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ORIGINAL RESEARCH

Assessing the conservation and restoration potential of biotopes in a central European region

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Abstract

Changing environmental conditions and land use are threatening biodiversity on a large scale, making successful conservation and restoration essential for maintaining biodiversity. Planning of such efforts profits from information about where conditions are suitable for biotopes, to evaluate how likely successful conservation or restoration is at these sites. This study uses the distribution model Maxent to identify varying levels of conservation and restoration potential for 29 different biotopes in the central European region of Bavaria, Germany, by comparing the environmentally suitable areas identified by models with the current distribution of each biotope. We identified a conservation potential when a biotope occurred under suitable environmental conditions and a restoration potential when suitable environmental conditions were present at a site where the biotope was not observed. We found that 69.57% of biotope observations occurred under suitable environmental conditions representing a large conservation potential. Also, 22 biotopes showed more restoration potential than their current distribution and both conservation and restoration potential showed a similar geographical distribution. The approach used in this study can provide valuable insights for conservation and restoration decision-making by suggesting priority areas for the conservation and restoration of multiple biotopes. Further, it could be applied in other regions globally and by incorporating future climate projections it could identify particularly resilient locations for biotope conservation or restoration.

Keywords Conservation potential · Restoration potential · Distribution modelling · Maxent

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Introduction

Biodiversity is experiencing global decline, with over 82,000 species at risk (Maxwell et al. 2016). This decline is largely attributed to land-use change (Newbold et al. 2015) and anthropogenic climate change (IPBES 2019; Newbold et al. 2020). To protect species at risk effectively and comprehensively *in situ*, an effective protected area network is needed (Guisan and Thuiller 2005). Such a network can be established through conservation projects that aim to preserve existing species and biotopes at environmentally suitable areas. However, land-use and climate change is causing profound alterations to environmental conditions, resulting in survival stress for many ecoregions (Beaumont et al. 2011). Consequently, species are being compelled to either adapt their environmental requirements (Sillero et al. 2022) or to migrate to more suitable areas. However, this process is often challenging, as the successful arrival of a species in new areas with environmentally suitable conditions remains uncertain due to landscape destruction and fragmentation (Hof 2021). Furthermore, even if a species can reach a new area with favourable environmental conditions where it did not occur until now, local human activities, such as land use, raise doubts about the establishment of the species (Franklin 1995). Therefore, alongside conservation efforts, restoration projects are necessary to ensure the establishment of a species or biotope at suitable areas where they do not occur yet. Such projects can promote biodiversity enrichment (Benayas et al. 2009) and improve biotope connectivity (Gilbert-Norton et al. 2010) beyond what conservation alone can achieve.

Conservation and restoration are established methods to mitigate biodiversity decline, but they often report low success rates mainly due to a knowledge gap in identifying environmentally suitable areas (Osborne and Seddon 2012). To address this gap, distribution models have been used in conservation and restoration studies (Elsäßer et al. 2013; Franklin 2010; Guisan et al. 2013; Swan et al. 2021; Wilson et al. 2011). These models assess the environmental requirements of species or biotopes based on their historical or current distribution, enabling the identification of environmentally suitable areas (Guisan and Thuiller 2005). By using these models, a comprehensive understanding of the disparities between the current and potential distribution of species and biotopes relevant to conservation and restoration can be obtained, providing a foundation for decision-making in conservation and restoration actions. Previous studies either focused on individual species or biotopes (Fehérvári et al. 2012; Hu et al. 2020) or considered only the most suitable biotope in a given area (Fischer et al. 2019). This ignores the fact that in a given area several species or biotopes could be conserved or restored. Studies also generally focus on either conservation or restoration (Liu et al. 2013; Olsson and Rogers 2009), even though an area could be suitable for both.

In this study, we modelled the potential distribution of 29 terrestrial biotopes in the central European region of Bavaria, Germany, using the distribution modelling algorithm Maxent including 16 abiotic environmental variables covering climate and soil properties (cf. Rubanschi et al. 2023). We aimed to identify the conservation and restoration potential of these biotopes by comparing their potential and current distributions. Areas with environmentally suitable conditions for a particular biotope were considered as having conservation potential for this biotope if it was already present in that area, and as having restoration potential if the biotope was absent. Using this approach, we were able to determine the general conservation and restoration potential of each biotope, as well as the conservation and restoration potential of any region in Bavaria considering all biotopes simultaneously. Thereby, we addressed the questions (a) whether the majority of biotope observations occurred under suitable environmental conditions, (b) whether there is potential for biotope restoration, and (c) whether the geographical distribution of conservation and restoration potential overlap.

Methods

Study area

The study took place in Bavaria (south-east Germany) covering 70,550 km2 between 47°16'-50°34'N and 8°58'-13°50'E. Bavaria has a varied elevation profile, including the Calcareous Alps (Mt. Zugspitze, 2,962 m a.s.l.), the Bavarian Forest (Mt. Arber, 1,455 m a.s.l.), the Franconian Jura (600-700 m a.s.l.), and lowlands (100-500 m a.s.l.). The climate ranges from sub-oceanic in the northwest to sub-continental in the plains and basins to montane climate in the Alps. The soil also varies, with granite and gneiss in the Bavarian Forest and limestone in the Alps and Franconian Jura. Bavaria's land use is dominated by agriculture (46.3%) and forestry (35.3%) (Bayerisches Landesamt für Statistik 2020).

The Bavarian biotope mapping

Biotopes are distinct landscape elements distinguished by specific communities of species, here primarily characterised by their plant species composition, which have evolved in response to particular environmental conditions (Colwell and Rangel 2009). Since 1985, the Bavarian Environment Agency (Bayerisches Landesamt für Umwelt) maps biotopes in entire Bavaria, aiming to monitoring all (semi-)natural areas that house specific biological communities, often including protected or threatened species (Rubanschi et al. 2022). This mapping effort also considers anthropogenic structures, such as hedges, when these are old, structurally rich, and consist of native species (Lang and Zintl 2018). Most of these biotopes are protected under federal and state-level nature conservation acts (§ 30 and 39 of the BNatSchG/Federal Nature Conservation Act, articles 16 and 23 of the BayNatSchG/Bavarian Nature Conservation Act). Moreover, their classification aligns with the Fauna-Flora-Habitat guidelines, that aim at safeguarding wild species and habitats and creating a Europe-wide habitat network to ensure comparability across Europe (European Community 2006; Lang and Zintl 2018). Each biotope is recorded with its spatial shape (polygon) and vegetation composition, which is then assigned to a biotope using a classification key (Lang and Zintl 2018). Many polygons contain a mixture of different biotopes due to fluctuations in species composition (e.g., 10 % “Lean old grass stands and fallow grassland”, 20 % “Lean grasslands, basophilic”, and 70 % “Hedges, near natural”). 1.7 million biotopes were recorded, covering 5% (3,723 km2) of Bavaria's area (Rubanschi et al. 2022).

For the biotope distribution modelling, we focused on terrestrial biotopes (shrubland, forests, and grasslands) with a sufficient number of observations and excluded peatland, water-associated, human-dominated biotopes and biotopes with less than 500 observations. This resulted in 29 biotopes (Appendix Table 2) with a total of 685,647 observations (39.5% of all biotope observations) covering 2,028 km2 (54.5% of the mapped biotope area) with an average polygon size of 0.51 ha (cf. Rubanschi et al. 2023).

