

## LETTER

# European Habitats Directive has fostered monitoring but not prevented species declines

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## Abstract

Strong biodiversity declines have been reported across the European Union, especially in insects, despite conservation policy such as the Habitats Directive that aims to halt biodiversity loss. Using 50 years of observational data, we examined indicators for the goals of the Directive in terms of improving monitoring efforts and occupancy trends of butterfly and dragonfly annex species in a central European region. We quantified annual monitoring effort and used occupancy-detection models to compare species trends for 18 years before and after legal implementation of the Directive. Monitoring efforts increased after implementation, while occupancy trends both improved and deteriorated. Contrary to its main goal, the European Habitats Directive did not prevent a worsening of all annex species' occupancy trends in the studied region. While the increased monitoring efforts aid biodiversity assessments, more serious broad-scale conservation measures are needed to halt biodiversity loss across Europe.

## KEYWORDS

biodiversity monitoring, Central Europe, Germany, insect conservation, insect declines, Lepidoptera, Natura 2000, Odonata, policy evaluation, special areas of conservation

## 1 | INTRODUCTION

Across the world, various policy and legal instruments have been enacted to halt and reverse biodiversity loss at national and international scales. In Europe, an important general instrument is the Habitats Directive (European Commission, 1992), a cross-country protective framework aiming to “ensure the long term survival of Europe’s most valuable and threatened species and habitats” that was adopted in 1992 (European Commission, 2021a). The Directive entails multiple obligations for participating countries, including regular reporting obligations on annex species as well as conservation actions such as protecting species

listed in annex IV across their whole range, and establishing protected areas (Special Areas of Conservation) for habitats and species listed in annexes I and II. Management plans for protected areas are required to preserve and restore optimal conditions, for example, by coordinating mowing times to support butterfly development (e.g., Dolek et al., 2017).

Although the Habitats Directive prohibits the deterioration of habitats and annex species, the European Union’s target of halting biodiversity loss by 2010 was not achieved (Butchart et al., 2010; European Environment Agency, 2009). Currently, the annexes list 117 insect species, but insect data are typically sparse and only few countries have

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established standardized monitoring schemes, despite the Directive's reporting obligations. Moreover, multiple studies have shown insect declines in Europe and beyond (e.g., Dirzo et al., 2014; van Klink et al., 2020; Wagner, 2020). Some of the strongest declines have been shown for insects in different regions of Germany (Hallmann et al., 2017; Seibold et al., 2019), but it is unclear whether these case studies represent wider declines.

By analyzing rarely used long-term occurrence datasets for multiple insect taxa, we examined indicators of the success of the Habitats Directive in the German federal state of Bavaria in terms of both species reporting and halting biodiversity loss. First, we analyzed whether the Habitats Directive has differentially affected monitoring efforts toward annex species compared with non-annex species. We expected increasing monitoring efforts, as EU member states are expected to submit regular reports on the status of annex species. Second, we compared the occupancy trends of annex species before and after legal implementation of the Directive using occupancy-detection models to account for heterogeneity in effort. In line with the main goal of the Directive, we expected annex species to either improve their occupancies or stay stable after implementation in national law in 1998, including possible delays to assumed improving conditions. We focused on annex species from two comparably well-sampled insect taxa, butterflies (Lepidoptera, Rhopalocera) and dragonflies and damselflies (Odonata, henceforth "dragonflies"). We show that while monitoring effort toward annex species has increased in various ways, some annex species are still declining, indicating that current protective measures are not yet sufficient. Our findings suggest that legal conservation instruments need more prioritization as well as explicit and measurable requirements. Modeling techniques such as occupancy models provide one approach to produce reliable species trends using the available data in order to evaluate the effectiveness of conservation policies.

## 2 | METHODS

### 2.1 | Data basis: Species occurrence data

Our analysis is based on occurrence records collected by the Bavarian Environment Agency (Bayerisches Landesamt für Umwelt/LfU) for 203 butterfly species (Lepidoptera, Rhopalocera) and 76 dragonfly species (Odonata), covering the federal state of Bavaria, Germany (70,542 km<sup>2</sup>). Data collected over the past 50 years of this database ("Bayerische Artenschutzkartierung (ASK)," [www.lfu.bayern.de/natur/artenschutzkartierung](http://www.lfu.bayern.de/natur/artenschutzkartierung)) are mostly the result of ongoing semi-systematic surveys

initiated in the 1980s by Bavarian officials, but also include previous collections (Bräu et al., 2013; Kuhn & Burbach, 1998; see also Engelhardt et al., 2022 for details). All records are validated by experts.

