

## Discussion

## Ecological theory provides strong support for habitat restoration

Peter Török <sup>a,\*</sup>, Aveliina Helm <sup>b</sup><sup>a</sup> MTA-DE Biodiversity and Ecosystem Services Research Group, 4032 Debrecen, Egyetem sq. 1, Hungary<sup>b</sup> Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, 51005 Tartu, Estonia

## ARTICLE INFO

## Article history:

Received 18 August 2016

Received in revised form 18 December 2016

Accepted 21 December 2016

Available online xxxx

## Keywords:

Colonisation credit

Dispersal

Extinction debt

Grassland restoration

Landscape heterogeneity

Species pool

## ABSTRACT

The involvement of ecological theory in habitat restoration has significantly increased in the past decade. However, despite the fact that the field of restoration ecology has grown academically strong in recent years, there are still visible gaps between the advancing discipline of theoretical ecology and current approaches of habitat restoration. We propose bridging these gaps by linking recent developments in theoretical plant ecology with the main questions every restoration practitioner should ask, namely: Q1) How to identify target species and baseline conditions for restoration of the selected habitat?; Q2) When can one count on spontaneous dispersal and when are additional efforts required for facilitating dispersal of desired species?; Q3) Which factors determine the successful establishment of target species and assembly of target communities?; and Q4) What time-scale needs to be considered for the evaluation of species colonisation and restoration success? Knowledge and experience accumulated in practical restoration can considerably benefit theoretical ecology for example by improving the understanding on (i) temporal changes in community, (ii) species assembly, (iii) species dispersal and establishment and (iv) landscape-scale dynamics of biodiversity. We emphasise that to improve joint thinking of practical restoration and theoretical ecology, restoration-problem-driven theoretical research is necessary. We suggest either (i) to translate and link the current findings of theoretical ecology to restoration strategies; and/or (ii) to summarise practical restoration needs by formulation of questions and testable hypotheses based on theory.

© 2016 Elsevier Ltd. All rights reserved.

## 1. Introduction

During the past century, most ecosystems have faced large-scale degradation as a result of increasing influence of agriculture, urbanisation, climate change and other human-related factors (Bakker and Berendse, 1999; Walther et al., 2009; Bullock et al., 2011; Steffen et al., 2015). To ensure a sustainable future, biodiversity conservation approaches must start shifting from traditional, often rather passive site preservation and small-scale site-level restoration to the direction of large-scale, holistic restoration and conservation efforts, grounded on a solid theoretical basis (Higgs et al., 2014; Perring et al., 2015).

The involvement of ecological theories in habitat restoration has significantly increased in the past decade, and a scientific framework for restoration has been established (Society for Ecological Restoration International Science & Policy Working Group, 2004). While the field of restoration ecology has grown academically strong, there are still visible gaps between advancing ecological theory and the actual approaches used during habitat restoration. Lack of strong application of ecological theory in habitat restoration and vice versa, application of

practical restoration experience to ecological theory, could be caused by insufficient communication between theoretical ecologists, restoration ecologists and practitioners. Problems and questions arising in practical restoration seldom find their way to theoretical works. Similarly, highly relevant but mostly rather complicated ecological theories are often not 'translated' into practically applicable solutions for restoration practitioners. The necessity of establishing a stronger scientific foundation for habitat restoration has already been emphasised by several authors (Young et al., 2005; Temperton, 2007; Perring et al., 2015). Similarly, although ecological restoration has long been recognized as 'the acid test of ecological theory', theoretical ecology does not fully exploit the opportunities offered by habitat restoration for testing ecological concepts and theories in the field (Bradshaw, 1987; Young et al., 2005).

We bridge these conspicuous gaps between practice and theory by linking recent theories in theoretical plant ecology with the main questions every restoration practitioner should ask: Q1) How to identify target species or baseline conditions in restoration for the selected habitat?; Q2) When can one count on spontaneous dispersal and when are additional efforts required for facilitating dispersal of desired species?; Q3) Which factors determine the successful establishment of target species and assembly of target communities?; and Q4) What

\* Corresponding author.

E-mail address: [molinia@gmail.com](mailto:molinia@gmail.com) (P. Török).

time-scale needs to be considered for the evaluation of species colonisation and restoration success? Being able to answer these questions not only positively influences the restoration outcome, but also helps in restoration planning (i.e. community and method selection), the implementation of habitat restoration and strongly supports the issues of sustainability (Fig. 1). In the second part of the paper we explore how restoration can contribute to refinement of or testing of ecological theories and we provide guidelines for future research.

We used Palaearctic grasslands as model communities for explaining theories, for several reasons. First, they cover a wide range of habitats characterised by diverse environmental conditions and have a considerable extent in the Palaearctic realm (Dengler et al., 2014; Dixon et al., 2014; Wesche et al., 2016). Second, they have a high conservation and restoration interest and harbour an extremely high biodiversity (Wilson et al., 2012). Finally, there has been a great deal of both theory and restoration driven research in Palaearctic grasslands in the last decades (Kiehl et al., 2010; Török et al., 2011; Dengler et al., 2014; Helm et al., 2015; Valkó et al., 2016).

## 2. How to identify target species and baseline conditions in restoration for the selected habitat?

Central goals of habitat restoration are (i) the establishment of a self-supporting ecosystem that is highly resistant and resilient to perturbation (Ruiz-Jaen and Mitchell Aide, 2005) or (ii) establishment of an ecosystem that can be managed in a sustainable way (i.e. semi-natural grasslands traditionally maintained by extensive mowing or grazing; Dengler et al., 2014; Kelemen et al., 2014). Most often, these goals are expected to be achieved through the restoration of species composition and functioning similar to the targeted reference habitat or to some kind of agreed baseline. Baseline or reference habitat is usually defined by the historical state or by using contemporary examples from good-quality target habitat (SER International Science & Policy Working Group,

2004). As technical reclamation is often expensive, it is vital for practitioners to find the most cost-effective, yet most efficient method for restoration by aiming for the most realistic restoration target and considering also the initial habitat conditions of potential receptor sites (Fig. 1).

The ambiguity in the determination of target habitat already provides the first obstacle for practitioners to overcome. It is increasingly difficult to identify reference habitat or the set of target species in a quickly changing environment where the historical conditions or ecological characteristics of the surrounding landscape are almost impossible to meet (Higgs et al., 2014). This obstacle can be overcome by engaging the *species pool concept* (Zobel et al., 1998; Pärtel et al., 1996; Zobel, 2016) and desirable species composition for restored habitats can be found by identifying the composition of a habitat specific species pool. The *habitat specific species pool* is a set of species that occur naturally in the given region and that are able to disperse to, establish, survive and reproduce in a particular site or habitat (Zobel, 2016).

