



# Soils and Landscape Restoration

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# Converting agricultural lands into heathlands: the relevance of soil processes

# 13

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## 13.1 Introduction

Heathlands in the Atlantic coastal region of Europe are in decline, and efforts are underway to restore them by recreating low fertility conditions. To speed up such impoverishment processes, nature managers have used alternative, rather drastic, techniques and stripped away the entire topsoil. Not only nutrients but also above- and belowground vegetation and the complete soil community are removed with such a technique, and recovery has to start from scratch.

Until the end of the 19th century, agricultural productivity in Europe was limited by natural soil fertility and locally produced fertilizers, mainly manure from animal husbandry. In regions with infertile soils, this led to a so-called infield–outfield system where organic material and animal dung were collected from large grazing areas and used to fertilize much smaller arable fields close to the settlements. In Western Europe, outfields were normally covered with heathlands, a vegetation type unique to the Atlantic coastal region that can survive on extremely impoverished soils and consists mainly of small dwarf shrubs from the *Ericaceae* (Loidi et al., 2010).

This practice changed radically at the beginning of the 20th century with the onset and massive expansion of industrial production of artificial fertilizers. Agricultural yields increased enormously because outfields could now be used for crop production, and existing farmland could produce much more than before. With the famines of the 19th century still in mind, politicians enthusiastically supported agricultural intensification programs, first at the national level and later via the Common Agricultural Policy at the European level.

From an agricultural point of view the intensification programs have been highly successful, but the ecological drawback is a large decline in surface area and quality of outfields. Heathlands are now classified as “vulnerable” at a European scale (Janssen et al., 2016) and have declined in surface between 30% and 50% during the last half century. Regionally, the decline can be even much larger (Pywell et al., 1994; Bakker et al., 2012). To counteract these unwanted developments, programs have been set up to increase heathland surface through restoration.

Starting from fertilized grasslands, a first and essential step is to lower site fertility, often through mowing and removal of the cuttings afterward but without adding fertilizer (Bakker, 1989). Unfortunately, it may take a very long time before such management results in nutrient-poor, yet species-rich grasslands (Bakker and Olf, 1995; Pywell et al., 2011; Redhead et al., 2014), and a further development to heathlands has yet to be observed. A major reason may be that nutrient availability is still too high. Nutrient balance calculations suggest that in regions with high external nutrient input, for example, via atmospheric N deposition, net nutrient export via mowing is very low (Jones et al., 2017) (Fig. 13.1).

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## 13.2 Soil chemistry

Soil N pools are generally larger than P pools (Verhagen, 2007), but accumulation of P may nevertheless be a serious bottleneck for the restoration of oligotrophic ecosystems. Decades of intensive agriculture may result in P saturation as deep as 20–100 cm of the profile (Smolders et al., 2008). Under dry conditions, P is highly immobile and P losses consist mainly of removal by mowing while accumulated N can be lost either by denitrification, leaching of nitrate or mowing. Moreover, plants contain on average 10–20 times more N than P (Larcher, 2001; Güsewell, 2004), and mowing therefore results in much larger removal of N than of P. Nevertheless, when the P pool is small, mowing may be an effective technique to remove so much P from the soil that it becomes a limiting element for vegetation productivity (Härdtle et al., 2009). Unfortunately, this is an exception to the general rule. Normally soil P pools in formerly fertilized fields are very large, and the fraction of P that is removed via mowing is negligible. Consequently, the productivity there is limited by N (Verhagen, 2007). The sites are highly susceptible to enhanced N availability through atmospheric deposition (Bobbink et al., 2010) and require constant on-site management to keep productivity low (Jones et al., 2017). Moreover, high levels of P may inhibit mycorrhizal association establishment.

Topsoil removal on former agricultural fields is a drastic measure that removes most of the N and P (Verhagen, 2007; Klimkowska et al., 2007), but recovery of the typical heathland vegetation is in many cases poor. It has been hypothesized that suboptimal soil conditions are a major cause of this limited



**FIGURE 13.1**

A yearly mown grassland that has not been fertilized for over 10 years that is still rather productive and poor in species.

success, more in particular a soil pH that lies outside the optimal range for heathland (Pywell et al., 1994) (Fig. 13.2).

Decomposition of organic material and mineralization of N and P are enhanced at higher pH, and the resulting nutrient availability may become so high that heathland species are outcompeted by fast(er) growing grasses and ruderals (Pywell et al., 1994; Pywell et al., 2011). The application of elemental S ( $S^0$ ) is sometimes proposed as a suitable measure after topsoil removal to lower soil pH toward the values appropriate for heathlands. Until now, the effects of  $S^0$  are little studied; only short-term effects on soil pH and *Calluna vulgaris* establishment have been shown in the United Kingdom (Owen et al., 1999; Owen and Marrs, 2000; Lawson et al., 2004; Tibbett and Diaz, 2005).

