



# Modelling forest biodiversity and recovery from acidification

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# 1. Introduction and background

## 1.1.1 *Reduced emissions but delayed recovery*

Acid deposition originating in emissions from fossil fuel use and agricultural practices, in the form of sulphur (S) and nitrogen (N), has resulted in the widespread acidification of terrestrial ecosystems (Bouwman et al. 2002). In recent decades however, international agreements on air pollution reduction, such as the Convention on Long-Range Transboundary Air Pollution (CLRTAP) in Europe have achieved substantial decreases in emissions, particularly in S. However, nitrogen emissions (which also have acidifying effects) decreased, but not to the same extent (EMEP, 2021). S in precipitation (in Europe) decreased by 73% between 1990 and 2012, while NO<sub>3</sub> in precipitation decreased by 33% (Colette et al., 2016). Despite these positive developments, there appears to be a long temporal delay between emissions reduction and changes in soil solution acidity (Johnson et al. 2018), and soil acidification shows non- uniform tendencies across Europe (Schmitz et al. 2018). Delayed recovery in soil chemistry also has implications for recovery in biodiversity, as chemical parameters such as soil pH and nutrient availability are critical for determining the vegetation community at the base of food webs. This study applies a model chain incorporating dynamic soil chemistry modelling and predicted probability of occurrence of plant species to investigate how well predictions match observed biodiversity data, and to model future recovery of vegetation communities after acidification.

## 1.1.2 *The role of long-term monitoring*

The International Cooperative Programme on Integrated Monitoring of Air Pollution Effects on Ecosystems (ICP IM) was set up to determine and predict the state and change of terrestrial ecosystems in a long-term perspective with respect to the impact of air pollutants, especially nitrogen and sulphur. The aim is to provide a scientific basis for decisions on emission controls, and an assessment of the ecological impact of such controls, within the UNECE CLRTAP (Convention on Long-range Transboundary Air Pollution). The programme conducts long-term simultaneous measurements of physical, chemical, and biological properties at permanent monitoring sites, mainly forested catchments located in natural or semi-

natural areas across Europe. The ICP IM Programme Centre is based at SLU, as part of the Department of Aquatic Sciences and Assessment.

Many ICP IM sites have multi-decadal time series that are invaluable both for modelling and policy guidance. Another strength of the ICP IM programme lies in the depth of ecosystem parameters covered, as data collection at the sites is based on a whole ecosystem perspective. The data gathered by ICP IM is used to investigate and model the impacts of air pollution and climate change on vegetation (responses to atmospheric deposition) and biogeochemical cycling (e.g. recovery from acidification and soil C and N turnover). The focus is on data analysis and on creating scientific knowledge and process understanding necessary to interpret the observations. Dynamic models are an integral part of this process as they provide a framework in which process understanding can be formulated and used to produce policy relevant outputs, e.g., predictions of future ecosystem status. Dynamic models are needed as many forest ecosystems are not in a steady-state, due to buffering processes such as sulphate desorption and cation exchange. These result in time lags between reductions in deposition and changes in soil chemistry and biological response. Models that include these buffering processes are therefore needed to understand the effects of changes in deposition over time.

### *1.1.3 Modelling work using ICP IM data*

While good use has been made of the biological data gathered by ICP IM e.g. (Bernhardt-Römermann et al. 2011; Dirnböck et al. 2014; Weldon et al. 2022), to date the modelling work at ICP IM has not had a primary focus on biodiversity change. Instead, the modelling work has mostly concentrated on understanding the biogeochemical aspects of acidification, recovery from acidification, nitrogen cycling and eutrophication. This is complementary to an interest in biodiversity, as modelling of biodiversity response to decreasing atmospheric deposition of course first needs an understanding of biogeochemical processes (e.g., soil chemistry, hydrology, etc.) in the area. This biogeochemical understanding underpins the necessary ecological understanding for credible modelling of biological responses. While biodiversity data is available only for vegetation at IM sites, plant diversity is known to be strongly linked to diversity at other trophic levels e.g. (Schuldt et al. 2019). Important work on linking dynamic models of forest soils to plant diversity was done in 2018 (Holmberg et al. 2018; Dirnböck et al. 2018), concluding that predicted reductions in N deposition according to current legislation would not prevent further declines in N sensitive forest plant species. While there has been only limited development in this area since those publications, attention is now turning to biodiversity again in the priorities of the UNECE Working Group on Effects (the body to which the ICPs belong) and more widely with the adoption of

the Kunming-Montreal Global Biodiversity Framework (CBD, 2022). The aim of the current report is to use dynamic modelling of the four Swedish ICP IM sites as a case study to explore possibilities and limitations of the approach when applied to biodiversity.

While ICP IM has excellent data in-depth, the geographical coverage is more limited than some other networks (e.g., ICP Forests, eLTER). However, it can fulfil an important role in the process of creating policy-relevant outputs by serving as a platform for model tests and development that can be expanded to larger networks. Regional assessments for policy purposes can be undertaken as a follow-up step in co-operation with networks with better regional coverage, using models and concepts developed and tested within ICP IM.

#### 1.1.4 Methods

Data from the four Swedish ICP Integrated Monitoring sites (SE04 Gårdsjön, SE14 Aneboda, SE15 Kindla and SE16 Gammtratten, see Fig.1) were used. These forest catchment sites gather data based on a range of subprogrammes, the most relevant here being those covering meteorology, air chemistry, precipitation and throughfall chemistry, soil and soil water chemistry, ground and runoff water chemistry, and forest floor vegetation. For full details of the monitoring methods please refer to the ICP IM Monitoring Manual (ICP IM, 2022). Site maps and further details of the sites can be found at DEIMS-SDR (Dynamic Ecological Information Management System - Site and dataset registry), accessible at [deims.org](https://deims.org), which is a database of long-term ecosystem research sites.

