Climate change aggravates bog species extinctions in the Black Forest (Germany)

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Abstract
Aim: Bogs and transition mires in Central Europe have undergone tremendous changes in the last decades, declining in spatial extent and favourable conservation status. However, species extinctions have been documented only rarely because of a lack of reliable floristic data. Here, we assessed species losses of bog complexes and analysed their potential drivers.

Location: Black Forest, Germany.

Methods: We made use of the unique situation that the majority of bogs in the Black Forest (124 sites) had been systematically surveyed from 1972 to 1980 and resurveyed the flora of the same sites between 2017 and 2020. In addition, we included further data from the preceding decades.

Results: Out of 88 species for which we compiled site occupancy data, two species went extinct in the whole study area and 37 decreased from 1972 to 2020, losing on average 33% of their initial frequency. In contrast, 46 species displayed a positive trend. While decreasing species were characteristic of raised bogs, moorland ponds and base-rich mires, increasing species were typical of poor mires, fens and wet meadows. Species losses were higher at low elevation, pointing to increasing temperature increase and decreasing precipitation as main drivers of extinction, while habitat area, distance to the nearest site and land use played no significant role. The mean altitude at which extinctions of populations occurred increased with time. Assuming a continuation of the observed negative trends for declining bog species, our models predict the extinction of further ten species by 2045.

Main Conclusion: Our study highlights the value of systematic and comprehensive past biodiversity surveys to assess biodiversity change. We demonstrated that low-mountain habitats have already suffered biodiversity loss as a result of climate change. There are only limited management options against rising temperatures and decreasing precipitation.

Keywords: biodiversity loss, biodiversity monitoring, bog vegetation, climate change, extinction, plants, transition mires
1 | INTRODUCTION

Peat bogs in Europe have come under high pressure because of land use change, climate change, pollution and peat extraction (IPBES, 2018; Kosonen et al., 2019). Among all habitats monitored under the Birds and Habitats Directive in Europe (EC Directive 92/43), peatland habitats show the highest proportion of assessments that are unfavourable or deteriorating (European Environment Agency, 2015). Bog sites are characterized by a mosaic of different habitat types, most of which are subjects of the European habitat directive. The centre of this mosaic is mostly occupied by raised and quaking bogs, sustained mainly by rainwater, with a water level generally higher than the surrounding water table, or transition mires, which develop under oligotrophic to mesotrophic water conditions, with characteristics intermediate between soligenous and ombrogenous types. In contrast, fens, which receive water from the surrounding landscape, are found in peripheral zones (van Kleef et al., 2012; Succow & Jeschke, 1990). In the following, we refer to this habitat complex simply as bog complexes.

According to the Red List of Germany (Bundesamt für Naturschutz, 2018), peatlands are among the habitats with the highest proportion of threatened species, only surpassed by oligotrophic water vegetation. Declines in bog, mire and fen species populations at the large spatial extent of southwest Germany have been reported for butterflies (Habel et al., 2019) and for a few plant species (Buse et al., 2015), while no attempt has been made yet to analyse floristic changes with site-specific data. Peat extraction, drainage and melioration have reduced bog areas in Central Europe since approximately 900 years (Dierßen & Dierßen, 2001). Only in the second half of the 20th century, peatlands have become focal objects of nature conservation (Joosten et al., 2017). However, drainage and eutrophication have remained a continuous threat (Kosonen et al., 2019). Climate change effects on bog species composition are well known from fossil records (Lamentowicz et al., 2019), but have not been documented at the temporal scale of the recent decades. Climate change impacts on bog complexes are complex, being both caused by warming, increasing evapotranspiration, and changed precipitation patterns (Gerdol et al., 2007). In Austria, the poor fens and transition mires have been predicted to be more affected by warming than by drought or N input (Hämmerle et al., 2018). This would also be relevant for Germany, where the current business-as-usual emission scenario (RCP 8.5) is expected to increase surface temperatures by 2.8–5.2°C in the period 2071–2100 (compared to 1971–2000), while the projections are rather uncertain with respect to precipitation, which according to different models may increase or decrease by up to ±26% (Deutscher Wetterdienst, 2018). Consequently, among all habitats in Europe, bogs and fens were identified as those that would be most threatened by the projected temperature rise and summer drought (Essl et al., 2012; Normand et al., 2007).

