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REVIEW PAPER

Soil disturbance as a restoration measure in dry sandy grasslands

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Abstract Severely disturbed habitats such as military training grounds, gravel pits and sand pits contribute to the species diversity of the agricultural landscape in Europe. They host a number of red-listed species not found elsewhere, illustrating that many plant species are threatened by extinction due to too little soil disturbance. Implementing a suitable disturbance regime is therefore crucial to ensure species-rich environments. We have reviewed the literature on soil disturbance as a restoration measure in dry sandy grasslands, with a special focus on xeric sand calcareous grasslands as these are severely threatened. Our objective was to elucidate the relations between diversity and disturbance regimes, and to determine how disturbance can be used to counteract acidification, to reduce nutrient availability and to create gaps in the vegetation. Our findings indicate that the current disturbance regime should be based on the historical disturbance regime, the productivity of the habitat and the propagule supply, in order to promote diversity at a landscape scale. Based on earlier studies and on the diversity/disturbance theory, we propose a conceptual model that can be used to determine the appropriate soil disturbance regime for restoration purposes. Our analysis highlights the importance of considering soil productivity, soil chemistry and dispersal limitations when choosing restoration measures and disturbance regimes for the conservation of biodiversity.

Keywords Calcium carbonate ($CaCO_3$) depletion · Conceptual model · Disturbance frequency · Plant diversity · Propagule supply · Site productivity

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Introduction

Military training areas, sand pits and gravel pits are recognised as sites with high biodiversity and large numbers of red-listed species (Gazenbeek 2005; Warren et al. 2007; Jentsch et al. 2009; Řehounková and Prach 2008; Widgren 2005; Lönnell and Ljungberg 2006), illustrating that many species are threatened by extinction due to too little soil disturbance. This is particularly true for sandy grasslands. Historically, low intensive arable farming created patches of bare soil in these grasslands (Mattiasson 1974; Tyler 2003; Poschlod et al. 2009), which were exposed to wind erosion and resulted in drifting sand (Mattiasson 1974; Poschlod et al. 2009; Persson 2000). Today, the old agricultural practices in these grasslands have been abandoned, and they have been turned into pine plantations or pastures (Mattiasson 1974; Tyler 2003). This has led to closed vegetation cover and an end to sand drift.

When the historical disturbance regime is replaced by grazing disturbance or no disturbance at all, the bare sand of dry sandy grasslands will eventually be covered by vegetation (Schnoor and Olsson 2010). There will be a natural accumulation of nutrients and organic matter (Eichberg et al. 2010), which will be further accelerated by atmospheric nitrogen deposition (Roem and Berendse 2000). This nutrient accumulation is a threat to all sandy grasslands, while calcareous sandy grasslands face the additional threat of decalcification and subsequent acidification of the topsoil (Olsson et al. 2009).

Sandy grasslands occur all over Europe on coastal and inland dunes, as well as glaciofluvial sediments in the north. Of particular interest is the threatened habitat xeric sand calcareous grassland (Natura 2000 code 6120, 2002/83/EC Habitat Directive), which is home to a large number of red-listed and endangered species of vascular plants (Mattiasson 1974; Olsson 1994; Eichberg et al. 2010), bryophytes (Tyler 2005), fungi (Hansson and Jeppson 2005; Olsson et al. 2010) and invertebrates (Ljungberg 1999). During the past century there has been a decrease in the area and species richness of these grasslands, caused mainly by changes in land use (Tyler 2003; Mattiasson 2009; Eichberg et al. 2010), and they are further threatened by acidification (Olsson et al. 2009; Mårtensson and Olsson 2010) and nutrient enrichment (Tyler 2005; Storm and Süss 2008; Mårtensson and Olsson 2010). There are 423 sites with xeric sand calcareous grasslands listed in the EUNIS database (European Environment Agency 2011), occurring in 11 European countries; Germany and Poland hold the highest number of sites. Several studies have been published on their diversity and possible restoration, in particular in Germany and Sweden (e.g. Röder and Kiehl 2006; Kiehl and Pfadenhauer 2007; Eichberg et al. 2010; Schnoor and Olsson 2010; Ödman et al. 2011). In Sweden for example, less than 50 ha of xeric sand calcareous grasslands remain (Olsson 1994; Tyler 2005). Xeric sand calcareous grasslands have a sub-continental centre of distribution (European Environment Agency 2011) and occur in summer-dry areas on sun-exposed, warm sites on calcareous, more or less humus-free, nutrient-poor and well drained sandy soils. They are also characterised by a discontinuous vegetation cover and many of the characteristic plant species depend on the open sand for regeneration (Olsson et al. 2009). These grasslands have developed on lime-rich glaciofluvial sand (Persson 2000; Olsson et al. 2009), a material which has been subjected to weathering since the end of the Weichselian glaciations ca. 15,000 years BP (before present). Most of the remaining xeric sand calcareous grasslands are found on eroded sites such as steep, wind exposed slopes (often south-facing), sand pits or military training grounds (Tyler 2003), where the underlying lime rich soil is exposed.