These relationships were further investigated in a heathland restoration study in the Northern Netherlands (see case study for more details) where topsoil was removed in 2011 on c. 160 ha former agricultural land. We analyzed the effects of soil pH manipulation and inoculation with biota via herbage or crumbled sods, in all possible combinations for 7 years (Weijters et al., 2015; van der Bij et al., 2017). The addition of  $S^0$  lowered soil pH and base cation concentrations and increased dissolved Al. We found a clear shift in soil abiotic conditions from those typical of a common grassland to conditions that lie within the range of



**FIGURE 13.2**

The situation 1 year after topsoil removal.

well-developed heathlands (De Graaf et al., 2009). Concentrations of available P, ammonium, and nitrate remained very low during the whole period, showing an effective reduction of site fertility after topsoil removal. Moreover, the addition of biota did not have any effect on the soil chemical parameters that we measured, implying that chemical alterations were not caused by the addition of herbage or sods. In conclusion, topsoil removal in combination with manipulation of the pH was highly successful in shifting soil abiotic conditions toward values suitable for heathlands.

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### 13.3 Vegetation

Depleting soil nutrients by regular mowing is used widely by nature managers. Over time, the vegetation becomes less productive and more open; competition for light decreases (Kotowski and van Diggelen, 2004; Hautier et al., 2009) and less-competitive species establish. However, even when the productivity lies within the target range, the vegetation may still remain highly undersaturated in species (Klimkowska et al., 2007). Apart from abiotic constraints, biotic bottlenecks such as high resistance of an existing canopy against invasion (Tilman, 1997;

Chytrý et al., 2008) in combination with a low seed pressure of uncommon species (Bekker et al., 1997; Ozinga et al., 2009) are major reasons for low diversity.

Topsoil removal changes these conditions, making them suitable for the establishment of species from low-productive environments. Competition with existing vegetation stays low for years, and establishment gaps are widely available. However, the problem of low seed pressure of less-common species remains, and the emerging vegetation mainly reflects the species palette of the neighborhood (Verhagen et al., 2001). A well-established technique to speed up establishment is the transfer of fresh herbage with ripe seeds of well-developed communities to an abiotically restored area (Kiehl et al., 2010).

In heathland restoration, there is only limited experience with soil transfer (Pywell et al., 2011; van der Bij et al., 2018), but the available evidence suggests additional beneficial effects, at least in the first years after application. Heathland species establish fast and reach a higher cover than in treatments without soil addition. To what degree this is to be attributed to the transfer of seeds with the added soil is unknown but seems only likely for uncommon species. Differences in establishment of dominant heathland species between herbage-only and soil addition treatments therefore suggest additional beneficial effects of the soil community (Fig. 13.3).



**FIGURE 13.3**

The situation three years after topsoil removal and addition of soil from a well-developed heathland.

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### 13.4 Soil microbial communities

Determining characteristics of the soil microbial community to inform progress toward a desired target condition has been well established (Harris, 2003). However, recognition of the role of the microbial community in facilitating or even determining the composition of the vegetation assembly is a more recent development (Harris, 2009; Wubs et al., 2016). Certainly, the composition of the microbial community can be changed by reducing the freely available nutrient pool to levels found in reference systems, increasing the size, and changing the composition, of the soil organic component but this is a very long-term process.

Reducing biomass through the removal of the top layers of topsoil in order to effect rapid change has shown to be effective—potentially leading to a change from the bacterial to the fungal channel of nutrient cycling. This is important as it has been suggested that bacterially dominated systems enhance rates of nutrient cycling, favoring ruderal species—particularly grasses—whereas fungal energy channels promote slow and conservative nutrient cycling (Wardle, 2002). Topsoil removal may shift the system to a different state and enable the start of heathland community development (Harris, 2013).

Van der Bij et al. (2017, 2018) have demonstrated that removal of topsoil reduces the size of the microbial biomass significantly, as might be expected. But this also shifts the F:B (fungal to bacterial) ratio from a bacterially to a fungally dominated system, which coincides with switching to a heather-dominated vegetation. Phospholipid fatty acid profiling also demonstrated that adding a soil inoculum of the target system rapidly establishes a microbial community similar to that of the target system but with a greatly reduced biomass (Van der Bij et al., 2017, 2018).

Conversion of former agricultural land into heathland not only requires changing from a bacteria-dominated microbial community into one more dominated by fungi but also changing the dominant mycorrhizal type. While most agricultural crops and temperate meadows form arbuscular mycorrhizae (AM), heather and most other *Ericaceae* species form ericoid mycorrhizae (ErM). These are formed with a select group of fungi, predominantly from the phylum Ascomycota (Read et al., 2004), and are composed of strongly inflated epidermal cells colonized by ErM fungi.

