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A comparative analysis of decline in the distribution ranges of orchid species in Estonia and the United Kingdom

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ABSTRACT

National databases were interrogated to analyse and compare proportional alterations in the distribution ranges of orchid species between two surveys in the UK (surveys completed in 1969 and 1999) and in Estonia (surveys completed in 1970 and 2004). Nearly every species declined between the surveys in both countries, and two species may have become extinct in the UK. Mean decline in distribution range for 49 species in the UK was 50% (range 14–100%), and 23 species declined by over 50%. The mean decline for 33 orchid species in Estonia was 25% (range 0–62%), and three species declined by over 50%. These results corroborate serious range declines recently reported for orchids in other regions of Europe (the Netherlands and Flanders, Belgium). In contrast with these other regions, we found that species associated with calcareous grassland and woodland habitats had suffered greater mean contractions in range than species of wet grassland habitats. Greater decline was recorded for species found on drier soils, and for species characteristic of open habitats. In addition, greater decline was found in species with short inflorescences, and in species that were short-lived, and clonal. Our results suggest that levels of decline shown both by groups of species associated with specific habitat types, and by particular species of orchid, depend strongly on local policies and specific conservation action, and indicate the habitat types on which conservation efforts may need to be concentrated in the future. The results suggest that grazing and mowing of competing vegetation, and avoidance of substrate disturbance, will produce the greatest rewards for the most vulnerable species.

1. Introduction

The abundance and distribution ranges of many plant species have undergone dramatic declines in recent decades (Gaston, 2002; Kull et al., 2002). Important factors that have contributed to these declines include habitat loss and fragmentation (Fischer and Stöcklin, 1997), and the smaller population sizes and greater degree of population isolation caused by these processes are also strongly associated with increased risk of further local population decline and extinction (Fischer and Stöcklin, 1997; Fischer and Matthies, 1998; Matthies et al., 2004). Despite considerable information having been assembled about reductions in the ranges of many species, it is not clear whether decline has been similar for groups of species characteristic of different habitat types, or whether particular species have suffered similar levels of decline in different parts of their range. Such information would allow limited funds and effort to be

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more closely focussed on conserving species that are at greatest risk of extinction, both locally and over a wider area.

The availability of detailed records of changes in the distribution of species over time provides opportunities for comparative analyses of declines in ranges both within and between ecological and taxonomic groupings, and between geographical areas. Pioneering work in this field has recently been published by Jacquemyn et al. (2005), who used records of the presence of orchid species in grid cells in Flanders, Belgium (based on 4 × 4 km cells, and records in 1930 and 2000) and in the Netherlands (based on 5 × 5 km cells, and records in 1950 and 2000) to examine decline in their range. In Flanders, over the time period considered, 26 species (over 80% of those for which there were data) suffered range contractions, and eight became extinct. In the Netherlands, 29 (78%) of the orchid species suffered range contractions, and five became extinct. Jacquemyn et al. also compared mean percentage changes in the distribution of orchid species characteristic of different types of habitat. In both Flanders and the Netherlands, orchids of wet grasslands and heathlands suffered greater levels of decline than orchids of calcareous grasslands or forest habitats.

The purpose of the present study was to conduct a comparative analysis of decline in the distribution ranges of species of orchids for two more widely separated European regions, namely the United Kingdom in western Europe, and Estonia in NE Europe. The UK supports a high human population density, and the associated infrastructure has caused considerable fragmentation and isolation of the remaining patches of semi-natural vegetation, many of which appear to be suffering considerable biodiversity loss. In contrast, Estonia has the lowest human population density in Europe, and maintains a high proportion of its semi-natural habitats in a protected state. Species range declines and loss of biodiversity to date in Estonia are thought to be modest compared with the UK. Our aim was to compare the range declines shown by individual orchid species, and groups of orchid species categorised by their environmental preferences and life-history traits, in these two contrasting countries. Comparison of such widely separated regions also enabled us to ascertain whether specific environmental factors and species traits have the same impact on decline over a wider geographical range than that considered by Jacquemyn et al. (2005). Identification of environmental factors and species traits that are correlated with range decline may enable recommendations for management to be made that will minimise or reverse range contraction.

2. Materials and methods

The area of the UK is 245,000 sq. km, and its flora includes almost 50 orchid species occurring in a wide range of habitat types. With an area of 45,000 sq. km. Estonia is only 18% as large as the UK, but it is rich in orchids, with 36 species recorded nationally (Leht, 1999). Thirty species of orchids are common to both countries.