Modelling the potential distribution of biotopes

To model the potential distribution of biotopes in Bavaria we collected in total 35 environmental variables, covering 19 climate variables (WorldClim Verion 2.1; Fick and Hijmans 2017), 9 soil chemical properties (Ballabio et al. 2019), 6 soil physical properties (Ballabio et al. 2016), and elevation as a topographical variable (European Environment Agency 2016). Due to different spatial resolution, we rescaled all the environmental variables to a raster size of 30 arc seconds (56.6 ha ± 0.9 ha, i.e., a square of c. 930 m x 610 m in the study region) using the geographic information system QGIS (QGIS Development Team 2020) resulting into a total of 126,697 raster cells. 385 of the raster cells were excluded since they were entirely covered by water bodies or sealed by artificial surfaces such as airports or cities. Then, we performed a variable selection excluding variables that correlated with $|r| > 0.7$ (Dormann et al. 2013) or had a variance inflation factor (VIF) > 3 (Zuur et al. 2010) using the 'vifcor' and 'vifstep' functions of the 'usdm' packaged 1.1-18 (Naimi et al. 2014) in R 3.6.1 (R Core Team 2020) leaving us 16 variables, including six climate variables, six chemical, and four physical soil properties.

The abiotic variables were organised in raster cells, and biotopes were recorded as polygons. 71.05% of the biotope polygons were found in individual raster cells that reflect their respective environmental conditions. The remaining 28.95% of biotope polygons extended over multiple raster cells. To determine the environmental conditions of these polygons, we calculated the weighted mean of environmental conditions for each polygon observation (cf. Rubanschi et al. 2023).

Since all biotope occurrences in Bavaria were observed, this dataset can be seen as a presence/absence dataset, however, we decided to treat this dataset rather as presence-only dataset because biotopes are land-cover types that can be displaced by anthropogenic land use and the absence of a biotope can therefore not be considered as evidence for unsuitable environmental conditions (cf. Elith et al. 2020; Lobo et al. 2010). To assess the potential distribution of the biotopes we used the algorithm Maximum Entropy (Maxent; Phillips et al. 2006), which was already used to predict the distribution of various vegetation communities (Fischer et al. 2019; Hemsing and Bryn 2012; Jiménez-Alfaro et al. 2018; Tarkesh and Jetschke 2012), and calculated a separate model for each biotope. The biotope distribution models were calculated with Maxent version 3.4.1 (Phillips et al. 2006) using the package 'dismo' 1.1-4 (Hijmans et al. 2017) in R 3.6.1 (R Core Team 2020) with the settings: maximum number of iterations = 10,000, convergence threshold = 0.00001, model output = logistic and a bootstrap of 100 repetitions with a 90/10 split (90% of the data as training data and 10% of the data as test data). The rest of the model settings were set to default. We used the environmental conditions of each observed biotope polygon as presence data and the raster cells not overlapping with the respective polygons as background data in the models. To assess the models' accuracy, we calculated the area under the receiver-operator curve (AUC; Mason and Graham 2002) and the true skill statistic (TSS; Allouche et al. 2006) for each model.

To condense the bootstrap repetition results, we calculated the mean and standard deviation of AUC and TSS for each biotope (Appendix Table 1). Each of the 100 model repetitions per biotope was used to predict the suitability of Bavarian raster cells, which was then averaged, resulting in a mean suitability map. Suitability values ranged from 0 (unsuitable) to 1 (perfectly suitable). 582 raster cells located at the U.S. military bases Grafenwöhr-Vilseck and Hohenfels, for which no biotope occurrence information was available, were excluded from the further analysis since we could not compare the potential distribution with the current distribution.

To decide which raster cells are potentially suitable for conservation or restoration the suitability values provided by the 29 biotope models needed to be translated into presence/absence maps which were then compared with the observed distribution. To turn the values into a presence/absence map, a suitability threshold is required. While usually a biotope specific threshold is chosen that reduces the difference between the predicted and observed distribution (Liu et al. 2005), this method relies on the observed biotope distribution, which can be influenced by anthropogenic land use. To avoid this, we treated the suitability value as a measure of the raster cells' environmental suitability for the specific biotope as intended by the models. Using this approach we were able to provide a comparable conversion of the suitability values over all biotopes (cf. Bailey et al. 2002; Rubanschi et al. 2023; Stockwell and Peterson 2002; Woolf et al. 2002). To quantify the sensitivity of the results to a chosen threshold, we compared the outcomes using a 0.25, a 0.50, a 0.75 and a biotope-specific threshold, based on the maximal TSS value (Allouche et al. 2006). The results of the different thresholds can be used if a different approach is preferred (a low suitability threshold accepts areas having minor suitability for biotopes while a high suitability threshold selects only areas with high suitability for biotopes). In our study we focused on the 0.5 threshold since this represents the most balanced interpretation of the suitability value. Additional details on the modelling methodology can be found in Rubanschi et al. (2023).

To verify the robustness of our results, we compared the suitability values of the Maxent models with those of generalised adaptive models (GAM) using the same presence and background data, though the number of iterations for GAM was reduced to 5. The comparison between the Maxent models and the GAMs showed a correlation between predicted suitability and similarities in model accuracy (cf. Rubanschi et al. 2023).

Quantifying conservation and restoration potential

Given that resources for conservation and restoration are limited, efforts should be concentrated on areas where they can expect promising results. To ensure the success of conservation and restoration actions, the area of interest should provide suitable environmental conditions. Therefore, we compared the distribution of environmentally suitable conditions for a biotope identified by the distribution models with the current biotope distribution to identify the potential for conservation or restoration. We determined the conservation potential of a biotope by the number of raster cells where a biotope was present and where the environmental conditions were identified to be suitable by the distribution model. The restoration potential of a biotope was determined by the number of raster cells where the biotope was not observed but the environmental conditions were suitable according to our models.

To quantify the conservation and restoration potential of a raster cell, we counted the number of biotopes in a raster cell for which the raster cell was considered suitable for conservation or restoration.

Results

Conservation and restoration potential of biotopes

According to the biotope models that employed the 0.5 threshold, more than half of each biotope's distribution was deemed to occur under suitable environmental conditions, thus indicating a conservation potential in the areas where they occur. The highest conservation potential, with 80.93% of the observed distribution, was found for "Hedges, near natural" and the lowest was found for "Dwarf shrubs and gorse heaths" with 53.32% of the observed distribution (Fig. 1C). Generally, the more frequently observed biotopes showed slightly higher conservation potential than less frequently observed biotopes (cf. Fig. 1; Pearson's correlation r = 0.741, p < 0.001).

The models identified the highest restoration potential for "Tall sedge beds outside the siltation zone" with 36.75% of all raster cells in Bavaria, while "Lean golden oat meadows" had the lowest restoration potential, with only 0.27% of all raster cells in Bavaria (Fig. 1A). The models revealed for 22 biotopes a higher number of raster cells having restoration potential compared to the number of raster cells where the biotopes were currently observed (Fig. 1B). The proportion of raster cells with restoration potential in that comparison was highest for "Black alder forest" at 95.9% and the lowest proportion was observed for "Alpine lawns" with 7.58% (Fig. 1B). Generally, the models of less frequent biotopes (observed in <10% of Bavarian raster cells, Fig. 1) showed that the number of raster cells with restoration potential was multiple times higher than the number of raster cells where the biotope was currently observed. Only "Lean golden oat meadows" and some alpine vegetation biotopes showed similar or lower numbers of raster cells with restoration potential compared to the number of raster cells where the biotope was observed.