The success and the speed of habitat recovery are strongly influenced by the availability of species in the surrounding landscape. Identification of the composition and size of habitat specific species pool provides knowledge of which species are to be expected to arrive at the habitat being restored and helps to set measurable goals for restoration and to help quantify success (Lewis et al., 2016). The size of the species pool is strongly related to local species richness (Pärtel et al., 1996; Tschamtké et al., 2012) and thus also to the expected diversity of the restored habitat site. For example, European calcareous grasslands usually have large species pools, i.e. there have historically been many species in the region that are suitable for such environmental conditions, rendering their historically characteristic local species richness high. Conversely, oligotrophic heaths have very few suitable species in their species pool. Thus, when setting restoration goal, these differences must be taken into account.

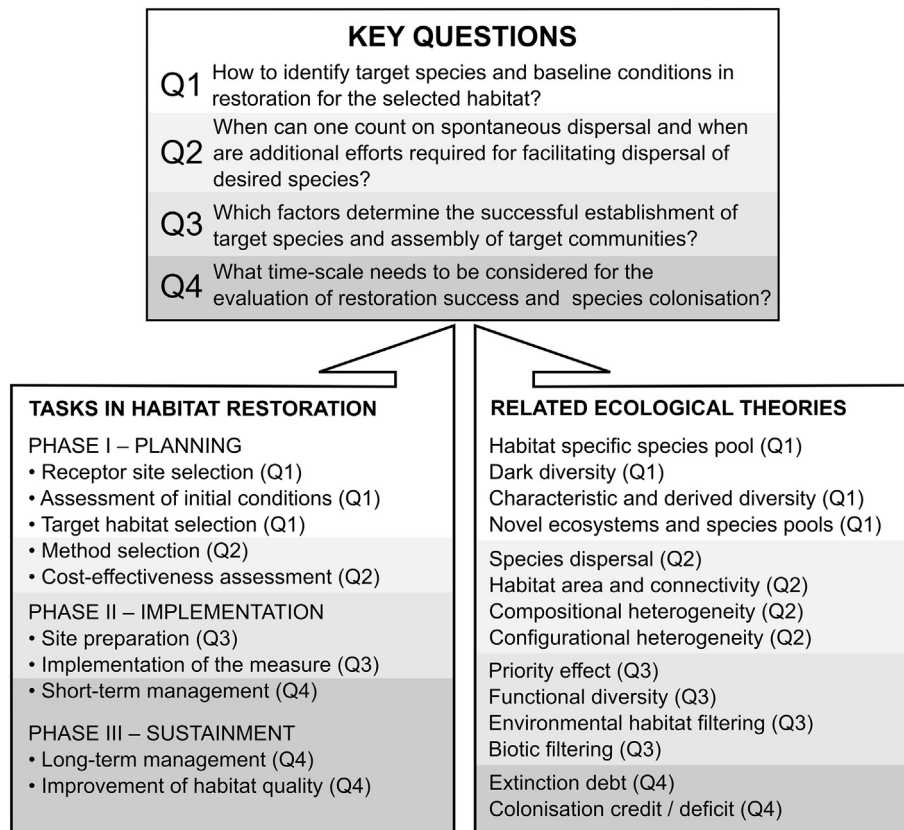


Fig. 1. A practice-driven link between habitat restoration and theoretical plant ecology: Key questions to be answered during habitat restoration

Similarly, knowledge about the species pools should be used while evaluating and monitoring restoration success. To take into account this variability in species pool sizes, and thus also in the expected restoration result, we can use concept of dark diversity and index of community completeness (Pärtel, 2014). *Dark diversity* is a set of species that are in the historically developed habitat-specific species pool for a particular site, but are currently absent (Pärtel et al., 2011). During restoration, all species from the species pool that have not yet arrived at the restoration site belong to dark diversity. The *Index of community completeness* is calculated as the logistic expression,  $\ln(\text{observed richness}/\text{dark diversity})$  and it expresses in relative terms how many species out of the total species pool are already present at the site and how many are in the dark diversity (Pärtel, 2014). An increase in value of the community completeness index should be the goal of every habitat restoration project.

Species pools can be estimated from information available for species geographical distribution, habitat requirements and dispersal abilities. In recent years, a number of publications have focused on the methodology of determining the composition of species pools, whether using binary thresholds (belonging or not belonging to particular species pool, e.g. Lewis et al., 2016; Helm et al., 2015; Pärtel et al., 2011) or probabilistic approaches (a species is part of a species pool for particular habitat with some kind of probability ranging from 0 to 1, e.g. Lessard et al., 2016; Karger et al., 2016). By acknowledging and identifying the composition of the species pool and thus identifying and recognising the amount and identity of species available for the restored habitat, we can set more realistic goals for restoration, or when deemed necessary, re-introduce the species to a deteriorated species pool and the restored site.

Often, there are also a number of species arriving at the restored habitat that do not belong to the habitat-specific species pool for a particular habitat, either being non-native or being more characteristic of other habitat types in the region. Thus, *total species richness* per se is not a suitable indicator for restoration needs or targets, and that following the restoration, we should be very cautious in interpreting the change in total species richness values. Thus, we advocate the use of a more ecologically reasoned approach that separates total species richness into two parts: the *characteristic diversity* i.e. characteristic species for the restoration target reference community, and the *derived diversity* i.e. other species, which are either problem plants or plants characteristic of other non-target habitat types (Helm et al., 2015). Most restoration actions should be focused on increasing the number and abundance of the first group, often referred to in restoration ecological terminology as ‘target species’ and suppress and/or prevent the establishment of the second group.

Ongoing climate change adds another angle of complexity to restoration ecology. Implications of changing climate should also be taken into account as much as possible during practical restoration in order to ensure the development of sustainable ecosystem (Harris et al., 2006). One theoretical solution that could have its direct influence on practical restoration would lie in our improved ability to predict the composition of novel species pools for altered environmental conditions (Hobbs et al., 2014a, b; Kasari et al., 2016). Novel species pools would include species that are expected to be part of ecosystems under changed conditions (Kasari et al., 2016). They can theoretically be both natives but also non-natives that are expected to increase/shift their range with changing climate. It may be potentially contentious to start introducing new ‘suitable’ species during restoration and hence go down the road of assisted migration. Hence, knowledge of the species and trait composition of novel species pool would allow us to foresee which species are less likely and which species are more likely to persist and contribute to a restored community in the future.

