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Change in the occurrence of common vascular plants in Finland between 1960–2000 and 2001–2019

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Data from a national vascular plant atlas, containing species occurrence data from 1-km squares in different parts of Finland over a period of 60 years, were used for detecting change in the commonness of 712 species. The dataset was divided into two parts, one containing squares inventoried between 1960 and 2000 (Period A, 4 596 squares) and the other containing squares from 2001 to 2019 (Period B, 3 692 squares). Of the 712 species analysed, we observed 124 species that showed consistent increase in commonness from Period A to Period B. Only eight species showing a decline from Period A to Period B were found. Our results indicate that human activities have been the main driving force behind the floristic change in Finland during the study period. The successful competitors are mostly alien and apophytic native species that are able to utilize habitats modified by cultural influence.

Introduction

Finland is one of the floristically well-known countries in the world. However, the chronological aspect of the flora – various patterns of floristic change over time – is rather poorly documented. Monitoring of rare and endangered species for conservation purposes has been a focal point in a number of assessments coordinated by the Finnish Environment Institute and carried out by voluntary amateur botanists together with professionals. Likewise, expansion of invasive alien plants has been a theme of growing interest in recent decades. However, the temporal dynamics of common native species, especially those with no economic value, has drawn less attention from botanists.

Here, we utilize the species occurrence data collected for an atlas of the vascular flora of Finland (see Kurtto & Lampinen 1999). The atlas is a coordinated national floristic survey initiated in 1985, but we have also included a number of additional 1-km squares inventoried with the same methods between 1960 and 1985. These data, collected by professional and amateur botanists from different parts of the country, include the occurrences of all vascular plant species found within the 1-km squares surveyed. The primary use of the data has been the publication of distribution maps for the species, originally as a commercial digital atlas (Lahti et al. 1994, 1997). Since 2006, the distribution maps have been published online and updated annually (see the atlas website at http://kasviatlas.fi).

The 60 years of occurrence data from 1960 to 2019 is a period sufficient for detecting at least the most rapid changes in the flora of Finland, especially among the most common species. Following these baseline settings, we focus here on examining the changes in prevalence in common species. We have excluded a large number of uncommon species from our analysis, because there are not enough occurrence data for detecting significant change in their commonness. Here, we focus on the average change in species' commonness throughout the country and ignore the spatial patterns of change and range shifts of the species. Specifically, we will examine the following questions:

1) How many of the 712 vascular plant species analysed show consistent change in commonness between the time periods of 1960–2000 and 2001–2019?

2) What is the relative proportion of increasing and decreasing trends in species commonness?

3) Are the observed changes in commonness occurring more often in certain types of plant species

Collection of floristic data

The floristic data used here were collected by professional and advanced amateur botanists in various localities of Finland. The basic unit of mapping has been a 1×1 km^2 square, aligned with the gridlines of the Finnish Uniform Grid (see Heikinheimo & Raatikainen 1971, 1981). The goal of the field workers has been to record all vascular plant species occurring within the 1-km targeted squares. Preprinted field forms, with different species lists in various parts of the country, were used to facilitate the surveys.

No systematic or randomized sampling schemes were used in the selection of the 1-km grid squares. Instead, each voluntary field worker was free to choose any available square, based on personal preferences. Certain outcomes from this have emerged that need to be taken into account in analysing the data and assessing the observed changes in species commonness.

First, with very few exceptions, each 1-km grid square was examined only once over the period from 1960 to 2019. Second, quadrats with locally richer floras were probably preferred over poorer quadrats by the workers. Third, the field workers were requested to assess whether the 1-km square was examined ”completely”, implying that a reasonably thorough survey of different parts of the quadrat has been completed. However, reaching completeness in species occurrence mapping is difficult, because there are considerable species-specific differences in observability (Kytövuori & Suominen 1967, Chen et al. 2009, 2013). Thus, all species occurring within the 1-km square are seldom recorded in real life. The potential impact of incomplete recording efficiency of the 1-km squares was compensated for by taking into account all the observations of the species made in the squares during the complete range of the two time periods used in the comparison.

On the other hand, with the exception of a small number of problematic taxa such as *Alchemilla* spp. and the *Poa pratensis*/*alpigena* complex, we are confident that the field workers were competent enough to identify the species found, so that the number of false-positives (species occurrences recorded in error) is close to zero. The floristic data used in the analysis are stored in the National Floristic Database Kastikka, maintained by the Finnish Museum of Natural History (see Kurtto & Lampinen 1999).

Analysis of data

Until late 2019, a total of 9262 squares were examined. Although the atlas mapping scheme officially began in 1985, there are 938 additional squares, examined with the same method between 1960 and 1985, that were included in the analysis. The original goal of the atlas mapping scheme was to complement the distribution maps of vascular plants in Finland, based on museum collections, publications and unpublished floristic notes (see Kurtto & Lampinen 1999).

In our previous studies and analysis of the data, the temporal distribution of the floristic observations was ignored. Instead, the focus was on using the spatial components (northern and eastern coordinates of the Finnish Uniform Grid) as explanatory variables. The goal here was to identify the species that have shown significant change in commonness in Finland during recent decades. For such species, temporal averaging of species occurrence data over several decades can hide important aspects of their past and present distribution patterns.

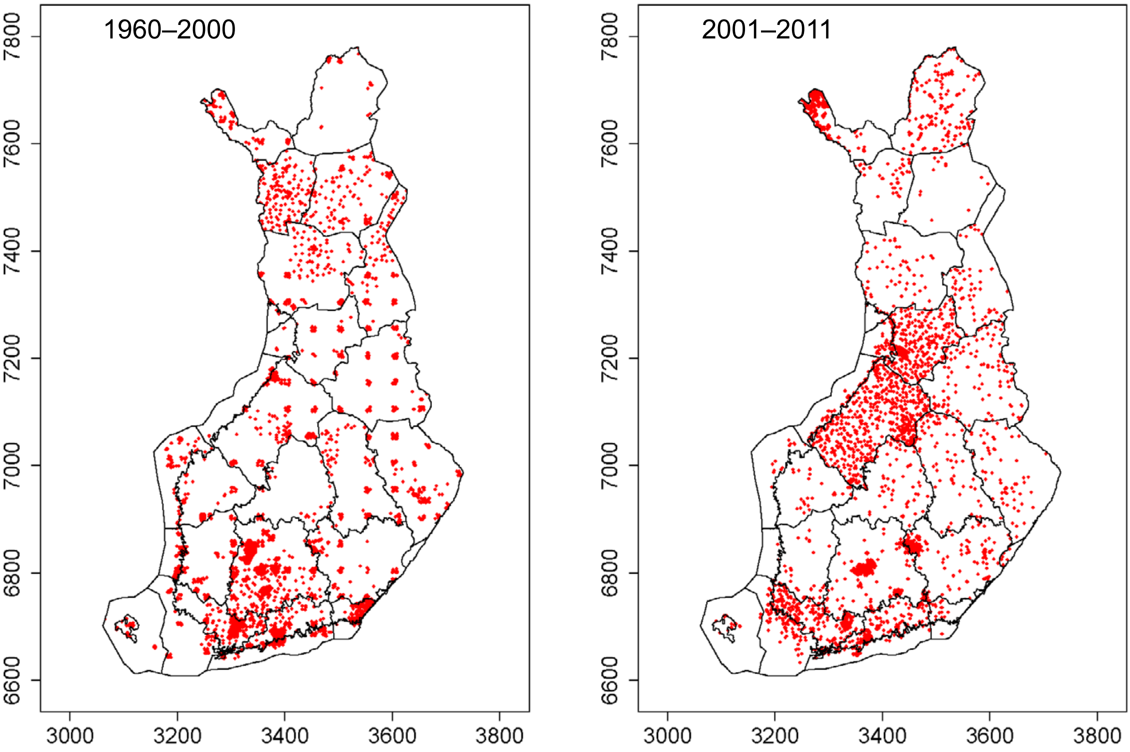

Figure 1. Locations of 1-km squares in Finland inventoried in Period A (1960–2000) and Period B (2001–2019).

