Changes in the abundance of Danish orchids over the past 30 years

Christian Damgaard, Jesper Erenskjold Moeslund, Peter Wind

Department of Bioscience, Aarhus University, Denmark

Abstract

Orchid abundance data collected during the past 30 years from 440 sites within the National Orchid Monitoring Program were analysed to quantify the population trends of orchids in Denmark, and the underlying reasons for the observed population trends were analysed and discussed. Twenty of the 45 monitored Danish orchids showed a significant decrease in abundance over the past 30 years (16, if only orchids with at least 50 observations each are selected), thus corroborating the previous observations of declining orchid abundances at European scale. Generally, there was a significant negative effect of overgrowing with tall-growing herbs and shrubs on the abundance of Danish orchids.

Keywords: Danish orchid species, Danish Red List, National Orchid Monitoring Program, Danish Orchid Database, citizen science, monitoring, vegetation, population size, population trend, plant abundance, plant diversity, pressures on orchid sites

Introduction

Orchids are generally in decline globally (Kull & Hutchings 2006; Tali et al. 2006; Vogt-Schilb et al. 2015). In Denmark, 33 taxa out of 51 species, subspecies and varieties of orchids (see Table 1) are assessed as either extinct, threatened or near threatened on the Danish Red List (Wind 2019). In this study, we use orchid abundance data collected during the 30 years between 1987 and 2016 from 440 sites within the National Orchid Monitoring Program to quantify the population trends of orchids in Denmark. Additionally, we analyse and discuss underlying reasons for the observed population trends.

In Northern Europe, orchids typically grow in woodlands, both broad-leaved forests and old conifer plantations, dry grasslands and heathlands, rich and poor fens, meadows and dune slacks (Pedersen & Faurholdt 2010). Sometimes, orchids also colonize abandoned marl and lime pits, but avoid saline marshes, arid white dune areas and intensively managed farmlands (Pedersen & Faurholdt 2010). The soil's structure and texture, hydrology, pH, mycorrhiza availability and composition of nutrients are important ecological factors that characterize suitable habitats for orchids (Djordjević et al. 2016; Hemrová et al. 2019; McCormick & Jacquemyn 2014; van der Heijden et al. 2015). Furthermore, light conditions, the degree of disturbance and, for some orchids, the presence of specific pollinators play important roles for habitat suitability (Pedersen & Faurholdt 2010; Schiestl 2005).

Most orchids in Northern Europe have declined because of habitat loss or habitat degradation, for example as a result of secondary succession following abandonment of former farming practises such as extensive grazing and hay cutting (Kull & Hutchings 2006; Mattiasson 1986; Schrautzer et al. 2011). The secondary succession can accelerate by changed interspecific competitive regimes following increased soil nutrient availability due to fertilizers and airborne nitrogen pollution (Ejrnæs et al. 2003). Other land use changes, such as urbanization, infrastructural constructions, lowering of the groundwater table, draining and cultivation, are equally important causes of orchid habitat loss (Kull & Hutchings 2006; Mattiasson 1986). In some cases, overgrazing can also constitute a threat to orchids (Catorci et al. 2013), e.g. by preventing seed development. In forests, many orchids grow in areas that have been left untouched for decades, and if the forests are disturbed, e.g. drained, clear-cut or fertilized, then orchids are at risk of disappearing (Whigham 2004). Despite being protected by law in many countries including Denmark (Miljøministeriet 2016), orchids are regularly picked for flower bouquets or dug up for gardening or trade, actions that both affect the fitness of an orchid population. For instance, three entire clones of *Cypripedium calceolus* were dug up from the Danish population of at Buderupholm in 2012 and moved from the fence that had been raised in order to protect the population, and in 2016, approximately 40 flowering shoots were picked from the

population (Himmerland Forest Department, pers.com. 2012, 2016). Additional, general public disturbance and outdoor activities, such as hiking, camping, and picnicking, may also affect orchid populations negatively (Handley & Heidel 2005; Kull 1999; Rocchio et al. 2006; Stewart 1989, 1996; Wood et al. 1984). For example, an *Epipactis leptochila* population at a slope on Møns Klint possibly went extinct due to the playing of children (N. Faurholdt, per.com 1996). Many orchid species are specialists, depending on only one or a few pollinators or mycorrhizal symbiont species (Phillips et al. 2011a; Rasmussen 1995). This can explain why orchids are intrinsically rare (Phillips et al. 2011b), but has probably also given orchids their reputation for being good indicators of intact or high-value nature (e.g. Laroche et al. 2012; Newman 2009).

The monitoring of orchid species provides a good basis for effective management and conservation of native orchid populations and their habitats, which is a complicated task due to the orchid species' complex ecology and the many and varied threats mentioned above. The annual collecting of information on orchid populations and the condition of their habitats for the National Orchid Monitoring Program is a way to achieve such adequate data that are useful for planning of management and conservation tasks and to describe the trend of the Danish orchid species. Besides, the program is an excellent example of an ongoing citizen science project, where Danish orchids have been monitored annually for more than 30 years from 440 selected orchid sites. The National Orchid Monitoring program is, to our knowledge, the most comprehensive and long-lived field-based orchid monitoring project in the world comprising many Danish members of the orchid family (see Appendix A for a detailed account of citizen science in Denmark).

Internationally, there are a few examples of long-term orchid monitoring programs of comparable duration as the monitoring of the Danish population of *Cypripedium calceolus*. One example is the annual census of a population of *Anacamptis pyramidalis* in a Dutch dune area that started in 1940 (Sterk 1976). The annual census has been continuously conducted until at least 1975, except for the Wold War years 1943, 1944 and 1945 (Sterk 1976). Another example is the Swedish ecologist, C.O. Tamm (1919-2007), who laid out the first plot in 1942 in a population of *Dactylorhiza sambucina* in order to document the effect of picking orchids (Tamm 1991). The annual Swedish census also involved other orchid species, *Dactylorhiza incarnata, Neottia ovata* and *Orchis mascula*. The monitoring seems to have ended in 1990. Additionally, long-time monitoring has been performed on *Orchis anthropophora* (L.) All. 1967-1980 (Wells 1981), *Dactylorhiza majalis* subsp. *integrata* 1973-1985 (syn. *D. praetemissa*), (Vanhecke 1988; Vanhecke 1991), *Dactylorhiza sambucina* 1968-1985 (Mattiasson 1986), *Orchis mascula* 1960-1970 (Willems 1989), *O. militaris* 1947-1962 (Farrell 1991; Waite & Farrell 1998), *O. palustris* (Högström 1991), and *Spiranthes spiralis* (Salkowski 1990; Wells 1981). Kull (2002) has made an overview of long-term field-based studies on population dynamics of

terrestrial orchids. The overview comprises 66 orchids with information on the ways of performing the monitoring: 1) monitoring in permanent plots, 2) counting of specimens in populations, 3) genet dynamics, where individuals are mapped, 4) measurement of fruit set, and 5) morphometrical parameters analysed. A characteristic feature of these studies is that they are generally short-termed compared to the National Orchid Monitoring Program and most studies only monitor a single species.

In our study, we analyse the data of The National Orchid Monitoring Program and report on the observed trends for the monitored orchids. Furthermore, we link the observed changes in orchid abundance to four observed potential pressures acting on orchid populations.

Materials and Methods

Orchid taxa in Denmark

Fifty one terrestrial orchids have been recorded in Denmark (Pedersen & Faurholdt 2010) and belong to 10 boreal genera of the orchid family (*Orchidaceae*). All of them are native to the Danish flora and comprise 31 species, 13 subspecies and 7 varieties. Two species, *Ophrys apifera* and *Orchis militaris*, recently appeared in Denmark in 2004 and 1981, respectively.

