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Data Availability Statement: All data used for this study are open source data and available from the following URLs: Natura 2000 habitat type distribution data: https://bd.eionet.europa.eu/; Grid map for Germany as used in our analyses: http:// www.orchids.de/haynold/tkg/KoordinatenErmittler. php; EUNIS habitat class distribution: https://www. eea.europa.eu/data-and-maps/data/ecosystemtypes-of-europe/; Distribution of plant species in Germany: www.floraweb.de.

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Evaluation of habitat protection under the European Natura 2000 conservation network -The example for Germany

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Abstract

The world's largest network of protected areas—Natura 2000 (N2000)—has been implemented to protect Europe's biodiversity. N2000 is built upon two cornerstones, the Birds Directive, which lists 691 bird species (plus one additional bird genus with no further classification) and the Habitats Directive, which lists next to a variety of species, 233 habitat types to be protected. There is evidence of the positive impact of the Directives on the EU's biodiversity, although the overall improvement reported for species in favourable condition in the last assessment was low. However, most of the assessments are species focused, while habitats have received very little attention. Here we developed a generic workflow, which we exemplified for Germany, to assess the status of habitat coverage within the N2000 network combining information from publicly available data sources. Applying the workflow allows identification of gaps in habitat protection, followed by the prioritization of potential areas of high protection value using the conservation planning software Marxan. We found that, in Germany, N2000 covers all target habitats. However, common habitats were proportionally underrepresented relative to rare ones, which contrasts with studies focussing on the representation of species. Moreover, the German case study suggests that especially highly protected areas (i.e. covered by more than 90% with N2000 sites) build an excellent basis towards a cost-effective and efficient conservation network. Our workflow provides a generic approach to deal with the common problem of missing habitat distribution data outside of N2000 sites, information which is however crucial for managers to plan conservation actions appropriately across Europe. To avoid a biased representation of habitat types within N2000, our results underpin the importance of defining qualitative and quantitative conservation targets which will allow assesment of the trajectory of habitat protection in Europe as well as adjustment of the network accordingly—a future necessity in the light of climate change.



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Introduction

In times of global biodiversity loss [1], large nature conservation networks will become increasingly important for mankind, as human wellbeing is closely linked to biodiversity [2]. The most important contribution to biodiversity conservation in Europe is Natura 2000 (N2000), the world's largest nature conservation network. N2000 is built upon two cornerstones: The Birds Directive (BD), introduced in 1979 (Council Directive 79/409/EEC) was established to protect bird species, their resting and nesting areas, and migration pathways through the implementation of special protection areas (SPAs). Since 1994, these SPAs are included in the N2000 network. The second cornerstone of N2000 is the Habitats Directive (HD; Council Directive 92/43/EEC), introduced in 1992, which is based on the designation of special conservation areas (SACs) that should ensure the protection of a broader range of species. Annex I lists more than 230 rare and characteristic habitat types which must be protected. Additionally, in the Annexes II, IV, and V, more than 1000 animal and plant species are listed which need protection across the EU.

The HD can be seen as the backbone of habitat conservation efforts in Europe and does not have a counterpart in the rest of the world [3, 4]. The explicit effort to protect habitats is a reaction to the increasing awareness that, besides species, habitats are also under great threat and essential for successful nature conservation (e.g. European Red List of Habitats; [5]). It is well known that an increased habitat diversity is beneficial for species diversity [6]. Additionally, habitats are commonly used as biodiversity indicators in conservation assessments [7]. Therefore, an evaluation of habitat coverage under N2000 is a good reflection of how well N2000 is covering biodiversity overall.

Despite a worldwide commitment, human pressures and inadequate conservation efforts limited the success of reducing the rate of biodiversity loss by 2010 [8] and new targets were set to 2020 [9]. These targets mandate that 17% of terrestrial areas, and 10% of coastal and marine areas should be covered by nature conservation networks (Target 11). Furthermore, by 2020 100% more habitat assessments should show an improved conservation status compared to current assessments (Target 1; [10]). Considering that N2000 currently protects 18% of Europe's terrestrial and 6% of the marine area [11] the BD and HD could be effective tools to deal with the biodiversity crisis in the EU. However, in the last "State of nature in the EU" report [12], the conservation status of more than half of the species legally protected by the Directives were considered unfavourable, and studies on the effectiveness of N2000 came to very diverse conclusions [13, 14]. Gruber et al. [15], for instance, analysed the representation of N2000 Annex II species in the entire network according to their distribution ranges and found that most target species are well represented. However, they also found a strong bias in protection status with an overrepresentation of species with a large distribution range, and an underrepresentation of species with a narrow distribution range. Additionally, a recent study by Hermoso et al. [16] showed that N2000 fails to adequately cover freshwater biodiversity in Spain with some species not present within the network and less than 20% of the analysed species distribution ranges covered on average. Abellàn et al. [17] found that the implementation of N2000 on the Iberian Peninsula will increase the protection status for raptor species. However, in terms of efficiency, defined as the proportion of nesting territories included within the system in relation to the surface of the system, the network consistently falls short of expectations. On the other hand, Pellissier et al. [18] showed for France that the abundance of common, mostly non-target birds, i.e. species not listed in the Birds Directive, is higher within N2000 than outside. They concluded that the designation of N2000 sites for target species is also beneficial for non-target bird species. One of the few studies focusing on habitat types, conducted by Miklín and Čížek [19], focused on open woodland habitats in Czech Republic, identifying habitat fragmentation and logging as the main causes for the disappearance of open woodland habitat types. Although open woodland habitat types are listed in the HD



Annex I, even after the implementation of N2000 in the Czech Republic, these habitat types still disappear and the effectiveness of N2000 to protect them remains questionable. In conclusion, although the implementation of N2000 has positive effects on some taxonomic groups, the effectiveness of the network still leaves a lot to be desired [20, 21].

