relationships between species taxonomic position and origin, residence time and invasive status, abundances in the area and biological characteristics of species, etc. Particularly, we asked whether the introduction mode — deliberate (often cultivated and pre- and post-introduction selected) *versus* accidental — and life history traits could be important factors for crossing the stages from the casual to naturalised to invasive, thus achieving greater abundances in the area. We also tested one of the emerging generalisations in invasion biology that the probability of invasion success (frequency in area and invasion status) increases with residence time (representing another dimension of propagule pressure).

Material and methods

Geographical, climatic and demographic conditions in Estonia

Estonia is located in northern Europe (58°–60°N, 22°–28°E) on the eastern coast of the Baltic Sea, and covers an area of 4 522 700 ha, thus belonging to the northern part of the temperate zone and to the transition zone between maritime and continental climates (Raukas 1995). The annual average temperature in Estonia (between 4.3 °C and 6.5 °C) is considerably higher than in more eastern areas lying at the same latitudes but having a more continental climate. The annual amount of sunshine hours varies between 1600 and 1900, and is higher on the coast and on the islands and lower on the uplands.

The vegetation period lasts for 180–195 days and the frost-free period for 103–164 days. Both are longer on the coast.

The annual average of the relative air humidity is 80%–83%. It is higher in winter and at its lowest in May, 70% on average. The annual average precipitation varies between 550 and 800 mm. As a rule, the coastal zone receives less rainfall than the inland areas. It is particularly dry on the coast in spring and in the first half of summer. The snow cover in Estonia is characterised by large territorial and temporal variations. The average duration of snow cover during winter is 75–135 days.

The main characteristics of Estonian soils are: (1) high relative importance of mires and swampy soils, (2) appearance of massive limestone in soil profiles, (3) high percentage of calcareous soils, (4) high proportion of stony soils, and (5) heterogeneity of soil types, which is a result of different mineral and chemical content of the soil matrix and also of a fluctuating water regime (Raukas 1995).

In 2006, Estonia had 1.34 million inhabitants. Approximately a third of the nation lived in the capital, Tallinn, and about 67% of the population resided in the cities. Human population density was 29.1 inhabitants per km^2. The total length of the road system was 56 850 km (1.13 km per km^2) and the length of the railroad network, 1026 km (0.0214 km per km^2). The agricultural area covered about 29% (arable land together with natural grasslands), forests ca. 47%, wetlands over 6% and under inland waters was 6% of the Estonian territory.

History and traditions of floristic research and data sources for compiling alien flora of Estonia

The first scientific studies on the flora of Estonia date back to the first half of the 18th century, when J. C. Buxbaum, a scholar of the Russian Academy of Science studied the flora of Ingermanland. In this work published in 1729, 1732 and 1740, Buxbaum described some species noticed occasionally in several locations near Narva where he stayed and rested. The first proper list of vascular plants growing in Estonia and Livonia was published by Hupel in 1777 in *Topografische Nachricten von Lief- und Ehstland*. Since the second half of the 19th century, the flora on the territory of Estonia has been very well studied, making Estonia one of the botanically best described areas in the region.

Today we have over 300 000 herbarium specimens and numerous databases. More than 8000 publications on Estonian flora have been published. A larger part of this vast information is summarised in *Flora of Estonian SSR* (1953–1984), published in 11 volumes during the period from 1953 to 1984. The most recently published data sources include *Vascular Plant Flora of Estonia* (Kukk 1999) and *Atlas of the Estonian Flora* (Kukk and Kull 2005). Alien species have been a topic since the first floristic investigations, but published data are occasional and unsystematic.

Terminology — history and actual state (residence time, invasive status)

It is a widely known fact that the quality and the quantity of written sources varies from country to country and from species group to species group. In the European context, many authors have suggested the use of 1492 as the dividing year (beginning of Spanish trips to America) to distinguish between the old and the more recent human-influenced introductions, termed as *archaeophytes* and *neophytes* respectively (Kowarik 1999, Richardson *et al.* 2000). In the Nordic area, the field of botany began developing after 1600 (Weidema 2000). Accordingly, for instance, in Finland the time limit for calling a plant an archaeophyte is