Undoubtedly, the Danish orchids belong to the most threatened group of vascular plants in the Danish flora. Thirty-three out of 51 (65 %) of the Danish orchids assessed for the Danish Red List (Wind 2019) are either extinct, threatened or near threatened by extinction based on the IUCN Red List Assessment methodology (IUCN 2012). Eight orchids are categorized Critical Endangered (CR), seven Endangered (EN), seven Vulnerable (VU) and eight Near Threatened (NT). Sixteen orchids are categorized Least Concern (LC), while two have not yet been assessed. Two species and one subspecies are now Regionally Extinct (RE) in Denmark (Table 1) (Wind 2019).

In the following, the term ‘orchid/orchids’ refers to taxa both on species and subspecies level unless anything else is specified, while the nomenclature follows Pedersen & Faurholdt (2010).

Orchid censuses in Denmark

The census of Danish orchid populations started long before the onset of the National Orchid Monitoring Program in 1987. *Cypripedium calceolus* was recorded for the first time in Denmark Rold Skov, a forest in Jutland, in 1884. The annual census of the population started in 1943 and has continued since then, except

for the year 1946 (Fig. 1). The monitoring of orchids expanded in the beginning of the 1980'ties, where three Danish counties commenced to perform an annual census of local populations of orchids such as *Anacamptis morio, Dactylorhiza maculata* subsp. *fuchsii, Dactylorhiza majalis, Epipactis palustris, Gymnadenia conopsea* and *Liparis loeselii.* In parallel, amateurs started regular annual censuses of selected populations of some of the rarest Danish orchids, e.g. *Anacamptis pyramidalis, Epipactis leptochila, Epipogium aphyllum* and *Pseudorchis albida* (Fig. 2).

The annual census of 18 Danish orchids was performed, including the populations of orchids that had already been monitored, as mentioned above, at the start of the National Orchid Monitoring Program. The annual census was continued for 14 of the 18 orchids throughout the first 30 years of the program. In 1989 and in 1990, four additional orchids were included in the program, of which the annual censuses were performed for one of them, *Epipactis phyllanthes*, during the rest of the period. For the three other orchids, the censuses of *Epipactis atrorubens* and *Neottia cordata* ended in 2009 and 2011, respectively, and those of *Epipactis helleborine* subsp. *neerlandica* were performed more irregularly on different sites (Fig. 2). The annual censuses of *Ophrys apifera* started in 2004, the year when the orchid species was observed for the first time in Denmark. Thus, 45 Danish orchids (30 species, 9 subspecies, and 6 varieties) have been monitored either continuously (31 orchids) or more irregularly. The latter was either because monitoring stopped (10 orchids) during the period 1987-2016 or since their first inclusion in the program. A full overview of the monitored orchids and their census periods can be found in Table 1 and Figure 2, respectively.

Two Danish orchid species, *Cypripedium calceolus* and *Liparis loeselii*, are included in the European Union Habitats Directive Annex 2 (EU 1992), and all known Danish populations of the two species have been monitored annually since the onset of the national monitoring program for species, terrestrial and aquatic nature in 2004.

Orchid abundance data

Local volunteers are of great importance in the National Orchid Monitoring Program as they perform the annual census of selected orchid populations. The surveyors in the program also include paid field-biologists. All participants possess an in-depth knowledge of the orchids. Not all Danish orchid sites were included in the program; many sites were selected in close distance to the surveyors' residences or they were selected based on their knowledge of the locations of the most important local populations. Only sites with more than 30 flowering orchid shoots at the start of the program were included (Løjtnant 1991). On

many sites, different orchids grow together, e.g. on fen sites comprising the two orchid species *Dactylorhiza incarnata* and *D. majalis.* In such instances, both species were monitored. At each of the selected 440 sites, the number of flowering shoots, either at the whole site or at a permanent plot within the site, were counted in the flowering season. A sub-sample of the collected abundance data is illustrated for four orchids (Fig. 3).

The surveyors also estimated the intensity of grazing, forest management, overgrowing with tall-growing herbs and shrubs and public disturbance at the orchid sites by using a four-step classification of the pressures, i.e. 1) none, 2) weak, 3) moderate and 4) hard or strong (Wind 1999).

Further details on the National Orchid Monitoring Program are compiled in Appendix B.

On August 8, 2019, the existing 9,688 records (observations) of flower numbers from 874 Danish orchid populations at the 440 orchid sites as well as 3,337 records on pressures had been retrieved from the Danish Orchid Database and provide the basis for the present analysis.

Statistical analysis

The observed changes in orchid species abundances were modelled based on the recorded flower numbers, and since the data structure was irregular, it was decided to model the change in abundance by a state-space model, where the species abundance at a specific site *i* at time *t* was modelled by latent variables, $x_{i,t}$. The observed abundance is denoted by $y_{i,t}$ and assumed to be Poisson distributed with the latent variables as the mean parameters, $y_{i,t} \sim Poisson(x_{i,t})$. The change in the log-transformed abundance was modelled by two linear models,

$$log(x_{i,t}) = \alpha + \vartheta_i + \beta\, t \qquad (1),$$

$$log(x_{i,t}) = \alpha + \vartheta_i + (\beta + \delta_i)\, t \qquad (2),$$

where α is the intercept and β is the mean annual change. The random effects of site and site * years are modelled by ϑ_i and δ_i, respectively, and both are assumed to be normally distributed. The two linear models differ in whether the random effect of site * years is included or not, i.e. whether the change in abundance varies among sites. Due to the log-transformation, the estimated doubling time of a population may be calculated as $\log(2)/\beta$ or $\log(2)/(\beta + \delta_i)$ in model 1 and 2, respectively.

The models were fitted in a Bayesian framework using integrated nested Laplace approximation (Rue et al. 2009). The implementation of the two models in R is shown in Appendix D and follows Blangiardo et al. (2013). The two models were compared by DIC (Spiegelhalter et al. 2002), and statistical inferences were made using the 95% credible interval of the parameter of interest.

In order to investigate possible causal relationships between the abiotic environment and the observed site-specific changes in abundance, the estimated site-specific random time coefficients, δ_i, of model 2 were regressed against the mean values of the four estimated pressures at each site with species as a random effect. Again, this model was fitted in a Bayesian framework using integrated nested Laplace approximation (Rue et al. 2009).

Results

Generally, the two linear models (1 and 2) gave the same qualitative results, i.e. the estimated trends, β, had approximately the same credibility interval. However, model 2 better supported the abundance data for the majority of the orchid species (Table 2), i.e. for most species the rate of change differed significantly among sites.

Eighteen of the 41 orchids showed a significant decrease in abundance, while two, *Epipactis helleborine* subsp. *neerlandica* and *Ophrys insectifera*, showed a significant increase in abundance. The abundance of the remaining 21 orchids did not show a significant change (Table 2). In order to ensure that the reported trends are general in both time and space and not due to extraordinary years or sites with uncharacteristic management practices, we added the supplementary constraint that at least 50 observations were needed for making robust and general inferences on the change in orchid abundance. Under this added constraint, 16 orchids showed a significant decrease, while none were found to be increasing (Table 2). In figure 3, the population decrease for four of the monitored orchids is illustrated.

The effects of the estimated pressures on the change in abundance are shown in Table 3. Generally, there was a significant negative effect of overgrowing with tall-growing herbs and shrubs on the abundance of orchids. The effects of the remaining three pressures were not statistically significant.