According to metapopulation theory, colonization and extinction events are not only driven by environmental drivers, but also by isolation and distance (Husband & Barrett, 1996). More isolated populations are more likely to go extinct because of lacking gene flow and stochastic effects. In addition, extinction risk might be associated with the species’ degree of specialization and the ability to persist and spread (Walker & Preston, 2006). Thus, species reproducing by vegetative organs might be less prone to extinction than those reproducing only generatively by seeds or spores.

We here studied extinction events and potential drivers in one of the focal regions of bog vegetation in Germany, the Black Forest in Baden-Württemberg (Figure 1). From 1972 to 1980, bog complexes had been systematically surveyed in this region by Klaus and Barbara Dierßen with respect to both flora and vegetation (Dierßen & Dierßen, 1984). We resurveyed the flora of the same sites between 2017 and 2020 and compiled all surveys with further data from the preceding decades. Our main objective was to assess occurrences, temporal stability and extinction of typical bog complex species across a large number of sites and to relate the observed changes to potential drivers. In particular, we hypothesized that (a) species extinctions in the Black Forest bog sites are ongoing and (b) that these are driven by climate change. At the level of bog sites, we tested (c) whether the proportion of declining species depended on elevation, area, distance to the nearest bog complex and land use. Finally, (d) we hypothesized that the altitude of extinction events increased with time. As extinctions are notoriously difficult to prove, we discuss the methodological difficulties of generating reliable results from the former survey data.

2 | MATERIAL AND METHODS

2.1 | Study site

The study area comprised the southern part of the Black Forest, an area of about 500 km² (Figure 1). While the study area only covers about one third of all bog sites in the Black Forest, the vast majority of rare and regionally typical bog species occurred here. Within the study region, elevation ranges from approximately 300 m above sea level in the Rhine valley in the south to almost 1,500 m above sea level at the summit of Mt. Feldberg in the northwest. This elevational gradient offers the opportunity to relate possible changes to climatic drivers, in particular to precipitation and temperature.

The majority of the bog complexes is located in forested valleys and on slopes and not used for forestry, except for some marginal areas. Some other bog complexes are found on sloping valley floors or plateaus that are used for low-intensity agriculture. Almost all bog complexes have been affected by drainage ditches, which in most cases were created more than 50 years ago and are no longer maintained today. To our knowledge, in the past few decades, new drainage ditches have only been established in exceptional cases, affecting only small areas (von Sengbusch, 2015). As we were not able to collect water level data at all sites and drainage conditions did not change in almost all sites, we did not include them in the subsequent analyses.
FIGURE 1  Map of the study area. Black = all bogs and mires in the area with survey between 1972 and 1980, magenta = the 124 bogs and transition mires analysed here. For the site codes, see Appendix Table S1 in Supporting Information.
2.2 | Data compilation

In total, species inventories of typical vascular plant species of bog complexes were compiled for 124 bogs with presence/absence. In particular, 106 bogs were included that had been surveyed by Barbara Dierßen and Klaus Dierßen four to five decades ago in the study area (Dierßen & Dierßen, 1984). Locations of all sites of bog complexes (as listed in Appendix Table S1 in Supporting Information) were digitized as polygons.

In addition to the bog sites surveyed by Dierßen & Dierßen themselves, Dierßen and Dierßen (1984) included a species list from one site from literature and eight further sites were included that had been recorded at the same time by Schuhwerk (1988). These records were made between 1972 and 1980 (Appendix Table S2 in Supporting Information). Further nine bog complexes were included that were only surveyed in the 1980s and 1990s. There are further bog sites inside the study region, which, however, are either very small or mostly very species-poor, and thus, not considered in our study. From 2017 to 2020, the first author resurveyed 123 sites, most of them twice. To complete these census species lists, we added occurrence data from habitat mapping campaigns carried out in these four years. For the period between 1980 and 2017, we collected occurrence data from habitat mapping campaigns, expert reports for nature conservation value of some of the sites, the species protection programme of the federal state of Baden-Württemberg and unpublished records based on the expertises of local biologists (Appendix Table S2 in Supporting Information).