1650 (associated with the first botanical document from the region). Due to similar considerations for other Nordic countries, 1700 has been chosen as a relevant dividing year. There are further differences between countries: some sources have included the archaeophytes as introduced, while others have considered these as natives. However, it has been shown that archaeophytes are ecologically distinct from native taxa (Pyšek *et al*. 2002, Pyšek *at al*. 2004b, Frank and Klotz 1990) and it is misleading to lump them together. Since all contemporary plant species (excluding the exceptional neo-endemic ones) have come to the Estonian area in some period not earlier than 12 000 years ago, we have only a theoretical distributive classification of species with respect to their status in the local flora: *indigenous* (or *native*) are the species that have arrived in the Estonian area without direct human help since the beginning of the Holocene and before the middle of the 18th century (first material from region, Fisher [1778]), and *archaeophytes* are the species that have arrived with human help but not later than the middle of the 18th century. In practice, *Vascular Plant Flora of Estonia* (Kukk 1999) has considered natives and archeophytes in the same inseparable group. In this study we analysed specifically only *alien neophytes* from this region.

Unfortunately, terminological confusions are common in and among research, management and public policy publications and discussions regarding invasive species. This all makes comparisons between areas and generalisations quite problematic. For example, in various Nordic countries the term ‘naturalised’ has been used with slightly varying meanings (Weidema 2000). In Estonia, the term ‘naturalised plants’ has historically been used to indicate the alien plants that are found in natural or in semi-natural communities and that have reproduced there without human help. Several distinctions have been used for other categories, but in the current work we have re-evaluated the species statuses in alien flora, applying the unifying principles and considering the work done in different parts of Europe. We found it reasonable to use the recommended terminology in plant invasion ecology (Richardson *et al*. 2000, Pyšek *et al*. 2004a). In our database *casuals* are the alien species that may flourish and even reproduce occasionally in an area, but which do not form self-replacing populations, and which rely on repeated introductions for their presence. *Naturalised* (*non-invasive*) are alien species that reproduced consistently and sustain populations over many life cycles without direct intervention by humans (or in spite of human intervention); they often recruit offspring freely, usually close to adult plants, and do not necessarily invade natural, semi-natural or man-made ecosystems. *Invasive* are these naturalised plants that produce reproductive offspring, often in very large numbers, at a considerable distance from parent plants, and thus have the potential to spread over a considerable area. We have used the last term without any indication of environmental or economic impact.

The database and statistical analysis

The present study uses the published floristic database for the country (Kukk 1999) and brings together all available data on alien species from the last 10 year period (specimens of the main Estonian herbariums, controlled unpublished data from different field researches, etc.) for compiling a comprehensive alien flora of Estonia. We included all alien neophytes recorded at least once in the wild in the country, and collected the basic information for each species (Table 1), where such information was available.

Overall, our data represent a rank ordering of observations rather than precise measurements; variables are also not normally distributed. Therefore for statistical analyses we used nonparametric Kruskal-Wallis ANOVA, comparing the differing characteristics of multiple independent samples (groups). Precise comparisons were determined for abundances and invasive statuses between accidentally and deliberately introduced species, life history traits among species with varying invasive statuses, as well as abundance classes and invasion statuses in concordance with residence time. In addition we used the t-test to evaluate proportional differences in species origin between the whole database and particular invasive status. For all analyses we used software package STATISTICA ver. 7, considering differences significant at $p < 0.05$.

Results

Alien Flora of Estonia contains altogether 787 neophyte taxa belonging to 83 families and 381 genera (Table 2). Of these, there are 42 taxa at subspecies level and 4 at varietal level. Of the total number of the neophyte taxa, 25 are hybrids. For comparison, the native and archaeophyte flora of Estonia includes 1441 species of vascular plants. The number also covers the taxa with uncertain status in the present Estonian flora (e.g., herbarium evidence proves the earliest existence, but no recent findings), and micro-species (Kukk 1999). If we add the 97

Table 1. Description of the species characteristics in the general database and respective categories assigned for each species.