In Figure 4, the results of three of the more noticeable changes in orchid abundance are presented. The orchids *Anacamptis morio*, *Dactylorhiza sambucina* and *Herminium monorchis* all show a significant decreasing abundance, which may be explained by a typical land use change from extensive grazing,

190 especially with cattle and hay-making, towards more intensive farming practices with the use of fertilisers.
191 Notice also that the chosen linear trend model does not always, provide an adequate description of the
192 observed trends, e.g. in the case of *Herminium monorchis*.

193 Discussion

194 Twenty of the 45 monitored Danish orchids showed a significant decrease in abundance over the past 30
195 years (16, if only orchids with at least 50 observations were selected), thus corroborating the previous
196 observations of declining orchid abundances at European scale (Kull & Hutchings 2006; Tali et al. 2006;
197 Vogt-Schilb et al. 2015). Thirteen of the declining 16 orchids are nationally red-listed (Wind 2019), status in
198 parenthesis): *Anacamptis morio* (NT)*, Corallorhiza trifida* (VU)*, Dactylorhiza sambucina* (EN), *Epipactis*
199 *atrorubens* (NT)*, E. leptochila* (NT)*, E. palustris* (NT)*, Gymnadenia conopsea* subsp. *conopsea* (CR),
200 *Hammarbya paludosa* (EN), *Orchis purpurea* (NT)*, Platanthera bifolia* subsp. *bifolia* (NT), *P. bifolia* subsp.
201 *latiflora* (EN), *Platanthera chlorantha* (NT) and *Pseudorchis albida* (CR) (Table 1).

202 Seven threatened orchids did not show a significant decrease in abundance: *Cephalanthera damasonium*
203 (VU), *C. longifolia* (EN), *C. rubra* (CR), *Cypripedium calceolus* (VU), *Herminium monorchis* (EN) and *Liparis*
204 *loeselii* (EN). Furthermore, the result of the analysis show a significant decrease in abundance among seven
205 orchids categorized Least Concern (LC): *Dactylorhiza incarnata* subsp. *incarnata, D. maculata* subsp. *fuchsii,*
206 *Epipactis phyllanthes, E. purpurata, Neottia ovata, N. nidus-avis* and *Orchis mascula*. However, all these
207 orchids still have a relatively large geographical distribution within Denmark (Hartvig 2015).

208 According to our analyses, the observed general decline in orchid abundance may be partially caused by
209 overgrowth with tall-growing herbs and shrubs caused by changes in the traditional farmland-use. This
210 inference is corroborated by the results from Timmermann et al. (2015), who found that reduced livestock
211 grazing most likely was an important factor in explaining the decline in abundance of some plant species.

212 Many orchids have relatively complex life-cycles and quite narrow ecological requirements for their habitat.
213 A number of orchid species are pollinated by one or two insect species (Joffard et al. 2019), but most are
214 pollinated by a more diverse insect fauna. For instance, *Ophrys insectifera* are pollinated by males of the
215 digger wasps *Argogorytes mystaceus* and *A. frageii,* while the flowers of *Cypripedium calceolus* are
216 pollinated by females of the genus *Andrena* and *Halictidae* (Pedersen & Faurholdt 2010). Hence, the decline
217 in such insects could also explain the decline in their dependent orchid species. Also, most orchid species
218 depend on certain mycorrhizae to germinate and thrive and are therefore prone to reduction in the

availability of these fungal relationships. For example, a recent study showed that the landscape-scale distribution of four European orchid species, *Cephalathera rubra, Epipactis atrorubens, E. helleborine* and *Neottia nidus-avis*, are primarily restricted by availability of fungal associates (Hemrová et al. 2019). We have not included such relationships in our analysis of pressures, as the surveyors did not collect mycorrhizal information, but we highly recommend that future studies pursue this and shed more light on the role of pollinators and mycorrhiza for the decline in orchid abundances.

Acknowledgements

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229 # Tables

230 Table 1. The 51 orchids recorded in Denmark, their taxonomic level (Pedersen & Faurholdt 2010), Danish
231 Red List status (Wind 2019) and period of monitoring of 45 orchids in the National Orchid Monitoring
232 Program. Red List Categories: RE = Regionally Extinct. CR = Critically Endangered. EN = Endangered. VU =
233 Vulnerable. NT = Near Threatened. LC = Least Concern. NE = Not Evaluated.

International name	Taxon level	Stat 202
Anacamptis morio (L.) R.M. Bateman, Pridgeon & M.W. Chase	Species	NT
Anacamptis pyramidalis (L.) Rich.	Species	VU
Cephalanthera damasonium (Mill.) Druce	Species	VU
Cephalanthera longifolia (L.) Fritsch	Species	EN
Cephalanthera rubra (L.) Rich.	Species	CR
Coeloglossum viride (L.) Hartm.	Species	RE
Corallorhiza trifida Châtel	Species	VU
Cypripedium calceolus L.	Species	VU
Dactylorhiza incarnata (L.) Soó subsp. *incarnata*	Subspecies	LC
Dactylorhiza incarnata (L.) Soo subsp. *lobelii* (Verm.) H.A. Pedersen	Subspecies	VU
Dactylorhiza incarnata (L.) Soó subsp. *incarnata* var. *ochroleuca* (Boll) Hyl.	Variety	EN
Dactylorhiza maculata (L.) Soó subsp. *fuchsii* (Druce) Hyl.	Subspecies	LC
Dactylorhiza maculata (L.) Soó subsp. *maculata*	Subspecies	LC
Dactylorhiza majalis (Rchb.) P.F. Hunt & Summerh. subsp. *calcifugiens* H.A. Pedersen	Subspecies	NE
Dactylorhiza majalis (Rchb.) P.F. Hunt & Summerh. subsp. *integrata* (E.G. Camus) H.A. Pedersen var. *integrata*	Variety	LC
Dactylorhiza majalis (Rchb.) P.F. Hunt & Summerh. subsp. *integrata* (E.G. Camus) H.A. Pedersen var. *junialis* (Verm.) H.A. Pedersen	Variety	VU
Dactylorhiza majalis (Rchb.) P.F. Hunt & Summerh. subsp. *lapponica* (Hartm.) H. Sund.	Subspecies	RE
Dactylorhiza majalis (Rchb.) P.F. Hunt & Summerh. subsp. *majalis*	Subspecies	LC
Dactylorhiza majalis (Rchb.) P.F. Hunt & Summerh. subsp. *purpurella* (T. & T.A. Stephenson) D.M. Moore & Soó var. *cambrensis* (R.H. Roberts) H.A. Pedersen	Variety	LC
Dactylorhiza majalis (Rchb.) P.F. Hunt & Summerh. subsp. *purpurella* (T. & T.A. Stephenson) D.M. Moore & Soó var. *purpurella*	Variety	LC

