¹ Changes in the abundance of Danish

² orchids over the past 30 years

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5 Abstract

6 Orchid abundance data collected during the past 30 years from 440 sites within the National Orchid 7 Monitoring Program were analysed to quantify the population trends of orchids in Denmark, and the 8 underlying reasons for the observed population trends were analysed and discussed. Twenty of the 45 9 monitored Danish orchids showed a significant decrease in abundance over the past 30 years (16, if only 10 orchids with at least 50 observations each are selected), thus corroborating the previous observations of 11 declining orchid abundances at European scale. Generally, there was a significant negative effect of 12 overgrowing with tall-growing herbs and shrubs on the abundance of Danish orchids.

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

17 Introduction

- 18 Orchids are generally in decline globally (Kull & Hutchings 2006; Tali et al. 2006; Vogt-Schilb et al. 2015). In
- 19 Denmark, 33 taxa out of 51 species, subspecies and varieties of orchids (see Table 1) are assessed as either
- 20 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
- 22 Orchid Monitoring Program to quantify the population trends of orchids in Denmark. Additionally, we
- analyse and discuss underlying reasons for the observed population trends.
- 24 In Northern Europe, orchids typically grow in woodlands, both broad-leaved forests and old conifer
- 25 plantations, dry grasslands and heathlands, rich and poor fens, meadows and dune slacks (Pedersen &
- 26 Faurholdt 2010). Sometimes, orchids also colonize abandoned marl and lime pits, but avoid saline marshes,
- 27 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
- 29 factors that characterize suitable habitats for orchids (Djordjević et al. 2016; Hemrová et al. 2019;
- 30 McCormick & Jacquemyn 2014; van der Heijden et al. 2015). Furthermore, light conditions, the degree of
- 31 disturbance and, for some orchids, the presence of specific pollinators play important roles for habitat
- 32 suitability (Pedersen & Faurholdt 2010; Schiestl 2005).

33 Most orchids in Northern Europe have declined because of habitat loss or habitat degradation, for example 34 as a result of secondary succession following abandonment of former farming practises such as extensive 35 grazing and hay cutting (Kull & Hutchings 2006; Mattiasson 1986; Schrautzer et al. 2011). The secondary 36 succession can accelerate by changed interspecific competitive regimes following increased soil nutrient 37 availability due to fertilizers and airborne nitrogen pollution (Ejrnæs et al. 2003). Other land use changes, 38 such as urbanization, infrastructural constructions, lowering of the groundwater table, draining and 39 cultivation, are equally important causes of orchid habitat loss (Kull & Hutchings 2006; Mattiasson 1986). In 40 some cases, overgrazing can also constitute a threat to orchids (Catorci et al. 2013), e.g. by preventing seed 41 development. In forests, many orchids grow in areas that have been left untouched for decades, and if the 42 forests are disturbed, e.g. drained, clear-cut or fertilized, then orchids are at risk of disappearing (Whigham 43 2004). Despite being protected by law in many countries including Denmark (Miljøministeriet 2016), 44 orchids are regularly picked for flower bouquets or dug up for gardening or trade, actions that both affect 45 the fitness of an orchid population. For instance, three entire clones of *Cypripedium calceolus* were dug up 46 from the Danish population of at Buderupholm in 2012 and moved from the fence that had been raised in 47 order to protect the population, and in 2016, approximately 40 flowering shoots were picked from the

48 population (Himmerland Forest Department, pers.com. 2012, 2016). Additional, general public disturbance 49 and outdoor activities, such as hiking, camping, and picnicking, may also affect orchid populations 50 negatively (Handley & Heidel 2005; Kull 1999; Rocchio et al. 2006; Stewart 1989, 1996; Wood et al. 1984). 51 For example, an *Epipactis leptochila* population at a slope on Møns Klint possibly went extinct due to the 52 playing of children (N. Faurholdt, per.com 1996). Many orchid species are specialists, depending on only 53 one or a few pollinators or mycorrhizal symbiont species (Phillips et al. 2011a; Rasmussen 1995). This can 54 explain why orchids are intrinsically rare (Phillips et al. 2011b), but has probably also given orchids their 55 reputation for being good indicators of intact or high-value nature (e.g. Laroche et al. 2012; Newman 2009).

