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ORIGINAL PAPER

Habitat preferences and distribution characteristics are indicative of species long-term persistence in the Estonian flora

Marek Sammul · Tiiu Kull · Kaire Lanno · Merit Otsus · Merike Mägi · Silja Kana

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Abstract Large-scale changes in regional floras provide direct information about changes in biodiversity through time and enable the evaluation of conservation targets. We compared the distribution ranges in 2004 of Estonian native terrestrial flora with the distribution ranges before 1970, using the Atlas of Estonian Flora. Relative persistence was related to species endemism, commonness, occurrence at its border of the global distribution range, main habitat type, sensitivity to human impact, life-form, conservation category, and Red List category. A literature-based database of the flora of Estonian habitat types was used to evaluate relative persistence of the flora of different habitats. Changes in the flora are largely dependent on human activities. The decrease in mire and grassland habitats and the increase in forests are reflected in the persistences of related species. Flora of mire habitats decreased the most. The fact that an almost ten-fold decrease of grasslands has not resulted in as large a decrease in the ranges of grassland species could serve as evidence of the extinction debt of these habitats. We also found a greater decrease among habitat specialists than habitat generalists and lower average persistence of the species of species-rich habitats. Our data show that current prioritization of species for conservation is in concordance with needs, as reflected in the changes in the range of species. However, conservation has not been entirely successful: the decrease of protected species continues. Our simple method for summarizing large databases was effective for the evaluation of large scale effects of conservation actions.

Keywords National flora · Distribution ranges · Eutrophication · Land-use change · Large-scale changes · Long-term changes · Monitoring · Species persistence

Introduction

There is general acknowledgment of large scale decline in global species diversity (Myers 1979; Wilson 1992; May et al. 1995; Brooks et al. 2002 etc). While the main reason for

M. Sammul (✉) · T. Kull · K. Lanno · M. Otsus · M. Mägi · S. Kana
Department of Botany, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Riia str 181, Tartu 51014, Estonia
e-mail: marek.sammul@emu.ee

such mass extinction is human impact, the causes can range from extirpation of populations to the effects of pollution and climate change. However, the main factor causing current species loss is the destruction of habitats (Soulé 1987; Tilman et al. 1994; Fischer and Stöcklin 1997; Riis and Sand-Jensen 2001 etc.), driven mostly by changing practices of land-use (including abandonment, and intensification of use of natural resources) (Chapin et al. 2000; Sala et al. 2000).

Habitat loss is often accompanied by other changes such as fragmentation and isolation of the remaining habitat patches. These processes have negatively influenced many plant populations (Henle et al. 2004; Honnay et al. 2005), and greater negative effects of the change in quality and quantity of habitat on specialist species than on generalists would be expected (Dupré and Ehrlén 2002). There may be a threshold for the area of habitat occupied by a species below which the probability of its extinction increases drastically (Tilman et al. 1994; Hanski 2000; Hanski and Ovaskainen 2002). Moreover, some long-lived perennial species can persist despite declining population size for a relatively long time. This is sometimes responsible for the apparent long-term maintenance of species richness even after quality and/or quantity of habitat has fallen (Eriksson 2000; Hedin 2003; Ikonen 2004; Helm et al. 2006). Analysis of long-term change in species distributions in relation to dynamics of habitats might reveal which species decrease in distribution mainly because of changed habitat quantity; appropriate measures for their conservation could then be undertaken.

To acquire long-term data on species abundance most countries have established some form of biodiversity monitoring. This is often accompanied by mapping of biodiversity or inventories of conservationally important species (e.g. Andersson 2002). Inventories and surveys provide important information regarding the spatial distribution of species, even though their usability for monitoring may be limited (e.g. Pavlik and Barbour 1988; Hutchings 1991). National atlases of plant species are becoming increasingly available (e.g. the Atlas of European flora, Jalas and Suominen 1972). Quite often these atlases provide information from various time periods (e.g. Preston et al. 2002; Kukk and Kull 2005) or are a repetition of an earlier similar study, enabling large-scale changes in the flora of a specific region to be estimated.

The most threatened habitat types and their flora vary depending upon the region and its land-use history. In the UK, orchids of calcareous grasslands and woodlands have suffered the greatest decline in range (Kull and Hutchings 2006), while on arable land rare plants have decreased the most and the largest changes in abundance of plants are related to increased nutrient load (Smart et al. 2005). Similarly, eutrophication, along with decrease of flora of saline habitats, and of aquatic and wet habitats has driven changes in the flora of the Netherlands (Tamis et al. 2005). In Sweden, species-rich dry to mesic semi-natural grasslands have decreased from 2 million ha to 200,000 ha (Bernes 1994). Their flora contains of a large number of habitat specialists (Cousins and Eriksson 2001), and the habitats are considered strongly threatened, probably possessing a large extinction debt (Eriksson et al. 2002). In the Finnish archipelago, forest plants have increased at the expense of grassland species due to depopulation and consequent abandonment of stock farming (von Numers and Korvenpää 2007).

To date, the Estonian native flora is thought to have suffered only a modest decline of diversity. However, Estonia has undergone large changes in the dominant practice of land use since World War II. These include the complete restructuring of agriculture due to enforced collectivisation (complete prohibition of private farms and establishment of collective farms) after invasion by the Soviet Union (Viiralt and Lillak 2006), massive drainage of wetlands (incl. various peatlands) (Ilomets 2005), abandonment of semi-natural grasslands and increased utilisation of hay-fields since the 1960s, a dramatic drop in agricultural activities in the early 1990s due to the economic downturn (Sammul et al. 2000), and intensification of forestry. It is reasonable to expect that these changes have affected the flora of Estonia. Earlier studies in Estonia have shown an increased human impact on several forest and mire habitats as well as decreased use of semi-natural habitats (Sammul et al. 2000; Kukk and Sammul 2006). Hence, we presume that most species with decreased distribution are associated with these habitat types.