Heathland plants and their mycorrhizal fungi are a very effective symbiosis. Within higher plants, *Ericaceae* have among the lowest nutrient content and decomposition rates (Cornelissen et al., 2001). Therefore in the typically infertile systems where they occur, most of the nutrients required for plant growth have to come from slowly cycling biomass. Mycorrhizal fungi help ericaceous plants take up organic N from their litter (Kerley and Read, 1997), which is largely inaccessible to other plants due to its high recalcitrance (Jalal et al., 1982). The same is true for uptake of N from fungal necromass (Kerley and Read, 1997), both of which lead to tight recycling of scarce nutrients. In contrast, the AM fungal symbionts of most grasses and forbs are especially

effective at increasing uptake of inorganic P and N but only have low capacity to release N from organic matter (Smith and Read, 2008), which means AM plants have a low competitive capacity when the recalcitrant heather litter is the main source of nutrients. Furthermore, the relatively fast turnover of AM mycelia compared with nutrient-conservative ErM mycelia (Olsson and Johnson, 2005; Verbruggen et al., 2017) leads to a high requirement of N in the former that is a poor match for systems of low fertility.

Indeed, ErM are associated with sites of lower productivity than AM systems, as well as a lower pH (Bueno et al., 2017). However, while there certainly is a favorable range of abiotic conditions that differ for these mycorrhizal types, these ranges have a high overlap (Soudzilovskaia et al., 2015; Bueno et al., 2017). Likewise, there is a large overlap of climatic and abiotic properties (nutrients, pH), under which both heather and grassland can come to dominate (Ransijn et al., 2015). The alignment of plant traits (nutrient content, growth rates), their mycorrhizal specificity, and the traits of these mycorrhizal fungi may therefore lead to a positive feedback with the power to stabilize one vegetation type when abundant.

Mono-dominant heathlands and grasslands are thought to represent two “alternative stable states” (Berendse and Scheffer, 2009). For this reason, restoration of an ecosystem of a different mycorrhizal type than the current undesired one is not just a matter of introducing appropriate fungi. In contrast, through the positive feedbacks described earlier, these fungi can be a pertinent source of soil legacy effects (Dickie et al., 2017) that may hamper the establishment of the desired vegetation. When considering restoration of heather vegetation, a situation must be put in place where the plant–mycorrhizal complex engages in a positive feedback—so for ErM plants low inorganic nutrient availability but potentially also a low abundance of AM hosts and AM propagules in soil.

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## 13.5 Soil faunal communities

The composition of soil fauna communities of productive grasslands is entirely different from those of oligotrophic heathlands, both in size and quality (Frouz et al., 2009). On the one hand, macrofauna communities of heathlands are small and to a large extent dominated by predators and omnivores such as centipedes, spiders, and carabid beetles. Grassland macrofaunal communities, on the other hand, are large and consist mainly of earthworms and macrosaprophagous groups involved in litter fragmentation, such as some families of Diptera and millipedes. In other words, grassland communities are dominated by species that process the litter and contribute to bioturbation (i.e., mixing of organic matter into the mineral soil). Decomposition studies have emphasized the important role of macrofauna in grasslands and shown that raw organic matter is converted much faster into humus when it can be accessed by macrofauna (Frouz et al., 2009). Also, the

composition of earthworm communities differs. Anecic and endogeic species make burrows in the soil and dominate grassland communities while litter-dwelling epigeic species dominate in heathland (Frouz et al., 2009).

Heathlands on the contrary harbor much larger populations of soil mesofauna of especially oribatid mites. These do not live in the soil but instead on top of it in the fermentation (Oe) layer that consists of partly decomposed plant material (Frouz et al., 2009). The mesofauna not only use this layer as habitat but also actively contribute to its formation by shredding raw organic remains into small, partly decomposed litter fragments (Frouz et al., 2009).

The distribution of organic matter in the soil profiles differs between habitats and is related both to the composition of the soil fauna and that of the vegetation. A high level of bioturbation is associated with high nutrient availability and fast-growing plants that produce large quantities of easily decomposable litter (Frouz, 2018). The microbial community and indeed the whole soil food web shift in the direction of a bacteria-driven system with fast decomposition and nutrient release. Bioturbation promotes the formation of an A horizon rich in organic matter and with high sorption capacity. This implies that an important part of the released nutrients can be stored in an easy accessible form in the soil, thus providing good conditions for fast-growing competitive plant species that produce highly decomposable organic matter. Conversely, accumulation of litter on the surface is characteristic of a food web dominated by fungi and characterized by low nutrient turnover rates. Stress-tolerant plant species with a conservative growth strategy dominate and produce recalcitrant organic matter (Frouz, 2018).