Regional conservation and restoration potential

Generally, the pre-alpine and alpine area, the regions of the Franconian Jura, Bavarian Forest, Spessart, Röhn, Steigerwald, and raster cells along the rivers in Bavaria showed high conservation and restoration potential for multiple biotopes. However, we also identified

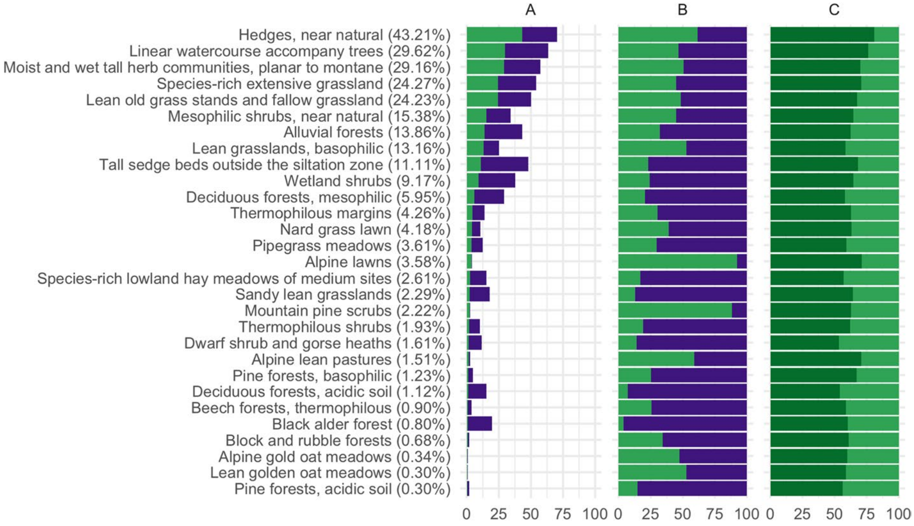

Fig. 1 Illustration of conservation and restoration potnetial of biotopes sorted by observation frequency (percentage observation in Bavarian raster cells). **A** Illustrates the percentage of Bavarian raster cells where biotopes was observed (light green) and raster cells attractive for restoration (purple); **B** Illustrates the scaled proportion between raster cells where the biotope was observed (light green) and raster cells attractive for restoration (purple); **C** Illustrates the percentage of raster cells occupied by actual biotope distribution that are attractive for conservation (dark green)

areas in the centre of Bavaria that showed no potential for conservation or restoration. The highest number of biotopes with conservation potential in a raster cell was 12 (Fig. 2A), and the highest number of biotopes with restoration potential in a raster cell was 16 (Fig. 2B). Further, most raster cells in Bavaria provided more restoration potential than conservation potential, with only few exceptions concentrated in the areas listed above that showed higher conservation potential.

Effects of different suitability thresholds

The results obtained from applying different suitability thresholds to identify raster cells suitable for a given biotope revealed differences in conservation and restoration potential (see comparison in Appendix Figs. 3 and 4). Unsurprisingly, the comparison showed that increasing the threshold resulted in a reduction in the conservation and restoration potential of biotopes. Comparing this to the biotope-specific threshold revealed that frequently observed biotopes had a relatively high threshold, while less frequently observed biotopes had a low threshold (Appendix Table 1). Consequently, frequent biotopes showed lower conservation and restoration potential, while less frequent biotopes showed higher conservation and restoration potential, in comparison to the 0.5 threshold outcome (Appendix Fig. 3).

Similar to the conservation and restoration potential of single biotopes, applying a higher threshold led to a decrease in the conservation and restoration potential of Bavarian raster cells, resulting in an increased number of raster cells showing neither conservation nor restoration potential (Appendix Fig. 4A-I). Comparing the results of the 0.5 threshold and the biotope-specific threshold, we observed for the biotope-specific threshold a slightly higher potential for both conservation and restoration. This is because most biotope-specific thresholds were lower than 0.5 (Appendix Table 1, 25% quantile showed a threshold of 0.12, 50% quantile showed a threshold of 0.30). A higher conservation and restoration potential when using the biotope-specific threshold could especially be found in the alpine region. The location and number of raster cells showing no conservation or restoration potential remained similar.

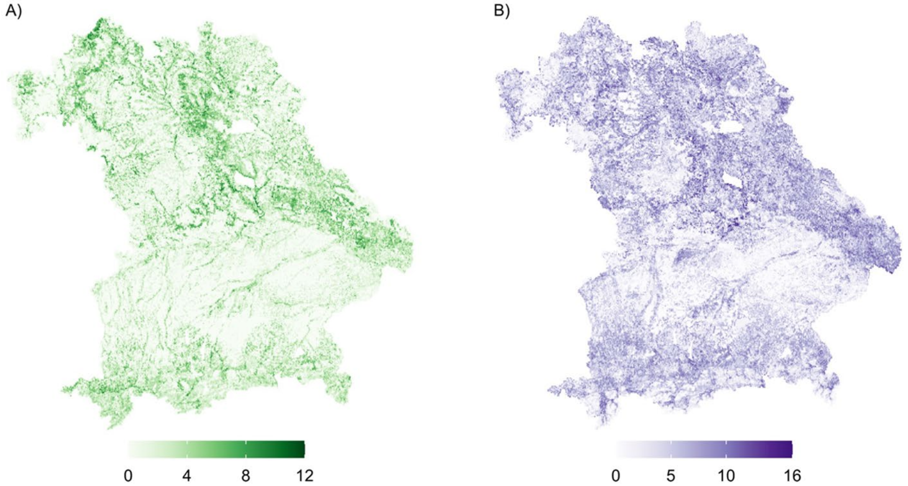

Fig. 2 Geographical distribution of conservation and restoration potential. **A** Illustrating the number of biotopes considered attractive for conservation in a raster cell. **B** Illustrating number of biotopes considered attractive for restoration in a raster cell

Discussion

Conservation potential of biotopes

The main role of conservation planning is to establish a network of biotopes that effectively and comprehensively protects biodiversity *in situ* (Guisan and Thuiller 2005). However, not every biotope observation can be considered an immediate indication of suitable environmental conditions, as natural systems may experience time lags between negative events and their consequences (Osborne and Seddon 2012). Changes in environmental conditions that occurred in the past may result in current conditions that deviate from a biotope's optimum, with negative impacts that may not be immediately apparent. Therefore, relying solely on biotope observations may reduce the success of conservation efforts if the environmental conditions do not meet the biotope's needs. To identify areas with high potential for conservation, distribution models can be used to provide a backbone for decision-making (Fehérvári et al. 2012). Our approach determined the general conservation potential of a biotope, by estimating how much of the observed biotope distribution already occurs under suitable environmental conditions.

Our analysis revealed that 69.57% of raster cells in which a biotope was observed were considered environmentally suitable, suggesting a potential for conserving the observed biotope within those cells. Even though more than half of each biotope's observed distribution was considered suitable for conservation, we see a declining trend of conservation potential from frequently observed biotopes (e.g. "Hedges, near natural" with 80.93% of raster cells providing conservation potential, Fig. 1C) to less frequently observed biotopes (e.g. "Pine forests, acidic soil" with 56.27% of raster cells providing conservation potential, Fig. 1C). This trend may be attributed to the fact that frequently observed biotopes are typically associated with a broad distribution range, which implies a larger environmental range that is suitable for the biotope. This increases the probability of finding suitable environmental conditions in a greater number of raster cells where the biotope was observed. However, less frequently observed biotopes, such as those found in alpine areas (see Appendix Fig. 5), tend to have narrow distribution ranges, which limits suitable environmental conditions to a similarly narrow range. Consequently, a smaller fraction of these biotopes' distribution is considered for conservation by the models, as not all raster cells where these biotopes were observed provide the required narrow range of environmental conditions. In such cases, conservation planning should prioritise efforts on the remaining biotope observations occurring under environmentally suitable conditions to ensure their conservation as sources for future restoration actions (Guisan et al. 2013).