The sites featured in this study have the following permanent identifiers:

Aneboda <https://deims.org/9dd45aa6-ed7a-49d2-bea4-7750351c55d0>

Kindla <https://deims.org/9aa88bb6-b4a9-4569-8520-3d26643e6de9>

Gårdsjön <https://deims.org/9abbb750-8325-4a00-a801-db9cf3a2df13>

Gammtratten <https://deims.org/27415652-8de8-40e7-92c1-f82526116a2d>



*Figure 1: Location of the four Swedish ICP IM sites*

*Table 1: Overview of study sites*

Site	Area (Ha)	Altitude (m above sea level)	Annual mean temperature	Precipitation (mm)
Gårdsjön SE04	3.7	114-140	+ 6.7°C	1000
Aneboda SE14	18.9	210-240	+ 5.8 °C	750
Kindla SE15	20.4	312-415	+ 4.2 °C	900
Gammtratten SE16	45	410-545	+ 1.2°C	750

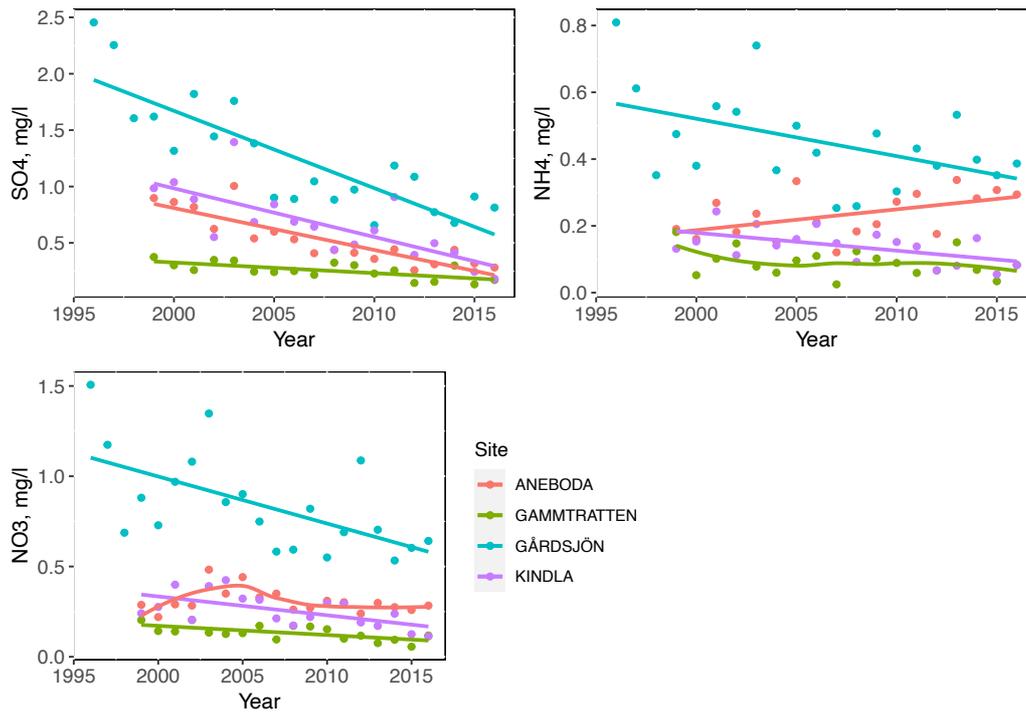


Figure 2: Mean annual concentrations in throughfall deposition S and N at ICP Integrated Monitoring sites situated along a north-south depositional gradient in Sweden. Smoothed lines indicate a non-significant trend (adapted from Weldon and Grandin, 2021)

### 1.1.5 Modelling method

The same modelling approach was adopted as in (Holmberg et al. 2018) and (Dirnböck et al. 2018)- a model chain integrated in VSD+ studio (Bonten, Reinds, and Posch 2016), incorporating a meteorological-hydrological pre-processor (MetHyd) a forest growth estimator (GrowUp) and the VSD+ (Very Simple Dynamic Model) dynamic model. This is designed to cover carbon and nitrogen cycling, charge balance, cation exchange, and weathering processes. VSD+ takes as inputs time series of N and S deposition, temperature and hydrology and predicts key soil attributes such as pH, carbon/nitrogen ratio and base saturation. The outputs of VSD+ are in turn input to the vegetation model PROPS.

### 1.1.6 Deposition and climate data

Deposition values of S and N are obtained from the modelling work undertaken by The Co-operative Programme for Monitoring and Evaluation of the Long-Range Transmission of Air Pollutants in Europe (the European Monitoring and Evaluation Programme, EMEP) (EMEP, 2021; Simpson et al., 2012), using the current legislation scenario (CLE) incorporating emissions reductions based on agreed

targets under current legislation (e.g. the Gothenburg Protocol). As the sites in Sweden are all forested catchments the modelled deposition values for forests were used. Climate variables were based on an RCP 4.5 scenario assuming a peak in emissions contributing to global heating around 2040. These data are based on a bias-adjusted regional climate model data produced by EURO-CORDEX (European Coordinated Regional Downscaling Experiment) (Jacob et al., 2014).

#### 1.1.7 *Meteorological-Hydrological Pre-processing (MetHyd)*

MetHyd performs meteorological and hydrological pre-processing. Given data on temperature, precipitation, and key soil properties, it calculates coefficients related to nitrogen and carbon cycling processes for the period to be simulated in VSD+.

#### 1.1.8 *Forest Growth Estimation (GrowUp)*

GrowUp (Bonten et al., 2016) is used to predict the dynamics of forest growth and nutrient cycling in woodland ecosystems. It calculates the uptake, retention and loss of nutrients from the system, accounting for tree species composition, biomass, management and yield.

#### 1.1.9 *Very Simple Dynamic Model (VSD+)*

The VSD+ model (version 5.6.3) is a well-tested dynamic geochemical soil model which can take as inputs values produced by MetHyd and Growup (see above). These inputs are key parameters related to soil chemistry and are used to provide outputs for vegetation relevant variables such as soil pH, soil C and N pools and C:N ratio that are in turn used by PROPS to predict plant species probability of occurrence (see next section for a description of PROPS). VSD+ uses time series data of atmospheric pollutant deposition (S and N), precipitation, temperature derived from modelling work such as climate and deposition models, and can be calibrated with available observations from locations of interest.

#### 1.1.10 *Calibration*

Observed data from the ICP IM database were used to calibrate and assess the model predictions. VSD+ Studio includes a calibration process based on Bayesian and Markov chain Monte Carlo methods (Bonten, Reinds, and Posch 2016). Measured data on pH and base saturation are used to calibrate initial C pool and C:N ratio, cation exchange and cation weathering rates. Similarly, data on soil solution concentrations and pH contributed to calibrating weathering rates. Not all variables may be calibrated but a visual comparison of measured and predicted values can also be performed (as well as statistical measures where needed). Once a satisfactory performance was achieved in VSD+, the model outputs were used in PROPS.