In the analysis of change, the dataset was divided into two temporally distinct periods. The first period (Period A, 4596 squares) covered data for the years 1960–2000. The second period (Period B, 3692 squares) covered data for the years 2001–2019. The locations of the 1-km squares analysed during these two periods are shown in Fig. 1.

The resulting two datasets were completely independent, i.e. there were no common squares studied in both datasets. A spatial data model, based on generalized additive models (GAMs; Hastie & Tibshirani 1990, see also Yee & Mitchell 1991, Wood 2017), was fitted to the binary occurrence data for each species in both time periods. Smoothing functions of the northern and eastern coordinates and their combination were used as explanatory variables of the additive model and logit transformation of the presence-absence data as a response variable.

Using the fitted GAMs for each species and time period, occurrence probabilities were estimated for each of the 3859 10×10 km^2 grid squares covering the land area of Finland. These projected probability values were then used for calculating the mean commonness of the species in each of the two time periods.

The confidence limits of the results were estimated by calculating 1 000 bootstrap replicas of the data for the most common species, based on the number of occurrences in the dataset. A total of 712 species were analysed with bootstrap. All calculations were done, using the R language. The GAMs were fitted, using the R package *mgcv* (Wood 2019, see also Wood 2017).

Due to the large number of species analysed, we used rather strict criteria for the indication of change. In a pairwise comparison of frequencies in Period A vs. Period B in each of the 1 000 bootstrap replicas, we recorded change only when the difference in commonness was at least 0.01 units upwards or downwards. We investigated only the absolute change in frequency, since it is biologically more interesting than the relative change.

The changes observed in species commonness between the two time periods may have been due to differences in the proportion of the various biotopes in the grid squares included in the analysis. To quantify such potential differences, we used the Corine 2012 biotope classification for Finland (see Härmä et al. 2015) to calculate the proportions of primary biotopes in the squares. The most important differences in biotope proportions between the two periods are for forests and bodies of water (Table 1). There is 12% more forest cover in the squares examined in Period B than in Period A. Correspondingly, the proportion of bodies of water in Period B is only 66% of that in Period A. The ratio of the other primary biotopes is between 0.90 and 0.95.

These differences imply that the expansion observed in forest species, as well as declining trends in aquatic species, may at least partially have been artefacts of uneven biotope proportions. This possible source of error will be discussed further in the species accounts.

Table 1. Proportion of primary biotopes in the quadrats inventoried during the two time periods. Period A covers years 1960--2000 and Period B years 2001–2019. The greatest differences in biotope proportions between periods are in forests and wetlands.

CORINE2012 land use class	Period		B/A ratio
	A	B	
Artificial surfaces	8.9	8.0	0.90
Agricultural areas	9.7	9.1	0.93
Forests and semi-natural areas	61.4	68.5	1.12
Wetlands	3.9	3.7	0.95
Water bodies	16.1	10.7	0.67

Taxonomy and species properties

Taxon circumscriptions and nomenclature follow the recent checklist of the vascular plants of Finland (Kurtto et al. 2019). The status categories of the species in Finland used in interpretation of the results were collected from Suominen & Hämet-Ahti (1993), Hämet-Ahti et al. (1998) and Kurtto et al. (2019). The habitat preferences of the species were obtained from Suominen & Hämet-Ahti (1993), Hämet-Ahti et al. (1998) and Hyvärinen et al. (2019). For some species, we made adjustments for habitat preferences, based on our own field experience. In our analysis, we used only the primary habitat in the classifications, although some species occur in several habitats. For apophytes, we used the habitats for native occurrences of the species.

Results and discussion

A scatterplot of mean commonness for the species in Period A vs. Period B is shown in Fig. 2. The corresponding linear regression equation is $B = 0.007 + 1.053 * A$. This relationship is slightly concave, because the frequency of the most common species has not changed significantly.

These results indicate that there are considerably more species showing an increase than a decrease in frequency from Period A to Period B. The same pattern is also visible in Fig. 3, which shows the frequency distribution of species as a function of mean change in commonness.

The number of species showing either a downward or an upward trend of at least 0.01 units in the bootstrap replicas with different confidence levels are shown in Table 2. Only those species that showed a consistent trend in all 1000 bootstrap replicas (implying $p < 0.001$, the first line of Table 2) were chosen for further analysis. There were 124 such species showing an upward trend and 8 species showing a downward trend. For interpretation of the results, we classified the species according to their status categories and habitat preferences in Finland.

Increase in alien species

In the group of 42 increased alien species (Table 3), 26 species (62%) were archaeophytes, i.e. species that are assumed to have arrived in Finland with the aid of humans before the mid-1600s. However, many of these species may occur as archaeophytes only in small areas inside the country, being neophytes elsewhere, especially *Aquilegia vulgaris*, which occurs most often as a recent and often only an ephemeral escape from cultivation. *Aquilegia vulgaris* was classified as a neophyte by Suominen & Hämet-Ahti (1993) and Hämet-Ahti et al. (1998), in contrast to Kurtto et al. (2019). Similarly, plants that have been cultivated for forage, e.g. *Trifolium pratense*, *Schedonorus pratensis* and *Dactylis glomerata*, have often escaped from cultivation. Ten species are an-