In this paper we estimate long-term distribution trends of vascular plant species and compare their persistence to changes in area of their habitats. Our objectives are (1) to compare the persistence of the flora of different habitat types, (2) to determine whether the species characteristics related to species habitat preference and distribution are related to long-term persistence, (3) to compare current species conservation priorities with species persistence, and (4) to provide recommendations for monitoring and conservation of plant species.

Methods

Mapping of species distribution

The compilation of the database for the Atlas of Estonian vascular plants (see Kull et al. 2002 for details) was undertaken at the beginning of the 1970s. Estonia was divided into 494 quadrats, each about 100 km^2 (11.1 $\times$ 9.45 km) in size, using the Central European grid system (6$'$ $\times$ 10$'$). The database includes the list of species in all 494 quadrats. All quadrats were inspected several times mainly by professional botanists. The help of amateurs has been used for some groups of species (e.g. orchids), in cases where qualified people were available. In each quadrate various habitats were visited and species presence was recorded. Additionally, records on species finds from herbaria, from reliable data from literature, and from different projects, have been included. Literature sources, herbaria, older vegetation analyses, older species counts in quadrats, and various sources of historical data on species distribution were used for mapping species presence in quadrats prior to 1970.

The apomictic genera *Alchemilla*, *Crataegus*, *Euphrasia*, *Hieracium*, *Pilosella* and *Taraxacum*, hydrophytes and most invasive species, were excluded from current analysis since data on their distribution are scarce and not readily comparable to that of the other taxa. Data about the distribution of 1,031 species was included in the current analyses. The taxonomy follows Kukk 1999a.

Species characteristics and habitat preferences

We used literature sources (Flora of Estonian SSR 1953–1984; Kukk 1999a; Kukk and Kull 2005) to compile a list of traits indicating commonness of a species (seven ordinal classes provided by the Flora of Estonian SSR 1953–1984 and Kukk 1999a: Very Rare—1–3 findings during the last 50 years; Rare—4–10 findings during the last 50 years; Uncommon—20–30 regionally restricted populations; Scattered—sparse distribution across Estonia; Occasional—common species within a restricted region; Common—abundant in suitable habitats, but regionally restricted; Frequent—abundant and common across Estonia); endemism in the Baltics and Fennoscandia (endemic or not); whether the species reaches the border of its global distribution range in Estonia (yes or no); sensitivity to human impact (anthropophyte—dependent on human activities, apophyte—benefiting from human activities, hemeradiaphor—indifferent to human influence, hemerophob—species harmed by human influence) (Kukk 1999a); life-form (according to Raunkiaer's classification). We also added indicator values of species requirements (environmental preferences for light, temperature, continentality, soil moisture, soil acidity, nutrients, and salinity) (Ellenberg 1974; Karrer and Killian 1990; Ellenberg et al. 1991; Englisch et al. 1991; Karrer 1992) as well as species conservation category according to Estonian legislation (three ordinal categories defining level of conservation priority: 1st—strictly protected, 2nd—moderately protected, 3rd—category of weakest protection) (Kukk 1999b) and species status in the Estonian Red List which does not imply legal obligations in Estonia (five ordinal categories: Endangered—species under strong threat of becoming extinct; Vulnerable—species whose populations are quickly declining; Rare—species with restricted distribution; Care Demanding—relatively common species whose status requires attention; Indeterminate—species whose degree of being endangered cannot be specified due to insufficient data) (Lilleleht 1998).

The main habitat of each species was determined using the following general categories of habitat types (Flora of Estonian SSR 1953–1984; Kukk 1999a; Leht 1999): dunes, shores (coastal habitats), bedrock outcrops and rocks, grasslands, forests, mires (bogs and fens), cultural habitats, no preference.

Typical flora of habitat types

Using various sources of literature (see Appendix 1) a database of typical species lists for habitat types found in Estonia was compiled. We used a habitat classification by Paal (1997) with some additional well-defined ecotone habitat types (a total of 46 habitat types; Appendix 2). According to the published phytosociological descriptions of the flora of habitat types (Appendix 1), the presence of each species in the typical flora of a particular habitat type was recorded on two levels: (1) dominant or characteristic species of a habitat; (2) other species commonly found in that particular type of habitat. (A single species can belong to a group of dominant species in several habitat types.) Only natural and semi-natural mainland habitats were included. Species that are found only occasionally in one or the other habitat type were omitted from the flora of that habitat type.

Species habitat specificity was estimated at two levels. Species limited to (i.e. occurring in the list of) less than 15% of habitat types (472 species) were considered to be habitat specialists while species occurring in more than 15% of habitat types were considered to be habitat generalists.

Data analysis

We calculated the persistence for each species as the percentage ratio of the number of quadrats occupied by the species between 1970 and 2004 in the Atlas of Estonian vascular plants (Kukk and Kull 2005) from the total number of quadrats occupied by the species in the Atlas (as in Kull et al. 2002 and Kull and Hutchings 2006).

Differences in mean persistence between species belonging to different groups of endemism, commonness, occurrence at the border of the global distribution range, main habitat type, sensitivity to human impact, life-form, conservation category, and Red List category were tested with one-way type III analysis of variance. Insufficient overlap between different groups prevented testing of interactions between factors. Correlation analysis was used to seek relationships between persistence and indicator values of species requirements.

