

REVIEW ARTICLE

# Restoration of plant species and genetic diversity depends on landscape-scale dispersal

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In the era of ongoing global change, it is highly important that restoration efforts lead to functioning, self-sustainable ecosystems that are resilient to disturbance and resistant to environmental changes. Therefore, it is necessary that restoration aims at achieving high genetic diversity of plant populations in addition to the recovery of characteristic species composition and diversity. Nevertheless, species- and gene-level biodiversity are rarely examined together in the context of restoration, although high genetic diversity of plant populations is a fundamental factor ensuring long-term success of restoration. Landscape-scale dispersal is the key process linked to the recovery of vegetation and maintaining both species and genetic diversity following restoration. In fragmented landscapes, dispersal of seeds and genetic material is often disrupted, leading to failure in spontaneous recovery of species richness as well as in establishment and maintenance of genetically diverse populations. Here, we review the linkages between landscape-scale dispersal of plants and the recovery of species richness and genetic diversity of plants during habitat restoration. We propose recommendations for restoration planners and practitioners to consider while aiming to restore self-sustainable ecosystems with high species- and gene-level biodiversity.

**Key words:** functional connectivity, gene flow, landscape genetics, landscape-scale restoration, local provenance, restoration success, species pool, species richness

## Implications for Practice

- Both species and genetic diversity should be considered during restoration.
- Recent advances in molecular tools allow employing genetic information for setting restoration goals, selecting appropriate restoration methods, and monitoring restoration success.
- Landscape scale (covering several km<sup>2</sup>) needs to be taken into account for ensuring development of high plant species richness, characteristic species composition, and high genetic diversity following the restoration.
- Availability of species pool, the presence of genetically diverse populations, and landscape functional connectivity determine the outcome of restoration during spontaneous succession.
- Active restoration measures need to be applied in landscape-scale restoration when species pool is impoverished and genetic diversity of populations is low.

## Introduction

In the era of ongoing global change, the role of ecological restoration has never been as important before (Haddad et al. 2015). Self-sustainability of ecosystems can only be achieved when restored habitats are integrated into a larger ecological matrix (SER 2004), which ensures not only connectivity between populations, but also helps to recover and maintain important ecological interactions and viable ecosystem services

(Bommarco et al. 2013; Kovács-Hostyánszki et al. 2017). The importance of landscape-scale processes on the restoration success of ecosystems has been emphasized in a number of studies (Prach et al. 2015a; Crouzeilles & Curran 2016). However, despite the recent calls to focus on a landscape-scale approach during restoration (e.g. Brudvig 2011; Helm 2015), both restoration planning as well as monitoring restoration success are still often largely confined to site scale (Watson et al. 2017). Furthermore, the need to integrate a restored ecosystem into a larger ecological matrix or a landscape has been very seldom set as a restoration goal (Gerla et al. 2012; Lengyel et al. 2012; Hallett et al. 2013).

Ecosystem restoration should focus on establishing self-supporting (or in case of seminatural habitats, maintained by moderate human intervention) communities that are resistant and resilient to perturbations (Hallett et al. 2013; Török & Helm 2017). However, the most often listed goal in the Global Restoration Network database is the recovery of the characteristic assemblage of species, based on the reference ecosystem (Hallett et al. 2013). Until recently, relatively little attention was paid to restoring genetic diversity, which is a

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prerequisite for establishing viable populations resilient to perturbations (Ruiz-Jaen & Mitchell Aide 2005; Brudvig 2011; Wortley et al. 2013; Mijangos et al. 2015). Yet, in order to ensure the sustainability of restored ecosystems, recovery of genetic diversity should be pursued with the same determination as the recovery of characteristic species richness and composition. Higher genetic diversity enhances the fitness of organisms and increases population viability (Leimu et al. 2006; Takkis et al. 2013). Without the buildup of genetic diversity, established populations are vulnerable to the effects of inbreeding and stochastic environmental conditions, threatening the long-term persistence of species (Hoffmann & Sgro 2011). Furthermore, altered environmental conditions, such as climate change and high-intensity land use, are increasingly threatening the presence of many species, and the ability of populations to respond to all these pressures largely depends on genetic diversity. Measures of genetic diversity and gene flow can also inform about important ecological processes. In particular, molecular tools offer a powerful means for gaining valuable insights into patterns and processes of plant dispersal and habitat connectivity, which are difficult to assess with traditional ecological tools (Broquet & Petit 2009; Lowe & Allendorf 2010).