Out of the species lists of all surveys, we selected 109 vascular plant species. On the one hand, the selected species can be considered typical of raised and quaking bogs and, in particular, transition mires. On the other hand, species were included that are common in peat woodlands, wet meadows and fens. Species from this second group are usually absent in undisturbed and intact bog complexes, but are widespread in degraded stands. These species were included to detect effects of drainage and eutrophication (see species’ habitat preferences in Appendix Table S3 in Supporting Information). We then checked for species with insufficient number of observations. From the initial pool of 109 target species, we removed those without repeated records and those that were not recorded by the majority of the authors or whose identification by some recorders was questionable. For example, we excluded Scutellaria minor because the species has never been recorded by Dierßen and Dierßen (1984) although its presence had been documented in bog complexes at low elevation since at least 1961 (Sebald et al., 1996). Species taxonomy follows Rothmaler (Jäger, 2017). We aggregated Dactylorhiza traunsteineri and D. majalis as D. majalis agg. because these species were not distinguished in all past surveys. Finally, 88 species remained, with a total of 5,076 occupancy change observations across all sites (for the data see Appendix Table S5 in Supporting Information). Across all sites, the mean number of occupancy change observations per species (i.e. whether a species was newly recorded at a site or no longer occurred) was 57.7 (min 1, max 118). Overall, the final database consisted of 814 species lists and a total of 72,268 presence/absence (p/a) observations, with on average 583 species records per site and 6.5 (min 1, max 16) repeated records per species per site. The lists vary in completeness. An exception is the most recent species inventory for the period 2017 to 2020, which can be considered nearly complete. The assessment of extinction events at the scale of hectares generally involves the difficulty that absences of every species have to be examined across the total area of every bog complex. Thus, even with the extensive data on which our study is based, past extinction events always pose a risk that species may have been overlooked (Beck et al., 2018). Thus, it is difficult to assess when exactly species that were absent in our last systematic survey from 2017 to 2020 went extinct. For example, Carex frigida went extinct at site 160 (Quellgebiet Sägenbach) between 1973, when the species was recorded by Dierßen and Dierßen (1984) and 2018. Within this period, the extinction could have happened any time because we had no further survey data.

2.3 | Species characteristics

Species characteristics were used to test whether the change in occupancy depended on certain traits. Types of reproduction were retrieved from the Bioflor database (Klotz et al., 2002). Species reproduce purely vegetatively or by seeds or by a combination of both. The species’ habitat preference (e.g. characteristic species of bogs and transition mires, of base-rich fens and mires) was compiled from Oberdorfer (1994), while the species’ geographic range type was extracted from Rothmaler (Jäger, 2017), coding for every species how far the geographic range extends across the five floristic zones (arctic, boreal, temperate, sub-meridional and meridional, Appendix Table S3).

2.4 | Attribution of change

We considered habitat size, distance to the closest conspecific population, climate and land use as possible drivers of the change of a species’ occupancy. Habitat size was obtained by measuring the surface area of each site using a Geographic Information System (QGIS, version 3.10.1). Area of bog sites ranged between 0.4 and 50 ha (mean 9.5 ha, median 7.1 ha). For each species, we calculated the distances between all sites in which a species occurred in any survey and then, for each site, identified the minimum distance to the closest site. For the analysis, it would have been desirable to know the area of raised and quaking bogs, transition mires and fens within the bog complex at each site. However, these habitat-specific area data are not available for most sites. If these habitats had been mapped, this has occurred only since 1993, thus precluding us to relate it to the conditions in the 1970s and 1980s. More importantly, the habitat types within bogs are mapped on the basis of species occurrences. Thus, if suitable habitat area would be defined by the presence of species for which the presence should be predicted, the whole approach would become circular.
The land use type of the bogs was recorded during the survey from 2017 to 2020. We distinguished forestry and agricultural use, which was either grazing or mowing. Bog complexes without current land use, except for maintenance measures by the nature conservation agencies, were classified as unused.

We considered to use atmospheric nitrogen deposition as potential driver for occupancy change. However, we were not able to obtain a time series from 1972 to 2019 for our study area. The Germany-wide trends show steadily decreasing atmospheric nitrogen deposition from 1990 to 2015 by more than 50% (Schaap et al., 2018). In contrast, climate data were available directly from the study region. We focused on precipitation and temperature as the most important drivers of evaporation, and thus, of mire desiccation. Climate data were obtained from the German Climate and Environment Consultancy Department (https://opendata.dwd.de/climate_environment/CDC/) for the meteorological stations 01346 (Mt. Feldberg, at 1,489 m a.s.l.) and 01443 (Freiburg, at 236 m a.s.l.), which are located in the centre and outside our study region, respectively (Figure 1). Air temperature data were available since 1921 and 1869 for Mt. Feldberg and Freiburg, respectively, while precipitation has been recorded since 1926 and 1885, respectively. The last observation year included in the analysis was 2019.

