# Mixed evidence that protected areas slow declines of threatened plant species in Germany

Marie Englert[1], Marten Winter[1,2], Christian Wirth[1,2,3] & Ingmar R. Staude[1,2]

*1. Institute of Biology, Leipzig University, 04103 Leipzig, Germany*

*2. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany*

*3. Max-Planck-Institute for Biogeochemistry, Jena, Germany*

**ORCID iDs:** Marie Englert, 0009-0004-9460-0951; Ingmar R. Staude, 0000-0003-2306-8780; Marten Winter, 0000-0002-9593-7300; Christian Wirth, 0000-0003-2604-8056

**Corresponding author:** Marie Englert; **m.englert@uni-leipzig.de**

**Author contribution statement:** Marie Englert: conceptualization (lead); methodology (equal); formal analysis (lead); data curation (lead); visualization (lead); writing – original draft (lead); writing – review & editing (equal).
Ingmar R. Staude: conceptualization (lead); methodology (equal); supervision (lead); project administration (lead); writing – original draft (supporting); writing – review & editing (equal).
Marten Winter: conceptualization (supporting); methodology (supporting); writing – review & editing (supporting).
Christian Wirth: conceptualization (supporting); methodology (supporting); writing – review & editing (supporting).

**Data availability statement:** The primary datasets used in this study are publicly available from the sources cited in Table S1. These include the occurrence-probability data of Eichenberg et al. (2021), the ReSurvey Germany vegetation-plot data of Jandt et al. (2022), HILDA+ land-cover data, protected-area boundaries from the World Database on Protected Areas, and the German Red List of vascular plants. Exact plot coordinates used to assign ReSurvey plots to protected areas were provided by the ReSurvey Germany data custodians and are not redistributed here. All derived data required to reproduce the analyses, together with the R code, are openly available on GitHub at https://github.com/moohkuh/threatened-plants-protected-area-publication.

**Acknowledgements:** We thank Helge Bruelheide, Ute Jandt and Florian Jansen for providing access to the plot coordinates of the ReSurvey Germany vegetation plots and for their valuable advice throughout the study. We are grateful to all contributors to the ReSurvey Germany project for collecting, compiling and making available the vegetation resurvey data used in this study. We also thank David Eichenberg for his advice and support regarding the occurrence probability-data. We further acknowledge all contributors to the underlying biodiversity and spatial datasets used in this study. This work was funded by the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG; project number 552574450).

ChatGPT (OpenAI) and Claude (Anthropic) were used to assist with R code development and debugging for the analyses. All analytical decisions were made by the authors, and all code was reviewed and executed by M.E. The authors take full responsibility for the analyses and results.

# Mixed evidence that protected areas slow declines of threatened plant species in Germany


## Abstract

1. A central credo of plant conservation is that the most effective way to protect native plants is to conserve the habitats in which they occur. Protected areas are therefore a cornerstone of plant conservation, and much research has focused on optimizing their representativeness across species. Far fewer studies, however, have tested whether protected populations actually persist over time. Here, we address this gap and assess whether protected areas in Germany promote persistence of threatened plant species.
2. Using a large-scale, 60-year occurrence dataset based on >29 million records for >2,100 plant species, together with >7,700 local plot time series spanning almost 100 years for 1,800 vascular plant species, we evaluated protected-area effectiveness across two spatial scales. We tested (i) whether greater coverage of threatened species' ranges by protected areas was associated with greater range retention, (ii) whether threatened species showed more favorable cover, colonization, and extinction dynamics in protected than unprotected plots, and (iii) whether these relationships differed among protected-area categories.
3. Greater protection of species' baseline ranges was associated with higher range retention, although protected-area coverage explained little variation, and category-specific positive associations were detected only for strictly protected areas (IUCN I–III and biosphere reserve core zones) and Natura 2000 sites. At the local scale, cover trends differed little between protected and unprotected plots and were generally negative, with weak evidence for more positive trends in Natura 2000 sites. Extinction odds of threatened species were lower in Natura 2000 and IUCN IV sites, both characterized by more active management, but higher in IUCN V areas. Colonization

counts were higher in Natura 2000 sites and strictly protected areas than outside protected areas.

4. *Synthesis:* Natura 2000 was the only protection category showing favorable effects across both spatial scales and multiple measures of persistence. More broadly, however, the effects of protection were modest and far from unequivocal or universal. Thus, our findings suggest that biodiversity targets focused on protected-area extent, like 30-by-30, whilst certainly benefiting several other attributes of biodiversity, are in themselves not a safe bet for the conservation of threatened flora.

## Introduction

Protected areas serve as an essential tool for combating the global biodiversity crisis and achieving internationally agreed biodiversity targets (Gray et al., 2016; Rodrigues & Cazalis, 2020). Currently, approximately 17.6% of the global terrestrial land area is covered by protected areas. While the Kunming-Montreal Global Biodiversity Framework (COP15) of 2022 set a new conservation target to protect and effectively manage 30% of the world's land and sea by 2030 (COP 2022; UNEP-WCMC and IUCN, 2024), quantifying the actual effectiveness of protected areas remains a central challenge in conservation ecology.

A useful framework to address this challenge distinguishes two complementary components (Gaston et al., 2006): (i) representativeness (*sensu* Pressey et al., 1993), or whether protected areas represent a sufficient fraction of regional biodiversity and (ii) persistence, or whether protected areas achieve the maintenance of biodiversity features. Representativeness constitutes a commonly used metric to quantify protected area effectiveness (Gruber et al., 2012; Maiorano et al., 2015; Rodrigues et al., 2004; Scott et al., 1993), in part because conservation planning approaches have largely been developed under the assumption of relatively slow and predictable environmental change (Heywood, 2019) and that maximum species representation ensures persistence of biodiversity (Cabeza & Moilanen, 2001). Yet representation does not necessarily translate into persistence. Sites can be too small to sustain viable populations, management may not match species' requirements, or conditions may change faster than a static network can accommodate. Thus, as species ranges shift and contract, snapshots of species representation at given points of time may reveal little about long-term conservation outcomes. Consequently, persistence rather than representation was proposed to be a more meaningful "currency for evaluating conservation success" (Williams & Araújo, 2002). Persistence, however, is much harder to quantify because it requires time-series data from both inside and outside protected areas, ideally for the same species.

Studies on mammals, birds or insects indicate positive but variable effects of protected areas on species persistence, depending on taxon, region and protection regime (Araújo et al., 2007; J. A. Brown et al., 2019; Hallmann et al., 2017; Rada et al., 2019; Wauchope et al., 2022; Xavier da Silva et al., 2018). Assessments for vascular plants remain, however, scarce. Notably, the most comprehensive synthesis to date, a global meta-analysis of counterfactual studies (Langhammer et al., 2024) reporting an overall positive effect of protected areas, included no study evaluating protected-area effectiveness for plants. This gap is particularly concerning for the majority of threatened plant species in Central Europe, which tend to be open habitat species dependent on nutrient-poor soils and traditional extensive land-use (Poschlod & Bonn, 1998; Staude et al., 2023). Protection may keep away some anthropogenic pressures, such as more intensive land use, but does not stop, at least on its own, successional vegetation dynamics that transform open habitats into closed ones. And even if management efforts are in place, global-change drivers such as nitrogen deposition and climate change transcend protected area boundaries and may erode habitat quality within them. Thus, it is unclear whether the central credo of plant conservation—that the most effective way to protect species is to protect the habitats in which they occur—is, in actuality, an effective strategy in an era of rapid environmental change.

Germany provides a particularly suitable setting for testing protected-area effectiveness for plants, as it combines a highly threatened flora—close to one in three native plant species is red-listed (Metzing et al., 2018)—with an extensive protected-area network that nominally exceeds the 30% target of the Kunming-Montreal Global Biodiversity Framework (www.protectedplanet.net/country/DEU). Yet this network spans protection categories of very different management regimes, from strict non-intervention to categories that permit continued land use. Evidence that protected areas improve the persistence of native flora in Germany nonetheless remains scarce. Existing assessments are largely based on current conservation

85 status or other non-temporal approaches and have often focused on Natura 2000 sites, where
86 conservation objectives more explicitly involve active habitat and species management
87 (Ellerbrok et al., 2025; Friedrichs et al., 2018; Kallimanis et al., 2015; Trochet & Schmeller,
88 2013). Such assessments provide important information on present conditions but cannot reveal
89 temporal trajectories or provide an explicit counterfactual outside protected areas. Time-series
90 studies have documented declines in German plant diversity in open habitats (Lüttgert et al.,
91 2025) and at the plot level shown that more species decrease than increase in cover (Jandt et
92 al., 2022), but have not tested whether protection affects these trends, particularly for threatened
93 flora. Germany therefore provides a critical test of whether meeting ambitious area-based
94 protection targets actually translates into improved persistence of threatened plants.

95 Assessing persistence within protected areas depends strongly on the spatial scale considered.
96 Studies conducted at coarse spatial resolution, such as those using species records aggregated
97 to grid-cells or species range maps, may be well suited to capture large-scale distributional
98 changes (e.g., Eichenberg et al., 2021) but obscure local population dynamics, since a species
99 is recorded as absent only once its last individual in a grid cell has disappeared (Keil et al.,
100 2018). For example, many orchid species show little decline in grid-cell occupancy despite the
101 loss of many local populations and marked reductions in population size (Ludwig et al., 2009).
102 Conversely, vegetation plot resurveys can reveal mean temporal trends in local abundance (e.g.
103 Steinbauer et al., 2018; Verheyen et al., 2018), but are, in comparison to grid cell data, subject
104 to greater stochasticity and plot selection bias, as resurveys are often conducted in relatively
105 intact habitats, and not in those most adversely affected by global environmental change factors
106 (Gonzalez et al., 2016). Combining monitoring data of varying grain sizes and extent can
107 therefore enable a more comprehensive assessment of protected-area effectiveness. Data on
108 changes in species distributions can be used to test whether greater coverage of species' ranges
109 by protected areas is associated with greater range retention over time, while plot-level time-

series data can reveal whether populations within protected areas show more favorable changes in abundance.

Two recent high-profile studies of vegetation change in Germany provide the necessary data for evaluating protected-area effectiveness for threatened plant species across spatial scales. Eichenberg et al. (2021) reconstructed national distributional change on a 5 x 5 km grid basis for 2,136 plant species from >29 million occurrence records spanning 1960–2017. Jandt et al. (2022), in turn, compiled 7,738 permanent and semi-permanent vegetation plots (0.5 to 2500 $m^2$) surveyed over almost a century, providing repeated local-scale measurements of occurrence and cover for 1,794 vascular plant species. Together, these datasets allow protected-area effectiveness to be evaluated both in terms of species' range retention and maintenance of local populations over time. Here, we use these data to test three hypotheses: (H1) threatened plant species with a larger fraction of their range under protection exhibit greater range retention over time (i.e., retained a greater fraction of grid cells occupied in 1960); (H2) threatened plant species exhibit more positive plot-level abundance trends, as well as higher colonization and lower extinction rates inside protected areas; and (H3) favorable trends are stronger in protected-area categories characterized by more active management. Our analysis provides, to our knowledge, the first quantitative insights into how protected area coverage relates to trends in national range size and local abundance of threatened flora in Germany.

## Methods

***Vegetation change data.*** We leveraged two complementary datasets capturing nationwide temporal changes in plant distributions and local abundance in Germany (Table S1). The first dataset provides modelled occurrence probability records for 2,136 plant species across 12,024 5 x 5 km grid cells ("Messtischblatt" quadrants, MTBQs) covering the entire terrestrial area of Germany for the three time periods T1=1960-1987, T2=1988-1996 and T3=1997-2017

(Eichenberg et al., 2021). Occurrence probabilities range from 0 to 1 and were estimated using the sampling bias correcting Frescalo algorithm (Eichenberg et al., 2021; Hill, 2012). The second dataset comprises 7,738 permanent and semi-permanent vegetation plots (0.5 to 2500 $m^2$) distributed across Germany and resurveyed between 1927 and 2020, with cover estimates for 1,794 plant species (Jandt et al., 2022). To filter threatened species, we taxonomically harmonized species names in the two datasets and the German Red List of vascular plants (Metzing et al., 2018) using the World Checklist of Vascular Plants (Govaerts et al., 2021) via the *rWCVP* and *rWCVPdata* packages (M. J. M. Brown et al., 2023). We then retained species assigned to Red List categories 0–3, R, G, and V (Table S2).

***Protected area data.*** We obtained shapefiles of protected area boundaries in Germany from the World Database on Protected Areas (WDPA; UNEP-WCMC and IUCN, 2024; https://www.protectedplanet.net/country/DEU; Table S1). We restricted analyses to polygon-based, terrestrial protected areas, excluding exclusively marine protected areas, one World Heritage Site located outside Germany's borders (WDPA ID 903141), and point-based natural monuments (e.g., individual trees or rocks; ~IUCN category III). Because WDPA protected area polygons from different legal designation categories (e.g., national parks, biosphere reserves) can spatially overlap (Notes S1; Tables S3–S4), we defined four focal categories for all subsequent analyses: strict protection (IUCN I-III and biosphere reserves core zones), IUCN IV, IUCN V and Natura 2000's Habitats Directive, hereafter referred to as "Natura 2000" (Table 1). Polygon-based National Natural Monuments (Nationale Naturmonumente) were grouped with strict protection (Notes S1). Areas designated solely under Natura 2000's Birds Directive were not included in our "Natura 2000" category, as they target birds rather than plants. For each focal category, corresponding WDPA polygons were merged into a single polygon layer. We also combined all protected areas into a single "All" category to assess associations across

159 the entire protected-area network. Note that our focal categories were still not mutually
160 exclusive (Table S3).