### 2.2 | Monitoring effort

To assess whether legal implementation of the Habitats Directive in 1998 increased monitoring effort toward annex species, we analyzed occurrence data since 1970. We calculated the annual number of occurrence records and the observed number of species, which reflect the combined efforts of all surveys in a year but might be affected by species' abundances. We also calculated the numbers of sampling days, of projects for the targeted recording of annex species, and of general project types, which summarize individual monitoring projects with a common aim. These metrics are independent of species' occurrences and reflect the monitoring efforts by officials. For each metric, we quantified the annual total numbers and the proportion of annex species' numbers out of all including non-annex species. We assumed that the total number of both annex and non-annex species indicates the general monitoring effort for each year, while the proportion of annex species in each metric indicates whether monitoring efforts focused on annex species changes. To visualize temporal changes of these metrics for annex compared with non-annex species, we fitted binomial generalized additive models from the R-package MGCV (Wood, 2006) with year as a spline term. The effective degrees of freedom (edf) indicate whether the relationship with time is linear (edf = 1), weakly non-linear (edf > 1 and < 2), or highly non-linear (edf > 2) (Zuur et al., 2009). We compared generalized additive models with generalized linear models with and without a year effect, based on the models' Akaike information criterion (Akaike, 1974). We assumed that in contrast to a lack of effect of year, evidence of a non-linear increase is consistent with a positive effect of the Directive, while a linear increase indicates a general, independent increase of monitoring effort.

### 2.3 | Species trends

To analyze effects of the Habitats Directive on species trends, we modeled species' occurrence probabilities from 1980 to 2019 (Engelhardt et al., 2022), and then compared species linear trends before and after implementation of the Directive, as well as all possible trend changes since 1980. We focused on this period because of the reasonably high observation numbers across all species (lowest number of yearly records: butterflies 996, dragonflies 357;

lowest number of sampled grid cells in a year: butterflies 105, dragonflies 48).

### 2.3.1 | Occupancy-detection models

We conducted our occupancy models following Kéry (2011) and Outhwaite et al. (2018). We first mapped the records to the common German grid of approximately 5 km × 5 km cells (TK25 quadrants). We estimated species annual occurrence probability over 40 years (1980–2019) by modeling the proportion of grid cells occupied by a species per year with the standard deviation (SD) of this estimate as a measure of its uncertainty. We estimated model convergence using the Gelman–Rubin statistic (Rhat, Gelman & Rubin, 1992). For details on the models, see Supporting InformationS1.

### 2.3.2 | Assessment of species' trends

We estimated each species' occurrence trend before and after legal implementation of the Habitats Directive in 1992. We calculated linear trends of 18 years before (1980–1998) and after (2000–2018) implementation, allowing for 2 years of transition. We fitted generalized linear models with year as a continuous predictor variable and annual occupancy estimate as the response, using the inverse of the occupancy estimate's standard deviation (1/SD) as weights to decrease the impact of years with greater uncertainty of the predicted annual occupancy estimate on the linear trend. We compared species' trends before and after implementation by adding a Before- versus After-interaction term to the year effect in the linear model ( $occupancy \sim year \times time-period$  where *time-period* is a factor with two levels—before vs. after). Species were classified as increasing if their 95% confidence intervals (CIs) on the trend changes were positive, as decreasing if the CIs were negative, and as unclear/stable if the CIs overlapped zero. We classified the results as unreliable for species whose model mean or median Rhat values during at least one of the study periods was above or equaled 1.1; in these cases, a comparison of the trends was not possible (compare Table S5). We used a chi-squared test to test the association between trend changes and annex status.

### 2.3.3 | Assessment of changes in trend direction

We additionally used a more flexible temporal analysis to examine how close changes in species' occupancy trends matched the changes in legislation. To analyze

whether species show changes in the directions of their trends in certain years, we fit segmented linear models to their annual occupancies. We used the SEGMENTED.LM function of the R-package SEGMENTED (Muggeo, 2017), see Supporting InformationS2 for details. We defined those breakpoints as improving where the change was from decrease to increase, decrease to stable, or stable to increase. We defined breakpoints as deteriorating if the change was from increase to decrease, increase to stable, or stable to decrease.

We conducted all analyses in R version 4.0.2. (R Core Team, 2020).