In this paper, we review the main factors influencing the restoration of landscape-scale dispersal of plants, and discuss how enhancing dispersal of propagules and pollen influence the recovery of both species- as well as gene-level diversity. We bring examples of how genetic tools can be used not only for estimating the fitness potential of plant populations, but also for assessing plant landscape-scale dispersal during planning and monitoring of landscape-scale restoration. Finally, we provide recommendations of how to improve (Fig. 1) and assess landscape-scale dispersal during restoration (Table 1).

## Main Issues to Consider for Restoring Landscape-Scale Dispersal of Plants

### Availability of Species Pool and Genetically Diverse Populations

The presence of suitable species (habitat-specific species pool) and genes (i.e. genetically diverse populations of target species) in the nearest surroundings plays a fundamental role in the development of high species and genetic diversity in restored habitats (Helsen et al. 2013; Lewis et al. 2017). Habitat-specific species pool is a set of species that occur naturally in the region, are able to disperse to a given habitat patch, and have life-history characteristics that enable them to establish, survive, and reproduce under environmental conditions typical to the particular habitat (Eriksson 1993; Pärtel et al. 2011; Helm et al. 2015). Small-scale species richness in a given habitat is generally correlated with the size of the species pool in the surroundings (Zobel et al. 2011). For example, humans have long transformed European nature and a large number of plant species is historically available for grasslands. Large species pool, along with moderate human disturbance, is also related to high small-scale (site level) plant diversity in European grassland habitats

(Dengler et al. 2014). A number of studies have indicated the importance of species pool diversity and composition on the recovery of plant diversity following restoration (Cousins & Lindborg 2008; Prach et al. 2015b). For example, Conradi and Kollmann (2016) found that the community structure of recovering calcareous grasslands was mainly driven by propagule pressure from historically old grasslands nearby. Foster et al. (2011) showed for the prairies in the United States that the availability of a rich species pool governs the capacity of ecological systems to adjust with and respond to environmental changes.

Similar to the role of the species pool in recovering the characteristic species composition of a habitat, the buildup of genetic diversity of plant populations constituting the restored community depends on the genetic diversity of populations surrounding the restoration sites. When the restored sites are located in a landscape inhabited by multiple genetically diverse plant populations, restored populations are more likely to recover high genetic diversity (Helsen et al. 2013; Ilves et al. 2015). Nevertheless, many landscapes have experienced severe fragmentation, which has seriously impoverished the local species pool. In that case, the establishment of viable target communities and the buildup of genetic diversity requires active restoration measures such as hay transfer (Rydgren et al. 2010; Auestad et al. 2016) or sowing natural (harvested) or commercially produced seeds (Kiehl et al. 2010; Baasch et al. 2016). For example, low genetic diversity in the naturally recruited populations of *Zostera marina* in restored habitats indicated a poor success of natural recolonization of this species, whereas restoration measures, which included sowing of seeds collected from a nearby good-quality habitat, led to genetically diverse populations (Reynolds et al. 2013). Additional analysis revealed that approximately 125–185 years may be needed in naturally recruited populations for reaching the same level of diversity that was observed in seeded populations. Careful selection of populations acting as sources of propagules for reintroduction may increase the genetic diversity of restored populations and can thus significantly support the long-term survival of restored plant populations (Reynolds et al. 2013; Kettenring et al. 2014).

The desirable outcome of restoration would be the establishment of locally adapted genotypes and recovery of high genetic diversity characteristic to viable populations. When introducing propagules, it is important to consider their quality and genetic diversity to avoid negative genetic and fitness consequences. Introduction of genetically impoverished propagules accompanied by low levels of pollen and seed flow between habitats hinders the long-term success of restoration measures (Aavik et al. 2013). In addition to ensuring sustainable levels of genetic diversity, it is also important to consider that the plant material used in active restoration would be adapted to the environmental conditions of restored habitats, while avoiding possible introduction of maladapted genotypes (Gallagher & Wagenius 2016). Assessment of the most appropriate source populations for collecting restoration material can be done experimentally (e.g. Aavik et al. 2014a; Gibson et al. 2016) or by using genetic approaches (e.g. Aavik et al. 2012; Shryock et al. 2017). Rapid methodological advances have

