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Beyond the species pool: modification of species dispersal, establishment, and assembly by habitat restoration

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Abstract

Species dispersal, establishment, and assembly are crucial stages of the life history of plants, and clear understanding of the governing forces and rules that shape species composition in a particular community is vital for successful ecological restoration. In this article, we focus on five aspects of seed dispersal and plant establishment, which should be considered during habitat restoration actions. In the first two sections, we discuss the success of spontaneous dispersal and establishment on restoration based on either spatial dispersal or local seed banks. In the third section, we assess the possibilities of species introduction and assisted dispersal. In the fourth section, we introduce some possibilities for the improvement of establishment success of spontaneously dispersed or introduced species. Finally, we highlight issues influencing long-term persistence and sustainability of restored habitats, related to the alteration of management type and intensity, climate change, and spread of non-native species. With the present article, we introduce the special issue entitled “Seed dispersal and soil seed banks – promising sources for ecological restoration” containing 15 papers by 62 authors from 10 countries arranged in the abovementioned five topics.

Implications for Practice

- The potential of spatial and temporal seed dispersal needs to be evaluated before site selection and restoration planning.
- Knowledge on seed bank, seed rain, and landscape-scale dispersal helps to identify the most proper, well-timed, and cost-effective restoration measures.
- Creation of small-scale environmental heterogeneity and favorable conditions for species establishment is crucial for maximizing restoration success.
- Suppression of unwanted species via prevention of immigration and depletion of their seed banks is crucial.
- It is vital to plan restoration at the landscape scale for ensuring the exchange of seeds and pollen between habitats, to apply the most suitable postrestoration management, and to ensure that established communities are resilient to climate change.

Introduction

Species dispersal and establishment are crucial stages in the life history of plant species, and clear understanding of governing forces and rules that shape species composition and assembly in a particular community is fundamental for a successful ecological restoration. Species dispersal and establishment success are influenced by a set of factors, including the composition of species pool, habitat conditions determining environmental filtering, and ecosystem dynamics (Kraft & Ackerley [2014](#)). The species pool represents a set of possibly colonizing species that are “filtered” to the final community by regional processes (e.g. dispersal), environmental and biotic factors (= filters), and interactions or internal dynamics (White & Jentsch [2004](#)). These filters must be considered as dynamic because communities are dynamic themselves. Additionally, different filters depend on each other via feedback loops (Belyea [2004](#); Fattorini & Halle [2004](#)). When determining the processes that filter species to communities, one can apply either a top down (from species pool to community) or bottom up (from community to species pool) approach (Temperton & Hobbs [2004](#)). Some authors proposed to divide the total species pool in two: the external species pool including species occurring in the landscape, and the internal species pool with species already present on site, e.g. in the seed bank, bud bank, egg bank, or still alive after the disturbance (Fattorini & Halle [2004](#)). This second pool is part of what White and Jentsch ([2004](#)) called disturbance legacy.

A simplified scheme of the interaction of species pools, filters, and restoration measures is introduced in Figure [1](#). Only a fraction of the total species pool is able to reach a particular site (i.e. available species), and species arrival is governed by spontaneous dispersal processes (Prach & Pyšek [2001](#)). Spontaneous species dispersal has a spatial component, which means that dispersal in space is facilitated by abiotic and biotic vectors. Although the spontaneous spatial dispersal has attracted quite high attention in the literature, the temporal component of dispersal, e.g. the formation of persistent seed and bud banks but also temporal dynamics of spatial dispersal, has gained so far much less attention (but see Pausas et al. [2018](#)). The available species pool (i.e. species able to arrive at a particular site) is generally further filtered by abiotic conditions of the respective habitat (i.e. abiotic filtering) and later by the respective species assembly at the site (i.e. biotic filtering). Although abiotic conditions filter species from the species pool, which are able to establish in a respective habitat, biotic filtering sorts out those species that are not able to assemble in a respective community. Due to successional changes, however, the species composition of an established community is not constant over time (Hobbs et al. [2007](#)). Fluctuations and internal community dynamics strongly influence the actual species composition in a site (Fig. [1](#)).