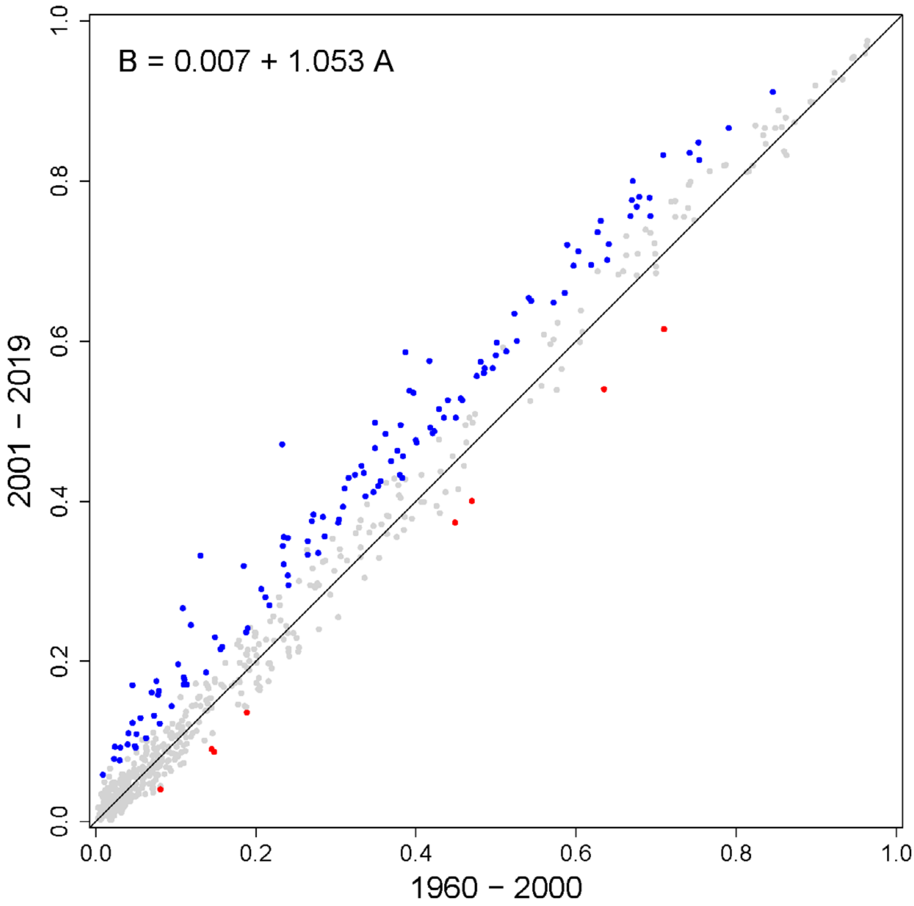

Figure 2. Scatterplot of mean commonness of species in Period A (1960–2000) vs. Period B (2001–2019). Each dot refers to one species. Species with consistent patterns of change in the bootstrap replicas are shown with blue (upward) and red (downward) symbols. Species with grey symbols indicated no consistent trend in the bootstrap analysis.

Table 2. Number of species showing downward or upward changes in commonness, with different confidence levels. Only species with all 1000 bootstrap replicas indicating change in the same direction (corresponding to p < 0.001) were chosen for further analysis.

Probability	Down	Up
p < 0.001	8	124
p < 0.01	12	150
p < 0.05	22	168
p < 0.10	31	188

nual weeds (listed in alphabetical order): *Capsella bursa-pastoris, Galium spurium*, *Gnaphalium uliginosum*, *Lapsana communis*, *Myosotis arvensis*, *Poa annua*, *Polygonum aviculare*, *Senecio vulgaris*, *Spergula arvensis* and *Viola arvensis*. Four *Alchemilla* species, *A. acutiloba*, *A. micans*, *A. monticola* and *A. subcrenata*, show slight increases between the two time periods. However, this trend may be partially an artefact caused by better identification abilities of field workers in the latter period.

The remaining 16 species (38%) are neophytes, i.e. species that are assumed to have arrived in Finland with the aid of humans after the mid-1600s. Most are rather recent arrivals, known to have arrived late in the 19th century or later. Six species – *Achillea ptarmica*, *Epilobium adenocaulon*, *E. ciliatum*, *Galium album*, *Matricaria discoidea* and *Senecio viscosus* – have not been cultivated in Finland. The remaining 10 species have escaped cultivation and include the woody species *Amelanchier spicata*, *Malus do-*

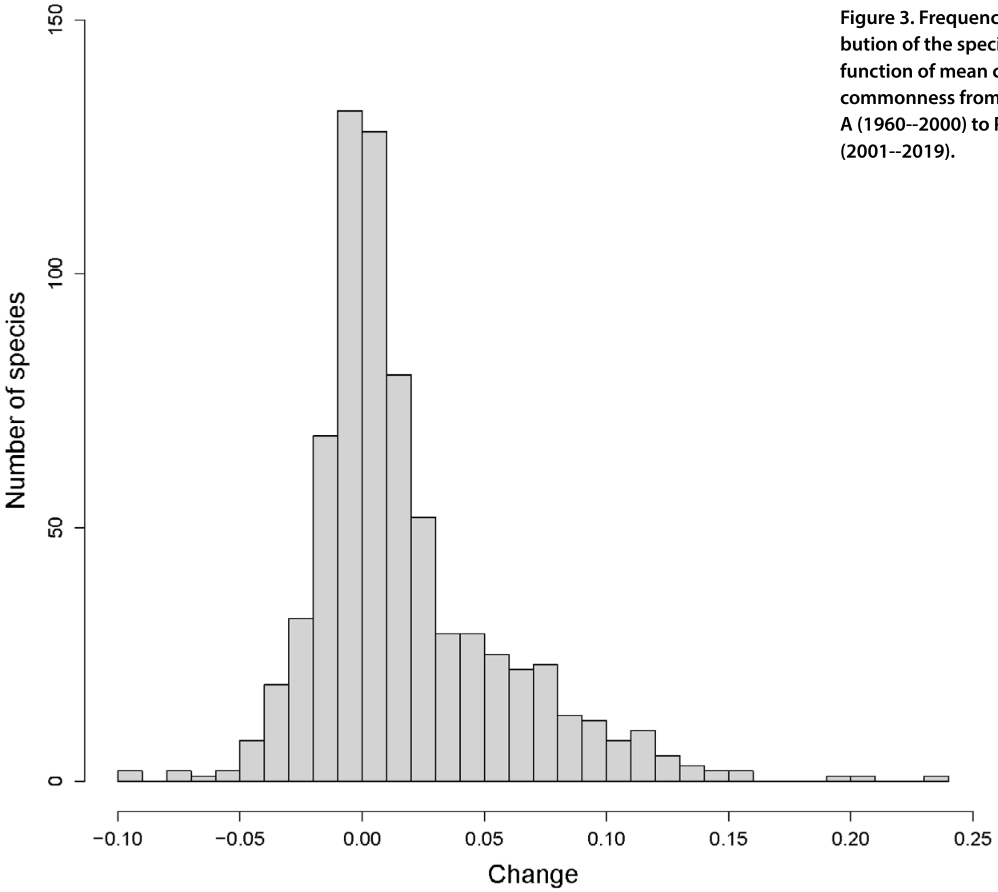

Figure 3. Frequency distribution of the species as a function of mean change in commonness from Period A (1960--2000) to Period B (2001--2019).

mestica, *Rosa rugosa*, *Rubus odoratus*, *Sambucus racemosa* and *Sorbaria sorbifolia*, as well as the herbs *Festuca stricta*, *Impatiens glandulifera*, *Lupinus polyphyllus* and *Trifolium hybridum* (in large proportion).

The change observed in *Euphrasia* species was complicated by identification problems. In addition to *E. nemorosa* shown in Table 3, *E. stricta* also increased (mean 0.055, range 0.005 to 0.116). However, only 998 out of 1 000 bootstrap replicas indicated increase, with two replicas showing change of less than 0.01 units. On the other hand, the northern species *E. wettsteinii* showed no consistent change (mean 0.020, range –0.042 to 0.085).