2.5 | Statistics

For each species and site, we assessed when a species was first and last recorded in any survey (Appendix Table S5, columns Year_first_obs and Year_last_obs), thus disregarding detection errors of surveys within this period. Excluding potentially wrong absences within this period is justified because the data of the intermediate surveys were mostly based on habitat mapping campaigns (Appendix Table S1), which cannot be considered complete. Our decision to disregard absences in intermediate incomplete surveys is justified also from the knowledge of the bog species’ general high persistence. Some species such as Betula nana or Drosera spec. are known from particular bog sites since the late glacial period (Dudová et al., 2014; Rösch, 2000). Thus, classical metapopulation dynamics that are characterized by frequent extinction and resettlement events across sites (Freckleton & Watkinson, 2003) cannot be expected for most study species. Typically, such species would be short-lived, highly habitat-specific, wind-dispersed and have a large amounts of seeds (Vanden Broeck et al., 2014). If the last record had been made before 2017, we also noted the year of the subsequent survey in which the species was no longer detected at that site (Appendix Table S5, Year_subsequent_survey). Using the date of the survey subsequent to one in which a species had been recorded the last time is a conservative assumption, resulting in underestimating the rate of extinctions. For each species, we calculated mean change in occupancy by counting the number of extinctions and new colonizations and dividing them by the total number of sites at which the species was encountered in any survey. For each species, we tested the null hypothesis that the number of extinctions was equal to the number of new colonizations, by applying a sign test for extinctions (−1) vs. new colonizations (+1) and using a significance level of 0.05. We carried out an analysis of variance omitting the intercept to test whether mean change in occupancy to either habitat specificity or mode of reproduction was significantly different from zero. The difference in the extension of the species’ geographic distribution ranges across the five floristic zones between declining and the whole set of species was tested with Pearson’s chi-squared test. For every declining species, we tested whether the probability of survival depended on the area of the site, distance to the next site at which a conspecific population had occurred in any survey, and altitude, using generalized linear models (glms) with logit link function and binomial error distribution. As this species-wise analysis was based on site occupancy, there was the risk that patterns were driven by spatial autocorrelation. We tested by spatial autocorrelation by applying Moran’s I statistic on the glm residuals in every model, using the MorancI function in the ape package (Paradis & Schliep, 2018). In addition, we incorporated spatial autocorrelation by expanding the glms into generalized additive models (gams). In addition to the glm part, the gam included a basis-penalty smoother spline on the sphere (bs="sos"), applied to the geographic coordinates of every site. The gams were implemented using the mgcv package (Wood, 2017). As the gams were not applicable to species with too few occurrences and did not converge in all cases, we report the p values both for the models without (glms) and with autocorrelation (gams).

The temporal change in occupancy was analysed separately for declining and increasing species (n = 37 and 46 species with a mean negative or positive change in occupancy, see Appendix Table S3). To account for the partly incomplete surveys in the first years of the investigation period, we made the assumption that all declining species were present at the beginning of the study period (1972). Thus, species could only decline, that is become extinct at sites. This assumption is reasonable as it was only applied to sites where the species was encountered at a later date than 1972. We thus did not increase the number of sites where the species was observed at any time, but only assumed that the species was overlooked before it was encountered the first time. We then plotted the decrease in relative occupancy (i.e. proportion of occupied sites, which is the number of occupied sites divided by the total number of sites at which a species had been observed in any survey) against the time when an extinction event was observed (using Appendix Table S5, Year_subsequent_survey and Ext_event). Across all declining species, we modelled the proportion of occupied sites with a general additive model (gam), using cubic regression splines. Results were similar when using the more robust approach of local polynomial regression fitting (loess), but regression splines allowed us to extrapolate the model to the time when relative occupancy reached zero, which is the year when all populations of declining populations would go extinct. We also applied these gams to estimate the year when the most declining first 12, 24 or all species would go extinct.

Likewise, we applied the same rationale to species that showed a significant mean increase in occupancy. Here, we made the assumption that a species could only increase, that is newly colonize
FIGURE 2  Relative change in occupancy of the 88 study species across the 124 bogs in this study. Red and blue dots show the mean change in occupancy with a negative and positive/neutral net change in occupancy, respectively. The red and blue areas show how much the contrasting trend of loss and gain in occupancy contribute to net occupancy. Thus, the total proportion of occurrences being lost and newly found is shown by the left-most red and right-most blue lines, respectively. * = statistically significant change according to a sign test.