The databases used were the New Atlas of the British and Irish Flora (Preston et al., 2002) and an unpublished database held at the Institute of Zoology and Botany of the Estonian Agricultural University in Tartu. In both countries the presence of orchid species was recorded on maps in grid squares 100 sq. km in size. Decline in distribution range was measured for all 49 orchid species in the UK and for 33 orchid species in Estonia, and compared for the 30 species that were common to both countries. Decline for each species in each country was measured as the change in the number of grid squares occupied in the national plant atlas databases between the two survey periods (between 1930 and 1969, and between 1987 and 1999 in the UK, and between 1921 and 1970, and between 1971 and 2004 in Estonia. Thus, there was an interval of 30 and 34 years between the ends of the first and second survey periods in the UK and Estonia, respectively. The data used in the analyses do not include information on the abundance of species in each grid square. For practical purposes, in large-scale comparative analyses of species decline, such as this, it has to be assumed that populations of all species are equally detectable in all habitats (see Kéry, 2004 for discussion of the problems associated with violation of this assumption).

To determine whether the magnitude of alteration in species' ranges was influenced by environmental preferences, Ellenberg indicator values (Ellenberg et al., 1991) were tabulated for as many of the species as possible, using the following abiotic variables: light preference, ranging from 1 (tolerant of full shade) to 9 (found in completely unshaded conditions); temperature, ranging from 1 (cold-tolerant) to 9 (tolerant of extremely warm conditions); continentality, ranging from 1 (euoceanic) to 9 (eucontinental); soil wetness, ranging from 1 (tolerant of very dry soils) to 12 (plants growing beneath water); soil reaction, ranging from 1 (highly acidic) to 9 (highly calcareous); nitrogen demand, ranging from 1 (soils extremely nitrogen-deficient) to 9 (soils extremely rich in nitrogen). In addition, the species were categorized according to the habitat type in which they occur most commonly: woodlands (w), calcareous grassland (c) or wet grassland (wg). In addition, Flora Europaea (Tutin et al., 1980) was used to categorise species by mean height of inflorescence as either short (<30 cm) or tall (>30 cm). Information from the literature was used to categorise species as either clonal or non-clonal (whether a species is capable of clonal spreading), and both published and unpublished estimates of life span were used to classify species as either short-lived (defined as those in which genet half-life is <3 years) or long-lived (those in which genet half-life is >3 years). The full database on which the analysis is based is presented in Appendix 1.

Statistical analysis was carried out using the SAS GLM procedure to determine the influence of different parameters on decline in the range of each species. The number of grid cells occupied at the second survey was treated as the dependent variable, with the number of grid cells occupied at the first survey as a covariate. The effects on species decline of environmental factors and biotic variables, and their interactions, were tested by stepwise selection. Three data sets were analysed separately, namely data for species in the UK, data for species in Estonia, and data for the species common to both countries. Because Ellenberg indicator values have not been published for all of the species recorded in both countries, the number of species analysed in these data sets was 38, 30 and 23, respectively. For the analysis using species common to both countries, the numbers of occupied squares for each species in the UK and in Estonia were clearly different. Therefore, centred values for both surveys (i.e. the differences between the actual number of occupied squares for each species, and the mean number of squares occupied by all species in the same country) were used in the analysis.

3. Results

In the UK, there was a mean (±SD) decline of 49.7 ± 22.0% (range 14–100%) in the distribution range of all orchid species over the 30-year period between the ends of the two surveys. The ranges of 23 of the 49 species declined by over 50% during this time (Fig. 1(a)). In comparison, the mean decline in the distribution of orchid species in Estonia over the 34-years between the two surveys was 25.0 ± 16.0% (range 0–62%, Fig. 1(b)), and of the 33 species, three had declined by over 50%. For the 30 species common to the two countries, the difference in decline is significant (mean for the UK = 52.0%, mean for Estonia = 28.5%, $t = 5.92$, $P < 0.001$, two-tailed test). The species that were most abundant in both the UK and Estonia at the end of the first surveys displayed relatively small percentage declines. Percentage decline in the range of rarer species was more variable, and in many cases greater. Very rare species (those recorded from less than one hundred 10 × 10 km squares during the first survey) showed anything from 0% to 100% decline in their range in the UK, and between 0% and 60% decline in Estonia (Fig. 1(c) and (d)).