Increase in apophytic species

The increase in apophytic species involved 66 species (Table 4) that are considered native at least somewhere in Finland, but have strongly benefited from artificial habitats in all parts of the country. This group has the highest number of species, indicating that the strategy of arriving early in Finland and later taking advantage of the disturbance caused by human activities is a successful life-history strategy. However, it is worth noting that many of the species in this group are native in Finland only in restricted areas, where their expansion to cultural biotopes is limited. The majority of occurrences may actually have been of alien origin. In some cases, the aliens may even have represented a race different from the native race. Some examples of these include:

1) Species occurring as natives along the Baltic coastline and other shore biotopes, aliens elsewhere: *Artemisia vulgaris* var. *coarctata* (native) and var. *vulgaris* (alien), *Elytrigia repens* subsp. *arenosa* (native) and subsp. *repens* (alien), *Plantago major* subsp. *intermedia* (native) and subsp. *major* (alien), *Sonchus arvensis* var. *maritimus* (native) and var. *arvensis* (alien). Other species

occurring as natives along the Baltic coastline include *Cirsium arvense*, *Convolvulus sepium*, *Linaria vulgaris*, *Tanacetum vulgare* and *Vicia cracca*. Species occurring natively both along the Baltic and inland shores include *Persicaria lapathifolia*, *Sagina procumbens* and *Stachys palustris* (Suominen & Hämet-Ahti 1993).

2) Species occurring as natives in northern Finland and as aliens in the south: *Cerastium fontanum* subsp. *fontanum* (native) and subsp. *vulgare* (alien), *Veronica serpyllifolia* subsp. *humifusa* (native) and subsp. *serpyllifolia* (alien) and *Potentilla norvegica*.

3) Species of other biotopes that have expanded in Finland primarily as aliens (see Suominen & Hämet-Ahti 1993): *Aegopodium podagraria*, *Anthriscus sylvestris*, *Campanula rotundifolia* (subsp. *rotundifolia*), *Juncus alpinoarticulatus* (subsp. *alpinoarticulatus*), *Poa trivialis*, *Tussilago farfara* and *Prunella vulgaris*. A special case are the species that have expanded their range by escaping cultivation, such as *Acer platanoides*, *Festuca rubra*, *Polemonium caeruleum* and *Quercus robur*.

Six of the increased species listed in Table 4 (*Agrostis capillaris*, *Carex leporina*, *Juncus conglomeratus*, *Persicaria lapathifolia*, *Rumex longifolius* and *Trifolium repens*) were regarded as native in Finland in the checklist of Kurtto et al. (2019), although Suominen & Hämet-Ahti (1993) and Hämet-Ahti et al. (1998) classified them as aliens. As noted by Suominen & Hämet-Ahti (1993), the native vs. alien status of many species in Finland remains unclear.

The most uncontroversially true apophytes, species that have started their expansion into cultural habitats from native populations, include *Calamagrostis canescens*, *Calamagrostis epigejos*, *Carex brunnescens*, *Cirsium palustre*, *Epilobium montanum*, *Equisetum arvense*, *Festuca ovina*, *Glyceria fluitans*, *Lycopodium clavatum*, *Orthilia secunda*, *Scirpus sylvaticus*, *Scrophularia nodosa* and *Valeriana sambucifolia*.

There is a wide variety of native habitats, plant sizes and life-history strategies among the species in this group, including forest species such as *Lycopodium clavatum*, *Orthilia secunda* and *Epilobium montanum*, shore plants like *Tanacetum vulgare*, wetland plants like *Tussilago farfara*, as well as aquatic plants like *Typha latifolia* and *Callitriche cophocarpa*. However, each of these species has adopted some way of taking advantage of human-influenced changes in the environment.

Increase in nonapophytic species

This group includes 16 perennial herbs from forest, shore and peatland habitats (Table 5). However, in the case of forest species, the increase observed in commonness may partly have been artefactual, due to the increased proportion of forested habitats in the inventoried squares from Period A to Period B (see Table 1).

Increases in seven species: *Athyrium filix-femina*, *Dryopteris carthusiana*, *Melica nutans*, *Milium effusum*, *Oxalis acetosella*, *Prunus padus* and *Salix aurita*, were documented earlier by Reinikainen et al. (2000). The authors also mentioned that *Dryopteris carthusiana* benefits from peatland ditching, thus indicating somewhat apophytic behaviour.

One species in Reinikainen et al. (2000) showing a pattern of change in contrast to our results is *Viola riviniana*. This species shows a declining trend in the forest vegetation data, whereas our data show an increase in frequency. Differences in quadrat sizes and habitat proportions may explain part of the contradiction.

Decline in species

The group of species in decline included only eight species of various origins and habitats (Table 6). The small number of species in this category is partly explained by the fact that many species, including those most nationally endangered, are so rare that our 1-km grid square data do not capture enough occurrences for assessing potential changes in their commonness.

For four species: *Antennaria dioica*, *Bistorta vivipara*, *Raphanus raphanistrum* and *Silene vulgaris*, the change in commonness is as expected. *Antennaria dioica* has declined primarily in southern Finland, whereas the northern population has remained rather stable. It is classified as Near Threatened in the latest Red Data Book of Finland (Hyvärinen et al. 2019).

Bistorta vivipara is a small apophytic perennial of moist fields and roadsides, and its decline may be associated with the overgrowth of these habitats. The decline in this species, especially in southern Finland, has also been reported in local floras (e.g. Hæggström & Hæggström 2010, Suominen 2013, Kuitunen 2016). It was classified as regionally threatened in SW Finland by Rassi et al. (2010).

The two varieties of *Silene vulgaris* differ in terms of distribution and temporal trend. *Silene vulgaris* var. *vulgaris*, the inland race of alien origin, occurs in all parts of the country and has declined, whereas the native var. *litoralis* occurs only in the coastal region and has remained rather stable.

The decline in *Eriophorum angustifolium*, especially in southern Finland, was also reported by Hotanen and Reinikainen (2000). The decline in this species seems to be steeper in the southern part of the country, whereas the northern populations have remained more stable.

The decline observed in *Poa pratensis* is somewhat surprising and may reflect taxonomic issues associated with the increasing trend of *P. alpigena*. Both are closely allied members of the same species aggregate (*Poa pratensis* coll., see Kurtto et al. 2019). Some field workers in Period A may have recorded *P. alpigena* as *P. pratensis*. Biotope differences between the two time periods may also partially explain the trend observed.

The aquatic *Sparganium angustifolium* is fairly difficult to observe and identify. Its moderate decline should be noted with caution requiring more investigation. The smaller proportion of aquatic habitats in period B (see Table 1) may be a partial explanation of the trend observed.

Montia fontana is a problematic species for analysis, due to methodological issues. It is a small species that early in the season either disappears completely or is hidden under higher vegetation. Regional differences in the distribution of the squares examined between Periods A and B may also have affected the lower commonness in the latter period. *Montia fontana* was classified as regionally endangered in the Lake District of southern Finland by Rassi et al. (2010).

General patterns of change

The general pattern of change among the common vascular plants of Finland, revealed by our data, is as expected: some species have increased in frequency, some have declined, and a large number of species has remained more or less unchanged in terms of commonness. A more interesting question is the number and properties of the species in each group. Our grouping of species according to their origins, habitat preferences and responses to human influence gives a rough estimate of the factors affecting the capacity of survival and potential for expansion under recent environmental changes.

Our results indicate that the proportion of expanded species is much higher than that of species in decline (Figs. 2 and 3). This pattern is in contrast to the trend observed among the endangered vascular plants in Finland. A comparison of the latest three Red Data Books of Finland (Rassi et al. 2001, 2010, Hyvärinen et al. 2019) shows a continuous increase in the numbers of endangered vascular plants from 2000 to 2019 (Table 7). The red-listed species in our data were too rare to be included in the analysis. Combining this trend with ours suggests a general pattern of change in the flora of Finland: common species either remain stable or become more common, and rare species, especially nonapophytic natives, become endangered to a greater extent.