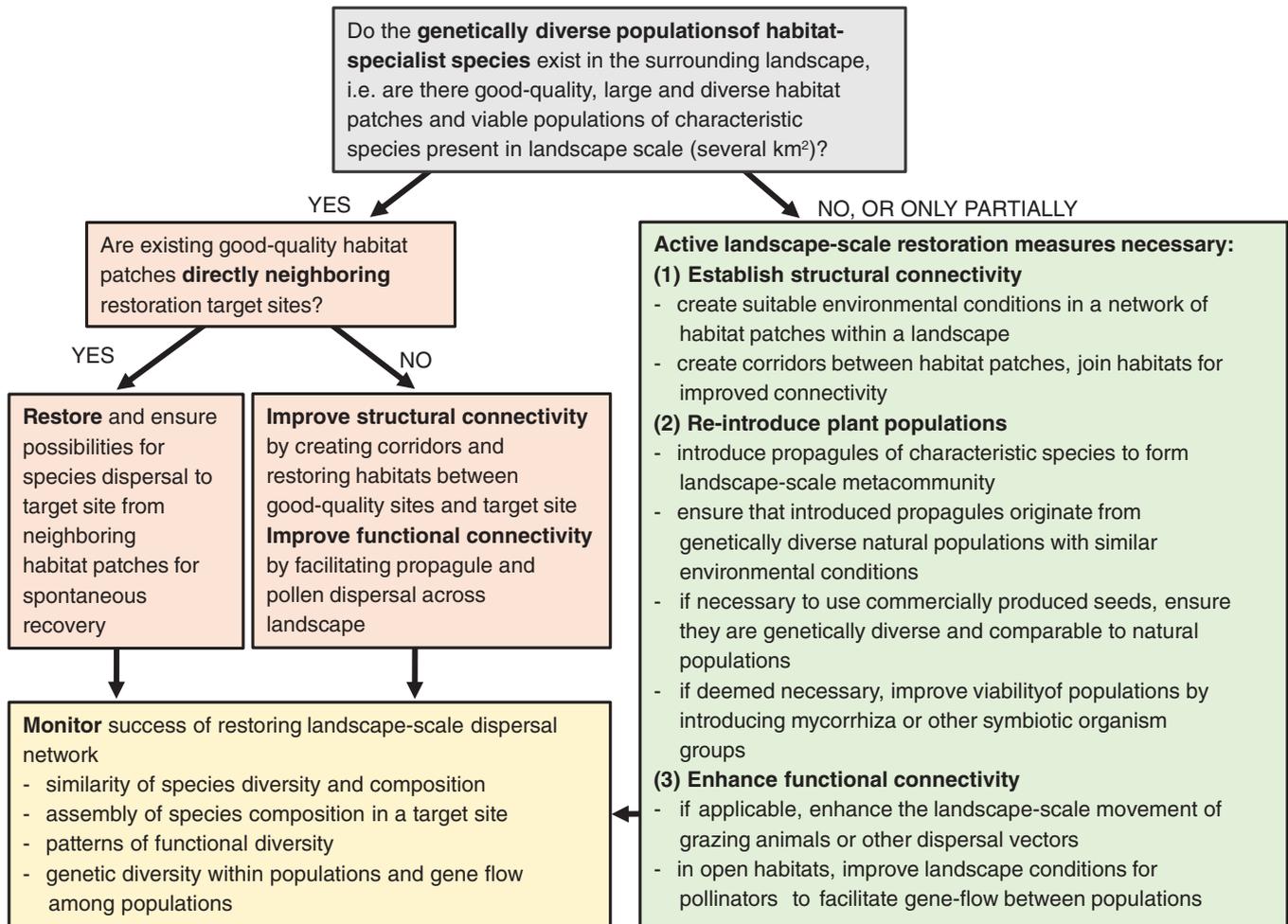


Figure 1. Guidelines for improving landscape-scale dispersal during habitat restoration. The graph provides an overview of alternative steps that need to be taken to maximize landscape-scale dispersal during restoration, depending on the context of the landscape, where habitats will be restored. Answering “Yes” to any question does not necessarily indicate that choices from the other path should not be considered, e.g. even in landscapes with relatively good structural connectivity, rotational grazing or improvement of conditions for the movement of pollinators may be strongly recommended.

significantly fostered research for improving fundamental knowledge on local adaptation (Flood & Hancock 2017), and can also provide valuable information for restoration applications (Shryock et al. 2017). Thus, choosing suitable plant material for active restoration should be accompanied by careful consideration of balancing local provenance on the one hand and maximizing genetic diversity for achieving adaptive capacity in the light of ongoing environmental change on the other hand.