It is recognised that soil disturbance and removal can be a successful restoration measure for sandy types of dry grasslands (Eichberg et al. 2010; Faust et al. 2011; Jentsch et al. 2009; Ödman et al. 2011). This review focuses on anthropogenic soil disturbances such as rotovation (breaking up the soil), ploughing, sod-cutting, deep soil perturbation and top-soil removal, and their usefulness as restoration measures with respect to their effects on the soil nutrient content, the $CaCO_3$ content of the top soil and the vegetation of sandy grasslands. We describe the anthropogenic and natural mechanisms behind acidification, nutrient enrichment and the subsequent vegetation degeneration in sandy calcareous grasslands. Based on earlier studies and theories concerning the effects of disturbance on diversity, we propose a conceptual model for the determination of the soil disturbance regimes appropriate for restoration purposes.

Threats to calcareous grasslands

The intensification of farming is a serious threat to calcareous grasslands, as is afforestation and the abandonment of grasslands formally utilised in low-intensity agriculture (Mattiasson 1974; Poschlod and WallisDeVries 2002; Tyler 2003; Poschlod et al. 2005). These grasslands experience a high degree of fragmentation and isolation as a result of changes in land use (Olsson 1994; Poschlod et al. 2009). Mitchley and Xofis (2005) investigated the importance of landscape structure and management regime on the state of calcareous grasslands in the UK. They found that unfavourable habitat conditions were related to a lack of management or to a high level of agriculture in the surrounding buffer zone (200 m around the site), and led to habitat degradation and nutrient enrichment. Wind erosion has been mentioned by several authors as an important factor in maintaining xeric sand calcareous grassland (Persson 2000; Poschlod et al. 2009). A high proportion of forest in the surrounding landscape or a continuous vegetation cover would most likely lead to less wind erosion and thus less drifting sand.

Acidification and nutrient enrichment pose considerable threats to species in sandy calcareous grasslands. The Ellenberg (1991) indicator values for pH are between 7 and 8 for most of the red-listed plant species in xeric sand calcareous grasslands. Soil pH was found to be the factor most strongly correlated with plant species diversity in grassland communities on sandy soil, with a decrease in species richness with decreasing pH in the range between pH 4 and 8 (Roem and Berendse 2000). Olsson et al. (2009) found a high number of red-listed plant species in nutrient-poor sandy grasslands, but the highest numbers were found on neutral to slightly alkaline soils, and a few species seemed to be restricted to alkaline soils. A later survey of the same grasslands revealed that decreasing pH brought about a shift from calcareous grassland vegetation towards heath vegetation dominated by *Corynephorous canescens* (Mårtensson and Olsson 2010). The grass heath (Natura 2000 code 2330) is also a protected vegetation type, but in Sweden this vegetation type is more abundant and has fewer red-listed species than xeric sand calcareous grassland (Olsson et al. 2009).

Wassen et al. (2005) showed that many endangered plant species in terrestrial ecosystems are found only under conditions of P limitation, and Janssens et al. (1998) reported that the maximum diversity and the highest number of rare species in grasslands are found at very low levels of available P. A significant negative relationship has been found between total species richness of bryophytes and extractable P in Swedish xeric sand calcareous grasslands, and most of the rare or red-listed species were restricted to, or most frequent in, plots where P availability was low (Tyler 2005). A high P availability may be due to the historical land use, for example, as a result of fertilisation (Smits et al. 2008), but there is also a relation between P availability and acidification. When an adequate amount of $CaCO_3$ is present in the soil, P is fixed in calcium phosphate (Golterman 1998), but when $CaCO_3$ is depleted, the availability of P increases markedly (Tyler 1992; Kooijman and Besse 2002; Olsson et al. 2009). One would thus expect P to be the limiting nutrient for vascular plants in soils with a high pH.

However, Mårtensson et al. (2012) found, in an investigation of xeric sand calcareous grassland, that N and not P seemed to be the limiting nutrient for vascular plants at both low and high pH. In another study of xeric sand calcareous grasslands in southern Sweden, a high N concentration was found to induce a shift from calcareous grassland vegetation towards vegetation dominated by the grass *Arrhenatherum elatius* (Mårtensson and Olsson 2010). When investigating the effect of nutrient addition on a nutrient-poor, calcareous inland sand ecosystem in Germany, Storm and Süss (2008) found that the above-ground production of vascular plants was doubled following N and NP treatments, and that the cover and/or height of nearly all the species investigated increased following high doses of N. P application alone had little effect, which may indicate that the system in question was N limited. They also found that N addition resulted in accelerated succession, i.e. perennial vascular plant species increased while others, particularly annuals and bryophytes, decreased due to increased competition, litter accumulation and the reduction of gaps. It seems thus that N and not P might be the limiting nutrient in these sandy calcareous grasslands.