Converting productive agricultural grasslands into oligotrophic heathlands requires replacing macrofauna living in an organic layer in the soil with mesofauna living in an organic layer on top of the soil. Simply substituting the dominant grass vegetation by heather and/or other oligotrophic species, for example, by sowing with a high seed density, does not automatically solve this problem. Saprophagous macrofauna live in the A horizon or under the litter on the soil surface, and these habitats remain there even if we replace the grassland vegetation. Conversely, a typical heathland mesofauna community is adapted to the litter layer on the surface, and this needs a certain time to develop. All in all, this implies that soil community processes may significantly retard ecosystem changes (Foster et al., 2003; Kardol et al., 2007; Brudvig et al., 2013; Hahn and Orrock, 2015).

Previous research showed that complete topsoil removal is highly effective in removing the saprophagous macrofauna community (Frouz et al., 2009; van der Bij et al., 2018), but the formation of a litter layer on the soil surface may take a long time (Frouz et al., 2009). The large-scale field experiment in the Dwingelderveld (see case study) showed a significantly increased recovery rate of the mesofaunal community after inoculation topsoil removal sites with fresh herbage, or even better sods, from undisturbed heathlands. The increased recovery of oribatid mites is especially relevant because this group is typically quite slow to colonize (Frouz et al., 2009), due to their low reproduction rate and poor dispersal capacity. Sod transfer is considered particularly effective because it reduces several constraints at the same time: sods transfer both soil fauna and part of the habitat that is needed by this fauna, thus facilitating its establishment (van der Bij et al., 2018).

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## 13.6 Effects of alternative restoration strategies

Decades of mowing of existing grasslands have resulted in less-productive and more open vegetation but unfortunately so far have not led to heathland development. Often this is attributed to depleted seed banks and limited dispersal rates (Kardol et al., 2008; Ozinga et al., 2009), but more inclusive views see a more active role for the soil community. In this view, microbial communities can keep the system locked in a previous stage by enhancing the performance of adapted species (Grime et al., 1987; van der Heijden, 2004; Dudenhoeffer et al., 2018). Since grasslands are dominated by bacteria and AM and heathlands by fungi and ErM, this suggests that, as long as the soil community has not been replaced, the performance of grasses is likely to be better than that of heather.

Such shift in soil community composition is not self-evident in existing vegetation. The close match between mycorrhizal type and vegetation composition implies that heather and ErM can only establish when they arrive at the same time in large enough numbers to be able to outcompete both the existing vegetation and the current AM. In addition, the legacy of the organic matter distribution in the soil profile can be a barrier (Schmidt et al., 2011). As long as organic matter stays well mixed with the upper soil layers and the soil fauna consists of bioturbators, decomposition rates will remain high (Frouz, 2018), and site fertility might still be high enough with a decreased nutrient pool size to enable competitive grassland species to outperform heathland vegetation.

Topsoil removal eliminates several of the constraints mentioned but adds others. Potentially superior competitors are no longer present, and soil legacies in the form of accessible and easily degradable organic matter have disappeared. At the same time the soil seed bank and the soil food web are gone, and species have to reach the site via dispersal. Dispersal probability decreases with distance (Bullock et al., 2017), and both the vegetation and the soil community are therefore mainly a reflection of the ecosystems in the neighborhood. On the one hand, mycorrhizal fungi are generally less dispersal limited than plants (Peay et al., 2010; Honnay et al., 2017), and this also is likely true for other microorganisms. Plant species on the other hand have more problems with dispersal, and the species composition of restored sites often consists predominantly of good dispersers (Kirmer et al., 2008). The same is true for certain soil faunal groups such as oribatid mites (Frouz et al., 2009). The soil community suffers from the additional constraint that most organic matter has been removed which is exactly the substrate they live on. Consequently, topsoil removal sites close to or surrounded by undisturbed heathlands can develop slowly in the desired direction but with a limited number of species (Verhagen et al., 2001; Frouz et al., 2009) and a lower microbial biomass (van der Bij et al., 2017). Isolated topsoil removal sites often develop in a totally different direction (van der Bij et al., 2017).

Inoculation of topsoil removal sites with sods solves many of the problems mentioned. Both the vegetation and the soil community are added, together with

some organic matter of the right composition, and more or less in the right place in the profile, namely, on the soil surface. Heathland development goes much faster with inoculation than in noninoculated topsoil removal sites, but there is still ongoing community change (see case study), suggesting that developments have not finished yet. Moreover, many characteristics of the soil community still differ considerably from those in undisturbed heathlands. Nevertheless, sites treated this way are closest to undisturbed reference heathlands.