56 The monitoring of orchid species provides a good basis for effective management and conservation of 57 native orchid populations and their habitats, which is a complicated task due to the orchid species' complex 58 ecology and the many and varied threats mentioned above. The annual collecting of information on orchid 59 populations and the condition of their habitats for the National Orchid Monitoring Program is a way to 60 achieve such adequate data that are useful for planning of management and conservation tasks and to 61 describe the trend of the Danish orchid species. Besides, the program is an excellent example of an ongoing 62 citizen science project, where Danish orchids have been monitored annually for more than 30 years from 63 440 selected orchid sites. The National Orchid Monitoring program is, to our knowledge, the most 64 comprehensive and long-lived field-based orchid monitoring project in the world comprising many Danish 65 members of the orchid family (see Appendix A for a detailed account of citizen science in Denmark).

66 Internationally, there are a few examples of long-term orchid monitoring programs of comparable duration 67 as the monitoring of the Danish population of Cypripedium calceolus. One example is the annual census of a 68 population of Anacamptis pyramidalis in a Dutch dune area that started in 1940 (Sterk 1976). The annual 69 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 70 71 plot in 1942 in a population of Dactylorhiza sambucina in order to document the effect of picking orchids 72 (Tamm 1991). The annual Swedish census also involved other orchid species, Dactylorhiza incarnata, 73 Neottia ovata and Orchis mascula. The monitoring seems to have ended in 1990. Additionally, long-time 74 monitoring has been performed on Orchis anthropophora (L.) All. 1967-1980 (Wells 1981), Dactylorhiza 75 majalis subsp. integrata 1973-1985 (syn. D. praetemissa), (Vanhecke 1988; Vanhecke 1991), Dactylorhiza 76 sambucina 1968-1985 (Mattiasson 1986), Orchis mascula 1960-1970 (Willems 1989), O. militaris 1947-1962 77 (Farrell 1991; Waite & Farrell 1998), O. palustris (Högström 1991), and Spiranthes spiralis (Salkowski 1990; 78 Wells 1981). Kull (2002) has made an overview of long-term field-based studies on population dynamics of

- 79 terrestrial orchids. The overview comprises 66 orchids with information on the ways of performing the
- 80 monitoring: 1) monitoring in permanent plots, 2) counting of specimens in populations, 3) genet dynamics,
- 81 where individuals are mapped, 4) measurement of fruit set, and 5) morphometrical parameters analysed. A
- 82 characteristic feature of these studies is that they are generally short-termed compared to the National
- 83 Orchid Monitoring Program and most studies only monitor a single species.
- 84 In our study, we analyse the data of The National Orchid Monitoring Program and report on the observed
- 85 trends for the monitored orchids. Furthermore, we link the observed changes in orchid abundance to four
- 86 observed potential pressures acting on orchid populations.

87 Materials and Methods

88 **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

- 91 species, 13 subspecies and 7 varieties. Two species, *Ophrys apifera* and *Orchis militaris*, recently appeared
- 92 in Denmark in 2004 and 1981, respectively.
- 93 Undoubtedly, the Danish orchids belong to the most threatened group of vascular plants in the Danish
- 94 flora. Thirty-three out of 51 (65 %) of the Danish orchids assessed for the Danish Red List (Wind 2019) are
- 95 either extinct, threatened or near threatened by extinction based on the IUCN Red List Assessment
- 96 methodology (IUCN 2012). Eight orchids are categorized Critical Endangered (CR), seven Endangered (EN),
- 97 seven Vulnerable (VU) and eight Near Threatened (NT). Sixteen orchids are categorized Least Concern (LC),
- 98 while two have not yet been assessed. Two species and one subspecies are now Regionally Extinct (RE) in
 99 Denmark (Table 1) (Wind 2019).
- 100 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).

102 Orchid censuses in Denmark

103 The census of Danish orchid populations started long before the onset of the National Orchid Monitoring

- 104 Program in 1987. *Cypripedium calceolus* was recorded for the first time in Denmark Rold Skov, a forest in
- 105 Jutland, in 1884. The annual census of the population started in 1943 and has continued since then, except

106 for the year 1946 (Fig. 1). The monitoring of orchids expanded in the beginning of the 1980'ties, where

- 107 three Danish counties commenced to perform an annual census of local populations of orchids such as
- 108 Anacamptis morio, Dactylorhiza maculata subsp. fuchsii, Dactylorhiza majalis, Epipactis palustris,
- 109 *Gymnadenia conopsea* and *Liparis loeselii*. In parallel, amateurs started regular annual censuses of selected
- 110 populations of some of the rarest Danish orchids, e.g. Anacamptis pyramidalis, Epipactis leptochila,
- 111 *Epipogium aphyllum* and *Pseudorchis albida* (Fig. 2).