### 1.1.11 PROPS

PROPS (Probability of Occurrence of Plant Species) is a model which predicts the probability of occurrence for plant species, based on their ecological niche (Reinds et al., 2015, Wamelink et al. 2020). Data on niches comes from a large database of over 4000 European plant species. This is in turn based on vegetation surveys (ca. 800 000) and a smaller dataset of ca 12 000 surveys where measured data on soil pH and/or C:N ratio are also available (these are mostly from the Netherlands, the United Kingdom, Ireland, Denmark and Austria, meaning species from other regions may not be present). PROPS can output the probability of occurrence of selected species and metrics such as diversity and habitat suitability indices derived from these, based on predicted temperature, precipitation, soil pH and C:N ratio, and atmospheric pollutant deposition.

The user must select which species will be included in the model. This is often based on characteristic species for a vegetation type (e.g. based on EUNIS habitat classifications, which are available to select in PROPS together with pre-set lists of species). In the current study however, the species actually found in the detailed vegetation surveys performed at the sites were selected in order to assess how well the predicted suitability of the site matched the measured community composition. Of the species present, a subset classified as acidophiles were also tested to investigate the impact of reduced deposition. These classifications were based on ecological indicator values for the species as assessed in Sweden (Tyler et al. 2021). Ecological indicator values (also known as Ellenberg values) are an assessment of the preferences or optima of a species for environmental factors such as soil acidity, nitrogen, temperature etc, based on surveys, experiments and expert opinion. In this case, species with R (Reaction, or acidity) value of under 5 were classed as acidophilic.

PROPS calculates the probability of a species occurring under a given set of environmental parameters. Obviously, probability of occurrence so conceived cannot be directly measured at a particular location – in reality a species is either present or absent, so the “probability of occurrence” is collapsed to 0 or 1. However, the current study uses the structure of the vegetation monitoring programme to create a value that would be expected to correlate with this probability of occurrence. The Vegetation Structure subprogramme of the ICP Integrated Monitoring programme is based on a grid of circular monitoring plots distributed at regular intervals across each site, within which all plant species are identified, and their abundances recorded (with an inventory performed every 5 years, although occasion deviations from this schedule have occurred). Consequently, the proportion of plots at which a species has been identified can be calculated and compared with the modelled probability of occurrence. This proportion was

calculated for each species at each inventory, and the mean value for each species across inventories used as the observed “probability of occurrence”.

#### *1.1.12 A note on critical loads*

The VSD+ model chain and related methods have been an important tool in setting critical loads for biodiversity, that is to say the limits for N and S deposition if plant species of concern are not to be lost. A two-step process is involved in calculating these. Firstly the (abiotic) parameters where species of concern are likely to be lost must be established (which involves the probability of species occurrence as a function of those parameters) and secondly a soil chemistry model is needed to calculate the maximum levels of deposition that equate to those key levels of abiotic parameters. The calculation of biodiversity critical loads is based on the Habitat Suitability index (the arithmetic mean of the normalised probabilities of occurrence of the defined species of interest). This HSI is output by PROPS, based on the species occurrence probabilities as a function of temperature, precipitation, soil solution pH, C:N ratio and N deposition. S deposition is derived with a SMB (simple mass balance) model, allowing HSI as a function of S and N deposition to be calculated for a location of interest. While critical loads are not included in the current study, it is important to note that biodiversity modelling using these methods has a high degree of policy relevance.

## 2. Results

The VSD+ models after calibration showed an acceptable performance. Pearson correlation coefficient between modelled and observed pH was 0.77, while for BC (base cations) the equivalent value was 0.73. The focus of this results section is on the vegetation modelling performed with PROPS, using the soil chemistry modelling to provide relevant inputs. However more detail on the VSD+ results can be found in the appendix.

### 2.1.1 Probability of occurrence (all species)

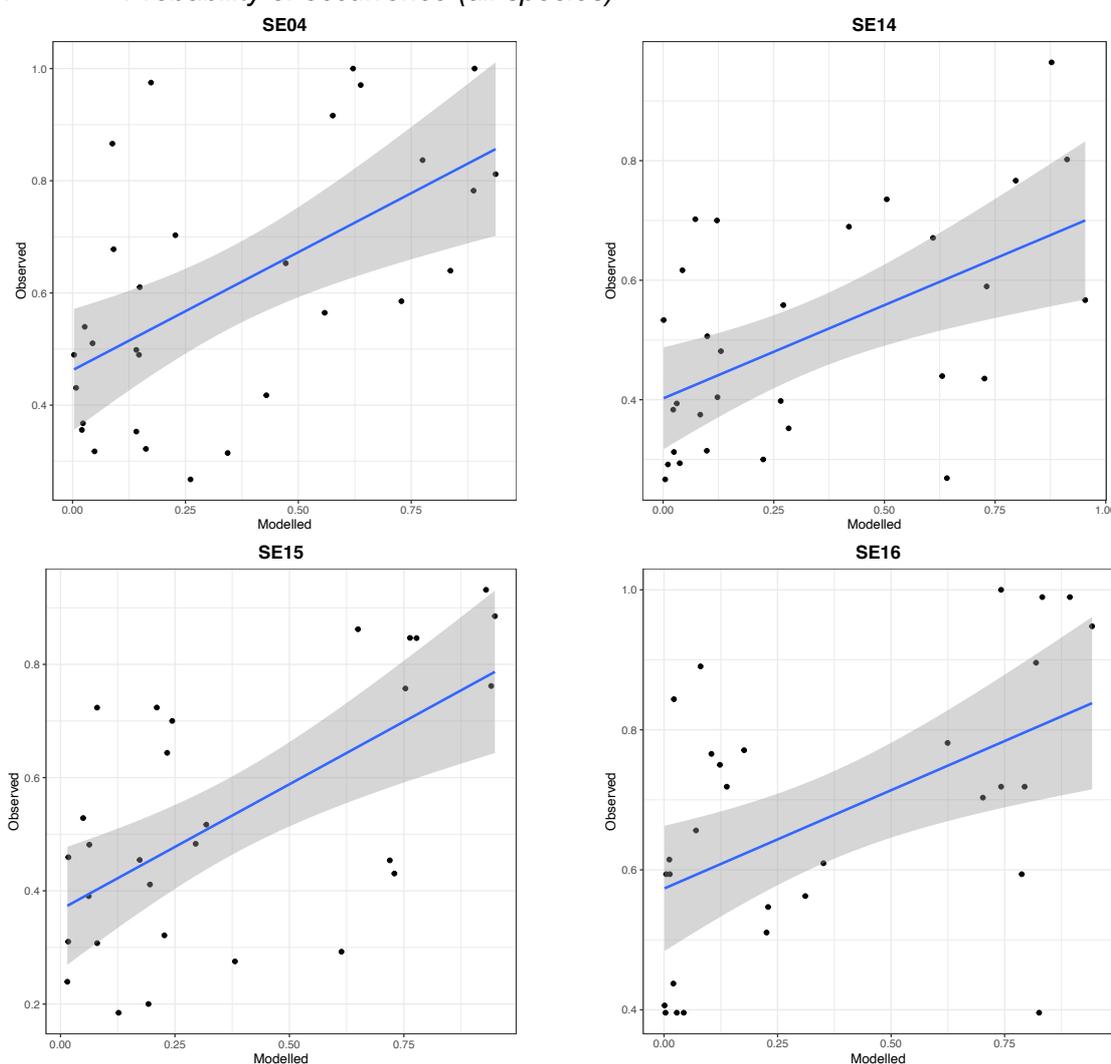


Figure 3: Proportion of plots in which a species was observed (y-axis) and modelled probability of occurrence in PROPS for the same species at the same site (x-axis), using the 30 species with highest proportion of occurrence.

