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Global change, novel ecosystems and the ecological restoration of post-industrial areas: The case of a former brown coal mine in Søby, Denmark

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Abstract

Questions: Can multi-decadal vegetation changes in a decommissioned brown coal mine be attributed to global-change forcing? Given novel drivers of community assembly and ongoing global change, what are sensible restoration goals and strategies for large post-industrial areas?

Location: A decommissioned brown coal mine near Søby, central Denmark (56°01′45′′ N, 9°04′4′′ E).

Methods: We resurveyed the plant communities of the mine 31 years after an initial survey. Changes in the prevalence of exotic species and species indicator values for environmental conditions were used to link the observed vegetation changes to global change factors.

Results: The plant communities, including their unmined reference sites, changed over the 31-year period toward plant communities with higher proportions of exotics, nitrophilous, warmth- and moisture-indicating species, and species of low foraging quality for deer. The changes are consistent with the novel drivers of community assembly at the site, such as the introduction of exotic species, increased nitrogen deposition, elevated temperatures, steadily increasing groundwater level post mining, and the massive comeback of red deer.

Conclusions: The global-change forcing of novel plant communities suggests that it is becoming increasingly difficult to restore historical references. It may thus be more sensible to acknowledge novelty and adopt an open-ended approach for the restoration of this and similar post-industrial areas, e.g. using rewilding principles to promote biodiverse self-sustaining ecosystems.

KEYWORDS
brown coal mining, ecological restoration, global change, novel ecosystems, open-endedness, rewilding

1 | INTRODUCTION

Human impacts on Earth are accelerating, with an increasing number of habitats being destroyed, fragmented or degraded (Venter et al., 2016; IPBES, 2019). To avert declines in biodiversity and ecosystem functioning, nature conservation managers are restoring degraded and destroyed ecosystems alongside the protection of remaining habitats. The goal of ecological restoration is to improve abiotic and biotic conditions and to provide new habitat for endangered and other target species, and its success is often measured by how well the biodiversity or ecosystem functions of a reference system are emulated (Benayas et al., 2009; Kollmann et al., 2016). Ecological restoration projects often use remnant (near-)intact patches or historical descriptions of ecosystems as references, but in some cases, the ecological or societal context makes a full restoration unlikely, for instance in heavily disturbed sites. In such cases, a partial restoration of a reference is a more feasible target (Gann et al., 2019).

Reference ecosystems have often assembled under conditions that are unlike those of today (often prior to the Industrial Revolution). Given the increasing novelty of ecological drivers, the use of reference ecosystems as restoration targets is thus increasingly questioned. In a recent contribution, Wilsey (2021) argued that multiple global change factors such as climate change, nutrient additions or altered regional species pools make it increasingly difficult to establish plant communities similar to reference ecosystems that assembled under very different conditions in the past (Choi, 2007; see also Harris et al., 2006). If novel drivers of community assembly promote the formation of plant communities that are unlike ancient reference points and force further continual change in ecosystems, managers will have to work increasingly hard and invest large amounts of precious resources to reach and maintain ancient reference points (Hobbs et al., 2006, 2009).

As an alternative to using references, restoration targets can also be more flexibly defined. For instance, restoration targets can be the provision of alternative habitat for certain species or — more forward-looking – projections of future vegetation states that are in equilibrium with future conditions (Gann et al., 2019; Conradi et al., 2020 — although such projections have considerable uncertainties; Thuiller et al., 2019). Alternatively, and open-ended approach may be adopted, where natural processes are restored that, under contemporary and future conditions, allow ecosystems to adapt on a new trajectory toward a desired ecosystem state (e.g. a biodiverse, spatio-temporal dynamic habitat mosaic) rather than prescribing a fixed vegetation target based on surroundings or history (Hughes et al., 2011, 2012).

The question of using references vs adopting an open-ended approach is pertinent in the restoration of decommissioned surface mines. In particular, spontaneous vegetation succession in decommissioned surface mines (i.e. passive restoration/rewilding) may serve as a prime example for the formation of novel ecosystems. Such mines have experienced profound and large-scale disturbances, including the removal of vegetation and soil, and often also artificial lowering of the groundwater table, which are necessary to extract resources from below-ground (Kirmer & Tischew, 2019). This results in the large-scale availability of newly exposed surfaces for succession, which promotes the establishment of non-native species (Theoharides & Dukes, 2007) that are common members of today's species pools (van Kleunen et al., 2015) and thus often immigrate from the surroundings or have been planted to stabilize soils and initiate succession (Dutta & Agrawal, 2003; Prach et al., 2015). Due to the absence of humans over vast areas, decommissioned mines often provide important habitat for wildlife that is likely to influence vegetation dynamics (Müller et al., 2017; Beale & Boyce, 2020; Lituma et al., 2021). Regarding the question of using references vs an open-ended approach, this is relevant because the presence or absence of large herbivores can strongly influence vegetation trajectories (Shiponeni & Milton, 2006; Thrippleton et al., 2018), and a desired reference state may not be reached if the animal community is (functionally) different from that of the reference state (Schweiger et al., 2019). Another interesting feature in some mines is that the successional dynamics are acting on an abiotic template in disequilibrium due to a constantly rising groundwater table after mining. This not only creates increasingly moister soil conditions in the lower parts of the mines, but can also lead to subsidence of slopes when pore space of the bedrock becomes filled with water (Højrup & Swanson, 2018; Hancock et al., 2020). In addition to these factors, the ecological dynamics are likely to be influenced by anthropogenic climate change (IPCC, 2014) and elevated rates of nutrient deposition relative to the conditions under which most reference ecosystems have assembled (Galloway et al., 2004; Bobbink et al., 2010). Decommissioned mines are thus true melting pots of novel ecological drivers, which may pose limitations to restoring and maintaining fixed references, especially if these references assembled under conditions that are unlike today's.

