

RESEARCH ARTICLE

Rehabilitated richness: biodiversity recovery in Germany's gypsum post-mining landscapes

Andreas von Heßberg¹, Saskia Knispel de Acosta^{1,3}, Benjamin Möller⁴, Marta De Giuli^{1,5} , Anke Jentsch^{1,2}

In light of European and international mandates to protect natural areas in order to preserve biodiversity, all unused or abandoned areas become invaluable resources. We examined the botanical and structural diversity of post-mining areas and surrounding landscapes across four major mining regions in Germany over a year-long study. We categorized our 66 study transects over 24 mining sites based on their structure and usage. Our results indicate that the vascular plant richness in restored post-mining landscapes is significantly higher than in the undisturbed, surrounding area. This research emphasizes the importance of these disturbed landscapes for Red List species and of recovering gypsum-mining sites in Germany for the protection of biodiversity. We also expose the strong effect of management in the value development of these areas, with particular importance being placed on rewilding and restoration projects as effective techniques to increase the nature conservation value of abandoned sites.

Key words: biodiversity, disturbance ecology, ecological restoration, gypsum mining, nature conservation, post-mining landscapes, Red List species, time-for-space concept

Implications for Practice

- The trends observed in rewilded and restored areas have important implications for future management plans, especially those focused on maximizing the preservation and promotion of floristic and faunal biodiversity. We recommend the following:
 - Long-term management plans are not strictly necessary for restoration areas (given back to agriculture or forestry), but they are essential for rewilding areas.
 - Regular mechanical disturbance impulses should be applied in a mosaic pattern every 3–5 years, using grazing animals, brush cutters, or heavy tillage machines (topsoil removal/tearing up).
 - After the dismantling of a (partial) extraction area, a large variety of structures with steep walls, shallow water, piles of rubble, and stone slabs should be constructed.
 - For the development of biodiversity, rewilding is preferable to restoration.

Introduction

The annual global production of gypsum in 2023 was approximately 160 million metric tons (USGS 2024). Germany ranks as the second largest producer of gypsum in Europe (USGS 2024), with over 5 million tons of gypsum and anhydrite mined there in 2023, valued at around €54 million (Baier et al. 2021). Gypsum has a long history of use as a building material due to its proximity to raw material sources, fire-resistant properties, and ease of processing (Arendt 2001). It has been used for construction, interior plastering, and artistic

purposes like stucco work and sculpture in Germany since the early Middle Ages (Zekert 1938; Scheidegger 1990). Germany's gypsum deposits are estimated to be between 210 and 110 million years old (Schulmeister 1998, Paul 2014). Although their chemical compositions vary, resulting in different geological structures, the most commonly mined form of gypsum is “massive” gypsum. Presently, most natural gypsum in Germany is extracted from surface quarries, but Germany is also a significant producer of synthetic gypsum. The construction sector boom since the 1980s has increased the demand for mineral raw materials, particularly stone and earth materials sourced domestically (Baier et al. 2021). Flue gas

Author contributions: AJ, AvH conceived and designed the research; AvH, SKdA, BM collected the field data and analyzed the data; AvH, BM, MDG, SKdA, AJ wrote and edited the manuscript.

¹Disturbance Ecology and Vegetation Dynamics, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätstraße 30, 95447 Bayreuth, Germany

²Address correspondence to A. Jentsch, email anke.jentsch@uni-bayreuth.de

³Institute for Meteorology and Climate Research (IMK-ASF) Geb, Karlsruhe Institute of Technology, 453 Hermann-von-Helmholtz Platz 1, 76344 Eggenstein-Leopoldshafen, Germany

⁴Petrology and Mineral Resources, University of Tübingen, Schnarrenbergstraße 94-96, 72076 Tübingen, Germany

⁵Institute for Alpine Environment, EURAC Research, Viale Druso 1, 39100 Bolzano, Italy

© 2025 The Author(s). Restoration Ecology published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.

This is an open access article under the terms of the [Creative Commons Attribution License](#), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

doi: 10.1111/rec.70220

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.70220/supinfo>

desulfurization (FGD) systems in brown coal-fired power plants have helped meet this demand by producing FGD gypsum.

With stricter environmental regulations and the phase-out of coal-fired power generation, a gypsum shortage is expected by 2030. Few remaining natural gypsum deposits in Germany are approved for mining, and they are unlikely to meet future industry and construction demand once FGD gypsum is no longer produced (Baier et al. 2021; Höding et al. 2021). Adaptation strategies from the stone and earth industries, including material flow management, recycling, alternative uses, and reuse of mining areas, are necessary (Arendt 2001; Lorite et al. 2021; Khater et al. 2003; Martins et al. 2020; Řehouňková et al. 2020). These strategies should consider the economic and environmental circumstances and aim to be climate- and biodiversity-resilient (Escudero et al. 2015; Corlett & Tomlinson 2020; Luzuriaga et al. 2020; Mota et al. 2021). The gypsum mining industry also bears responsibility for interventions in cultural and natural landscapes and biodiversity (Martins et al. 2020). As habitat fragmentation and destruction continue globally (Bonn & Poschlod 1998; Caballos et al. 2020; EEA 2020; Cowie et al. 2022), this role becomes increasingly crucial. While expanding gypsum quarries pose a threat to naturally occurring habitats, properly managed post-mining landscapes can serve as important conservation tools and hotspots of species richness in the surrounding agricultural landscape.

Quarries and raw material extraction areas provide unique bare soil environments in landscapes (see Fig. S1) typically dominated by closed vegetation cover (Poschlod 1997; Poschlod & Tränkle 1997; Schulmeister 1998; von Heßberg 2022). Since there are now few naturally occurring areas of gravel or fine material along riverbanks in Central Europe (de Acosta 2018; Müller 2020), quarries, with their diverse raw soil habitats and primary succession areas (Fig. S1), often represent the last large-scale refugia for these specialists (von Heßberg 2003; Gilcher & Tränkle 2005). Many specialized, often poorly competitive plant species, including some Red List species (Finck et al. 2017; Metzging et al. 2018), depend on these open areas (Poschlod 1997). The few near-surface gypsum deposits in Germany are additionally valuable for nature conservation as they provide a starting substrate for the development of specialized “gypsum flora” or “Pannonian steppe flora” habitats (with plant species like *Adonis vernalis*, *Scozonera purpurea*, *Astragalus danicus*, *Euphorbia segueriana*). This relict vegetation is often only found in areas with slightly disturbed (i.e., by short-term sheep grazing), near-surface gypsum, such as “semi-natural dry grasslands and scrubland facies on calcareous substrates” (EU habitat type 6210) in Lower and Middle Franconia (Raab et al. 2002; Raab & Reimann 2013), east Württemberg (Raab et al. 2002), and southern Harz (Schönfelder 1978; Seifert & Etges 2005; Finck et al. 2017). Raw material habitats with their raw soil environments play a crucial role in the establishment of pioneer grasslands with species from dry grassland habitats (Poschlod 1997; Palacio et al. 2007; von Heßberg 2022). These habitats also form important refugia for arable flora (“segetal flora”), one of the most threatened plant groups in our cultural landscape (Stumpf & Offenberger 2018; Bergmeier

et al. 2021). The large-scale industrial gypsum mining has emerged in recent decades in areas where gypsum was easily accessible close to the surface. Gypsum mining areas are therefore often close to rare dry steppe grasslands.

Their abandonment or management, after mining cessation, provides us with a perfect study design to investigate recovery from disturbance in these environments. Typically, once an extraction site has been exploited, the volume is filled with uncontaminated excavated soil from other construction sites, and the original topsoil deposited next to the extraction site is applied as the top layer of soil. This process is called back-filling and is usually done to return the extraction site to its previous agricultural use. The landowner decides on post-extraction management, and since many of the extraction sites are leased areas, the decision is up to local communities or private individuals. In the case of areas purchased by quarries, it is much easier to allow rewilding instead of restoration. Both situations present us with opportunities to observe successional processes after disturbance.