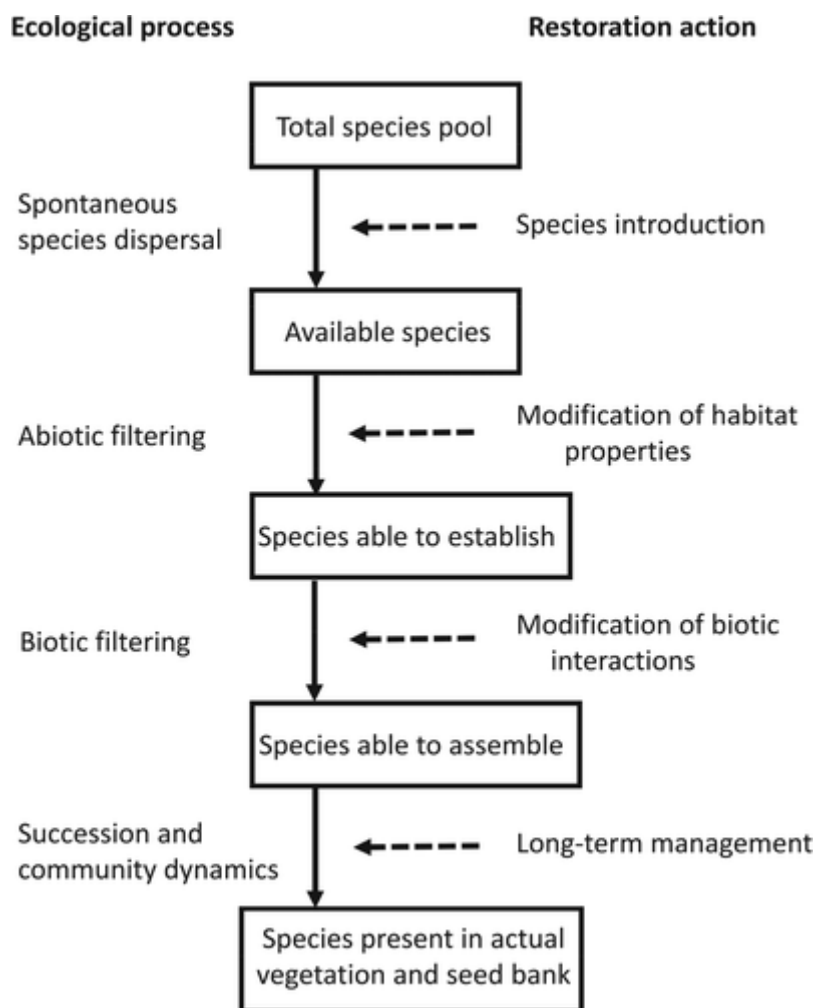


Figure 1

A conceptual framework linking the ecological processes filtering the species pool and ways how active habitat restoration can modify community assembly.

Applied to restoration, this scheme makes it possible to draw some generalities from various projects and provide guidelines (Temperton & Hobbs [2004](#)). It implies that for each restoration project, one must consider (1) the regional processes determining the composition of species pool and species dispersal; (2) the actual and predicted environmental conditions and habitat characteristics favoring the species of the target community; and (3) biotic interactions (Menninger & Palmer [2006](#)). In this context, it is crucial to know that different filters can be important at different restoration stages (Hobbs & Norton [2004](#)). Identifying the key filters allows the determination of the steps needed to be taken during the restoration process (Hobbs & Norton [2004](#)) and to decide if active restoration measures are needed or if passive restoration by unassisted succession may be sufficient to reach restoration goals (Prach et al. [2007](#)). In the last few decades, there has been an increasing demand to link ecological theory with the practice of restoration, and it was argued that the implication of theories in restoration increases its applicability and success (Prach & Hobbs [2008](#); Török & Helm [2017](#)). The special feature and review focus on five topics of restoration clearly linked to the above introduced filtering scheme (Fig. [1](#)).