The annual census of 18 Danish orchids was performed, including the populations of orchids that had 112 113 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 114 115 and in 1990, four additional orchids were included in the program, of which the annual censuses were 116 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 117 118 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 119 first time in Denmark. Thus, 45 Danish orchids (30 species, 9 subspecies, and 6 varieties) have been 120 121 monitored either continuously (31 orchids) or more irregularly. The latter was either because monitoring 122 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, 123 respectively. 124

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.

129 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 fieldbiologists. 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

- 136 many sites, different orchids grow together, e.g. on fen sites comprising the two orchid species
- 137 Dactylorhiza incarnata and D. majalis. In such instances, both species were monitored. At each of the
- 138 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
- 140 for four orchids (Fig. 3).
- 141 The surveyors also estimated the intensity of grazing, forest management, overgrowing with tall-growing
- 142 herbs and shrubs and public disturbance at the orchid sites by using a four-step classification of the
- 143 pressures, i.e. 1) none, 2) weak, 3) moderate and 4) hard or strong (Wind 1999).
- 144 Further details on the National Orchid Monitoring Program are compiled in Appendix B.
- 145 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
- 147 Danish Orchid Database and provide the basis for the present analysis.

148 Statistical analysis

- 149 The observed changes in orchid species abundances were modelled based on the recorded flower
- 150 numbers, and since the data structure was irregular, it was decided to model the change in abundance by a
- 151 state-space model, where the species abundance at a specific site *i* at time *t* was modelled by latent
- 152 variables, $x_{i,t}$. The observed abundance is denoted by $y_{i,t}$ and assumed to be Poisson distributed with the
- 153 latent variables as the mean parameters, $y_{i,t} \sim Poisson(x_{i,t})$. The change in the log-transformed 154 abundance was modelled by two linear models,

155
$$log(x_{i,t}) = \alpha + \vartheta_i + \beta t$$
 (1),

156
$$log(x_{i,t}) = \alpha + \vartheta_i + (\beta + \delta_i) t$$
 (2),

157 where α is the intercept and β is the mean annual change. The random effects of site and site * years are 158 modelled by ϑ_i and δ_i , respectively, and both are assumed to be normally distributed. The two linear 159 models differ in whether the random effect of site * years is included or not, i.e. whether the change in 160 abundance varies among sites. Due to the log-transformation, the estimated doubling time of a population 161 may be calculated as $\log(2)/\beta$ or $\log(2)/(\beta + \delta_i)$ in model 1 and 2, respectively.

162 The models were fitted in a Bayesian framework using integrated nested Laplace approximation (Rue et al.

- 163 2009). The implementation of the two models in R is shown in Appendix D and follows Blangiardo et al.
- 164 (2013). The two models were compared by DIC (Spiegelhalter et al. 2002), and statistical inferences were
- 165 made using the 95% credible interval of the parameter of interest.
- 166 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
- 168 were regressed against the mean values of the four estimated pressures at each site with species as a
- 169 random effect. Again, this model was fitted in a Bayesian framework using integrated nested Laplace
- 170 approximation (Rue et al. 2009).

171 **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.

176 Eighteen of the 41 orchids showed a significant decrease in abundance, while two, Epipactis helleborine 177 subsp. neerlandica and Ophrys insectifera, showed a significant increase in abundance. The abundance of 178 the remaining 21 orchids did not show a significant change (Table 2). In order to ensure that the reported 179 trends are general in both time and space and not due to extraordinary years or sites with uncharacteristic 180 management practices, we added the supplementary constraint that at least 50 observations were needed 181 for making robust and general inferences on the change in orchid abundance. Under this added constraint, 182 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. 183

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).
- According to our analyses, the observed general decline in orchid abundance may be partially caused by overgrowth with tall-growing herbs and shrubs caused by changes in the traditional farmland-use. 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.
- 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
- 221 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
- 223 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.

225 Acknowledgements

- 226 We sincerely thank all the surveyors (see Appendix C) of the National Orchid Monitoring Program for
- collecting the data used here and the Danish foundation '15. Juni Fonden' for economic support for the
- analysis of the collected data.

229 Tables

- 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
- Program. Red List Categories: RE = Regionally Extinct. CR = Critically Endangered. EN = Endangered. VU =
- 233 Vulnerable. NT = Near Threatened. LC = Least Concern. NE = Not Evaluated.

		Stat
International name	Taxon level	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.		
<i>junialis</i> (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. <i>purpurella</i>	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
- 237 decrease), β , and the model (eqn. 1 or eqn. 2) that was best supported by the data.