No species increased its distribution range, in either country, over the time periods considered. Out of all the species common to both countries, *Epipogium aphyllum* exhibited the greatest percentage decline both in the UK (perhaps 100% decline) and in Estonia (61% decline), whereas *Dactylorhiza fuchsii* and *D. praetermissa*, exhibited no decline in Estonia, and the smallest declines (14% and 20%, respectively) in the UK. Other species declining by over 50% in Estonia were *Coeloglossum viride* (56%) and *Corallorhiza trifida* (58%). Species showing the highest (<80%) levels of decline in the UK were *Cypripedium calceolus* (95%), *Himantoglossum hircinum* (83%), *Orchis militaris* (84%), *O. simia* (80%) and *O. ustulata* (79%). Percentage decline in the 30 species

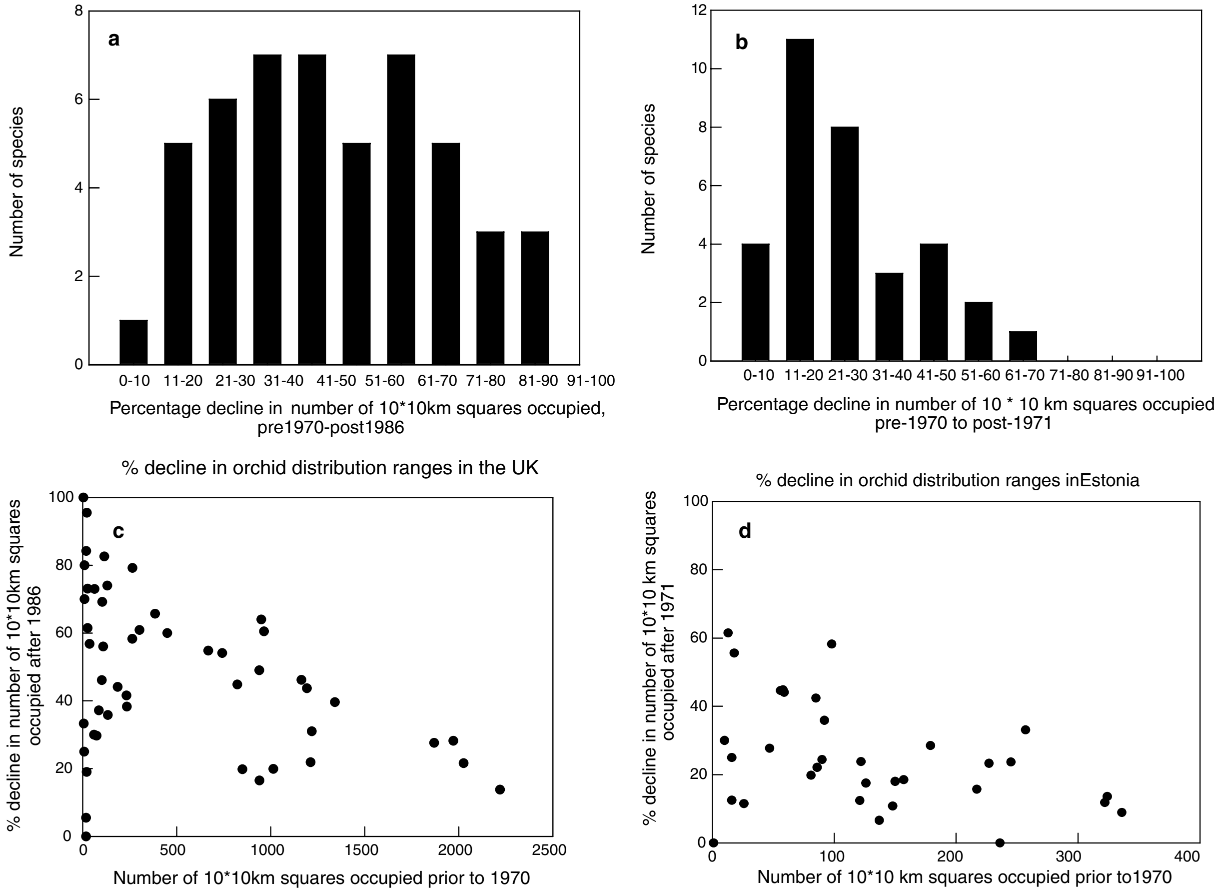

Fig. 1 – Histograms of percentage change in the distribution ranges of (a) 49 orchid species in the UK, and (b) 33 orchid species in Estonia between the first and second survey dates. (c) Percentage change in number of grid squares in which 49 species of orchid were recorded at the second survey in the UK, and (d) 33 species of orchid were recorded in the second survey in Estonia, plotted against number of squares occupied at the first survey in each country.