Properties of expanded species

As shown in Tables 3–5, a majority of expanded species includes those that have arrived as a result of human activities (aliens) or native species that have been able to benefit from cultural influence (apophytes). On the average, apophytes have enjoyed a head start over aliens, due to earlier arrival, but species-specific traits determine the actual speed of expansion. In some cases, taxonomic differentiation at the infraspecific level is also associated with the expansion.

In his classic article, Linkola (1918) documented the expansion of a number of species over a period of 60–70 years, covering the time frame where reliable data on the flora of Finland were made available for the first time in history. The species discussed by Linkola were (in the original order) *Matricaria discoidea*, *Elodea canadensis*, ”*Thlaspi alpestre*” (*Noccaea caerulescens* s.lat.), *Silene dichotoma*, *Sisymbrium altissimum*, *Cerastium arvense*, *Barbarea vulgaris*, *Achillea ptarmi-*

ca, ”*Galium mollugo*” (*G. album*, previously *G. mollugo* subsp. *erectum*) and ”*Potentilla Goldbachii*” (*P. thuringiaca*). Our data show that *Matricaria discoidea*, *Achillea ptarmica* and *Galium album* are still continuing their expansion in Finland, now a century later (see Table 3).

Overall, cultural influence seems to be the main driver of the dynamics of the vascular flora of Finland. However, species-specific traits determine the nuances of the influence. For example, two alien species showing the fastest expansion during the study period, *Epilobium adenocaulon* and *Lupinus polyphyllus* (see Table 3), differ greatly in terms of their dispersal strategy. The seeds of *L. polyphyllus* are shed very close to the parent plant, and their wider dispersal is made possible by transfer of land masses in human construction activities. Furthermore, the use of *L. polyphyllus* as an ornamental plant in different parts of the country has accelerated the dispersal of the species.

In contrast, the rapid dispersal of *Epilobium adenocaulon*, as well as its close relative *E. ciliatum*, is made possible by wind-dispersed seeds without human assistance. Human influence for these species is more important in the form of creating suitable habitats for seedling establishment. Expansion of *Epilobium adenocaulon* in Finland has been documented, e.g. by Hiitonen (1938), Erkamo (1945) and Piispala (1964). Local floras, such as Suominen (2013) and Kuitunen (2020), discuss the smaller-scale patterns of its distribution and dynamics.

The small group of nonapophytic natives (16 species, see Table 5) contains mainly species of forest or forested peatland habitats. Considering the amount of forest biotopes in Finland, this pattern is not surprising. The slightly higher proportion of forested habitats in the squares examined in the latter period (see Table 1) may explain part of the expansion observed.

Concluding remarks

For the purpose of analysing the dynamics of the national flora, our data available from Finland display a number of deficiencies. The fact that there are no repeated inventories of the same squares over time, as well as subjective selection of squares by field workers in different parts of the country, make detection of consistent patterns in the dynamics of the flora challenging. Due to the potential limitations in our analysis of the changes in species commonness, we opted to abandon a rigorous statistical analysis of the data, e.g. comparable to that of Braithwaite el al. (2006) in Britain. However, we believe that our data are nevertheless suitable for illustrating the general patterns of change in the vascular flora of Finland during recent decades. In other words, although our assessment is not conclusive, the results derived draw attention to those species worth further analysis.

Moreover, the wide geographic coverage of our atlas data, capturing biotopes from the southwestern hemiboreal region via the boreal biogeographic zone up to subarctic environments makes it possible to detect large-scale patterns of distribution and change in the flora. As far as we know, the only botanical dataset in Finland comparable to our plant atlas data in terms of geographic coverage is that of forest and peatland vegetation, collected in association with national forest inventories and spanning a time frame from 1951 to 1995 (see Reinikainen et al. 2000).

The field work for the plant atlas of Finland is still continuing, and some 150–200 new 1-km squares have been inventoried annually in recent years. An important future direction would be to develop a national monitoring scheme for the vascular flora of Finland, based on the existing atlas data and methods, which would enable a more detailed analysis of changes in plant species distributions. To be successful, it would require devoted planning, coordination and sufficient funding (cf. Pescott et al. 2019).

Acknowledgements. Our analysis is based on the field work of about 450 voluntary field workers, both professional botanists and advanced amateur naturalists, too numerous to mention here. We are grateful to them all for their invaluable effort. The manuscript was greatly improved by the comments of Risto Heikkinen, Arto Kurtto and Jaakko Nurmi. The Botanical Unit of the Finnish Museum of Natural History provided us with the resources needed for analysis of the data and preparation of the manuscript.

Table 3. List of alien species showing increasing trend between the time periods, listed in decreasing order of change. The values are means of 1000 bootstrap replicas; the range of values is given in parentheses. Status of occurrence is given after the taxon name. See the last column and text for species-specific notes.