In less disturbed habitats, the availability of the seed bank has been sometimes shown to be important in reestablishing species richness following restoration (Metsoja et al. 2014) and maintaining genetic variation of aboveground populations (Honnay et al. 2008; Oudot-Canaff et al. 2013). However, in some cases, the seed bank can already be depleted or the species for a particular community do not form persistent seed banks (Török et al. 2017). Thus, relying only on the seed bank is not considered feasible (Bossuyt & Honnay 2008). In addition, even if the seed bank provides an initial boost for the recovery

of species richness and genetic diversity following restoration, it does not necessarily ensure the long-term persistence of diversity in isolated habitats. Therefore, restoration securing efficient dispersal of characteristic species at the landscape scale should deserve high priority.

### Structural Connectivity of Habitats

The presence of species with genetically diverse populations in the landscape is insufficient for creating self-sustainable high-diversity ecosystems unless landscape-scale habitat connectivity is achieved (Christie & Knowles 2015). Habitat connectivity is a landscape-scale measure of connectedness between the existing habitat patches and is necessary for the vital processes of populations and ecosystems—movement of individuals, dispersal of seeds, and the exchange of genetic material between individual habitat patches (Fischer & Lindenmayer 2007). Connectivity can be differentiated into components of structural and functional connectivity.

**Table 1.** Examples of ecological and genetic methods that can be applied for assessing landscape-scale dispersal during restoration. The list is not complete and represents the most commonly used tools; however, a variety of additional ecological and genetic methods is available for assessing landscape dispersal of pollen and seed (e.g. see Bullock et al. 2006 and Auffret et al. 2017) that may be appropriate depending on specific study system and research question.

<i>Method</i>	<i>General Application</i>	<i>Relevance for Monitoring Landscape-Scale Dispersal</i>	<i>Examples</i>
<i>Ecological tools</i>			
Direct observations			
(a) Trapping propagules (e.g. seed traps, containers on the substrate)	Allows to estimate seed rain. Possible to quantify the amount and identity of dispersed seeds as well as spatial pattern of dispersed seeds	One of the most often used methods for estimating the availability and presence of seeds in the restored area. Together with mapping the distribution of source populations, it can be considered a good and informative method, but requires sufficient sampling effort.	Bullock et al. (2006) (methodological overview); Buisson et al. (2006); Schwab et al. (in press)
(b) Tracking propagules	Assessing actual dispersal events via trapping marked propagules	The most direct approach for quantifying realized dispersal events, but time-consuming and laborious.	Herrmann et al. (2016); Carlo et al. (2009)
(c) Tracking pollen analogs (e.g. fluorescent dye)	Assessing realized pollen dispersal	Helps to determine whether restored habitats support connectivity through pollen flow and evaluate where implementation of connecting landscape elements might be necessary.	Van Geert et al. (2010); Van Rossum and Triest (2012)
Indirect observations			
Mechanistic models using life-history traits	Predicting species dispersal ability, seed-dispersion patterns	Can be used to estimate potential dispersal distance and dispersal kernels of expected target species. Pre- and after-restoration sampling of existing vegetation on restored sites and in landscapes allows to estimate the effect of restoration on species with differing dispersal ability.	Thomson et al. (2010); Tamme et al. (2014); Bullock et al. (2017); Nathan & Muller-Landau (2000)
Distribution mapping of target species	Estimating existing and potential distribution of species in the landscape	Allows to quantify the availability of potential source populations for target species and monitor their effect on colonization of restored sites. Helps to identify target species that are rare or lacking in the landscape.	Donath et al. (2003)
Taxonomic or functional dissimilarity matrices	Estimating the effect of structural connectivity on species dispersal	Enables to improve the planning of landscape elements needed for enhancing functional connectivity.	Thiele et al. (2017)
<i>Genetic tools</i>			
Within-population genetic diversity	Measuring genetic diversity within populations	Helps to evaluate the buildup of genetic diversity within populations during habitat restoration.	Helsen et al. (2013); Favre-Bac et al. (2016); Ilves et al. (2015); DiLeo et al. (2017)
Pairwise genetic distances among populations (e.g. genetic differentiation $F_{ST}$ )	Assessing genetic differences between populations	Pairwise genetic distances are the most widely used response variables in landscape genetic analyses, which help to infer elements hindering or fostering gene flow. However, because these measures reflect the outcome of gene flow over many generations (i.e. reflect historical gene flow), they may not be applicable for assessing the effectiveness of recent restoration measures.	Vandepitte et al. (2012); Helsen et al. (2013); Rico et al. (2014)
Assignment tests	Assessing recent gene flow events and determination of first-generation migrants	Depicting gene flow events during last generation(s), assignment tests are suitable for assessing the effectiveness of recent restoration measures. However, the results may contain uncertainties when populations are genetically very similar to each other.	Van Looy et al. (2009); Jacquemyn et al. (2010); Aavik et al. (2013); Vanden Broeck et al. (2015)
Clustering methods	Creation of genetic groups based on multilocus genotypic data	Inferences about the amount of gene flow between populations before and after restoration can be made on the basis of identified genetic clusters.	Aavik et al. (2012); Helsen et al. (2013)
Kinship analysis	Assessment of genetic relatedness among individuals	When combined with spatial information about the distance of sampled individuals from each other, kinship analysis can provide insight about the effect of Euclidian distance (or landscape properties) on gene flow.	Favre-Bac et al. (2016); Helsen et al. (2015)