The ultimate goal of habitat restoration is to reach a species composition and community functioning similar to a predefined idealized target community (van Andel & Aronson [2012](#); Helm et al. [2015](#)). This means that during active restoration we aim at modifying the species

composition of a particular site by directing compositional changes or development of the species assembly toward a desirable targeted direction (Kiehl et al. [2010](#); Tischew et al. [2014](#)). For cost-effective planning and implementation of target species transfer, as well as for ensuring long-term viability of the restored community, it is vital to know in which magnitude a restoration action can be based on spontaneous spatial dispersal and local seed banks. Spontaneous succession or assisted regeneration is increasingly promoted (Prach & Hobbs [2008](#)). Spontaneous succession is either based on local propagule banks or on spatial dispersal of target species. These topics are introduced in the following sections 1 and 2. In section 3, we focus on species introduction, with which it is possible to overcome dispersal limitation. This is generally done by sowing of seed mixtures or plant material transfer (Kiehl et al. [2010](#); Török et al. [2011](#)). For an effective establishment of species from the habitat-specific species pool (Helm et al. [2015](#)), it is often necessary to modify abiotic and biotic habitat conditions in degraded landscapes (section 4). Finally, the long-term persistence of restored communities is strongly linked to the long-term modification and direction of internal community dynamics. Long-term sustainability can be strongly influenced by climate change or by the spread of invasive non-native species and the suitability of management measures for reaching restoration targets (section 5).

This special issue entitled “Seed dispersal and soil seed banks – promising sources for ecological restoration” contains 15 papers by 62 authors from 10 countries arranged in the abovementioned five topics. The special issue was initiated during the SER Europe Conference 2016 on “Best practice in restoration” (Freising, Germany, 22–26 August, 2016). The contributing author teams were mostly invited from the special session “Soil seed banks and seed dispersal – promising sources for restoration” organized by the guest editors. The special issue is developed with the collaboration and support of the European chapter of the Society for Ecological Restoration (Box [1](#)).

Box 1. About SER Europe.



SER Europe is an official chapter of SER International and an international nonprofit organization for ecological restoration. The mission of SER Europe is to promote ecological restoration essential for sustainable recovery of the natural biodiversity in Europe and to facilitate the reestablishment of an ecologically healthy relationship between nature and human culture. SER Europe commits to (1) facilitate discussion between researchers, practitioners, and stakeholders by organizing conferences, workshops, and training courses; (2) support practitioners and stakeholders with evidence-based knowledge reaching a cost-effective restoration; (3) encourage the development of research and policy networks over the continent and beyond; (4) contribute the sustainment and scientific mission of the journal *Restoration Ecology*; (5) provide scientific background and support for restoration activities; and (6) provide decision support and contribute to public policy discussions in the field of environmental restoration.

Success of Spontaneous Dispersal and Colonization

Species spontaneous colonizations and extinctions are fundamental components of community dynamics. In ecological restoration, spontaneous dispersal of propagules is a highly relevant process that has to be carefully incorporated in restoration planning (Török & Helm [2017](#)). Patterns of unassisted dispersal of target and nontarget species and the potential of target communities to benefit from seed rain determine which restoration measures are needed and how restoration has to be carried out. When target species are expected to arrive fast, restoration can largely focus on re-creating necessary physical conditions and on ensuring the establishment success (Prach & Pyšek [2001](#); Valkó et al. [2017](#); Aradóttir & Halldorsson [2018](#)). When spontaneous colonization of target species is unlikely to occur, or can result in arrival of unwanted species, species introductions and assisted dispersal are needed (see section 3 and Kiehl et al. [2010](#)).