Table 2: R<sup>2</sup> and p-values for linear regression (observed and modelled probabilities as shown in Fig 3 above).

Site	R <sup>2</sup>	P-values
Gårdsjön SE04	0.3294	≤ 0.001 ***
Aneboda SE14	0.2924	≤ 0.01 **
Kindla SE15	0.3909	≤ 0.001 ***
Gammtratten SE16	0.2661	≤ 0.01 **

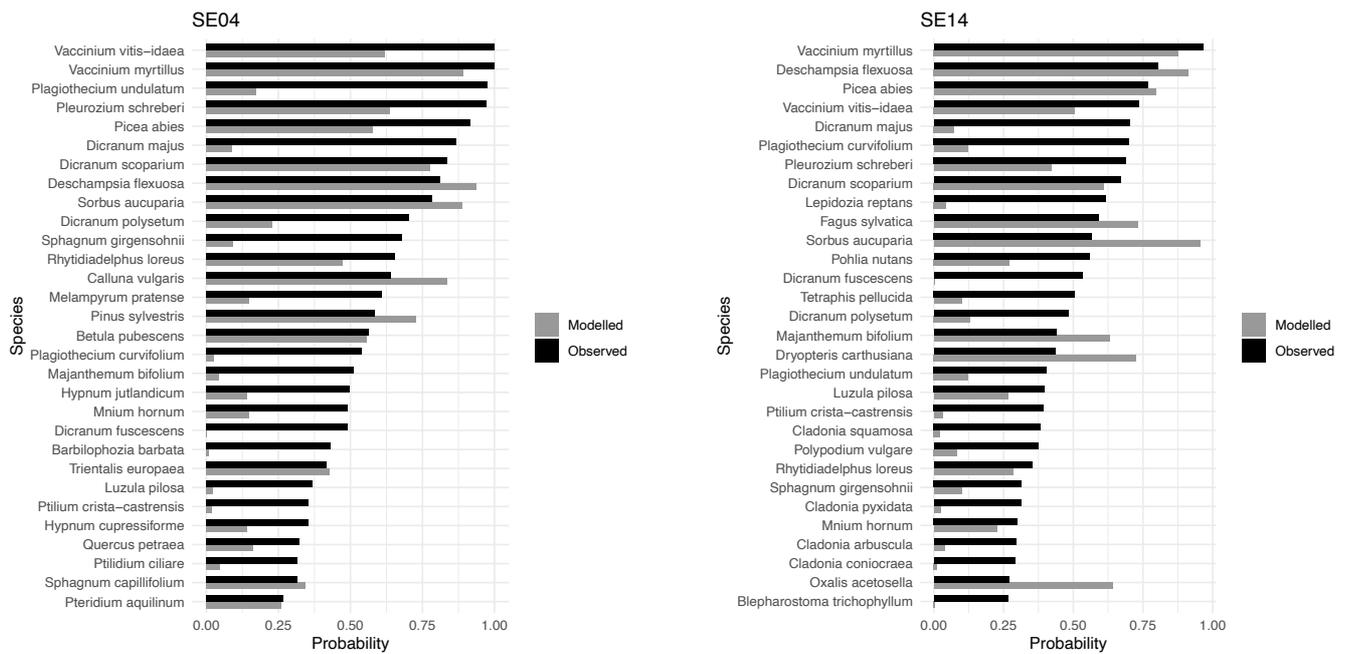


Figure 4: Proportion of plots in which a species was observed ("Observed") and the modelled probability of occurrence for the same species, as calculated in PROPS for each site ("Modelled")