The result that about 30% of raster cells with biotope observations were associated with suboptimal environmental conditions may have many reasons. One possibility is that these biotopes were located in areas where suitable conditions existed in the past but have changed since (Osborne and Seddon 2012). Another possibility is that the environmental conditions of the raster cell lie at the edge of the model's estimated environmental niche for the biotope, meaning that the raster cell provides good environmental conditions, but it did not exceed the 0.5 suitability threshold. While both explanations assume that the environmental conditions should be at least close to suitable conditions, it is uncertain whether former suitable conditions can be restored or modified in favour of the biotope.

Nevertheless, it is important not to discard biotope occurrences that were observed under suboptimal environmental conditions. Some of these biotopes may occur in small patches within a raster cell that provided suitable environmental conditions (cf. average biotope polygon size of 0.51 ha), and these environmental conditions may differ from the average condition of the entire raster cell (average size of 56.6 ha). These small patches may emerge due to heterogeneity and fluctuations within the landscape, which are not adequately represented by the averaged value of larger raster cells (Seo et al. 2009). Therefore, raster cells where a biotope was observed under unsuitable environmental conditions should not be categorically excluded from conservation projects but rather thoroughly examined before including, to avoid losing critical biodiversity but also to invest limited resources at suboptimal sites.

Restoration potential of biotopes

Efforts to restore biotopes can have a variety of aims, such as enriching biodiversity, providing ecosystem services (Benayas et al. 2009) and improving biotope connectivity (Gilbert-Norton et al. 2010). Reaching these aims may involve actions, from rebuilding devastated areas (like mine sites) to managing unmodified ones (Hobbs and Norton 1996). Unfortunately, restoration projects often report low success rates, partly due to the lack of knowledge of suitable areas (Osborne and Seddon 2012). To address this challenge, distribution models can be used to identify suitable areas where specific species or biotopes were not previously observed (Elsäßer et al. 2013; Franklin 2010; Guisan et al. 2013; Swan et al. 2021; Wilson et al. 2011). By applying this approach, our study provides insides into which biotopes may have a high potential for successful restoration.

Overall, our study identified varying levels of restoration potential for different biotopes in Bavaria. For 15 of the analysed biotopes, more than 10% of Bavarian raster cells were considered environmentally suitable for restoration (Fig. 1A) ranging from 11.8% of Bavarian raster cells for “Lean grasslands, basophilic” to 36.75% for “Tall sedge beds outside the siltation zone” (Fig. 1A). Further, the models revealed that for 22 biotopes, there were more raster cells suitable for restoration than those where the biotope was observed (Fig. 1B). Such large restoration potential appears to be common in spatial analyses using distribution models (cf. Guisan et al. 2013; Olsson and Rogers 2009; Swan et al. 2021). Reason for that is when transferring the environmental niche, determined by a distribution models, into geographical space, areas could be environmentally suitable but other requirements for their occurrence beyond environmental conditions may not be given (Franklin 1995; Osborne and Seddon 2012). This argument is transferable to biotopes where environmental conditions may be good, however the biotope is not realised due to the fact that other needs such as management or disturbances (Franklin 1995) were not present.

The predominance of other land-use types such as agriculture (46.3%), forestry (35.3%) and artificial area (12.1%) (Bayerisches Landesamt für Statistik 2020), as well as the absence of biotope-specific management, appeared to contribute to the underrepresentation of biotopes in Bavaria (Fig. 2B) (Rubanschi et al. 2023). For example, the decline of continuous grassland and the expansion of agricultural areas in critical regions, particularly in the pre-alpine areas of Bavaria between 1999 and 2016, may contribute to the limited occurrence of biotopes restoration (Kieslinger et al. 2022). Additionally, from a socio-ecological perspective, challenges arise to identify areas for restoration, due to ambitious goals without result obligations, conflicts of interest across stakeholders involving agriculture, nature conservation, and the energy industry, as well as overlapping responsibilities at different action levels (Pohle et al. 2022). These factors collectively impede the successful restoration of biodiversity. These Bavarian trends are consistent with global reports of declining biodiversity, where human land-use activities pose a threat to both biodiversity and ecosystem services (Felipe-Lucia et al. 2020; Maxwell et al. 2016; Newbold et al. 2015). To mitigate biodiversity decline and to ensure the provision of ecosystem services and biotope connectivity, successful restoration projects are urgently needed (Benayas et al. 2009; Gilbert-Norton et al. 2010). Our study can assist such restoration efforts by identifying areas for biotopes with high restoration potential.

Regional conservation and restoration potential

When we analysed the conservation and restoration potential of each biotope geographically and stacked the results, we found that certain regions showed high incidences of both conservation and restoration potential where, in some cases, a greater potential for restoration was observed (see Fig. 2 and Appendix Fig. 4D-F). One reason for the overlap in high potential for both conservation and restoration is that the environmental conditions of a single raster cell may be suitable for multiple biotopes, whether or not they have been observed (Rubanschi et al. 2023). This is consistent with the findings of the Bavarian biotope mapping, which recorded the occurrence of up to 14 different biotopes in a single raster cell (Rubanschi et al. 2023). Further, the concentration of conservation and restoration potential in specific regions can be explained by the fact that if suitable environmental conditions for a biotope were observed in a raster cell, neighbouring raster cells are likely to provide similar suitable conditions, since these conditions should not change dramatically over small distances.

While we observed high restoration potential in many regions (Fig. 2B), these regions may currently be occupied by other land-use types which have replaced the biotopes. This potential replacement effect becomes more evident when we consider that Bavaria is predominantly characterised by agriculture (46.3%), forestry (35.3%) and artificial area (12.1%) (Bayerisches Landesamt für Statistik 2020) which is further confirmed by satellite-borne land-use classification (Agency European Environment 2020). Despite this, by considering both the potentially restorable biotopes and current land-use, restoration projects can better coordinate their efforts and estimate the degree of difficulty in transforming the current land-use type into the desired biotope (Hu et al. 2020).

Besides the high incidences of high conservation and restoration potential we identified regions where neither conservation nor restoration potential was estimated (Appendix Fig. 4F). The reason for that may be technical, since there were only few biotopes recorded by the Bavarian biotope mapping (Rubanschi et al. 2022) and the occurring environmental conditions were not considered optimal by the distribution models for any of the biotopes (Rubanschi et al. 2023). When we then compare what land-use is realised in these regions, we saw a high density of anthropogenic land-use (Agency European Environment 2020). This illustrates that in certain areas in Bavaria, anthropogenic land-use suppresses the occurrence of biotopes to such an extent that it is unknown if the areas are suitable for any analysed native biotope. Of course, we did not analyse every native biotope in Bavaria and some of these non-analysed biotopes may occur there, however, including them into the analyse would introduce other problems like insufficient number of biotope observation for modelling.