Disturbance–diversity theory

Restoration of calcareous sandy soils has the potential to increase biodiversity at a landscape scale, since it has been shown to favour a large number of threatened disturbance-dependent species (Olsson et al. 2009). The diversity of native species at the landscape level is assumed to be greatest when the disturbance regime matches its historical pattern (Denslow 1980). It has been suggested that restoration and management practices in calcareous grasslands should take into account the former dynamics that maintained these systems (Poschlod and WallisDeVries 2002).

The intermediate disturbance hypothesis (IDH) states that diversity will be highest at a moderate rate of disturbance (Grime 1973). The disturbance factor can be defined as the frequency of disturbance (time between disturbances), the time since the last disturbance, or the severity of disturbance, referred to together as the disturbance regime (Sousa 2001). The IDH assumes that a system is in non-equilibrium, with interspecific interactions and abiotic constraints interacting to structure ecological systems. After a disturbance event, propagules from different organisms enter the system, utilising the open spaces and resources created by the disturbance, increasing species diversity. As the time since the latest disturbance passes, or if only low-intensity or small-scale disturbances occur, competition between species becomes stronger, eventually leading to competitive exclusion of some species. At high levels of disturbance, on the other hand, only a few species in the system are able to survive. In a study on the effect of military training on the vegetation and soil of the Great Plains grasslands, Leis et al. (2005) suggested that the IDH could be useful for predicting changes in species richness and composition. In xeric sand calcareous grassland on the other hand Olsson et al. (2009) found a negative correlation between disturbance and species richness. This showed that diversity at a plot scale (1 m^2) was not promoted by further disturbance in this highly stressed habitat. On the other hand, richness of red-listed species showed no relation to disturbance level, and some of the target species were related to sites with high amounts of bare ground. This highlights the importance of variation in disturbance intensity and successional stages within a grassland ecosystem (Warren et al. 2007).

Disturbance in stressed habitats may easily be too intensive, and there are very few plant species that can cope with both high stress and disturbance (Grime 1977). For this reason it is particularly important to also consider productivity when analysing disturbance regimes in sandy grasslands. Huston (1979, 1994) formulated the model of dynamic equilibrium (DE), in which species richness is affected by disturbance as well as community productivity. According to the DE model, these two factors interact in determining species richness. At low productivity, the system can only maintain a few species able to cope with the high stress. As productivity increases, the possibility of both specialist and generalist species to survive in the system increases, thereby increasing species richness. As productivity increases further, a few strong competitors are able to dominate the system through effective use of resources and competitive exclusion, leading to a decrease in species richness. If only disturbance is considered, the relationship between disturbance and species richness is the same as in the IDH. However, combining disturbance and community productivity gives a more complex representation, where the species richness is a function of both. For example, at high productivity and low disturbance, dominant competitors will exclude many species, leading to a species-poor system. But, as disturbance increases, the dominant species disappear, resulting in more space and resources becoming available. This may then lead to higher species diversity. Analogous reasoning can be applied in the case of low productivity, but here species richness will decrease at much lower disturbance levels or frequencies. Since calcareous grasslands are strongly nutrient-limited systems, it is important to consider the DE model when determining the disturbance regime. This means that the disturbance regime appropriate for a fertile environment cannot be applied to a nutrient-poor one.

Anthropogenic soil disturbance as potential restoration measures

The two disturbance theories described above provide a theoretical basis for the use of disturbance as a restoration measure in habitats with a history of disturbance, such as calcareous grasslands. Since sandy grasslands are highly stressed habitats, the DE model may prove useful for understanding the effect of disturbance. The extent, intensity and frequency of disturbances must be carefully evaluated, in particular the ways in which they influence the diversity of different groups of threatened organisms.

The extent (depth and area), frequency (Denslow 1980) and timing (Crawley 2004; Kotanen 1996) of soil disturbances are important. The least intensive mechanical soil disturbance measures are harrowing and rotovation, during which the soil surface and vegetation cover are broken up, but not turned over. Ploughing or deep perturbation (mixing of the soil), on the other hand, creates a more intensive disturbance by turning the soil over, burying the nutrient rich top-soil. Top-soil removal and sod-cutting, during which the vegetation and the nutrient-rich top-soil are removed to a depth of 30–40 cm (de Graaf et al. 1998; Röder and Kiehl 2006; Kiehl and Pfadenhauer 2007; Eichberg et al. 2010), have a much greater potential for reducing nutrient availability and increasing the pH than rotovation and ploughing.

