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

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Abstract

Orchid abundance data collected over the past 30 years (1987-2016) 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 were 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 mainly caused by change of farming practises, as extensive management, such as grazing or mowing of light-open grassland areas, has decreased.

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; farming practise

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 the present study, we use orchid abundance data collected in 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, habitat fragmentation or habitat degradation, for example as a result of secondary succession following abandonment of former farming practises, such as extensive grazing with livestock and mowing (Jacquemyn et al. 2005; 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), prohibiting digging or pricking of specimens, collecting seeds or in any way harming the individual specimen, 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 at

Buderupholm in 2012 and moved from a 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). Additionally, 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 censuses of orchid populations performed within the National Orchid Monitoring Program is an example of such monitoring that provides important information on abundance trends 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 most 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 was conducted continuously 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). A study of 47 orchid species at 26 sites with three different habitat types, grassland, shrubland and woodland, was performed between March and May for an 8 years period (2006-2013) in the Mediterranean part of France, where the flowering plants were recorded on sites ranging between 500 and 2000 m^2 in size (Vogt-Schilb et al. 2013).

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 or a few species.

There is a need for monitoring data to support decision making in nature conservation and restoration, especially for species groups that are good indicators of the status of nature. In this study, we demonstrate the importance of long term monitoring of such species for nature management. More specifically, we use data from the long term (30 years) National Orchid Monitoring Program to address the following questions: Which orchid species are declining and which are not? What is the degree of decline? What are the most important pressures that can explain the population dynamics that we have observed?

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, *Orchis militaris* with one flowering plant in a calcareous pit and *Ophrys apifera* with 50 flowering plants in an abandoned marl pit, were recorded for the first time in Denmark in 1981 and 2004, respectively (Løjtnant 1981; Petersen & Høyer-Nielsen 2005). In 1989, the population of *O. militaris* was destroyed as a result of replenishment and planning work in part of the lime pit (Pedersen & Faurholdt 2010). The orchid was rediscovered with one flowering plant in another part of Denmark in 2016 (Correll 2016).

In the following, the term 'orchid/orchids' refers to taxa on species level and lower levels, unless otherwise specified, while the nomenclature follows Pedersen & Faurholdt (2010).

Status, biology and habitats of Danish orchids

Undoubtedly, the Danish orchids belong to one of 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). In addition, orchids constitute 10 % of the 324 threatened Danish taxa. 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).

The rareness and threatened status are also reflected in the national mapping of the vascular plants in Denmark, *Atlas Flora Danica* (Harvig 2015), where the extant Danish orchids have been recorded from *Epipogium aphyllum* in one to *Epipactis helleborine* subsp. *helleborine* in 677 grid-squares of 5x5 km^2. The number of orchid sites varies from one (various orchids) to *Dactylorhiza majalis* subsp. *Majalis,* which are present on at least 830 sites (Table 2).

All Danish orchids are terrestrial perennials supplied with either tubers (31 orchids), rhizomes (18 orchids), pseudobulbs (two orchid) or tuberous roots by the extinct *Spiranthes spiralis* – all subterranean organs that are responsible for storing of nutrients for the following year's formation of over ground parts like aerial stems, leaves and inflorescences. During the summer season, a new tuber or a pseudobulb substitutes the old one. In some instances, more tubers or pseudobulbs are formed, giving rise to more new independent daughter offspring genetically identical with the mother plant the following year. The rhizome can divide vegetative into several separate units that can form aerial shoots that are impossible to separate from each other without digging the rhizome complex up and, thus, functions as a clone. All aerial shoots are therefore counted separately.

Most Danish orchids have conspicuous flowers, which makes it easy to identify and determine the particular orchids in a dense vegetation cover, especially in species-rich fens. A few have more inconspicuous flowers, e.g. Hammerbya paludosa and Pseudorchis albida, and can easily be overlooked,

especially the latter when growing together with *Platanthera* ssp., a problem that Voigt-Schilb et al. (2016) have realised, too.

Pollination of the orchid flowers implies that the individual plants are able to produce capsules with ripe seeds. The fertilisation is carried out by obligate cross-pollination (42 orchids), although more than half of the species produce no nectar that can attract pollinators. Five orchids are obligate self-pollinators. The flowers of four orchids are originally designed for cross-pollination, but due to various mechanisms in the flower self-pollination takes over (Table 2), which the Danish botanist Hagerup (1941) has demonstrated for *Liparis loeselii*.

Many Danish orchids have narrow ecologically requirements, as they are confined to only one habitat type either as shade-requiring under more protected, shaded conditions in woodland, or as shade-intolerant under light-open, moist or dry, calcareous conditions. As pointed out by Swarts & Dixon (2009), the adaptability to one or more mycorrhizae, the attractiveness of the orchid flowers for one or more pollinators and the ability for dispersal of the ripe seeds are all parameters that limit the distribution and the different orchids' choice of habitat.

Even though the Danish terrestrial area in 43.000 km^2 is quite small compared to many other countries, there is a great difference in the annual precipitation between the different parts of Denmark. Preciptitation is lowest in the coastal areas, especially in the Storebælt area, and highest in the interior parts, which is reflected in the distribution pattern of many plant species and orchids as well. Additionally, the composition of the soil influences the distribution of plants, including orchids. The western part of Jutland was ice-free during the latest Weichel Ice Age, resulting in a sandier, nutrient-poor soil, while clay or calcareous moraine cover most of the remaining areas of Denmark.