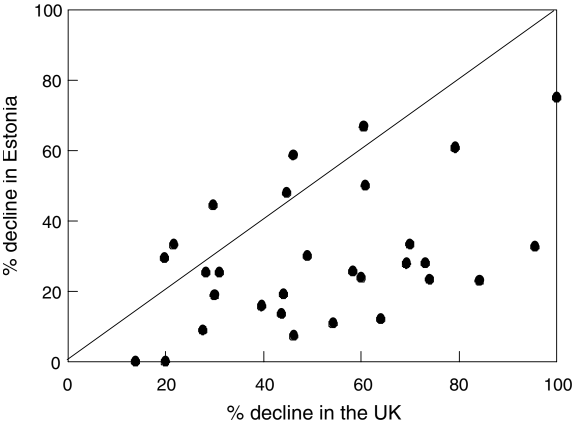

Fig. 2 – A comparison of percentage alteration in distribution range of the 30 species of orchid common to the UK and Estonia. The diagonal line indicates equal percentage change in distribution range in the two countries. Points above and below the line indicate greater decline in Estonia and in the UK, respectively.

common to both the UK and Estonia was significantly correlated ($r = 0.46$, $P = 0.01$, $n = 30$, Fig. 2). Only six of the species common to both countries declined more in Estonia than in the UK (*Anacamptis pyramidalis*, *C. viride*, *Corallorhiza trifida*, *D. maculata*, *D. traunsteineri*, *Listera cordata*).

3.1. *Factors responsible for decline*

Parameters that were significantly correlated with species decline in all three data sets (i.e. for the UK and Estonia separately, and for the two countries combined) were habitat, and species life-span. On average, species of wet grasslands declined by little more than half as much as species characteristic of calcareous grassland and woodland (Table 1 and Fig. 3). Decline in the range of orchid species in the UK was also significantly correlated with soil wetness preference, with species confined to dry soils showing greater decline than those characteristic of wetter soils. Species life-span had a significant influence on the extent of decline, with short-lived species showing greater decline in both countries than longer-lived species (Fig. 4(a)). In addition, for species in the UK, height of species when in flower was a significant predictor of decline, with species of short stature showing significantly greater decline than tall species (Fig. 4(b)). In Estonia, species associated with more open habitats suffered greater decline. When data from both countries were combined (data were available for 23 species common to both countries), significant parameters beside habitat and life-span were soil reaction and species nitrogen demand. Species associated with soils of higher pH and with higher nitrogen demand declined more than species tolerant of lower pH and species found on substrates of lower nitrogen status.

Table 1 – Analysis of parameters having significant impact on decline in range of orchid species in the UK, in Estonia, and in both countries together

Parameter	Estimate	Standard error	*t*-Value	P > /t/
UK				
Intercept	−29.68	16.29	−1.82	0.078
Start	0.899	0.129	6.94	<0.0001
Start*Habitat c vs. w	0.028	0.046	0.60	0.552
Start*Habitat c vs. wg	−0.175	0.060	−2.93	0.006
Start*Habitat w vs. wg	−0.203	0.057	−3.54	0.001
Start*life-span (long)	0.174	0.046	3.78	0.001
Start*plant height (short)	−0.206	0.057	−3.63	0.001
Start*soil wetness	−0.036	0.015	−2.37	0.024
Estonia				
Intercept	−5.509	2.740	−2.01	0.056
Start	0.610	0.079	7.70	<0.0001
Start*Habitat c vs. w	−0.063	0.039	−1.64	0.114
Start*Habitat c vs. wg	0.148	0.037	3.95	0.001
Start*Habitat w vs. wg	0.211	0.034	6.11	0.0001
Start*life-span (long)	−0.121	0.030	−3.99	0.001
Start*light	0.033	0.010	3.45	0.002
Both countries together				
Intercept	−14.36	9.319	−1.54	0.131
Start*Habitat c vs. w	−0.048	0.075	−0.65	0.521
Start*Habitat c vs. wg	−0.291	0.063	−4.64	0.0001
Start*Habitat w vs. wg	−0.243	0.074	−3.26	0.002
Start*life-span (long)	0.227	0.057	3.98	0.0001
Start*soil pH	0.044	0.016	2.69	0.010
Start*soil fertility (N demand)	0.039	0.019	2.07	0.045

The dependent variable was the number of grid cells occupied by species at the second survey. Start – number of grid cells occupied at the first survey; c calcareous grassland; w – forest; wg – wet grassland and mires.