Ecological novelty in decommissioned mines is often discussed as a consequence of irreversible changes to the substrates for plant growth due to mining. However, after this singular disturbance event, global changes continue and further alter this novel template. Continual environmental change is expected to be forcing changes in plant communities toward increasing novelty (in terms of difference to the baseline), implying that any fixed restoration goal may soon be in disequilibrium with the abiotic and biotic factors of plant community assembly (Williams et al., 2021).

There are few empirical studies that have attempted to attribute long-term vegetation dynamics in decommissioned mines to multiple global change factors. Attributing the causes of vegetation change is critical for developing effective and global change-robust restoration strategies. For instance, if no fingerprint of global change on vegetation change is diagnosed, using historical and other fixed references as restoration targets may be well justified. By contrast, if global-change forcing of vegetation dynamics is diagnosed, an open-ended approach to restoration in which ecosystems are allowed to adapt on a new desirable trajectory rather than managed to resemble a reference state may be more practicable (Hughes et al., 2011, 2012).

In this contribution, we present a case study of long-term (31 years) spontaneous vegetation dynamics in a decommissioned brown coal mine in Denmark. Our goal is not to evaluate the success of this passive restoration in terms of the similarity to reference ecosystems or how many rare species established. Rather, our goals are to detect vegetation change and assess its links to multiple novel drivers of community assembly. We see the greatest value of this analysis in revealing if and which global change drivers act upon vegetation dynamics in the mine (these drivers should also influence actively restored sites), and use our findings to discuss possible restoration targets and strategies (i.e., fixed state vs open-ended) for this and similar post-industrial ecosystems.

2 | METHODS

2.1 | Study site

Our study site is a former brown coal mine near Søby, Denmark (56°01′45′′ N and 9°04′45′′ E) with a size of ca. 1,100 ha. The mine is surrounded by a flat agricultural landscape, small villages and coniferous plantations. Mean annual temperature is 7.5°C, the highest monthly mean occurs in August with 20.1°C (day) and the lowest in February with −3.1°C (night). Mean annual precipitation is 781 mm and distributed evenly among the months, but with a peak from September to November. The surface is up to 30 m of uncompacted Pleistocene sand perched on brown coal layers. The natural vegetation in the region would likely be oak-dominated woodland (with *Quercus petraea* and *Quercus robur*) as well as open grass- and heathland areas (Odgaard, 1994), but the landscape had been transformed into a *Calluna vulgaris* heathland maintained by sod cutting and sheep grazing centuries before industrial mining started during World War I (Odgaard, 1994). To extract the coal, the groundwater table in the area was artificially lowered and sand layers were removed. The sand was deposited within the mining site, creating a topographically diverse landscape with large hills of sand and pits where coal was extracted.

When brown coal mining ended in 1971, the groundwater table rose again — a process that is continuing. This turned some of the pits into lakes, and creates increasingly moister conditions in habitats that once were well elevated above the groundwater table. Another consequence of the rising groundwater table is the filling of pores in the loose sand, making the terrain susceptible to subsidence and the ground surface can drop several meters in such events. In addition, landslides occur frequently at lake sides (Højrup & Swanson, 2018). To reduce sand drift by wind into surrounding areas, exotic lodgepole pine (*Pinus contorta*) was planted in parts of the mining site as a reclamation measure in the 1950s and 60s and into the early 70s (just after the brown coal extraction stopped) and has since naturalized at the site. The area has also seen a massive comeback of large herbivores, in particular red deer (*Cervus elaphus*), but also fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*). Population densities at the site are estimated to be 27 red deer km^{-2}, five fallow deer km^{-2} and five roe deer km^{-2} (Dahm, 2013). As in most industrial regions, atmospheric nitrogen deposition strongly increased throughout the late 19th and the 20th century. In 1860 and 1990, i.e., 50 years before and 20 years after mining, respectively, atmospheric N deposition was estimated to be 100–250 mg N m^{-2} $year^{-1}$ and 1,000–2,000 mg N m^{-2} $year^{-1}$ respectively (Galloway et al., 2004). Nitrogen deposition rates have declined in Denmark since 1990, but were still high in 2016 with 1,300 mg m^{-2} $year^{-1}$ (Denmark-wide average), exceeding critical loads for sensitive ecosystems (Ellermann et al., 2018).

2.2 | Vegetation sampling

Sørensen (1984) conducted a first survey of the floristic composition of six habitat types in the former mining site: open sand, dry and wet meadow, heathland, broad-leaved deciduous forest, and conifer plantations (Figure 1). From each habitat type, he selected up to six sites where mining had taken place and were then recovering, and one or two reference sites that were not mined, resulting in a total of 36 sites. No reference sites were available for the open sand habitat, but, as mentioned above, our goal was not to assess convergence toward reference sites, but detection and attribution of vegetation changes. For each site, Sørensen (1984) recorded a comprehensive species list.

We resurveyed 35 sites in June and July 2015, but with a different vegetation sampling approach. Within each site, five plots of 5-m radius were randomly selected in a Geographic Information System software, and the presence of vascular plant species in these plots was noted. Trees >2 m tall were not recorded by us because we focused on spontaneous dynamics since 1984 and the majority of the trees had been planted for erosion control or forestry purposes. The minimum distance between plots was constrained by the size of the sites, with a minimum distance of 12 m, 30 m and 55 m for sites up to 2 ha, 7.5 ha and 20 ha, respectively. In larger sites, the minimum distance between plots was 90 m. If the randomly generated plot coordinates were in a lake, we selected the next closest terrestrial location. We pooled the plots from each site to obtain one species list per site, which we compared to Sørensen's species list from 1984. Because we sampled a smaller total area than Sørensen (1984), low-abundant species may have been recorded with lower probability by our survey, but we believe this does not introduce a systematic bias to our results. The nomenclature follows Frederiksen et al. (2006).