Species	Status	Period A	Period B	Change	Notes
Epilobium adenocaulon	neophyte	0.233 (0.208..0.267)	0.471 (0.435..0.506)	0.238 (0.192..0.281)	arrived in the early 1900s
Lupinus polyphyllus	neophyte	0.131 (0.110..0.158)	0.332 (0.292..0.370)	0.201 (0.162..0.242)	escaped from cultivation
Euphrasia nemorosa	archaeophyte	0.109 (0.091..0.140)	0.266 (0.230..0.296)	0.157 (0.107..0.196)	perhaps sometimes mixed up with *E. stricta*
Omalotheca sylvatica	archaeophyte	0.349 (0.316..0.375)	0.498 (0.452..0.539)	0.148 (0.093..0.198)	might even be native
Impatiens glandulifera	neophyte	0.046 (0.022..0.075)	0.170 (0.142..0.204)	0.124 (0.081..0.176)	also cultivated
Gnaphalium uliginosum	archaeophyte	0.349 (0.321..0.377)	0.466 (0.427..0.506)	0.117 (0.066..0.165)	weed
Matricaria discoidea	neophyte	0.523 (0.493..0.554)	0.634 (0.586..0.673)	0.111 (0.055..0.163)	weed
Poa annua	archaeophyte	0.627 (0.589..0.664)	0.736 (0.697..0.781)	0.109 (0.057..0.163)	weed
Galium album	neophyte	0.270 (0.246..0.303)	0.375 (0.332..0.410)	0.104 (0.058..0.147)	
Epilobium ciliatum	neophyte	0.076 (0.060..0.098)	0.175 (0.149..0.208)	0.099 (0.061..0.133)	weed
Dactylis glomerata	archaeophyte	0.284 (0.264..0.310)	0.380 (0.346..0.414)	0.096 (0.055..0.137)	sometimes cultivated
Trifolium pratense	archaeophyte	0.597 (0.566..0.624)	0.694 (0.646..0.734)	0.096 (0.043..0.140)	also cultivated
Achillea millefolium	archaeophyte	0.753 (0.724..0.779)	0.848 (0.807..0.883)	0.096 (0.044..0.135)	
Sambucus racemosa	neophyte	0.103 (0.085..0.126)	0.196 (0.160..0.231)	0.093 (0.044..0.137)	escaped from cultivation
Spergularia rubra	archaeophyte	0.070 (0.058..0.084)	0.161 (0.132..0.190)	0.091 (0.064..0.119)	
Senecio viscosus	neophyte	0.079 (0.065..0.101)	0.163 (0.134..0.191)	0.084 (0.052..0.114)	
Schedonorus pratensis	archaeophyte	0.309 (0.272..0.345)	0.393 (0.358..0.433)	0.084 (0.039..0.130)	also cultivated
Leucanthemum vulgare	archaeophyte	0.500 (0.470..0.530)	0.582 (0.543..0.624)	0.081 (0.036..0.128)	sometimes cultivated for ornament
Polygonum aviculare	archaeophyte	0.486 (0.458..0.516)	0.566 (0.524..0.601)	0.080 (0.032..0.128)	weed
Aquilegia vulgaris	archaeophyte	0.078 (0.060..0.100)	0.158 (0.115..0.195)	0.080 (0.035..0.121)	archaeophytic status doubtful; Hämet-Ahti et al. 1998 regarded as neophyte
Achillea ptarmica	neophyte	0.619 (0.588..0.644)	0.695 (0.660..0.730)	0.076 (0.029..0.126)	
Myosotis arvensis	archaeophyte	0.400 (0.369..0.429)	0.476 (0.442..0.513)	0.076 (0.031..0.118)	weed
Alchemilla monticola	archaeophyte	0.304 (0.279..0.329)	0.377 (0.338..0.412)	0.073 (0.025..0.114)	
Trifolium hybridum	neophyte	0.286 (0.256..0.325)	0.356 (0.321..0.395)	0.070 (0.016..0.113)	also cultivated
Glechoma hederacea	archaeophyte	0.110 (0.089..0.135)	0.180 (0.150..0.227)	0.070 (0.030..0.121)	also cultivated
Capsella bursa-pastoris	archaeophyte	0.435 (0.404..0.464)	0.504 (0.469..0.544)	0.070 (0.023..0.118)	weed
Spergula arvensis	archaeophyte	0.458 (0.421..0.491)	0.526 (0.485..0.560)	0.069 (0.016..0.117)	weed
Hypericum maculatum	archaeophyte	0.337 (0.316..0.359)	0.406 (0.372..0.437)	0.069 (0.032..0.100)	
Festuca stricta	neophyte	0.041 (0.022..0.072)	0.110 (0.082..0.150)	0.068 (0.022..0.113)	largely cultivated on road banks; observer-specific differences in recording possible
Alchemilla subcrenata	archaeophyte	0.265 (0.239..0.299)	0.333 (0.298..0.374)	0.068 (0.022..0.116)	
Viola arvensis	archaeophyte	0.353 (0.326..0.389)	0.419 (0.384..0.454)	0.066 (0.015..0.117)	weed
Galium spurium	archaeophyte	0.110 (0.089..0.132)	0.171 (0.140..0.214)	0.060 (0.027..0.101)	weed
Sorbaria sorbifolia	neophyte	0.023 (0.011..0.054)	0.078 (0.054..0.108)	0.055 (0.019..0.089)	escaped from cultivation
Amelanchier spicata	neophyte	0.040 (0.026..0.060)	0.096 (0.062..0.148)	0.055 (0.021..0.112)	escaped from cultivation
Lapsana communis	archaeophyte	0.241 (0.219..0.268)	0.295 (0.261..0.341)	0.055 (0.017..0.107)	weed
Alchemilla acutiloba	archaeophyte	0.190 (0.167..0.215)	0.241 (0.205..0.273)	0.051 (0.018..0.084)	
Rubus odoratus	neophyte	0.009 (0.002..0.032)	0.058 (0.040..0.102)	0.049 (0.015..0.098)	escaped from cultivation
Senecio vulgaris	archaeophyte	0.138 (0.120..0.162)	0.186 (0.153..0.224)	0.049 (0.015..0.089)	weed
Alchemilla micans	archaeophyte	0.030 (0.019..0.051)	0.076 (0.054..0.107)	0.046 (0.022..0.076)	
Campanula patula	archaeophyte	0.383 (0.360..0.406)	0.429 (0.406..0.457)	0.046 (0.010..0.080)	
Rosa rugosa	neophyte	0.049 (0.031..0.068)	0.094 (0.075..0.119)	0.045 (0.014..0.074)	escaped from cultivation
Malus domestica	neophyte	0.050 (0.037..0.075)	0.092 (0.069..0.119)	0.042 (0.014..0.070)	escaped from cultivation

Table 4. List of apophytic native species showing increasing trend between the time periods, listed in decreasing order of change. The values are means of 1000 bootstrap replicas; range of values is given in parentheses. Native habitat and weedy status are given after the taxon name. See the last column and text for species-specific notes.