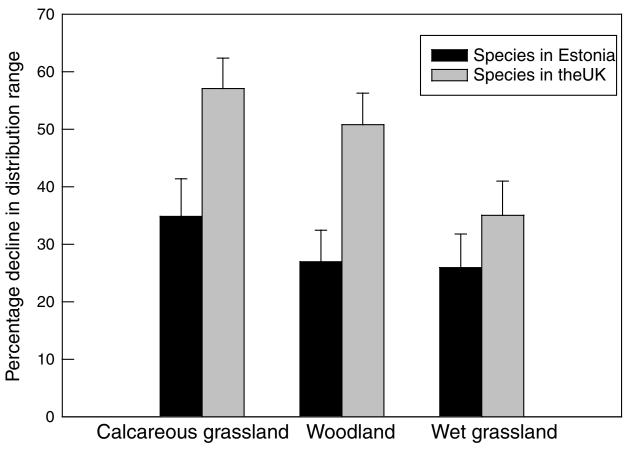

Fig. 3 – Mean ± SE percentage decline in distribution range of orchid species associated with calcareous grassland, woodland and wet grassland habitat, in Estonia and the UK.

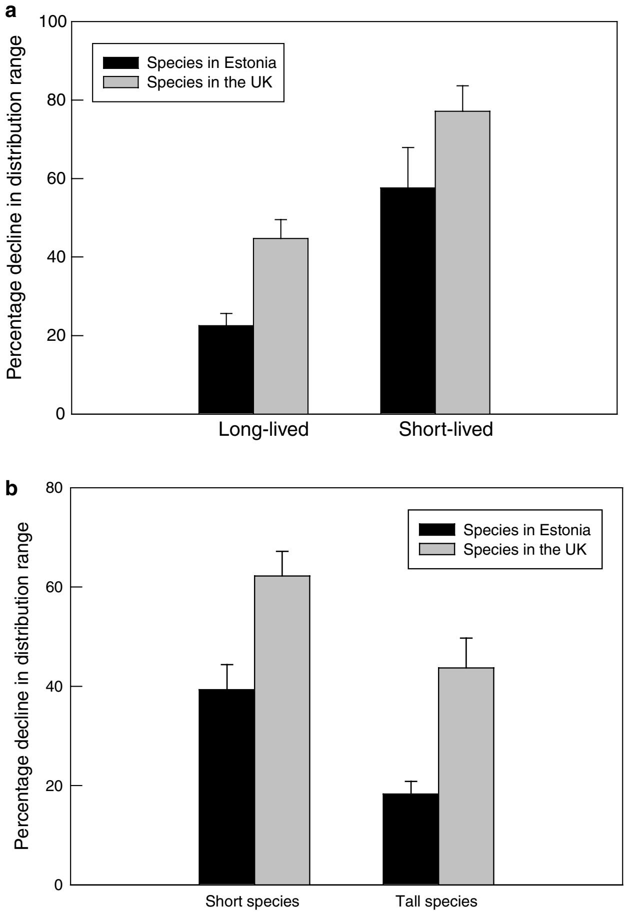

Fig. 4 – Comparisons of mean ± SE percentage decline in distribution range of orchid species in Estonia and the UK. (a) Long-lived vs. short-lived species and (b) species with short vs. tall stature.

4. Discussion

Apart from some species of *Dactylorhiza*, all species for which distribution ranges were analysed in the UK and Estonia suffered some range contraction during the intervals considered. Overall, the range of orchid species in the UK contracted by an average of 50% over a 30-year period. In Estonia the corresponding mean decline over a 34-year time period was 25%. Corresponding figures for Flanders over a 70-year period, and for the Netherlands over 50 years, were 48% and 37%, respectively (Jacquemyn et al., 2005).