Using the species' persistences three groups of species were selected: (a) species with no decrease or only a slight decrease in distribution range (persistence 70–100%); (b) species with intermediate decrease in range (persistence 40–70%); (c) species that had suffered a large decrease in range (persistence 0–40%). We used one-way type III analysis of variance to test whether the proportion of species belonging to each persistence group in the typical flora of a particular habitat type differed between the following groups of habitat types: forest habitats, other forest-related habitats (clear-cuts, forest edges, forest survey lines, electricity and other tracks, and burnt-over areas), shrubland habitats, mires, grasslands, dunes and sandy plains, and coastal habitats (see Appendix 2 for a complete list). Bedrock outcrop habitats had to be omitted from this analysis due to lack of replicates. To correct for the mass effect in all results of analyses of variance we employed the Bonferroni-type correction with the Dunn-Šidák method (Sokal and Rohlf 1995) and obtained the critical experiment-wise error rate using the following equation:

$$p_{\text{critical}} = 1 - (1 - 0.05)^{1/k} \tag{1}$$

Here 0.05 is the original level of probability of type I error and k stands for the number of statistical tests.

The weighted average of persistence value (*PV*) was calculated for the flora of each habitat type (h) as follows:

$$PV_h = \left(\sum PV_i * W_{ih}\right) \Big/ \sum W_{ih} \tag{2}$$

Here PV_i is the persistence of species i and W_{ih} is the importance weight of species i in habitat h. An importance weight of 2 was given to dominant and characteristic species of a habitat, and an importance weight of 1 was given to other species in that habitat type. Correlation between the weighted average of persistence of a habitat and the number of species in a flora of a habitat was tested, along with a test of the difference in weighted average of persistence between different groups of habitat types.

Results

Traits of decreased species

The distribution range of almost half (49% of the total) of the species in the Estonian flora has remained within 80% of the original range in the post-1970 period (Fig. 1). There are 18 species in which the persistence is lower than 10%, 120 species (11.6%) persisted in less than 40% of their original quadrats and 261 species (25.4%) persisted in 40–70% of quadrats.

Different groups of main habitat type, life-form, border of the distribution range, and sensitivity to human impact all differed in their persistence (Tables 1 and 2). Endemic species had lower mean persistence than those with wider distribution, but this difference was not significant. There was a mixed trend regarding species tolerance to human influence. Hemerophob species showed the strongest decrease in range, but this group did not differ significantly from anthropophytes (Tukey HSD test, $P = 0.26$). Apophytes had the highest persistence and formed a single homogeneous group ($P < 0.001$). Hemeradiaphor species, which were second in persistence, differed significantly from hemerophob species ($P < 0.003$), but did not differ from anthropophytes. Species at their border of the distribution range were less persistent than species within their distribution range. Even

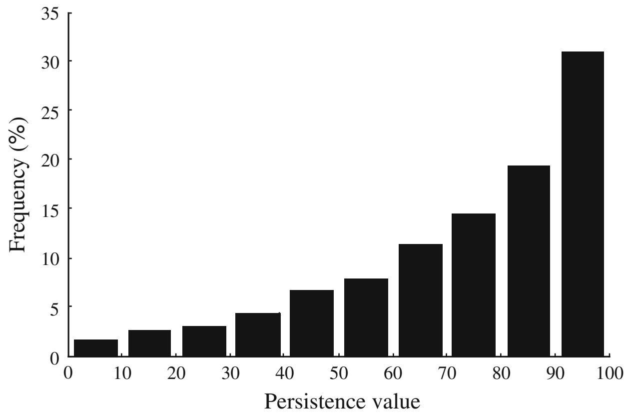


Fig. 1 Frequency distribution of persistences of plant species in the Estonian flora

though we did not separate between various borders, species at their south-western or western border were least persistent. Of the various life-form groups, phanerophytes were the most persistent and therophytes the least persistent. There was no difference in persistence rate between chamaephytes, hemicryptophytes and geophytes.

There were only minor variations in persistence between groups of species with different main habitat preference. We found that species of mires exhibited significantly lower mean persistence than forest and grassland species ($P < 0.002$ and $P < 0.016$ respectively). Species inhabiting either bedrock outcrops or dunes had on average the lowest persistence, but due to the very high level of within-group variation, there was no statistically significant difference between these and other species groups. However, there was considerable difference in average persistence between species with different habitat specificity. Habitat generalists had significantly higher persistence than habitat specialists.

Species belonging to various groups of commonness, conservation, and Red List categories also differed significantly in their persistence (Table 3). Persistence declined with increasing level of rarity. The highest persistence was observed for 'frequent' species (Fig. 2a), followed by 'common' species. 'Occasional' and 'scattered' species formed one homogeneous group, while 'uncommon', 'rare' and 'very rare' species formed another homogeneous group with the lowest persistence. The conservation status of species was also consistent with the persistence of the species (Fig. 2b): those most strictly protected are species with the lowest persistence. However, there is no significant difference between the persistence of species of two most strict conservation categories (1st and 2nd categories). Moreover, the lowest conservation category species (3rd category) exhibited the same persistence as unprotected species. Of the Red List categories, species with 'indeterminate' status (see Lilleleht 1998 for definitions) were least persistent, followed by groups in decreasing threat categories (Fig. 2c).

We found three significant correlations between species persistence and indicator values of species' requirements (Table 4, Fig. 3). Light-demanding species were less persistent than shade-tolerant species; species preferring alkaline soils were more persistent than species of more acidic habitats, and species preferring nutrient-rich habitats were more persistent than species of nutrient-poor conditions.