161 **Table 1.** Protected-area designation categories in Germany, their corresponding IUCN management categories,
162 and their assignment to the four focal categories analyzed separately in this study. Designations are ordered by
163 decreasing restriction on human intervention. Strict protection comprises IUCN categories I–III and biosphere
164 reserve core zones. "All only" refers to designations that were included only in analyses combining all protected
165 area categories into a single "All" category and were not analyzed separately. Designation types may overlap
166 spatially.

| IUCN category | German designation | English term | Intervention | Conservation objective | Combined category |
|---|---|---|---|---|---|
| Ia/Ib | Wildnisgebiete | Wilderness areas | None | Natural processes | Strict |
| – | Biosphärenreservat – Kernzone | Biosphere reserve core zone | None | Natural processes | Strict |
| II | Nationalparks | National parks | Minimal; zoned | Natural processes | Strict |
| III | Naturdenkmäler | Natural monuments | Feature-specific | Specific features | Strict |
| IV | Naturschutzgebiete | Nature reserves | Active | Habitats / species | IUCN IV |
| V | Landschaftsschutzgebiete | Landscape protection areas | Continued human use | Cultural landscape | IUCN V |
| – | Flora Fauna Habitat (FFH)-Gebiete | Natura 2000 / Habitats Directive – Special Areas of Conservation (SACs) & Site of Community Importance (SCIs) | Active | Favourable conservation status of Annex features | Natura 2000 |
| – | Vogelschutzgebiete | Natura 2000 / Birds Directive – Special Protection Areas (SPAs) | Active | Bird conservation | All only |
| – | Biosphärenreservat – Pflege-/Entwicklungszone | Biosphere reserve – buffer / transition zone | Continued human use | Sustainable use | All only |
| – | Ramsar-Gebiete | Ramsar sites | Variable | Wetland conservation | All only |
| – | Ostsee-Schutzgebiete | Baltic Sea Protected Areas (HELCOM) | Variable | Marine / coastal habitats | All only |
| – | Welterbestätten | World Heritage Sites | Variable | Outstanding universal value | All only |

167

168 ***Quantifying range protection and retention.*** To test H1 (and H3), we derived two species-level
169 metrics from the gridded occurrence data of Eichenberg et al. (2021): the proportion of the
170 baseline range under protection, calculated separately for each protected-area category, and
171 subsequent baseline-range retention. For each species, we defined the baseline range as all
172 MTBQs with occurrence probability >0 in T1 (1960–1987).

173 *Range protection.* To quantify the proportion of the baseline range under protection, we
174 intersected baseline-range MTBQs with protected-area polygons separately for each protected-
175 area category. We then calculated, for each species and category, the occurrence-probability-
176 weighted mean proportion of protected area across all MTBQs in its baseline range (Notes S2).

We used protected area data irrespective of designation date. Although later-designated areas may have been formally unprotected at baseline, those areas typically already retained the ecological value that ultimately motivated protection, as designation generally targets relatively intact rather than heavily transformed land. We restricted analyses to 11,030 MTBQs whose centroids were located within Germany because protected area data was unavailable for portions of cells extending beyond the national border. We further excluded MTBQs with >50% urban area cover in 1960, as high urbanization may constrain plant persistence independently of protection status. Urban area cover for 1960 was obtained from HILDA+ (Winkler et al., 2021), leaving 10,519 MTBQs for analysis (Notes S2).

*Range retention.* To quantify a species' range retention, we summed occurrence probabilities across all MTBQs occupied by that species at baseline and repeated this calculation for later periods using the same set of baseline-occupied cells. This captures change within the baseline range while excluding newly colonized cells. Range retention was expressed as the log-ratio of summed occurrence probabilities in T3 relative to T1 (Notes S2). Values near zero indicate little overall change, negative values indicate loss within the baseline range, and positive values indicate increases in occurrence probability within the MTBQs occupied at baseline. Two species for which range retention could not be calculated were excluded (*Anagallis tenella*, category 2: zero occurrence probability at T3, yielding a non-finite log-ratio; *Minuartia austriaca*, category R: no detectable baseline occurrence), leaving 860 species for analysis from which 658 belong to the more severely threatened species of Red List categories 0-3 and R (Table S5).

***Quantifying local population dynamics inside and outside protected areas.*** To test H2 (and H3), we derived three species-level metrics from the vegetation resurvey data of Jandt et al. (2022) following the R code by Jandt et al. 2022[1]: mean annual cover change, colonization, and

[1] https://github.com/idiv-biodiversity/ReSurveyGermany_Analysis/blob/main/SupplementaryCode1.txt

extinction inside versus outside protected areas and across protected-area categories. Plot coordinates were spatially intersected with protected-area polygons to assign protection status separately for each protected-area category (Notes S3.1; Table S7).

*Mean annual cover change.* For each threatened plant species and plot, relative cover change was calculated as the difference in cover between consecutive surveys, divided by the maximum cover of that species observed across the plot's time series. To account for unequal survey intervals, we divided relative cover changes by the number of years between consecutive surveys. Annualized cover changes were first averaged within each species × plot combination for plots with more than one resurvey and then across plots, separately for plots inside and outside each protected-area category. This two-step averaging prevented plots with multiple resurveys from receiving disproportionate weight and yielded, for each species, one mean annualized cover-change value inside and one outside protected areas. We used these species-level estimates for the main analysis because they allow a direct paired within-species comparison of cover change inside versus outside protected areas, while giving equal weight to each species. But note we also analyzed the (unaveraged) plot-level observations in a supplementary analysis (Table S12). To ensure that these paired estimates were based on sufficient spatial replication, we retained only species represented by at least five distinct plots both inside and outside each protected-area category (Table S9).

*Colonization and extinction.* Colonization was defined as a transition from absence to presence between consecutive surveys, and extinction as the reverse transition. For plots with multiple resurveys, colonization events were retained only if they were not followed by a later extinction of the same species, and extinction events only if they were not followed by subsequent recolonization of the same species. This was done in order to minimize the influence of stochastic fluctuations in species occurrence. Colonization events were summed across all threatened species and survey intervals within each plot to obtain plot-level colonization counts.

For the extinction analysis, we considered all threatened species that were present in a plot at the start of at least one survey interval and therefore could potentially be lost from that plot. Each species was counted only once per plot. For each plot, we recorded the number of threatened species that could go extinct and the number that ultimately underwent local extinction. Plots with no threatened species present at the start of any survey interval were excluded from the extinction analysis. In contrast, colonization could also be assessed in plots where no threatened species were present at the beginning of the time series.

***Statistical Analyses.*** To test H1 (and H3), we fitted separate linear models for each protected-area category, relating species' range retention to the proportion of their baseline range under protection. Because baseline range size was associated with the proportion protected (Figure S2; Table S6), we included log-transformed baseline range size as a covariate. Variance inflation factors were low (VIF = 1.01–1.35; Fox & Weisberg, 2019), and model diagnostics indicated no violations of model assumptions. Near-threatened species (category V) were excluded from the analysis reported in the main text, but we tested whether results are robust to their inclusion (Figure S4). To assess whether associations were robust to the choice of baseline period, we repeated the analysis for T2–T3, redefining species' baseline ranges at the beginning of T2 (Notes S2; Table S6; Figure S3).

To test H2 (and H3), we first related species' mean annual cover change to protection status (inside vs. outside protected areas), fitting separate species-level linear mixed-effects models for each protected-area category. Species identity was included as a random intercept to account for the paired inside–outside structure of the data. Models were fitted using the *lme4* and *lmerTest* package (Bates et al., 2015; Kuznetsova et al., 2017), and marginal means and inside–outside contrasts were estimated using the *emmeans* package (Lenth, 2025). Near-threatened species were retained in this analysis because excluding them strongly reduced the sample size

in strictly protected areas. We assessed the robustness of the results to their exclusion for all protected-area categories except strict protection, for which the model did not converge (Figure S5). Because model diagnostics indicated deviations from model assumptions for some protected-area categories, we additionally performed paired Wilcoxon signed-rank tests as a non-parametric analysis (Notes S3.2; Table S10). We further assessed the robustness of the results using mixed-effects models with robust estimation, fitted to species × plot-level mean annual cover changes. These models retained (unaveraged) multiple plot-level observations per species within each protection status (Table S12). We then related colonization and extinction to protection status (inside vs. outside protected areas), fitting separate generalized linear mixed-effects models for each protected-area category using the *glmmTMB* package (Brooks et al., 2017; McGillycuddy et al., 2025). All models included log-transformed plot size and total survey duration as covariates, and resurvey project as a random intercept to account for regional, habitat-specific, and methodological differences among projects (cf. Jandt et al., 2022). Near-threatened species were excluded from these analyses because sample sizes were sufficient without them, but we assessed the robustness of the results to their inclusion (Figure S6). Colonization was modeled as the total number of colonization events involving threatened species per plot using a negative binomial distribution, with protection-status effects expressed as incidence rate ratios (IRRs). Extinction was modeled using a binomial model, with the number of unique threatened species experiencing final local extinction modeled relative to the number of unique threatened species that could potentially go locally extinct during the observed plot time series, thereby accounting for differences among plots in the number of species available to be lost. Protection-status effects were expressed as odds ratios (ORs). For both responses, values > 1 indicate higher colonization rates or extinction odds inside protected areas, respectively. Model diagnostics indicated no substantial problems with model fit or dispersion.

For all three plot-scale responses (cover change, colonization, and extinction), we additionally tested whether protected-area size was associated with local population dynamics. These analyses were restricted to plots located inside the respective protected-area category because protected-area size could not be assigned to plots outside protected areas (Notes S3.4; Tables S17–S18).

## Results

***Range retention in relation to baseline-range protection.*** Despite an overall decline in summed occurrence probability within baseline ranges (541 of 658 species, 82.2%), species retained more of their baseline range when a greater proportion of it was protected ($\beta = 0.006$, $p < 0.01$), although the explained variance was very low ($R^2 = 0.09$). When analyses were separated by protected-area category, a positive association between range protection and retention was evident for strictly protected areas (IUCN I-III and biosphere core zones; Figure 1b; $\beta = 0.018$, $p < 0.001$, $R^2 = 0.11$) and Natura 2000 sites (Figure 1e; $\beta = 0.007$, $p < 0.01$, $R^2 = 0.09$). No association between range protection and retention was detected for IUCN IV or IUCN V areas (Figure 1c–d; Table S6). These results were consistent when near-threatened species were included (Figure S3). When using a later time period (1988) to define species' baseline ranges (Figure S4), the association between range protection and retention remained positive for strictly protected areas ($\beta = 0.022$, $p < 0.001$), was significantly negative for IUCN IV areas ($\beta = -0.007$, $p = 0.001$), and was no longer significant for Natura 2000 areas ($p = 0.084$). These associations were broadly consistent when near-threatened species were additionally included (strictly protected: $\beta = 0.023$, $p < 0.001$; IUCN IV: $\beta = -0.006$, $p = 0.001$), except that the positive association for Natura 2000 areas reappeared ($\beta = 0.003$, $p = 0.019$).