The species suffering the greatest decline in both countries was *Epipogium aphyllum*. It may have become extinct in the UK, and in Estonia its range declined by 61% during the period considered. Although *E. aphyllum* is hard to record due to its irregular flowering, monitoring programmes in two small remnant populations in Estonia still record flowering plants in most years. The main reason for decline of this species is probably loss of suitable forest habitat. In most parts of Europe, the forests on fertile soils that are its preferred habitat are heavily managed, resulting in its elimination. *E. aphyllum* is also among the orchid species displaying the most serious level of decline in Germany (Baumann et al., 2005). Another species suffering serious decline in both the UK and Estonia is *O. ustulata*, a species of calcareous grasslands. Abandonment of traditional management on sites where it occurs quickly results in increased vegetation height and loss of *O. ustulata*, which is short in stature (Tali et al., 2004). Some species have declined dramatically in either the UK or Estonia, but less in the other country. For example, *O. militaris* has suffered very severe (>80%) decline in the UK, but only 18% decline in Estonia. Although *O. militaris* inhabits similar sites to those of *O. ustulata*, it is taller, longer lived, and probably less sensitive than *O. ustulata* to eutrophication (for example, it often grows on roadsides in Estonia). Another species that has suffered severe decline in the UK is *Cypripedium calceolus*. Although this species has declined by 28% in Estonia, there are still many sites where it occurs, some of which support thousands of ramets. However, heavy logging during the last decade has destroyed a considerable number of its sites. In the UK, *Himantoglossum hircinum* declined by over 80% during the recording interval, although it has been increasing again in recent years, possibly in response to climate change (Carey, 1999; Carey et al., 2002). The distribution of *Ophrys sphegodes* has followed a similar trajectory, see Hutchings, 1987, and unpublished results). *H. hircinum* has also increased its range in Flanders and the Netherlands during the periods investigated by Jacquemyn et al. (2005). Both in Estonia and in the UK there has been severe decline in the range of *Coeloglossum viride*, a short-lived species (Willems and Melser, 1998) inhabiting grasslands that are neutral or mildly acidic. *C. viride* has also dramatically decreased in the Netherlands, Flanders and Germany (Jacquemyn et al., 2005; Baumann et al., 2005). In contrast to these rapid range contractions, some species declined by relatively small amounts (Appendix 1). These included common species such as *D. fuchsii* in the UK, and some very rare species, such as *Gymnadenia odoratissima* in Estonia, and *D. praetermissa* in Estonia and the UK. The distribution ranges of several rare species have been largely maintained as a result of careful management for conservation. Thus, although the statistics about range declines are worrying, there is cause for optimism that, if appropriate management is implemented, local extinction can be avoided even in very rare species.

The effects of human activities upon the natural world differ in severity at regional scales, and this has strong effects on species decline. Level of decline was on average twice as high in the UK as in Estonia, where population density is much lower, despite the fact that the time interval between successive surveys was similar for both countries. Altogether, only six of the 30 species common to both regions declined more in Estonia than in the UK. Of these, *Anacamptis pyramidalis* and *C. viride* are mainly characteristic of grassland habitats, whereas the other four (*Corallorhiza trifida*, *Dactylorhiza maculata*, *D. traunsteineri* and *Listera cordata*) are species of wet forest habitats. Many natural grasslands in Estonia have been abandoned from management or cultivated in recent decades, and many wet forest habitats were subjected to drainage between 1970 and 1990. These changes in traditional management practises are probably major causes of the relatively severe declines of these species in Estonia.

Our results showed that, in the UK, species of calcareous grasslands and woodland have suffered greater range losses than species of wet grasslands. This is probably associated with the loss of a very high percentage of traditional sheep-grazed calcareous grasslands, which are a very important habitat for many orchid species in the UK (Blackwood and Tubbs, 1970; Anonymous, 1984a,b; Ratcliffe, 1984). In contrast, in the Netherlands and Belgium, orchids of wet grasslands and heathlands suffered greater decline than those of forests and calcareous grasslands (Jacquemyn et al., 2005). It is clear that the same types of habitats are subjected to different levels of anthropogenic pressure in different countries, depending on local conditions and policies. Moreover, conservation efforts to avert species decline have differed between regions, and consequently the pattern of species decline varies between different parts of Europe. While the patterns of decline for orchids of different habitat types appear to be consistent in Flanders and the Netherlands (Jacquemyn et al., 2005), it should be noted that the data for Flanders are actually based on very small numbers of grid squares (mean number of squares occupied by orchids was only 10.8 at the start of the study period and 5.6 at the end). Given such small numbers, caution should be exercised when making comparisons of species decline in specific habitat types between different regions. The contrasting results obtained by ourselves and Jacquemyn et al. also suggest that we should be cautious before accepting the proposal that the relative risks of extinction for orchid species in different types of habitat are similar across widely separated regions.