Topic	Characteristic	Used categories or references
Species identity and taxonomic position	Genus, species, subspecies, synonyms, family; source of information	
Invasiveness on Estonian territory	Invasive status	Casual (1) Naturalised (non-invasive)(2) Invasive (3)
	Year of introduction	
	Year of the first record in the wild	
	Type of invaded habitats	Natural (1): natural forests and naturally treeless habitats, and/or semi-natural (2): managed landscape except of settlements, communications and arable land; and/or man-made (artificial) (3)
	Abundance in the wild (frequency classes)	Rare (1): one to 10 proved findings during the last 50 years Uncommon (2): 11–30 locations; usually in one and the same region Scattered or occasional (3): distributed all over Estonia, but sparse everywhere or sparse, but rather common in certain regions Common (4): grows in suitable locations all over Estonia, sometimes in large numbers
	Introduction mode	Accidental (1) Deliberate (2) Both ways (3) (for statistical analyses, only one prevailing mode per species was used)
Native distribution	Area of origin (floristic element; Kukk 1999: 302–303)	America, Asia, Europe, Eurasia, Eurosiberia, Circumpolar, Africa, Australia, Homeless (known only from cultivation)
Biological and ecological characteristics	Life history	Annual/biennial (1) (annual or annual/biennial or biennial) Intermediate (2) (annual to perennial or biennial to perennial) Perennial (3) Shrub (4) (semi-shrub or shrub) Tree (5)
	Raunkiaer's life forms*	Ellenberg 1988, Lindacher 1995
	Grime's life strategy*	Grime 1979
	Clonality type*	Klimeš *et al.* 1997
	Ellenberg's indicator values*	Ellenberg *et al.* 1991
	Pollination and dispersal type*	Lindacher 1995

* Not used in the current paper.

subspecies, the total number of taxa increases to 1538. These indigenous species and archaeophytes altogether belong to 113 families and 443 genera. Roughly one-third of the Estonian wild flora consists of neophytes.

Of all the neophytes in Estonia, 555 species have casual status, 232 species have become naturalised and of those, 37 are considered invasives (Tables 2 and 3). Consequently, approximately 16% of the naturalised species and approximately 5% of all aliens have reached invasive status. There were remarkable differences between accidentally and deliberately introduced species characteristics. First, the abundances (Kruskal-Wallis: $H = 37.48$, df = 1, $N = 787$, $p < 0.0001$) and invasive status (Kruskal-Wallis: $H = 33.13$, df = 1, $N = 787$, $p < 0.0001$) of deliberately introduced species were higher than of those of accidentally introduced (Fig. 1). Second, there were more long-lived species among naturalised non-invasive species than among the casuals or invasive species (Kruskal-Wallis: $H = 65.77$, df = 2, $N = 787$, $p < 0.0001$; Table 2 and Fig. 1).

The most represented families in the alien flora involved the families whose representatives commonly invade in temperate climates (Pyšek 1998), with *Asteraceae* (89 species, 11.3% of all), *Brassicaceae* (59 species, 7.5%) and *Poaceae* (57 species, 7.2%), but also (surprisingly) *Rosaceae* are quite frequent among the aliens (72 species, 9.1%). In contrast with the family *Asteracea*, which maintain species through all invasive stages (27 naturalised species and 12 invasive species), the family *Rosaceae* is especially frequently represented among deliberately introduced casuals and naturalised species (61 species from 72). Species in casual status have also the most representatives in family *Asteraceae* and *Brassicaceae*, with 62 and 47 species respectively. Some large families contain exclusively alien species (e.g., *Malvaceae*: 15 species, *Amaranthacheae*: 11 species), or exclusively native species (e.g., *Cyperaceae*: 95 in native and archeophytes flora and 1 species among neophytes, *Orchidaceae*: all 36 are native species). Altogether 24 families appear only in

Table 2. Classification of species of Estonian Alien Flora in terms of invasive status.

Characteristic	Invasive status				
	All alien	Casual	All naturalised	Non-invasive	Invasive
No. of species	787	555	232	195	37
transition rates between stages (%)	100	70.5	29.5		
naturalised (%)				84.1	15.9
total (%)				24.8	4.7
Taxonomy					
no. of represented families	83	75	52	51	15
Origin (%)					
Europe	27.6	28.1	26.3	28.7	13.5
Eurasia	20.1	20.6	19.3	11.8	18.9
Eurosiberia	7.2	5.0	12.5	19.4	16.2
America	17.9	16.0	22.4	21.0	29.7
Asia	17.6	18.9	14.7	15.4	10.8
others	9.6	11.4	4.8	3.7	10.9
Introduction mode (%)					
deliberate	57	50	74	78	51
accidental	43	50	26	22	49
Life history (%)					
short-lived herbaceous	45	54	24	21	38
perennial herbaceous	33	29	41	41	46
shrubs and trees	22	17	35	38	16
Habitat preferences (%)					
only in human made	57	76	18	23	0
at least met in semi-natural/ natural	43	24	82	77	100

Table 3. List of naturalised invasive species in Estonian Alien Flora (definitions in the text).