FIGURE 3  Survival probability of populations as function of altitude. All species are shown that have a significant slope in a generalized linear model (at \( p < .05 \)). a) Carex pauciflora, b) Drosera rotundifolia, c) Eriophorum vaginatum, d) Parnassia palustris. e) Pinguicula vulgaris, f) Trichophorum cespitosum. For all other species, see Appendix Table S4.
In the past five decades, 37 out of the 88 species decreased in occupancy at a site, and would be present at all sites in 2020 where it had been observed at any time before. We then plotted the increase in relative occupancy against the time when a colonization event had been observed. Here, we modelled the proportion of occupied sites with a gam, using local polynomial regression fitting (loess) because the number of observations was too low for obtaining smooth curves with cubic regression splines.

At the site level, we calculated the change as the mean sum of changes in the status of occupancy (number of species that changed from 0 to 1 minus number of species that changed from 1 to 0), based on all species that showed a significant decline. Then, gsms with logit link function and binomial error distribution were used to test whether the change per site depended on site area, distance to the next site, elevation or land use. We used the predictors one by one in separate models and jointly in a multiple generalized regression model. The full model was then simplified by backward elimination of predictors using Akaile's information criterion (AIC). As for the species-wise analysis (see above), we additionally report the spatial autocorrelation of residuals using Moran's I and the results from gams with a basis-penalty smoother spline on the sphere.

To test whether the altitude of extinction events increased with time, we used all declining species and calculated linear mixed effect models, taking species as random factor. We employed AIC to compare random intercept with random slope models, where we allowed the altitude-slope relationship to vary by species.

All calculations were made with R 3.6.2 (R Core Team, 2019), using the packages sp, rgdal, maptools, data.table, ape, mgcv, dplyr, reshape2, BSDA, ImerTest and ggplot2.

### RESULTS

In the past five decades, 37 out of the 88 species decreased in occupancy, and on average, lost 33% of their initial frequency (Figure 2). Fourteen of the declining species displayed a significantly negative trend according to a sign test. Among the declining species that showed no significant trend, 11 further species lost 20% or more of initial occupancy (Appendix Table S3). Among them were two species that went extinct in the whole study area (Juncus alpinoarticulatus, Utricularia minor), which, however, had occurred in too few sites (four in both cases) to pass the threshold of significance (Appendix Table S3). Species with a significant decline decreased between 68% (Carex dioica) and 10% (Eriophorum vaginatum). Figure 2 shows that the direction of trends was quite consistent, as the proportion of occurrences with opposing trends (i.e., being newly found in decreasing species or being lost in increasing species, as indicated by the blue and red areas in Figure 2) was lower than 25% for nearly all species. Only five species did not suffer any losses (Agrostis canina, Betula nana, Calamagrostis phragmitoides, Soldanella alpina and Trifolium spadiceum, which each occurred only at one to three sites). Among the significantly declining species are not only characteristic species of raised bogs, such as Drosera rotundifolia or Vaccinium oxyccos, and moorland ponds, such as Scheuchzeria palustris or Lycopodiella inundata, but also those typical of base-rich mires, such as Carex davalliana, C. dioica or Eriophorum latifolium, as well as widespread bog species such as Eriophorum vaginatum (Appendix Table S3). In contrast, 46 species increased in the last five decades, 18 of them with a significant trend, while five species displayed no change in occupancy (Figure 2, Appendix Table S3). A significant increase was encountered for species typical of poor fens, such as Agrostis canina, and of wet meadows and fens, such as Cirsium palustre, Lotus pedunculatus or Ranunculus repens. In addition, tree and shrub species increased, such as Picea abies and Salix cinerea. Mean relative change in occupancy was not significantly related to the species’ dispersal mode or to the species range type (Appendix Table S3). All species characteristic of bogs and transition mires as well as base-rich fens and mires (categories “B” and “R” in Appendix Table S3) showed a significant decline, while those typical of fens and wet meadows (“F”) displayed a significant increase (all at $p < .0001$).