Effects of soil disturbance on soil chemistry and vegetation

Soil disturbance has the potential to successfully restore the chemical properties of the soil in formerly nutrient-poor grasslands by lowering the nutrient content in the top-soil, as will be seen in the following paragraph. When Dolman and Sutherland (1994) performed a perturbation experiment in a Breckland grass heath, they found that levels of total N, extractable P, K and Mg were consistently lower in ploughed or rotovated areas compared to the controls, whereas total P did not react to the treatment. In an area of degenerated xeric sand calcareous grassland, harrowing and ploughing did not affect the total P concentration, and there was even a slight increase in extractable P after harrowing (Schnoor and Olsson 2010). A deep soil disturbance experiment (mixing of soil down to 100 cm) in a nearby degenerated xeric sand calcareous grassland resulted in decreased concentrations of extractable N and P compared to the controls (Ödman et al. 2011) but top-soil removal resulted in even lower extractable N and P concentrations (Olsson and Ödman unpublished results).When studying the effects of sod-cutting on soil conditions in Dutch dry heath, de Graaf et al. (1998) found that sod-cutting down to the mineral soil layer reduced N and P. In a 9 year study of calcareous grasslands in Germany, top-soil removal down to the calcareous gravel at 40 cm depth was a very efficient method to reduce litter cover and soil nutrient content to the level of the ancient, species-rich, calcareous grasslands in a nearby natural reserve (Kiehl and Pfadenhauer 2007). Röder and Kiehl (2006) also studied the effects of top-soil removal on calcareous grasslands in Germany and they found that litter cover was lowest on the top-soil removal sites.

In addition, Dolman and Sutherland (1992, 1994), Jones et al. (2010) and Ödman et al. (2011) found that soil disturbance could increase the pH in the top-soil by bringing up $CaCO_3$ from the lower soil layers. However, top-soil removal seems to be the most successful method for increasing the $CaCO_3$ concentration of the top-soil by simply removing the decalcified soil (Olsson and Ödman unpublished results). In a study by Schnoor and Olsson (2010), neither harrowing nor ploughing reached down to the $CaCO_3$ horizon in the decalcified plots and no increase in the pH was achieved. This emphasises the importance of sufficiently deep disturbance when restoring decalcified grasslands.

The vegetation responds to soil disturbance both directly, through the creation of gaps, and indirectly, through changes in soil chemistry. Gap creation gives new individuals the opportunity to become established, but may also suppress dominant species, thereby allowing less competitive species to persist (Hobbs and Huenneke 1992). Rotovation and ploughing reduced the height of the vegetation, reduced the dominant species, increased the percentage cover of target species and bare ground, and ensured continuous soil disturbance by increasing the rabbit activity in a Breckland grass heath (Dolman and Sutherland 1992, 1994). However, when choosing between these two methods it is important to consider that ploughing buries the vegetation leaving an open soil surface, while rotovation allows in situ regeneration (Dolman and Sutherland 1992, 1994). Schnoor and Olsson (2010) investigated the restoration potentials of harrowing and ploughing in a dry sandy calcareous grassland, and found that both treatments had a positive effect on some annual target species (calcareous grassland species at which the restoration efforts were aimed), but harrowing resulted in a vegetation closer to the target. In a similar grassland, Ödman et al. (2011) reported colonisation by the target species *Koeleria glauca* in plots 4 years after deep soil disturbance (mixing of soil down to 100 cm). The most intensive of the investigated soil disturbances, top-soil removal, has been found to reduce the dominant species, and increase the percentage cover of target species and bare ground in calcareous grassland (Eichberg et al. 2010). In another study performed in degenerated xeric sand calcareous grasslands, Olsson and Ödman (unpublished results) found that top-soil removal seems to be a far more efficient method than deep soil perturbation in restoring the target vegetation.

As seen above, the abundance of bare ground increases after soil disturbance, but other effects that have also been observed, such as increased rabbit activity (Dolman and Sutherland 1994) and increased wind erosion (Jones et al. 2010). These cause additional soil disturbance and prolong the effect of the disturbance treatments.

All these kinds of disturbance have potential as restoration methods in degenerated xeric sand calcareous grassland areas, but, as discussed above, the choice should depend on the chemistry of the top-soil. Former xeric sand calcareous grasslands with a low nutrient content and a high pH could be restored using a method that opens up the sward (e.g. trampling or harrowing), whereas areas with a high nutrient content and a low pH will need a more intensive form of disturbance that removes or buries the top-soil and extends down into the $CaCO_3$-containing layer.