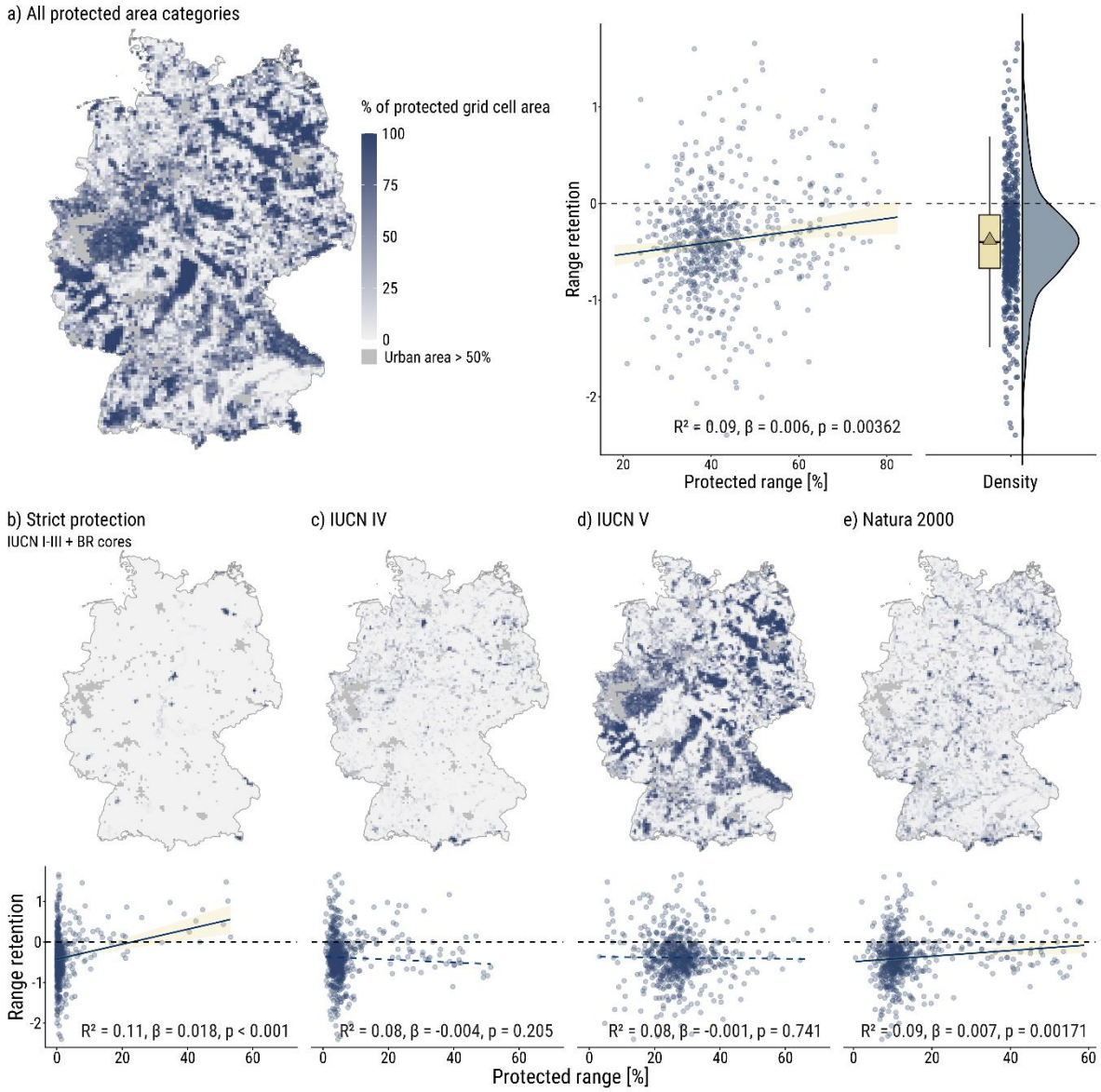



**Figure 1. Relationship between the proportion of species' baseline ranges protected and subsequent range retention in threatened plant species in Germany.** a) Total protected-area coverage in Germany and the relationship between the proportion of each species' baseline range protected and its range retention from T1 (1960) to T3 (2017), across 658 threatened plant species (including Red List categories 0-3, R). The marginal panel shows the distribution of range-retention values across species; the boxplot indicates the median and interquartile range, and the density curve shows the overall distribution. b)–e) The same relationship shown separately for strictly protected areas (IUCN I–III and biosphere reserve core zones), IUCN IV areas, IUCN V areas, and Natura 2000 Habitats Directive sites. Points represent species, lines show the fitted linear relationship, and the shaded band indicates the 95% confidence interval. Solid regression lines indicate significant relationships ($p < 0.05$).

***Local population dynamics inside and outside protected areas.*** Mean annualized cover changes of threatened plant species tended to be negative both inside and outside protected areas (Figure 2; Table S8), although the proportion of species with positive versus negative trends varied by protected-area category (Table S11). Paired within-species comparisons revealed no clear differences between protected and unprotected plots across protected-area

categories. However, the estimated contrasts were marginally significant for Natura 2000 sites ($\beta = 0.009$, 95% CI: −0.000–0.018, $p = 0.051$), suggesting that, within species, cover change was somewhat less negative inside Natura 2000 sites than outside. Wilcoxon signed-rank tests likewise indicated that cover change was slightly less negative inside than outside protected areas for Natura 2000 sites ($p = 0.020$; Table S10). These inside–outside differences were less pronounced when near-threatened species were excluded (Figure S5). A supplementary analysis using the unaveraged annualized cover changes in a hierarchical model (Table S12) showed no clear inside–outside differences; the marginal Natura 2000 contrast was not retained. Extending this model to include protected-area size indicated that size was not associated with cover change of threatened species (Table S17).

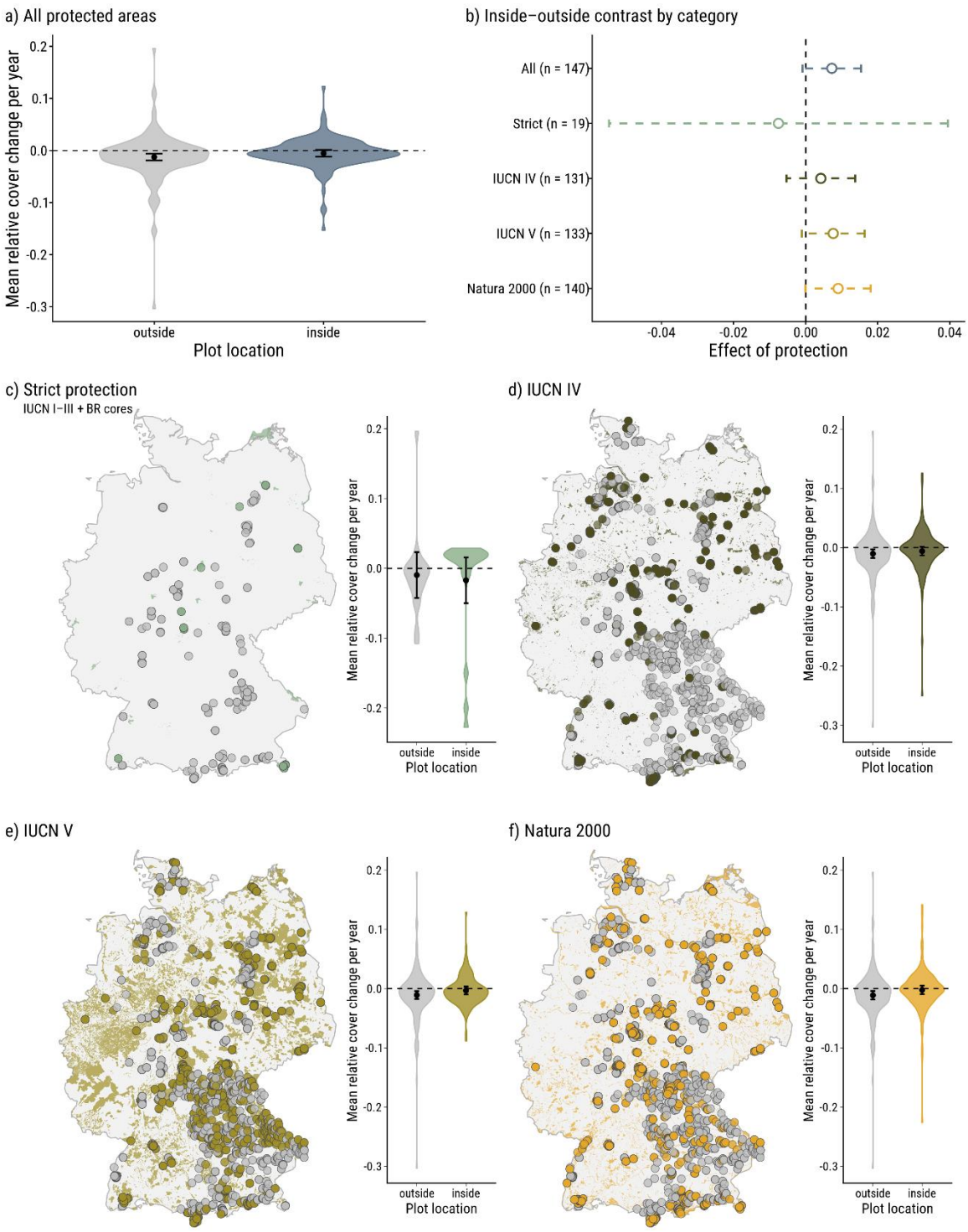



**Figure 2. Within-species comparisons of mean relative annualized cover change inside versus outside of protected areas across Germany.** Analyses include nationally red-listed species from categories 0–3, R, G, and V. a) Species-level mean annualized relative cover change in plots inside versus outside protected areas, considering all protected-area categories combined. b) Model-estimated inside–outside contrasts with 95% confidence intervals for each protected-area category; positive values indicate more positive cover change inside protected areas. Dashed confidence intervals indicate non-significant contrasts at $\alpha = 0.05$, and the vertical dashed line denotes no difference. (c–f) Plot locations and corresponding within-species comparisons for the individual protected-area categories. Violin plots show the distribution of species-level mean cover changes; black points show estimated marginal means ± 95% confidence intervals from the linear mixed-effects models. n denotes the sample size, i.e., the number of species represented by at least five plots both inside and outside the respective protected-area category. Relative cover change is calculated as the annualized change in species cover divided by

each species' maximum observed cover within its time series (Methods), and is therefore a dimensionless, species-normalized quantity, not a measure of absolute cover in percentage points.

Colonization and extinction event counts differed among protected-area categories (Figure 3; Table S13). Colonization rates of threatened species (Table S15) were higher in strictly protected areas (IRR = 1.52, 95% CI: 1.01–2.29, p = 0.047) and Natura 2000 sites (IRR = 1.34, 95% CI: 1.09–1.63, p = 0.005), corresponding to 52% and 34% higher expected colonization counts than in unprotected plots, respectively. No clear differences in colonization were detected between protected and unprotected plots for IUCN IV, IUCN V, or all protected areas combined. The odds of local extinction were clearly lower in IUCN IV areas (OR = 0.65, 95% CI: 0.48–0.88, p = 0.005) and Natura 2000 sites (OR = 0.64, 95% CI: 0.49–0.82, p < 0.001), corresponding to approximately 35% and 37% lower odds than in unprotected plots, respectively. In contrast, extinction odds were higher in IUCN V areas (OR = 1.32, 95% CI: 1.00–1.75, p = 0.0496), while no clear differences were detected for strictly protected areas or all protected areas combined. Including near-threatened species resulted in significant positive associations between protection and colonization in additional protected-area categories (Table S16), although the positive association for strictly protected areas was no longer significant. Similarly, the reduced extinction observed in Natura 2000 sites was no longer evident (Figure S6; Tables S14-S16). A supplementary analysis found no consistent associations of protected area size with extinction and colonization rates (Table S18).

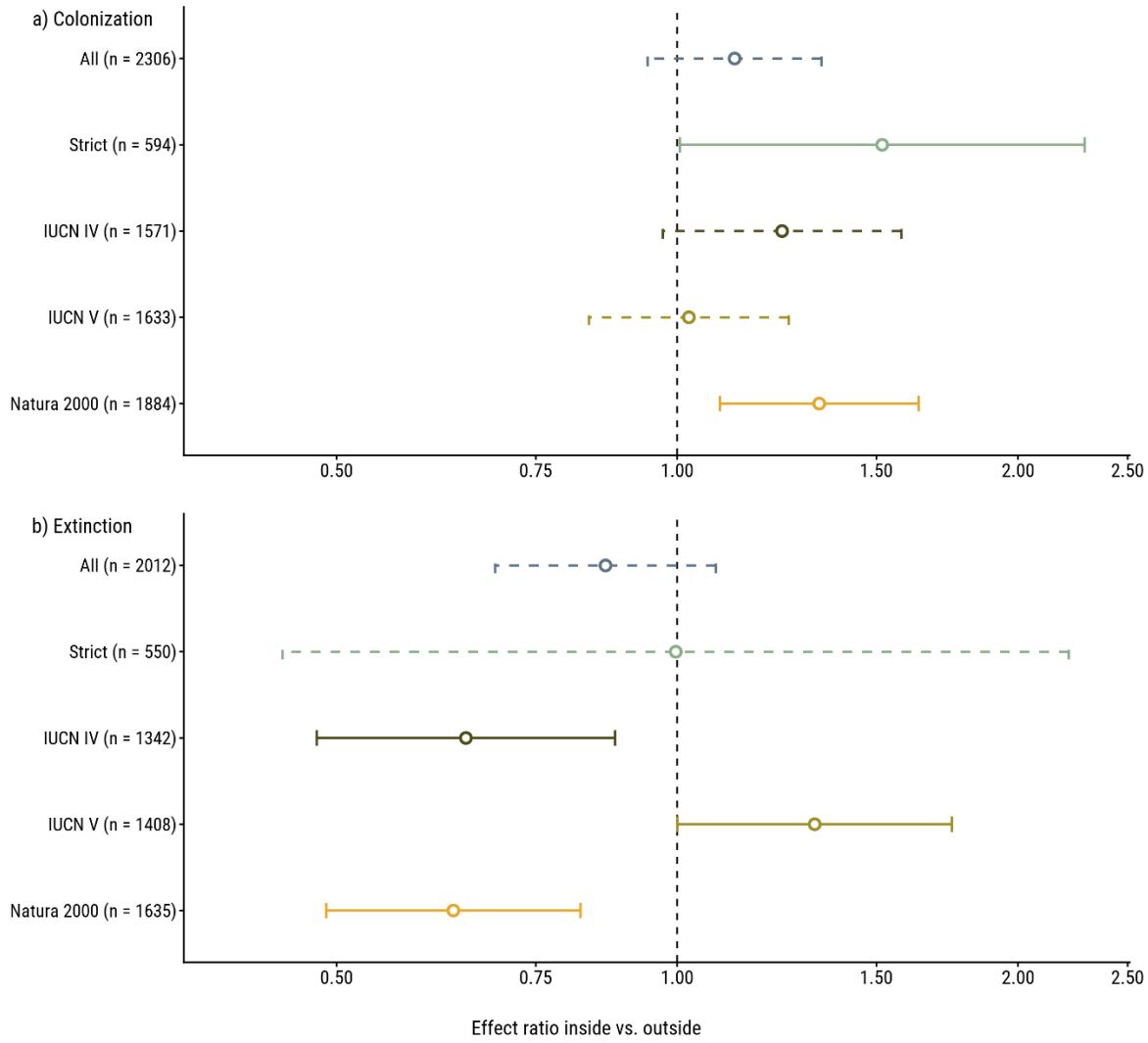



**Figure 3. Plot-level colonization and extinction of threatened plant species (Red List categories 0-3, R, G) inside versus outside protected areas.** Points show a) incidence rate ratios (IRR) for colonization and b) odds ratios (OR) for extinction, with horizontal lines indicating 95% confidence intervals. The dashed vertical line marks IRR/OR = 1 (no difference between protected and unprotected plots); values >1 indicate higher expected colonization counts or higher odds of final local extinction inside protected areas, whereas values <1 indicate the reverse. Dashed confidence intervals indicate non-significant differences at $\alpha = 0.05$; n indicates the number of plots included in the respective colonization or extinction model. Effect ratios are plotted on a log10-transformed x-axis. Near-threatened species (V) were excluded from this analysis; see Figure S6 for results including near-threatened species.