Ecological changes (disturbances) usually take place as singular events: disruptions that are clearly constrained in time and space. The sum of these disturbances acts as a disturbance regime, which shifts the ecological network and allows existing elements to morph and new elements to emerge, thus enabling dynamic stability in ecosystems (Jentsch et al. 2019). Nature possesses a wide range of response mechanisms to disturbance events, allowing it to restore dynamic landscape sections to their original state or to establish new species and structural configurations (von Heßberg & Jentsch 2022). There is ongoing debate about the relationship between species richness and ecosystem functions. However, it is generally agreed that the loss of species leads to a decrease in ecosystem functions. Conversely, ecosystem functions can be enhanced by increasing habitat heterogeneity and species richness through external factors, such as reintroducing mechanical disturbances, fires in areas with historical fire regimes, or rehabilitating areas through seeding native species and removing invasive species (Tilman et al. 2014; Frank 2022; Hong et al. 2022; Spangenberg 2023).

The extraction of deposits is influenced by the geological thickness, accessibility, and therefore economic efficiency of extraction: thus, limited in space and time. After the cessation of mining activities, a variety of possibilities arise for restoration (e.g., to agricultural or forested areas) or rewilding, allowing rare steppe species to migrate into these secondary habitats and to stabilize or expand their populations (Gilcher & Bruns 1999). Due to this, future mining areas will be included in the regional development strategies of the federal states for nature conservation and the biodiversity strategy (Rademacher & Hoffeins 2008). The rewilding or restoration of mining areas is now mandatory in all federal states (Martins et al. 2020), and the implementation of global agreements is mandatory for the gypsum industry in Germany (Bundeskabinett 2020; EEA 2020). What is missing in Germany, however, is scientific literature on the economic evaluation of gypsum-mining ecosystems and their post-mining landscapes (Lorite et al. 2021).

As a first step to fill this gap, we look to study the impact of gypsum mining in Germany on vascular plant richness by analyzing post-gypsum mining landscapes. We are convinced that this study can provide a foundation for future research because no scientifically independent studies on the ecological status of German gypsum mining sites have been conducted. We asked the following research questions:

- (1) How species-rich are gypsum post-mining landscapes compared to the surrounding areas?
- (2) How does the age of gypsum post-mining landscapes relate to their floristic species richness?
- (3) How does habitat heterogeneity affect the species richness of these landscapes?

Methods

Site Description

Gypsum deposits worth mining in Germany are located in the regions of Lower Saxony, Hesse, Thuringia, Bavaria, and Baden-Württemberg (Schöneich 1991) (Fig. 1). We included the following subset of regions in our investigations: southern Harz, northeast Hesse, Lower and Middle Franconia (Bavaria), and eastern Württemberg. In each of these regions, four to five mining areas were selected for vegetation mapping. Natural protected areas (NPAs) with clear gypsum-dominated vegetation communities in the surrounding landscape were also selected as investigation sites. We did not take into consideration the companies operating in the areas for our analysis. The selection of the study areas and NPAs was done to be able to form a chrono sequence using the plant data collected on species richness in a proxy time series (“space for time” concept).

All study areas were classified by land use category: mining dumps (continuously but partly disturbed topsoil dumps), rewilding, restoration, NPAs, and expansion areas (Table 1). While grazed areas were present, they only occurred in two rewilding areas and one NPA and were thus excluded from further analyses (Fig. S2). NPAs with near-surface gypsum were not always available near the mining areas for comparison. For safety reasons, no mapping was carried out in active mining areas and on very steep slopes. Age (since cessation of mining) for each respective area was provided by the mining companies and, when this data was not available, was estimated based on the present vegetation.

Areas characterized as “expansion” land use areas (see Table 1 for a definition of each land use category) are covered with either permanent grassland or managed forest. Since no precise age could be determined for these areas, we used an approximation of 100 years. These expansion areas are clustered on the right edge of Figure 3 and serve as a measure of the species richness beyond the mining areas, in the environmental matrix, as a reference for climax vegetation in each region. We examined three NPAs, which could also not be assigned a fixed successional age and were set to 50 years to serve as comparison points for the typical gypsum steppe vegetation.

Landscape and Vegetation Mapping

In each site we used planar structural mapping to delineate each structural class present (see Fig. 2 for structural classes and an example map). We then performed two vegetation surveys (spring and summer of 2022) along a 10-m-wide line transect through each study area so that the maximum length or width of the respective area was covered (Tränkle & Poschold 1994; Friedel et al. 2008). In this way, the saturation area of the species-area curve was always reached long before the transect was finished. Using the GPS-fixed transects, we created a list of all vascular plant species for each study area. Care was taken to use the most current nomenclature according to the TRNS database (Boyle et al. 2013).

We quantified the structural diversity as the number of different structural elements per area: we mapped the landscape in each area landscape on coarse grids, entering landscape elements and biotope types, giving priority to those that occupied a significant proportion of the total mapping section of the mining area (up to a maximum of 500 m outside the company premises, even if the predominant biotope type was not present there). Examples of mapped elements include rock walls, rubble heaps, water areas, bank areas, raw soil areas, bushy areas, forests, and piles of topsoil (removed from mining areas)—see Figure 2.

We recorded a total of 66 transects ranging from about 50 m to 300 m in length. The number of habitats intersected was correlated with the average number of species (richness of vascular plant species) in each transect (Fig. 5). This methodology allows us to record approximately 50–70% of the vascular plant species effectively occurring in an area (Friedel et al. 2008). The transect dataset was tested for the dependence of the number of plant species (species richness) on different succession ages. The entire dataset was tested (5,343 individual entries) to understand if species numbers correlated with the area sizes of the transects.

The data were evaluated using MS Excel 16.0 and “R-Studio” running R version 4.2.1.

The spatial analysis and representation of the structural mapping was carried out using QGIS Desktop 3.16.14. With the help of aerial photographs and transect data, we calculated the area of each vegetation type for all study areas. When combining the individual data sets, vegetation units of similar age were adjusted to ensure better comparability.

Results

A total of 66 transects across 26 study areas covering over 11 km in length were surveyed twice in 2022 in four major regions of Germany. In total, 657 vascular plant species (including *Achillea setacea*, *Leonurus cardiaca*, *Onobrychis vicifolia*) and 75 moss species (including *Aloina aloides*, *Preissia quadrata*, and *Encalypta vulgaris*) were recorded. The complete species list is provided in Table S1. The complete dataset of all mappings consists of 5,343 entries for vascular plant species. Of these, only 13% (87 species) are woody plants (including *Acer campestre*, *Cornus mas*, *Ulmus minor*). A total of 25% of