Modelling the survival probability for each of the 37 declining species as function of area of the site, isolation and altitude revealed species-specific responses to these potential drivers of extinction (Appendix Table S4 in Supporting Information). The survival of only one species depended positively on habitat area (Eriophorum vaginatum, Appendix Figure S1 in Supporting Information). Another one responded negatively to the distance to the next conspecific population (Drosera rotundifolia, Appendix Figure S2 in Supporting Information). However, the direction of trends was to some degree ambiguous, because single species also responded positively to increasing distance. In contrast, the trends with respect to altitude were unequivocal. In total, survival of six species increased significantly with altitude (Figure 3, Appendix Table S4 in Supporting Information). Summarizing the trends across all declining species at the site level and relating the proportion of extinctions per site to land use showed no significant effects ($p > .05$ for forestry, grazing, mowing and absence of use, respectively). Similarly, the proportion of extinctions per site across all 37 declining species were also not related to area of the site or distance to the next site ($p = .76$ and .48, respectively, both for the glm without and for the gam with accounting for autocorrelation). The residuals neither of the gms nor of the gams were spatially autocorrelated ($p = .928$ with Moran’s I statistic). However, there was a marginally significant relationship to altitude (glm $p = .07$, gam $p = .08$, Appendix Figure S3 in Supporting Information). This relationship became significant ($p = .006$, both for the glm and gam) when only including the 14 species with a significant decline. Altitude was also the only predictor that remained after simplifying the generalized linear model that related the proportion of extinctions of the 37 declining species to all predictors mentioned before.

When analysing the temporal course of decline of the 37 species with a decrease in occupancy relative to the initial occupancy of sites in 1972, it became apparent that for the species with largest losses such as Carex dioica, the losses occurred already before the end of the second systematic survey by biotope mapping in 1998 (Figure 4). In contrast, for species with moderate losses these losses occurred only in the last 20 years. We have to consider that the sharp declines
in many declining species in the two periods 1993 to 1998 and 2017 to 2020 may be the result of an increased survey intensity, as either extensive biotope mapping or our own systematic survey took place in this period. Therefore, the temporal curves do not reflect the exact course of the declines. At the end of the study period in 2020, 12 species had lost 50% or more of their previous occurrences. If this trend will continue, the general additive model predicts that the mean relative occupancy of these 12 species would have reached zero by the year 2042. Another 12 species would be completely lost by the year 2067, and all 37 declining species would have gone extinct by the year 2,161. Out of the 37 declining species, 16 are typical of base-rich mires and 14 of bogs. In contrast, no typical bog species showed an increase. Out of the 46 increasing species, 19 were fen species and 16 were meadow species (Appendix Table S3). The temporal course of newly found occurrences shows that these species increased either in the 1990s or between 2010 and 2020 (Appendix Figure S4 in Supporting Information).

Altitude of extinction events across all 37 decreasing species increased with time (Figure 5). The altitudinal mean of extinction events increased by 17.86 m per decade, or about 89.3 m over the whole study period from 1972 to 2020. The temporal course of extinctions (Figure 4) coincided with an increase in air temperature (Figure 6). While mean annual temperature did not significantly increase before 1972 in Freiburg outside the study area, it significantly increased since then, by 1.1K between 1972 and 2019, which is 0.23K/decade. This temperature increase at Mt. Feldberg was much stronger than in Freiburg. During the investigation period from 1972 to 2019, mean annual temperatures at Mt. Feldberg increased by 1.75K or 0.37K/decade. While precipitation showed no significant trend at Freiburg, since 1926 it decreased by 337 mm or 36 mm/decade at Mt. Feldberg.
4 | DISCUSSION

The overall decrease in species occupancy and the high number of significantly declining species fully support our first hypothesis of ongoing species extinctions in the Black Forest bog complexes. Almost all studied species (94%) suffered from local extinctions, which is much higher than the 39% of the plant species in a global meta-analysis on climate-related local extinction (Wiens, 2016). The magnitude of extinction events is unprecedented for bog habitats in Central Europe in the last 30 years and is only comparable with destruction of peatland habitats in the 19th and 20th century (Joosten et al., 2017; Walker & Preston, 2006).

Overall, we only find little support for the impact of habitat area, isolation and land use for the decline of species and have to reject these parts of hypothesis 2 and 3. These findings conform to other studies that neither detected an effect of habitat area on fen vegetation in the Western Carpathian Mountains (Horsák et al., 2018) or only weak effects of isolation (Krause et al., 2015). With respect to the absent effect of land use, we have to acknowledge that our land use assessment only reflected the most recent situation from 2017 to 2020 and thus, might not capture past conditions. The lack of influence of mowing on the decline of species might be explained by a more recent application of this land use type as management measures of Natura 2000 habitats in the last two decades (LUBW, 2017). Similarly, grazing intensity has increased in the Black Forest in recent years. From our data, we cannot conclude whether mowing and grazing contributed to the species decline or rather alleviated it. Overall, we only find little support for the impact of habitat area, isolation and land use for the decline of species and have to reject these parts of hypothesis 2 and 3.