Taxon	Family	First reported presence in the area	Estimated abundance (S: scattered or occasional; U: uncommon; C: common)	Introduction mode (D: deliberate; A: accidental)	Habitat (N: natural, S: seminatural, H: human-made)	Origin	Life history
Amelanchier spicata	Rosaceae	1934	S	D	N,S,H	America	shrub
Aster lanceolatus	Asteraceae	1903	S	D	S,H	America	perennial
Aster × *salignus*	Asteraceae	1820	S	D	S,H	Homeless	perennial
Bromus inermis	Poaceae	1805	C	D, A	N,S,H	Eurasia	perennial
Bunias orientalis	Brassicaceae	1796	C	A	N,S,H	Eurosiberia	biennial/perennial
Chaenorhinum minus	Scrophulariaceae	1803	S	A	S,H	Europe	annual
Chamomilla recutita	Asteraceae	1777	S	D	S,H	Eurasia	annual
Chamomilla suaveolens	Asteraceae	1823	C	A	S,H	Circumpolar	annual
Cichorium intybus	Asteraceae	1777	S	D	S,H	Eurosiberia	perennial
Conyza canadensis	Asteraceae	1784	C	A	S,H	America	annual
Cotoneaster lucidus	Rosaceae	1883	S	D	N,S,H	Asia	shrub
Echinochloa crus-galli	Poaceae	1839	S	A	S,H	Eurasia	annual
Elodea canadensis	Hydrocharitaceae	1905	C	A	N,S,H	America	perennial
Epilobium adenocaulon	Onagraceae	1930	C	A	N,S,H	America	perennial
Erucastrum gallicum	Brassicaceae	1823	S	A	S,H	Europe	annual/biennial
Galega orientalis	Fabaceae	1807	S	D	N,S,H	Asia	perennial
Galinsoga ciliata	Asteraceae	1841	S	A	S,H	America	annual
Heracleum sosnowskyi	Apiaceae	1957	S	D	N,S,H	Asia	perennial
Impatiens parviflora	Balsaminaceae	1852	C	A	N,S,H	Eurasia	annual
Juncus tenuis	Juncaceae	1955	S	A	S,H	America	perennial
Lactuca serriola	Asteraceae	1803	S	A	N,S,H	Eurosiberia	annual
Lactuca tatarica	Asteraceae	1931	S	A	N,S,H	Circumpolar	perennial
Lepidium densiflorum	Brassicaceae	1931	U	A	S,H	America	annual/biennial
Lolium perenne	Poaceae	1791	C	D	S,H	Eurosiberia	perennial
Lupinus polyphyllos	Fabaceae	1807	S	D	N,S,H	America	perennial
Medicago × *varia*	Fabaceae	1925	S	D	S,H	Eurasia	perennial
Melilotus albus	Fabaceae	1839	C	A	N,S,H	Circumpolar	annual/biennial
Petasites hybridus	Asteraceae	1777	S	D	N,S,H	Europe	perennial
Populus balsamifera	Salicaceae	1805	S	D	N,S,H	America	tree
Rosa rugosa	Rosaceae	1825	S	D	N,S,H	Asia	shrub
Rumex confertus	Polygonaceae	1933	S	A	N,S,H	Eurasia	perennial
Sambucus racemosa	Caprifoliaceae	1805	C	D	N,S,H	Eurasia	shrub
Sambucus nigra	Caprifoliaceae	1777	S	D, A	S,H	Europe	shrub
Saponaria officinalis	Caryophyllaceae	1777	C	D	S,H	Eurosiberia	perennial
Senecio viscosus	Asteraceae	1839	C	A	N,S,H	Europe	annual
Solidago canadensis	Asteraceae	1807	S	D	N,S,H	America	perennial
Trifolium hybridum ssp. *hybridum*	Fabaceae	1791	C	D	N,S,H	Eurosiberia	biennial/perennial