### 3. When can one count on spontaneous dispersal and when are additional efforts required for facilitated dispersal of desired species?

The assigned costs and implementation facility (i.e. machinery, manpower) for restoration actions are usually limited – most cases

restoration actions are funded by a private company or government, which expect results and successes. Thus, it is important to know which methods can be most easily and cost effectively applied. In such decisions, considering the surrounding landscape structure and composition is critical. It helps to assess whether it is possible to rely on spontaneous dispersal in restoration or whether species transfer by technical methods is needed to achieve the desired outcome. During the past decade, the importance of incorporating landscape context to both conservation management and habitat restoration has been stressed by several authors, because factors that determine the diversity, resistance and resilience of natural communities often operate at the landscape scale (Tscharrntke et al., 2012; Auffret et al., 2015). However, until recently, landscape context has rarely been considered in restoration planning. It is important to stress that the (i) *total area and connectivity of habitats* in the landscape, (ii) *landscape compositional heterogeneity* (i.e. larger variety of different habitat types) and (iii) *configurational heterogeneity* (i.e. spatial arrangement of habitat patches) have significant effects on species dispersal patterns and on local biodiversity (Fahrig, 2003; Fahrig et al., 2011, Tscharrntke et al., 2012; Dengler et al., 2014). For grassland plants, Loos et al. (2014) found that local plant species diversity was highly dependent on grassland area and continuity, and have also emphasised the importance of the mosaic character of the landscape. Duflot et al. (2014) showed that landscape heterogeneity, i.e. diversity of habitat types, and the area of the dominant habitat type in the landscape were the main predictors for functional composition and dispersal traits of grassland plant communities. In addition to plants, habitat connectivity, landscape heterogeneity and habitat area have been shown to be important to diversity of a number of animal groups (Kormann et al., 2015; Rösch et al., 2013; Brückmann et al., 2010). Restoration success can also be strongly influenced by the size and shape of the restoration site; large sites without adjacent grassland patches are less likely to be colonised than small sites with neighbouring grasslands (Cousins and Lindborg, 2008).

However, not all species are similarly affected by landscape structure and habitat spatial composition, and those species that are most susceptible to habitat loss and fragmentation are often the ones that need the most active approaches during habitat restoration. Species dispersal likelihood, local persistence and competitive ability are among the main life-history traits that determine species capacity to persist following habitat fragmentation or to re-colonise restoration sites (Redhead et al., 2014). Species dispersal is limited in space and for many grassland plants, the realistic dispersal range is only up to a few hundreds of metres (Turnbull et al., 2000; Cousins and Lindborg, 2008). Thus, for spontaneous recovery, proper seed sources for an effective dispersal in the nearest vicinity of the restored habitat are crucial (Benayas et al., 2008). Nearest vicinity for grassland plants can be considered as being in the direct contact with restored area with up to few hundred metres (Prach et al., 2015). For example, in the ten years following restoration Donath et al. (2003) recorded the colonisation of target species to new areas only if the sources were closer than 50 m (mostly even less than 20 m). At maximum, the distance to possible seed sources should not be more than 1 km, as it is highly unlikely that migration or gene flow will occur over larger distances (Aavik et al., 2013; Prach et al., 2015). When there are no seed-sources nearby, species transfer is required, preferably from natural populations in the same region (Mijnsbrugge et al., 2010; Aavik et al., 2013). In small isolated habitats where exchange of genetic material with other populations is unlikely, species transfer needs to be repeated over several consecutive years for building up and maintaining viable and genetically diverse populations. The latter is especially important for species with relatively good dispersal abilities and with special dispersal vectors as they have historically benefited the most from well-connected meta-communities (Saar et al., 2012; Soons and Heil, 2002) and due to the trade-off between local competitive ability and dispersal ability (Westoby et al., 1996), they are relatively less favoured in current landscapes and in more nutrient rich conditions nowadays. For the assessment of dispersal capacity of



plant species, one can use a model by Tamme et al. (2014) that predicts seed dispersal distances from simple plant traits.

Lack of suitable dispersal vectors can considerably hinder the successful colonisation of species. A number of plant species have propagules with special adaptations for dispersal, e.g. awns and hooks for attaching to mammalian fur, or special structures (e.g. pappi) for being carried by wind. Ozinga et al. (2009) showed that species with adaptations for dispersing via water or that use the fur of mammals for dispersal are over-represented among declining species in NW Europe. Many grassland species in Europe are adapted to disperse with the help of animals, whether in fur (Fischer et al., 1996) or via dung (Malo & Suárez, 1995). Spatially too concentrated grazing, lack of landscape-scale movement of animals (either wild or domesticated) between habitat patches can substantially hinder the dispersal patterns and success of restoration and persistence of species diversity (Bakker & Berendse, 1999).

Considering and understanding landscape-scale patterns and dispersal processes allow the identification of suitable restoration sites and aim for better restoration outcome (Auffret et al., 2015). For background information, there is a magnitude of literature tackling the effect of landscape-scale factors on biodiversity. For example, detailed review and methods for quantifying landscape scale factors on local and landscape-scale species richness are provided by Fahrig et al. (2011). Kumar et al. (2006) have proposed a general methodology for the assessment and quantification of spatial heterogeneity and to evaluate its role in influencing patterns of habitat diversity.

#### 4. What determines the successful establishment and assembly of target species?

Habitat history, site conditions, severity of disturbance and existing species composition can influence the structural development of restored communities and their “openness” to colonisation (Montoya et al., 2012; Eriksson et al., 2006; Walker et al., 2014). Understanding the accompanying factors related to assembly rules, i.e. constraints to species co-existence, are highly relevant in restoration (Götzenberger et al., 2012; Montoya et al., 2012). If the arrival of species is not limited by the availability of seed sources, or when species are directly transferred, species establishment is driven by the abiotic conditions of a given site (i.e. *environmental habitat filtering*) or by the respective species assemblage at the site (i.e. *biotic filtering*) (Lhotsky et al., 2016). During environmental filtering, species with more or less similar functional characteristics are favoured, leading to a functionally less diverse community (Lhotsky et al., 2016; de Bello et al., 2012). To take into account environmental filtering and recognize species that are filtered due to environmental conditions, one can consider the patterns of species habitat preferences (e.g. Ellenberg indicator values, Diekmann, 2003). For example, if community is dominated by species with low light requirement, it indicates the environmental filtering out of species that prefer more light.