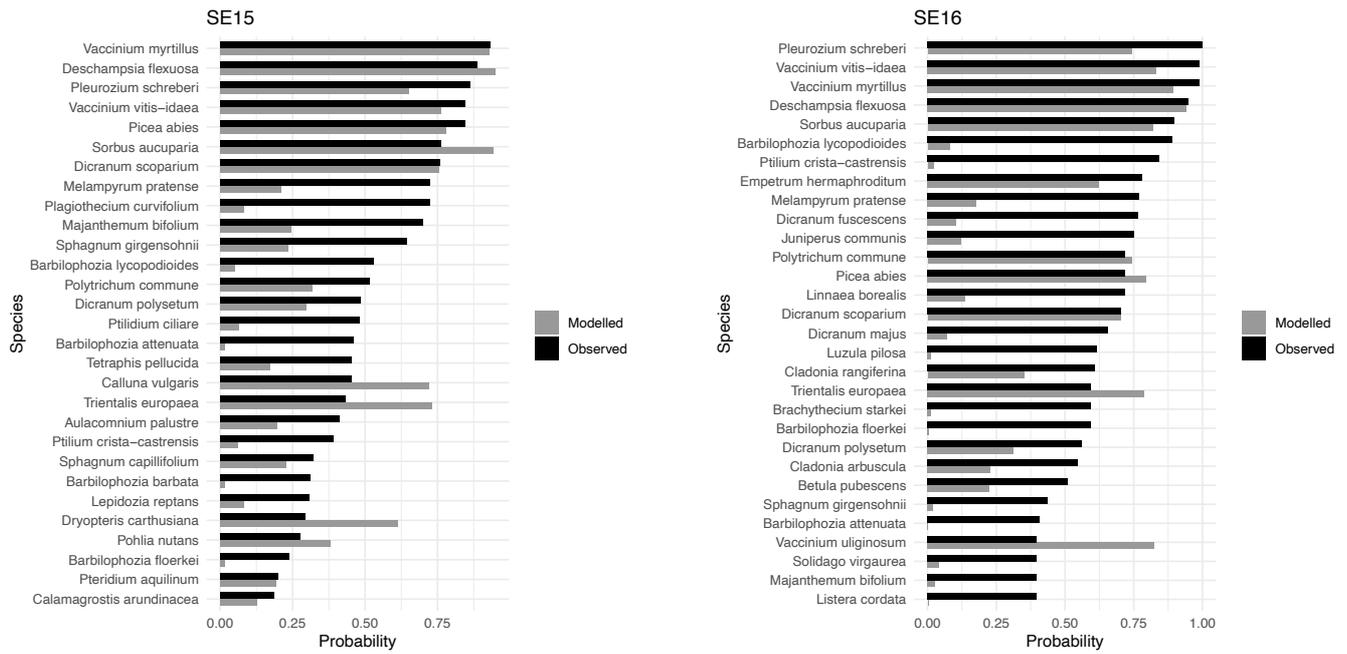


Figure 5: Proportion of plots in which a species was observed ("Observed") and the modelled probability of occurrence for the same species, as calculated in PROPS for each site ("Modelled")

While significant relationships between modelled and observed probabilities were found in all cases (Table 2), the points are widely scattered (Fig. 3) and the R square values are rather low (Table 2). The reason for this can be seen more clearly when plotting results for each species included (Fig. 4 and 5). While there is a high correlation between the modelled and observed values for many species, there is a large gap for some species, particularly non-vascular species (mosses, liverworts and lichens, Table 3).

Table 3: Spearman rank correlation between modelled and observed probability of occurrence for vascular and non-vascular species

Site	Vascular correlation	Non-vascular correlation
Gårdsjön SE04	0.72	0.42
Aneboda SE14	0.65	0.44
Kindla SE15	0.81	0.60
Gammtratten SE16	0.63	0.48

## 2.1.2 Habitat suitability index (acidophiles)

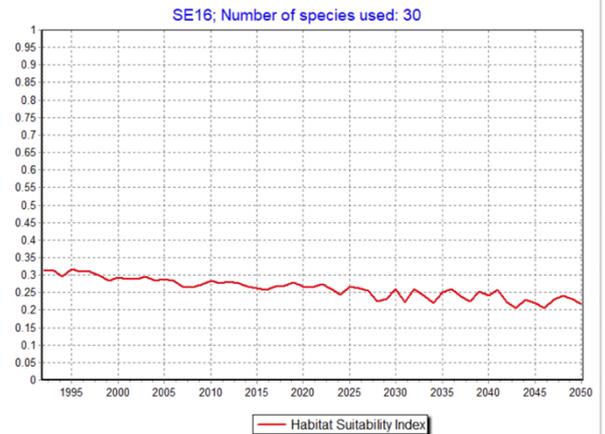
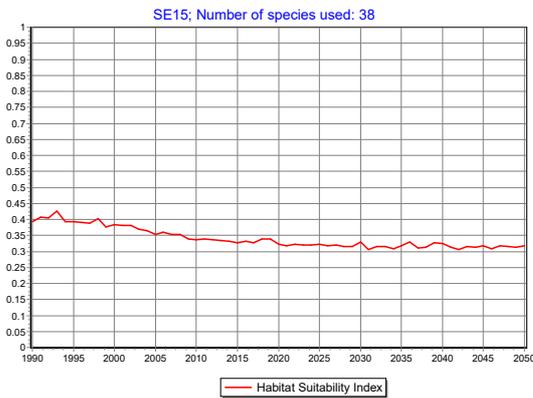
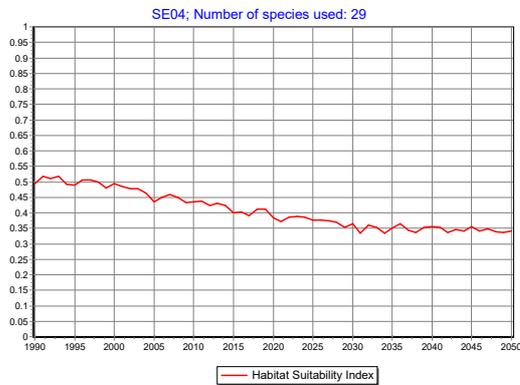


Figure 6: Modelled Habitat Suitability Index for species classified as acidophiles, calculated independently for each site using PROPS

The modelled Habitat Suitability Index (HSI) for the species found in vegetation surveys that were classified as acidophiles showed a decline during the period up to approximately 2010 at all sites before levelling off, but the decline is more noticeable for SE04 and SE14 than for the more northerly sites (Fig. 6). Particularly the most northern sites, SE16, shows little change other than a slow decline in HSI.

### 3. Discussion

The PROPS predictions of Habitat Suitability Index for the acidophilic species reflects the geographical gradient in acidifying deposition, with the southern sites (SE04 and SE14) which have historically received much higher deposition than the more northerly sites (SE15 and SE16) showing a sharp decline in suitability for species which favour acid conditions (Fig. 6).

When looking at predicted probability of occurrence at a species level, the metric of “probability of occurrence” based on the proportion of plots at a given site where a species was found in surveys corresponds reasonably well with the PROPS predictions of probability of occurrence overall (Fig. 3) and in many cases very well (Fig. 4, Fig. 5). A very high degree of correlation is probably unrealistic to expect - observational data will always include variation due to recording errors of various kinds while models are inherently a simplification that disregard some processes that cause variation in the real world. However, there is considerable variation in the degree of correlation depending on the species, and many species are underestimated by PROPS. It is notable that these are largely the non-vascular parts of the vegetation community (mosses, liverworts and lichens, the latter of which are of course not plants but are often included in plant surveys). SE15 and SE16 for example both show a high degree of correlation between modelled and observed values for the most commonly occurring species until we come to the mosses *Plagiothecium curvifolium*, *Dicranum majus*, and *Ptilium crista-castrensis*, and the liverwort *Barbilophozia lycopodioides* occur, all of which have a much lower value for modelled than observed probability. This is a general pattern found across all four sites (Table 3). A likely explanation for this pattern is that PROPS is based on a large body of data which is concentrated in certain regions (the Netherlands, the United Kingdom, Ireland, Denmark and Austria are heavily featured). Bryophytes, lichens and liverworts are an important and often dominant part of boreal and boreo-nemoral forest understorey vegetation (Esseen et al. 1997; Turetsky et al. 2012), which will not be reflected in probabilities of occurrence based on central or north-west European data. This is not a fault of PROPS and is a reflection of the data that are available for developing such models, but this should be borne in mind when modelling sites in areas where non-vascular vegetation is a more important part of the vegetation community than is typically the case in Europe.