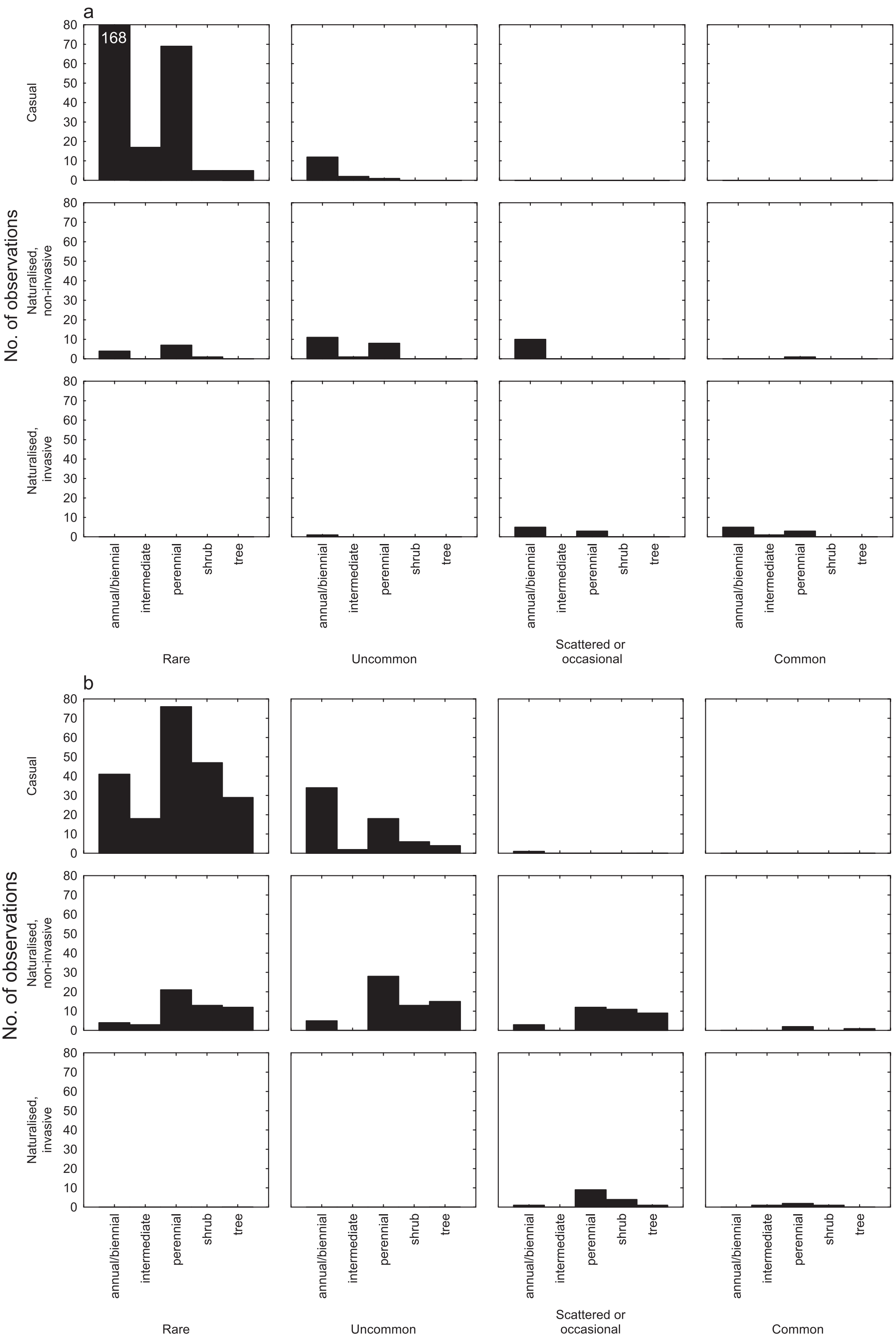

Fig. 1. Abundances and life history traits between (**a**) accidentally and (**b**) deliberately introduced alien neophytes. The abundances of deliberately introduced species were higher than those of accidentally introduced. Long-lived species prevailed in species of naturalised non-invasive status as compared with casuals or invasive species.