Biotic filtering is a process where biotic interactions, e.g. competition or facilitation drive the species co-existence (Mittelbach, 2012). One of the crucial mechanisms in biotic filtering is the *priority effect of species establishment*. Priority effects occur when the species that arrive first affect the establishment, growth or reproduction of species arriving later mostly via (i) size-asymmetric competition, (ii) soil modification by plant-soil feedback, or by (iii) nitrogen facilitation in the case of initially colonising legumes (von Gillhausen et al., 2014). This means that changes in the composition of spontaneous seed dispersal or manipulation of the order of arrival of species via propagule addition can create alternative successional pathways, change community composition and assembly and community functioning (Körner et al., 2008; von Gillhausen et al., 2014). *Functional diversity* is considered to be important in maintaining ecological processes and services (Cadotte et al., 2011). For example, community stability has been shown to be related to the number of species with different functional characteristics

(Biswas and Mallik, 2011). In most natural communities, functional groups are generally represented by multiple species, enabling the community to retain important ecosystem functions in case of decreasing diversity and the loss of some species (i.e. high functional redundancy, Török et al., 2016).

Although we are not yet able to fully orchestrate ecosystem development via trait-based ecosystem engineering, the trait-based approach can help to maximise the ecosystem functions and services following restoration (Pywell et al., 2003). Recently, functional indicators have been developed to assess and monitor success of restoration actions (de Bello et al., 2010; Engst et al., 2016). Currently, the potential of the trait-based approach both in restoration planning and for restoration monitoring has been clearly underused. Functional trait composition of the restored habitat should ideally represent the whole range of traits available in the species pool for the particular habitat (Botta-Dukát and Czúcz, 2016; de Bello et al., 2010). Dominance of certain trait values (e.g. more tall-growing species or higher abundance of monocots and shrubs compared to random expectation selecting from the potential pool of species) can provide a warning signal of the failure to re-create a diverse community and indicate the need for immediate management intervention or other action.

#### 5. What time-scale needs to be considered for the evaluation of restoration success and species colonisation?

Restoration is not a fast process, although promising results within a short timeframe are often expected by funders. Thus, rapid species colonisation and increase in species diversity is often required and expected following restoration activities. In most restoration projects, the monitoring period is relatively short (often also due to funding issues), resulting in short timeframes for scientific studies that evaluate restoration success and sustainability (Lengyel et al., 2008). How the desirable state of the restored community is sustained over a longer period, is often not studied and not known (Kelemen et al., 2014). However, this kind of knowledge is already crucial in the planning phase of restoration actions (Török et al., 2011).

Spontaneous development of characteristic community composition and high diversity is often a long-term process that can take decades (Fagan et al., 2008). Local species diversity in grasslands has built up over centuries and even millennia, first by the impact of wild ungulates and later by moderate management, enhancing species dispersal and facilitating metapopulation dynamics within habitats (Dengler et al., 2014; Hanski and Ovaskainen, 2000). For example, plant species diversity in grasslands have been shown to be related to past human impacts of up to 1000 years ago (Bruun et al., 2001; Pärtel et al., 2007), indicating very slow species diversity dynamics which makes it challenging to observe and estimate restoration success (Dullinger et al., 2012; Dengler et al., 2014).

There are considerable time lags detected in species extinctions following environmental change, termed “extinction debt” (Hanski, 2000). *Extinction debt* develops because populations do not respond immediately to changing conditions due to their slow dynamics, but persist for some time despite unsuitable conditions (Kuussaari et al., 2009; Hylander and Ehrlén, 2013). If left disregarded and unaccounted, delays in species response to environmental changes can lead to considerable loss of biodiversity and complete failure of conservation activities. The magnitude of already triggered extinctions is considered by some authors to be massive. According to Dullinger et al. (2012), a large proportion of threatened species in Europe are currently in extinction debt. For example, Helm et al. (2006) estimated extinction debt to occur for ca 40% of habitat characteristic plants in Estonian grasslands. Kitzes and Harte (2015) estimated extinction debt to occur for 30–50% of bird species in the world’s biodiversity hotspots. However, time lags also provide an opportunity to avoid extinctions that have already been destined to occur and to save species before the debt is paid. Hylander and Ehrlén (2013) argued that, depending on the key factors behind

the development of extinction debt, different actions should be implemented for successful restoration. Threat of future extinctions due to changed environmental conditions requires rapid improvement of local habitat quality, extinctions due to small population size require enlargement of habitat area and loss of metapopulation structure requires the increase of habitat connectivity. However, these factors often work hand-in-hand, thus it is important to ensure that suitable habitat quality, large habitat area and sufficient connectivity have been achieved during restoration.

Similarly to delays in already triggered extinctions, expected colonisations can take a considerable amount of time following restoration (Jackson and Sax, 2010; Cristofoli et al., 2010). Delays in colonisations, termed as *colonisation credit* or *colonisation deficit*, have previously been studied in invasion ecology and in relation to climate change (Menéndez et al., 2006), but this has been recently recognized as a topic of high importance in habitat restoration (Ozinga et al., 2009; Gijbels et al., 2012; Cristofoli et al., 2010; Naaf and Kolk, 2015). Colonisation credit is the number of species yet to colonise a suitable habitat (Jackson and Sax, 2010). Delay in species colonisation to suitable habitat is caused by the slow and random nature of seed dispersal and establishment success. Similarly to extinction debt, that is often related to habitat spatial configuration and habitat fragmentation (Helm et al., 2006; Lindborg and Eriksson, 2004), colonisation credit can be attributed to factors acting at a landscape-scale. Time of arrival for different species can be dependent on habitat availability in the surroundings (Bagaria et al., 2015; Naaf and Kolk, 2015), magnitude of habitat area loss (Piqueray et al., 2011), presence of mutualistic assemblages such as pollinators or mycorrhiza (van der Heijden et al., 1998; Gijbels et al., 2012) or availability of suitable dispersal vectors (Ozinga et al., 2009). Different species respond differently to abovementioned factors, depending on species individual characteristics (species traits). Species with poor dispersal abilities or with necessity for use specific dispersal vectors, species with limited competitive ability and rare species are expected to establish larger colonisation credit. As with extinction debt, colonisation credit can take decades or centuries before it is 'paid'. Naaf and Kolk (2015) studied colonisation of forest species in younger and older forest patches and found that colonisation credit can last up to 230 years. Gjerde et al. (2012) found, for young forest patches, that colonisation of epiphytic lichens can take up to 100–150 years before same diversity levels are achieved as in old patches. Cristofoli et al. (2010) found that in wet heathland plant communities, colonisations had occurred relatively rapidly following restoration (in less than 25 years), but for some species groups, colonisations were delayed for more than 25 years and smaller habitat patches experienced a greater delay.