Scale, timing and frequency

Different species show contrasting responses to different kinds of management (Wallis-DeVries 2002), as they will profit from early, mid or late successional stages depending on their life history traits and not all species will benefit from soil disturbance. Denslow (1980) suggests that at sites where large-scale disturbances dominate, most species would become established in larger gaps, and that species richness will decline with time and succession. In contrast, in an ecosystem where small-scale disturbances are dominating, most species will become established in small gaps or undisturbed sites, and diversity will increase with time after a large disturbance (Denslow 1980). The highest species richness is said to be achieved by creating a mosaic of different successional stages (Steffan-Dewenter and Tscharntke 2002; Warren et al. 2007), which probably reflects the historical agricultural land-use where small plots were cultivated each year and then left for long periods of fallow (Mattiasson 1974; Tyler 2003).

The timing of soil disturbance is of importance regarding the effect it will have on a community (Crawley 2004; Kotanen 1996), and most species seem to be favoured by a disturbance regime that matches their germination behaviour (Crawley 2004). The timing of disturbance is especially important for species that lack a persistent seed bank (Crawley 2004), and should be considered when planning restoration in grasslands with a short-term seed bank (Bossuyt et al. 2006). This will, however, be most important when using small-scale or less intense disturbance methods that leave the seed bank intact.

In order to maintain the positive results of a disturbance, repeated disturbances are sometimes necessary. This is especially true in habitats such as xeric sand calcareous grasslands that depend on open soil with a low nutrient content and a high pH for its establishment and existence. There are already ongoing restoration projects in Europe in which repeated soil disturbances are used in various types of dry grasslands, such as sand dunes in the Netherlands (e.g. Arens et al. 2005), Brecklands (Leonard 2006) and Prees Heath in England (Putwain and Haynes 2009). In the study performed by Dolman and Sutherland (1992), the positive results of rotovation on the vegetation lasted up to at least 20 years after the treatment. This also coincides with the time at which gaps disappeared after disturbance by military training, according to an investigation by Hirst et al. (2005). Disturbances more frequent than every 10 years, on the other hand, did not give the vegetation a sufficient time for recovery, according to a study by Kotanen (2004). One of the side effects of soil disturbance is that it facilitates the invasion of non-native species (Hobbs and Huenneke 1992). However, Kotanen (2004) found that exotic species increased rapidly shortly after most types of disturbance, but that after 10 years the vegetation had recovered and was again dominated by native species. The problem of exotic invasion following disturbance could thus be avoided if the disturbance is not repeated too frequently. The above-mentioned results give an indication of the appropriate time intervals, but it is important to remember that it is probably the productivity of the site that ultimately determines the appropriate interval between disturbances (Huston 1979, 1994).

Propagule supply

The majority of typical calcareous grassland species produce transient seeds (Graham and Hutchings 1988; Matus et al. 2003; Bossuyt et al. 2006; (Eichberg et al. 2006). Therefore, in most cases the seed bank cannot be an effective source for calcareous grassland restoration (Graham and Hutchings 1988; Eichberg et al. 2010). Pärtel et al. (1998) and Bossuyt et al. (2006) found that when restoring calcareous grasslands that had been left without management for more than 15 years, one can no longer rely on the seed bank for regeneration of target species. These species must instead rely on dispersal from adjacent species-rich calcareous grasslands (Pärtel et al. 1998; Matus et al. 2003). Seed dispersal is, however, considered a limiting factor in calcareous grasslands (Graham and Hutchings 1988). For example, Verhagen et al. (2001) found that the establishment of target species in their top-soil removal sites was low, even when there was a local pool of appropriate species present in an adjacent nature reserve. This evidence of low dispersal ability indicates that the restoration of isolated calcareous grasslands would require seed addition.

Most seeds and buds occur at or near the soil surface, meaning that they are very sensitive to soil disturbances leading to the removal or burying of the upper soil layer (Kotanen 1996). Ploughing may lead to low seed abundance in the shallow soil layer (Luzuriaga et al. 2005), and during top-soil removal, a large part of the seed bank is removed together with the soil (Kiehl and Pfadenhauer 2007). However, since the seed banks of calcareous grassland species are transient, top-soil removal could have a positive effect on the chances of re-establishing the target species on degenerated grasslands, by removing the seed bank of potential competitors.

Most top-soil removal experiments have been carried out in combination with the addition of seeds, or seed-containing hay. Greater success has been achieved in plots undergoing both soil disturbance and seed addition, than in plots where only soil disturbance was applied (Kiehl and Pfadenhauer 2007; Szabó et al. 2008; Eichberg et al. 2010). Seed addition could provide a solution when there are no adjacent species-rich calcareous grasslands from which the target species could be dispersed. Seed addition will, however, only be successful if the preceding restoration measures create the appropriate conditions for the species in question. It is also important to consider groups other than vascular plants since, for example, the only bryophytes favoured by hay transfer in a study by Jeschke and Kiehl (2008) were pleurocarpous mosses. Xerophytic mosses and lichens in low-productive grasslands would instead benefit from the transfer of raked cryptogam material.