Europe stands out as one of the areas in the world with the largest human footprint, indicating a high anthropogenic pressure on ecosystems [22]. The limited available space biases the designation of nature conservation areas towards remote or abandoned regions of low commercial interest [23]. Additionally, adding new areas to existing networks is often connected with high costs [24] and is politically challenging. For N2000, although continuously growing, this results in a static, inflexible network [14], including in some countries such as Germany, with many small and unconnected protected areas [25]. In particular for the 233 habitat types listed under Annex I, this could result in serious conservation problems due to, for example, habitat fragmentation which is one of the key drivers for biodiversity loss [26], and resulting edge-effects [27]. An additional challenge for applying the HD is that there are no specific area targets set for each habitat type. This uncertainty may lead to misinterpretations regarding the degree of protection of individual habitat types and biased conservation efforts towards 'charismatic' habitats, as this has been shown for species conservation [28, 29].

Despite these preconditions, including the fact that the conservation status of the N2000 habitat types is generally worse than that for species [30], surprisingly few studies have concentrated on the degree of protection of habitat types (but see [19, 31–34]) compared to the vast amount of studies focusing on single species or groups of species [15, 16, 18, 35–40]. A likely reason for this bias is the lack of information on N2000 habitat types outside the current N2000 network [41, 42]. For example, the "Mid-term review of the EU Biodiversity Strategy to 2020" [43] identified the lack of information on forest habitat types distribution outside N2000 as the reason for not significantly improving towards the Target 3b 'Increase the contribution of forestry to maintaining and enhancing biodiversity'. As a consequence, studies addressing habitat protection under N2000 have either i) focussed on only a small number of habitats occurring in a country [19], ii) assessed the status of habitat protection in only a small area of a country [44] or iii) made rather vague assumptions to estimate the occurrence of N2000 habitat types outside existing protected areas [32].

Hence, the two main objectives of our study were 1) to develop a workflow to map habitat types outside N2000, information needed to evaluate the protection status of all habitat types considered in the HD at a country scale, and 2) to demonstrate how to identify areas in order to fill protection gaps effectively and cost-efficiently. To do so, we i) mapped the spatial distribution of habitat types at a 30 km² resolution. Based on this information, ii) we performed a gap analysis to identify habitats that are currently not sufficiently protected, and iii) used the conservation planning software Marxan to spatially optimize the current N2000 network testing for different targets, including a 17% target to account for Aichi target 11 [9]. We demonstrate this approach for Germany as a case study. Germany is one of the most densely populated countries in the EU [22], thus representing an additional challenge when establishing meaningful conservation areas. To the best of our knowledge, this is the first study that provides generic guidance on how to evaluate the representation of N2000 target habitats with a subsequent optimization to inform potential future management.

Methods

Study area

We selected Germany as the study area as covered by the German ordnance survey map based on TK25 quadrant map sheets (hereafter called TK25 map; [45]). The TK25 map consists of



12028 grid cells and includes the terrestrial area of Germany, but excludes most of the marine territory, covering an area of approximately $360,000 \text{ km}^2$. From the 233 habitats designated under N2000, 92 occur in Germany (from which we analysed 83). The German N2000 network consists of more than 5300 mostly small (median area = 2 km^2), single sites covering an area of about $80,000 \text{ km}^2$.

Distribution of natura 2000 habitats

To determine the gaps in habitat coverage under N2000, and to eventually identify priority areas for filling these gaps for habitats that are not adequately covered, we needed maps with habitat-specific occurrence information. EU member states have to report N2000 habitat types within 10×10 km squares (100 km^2 ; https://bd.eionet.europa.eu/). Because most of the German habitat mapping to date is based on the TK25 map, with 11×11 km grid cells (121 km^2), Germany is currently using these quadrants to report N2000 habitat types. However, this information is of limited use for meaningful conservation planning, because i) these grid cells are too large to be considered for on-ground implementation by policy makers and stakeholders, and ii) fewer larger areas mean less flexibility in the conservation planning process.

In order to refine the information given on grid cell level, we divided each grid cell into four quadrants of equal size (which is the unit we further used as planning unit (PU); 1 PU \sim 30 km²; total number of PUs = 48112; Fig 1C). Since the TK25 map only states whether or not a habitat occurs within a grid cell (and gives no information about its extent or location), we had to verify whether the habitat is located in one, two, three, or all four of the respective PUs. To do so, first we combined the divided TK25 map with a European Nature Information System (EUNIS) habitat class map (section 2.2.1 "Assignment of EUNIS habitat classes to N2000 habitats"; European Environment Agency, 2016a; Fig 1D). In a second step, we verified habitat occurrence on PU-level by using occurrence data of characteristic plant species (section 2.2.2 "Assignment of plant species to Natura 2000 habitats"; Fig 1E). With this process, we excluded PUs that have a high improbability of containing the target habitat. For further analyses, we used presence/absence data of habitats within a PU.