Possible methods for evaluating the existence of extinction debt include monitoring of the population characteristics e.g. changes in population size, fitness or in genetic diversity, or evaluating community parameters, whether testing the relationship between current diversity parameters and past habitat configuration or environmental conditions (Kuussaari et al., 2009) or by using the measurements of abundance distributions and species spatial patterns in communities (Kitzes and Harte, 2015). Assessing the magnitude of colonisation credit and identification of the species potentially inhabiting the site requires quantification of the habitat suitability for the species that occur in the region. The dark diversity concept, described above, provides an opportunity to quantify the set of potential colonizers (Pärtel et al., 2011). Providing that there is sufficient time for monitoring of restoration success, lasting at least a decade (but ideally longer) following the restoration, it is possible to track the arrival time for different species.

Changing climatic conditions are necessary to take into account as much as possible under current knowledge. Information provided by climate-change studies and respective scenarios can help to set more realistic goals as well as to work towards the mitigation of climate change effects (Harris et al., 2006). Information about novel species pools (described above) during monitoring process could help to adjust

the restoration targets, enables to recognize species and habitats for which conditions have become unsuitable and allows timely detect deviations in the successful recovery.

## 6. How can restoration support ecological theory? – conclusions and outlook

As we pointed out in the former sections, the visible knowledge gap between theoretical ecology and practice driven restoration still exists – caused mostly by the different approaches combined with insufficient communication – but it can be bridged by theory-driven restoration (see also Laughlin, 2014). However, it is not only practical restoration that can benefit from the advances in theoretical ecology: implemented activities during habitat restoration also provide an excellent playground for testing various ecological concepts and theories in 'real world' conditions. Increasing magnitude of habitat restoration activities have revealed, and will continue to reveal, a number of practical, principal and conceptual questions and challenges that also boost and direct theoretical ecological research (Young et al., 2005).

During the past decades many practical grassland restoration projects have been implemented in Palaearctic grasslands. By using the search filters of 'restoration measure' and 'grassland ecosystems', query in the database of EU-funded LIFE projects leads to 118 funded projects between 1992 and 2016 (EU Life Program, 2016). Most of these and also other restoration projects aim to manipulate site-level conditions and to facilitate the establishment of a functioning target community by using species transfer and improved local propagule availability (Young et al., 2005). Similarly, most habitat restoration related research has been conducted to understand the role of local processes and habitat properties (i.e. site level filters) on species establishment and target grassland recovery, while landscape-scale approach on restoration has been very rarely addressed (Brudvig, 2011). In Europe, several large-scale grassland restoration projects have been conducted and reported during the last decades (Lengyel et al., 2012; Prach et al., 2013; Pywell et al., 2011), but only a small fraction of these habitat restoration activities were carried out while considering landscape level factors, land use changes or habitat history (Brudvig, 2011). However, most grassland restoration projects conducted so far are able to provide information about (i) initial habitat conditions (e.g. soil properties), (ii) species transfer rates (number and identity of transferred target species and reference habitat species), (iii) data on the spread or suppression of problem species, and data (iv) on the measures and techniques used for site preparation, species transfer or short- and long-term post-restoration management (Kiehl et al., 2010; Török et al., 2011). By compiling and analysing this kind of information, theories linked to local species establishment and assembly rules can be tested and improved.

To conduct better and more informed research both in restoration ecology and in theoretical ecology, and for obtaining better restoration results, we suggest that international/continental scale databases containing thorough information about restoration projects and about the results and methodology of their monitoring are necessary. Large scale databases already exist for example for plant traits, encompassing a huge number of species (Kattge et al., 2011). For the restoration database, the very first steps have already been taken by the launch of the SER Europe Knowledge Base (<http://chapter.ser.org/europe/knowledge-base/overview/>).

It is highly desirable that every theoretical ecologist would at least to some extent participate in practical nature conservation activities, leading to better link between disciplines and improved communication. More active participation of theoretical scientists in conservation works can be facilitated by scientists themselves wanting to improve the link between theory and practice. However, it can also be facilitated by improved requirements in restoration projects, demanding the inclusion and participation of actively publishing scientists.

Knowledge and experience accumulated in practical restoration can considerably benefit theoretical ecology by improving the understanding of (i) temporal changes in community (e.g., state transitions; habitat succession and effect of different starting conditions, convergent and divergent vegetation development; determinants of species turnover; priority effect vs. 'year' effects; time-lags in community dynamics); (ii) species assembly (e.g. functional diversity vs. species diversity; community and ecosystem stability; functional diversity and functional redundancy; keystone species; community structure and functioning); (iii) species dispersal and establishment (e.g. dispersal vs. establishment limitation); (iv) landscape-scale dynamics of biodiversity (e.g. landscape-scale determinants of genetic diversity, functional and phylogenetic diversity). However, these are only few examples where experiences from habitat restoration can boost theoretical research (see also Young et al. 2005, Palmer et al., 1997, and Temperton, 2007).

We emphasise that for increasing joint thinking and improving the outcome of both practical restoration and theoretical ecology, ecological research must focus more on untangling the issues that arise during restoration. Focused theoretical research that would solve the difficult practical problems frequently occurring in ecological restoration would not only increase our understanding of community assembly and functioning, but also would improve the practical implementation of restoration. For example, detected differences, failures or even successes in target species establishment and the linkages to ecological assembly rules may facilitate the development of adaptive trait-based multispecies seed mixtures, improve cost-effectiveness of restoration and help to create resilient ecosystems in the light of global changes.

In conclusion, differences and gaps between typical practice-driven, time and resource limited actions of ecological restoration and theoretical research are still visible. However, considerable improvement would arise if in future we could (i) translate and link the current findings of theoretical ecology to restoration strategies; and (ii) to summarise the practical needs of restoration to obtain support from theoretical ecology.

## Acknowledgements

The authors are thankful to R. Pakeman, O. Valkó and an anonymous reviewer for the comments made on an earlier draft of the paper. The first author thanks NKFIH K 119 225 for grant support and colleagues of MTA-DE Biodiversity and Ecosystem Services Research Group for fruitful discussions. A.H. was supported by the Estonian Ministry of Education and Research (IUT 20-29) and by the European Commission through the European Regional Development Fund (Centre of Excellence EcolChange). Jonathan Mitchley (University of Reading) kindly improved our English.