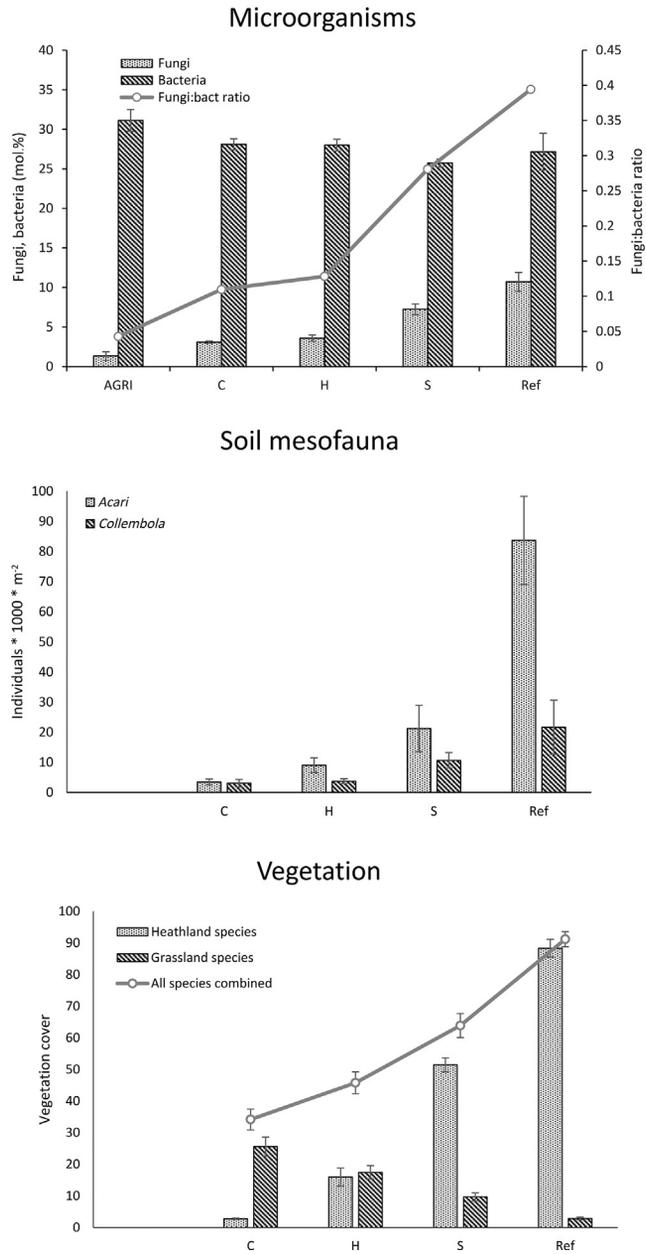
Supplying topsoil removal sites with only herbage brings the system into an undefined and, potentially static, intermediate state. Together with the herbage, some of the belowground community is introduced in small numbers in the restoration site, but the site remains open to dispersal from the surroundings. Organic matter availability is limited, and first needs to be built up by the establishing vegetation. The outcome of such a process is highly unpredictable, but a mismatch between above- and belowground communities is likely (van der Bij et al., 2018). This could lead to a lowered performance of heather as compared to competing species and might ultimately lead to a failure of restoration attempts that seem successful during early stages but then develop back into species-poor grasslands of low conservation value.

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### 13.7 The Noordenveld experiment

The Noordenveld is a former heathland of about 160 ha in the center of the National Park Dwingelderveld in the Northern part of the Netherlands. It was converted into arable fields and grasslands in the 1930s and restored back in 2011 when c. 30 cm of topsoil was removed to quickly reach the low nutrient levels required for heathlands. This restoration was accompanied by a large-scale field experiment with plots of 15 m × 15 m. Different restoration measures were compared: topsoil removal only, topsoil removal + addition of freshly mown herbage from nearby heathlands with ripe seeds to eliminate possible plant dispersal barriers, and topsoil removal + addition of sod cut soil from nearby heathlands to eliminate possible dispersal barriers for both plants and soil organisms. In addition, soil pH was manipulated in a full factorial treatment independent of biota addition: (1) pH was lowered by addition of elemental sulfur ( $S^0$ ), (2) pH unaltered, and (3) pH increased by addition of dolomite. Soil chemistry and vegetation were monitored each year. Soil fauna and soil microbes were measured immediately after topsoil removal, in the third year after the start of the experiment and will be again in the seventh year. The results presented here (Fig. 19.1) are those in the third year after topsoil removal and based upon Weijters et al. (2015) and van der Bij et al. (2018). By that stage, there were no significant effects of pH manipulation on the performance of biota.

The composition of the soil microorganism community in terms of the F:B ratio clearly differed between treatments with the sod addition treatment being closest to the reference. The control treatment with topsoil removal only is still close to the starting situation, and the treatment with herbage addition shows



**FIGURE 13.4**

Response of several biotic parameters on alternative restoration treatments. AGRI, starting situation before topsoil removal; C, control; H, herbage; S, sods; and Ref, reference.

intermediate values. The results also demonstrate that the changes in ratio are not caused by differences in bacterial content but instead by increases in the amount of fungal material when going from control to sod addition and reference.