While this model chain (and similar approaches) can predict environmental conditions that are important for plant species occurrence and use these to provide a probability of occurrence for species of interest, an important factor that is not included is limitation by dispersal and establishment. The predictions are based on observations (i.e., environmental conditions in which the species has been found) but it cannot be assumed that a species will be found everywhere conditions are suitable for it. Indeed, PROPS is explicit in modelling precisely suitability rather than predicting actual occurrence or abundance. Nevertheless, if we are interested in biological recovery and a desired increase in species threatened by the previous high deposition of S (and/or N), the existence of a suitable habitat is necessary but not sufficient.

This can be seen when considering a simpler approach to assessing habitat quality that avoids dealing with the complexity of modelling both soil chemistry and ground vegetation. Epiphytic lichens have long been used as bioindicators for air quality due to their sensitivity to airborne pollutants (Nash and Gries 1991). The expected recovery of S sensitive species in areas where S deposition levels have fallen has been found in some long-term datasets (Pescott et al. 2015; Outhwaite et al. 2020) but failures of recolonization have also been recorded (Bates, Bell, and Massara 2001), including in a recent study at the Swedish sites currently in focus (Weldon and Grandin 2021). While declines in sensitive epiphytic lichens seem to reliably occur when S (and N) deposition levels increase, the reverse process of recovery is more complex. As with forest floor vegetation, other factors such as dispersal and establishment limitation must also be taken into account if an accurate overview of current species distributions are to be estimated. Additionally, the continued moderate level of N deposition coupled with greatly decreased S deposition in Southern Sweden (a pattern repeated across much of Europe in recent decades) can change communities in contrasting directions (Giordani et al. 2014, 2018). In the Swedish case, depleted regional species pools due to both previous high levels of deposition, continued N deposition, and the ongoing intensive production focused forestry practices are probably the key factors in the observed weak recovery of sensitive lichens (Weldon and Grandin 2021). Of course, the complexities of soil chemistry cannot be avoided if we are interested in ground vegetation rather than only epiphytes, but to those complexities we should also add a consideration of the question of dispersal and establishment.

Another factor to consider is competition. PROPS and similar models are based on the realised niche of species in the data, so information about competitive exclusion is implicitly included. However given that model chains such as VSD+PROPS are typically used to model conditions decades in the future under scenarios

of climate change and various deposition predictions, there is the possibility of novel vegetation communities emerging (Staples, Kiessling, and Pandolfi 2022; Lurgi, López, and Montoya 2012). Competitive relations among species that do not normally compete under current environmental conditions and species distributions will not be reflected in currently available training data.

Expanding the modelling framework to include dispersion/establishment limitations and relations within the communities, while desirable, would be a major undertaking, and the HSI framework is already well used in policy relevant settings. Nevertheless, a clear view of the strengths and weaknesses of the approach described here is important in applying it appropriately.

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# Appendix

PROPS modelled probability (maximum probability of individual species using Local Maxima 2-D (over pH, Ndep)) and actual occurrence (presented as the proportion of survey plots in which a species occurred, averaged over all survey years where data were available). Only the 30 species with highest probability as modelled in PROPS are presented here.

## SE04

Species	Actual	Modelled
<i>Vaccinium myrtillus</i>	1	0.890293
<i>Vaccinium vitis-idaea</i>	1	0.621219
<i>Plagiothecium undulatum</i>	0.975	0.173727
<i>Pleurozium schreberi</i>	0.970588	0.638116
<i>Picea abies</i>	0.916176	0.576312
<i>Dicranum majus</i>	0.866176	0.088223
<i>Dicranum scoparium</i>	0.836765	0.775213
<i>Deschampsia flexuosa</i>	0.811765	0.936809
<i>Sorbus aucuparia</i>	0.782353	0.888131
<i>Dicranum polysetum</i>	0.702941	0.227678
<i>Sphagnum girgensohnii</i>	0.677941	0.090901
<i>Rhytidiadelphus loreus</i>	0.652941	0.472177
<i>Calluna vulgaris</i>	0.639706	0.836867
<i>Melampyrum pratense</i>	0.610294	0.148803
<i>Pinus sylvestris</i>	0.585294	0.728351
<i>Betula pubescens</i>	0.564706	0.558294
<i>Plagiothecium curvifolium</i>	0.539706	0.027012
<i>Majanthemum bifolium</i>	0.510294	0.044343
<i>Hypnum jutlandicum</i>	0.498529	0.141165
<i>Dicranum fuscescens</i>	0.489706	0.003232
<i>Mnium hornum</i>	0.489706	0.147146
<i>Barbilophozia barbata</i>	0.430882	0.007781
<i>Trientalis europaea</i>	0.417647	0.429167
<i>Luzula pilosa</i>	0.367647	0.023043
<i>Ptilium crista-castrensis</i>	0.355882	0.020672
<i>Hypnum cupressiforme</i>	0.352941	0.141165
<i>Quercus petraea</i>	0.322059	0.162406
<i>Ptilidium ciliare</i>	0.317647	0.048744

Sphagnum capillifolium	0.314706	0.343487
Pteridium aquilinum	0.267647	0.261128

SE14

Species	Actual	Modelled
Vaccinium myrtillus	0.964583	0.877576
Deschampsia flexuosa	0.802083	0.912675
Picea abies	0.766667	0.796725
Vaccinium vitis-idaea	0.735417	0.505262
Dicranum majus	0.702083	0.072717
Plagiothecium curvifolium	0.7	0.121641
Pleurozium schreberi	0.689583	0.419849
Dicranum scoparium	0.670833	0.609789
Lepidozia reptans	0.616667	0.043636
Fagus sylvatica	0.589583	0.731061
Sorbus aucuparia	0.566667	0.953614
Pohlia nutans	0.558333	0.271636
Dicranum fuscescens	0.533333	0.001232
Tetraphis pellucida	0.50625	0.099723
Dicranum polysetum	0.48125	0.130618
Majanthemum bifolium	0.439583	0.630583
Dryopteris carthusiana	0.435417	0.726111
Plagiothecium undulatum	0.404167	0.122741
Luzula pilosa	0.397917	0.265786
Ptilium crista-castrensis	0.39375	0.030839
Cladonia squamosa	0.383333	0.022821
Polypodium vulgare	0.375	0.083882
Rhytidiadelphus loreus	0.352083	0.28375
Sphagnum girgensohnii	0.314583	0.098688
Cladonia pyxidata	0.3125	0.024456
Mnium hornum	0.3	0.226214
Cladonia arbuscula	0.29375	0.037581
Cladonia coniocraea	0.291667	0.010894
Oxalis acetosella	0.26875	0.641189
Blepharostoma trichophyllum	0.266667	0.004655