Concerning the choice of habitat, 14 Danish orchids grow solely in rich fens and dune slacks, while four of them are restricted to calcareous grassland and two to calcareous dunes. Thus, all 18 orchids can be characterised as shade-intolerant. Three orchids are found in deciduous woodland on chalk only, while six others are limited to other types deciduous woodland, especially beech forest, and thus can be characterized as shade-requiring. The rest of the Danish orchids have more broad ecological requirements and can be found in different habitat types as deciduous woodland and on grassland both with and without calcareous soil (Table 2).

Orchid censuses in Denmark

The census of Danish orchid populations started long before the onset of the National Orchid Monitoring Program in 1987. The monitoring of orchids expanded in the beginning of the 1980s, where three Danish counties began 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.* At the same time, 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. 1).

The annual census of 18 Danish orchids was performed at the start of the National Orchid Monitoring Program, including the populations of orchids that had already been monitored, as mentioned above. 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 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 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. 2).

The surveyors also estimated the intensity of grazing with livestock, 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 flowering shoots 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 number of flowering shoots, 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 is 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 (INLA) (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 using INLA (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 3), 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 3). 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 3). In figure 2, 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 4. 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 3, 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 livestock grazing, especially with cattle and mowing, towards more intensive farming practices with the use of

fertilisers. Notice also that the chosen linear trend model does not always provide an adequate description of the observed trends, e.g. in the case of Herminium monorchis, which for unknown reasons show large inter-annual variation in abundance.

Discussion

Twenty orchids have shown a significant decrease in abundance over the past 30 years (16, if only orchids with at least 50 observations are considered), thus corroborating the previous observations of declining orchid abundances at European scale (Kull & Hutchings 2006; Tali et al. 2006; Vogt-Schilb et al. 2015). Twelve of the declining 16 orchids are nationally red-listed (Wind 2019), status in parenthesis): *Anacamptis morio* (NT)*, Corallorhiza trifida* (VU)*, Dactylorhiza sambucina* (EN), *Epipactis atrorubens* (NT)*, E. leptochila* (NT)*, E. palustris* (NT)*, Gymnadenia conopsea* subsp. *conopsea* (CR), *Hammarbya paludosa* (EN), *Orchis purpurea* (NT)*, Platanthera bifolia* subsp. *bifolia* (NT), *P. bifolia* subsp. *latiflora* (EN), *Platanthera chlorantha* (NT), and *Pseudorchis albida* (CR). The four not red-listed orchids are *Epipactis helleborine* subsp. *helleborine, Neottia nidus-avis, N. ovata* and *Orchis mascula* (Table 1).

There is no clear pattern between the significant decline of the 16 orchids and their abundance, biology and habitat. Both some of the very rare and of the more common species are represented among the 16 orchids with both tuberous, rhizomatous orchids as well as *Hammabya paludosa* with pseudobulbs. Seven of the 16 orchids are confined to light-open habitats, e.g. grassland, dune slacks, rich or poor fens and blanket bogs. The remaining orchids grow on both light-open and shaded habitats. Thus, our results do not corroborate the findings of Vogt-Schilb et al. (2016), where the abundance of shade-intolerant orchids declined more sharply than that of shade-requiring orchids on the Mediterranean island Corsica.

Seven threatened orchids did not show a significant decrease in abundance: *Cephalanthera damasonium* (VU), *C. longifolia* (EN), *C. rubra* (CR), *Cypripedium calceolus* (VU), *Herminium monorchis* (EN), and *Liparis loeselii* (EN). These are all species that are either red-listed because of a very small distribution or because their main habitats are in decline, which is also a significant factor considered in the redlisting process. Furthermore, the result of the analysis shows a significant decrease in abundance among seven orchids categorized Least Concern (LC): *Dactylorhiza incarnata* subsp. *incarnata, D. maculata* subsp. *fuchsii, Epipactis phyllanthes, E. purpurata, Neottia nidus-avis, N. ovata* and *Orchis mascula*. This incongruence can probably be explained by the fact that they are all still relatively widely distributed in Denmark (Hartvig 2015), but, even more importantly, in our study only a subset of the monitored Danish populations were included compared to the number of estimated sites of Danish orchids in Table 2. Hence, most populations

of these species are probably not in decline nationally, but only locally, and therefore our results regarding these species should be interpreted with this in mind.

Two of the 45 monitored Danish orchids, *Epipactis helleborine* subsp. *neerlandica* and *Ophrys insectifera* have shown a significant increase in abundance. The likely reason for the increase of *E. h.* subsp. *neerlandica,* which is not common and nationally red-listed in least concern (LC), is that the orchid grows in calciferous dune slacks in the Danish coastal zone that are not heavily affected by the various pressures that other orchids are confronted with. Besides, the coastal zone and the dune areas are legally protected to prevent human changes of the coastal habitats. In Denmark, there is only one population of *O. insectifera* growing in a light-open forest on calciferous soil on Zealand, nationally red-listed in critical endangered (CR). The forest on 65 ha is now owned by 'Danmarks Naturfond', a private, independent foundation under 'Danmarks Naturfredningsforening'. The aim of the foundation is to preserve landscapes and cultural historical values, to protect plant and animal life and to provide recreational areas for the population. Volunteers perform annual nature management to keep the sites in the forest for the *O. insctifera* light-open.