Structural connectivity describes the physical characteristics of a landscape, such as habitat spatial configuration or area of habitats in the landscape (Watson et al. 2017). Plant functional connectivity describes the actual flow of propagules and pollen among habitat patches (Auffret et al. 2017). Functional connectivity depends on the amount of habitat in the landscape, spatial vicinity of the habitat patches, species dispersal abilities, and quality of the matrix surrounding the habitat patches (Villard & Metzger 2014). Landscape-scale habitat loss and decreasing structural connectivity have large, consistently negative consequences on all levels of biodiversity, resulting in decreases in species and genetic diversity, reduced abundance and viability of populations, and disruptions in the functioning of biotic interactions (Aguilar et al. 2006; Fischer & Lindenmayer 2007; Leimu et al. 2010; Frankham et al. 2014; Humphrey et al. 2015).

A number of studies have demonstrated the high importance of landscape structure on the recovery and persistence of species and genetic diversity. In a modeling study, Christie and Knowles (2015) indicated that improved connectivity via suitable corridors provides long-term conservation benefits irrespective of species dispersal abilities or population sizes. In a global meta-analysis, Crouzeilles and Curran (2016) showed that restoration success of forests, estimated via changes in species diversity, directly depended on undisturbed forest cover in 10 km radius. In particular, adjacent (directly neighboring) land use plays a key role in determining the recovery of species richness (Öster et al. 2009; Winsa et al. 2015; Prach et al. 2015a, 2015b) or genetic diversity of habitats (Aavik et al. 2013; Helsen et al. 2013). In sites where target vegetation is abundant and structural connectivity is high, restoration can be successful by introducing only a few basic species and by facilitating the colonization of plants via dispersal from neighboring good-quality habitat patches (e.g. Öster et al. 2009; Lengyel et al. 2012). Although the relative effect of spatial proximity on recolonization success and gene flow may depend on various factors, such as species characteristics, habitat type, and the history of land use of restored sites (Lengyel et al. 2012), the distances that are shown to be beneficial for spontaneous recovery can be only up to 10–20 m to source habitat, and distances exceeding 100 m might be already too large to support species colonization or exchange of genetic material (Prach et al. 2015b). For example, in fragmented forest habitats in Belgium, Honnay et al. (2002) showed that colonization rates for 85% of the forest plant species to suitable habitat fragments were not higher than a few meters per year. Similarly, Butaye et al. (2001) demonstrated that the probability of occurrence of isolation-sensitive species in forest fragments is almost zero if the nearest source patch is situated further than 200 m. Aavik et al. (2013) found that almost no dispersal of either seeds or pollen took place between old and restored populations of a grassland plant *Lycnis flos-cuculi* at distances larger than 1 km.