Table 1 Averages, standard deviations and sample size of persistences of categories of species distribution and habitat preference

Species category	Persistence		N
	Average	SD	
Main habitat type			
Mires	66	24	122
Bedrock outcrops and rocks	62	31.6	14
Dunes	67	23.8	28
Coastal habitats	72	20.4	68
Shores	71	24.7	110
Grasslands	75	23.8	309
Forests	77	22.2	229
Cultural habitats	72	25.2	140
Sensitivity to human impact			
Hemerophob	61	25.4	99
Hemeradiaphor	70	23.8	490
Apophyte	81	19.8	362
Anthropophyte	67	27.8	77
Endemism			
Nonendemic	73	23.8	1,016
Endemic	71	27.1	15
Border of distribution range			
Not at the border of range	78	21.6	617
At the border of range	65	24.8	413
Life-form			
Therophytes	70	23.2	156
Chamaephytes	76	18.3	57
Geophytes	77	20.5	137
Hemicryptophytes	76	20.9	426
Phanerophytes	87	17.6	59
Habitat specificity			
Generalist	81	18	507
Specialist	65	25.7	472

Changes in floristic composition of habitat types

The weighted averages of persistence of species from most habitats were between 70 and 75%. The lowest average persistence was observed in flora of deciduous shrublands (mostly *Corylus avellana* habitats) while the highest average persistence was found in flora of dry boreal forests and in floodplain willow shrublands (Appendix 2). Of the groups of habitat types, the flora of bedrock outcrops had the lowest average persistence (69.6%), followed by habitats of shrublands (70.1%), while forest habitat types had the highest average persistences (76.6%).

We divided the flora of Estonia into three groups according to their persistence. Species with persistence under 40% were most abundant in cliff habitat types and in sandy and dune habitats (Fig. 4). However, this difference was not significant (Table 5). There was a

Table 2 Differences in persistence between species groups with various traits as tested with one-way ANOVA

Factor	Source of variation	SS	d.f.	MS	F-value	P
Main habitat type	Intercept	2,052,703	1	2,052,703	3,658	**<0.0001**
	Factor	13,035	7	1,862	3.32	**0.0017**
	Error	567,841	1,012	561		
Sensitivity to human impact	Intercept	2,798,578	1	2,798,578	5,306	**<0.001**
	Factor	45,972	3	15,324	29	**<0.001**
	Error	540,090	1,024	527		
Endemism	Intercept	303,721	1	303,720.9	533	**<0.0001**
	Factor	77	1	77	0.14	0.71
	Error	586,609	1,029	570.1		
Border of the distribution range	Intercept	5,054,831	1	5,054,831	9,644	**<0.001**
	Factor	47,335	1	47,335	90	**<0.001**
	Error	539,351	1,029	524		
Life-form	Intercept	2,938,437	1	2,938,437	6,734	**<0.0001**
	Factor	12,170	4	3,042	6.97	**0.00002**
	Error	362,199	830	436		
Habitat specificity	Intercept	5,480,158	1	5,480,158	10,948	**<0.001**
	Factor	71,600	1	71,600	143	**<0.001**
	Error	515,086	1,029	501		

Differences between groups are statistically significant (after Bonferroni-type correction) at the P-level < 0.0085

Table 3 Differences in persistence between groups with different levels of commonness in the flora, conservation priority and threat (red list) as tested with one-way ANOVA

Factor	Source of variation	SS	d.f.	MS	F-value	P
Commonness	Intercept	3,701,073	1	3,701,073	9,703	**<0.001**
	Factor	192,487	6	32,081	84	**<0.001**
	Error	388,684	1,019	381		
Conservation category	Intercept	1,047,640	1	1,047,640	1,920	**<0.0001**
	Factor	26,214	3	8,738	16	**<0.0001**
	Error	560,472	1,027	545		
Red List category	Intercept	856,866	1	856,866	1,768	**<0.001**
	Factor	85,919	5	17,184	35	**<0.001**
	Error	496,205	1,024	485		

Differences between groups are significant (after Bonferroni-type correction) at the P-level < 0.017

significantly higher number of species with persistence values between 40 and 70% in mire habitat types than in forest habitat types (Tukey HSD test, $P < 0.001$) or in other forest-related habitats ($P = 0.02$). The proportion of species with persistence over 70% was significantly smaller in mire habitat types than in forest habitat types ($P = 0.01$).

We found a significant non-linear negative correlation between species richness in the flora of a habitat type and the weighted average of persistence of species from a habitat type ($R^2 = 0.28$; $P < 0.05$) (Fig. 5).