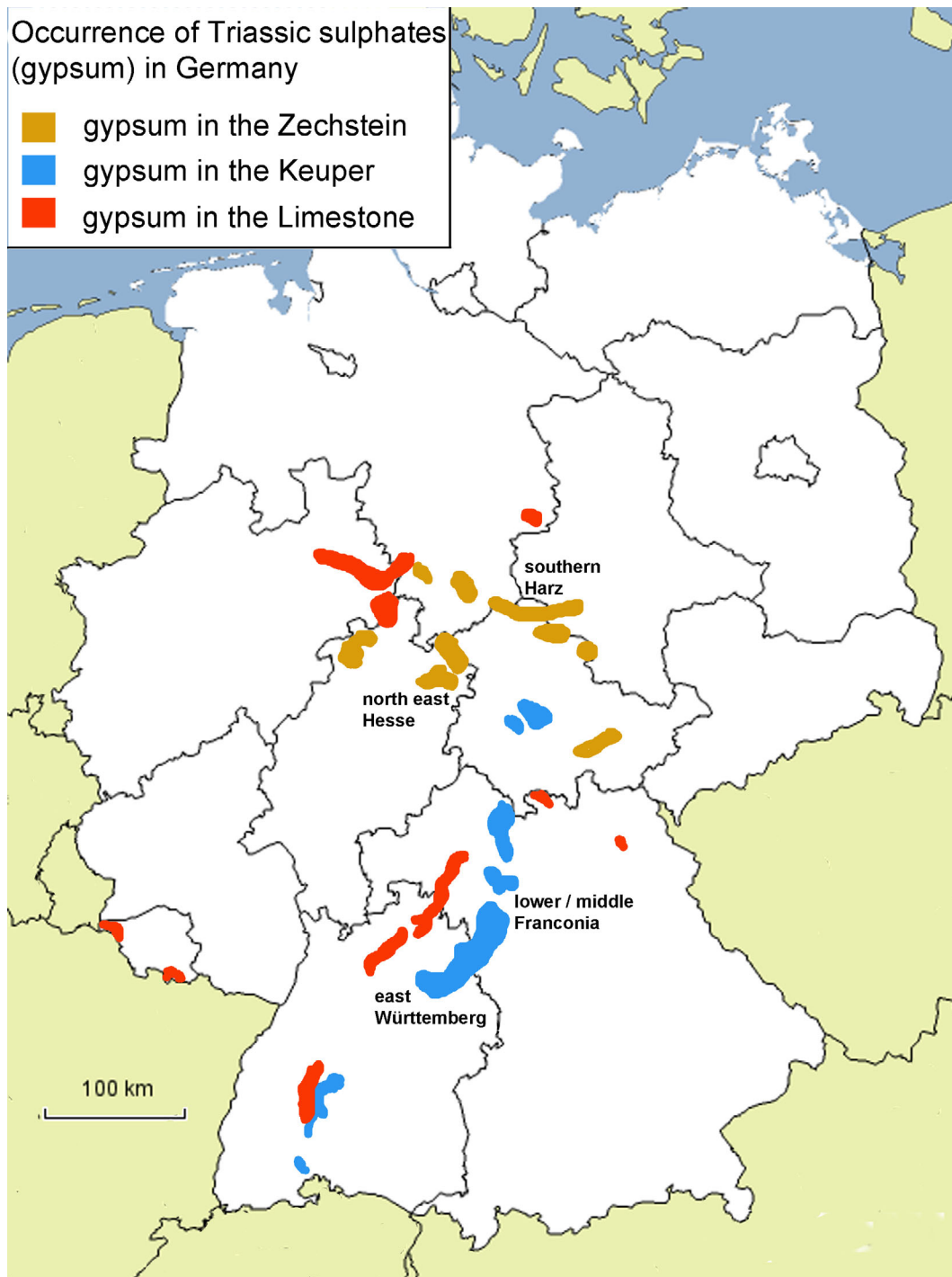


Figure 1. Map of gypsum deposits in Germany (modified from BdG 2006). The exact location of the study sites will remain unpublished to maintain the anonymity of the collaborating parties.

the species are wind-pollinated (including *Briza media*, *Koeleria pyramidata*, *Stipa pennata*) and 75% are insect-pollinated (including *Carduus nutans*, *Melampyrum pratense*, *Veronica teucrium*). Finally, 5% (33) of the plant species are classified as neophytes (including *Acer negundo*, *Laburnum anagyroides*, *Syringia vulgaris*).

Only 5% of the 66 transects were in NPA land use areas, while 47% of them were rewilding areas (Table 1). The total mapped area of all transects was approximately 120,000 m² with an average area size of the 66 study transects (each 10 m wide) of 1,800 m² (± 860 m²). An average of 75 vascular plant species (± 12) were mapped per transect.

Table 1. Classification of the mapped transects within all recorded gypsum extraction sites into five land-use categories and their descriptions.

Land-Use Category	Description	% Share of Transects
Mining dumps (0–3 years old)	Areas on which the first initial succession processes (usually up to 3 years old) can take place—usually topsoil dumps.	3
Rewilding (3–99 years old)	Passively renatured mining area with a proportion of bare raw soil or rock rubble. Free, un-aided succession, with no topsoil addition or planting (see Fig. S2).	47
Restoration (3–99 years old)	Areas where succession has been specifically controlled or accelerated through management measures, for example by applying fertile topsoil, planting trees and shrubs or sowing ground-covering herbaceous vegetation. Actively restored mining area.	29
Natural protected areas (NPA) (50 years or older)	The examined NPAs that contain gypsum rock close to the surface are located in the immediate surroundings of active mining areas and represent an important part of the environmental matrix in terms of the species pool. They are refuges for rare species and specialized species communities in the gypsum landscape and starting areas for spread to nearby mining areas.	5
Expansion areas (100 years or older)	Areas that will be available for gypsum mining in the next few years and for which there are mining permits. These areas, together with the NPAs, form the areas of the environmental matrix that support the species pool. Varied habitat structures: forests used for forestry purposes; agriculturally used fields or meadows; components of the cultural landscape. Used as the starting point for species diversity comparisons with post-mining sites.	17

The total richness of 657 vascular plant species across all mapped sites is unevenly distributed across the five land use categories, with rewilding areas being the most diverse with 523 vascular plant species. NPA and expansion areas each had about half as many species (262 and 271, respectively), while restored areas were middlingly diverse with 389 recorded species (Fig. 3). The areas on active mining dumps had a much lower species richness than the other sites (97 species). It seems that post-mining landscapes harbor more species richness than their surrounding areas. This trend is also present in the number of uniquely occurring species in each land use category. Here too, the rewilding areas have a higher number of species compared to the NPA and expansion areas (94, 17, and 21 species, respectively). The restoration areas, again, bridge the difference with 52 unique species. Accounting for the unequal sample size of some of the categories, we found no species–area dependence within our dataset.

In order to identify a possible regional effect in the study results, we also broke down the richness of each land use category into the four German bioregion study areas (Fig. 4). In the rewilding category, the number of species in Lower/Middle Franconia (356 species) is significantly higher than in the areas of East Württemberg (188) and Northeast Hesse (237). The area in Southern Harz also has a slightly lower richness (307). In the restoration category, the richness in East Württemberg is significantly higher at 256 than in the other three areas. In the NPA and expansion categories, the regional differences are not as pronounced.

Of the 657 mapped vascular plant species, 84.6% (557 species) are listed as not endangered or lack an entry in the German Red List. A total of 15% (100 species) of the mapped vascular plant species have an endangered status (Fig. 5); 64 species

(9.7%) are near threatened (vulnerable); 30 species (4.6%) have a Red List status 3 (endangered e.g., *Astragalus danicus*, *Adonis vernalis*); and 7 species (1.1%) have an RL 2 status (highly endangered) (*Astragalus arenarius*, *Carex dioica*, *Leonurus cardiaca*, *Ranunculus reptans*, *Scorzonera purpurea*, *Teucrium scordium*, *Trifolium ochroleucon*); for selected pictures see Figure S3. Even considering only the species listed as endangered, highly endangered, and threatened with extinction (RL 3 to RL 1), the rewilding areas in Lower/Middle Franconia and southern Harz represent refugia for certain species (Fig. 4). This is further supported by the significantly higher number of RL species in the mapped rewilding areas compared to NPAs (Fig. 4).

The richness in rewilding and restoration areas peaks around 15 years after mining activity cessation (YAC) (Fig. 6). This maximum is reached slightly earlier in the restoration areas (approximately 10 YAC) and then levels off faster than in the rewilding areas.

In just over half of the cases (37 of 66), the transect only intersected one structural element (see Fig. 2), while a few transects intersected up to 10 structural elements (see Fig. 2 for an example transect crossing five different structural elements). We found that the average number of species present, vascular plant species richness, was positively related to the number of structural elements intersected by the respective transect (Fig. 7).

Of the eight transects with five or more intersected habitat structures, only one was in a restoration area—the remaining seven were split between rewilding areas and NPAs (6 and 1, respectively). Of the 37 transects with only one habitat structure, 13 were in rewilding and restoration areas. The number of species thus seems to depend on the heterogeneity of the landscape rather than the land use category.