However, the scientific knowledge about the positive and negative effects of spontaneous dispersal is far from complete (Arruda et al. [2018](#)). Recovery of vegetation via spontaneous dispersal is a complicated process and depends on multitude of factors such as composition of the species pool, landscape structure and connectivity, land use history, dispersal ability of species, availability and behavior of dispersal vectors as well as on aspects related to seed production and predation (Marteinsdóttir [2014](#); Johanidesová et al. [2014](#); Prach et al. [2015](#); Solbreck & Knape [2017](#); Arruda et al. [2018](#); Schwab et al. [2018](#)). The capacity to incorporate all the aspects in practical restoration is hindered both by the lack of standardization in approaches and methods, as well as by the lack of basic knowledge of the processes. Based on a systematic review of grassland literature, Arruda et al. ([2018](#)) point out that there are significant knowledge gaps in seed rain research depending on grassland types and concerning the role of native animals as seed dispersers, predispersal, and postdispersal seed predation and the effect of seed rain on arrival of non-native species. Aavik and Helm ([2018](#)) additionally emphasize that not only dispersal of seeds needs to be considered but the drivers of gene flow in general: successful restoration also needs to result in the recovery of genetic diversity, which is dependent both on seed and pollen flow in the landscape, as well as on population size. Thus, in order to ensure that restored ecosystems will harbor viable, genetically diverse populations, and diverse communities, restoration planning should specifically aim for the recovery of landscape-scale spontaneous dispersal of target species (Török & Helm [2017](#); Aavik & Helm [2018](#)). Aavik and Helm ([2018](#)) list a number of genetic and ecological tools that allow assess landscape-scale dispersal for selecting appropriate restoration methods and monitor restoration success. They also propose recommendations for restoration planners and practitioners to consider while aiming to restore self-sustainable ecosystems with high species- and gene-level biodiversity.

The knowledge of factors influencing spontaneous dispersal in watercourses is even scarcer than in terrestrial habitats (Bourgeois et al. [2016](#)). Schwab et al. ([2018](#)) studied the effects of the surrounding vegetation and the local species pool on seed dispersal from the Danube to a newly connected watercourse in the Danube floodplain and between different habitat types within the restored floodplain. They found that connecting restoration sites with upstream donor habitats enhanced restoration success but also pointed out that upstream seed sources of potentially invasive nontarget species have to be reduced.

An integral component of spontaneous colonization is the establishment success following seed dispersal (section 4). Aradóttir & Halldorsson ([2018](#)) showed in severely degraded and erosion-prone landscapes in Iceland that colonization of woody species has been both seed and microsite limited; thus, both aspects need to be addressed for successful restoration. In

their study, creation of colonization and establishment nuclei via planting “woodland islets” served as a tool to overcome both seed and microsite limitation.

In general, knowledge-based approaches to reconnect habitats and to improve conditions for target seed dispersal will enhance success (see also other studies in this issue). Each restoration project, however, has its specific conditions and often large efforts are necessary prior restoration for incorporating spontaneous dispersal effects and maximizing restoration success, as well as after restoration for monitoring ecological consequences of implemented measures (Watson et al. [2017](#); Arruda et al. [2018](#)).

Effectiveness and Role of Seed Bank in Restoration

The quality and quantity of the soil seed bank of restoration sites is one of the most important prerequisites, which determines the required actions and the rate and type of species introductions. In their meta-analysis, Bossuyt and Honnay ([2008](#)) found that in most grassland and forest communities, target species with persistent seed bank are too scarce to effectively support spontaneous recovery. This is especially true, because most of the rare species, and also several characteristic matrix species generally lack persistent seed banks in these communities (Kiss et al. [2016](#); Klaus et al. [2018](#); Godefroid et al. [2018](#); Török et al. [2018](#)). In wetlands, heathlands, and habitats with frequent and unpredictable disturbances, regeneration from the seed bank is more important and thus persistent seed banks can support the spontaneous recovery of these habitats better than in grasslands or forests (Bossuyt & Honnay [2008](#), Kiss et al. [2018](#)). In general, the role of seed banks in recovery decreases with increasing community stability. Thus, in stable communities, due to the lack of disturbances creating gaps for germination and establishment most species do not have persistent seed banks (Bossuyt & Honnay [2008](#); Schwab & Kiehl [2017](#)). But also in ancient grassland habitats regularly disturbed by fire, such as old-growth *campo rupestre* grasslands, the seed bank was found to be insufficient for community recovery after severe anthropogenic disturbance (Le Stradic et al. [2018](#)). Obviously the bud bank is more important in regularly burnt old-growth grasslands than the seed bank (Fidelis et al. [2014](#); Pausas et al. [2018](#)) and resprouting seems to be the major way of plant regeneration (see also Kiss et al. [2018](#)).