The soil mesofauna show a similar trend, but the absolute numbers are still much lower than those in the reference site. Moreover, the relative abundance of springtails (*Collembola*) as compared to soil mites (*Acari*) was much closer to one in all treatments than in the reference site, where the drought-resistant *Acari* are much more common than the drought-avoiding *Collembola*. The absolute numbers in all experiments are much lower than in the reference site, possibly because the organic matter content is much lower.

Finally, the vegetation composition shows two clearly diverging trends: from control with only topsoil removal to reference, there is a clear increase in both total vegetation cover and percentage of heathland plant species; whereas the opposite is true for grassland species. In other words, after 3 years the control sites are still a grassland—admittedly of much lower productivity—and the sites with crushed sod addition are already close to a heathland, though with lower standing biomass (Fig. 13.4).

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## References

- Bakker, J.P. (Ed.), 1989. *Nature Management by Grazing and Cutting: On the Ecological Significance of Grazing and Cutting Regimes Applied to Restore Former Species-Rich Grassland Communities in the Netherlands*. Kluwer, Dordrecht.
- Bakker, J.P., Olf, H., 1995. Nutrient dynamics during restoration of fen meadows by hay making without fertilizer application. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J., Robertson, A. (Eds.), *Restoration of Temperate Wetlands*. Wiley, Chichester, pp. 143–166.
- Bakker, J.P., Van Diggelen, R., Bekker, R.M., Marrs, R.H., 2012. Restoration of dry grasslands and heathlands. In: van Andel, J., Aronson, J. (Eds.), *Restoration Ecology*. Wiley, Chichester, pp. 173–188.
- Bekker, R.M., Verweij, G., Smith, R.E.N., Reiné, R., Bakker, J.P., Schneider, S., 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? *J. Appl. Ecol.* 34, 1293–1310.
- Berendse, F., Scheffer, M., 2009. The angiosperm radiation revisited, an ecological explanation for Darwin's "abominable mystery". *Ecol. Lett.* 12, 865–872.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., et al., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* 20, 30–59.
- Brudvig, L.A., Grman, E., Habeck, C.W., Orrock, J.L., Ledvina, J.A., 2013. Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands. *For. Ecol. Manage.* 310, 944–955.
- Bueno, C.G., Moora, M., Gerz, M., Davison, J., Öpik, M., Pärtel, M., et al., 2017. Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Global Ecol. Biogeogr.* 26, 690–699.

- Bullock, J.M., Mallada González, L., Tamme, R., Götzenberger, L., White, S.M., Pärtel, M., et al., 2017. A synthesis of empirical plant dispersal kernels. *J. Ecol.* 105, 6–19.
- Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L., et al., 2008. Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89, 1541–1553.
- Cornelissen, J., Aerts, R., Cerabolini, B., Werger, M., Van der Heijden, M., 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia* 129, 611–619.
- De Graaf, M.C.C., Bobbink, R., Smits, N.A.C., Van Diggelen, R., Roelofs, J.G.M., 2009. Biodiversity, vegetation gradients and key biogeochemical processes in the heathland landscape. *Biol. Conserv.* 142, 2191–2201.
- Dickie, I.A., Bufford, J.L., Cobb, R.C., Grelet, G., Hulme, P.E., Klironomos, J., et al., 2017. The emerging science of linked plant – fungal invasions. *N. Phytol.* 215, 1314–1332.
- Dudenhoeffer, J.-H., Ebeling, A., Klein, A.-M., Wagg, C., 2018. Beyond biomass: soil feedbacks are transient over plant life stages and alter fitness. *J. Ecol.* 106, 230–241.
- Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., et al., 2003. The importance of land-use legacies to ecology and conservation. *Bioscience* 53, 77–88.
- Frouz, J., 2018. Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. *Geoderma* 332, 161–172.
- Frouz, J., Van Diggelen, R., Pižl, V., Starý, J., Háněl, L., Tajovský, K., et al., 2009. The effect of topsoil removal in restored heathland on soil fauna, topsoil microstructure, and cellulose decomposition: implications for ecosystem restoration. *Biodivers. Conserv.* 18, 3963–3978.
- Grime, J.P., Mackey, J.M.L., Hillier, S.H., Read, D.J., 1987. Floristic diversity in a model system using experimental microcosms. *Nature* 328, 420–422.
- Güsewell, S., 2004. N:P ratios in terrestrial plants: variation and functional significance: Tansley review. *N. Phytol.* 164, 243–266.
- Hahn, P.G., Orrock, J.L., 2015. Land-use history alters contemporary insect herbivore community composition and decouples plant-herbivore relationships. *J. Anim. Ecol.* 84, 745–754.
- Härdtle, W., von Oheimb, G., Gerke, A.-K., Niemeyer, M., Niemeyer, T., Assmann, T., et al., 2009. Shifts in N and P budgets of heathland ecosystems: effects of management and atmospheric inputs. *Ecosystems* 12, 298–310.
- Harris, J., 2009. Soil microbial communities and restoration ecology: facilitators or followers? *Science* 325, 573–574.
- Harris, J.A., 2003. Measurements of the soil microbial community for estimating the success of restoration. *Eur. J. Soil Sci.* 54, 801–808.
- Harris, J.A., 2013. Case study: do feedbacks from the soil biota secure novelty in ecosystems? *Novel Ecosystems*. John Wiley & Sons, Ltd, pp. 124–126.
- Hautier, Y., Niklaus, P.A., Hector, A., 2009. Competition for light causes plant biodiversity loss after eutrophication. *Science* 324, 636–638.
- Honnay, O., Helsen, K., Van Geel, M., 2017. Plant community reassembly on restored semi-natural grasslands lags behind the assembly of the arbuscular mycorrhizal fungal communities. *Biol. Conserv.* 212, 196–208.
- Jalal, M.A., Read, D.J., Haslam, E., 1982. Phenolic composition and its seasonal variation in *Calluna vulgaris*. *Phytochemistry* 21, 1397–1401.