Dactylorhiza majalis (Rchb.) P.F. Hunt & Summerh. subsp. *sphagnicola* (Höppner) H.A. Pedersen & Hedrén	Subspecies	CR
Dactylorhiza sambucina (L.) Soó	Species	EN
Epipactis atrorubens (Hoffm. ex Bernh.) Besser	Species	NT
Epipactis helleborine (L.) Crantz subsp. *helleborine*	Subspecies	LC
Epipactis helleborine (L.) Crantz subsp. *neerlandica* (Verm.) Buttler var. *neerlandica*	Variety	LC
Epipactis helleborine (L.) Crantz subsp. *neerlandica* (Verm.) Buttler var. *renzii* (Rob.) J.Claess., Kleynen & Wielinga	Variety	NT
Epipactis leptochila (Godfery) Godfery	Species	NT
Epipactis palustris (L.) Crantz	Species	NT
Epipactis phyllanthes G.E. Sm.	Species	LC
Epipactis purpurata Sm.	Species	LC
Epipogium aphyllum Sw.	Species	CR
Goodyera repens (L.) R. Br.	Species	LC
Gymnadenia conopsea (L.) R. Br. subsp. *conopsea*	Subspecies	CR
Gymnadenia conopsea (L.) R. Br. subsp. *densiflora* (Wahlenb.) K Richt.	Subspecies	CR
Hammarbya paludosa (L.) Kuntze	Species	EN
Herminium monorchis (L.) R. Br.	Species	EN
Liparis loeselii (L.) Rich.	Species	EN
Neotinea ustulata (L.) R.M. Bateman, Pridgeon & M.W. Chase	Species	CR
Neottia cordata (L.) Rich.	Species	LC
Neottia nidus–avis (L.) Rich.	Species	LC
Neottia ovata (L.) Bluff & Fingerh.	Species	LC
Ophrys apifera Huds.	Species	VU
Ophrys insectifera L.	Species	CR
Orchis mascula (L.) L.	Species	LC
Orchis militaris L.	Species	NA
Orchis purpurea Huds.	Species	NT
Platanthera bifolia (L.) Rich. subsp. *bifolia*	Subspecies	NT
Platanthera bifolia (L.) Rich. subsp. *latiflora* (Drejer) Løjtnant	Subspecies	EN
Platanthera chlorantha (Custer) Rchb.	Species	NT

Pseudorchis albida (L.) À & D. Löve	Species	CR
Spiranthes spiralis (L.) Chevall.	Species	RE

Table 2. The number of observations, N, percentiles of the marginal distribution of the average change over time (bold green numbers denotes a significant increase and bold red numbers denotes a significant decrease), β, and the model (eqn. 1 or eqn. 2) that was best supported by the data.

Species	N	2.5 %	50 %	97.5 %	Model
Anacamptis morio	433	**-0,1378**	**-0,0715**	**-0,007**	2
Anacamptis pyramidalis	100	-0,009	0,1233	0,242	2
Cephalanthera damasonium	137	-0,1002	-0,0102	0,0662	2
Cephalanthera longifolia	182	-0,066	-0,0265	0,0094	2
Cephalanthera rubra	60	-0,2268	-0,017	0,1976	2
Corallorhiza trifida	189	**-0,4227**	**-0,2633**	**-0,1144**	2
Cypripedium calceolus	83	-0,1162	-0,0157	0,0746	2
Dactylorhiza incarnata	641	-0,2437	-0,1155	0,0086	2
Dactylorhiza maculata subsp. *fuchsii*	182	**-0,0851**	**-0,0491**	**-0,0176**	2
Dactylorhiza maculata subsp. *maculata*	391	-0,1085	0,0153	0,1329	2
Dactylorhiza majalis subsp. *majalis*	928	-0,0439	0,012	0,0666	2
Dactylorhiza majalis subsp. *integrata*	33	-0,1851	0,3126	0,8105	2
Dactylorhiza majalis subsp. *purpurella*	158	-0,1351	-0,0363	0,058	2
Dactylorhiza sambucina	231	**-0,2581**	**-0,1358**	**-0,0245**	2
Epipactis atrorubens	38	**-0,0823**	**-0,0599**	**-0,038**	1
Epipactis helleborine subsp. *helleborine*	652	**-0,1575**	**-0,1173**	**-0,0781**	2
Epipactis helleborine subsp. *neerlandica*	20	**0,0058**	**0,0228**	**0,0404**	1
Epipactis leptochila	217	**-0,1834**	**-0,1208**	**-0,0608**	2
Epipactis palustris	310	-0,3607	-0,1382	0,0771	2
Epipactis phyllanthes	232	**-0,2395**	**-0,1625**	**-0,0967**	2
Epipactis purpurata	247	-0,0742	-0,0352	0,0014	2
Epipogium aphyllum	26	-0,1018	0,0223	0,1545	2
Goodyera repens	45	-1,3174	-0,5082	0,2319	2
Gymnadenia conopsea subsp. *conopsea*	63	**-0,2497**	**-0,1098**	**-0,0264**	2

Gymnadenia conopsea subsp. *densiflora*	20	-0,099	0,0926	0,287	2
Hammarbya paludosa	122	**-0,4299**	**-0,2721**	**-0,1274**	2
Herminium monorchis	131	**-0,3406**	**-0,1741**	**-0,004**	2
Liparis loeselii	408	-0,124	-0,0418	0,0391	2
Neotinea ustulata	32	-0,1095	0,0433	0,1952	2
Neottia cordata	31	-0,6676	-0,1139	0,4011	2
Neottia nidus-avis	163	**-0,116**	**-0,0576**	**-0,002**	2
Neottia ovata	447	**-0,08**	**-0,0411**	**-0,0054**	2
Ophrys apifera	21	-0,1546	0,7153	1,5831	2
Ophrys insectifera	18	**0**	**0,0344**	**0,0689**	2
Orchis mascula	795	**-0,0678**	**-0,0361**	**-0,005**	2
Orchis militaris	6	**-1,9705**	**-1,085**	**-0,4714**	2
Orchis purpurea	140	-0,0725	-0,0272	0,0208	2
Platanthera bifolia subsp. *bifolia*	281	**-0,3781**	**-0,2153**	**-0,074**	2
Platanthera bifolia subsp. *latiflora*	82	**-0,1708**	**-0,1162**	**-0,0683**	2
Platanthera chlorantha	315	-0,1442	0,059	0,2744	2
Pseudorchis albida	181	**-0,0725**	**-0,0606**	**-0,049**	1

240 Table 3. The percentiles of the marginal distribution of the estimated posterior distribution of the effect of
241 the mean estimated pressures at each site on the site-specific random time coefficients, δ_i, of model 2.

Effect	2.5 %	50 %	97.5 %
Intercept	-0.061	0.023	0.108
Intensity of grazing	-0.009	0.016	0.040
Intensity of forest management	-0.031	0.006	0.043
Overgrowth with tall-growing herbs and shrubs	-0.052	-0.029	-0.006
Public disturbance	-0.038	-0.004	0.030

242

Figures

Fig. 1. *Cypripedium calceolus.* The annual census of flowering aerial shoots in Buderupholm Forest 1943-2016.