2.3 | Data analysis

We analyzed vegetation changes between the 1984 and 2015 censuses in relation to changes in abiotic factors and herbivory. To this end, we extracted for each plant species Ellenberg Indicator Values (EIVs) from Ellenberg et al. (1992) for light, temperature, nitrogen, soil reaction and soil moisture, as well as the foraging value for deer from Briemle et al. (2002). The EIVs characterize the environmental

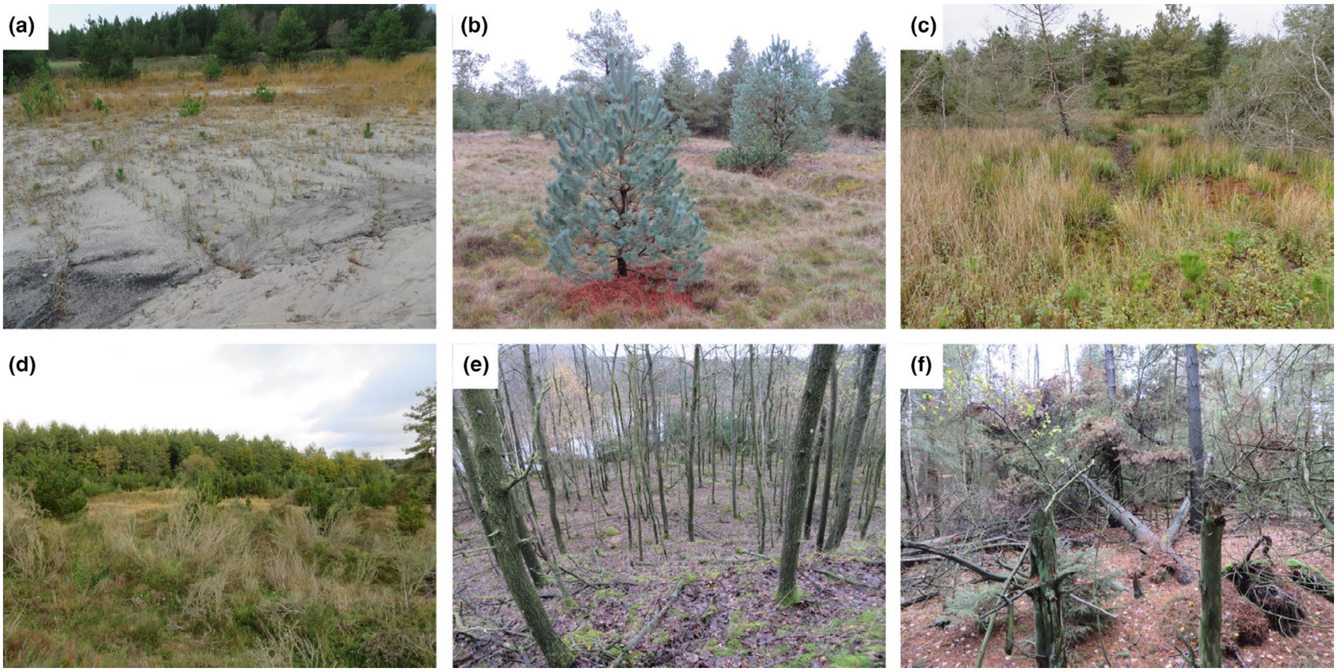

FIGURE 1 Terrestrial habitat types of a former brown coal mine near Søby, Denmark. (a) Open sand; (b) dry meadow with self-sown *Pinus sylvestris* (the only pine native to northern Europe, albeit historically exterminated from Jutland); (c) wet meadow; (d) heathland; (e) broad-leaved forest; (f) conifer forest. The conifer visible on most pictures is lodgepole pine (*Pinus contorta*), a North American tree species that has been planted for erosion control in the 1950–70s and is now very common and widely naturalizing at the site. Picture credits: Jens-Christian Svenning

conditions under which plant species occur most frequently in plant communities and have been assigned by experts. They range from 1 to 9 (except moisture, which ranges from 1 to 12), with a low value indicating that a species is occurring mostly in habitats with e.g. low light or moisture availability. Because they are good surrogates of the actual environmental conditions, EIVs are frequently used by European plant ecologists to infer spatial or temporal changes in environmental conditions (Diekmann, 2003). We used the species' EIVs to compute community mean indicator values for each site in each census year.

For each of the six habitats, we performed non-metric multidimensional scaling (NMDS) of the site species lists from 1984 and 2015 to visualize compositional differences between sites and censuses. Compositional dissimilarity was quantified using the Sørensen index. We fitted environmental vectors (linear trends) of the mean indicator values to find directions in the ordination space toward which the community mean indicator values change most rapidly and to which they have maximal correlations with the ordination configuration. The NMDS and the fitting of environmental vectors were conducted using the *vegan* package in R (Oksanen et al., 2019). The NMDS and the mean indicator values are computed from the same information, i.e., species composition. Their correlation is thus inflated and we therefore do not report the correlation coefficients or judge significance, but the environmental vectors are still useful for interpretation (Zelený & Schaffers, 2012).