According to our analyses, the observed general decline in orchid abundance may be partially caused by overgrowth with tall-growing herbs and shrubs, which most likely is caused by changes in the traditional farmland-use, especially livestock grazing or mowing. The speed of the natural vegetation dynamics may in many instances be increased by the intensive agricultural use of fertilizers and manure on neighboring fields to orchid sites. This inference is corroborated by the results from Timmermann et al. (2015), who found that reduced livestock grazing most likely was an important factor in explaining the decline in abundance of some plant species. On the contrary, we did not find a significant effect of public disturbance and forest management on the observed changes in orchid abundance in this study.

Many orchids have relatively complex life-cycles and quite narrow ecological requirements for their habitat. A number of orchid species are pollinated by one or two insect species (Joffard et al. 2019), but most are pollinated by a more diverse insect fauna. For instance, *Ophrys insectifera* are pollinated by males of the digger wasps *Argogorytes mystaceus* and *A. frageii,* while the flowers of *Cypripedium calceolus* are pollinated by females of the genus *Andrena* and *Halictidae* (Pedersen & Faurholdt 2010). Hence, a decline in such pollinating insects could also explain the decline in their dependent orchid species. Also, most orchid species 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, *Cephalanthera rubra, Epipactis atrorubens, E.*

helleborine and *Neottia nidus-avis*, are primarily restricted by availability of fungal associates (Hemrová et al. 2019).

Conservation and protection of Danish orchids

There are several legal and administrative tools that can be applied to protect the population of the Danish orchids and their habitats. 1) All orchids are protected against harming and picking the plants, collection of their seed and digging by the Danish species conservation act nr. 1466 of 6th December 2018. 2) The legal protection of specific orchid sites. 3) Paragraph three in the Danish nature protection law that states a general protection of the light-open, terrestrial nature types, dry grassland, heathland, fens and fresh and saline meadows over a certain size against changes of their present state. 4) The establishment of National Parks. 5) The implementation of the Habitats Directive (the European Council Directive 92/43/EEC of 21 May 1992) on the conservation of natural habitats and of wild fauna and flora.

However, none of the tools are sufficient to protect Danish orchids. 1) Despite general legal protection with a criminal frame, Danish orchids are continuously picked or dug up where even a tight fence cannot prevent the theft of flowering or entire clones of *Cypripedium calceoulus,* and although the thefts are reported to the police, no one has been charged. Presumably, the thefts of orchids normally take place during times of the day where the thieves can fulfill their illegal mission undisturbed. On the other hand, information from the Danish authorities on the protected species is scant and often random. 2) A few sites have been legally protected because of the presence of orchids. An example is the limestone cliffs and forest on the island of Møn, which have been protected since 1921, among other things because of the great amounts of orchids found here. Information stands inform the public of the protected species at the entrances to the protected areas of Møn. 3) The protection of light-open Danish nature types is a general tool. If a landowner wishes to alter the state or use of an area with a protected nature type, he/she must seek permission from the local community. Unfortunately, the general protection cannot prevent farmland-use of a legally protected area from being stopped, allowing the natural vegetation dynamics to continue. This may result in overgrowth with tall herbs and shrubs and outcompeting of the low-growing species, such as orchids. 4) In Denmark, five national parks have been designated. Of these, none has been appointed in order to specially protect orchids. Voluntarily, the staff of National Park Mols Bjerge in Jutland has chosen to map the distribution of 20 key vascular plant species in order to map, gain inform and protect them. *Orchis mascula* is one of the target species. The project is still running. 5) Apart from habitat type 6210 'Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)', where 'important orchid sites' are prioritized, no habitat type has been appointed because of the presence

of orchids. In addition, two Danish orchids, *Cypripedium calceolus* and *Liparis loeselii,* are listed in the Habitats Directive Annex II and IV. This implies for species listed on Annex II that the core areas of their habitat are designated as sites of Community importance and included in the Natura 2000 network. These sites must be managed in accordance with the ecological needs of the species. According to the species listed in Annex IV, a strict protection regime must be applied across their entire natural range within the EU, both within and outside Natura 2000 sites.

As of yet, no specific national conservation strategy for orchids has been worked out in Denmark. A national conservation strategy should be developed in collaboration between scientists and authorities, i.e. the Danish Nature Agency. To work out an effective national conservation strategy, it is necessary to understand the orchids' biology, which requires further research into areas including pollination, mycorrhizal associations, population genetics and demographics, as Fay (2018) has pointed out.

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Tables

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

International name	Taxon status	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. Status, biology and habitats of Danish orchids. The number in parenthesis in No grid-squares is the number cited in Hartvig (2015), while the next number without parenthesis is the actual number. The estimated number of sites is based on unpublished data provided by P. Wind. Information on biology and habitats is based on Pedersen & Faurholdt (2010) and Hartvig (2015). Abbreviations of orchid names: *Ana mor – Anacamptis morio, Ana pyr – A. pyramidalis, Cep dam – Cephalanthera damasonium, Cep lon – C. longifolium, Cep rub – C. rubra, Coe vir – Coeloglossum viride, 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 – D. maculata* subsp. *fuchsii, Dac mac mac – D. m.* subsp. *maculata, Dac maj int int – D. majalis* subsp. *integrata* var. *integrata, Dac maj int jun – D. m.* subsp. *i.* var. *junialis, Dac maj lap – D. m.* subsp. *lapponica, 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 bif lat– P. b.* subsp. *latiflora, Pla chl – P. chlorantha, Pse alb – Pseudorchis albida. Spi spi – Spiranthes spiralis*.