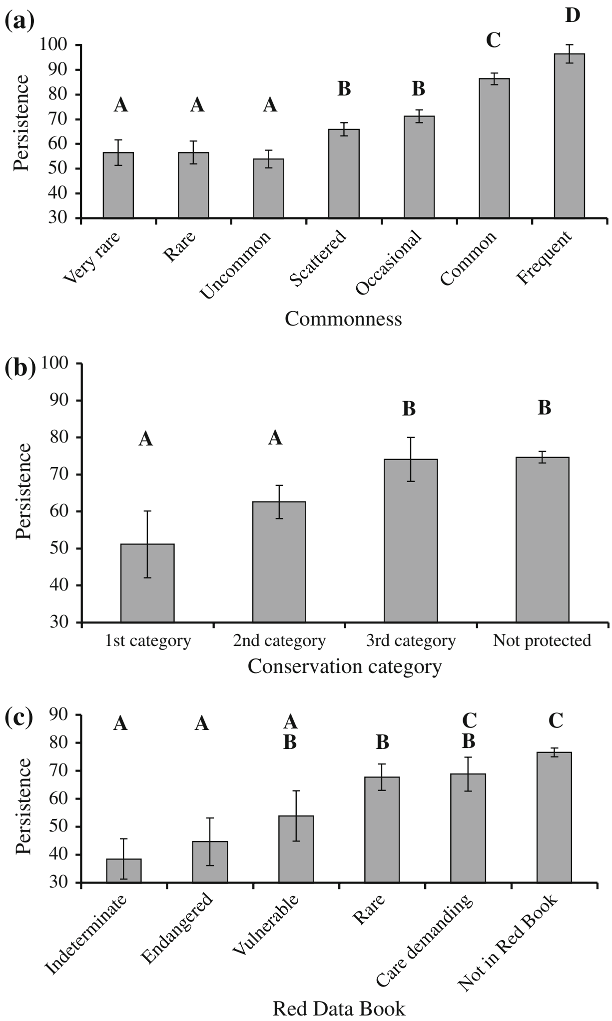


Fig. 2 Mean persistence for species with different levels of commonness (**a**), conservation category (**b**; 1st category is the most strictly protected one), and Red List category (**c**). The same letters above columns denote homogeneous groups while bars indicate 95% confidence intervals of means

Discussion

Effects of changing land use

Due to large changes in land-use the Estonian land cover has experienced considerable change during the last 50 years. The total area of grasslands has decreased by about 90%; the area of mires has decreased by two-thirds while that of forest habitats has doubled (Fig. 6). Obviously, corresponding changes in the flora would be expected.

Increase of forest area has been used as an indicator of positive changes in forest biodiversity, which in some cases is supported with evidence (e.g. von Numers and Korvenpää 2007). However, as shown by our data, such a simplified approach is not

Table 4 Spearman rank order correlations between persistence and indicator values of species requirements

Ellenberg indicator value	Valid N	Spearman R	$t_{(N-2)}$	*P*-level
Light	919	−0.147	−4.51	**<0.001**
Temperature	705	−0.007	−0.17	0.862
Continentality	784	−0.037	−1.03	0.301
Soil moisture	867	−0.039	−1.13	0.257
Soil acidity	737	0.115	3.12	**<0.002**
Nutrients demand	845	0.216	6.41	**0.001**
Salinity	863	0.063	1.85	0.064

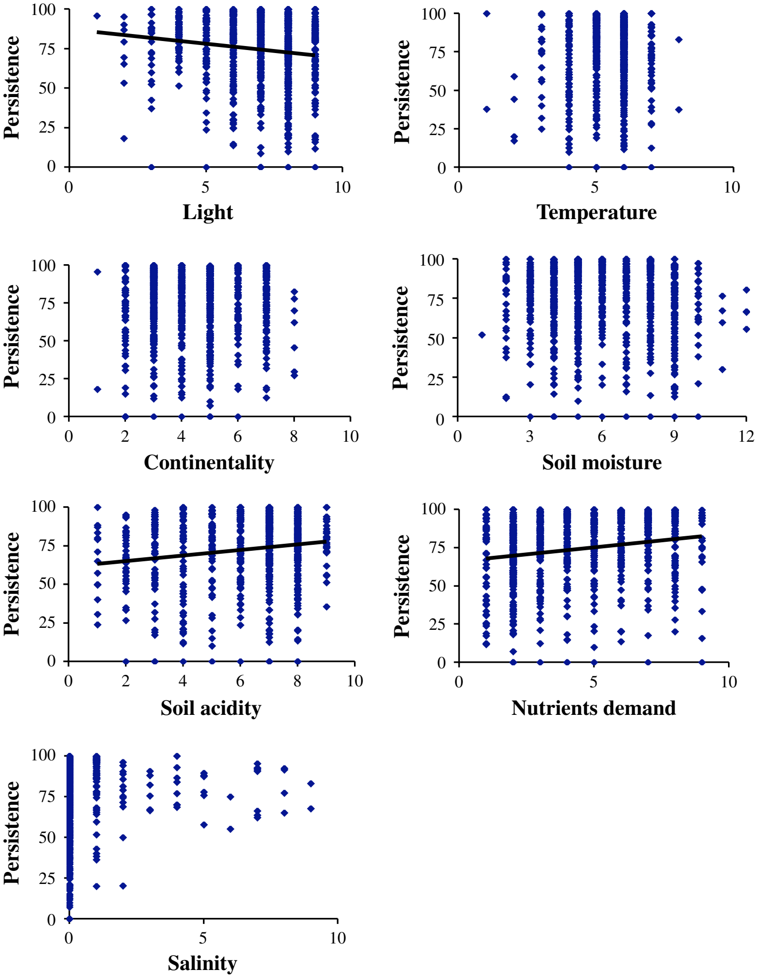


Fig. 3 Correlations between persistence and Ellenberg indicator values of species requirements. Only statistically significant trendlines (Table 4) have been plotted

Fig. 4 Proportion of species with different persistence values in various groups of habitat types