Spatial proximity of genetically diverse populations together with good structural connectivity will significantly enhance the buildup of genetic diversity of plant populations at restoration sites. For example, Helsen et al. (2013) detected rapid colonization of a grassland specialist *Origanum vulgare* to recently

restored grasslands from multiple sources. They also found that gene flow into restored patches occurred primarily from spatially nearby grasslands, which demonstrates the importance of creating structural connectivity for achieving functional connectivity. Low structural connectivity, on the other hand, may lead to failure in landscape-scale dispersal and is related to low genetic diversity of plant populations at restoration sites jeopardizing the long-term success of restoration measures (Kettle et al. 2012). For example, Vandepitte et al. (2012) found that even after 40 years since restoration, gene flow among the populations of *Dactylorhiza incarnata* and genetic diversity within populations were low indicating insufficient dispersal, most likely owing to a low number of spatially isolated source populations.

Occasional long-distance seed dispersal events may foster recolonization of restoration sites from distances beyond landscape scale. For example, Kirmer et al. (2008) found that for about one-fifth of the establishing events of Red List species in former mining areas, the nearest seed source was located further than 10 km from recolonized habitats. Similarly, suitable matrix conditions can support pollen flow in insect-pollinated plants over distances of 10 km (Kamm et al. 2010). However, long-distance dispersal events are likely to be rare compared to landscape-scale dispersal, which is why the creation and maintenance of landscape-scale connectivity among habitats is of higher priority for enhancing the recovery of characteristic vegetation as well as genetic diversity at restored habitats.

#### Availability of Seed and Pollen Vectors

Many plants depend on biotic vectors for effective pollen and seed flow (Ollerton et al. 2011; Farwig & Berens 2012). Hence, the presence of pollen and propagule vectors and favorable matrix conditions between habitats or corridors for the movement of dispersal agents are among the most important prerequisites for restoring a functionally connected network of habitats (Aguilar et al. 2006; Donald & Evans 2006; Öckinger et al. 2012; Török & Helm 2017). For example, rotational grazing is a practice that traditionally ensured the dispersal of seeds of characteristic grassland species from one pasture to another (Fischer et al. 1996). In addition to fostering recolonization of restored habitats with grassland species (Rico et al. 2012), such rotational grazing supports gene flow among pastures and thus helps to improve and maintain genetic diversity within plant populations. Rico et al. (2014) observed significantly higher levels of gene flow among those populations of *Dianthus carthusianorum* which were connected by grazing sheep herds compared to populations located on grasslands not connected by grazers. However, as currently landscape-scale shepherding has almost completely been replaced by stationary paddocks, special incentives are necessary for reintroducing landscape-scale movement of grazing animals when restoring seminatural grassland habitats (Fischer et al. 1996; Poschlod & WallisDeVries 2002). Effective restoration of landscape-scale seed dispersal can also be highly dependent on the presence and suitable roaming conditions for wild animals, e.g. mammals and birds, but also ants, acting as important dispersal vectors

for many plant species (Magrath et al. 2012; González-Varo et al. 2013; González-Varo et al. 2017).

The exchange of pollen between populations is an important mechanism helping to maintain high levels of genetic diversity and consequent fitness (Fischer & Matthies 1997). Biotic pollination is a dominant mechanism for pollen flow in flowering plants (Menz et al. 2011). However, habitat fragmentation has significantly altered the diversity and composition of pollinators, which makes plants depending on biotic pollination particularly susceptible to the negative consequences of habitat fragmentation (Aguilar et al. 2006). To ensure effective pollen exchange between habitats, it is highly important to foster the movement of pollinating insects by creating wildflower strips or hedgerows in unsuitable matrix (Van Geert et al. 2010; Menz et al. 2011; Fig. 1). Depending on the type of dispersal or pollination mechanism and the group of organisms acting as dispersal and pollen vectors, the level of structural connectivity necessary for ensuring functional connectivity may substantially vary, which needs to be carefully considered during restoration planning (Menz et al. 2011; McConkey et al. 2012).