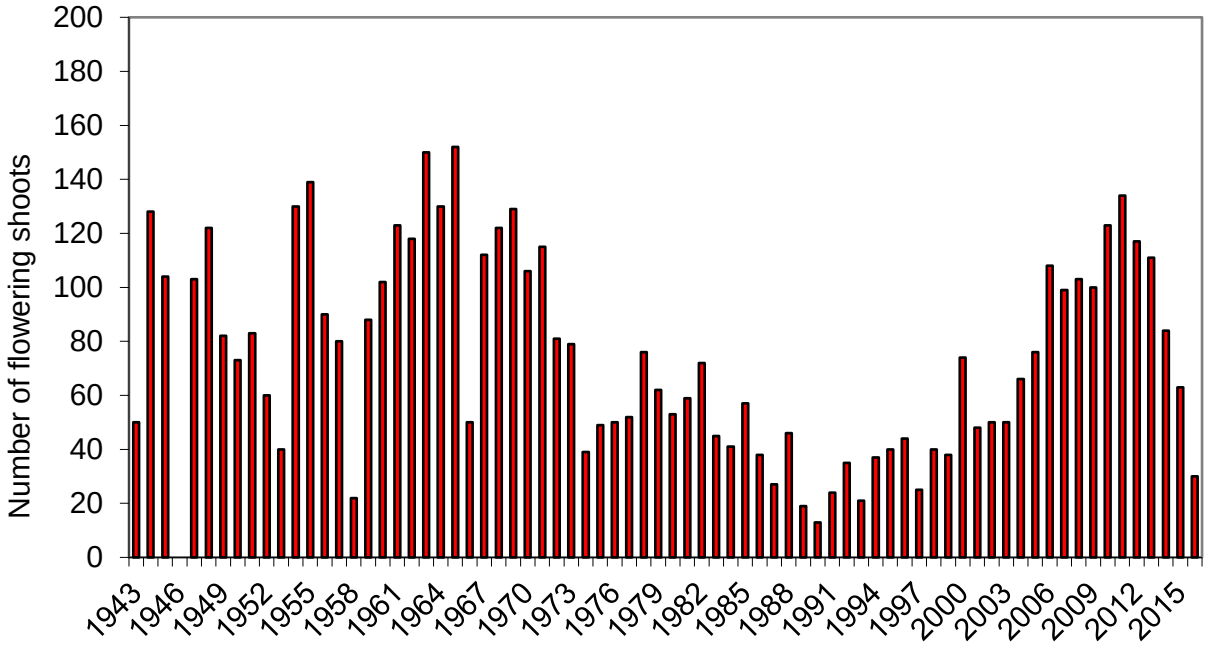
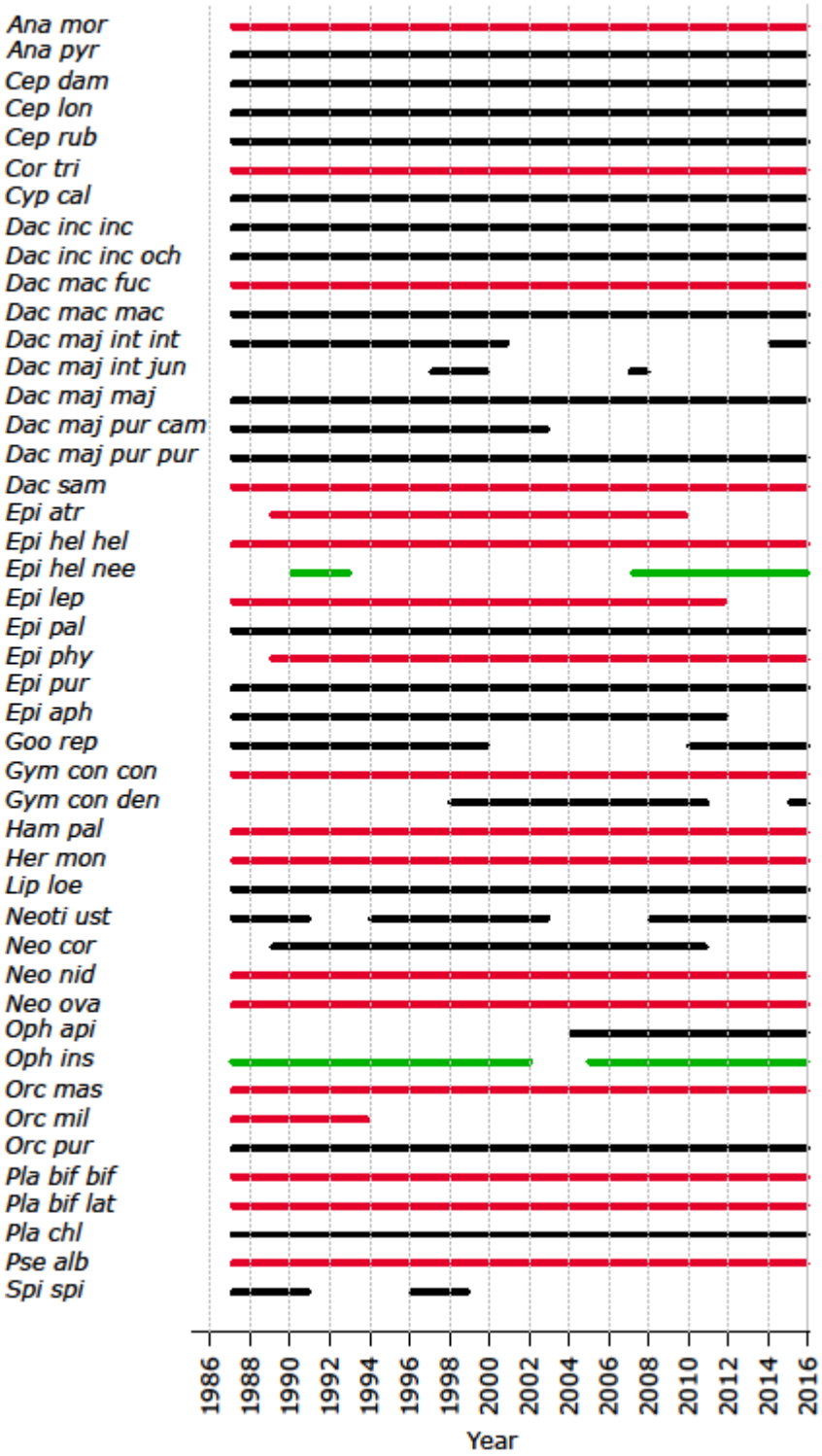


Fig. 2. Onset and continuity of the annual census of 45 Danish orchids based on the data in the Danish Orchid Database. Abbreviations: *Ana mor – Anacamptis morio, Ana pyr – A. pyramidalis, Cep dam – Cephalanthera damasonium, Cep lon – C. longifolium, Cep rub – C. rubra, Cor tri – Corallorhiza trifida, Cyp cal – Cypripedium calceolus, Dac inc inc – Dactylorhiza incarnata* subsp. *incarnata, Dac inc inc och – D. i.* subsp. *i.* var. *ochroleuca, Dac mac fuc – C. maculata* subsp. *fuchsii, Dac mac mac – D. m.* subsp. *maculata, Dac ma int int – D. majalis* subsp.*integrata* var. *integrata, Dac maj int jun – D. m.* subsp. *i.* var. *junialis, Dac maj maj – D. m.* subsp. *majalis, Dac maj pur cam – D. m.* subsp. *purpurella* var. *cambrensis, Dac maj pur pur – D. m.* subsp. *p.* var. *purpurella, Dac sam – D. sambucina, Epi atr – Epipactis atrorubens, Epi hel hel – E helleborine* subsp. *helleborine, Epi hel nee – E. h.* subsp. *neerlandica, Epi lep – E. leptochila, Epi pal – E. palustris, Epi phy – E. phyllanthes, Epi pur – E. purpurata, Epi aph – Epipogium aphyllum, Goo rep – Goodyera repens, Gym con con – Gymnadenia conopsea* subsp. *conopsea, Gym con den – G. c.* subsp. *densiflora, Ham pal – Hammarbya paludosa, Her mon – Herminium monorchis, Lip loe – Liparis loeselii, Neoti ust – Neotinea ustulata, Neo cor – Neottia cordata, Neo nid – N. nidus-avis, Neo ova – N. ovata, Oph api – Ophrys apifera, Oph ins – O. insectifera, Orc mas – Orchis mascula*. *Orc mil – O. militaris, Orc pur – Orchis purpurea, Pla bif bif – Platanthera bifolia* subsp. *latiflora, Pla bi flat – P. b.* subsp. *latiflora, Pla chl – P. chlorantha, Pse alb – Pseudorchis albida. Spi spi – Spiranthes spiralis*.