- Janssen, J.A.M., Rodwell, J.S., García Criado, M., Gubbay, S., Haynes, T., Nieto, A., et al., 2016. European Red List of Habitats. Part 2. Terrestrial and Freshwater Habitats. Publications Office of the European Union, Luxembourg.
- Jones, L., Stevens, C., Rowe, E.C., Payne, R., Caporn, S.J.M., Evans, C.D., et al., 2017. Can on-site management mitigate nitrogen deposition impacts in non-wooded habitats? *Biol. Conserv.* 212, 464–475.
- Kardol, P., Cornips, N.J., van Kempen, M.M.L., Bakx-Schotman, J.M.T., van der Putten, W.H., 2007. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. *Ecol. Monogr.* 77, 147–162.
- Kardol, P., Wal, A.V., der, Bezemer, T.M., Boer, W., de, Duyts, H., Holtkamp, R., et al., 2008. Restoration of species-rich grasslands on ex-arable land: seed addition outweighs soil fertility reduction. *Biol. Conserv.* 141, 2208–2217.
- Kerley, S.J., Read, D.J., 1997. The biology of mycorrhiza in the *Ericaceae*. XIX. Fungal mycelium as a nitrogen source for the ericoid mycorrhizal fungus *Hymenoscyphus ericae* and its host plants. *N. Phytol.* 136, 691–701.
- Kiehl, K., Kirmer, A., Donath, T.W., Rasran, L., Hölzel, N., 2010. Species introduction in restoration projects – evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic. Appl. Ecol.* 11, 285–299.
- Kirmer, A., Tischew, S., Ozinga, W.A., von Lampe, M., Baasch, A., van Groenendael, J.M., 2008. Importance of regional species pools and functional traits in colonization processes: predicting re-colonization after large-scale destruction of ecosystems. *J. Appl. Ecol.* 45, 1523–1530.
- Klimkowska, A., Van Diggelen, R., Bakker, J.P., Grootjans, A.P., 2007. Wet meadow restoration in Western Europe: a quantitative assessment of the effectiveness of several techniques. *Biol. Conserv.* 140, 318–328.
- Kotowski, W., van Diggelen, R., 2004. Light as an environmental filter in fen vegetation. *J. Veg. Sci.* 15, 583–594.
- Larcher, W., 2001. *Ökophysiologie der Pflanzen: Leben, Leistung und Streßbewältigung der Pflanzen in ihrer Umwelt*. Ulmer, Stuttgart.
- Lawson, C.S., Ford, M.A., Mitchley, J., Warren, J.M., 2004. The establishment of heathland vegetation on ex-arable land: the response of *Calluna vulgaris* to soil acidification. *Biol. Conserv.* 116, 409–416.
- Loidi, J., Biurrun, I., Campos, J.A., García-Mijangos, I., Herrera, M., 2010. A biogeographical analysis of the European Atlantic lowland heathlands: biogeographical analysis of European Atlantic lowland heathlands. *J. Veg. Sci.* 21, 832–842.
- Olsson, P.A., Johnson, N.C., 2005. Tracking carbon from the atmosphere to the rhizosphere. *Ecol. Lett.* 8, 1264–1270.
- Owen, K.M., Marrs, R.H., 2000. Creation of heathland on former arable land at Minsmere, Suffolk, UK: the effects of soil acidification on the establishment of *Calluna* and ruderal species. *Biol. Conserv.* 93, 9–18.
- Owen, K.M., Marrs, R.H., Snow, C.S.R., Evans, C.E., 1999. Soil acidification—the use of sulphur and acidic plant materials to acidify arable soils for the recreation of heathland and acidic grassland at Minsmere, UK. *Biol. Conserv.* 87, 105–121.
- Ozinga, W.A., Römermann, C., Bekker, R.M., Prinzing, A., Tamis, W.L.M., Schaminée, J.H.J., et al., 2009. Dispersal failure contributes to plant losses in NW Europe. *Ecol. Lett.* 12, 66–74.