SE15

Species	Actual	Modelled
Vaccinium myrtillus	0.931642	0.929504
Deschampsia flexuosa	0.88513	0.948821
Pleurozium schreberi	0.862051	0.649756

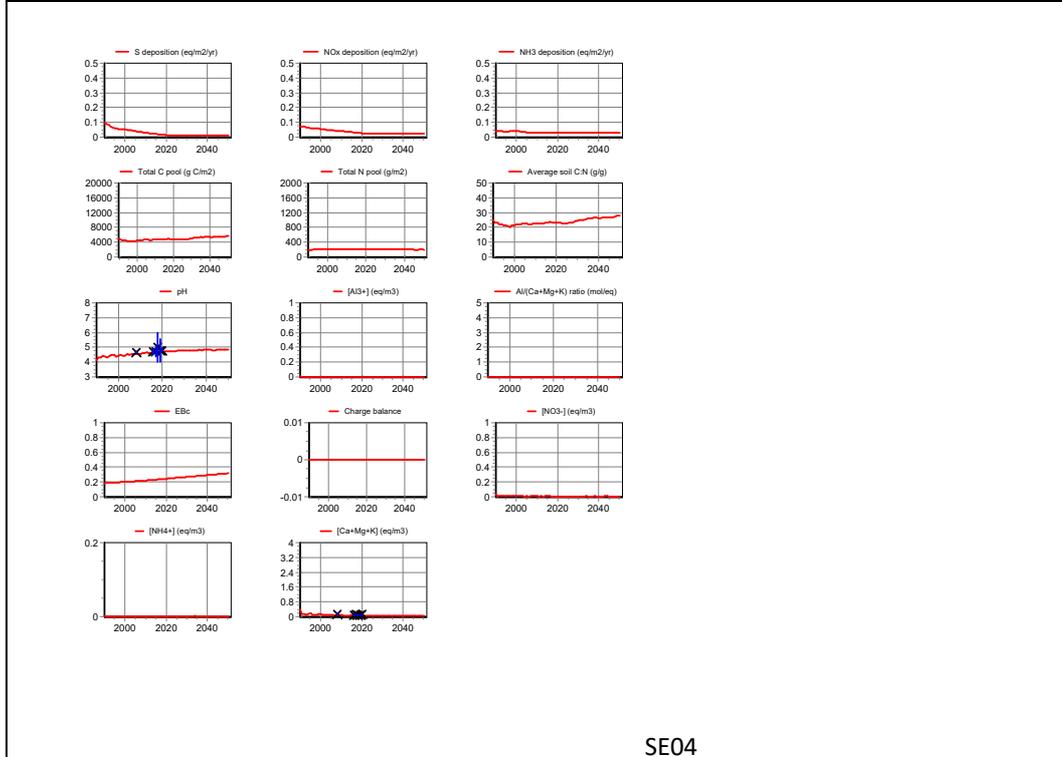
Vaccinium vitis-idaea	0.846723	0.76338
Picea abies	0.846371	0.777786
Sorbus aucuparia	0.761804	0.940751
Dicranum scoparium	0.7574	0.753411
Melampyrum pratense	0.723749	0.210349
Plagiothecium curvifolium	0.723573	0.07987
Majanthemum bifolium	0.700141	0.244032
Sphagnum girgensohnii	0.643763	0.232968
Barbilophozia lycopodioides	0.528541	0.049504
Polytrichum commune	0.516913	0.318455
Dicranum polysetum	0.483087	0.295221
Ptilidium ciliare	0.481501	0.063016
Barbilophozia attenuata	0.459302	0.017214
Tetraphis pellucida	0.454545	0.173018
Calluna vulgaris	0.453841	0.719238
Trientalis europaea	0.430585	0.72933
Aulacomnium palustre	0.411205	0.195458
Ptilium crista-castrensis	0.390592	0.061686
Sphagnum capillifolium	0.321353	0.226893
Barbilophozia barbata	0.310254	0.016848
Lepidozia reptans	0.307611	0.080024
Dryopteris carthusiana	0.292459	0.613681
Pohlia nutans	0.27537	0.381073
Barbilophozia floerkei	0.239429	0.014979
Pteridium aquilinum	0.200141	0.192079
Calamagrostis arundinacea	0.184637	0.126883