## References

Aavik, T., Holderegger, R., Edwards, P.J., Billeter, R., 2013. Patterns of contemporary gene flow suggest low functional connectivity of grasslands in a fragmented agricultural landscape. *J. Appl. Ecol.* 50, 395–403.

Auffret, A.G., Plue, J., Cousins, S.A.O., 2015. The spatial and temporal components of functional connectivity in fragmented landscapes. *Ambio* 44, 51–59.

Bagaria, G., Helm, A., Rodà, F., Pino, J., 2015. Assessing coexisting plant extinction debt and colonization credit in a grassland–forest change gradient. *Oecologia* 179, 823–834.

Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol. Evol.* 14, 63–68.

Benayas, J.M.R., Bullock, J.M., Newton, A.C., 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Front. Ecol. Environ.* 6, 329–336.

Biswas, S.R., Mallik, A.U., 2011. Species diversity and functional diversity relationship varies with disturbance intensity. *Ecosphere* 2, 1–10.

Botta-Dukát, Z., Czúcz, B., 2016. Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. *Methods Ecol. Evol.* 7, 114–126.

Bradshaw, A.D., 1987. Restoration: the acid test for ecology. In: Jordan, W.R., Gilpin, M.E., Aber, J.D. (Eds.), *Restoration Ecology: A Synthetic Approach to Ecological Research*. Cambridge University Press, Cambridge, UK, pp. 23–29.

Brückmann, S.V., Krauss, J., Steffan-Dewenter, I., 2010. Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *J. Appl. Ecol.* 47, 799–809.

Brudvig, L.A., 2011. The restoration of biodiversity: where has research been and where does it need to go? *Am. J. Bot.* 98, 549–558.

Bruun, H.H., Fritzberger, B., Rindell, P.O., Hansen, U.L., 2001. Plant species richness in grasslands: the relative importance of contemporary environment and land-use history since the Iron Age. *Ecography* 24, 569–578.

Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F., Rey-Benayas, J.M., 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends Ecol. Evol.* 26, 541–549.

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087.

Cousins, S.A.O., Lindborg, R., 2008. Remnant grassland habitats as source communities for plant diversification in agricultural landscapes. *Biol. Conserv.* 141, 233–240.

Cristofoli, S., Piqueray, J., Dufrene, M., Bizoux, J.-P., Mahy, G., 2010. Colonization credit in restored wet heathlands. *Restor. Ecol.* 18, 645–655.

de Bello, F., Lavorel, S., Gerhold, P., Reier, U., Pärtel, M., 2010. A biodiversity monitoring framework for practical conservation of grasslands and shrublands. *Biol. Conserv.* 143, 9–17.

de Bello, F., Price, J.N., Münkemüller, T., Liira, J., Zobel, M., Thuiller, W., Gerhold, P., Götzenberger, L., Lavergne, S., Lepš, J., Zobel, K., 2012. Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93, 2263–2273.

Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palearctic grasslands: a synthesis. *Agric. Ecosyst. Environ.* 182, 1–14.

Diekmann, M., 2003. Species indicator values as an important tool in applied plant ecology – a review. *Basic Appl. Ecol.* 4, 493–506.

Dixon, A.P., Faber-Langendoen, D., Josse, C., Morrison, J., Loucks, C.J., 2014. Distribution mapping of world grassland types. *J. Biogeogr.* 41, 2003–2019.

Donath, T.W., Hölzel, N., Otte, A., 2003. The impact of site conditions and seed dispersal on restoration success in alluvial meadows. *Appl. Veg. Sci.* 6, 13–22.

Dufloy, R., Georges, R., Ernoult, A., Aviron, S., Burel, F., 2014. Landscape heterogeneity as an ecological filter of species traits. *Acta Oecol.* 56, 19–26.

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnbock, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J.-C., Psomas, A., Schmatz, D.R., Silc, U., Vittoz, P., Hulber, K., 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat. Clim. Chang.* 2, 619–622.

Engst, K., Baasch, A., Erfmeier, A., Jandt, U., May, K., Schmiede, R., Bruelheide, H., 2016. Functional community ecology meets restoration ecology: assessing the restoration success of alluvial floodplain meadows with functional traits. *J. Appl. Ecol.* 53, 751–764.

Eriksson, O., Wikström, S., Eriksson, A., Lindborg, R., 2006. Species-rich Scandinavian grasslands are inherently open to invasion. *Biol. Invasions* 8, 355–363.

EU Life Program, 2016. LIFE Project Database. Updated: 06/27/2016; Accessed: 07/26/2016. <http://ec.europa.eu/environment/life/project/Projects/>.

Fagan, K.C., Richard, F., Bullock, J.M., Marrs, R.H., 2008. Do restored calcareous grasslands on former arable fields resemble ancient targets? The effect of time, methods and environment on outcomes. *J. Appl. Ecol.* 45, 1293–1303.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.* 14, 101–112.

Fischer, S.F., Poschlod, P., Beinlich, B., 1996. Experimental studies on the dispersal of plant and animals on sheep in calcareous grasslands. *J. Appl. Ecol.* 33, 1206–1222.

Gijbels, P., Adriaens, D., Honnay, O., 2012. An orchid colonization credit in restored calcareous grasslands. *Ecoscience* 19, 21–28.

Gjerde, I., Blom, H.H., Lindblom, L., Sætersdal, M., Schei, F.H., 2012. Community assembly in epiphytic lichens in early stages of colonization. *Ecology* 93, 749–759.

Götzenberger, L., de Bello, F., Bräthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., Zobel, M., 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biol. Rev.* 87, 111–127.

Hanski, I., 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Ann. Zool. Fenn.* 37, 271–280.

Hanski, I., Ovaskainen, O., 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404, 755–758.

Harris, J.A., Hobbs, R.J., Higgs, E., Aronson, J., 2006. Ecological restoration and global climate change. *Restor. Ecol.* 14, 170–176.

Helm, A., Zobel, M., Moles, A.T., Szava-Kovats, R., Pärtel, M., 2015. Characteristic and derived diversity: implementing the species pool concept to quantify conservation condition of habitats. *Divers. Distrib.* 21, 711–721.

Helm, A., Hanski, I., Pärtel, M., 2006. Slow response of plant species richness to habitat loss and fragmentation. *Ecol. Lett.* 9, 72–77.