In general, sites with a shorter history of degradation can be restored with higher success based on the local seed bank (Bekker et al. [1997](#)). This finding should be considered in restoration prioritization: if resources for restoration are limited, site managers should select less severely degraded sites for spontaneous recovery or assisted restoration. Given the low contribution of soil seed banks to vegetation recovery, enabling the spatial component of seed dispersal is crucial in restoration projects (see Török et al. [2018](#)). Landscape-scale extent and spatial configuration of reference grasslands should be evaluated and sites where spatial dispersal of target species is more promising and where unwanted invasive species are absent should be prioritized for spontaneous recovery.

In general, the soil seed bank of degraded sites mainly consists of undesired species (Török et al. [2012](#); Hess et al. [2018](#); Klaus et al. [2018](#); Török et al. [2018](#)). Thus, information about the composition of the seed bank can inform site managers about the most important future threats, such as the encroachment of weeds and invasive species. With this knowledge, they can also plan the necessary restoration actions. If the seed bank contains mainly undesired species, it is important not to allow its activation, thus drastic site preparation by soil disturbance without additional introduction of target species should be avoided (see Valkó et al. [2016](#); Klaus et al. [2018](#)). If the seed bank is largely infested by invasive species, only its

complete removal can prevent future invasion. Hess et al. (2018) provided a novel approach for eradicating the seed bank of undesired species by microwave heating of soils. Even though the method is currently being fine-tuned for larger-scale field application, it seems to be a promising and innovative approach to fight against invasive species without pesticide application.

Finally, knowledge on soil seed banks also supports the monitoring of restoration success and helps us estimate the resilience of the restored communities. Török et al. (2018) evaluated the success of spontaneous recovery of sandy old-fields in a chronosequence study and showed that the development of seed banks is also a proper indicator of restoration success. The seed bank informs us about community resilience, which is especially important faced with changing climate as shown by Kiss et al. (2018). This study highlighted that in stable habitats, characterized by predictable and less severe disturbance, such as nonfire-prone temperate grasslands, climate-induced changes in disturbance regimes cannot be buffered by soil seed banks in the future. They showed that climate-driven changes in disturbance regimes can lead to directional and irreversible changes in species composition and density of soil seed banks, especially in currently stable ecosystems.

Species Introduction and Assisted Dispersal

As mentioned above, the restoration of grassland ecosystems is often limited by seed availability because of depleted seed banks and limited dispersal of diaspores due to a lack of dispersal vectors, especially for long-distance dispersal (Walker et al. 2004; Buisson et al. 2006a; Klaus et al. 2018; Török et al. 2018). Also in other plant communities of ancient cultural landscapes, e.g. in arable ecosystems, populations of rare and threatened target species are often fragmented due to changed land use techniques (e.g. herbicide application, changed crop rotation, seed cleaning of crops in arable ecosystems). Nowadays, most rare and threatened arable weed species are not able to disperse over longer distances (Mayer & Albrecht 2008, Lang et al. 2018).

Therefore, active species introduction is necessary when target species are absent on restoration sites in fragmented landscapes and are not able to reach them by natural dispersal (Kiehl 2010; Tischew et al. 2014). Suitable restoration measures include, e.g. the transfer of freshly harvested seed-containing hay or raked material, seeding of site-specific seed mixtures (Hedberg & Kotowski 2010; Kiehl et al. 2010, 2014). The transfer of diaspore-rich topsoil can also be used to introduce target species (Scotton et al. 2012; Jaunatre et al. 2014), but it strongly damages the donor site and should mainly be used when donor sites are destroyed anyway, e.g. by construction works. Although many studies have shown a successful restoration of ecosystems by topsoil transfer, information about practical details of species introduction techniques and about mechanisms of target species establishment is still missing for different types of plant communities.