Assignment of EUNIS habitat classes to natura 2000 habitats. The EUNIS habitat classification map offers habitat information with a spatial resolution of 100×100 m grid cells, which is much more detailed than the TK25 maps. However, its thematic resolution is less detailed, considering only 40 different habitat classes in Germany (\$1 Table). Eight of these habitat classes belong to highly artificial areas and were excluded from further analyses (\$1 Table, asterisks). Within the remaining 32 habitat classes, only three different categories exist for forests, whereas in Annex I of the HD 18 different forest habitats are listed, plus another two habitats which are closely related to forests. To make use of the high spatial resolution of the EUNIS habitat classification map, we had to find matching combinations of the remaining 32 habitat classes to describe the 92 N2000 habitats occurring in Germany. Although recommendations on how habitat classes can be translated into N2000 habitats exist [46], we found this exercise challenging. To provide a better correspondence between the TK25 maps and the EUNIS habitat classes, first we checked each EUNIS habitat class definition and searched for similarities in N2000 habitat definitions. Additionally, we used example pictures showing N2000 habitats from guidelines for field monitoring from different German Federal States and checked the reports from the German Federal Agency for Nature Conservation (BfN) for habitat-specific plant species. We used this information to find more similarities between plant species and EUNIS habitat classes. For example, N2000 habitat 3260 'Water courses of plain to montane levels with the Ranunculion fluitantis and Callitricho-Batrachion vegetation' is described by the BfN as mainly consisting of streams and running waters, but also containing



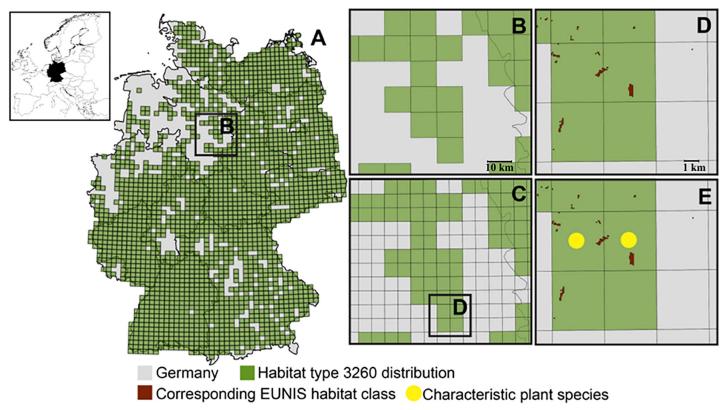


Fig 1. Example of PU-specification of N2000 habitats. A) Distribution of habitat 3260 "Water courses of plain to montane levels with the Ranunculion fluitantis and Callitricho-Batrachion vegetation" in Germany (upper left panel indicates the location of Germany within Europe) as reported by the German Federal Agency for Nature Conservation (BfN; BfN, 2013) on TK25 grid cell level (each grid cell is ~ 120 km2). B) Enlargement of a random area (grid size ~ 120 km²) to better visualize the partitioning of TK25 grid cells into four equal quadrants (PUs; area ~ 30 km2) as seen in C. D) Single, partitioned TK25 grid cell (in the centre in green) combined with the EUNIS habitat class which accounts for habitat 3260. The lower right PU was excluded from further considerations of habitat 3260 occurrence, since it does not contain any EUNIS habitat class accounting for habitat 3260. E) Single, partitioned TK25 grid cell and the EUNIS habitat class combined with occurrence data of plant species characteristic for habitat 3260 (yellow circles). Since in the lower left PU not a single characteristic plant species accounting for habitat 3260 occurred, this PU was excluded from further considerations of potential habitat occurrence. In this example, habitat 3260 most likely occurs only in the upper two PUs.

backwaters and near natural drains with natural vegetation [47]. The recommended matching EUNIS land cover class is 'Surface running waters' [46]. However, by using just this recommendation, we would have missed a high amount of PUs in which habitat 3260 occurs in Germany. Therefore, we additionally matched the EUNIS land cover class 'Surface standing waters' to the habitat 3260, since this class contains canals, man-made freshwater bodies, and reservoirs [48]. Moreover, because the EUNIS habitat classification is based on satellite images, and therefore does not indicate sub-surface habitats, we had to exclude N2000 habitat 8310 (Caves not open to the public) from further analyses. We also excluded the habitats 1110 (Sandbanks which are slightly covered by sea water all the time), 1130 (Estuaries), 1140 (Mudflats and sandflats not covered by seawater at low tide), 1160 (Large shallow inlets and bays), and 1170 (Reefs), as they belong to open sea and tidal areas. Additionally, these habitats mostly refer to areas which are not covered by the TK25 map.