Ana mor
Ana pyr
Cep dam
Cep lon
Cep rub
Cor tri
Cyp cal
Dac inc inc
Dac inc inc och
Dac mac fuc
Dac mac mac
Dac maj int int
Dac maj int jun
Dac maj maj
Dac maj pur cam
Dac maj pur pur
Dac sam
Epi atr
Epi hel hel
Epi hel nee
Epi lep
Epi pal
Epi phy
Epi pur
Epi aph
Goo rep
Gym con con
Gym con den
Ham pal
Her mon
Lip loe
Neoti ust
Neo cor
Neo nid
Neo ova
Oph api
Oph ins
Orc mas
Orc mil
Orc pur
Pla bif bif
Pla bif lat
Pla chl
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Spi spi
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263

Fig. 3. Populations of four analysed orchids. Only populations that were monitored at least three years within the first and last ten years of the study period are shown. The size of the dots corresponds to the mean number of flowering shoots 1987–1996 showing the initial population sizes. The color gradient from green to red reflects the reduction of flowering shoots from the initial period (1987–1996) to the 2007–2016 period. The insert shows the island of Bornholm. (a): *Dactylorrhiza sambucina*, (b): *Epipactis helleborine* subsp. *helleborine*, (c): *Herminium monorchis*, (d): *Anacamptis morio*. Photos: a, c & d Jesper Moeslund. b Peter Wind.

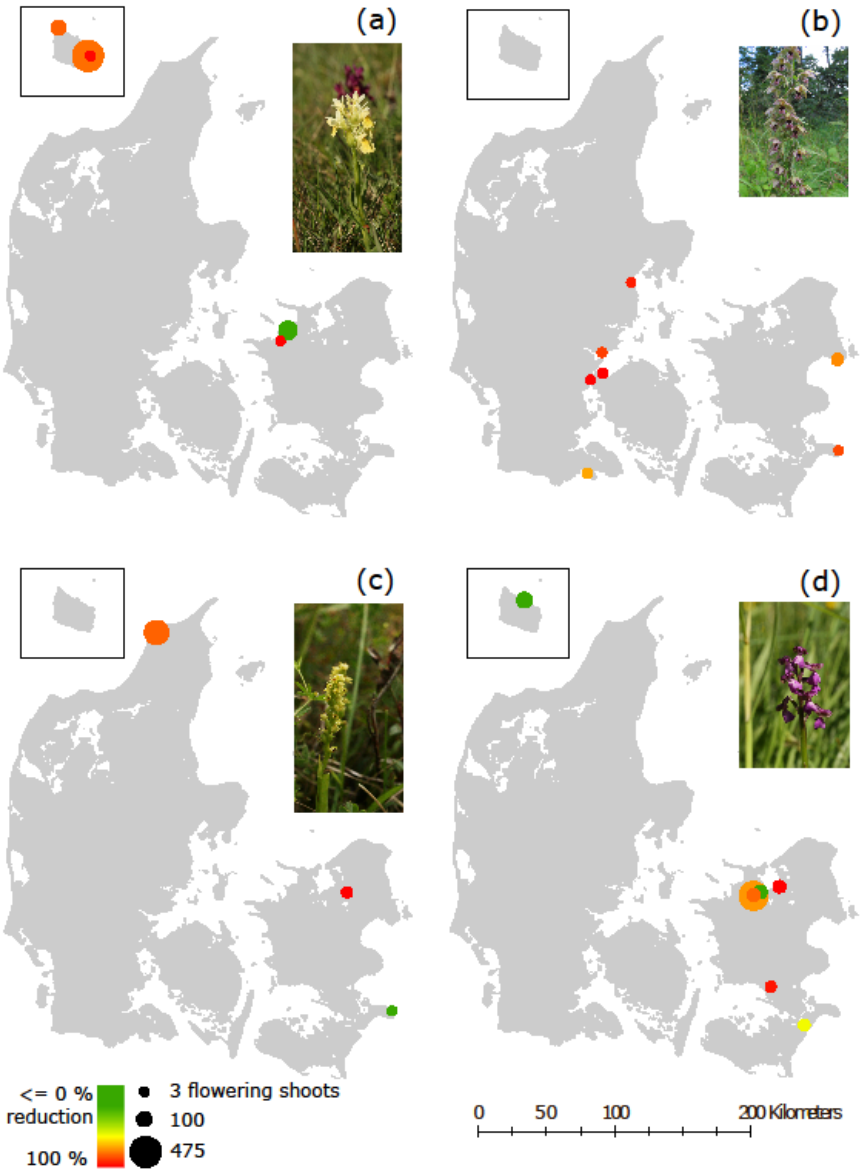
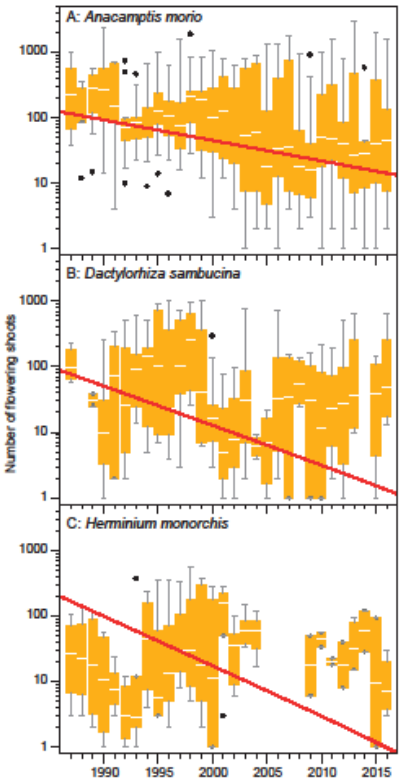


Fig. 4. The observed number of flowering shoots changes for three orchid species shown as box plots of the mean site abundance (white line: medians, yellow box: 25% - 75%, whiskers: 2.5%-97.5%, points: outliers), and the red line illustrates the estimated annual change in the linear model (2). The shown Box-plots are a summary of the hierarchical repeated-measure abundance data and cannot be eyeball-fitted to the back-transformed median slope. A: *Anacamptis morio,* B: *Dactylorhiza sambucina,* C: *Herminium monorchis*



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Electronic supplements

Appendix A: Citizen Science in Denmark

In Denmark, there is a long-time tradition for national species surveillance involving voluntary citizens. Birds were the first group of organisms to be involved in a species-monitoring program. In 1899, the Danish ornithologist Hans C.C. Mortensen (1856-1921) founded the project of ringing birds in order to follow the migration of bird species. During the 20th Century, many Danish Natural History Societies launched national surveillance programs that in a modern term are characterised as 'Citizen Science'. In 1904, The Danish Botanical Society started a complete monitoring program of the Danish flora of vascular plants – the Botanical Topographic Investigation of Denmark (TBU). The aim of the project was to gather information of the distribution and state of the Danish vascular plant flora. Officially, 262 voluntary persons participated, but more than half of them never became active (Hartvig 2015). In Denmark, 57 topographical-botanical districts were established in order to collect information that was more detailed on the vascular plant distribution. Field monitoring ended in 1923. The results of the monitoring were worked up and published in family order, starting with the *Fabaceae* (*Papilionaceae*) in 1931 (Jessen 1931). The final scientific paper on the *Portulacaceae* and the *Valerianaceae* (Hansen & Pedersen 1976) was published in 1976. In total, 41 scientific papers have been published on the distribution of the Danish vascular plant flora. In 1989, a scientific paper (Vestergaard & Hansen 1989) on the general distribution pattern of the Danish vascular plant flora was issued, which formally closed the project.