#### Delayed Responses of Species and Genetic Diversity to Landscape Change

Extinction threshold is a critical amount of habitat in a landscape necessary for species to persist (Ewers & Didham 2006). Estimates of extinction thresholds vary from 5 to 90% habitat loss in the landscape, depending on both the species' responses to habitat fragmentation (sensitivity to habitat area and/or edge effects) and the spatial arrangement of the remaining habitat (Swift & Hannon 2010). Such thresholds are often considered to have a potential for setting targets for habitat restoration (Huggett 2005), indicating minimum viable area required for preserving or introducing species to the landscape. However, it is important to point out that determination of extinction thresholds is complicated by time-delayed responses, as the actual disappearance of species can still take considerable amount of time even if the extinction thresholds are exceeded (Hanski & Ovaskainen 2002; Kuussaari et al. 2009). Thus, Swift and Hannon (2010) warn that below some "restoration threshold," restoration of population size or habitat area would not necessarily prevent extinction. Similar to the delayed response of species to habitat fragmentation, recolonization of habitats after restoration may exhibit time lags. Hence, when assessing the effect of restoration on landscape-scale dispersal, one has to take into account the phenomenon of colonization credit, which encompasses species to colonize a patch following habitat restoration which have not yet arrived at the restoration site, owing to, e.g. poor dispersal ability (Aavik et al. 2008; Cristofoli et al. 2010). Not considering potential time delays in the response of species patterns to improvement of structural connectivity may lead to incorrect inferences about the consequences of restoration for landscape-level dispersal of propagules.

Genetic tools can provide valuable information about the level of dispersal following habitat restoration. Nevertheless, similarly to the dynamics of species richness, time lags may be present in the response of genetic patterns to the change

of habitat conditions and landscape connectivity (Helm et al. 2009; Vranckx et al. 2012; Münzbergová et al. 2013; Plue et al. 2017). It has to be noted that the method, which is used for assessing landscape-scale dispersal, should fit the spatial and temporal scale of the study because different measures of genetic diversity and gene flow can reflect processes at varying time scales (Anderson et al. 2010). For example, genetic distances (e.g. genetic differentiation  $F_{ST}$ ) between populations, which are often used as proxies for gene flow, rather mirror historical gene flow. Such measures may therefore be unsuitable for assessing the effect of recent restoration measures on the recovery of functional connectivity (Holderegger et al. 2010; Dyer 2015). In contrast, measures of contemporary gene flow, such as assignment tests or parentage analysis (Manel et al. 2005), may be more appropriate for assessing the effect of recent restoration events on landscape-scale dispersal (Jacquemyn et al. 2010; Aavik et al. 2013). The relative influence of time lags on the observed patterns of plant genetic diversity has remained largely unexplored and therefore deserves more attention in future studies (Manel & Holderegger 2013).

#### Tools for Assessing Landscape-Scale Dispersal in Restoration Context

Estimating the structural and functional connectivity of the landscape and observing the effects of restoration on the effectiveness of landscape-scale dispersal should be an integral part of both restoration planning as well as monitoring schemes (Watson et al. 2017). Indicators of the surrounding landscape and species pool composition will help to set realistic restoration goals, advise about necessary restoration measures, and make veritable assumptions about actual restoration success (De Bello et al. 2010; Török & Helm 2017). Below, we outline the ecological and genetic approaches most commonly used for informing restoration about landscape-scale dispersal (explained more depth in Table 1).

Measuring dispersal of seeds and pollen in landscape scale has always been a challenging task. Direct measurements of dispersal have usually been carried out by trapping and/or tracking propagules and pollen (or its analogs, e.g. fluorescent dye) (Bullock et al. 2006; Carlo et al. 2009; Van Rossum & Triest 2012; Herrmann et al. 2016). Various life history traits such as plant height, seed mass, terminal velocity, dispersal mode, or fruit and seed morphology have been shown to be strongly linked to dispersal or colonization ability (Tamme et al. 2014; Baeten et al. 2015). Thus, indirect estimates of dispersal have been developed by using species life history traits for building mechanistic models predicting seed dispersal distances, shape of seed dispersal kernels and seed-dispersion patterns (Thomson et al. 2010; Tamme et al. 2014; Bullock et al. 2017). A variety of ecological methods that allow indirect estimates of dispersal in restoration context involve mapping and modeling of realized and potential distribution of target species in landscape around restoration areas and comparison of taxonomic and functional dissimilarity of communities within landscape

to evaluate functional connectivity (Donath et al. 2003; Thiele et al. 2017). In any case, knowledge about dispersal-related characteristics of target species (e.g. dispersal distance and dispersal mode), their distribution and composition in the landscape, as well as in the existing landscape conditions surrounding the restoration areas allows to considerably improve planning of landscape elements that are necessary for enhancing functional connectivity (Lewis et al. 2017; Thiele et al. 2017; Török & Helm 2017).