To compare the community mean indicator values between 2015 and 1984 we computed an effect size, the log response ratio for each habitat as $\ln(\overline{X}_{2015}/\overline{X}_{1984})$. Therein, $\overline{X}_{2015}$ and $\overline{X}_{1984}$ are the average mean indicator values of all sites in 2015 and 1984 respectively (Hedges et al., 1999). A positive effect size indicates an increase of the community mean indicator value between the censuses. The standard deviation of the effect sizes of the individual sites was also computed. The analysis of effect sizes is not affected by inflated correlations and offers a straightforward temporal comparison, whereas the NMDS also visualizes differences between the sites of each census.

In addition, we had a closer look at the species that were found in 2015, but not in the 1984 census. Specifically, we examined their indicator values and prevalence across our sampling plots. This was done for each habitat separately.

3 | RESULTS

All sites and habitats showed marked compositional changes between 1984 and 2015 (Figure 2). This is reflected by the 1984 and 2015 species lists clustering at opposite ends of the ordination diagrams. The temporal change analysis using the response ratios (Figure 3) supported the environmental trends seen in the NMDS. The vegetation changes in all habitats appear to be driven by succession toward more closed communities, as indicated by the increasing dominance of shade-tolerant plant species. Nutrient-demanding species increased in all except the dry meadow and broad-leaved forest habitats. Warmth-demanding species increased in all but the wet meadow and broad-leaved forest habitats. Moisture-indicating

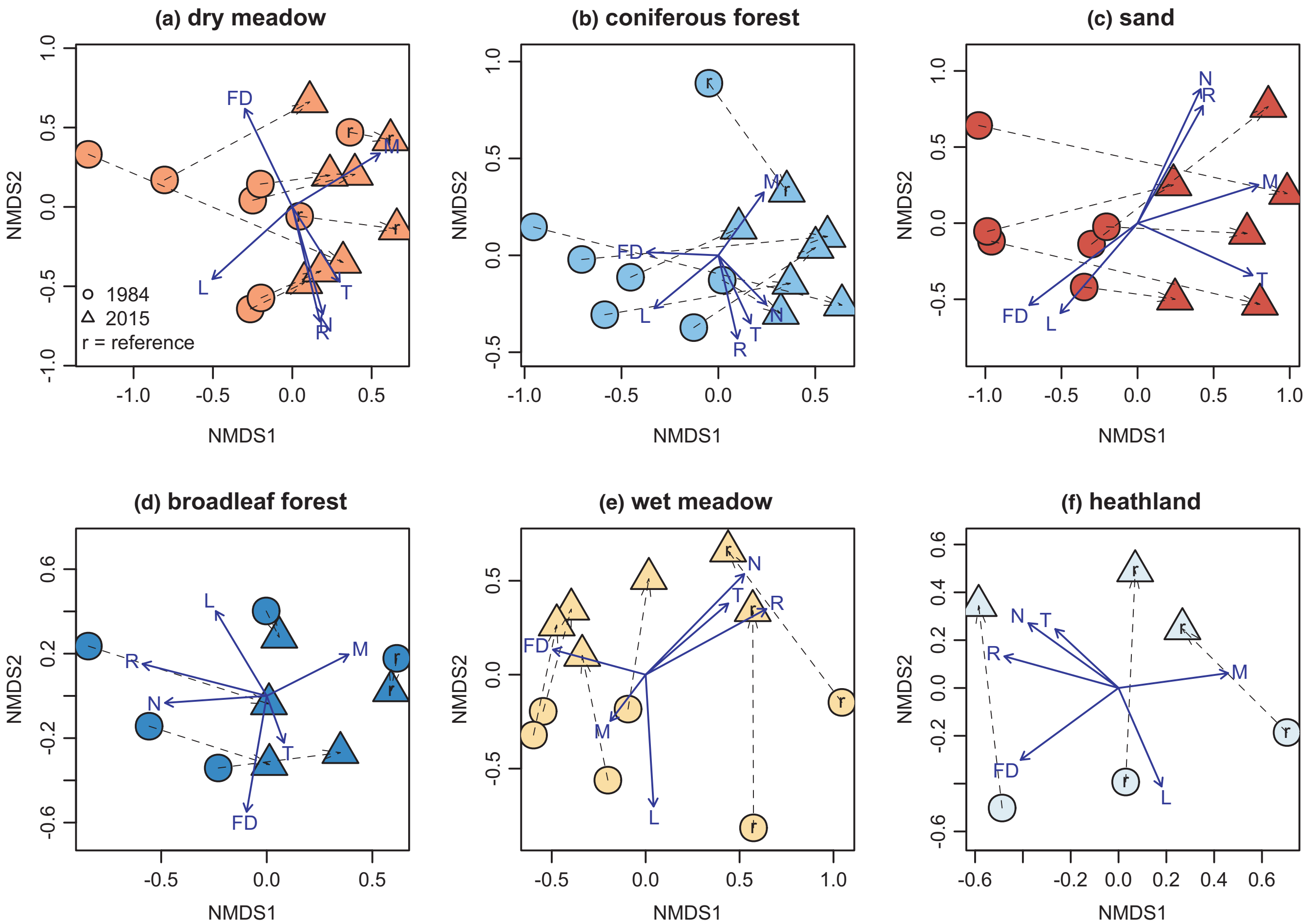

FIGURE 2 Non-metric multidimensional scaling (NMDS) of plant species lists from six habitat types of a former brown coal mine near Søby, Denmark. Symbols represent sampling sites and census year (circles, 1984; triangles, 2015). Black arrows link the 1984 and 2015 species lists of the same site. Blue arrows show linear trends of community mean indicator values: *L* = light; *M* = soil moisture; N = soil nitrogen, *R* = soil reaction; *T* = temperature, *FD* = foraging value for deer. Community mean indicator values without significant correlation with the NMDS are not shown. No reference sites were available for the sand habitat

species increased in the sand patches and in some of the dry meadows and coniferous forests, probably as a result of the continuously increasing ground water table at the mining site. In the coniferous forest and some of the sand and heathland sites, there was also a shift toward species with low foraging value for deer throughout the study period. In the other habitats, temporal shifts in species composition were not related to foraging value for deer (Figure 3), although foraging value was related to spatial variation in species composition (Figure 2). Soil reaction seems to have increased in all but the broadleaved forest habitat. Notably, there were also strong temporal dynamics in the unmined reference sites of most habitats (Figure 2).