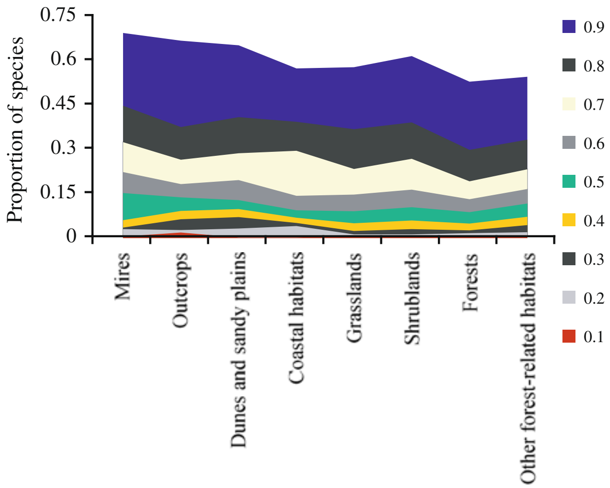
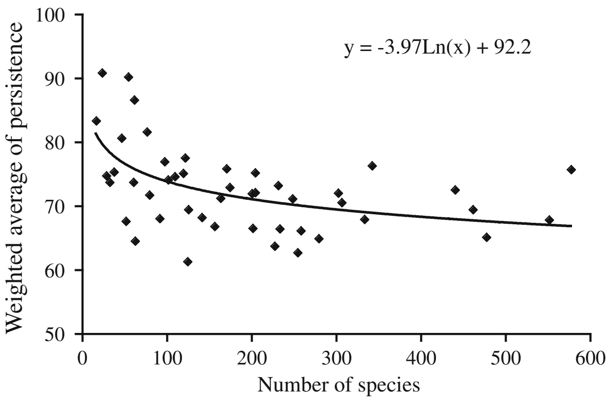


Table 5 Difference between different groups of habitat types in relative number of species of various ranges of persistence (PV)

Source of variation	SS	d.f.	MS	*F*-value	*P*
PV < 40%					
Intercept	0.168	1	0.168	134	**<0.0001**
Habitat type	0.007	6	0.001	0.98	0.45
Error	0.051	41	0.001		
PV > 40–70%					
Intercept	1.45	1	1.45	510	**<0.0001**
Habitat type	0.078	6	0.013	4.55	**0.0013**
Error	0.117	41	0.003		
PV > 70–100%					
Intercept	20.0	1	20.0	3,272	**<0.0001**
Habitat type	0.10	6	0.017	2.81	**0.022**
Error	0.25	41	0.006		

Fig. 5 Relationship between weighted average of persistence value of the flora of a habitat type in relation to number of species in the flora of a habitat type



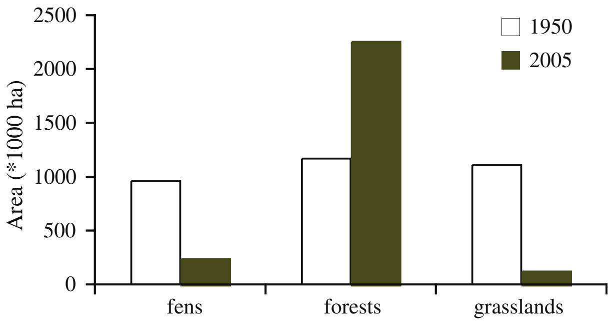


Fig. 6 Changes in area of mires, forests, and grasslands in Estonia from 1950 to 2005 (based on Laasimer 1965; Metsakaitse 1999; Sammul et al. 2000; Kukk and Sammul 2006; Statistics Estonia 2007).

justified, and increase in forest area does not necessarily indicate a shift towards higher forest biodiversity. Nor does it reflect the increased intensity of use of forest resources, the resulting scarcity of high quality, old-growth forests (Andersson et al. 2003; Lõhmus et al. 2004), and decrease of biodiversity. Decrease of old-growth forests in Estonia is approaching a point at which conservation targets (Lõhmus et al. 2004) cannot be met. In time, major landscape- and habitat-changing processes, such as drainage, creation of fields, increased construction of roads, abandonment of managed land, etc, will also have an increasingly negative effect on the fauna and flora of forests. So far, the flora of forests, as well as shade-tolerant plants, has in total suffered least, but fresh boreal forests and boreal heath forests, which are among habitats that provide the best wood and thus suffer highest cutting pressure, already demonstrate strong decline in species richness (Appendix 2).

The decrease in area of grasslands includes a decrease of high-diversity and conservationally important semi-natural grasslands (Kukk and Sammul 2006). Estonia is known for its high diversity grasslands (Kull and Zobel 1991; Kukk and Kull 1997; Sammul et al. 2000). However, even though our results indicate moderate persistence of grassland species, we have detected a relatively higher decline in diversity of species-rich communities (mostly grasslands). Hence, the preservation of high diversity grasslands is not guaranteed and degradation, analogous to most other European countries (e.g. Willems 1983; Bakker 1989; Smart et al. 2003) could continue, partly also due to loss of species and decrease in size of species pool.

The decrease of mires has been habitat type-dependent (see Ilomets 2005) and has resulted in loss of almost all Estonian fens while the reduction in area of raised bogs has been much smaller (Pajula 2006). We detected lower persistence among mire species than among grassland species. Thus, local extinctions seem to be faster in mires than in grasslands, despite the greater decrease of grassland area. Partial habitat destruction in mires is usually coupled with wide-reaching impacts on the quality of the remaining habitat patches. The rapid change in ecological conditions in degraded mires leads to the rapid floristic changes revealed by our data (see also Fojt and Harding 1995). The loss of grassland habitats is primarily due to direct destruction, or abandonment and subsequent overgrowth. Therophytes respond quickly to such successional changes while clonality helps to resist the habitat change. Still, the relatively persistent floristic composition of grasslands may only be transient (von Numers and Korvenpää 2007) and may mask a high extinction debt (see also Helm et al. 2006). It should also be noted that mire flora has much higher habitat specificity than grassland flora. It has been shown before that grassland species can sometimes find refuges in new, man-made habitats such as road verges (e.g. Tikka et al. 2000; Cousins and Eriksson 2001). These habitats are not nearly equal in quality to the true grasslands (Tikka et al. 2000), but may sometimes serve as migration corridors and provide a transient habitat. The very specific habitat conditions of wetlands, however, are hardly ever replicated by humans. Quite the contrary: draining wet areas and turning them into utilisable land has been a major undertaking (e.g. Krug 1993; Ilomets 2005).