Higgs, E., Falk, D.A., Guerrini, A., Hall, M., Harris, J., Hobbs, R.J., Jackson, S.T., Rhemtulla, J.M., Throop, W., 2014. The changing role of history in restoration ecology. *Front. Ecol. Environ.* 12, 499–506.

Hobbs, R.J., Higgs, E., Hall, C.M., Bridgewater, P., Chapin, F.S., Ellis, E.C., Ewel, J.J., Hallett, L.M., Harris, J., Hulvey, K.B., 2014a. Managing the whole landscape: historical, hybrid, and novel ecosystems. *Front. Ecol. Environ.* 12, 557–564.

Hobbs, R.J., Higgs, E., Hall, C.M., Bridgewater, P., Chapin, F.S., Ellis, E.C., Ewel, J.J., Hallett, L.M., Harris, J., Hulvey, K.B., Jackson, S.T., Kennedy, P.L., Kueffer, C., Lach, L., Lantz, T.C., Lugo, A.E., Mascaro, J., Murphy, S.D., Nelson, C.R., Perring, M.P., Richardson, D.M., Seastedt, T.R., Standish, R.J., Starzomski, B.M., Suding, K.N., Tognetti, P.M., Yakob, L., Yung, L., 2014b. Managing the whole landscape: historical, hybrid, and novel ecosystems. *Front. Ecol. Environ.* 12, 557–564.