- Peay, K.G., Garbelotto, M., Bruns, T.D., 2010. Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. *Ecology* 91, 3631–3640.
- Pywell, R.F., Webb, N.R., Putwain, P.D., 1994. Soil fertility and its implications for the restoration of heathland on farmland in southern Britain. *Biol. Conserv.* 70, 169–181.
- Pywell, R.F., Meek, W.R., Webb, N.R., Putwain, P.D., Bullock, J.M., 2011. Long-term heathland restoration on former grassland: the results of a 17-year experiment. *Biol. Conserv.* 144, 1602–1609.
- Ransijn, J., Kepfer-Rojas, S., Verheyen, K., Riis-Nielsen, T., Schmidt, I.K., 2015. Hints for alternative stable states from long-term vegetation dynamics in an unmanaged heathland. *J. Veg. Sci.* 26, 254–266.
- Read, D.J., Leake, J.R., Perez-Moreno, J., 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Can. J. Bot.* 82, 1243–1263.
- Redhead, J.W., Sheail, J., Bullock, J.M., Ferreruella, A., Walker, K.J., Pywell, R.F., 2014. The natural regeneration of calcareous grassland at a landscape scale: 150 years of plant community re-assembly on Salisbury Plain, UK (L. Fraser, Ed.), *Appl. Veg. Sci.*, 17. pp. 408–418.
- Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., et al., 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478, 49–56.
- Smith, S.E., Read, D.J., 2008. *Mycorrhizal Symbiosis*, third ed. Academic Press, London.
- Smolders, A.J.P., Lucassen, E.C.H.E.T., van der Aalst, M., Lamers, L.P.M., Roelofs, J.G.M., 2008. Decreasing the abundance of *Juncus effusus* on former agricultural lands with noncalcareous sandy soils: possible effects of liming and soil removal. *Restor. Ecol.* 16, 240–248.
- Soudzilovskaia, Na, Douma, J.C., Akhmetzhanova, Aa, van Bodegom, P.M., Cornwell, W.K., Moens, E.J., et al., 2015. Global patterns of plant root colonization intensity by mycorrhizal fungi explained by climate and soil chemistry. *Global Ecol. Biogeogr.* 24, 371–382.
- Tibbett, M., Diaz, A., 2005. Are sulfurous soil amendments ( $S^0$ ,  $Fe(II)SO_4$ ,  $Fe(III)SO_4$ ) an effective tool in the restoration of heathland and acidic grassland after four decades of rock phosphate fertilization? *Restor. Ecol.* 13, 83–91.
- Tilman, D., 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78, 81–92.
- van der Bij, A.U., Pawlett, M., Harris, J.A., Ritz, K., van Diggelen, R., 2017. Soil microbial community assembly precedes vegetation development after drastic techniques to mitigate effects of nitrogen deposition. *Biol. Conserv.* 212, 476–483.
- van der Bij, A.U., Weijters, M.J., Bobbink, R., Harris, J.A., Pawlett, M., Ritz, K., et al., 2018. Facilitating ecosystem assembly: plant-soil interactions as a restoration tool. *Biol. Conserv.* 220, 272–279.
- van der Heijden, M.G.A., 2004. Arbuscular mycorrhizal fungi as support systems for seedling establishment in grassland. *Ecol. Lett.* 7, 293–303.
- Verbruggen, E., Pena, R., Fernandez, C.W., Soong, J.L., 2017. Mycorrhizal interactions with saprotrophs and impact on soil carbon storage. In: Johnson, N.C., Gehring, C., Jansa, J. (Eds.), *Mycorrhizal Mediation of Soil. Fertility, Structure, and Carbon Storage*. Elsevier, Amsterdam, pp. 441–460.

- Verhagen, H.M.C., 2007. Changing Land Use: Restoration Perspectives of Low Production Communities on Agricultural Fields After Top Soil Removal (Ph.D. thesis). University of Groningen.
- Verhagen, R., Klooker, J., Bakker, J.P., Diggelen, Rvan, 2001. Restoration success of low-production plant communities on former agricultural soils after top-soil removal. *Appl. Veg. Sci.* 4, 75–82.
- Wardle, D.A., 2002. *Communities and Ecosystems*. Princeton University Press, Princeton.
- Weijters, M.J., van der Bij, A.U., Bobbink, R., Van Diggelen, R., Harris, J.A., Pawlett, M., et al., 2015. Praktijkproef heideontwikkeling op voormalige landbouwgrond in het Noordenveld. Resultaten 2011-2014. Report B-Ware. Nijmegen.
- Wubs, E.R.J., van der Putten, W.H., Bosch, M., Bezemer, T.M., 2016. Soil inoculation steers restoration of terrestrial ecosystems. *Nat. Plants* 2, 16107.