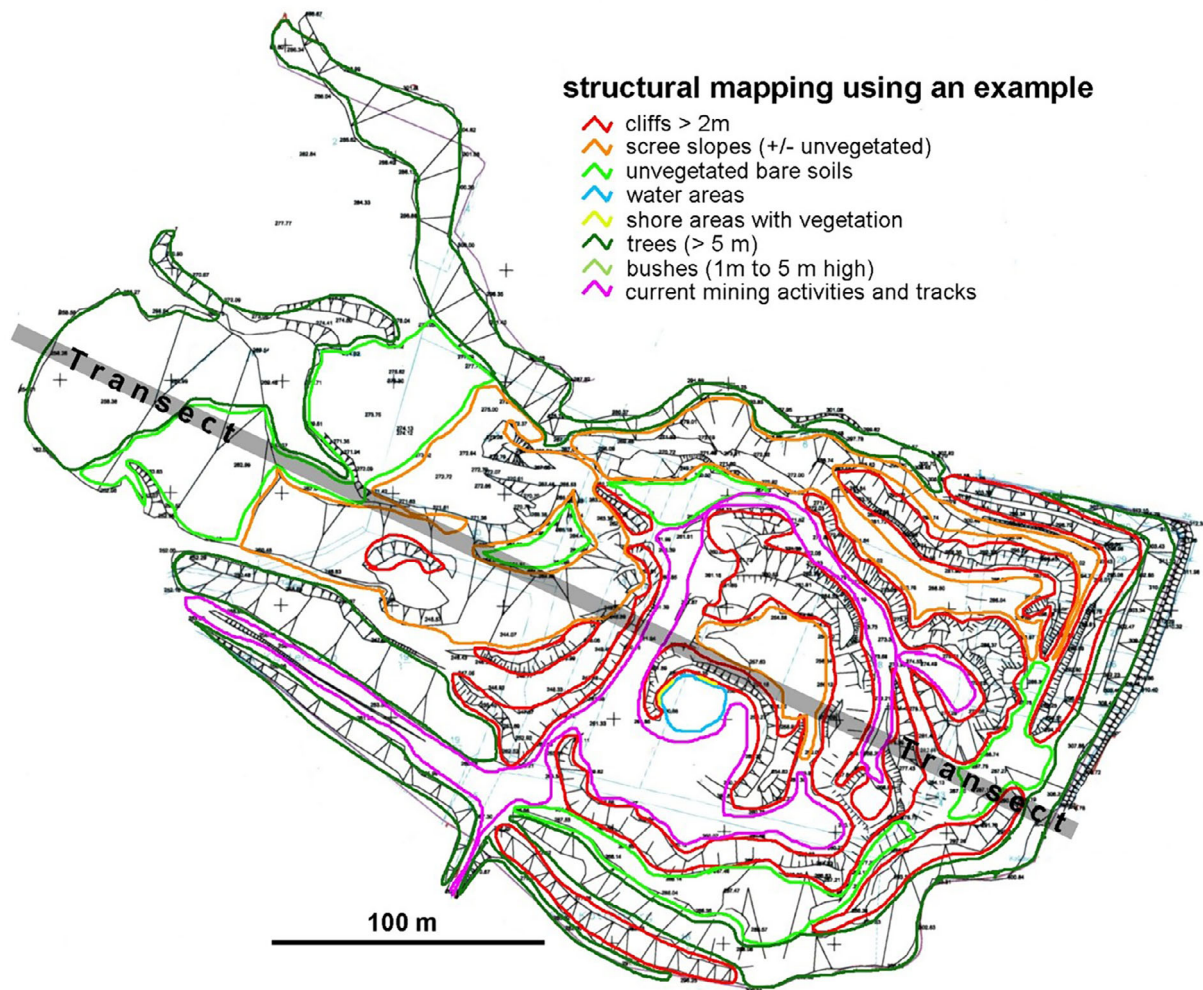


Figure 2. Example sketch of a mining site with a selection of mapped landscape structures and the 10 m wide sampling transect laid through the area.

In our study areas, uniform landscapes with a low number of structural elements support a low number of plant species. Among the eight transects with more than five different habitat structures, only one transect did not contain water, while in transects with four or fewer habitat structures, only one transect intersected a water body. This shows the importance of the creation of water areas, as they can relatively easily increase structural diversity in post-mining landscapes for the floristic (and faunistic) species richness that develops there.

Discussion

Habitat fragmentation and destruction are on the rise globally (Bonn & Poschlod 1998; Caballos et al. 2020; EEA 2020; Cowie et al. 2022), even with the rising understanding of the importance of biodiversity for ecosystem functioning. Given these circumstances, any degraded area can be seen as a potential conservation target. Gypsum extraction areas, in particular, can provide an important opportunity for conservation. Their raw soil environments can play a crucial role in the establishment of pioneer

grasslands with species from dry grassland habitats (Poschlod 1997; von Heßberg 2022) and form important refugia for arable flora (Stumpf & Offenberger 2018; Bergmeier et al. 2021). A firm scientific understanding of the effects of different restoration practices in post-mining landscapes in Germany has yet to be developed, though. Here we try to fill that gap, focusing on species richness, successional dynamics, and habitat structure.

Post-mining landscapes are often considered suitable only for ruderal vegetation common in the surrounding area rather than botanical highlights or rare Red List species. However, as we observe, these landscapes act as refugia for many Red List species (similarly reported by Mota et al. (2004) and Mota et al. (2021) for landscapes on the Iberian Peninsula, and König (2017) for the Pomeranian Islands). Ruderal species, though, while often referred to as “everyday species,” also play an important role in biodiversity and trophic interactions and should not be overlooked. Not only are they a valuable food source for many pollinators and herbivores; they are also becoming increasingly rare on agricultural land due to intensified use (e.g., Pinke et al. 2011; Feledyn-Szewczyk et al. 2019).

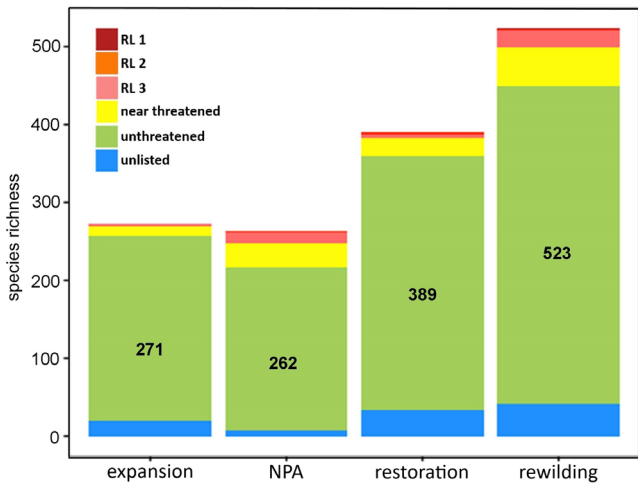


Figure 3. Distribution of Red List species by category in the four land-use types (category “mining dump” is excluded here). The black numbers represent the total number of species.

The landscape surrounding these gypsum quarries is dominated by land used for agriculture or forestry that has been anthropogenically molded several times in recent centuries, yielding a high level of biodiversity in the cultural landscape of central Germany. Many species, both vegetable and animal, native to hedgerows and species-rich hay meadows are being increasingly pushed into secondary habitats due to the

intensification of agriculture and its associated loss of biodiversity (e.g., Graham et al. 2018). As a result, the post-mining landscapes we surveyed, as habitats for these hedge and meadow species, represent important refugia for a wide range of species groups and communities, including birds such as *Lanius colurio*, reptiles such as *Lacerta agilis*, amphibians such as *Alytes obstetricans*, insects such as *Papilio machaon*, spiders such as *Argiope bruennichi*, and mollusks such as *Helix pomatia*.

Our surveys indicate that these areas are not only richer in species than the surrounding agricultural areas; they also host a higher species richness than protected and forested areas in their vicinity. This highlights the potential that well-managed post-mining landscapes have for conservation purposes. We suggest that this is likely driven by two factors: succession and habitat diversity.