We found that in Estonia the average persistence of species is lower in habitats that contain more species. This could be because more diverse habitats are more likely to contain species with low persistence. However, the pattern of the relationship (Fig. 5) implies that the relationship is primarily caused by low diversity habitats where flora has not declined. Alternatively, it could be an effect of eutrophication, which has a relatively stronger negative effect on nutrient-poor communities. The latter, especially on calcareous soils, are among the most diverse communities in Estonia. This hypothesis is supported by similar observations from other countries, where negative effect of eutrophication has been detected (McCollin et al. 2000; Tamis et al. 2005; Piessens and Hermy 2006; Smart et al. 2006; Römermann et al. 2008), and by higher persistence of nutrient-demanding species in our data (Table 4, Fig. 3). The issue demands further detailed study, because if the stronger decline of the flora of diverse communities is a general trend it has serious implications for conservation strategies.

Persistence of species with different characteristics

Species with specific ecological requirements are often restricted to few habitat types and are therefore more likely to be rare (Cousins and Eriksson 2001; Dupré and Ehrlén 2002). The persistence of rare species is always influenced by stochasticity of the environment. Loss of one local population has a relatively larger negative impact for habitat specialists than for ubiquitous species. Our data showed decreased persistence with decreasing species commonness (Fig. 2), as well as strong negative effect of habitat specificity on persistence. Often, changed landscapes act as a dispersal barrier for habitat specialists and their negative growth rate is not balanced by immigration from other propagule sources. It is thus important to concentrate conservation efforts on sustaining habitats which provide specific environmental conditions and habitats for rare and specialized species.

Our results revealed that species at the border of their global distribution range had low persistence in the Estonian flora. Such populations are mostly limited by unsuitable climatic conditions and the implications of the lower persistence probability of this group of species should be considered in planning both national and international conservation networks. Further analysis of range shifts might provide valuable information in the context of the global climate change and species protection at a pan-European scale.

Higher persistence of nutrient-demanding species indicates the widely recorded trend of eutrophication of ecosystems (McCollin et al. 2000; Smart et al. 2005; Piessens and Hermy 2006; Römermann et al. 2008). Above all the enrichment concerns grasslands, many of which have been fertilized for agriculture, but probably also other habitats due to atmospheric deposition. Together with species at the border of their distribution range, hemerophobs, and of habitat specialists, all of which have suffered at least 35% decline, a set of vulnerable species is formed, that deserves further attention both from a conservation point of view and also scientifically.

Data restrictions

The data-set that was used in this study is a result of rather large generalizations. First, the mapping of species distributions was carried out over a long time interval (35 years is considered as “current”), during which Estonian habitats have undergone a series of huge changes. Secondly, the mapping of the Estonian flora has been carried out by counting species in quadrats that have an area of about 100 km^2. Hence, there could be considerable changes occurring within these quadrats both spatially and temporally (including changes in area of various habitat types located within quadrat) that are overlooked. Thirdly, the amount of data acquired before 1970 is relatively scarce. Hence, we are only able to estimate the decline of species range; an estimated increase in species range since 1970 may be caused by the lack of information from previous periods. However, considering such restrictions only strengthens our results as all the points raised above reduce the detectability of changes.

Monitoring methodology

Due to the large effort needed for monitoring general trends in biodiversity as well as the fulfillment of national and international conservation targets, recent efforts have concentrated primarily on changes in biodiversity. Persistence could be used for evaluation of large-scale conservation efforts which are rarely documented (Pullin et al. 2004; Sutherland et al. 2004). The 2010 target (Balmford et al. 2005) requires information about dynamics of the complete biota. Plants are among the few species groups for which this task is actually realistic. Surveys like mapping of flora (combined with various inventories) are the only mechanisms that provide data on the condition of the entire flora and could alert us to a decline of a species that is not currently protected (e.g. see Kull et al. 2002) as species that are not protected are usually not monitored. Monitoring of change in common species is an important but rather neglected task in conservation planning. It is best to know when a species starts to decline and to take action before it has become rare. Moreover, such warnings are not just indicative of changes in individual species, but if several species show a consistent pattern of change, it also signals changes in the quality of habitats or environmental conditions.

Large scale floristic censuses are quite rare. There are a few atlases of flora of whole countries which include data from various time periods (e.g. Flora of UK, Preston et al. 2002) and few similar databases, such as the flora of the Netherlands (Tamis et al. 2005). Even though such species lists lack the precision that comes with detailed and repeated vegetation analyses or even with simple addition of abundance data (Balmer 2002), they are still useful for covering large areas and for estimation of coarse changes. In order to provide comparative material and to evaluate pan-European shifts in plant species richness, publication of similar data from other countries is badly needed.