Those species that we could categorise as short-lived in our study showed greater levels of decline, both in the UK and in Estonia, than longer-lived species. In addition, species that have shorter stature when in flower have declined more than those with taller inflorescences, probably because they have been unable to survive increased competition from associated species which have grown taller as a consequence of habitat eutrophication (see also Jacquemyn et al., 2005). Greater height of competing species can affect orchids especially during the vegetative phase, as many species, especially those with smaller inflorescences, produce rosettes of short leaves that are held very close to the ground. Species of smaller stature are also more threatened after abandonment of traditional hay management practises in semi-natural grasslands, as has occurred in many sites in Estonia. Analysis of environmental preferences showed that light was a significant explanatory variable for orchid decline in Estonia, with species of open conditions declining more than those tolerant of at least some shade. Although life-form was not a significant predictor of the level of decline suffered by species, rhizomatous (clonal) species declined to a greater extent than tuberous (non-clonal) species. Fischer and Stöcklin (1997) and Eriksson and Ehrlén (2001) report that clonal species, and species with colonising ability, have lower extinction risks than non-clonal species. In general, clonal species are usually more buffered against habitat deterioration and increased competition than non-clonal species, as a result of being able to produce multiple ramets distributed over a wider area, the ability to move in space, and being able to allocate more resources to storage. However, most rhizomatous orchid species have low mobility because their rhizomes have short annual increments (Kull and Kull, 1991; Püttsepp, 1994; Tatarenko, 1996). At least in Estonia, rhizomatous orchid species with long annual rhizome increments, such as *Listera ovata*, *Epipactis palustris* and *Goodyera repens*, have shown relatively small declines during the study periods (Appendix 1). Further studies are still needed to provide autecological and demographic information about many species to strengthen the analyses we present here, and to guide management for conservation.

5. Conclusions

The analyses presented here demonstrate that, in widely separate regions in Europe, orchid species have suffered severe declines in range during the time periods considered. Whereas several orchid species expanded their ranges in Flanders and the Netherlands over the time periods considered by Jacquemyn et al. (2005), no species increased its range in either the UK or Estonia, and the ranges of virtually all species contracted. Although this appears to suggest that orchids were less threatened in the regions studied by

Jacquemyn et al., several species became extinct both in Flanders and the Netherlands during their study period, whereas there were no extinctions in Estonia, and no more than two in the UK. This might reflect greater investment in the conservation of the rarest species in Estonia and the UK, and maintenance of natural and semi-natural habitat in Estonia.

Whereas our data demonstrate more severe declines in species associated with calcareous grasslands and woodland habitat, Jacquemyn et al. showed that orchids of heathland and wet grassland suffered greater declines. Thus, the level of decline shown both by groups of species associated with specific habitat types, and by particular species of orchid, may depend strongly on local conditions, policies and conservation action. Orchids of small stature declined more than taller orchids, possibly reflecting both abandonment of traditional management practises, and eutrophication. These results provide some basis for selecting habitat types on which to concentrate conservation efforts. They suggest that management practises such as grazing and mowing, and avoidance of substrate disturbance, may produce the greatest benefits.

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Appendix A

Species	1	2 (UK Number of squares since 1986)	3 (Est 1921–1970)	4 (Est number of squares 1971–2004)	5	6	7	8	9	10	11	12	13	14	15
Aceras anthropophorum	109	48			c	t	l	t	35	7	7	2	4	8	3
Anacamptis pyramidalis	849	681	16	12	c	t	l	t	45	8	7	2	3	9	2
Cephalanthera damasonium	233	136			w	r	l	t	37	3	6	2	4	7	4
Cephalanthera longifolia	131	34	26	23	w	r	l	t	37	5	5	3	4	6	4
Cephalanthera rubra	10	3	47	34	w	r	l	t	40	4	5	4	3	8	4
Coeloglossum viride	964	381	18	8	c	t	s	s	23	8	indiff	indiff	4	4	2
Corallorhiza trifida	102	55	98	41	w	r	s	s	19	indiff	4	7	5	3	indiff
Cypripedium calceolus	22	1	179	128	w	r	l	t	32	5	5	5	4	8	4
Dactylorhiza baltica			121	106	wg	t	l	t	*	*	*	*	*	*	*
Dactylorhiza fuchsii	2219	1913	236	236	wg	t	l	t	30						
Dactylorhiza incarnata	1192	671	324	280	wg	t	s	t	35	8	5	3	8	7	2
Dactylorhiza lapponica	18	18			wg	t	l	s							
Dactylorhiza maculata	2025	1587	257	172	wg	t	l	t	30	7	indiff	2	8	7	2
Dactylorhiza majalis	26	10			wg	t	l	t	37	8	5	3	8	7	2
Dactylorhiza praetermissa	1014	812	1	1	wg	t	l	t	33	9	5	?	9	8	2
Dactylorhiza purpurella	1212	946			wg	t	l	s	32						
Dactylorhiza traunsteineri	74	52	92	59	wg	t	l	t	30	8	4	4	9	4	2
Epipactis atrorubens	60	42	126	104	w	r	l	t	57	6	indiff	3	3	8	2
Epipactis helleborine	1218	840	227	174	w	r	l	t	67	3	5	3	5	7	5
Epipactis leptochila	86	54			w	r	l	t	45	3	6	3	4	9	4
Epipactis palustris	450	180	245	187	wg	r	l	t	42	8	5	3	9	8	2
Epipactis phyllanthes	134	86			w	r	l	t	37						
Epipactis purpurata	235	145			w	r	l	t	45	2	6	4	6	8	6
Epipogium aphyllum	4	0	13	5	w	r	s	s	13	2	4	6	5	7	4
Goodyera repens	186	104	150	123	w	r	l	s	17	5	indiff	7	4	indiff	2
Gymnadenia conopsea	1341	810	217	183	c	t	l	t	40	7	indiff	2	7	8	3
Gymnadenia odoratissima			16	14	wg	t	l	s	30	6	indiff	4	4	9	2
Hammarbya paludosa	302	118	58	32	wg	t	l	s	7	9	5	3	9	2	2
Herminium monorchis	104	32	81	65	c	t	l	s	16	7	5	7	5	8	2
Himantoglossum hircinum	115	20			c	t	l	t	55	7	7	2	3	9	2
Liparis loeselii	26	7	86	67	wg	t	s	s	13	8	6	4	9	9	2