Succession in Iberian gypsum quarries has been studied quite extensively (e.g., Mota et al. 2004; Cañadas et al. 2015; Mota et al. 2021 to name a couple) and spontaneous succession has been observed in most cases. We observe a similar phenomenon in our sites, following a shorter timeline likely due to climatic factors, with the cessation of disturbance caused by the mining machines being followed within the first growing season by the establishment of a pioneer flora. As succession progresses, often within the second year, these pioneers are replaced by perennial ruderal shrubs (e.g., *Crataegus spec.*) and grasses (e.g., *Arrhenatherum elatius*). The first woody plants appear within the first 3 years (e.g., *Pinus sylvestris*, *Betula pubescens*, *Salix spec.*, *Alnus glutinosa*, *Euonymus europaeus*, *Viburnum*

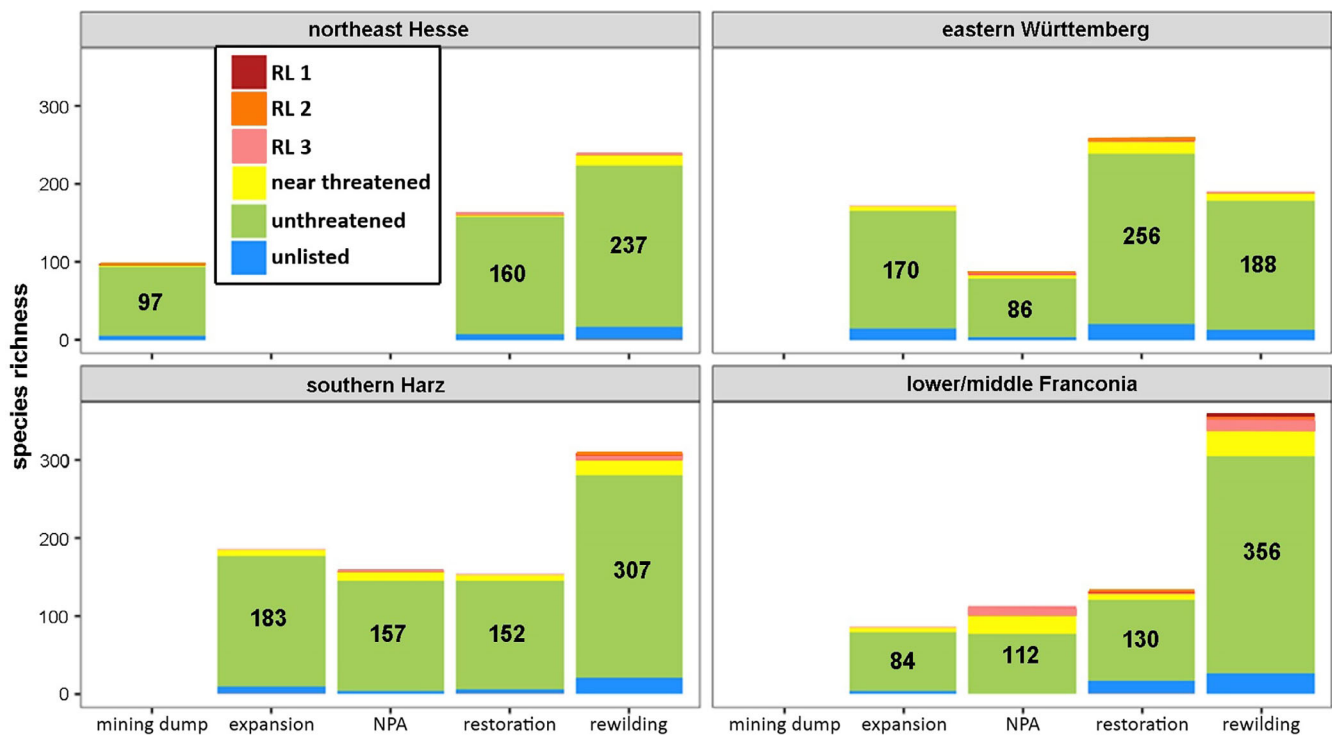


Figure 4. Sub-division of the distribution of Red List species by category in the five land use types by the four mining regions. The black numbers represent the total number of species in these four utilization categories.

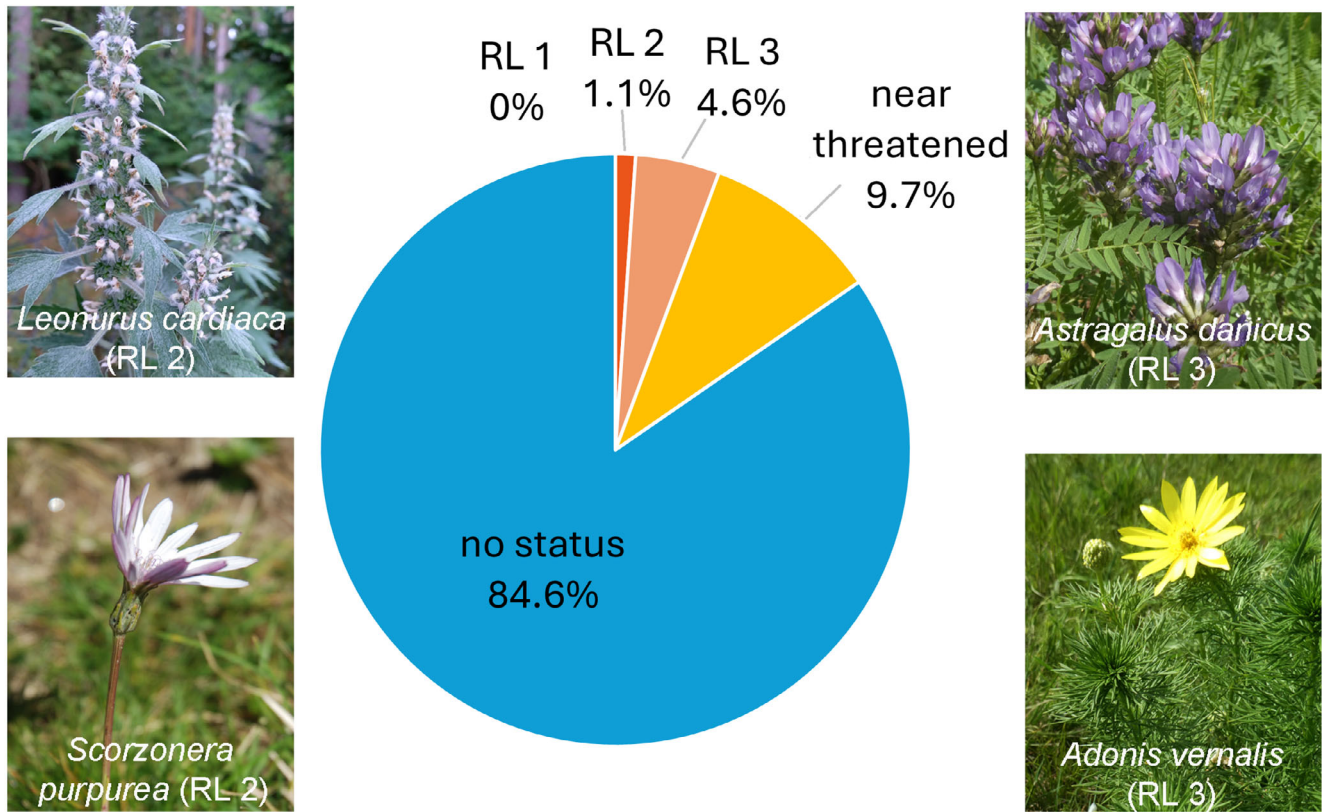


Figure 5. Percentage distribution of the protection status of all 657 mapped vascular plant species based on their German Red List (RL) classification and four of these RL species with their respective Red List protected class in brackets under the scientific name.