Assignment of plant species to natura 2000 habitats. The BfN assigns a set of characteristic plant species based on plant communities to the majority of N2000 habitats occurring in Germany (i.e. to 83 of the 85 habitats that we included in this study). We used this information to further downscale the N2000 habitat distribution information provided by the BfN. We used occurrence data of plant species provided by www.floraweb.de (FloraWeb-data and



information on plants and vegetation in Germany), which reports information on the same grid cell level, i.e. PU level, as we used for our analyses (30 km²). The classification of these communities is based on syntaxonomy, with the plant association as the highest syntaxonomic rank, which is further separated into alliances, orders, and classes [49]. For each syntaxonomic rank, a so called character species or group of character species exists. Character species are plant species, which define a certain syntaxonomic rank. Additionally, differential species are used to distinguish between ranks. That means that these plant species are used to separate two closely related ranks, which could have a similar set of character species. We checked habitat descriptions provided by the BfN as well as (where available) descriptions provided from the German Federal States for field habitat mapping (e.g. https://www.lubw.badenwuerttemberg.de for Baden-Würtemberg, https://lau.sachsen-anhalt.de for Saxony-Anhalt etc.) to evaluate which plant community classes or orders are typical for each N2000 habitat. We used the lowest syntaxonomic rank possible. First, we included character species of the identified communities in our analyses. In case there were not enough character species, we used differential species to reach a number of ten plants per habitat (S2 Table). If more than one plant community was recommended for a habitat, we selected an equal number of plant species across the communities for our analyses. Additionally, for each habitat, we checked if the species named as the character species by Pott (1995) also occured in the plant species list provided by the BfN. If that was the case, we then used a plant species for our downscaling approach.

Assessing habitat coverage

To assess the coverage of habitats under N2000, we first had to decide whether a PU can be considered as protected or not. To do so, we calculated the area of each PU covered by N2000 using the most current N2000 layer [50]. We built four scenarios using different thresholds of the percentage of a PU area covered by N2000 sites (90%, 75%, 50%, and 25%; scenario 90, scenario 75, scenario 50 and scenario 25, respectively). Next, we tested each scenario for missing habitats, i.e. habitats that did not occur in any of the PUs considered as protected. We then evaluated whether a habitat can be considered as sufficiently covered. As a habitat-specific target, we used 17% of the total number of PUs where the respective habitat occurs, adopting Aichi target 11 for lack of specific area targets in the HD (for more information see \$2 Table). For example, if a habitat occured in 100 PUs, the habitat-specific target was set to 17 PUs. To test whether the habitat-specific frequency of occurrence, measured as the amount of PUs in which a habitat occurs, influences its coverage within N2000, we separated habitats in three groups: "rare" habitats found in less than 100 PUs, "intermediate" habitats found in between 100 to 1000 PUs, and "common" habitats occuring in more than 1000 PUs. To test for differences in coverage between the three groups within a scenario, we used a Kruskall Wallis Test and as a post-hoc test a Dunn's Test with Benjamini-Hochberg p-value adjustment.

Identification of priority areas using Marxan

To identify a minimum set of PUs to improve the representation of habitats in N2000, we used the conservation planning software Marxan [51]. Marxan solves the so-called minimum-set problem by trying to represent all conservation features at the minimum cost, while attending to other spatial constrains like connectivity [51]. In our study, we ran Marxan for five different scenarios. In scenario 90, 75, 50, and 25, we locked-in the PUs, i.e. we forced Marxan to use the PUs in the planning exercise, which are covered by N2000 in more than 90%, 75%, 50%, or 25%. In an additional free-choice scenario, we let Marxan choose from all PUs, apart from 173 PUs located at the North and Baltic Sea, which we locked-in (in all scenarios). In these PUs



that cover mainly marine habitats and only partly terrestrial ones, N2000 sites were most likely implemented to protect habitats which we excluded from our analyses (see above). We used the average human footprint value [22, 52], a measure of human impact in each PU (Fig 2; [53]) as a surrogate for cost (human footprint penalty = HFPP). Details of the Marxan analyses are elaborated on in the S1 File.

The result of high human footprint values in PUs represents a reduced likelihood for these PUs to be included in the conservation network, since they are most likely heavily degraded and therefore of lower quality, or their inclusion would be very costly. As there are no specific area targets for habitats mentioned in the HD, we ran sensitivity analyses for seven different area targets (1%, 5%, 10%, 15%, 17% (the Aichi Target 11), 20%, and 25%) calculated as percentages of the total number of PUs in which a habitat occurs, for all scenarios. We set the species penalty factor (SPF, specifies the magnitude of penalty for unmet targets) to 10 for all habitats, because we wanted to include all habitats with the same probability in our planning solution and calibrated the boundary length modifier (BLM, specifies the connectivity within the proposed conservation network) to two. For each target, we ran 100 replicates with 1,000,000 iterations each.

Results

Habitat coverage

Analysing habitat coverage revealed that the number of total missing habitats ranged from zero in scenario 25 to seven in scenario 90 (Table 1). Considering 17% of the total number of PUs in which a habitat occurs as a conservation target for each habitat, scenario 25 adequately covers 83 of 85 habitats. Hence, the two missing habitats were included in N2000 sites, but not covered enough to meet the 17% target. In scenario 50, the number of sufficiently protected habitat types dropped to 37, and in scenario 90 15 habitats were inadequately covered (Table 1).

We found a significant decrease in covereage from rare to intermediate to common habitats for all scenarios (Dunn's Test, p< 0.05; Fig 3). In scenario 25, i.e. in the least restrictive scenario, all three habitat categories were covered by more than 17% of the total N2000 area with a mean proportion of $56.8 \pm 21.3\%$ (mean \pm SD) for rare habitats, $44.8 \pm 20.3\%$ for intermediate, and $26.7 \pm 4.7\%$ for common habitats (Fig 3). Contrarily, in scenario 90, the proportional areas covered by N2000 were below 17% for all three categories ($16.0 \pm 17.8\%$ for rare, $10.9 \pm 12.3\%$ for intermediate and $2.5 \pm 2.0\%$ for common habitats; Fig 3). Scenarios 50 and 75 ranged in between these two scenarios, but showed the same trend of decreasing coverage with increasing number of PUs in which a habitat occurs (Fig 3).