Nonetheless, seed addition should not be used lightly, and requires careful consideration. In a study of the genetic effects of using seed mixtures to restore wildflowers in Switzerland, two of the three species showed clear effects of outbreeding depression when local genotypes were crossed with plants of German origin (Keller et al. 2000). The recommendations of Hufford and Mazer (2003) are that seed collection be made from populations as geographically close to the restoration site as possible, to avoid outbreeding depression. They also recommended maximising the genetic variation among the individuals introduced to avoid severe genetic bottlenecks. Choosing the right donor population is thus of great importance for the success of reintroduction.

Seed transportation by animals has been shown to be of great importance for the spreading of sandy grassland species in Germany. As a way of connecting fragments of these grasslands, it has been suggested that animals can be used as living corridors to transport seeds between them, something which could also be used to reintroduce species after restoration (Poschlod et al. 2009).

Conceptual model

The main reason for loss of diversity in sandy grassland areas is that threatened specialists are replaced by dry grassland generalists. To illustrate the possible effects of different disturbance regimes on threatened target species and some of the underlying mechanisms, we designed a simple model of a competitive plant community. The model has a set of target species, representing the sandy grassland species at which restoration is aimed, adapted to low nutrient conditions and with poor competitive capacity. It also includes a set of non-target species, the type of species we would expect in a degraded grassland, which are assumed to be good competitors that depend on the high availability of soil nutrients for rapid growth. We assumed that favouring the biomass of threatened species will favour the biodiversity at the landscape scale. The "heterogeneous disturbance hypothesis" proposed by Warren et al. (2007) shows that even if disturbance may not increase diversity at the plot scale, it may do so at a landscape scale.

The model has a single variable representing nutrients accumulated in the system (mainly N), which increases in concentration in proportion to the total plant biomass in the community. The plant populations were modelled with Lotka–Volterra dynamics while the soil nutrients were modelled with chemostat-type dynamics. We modelled two different disturbances, soil perturbation and top-soil removal, at regular intervals. Soil perturbation means that all plant populations are reduced to a minimal level, but the soil nutrients are only slightly reduced by the mixing of the top-soil with the underlying soil. This could be achieved through ploughing or harrowing, and at a very small scale even through trampling by grazers. The effects of top-soil removal are similar, except that the soil nutrient content is reduced by a factor of 100 since the nutrient-rich top-soil is removed. Top-soil removal can be implemented as a restoration measure, but the effects of erosion and sand-drift could be similar. At a very small scale even digging by rabbits and rodents may have similar effects.

Simulations were started at the minimal level for all populations, representing a constant seed rain or seed bank. The minimal level of target species was 1/10 of that of non-target species, which reflects dispersal limitations or short-lived seeds. For model details and parameter values see Appendix. We emphasise that this model is highly simplified and is purely for illustrational purposes. Our results should therefore not be taken too literally, but instead be used as a basis for the discussion and interpretation of observed vegetation processes in the modelled habitat type.

The modelled treatments were: no disturbance (Fig. 1a), soil perturbation (Fig. 1b), top-soil removal at short intervals (Fig. 1c) and top-soil removal at long intervals (Fig. 1d). In the control case (no disturbance), there was an accumulation of nutrients followed by an increase in biomass; target species eventually being replaced by non-target species. The perturbation treatment created open soil for establishment, but without substantially lowering the nutrient content. This slowed down the succession from target to non-target