## Discussion

Our results provide mixed evidence for the effectiveness of protected areas in conserving threatened plant species. Species whose baseline ranges (1960-1987) were more extensively covered by protected areas retained more of their range over time (H1), although the effect was weak and significant only for stricter protected-area categories and Natura 2000 sites. Likewise, at the local scale, protected plots did not show universally more favorable population dynamics

371 (H2). Cover trends differed little between protected and unprotected plots, despite weak
372 evidence for more positive cover trends in Natura 2000 sites, and were generally negative both
373 inside and outside protected areas. Per contra, the odds of extinction of threatened species were
374 clearly lower in the more actively managed Natura 2000 and IUCN IV (nature reserves) sites.
375 The likelihood of colonization by a new threatened species was likewise higher in Natura 2000
376 sites and in stricter protected areas. Given that Natura 2000 sites showed the most consistent
377 favorable effects of protection, we find some support for the hypothesis that protection is most
378 effective under more active management (H3). However, because the most widespread
379 protection category in Germany, IUCN V (landscape protection areas), showed no detectable
380 benefit for any metric studied, and in fact, showed increased extinction odds relative to outside
381 protected areas, our findings also suggest global biodiversity targets focused on protected-area
382 extent, like 30-by-30, whilst potentially benefiting other attributes of biodiversity, are not in
383 themselves very safe targets for the conservation of native flora.

384 Among the individual protected-area categories, Natura 2000 sites provided the clearest and
385 most consistent evidence of benefits for threatened plants. Greater Natura 2000 coverage was
386 associated with higher range retention, cover trends were marginally more positive inside than
387 outside Natura 2000 sites, colonization was elevated, and local extinction odds were reduced.
388 No other protection category showed favorable effects across both spatial scales and multiple
389 measures of persistence. This convergence is consistent with our hypothesis that more actively
390 managed protected areas (as Natura 2000 sites) are more effective at preserving threatened
391 species. Although management practices vary considerably among Natura 2000 sites and
392 primarily target species and habitats listed in the Annexes of the Directive, they aim to maintain
393 specific habitat conditions and may therefore generate an umbrella effect that benefits
394 threatened species beyond these explicit conservation targets (Van Der Sluis et al., 2016). The
395 disappearance of the reduced-extinction signal when near-threatened species (Table S16) were

included is also consistent with benefits being concentrated among the more severely threatened species. More explicit integration of nationally threatened species into Natura 2000 management could therefore further strengthen the network's contribution to national and European biodiversity goals.

Strictly protected areas and IUCN IV nature reserves showed more selective benefits. Strict protection was associated with greater range retention and increased colonization events of threatened species, but not with reduced local extinction counts or positive cover trends. The positive range-retention signal is somewhat surprising because many threatened plants in Germany occur in open ecosystems (Staude, Segar, et al., 2023), where strict non-intervention can promote succession, shading, and competitive exclusion. A purely "hands-off" mechanism therefore seems unlikely to explain the strict-protection signal. Instead, the extensive overlap among designation types may contribute to this pattern: 86% of strictly protected areas overlap with other protected-area designations, including 76% with Natura 2000 sites (Tables S3–S4), such that active management (e.g., extensive mowing, conservation grazing, or removal of encroaching woody vegetation) in overlapping areas may partly underlie the apparent benefit of strict protection (Ellerbrok et al., 2025). IUCN IV areas (nature reserves in Germany) showed almost the inverse pattern. Extinction odds were reduced, but there was no detectable benefit for range retention, colonization, or cover change. Their generally small size (median = 0.35 $km^2$; Notes S1; Figure S1) may leave populations exposed to edge effects and pressures originating outside reserve boundaries, such as nitrogen pollution and pesti- and insecticide inputs from surrounding agricultural land (Köthe et al., 2023). However, our supplementary analysis did not support a role of protected-area size in explaining local population dynamics of threatened flora (Table S18).

The clearest counterpoint was provided by IUCN V areas (i.e. Landscape Protection Areas in Germany). Despite constituting the major share of Germany's protected-area network, they

showed no detectable benefit for range retention, cover change, or colonization, while extinction odds were even higher than outside protected areas. This may partly reflect the purpose of this designation. IUCN V areas are intended to maintain landscapes shaped by long-term interactions between people and nature (Dudley, 2008) and permit comparatively broad human use. Consequently, designation as IUCN V may say relatively little about whether the local habitat conditions required by threatened plants are maintained. However, higher extinction odds relative to unprotected plots do not imply that IUCN V areas perform worse than unprotected habitats more generally. Vegetation resurveys are typically conducted in sites that have remained sufficiently intact to be resurveyed, and unprotected plots may therefore underrepresent the full spectrum of human pressures outside protected areas (Gonzalez et al., 2016). This site-selection bias could make the unprotected plots a particularly demanding counterfactual against which to detect benefits of protection. Nonetheless, the weak performance of this widespread category is relevant to area-based conservation targets. Increasing the extent of land under protection may make an important contribution to biodiversity conservation, but our results show that gains in protected-area coverage need not translate into improved persistence of threatened flora.

Finally, even where protection was associated with more favorable outcomes, however, these effects remained modest. At the range scale, protected-area coverage explained only a very small fraction of the variation in range retention ($R^2 = 0.09$), indicating that protection is only one among many factors shaping long-term range dynamics. Range retention is shaped by many factors beyond protected-area coverage, and one likely source of the low explained variance is spatial heterogeneity in pressures across species' ranges. Our analysis does not isolate protection from this variation, and species with similar levels of protection may therefore experience very different pressures across the unprotected portions of their ranges. Thus, greater protected-area representation appears to contribute to range retention but is clearly not a strong

predictor. At the local scale, threatened species generally declined in cover both inside and outside protected areas, including within the protection categories that otherwise showed the clearest benefits. Such widespread declines suggest that protected-area designation alone cannot shield populations from broader drivers of vegetation change, including atmospheric nitrogen deposition, climate change, and successional change following land-use abandonment (Lüttgert et al., 2025; Sanczuk et al., 2024; Staude, Weigelt, et al., 2023). Thus, while some protection regimes appear to improve some components of threatened-plant persistence, the overall evidence for their benefits was far from unequivocal.

## Conclusion

Our study provides, to our knowledge, the first quantitative, cross-scale evaluation of how the German protected-area network relates to trends in threatened plant species. We do not find clear-cut evidence that protection universally increases the likelihood of persistence, although some benefits for threatened flora emerge in more actively managed and stricter protected sites. However, the absence of detectable benefits at either spatial scale for some of Germany's most extensive protected-area categories suggests that area-based targets alone may overestimate conservation gains for threatened plants. As Germany and the EU pursue the 30-by-30 target, evaluating and improving the effectiveness of existing protected areas to sustain the diversity of native flora needs to accompany further expansion of the protected-area network. Restoration will also play a major role, alongside ex-situ conservation and, perhaps more provocatively, more participatory approaches to conserving declining native plants (Segar et al., 2022). Returning to the example from the Introduction for orchids that retain much of their range whilst declining locally: many hardy orchids are not so hard to propagate and cultivate but remain almost entirely excluded from nurseries (Tullock, 2005). More widespread ex-situ efforts, together with more creative use of native threatened plants in the spaces humans create, may be

important complements to the protection of historical native habitats and to sustaining plant persistence in a rapidly changing world.

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**Supplementary Material for**

# Mixed evidence that protected areas slow declines of threatened plant species in Germany

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## Supplementary Notes

### Notes S1: Additional notes on protected area categories

Protected-area data were downloaded from the WDPA in January 2025. The terrestrial protected area polygons included in our spatial analysis belong to a variety of designation categories, i.e. one Wilderness area (corresponding to IUCN Ib), national parks (IUCN II), natural monuments (IUCN III), nature reserves (IUCN IV), landscape protection areas (IUCN V), Biosphere reserves (split up into Core-, Buffer-, and Transition-Zones), Natura 2000 Birds-Directive sites (79/409/EEC; a Directive for the Conservation of Wild Birds), Natura 2000 Habitats Directive sites (92/43/EEC; a Directive on the Conservation of Natural Habitats and Wild Fauna and Flora), Ramsar Sites, Baltic Sea Protected Areas (HELCOM; the terrestrial over-laps) and World Heritage Sites. For the category-specific analyses, IUCN categories I-III and biosphere reserve core zones were grouped as “strict protection” because of their limited spatial extent in Germany and their shared emphasis on minimizing human intervention. Polygon-based National Natural Monuments (Nationale Naturmonumente) were retained and grouped with strict protection because they are substantially larger (median 8.8 $km^2$ vs. 0.35 $km^2$ for IUCN IV) and primarily managed for non-intervention (§24(4) BNatSchG).

**Notes S2: Additional notes on range-scale analses**

Occurrence records were provided in geographic coordinates (WGS84) as grid cell centroids and linked to the corresponding MTBQ grid-cell geometries using their unique MTBQ identifiers. MTBQ polygons were obtained from the Recorder 6 resource portal (Table S1) and processed in ETRS89 / UTM zone 32N (EPSG:25832). Because some MTBQ cells extend beyond Germany's national boundary and corresponding protected-area information was unavailable for areas outside Germany, analyses were restricted to the 11,030 grid cells whose centroids were located within Germany.

Historical urban cover was obtained from the HILDA+ database (Winkler et al., 2021; Table S1) for 1960, corresponding to the baseline period of the occurrence data, and spatially intersected with the MTBQ grid. This excluded 511 cells (16,661 km²; 4.6% of the total MTBQ area), leaving 10,519 grid cells for the range-scale analyses.

*Anagallis tenella* (Red List category 2) had a summed occurrence probability of zero at T3 within its baseline range, resulting in a non-finite log-ratio. *Minuartia austriaca* (Red List category R) had no detectable occurrence probability at baseline and therefore fell outside the scope of the baseline-retention analysis. *Rhinanthus serotinus* was already excluded during the data processing pipeline, as the species had conflicting occurrence probability records in the raw data. The final range-persistence analysis therefore comprised 860 nationally red-listed species (when including near-threatened species; Red List category V); of these, 658 species belonging to Red List categories 0–3 and R were retained for the main analysis, which excludes category V.

## Notes S3: Additional notes on plot-level analyses

***S3.1 Plot assignment and protected-area overlap.*** Plot coordinates (WGS84, EPSG:4326) were converted to spatial points, reprojected to ETRS89 / UTM zone 32N (EPSG:25832), and spatially joined with WDPA polygons. Because individual plots could intersect multiple WDPA polygons, the spatial join could produce multiple records per plot × species × survey interval combination. We therefore collapsed polygon-level information to the plot level and created separate binary indicators for strict protection, IUCN IV, IUCN V, Natura 2000 and all protected areas. Plots could belong to more than one focal category, if these protected area categories were overlapping, whereas plots classified as "outside" were required not to intersect any protected area (Table S7).

***S3.2 Sensitivity analyses of cover change.*** To assess the robustness of the species-level cover-change results, we conducted three complementary analyses. First, we repeated the inside-outside comparisons using paired Wilcoxon signed-rank tests as a non-parametric sensitivity analysis (Table S10). Second, we repeated the species-level mixed-effects models after excluding near-threatened species (Red List category V; Figure S5). Third, we retained the species × plot-level mean annualized cover changes rather than averaging them further to one inside and one outside value per species. Because these plot-level values showed strong deviations from Gaussian model assumptions and included influential extreme observations, we analyzed them using robust linear mixed-effects models fitted with the robustlmm package (Koller, 2016). Protection status (inside vs. outside) was included as a fixed effect, with random intercepts for species, ReSurvey project, and plot. Robust estimation reduces the influence of observations with large residuals without removing them from the analysis. The variance of the plot random intercept was estimated at zero in all models; it was nevertheless retained to keep the random-effect structure identical across protected-area categories. Species were restricted to the same sets used in the corresponding main species-level comparisons, i.e. species represented by at least five distinct plots both inside and outside the respective protected-area category.***S3.3 Plot-level colonization and extinction.*** For the main analysis, we excluded near-threatened species (Red List category V) and retained species assigned to categories 0-3, R and G; analyses including category V were conducted as a sensitivity analysis (Figure S6; Tables S14, S16). Following Jandt et al. (2022), we treated observed transitions between presence and absence as ecologically meaningful because resurveys were conducted by experienced vegetation scientists.

***S3.4 Protected area size analyses.*** To test whether local population dynamics varied with protected-area size, we conducted additional analyses restricted to plots located inside the respective protected area category. For cover change, annualized relative cover changes were first averaged across survey intervals within each species × plot combination and then analyzed using linear mixed-effects models with log-transformed and centered protected-area size as predictor and random intercepts for species, plot, and protected-area identity. Colonization was analyzed at the plot level using negative-binomial GLMMs, whereas final local extinction was analyzed using binomial GLMMs based on the number of final extinctions relative to the number of species at risk. Event models additionally included plot area and total survey

duration as covariates and resurvey project and protected-area identity as random intercepts (Tables S17–S18).