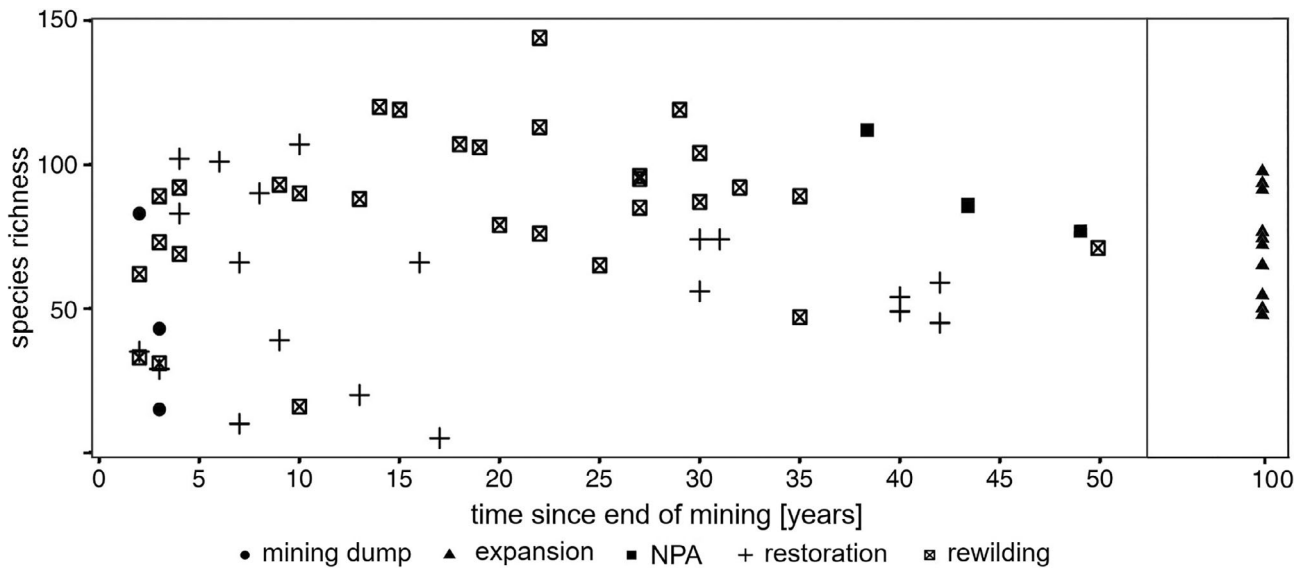


Figure 6. Distribution of the number of vascular plant species in the 66 study transects as a function of plot age (number of years after the end of active gypsum mining or soil movements).

spec., *Prunus spec.*, *Populus spec.*). The number of plant species in the sampled post-mining landscapes increases with increasing age of succession (which supports both experiments on the

Iberian Peninsula by Mota et al. (2023) and observations in the Pomeranian Islands by König 2017). The accelerated tree succession we observed in restoration areas is likely due to the

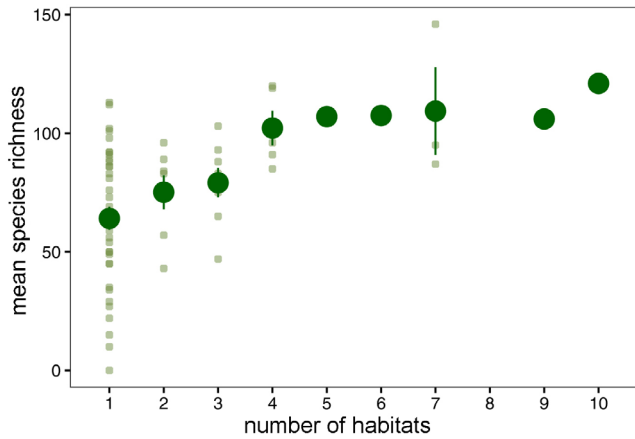


Figure 7. The average species richness by number of intersected habitats of each transect (see list of habitats in Fig. 2).

application of topsoil and the planting of young trees, following findings of work by Ballesteros et al. 2012.

Currently, post-mining landscapes in Germany are most frequently either restored or rewilded. In the former scenario, areas destined for agriculture or forestry are restored and actively managed, with a pattern of frequent disturbance (e.g., biomass harvest, sheep grazing). In the latter case, the areas are returned to nature for free succession, which will tend towards a forested “climax” state in the absence of external disturbances. In both cases, though more strongly in rewilded areas, we observe a temporal evolution of species diversity across our sites consistent with the classic distribution of species richness at different stages of succession. As competition for light, space, nutrients, and water increases, much of the former ruderal vegetation disappears, and shade-tolerant shrubs and forest species immigrate. This trend mimics the curve defined by the intermediate disturbance hypothesis (IDH; Connell 1978), which states that maximum species richness coincides with medium levels of disturbance.

While natural gypsum deposits are only found on a few cliffs in the southern Harz region of Germany, in the other regions, gypsum is naturally hidden under geological Keuper layers. The few places in Germany where gypsum appears close to the surface are in most cases of anthropogenic origin, namely due to the extraction of gypsum since the early Middle Ages. These areas have developed into sites with a low nutrient supply and edaphic, seasonal dryness, enabling the specialized species of the “Pannonian steppe flora” to grow with low competition from the surrounding flora. These unique locations have historically been used primarily for grazing purposes, resulting in ongoing nutrient depletion, and somewhat paradoxically the maintenance of these steppe flora environments. A disturbance regime is thus a crucial factor to include when creating management plans.

We observe that managed post-mining landscapes with a greater habitat richness support a greater number of plant species. This mirrors results found in other ecosystems—agriculture (see Benton et al. 2003), boreal forests (see Hekkala et al. 2023), and even the deep ocean (Buhl-Mortensen

et al. 2010) where biodiversity increased with increased habitat diversity, hinting that active management, not just successional dynamics, is valuable to increase the conservation value of these areas.

Large-scale mapping of the vegetation in the sites would likely result in more extensive and perhaps precise species lists and proper successional experiments (such as those run by Mota et al. 2023), clearer successional trajectories. Our goal, outside of merely describing the botanical communities in these areas, was also to develop an efficient metric to measure gypsum-mine recovery which could be replicated, without a hindering time commitment, in any site. We leveraged the “space for time” concept, selected areas, and defined transects to form a proxy time series post-cessation. Working with transects, even if only 50% to 70% of vascular plant species actually occurring in an area can be recorded (Friedel et al. 2008), improved efficiency and comparability between sites. This permits us to provide a general overview of the relationship between post-mining management and vascular biodiversity.

We conclude that the most important factor in the active management for biodiversity in these landscapes is a high diversity of structures to create a variety of habitats. This can be done as a last step after finishing the extraction of gypsum, but only in agreement with the landowners. In light of the recent adoption of the EU Nature Restoration Regulation, all degraded ecosystems within the EU become opportunities to achieve the ambitious targets set by the Environmental Council. The relatively rare and highly biodiverse communities supported by gypsum substrate combined with the large area these post-mining landscapes cover make these sites ideal targets for German conservation action. An improvement in goal communication between companies, legislating bodies, other stakeholders of these sites, and science needs to occur though if we are to prioritize these areas for biodiversity conservation.

Acknowledgments

We thank the various mining companies for site access, the Federal Association of the Gypsum Industry for fruitful discussions, and our team of field investigators, including Pia Bradler and Wiebke Richter, and data analysts including Max Schuchardt. Open Access funding enabled and organized by Projekt DEAL.