Orchid name	No grid-squares	No of sites	Underground part	Vegetative propagation	Fertilisation	Production of nectar	Pimary habitat(s)
Ana mor	26	34	Tuber	Formation of more tubers	Cross-fertilisation	No	Grassland
Ana pyr	(2) 3	4	Tuber	Formation of more tubers	Cross-fertilisation	No	Calcareous grassland
Cep dam	20	21	Rhizome	Devision of rhizome	Self-fertilisation	No	Decideous woodland on ch
Cep lon	13	13	Rhizome	Devision of rhizome	Cross-fertilisation	No	Decideous woodland on ch
Cep rub	3	5	Rhizome	Devision of rhizome	Cross-fertilisation	No	Decideous woodland on ch

Coe vir	0	0	Tuber	Formation of more tubers	Cross-fertilisation	Yes	Grassland
Cor tri	20	21	Rhizome	Devision of rhizome	Cross- & self-fertilisation	No	Decideous woodland on ch wooded poor fen
Cyp cal	2	2	Rhizome	Devision of rhizome	Cross-fertilisation	No	Decideous woodland on ch calcareous grassland
Dac inc inc	338	384	Tuber	Formation of more tubers	Cross-fertilisation	No	Rich fen
Dac inc lob	4	7	Tuber	Formation of more tubers	Cross-fertilisation	No	Rich fen
Dac inc inc och	(4) 3	3	Tuber	Formation of more tubers	Cross-fertilisation	No	Rich fen
Dac mac fuc	71	130	Tuber	Formation of more tubers	Cross-fertilisation	No	Decideous woodland
Dac mac mac	268	424	Tuber	Formation of more tubers	Cross-fertilisation	No	Grassland, heathland, fen
Dac maj cal	7	10	Tuber	Formation of more tubers	Cross-fertilisation	No	Dune slack, rich fen
Dac maj int int	9	11	Tuber	Formation of more tubers	Cross-fertilisation	No	Rich fen
Dac maj int jun	4	7	Tuber	Formation of more tubers	Cross-fertilisation	No	Rich fen
Dac maj lap	0	0	Tuber	Formation of more tubers	Cross-fertilisation	No	Fen
Dac maj maj	556	830	Tuber	Formation of more tubers	Cross-fertilisation	No	Rich fen
Dac maj pur cam	12	30	Tuber	Formation of more tubers	Cross-fertilisation	No	Dune slack, rich fen
Dac ma pur pur	73	60	Tuber	Formation of more tubers	Cross-fertilisation	No	Dune slack, rich fen
Dac maj sph	3	3	Tuber	Formation of more tubers	Cross-fertilisation	No	Poor fen
Dac sam	7	13	Tuber	Formation of more tubers	Cross-fertilisation	No	Grassland, heathland
Epi atr	2	3	Rhizome	Devision of rhizome	Cross-fertilisation	Yes	Conifer and decideous woodland on chalk, grassla
Epi hel hel	677	701	Rhizome	Devision of rhizome	Cross-fertilisation	Yes	Decideous woodland, grassland
Epi hel nee nee	19	30	Rhizome	Devision of rhizome	Cross-fertilisation	Yes	Calcareous dune
Epi hel nee ren	3	4	Rhizome	Devision of rhizome	Self-fertilisation	No	Calcareous dune
Epi lep	7	11	Rhizome	Devision of rhizome	Self-fertilisation	No	Decideous woodland
Epi pal	123	231	Rhizome	Devision of rhizome	Cross-fertilisation	Yes	Dune slack, rich fen

Epi phy	70	119	Rhizome	Devision of rhizome	Self-fertilisation	No	Decideous woodland
Epi pur	23	52	Rhizome	Devision of rhizome	Cross-fertilisation	Yes	Decideous woodland
Epi aph	1	1	Rhizome	Devision of rhizome	Cross-fertilisation	Yes	Decideous woodland
Goo rep	17	18	Rhizome	Devision of rhizome	Cross-fertilisation	Yes	Conifer forest
Gym con con	(4) 1	1	Tuber	Formation of more tubers	Cross-fertilisation	Yes	Rich fen
Gym con den	(1) 2	2	Tuber	Formation of more tubers	Cross-fertilisation	Yes	Rich fen
Ham pal	18	21	pseudobulb	Formation of more pseudobulbs and bulbils at leaftips	Cross-fertilisation	Yes	Poor fen, blanket bog
Her mon	10	18	Tuber	Formation of more tubers	Cross-fertilisation	No	Dune slack, rich fen
Lip loe	15	20	pseudobulb	Formation of more pseudobulbs	Cross- & self-fertilisation	No	Dune slack, rich fen
Neoti ust	2	3	Tuber	Formation of more tubers	Cross-fertilisation	No	Calcareous grassland
Neo cor	18	21	Rhizome	Devision of rhizome	Cross-fertilisation	Yes	Conifer forest, wooded poo fen
Neo nid	119	149	Rhizome	Devision of rhizome	Cross- & self-fertilisation	No	Decideous woodland
Neo ova	306	495	Rhizome	Devision of rhizome	Cross-fertilisation	Yes	Decideous woodland, grassland, rich fen
Oph api	2	5	Tuber	Formation of more tubers	Self-fertilisation	No	Grassland
Oph ins	2	1	Tuber	Formation of more tubers	Cross-fertilisation	No	Calcareous grassland
Orc mas	301	576	Tuber	Formation of more tubers	Cross-fertilisation	No	Decideous woodland, grassland
Orc mil	(0) 1	1	Tuber	Formation of more tubers	Cross-fertilisation	No	Calcareous grassland
Orc pur	9	10	Tuber	Formation of more tubers	Cross-fertilisation	No	Decideous woodland on ch calcareous grassland
Pla bif bif	90	123	Tuber	Formation of more tubers	Cross-fertilisation	Yes	Grassland, heathland
Pla bif lat	3	3	Tuber	Formation of more tubers	Cross-fertilisation	Yes	Decideous woodland on ch
Pla chl	231	374	Tuber	Formation of more tubers	Cross-fertilisation	Yes	Decideous woodland, grassland