Species	Ν	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	- 0,25 81	-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	- 0,23 95	-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

238

240 Table 3. 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 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

243 Figures

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

245 2016.



247 Fig. 2. Onset and continuity of the annual census of 45 Danish orchids based on the data in the Danish

- 248 Orchid Database. Abbreviations: Ana mor Anacamptis morio, Ana pyr A. pyramidalis, Cep dam –
- 249 Cephalanthera damasonium, Cep Ion C. longifolium, Cep rub C. rubra, Cor tri Corallorhiza trifida, Cyp
- 250 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,
- 252 Dac ma int int D. majalis subsp.integrata var. integrata, Dac maj int jun D. m. subsp. i. var. junialis, Dac
- 253 maj maj D. m. subsp. majalis, Dac maj pur cam D. m. subsp. purpurella var. cambrensis, Dac maj pur pur
- 254 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.
- 256 palustris, Epi phy E. phyllanthes, Epi pur E. purpurata, Epi aph Epipogium aphyllum, Goo rep –
- 257 Goodyera repens, Gym con con Gymnadenia conopsea subsp. conopsea, Gym con den G. c. subsp.
- 258 densiflora, Ham pal Hammarbya paludosa, Her mon Herminium monorchis, Lip loe Liparis loeselii,
- 259 Neoti ust Neotinea ustulata, Neo cor Neottia cordata, Neo nid N. nidus-avis, Neo ova N. ovata, Oph
- 260 api Ophrys apifera, Oph ins O. insectifera, Orc mas Orchis mascula. Orc mil O. militaris, Orc pur –
- 261 Orchis purpurea, Pla bif bif Platanthera bifolia subsp. latiflora, Pla bi flat P. b. subsp. latiflora, Pla chl –
- 262 P. chlorantha, Pse alb Pseudorchis albida. Spi spi Spiranthes spiralis.



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
- 273 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-
- 276 transformed median slope. A: Anacamptis morio, B: Dactylorhiza sambucina, C: Herminium monorchis



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382

384 **Electronic supplements**

385 Appendix A: Citizen Science in Denmark

In Denmark, there is a long-time tradition for national species surveillance involving voluntary citizens. Birds 386 were the first group of organisms to be involved in a species-monitoring program. In 1899, the Danish 387 388 ornithologist Hans C.C. Mortensen (1856-1921) founded the project of ringing birds in order to follow the 389 migration of bird species. During the 20th Century, many Danish Natural History Societies launched national 390 surveillance programs that in a modern term are characterised as 'Citizen Science'. In 1904, The Danish 391 Botanical Society started a complete monitoring program of the Danish flora of vascular plants – the 392 Botanical Topographic Investigation of Denmark (TBU). The aim of the project was to gather information of 393 the distribution and state of the Danish vascular plant flora. Officially, 262 voluntary persons participated, 394 but more than half of them never became active (Hartvig 2015). In Denmark, 57 topographical-botanical 395 districts were established in order to collect information that was more detailed on the vascular plant 396 distribution. Field monitoring ended in 1923. The results of the monitoring were worked up and published 397 in family order, starting with the Fabaceae (Papilionaceae) in 1931 (Jessen 1931). The final scientific paper 398 on the Portulacaceae and the Valerianaceae (Hansen & Pedersen 1976) was published in 1976. In total, 41 399 scientific papers have been published on the distribution of the Danish vascular plant flora. In 1989, a 400 scientific paper (Vestergaard & Hansen 1989) on the general distribution pattern of the Danish vascular 401 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
- 415 counted, and 1946, where no recordings of the aerial shoots were performed at all (Figure 1).
- 416 Many other national surveillance terrestrial programs have been performed in Denmark, focusing on other
- 417 organism groups where volunteer citizens have been involved. Examples are: 1) the national bird-
- 418 monitoring program based on Point Count Census covering the trends in breeding populations of 90 species
- 419 launched in 1975 and organised by the Danish Ornithological Society. 2) monitoring of amphibians and
- 420 reptiles started in 1976 and is organised by the youth society 'Natur og Ungdom'. 3) monitoring of the
- 421 Danish otter was launched in 1984 by World Wildlife Fund and the Danish Animal Welfare Society and is
- 422 conducted in cooperation with the Natural History Museum in Aarhus (Asbirk & Orth 1987). Besides, the
- 423 Danish Ornithological Society has performed three national atlas surveys of bird species in 1971 1974,
- 424 1993-1996 and latest in 2014 2017 using the same five x five km squares in the UTM grid as in the
- 425 botanical AFD-project.