LITERATURE CITED

- Arendt M (2001) Kreislaufwirtschaft im Baubereich: Steuerung zukünftiger Stoffströme am Beispiel Gips. PhD dissertation. University of Heidelberg.
- Baier M, Bookhagen B, Eicke C, Elsner H, Henning S, Kuhn K, et al. (2021) Deutschland—Rohstoffsituation 2020. Deutsche Bundesanstalt für Geowissenschaften und Rohstoffe (BGR), Hannover, Germany
- Ballesteros M, Cañadas EM, Foronda A, Fernández-Ondoño E, Peñas J, Lorite J (2012) Vegetation recovery of gypsum quarries: short-term sowing response to different soil treatments. *Applied Vegetation Science* 15:187–197. <https://doi.org/10.1111/j.1654-109X.2011.01166.x>
- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution* 18:182–188. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9)

- Bergmeier E, Meyer S, Pape F, Dierschke H, Härdtle W, Heinken T, et al. (2021) Ackerwildkraut-Vegetation der Kalkäcker (Caucalidion): Pflanzengesellschaft des Jahres 2022. *Tuexenia* 41:299–350. <https://doi.org/10.14471/2021.41.021>
- Bonn S, Poschlod P (1998) Ausbreitungsbiologie der Pflanzen Mitteleuropas Verlag. UTB, Stuttgart, Germany
- Boyle B, Hopkins N, Lu Z, Garay JAR, Mozzherin D, Rees T, et al. (2013) The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics* 14:1–15. <https://doi.org/10.1186/1471-2105-14-16>
- Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology* 31:21–50. <https://doi.org/10.1111/j.1439-0485.2010.00359.x>
- Bundeskabinett (2020) Gipsabbau in Deutschland und Auswirkungen auf Naturschutz. Drucksache 19/21494 Deutscher Bundestag 19. Wahlperiode, Berlin, Germany
- Bundesverband der Gipsindustrie e.V (2006) Tierwelt in Gipssteinbrüchen. GIPS schafft Freiräume, Darmstadt, Germany
- Caballos G, Ehrlich PR, Raven PH (2020) Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings of the National Academy of Sciences of the United States of America* 117:13596–13602. <https://doi.org/10.1073/pnas.1922686117>
- Cañadas EM, Ballesteros M, Foronda A, Navarro FB, Jiménez MN, Lorite J (2015) Enhancing seedling production of native species to restore gypsum habitats. *Journal of Environmental Management* 163:109–114. <https://doi.org/10.1016/j.jenvman.2015.08.006>
- Connell J (1978) Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. *Science* 199:1302–1310. <https://doi.org/10.1126/science.199.4335.1302>
- Corlett R, Tomlinson KW (2020) Climate change and edaphic specialists: irresistible force meets immovable object. *Trends in Ecology & Evolution* 35:367–376. <https://doi.org/10.1016/j.tree.2019.12.007>
- Cowie RH, Bouchet P, Fontaine B (2022) The sixth mass extinction: fact, fiction or speculation? *Biological Reviews of the Cambridge Philosophical Society* 97:640–663. <https://doi.org/10.1111/bvr.12816>
- de Acosta SK (2018) Auswirkungen von anthropogenen Eingriffen in die Wildflusslandschaften der nördlichen Kalkalpen. M.Sc. Dissertation. Karlsruher Institut für Technologie, Karlsruhe, Germany
- EEA (2020) The European environment—state and outlook 2020 knowledge for a transition to a sustainable Europe. https://www.eea.europa.eu/publications/soer-2020/at_download/file
- Escudero A, Palacio S, Maestre FT, Luzuriaga AL (2015) Plant life on gypsum: a review of its multiple facets. *Biological Reviews* 90:1–18. <https://doi.org/10.1111/bvr.12092>
- Feledyn-Szewczyk B, Matyka M, Staniak M (2019) Comparison of the effect of perennial energy crops and agricultural crops on weed flora diversity. *Agronomy* 9:695. <https://doi.org/10.3390/agronomy9110695>
- Finck P, Heinze S, Raths U, Riecken U, Ssymank A (2017) Rote Liste der gefährdeten Biotoptypen Deutschlands, 3. Auflage. Vol 156. Bundesamt für Naturschutz, Bonn, Germany
- Frank D (2022) Science and values in the biodiversity-ecosystem function debate. *Biology & Philosophy* 37:7. <https://doi.org/10.1007/s10539-022-09835-4>
- Friedel G, Rademacher M, Tränkle U, Offenwanger H, Schuler A, Röhl M, Steimle B, Hübner F (2008) Nachhaltigkeitsindikatoren für ein integriertes Rohstoff- und Naturschutzmanagement: Pilotprojekt im Zementwerk Schelklingen—Projektsergebnisse. Bundesverband der Deutschen Zementindustrie, Düsseldorf, Germany
- Gilcher S, Bruns D (1999) Renaturierung von Abbaustellen. Ulmer, Stuttgart, Germany
- Gilcher S, Tränkle U (2005) Steinbrüche und Gruben Bayerns und ihre Bedeutung für den Arten- und Biotopschutz. Bayerischer Industrieverband Steine und Erden e.V., Bayerisches Landesamt für Umwelt, München, Germany
- Graham L, Gaulton R, Gerard F, Staley JT (2018) The influence of hedgerow structural condition on wildlife habitat provision in farmed landscapes. *Biological Conservation* 220:122–131. <https://doi.org/10.1016/j.biocon.2018.02.017>
- Hekkala AM, Jönsson M, Kärvelo S, Strengbom J, Sjögren J (2023) Habitat heterogeneity is a good predictor of boreal forest biodiversity. *Ecological Indicators* 148:110069. <https://doi.org/10.1016/j.ecolind.2023.110069>
- Höding T, Szurliés M, Kimmig B, Poschlod K, Fritsche G, Börner A, et al. (2021) Bestandsaufnahme der Gipsvorkommen in Deutschland. Bund-Länder-Arbeitsgruppe der staatlichen Geologischen Dienste, Hannover, Germany
- Hong P, Schmid B, De Laender F, Eisenhauer N, Zhang X, Chen H, et al. (2022) Biodiversity promotes ecosystem functioning despite environmental change. *Ecology Letters* 25:555–569. <https://doi.org/10.1111/ele.13936>
- Jentsch A, Seidl R, Wohlgemuth T (2019) Definitionen und Quantifizierungen von Störungen. Pages 21–39. In: Wohlgemuth T, Jentsch A, Seidl R (eds) *Störungsökologie*. UTB Haupt Vlg, Bern, Stuttgart, Germany
- Khater C, Martin A, Maillat J (2003) Spontaneous vegetation dynamics and restoration prospects for limestone quarries in Lebanon. *Applied Vegetation Science* 6:199–204. <https://doi.org/10.1111/j.1654-109X.2003.tb00580.x>
- König P (2017) Plant diversity and dynamics in chalk quarries on the islands of Rügen and Wolin (Western Pomerania/Germany and Poland). *Biodiversity: Research and Conservation* 47:23–39. <https://doi.org/10.1515/biorc-2017-0014>
- Lorite J, Ballesteros M, García-Robles H, Cañadas EM (2021) Economic evaluation of ecological restoration options in gypsum habitats after mining. *Journal for Nature Conservation* 59:125935. <https://doi.org/10.1016/j.jnc.2020.125935>
- Luzuriaga AL, Ferrandis P, Flores J, Escudero A (2020) Effect of aridity on species assembly in gypsum drylands: a response mediated by the soil affinity of species. *AoB Plants* 12:plaa020. <https://doi.org/10.1093/aobpla/plaa020>
- Martins WB, Lima MD, Junior UD, Amorim LS, de Assis Oliveira F, Schwartz G (2020) Ecological methods and indicators for recovering and monitoring ecosystems after mining: a global literature review. *Ecological Engineering* 145:105707. <https://doi.org/10.1016/j.ecoleng.2019.105707>
- Metzing D, Garve E, Matzke-Hajek G (2018) Rote Liste und Gesamtartenliste der Farn- und Blütenpflanzen (Tracheophyta) Deutschlands. Pages 13–358. In: Metzing D, Hofbauer N, Ludwig G, Matzke-Hajek G (eds) *Rote Liste der gefährdeten Tiere, Pflanzen und Pilze Deutschlands*. Vol 7. Bundesamt für Naturschutz, Bonn. *Naturschutz und Biologische Vielfalt* 70 (7)
- Mota JF, Martínez-Hernández F, Salmerón-Sánchez, E, Mendoza-Fernández AJ, Pérez-García FJ, & Merlo, ME (2023) Spontaneous Primary Succession and Vascular Plant Recovery in the Iberian Gypsum Quarries: Insights for Ecological Restoration in an EU Priority Habitat. *Plants* 12(5):1162. <https://doi.org/10.3390/plants12051162>
- Mota J, Merlo E, Martínez-Hernández F, Mendoza-Fernández AJ, Pérez-García FJ, Salmerón-Sánchez E (2021) Plants on rich-magnesium dolomite barrens: a global phenomenon. *Biology* 10:38. <https://doi.org/10.3390/biology10010038>
- Mota J, Sola A, Jiménez-Sánchez M, Pérez-García F, Merlo ME (2004) Gypsicolous flora, conservation and restoration of quarries in the southeast of the Iberian Peninsula. *Biodiversity and Conservation* 13:1797–1808. <https://doi.org/10.1023/B:BIOC.0000035866.59091.e5>
- Müller N (2020) Hoffnung für die Populationsentwicklung von Wildflussarten der Alpen? Rückgang und aktuelle Bestandssituation von Zwergrohrkolben (*Typha minima* Hoppe), Deutscher Tamariske (*Myricaria germanica* Desv.) und Uferreitgras (*Calamagrostis pseudophragmites* Koeler) in Bayern. Vol 89. *Berichte Der Bayerischen Botanischen Gesellschaft*, München, Germany
- Palacio S, Escudero A, Montserrat-Martí G, Maestro M, Milla R, Albert MJ (2007) Plants living on gypsum: beyond the specialist model. *Annals of Botany* 99:33–343. <https://doi.org/10.1093/aob/mcl263>
- Paul J (2014) Gypsum domes and diapirs: common features in the Zechstein (Upper Permian) of Germany. *Geological Quarterly* 58:521–530. <https://doi.org/10.7306/gq.1192>
- Pinke G, Király G, Barina Z, Mesterházy A, Balogh L, Csiky J, Schmotzer A, Molnár AV, Pál RW (2011) Assessment of endangered synanthropic plants of Hungary with special attention to arable weeds. *Plant Biosystems* 145:426–435. <https://doi.org/10.1080/11263504.2011.563534>