Pse alb	(6) 3	3	Tuber	Formation of more tubers	Cross- & self-fertilisation	No	Grassland
Spi spi	0	0	Tuberous root	Devision of tuberous roots	Cross-fertilisation	Yes	Grassland

Table 3. The number of observations, N, percentiles of the marginal distribution of the average change over time (bold green numbers denote a significant increase and bold red numbers denote 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 subsp. *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

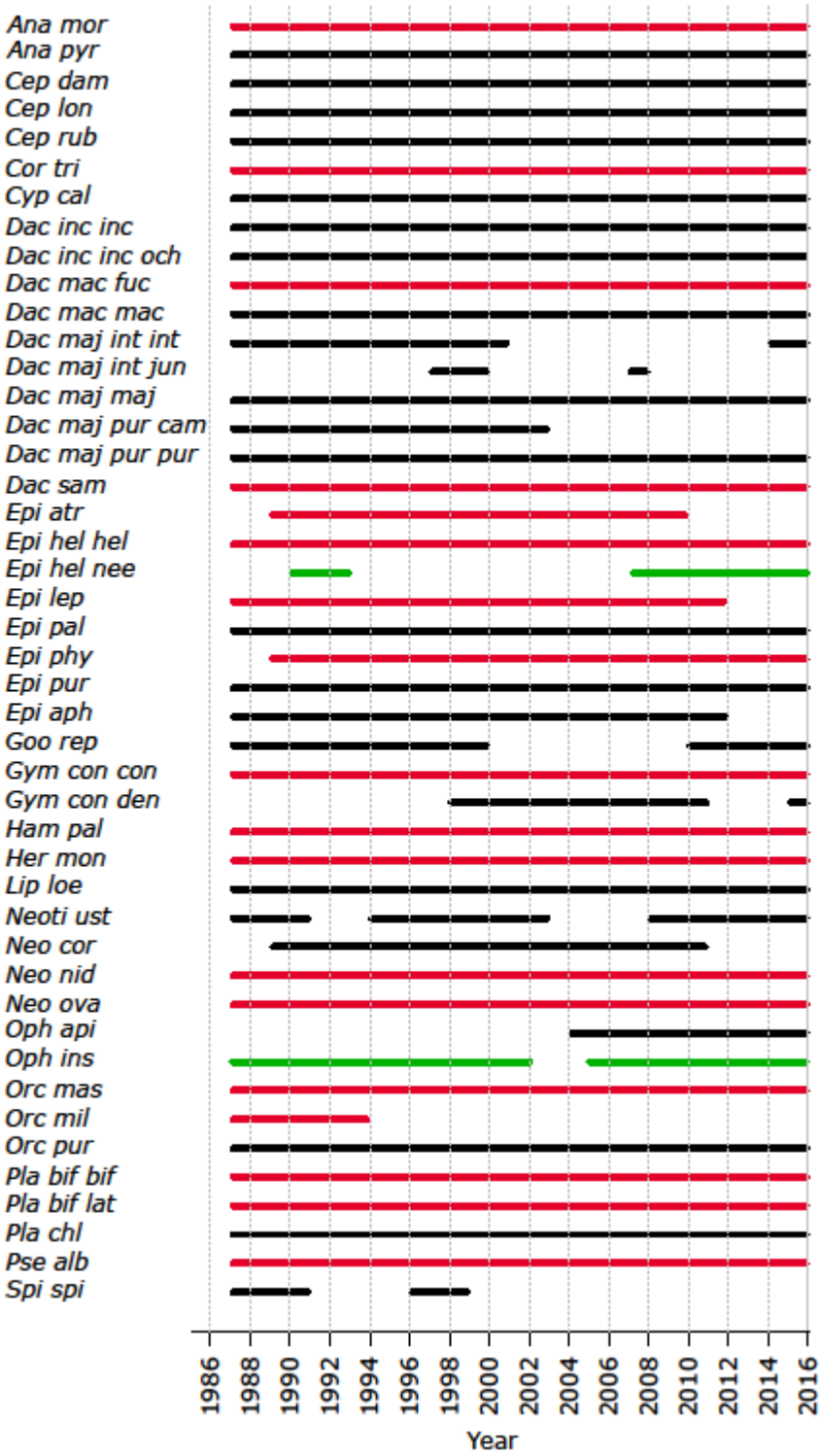
Goodyera repens	45	-1,3174	-0,5082	0,2319	2
Gymnadenia conopsea subsp. *conopsea*	63	**-0,2497**	**-0,1098**	**-0,0264**	2
Gymnadenia conopsea subsp. *densiflora*	20	-0,099	0,0926	0,287	2
Hammarbya paludosa	122	**-0,4299**	**-0,2721**	**-0,1274**	2
Herminium monorchis	131	**-0,3406**	**-0,1741**	**-0,004**	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