In 1991, the Danish Botanical Society launched a follow-up project to the TBU-project called Atlas Flora Danica (AFD). The AFD project was a time-limited survey, 1991-2012, of the actual flora based on standardized method. The survey included all vascular plants, native as well as alien, outside cultivated areas. The recording units were five x five km squares in the UTM grid. A total of 2.228 squares cover Denmark. Of the 2.228 squares, 1.300 were surveyed thoroughly. The project was completed in 2015 with the publication of a three-volume book containing a presentation of the recorded vascular plant species in the project and distribution maps for most of the species (Hartvig 2015).

The Buderupholm Forest District (now Himmerland Forest District) started the annual census of the local population of *Cypripedium calceolus* in 1943, which is one of oldest and still ongoing surveillances of a single species. The position of the clones of *C. calceolus*, which are surrounded by a fence to protect the plants from pricking of the shoots and digging of the plants, has been mapped precisely in order to follow the development of the individual clone. The number of both vegetative and flowering aerial shoots has

been recorded every year since 1943, except for 1945, where only the flowering aerial shoots were counted, and 1946, where no recordings of the aerial shoots were performed at all (Figure 1).

Many other national surveillance terrestrial programs have been performed in Denmark, focusing on other organism groups where volunteer citizens have been involved. Examples are: 1) the national bird-monitoring program based on Point Count Census covering the trends in breeding populations of 90 species launched in 1975 and organised by the Danish Ornithological Society. 2) monitoring of amphibians and reptiles started in 1976 and is organised by the youth society 'Natur og Ungdom'. 3) monitoring of the Danish otter was launched in 1984 by World Wildlife Fund and the Danish Animal Welfare Society and is conducted in cooperation with the Natural History Museum in Aarhus (Asbirk & Orth 1987). Besides, the Danish Ornithological Society has performed three national atlas surveys of bird species in 1971 – 1974, 1993- 1996 and latest in 2014 – 2017 using the same five x five km squares in the UTM grid as in the botanical AFD-project.

Appendix B: The National Orchid Monitoring Program

The Nature Protection Agency in cooperation with other national institutions held a symposium in October 1986 in order to get an overview of the many Danish surveillance programs run by other national agencies, county counsels, universities, and natural history societies. The aim of the symposium was to get inspiration on how to work out a national terrestrial monitoring program that could support effective nature management.

At the turn of year 1986/1987, a fusion of the Forest Agency and the Nature Protection Agency resulted in the establishment of the Forest and Nature Agency under the Ministry of Environment. One of the first tasks of the new agency was to work out and launch a national monitoring program based on the recommendations of the 1986-symposium.

The National Orchid Monitoring Program, which was launched in cooperation with the Danish Botanical Society in 1987, is one example. The aim of the program is to monitor the state and possible changes in orchid abundance in representative Danish orchid populations by means of annual censuses (Løjtnant 1991). Besides monitoring orchid abundance, the aim of the monitoring programme is to document the effects of joint legislation on biodiversity and to collect data that may be used to understand the causal mechanisms underlying the observed changes in the state of the orchid populations.

The National Orchid Monitoring Program relies on volunteer citizens to conduct the annual census of the selected orchid populations in the field. Therefore, volunteers have been recruited as surveyors to carry out the annual censuses together with professionals already involved in orchid censuses. Approximately 170 surveyors have contributed to the project over the past 30 years since it started in 1987 (see Appendix C). Some surveyors have contributed to the monitoring program from the beginning, whereas others have contributed for shorter periods or have joined after the onset of the program and are still involved. Sadly, a few surveyors have passed away.

In 1994, The National Environmental Research Institute (NERI) under the Ministry of Environment overtook the coordination and maintenance of the monitoring program. NERI had set-up the Danish Orchid Database for storing the collected data of the program and ensuring that data were accessible on the web (http://bios.au.dk/raadgivning/natur/planter/). When NERI was included in the Department of Bioscience at Aarhus University in 2007, the university became responsible for coordinating and maintaining the monitoring program.

Methodology

The Danish orchid expert Bernt Løjnant was the first coordinator of the National Orchid Monitoring Program. He launched four methods for performing the annual censuses of the aerial shoots of flowering and vegetative orchid specimens. 1) A total count of all specimens in an orchid population. The benefit of the method is that the method follows the orchid population that can emerge on different locations on a site from year to year. 2) A count of all specimens within a number of randomly laid out, permanent squares on one m^2 or circles on 0.1 m^2. 3) A total count of specimens within a permanent 'strip', e.g. 50 m in length and one m width in an orchid population. The method has been used on a large Danish population of *Liparis loeselii* on Zealand comprising thousands of plants. 4) A total count of all specimens within a permanent plot with a size of up to 100 m^2. The coordinator recommended generally using the latter method (Løjtnant 1991). A disadvantage to this is that many orchids disappear from the permanent plots and appear outside of the plots. In addition, a permanent plot may vanish, especially plots established on plastic soil where the plot and the orchid population may slide into the sea. The most applied methods in the program have proved to be methods 1 and 4, where the flowering shoots are counted and, if at all possible, the vegetative shoots are counted eventually as well, although they can be hard to identify in a dense vegetation cover and difficult to identify to a particular species when more orchids grow together on the same site.

Pressures

Another important field observation is the state of the pressures, their strength and influence on the individual orchid population. The pressures comprise all factors, both natural and human, that affect the growth of an orchid population on a site. The pressures are divided into five main categories. 1) Grazing. 2) Intensity of forest management. 3) Overgrowth of tall-growing herbs and shrubs. 4) Public disturbance. 5) Other impacts (not included in the previous four).

1) *Grazing* comprises all kinds of impacts that grazing livestock carry out on the orchid sites. Thus, the category does not include the influence of wild animals, e.g. red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and geese (*Anser anser*). Their influence is noted in category five.

2) *Forest management* is the impact caused by forestry on the orchid sites. The impact includes everything from felling of selected trees over pollarding to intensive management.

3) *Overgrowth with tall-growing herbs and shrubs* comprises the pressure caused by the surrounding vegetation influencing the growth of an orchid population on a site. Overgrowth typically occurs where the

previous management has been changed or has ended. This includes all degrees of overgrowth, from increased dominance of tall-growing herbs to the growth of woody plants.

4) *Public disturbance* is the impact caused by recreational activities on the orchid sites. Thus, the category comprises the degree of impact caused by everything from random human damage to picking flowers for a bouquet to targeted plant collection and digging of entire plants or clones for gardening or commercial use.

5) The category comprises impacts caused by the use of other management practices than those described in the previous categories. A typical example is hay mowing.

The Intensity of the pressures is, as mentioned in the body text, divided into a four-step scale defined by the types of impacts and are shown in Table B1-B4.

Unfortunately, some of the definitions are rather weakly defined, which leaves open the possibility of subjective interpretation by the surveyors. The bias in the interpretation has caused surveyors to doubt whether to use one category or the other and induced them to have chosen to report intermediately between the two categories. The intermediate choice is inappropriate when the collected data is to be used for analysis of the degree of pressure.

Table B1. Degrees of impact by grazing with livestock (from Wind 1999).