427 Appendix B: The National Orchid Monitoring Program

- 428 The Nature Protection Agency in cooperation with other national institutions held a symposium in October
- 429 1986 in order to get an overview of the many Danish surveillance programs run by other national agencies,
- 430 county counsels, universities, and natural history societies. The aim of the symposium was to get
- 431 inspiration on how to work out a national terrestrial monitoring program that could support effective
- 432 nature management.
- 433 At the turn of year 1986/1987, a fusion of the Forest Agency and the Nature Protection Agency resulted in
- 434 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
- 436 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.

456 Methodology

The Danish orchid expert Bernt Løjnant was the first coordinator of the National Orchid Monitoring 457 458 Program. He launched four methods for performing the annual censuses of the aerial shoots of flowering 459 and vegetative orchid specimens. 1) A total count of all specimens in an orchid population. The benefit of 460 the method is that the method follows the orchid population that can emerge on different locations on a 461 site from year to year. 2) A count of all specimens within a number of randomly laid out, permanent squares on one m² or circles on 0.1 m². 3) A total count of specimens within a permanent 'strip', e.g. 50 m 462 463 in length and one m width in an orchid population. The method has been used on a large Danish population 464 of Liparis loeselii on Zealand comprising thousands of plants. 4) A total count of all specimens within a 465 permanent plot with a size of up to 100 m². The coordinator recommended generally using the latter 466 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 467 468 plastic soil where the plot and the orchid population may slide into the sea. The most applied methods in 469 the program have proved to be methods 1 and 4, where the flowering shoots are counted and, if at all 470 possible, the vegetative shoots are counted eventually as well, although they can be hard to identify in a 471 dense vegetation cover and difficult to identify to a particular species when more orchids grow together on 472 the same site.

473 Pressures

474 Another important field observation is the state of the pressures, their strength and influence on the

475 individual orchid population. The pressures comprise all factors, both natural and human, that affect the

476 growth of an orchid population on a site. The pressures are divided into five main categories. 1) Grazing. 2)

- 477 Intensity of forest management. 3) Overgrowth of tall-growing herbs and shrubs. 4) Public disturbance. 5)
- 478 Other impacts (not included in the previous four).

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

482 2) *Forest management* is the impact caused by forestry on the orchid sites. The impact includes everything
483 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, fromincreased dominance of tall-growing herbs to the growth of woody plants.

- 488 4) *Public disturbance* is the impact caused by recreational activities on the orchid sites. Thus, the category
- 489 comprises the degree of impact caused by everything from random human damage to picking flowers for a
- 490 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
- 492 in the previous categories. A typical example is hay mowing.
- 493 *The Intensity of the pressures* is, as mentioned in the body text, divided into a four-step scale defined by the 494 types of impacts and are shown in Table B1-B4.
- 495 Unfortunately, some of the definitions are rather weakly defined, which leaves open the possibility of
- 496 subjective interpretation by the surveyors. The bias in the interpretation has caused surveyors to doubt
- 497 whether to use one category or the other and induced them to have chosen to report intermediately
- 498 between the two categories. The intermediate choice is inappropriate when the collected data is to be used
- 499 for analysis of the degree of pressure.
- 500 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

502 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

503

501

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

505

506 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

507

508	Finally, the surveyor must assess the suitability of the pressure on the orchid population. The aim of the
509	assessment of the suitability is to see whether the intensity of the pressure is good for the growth of the
510	orchid population on the site in question or whether it will harm it. Many orchid species require balanced
511	regulation of vegetation height and extent at the site in order for the population to thrive. For example, a
512	certain grazing pressure may cause the low-growing vegetation at a given site to be maintained when the
513	combination of bite and tramp is optimal. If grazing pressure is too high, it can cause damage to the
514	vegetation cover in the form of abrasion and curbing, while too low grazing pressure can cause problems in
515	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).

520 When the surveyors have finished the field work, all information is noted on data sheets that are sent to

521 the program manager at Aarhus University at the end of the season. The program manager examines the

- 522 received sheets making a quality check of the information to secure its validity before the data are stored in
- 523 the Danish Orchid Database.
- 524 In conclusion, the National Orchid Monitoring Program is an outstanding project supported by a core of
- 525 surveyors, mostly volunteers, willing to perform the annual census. The program was established long
- 526 before the term 'Citizen Science' was brought into everyday use. Thanks to the program, unique series of
- 527 data on orchid population trends have been collected over the years, forming a more solid basis for the
- 528 red-list assessment of the state of Danish orchids.