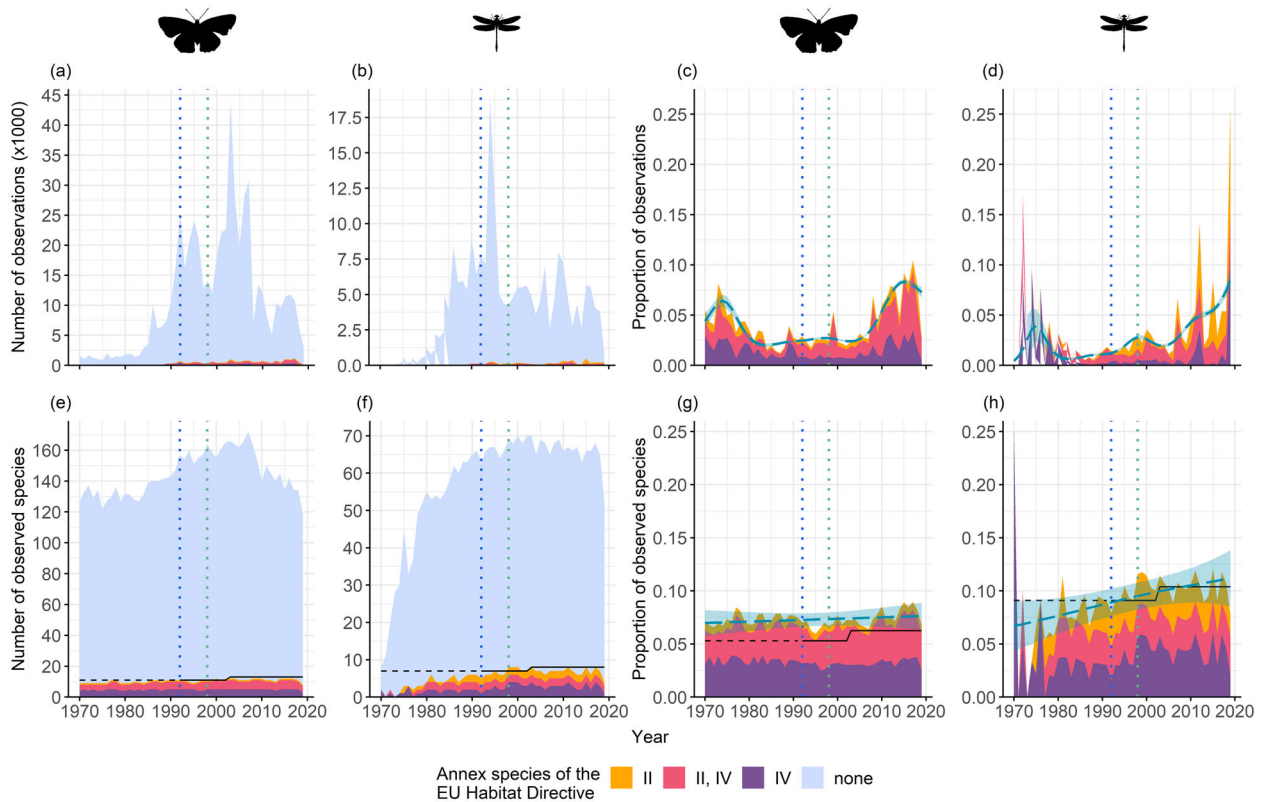
## 3 | RESULTS

### 3.1 | Monitoring effort

The European resolution for the Habitats Directive in 1992 came at a time of already increasing monitoring efforts in our study region, due to the establishment of a database of occurrence records starting in the 1980s. In the late 2000, the number of occurrence records, number of observed species and sampling days began to decrease again (Figures 1 and 2). However, this decrease did not affect annex species, leading to increasing proportions of observations of annex species and significant, non-linear relationships with time in most metrics of monitoring effort (observation numbers—butterflies: edf = 8.94, dragonflies: edf = 8.91, Figure 1a–d; sampling days—butterflies: edf = 7.85, dragonflies: edf = 6.15, Figure 2a–d; all *p*-values < 0.001; see Table S3).

The first projects targeting annex species were established after 1992 for butterflies (see Figure 2i,j), but their number strongly increased only after 2006 when targeted dragonfly monitoring started as well (butterflies: edf = 3.39, dragonflies: edf = 3.6, both *p*-values < 0.001, Figure 2k,l). Nevertheless, the proportion targeting annex species did not consistently change, remaining under 25% of all projects. The increase could be linked to a general increase in the number of monitoring projects. For both taxa, the number of project types increased strongly after legal implementation of the Directive (Figure 2e,f), but the proportion reporting annex species had a non-significant relationship with time (butterflies: edf = 1, *p*-value = 0.0628, dragonflies: edf = 1, *p*-value = 0.0531; see Figure 2g,h).