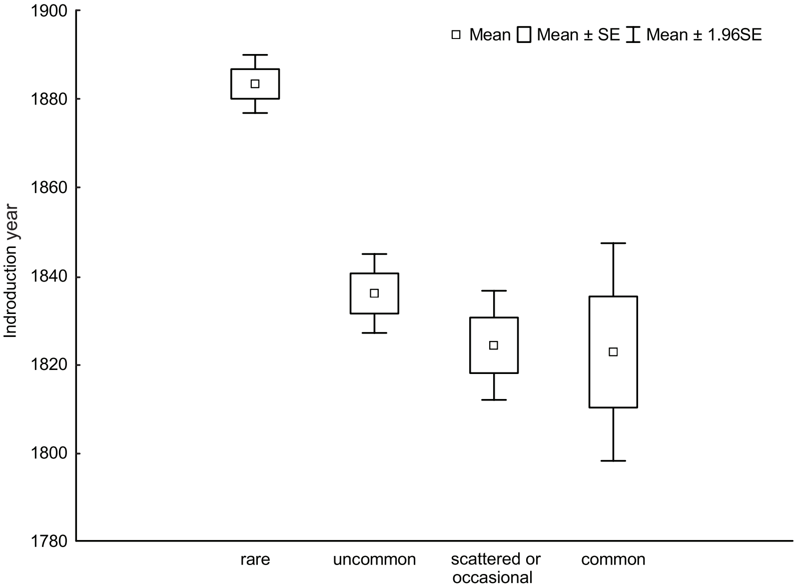

Fig. 2. Relationship between the abundance type and the introduction time.

the alien flora. The most common genera among alien taxa are: *Bromus* (15), C*henopodium* (15), *Populus* (14) and *Atriplex* (12).

According to the floristic elements, one-third of the alien species in Estonia come from Europe; additionally, there are some from Eurasia, America and Asia (about one-fifth from each) (Table 2). Only nine species originate from Africa (all casuals, six deliberately introduced) and one species is native to Australia (casual, accidental species). Four percent of the species have non-identified origin. In the entire database, among invasives there are more species originating from America (two-sided difference test between two proportions, $p = 0.04$), whereas species from near locations have easily become naturalised, but non-invasive (European origin in whole flora compared to invasive species; one-sided difference test between two proportions, $p = 0.02$).

Statistical analyses showed that species with longer residence time have reached higher abundances in the area (Kruskal-Wallis: $H = 88.37$, df = 3, $N = 687$, $p < 0.0001$; Fig. 2). Length of residence affects not only the range and frequency of an alien species, but also its invasion status, i.e. whether it persists as a casual or becomes naturalised or invasive (Kruskal-Wallis: $H = 49.73$, df = 2, $N = 687$, $p < 0.0001$; Fig. 3). These two measures, abundance and status, are closely related but are not necessarily so: many species are naturalised only locally and some of the casuals may be abundant (but still rely on repeated introduction of seeds or plants).

The 787 species pooled into five life history categories are grouped unequally regarding their invasive statuses (Table 2 and Fig. 1). In all, approximately 45% of the alien flora of Estonia consists of short-lived species, but only 24% of the naturalised flora belongs to this group. Hence, long-lived species have advantages for crossing the environmental and biotic barriers and for becoming naturalised. This is observed in particular among deliberately introduced species (Fig. 1b). Among the invasive species, the proportions of species life history traits are quite similar to the proportions in the entire database, but the most problematic invasive species can be classified as deliberately introduced perennial species (*see* also Table 3). Such species also prevailed in natural or semi-natural areas (Table 2).

Discussion

It is widely known that only a small fraction of the biotic material that lands in new territory actually becomes naturalised, and an even smaller fraction becomes a serious problem (Williamson and Brown 1986, Williamson and Fitter 1996). As expected, the majority of species

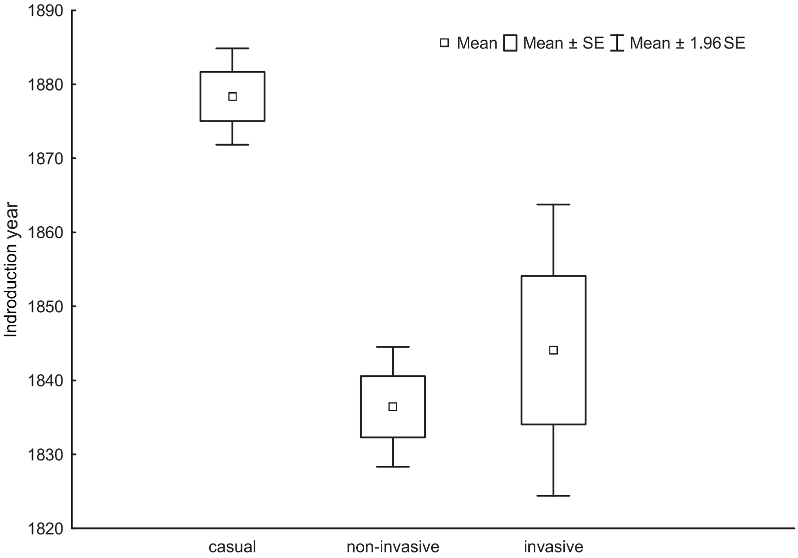

Fig. 3. Relationship between the invasive status and the introduction time.