Species	Native habitat	Weedy	Period A	Period B	Change	Notes
Sagina procumbens	shore	yes	0.387 (0.350..0.419)	0.586 (0.537..0.628)	0.199 (0.140..0.255)	native on sea and lake shore rocks; rapid stones; springs
Silene dioica	forest		0.417 (0.384..0.444)	0.575 (0.530..0.618)	0.158 (0.104..0.220)	native in black alder swamps and groves, river shore meadows, forest edges, fell precipices
Tussilago farfara	shore		0.392 (0.368..0.415)	0.538 (0.501..0.569)	0.146 (0.100..0.183)	not native in the south (Hämet-Ahti et al. 1998)
Tanacetum vulgare	shore		0.397 (0.366..0.425)	0.535 (0.494..0.590)	0.138 (0.085..0.202)	regarded as native only on seashores (Hämet-Ahti et al. 1998)
Typha latifolia	aquatic		0.185 (0.165..0.208)	0.319 (0.289..0.349)	0.133 (0.096..0.169)	
Anthriscus sylvestris	forest	yes	0.589 (0.562..0.622)	0.720 (0.678..0.763)	0.132 (0.084..0.178)	apparently native only in Åland and parts of Lapland
Scorzoneroides autumnalis	shore	yes	0.671 (0.645..0.700)	0.800 (0.763..0.843)	0.129 (0.087..0.185)	native only on seashore and in N Finland
Acer platanoides	forest		0.119 (0.103..0.161)	0.245 (0.210..0.283)	0.126 (0.073..0.169)	commonly escaping from cultivation, also outside the native range
Cerastium fontanum	shore	yes	0.709 (0.682..0.737)	0.832 (0.786..0.872)	0.123 (0.078..0.166)	native only in N Finland (subsp. *fontanum*); subsp. *vulgare* otherwise as an alien
Cirsium arvense	shore	yes	0.362 (0.337..0.394)	0.484 (0.453..0.530)	0.122 (0.076..0.174)	native only on seashores (var. *arvense*)
Ribes nigrum	forest		0.235 (0.210..0.260)	0.355 (0.320..0.399)	0.120 (0.075..0.177)	also cultivated and escaping
Plantago major	shore	yes	0.631 (0.608..0.657)	0.750 (0.712..0.796)	0.119 (0.077..0.165)	native probably only on seashores (subsp. *intermedia*); elsewhere as an alien
Phalaroides arundinacea	shore		0.381 (0.347..0.414)	0.495 (0.450..0.546)	0.114 (0.042..0.180)	also cultivated
Poa alpigena	peatland		0.240 (0.204..0.270)	0.354 (0.320..0.393)	0.113 (0.070..0.159)	
Urtica dioica	forest		0.541 (0.510..0.571)	0.654 (0.606..0.693)	0.113 (0.059..0.162)	seashore forest (subsp. dioica); herb-rich forest on brook shores and at the foot of precipices (subsp. *sondenii*)
Lycopodium clavatum	forest		0.316 (0.280..0.352)	0.429 (0.368..0.479)	0.113 (0.044..0.173)	
Poa palustris	shore		0.272 (0.249..0.301)	0.383 (0.339..0.428)	0.111 (0.055..0.165)	
Aegopodium podagraria	forest		0.234 (0.207..0.263)	0.344 (0.317..0.377)	0.110 (0.069..0.150)	apparently native in herb-rich forests and brook shores
Poa trivialis	shore	yes	0.324 (0.292..0.357)	0.433 (0.390..0.480)	0.109 (0.064..0.150)	
Carex brunnescens	rock		0.603 (0.568..0.634)	0.712 (0.672..0.765)	0.109 (0.058..0.171)	
Festuca rubra	shore	yes	0.670 (0.640..0.713)	0.776 (0.736..0.816)	0.106 (0.054..0.152)	native at least on seashore; elsewhere largely as an alien; commonly cultivated
Artemisia vulgaris	shore	yes	0.311 (0.285..0.345)	0.416 (0.381..0.450)	0.105 (0.056..0.152)	native only on seashores (var. *coarctata*); var. *vulgaris* elsewhere as an alien
Rumex longifolius	unclear	yes	0.544 (0.515..0.582)	0.650 (0.605..0.697)	0.105 (0.050..0.159)	native in Kurtto et al. 2019; alien in Hämet-Ahti et al. 1998
Trifolium repens	unclear	yes	0.679 (0.651..0.710)	0.780 (0.745..0.825)	0.100 (0.059..0.152)	native in Kurtto et al. 2019; alien in Hämet-Ahti et al. 1998; commonly cultivated
Sonchus arvensis	shore	yes	0.335 (0.314..0.358)	0.435 (0.408..0.464)	0.100 (0.059..0.141)	native only on seashores (var. *maritimus*); var. *arvensis* elsewhere as an alien
Cirsium palustre	peatland	yes	0.501 (0.478..0.525)	0.598 (0.559..0.639)	0.097 (0.050..0.141)	
Equisetum arvense	peatland	yes	0.742 (0.706..0.778)	0.835 (0.792..0.872)	0.094 (0.042..0.142)	shore, peatland, forest, spring, fell
Festuca ovina	rock		0.676 (0.646..0.707)	0.768 (0.728..0.808)	0.092 (0.039..0.146)	rock, forest, peatland
Orthilia secunda	forest		0.692 (0.665..0.729)	0.779 (0.741..0.818)	0.087 (0.035..0.126)	decline in Reinikainen et al. (2000)
Juncus alpinoarticulatus	shore		0.377 (0.336..0.409)	0.463 (0.423..0.504)	0.087 (0.030..0.147)	
Potentilla norvegica	rock	yes	0.265 (0.238..0.291)	0.350 (0.318..0.383)	0.086 (0.041..0.126)	regarded as native only in Inari Lapland (Hämet-Ahti et. 1998)
Carex leporina	unclear	yes	0.440 (0.417..0.462)	0.526 (0.487..0.560)	0.086 (0.041..0.126)	native in Kurtto et al. 2019; alien in Hämet-Ahti et al. 1998

Table 4 cont.

Species	Native habitat	Weedy	Period A	Period B	Change	Notes
Campanula rotundifolia	forest		0.429 (0.391..0.467)	0.515 (0.475..0.558)	0.086 (0.024..0.138)	even subsp. *rotundifolia* as native in Kurtto et al. 2019; alien in Hämet-Ahti et al. 1998
Epilobium montanum	forest		0.207 (0.178..0.233)	0.290 (0.256..0.322)	0.083 (0.035..0.123)	
Scrophularia nodosa	forest		0.149 (0.129..0.169)	0.230 (0.200..0.271)	0.081 (0.046..0.119)	
Prunella vulgaris	forest	yes	0.369 (0.342..0.392)	0.450 (0.421..0.475)	0.080 (0.042..0.120)	regarded as native only in the southern half of the country (Hämet-Ahti et al. 1998)
Vicia cracca	shore	yes	0.641 (0.608..0.671)	0.721 (0.682..0.757)	0.080 (0.033..0.122)	native only on seashores
Lathyrus pratensis	forest		0.476 (0.448..0.506)	0.556 (0.515..0.596)	0.080 (0.029..0.137)	regarded as native only in the southern provinces (Hämet-Ahti et al. 1998)
Elytrigia repens	shore	yes	0.572 (0.540..0.605)	0.648 (0.608..0.688)	0.077 (0.029..0.135)	native only on seashore (subsp. *arenosa*); subsp. *repens* as an alien
Senecio sylvaticus	rock		0.046 (0.035..0.064)	0.123 (0.096..0.146)	0.076 (0.049..0.108)	rock
Agrostis capillaris	unclear		0.791 (0.764..0.817)	0.866 (0.826..0.902)	0.076 (0.034..0.118)	native in Kurtto et al. 2019; alien in Hämet-Ahti et al. 1998
Agrostis canina	shore		0.418 (0.389..0.443)	0.492 (0.440..0.541)	0.075 (0.013..0.130)	
Calamagrostis epigejos	forest		0.526 (0.504..0.550)	0.600 (0.573..0.628)	0.074 (0.038..0.110)	forest, rock, shore, peatland
Galium uliginosum	shore		0.586 (0.551..0.634)	0.660 (0.616..0.699)	0.074 (0.016..0.123)	shore, springy forest
Quercus robur	forest		0.056 (0.039..0.081)	0.129 (0.100..0.169)	0.073 (0.032..0.112)	commonly escaping from cultivation, also outside the native range
Vicia sepium	forest		0.384 (0.360..0.413)	0.456 (0.426..0.495)	0.072 (0.027..0.119)	regarded as native only in the southern provinces (Hämet-Ahti et al. 1998)
Calamagrostis canescens	peatland		0.401 (0.371..0.431)	0.473 (0.424..0.527)	0.072 (0.013..0.124)	
Linaria vulgaris	shore		0.303 (0.274..0.335)	0.373 (0.346..0.415)	0.071 (0.027..0.116)	regarded as native only on seashores (Hämet-Ahti et al. 1998)
Convolvulus sepium	shore		0.024 (0.008..0.056)	0.093 (0.070..0.124)	0.069 (0.025..0.111)	regarded as native only on seashores in the south (Hämet-Ahti et al. 1998); elsewhere mainly an escape from cultivation
Scirpus sylvaticus	peatland		0.212 (0.188..0.241)	0.280 (0.253..0.311)	0.068 (0.032..0.103)	peatland
Valeriana sambucifolia	shore		0.240 (0.217..0.275)	0.307 (0.275..0.349)	0.067 (0.022..0.112)	shore
Deschampsia cespitosa	shore		0.846 (0.817..0.870)	0.911 (0.882..0.943)	0.066 (0.028..0.107)	shore, spring, thin-peated rich spruce mire
Veronica officinalis	rock		0.423 (0.402..0.447)	0.487 (0.459..0.516)	0.064 (0.031..0.100)	rock
Veronica chamaedrys	forest		0.421 (0.393..0.443)	0.485 (0.456..0.523)	0.064 (0.023..0.107)	
Veronica serpyllifolia	shore	yes	0.347 (0.320..0.376)	0.411 (0.365..0.457)	0.064 (0.012..0.119)	only subsp. *humifusa* native in the north; more widespread subsp. serpyllifolia is alien (Hämet-Ahti et al. 1998)
Stellaria graminea	rock		0.693 (0.665..0.727)	0.756 (0.717..0.792)	0.063 (0.013..0.110)	
Lactuca muralis	forest		0.031 (0.019..0.055)	0.092 (0.064..0.133)	0.061 (0.026..0.101)	herb-rich forest
Solanum dulcamara	shore		0.073 (0.059..0.090)	0.132 (0.106..0.176)	0.059 (0.026..0.109)	shore
Juncus conglomeratus	unclear		0.156 (0.137..0.181)	0.215 (0.188..0.253)	0.059 (0.019..0.101)	native in Kurtto et al. 2019; alien in Hämet-Ahti et al. 1998
Polemonium caeruleum	forest		0.051 (0.035..0.078)	0.109 (0.084..0.141)	0.058 (0.021..0.096)	regarded as native only in two provinces (Hämet-Ahti et al. 1998); mostly an escape from cultivation
Callitriche cophocarpa	aquatic		0.114 (0.091..0.145)	0.171 (0.137..0.209)	0.057 (0.017..0.091)	aquatic
Glyceria fluitans	shore		0.217 (0.189..0.240)	0.270 (0.243..0.301)	0.053 (0.013..0.092)	shore
Persicaria lapathifolia	shore		0.380 (0.353..0.408)	0.433 (0.403..0.466)	0.053 (0.011..0.109)	native in Kurtto et al. 2019; alien in Hämet-Ahti et al. 1998
Poa angustifolia	forest		0.095 (0.077..0.116)	0.144 (0.113..0.173)	0.049 (0.012..0.080)	perhaps between-observer differencies in identifying this species
Stachys palustris	shore		0.080 (0.069..0.112)	0.122 (0.099..0.157)	0.042 (0.012..0.082)	shore
Geum urbanum	forest		0.063 (0.047..0.079)	0.104 (0.075..0.137)	0.041 (0.011..0.081)	seashore forest