Despite the predominance of anthropogenic land use in Bavaria, analysing the geographical distribution of conservation and restoration potential can be useful. If there are conservation or restoration actions planned in a specific geographical area, results from studies like ours can be used to integrate additional biotopes with conservation or restoration potential. This allows for more comprehensive and effective conservation and restoration efforts, maximizing the impact of these projects.

Effects of different suitability thresholds

The results of this study strongly depend on the choice of suitability threshold used to convert the continuous suitability values into presence/absence data (Appendix Figs. 3 and 4). A higher threshold means that the environmental conditions of a raster cell must closely match the biotope's optimal conditions, resulting in more conservative estimates of conservation and restoration potential. For example, using a low threshold (e.g. 0.25; Appendix Fig. 3 first figure and Fig. 4A-C) resulted in nearly all raster cells where a biotope was observed being considered as conservation potential, and many raster cells being considered as restoration potential. However, many of these predicted presences may provide suboptimal environmental conditions, likely leading to low conservation or restoration success (Osborne and Seddon 2012). Using a high threshold (e.g. 0.75; Appendix Fig. 3 third figure and Fig. 4G-I) presented a different picture, with only highly suitable raster cells being considered as conservation or restoration potential, resulting in a low amount of conservation and restoration potential being identified. While conservation and restoration efforts would likely be more successful in these areas, many raster cells providing above-average suitable environmental conditions would be ignored. Thus, we considered the 0.5 threshold as best-balanced threshold for this study since it considers all suitability values above average and not only the extremely high suitability values.

When comparing the results of the 0.5 threshold with the biotope-specific threshold, we generally observed lower conservation and restoration potential with the 0.5 threshold, particularly for less frequent biotopes (observed in <10% of Bavarian raster cells; Appendix Fig. 3 second and fourth figure, Fig. 4D-F and J-L). The reason for this is that the biotope-specific threshold primarily selected threshold below 0.5, often far below 0.25 (Appendix Table 1), resulting in high conservation and restoration potential. Methodically the selection of a threshold is based on the ratio between the sensitivity (true positive rate) and specificity (true negative rate) of the prediction (Liu et al. 2011). However, for less frequently observed biotopes, the sensitivity is more affected by each correctly predicted presence than the specificity by a high number of incorrectly predicted absence. In other words, the threshold selection for less frequently observed biotopes recognises high conservation potential and accepts much larger restoration potential, even though the environmental conditions may be suboptimal. While this approach of identifying the biotope-specific suitability threshold can detect all known and previously unknown presences of a species or biotope (cf. Guisan et al. 2013; Jiménez-Valverde and Lobo 2007), it is important to remember that the occurrence of a species or biotope is not always a clear indicator for suitable environmental conditions (Osborne and Seddon 2012). Therefore, it is debatable whether it is beneficial for conservation and restoration project to consider areas that provide such poorly environmental conditions.

To maximise the chances of success for conservation and restoration projects, a selection of higher suitability thresholds should be considered to ensure optimal environmental conditions. However, if the objective is to identify multiple potential sites, lower suitability values may be appropriate. Thus, depending on the project's approach, suitability values from the distribution models can be directly used, and a threshold aligned with the specific approach can be selected.

Effects of climate and land-use change

Our study identified substantial disparities between the observed distribution of biotopes and their potential distribution under current environmental conditions. These disparities include instances where a biotope could occur but was not observed, as well as cases where biotopes were observed despite the model indicating unsuitable local conditions. Such discrepancies strongly suggest that climate and land-use changes have already altered conditions to an extent where certain biotope observations no longer align with suitable environmental conditions. Biotopes occurring under unsuitable conditions are raising concerns regarding their ability to persist these environmental conditions before potential degeneration, posing a risk of biodiversity loss. Preserving these biotopes required conservation and restoration actions, either by imporving environmental conditions at their current location or relocating them to more suitable areas with restoration potential. In future, the demand for conservation and restoration efforts can be expected to increase further due to impending threats from climate and land-use changes, which could lead to the disappearance of some biotopes in the near future (Maxwell et al. 2016; Newbold et al. 2020).

Conclusion

This study provides a comprehensive analysis of the conservation and restoration potential of various central European biotopes based on their environmental conditions, which is translated to a geographical scale. We demonstrate that not all biotope observations currently occur in areas with suitable environmental conditions, and that many areas may be potentially suitable for biotopes, where they have not been observed. This highlights the disparity between the potential and realised biotope distributions, which can be potentially attributed to changes in environmental conditions and land use. Successful conservation and restoration efforts are crucial to ensure the preservation of the biotopes and their biodiversity under changing circumstances. Our findings provide a foundation for decision-making regarding conservation and restoration in the central European region of Bavaria, which surpasses previous studies by suggesting conservation and restoration options for multiple biotopes. However, our approach is not limited to Bavaria but can be readily applied to other countries and even continents. Furthermore, this study can serve as a baseline for future efforts in assessing the suitability of areas for biotopes based on climate projections. This can facilitate the identification of particularly resilient locations for biotope conservation or restoration.

Appendix

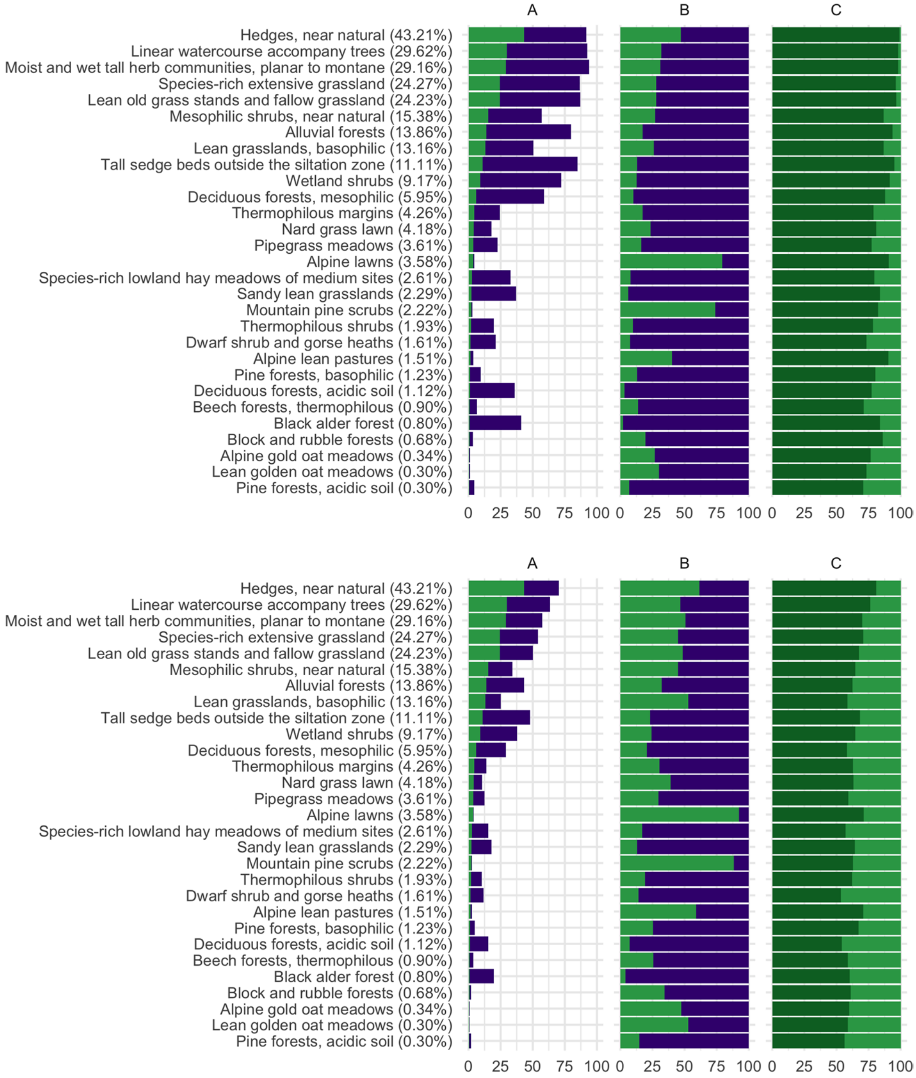

Fig. 3 Comparison between outputs when applying different suitability threshold (first figure 0.25 threshold, second figure 0.5 threshold, third figure 0.75 threshold and fourth figure biotope-specific threshold see Appendix Table 1) of each biotope (cf. Fig. 1)