Identification of priority areas to fill habitat gaps using Marxan

To fill the identified habitat gaps, we ran sensitivity analyses in Marxan for each of the four scenarios and the free choice scenario. The analyses revealed that the lower the threshold was set for a PU to be considered as protected, the more PUs were needed to reach a target and, therefore, the higher the total HFPP was (Fig 4; Table 2; S2 Table). This resulted in the highest total number of 2700 PUs needed in scenrio 25, and a total HFPP of 427.1, to fulfil the 17% target for all habitats. However, because N2000 in scenario 25 already consisted of 2687 PUs, only 13 PUs would have to be added (Table 2). Even for a 20% target, the number of additional PUs needed remained low (Fig 4). Scenario 90 required the fewest PUs to be protected (1730) with the lowest HFPP (227.0; Table 2; Fig 4). Numbers of PUs and HFPP in scenarios 50, 75, and in free-choice ranged in between these two scenarios (Table 2). All scenarios considering the current N2000 network in the Marxan analyses, except scenario 90, were less efficient. This means



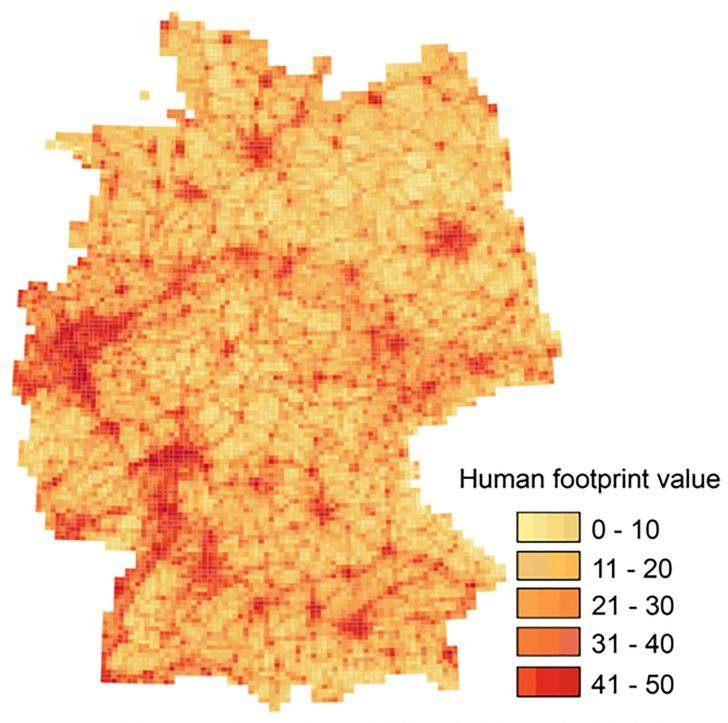


Fig 2. Human footprint (HFP) map of Germany. The HFP was used as a surrogate for highly humanized PUs for the Marxan analyses. A higher value indicates greater human impacts on a PU, i.e. a higher cost-penalty for adding a PU. HFP Values based on Sedac, 2016.

that they needed more PUs to reach a certain target compared to the free-choice scenario, regardless of the targets used (Table 2).

However, in all five scenarios habitat targets could be reached. This means that it was possible to represent the 85 habitats adequately by adding the identified PUs (Fig 5).



Table 1. Overview of missing habitats in the four different scenarios. The table shows for each scenario: the number of PUs considered as protected, the number of total missing habitats, the number of habitats protected sufficiently when considering the 17% target (maximum 85 habitats), and the mean number of PUs which have to be additionally protected for each habitat to reach the 17% target.

	N° of PUs considered as protected	Total N° of missing habitats	N° of habitats protected sufficiently (17% target) out of all habitats (85)	Mean (± SD) PUs missing for each habitat to fulfil 17% target
25	2687	0	83	< 10
50	1363	2	37	122 (± 173)
75	674	3	21	211 (± 294)
90	249	7	15	255 (± 330)

Finally, to evaluate if the current set of protected PUs under N2000 is the most effective way to cover habitats across all scenarios, we compared the spatial overlap of each scenario with the free-choice scenario (assuming that this scenario represents a highly efficient way of achieving the representation targets for all habitats; Fig 5). We found an increase in spatial overlap, when the threshold for considering a PU as protected, increased. In scenario 25, for example, we

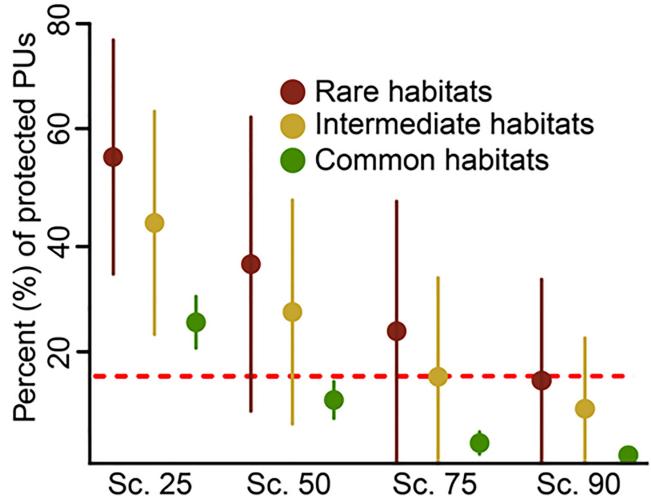


Fig 3. The rate of protection of N2000 habitats. Representation of the three habitat categories (proportion covered by Natura 2000 sites, mean \pm SD) in the current N2000 network based on the four different scenarios (Scenario 25, scenario 50, scenario 75 and scenario 90). Rare habitats occur in less than 100 PUs (n = 18), intermediate in a range of 100 to 1000 PUs (n = 39), and common habitats occur in more than 1000 PUs (n = 28). The red dashed line indicates the 17% target.