Appendix S1 in the Supporting Information shows newcomer species per habitat, i.e., species that were found in a habitat in 2015, but not in 1984, and their prevalence in the plots of each habitat type in 2015. A consistent pattern was the widespread establishment of woody species, such as broad-leaved trees that are dominants (*Fagus sylvatica*) and subdominants (*Quercus petraea*, *Quercus robur*) of late-successional forests on acidic soils, but also nutrient-demanding trees such as *Acer pseudoplatanus*, which is not historically native to Denmark (albeit very widely naturalized since its introduction from Germany in the 18th century). Notable is the abundant establishment of two North American tree species, black cherry (*Prunus serotina*) and lodgepole pine (*Pinus contorta*), the latter widely planted in the mining site in the 1950s–70s as part of the reclamation efforts.

The newcomer species often had different habitat requirements than species that were lost from a habitat type between the two censuses (see Appendices S2–S7). For example, in most habitats, newcomer species had lower indicator values for light and higher indicator values for nitrogen than species that were lost from a habitat type.

4 | DISCUSSION

4.1 | Novel drivers of community assembly

The successional dynamics at the Søby mine area show numerous symptoms of global change (Table 1). We do not have time series of environmental data from our study site or records of the changing

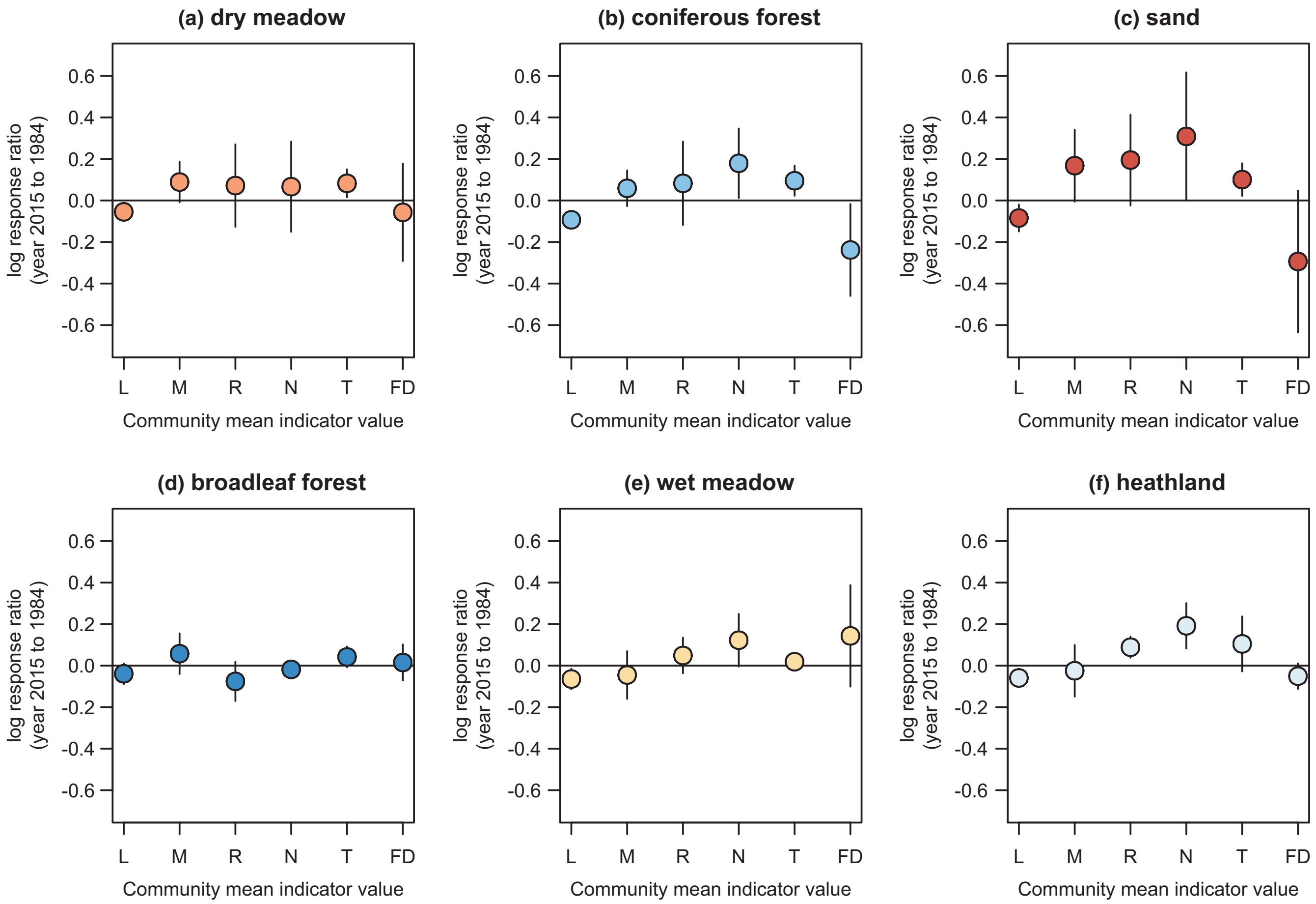

FIGURE 3 Relative difference in community mean indicator values between the 1984 and 2015 surveys of six habitat types of a former brown coal mine near Søby, Denmark. The difference is expressed as the log response ratio (dots) of the community mean indicator values in 2015 and 1984. Positive values indicate an increase in mean indicator values between 1984 and 2015. Bars indicate the standard deviation