(continued on next page)

Appendix A – *continued*

Species	1	2 (UK Number of squares since 1986)	3 (Est 1921–1970)	4 (Est number of squares 1971–2004)	5	6	7	8	9	10	11	12	13	14	15
Listera cordata	822	454	85	49	wg	r	l	s	12	3	4	3	7	2	2
Listera ovata	1869	1354	336	306	w	r	l	t	40	6	indiff	3	6	7	7
Malaxis monophyllos			56	31	wg	t	l	s	19	3	4	5	8	6	6
Neottia nidus-avis	742	340	148	132	w	r	s	t	32	2	5	3	5	7	5
Ophrys apifera	264	110			c	t	l	s	32	7	6	2	4	9	2
Ophrys fuciflora	940	785			c	t	*	s	35						
Ophrys insectifera	6	4	122	93	c	t	*	t	30	7	5	4	4	9	3
Ophrys sphegodes	63	17			c	t	s	s	27	8	8	4	4	9	3
Orchis laxiflora	8	6			WG	t	*	t	55	9	6	5	9	8	2
Orchis mascula	1971	1416	90	68	W	t	l	t	40	6	indiff	3	4	8	indiff
Orchis militaris	19	3	157	128	C	t	l	t	32	7	6	5	3	9	2
Orchis morio	939	479	10	7	C	t	l	s	27	7	5	3	4	7	3
Orchis purpurea	37	16			C	t	*	t	55	5	7	4	4	8	3
Orchis simia	10	2			C	t	l	t	32	8	8	2	3	8	2
Orchis ustulata	265	55	59	33	C	t	s	s	23	7	5	5	4	indiff	3
Platanthera bifolia	950	342	322	284	w	t	l	t	37	6	indiff	3	5	7	indiff
Platanthera chlorantha	1163	626	137	128	w	t	l	t	37	6	indiff	3	7	7	indiff
Pseudorchis albida	385	132			wg	t	*	s	27	8	4	2	5	2	2
Spiranthes aestivalis	3	0			wg	t	*	t	31	8	6	4	9	9	2
Spiranthes romanzoffiana	21	17			wg	t	*	t	20						
Spiranthes spiralis	668	302			c	t	l	s	20	8	6	2	4	5	2

Variables used in model: (1) number of grid cells occupied between 1930 and 1969 in the UK, (2) number of grid cells occupied between 1987 and 1999 in the UK, (3) number of grid cells occupied between 1921 and 1970 in Estonia, (4) number of grid cells occupied between 1971 and 2004 in Estonia, (5) habitat preferences (c – calcareous grassland, w – woodland, wg – wet grassland and mire), (6) growth habit (r – rhizomatous, t – tuberous), (7) life-span (l – long-lived, s – short-lived), (8) tall (t) or short (s) species, (9) height of a species in cm, (10) Ellenberg indices for light, (11) temperature, (12) continentality, (13) soil humidity, (14) soil pH and (15) soil fertility. * value missing, indiff-species is indifferent.

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