registered as growing in the wild in the study area have achieved only rare distribution and/or casual status. The highly dynamic nature of invasions means that alien species surveys become outdated in a very short period of time. Alien Flora of Estonia (as all similar lists) can only be a snapshot that can be used to understand and test theories. A list of species tends to be regenerated over time, and taxonomists are not in the habit of checking whether species reported at earlier times still persist in the wild. It has been pointed out, and we agree, since we have good or at least satisfactory knowledge of alien establishment, that local extinctions are poorly investigated and understood (Arroyo *et al.* 2000). Consequently, an unknown percentage of species of casual status is probably no longer a part of the Estonian flora. In a list of alien neophytes of the Czech Republic, local extinctions accounted for almost 30% of all casuals (Pyšek *et al.* 2002).

Although the whole invasion process is a continuum, it has been divided into several phases or stages in the conceptual framework proposed by Williamson (1996, 1999). In recent years, new complementary theories of stages have been published (Heger and Trepl 2003, Ruiz and Carlton 2003, Coulatti and McIsaac 2004, Lockwood *et al.* 2005). Richardson and Pyšek (2006) reviewed the published concepts, hypotheses and theories that can be linked to the naturalisation-invasion continuum concept, being related to invasion processes with a sequence of environmental and biotic barriers that an introduced species must negotiate to become casual, naturalised and invasive.

The potential reasons for naturalisations of alien species have previously been explained on the bases of both global and local factors. There are interpretations ranging from widely changed land-use (Hobbs 2000), and climate (Dukes 2000) to certain both abiotic and biotic characters of species and/or habitats promoting naturalisation in the recipient territory (e.g. fluctuating resources and disturbance regime: Davis *et al.* 2000, Mack and D'Antonio 1998, Hansen and Clevenger 2005, vegetation structure and soil properties: Vilà *et al.* 2006, Meiners *et al.* 2001, Wolfe and Klironomos 2005, facilitating biotic interactions: Richardson *et al.* 2000, Rodriguez 2006). As was summarized by Mack (2000), despite 150 years of history and a tremendous amount of literature there are only few widely-recognized observations on the fates of immigrant species.

As compared with the data from central Europe (Pyšek *et al.* 2002), the rate of naturalisation in Estonia is rather high. We seem to have proportionally more naturalised species but fewer species among naturalised species which have become invasive. This is especially true on our western islands where the climate is milder, since representatives of the same taxon may suffer severely from frost damage and do not reproduce naturally in eastern Estonia. Previously it has been shown that the total number of naturalised species can also be a reliable predictor of alien pest species. In general, a high number of naturalised species represents a red flag: there are problems with at least 15% of those species (Rejmánek and Randall 2004). As we showed earlier, transition rates in gradation from naturalised to invasive in Estonia are rather low (only part of them are problematic). Nevertheless, about 16% of naturalised neophytes and approximately 5% of all neophytes become invasive. The impact of problematic species is higher than their proportion in the list (e.g., the alien *Heracleum* sp. covered nowadays over 1470 ha altogether which is 0.03 percent of the area of Estonia).

Our results demonstrate that, according to the floristic elements, only one-third of the alien species in Estonia come from Europe. The proportion of species originating from America is higher among invasives than among the whole set of aliens (*see* Table 2), whereas species from near locations have easily become naturalised, but not invasive. This may be due to the fact that the species from far locations have weak biotic interactions in a new area. Of course, species have very different strategies to become invasive and possible effects of regional factors are not well understood (Guo *et al.* 2006).

As demonstrated by the data from central Europe, invasions frequently result from an inter-play of biological and anthropogenic mechanisms. The latter, however, cannot be explained or predicted by ecological rules (Kowarik 2003). Furthermore, economic and landscape factors are important in determining the rate of spread: the rate of spread is almost always fast and probably a result of human activity rather than simple biology (Willamson *et al.* 2005). Some particular cases have shown that cultivar selection prior to introduction may increase invasiveness of certain species (Kitajima *et al.* 2006), and for woody species planted for forestry purposes, planting history and propagule pressure may predict invasions (Křivánek *et al.* 2005). Propagule pressure created by the long presence of an ornamental plant on the market and their ability to escape from cultivation and establish in the wild are among the factors that have had important effects on the invasion processes (Dehnen-Schmutz and Williamson 2006, Dehnen-Schmutz *et al.* 2007). The important factors (socio-economic, geographical, ecological and evolutionary) throughout each stage often vary, yet all factors can affect all stages (Williamson 2006).