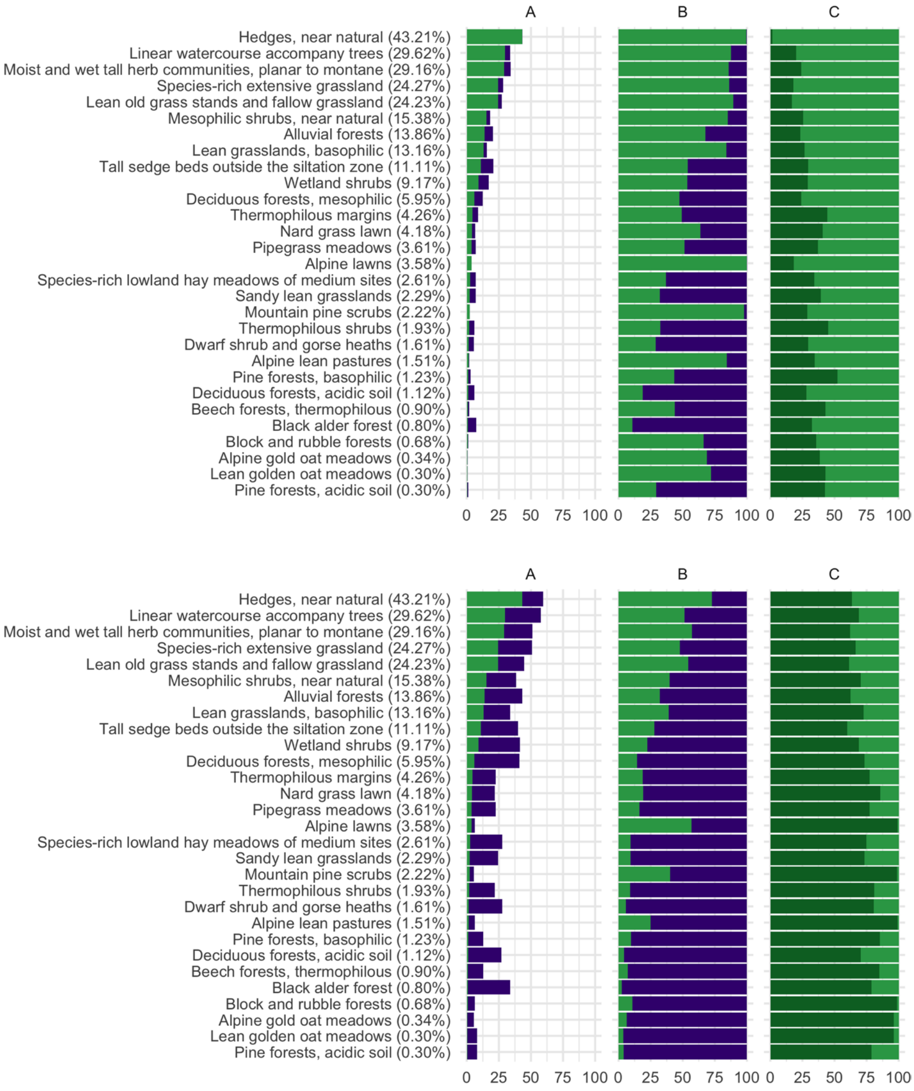

Fig. 3 (continued)

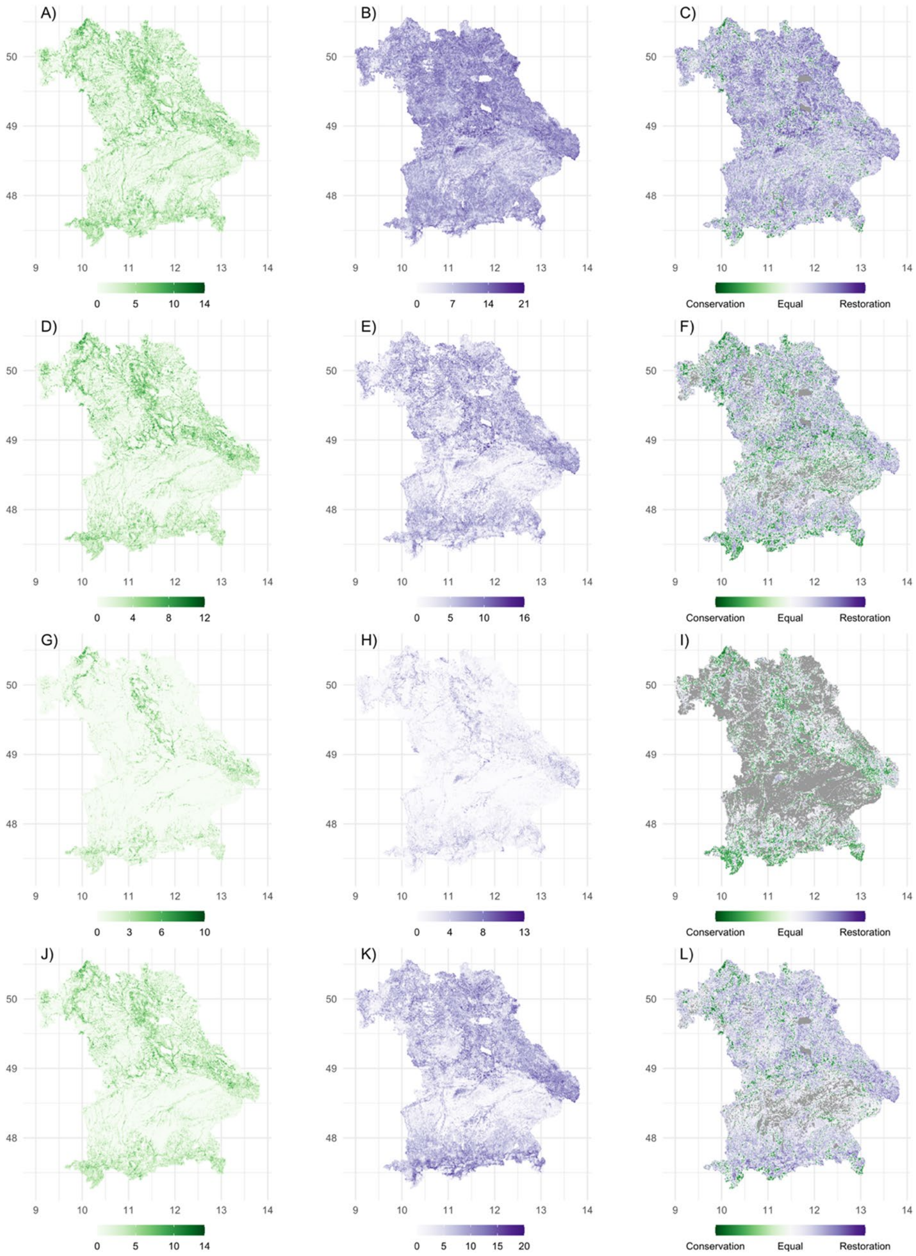

Fig. 4 Comparison between geographical conservation and restoration potential (cf. Fig. 2) using different suitability threshold. **A**-**C** 0.25 threshold, **D**-**F** 0.50 threshold, **G**-**I** 0.75 threshold and **J**-**L** biotope-specific threshold (see Appendix Table 1). Figure **C**, **F**, **I**, **K** illustrates the ratio between the number of biotopes considered attractive for restoration or conservation in a raster cell, indicating more biotopes for conservation with a green colour and more biotopes for restoration with a purple colour no potential is illustrated in grey