530 Appendix C: Surveyors

531 The surveyors that have contributed or still contribute to the National Orchid Monitoring Program are: 532 Allan Damborg, Asta Israelsen, Allan Weimann, Aage Pedersen, Aksel Voigt, Bo Boysen Larsen, Bodil 533 Grønborg Brun, Bjarne Hemmingsen, Bodil Holt, Birthe Kristensen, Bernt Løjtnant, Birte Hvarregaard, Bo 534 Normander, Bodil Stoltze, Brian Rudebeck, Bent Vestergaard Petersen, Birthe Zimmermann, Carsten Horup 535 Bille, Camilla Nielsen, Ellen & Claus Ole Madsen, Christian Roesdahl, Christian Rørdam, Christian Bertelsen, 536 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 537 538 Bjerregaard, Finn K. Hansen, Finn Lindhart, Flemming Thorning-Lund, Gudmund Fajstrup, Gudrun Larsen, 539 Gerda Madsen, Gerth Nielsen, Hanne Bau Jensen, Hanne Jensen, Hans Anker Nielsen, Henrik Bavnhøj, 540 Henrik Bjørn Holck, HC Gravesen, Hans Ditley, Hans Guldager Christiansen, Hans Hjeds, Hanne Holst, Hans 541 Jørn Christensen, Hans Jørgen Degn, Harald K. Hansen, Helle Møller-Madsen, Henning Petersen, Henning 542 Poulsen, Hans Rasmussen, Henrik Tranberg, Henrik Ærenlund Pedersen, Hans Øllgaard, Ian Heilmann, Inge 543 Nagstrup, Jan Germundsen, Jan Martin, Jens Amtkjær, Jens Blædel, Jens Christensen, Jens Christian Schou, 544 Jens Erik Lindgaard, Jens Gregersen, Jens Hohwü-Christensen, Jens Rye Larsen, Jens Vahl, Jes Phillipsen 545 Schmidt, Jesper Ratjen, Jimmy Lassen, John Brandbyge, John Holst, John Mønsted Jensen, Johannes Skov, 546 Jon Buttenschön, Jørgen Hyhne, Jørgen Peter Kjeldsen, Jørgen Terp Laursen, Kaj Halberg, Karen 547 Thingsgaard, Karin Sloth, Karsten Nørgaard, Kirsten Juul, Knud Rasmussen, Kurt Ærenlund Pedersen, Lars 548 Bjarne Pedersen, Lars Christiansen, Lars Jakobsen, Lasse Werling, Lene Kofoed, Lisbeth Emsholm, Lis 549 Kristensen, Lis Ravnsted-Larsen, Louise Lyng Bojesen, Lone Godske, Maria Mortensen, Marian Würtz 550 Jensen, Marianne Helkjær, Mikael Landt, Mogens B. Hansen, Mogens Frost Christensen, Mogens Holmen, 551 Morten Lyngsaa, Molly Hougaard, Niels Faurholdt, Nikolaj Hedegaard Correll, Niels Kornum, Niels 552 Westergaard Knudsen, Nina Kjær Pedersen, Ole Lyshede, Peer Høgsberg, Per Egge Rasmussen, Peter Echard 553 Mortensen, Peter Holm, Peter Leth, Rasmus Fuglsang Frederiksen, Rita Merete Buttenschön, Rikke Strøm-554 Ringstrøm, Sten Moeslund, Stig Jeppesen, Stig Mortensen, Stine Lindstrøm, Sten Asbirk, Susanne Bruhn 555 Aaen, Søren Grøntved Christiansen, Søren Holst Kjeldsen, Søren Vinding, Terkel Arnfred, Terje Seidenfaden, 556 Thea Illum, Thomas Eske Holm, Thomas M. Petersen, Thomas Plesner, Thomas Retsloff, Thomas Vikstrøm, 557 Toni Reese Næsborg, Torben Ebbensgaard, Vibeke Dunn-Andersen, Vibeke Rahbek, Westy Esbensen and 558 Aase Arbirk.

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561 Appendix D: Statistical model

562 The two models were implemented in R-INLA as

563	Model1=Present~Year+f(Site,model="iid")	(S1),
564	Model2=Present~Year+f(Site,model="iid")+f(Site1,Year,model="iid")	(S2).
565	Both model were fitted by, fit=inla(Model, data, family="poisson", E=1, control.compute=list(dic=TRL	E))
566	(S3).	