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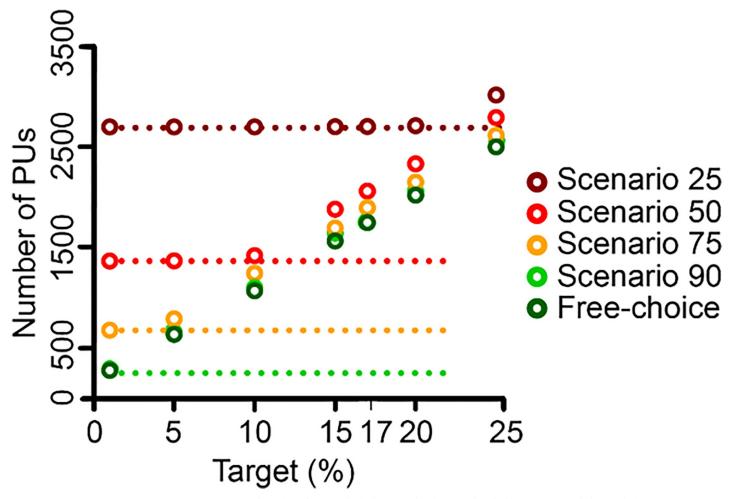


Fig 4. Sensitivity analysis for habitat target setting. Total number of PUs (i.e. locked-in PUs plus the ones identified by Marxan) needed to reach the 1%, 5%, 10%, 15%, 17%, 20%, or 25% target. Targets where calculated as a percentage of the maximum number of PUs in which a certain habitat occurs. For example, the 5%, 10%, 20% targets for a habitat which occurs in 100 PUs were 5, 10, and 20 PUs, respectively. Dashed lines indicate the number of PUs in each scenario, which were considered as initially protected, i.e. covered by N2000 and therefore locked-in for Marxan analyses (Table 1).

found 22.2% of the initially protected PUs also being selected by Marxan in the free-choice scenario, whereas 35.5% of PUs overlapped in scenario 90. Scenarios 50 and 75 shared 26.4% and 29.1% of PUs with the free-choice scenario respectively.

Discussion

Multiple conservation needs within each EU member state could easily lead to an ineffective distribution of nature conservation funds, i.e. protecting areas because of country-specific

Table 2. Specifics on Marxan solutions. Detailed information about necessities to protect 17% of each N2000 habitat in each scenario. HFPP = human footprint penalty.

Scenario	Locked-in PUs	N° of additional PUs needed to fulfil the 17% target	Total number of PUs	HFPP for additional PUs	Total HFPP
25	2687	13	2700	1,32	427,1
50	1363	685	2058	91,05	284
75	674	1219	1893	155,89	243,4
90	249	1484	1733	193,43	227
Free-choice	173	1545	1745	203,75	233,93

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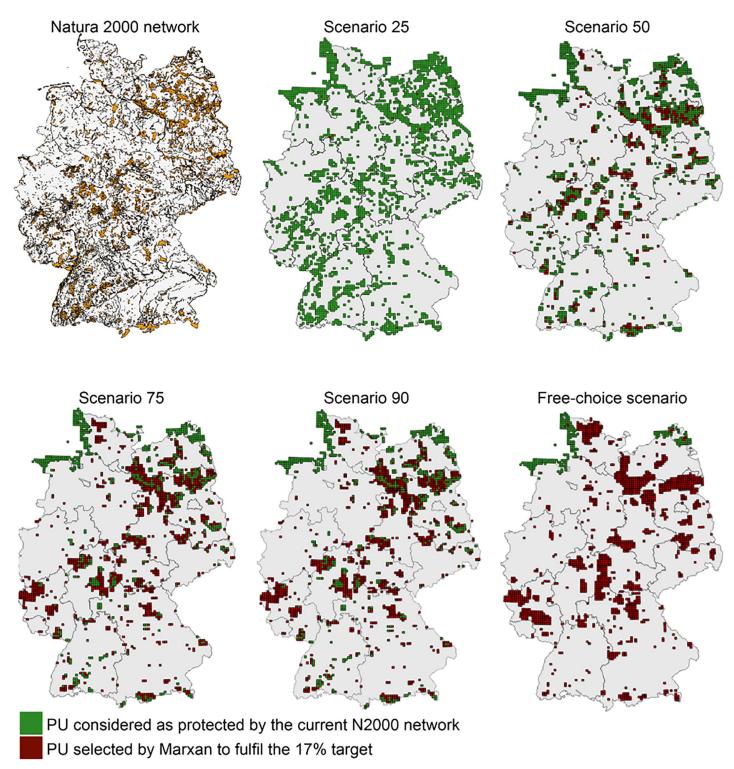