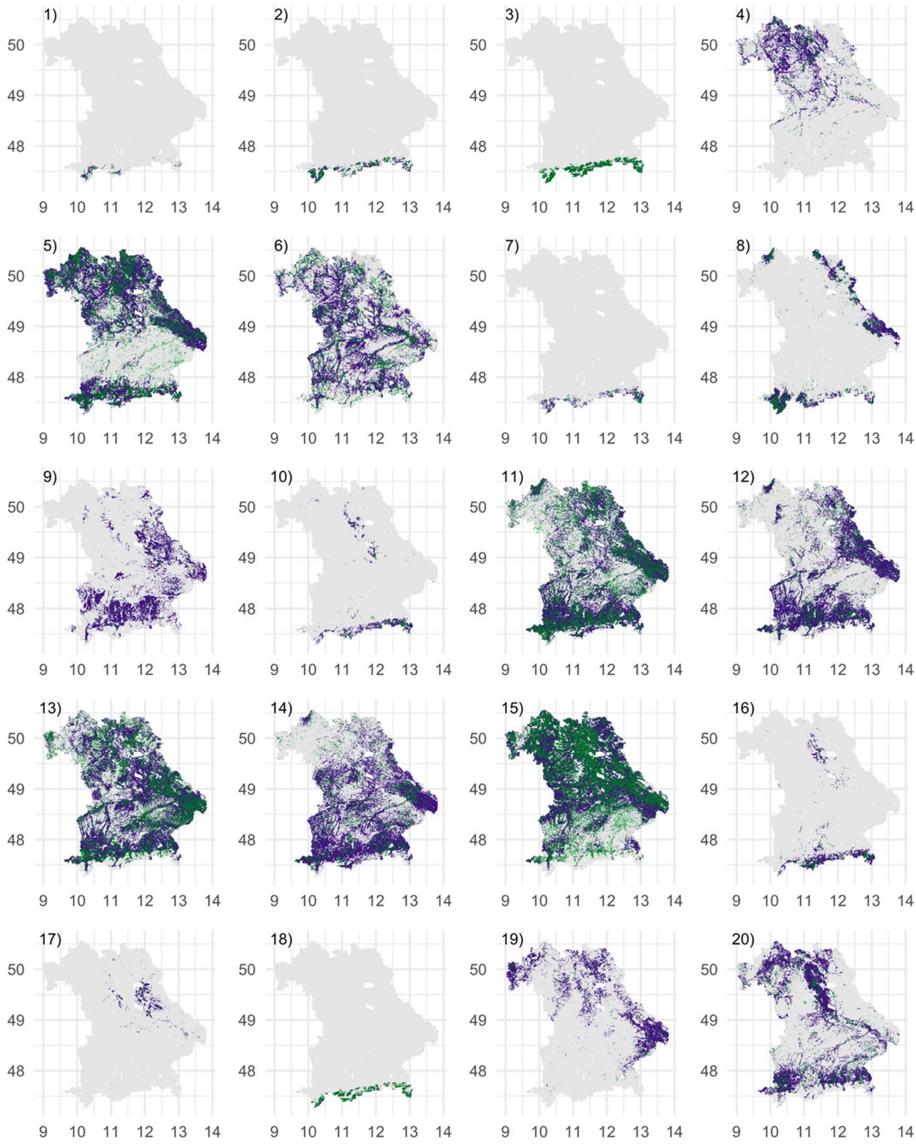

Fig. 5 Illustration of conservation and restoration potential for the individual biotopes (numbers in Appendix Table 1) using the 0.50 threshold; Raster cells providing conservation potential are coloured dark green, restoration potential is coloured purple, raster cells where a biotope was observed under unsittable conditions are coloured light green and raster cells showing no potential are coloured grey

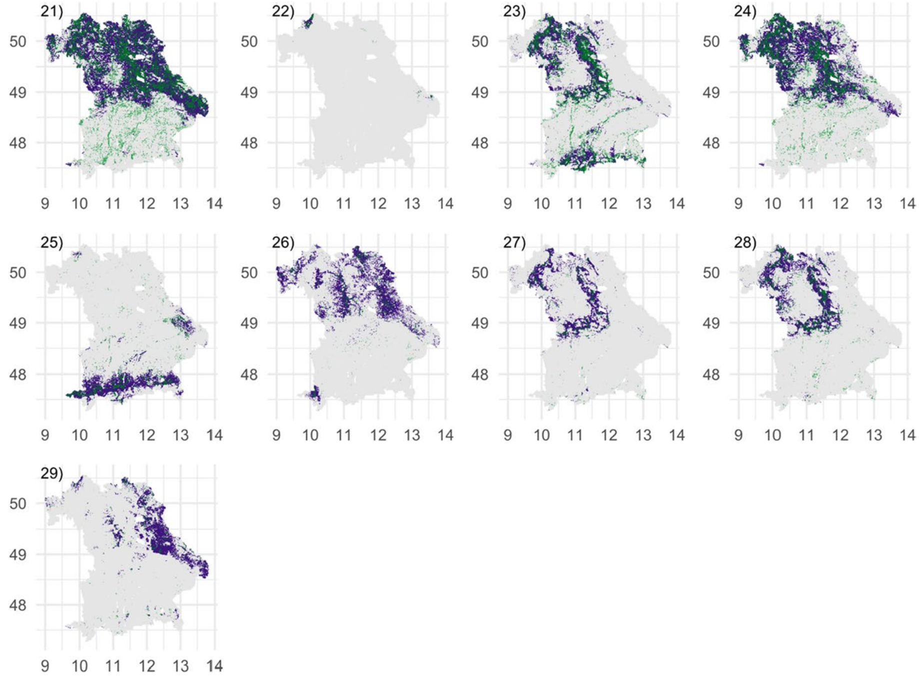

Fig. 5 (continued)

Table 1 Biotope-specific threshold (BST) selected by the models, mean accuracy values AUC and its standard deviation (SD) and mean TSS and its standard deviation (SD) for each biotope model