numbers of exotic species in the surrounding area that would have enabled a more direct attribution of the observed vegetation changes to global changes. However, the observed symptoms can be interpreted as circumstantial evidence because they are consistent with findings from other studies and would not be expected in a succession that is not influenced by global changes, e.g. a succession that would have taken place in the pre-industrial era. For instance, the increase of warmth-demanding species is consistent with positive anomalies of mean annual temperatures in Denmark in most years after 1985 (relative to the 1981–2010 mean; in contrast to almost entirely negative anomalies prior to 1985) (Cappelen, 2019) and with the period 2001–2010 being the warmest decade since Danish records began (Rasmussen, 2018), and mirrors the temperature-driven compositional changes reported from other ecosystems (IPCC, 2014). The increase in thermophilous species is not driven by the exotics, which were less warmth-demanding than the native species in our data set (Appendix S8 and S9). The results are also robust to removing the most "thermophilous" exotic species, *Prunus serotina*, which is also the most frequent newcomer (see Appendixes S10 and S11). The high abundance of exotic species reflects that intended and unintended introductions of exotic plant species to the region have increased the number of potential community members, some of which have been purposefully widely planted at Søby (prior to the first survey) and are now spreading to other habitat types (e.g. *Pinus contorta*), whereas others established largely spontaneously in large numbers (e.g. *Prunus serotina*). A recent analysis of the long-term monitoring program of Danish habitats has found these two species to be among the most invasive exotic species, with both exhibiting increasing trends (Damgaard et al., 2019). Establishment in early phases of succession is an important determinant of successional trajectories (Tischew et al., 2014; Conradi & Kollmann, 2016), and immigration into abandoned open-cast mines strongly depends on the species pools in the surroundings (Kirmer et al., 2008; Prach et al., 2015). While exotic species are not necessarily more abundant in decommissioned mines than in their surroundings if succession is sporadic (Tischew et al., 2014), exotics are often planted in mine reclamation due to their ability to achieve rapid ground cover and stabilize soils. Both has happened at Søby, which may result in exotic species being permanent members of the plant communities in this decommissioned mine.

In four habitats, we observed an increasing community mean nitrogen indicator value between 1984 and 2015. This was driven by

TABLE 1 Factors of novel ecosystem emergence in post-industrial areas and their symptoms in the vegetation of Søby mine

Factor	Symptom at Søby
Natural processes	
• Succession	• Decrease of light-demanding species • Establishment of woody species
Local anthropogenic environmental modification	
• Rising groundwater table after mining	• Increase of moisture-demanding species
• Unstable geomorphology	• Not investigated, but frequent slope subsidence
• Creation of virgin soil	• Presence of initial vegetation (sand slacks)
Global change factors	
• Climate change	• Increase of warmth-demanding species
• Exotic species in species pool	• Increased prevalence of exotic species
• Nitrogen deposition	• Increase of N-demanding
• Megafauna recovery	• Selection for species with low palatability for deer
Intended post-industrial use (not analyzed)	
• Nature conservation	• Management of open habitats
• Recreation	• Hunting (influencing red deer movement)
• Forestry	• Conifer plantations[a]
• Agriculture	• Not applicable

[a]Largely abandoned since planting the unstable ground did not allow use of heavy forestry machines.

both a loss of species associated with nutrient-poor habitats and the immigration of new species with high nutrient demands (Appendixes S2-S7 sites with semi-natural ecosystems in Denmark also found species with high EIV for N to have increased and species with low EIV for N to have decreased (Timmermann et al., 2015). The loss of species associated with nutrient-poor habitats may be explained by high atmospheric N deposition rates in Denmark (Ellermann et al., 2018). The effects of atmospheric N deposition vary in type and magnitude by ecosystem (Simkin et al., 2016), but one important effect is elevated soil N availability (Bobbink et al., 1998, 2010), which may have led to the competitive exclusion of species with low N indicator value at Søby. Elevated soil N availability may have also favored the establishment of the new species with higher nutrient demands between 1984 and 2015 at Søby. Søby mine was already surrounded by an intensively used agricultural matrix before the 1984 survey (pers. obs.), so it is unlikely that the increased occurrence of N-demanding species is due to an increased propagule pressure from the matrix. It is more likely that the establishment (rather than the dispersal) of these species is no longer limited. An alternative explanation may be that soils have matured between the two censuses. However, even the unmined reference sites on mature soils exhibited higher mean nitrogen indicator values in 2015 (Appendix S12), indicating that soil maturation is not the primary driver behind the higher proportions of nutrient-demanding species.

Lastly, there has been a massive comeback of a large herbivore at Søby, the red deer (*Cervus elaphus*; Müller et al., 2017), and consumptive uptake by red deer is a significant factor of species composition in most habitats at Søby (Figure 2). Red deer has been shown to influence plant dispersal (Heinken & Raudnitschka, 2002) and the recruitment and composition of tree species (Kuijper et al., 2010), and to sometimes maintain open vegetation (Tschöpe et al., 2011; Riesch et al., 2019, 2020). Wild large herbivores such as red deer are not a "novel" component of European ecosystems, but have shaped ecosystem structure and nutrient cycling for millennia prior to their widespread extinctions in the Late Pleistocene and the sharp range contractions of many remaining species through the Holocene (Sandom et al., 2014; Crees et al., 2016; Schowanek et al., 2021). However, the baseline for the conservation of many natural ecosystems often is a Holocene-to-preindustrial state with only small populations of wild large herbivores. Previously extirpated or near-extirpated large herbivores are currently repopulating many areas across Europe (Deinet et al., 2013), with vast decommissioned mining sites serving as important stepping stones. Our finding of vegetation modification by returning red deer suggests that its influence on vegetation dynamics and species composition needs to be considered in the definition of achievable restoration goals for our study site.