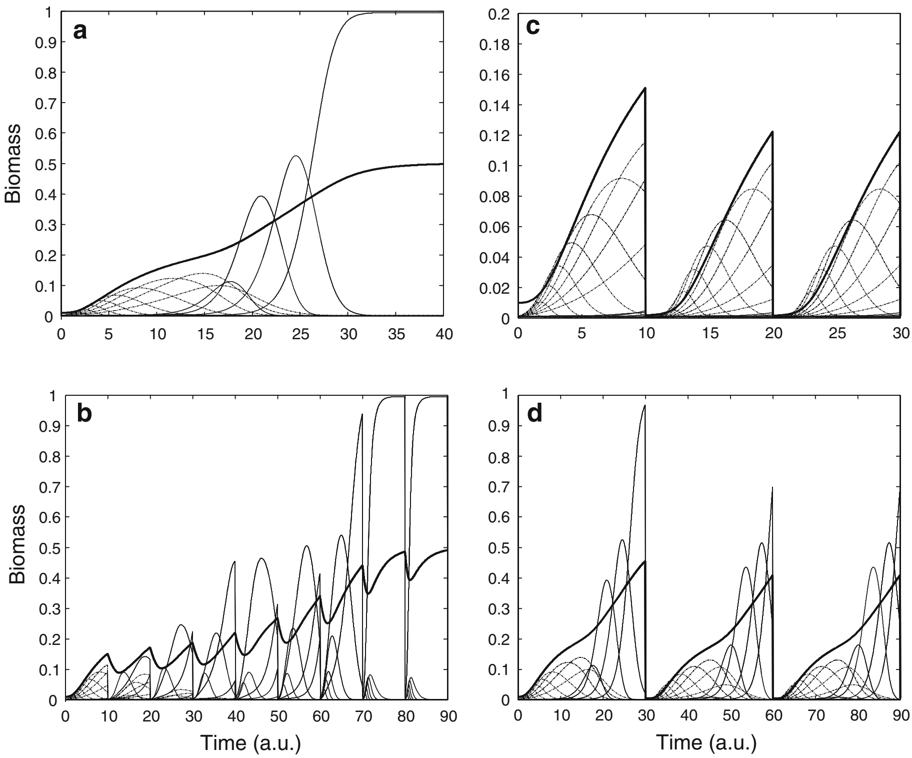

Fig. 1 Illustration of vegetation succession after different kinds of disturbance regimes modelled using Lotka–Volterra dynamics for the plant populations and chemostat-type dynamics for the soil nutrients. The modelled treatments were: **a** no disturbance, **b** soil perturbation, **c** topsoil removal at high frequency (interval = 10) and **d** top-soil removal at low frequency (interval = 30). The time scale is arbitrary and should only be used to compare the different treatments. The *dotted lines* illustrate the biomass of target species, the *solid lines* show the biomass of non-target species, and the *bold lines* denote the nutrient accumulation in the soil

species, but did not completely prevent it. Top-soil removal, which both created open soil and lowered the nutrient content, halted the succession, but the short-interval treatment kept the vegetation at an early successional stage with target species dominating, whereas the long-interval allowed some non-target species to become established and eventually outcompete the target species. Another important feature which singled out the short-interval treatment as the most successful was the total biomass. While the modelled biomass after no disturbance or soil perturbation amounted to 1 and the biomass after top-soil removal at long intervals stabilized at a level above 0.6, the biomass after the short-interval treatment stayed below 0.4. As mentioned earlier, discontinuous vegetation cover, and thereby low biomass, is a prerequisite for the regeneration of many of the target species.

The appropriate interval and the effect of the disturbance are highly dependent on the productivity of the area being restored. The DE model (Huston 1979, 1994) suggests that the intensity of the disturbance should be lower on low productivity sites. It has been reported that the frequency of disturbance should be about 20 years at sites with low productivity (Dolman and Sutherland 1992; Kotanen 2004; Hirst et al. 2005). This is in accordance with the observation that target vegetation may develop by spontaneous succession in sand pits within 25 years (Řehounková and Prach 2008). Sites with higher productivity could be managed with shorter disturbance cycles (Grime 1973). Habitats with low productivity can be those where plants are stressed by arid or nutrient deficient conditions, whereas habitats with naturally higher productivity are those with higher water and nutrient availability (Grime 1977). The highest productivity is seen at sites that have experienced anthropogenic fertilisation and the only applicable restoration measure in such areas may be top-soil removal or sod-cutting. Large scale top-soil removal can be applied on fertilised as well as acidified sites, but should be applied on smaller scales at low-productive sites to increase the gaps available for the establishment of new individual plants. In areas low in nutrients, sod-cutting may be sufficient to create sustainable gaps, while more drastic soil perturbation may be required to create small-scale variation in both topography and disturbance.

In addition to reducing nutrient availability, top-soil removal may also prevent decalcification by exposing the lime rich soil. With substantial amounts of lime in the top-soil, decalcification may be prevented for very long time-periods (Olsson et al. 2009). Top-soil removal could also induce erosion that prolongs the effect of the disturbance by continuous removal of the top-soil, which could possibly also influence surrounding vegetation through the spread of nutrient poor and lime rich sand.

Implications for management

The first step when planning the restoration and management of calcareous grasslands should be a thorough investigation of the site. Knowledge about the historical management regime and the soil properties, such as soil type, nutrient content and $CaCO_3$ content, is essential when choosing a suitable soil disturbance method, as well as the appropriate scale and interval for disturbance. Time-series and dated disturbance events, such as the one described by Faust et al. (2011), can be used to decide time intervals in the model. The restoration treatment should be repeated often enough to counteract gap reduction, $CaCO_3$ depletion and nutrient enrichment, but sufficient time must be given between disturbances to allow the target vegetation to recover. When trying to restore acidified soil to a neutral to alkaline pH, the depletion depth will determine how deep the disturbance must be to bring $CaCO_3$ up to the surface. The optimal size of the disturbance is determined by the historical disturbance regime, as the vegetation is accustomed to either small- or large-scale disturbances. Species richness benefits from a mosaic of successional stages, and it is therefore recommended that the area treated at any one time should not be too large. By disturbing different sections of a grassland at different times, it is possible to preserve all successional stages. As shown by the model, soil perturbation can be used to prolong the existence of target species in a habitat. Therefore a mixture of severe and moderate soil disturbances can be used, with longer time periods between the severe types of disturbance.