Fig 5. Best Marxan solutions for the five scenarios. Spatial distribution of PUs considered as protected (i.e. locked-in in the optimization analyses) and PUs selected by Marxan to fulfil the 17% target for all habitat types for the five scenarios. All scenarios met the 17% target for all habitat types (n = 85). Note that we locked-in PUs (green) being part of the coastal areas of North and Baltic Sea for the free-choice scenario (see Methods).



interests, while these areas are not effective when considering EU-wide targets [54, 55]. Thinking of N2000 as a network covering 28 EU member states, different policies and opposing interests between them result in an additional challenges for establishing N2000 sites (cost)-efficiently [37]. Hence, it is essential for N2000 and the related directives to assess their effectiveness and identify potential for future progress regularly. Our results indicate that, even if established in a highly populated country like Germany [22], N2000 could cope with multiple interests and potentially cover an unbiased representation of habitats. However, we also identified room for improvement for which the current N2000 network can build an excellent basis.

Missing habitats and underrepresentation of common habitats

Our gap analyses did not identify any missing habitats for scenario 25, and the number of missing habitats even remained low for the most conservative scenario (i.e. scenario 90 with seven missing habitats). This is an achievement for N2000, especially when considering that studies which focus on species protection in N2000 often found a varying number of species not being effectively protected [15]. Although N2000 is successful when considering the number of habitats protected, we found that common habitats are underrepresented compared to rare ones which are on average well covered (>17% of their distribution included in N2000). This is an interesting finding, since it is not in line with studies that consider species as conservation targets, which often found that rare and endemic species are underrepresented in conservation networks [56–58]. The good representation of rare habitats under N2000 in Germany could be the result of the thresholds we used for PUs to be considered as protected. As we cannot evaluate for which habitats a N2000 site was initially designated, it is possible that a PU, which for example is currently covered 25% by N2000 to protect a large lake, concurrently protects one or several rare habitats that happen to occur in the same PU. The likelihood of erroneously considering a habitat adequately covered by N2000 increases, the lower the threshold is for considering a PU as protected. Additionally, as N2000 sites cover on average 6% of a PU (with half of all PUs being covered between 0.1 and 21%), we labelled many PUs as not sufficiently protected. Therefore, we are likely to have missed some protected areas. These disregarded PUs could theoretically increase the coverage of common habitats. However, as they are only covered by small patches of N2000, it is more likely that including these PUs would have increased the representation of rare habitats. Finally, we found that the median area of a N2000 site in Germany is 2 km² with 75% of the sites being smaller than 9 km². This means that, despite Germany declaring by far the most N2000 sites (5206), the total area covered by these sites is comparably small (80,773 km² total area including 55,170 km² terrestrial area, compared to Spain covering the largest N2000 area with 1863 sites covering 222,142 km² total area including 137,757 km² terrestrial area, European Commission 2016b). Hence, the amount and/or the size of N2000 sites may be insufficient to protect common habitats adequately in Germany [59], which is a common issue conservation networks are facing [60].

Call for specific area targets to avoid over- or underrepresentation of habitats

It is impossible to evaluate the progress in habitat protection in Europe without measurable targets [61]. The Aichi target 11, which aims to protect 17% of terrestrial areas, could easily be applied for each habitat. In Germany (for example when considering scenario 25), only a small amount of areas would need to be added to the current N2000 network to reach a 17% target for all habitats. We used a percentage of the total distribution of habitats to set our targets to test the Aichi target 11 which treats all habitats equally, i.e. fosters the protection of the same



proportion of all of them. Additionally, we chose targets for the habitats in proportion to their representation within Germany's territory as recommended by the HD (92/43/EEC, Article 3, paragraph 2). Using proportional targets, we may have emphasised common, large habitats (mainly meadows and forests in our study). In doing so, however, we accounted for the fact that large-area habitats, for example forests, simply need more space to be protected sufficiently [41, 59] which is crucial for endangered, large, terrestrial mammals [62].

Considering area targets for each habitat in the HD would ensure i) a balanced habitat protection within Europe, and ii) evaluation of the trajectory of habitat protection compared to a current baseline. Since the HFPP for reaching the 17% target in scenario 25 was low (Table 2), the necessary PUs are likely to be situated in natural and semi-natural areas. Hence, it could be expected that the costs for adding these PUs would also be low, which is important when planning for future conservation [24].

N2000 compared to the free-choice scenario

The free-choice scenario consistently performed better in terms of minimizing the HFPP and the total number of PUs than most other scenarios, except from scenario 90 which performed similarly well. Additionally, we found that the spatial overlap with the free-choice scenario increased when the threshold for considering a PU as protected increased. The much higher number of PUs necessary to reach all the targets, together with the low spatial overlap of 22.2% when compared to the free-choice scenario, indicates that in scenario 25 a lot of PUs considered as protected do not contribute much to the conservation status of habitats. Although we found only 35.5% spatial overlap between the free-choice scenario and scenario 90, the free-choice scenario did not perform better than scenario 90 in terms of total HFPP and number of PUs. This indicates that PUs which are currently covered 90% or more by N2000 sites, have the potential to build the basis for an efficient conservation network. However, since in scenario 90 only 250 PUs were initially considered as protected i.e. locked-in, another 1500 PUs would be needed to fulfil the 17% target for each habitat type.