Table 5. List of nonapophytic native species showing increasing trend between the time periods, listed in decreasing order of change. The values are means of 1000 bootstrap replicas; range of values is given in parentheses. The primary habitat is given after the taxon name. See the last column and text for species-specific notes.

Species	Habitat	Period A	Period B	Change	Notes
Salix myrsinifolia	shore	0.332 (0.300..0.372)	0.444 (0.386..0.488)	0.112 (0.061..0.161)	
Athyrium filix-femina	forest	0.481 (0.456..0.511)	0.574 (0.543..0.615)	0.093 (0.049..0.140)	slight increase in Reinikainen et al. (2000)
Dryopteris carthusiana	forest	0.668 (0.645..0.693)	0.756 (0.720..0.788)	0.088 (0.036..0.134)	increase in Reinikainen et al. (2000), benefits from peatland ditching
Carex digitata	forest	0.235 (0.212..0.265)	0.321 (0.287..0.358)	0.086 (0.042..0.128)	no consistent trend in Reinikainen et al. (2000)
Salix aurita	forested peatlands	0.485 (0.458..0.515)	0.560 (0.525..0.601)	0.075 (0.032..0.123)	increase in Reinikainen et al. (2000), benefits from peatland ditching
Melica nutans	forest	0.513 (0.481..0.545)	0.587 (0.546..0.630)	0.073 (0.027..0.127)	slight increase in Reinikainen et al. (2000)
Prunus padus	forest	0.456 (0.421..0.491)	0.528 (0.485..0.570)	0.072 (0.019..0.118)	increase in Reinikainen et al. (2000), benefits from peatland ditching
Linnaea borealis	forest	0.754 (0.726..0.785)	0.826 (0.788..0.860)	0.072 (0.017..0.118)	decline in coverage, no change in frequency in Reinikainen et al. (2000)
Phegopteris connectilis	forested peatlands	0.496 (0.459..0.537)	0.566 (0.522..0.601)	0.070 (0.012..0.121)	
Salix cinerea	shore	0.356 (0.327..0.384)	0.425 (0.384..0.461)	0.069 (0.025..0.116)	
Iris pseudacorus	shore	0.111 (0.094..0.128)	0.177 (0.148..0.211)	0.067 (0.030..0.106)	
Viola palustris	shore	0.639 (0.612..0.665)	0.701 (0.668..0.751)	0.062 (0.020..0.115)	
Moehringia trinervia	forest	0.158 (0.140..0.173)	0.218 (0.187..0.245)	0.060 (0.018..0.098)	
Viola riviniana	forest	0.278 (0.254..0.305)	0.335 (0.305..0.369)	0.057 (0.016..0.104)	decline in Reinikainen et al. (2000)
Oxalis acetosella	forest	0.450 (0.425..0.477)	0.504 (0.471..0.538)	0.054 (0.015..0.097)	increase in frequency in Reinikainen et al. (2000)
Milium effusum	forest	0.188 (0.162..0.213)	0.236 (0.200..0.270)	0.048 (0.010..0.109)	increase in Reinikainen et al. (2000), benefits from peatland ditching

Table 6. List of species showing decreasing trend between the time periods, listed in decreasing order of change. The values are means of 1000 bootstrap replicas; range of values is given in parentheses. Occurrence status, primary habitat and apophytic status are given after the taxon name. See the text for species-specific notes.

Species	Status	Habitat	Period A	Period B	Change
Poa pratensis	alien	cultural	0.635 (0.609..0.665)	0.540 (0.501..0.583)	-0.095 (-0.136..-0.048)
Eriophorum angustifolium	apophytic native	peatland	0.710 (0.676..0.740)	0.615 (0.573..0.653)	-0.095 (-0.145..-0.049)
Bistorta vivipara	apophytic native	cultural	0.449 (0.412..0.486)	0.373 (0.331..0.415)	-0.076 (-0.129..-0.025)
Antennaria dioica	apophytic native	forest	0.470 (0.437..0.505)	0.400 (0.357..0.444)	-0.070 (-0.121..-0.016)
Raphanus raphanistrum	alien	cultural	0.148 (0.127..0.168)	0.087 (0.068..0.127)	-0.061 (-0.093..-0.015)
Sparganium angustifolium	native	aquatic	0.145 (0.118..0.169)	0.090 (0.065..0.127)	-0.055 (-0.097..-0.014)
Silene vulgaris	apophytic native	shore	0.189 (0.165..0.212)	0.136 (0.107..0.163)	-0.053 (-0.088..-0.013)
Montia fontana	native	shore	0.081 (0.066..0.100)	0.040 (0.021..0.062)	-0.042 (-0.074..-0.013)

Table 7. Number of endangered vascular plant species in Finland according to three national Red Data Books, published in 2001, 2010 and 2019. Key to IUCN categories: CR = Critically Endangered, EN = Endangered, VU = Vulnerable.

Year	CR	EN	VU	Total
2000	32	52	96	180
2010	31	88	78	197
2019	35	101	76	212

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