Table 4. The percentiles of the marginal distribution of the estimated posterior distribution of the effect of 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 livestock 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

Figures

Fig. 1. Onset and continuity of the annual census of 45 Danish orchids based on the data in the Danish Orchid Database. Bars in red indicate that the number of flowering shoots of the species in question is in decline, black means that it is stable and green that it is increasing. 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 – D. maculata* subsp. *fuchsii, Dac mac mac – D. m.* subsp. *maculata, Dac maj 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 bif lat– P. b.* subsp. *latiflora, Pla chl – P. chlorantha, Pse alb – Pseudorchis albida. Spi spi – Spiranthes spiralis*.


Ana mor
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Dac maj pur pur
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Epi atr
Epi hel hel
Epi hel nee
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Epi pal
Epi phy
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Goo rep
Gym con con
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Ham pal
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Lip loe
Neoti ust
Neo cor
Neo nid
Neo ova
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Fig. 2. 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.

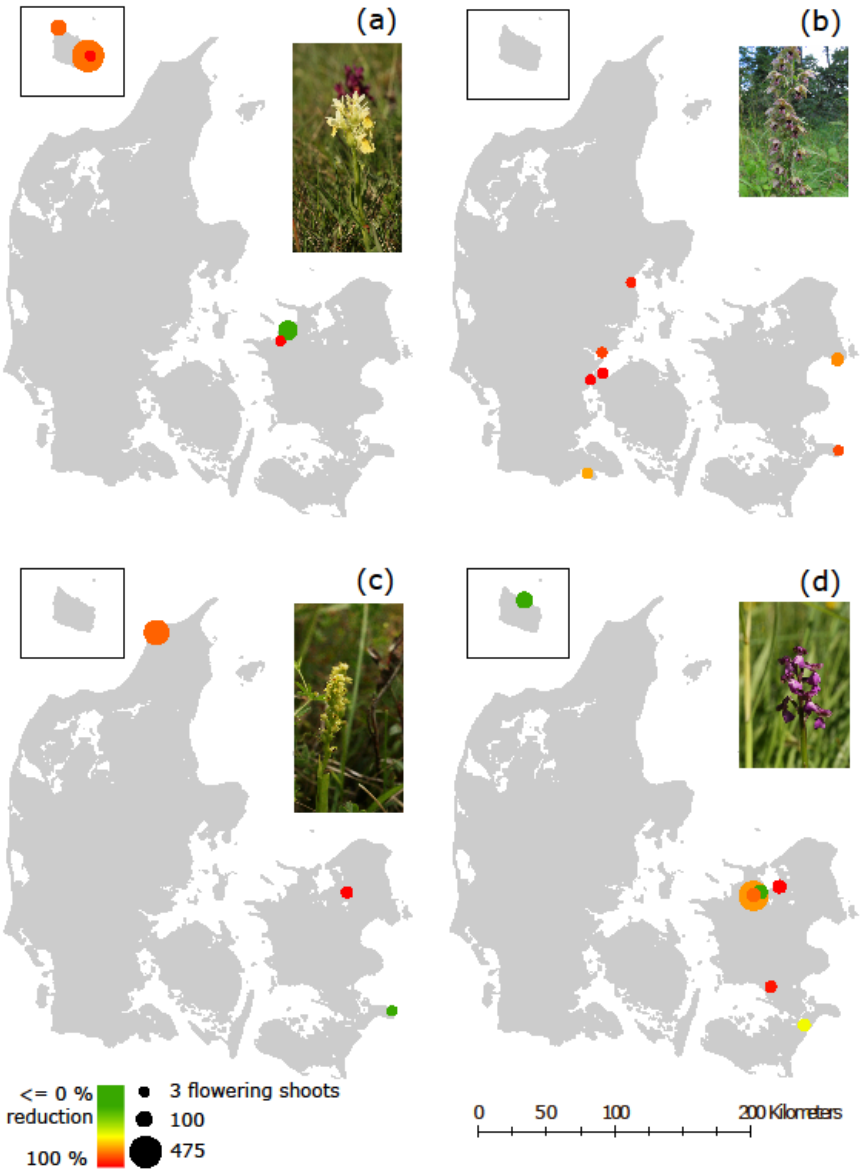
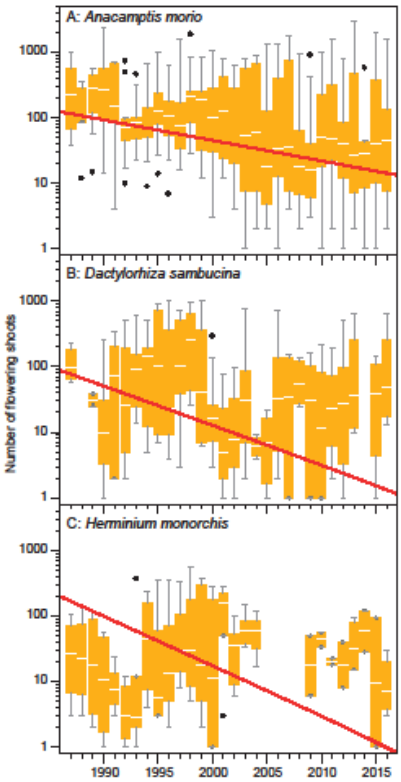


Fig. 3. The observed number of flowering shoots changes for three orchid species shown as box plots of the mean site abundance (white line: medians, yellow box: 25% - 75%, whiskers: 2.5%-97.5%, points: outliers), and the red line illustrates the estimated annual change in the linear model (2). The shown 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*



References

Blangiardo, M., M. Cameletti, G. Baio, and H. Rue. 2013. Spatial and spatio-temporal models with R-INLA. Spatial and Spatio-temporal Epidemiology **4**:33-49.