In addition to ecological methods, the toolbox of genetic methods for evaluating landscape-scale dispersal has never been as versatile as now (Table 1, Angeloni et al. 2012; Williams et al. 2014; Keller et al. 2015; Mijangos et al. 2015). In restoration ecology, measures of genetic diversity within plant populations have generally been used for evaluating the fitness potential of plants (Leimu et al. 2006; Mijangos et al. 2015). Nevertheless, as demonstrated in previous sections, genetic diversity of plant populations at restored sites may also inform about seed and pollen flow into the focal habitat from other surrounding habitats (DiLeo & Wagner 2016). Landscape-scale dispersal can be inferred from the measures of gene flow either (1) indirectly, assessing genetic distances (e.g. genetic differentiation  $F_{ST}$ ) between populations as a proxy for gene flow, or (2) directly, using assignment tests (Manel et al. 2005; Table 1). Landscape genetics is an evolving discipline, which links the measures of genetic diversity and gene flow with structural variation of a landscape and can hence provide valuable information about the restoration and monitoring of functional connectivity (Holderegger et al. 2010; Baguette et al. 2013; Bolliger et al. 2014; Watson et al. 2017). First, landscape genetics can help to determine the dispersal capacity of species (e.g. Mosner et al. 2012) as well as to assess which landscape elements enhance or inhibit dispersal (Aavik et al. 2014b; Favre-Bac et al. 2016). This information, in turn, can guide restoration planning toward establishing an optimal structural connectivity of habitats. Second, landscape genetics can also be used for assessing the effectiveness of restoration measures (Ritchie & Krauss 2012; Aavik et al. 2013; Reynolds et al. 2013).

Until recently, microsatellites (simple sequence repeats in generally noncoding part of the genome) were the main choice of genetic markers in studies of conservation and restoration genetics. However, due to significant methodological advances, detection of thousands of single nucleotide polymorphisms (SNPs) occurring all over the genome in noncoding regions as well as within or near regions of adaptive relevance has become now more feasible and affordable not only in fundamental research, but also in studies of conservational relevance (Benestan et al. 2016; Puckett 2017). However, although genetic toolbox has significantly improved due to high throughput molecular methods, restoration research rarely makes use of such data (Driscoll et al. 2014). We encourage researchers to exploit these tools for assessing adaptive genetic diversity of restored populations as well as of plant material used in restoration for achieving high evolutionary potential of restored populations (Shryock et al. 2017). On the other hand, studying neutral genetic diversity with the help of microsatellites or SNPs from noncoding part of the genome can provide valuable information

for planning restoration measures and for assessing restoration success in recovering landscape-scale dispersal (Michalski & Durka 2012; Helsen et al. 2013; Bolliger et al. 2014).

### Monitoring Restoration Success Provides Support for Ecological Theory

It is vital that ecological theory provides support for evidence-based restoration practices (Török & Helm 2017). However, restoration activities can also provide valuable information for improving various ecological theories. For example, it has been suggested that similar processes may govern the development of species diversity within a community and within-population genetic diversity, leading to the positive correlation between these two levels of biodiversity at local scale (Vellend 2005; Vellend & Geber 2005; Struebig et al. 2011; Taberlet et al. 2012). This ongoing debate, which is still largely theory-based, could gain a lot from simultaneous observations of the change in species and genetic diversity in response to the recovery of landscape structure and habitat conditions. Pre- and post-restoration monitoring of landscape-scale dispersal can provide additional insight into the understanding about colonization capacity and dispersal distance of species (Herrmann et al. 2016). Comparing data from pre- and post-restoration state may provide valuable information on the ability of species to track climate change.

### Conclusions

Although molecular tools have revolutionized fundamental research in ecology and evolutionary biology during the last decades, genetic methods are still underutilized in practical restoration activities (Mijangos et al. 2015). In most restoration projects, we lack knowledge if the visible target of restoration—the recovery of species diversity—will also bring along a parallel increase in the invisible, yet important genetic diversity. Owing to projected human-induced climate change, many species will be facing novel environmental conditions in the future (Chen et al. 2011). Coping with these changes depends on species ability to adapt to novel environments as well as to track the change in environmental conditions by dispersing propagules and pollen to favorable habitats. In the era of vast global changes, it is thus important that restoration aims to (1) maintain and restore plant populations with high evolutionary potential and (2) create landscapes fostering the movement of potentially beneficial genotypes, which help to cope with environmental pressures. For achieving these goals, we argue that, in addition to restoring characteristic species composition in restored habitats, it is also critical to consider diversity at the genetic level and to foster the landscape-scale dispersal of individuals and genes.

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