Implications for plant conservation

Our analysis points out that despite conservation efforts plant diversity in Estonia continues to decline and this is mostly due to human influence. The decrease of hemerophobs, of mire species, and of species preferring conditions with low nutrient availability indicates increasing negative human influence. Drainage and eutrophication are probably amongst the most dangerous effects. At the same time, a decrease of anthropophytes, light-demanding species and grassland species, indicates a decrease in positive human influence (e.g. grassland management). The majority of plants now considered rare have reached that status because of changes in land use in Estonia (Fig. 2a; see also Pärtel et al. 2005). Moreover, the number of rare species has not decreased (Kukk 2003); instead, our results suggest that it could continue to increase. Hence, it could be argued that conservation efforts have been only partially successful in preserving plant diversity.

Still, our results show that, on average, both legal protection categorisation and Red Data Book categorisation give high priority to recently-decreasing species (Fig. 2) and, hence, are addressing the problems to same extent (but see Pärtel et al. 2005). As an evidence for at least some success of conservation actions, most species that were rare at previous surveys are still extant: e.g. there are several species that remain viable despite miniscule populations in Estonia (Ryttäri et al. 2003).

Conclusions

Our results emphasize that habitat plant diversity could change asynchronously with changes in the habitat area and depends on habitat vulnerability. We don't want to underestimate the importance of stopping decline in habitats, quite the contrary, but point out that separating quantity and quality could enhance conservation planning for fulfillment of large-scale and long-term conservation targets. Estonia, which is often lauded for well-preserved biodiversity, should also, at least partly, reconsider its plant conservation strategies. Our data reveals troubling trends in the continuing decline of rare species and even of species with legal protection, in less persistent flora of species-rich habitats, and in effects of eutrophication. Land-use changes (e.g. Bernes 1994; Henle et al. 2004; Honnay et al. 2005; von Numers and Korvenpää 2007) and eutrophication (e.g. McCollin et al. 2000; Van der Veken et al. 2004; Tamis et al. 2005; Piessens and Hermy 2006) seem to be the main driver behind changes in plant diversity throughout the Europe. Conservation specialists have recognized some of these negative developments and measures have been planned to prevent continuation of these processes (see e.g. Sammul and Lõhmus 2005 for an overview). A preservation of habitats for specialist species should be given highest priority in the near future.

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Appendix 1

List of sources used to compile a database of species presence in various habitats.

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Eichwald K, Kask M, Talts S et al (1959) Eesti NSV floora. 3. Eesti Riiklik Kirjastus, Tallinn

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Eichwald K, Talts S, Vaga A et al (1956) Eesti NSV floora. 2. Eesti Riiklik Kirjastus, Tallinn

Eilart J, Kask M, Kuusk V et al (1973) Eesti NSV floora. 5. Valgus, Tallinn

Kalda A (1960) Eesti NSV laialehiste lehtmetsade taimkate. TRÜ toimetised 83. Botaanika-alased tööd IV:123–155

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Kuusk V, Talts S, Viljasoo L (1979) Eesti NSV floora.11. Valgus, Tallinn

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Botany, Latvian Academy of Sciences, Institute of Biology. Lithuanian Academy of Sciences, Institute of Botany. Tartu

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Appendix 2

Habitat types and basic descriptive characteristics of their flora used in this study.

Habitat type	Habitat group	Weighted average of persistence	Number of species
Alvar forests and shrublands	Forests	66	155
Boreal heath forests	Forests	66	257
Dry boreal forests	Forests	91	22
Fresh boreal forests	Forests	65	278
Dry boreo-nemoral forests	Forests	87	60
Fresh boreo-nemoral forests	Forests	74	332
Floodplain forests	Forests	78	169
Floodplain willow shrublands	Forests	90	53
Rich paludified forests	Forests	77	230
Poor paludified forests	Forests	75	108
Minerotrophic swamp forests	Forests	75	203

Appendix continued

Habitat type	Habitat group	Weighted average of persistence	Number of species
Mixotrophic (transitional) bog forests	Forests	78	120
Ombrotrophic bog forests	Forests	74	59
Drained peatland forests	Forests	75	118
Wooded meadows	Grasslands	76	576
Alvar grasslands	Grasslands	72	301
Boreal heath grasslands	Grasslands	80	45
Boreal grasslands	Grasslands	67	232
Boreo-nemoral grasslands	Grasslands	70	550
Floodplain grasslands	Grasslands	73	439
Coastal meadows	Grasslands	77	341
Paludified grasslands	Grasslands	71	460
Minerotrophic fens	Mires	71	305
Floodplain swamps	Mires	74	100
Mixotrophic (transitional) fens	Mires	72	199
Spring fens	Mires	68	90
Heath moors	Mires	84	15
Treeless and treed ombrotrophic raised bogs	Mires	66	50
Vegetation of bedrock outcrops	Outcrops	70	124
Salt marshes	Coastal habitats	74	27
Rubble, pebble and gravel ridges	Coastal habitats	71	162
Fucous ridges	Coastal habitats	77	96
Vegetation of coastal dunes	Dunes and sandy plains	73	173
Depressions between dunes	Dunes and sandy plains	76	36
Vegetation of inland dunes and sandy plains	Dunes and sandy plains	67	200
Alvar juniper shrubs	Shrublands	71	247
Juniper shrubs with deciduous species	Shrublands	82	75
Juniper shrubs on sands	Shrublands	65	61
Corylus avellana bushes	Shrublands	62	123
Alnus incana bushes	Shrublands	66	140
Willow bushes	Shrublands	71	78
Forest margins on mineral soils	Other forest-related habitats	65	476
Forest margins on swampy soils	Other forest-related habitats	72	203
Forest survey lines, electricity and other tracks	Other forest-related habitats	63	253
Burnt-over areas	Other forest-related habitats	74	31
Cut-over areas	Other forest-related habitats	64	226

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