## Supplementary Tables

### Table S1: Summary and description of the data sources used.

| Data | Variables used in our analysis | Dataset details | Resolution | Authors | URL |
|---|---|---|---|---|---|
| **Occurrence Probabilities across Germany** | Occurrence probabilities | Raster-based species occurrence probability time series (1960-2017) | Germany-wide; 25 $km^2$ | Eichenberg et al. 2021 | https://doi.org/10.1111/gcb.15447; https://idata.idiv.de/ddm/Data/ShowData/1875?version=9 |
| **ReSurvey Germany; vegetation plot resurvey data for Germany** | Species cover change, plot ID, year, coordinates, project ID, colonization/extinction information | Plot-based vegetation survey time series (1927-2020; repeated resurveys), 1 - 53 resurvey intervals per plot (median = 1) | Germany-wide; point locations (1-1000 $m^2$ plots) | Jandt et al. 2022 | https://doi.org/10.1038/s41586-022-05320-w; https://github.com/idiv-biodiversity/ReSurveyGermany_Analysis/blob/main/SupplementaryCode1.txt; https://idata.idiv.de/ddm/data/Showdata/3514 |
| **HILDA+ v1.0 (HIstoric Land Dynamics Assessment +)** | Urban areas | Time-series raster data (1960-2019) | Global; 1 $km^2$ | Winkler et al. 2021 | https://doi.pangaea.de/10.1594/PANGAEA.921846?format=html#download |
| **World Database on Protected Areas (WDPA)** | Protected areas polygons | Vector polygons; time-stamped (designation years) | Global and national; shapefiles | UNEP-WCMC & IUCN 2024 | https://www.protectedplanet.net/DEU (accessed in January 2025) |
| **Recorder 6 MTBQ Grid** | MTBQ grid in WGS84 (EPSG:4326) for Germany | 12,024 Grid-cells as one vector polygon (11,030 fully within German borders) | Germany-wide; 25 $km^2$ | Zentrum für Bio-dokumentation | http://www.recorder-d.de/index.php/downloads/viewdownload/8-rastergrenzen/15-mtb-raster-deutschland-wgs84-shapeformat |
| **Red List Germany** | German Red List category in 2018 | List of vascular plants and their threat status in 2018 | Germany-wide | Metzing et al., (2018) | https://www.floraweb.de/downloads.html |

**Table S2: German Red List categories for vascular plants and their IUCN equivalent.** Categories are based on the national Red List for Germany (Metzing et al. 2018) as proposed by the German Federal Nature Conservation Agency (BfN).

| RL categories | Definition | Approx. IUCN equivalent |
|---|---|---|
| **0** | No wild population remains within the assessed geographical area. | RE (Regionally Extinct) |
| **1** | At extremely high risk of extinction in the near future without effective conservation action. | CR (Critically Endangered) |
| **2** | Strong population decline or severe ongoing or anticipated threats indicate a very high risk of extinction. | EN (Endangered) |
| **3** | Marked population decline or other substantial threats indicate a high risk of extinction. | VU (Vulnerable) |
| **G** | Clearly threatened, but available information is insufficient to assign the species reliably to categories 1–3. | No direct equivalent |
| **R** | Very rare or geographically restricted, but without evidence of a substantial current decline. | No direct equivalent |
| **V** | Declining or exposed to threats but not currently meeting the criteria for categories 1–3. | NT (Near Threatened) |

**Table S3: Pairwise spatial overlap among protected-area categories within Germany.** Percentages are calculated relative to the focal category in each row. Percentages are asymmetric as for example, a large proportion of strict protected areas may overlap with Natura 2000 sites, while only a small proportion of Natura 2000 sites overlaps with strict protected areas. Row values are not additive because areas may overlap with multiple protected-area groups.

| Category | Area (km²) | Overlaps with | Shared area (km²) | % of focal group |
|---|---|---|---|---|
| **IUCN IV** | 13,708 | Natura 2000 | 10,577 | 77.2 |
| | | IUCN V | 3,995 | 29.1 |
| | | Strict protection | 362 | 2.6 |
| **IUCN V** | 98,181 | Natura 2000 | 13,843 | 14.1 |
| | | IUCN IV | 3,995 | 4.1 |
| | | Strict protection | 712 | 0.7 |
| **Natura 2000** | 32,117 | IUCN V | 13,843 | 43.1 |
| | | IUCN IV | 10,577 | 32.9 |
| | | Strict protection | 1,813 | 5.7 |
| **Strict protection** | 2,374 | Natura 2000 | 1,813 | 76.4 |
| | | IUCN V | 712 | 30 |
| | | IUCN IV | 362 | 15.3 |

**Table S4: Summary of protected-area coverage within Germany's terrestrial area.** Shown are the total area (km²) and percentage of the analysis area covered by each protected-area group, as well as the proportion of each group overlapping with other protected areas.

| Category | Area (km²) | % of area | % total shared area |
|---|---|---|---|
| **Strict protection** | 2373.65 | 0.7 | 85.95 |
| **IUCN IV** | 13708.4 | 4.02 | 81.35 |
| **Natura 2000** | 32116.78 | 9.41 | 68.96 |
| **IUCN V** | 98181.15 | 28.76 | 14.86 |

**Table S5: Number of species per German Red List category (Metzing et al., 2018) included in the range-persistence analysis.** *Anagallis tenella* and *Minuartia austriaca* were excluded because range retention could not be calculated for these species, resulting in a final sample of 860 species. See Table S2 for full Red List category definitions.

| RL category | Definition (short) | n species |
|---|---|---|
| **0** | Extinct | 5 |
| **1** | Critically endangered | 66 |
| **2** | Endangered | 220 |
| **3** | Vulnerable | 302 |
| **G** | Threat of unknown extent | 0 |
| **R** | Extremely rare | 65 |
| **V** | Near threatened | 202 |
| **Total** | | 860 |

**Table S6: Association between occurrence-probability-weighted protected area coverage and range retention of nationally red-listed plant species, compared across two time intervals.** Range retention was modelled as log(SOP_end / SOP_start) as a function of the proportion of a species' range covered by the respective protected area category (expressed as a percentage) and of baseline range size, fitted as separate linear models per category. Baseline cells are those with a non-zero occurrence probability at the start of the respective interval, so the T1-T3 models use OP_T1 > 0 and log(SOP_T1), and the T2-T3 models use OP_T2 > 0 and log(SOP_T2). Intervals differ in length and in baseline, so coefficients are not directly comparable on a per-year basis; the comparison concerns the presence and direction of associations rather than their absolute size. Both model terms are reported; $R^2$ refers to the full model. For both intervals, results are shown for the species set excluding (main analysis) and including (sensitivity analysis) IUCN category V (Near Threatened) species, labelled "without V" and "with V" blocks, respectively below. Bold indicates $p < 0.05$ for the protected range predictor.

| | Category | Term | β | se | 95% CI | *p* | $R^2$ |
|---|---|---|---|---|---|---|---|
| **$T_1$-$T_3$** (n= 658) *Without V* | All | log(SOP_T1) | -0.0708 | 0.013 | -0.097 - -0.0446 | <0.001 | 0.089 |
| | | **range protected** | **0.0062** | **0.002** | **0.002 - 0.0103** | **0.004** | **0.089** |
| | Strict | log(SOP_T1) | -0.0648 | 0.013 | -0.0894 - -0.0401 | <0.001 | 0.115 |
| | | **range protected** | **0.0184** | **0.003** | **0.0116 - 0.0252** | **<0.001** | **0.115** |
| | IUCN IV | log(SOP_T1) | -0.095 | 0.013 | -0.1207 - -0.0694 | <0.001 | 0.079 |
| | | range protected | -0.0035 | 0.003 | -0.009 - 0.0019 | 0.205 | 0.079 |
| | IUCN V | log(SOP_T1) | -0.0882 | 0.012 | -0.1118 - -0.0647 | <0.001 | 0.077 |
| | | range protected | -0.0008 | 0.003 | -0.0059 - 0.0042 | 0.741 | 0.077 |
| | Natura 2000 | log(SOP_T1) | -0.0661 | 0.014 | -0.0933 - -0.0389 | <0.001 | 0.09 |
| | | **range protected** | **0.0069** | **0.002** | **0.0026 - 0.0111** | **0.002** | **0.09** |
| **$T_1$-$T_3$** (n= 860) *With V* | All | log(SOP_T1) | -0.0335 | 0.01 | -0.0529 - -0.0141 | <0.001 | 0.051 |
| | | **range protected** | **0.0074** | **0.002** | **0.0037 - 0.0112** | **<0.001** | **0.051** |
| | Strict | log(SOP_T1) | -0.0296 | 0.009 | -0.0481 - -0.0111 | 0.002 | 0.076 |
| | | **range protected** | **0.0201** | **0.003** | **0.0138 - 0.0264** | **<0.001** | **0.076** |
| | IUCN IV | log(SOP_T1) | -0.0527 | 0.01 | -0.0722 - -0.0331 | <0.001 | 0.034 |
| | | range protected | -0.002 | 0.003 | -0.0071 - 0.0031 | 0.443 | 0.034 |
| | IUCN V | log(SOP_T1) | -0.0498 | 0.009 | -0.0677 - -0.0319 | <0.001 | 0.034 |
| | | range protected | 0.0007 | 0.002 | -0.0038 - 0.0053 | 0.751 | 0.034 |
| | Natura 2000 | log(SOP_T1) | -0.0276 | 0.01 | -0.0481 - -0.0071 | 0.008 | 0.053 |
| | | **range protected** | **0.0083** | **0.002** | **0.0044 - 0.0122** | **<0.001** | **0.053** |
| **$T_2$-$T_3$** (n= 653) *Without V* | All | log(SOP_T2) | -0.0536 | 0.01 | -0.0735 - -0.0337 | <0.001 | 0.056 |
| | | range protected | 0.0013 | 0.002 | -0.0018 - 0.0044 | 0.409 | 0.056 |
| | Strict | log(SOP_T2) | -0.0341 | 0.009 | -0.0526 - -0.0156 | <0.001 | 0.13 |
| | | **range protected** | **0.0222** | **0.003** | **0.0164 - 0.028** | **<0.001** | **0.13** |
| | IUCN IV | log(SOP_T2) | -0.0702 | 0.01 | -0.0899 - -0.0506 | <0.001 | 0.071 |
| | | **range protected** | **-0.0069** | **0.002** | **-0.011 - -0.0029** | **0.001** | **0.071** |
| | IUCN V | log(SOP_T2) | -0.0568 | 0.009 | -0.075 - -0.0386 | <0.001 | 0.057 |
| | | range protected | -0.0023 | 0.002 | -0.0062 - 0.0016 | 0.241 | 0.057 |
| | Natura 2000 | log(SOP_T2) | -0.0485 | 0.01 | -0.0691 - -0.0279 | <0.001 | 0.059 |
| | | range protected | 0.0029 | 0.002 | -0.0004 - 0.0061 | 0.084 | 0.059 |
| **$T_2$-$T_3$** (n= 855) *With V* | All | log(SOP_T2) | -0.0342 | 0.007 | -0.0483 - -0.0201 | <0.001 | 0.04 |
| | | range protected | 0.0021 | 0.001 | -0.0006 - 0.0048 | 0.132 | 0.04 |
| | Strict | log(SOP_T2) | -0.0203 | 0.007 | -0.0335 - -0.007 | 0.003 | 0.114 |
| | | **range protected** | **0.0229** | **0.003** | **0.0176 - 0.0281** | **<0.001** | **0.114** |
| | IUCN IV | log(SOP_T2) | -0.0476 | 0.007 | -0.0618 - -0.0334 | <0.001 | 0.049 |
| | | **range protected** | **-0.006** | **0.002** | **-0.0096 - -0.0023** | **0.001** | **0.049** |

| | | | | | | |
|---|---|---|---|---|---|---|
| IUCN V | log(SOP_T2) | -0.0379 | 0.007 | -0.0511 - -0.0248 | <0.001 | 0.038 |
| | range protected | -0.0011 | 0.002 | -0.0045 - 0.0023 | 0.520 | 0.038 |
| Natura 2000 | log(SOP_T2) | -0.0299 | 0.008 | -0.0447 - -0.0151 | <0.001 | 0.043 |
| | **range protected** | **0.0034** | **0.002** | **0.0006 - 0.0063** | **0.019** | **0.043** |

**Table S7: Number of protected area types intersecting each plot and resulting number of plot x species x interval records after spatial join.**

| Number of overlapping protected area types | Number of plots | Number of species x plot x interval records |
|---|---|---|
| **0** | 3320 | 129,846 |
| **1** | 1891 | 174,666 |
| **2** | 1407 | 93,844 |
| **3** | 652 | 24,692 |
| **4** | 360 | 27,168 |
| **5** | 96 | 7,677 |
| **6** | 12 | 418 |

**Table S8: Estimated marginal means and contrasts for species-specific mean annual relative cover change inside vs. outside five protected area categories**, derived from linear mixed models with species as random intercept. EMM = estimated marginal mean with 95% confidence interval. Contrasts represent the difference in EMMs (inside minus outside) and serve as effect size estimates. Positive values indicate smaller declines or greater increases inside protected areas. CI = 95% confidence interval of the contrast. $p < 0.05$ indicates a statistically significant effect.