Our study design poses some limitations to making causal inferences about the directionality of the observed vegetation change and its underlying drivers, however. For instance, with a comparison of just two time points, we cannot rule out the possibility that the observed compositional changes are transient. Related to this, we assumed directional environmental change, but environmental conditions may in fact have varied between the censuses. There is thus a possibility that some species may have established during times that were favorable for their establishment and are now persisting and influencing our community mean indicator values, which would then be misleading. On the other hand, the reported vegetation changes at Søby have also been observed elsewhere, e.g. the increasing prevalence of nitrophilous, thermophilous and exotic species (Feeley et al., 2020; Staude et al., 2020; e.g. Stohlgren et al., 2008), supporting the role of these global drivers of directional plant community change also in the Søby mining area.

4.2 | Restoration targets post mining

Given novel drivers of community assembly and ongoing global change, this raises the question what a sensible restoration target for Søby and similar post-industrial ecosystems should be (Figure 4). Should ecosystem managers target the full or partial restoration of a reference that has assembled in the past or target another fixed restoration goal (e.g. potential natural vegetation) that may soon be in disequilibrium with future environmental conditions? Or should managers adopt an open-ended approach that targets a desirable ecosystem trajectory? If so, can the system be put on such a trajectory using passive restoration/rewilding, or should managers actively promote ecosystem integrity and species richness (e.g., active rewilding, including species introductions)?

In Søby, historical references could be a Holocene-style near-natural woodland or mosaic of (semi-)closed and open natural ecosystems (Odgaard, 1994), a pre-industrial management-dependent *Calluna* heathland, or a mosaic of pre-industrial and Holocene ecosystems to maximize biodiversity. However, the changes to lithology and geomorphology after mining are often hard to reverse (Doley & Audet, 2013; Hancock et al., 2020) and ongoing global change has deflected ecosystems from Holocene and pre-industrial conditions at our study site (Figure 2; Appendix S1). It may thus require strong management and ecological engineering to develop and then maintain ecosystems that resemble historical references well. At Søby for instance, we detected an increased abundance of exotic and acid-tolerant species in the heathlands and broad-leaved forests after 31 years of vegetation development. These novel components suggest that emulating historical references would require continuous removal of exotic species and soil amelioration. The heathlands and broad-leaved forests at Søby also exhibited an increase in warmth-demanding species, and it is likely that future climatic warming will force further changes in the composition and abundance of species (Conradi et al., 2020). In summary, there are indications that the ecosystems at Søby are increasingly forced away from historical references, implying that it becomes increasingly hard at this site to restore any fixed target that is (implicitly or explicitly) assumed to be in equilibrium with past or present-day environmental conditions.

In this light, the site managers may adopt the view that it is not practicable to aim for the restoration of pre-industrial or Holocene reference ecosystems or other fixed restoration goals (Doley & Audet, 2013). One alternative strategy for managing the abandoned post-industrial system at Søby is passive rewilding that targets the development of self-sustaining ecosystems (Navarro & Pereira, 2012; Perino et al., 2019), where natural processes are allowed to happen with minimal human intervention and where species fitting into the system arrive over time. However, this low-intervention strategy may produce undesired outcomes at Søby mine because the intensively used surrounding landscape may not provide sufficient colonization rates of native focal species (Conradi & Kollmann, 2016), site degradation is high and because open ecosystems and overall habitat heterogeneity may disappear in later stages of succession if the developing ecosystems lack important disturbance agents (Conti & Fagarazzi, 2005; Holl & Aide, 2011; Řehounková et al., 2016; Prach et al., 2020). Indeed, the observed decrease of light-demanding species in all habitats at Søby (Figure 3) suggests that the biodiversity associated with open ecosystems may decline in the midterm in the absence of disturbances.

Promoting a mosaic of open, semi-open and closed ecosystems with a high native biodiversity at Søby may thus require active