Data robustness

As a full monitoring has not yet been completed for N2000 habitat types outside of the N2000 network in Germany, the habitat information contained in the TK25 maps we used here is based on expert judgments and/or modeling approaches. Hence, our estimations of the distribution of N2000 habitat types are likely to contain some uncertainty. Combining these data with the EUNIS habitat class map to downscale the resolution of the TK25 maps, and to run a meaningful conservation exercise, adds another layer of uncertainty to our analyses. Uncertainties in habitat type distribution can be a challenge [32] which we accounted for by three means: 1) comparing the definitions of N2000 habitat types and EUNIS habitat classes using the official translation tables provided by EEA, 2) manually checking the spatial overlap between N2000 habitat types and EUNIS habitat classes, and 3) verifying our habitat distribution estimations with plant species distribution data.

Applying the workflow to other EU member states

To apply the proposed workflow to other EU member states, two main data sets are needed: 1) A country-specific EUNIS habitat class map, which is open source and available for all EU member states (http://eunis.eea.europa.eu/about). This data set provides information on the occurrence of habitat classes (see more information in the method's section above) and recommendations on how those can be linked to N2000 habitat types. In caseWhere country-specific N2000 habitat maps exist (as the TK25 map for Germany), they can be combined with the



EUNIS habitat class map (see above). 2) To verify and downscale the EUNIS habitat class map (or a combined EUNIS-N2000 habitat map), plant distribution data is needed. Similar data sets asto the one we used for Germany can be found for other countries. Examples of such data sets are include: The "Raster der floristischen Kartierung" (https://www.gbif.org/dataset/85ab1bf8-f762-11e1-a439-00145eb45e9a) providing plant distribution data with an identical resolution asto the German one for Austria; the Species Observation System "Artportalen" with more than 53 million occurrence records from plants, animals, and funghi (https://www.artdatabanken.se/en/species-observations/) covering Sweden; orand the information system "Anthos" (http://www.anthos.es/index.php?lang=en) with plant occurrence information for Portugal and Spain, containing more than 1.8 million occurrence points for plants across the Iberian Peninsula alone; to just name a few.

Future conservation management practices: Quantitative vs. qualitative targets

Conservation targets such as the CBD Aichi target 11, that assess a purely quantitative progress in nature conservation efforts, have recently been challenged [63, 64]. Barnes et al. (2018) argues that nature conservation efforts must focus on the quality of protected areas and not on their quantity. Our study shows that one consequence of using quantitative targets is identifying an overrepresentation of rare conservation features. This clearly contrasts the current focus on implementing protected areas for rare conservation features [65]. For habitats in the N2000 network, this focus finds its expression in the discrimination between habitats which are only listed for protection, and those among them which are given priority because they are particularly vulnerable. In our study, we found the highest proportion of priority habitat types in the rare habitat group (28%, and 23% and 21% in the intermediate and common habitat groups respectively). Hence, overrepresentation of rare N2000 habitat types is partly anchored in the HD itself.

Focusing on rare or threatened conservation features will always result in a 'reaction-behaviour' of conservation efforts; i.e. nature assets must be (or become) rare or threatened, before conservation resources will be allocated. This stands in contrast to recent evidence found for a dramatic decline in species groups which have not been in the focus of conservation efforts, because they were considered abundant and non-threatened [66, 67]. Hence, we conclude that for an effective biodiversity protection a mixture of both, qualitative and quantitative targets, is needed. Here "qualitative" expresses a general active management of local conservation actions, some of which are hard to quantify. However, such local actions are vital to make conservation effective in practice. Consequently, in the HD a discrimination between priority and non-priority habitats is helpful to protect rare and threatened habitats, which currently need most attention. Additionally however, we argue for quantitative targets to foster conservation efforts towards common, large habitat types to protect them from becoming rare or threatened in the first place.

Conclusions

To cope with the pressing biodiversity issues that Europe is currently facing, we need protected areas that allow conservation efforts to tackle the specific challenges. First, allowing for flexibility to cope with arising climate- and land-use changes [68]; second, accounting for cost-effectiveness when planning new or adjusting existing protected areas [24, 54]; and third, striving for tangible targets, because effective nature conservation needs more than just an arbitrary amount of protected area [58, 64]. The workflow we presented here, based on publicly available data sets, allows identification of gaps and biases in habitat representation within the



N2000 network in Europe, with the subsequent prioritization of areas with high conservation value. In Germany, the N2000 network is effective in covering the HD Annex I habitats, but rare habitats are overrepresented compared to common habitats when using the same quantitative proportional targets for all of them. The German case study additionally suggests that especially highly protected PUs (PUs covered by more than 90% with N2000 sites) build an excellent basis towards an effective and efficient network that can fulfil its role as the world's largest nature conservation network. Our results enhance the value of N2000 at preserving habitats in Germany, whereas the proposed generic workflow helps guide future assessment and conservation efforts in Europe.

Supporting information

S1 File. Description of how Marxan variables were set; species penalty factor (SPF) and boundary length modifier (BLM).
(DOCX)

S1 Table. EUNIS habitat classes occurring in Germany with corresponding numerical codes. Habitat classes marked with an asterisk were not used to describe Natura 2000 habitats (see explanation in text).

(DOCX)

S2 Table. Natura 2000 habitat types and corresponding EUNIS habitat classes and plant species. Additionally, the maximum number (n°) of PUs in which a habitat type occurs, the number of PUs covered by N2000 in each scenario (Sc. 90, Sc. 75, Sc. 50, and Sc. 25), and the number of PUs which have to be protected to reach the 17% Aichi target, are given. PU = planning unit. (DOCX)

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