| Category | EMM | | Contrast | 95% CI | *p* |
|---|---|---|---|---|---|
| | Outside | Inside | | | |
| **All** | -0.013 [-0.019, -0.006] | -0.005 [-0.012, 0.001] | 0.007 | [-0.001, 0.015] | 0.079 |
| **Strict** | -0.010 [-0.042, 0.023] | -0.017 [-0.050, 0.016] | -0.007 | [-0.055, 0.039] | 0.740 |
| **IUCN IV** | -0.010 [-0.018, -0.003] | -0.006 [-0.013, 0.001] | 0.004 | [-0.005, 0.014] | 0.381 |
| **IUCN V** | -0.011 [-0.018, -0.004] | -0.003 [-0.010, 0.003] | 0.007 | [-0.001, 0.016] | 0.084 |
| **Natura 2000** | -0.011 [-0.018, -0.004] | -0.002 [-0.009, 0.005] | 0.009 | [-0.000, 0.018] | 0.051 |

**Table S9: Sample sizes for the species-level cover change analysis per protected area category.** Relative cover change was first annualized by dividing by the number of survey years per interval. These annualized values were then averaged across all resurvey intervals within each plot, yielding one plot mean per species x plot combination. Plot means were subsequently averaged across plots within each species and plot location (inside/outside protected areas), serving as the response variable in the linear mixed models. n species = number of species with at least five plot means on both sides of the comparison; n plot means inside/outside = total number of species x plot combinations contributing to the analysis per side. "Outside" refers in all scenarios to plots located outside any protected area.

| Category | n species | n plot means | | n plots | |
|---|---|---|---|---|---|
| | | Inside | Outside | Inside | Outside |
| **All** | 147 | 15051 | 4709 | 2710 | 1243 |
| **Strict** | 19 | 332 | 487 | 89 | 303 |
| **IUCN IV** | 131 | 8816 | 4514 | 1369 | 1215 |
| **IUCN V** | 133 | 10695 | 4582 | 1704 | 1233 |
| **Natura 2000** | 140 | 11568 | 4561 | 1856 | 1238 |

**Table S10: Wilcoxon signed-rank test results comparing species-level mean annual relative cover change (per year) between plots inside and outside protected areas.** n species = number of species meeting the minimum plot threshold (≥5 plots per side). The pseudo-median (median of all possible pairwise differences) represents the estimated median difference in mean annual cover change (inside minus outside). V = Wilcoxon test statistic. CI = 95% confidence interval of the pseudo-median.

| Category | n species | V-statistic | Pseudo-median | 95% CI | *p* |
|---|---|---|---|---|---|
| **All** | **147** | **6402** | **0.006** | **[0.0007; 0.0121]** | **0.029** |
| **Strict** | 19 | 117 | 0.018 | [-0.0624; 0.0403] | 0.387 |
| **IUCN IV** | 131 | 4985 | 0.005 | [-0.0014; 0.0116] | 0.129 |
| **IUCN V** | 133 | 5010 | 0.005 | [-0.0018; 0.0119] | 0.159 |
| **Natura 2000** | **140** | **5970** | **0.007** | **[0.0012; 0.0144]** | **0.020** |

**Table S11: Direction of species-level mean annual relative cover-change trends inside protected areas, by protected area category.** n species = number of species meeting the minimum plot threshold (≥5 plots inside and ≥5 outside; see Methods). ↑ inside PA / ↓ inside PA = number (%) of species with a positive/negative mean annual relative cover-change estimate inside the respective category; species with an estimate of exactly zero are not counted in either column, which is why counts do not sum to n species for All PAs, IUCN V, and Natura 2000. Less negative inside PA = number (%) of species for which the inside estimate exceeded (i.e., was less negative than) the matched outside estimate, regardless of the sign of either value. Note that this is not equivalent to a positive trend inside. Species of Red List categories 0-3, R, G and V are included.

| Category | n species | ↑ inside PA | ↓ inside PA | less negative inside PA |
|---|---|---|---|---|
| **All** | 147 | 55 (37.4%) | 91 (61.9%) | 85 (57.8%) |
| **Strict** | 19 | 14 (73.7%) | 5 (26.3%) | 13 (68.4%) |
| **IUCN IV** | 131 | 59 (45%) | 72 (55%) | 74 (56.5%) |
| **IUCN V** | 133 | 49 (36.8%) | 83 (62.4%) | 68 (51.1%) |
| **Natura 2000** | 140 | 65 (46.4%) | 74 (52.9%) | 82 (58.6%) |

**Table S12: Estimated contrasts and sample sizes for species × plot-level mean annual relative cover change inside versus outside five protected-area categories**, derived from robust linear mixed-effects models with species, ReSurvey project, and plot identity as random intercepts. Contrasts represent the inside-minus-outside difference and serve as effect-size estimates; positive values indicate more positive cover changes inside protected areas. Wald 95% confidence intervals (CIs) and normal-approximation p-values were calculated from the robust coefficient estimates and their standard errors. Values of $p < 0.05$ indicate a statistically significant inside–outside difference. Robust estimation was used because plot-level cover changes showed strong deviations from Gaussian residual assumptions and contained influential extreme observations, partly reflecting complete local disappearances and new colonization events that could produce relative cover changes at or near -1 and +1. Robust estimation reduces the influence of observations with large residuals without excluding them from the analysis.

| Category | n species | n species x plot means | n plots | β | SE | 95% CI | *p* |
|---|---|---|---|---|---|---|---|
| **All PAs** | 147 | 19760 | 3953 | -0.0012 | 0.0009 | [-0.0031, 0.0006] | 0.198 |
| **Strict** | 19 | 819 | 392 | 0.0059 | 0.0076 | [-0.0090, 0.0209] | 0.437 |
| **IUCN IV** | 131 | 13330 | 2584 | 0.0013 | 0.0015 | [-0.0016, 0.0043] | 0.377 |
| **IUCN V** | 133 | 15277 | 2937 | -0.0019 | 0.0011 | [-0.0040, 0.0002] | 0.072 |
| **Natura 2000** | 140 | 16129 | 3094 | 0.0003 | 0.0012 | [-0.0021, 0.0026] | 0.813 |

**Table S13: Summary of plot-level colonization and final-extinction datasets for the analysis excluding near-threatened species (Red List category V).** Panel A reports the number of plots, total number of survey intervals, total retained colonization events, and median total survey duration per plot for each inside–outside comparison. Panel B reports the corresponding number of plots and survey intervals for the final-extinction analysis, together with the total number of unique threatened species at risk of final local extinction and the number experiencing final extinction. Species were considered at risk if they were present at the beginning of at least one observed survey interval and were counted at most once per plot. Survey duration was calculated as the sum of all interval lengths per plot before taking the median across plots.

**Panel A**

| Category | location | n plots | total n intervals | total col | median years |
|---|---|---|---|---|---|
| **All** | outside | 513 | 717 | 226 | 24 |
| | inside | 1793 | 4468 | 1878 | 23 |
| **Strict** | outside | 513 | 717 | 226 | 24 |
| | inside | 81 | 148 | 230 | 15 |
| **IUCN IV** | outside | 513 | 717 | 226 | 24 |
| | inside | 1058 | 3138 | 1229 | 23 |
| **IUCN V** | outside | 513 | 717 | 226 | 24 |
| | inside | 1120 | 3191 | 1122 | 24 |
| **Natura 2000** | outside | 513 | 717 | 226 | 24 |
| | inside | 1371 | 3650 | 1673 | 23 |

**Panel B**

| Category | location | n plots | total n intervals | n sp. at risk | final ext | median years |
|---|---|---|---|---|---|---|
| **All** | outside | 470 | 674 | 998 | 633 | 24 |
| | inside | 1542 | 4217 | 4856 | 2333 | 24 |
| **Strict** | outside | 470 | 674 | 998 | 633 | 24 |
| | inside | 80 | 147 | 388 | 120 | 15 |
| **IUCN IV** | outside | 470 | 674 | 998 | 633 | 24 |
| | inside | 872 | 2952 | 2896 | 1395 | 25 |
| **IUCN V** | outside | 470 | 674 | 998 | 633 | 24 |
| | inside | 938 | 3009 | 3052 | 1506 | 25 |
| **Natura 2000** | outside | 470 | 674 | 998 | 633 | 24 |
| | inside | 1165 | 3444 | 4134 | 1874 | 23 |

**Table S14: Summary of plot-level colonization and final-extinction datasets for the sensitivity analysis including near-threatened species (Red List category V).** Panel A reports the number of plots, total number of survey intervals, total retained colonization events, and median total survey duration per plot for each inside–outside comparison. Panel B reports the corresponding number of plots and survey intervals for the final-extinction analysis, together with the total number of unique threatened species at risk of final local extinction and the number experiencing final extinction. Species were considered at risk if they were present at the beginning of at least one observed survey interval and were counted at most once per plot. Survey duration was calculated as the sum of all interval lengths per plot before taking the median across plots.

**Panel A**

| Category | location | n plots | total n intervals | total col | median years |
|---|---|---|---|---|---|
| **All** | outside | 1236 | 1570 | 875 | 24 |
| | inside | 2887 | 6960 | 5154 | 23 |
| **Strict** | outside | 1236 | 1570 | 875 | 24 |
| | inside | 105 | 184 | 342 | 15 |
| **IUCN IV** | outside | 1236 | 1570 | 875 | 24 |
| | inside | 1458 | 4675 | 3355 | 26 |
| **IUCN V** | outside | 1236 | 1570 | 875 | 24 |
| | inside | 1838 | 4889 | 3506 | 24 |
| **Natura 2000** | outside | 1236 | 1570 | 875 | 24 |
| | inside | 1968 | 5281 | 4282 | 23 |

**Panel B**

| Category | location | n plots | total n intervals | n sp. at risk | final ext | median years |
|---|---|---|---|---|---|---|
| **All** | outside | 1155 | 1489 | 4317 | 2395 | 24 |
| | inside | 2690 | 6763 | 15935 | 6679 | 23 |
| **Strict** | outside | 1155 | 1489 | 4317 | 2395 | 24 |
| | inside | 97 | 176 | 588 | 201 | 15 |
| **IUCN IV** | outside | 1155 | 1489 | 4317 | 2395 | 24 |
| | inside | 1355 | 4572 | 9582 | 3822 | 26 |
| **IUCN V** | outside | 1155 | 1489 | 4317 | 2395 | 24 |
| | inside | 1720 | 4771 | 11403 | 4638 | 24 |
| **Natura 2000** | outside | 1155 | 1489 | 4317 | 2395 | 24 |
| | inside | 1852 | 5165 | 12578 | 5039 | 23 |

**Table S15: Protection-status effects on plot-level colonization and final local extinction of threatened plant species, excluding near-threatened species (Red List category V).** Colonization was analyzed using negative binomial generalized linear mixed-effects models and is reported as incidence rate ratios (IRRs). Local extinction was analyzed using binomial generalized linear mixed-effects models and is reported as odds ratios (ORs). Models included resurvey project as a random intercept and log-transformed plot area and total survey duration as covariates. "Outside" refers to plots located outside all protected areas. Values above 1 indicate higher expected colonization counts or higher odds of final local extinction inside protected areas, whereas values below 1 indicate the reverse. Bold values indicate significant differences ($p < 0.05$).

| Category | Event | Effect type | Estimate | 95% CI | *p* |
|---|---|---|---|---|---|
| **All PAs** | Colonization | IRR | 1.124 | [0.94-1.34] | 0.196 |
| | Extinction | OR | 0.864 | [0.69-1.08] | 0.203 |
| **Strict** | **Colonization** | **IRR** | **1.517** | **[1.01-2.29]** | **0.047** |
| | Extinction | OR | 0.997 | [0.45-2.21] | 0.994 |
| **IUCN IV** | Colonization | IRR | 1.238 | [0.97-1.58] | 0.085 |
| | **Extinction** | **OR** | **0.651** | **[0.48-0.88]** | **0.005** |
| **IUCN V** | Colonization | IRR | 1.024 | [0.84–1.25] | 0.819 |
| | **Extinction** | **OR** | **1.323** | **[1.00-1.75]** | **0.050** |
| **Natura 2000** | **Colonization** | **IRR** | **1.335** | **[1.09-1.63]** | **0.005** |
| | **Extinction** | **OR** | **0.634** | **[0.49-0.82]** | **<0.001** |

**Table S16: Protection-status effects on plot-level colonization and final local extinction of threatened plant species including near-threatened species (Red List category V).** Colonization was analyzed using negative binomial generalized linear mixed-effects models and is reported as incidence rate ratios (IRRs). Local extinction was analyzed using binomial generalized linear mixed-effects models and is reported as odds ratios (ORs). Models included resurvey project as a random intercept and log-transformed plot area and total survey duration as covariates. "Outside" refers to plots located outside all protected areas. Values above 1 indicate higher expected colonization counts or higher odds of final local extinction inside protected areas, whereas values below 1 indicate the reverse. Bold values indicate significant differences ($p < 0.05$).