The total number of observed species increased over time for both butterflies and dragonflies, but the number of observed butterfly species strongly decreased since the late 2000s (Figure 1e–h). Butterflies and dragonflies also differed in how much this change was due to annex species. For dragonflies, the proportion of observed annex species



**FIGURE 1** Monitoring efforts during the past 50 years (1970–2019). The colours represent the annexes in which the species are listed. Dotted vertical lines in blue indicate the year 1992 when the European Union implemented the Habitats Directive, and lines in green indicate the year 1998 when Germany implemented the Habitats Directive in national law. (a), (c), (e), (g): butterfly data; (b), (d), (f), (h): dragonfly data. (a), (b): Total number of occurrence records; (c), (d): Proportion of observations of annex species, blue line represents the generalized additive model with light blue ribbons indicating 95% confidence intervals, (e), (f): Number of observed species, horizontal line marks the full number of annex species, where in 2003 two butterfly and one dragonfly species were added. (g), (h): Proportion of observed species, blue line represents the generalized additive model with light blue ribbons indicating 95% confidence intervals, horizontal line marks the proportion of annex species.

linearly increased, with the trend starting before the Directive (edf = 1.27,  $p$ -value = 0.0495; see Table S3). However, for butterflies, the proportion of observed annex species remained mostly constant over time (see Table S4).

### 3.2 | Species trends

Before the Directive, six species were declining, three were stable, and 10 were increasing (see Table S8). Since the year 2000, following legal implementation, five species declined, four species were stable, and nine species showed positive trends (see Table 1). One species went extinct (*Colias myrmidone*), for others we were unable to assess reliable occupancy estimates throughout the study period (*Gomphus flavipes*) or during the period before the Directive (*Coenonympha oedippus*, *Lycaena dispar*). When we compared recent trends with those before implementation (see Figure 3), eight species improved, six of them now increasing, while nine species deteriorated, five of which are now decreasing (compare Figures S6 and S7). We did

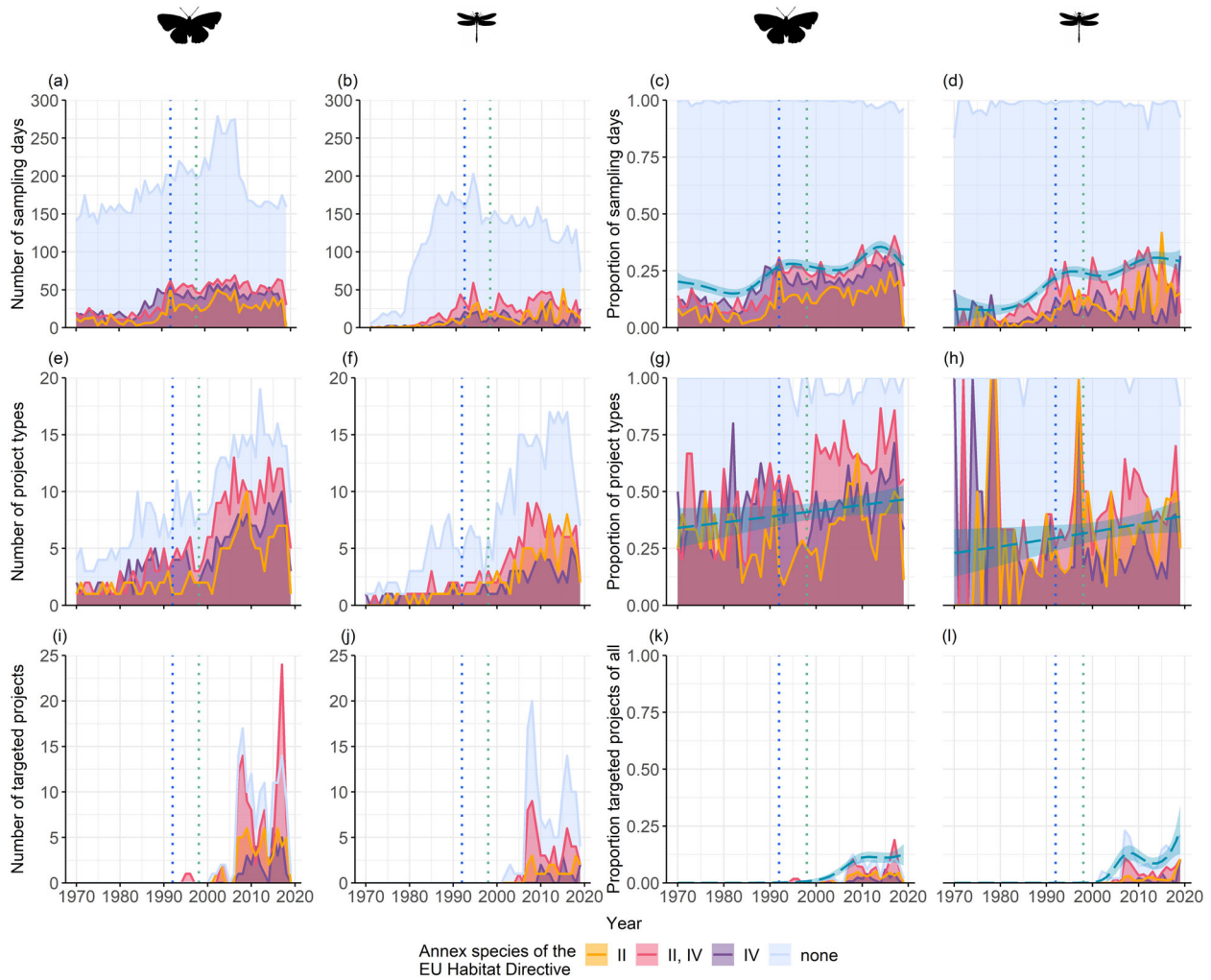
not find an association between annex status and species trend change from before to after implementation of the Directive (X-squared = 3.79,  $p$ -value = 0.15). Additionally, we did not find a relationship between temperature preference and species trend change (see Figure S10).