- Hylander, K., Ehrlén, J., 2013. The mechanisms causing extinction debts. *Trends Ecol. Evol.* 28, 341–346.
- Jackson, S.T., Sax, D.F., 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* 25, 153–160.
- Karger, D.N., Cord, A.F., Kessler, M., Kreft, H., Kühn, I., Pompe, S., Sandel, B., Sarmiento Cabral, J., Smith, A.B., Svenning, J.-C., Tuomisto, H., Weigelt, P., Wesche, K., 2016. Delineating probabilistic species pools in ecology and biogeography. *Glob. Ecol. Biogeogr.* 25, 489–501.
- Kasari, L., Saar, L., de Bello, F., Takkis, K., Helm, A., 2016. Hybrid ecosystems can contribute to local biodiversity conservation. *Biodivers. Conserv.* 25, 3023–3041.
- Kattge, J., Ogle, K., Bönnisch, G., Díaz, S., Lavorel, S., Madin, J., Nadrowski, K., Nöllert, S., Sartor, K., Wirth, C., 2011. A generic structure for plant trait databases. *Methods Ecol. Evol.* 2, 202–213.
- Kelemen, A., Török, P., Valkó, O., Deák, B., Migléc, T., Tóth, K., Ölvedi, T., Tóthmérész, B., 2014. Sustaining recovered grasslands is not likely without proper management: vegetation changes after cessation of mowing. *Biodivers. Conserv.* 23, 741–751.
- 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.
- Kitzes, J., Harte, J., 2015. Predicting extinction debt from community patterns. *Ecology* 96, 2127–2136.
- Kormann, U., Rösch, V., Batáry, P., Tschamtkte, T., Orci, K.M., Samu, F., Scherber, C., 2015. Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. *Divers. Distrib.* 21, 1204–1217.
- Körner, C., Stöcklin, J., Reuther-Thiébaud, L., Pelaez-Riedl, S., 2008. Small differences in arrival time influence composition and productivity of plant communities. *New Phytol.* 177, 698–705.
- Kumar, S., Stohlgren, T.J., Chong, G.W., 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87, 3186–3199.
- Kuusaaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodá, F., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2009. Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* 24, 564–571.
- Laughlin, D.C., 2014. Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecol. Lett.* 17, 771–784.
- Lengyel, S., Kobler, A., Kutnar, L., Framstad, E., Henry, P.-Y., Babij, V., Gruber, B., Schmeller, D., Henle, K., 2008. A review and a framework for the integration of biodiversity monitoring at the habitat level. *Biodivers. Conserv.* 17, 3341–3356.
- Lengyel, S., Varga, K., Kosztyi, B., Lontay, L., Déri, E., Török, P., Tóthmérész, B., 2012. Grassland restoration to conserve landscape-level biodiversity: a synthesis of early results from a large-scale project. *Appl. Veg. Sci.* 15, 264–276.
- Lessard, J.-P., Weinstein, B.G., Borregaard, M.K., Marske, K.A., Martin, D.R., McGuire, J.A., Parra, J.L., Rahbek, C., Graham, C.H., 2016. Process-based species pools reveal the hidden signature of biotic interactions amid the influence of temperature filtering. *Am. Nat.* 187, 75–88.
- Lewis, R.J., de Bello, F., Bennett, J.A., Fibich, P., Finerty, G.E., Götzenberger, L., Hiiesalu, I., Kasari, L., Lepš, J., Májeková, M., Mudrák, O., Riibak, K., Ronk, A., Rychtecká, T., Vitová, A., Pärtel, M., 2016. Applying the dark diversity concept to nature conservation. *Conserv. Biol.* (in press).
- Lhotsky, B., Kovács, B., Ónodi, G., Csécserits, A., Rédei, T., Lengyel, A., Kertész, M., Botta-Dukát, Z., 2016. Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *J. Ecol.* 104, 507–517.
- Loos, J., Dorresteijn, I., Hanspach, J., Fust, P., Rakosy, L., Fischer, J., 2014. Low-intensity agricultural landscapes in Transylvania support high butterfly diversity: implications for conservation. *PLoS One* 9, e103256.
- Lindborg, R., Eriksson, O., 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85, 1840–1845.
- Malo, J.E., Suárez, F., 1995. Establishment of pasture species on cattle dung: the role of endozoochorous seeds. *J. Veg. Sci.* 6, 169–174.
- Menéndez, R., Megías, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B., Thomas, C.D., 2006. Species richness changes lag behind climate change. *Proc. R. Soc. B Biol. Sci.* 273, 1465–1470.
- Mijnsbrugge, K.V., Bischoff, A., Smith, B., 2010. A question of origin: where and how to collect seed for ecological restoration. *Basic Appl. Ecol.* 11, 300–311.
- Mittelbach, G.G., 2012. Community Ecology. Sinauer Associates Inc., Sunderland, USA.
- Montoya, D., Rogers, L., Memmott, J., 2012. Emerging perspectives in the restoration of biodiversity-based ecosystem services. *Trends Ecol. Evol.* 27, 666–672.
- Naaf, T., Kolk, J., 2015. Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation. *Biol. Conserv.* 182, 155–163.
- Ozinga, W.A., Römermann, C., Bekker, R.M., Prinzing, A., Tamis, W.L.M., Schaminée, J.H.J., Hennekens, S.M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J.P., Van Groenendael, J.M., 2009. Dispersal failure contributes to plant losses in NW Europe. *Ecol. Lett.* 12, 66–74.
- Palmer, M.A., Ambrose, R.F., Poff, N.L., 1997. Ecological theory and community restoration ecology. *Restor. Ecol.* 5, 291–300.
- Pärtel, M., Zobel, M., Zobel, K., van der Maarel, E., 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos* 111–117.
- Pärtel, M., Helm, A., Reitalu, T., Liira, J., Zobel, M., 2007. Grassland diversity related to the Late Iron Age human population density. *J. Ecol.* 95, 574–582.
- Pärtel, M., Szava-Kovats, R., Zobel, M., 2011. Dark diversity: shedding light on absent species. *Trends Ecol. Evol.* 26, 124–128.
- Pärtel, M., 2014. Community ecology of absent species: hidden and dark diversity. *J. Veg. Sci.* 25, 1154–1159.
- Perring, M.P., Standish, R.J., Price, J.N., Craig, M.D., Erickson, T.E., Ruthrof, K.X., Whiteley, A.S., Valentine, L.E., Hobbs, R.J., 2015. Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere* 6, 1–25.
- Piqueray, J., Bottin, G., Delescaille, L.-M., Bisteau, E., Colinet, G., Mahy, G., 2011. Rapid restoration of a species-rich ecosystem assessed from soil and vegetation indicators: the case of calcareous grasslands restored from forest stands. *Ecol. Indic.* 11, 724–733.
- Prach, K., Jongepierová, I., Řehounková, K., 2013. Large-scale restoration of dry grasslands on ex-arable land using a regional seed mixture: establishment of target species. *Restor. Ecol.* 21, 33–39.
- Prach, K., Fajmon, K., Jongepierová, I., Řehounková, K., 2015. Landscape context in colonization of restored dry grasslands by target species. *Appl. Veg. Sci.* 18, 181–189.
- Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L., Walker, K.J., Rothery, P., 2003. Plant traits as predictors of performance in ecological restoration. *J. Appl. Ecol.* 40, 65–77.
- 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.
- Redhead, J.W., Sheail, J., Bullock, J.M., Ferreruela, 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. *Appl. Veg. Sci.* 17, 408–418.
- Rösch, V., Tschamtkte, T., Scherber, C., Batáry, P., 2013. Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *J. Appl. Ecol.* 50, 387–394.
- Ruiz-Jaen, M.C., Mitchell Aide, T., 2005. Restoration success: how is it being measured? *Restor. Ecol.* 13, 569–577.
- Saar, L., Takkis, K., Pärtel, M., Helm, A., 2012. Which plant traits predict species loss in calcareous grasslands with extinction debt? *Divers. Distrib.* 18, 808–817.
- SER (Society for Ecological Restoration) International Science & Policy Working Group, 2004e. The SER International Primer on Ecological Restoration. [www.ser.org](http://www.ser.org) & Tucson: Society for Ecological Restoration International.
- Soons, M.B., Heil, G.W., 2002. Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. *J. Ecol.* 90, 1033–1043.
- Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., de Vries, W., de Wit, C.A., Folke, C., Gerten, D., Heinke, J., Mace, G.M., Persson, L.M., Ramanathan, V., Rayers, B., Sörlin, S., 2015. Planetary boundaries: guiding human development on a changing planet. *Science* 347. <http://dx.doi.org/10.1126/science.1259855>.
- Tamme, R., Götzenberger, L., Zobel, M., Bullock, J.M., Hooftman, D.A.P., Kaasik, A., Pärtel, M., 2014. Predicting species' maximum dispersal distances from simple plant traits. *Ecology* 95, 505–513.
- Tschamtkte, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biol. Rev.* 87, 661–685.
- Temperton, V.M., 2007. The recent double paradigm shift in restoration ecology. *Restor. Ecol.* 15, 344–347.
- Török, P., Vida, E., Deák, B., Lengyel, S., Tóthmérész, B., 2011. Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. *Biodivers. Conserv.* 20, 2311–2332.
- Török, P., T-Krasznai, E., B-Béres, V., Bácsi, I., Borics, G., Tóthmérész, B., 2016. Functional diversity supports the biomass-diversity humped-back relationship in phytoplankton assemblages. *Funct. Ecol.* 30, 1593–1602.
- Turnbull, L.A., Crawley, M.J., Rees, M., 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88, 225–238.
- Valkó, O., Zmihorski, M., Biurrun, I., Loos, J., Labadessa, R., Venn, S., 2016. Ecology and conservation of steppes and semi-natural grasslands. *Hacquetia* 15, 5–14.
- van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglou, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396, 69–72.
- von Gillhaussen, P., Rascher, U., Jablonowski, N.D., Plücker, C., Beierkuhnlein, C., Temperton, V.M., 2014. Priority effects of time of arrival of plant functional groups override sowing interval or density effects: a grassland experiment. *PLoS One* 9 (1), e86906.
- Walker, L.R., Hölzel, N., Marr, R., del Moral, R., Prach, K., 2014. Optimization of intervention levels in ecological restoration. *Appl. Veg. Sci.* 17, 187–192.
- Walther, G.R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarošík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semchenko, V., Solarz, W., Thuiller, W., Vilá, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. *Trends Ecol. Evol.* 24, 686–693.
- Wesche, K., Ambarlı, D., Kamp, J., Török, P., Treiber, J., Dengler, J., 2016. The Palaearctic steppe biome: a new synthesis. *Biol. Conserv.* 25, 2197–2231.
- Westoby, M., Leishman, M., Lord, J., Poorter, H., Schoen, D.J., 1996. Comparative ecology of seed size and dispersal [and discussion]. *Philos. Trans. R. Soc. Lond. B* 351, 1309–1318.
- Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. *J. Veg. Sci.* 23, 796–802.
- Young, T.P., Petersen, D.A., Clary, J.J., 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecol. Lett.* 8, 662–673.
- Zobel, M., van der Maarel, E., Dupré, C., 1998. Species pool: the concept, its determination and significance for community restoration. *Appl. Veg. Sci.* 1, 55–66.
- Zobel, M., 2016. The species pool concept as a framework for studying patterns of plant diversity. *J. Veg. Sci.* 27, 8–18.