| Category | Event | Effect type | Estimate | 95% CI | *p* |
|---|---|---|---|---|---|
| **All PAs** | Colonization | IRR | 1.353 | [1.21-1.51] | <0.001 |
| | Extinction | OR | 1.064 | [0.96-1.18] | 0.246 |
| **Strict** | Colonization | IRR | 1.251 | [0.81-1.94] | 0.318 |
| | Extinction | OR | 1.554 | [0.98-2.47] | 0.064 |
| **IUCN IV** | Colonization | IRR | 1.668 | [1.40-1.99] | <0.001 |
| | Extinction | OR | 0.814 | [0.68-0.96] | 0.019 |
| **IUCN V** | Colonization | IRR | 1.212 | [1.07-1.38] | 0.003 |
| | **Extinction** | **OR** | **1.149** | **[1.01-1.31]** | **0.033** |
| **Natura 2000** | **Colonization** | **IRR** | **1.653** | **[1.45-1.89]** | **<0.001** |
| | Extinction | OR | 0.937 | [0.82-1.06] | 0.322 |

**Table S17: Effect of protected-area size on annual relative cover change within protected areas.** Annualized relative cover changes were first averaged across survey intervals within each species × plot combination. Separate linear mixed-effects models were then fitted for each protected-area category, with log-transformed and centered protected-area size (log10 $km^2$) as the predictor and random intercepts for species, plot, and protected-area identity. For plots intersecting multiple protected areas of the same category, the largest intersecting protected area was used. Reported are the estimated slope (β), 95% confidence interval, p-value, and sample sizes. Positive β values indicate more positive annual cover change with increasing protected-area size.

| Category | β | n species | n plots | n PAs | 95% CI | p |
|---|---|---|---|---|---|---|
| **Strict** | -0.089 | 130 | 104 | 13 | -0.243-0.066 | 0.29 |
| **IUCN IV** | 0.002 | 400 | 1490 | 131 | -0.011-0.016 | 0.73 |
| **IUCN V** | -0.006 | 408 | 1555 | 102 | -0.026-0.013 | 0.52 |
| **Natura 2000** | 0.004 | 437 | 1879 | 146 | -0.008-0.016 | 0.55 |

**Table S18: Effect of protected-area size on plot-level colonization and extinction within each protected-area category.** Analyses were restricted to threatened species (Red List categories 0–3, R and G), excluding near-threatened species (category V), consistent with the main colonization and extinction analyses. Colonization was modeled using negative binomial GLMMs and extinction using binomial GLMMs, restricted to plots inside the respective category. Models included log-transformed, centered protected-area size (log10 km2) as the predictor of interest, with plot area and survey duration as covariates and resurvey project and protected-area identity as random intercepts. Effects are reported as incidence rate ratios (IRRs) for colonization and odds ratios (ORs) for extinction. Bold indicates $p < 0.05$. The strict-protection colonization model did not converge and is therefore not shown.

| Category | Event | Effect type | Estimate | 95% CI | *p* |
|---|---|---|---|---|---|
| **Strict** | Colonization | IRR | *Model did not converge* | | |
| | Extinction | OR | 0.331 | [0.02-4.52] | 0.406 |
| **IUCN IV** | Colonization | IRR | 1.236 | [0.96-1.58] | 0.093 |
| | Extinction | OR | 0.885 | [0.61-1.28] | 0.518 |
| **IUCN V** | Colonization | IRR | 1.480 | [1.06-2.06] | 0.020 |
| | Extinction | OR | 1.288 | [0.81-2.04] | 0.283 |
| **Natura 2000** | Colonization | IRR | 1.190 | [0.92-1.53] | 0.181 |
| | Extinction | OR | 1.183 | [0.79-1.76] | 0.412 |

## Supplementary Figures

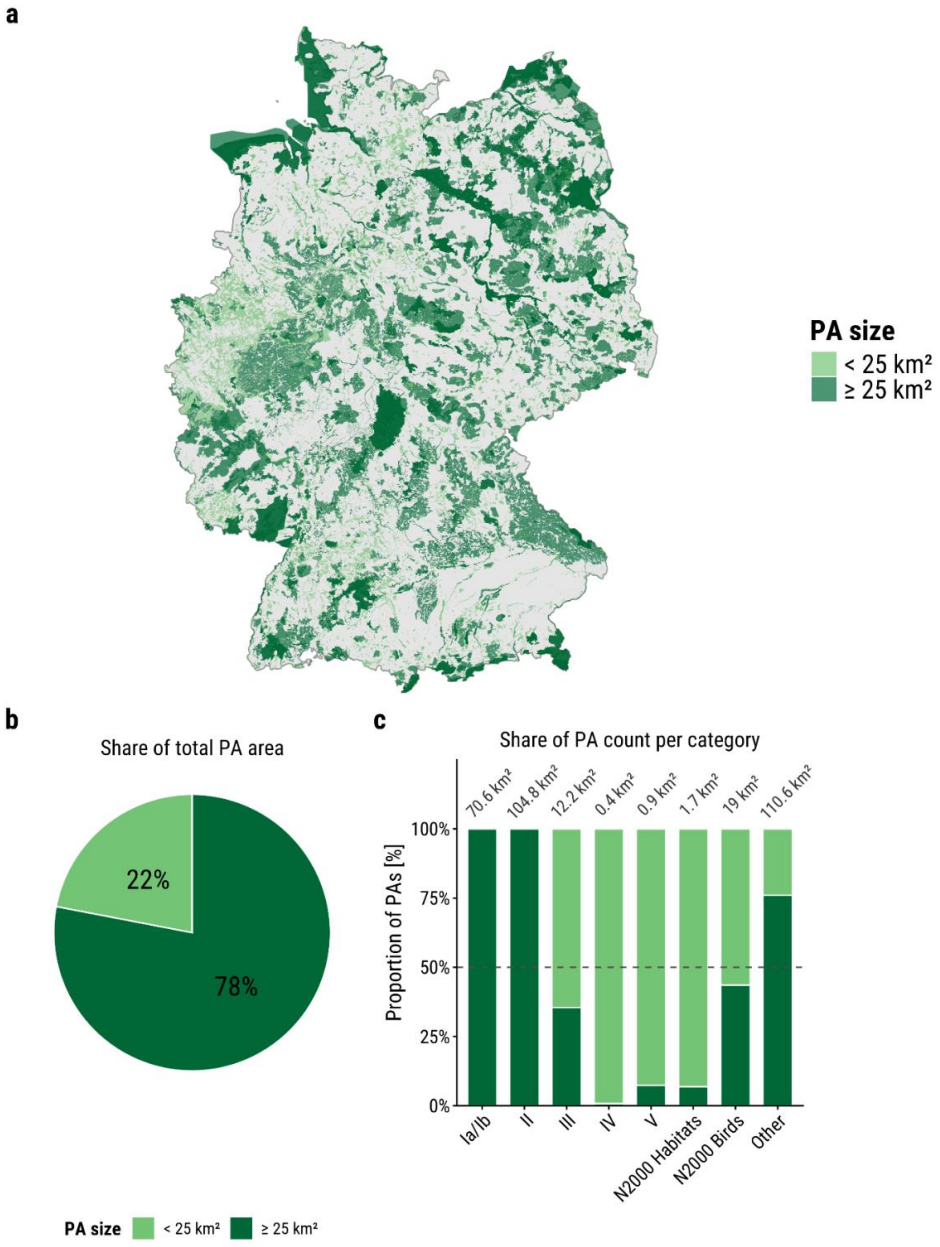



**Figure S1: Size distribution of protected areas in Germany.** a) Map of all protected areas in Germany. Dark-green colors indicate protected areas larger than 25 km$^2$. Light-green indicates protected areas smaller than 25 km$^2$. b) Percentage of protected areas with an area of less than or more than 25 km² relative to the total protected area coverage in Germany. c) Percentage of protected areas larger than or smaller as 25 km2 per protected area designation category.

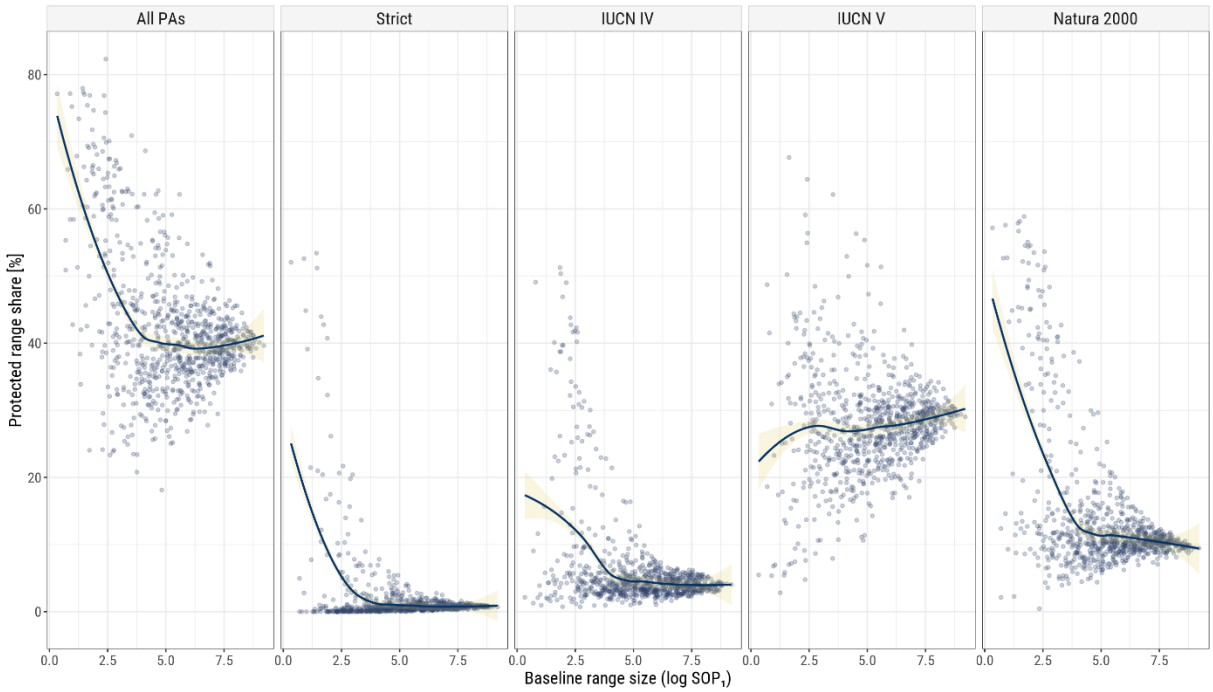



**Figure S2: Relationship between red-listed plant species' baseline range size (log(SOPT1)) and the occurrence-probability-weighted protected range share.** Lines show LOESS smoothers. Smaller-ranged species tended to have a larger proportion of their baseline ranges under protection; baseline range size was therefore included as a covariate in all range-persistence models. Linear-model estimates are reported in Table S6.

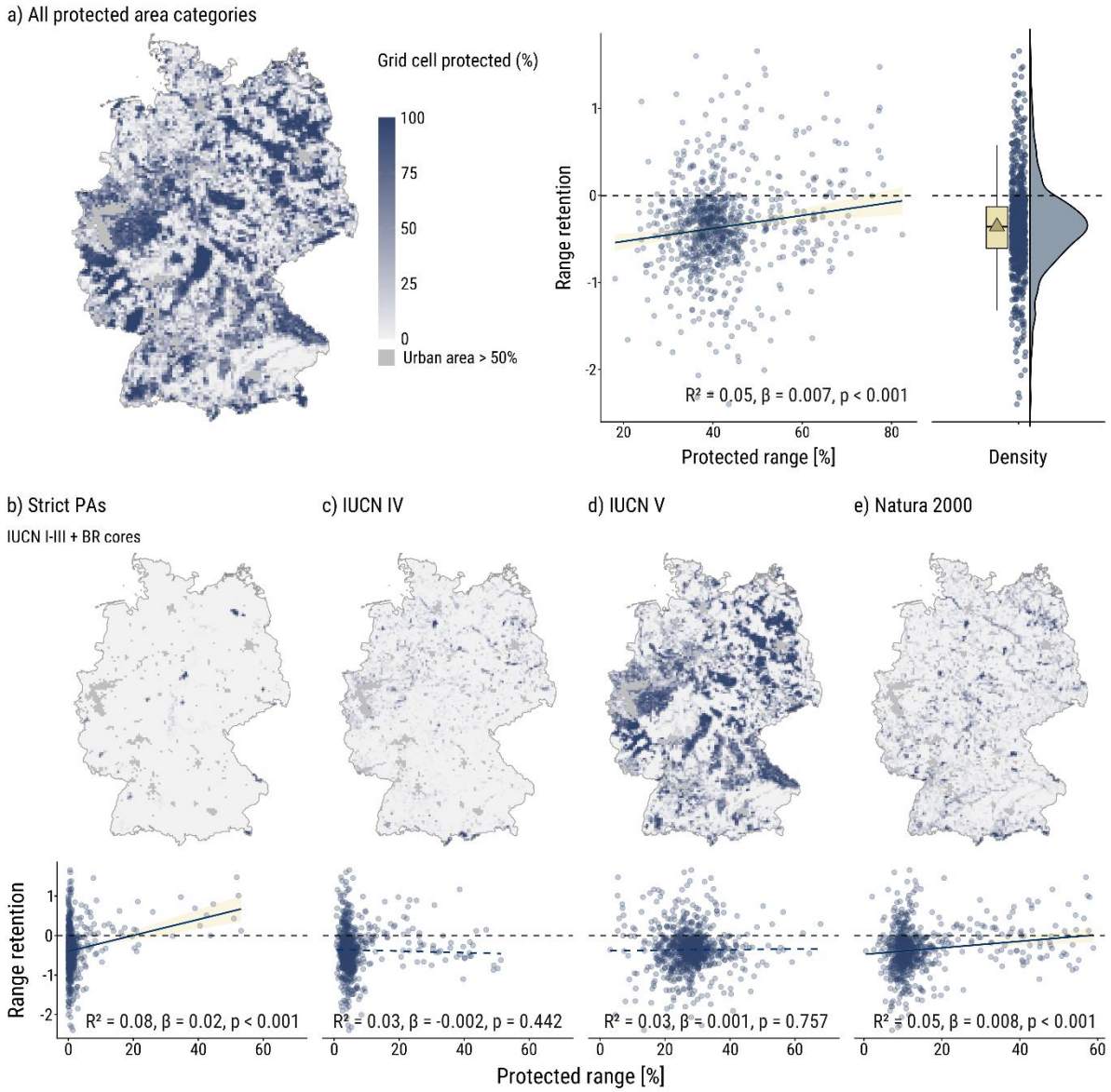



**Figure S3: Effect of protected area coverage on baseline range retention between T1 (1960-1987) and T3 (1997-2017) of red listed plant species in Germany including Red List category V (near-threatened species).** a) Total protected-area coverage in Germany and the relationship between the proportion of each species' baseline range protected and its range retention from T1 (1960) to T3 (2017), across 860 threatened plant species (including Red List categories 0-3, R, V). The marginal panel shows the distribution of range-retention values across species; the boxplot indicates the median and interquartile range, and the density curve shows the overall distribution. b)–e) The same relationship shown separately for strictly protected areas (IUCN I–III and biosphere reserve core zones), IUCN IV areas, IUCN V areas, and Natura 2000 Habitats Directive sites. Points represent species, lines show the fitted linear relationship, and the shaded band indicates the 95% confidence interval. Solid regression lines indicate significant relationships ($p < 0.05$).