In contrast, the strong effect of altitude on the decline of peatland species in the Black Forest points to climate impacts. Altitude was the most important driver at the level of species (hypothesis 2) and sites (hypothesis 3). Furthermore, the decline in occupancy strongly mirrored the increase in temperature and decrease in precipitation. Peatland species are supposed to be most threatened from climate change. Of the 84 plant species for which Normand et al. (2007) assessed the proportional change in bioclimatic suitability, those growing in raised bogs and fens lost most of their suitable habitat space. The loss ranged between −48% and −65%, depending on the chosen climate change scenario. A study modelling the impact of environmental variables (climate, soil conditions, land cover, topography) on the geographic distribution of 18 vascular plant species in southern Germany found the mire species Carex limosa and C. pulicaris to be particularly dependent on climate (Buse et al., 2015). For example, populations of C. pulicaris that went extinct in West Germany in the period 1950–2009 occurred at lower elevation at sites that were warmer and drier than extant populations (Buse et al., 2015). Our finding that base-richness indicators are disproportionately stronger declining than other peatland species contrasts reports from the Carpathians, where, for example, the occurrence of Eriophorum latifolium and other calcareous fen species responded positively to warmer conditions (Horsák et al., 2018). However, given that base-richness indicators in bog habitats are highly specialized species, the strong decline in this group conforms to findings that specialist species suffer the highest extinction risk (Walker & Preston, 2006). Accordingly, in studies on calcareous grassland species in Switzerland (Fischer & Stöcklin, 1997) or prairie species in Kalamazoo County (Michigan, USA; Zettlemoyer et al., 2019) habitat specialists contributed to the highest proportion of local extinctions. In addition, very low germination rates have been reported for the majority of our declining bog species (Poschlod, 1990). Colonization by generative reproduction events is highly unlikely for these species, which was also apparent in the absence of any significant effect of the species’ dispersal mode on change in occupancy. That the species’ degree of decline did not depend on the species’ geographic

FIGURE 6 Temporal course of climate in the study region. a) Mean annual air temperature (MAT) and b) precipitation (MAP) at Mt. Feldberg (1,489 m, highest elevation in the study region) and c) MAT and d) MAP at Freiburg (236 m, outside the study region). Solid lines = significant linear regressions at p < .05, broken lines = insignificant trend. For MAT, separate regressions were calculated for before (<1972) and within the study period (≥1972)
distribution range types can be explained by the selection of all study species, which almost exclusively had ranges extending into the boreal and arctic zone. However, compared with the whole flora of that region, these species with distribution into arctic and boreal ranges can be expected to suffer most from climate change (Wiens, 2016).

Climate change particularly affects the bog complexes in summer, when increased evapotranspiration results in superficial drying up. During our studies from 2017 to 2020, it was not uncommon to walk over the raised bogs with dry feet (pers. obs.). This resulted in decreased waterlogging and increased mineralization, which promoted species of fens and wet meadows, which significantly increased in particular in the last two decades. Recurrent droughts may contribute to a decrease of spring water influx into transition mires. This would explain the disproportionately large losses of base indicator species as in the studied bog complexes, these species depend on cations and comparably high pH values brought about by spring water (Flintrop, 1994). In single cases, establishment of drinking water wells in the water catchment area of the bog complexes may have contributed to lowering the groundwater table. Other rare interventions in the water table regime are road constructions (von Sengbusch, 2015). Unfortunately, the unsystematic spacing of observation events precludes a closer analysis on the relationship of species declines with particular drought events. As pointed out above, the moderate losses between 1999 and 2016, resulting in the less steep slope of the regression line in Figure 4, cannot be interpreted as a period of fewer extinctions, but was probably only brought about by fewer observations in this interval.

Of course, we cannot rule out further factors that drove species extinctions, such as atmospheric nitrogen additions. It is an open question, whether without temperature and precipitation change, nitrogen deposition alone might have caused similar trends. In a field manipulation experiment, Olid et al. (2017) demonstrated that nitrogen addition alone increased availability of other nutrients. As a consequence, the combination of warming and nitrogen addition accelerated peat decomposition (Gerdol et al., 2007). This would have resulted in more suitable conditions for fen and wet meadow species, as we observed in our study. However, we have no means to estimate nitrogen deposition effects that accumulated over time. Models that show nitrogen critical load exceedance values (Schaap et al., 2017) have a too low spatial resolution to be applicable for our site-based analysis. Considering that wet deposition in more natural regions in Germany is about ten times more important than the dry flux (Schaap et al., 2017) and that wet deposition increases with precipitation (Kruif et al., 2014), nitrogen deposition would be expected to increase with elevation, with concomitant effects on the bog vegetation. However, we observed the opposite effect with extinction rates decreasing with elevation. This would imply that increased wet N deposition rates are less harmful for bog plant species as long as precipitation is sufficient. Evidence for the interpretation is provided by an experimental increase of wet nitrogen deposition in a Scottish bog, where up to 56 kgN/ha\textsuperscript{-1} yr\textsuperscript{-1} caused only few significant changes in cover of the bog species and did not result in considerable changes in community composition over nine years (Sheppard et al., 2014).