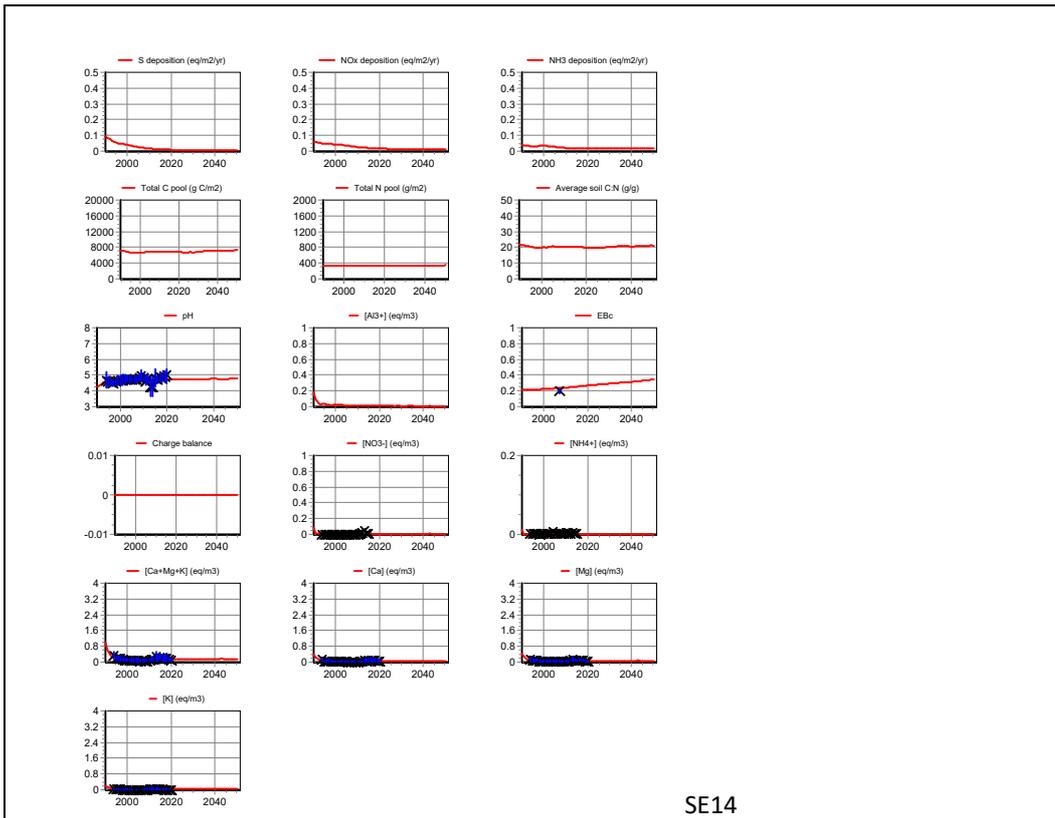
SE16

Species	Actual	Modelled
Pleurozium schreberi	1	0.742204
Vaccinium myrtillus	0.9895833	0.89367
Vaccinium vitis-idaea	0.9895833	0.832882
Deschampsia flexuosa	0.9479167	0.94255
Sorbus aucuparia	0.8958333	0.819265
Barbilophozia lycopodioides	0.890625	0.080417
Ptilium crista-castrensis	0.84375	0.021817
Empetrum hermaphroditum	0.78125	0.624552
Melampyrum pratense	0.7708333	0.176361
Dicranum fuscescens	0.765625	0.104337
Juniperus communis	0.75	0.123007
Linnaea borealis	0.71875	0.13816

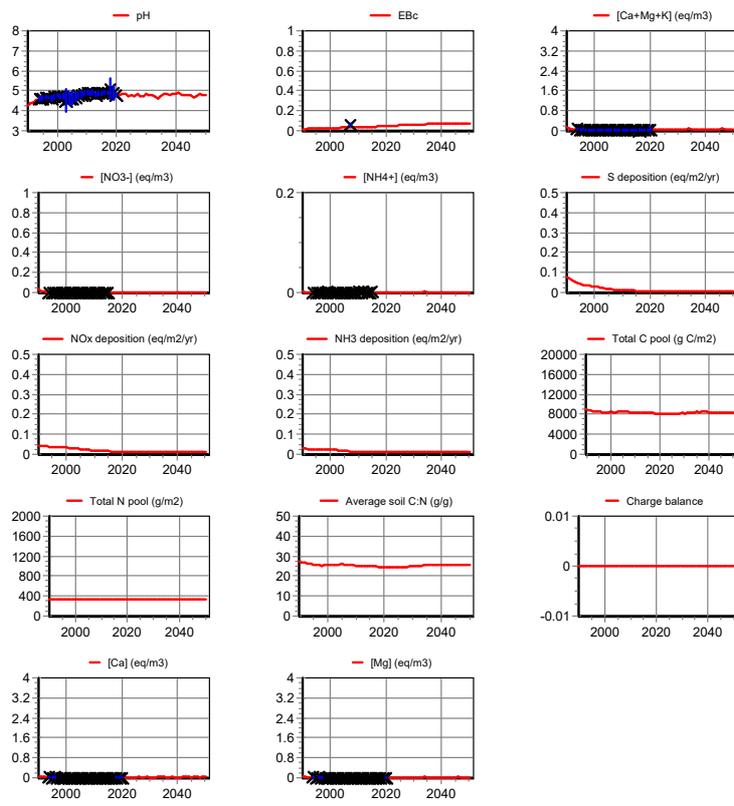
<i>Picea abies</i>	0.71875	0.794012
<i>Polytrichum commune</i>	0.71875	0.742204
<i>Dicranum scoparium</i>	0.703125	0.702233
<i>Dicranum majus</i>	0.65625	0.070451
<i>Luzula pilosa</i>	0.6145833	0.011713
<i>Cladonia rangiferina</i>	0.609375	0.351028
<i>Barbilophozia floerkei</i>	0.59375	0.004725
<i>Brachythecium starkei</i>	0.59375	0.012693
<i>Trientalis europaea</i>	0.59375	0.787724
<i>Dicranum polysetum</i>	0.5625	0.31114
<i>Cladonia arbuscula</i>	0.546875	0.229275
<i>Betula pubescens</i>	0.5104167	0.225857
<i>Sphagnum girgensohnii</i>	0.4375	0.020612
<i>Barbilophozia attenuata</i>	0.40625	0.001218
<i>Listera cordata</i>	0.3958333	0.003233
<i>Majanthemum bifolium</i>	0.3958333	0.028156
<i>Solidago virgaurea</i>	0.3958333	0.04337
<i>Vaccinium uliginosum</i>	0.3958333	0.825948

VSD+ outputs (observed values in blue, modelled values in red)

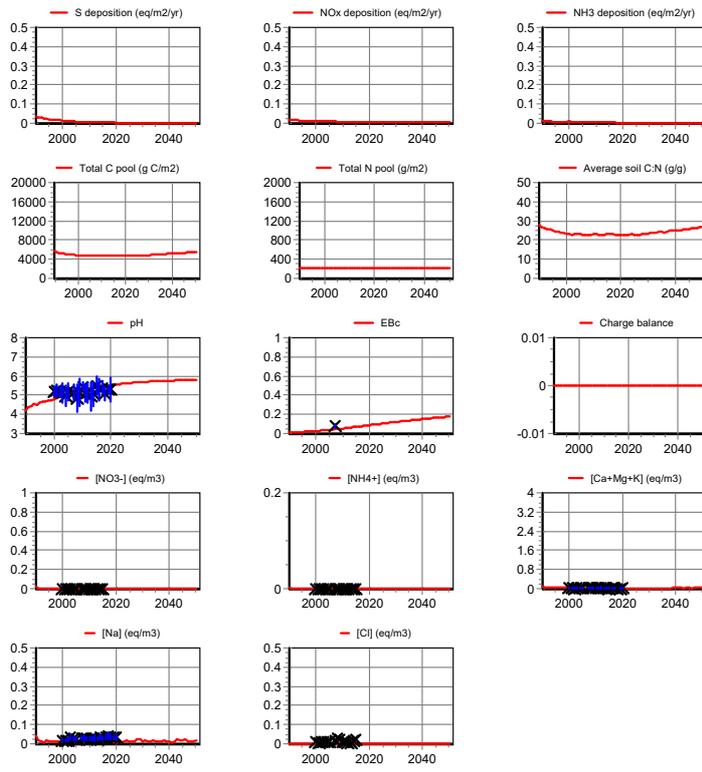




SE14



SE15



SE16