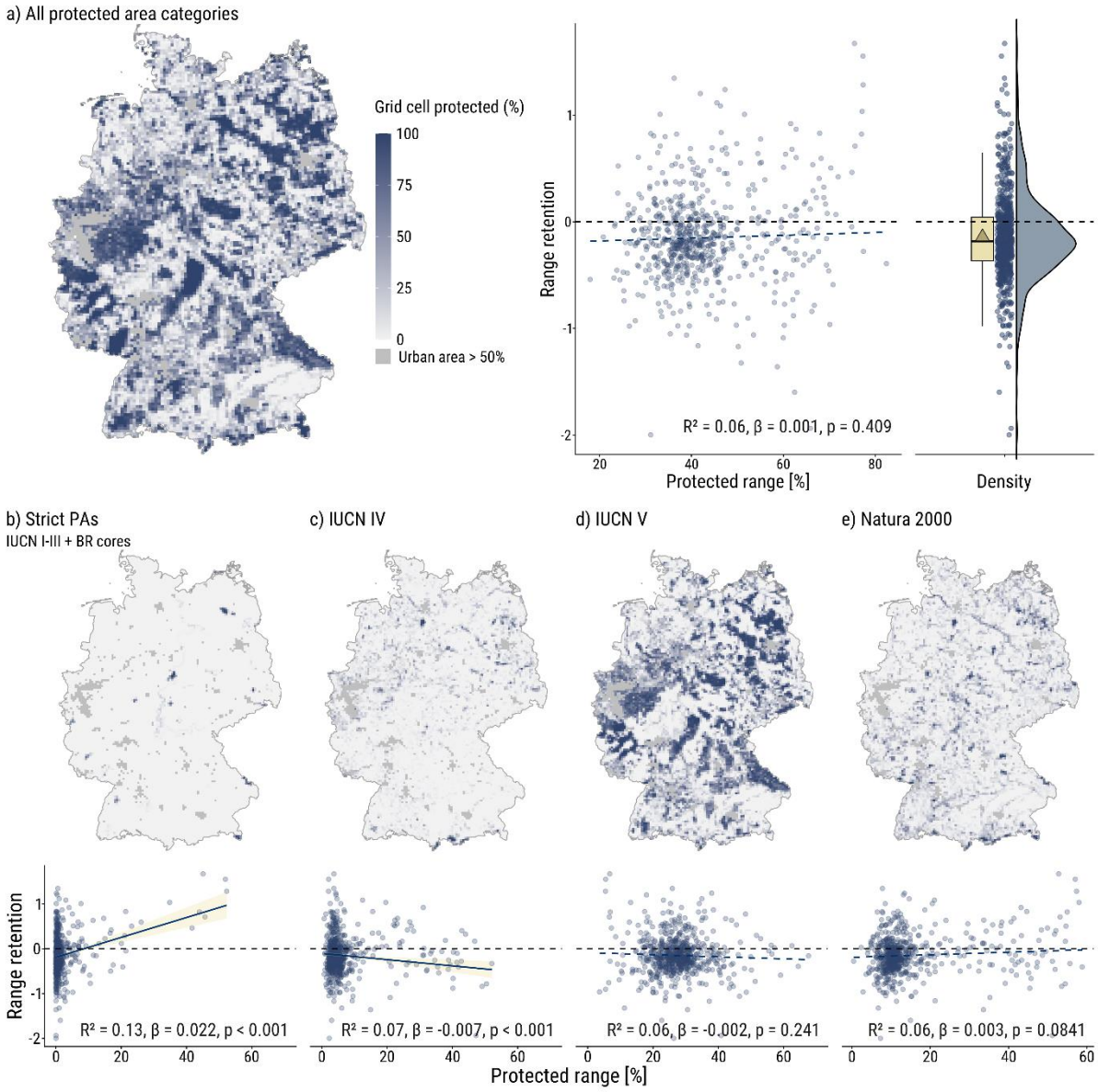



**Figure S4: Effect of protected area coverage on baseline range retention between T2 (1988-1996) and T3 (1997-2017) of red listed plant species in Germany.** a) Total protected-area coverage in Germany and the relationship between the proportion of each species' baseline range protected and its range retention from T2 (1988) to T3 (2017), across 653 threatened plant species (including Red List categories 0-3, R). The marginal panel shows the distribution of range-retention values across species; the boxplot indicates the median and interquartile range, and the density curve shows the overall distribution. b)–e) The same relationship shown separately for strictly protected areas (IUCN I–III and biosphere reserve core zones), IUCN IV areas, IUCN V areas, and Natura 2000 Habitats Directive sites. Points represent species, lines show the fitted linear relationship, and the shaded band indicates the 95% confidence interval. Solid regression lines indicate significant relationships ($p < 0.05$).

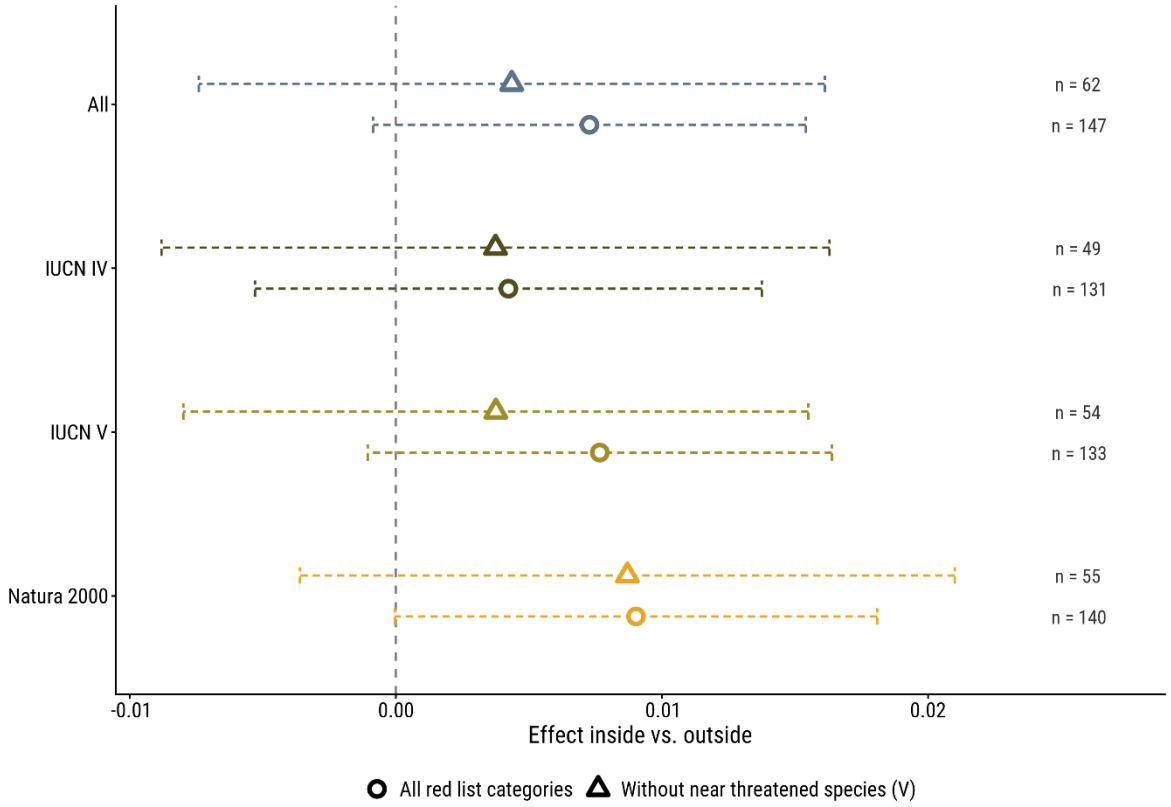



**Figure S5: Model-estimated contrasts of within-species comparisons of mean annualized cover changes inside versus outside of protected areas across Germany** with 95% CIs. Contrasts are shown for comparisons of red-listed species including the near-threatened Red List category (V; circles) and without near-threatened species (Red List categories 0-3, R, G; triangles). Dashed CIs represent non-significant contrasts with a significance threshold of $\alpha = 0.05$. The vertical dashed line marks the point of zero-differences. The model excluding category V species did not converge for strict protected areas because of the reduced sample size and is therefore not shown. n indicates the number of species included in the respective model.

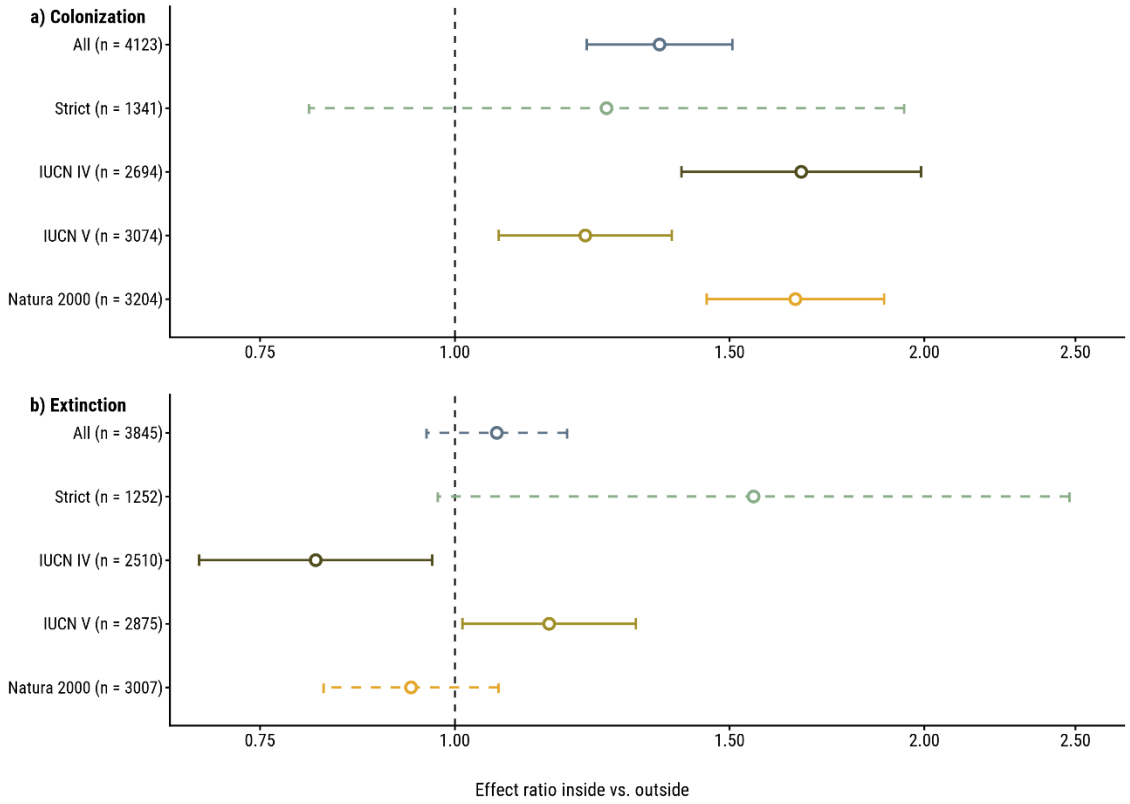



**Figure S6: Incidence rate ratios (IRRs) for colonization and odds ratios (ORs) for extinction of Red List plant species (including near-threatened species), inside versus outside protected areas.** Points show IRRs for colonization estimated from negative binomial GLMMs and ORs for final extinction estimated from binomial GLMMs, with horizontal lines indicating 95% confidence intervals. The dashed vertical line marks IRR/OR = 1 (no difference between protected and unprotected plots); values >1 indicate higher expected colonization counts or higher odds of final local extinction inside protected areas. Dashed confidence intervals indicate non-significant differences at $\alpha = 0.05$. Effect ratios are plotted on a log10-transformed x-axis. n indicates the number of plots included in the respective colonization or extinction model.

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