Category	**Definition**
None	The site is not grazed by livestock
Weak	The vegetation cover is coherent and dominated by tall-growing herbs and woody plants. Tussock and hillock structure is only seen to a lesser extent
Moderate	The vegetation cover is coherent and dominated by low-growing, light-depending species. Often, a tussock and hillock structure has developed with minor vegetation less gaps
Strong	The vegetation cover has been grazed intensively and is incoherent. Because of trampling, gaps in the vegetation cover have been created, and the

	tussocks and hillocks are often stepped on and destroyed

Table B2. Degrees of forestry management (from Wind 1999)

Category	Definition
None	The site is characterized as natural forest or untouched forest
Weak	The picking of selected trees or coppicing is carried out extensively, whereby the forest floor is only illuminated to a small extent. Forest regeneration occurs through continuous self-regeneration of trees and shrubs
Moderate	The picking of selected trees or coppicing is carried out to such a degree that the forest floor is partly illuminated. Forest regeneration occurs by strong self-regeneration of seed plants or by self-growth of trees and shrubs
Hard	Clear cutting, establishment of new cultures of woody plants, cultivation of the forest floor, use of fertilizers and pesticides and heavy pruning of the forest vegetation

Table B3. Degrees of overgrowth with tall-growing herbs and shrubs (from Wind 1999)

Category	Definition
None	No sign of overgrowth on the site
Weak	The overgrowth is so modest that, in a practical sense, it does not affect the growth of the orchid population

Moderate	The overgrowth is such that it will affect the growth of the orchid population in the long term
Hard/strong	The overgrowth is such that it will affect the growth of the orchid population in the short term

Table B4. Degrees of public disturbance (from Wind 1999)

Category	Definition
None	Unintended traffic, pricking or digging of orchids has not been recorded
Weak	Unintended traffic in an orchid population has been recorded
Moderate	Unintended traffic, pricking or digging of orchids has been recorded to a moderate degree
Hard/strong	Targeted digging of parts of or entire populations of orchids or a great degree of traffic has been recorded

Finally, the surveyor must assess the suitability of the pressure on the orchid population. The aim of the assessment of the suitability is to see whether the intensity of the pressure is good for the growth of the orchid population on the site in question or whether it will harm it. Many orchid species require balanced regulation of vegetation height and extent at the site in order for the population to thrive. For example, a certain grazing pressure may cause the low-growing vegetation at a given site to be maintained when the combination of bite and tramp is optimal. If grazing pressure is too high, it can cause damage to the vegetation cover in the form of abrasion and curbing, while too low grazing pressure can cause problems in the form of overgrazing.

The suitability of the intensity of the impact depends on the ecology of each orchid species. Some species thrive best in direct sunlight, while others prefer shade. For example, the number of *Orchis mascula* and *Neottia ovata* increases after coppicing the woodland, while the *Epipactis* and *Cephalanthera* species thrive in untouched forest (Wind 1989).

When the surveyors have finished the field work, all information is noted on data sheets that are sent to the program manager at Aarhus University at the end of the season. The program manager examines the received sheets making a quality check of the information to secure its validity before the data are stored in the Danish Orchid Database.

In conclusion, the National Orchid Monitoring Program is an outstanding project supported by a core of surveyors, mostly volunteers, willing to perform the annual census. The program was established long before the term ‘Citizen Science’ was brought into everyday use. Thanks to the program, unique series of data on orchid population trends have been collected over the years, forming a more solid basis for the red-list assessment of the state of Danish orchids.

Appendix C: Surveyors

The surveyors that have contributed or still contribute to the National Orchid Monitoring Program are: Allan Damborg, Asta Israelsen, Allan Weimann, Aage Pedersen, Aksel Voigt, Bo Boysen Larsen, Bodil Grønborg Brun, Bjarne Hemmingsen, Bodil Holt, Birthe Kristensen, Bernt Løjtnant, Birte Hvarregaard, Bo Normander, Bodil Stoltze, Brian Rudebeck, Bent Vestergaard Petersen, Birthe Zimmermann, Carsten Horup Bille, Camilla Nielsen, Ellen & Claus Ole Madsen, Christian Roesdahl, Christian Rørdam, Christian Bertelsen, David Boertmann, Erik B. Andersen, Erik Christensen, Erik Ehmsen, Erik Hansen, Erik Hammer, Erling Krabbe, Eigil Plöger, Erik Sand, Erik Skov Nielsen, Einer T. Ludvigsen, Erik Vinther, Eiler Worsøe, Finn Bjerregaard, Finn K. Hansen, Finn Lindhart, Flemming Thorning-Lund, Gudmund Fajstrup, Gudrun Larsen, Gerda Madsen, Gerth Nielsen, Hanne Bau Jensen, Hanne Jensen, Hans Anker Nielsen, Henrik Bavnhøj, Henrik Bjørn Holck, HC Gravesen, Hans Ditlev, Hans Guldager Christiansen, Hans Hjeds, Hanne Holst, Hans Jørn Christensen, Hans Jørgen Degn, Harald K. Hansen, Helle Møller-Madsen, Henning Petersen, Henning Poulsen, Hans Rasmussen, Henrik Tranberg, Henrik Ærenlund Pedersen, Hans Øllgaard, Ian Heilmann, Inge Nagstrup, Jan Germundsen, Jan Martin, Jens Amtkjær, Jens Blædel, Jens Christensen, Jens Christian Schou, Jens Erik Lindgaard, Jens Gregersen, Jens Hohwü-Christensen, Jens Rye Larsen, Jens Vahl, Jes Phillipsen Schmidt, Jesper Ratjen, Jimmy Lassen, John Brandbyge, John Holst, John Mønsted Jensen, Johannes Skov, Jon Buttenschön, Jørgen Hyhne, Jørgen Peter Kjeldsen, Jørgen Terp Laursen, Kaj Halberg, Karen Thingsgaard, Karin Sloth, Karsten Nørgaard, Kirsten Juul, Knud Rasmussen, Kurt Ærenlund Pedersen, Lars Bjarne Pedersen, Lars Christiansen, Lars Jakobsen, Lasse Werling, Lene Kofoed, Lisbeth Emsholm, Lis Kristensen, Lis Ravnsted-Larsen, Louise Lyng Bojesen, Lone Godske, Maria Mortensen, Marian Würtz Jensen, Marianne Helkjær, Mikael Landt, Mogens B. Hansen, Mogens Frost Christensen, Mogens Holmen, Morten Lyngsaa, Molly Hougaard, Niels Faurholdt, Nikolaj Hedegaard Correll, Niels Kornum, Niels Westergaard Knudsen, Nina Kjær Pedersen, Ole Lyshede, Peer Høgsberg, Per Egge Rasmussen, Peter Echard Mortensen, Peter Holm, Peter Leth, Rasmus Fuglsang Frederiksen, Rita Merete Buttenschön, Rikke Strøm-Ringstrøm, Sten Moeslund, Stig Jeppesen, Stig Mortensen, Stine Lindstrøm, Sten Asbirk, Susanne Bruhn Aaen, Søren Grøntved Christiansen, Søren Holst Kjeldsen, Søren Vinding, Terkel Arnfred, Terje Seidenfaden, Thea Illum, Thomas Eske Holm, Thomas M. Petersen, Thomas Plesner, Thomas Retsloff, Thomas Vikstrøm, Toni Reese Næsborg, Torben Ebbensgaard, Vibeke Dunn-Andersen, Vibeke Rahbek, Westy Esbensen and Aase Arbirk.

Appendix D: Statistical model

The two models were implemented in R-INLA as

```
Model1=Present~Year+f(Site,model="iid")                                    (S1),

Model2=Present~Year+f(Site,model="iid")+f(Site1,Year,model="iid")          (S2).
```

Both model were fitted by, fit=inla(Model, data, family="poisson", E=1, control.compute=list(dic=TRUE)) (S3).