We could demonstrate that the mean altitude of extinction events increased with time, thus confirming hypothesis 4. This finding evokes the picture of an extinction wave that climbs upslope. According to our model extrapolations, this wave will have reached the highest peaks in about 30 years. In contrast to the Alps (Rumpf et al., 2018), the Andes (Morueta-Holme et al., 2015) or Hawai‘i (Koide et al., 2017), where climate warming has resulted in upwards shifts of plant ranges, the low-mountain ranges of Central Europe, such as the Black Forest, do not provide alternative habitats at higher altitude. Here, bog species suffer the same fate as mountain-top species, for which a global significant range shrinkage has been documented (Freeman et al., 2018). Thus, it can be expected that these low-mountain habitats suffer more from biodiversity loss than high mountains.

Our study highlights the value of systematic and comprehensive past biodiversity surveys to assess biodiversity change. Without the meticulous work of Dierßen and Dierßen (1984) the changes, we report here would have happened undocumented. Most of the difficulties we encountered were not the availability of records of species presences but absences. Such absences are notoriously difficult to document, but are the key for reliable temporal models. Thus, we would recommend for future nature conservation monitoring programmes to spend a defined effort on the documentation of lacking target species. In addition, detectability of changes is much larger when being based on population density (Lesica & Crone, 2017). It should be considered to start monitoring populations of individual plants of the strongly declining species. We would also suggest to map the available habitat area of raised and quaking bogs, transition mires and fens within the bog complex at each site. Finally, our findings of a strong signal of climate on bog species extinctions in the Black Forest in Central Europe have general implications for peatland vegetation in mountain ranges of similar altitudinal limits worldwide. While many studies have already alerted the scientific community about the vulnerability of such systems in Central Europe (Essl et al., 2012) or eastern North America (Schultheis et al., 2010), ours are the first to document that these changes have already happened. Obviously, management options for bog complexes against rising temperatures and decreasing precipitation are strongly limited. No countermeasure is conceivable against the physiological effects of rising temperatures. Rewetting measures of raised and transitional bogs (Hedberg et al., 2012) would become ineffective with increasingly long drought periods that can be expected in the future. However, a very sophisticated irrigation system fed by reservoirs or groundwater bodies may preserve some of the bog species in this climate zone. These irrigation measures would also be counteract the rapidly increasing peat mineralization and thus prevent a further increase in release of CO\textsubscript{2}.

ACKNOWLEDGEMENTS

We are grateful to Barbara and Klaus Dierßen for their seminal work. We would like to express our gratitude to Anja Görger as the Officer for Species Protection at the regional council of Freiburg...
and to Dietlinde Köppler and Carola Seifert (botanists and environment project managers) without their support this study would not have been possible. We are grateful to Gunnar Seidler for preparing the map, to Erik Welk for providing the information on the geographic ranges and to Ute Jandt for proofreading. We much appreciate the support of the German Research Foundation (DFG) for funding the sMon working group (trend analysis of biodiversity data in Germany) as one of iDiv’s strategic projects (DFG FZT 118, 202548816). The manuscript was greatly improved by very competent comments of three anonymous reviewers and the handling editor Amanda Taylor. Open access funding enabled and organized by ProjektDEAL.

AUTHORS’ CONTRIBUTIONS
TS and HB conceived the idea, designed the study and wrote the manuscript. TS collected the data; HB analysed the data.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13184.

DATA AVAILABILITY STATEMENT
All survey data are included in: Bruehlheide, Helge; Sperle, Thomas (2020), Table S5: Occupancy change observations in bog species in the Black Forest (Germany) across all sites from 1972 to 2019, Dryad, Dataset, https://doi.org/10.5061/dryad.mw6m905vj.

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SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Sperle T, Bruelheide H. Climate change aggravates bog species extinctions in the Black Forest (Germany). Divers Distrib. 2021;27:282–295. https://doi.org/10.1111/ddi.13184