No.	Biotope	BST	AUC	AUC SD	TSS	TSS SD
1)	Alpine gold oat meadows	0.016	0.992	0.001	0.911	0.0014
2)	Alpine lean pastures	0.034	0.986	0.001	0.944	0.0005
3)	Alpine lawns	0.023	0.980	0.001	0.964	0.0002
4)	Species-rich lowland hay meadows of medium sites	0.304	0.856	0.007	0.492	0.0011
5)	Species-rich extensive grassland	0.524	0.676	0.003	0.313	0.0004
6)	Alluvial forests	0.501	0.731	0.004	0.284	0.0007
7)	Block and rubble forests	0.046	0.985	0.004	0.928	0.0015
8)	Nard grass lawn	0.182	0.909	0.005	0.673	0.0007
9)	Black alder forest	0.319	0.830	0.018	0.453	0.0038
10)	Beech forests, thermophilous	0.107	0.946	0.012	0.730	0.0031
11)	Moist and wet tall herb communities, planar to montane	0.547	0.668	0.003	0.310	0.0005
12)	Wetland shrubs	0.467	0.744	0.006	0.337	0.0005
13)	Linear watercourse accompany trees	0.535	0.660	0.003	0.290	0.0004
14)	Tall sedge beds outside the siltation zone	0.558	0.703	0.005	0.274	0.0006
15)	Hedges, near natural	0.571	0.593	0.002	0.346	0.0003
16)	Pine forests, basophilic	0.178	0.942	0.008	0.737	0.0020
17)	Pine forests, acidic soil	0.119	0.957	0.014	0.706	0.0042
18)	Mountain pine scrubs	0.016	0.989	0.002	0.955	0.0004
19)	Deciduous forests, acidic soil	0.332	0.848	0.015	0.442	0.0025
20)	Deciduous forests, mesophilic	0.383	0.781	0.005	0.360	0.0009
21)	Lean old grass stands and fallow grassland	0.555	0.671	0.003	0.342	0.0003
22)	Lean golden oat meadows	0.013	0.989	0.004	0.881	0.0040
23)	Lean grasslands, basophilic	0.381	0.781	0.003	0.487	0.0006
24)	Mesophilic shrubs, near natural	0.451	0.746	0.003	0.428	0.0006
25)	Pipegrass meadows	0.252	0.887	0.006	0.580	0.0008
26)	Sandy lean grasslands	0.403	0.856	0.009	0.507	0.0013
27)	Thermophilous shrubs	0.219	0.896	0.008	0.605	0.0017
28)	Thermophilous margins	0.276	0.875	0.006	0.579	0.0008
29)	Dwarf shrub and gorse heaths	0.169	0.895	0.009	0.538	0.0015

Table 2 German biotope names alongside their translations and associated phytosociological groups (Lang and Zintl 2018)

German biotope	English biotope	Associated phytosociological groups
Alpengoldhaferwiesen	Alpine gold oat meadows	*Polygono-Trisetion*
Alpenmagerweiden	Alpine lean pastures	*Festuco-Brometea, Seslerietalia variae, Nardo-Callunetea,* further
Alpine Rasen	Alpine lawns	*Trifolio-Festucetum violaceae, Campanulo-Festucetum noricae, Seslerietalia variae,* further
Artenreiche Flachland-Mähwiesen mittlerer Standorte	Species-rich lowland hay meadows of medium sites	*Arrhenatheretum elatioris, Alopecurus pratensis,* further
Artenreiches Extensivgrünland	Species-rich extensive grassland	*Arrhenatherion elatioris, Polygono-Trisetion, Crepido-Festucetum rubrae,* further
Auwälder	Alluvial forests	*Pruno-Fraxinetum, Querco roboris-Ulmetum minoris,* further
Block- und Hangschuttwälder	Block and rubble forests	*Vaccinio-Piceetea, Querco-Fagetea*
Borstgrasrasen	Nard grass lawn	*Nardo-Callunetea, Caricetalia curvulae, Lycopodio alpini-Nardetum,* further
Bruchwälder	Black alder forest	*Alnion glutinosae, Carici elongatae-Alnetum glutinosae*
Buchenwälder, wärmeliebend	Beech forests, thermophilous	*Cephalanthero-Fagenion, Luzulo-Fagetum tanacetosum corymbosi*
Feuchte und nasse Hochstaudenfluren, planar bis montan	Moist and wet tall herb communities, planar to montane	(see, Lang and Zintl 2018)
Feuchtgebüsche	Wetland shrubs	*Salicion cinereae, Betulo-Salicetum repentis, Alno-Salicetum cinereae,* further
Gewässer-Begleitgehölze, linear	Linear watercourse accompany trees	*Salicetalia purpureae, Alno-Ulmion*
Großseggenriede außerhalb der Verlandungszone	Tall sedge beds outside the siltation zone	*Phragmitetea, Magnocaricion, Molinio-Arrhenatheretea,* further
Hecken, naturnah	Hedges, near natural	*Pruno-Ligustretum, Rhamno-Cornetum, Corylo-Rosetum,* further
Kiefernwälder, basenreich	Pine forests, basophilic	*Erico-Pinion, Molinio-Pinetum, Cytiso-Pinetum,* further
Kiefernwälder, bodensauer	Pine forests, acidic soil	*Leucobryo-Pinetum, Pyrolo-Pinetum*
Latschengebüsche	Mountain pine scrubs	*Erico-Pinetea, Erico-Rhododendretum hirsuti, Piceetalia abietis,* further

Table 2 (continued)

German biotope	English biotope	Associated phytosociological groups
Laubwälder, bodensauer	Deciduous forests, acidic soil	*Luzulo-Fagenion, Quercion robori-petraeae*
Laubwälder, mesophil	Deciduous forests, mesophilic	*Stellario-Carpinetum, Galio odorati-Fagenion,* further
Magere Altgrasbestände und Grünlandbrache	Lean old grass stands and fallow grassland	*Arrhenatheretalia, Agropyretea intermedii-repentis*
Magere Goldhaferwiesen	Lean golden oat meadows	*Polygono-Trisetion*
Magerrasen, basenreich	Lean grasslands, basophilic	*Brometalia erecti, Trifolion medii, Festucetalia valesiacae,* further
Mesophiles Gebüsche, naturnah	Mesophilic shrubs, near natural	*Sambuco-Salicion, Pruno-Ligustretum, Rhamno-Cornetum,* further
Pfeifengraswiesen	Pipegrass meadows	*Molinietalia caeruleae, Juncion acutiflori, Molinion caeruleae,* further
Sandmagerrasen	Sandy lean grasslands	*Sedo-Sclerenthetea, Koelerion glaucae, Armerio-Festucetum trachyphyllae,* further
Wärmeliebende Gebüsche	Thermophilous shrubs	*Berberidion, Prunetum mahaleb,* further
Wärmeliebende Säume	Thermophilous margins	*Geranion sanguinei, Trifolio-Agrimonietum eupatoriae, Agrimonio-Vicietum cassubicae,* further
Zwergstrauch- und Ginsterheiden	Dwarf shrub and gorse heaths	*Vaccinio-Genistetalia, Genisto pilosae-Callunetum, Sarothamnion,* further

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Data availability The data that support the findings of this study are openly available: Bavarian biotope mapping https://www.lfu.bayern.de/umweltdaten/geodatendienste/pretty_downloaddienst.htm?dld=biotopkartierung accessed 31.03.2020; soil chemical properties at https://esdac.jrc.ec.europa.eu/content/chemical-properties-european-scale-based-lucas-topsoil-data accessed 02.02.2020; soil physical properties at https://esdac.jrc.ec.europa.eu/content/topsoil-physical-properties-europe-based-lucas-topsoil-data accessed 02.02.2020; climate variables https://www.worldclim.org/data/worldclim21.html accessed 23.05.2020.

Declarations

Competing interests The authors declare no competing interests.

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