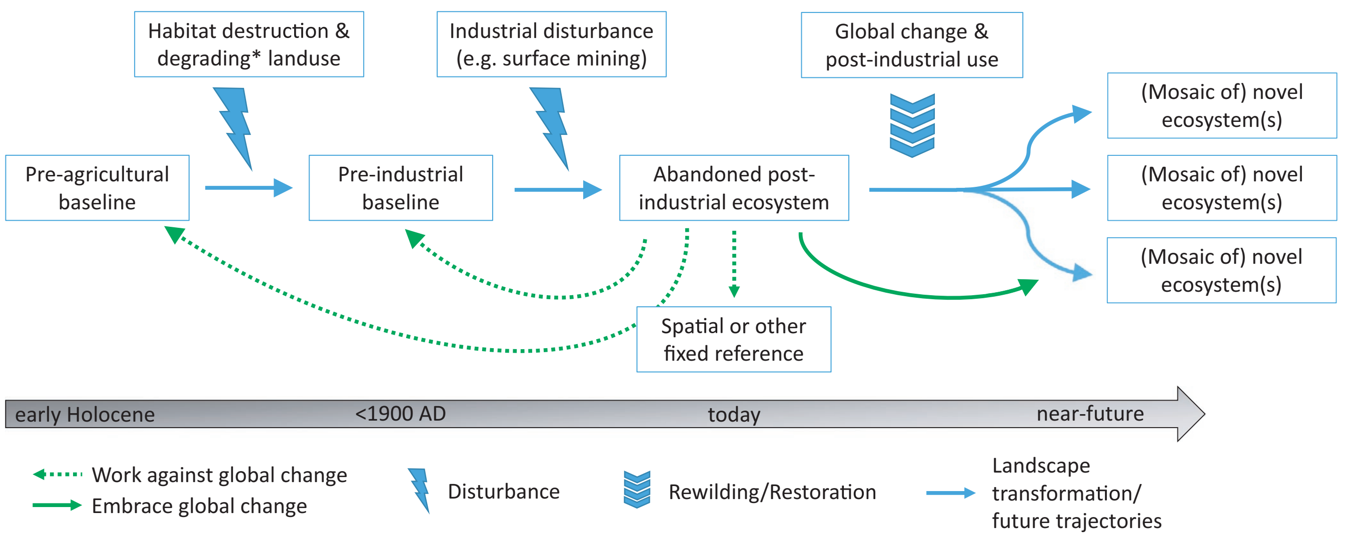

FIGURE 4 Phases of landscape transformation in industrial landscapes and potential targets for restoration. Novel starting conditions after disturbance and ongoing global change mean that restoring fixed targets becomes increasingly difficult. These include e.g. early-Holocene or pre-industrial baselines, but also fixed goals assumed to be in equilibrium with today's (but not future) conditions. Alternatively, restoration targets can be desirable ecosystem trajectories where ecosystems are allowed to change, as in open-ended approaches (Hughes et al., 2011, 2012). * Pre-industrial land use practices degraded forest ecosystems and soils, but promoted biodiverse open and semi-open ecosystems in central and northwestern Europe

restoration and rewilding measures. These could include assisted migration of native species (Hofmann et al., 2020; e.g. Kiehl et al., 2010) in combination with the reintroduction of a functionally diverse large-herbivore fauna ("trophic rewilding") as a tool for managers for promoting open and semi-open habitats and enhancing the area's overall biodiversity (Svenning et al., 2016, 2019; Schowanek et al., 2021), especially given the large size of Søby which makes maintaining open ecosystems with machines not feasible. The heterogeneous vegetation structures and high dispersal rates produced by large herbivores are also expected to increase species' resilience to climate change via the provision of diverse microclimates and by reducing dispersal limitation to track the changing climate (Svenning, 2020).

If active rewilding is chosen at Søby, it may be best implemented in an open-ended approach (Svenning et al., 2016). This is because of both the high ecosystem heterogeneity and dynamism created by large herbivores and the expected continued forcing of vegetation change. Søby mine exhibits a number of additional characteristics that makes it a suitable candidate for open-ended restoration, including its large size, the novelty of starting conditions that even with strong technical restoration interventions may be hard to reverse (Doley & Audet, 2013), dependence on processes external to the site (e.g. colonization rates) and high levels of abiotic ecosystem dynamism (Hughes et al., 2012). Adopting an open-ended approach for Søby and comparable post-industrial ecosystems will of course require the definition of acceptable ecosystem states (e.g. minimum abundances of focal species or a dynamic habitat mosaic of open, semi-open and closed ecosystems) and their monitoring (Hughes et al., 2011). In the case of Søby, the land has already passed to the state and a national authority has the power to alter its restoration strategies toward restoring processes that promote a self-sustaining biodiverse habitat mosaic through e.g. the rewilding measures suggested above. In mines where commercial operators are responsible for the restoration, the operator could be relieved from their obligations if it is evaluated after some years that these dynamic processes operate across the restoration area.

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AUTHOR CONTRIBUTIONS

JCS and MVJH conceived of and designed the research; MVJH collected the data; TC analyzed the data and led the writing; JCS and MVJH edited the manuscript.

DATA AVAILABILITY STATEMENT

The species lists and associated metadata are available in the article supporting information Appendices S12–S15.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Newcomer species and their prevalence across sampling plots in the 2015 census in six habitats of a former brown coal mine near Søby, Denmark.

Appendixes S2. Indicator values of species new to, lost from and persisting in dry meadows of a former brown coal mine near Søby, Denmark between 1984 and 2015.

Appendixes S3. Indicator values of species new to, lost from and persisting in coniferous forests of a former brown coal mine near Søby, Denmark between 1984 and 2015.

Appendixes S4. Indicator values of species new to, lost from and persisting in sand habitats of a former brown coal mine near Søby, Denmark between 1984 and 2015.

Appendixes S5. Indicator values of species new to, lost from and persisting in broadleved forests of a former brown coal mine near Søby, Denmark between 1984 and 2015.

Appendixes S6. Indicator values of species new to, lost from and persisting in wet meadows of a former brown coal mine near Søby, Denmark between 1984 and 2015.

Appendixes S7. Indicator values of species new to, lost from and persisting in heathlands of a former brown coal mine near Søby, Denmark between 1984 and 2015.

Appendix S8. Temperature indicator values of exotic and native species at Søby, Denmark.

Appendix S9. Comments on exotic status assignment.

Appendix S10. Non-metric multidimensional scaling (NMDS) of plant species lists from six habitat types of a former brown coal mine near Søby, Denmark, with *Prunus serotina* removed from the analysis.

Appendix S11. Relative difference in community mean indicator values between the 1984 and 2015 surveys of six habitat types of a former brown coal mine near Søby, Denmark, with *Prunus serotina* removed from the analysis.

Appendix S12. Community mean nitrogen indicator values of unmined reference sites in 1984 and 2015.

Appendix S13. Species lists of the habitats of a former brown coal mine near Søby, Denmark, in the 1984 and 2015 census.

Appendix S14. Descriptors of the species lists in Appendix S1.

Appendix S15. Metadata description file for Appendix S13 and S14.

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