Segmentation analysis revealed 16 improving and 21 deteriorating trend changes among annex species (see Figure 4), and two species with stable trends, over the whole study period (compare Table S9). We found shorter term change following implementation of the Directive. While five annex species improved in the 3 years following implementation, three of those deteriorated in later years. Since 1998, another three annex species showed improvements and six species deteriorated.

## 4 | DISCUSSION

Our results demonstrate that while we found increased monitoring efforts toward annex species after legal implementation of the Habitats Directive, it did not halt








**FIGURE 2** Monitoring efforts during the past 50 years (1970–2019), where. Dotted vertical lines in blue indicate the year 1992 when the European Union implemented the Habitats Directive, lines in green indicate the year 1998 when Germany implemented the Habitats Directive in national law. (a), (c), (e), (g), (i), (k): Butterfly data. (b), (d), (f), (h), (j), (l): Dragonfly data. (a), (b): Yearly number of sampling days. (c), (d): Proportion of sampling days on which annex species were reported, and dashed blue line represents the generalized additive model with light blue ribbons indicating 95% confidence intervals. (e), (f): Yearly number of project types that describe categories summarizing individual projects with a common aim or a certain group of people sampling repeatedly. (g), (h): Proportion of project types reporting annex species, dashed blue line represents the generalized additive model with light blue ribbons indicating 95% confidence intervals. (i), (j): Number of individual projects dedicated toward sampling of species listed in the Habitats Directive. (k), (l): Proportion of individual projects for the targeted recording of annex species of the Habitats Directive of the total number of projects, dashed blue line represents the generalized additive model with light blue ribbons indicating 95% confidence intervals. For details on the generalized additive models, see Table S3.

deteriorations in all annex species’ occupancy trends. Contrary to the Directive’s main goal of preventing a worsening of species’ status, occupancies of several species deteriorated. Other annex species, however, improved their occupancies or remained stable. As about 11% of the study region is protected under the European framework (Bayerisches Staatsministerium für Umwelt und Verbraucherschutz, 2021), only a small fraction of these trends may be attributed to local conservation measures. The contrasting trends of annex species indicate that the Habitat Directive has so far been insufficient at a regional level.

While by now the Directive has been implemented in German as well as in regional law, its protective power could be called into question, as our species trends indicate, as well as other studies showing decreasing species richness in butterflies (Rada et al., 2019) and declines in insect biomass (Hallmann et al., 2017) even in protected areas. Large proportions of habitat types listed to be protected under the Directive are in bad or insufficient condition and deteriorating (Adelmann, Hoiß, Riehl, & Stein, 2017).

Conflicts arise over different land-use priorities, with nature protection measures being relatively underfunded

**TABLE 1** Overview of recent trends of butterfly and dragonfly species protected under the European Union's Habitats Directive present in the German state of Bavaria