Buisson et al. (2018) evaluated the effects of the transfer ratio and the timing of topsoil transfer on the establishment of typical dry grassland species in Mediterranean grasslands. Although the seed bank contained more species in summer than in spring in their study, topsoil transfer in spring was more successful for the establishment of target species concerning both species richness and species composition compared to topsoil translocation in autumn. The different transfer ratios of 1:1 and 1:3 (donor:receptor site) had no significant effect on vegetation development, which indicates that a ratio of 1:3 was sufficient for dry grassland restoration in Southern France. Long-term establishment of target communities was,

however, mainly affected by the underlying seed bank at the receptor site, which contained competitive nontarget species hampering restoration success (see also Jaunatre et al. [2014](#)).

Lang et al. ([2018](#)) introduced arable weed species, which had become rare due to herbicide application in conventional farming, to organic farms where the probability of population persistence is higher under suitable management. They showed that it was possible to establish new populations by seeding, but only two out of three species (*Consolida regalis*, *Legousia speculum-veneris*) were able to build up a persistent soil seed bank at the restoration sites. In contrast, the available seed bank of *Lithospermum arvense* was rapidly depleted in unfavorable years (e.g. by mice feeding). Cultivation techniques led to a short distance dispersal of seeds over 16 m within fields in 3 years indicating that species may disperse further in the future especially when sown strips of target species are set up rectangular to the direction that cultivation is carried out, instead along the field margins.

Wagner et al. ([2018](#)) investigated not only the establishment of introduced target species but also the seed bank dynamics in soils of grasslands restored by sowing of low- and high-diversity seed mixtures. Sowing of species-rich grass-forb mixtures was reflected in a faster build-up of sown forbs in the seed bank and a faster decline of nontarget forbs in comparison to species-poor mixtures containing only grasses. Interestingly, seed bank composition and dynamics were more affected by the composition of the seed mixtures than by cultivation techniques prior to sowing (deep vs. shallow cultivation).

Improvement of Establishment Success

Following their arrival in a given community, species need to germinate, survive, grow, and reproduce. Only species with the physiological capacities to establish in particular environmental conditions can do so. One main restoration action is therefore to manipulate and reestablish adequate abiotic conditions before introducing species or leaving spontaneous succession to work (Fig. [1](#)). This may include manipulation of soil texture and nutrient concentrations (Hobbs & Norton [2004](#); Heneghan et al. [2008](#); Melnik et al. [2018](#)). In general, species diversity increases with habitat heterogeneity, which provides more niches for different species. Thus, ecological restoration often aims at creating structurally complex habitats and safe sites (del Moral et al. [2007](#); Aradóttir & Halldorsson [2018](#)) by modifying the abiotic and the biotic components of ecosystems: microtopography, substrate heterogeneity, biocrust and ecosystem engineers, such as ant mounds, thin moss, tussock grasses, and dwarf-shrubs, can play a major role in creating this heterogeneity (Whisenant [2002](#); Larkin et al. [2006](#); Menninger & Palmer [2006](#); Aradóttir & Halldorsson [2018](#)). Indeed, Melnik et al. ([2018](#)) found that variability in microtopography and substrate can support the expression of a wide range of species from the seed bank. They showed that site managers can make use of this method even at the operational scale. Aradóttir & Halldorsson ([2018](#)) showed that, in severely degraded and erosion-prone landscapes in Iceland, colonization of woody species is microsite limited, and the creation of establishment nuclei via planting “woodland islets” is useful.