The majority of alien species in Estonia that are able to naturalise originate from deliberate introduction. The pattern of invasive species is quite diverse, but among the most problematic species most are deliberately introduced perennials, which have run wild from cultivation (*see* Table 3; e.g., *Heracleum* sp., *Galega orientalis*, *Lupinus polyphyllus*, *Solidago canadensis*, etc.). Ornamental horticulture has previously been recognized as the main anthropogenic pathway for plant invasions worldwide. For example, the history of the majority of species now naturalised in the United States indicates deliberate introduction and post-immigration cultivation (Mack and Erneberg 2002). The mode of introduction has also been assessed for alien species in Denmark, Finland, Iceland, Norway and Sweden along with the Åland Island, the Faeroe Island, and Greenland (Weidema 2000). Here again, many naturalised species appear to have a history of deliberate introduction, but the role of accidental introduction appears to be larger than in the United States or southern Australia (Table 4). These values from northern Europe require further interpretation due to a lack of consensus on the definition of 'naturalised' among Nordic investigators; the values reported may also include casuals.

One robust emerging generalization of invasion biology is that the probability of invasion success increases with residence time (Rejmánek 2000, Pyšek and Jarošik 2005), i.e. the length of time since the introduction of a taxon to a new area. Residence time represents another dimension of propagule pressure: the longer the species is present in the region, the more propagules are spread and the probability of establishing new populations increases (Rejmánek *et al.* 2005). Residence time affects not only the range and frequency of alien species but also whether it persists as a casual or becomes naturalised or invasive (Richardson *et al.* 2000). Our results also showed that invasive status and abundance in an area tends to increase with residence time. For

Table 4. Modes of introduced for naturalised species.

	Estonia[1]	Nordic countries[2]	Switzerland[3]	South Australia[4]	United States[5]
Total number of naturalised species (= 100%)	232	1087	20	904	587
Species introduced deliberately (%)	74	43	75	57	61
Species introduced accidentally (%)	26	43	20	24	11
Unknown mode of introduction (%)	0	14	5	19	28

[1] authors' data.

[2] naturalised in at least one Nordic country as presented in Weidema (2000).

[3] only problematic plants as presented in Gassmann and Weber (2005).

[4] Kloot (1987).

[5] Numbers are means of percentages for 5 different regions in the United States as presented in Mack and Erneberg (2002).

invasive species the variation of residence time is higher than for naturalised species. In some cases invasively spreading species may be present for even less time than species of casual status. First, the species found in more localities might have been spread more efficiently by human mediation. Second, in some cases, invasiveness (rate of spread, competition ability) might have been higher and more important than residence time.

Recent progress suggests that it is possible for a new invader to transform an older invader into a serious new management problem by means of positive indirect interactions that may produce an invasional meltdown (Grosholz 2005). The latter term is widely used when referring to an escalation of the net effects of invasive organisms at the site. Basically, the presence of alien species is making some areas more susceptible to invasion by other alien species (Richardson and Pyšek 2006; *see* the conclusions in Richardson *et al*. 2000). In addition to preventing future introductions, it may be necessary to mitigate the impacts of alien species that have already become established, while realizing that such mitigations may, themselves, have unexpected impacts because of indirect interactions.

Conclusion

We have demonstrated that the establishment and naturalisation of introduced species depend on the level and type of human mediation. This effect may particularly characterise relatively harsh climatic areas. Our data supports an earlier presumption that humans are not just dispersers of the alien species but could raise the propagule pressure created by cultivar selection prior to introduction and/or the long presence of a species in the area (e.g., in the case of ornamental plants via their presence on the market). To summarise, there is a strong circumstantial link between cultivation and subsequent naturalisation.

To follow the problems caused by invasive species and the many pathways by which they enter, we must work to deliberately reduce the introduction and impact of such species (Snow 2002). As pointed out by Reichard and White (2003): "As scientists, we will need to ensure that our science is not only viewed by our peers, as is traditional, but that agencies managing invasive species are also aware of our findings. […] These discoveries, if implemented in management and policy practices, may play a substantial role in lessening environmental degradation through invasions. "

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