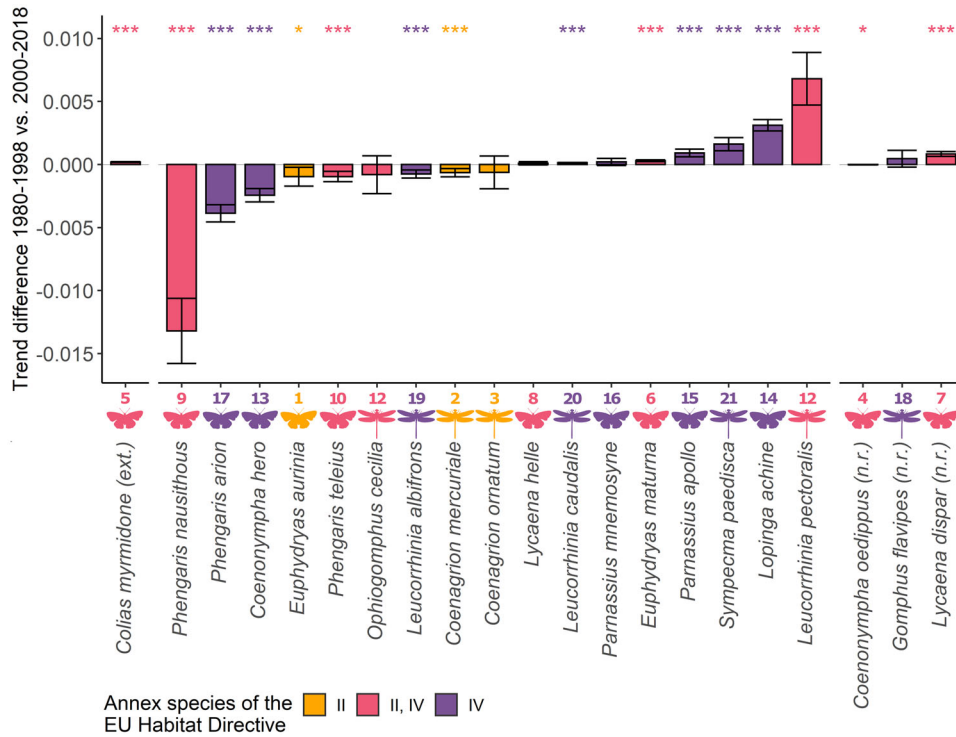
Annex	Order	Species	Trend 2000–2018		l. CI	u. CI	Compared 1980–1998
II		<sup>1</sup> <i>Euphydryas aurinia</i>	−0.0011	**	−0.0017	−0.0005	Deteriorating
		<sup>2</sup> <i>Coenagrion mercuriale</i>	−0.0002	*	−0.0004	0.0	Deteriorating
		<sup>3</sup> <i>Coenagrion ornatum</i>	0.0008		−0.0002	0.0019	Unclear/stable
II, IV		<sup>4</sup> <i>Coenonympha oedippus</i>	0.0		0	0	Unreliable
		<sup>5</sup> <i>Colias myrmidone</i>	0.0		0	0	Extinct
		<sup>6</sup> <i>Euphydryas maturna</i>	0.0001	*	0	0.0001	Improving
		<sup>7</sup> <i>Lycaena dispar</i>	0.0008	***	0.0006	0.0010	Unreliable
		<sup>8</sup> <i>Lycaena helle</i>	0.0004	***	0.0003	0.0005	Improving
		<sup>9</sup> <i>Phengaris nausithous</i>	0.0014		−0.0005	0.0032	Deteriorating
		<sup>10</sup> <i>Phengaris teleius</i>	0.0007	***	0.0004	0.0011	Deteriorating
		<sup>11</sup> <i>Leucorrhinia pectoralis</i>	0.0012		−0.0002	0.0026	Improving
		<sup>12</sup> <i>Ophiogomphus cecilia</i>	0.0027	**	0.0011	0.0042	Unclear/stable
		IV		<sup>13</sup> <i>Coenonympha hero</i>	−0.0023	***	−0.0026
<sup>14</sup> <i>Lopinga achine</i>	0.0022			***	0.0019	0.0025	Improving
<sup>15</sup> <i>Parnassius apollo</i>	0.0002			*	0.0	0.0003	Improving
<sup>16</sup> <i>Parnassius mnemosyne</i>	0.0004			*	0.0001	0.0007	Improving
<sup>17</sup> <i>Phengaris arion</i>	−0.0015			***	−0.0020	−0.0010	Deteriorating
<sup>18</sup> <i>Gomphus flavipes</i>	0.0004				−0.0004	0.0011	Unreliable
<sup>19</sup> <i>Leucorrhinia albifrons</i>	−0.0004			*	−0.0007	−0.0001	Deteriorating
<sup>20</sup> <i>Leucorrhinia caudalis</i>	0.0001			***	0.0001	0.0002	Improving
<sup>21</sup> <i>Sympecma paedisca</i>	0.0003				−0.0001	0.0007	Improving