Since most calcareous grassland species have been shown to lack a persistent seed bank, areas that have been abandoned and degraded for more than 10–15 years will probably have to rely solely on an external seed source. When this is the case, at least one suitable donor site must be identified in the close vicinity of the restoration site, since calcareous grassland species are generally also poor dispersers. In cases were both seed bank and donor vegetation are lacking, seed addition will be necessary for successful restoration, but this should be done with caution. Only when all the characteristics of the grassland in question are known, can the optimal restoration measures and management regime be decided.

Something which was not discussed in this article but which is of great importance for the long term outcome of restoration is the site area or level of habitat fragmentation. This must be considered to make sure that the vegetation of the restored site will not suffer from isolation and inbreeding depression. Due to the risk of insufficient dispersal of threatened species between existing populations, as mentioned above, it is recommended that restoration measures should be undertaken close to existing target habitats. To increase the connectivity between existing areas of xeric sand calcareous grassland the use of animals as moving corridors could be considered.

Even if suitable abiotic conditions can be achieved through the suggested restoration measures, other problems such as reduced genetic diversity, loss of mutualistic biotic interactions and introduced invasive species may remain. This must be taken into account in the planning of restoration actions and there is a need for further research on these factors in fragmented and diminishing habitats.

Appendix

Detailed model description

The model has 16 competing plant species governed by Lotka–Volterra dynamics (see below). The first 10 species ($i = 1\ldots10$) are considered 'target' species, adapted to poor nutrient conditions but dispersal limited, and species 11–16 are non-target, dependent on higher levels of soil nutrients but with a more rapid colonisation at appropriate soil conditions. In addition to plant population dynamics, soil nutrients are modelled as a single dynamic variable U, which adds up to a system of 17 differential equations:

$$\begin{cases} \frac{dN_{\mathrm{i}}(t)}{dt} = r_{\mathrm{i}}(t)\left(1 - \frac{N_{\mathrm{tot}}(t)}{K_{\mathrm{i}}}\right), \ i = 1, \ldots, 16 \\ \frac{dU}{dt} = cN_{\mathrm{tot}}(t) - \mu_{\mathrm{U}}U(t) \end{cases}, \tag{1}$$

where

$$N_{\mathrm{tot}}(t) = \sum_{i=1}^{16} N_{\mathrm{i}}(t) \tag{2}$$

$N_{\mathrm{i}}(t)$ is abundance (biomass) of population i at time t. r_{i} and K_{i} are species specific intrinsic growth rates and carrying capacities, respectively, chosen such that there is a trade-off between fast growth (a high r) and a high carrying capacity (K) (see below). The soil nutrient U increases at a rate c per unit total plant biomass (N_{tot}) and leaks out of the system at a rate μ_{U} per mass unit.

All target species ($i = 1..10$) have a constant, but unique, intrinsic growth rates r_{i}, whereas the r-values of non-target species increase with the amount of available soil nutrients according to

$$r_i(t) = \begin{cases} r_{0,\mathrm{i}}, & i = 1..10 \\ r_{0,\mathrm{i}} + kU(t), & i = 11..16 \end{cases} \tag{3}$$

All biomasses are kept at or above a minimal level corresponding to a constant rain of seeds. The minimal level is set to 10^{-4} for target species and 10^{-3} for non-target species, in accordance with the assumption that target species are more dispersal-limited than non-target species.

A ‘ploughing’ disturbance is implemented such that at regular intervals all biomasses are set to their minimal levels, but the soil nutrient content (U) is left intact. ‘Top soil removal’ means the same thing except the soil nutrient content is divided by a factor 100.

Numerical solutions to the differential equations were found by discretizing time (Euler method, $\Delta t = 0.01$).

Parameter values, target species ($i = 1..10$):

$K_{1-10} = 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50$
$r_{0,\ i} = 3\text{–}4.5\ K_{\mathrm{i}},\ i = 1..10$

Parameter values, non-target species ($i = 11..16$):

$K_{11-16} = 0.25, 0.40, 0.55, 0.70, 0.85, 1$
$r_{0,\ i} = 1\text{–}4.5\ K_{\mathrm{i}},\ i = 11..16$
$k = 20$

Parameter values, soil nutrient U:

$c = 0.15$
$\mu_{\mathrm{U}} = 0.3$

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