Species also interact with each other: these interactions can be negative (competition) or positive (facilitation), and both of them can considerably influence restoration success (Fig. [1](#)). Plant species compete for limited resources, such as water, nutrients, light, whereas animal species compete for prey and space. Plant and animal communities also interact. Although everyone agrees that primary producers have the primacy in controlling the structuring of communities, predator–prey interactions also play an important role. Dense

stands of exotic or ruderal species can reduce or enable native target species to establish (Buisson et al. [2006b](#), [2008](#); Buisson et al. [2018](#)). Grazing is widely studied to restore open landscapes (e.g. Fischer et al. [1996](#); Opperman & Merenlender [2000](#); Yates et al. [2000](#); Kiehl & Pfadenhauer [2007](#)) as it can limit competition, favor some species, and introduce new species. Eichberg and Donath ([2018](#)) studied the effects of simulated trampling by artificial sheep hooves on germination and seedling recruitment of plant species from dry sandy grasslands and of ruderals in a laboratory experiment. They showed that trampling pressed seeds into the upper soil layers and strongly promoted seedling emergence due to positive effects on microclimate. Not only target species but also ruderal species profited from trampling, which means that in practical conservation and restoration of sandy grasslands appropriate grazing management is necessary to reduce the abundance of nontarget species and to promote target species (see also Stroh et al. [2002](#)).

In the past 20 years, positive interactions between plants have been studied in detail (e.g. Callaway & Walker [1997](#); Brooker et al. [2008](#)) and have been applied to restoration (e.g. Gómez-Aparicio et al. [2004](#); Padilla & Pugnaire [2006](#); Aradóttir & Halldorsson [2018](#)). At the same time, there has been a growing interest in the linkage between belowground and aboveground biota because it influences community and ecosystem processes and properties (Wardle et al. [2004](#)). To conclude, both negative and positive interactions must be taken into account in ecological restoration in order to improve restoration efforts (Menninger & Palmer [2006](#); Halpern et al. [2007](#); Wagner et al. [2018](#)).

Long-Term Persistence, Sustainability, and Management

Natural fluctuations and internal community dynamics strongly influence species establishment and assembly in natural ecosystems (Fig. [1](#)). Both processes are strongly linked to the degradation of the species composition and functioning of ecosystems directly driven by altered intensity of management and climate change as well as by the spread of invasive species (Nelson et al. [2006](#)).

Changes in management intensity that is intensification or cessation of former use can shift the species composition and ecosystem functioning in an undesired direction causing species loss. Management intensity changes were identified as the most crucial drivers of species loss in grasslands and other open habitat types over the Palaearctic (Carboni et al. [2015](#); Török & Dengler [2018](#); Valkó et al. [2018](#)). In most cases, decreased management intensity will cause an increase in abundance and number of potentially dominant competitors of the subjected grassland community. During restoration planning, postrestoration management should be carefully selected because cessation or improper management can strongly threaten restoration success (Kelemen et al. [2014](#); Eichberg & Donath [2018](#)). Successful management of restored sites creates favorable light conditions, ensures the presence of gaps needed for the regeneration of target species, and provides control of potentially dominant native and non-native nontarget species (Tischew et al. [2014](#)).

Climate change has become an emerging threat to both original and restored ecosystems (Harris et al. [2006](#)), and together with the alteration of spatial and temporal patterns in precipitation and temperature, it also increases the chance of weather extremities. Climate change can induce community shifts by changing global and regional patterns of species distributions (Thuiller et al. [2005](#)), by affecting population sizes and the timing of reproduction (Nelson et al. [2006](#)), and by the facilitation of the spread of pests and biological invasions (Walther et al. [2009](#)). The magnitude in which climate change affects ecosystems is

highly variable in respect to the habitat type, and is often masked by other drivers including land use and management changes. Impacts of global changes can be mitigated by ecological restoration via creation of resilient communities of native plant species with as high evolutionary potential as possible, as well as via fostering the landscape-scale movement of seeds and pollen in order to build up high habitat-specific species and gene-level diversity (Aavik & Helm [2018](#)).

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