Catorci, A., S. Cesaretti, and R. Gatti. 2013. Effect of long-term abandonment and spring grazing on floristic and functional composition of dry grasslands in a Central Apennine farmland. Polish Journal of Ecology **61**:505--517.

Correll, N. H. 2016. Ridderen vender tilbage. URT **40**:42-45.

Djordjević, V., S. Tsiftsis, D. Lakušić, S. Jovanović, and V. Stevanović. 2016. Factors affecting the distribution and abundance of orchids in grasslands and herbaceous wetlands. Systematics and Biodiversity **14**:355-370.

Ejrnæs, R., D. N. Hansen, and E. Aude. 2003. Changing course of secondary succession in abandoned sandy fields. Biological Conservation **109**:343-350.

EU. 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora in E. Commission, editor.

Farrell, L. 1991. Population changes and management of Orchis militaris at two sites in England. Pages 63-68 in T. C. E. Wells, and J. H. Willems, editors. Population ecology of terrestrial orchids.

Fay, M. F. 2018. Orchid conservation: how can we meet the challenges in the twenty-first century? Botanical Studies **59**:16.

Hagerup, O. 1941. Bestøvningen hos Liparis og Malaxis. Bot. Tidsskr. **45**:396-402.

Handley, J., and B. Heidel. 2005. Amerorchis rotundifolia (Banks ex Pursh) Hultén (roundleaf orchid): A Technical Conservation Assessment. USDA Forest Service, Rocky Mountain Region.

Hartvig, P. 2015. Atlas Flora Danica. Gyldendal, København.

Hemrová, L., M. Kotilínek, M. Konečná, R. Paulič, J. Jersáková, T. Těšitelová, J. Knappová, and Z. Münzbergová. 2019. Identification of drivers of landscape distribution of forest orchids using germination experiment and species distribution models. Oecologia **190**:411-423.

Högström, S. 1991. Kärrnycklar, Orchis palustris, på Gotland 1982-1990. Svensk Bot. Tidskr. **85**:355-376.

Jacquemyn, H., R. Brys, M. Hermy, and J. H. Willems. 2005. Does nectar reward affect rarity and extinction probabilities of orchid species? An assessment using historical records from Belgium and the Netherlands. Biological Conservation **121**:257-263.

Joffard, N., F. Massol, M. Grenié, C. Montgelard, and B. Schatz. 2019. Effect of pollination strategy, phylogeny and distribution on pollination niches of Euro-Mediterranean orchids. Journal of Ecology **107**:478-490.

Kull, T. 1999. Cypripedium calceolus L. Journal of Ecology **87**:913-924.

Kull, T. 2002. Population Dynamics of Nort Temperate Orchids in T. Kull, and J. Arditti, editors. Orchid Biology: Reviews and Perspectives, VIII. Kluwer Academic Publishers, Dordrecht/Boston/London.

Kull, T., and M. J. Hutchings. 2006. A comparative analysis of decline in the distribution ranges of orchid species in Estonia and the United Kingdom. Biological Conservation **129**:31-39.

Laroche, V., S. Pellerin, and L. Brouillet. 2012. White Fringed Orchid as indicator of Sphagnum bog integrity. Ecological Indicators **14**:50-55.

Løjtnant, B. 1981. Orchis militaris L. (Ridder-Gøgeurt) – ny for Danmark. Flora og Fauna **87**:59-62.

Løjtnant, B. 1991. Overvågning af Orchideer 1987-89. Flora og Fauna **97**:63-121.

Mattiasson, G. 1986. Adam og Eva dör ut inom naturreseratet Kungsmarken. Svensk Bot. Tidskr. **80**:17-25.

McCormick, M. K., and H. Jacquemyn. 2014. What constrains the distribution of orchid populations? New Phytologist **202**:392-400.

Miljøministeriet. 2016. Bekendtgørelse af 27/06/2016 om fredning af visse dyre- og plantearter og pleje af tilskadekommet vildt in Miljøministeriet, editor.

Newman, B. 2009. Orchids as Indicators of Ecosystem Health in Urban Bushland Fragments. Murdoch University.

Pedersen, H. Æ., and N. Faurholdt 2010. Danmarks vilde orkidéer. Gyldendal, Copenhagen.