Note: Annex II species require the designation of Special Areas of Conservation, while annex IV species are under strict protection but occur in larger habitats or scattered. Icons indicate the order, each annex category first showing butterfly and then dragonfly species. Species' linear occupancy trends (Trend) since after implementation of the Habitats Directive from 2000 to 2018, calculated using generalized linear models on occupancy model results (see Figure S6 for occupancy models). Asterisks indicate the level of significance for effects with  $p < 0.05$  (\*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $p < 0.05$ ). l. CI gives lower 95% confidence intervals, u. CI gives upper 95% confidence intervals of the trends. Compared 1980–1998 gives a comparison of the trends before implementation of the Habitats Directive in 1998 with the trend after, see also Table S8 for trends from 1980 to 1998 and Figure S7. Improving: positive trend changes; deteriorating: negative trend changes; unclear/stable: 95% CI of change overlaps zero; extinct: no more observations and modeled occurrence of the species after implementation of the Habitats Directive is zero; unreliable: model reliability (based on Rhat) not deemed sufficient to provide reliable model results during at least one of the study periods (compare Table S5). Lighter font indicates low model reliability (Rhat) throughout both study periods; therefore, neither an after nor a before the trend for comparison can be provided. Species are numbered for comparison to Figures 3 and 4.

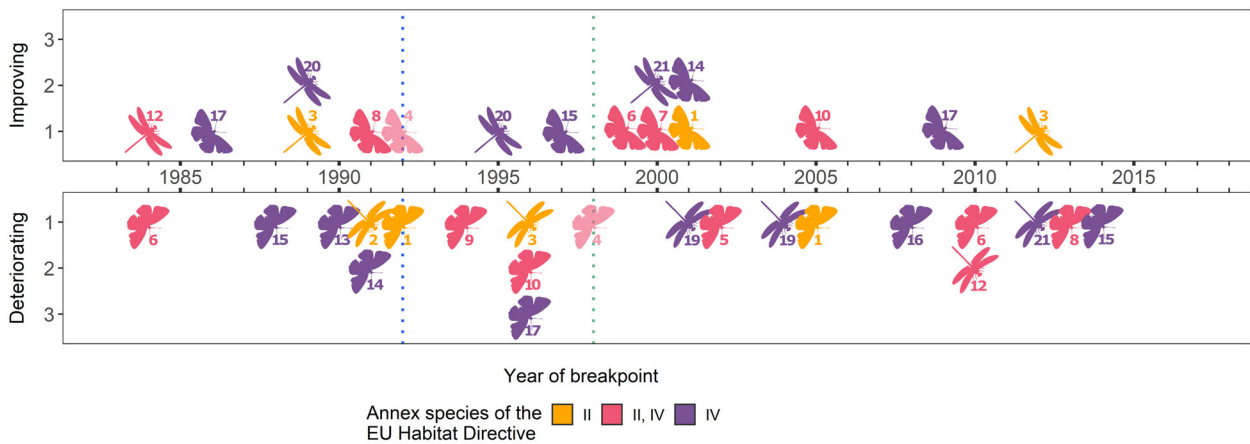
compared to, for example, the European Common Agricultural Policy (CAP) (Hodge, Hauck, & Bonn, 2015). Additionally, the implementation of both agricultural measures aiming to align agriculture and conservation in the CAP and conservation measures defined by management plans of the Habitats Directive is carried out voluntarily (Bayerisches Staatsministerium für Umwelt und Verbraucherschutz, 2021). Such soft rules are unhelpful when trying to protect annex species and habitats against systemic problems like pesticides, fertilizers, or other factors associated with high land-use intensity (Habel, Ulrich, Biburger, Seibold, & Schmitt, 2019; Seibold et al., 2019), while at the same time active, careful

site management is necessary especially for butterflies (Rundlöf, Bengtsson, & Smith, 2008; Scherer, Löffler, & Fartmann, 2021; van Swaay et al., 2012). Currently, Germany is being sued again by the European Commission because of the poor implementation of the Habitats Directive in general (European Commission, 2021b) and insufficient protection of flower-rich meadows (European Commission, 2021c). Our study is in agreement with the notion that stronger conservation action is needed at a landscape level (Maes et al., 2013).

Recent studies indicate that protected areas, which mainly target well-sampled groups like mammals or birds, are not necessarily suitable for insect protection. For



**FIGURE 3** Trend change between before (1980–1998) and after (2000–2018) legal implementation of the Habitats Directive in 1998, as proportion of occupied grid cells. Colors indicate the annexes species are listed in, species symbols indicate order, numbers are for comparison to Figure 4. Ext. = species went extinct during the “after” period; n.r. = non reliable trend estimates, model reliability (Rhat) not deemed sufficient to provide reliable model results during at least one of the study periods (compare Table S5). Asterisks indicate level of significance for effects with  $p < 0.05$  (\*\*\*)  $p < 0.001$ ; (\*\*)  $p < 0.01$ ; (\*)  $p < 0.05$ ). Error bars indicate 95% confidence intervals. For linear trends before and after 1998 see Figure S7, Table 1 and Table S8.