- Poschold P (1997) Ökologische und naturschutzfachliche Aspekte von Störungen und Dynamik bei Rohstoffentnahmen. Pages 65–78. In: Böcker R, Kohler A (eds) Abbau von Bodenschätzen und Wiederherstellung der Landschaft. Hohenheimer Umwelttagung. Vol 29. Vlg. Universität Hohenheim, Hohenheim, Germany
- Poschold P, Tränkle U (1997) Steinbrüche und Folgenutzung Naturschutz—Perspektive oder Konflikt? Pages 5–15. In: Poschold P, Tränkle U, Böhmer J, Rahmann H (eds) Steinbrüche und Naturschutz. Sukzession und Renaturierung. ecomed Verlag, Landsberg, Germany
- Raab B, Reimann M (2013) Steppenrasen in Gipssteinbrüchen—Flora und Vegetation einer sekundären Naturlandschaft. Pages 70–79. In: Siegesmund S, Sneathlage R (eds) Naturstein in der Kulturlandschaft. Mitteldeutscher Verlag, Halle, Germany
- Raab B, Reimann M, Lütkehaus M, Hotzy R (2002) Gipsabbau und Biologische Vielfalt. Renaturierung von Gipssteinbrüchen in Süddeutschland. Steine und Erden Service GmbH, Ostfildern, Germany
- Rademacher M, Hoffeins M (2008) Nature conservation and public relations as instruments of sustainable raw material procurement. In: Escher H, Härtling JW, Kluttig T, Meuser H, Mueller K (eds) Proceedings of the 3rd International UNESCO Conference on Geoparks. Global Geoparks Network, Mytilene, Greece
- Řehounková K, Vitovcová K, Prach K (2020) Threatened vascular plant species in spontaneously revegetated post-mining sites. *Restoration Ecology* 28: 679–686. <https://doi.org/10.1111/rec.13027>
- Scheidegger F (ed) (1990) *Aus der Geschichte der Bautechnik*. Bd. 1. Birkhäuser, Basel, Switzerland
- Schöneich H (1991) Die nutzbaren Lagerstätten mineralischer Rohstoffen in der Bundesrepublik Deutschland. Wandkarte Verlag Glückauf, Essen, Germany
- Schönfelder P (1978) Vegetationsverhältnisse auf Gips im südwestlichen Harzvorland. Vol 8. Naturschutz und Landschaftspflege in Niedersachsen, Hannover, Germany
- Schulmeister A (1998) Sukzession in Gipssteinbrüchen. Fachbereich Landwirtschaft, Internationale Agrarentwicklung und Ökologische Umweltsicherung, Gesamthochschule Kassel-Witzenhausen, Kassel-Witzenhausen, Germany
- Seifert M, Etges T (2005) Entwicklung eines rekultiviertes Gipssteinbruches bei Städtoldendorf. *Berichte Der Naturhistorischen Gesellschaft Hannover* 147:3–35. https://www.zobodat.at/pdf/Ber-Nathist-Ges-Hannover_147_0005-0035.pdf (accessed 15 Sep 2024)
- Spangenberg JH (2023) Supporting the global biodiversity framework monitoring with LUI, the land use intensity indicator. *Land* 12:820. <https://doi.org/10.3390/land12040820>
- Stumpf T, Offenberger M (2018) Erfolge beim Schutz der Segetalflora. *Naturschutz Und Landschaftspflege* 50:386–393. <https://doi.org/10.1007/s10342-018-1172-3>
- Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* 45:471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>
- Tränkle U, Poschold P (1994) Vegetationskundliche Untersuchungen zur Sukzession von Steinbrüchen unter besonderer Berücksichtigung des Naturschutzes. Erste Ergebnisse zum Einfluss der Umgebungsvegetation auf die Vegetationsentwicklung und zur gelenkten Sukzession mit Hilfe von Mähgut. Veröff. PAÖ 8:353–367
- U.S. Geological Survey (2024) Mineral commodity summaries 2024. Mineral Commodity Summaries. <https://doi.org/10.3133/mcs2024>
- von Heßberg A (2003) Renaturierungsmaßnahmen an Main und Rodach (Oberfranken) und ihr Einfluss auf die flussnahen Vegetationsstrukturen. Pages 23–35. In: Böcker R, Rosenthal G (eds) Bericht der Jahrestagung des AK Restaurationecology innerhalb der GfÖ. Vol 17. Berichte des Institutes für Landschafts- und Pflanzenökologie der Universität Hohenheim. Hohenheim, Germany
- von Heßberg A (2022) Störungsregime in einer natürlichen, alpinen Flusslandschaft. *Regio Basiliensis* 63:167–176. [https://www.gegbasel.ch/regio-basiliensis-archiv/\\$/Nr.-63-2-Storungsokologie/201](https://www.gegbasel.ch/regio-basiliensis-archiv/$/Nr.-63-2-Storungsokologie/201) (accessed 15 Sep 2024)
- von Heßberg A, Jentsch A (2022) Die Vegetationszonen der Erde und deren typische Störungsregime und Klimaextreme. *Regio Basiliensis* 63:99–111. [https://www.gegbasel.ch/regio-basiliensis-archiv/\\$/Nr.-63-2-Storungsokologie/201](https://www.gegbasel.ch/regio-basiliensis-archiv/$/Nr.-63-2-Storungsokologie/201) (accessed 15 Sep 2024)
- Zekert O (1938) *Dispensatorium pro pharmacopoeis Viennensibus Austria 1570*. In: Österreichischer Apothekerverein und Gesellschaft für Geschichte der Pharmazie. Deutscher Apotheker-Verlag Hans Hösel, Berlin, Germany

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Gypsum-mining-landscapes.

Figure S2. A gypsum mine that was abandoned 50 years ago.

Figure S3. Plant species typical of Gypsum habitats in Germany.

Table S1. Complete species list of all sampled sites.

Coordinating Editor: Stephen Murphy

Received: 12 November, 2024; First decision: 15 January, 2025; Revised: 23 September, 2025; Accepted: 23 September, 2025