Petersen, B. V., and J. Høyer-Nielsen. 2005. Biblomst, Ophrys apifera Huds. – nu i Danmark. URT **29**:16-19.
Phillips, R. D., M. D. Barrett, K. W. Dixon, and S. D. Hopper. 2011a. Do mycorrhizal symbioses cause rarity in orchids? Journal of Ecology **99**:858-869.
Phillips, R. D., A. P. Brown, K. W. Dixon, and S. D. Hopper. 2011b. Orchid biogeography and factors associated with rarity in a biodiversity hotspot, the Southwest Australian Floristic Region. Journal of Biogeography **38**:487-501.
Rasmussen, H. 1995. Terrestrial orchids from seed to mycotrophic plant. Cambridge University Press, Cambridge.
Rocchio, J., M. March, and D. G. Anderson. 2006. Epipactis gigantea Dougl. ex Hook. (stream orchid): A Technical Conservation Assessment. USDA Forest Service, Rocky Mountain Region.
Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian models using integrated nested Laplace approximations (with discussion). Journal of the Royal Statistical Society, Series B **71**:319-392.
Salkowski, H.-E. 1990. 20 Jahre Spiranthes spiralis (L.) Chevall. Im Rabengrund bei Wiesbaden. Ber. Arbeitskr. Heim. Orchid. **7**:73-76.
Schiestl, F. P. 2005. On the success of a swindle: pollination by deception in orchids. Naturwissenschaften **92**:255-264.
Schrautzer, J., A. Fichtner, A. Huckauf, L. Rasran, and K. Jensen. 2011. Long-term population dynamics of Dactylorhiza incarnata (L.) Soó after abandonment and re-introduction of mowing. Flora - Morphology, Distribution, Functional Ecology of Plants **206**:622-630.
Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. Journal of Royal Statistical Society B **64**:583-639.
Sterk, A. A. 1976. Anacamptis pyramidalis bij Wijk aan Zee. Gorteria **8**:81-85.
Stewart, J. 1989. La conservation des orchidées européennes. T-PVS (89) 3. Conseil de l'Europe, Strasbourg.
Stewart, J. 1996. Commercial trade. Pages 38-42, 43-44. Orchids – status survey and conservation action plan. IUCN/SCC Orchid Specialist Group, Gland and Cambridge.
Swarts, N. D., and K. W. Dixon. 2009. Terrestrial orchid conservation in the age of extinction. Annals of botany **104**:543-556.
Tali, K., M. F. Fay, and R. M. Bateman. 2006. Little genetic differentiation across Europe between early-flowering and late-flowering populations of the rapidly declining orchid Neotinea ustulata. Biological Journal of the Linnean Society **87**:13-25.
Tamm, C. O. 1991. Behaviour of some Orchid Population in a Changing Environment. Observations on Permanent Plots, 1943-1990. Pages 1-13 in T. C. E. Wells, and J. H. Willems, editors. Population ecology of terrestrial Orchids, The Hague.
Timmermann, A., C. Damgaard, M. T. Strandberg, and J.-C. Svenning. 2015. Pervasive early 21st-century vegetation changes across Danish semi-natural ecosystems: more losers than winners and a shift towards competitive, tall-growing species. Journal of Applied Ecology **52**:21-30.
van der Heijden, M. G. A., F. M. Martin, M.-A. Selosse, and I. R. Sanders. 2015. Mycorrhizal ecology and evolution: the past, the present, and the future. New Phytologist **205**:1406-1423.
Vanhecke, L. 1988. Veranderingen in én kustpopulatie van de Rietorchis (Dactylorhiza praetermissa) tussen 1973 en 1985. de Levende Natuur **2**:44-49.
Vanhecke, L. E. M. 1991. Population dynamics of Dactylorhiza praetermissa in relation to topography and inundation. Pages 15-32 in T. C. E. Wells, and J. H. Willems, editors. Population ecology of terrestrial orchids.
Vogt-Schilb, H., P. Geniez, R. Pradel, F. Richard, and B. Schatz. 2013. Inter-annual variability in flowering of orchids: lessons learned from 8 years of monitoring in a Mediterranean region of France. European Journal of Environmental Science **3**:129-113.
Vogt-Schilb, H., F. Munoz, F. Richard, and B. Schatz. 2015. Recent declines and range changes of orchids in Western Europe (France, Belgium and Luxembourg). Biological Conservation **190**:133-141.

Vogt-Schilb, H., R. Pradel, P. Geniez, L. Hugot, A. Delage, F. Richard, and B. Schatz. 2016. Responses of orchids to habitat change in Corsica over 27 years. Annals of botany **118**:115-123.

Waite, S., and L. Farrell. 1998. Population biology of the rare military orchid (Orchis militaris L.) at an established site in Suffolk, England. Botanical Journal of the Linnean Society **126**:109-121.

Wells, T. C. E. 1981. Population ecology of terrestrial orchids. Pages 281-295 in H. Synge, editor. The Biological Aspects of Rare Plants Conservation.

Whigham, D. F. 2004. Ecology of Woodland Herbs in Temperate Deciduous Forests. Annual Review of Ecology, Evolution, and Systematics **35**:583-621.

Willems, J. H. 1989. Population dynamics of Spiranthes spiralis in South-Limburg, the Netherlands. Mémoires de la Société Royale de Botanique de Belgique **11**:115-121.

Wind, P. 1999. Overvågning af orkidéer 1998. Påvirkningsfaktorer. Arbejdsrapport. Danmarks Miljøundersøgleser, Miljø- og Energiministeriet.

Wind, P. 2019. Karplanter in J. E. m. f. Moeslund, editor. Den danske Rødliste 2019, Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi.

Wood, J., M. Clements, and H. Muir. 1984. PLANTS IN PERIL, 2. The Kew Magazine **1**:139-142.