**FIGURE 4** Best estimate of years of breakpoints from segmented linear models on occupancy models of Habitats Directive annex species between 1980 and 2019. Colors indicate the annexes and lighter colors indicate unreliable occupancy estimates. Numbers indicate the species (compare for example, Table 1). Upper panel indicates improving trend changes, lower panel indicates deteriorating trend changes. See Figure S6 for single species occupancy models and Table S9 for single species information and confidence intervals.

instance, while the designated Special Areas of Conservation appear sufficient with regard to global protection targets (Beresford, Buchanan, Sanderson, Jefferson, & Donald, 2016), terrestrial vertebrates and increased connectivity of protected area networks (Koleček et al., 2014;

Maiorano et al., 2015; Trochet & Schmedler, 2013), studies focusing on invertebrates have come to more pessimistic conclusions regarding insect coverage (D’Amen et al., 2013; Guareschi, Bilton, Velasco, Millán, & Abellán, 2015; Trochet & Schmedler, 2013), except for butterflies (van der

Sluis et al., 2016; Verovnik, Govedič, & Šalamun, 2011). Especially in the face of climate change, which has been shown to affect insect long-term trends (Engelhardt et al., 2022), a wider consideration of different taxa is needed. However, a large-scale, cross-taxon assessment of the effectiveness of conservation measures is often hampered by a lack of reliable landscape-level data.

For the success of nature conservation targets like the European biodiversity strategy for 2030 (European Commission, 2021a), clear guidelines are needed to assess the effectiveness of conservation actions. The increased monitoring effort that we found might also be a result of strict requirements for regular reports, indicating the effectiveness of measurable requirements for which countries can be held responsible. Modeling techniques, such as occupancy models, could use these data to help create a baseline to which present species' trends can be compared especially with regard to understudied groups such as insects. Therefore, it is important to not only increase future monitoring efforts (e.g., Warren et al., 2021), but also use existing datasets on past species observations in combination with modern modeling techniques to assess the effectiveness of conservation measures. We have shown here how opportunistic data can be used to assess trends of species, but the data could also be used to assess the evidence-base for the effectiveness of conservation actions using a counterfactual approach (Ferraro & Pressey, 2015).

While we are raising some concerns regarding the effectiveness of the Habitats Directive, our study comes with three limitations that need to be considered. First, the increased monitoring efforts that we find in our database might not be a consequence of the Directive, but of independent efforts by the Bavarian Environment Agency to collect observations into their database. However, we would argue that the database is a good representation of public and institutional interest in insect monitoring. Second, also with regard to our occupancy models, the data basis for small-ranged species such as most of the annex species might be limited, which could potentially affect the reliability of modeled trends (but see also Out-hwaite et al., 2018). Lastly, local increases or decreases in species' abundances are possible despite different overall mean occupancy trends, as the latter use the whole spatial coverage of species, which could be decoupled from local population trends (Dennis et al., 2019; Kamp et al., 2016). Despite these limitations, occupancy models present a great opportunity for conservation, as they can analyze past species' data in cases where systematic monitoring has not been implemented (see also Hochkirch et al., 2013).

Our study shows how the establishment of a legal conservation instrument increased monitoring toward target species, while at the same time it did not halt deteriorating trends for some species. This highlights how

conservation instruments might fail to reach the intended protection effects on a large scale, due to implementation time lags, diffuse legal competences and a lack of political will to prioritize serious conservation measures in contrast to financial support of intensive farming. While increased sampling might indicate a chance for more public interest toward improved nature protection, it is also a result of strict requirements for regular reports. Therefore, legal conservation instruments should include measurable requirements for which countries can be held responsible, for example, in forms of efficient sanctions such as decreased European funding toward local stakeholders. Models of species' trends should be used for the assessment of the efficacy of large-scale conservation instruments, as they level out effects of sampling bias toward target species, especially where long-term, large-scale monitoring is insufficient. In the face of global biodiversity loss and the increasing threat of climate change, not only are large-scale protected area networks important, but also their effective implementation on the ground as well as addressing systemic problems beyond.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the Bavarian State Agency for the Environment (Bayerisches Landesamt für Umwelt, LfU). Restrictions apply to the availability of these data, which were used under license for this study. Species' annual occupancy estimates and code for occupancy models are available under <https://doi.org/10.5061/dryad.4f4qrjff5> and code for further analyses is available in Supporting Information: Code.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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