



Mix and match: regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration

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Abstract

One of the main questions in ecosystem restoration is where to obtain the seeds to re-establish plant communities. While the most commonly advocated approach is to use seeds from local sources, some experts argue against this because local populations may harbour little genetic variability for the restored populations to be able to adapt to and survive global change. Instead, they propose alternative strategies such as mixing seeds from various sources to increase genetic variability and adaptive potential, or using seeds from populations that have a similar climate as predicted for the target locality in the future. All these alternative seed-sourcing strategies have in common that they involve a transplanting of plant ecotypes, sometimes over large spatial scales. This is risky because plants from distant origins may be maladapted to the current local abiotic and biotic environment. In addition, introduction of non-local provenances will disrupt natural patterns of within-species biodiversity and will affect ecological networks, with unpredictable consequences. To balance the value of local adaptation with the need for future adaptation potential, we propose ‘regional admixture provenancing’ as a compromise strategy. Here seeds are sourced from multiple populations within the same region as the target locality and mixed prior to use. The mixing of seeds will increase the genetic diversity necessary for future adaptation, while restricting seed origins to a regional scale will maintain regional adaptation and reduce the risk of unintended effects on other biota. This approach is feasible in practice and has recently been implemented in Germany. We believe that it represents a compromise to reconcile opposing views on ecological restoration.

Keywords Local adaptation · Regional adaptation · Region of origin · Seed mixture · Seed sourcing strategy · Seed transfer zone

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Introduction

Ecologists and environmental managers often wish to restore the biodiversity and ecological integrity of degraded ecosystems (SER 2004). In many cases, the first critical step in such ecological restoration is to re-introduce target plant communities that will successfully establish, persist for a long time, and provide essential ecosystem functions (Kettenring et al. 2014). Under favourable conditions, restoration can rely on natural succession as a ‘passive restoration’ (Prach et al. 2015a, b; Prach and del Moral 2015; Gilhaus et al. 2015), but in most cases it is necessary to introduce seeds from other sources to ensure restoration success (Hölzel et al. 2012). There has been an intensive debate on which specific seed sources to use for this (e.g. Broadhurst et al. 2008; Sgrò et al. 2011; Breed et al. 2013; Bucharova 2017).

The selection of appropriate seed source for restoration is affected by how large and how urgent the restoration project is. In intentionally planned projects, it is feasible to select and produce optimal seed. This type of restoration is the main focus of this article. We acknowledge that cases may exist, e.g. after large-scale disasters, where it is impossible to optimally source seeds. There, any native seed will serve the main purpose, that is revegetation in order to prevent spread of invasive species and further land degradation.

Current seed-sourcing strategies

Cultivars

A common seed source for restoration are commercial cultivars (e.g. Aubry et al. 2005). Cultivars are plant materials that are bred for specific target traits and propagated for large-scale use in fodder production or restoration. The seeds of cultivars are readily available in large amounts, which makes them an easy choice when large amounts of seeds are needed. Although seed availability is a key prerequisite of any restoration project, use of cultivars can be problematic, because the traits for which cultivars were bred differ from the traits that are favoured in the field, in restored populations (Leger and Baughman 2015). For example, grass cultivars have been bred for forage quality and yield, high seed production, seedling vigour, or drought tolerance. Although these traits seem intuitively advantageous for successful restoration, natural selection in the field favours different traits including early flowering, small plant size and higher root allocation (Leger and Baughman 2015).

The genetic background of cultivars is variable: some are clonal or highly inbred, while others are derived from

polycrosses of multiple parents (Jones 2003; Kettenring et al. 2014). Cultivars with a narrow genetic basis will constitute genetically uniform populations that support less diverse ecological networks and fewer ecosystem functions (Barbour et al. 2016; Harvey et al. 2017). Many cultivars have low phenotypic variability, e.g. with respect to flowering phenology or secondary chemistry, and thus support a limited number of dependent organisms, which results in homogenization of communities across trophic levels (Zytnyska and Preziosi 2011; Tahmasebi et al. 2014; Mody et al. 2017). Part of these problems can be counteracted by the use of polycrosses, but these genetically more diverse cultivars remain problematic, because they still constitute an introduction of foreign genotypes with risks of maladaptation and unpredictable effects on dependent organisms. Because of these problems, the use of cultivars should ideally be restricted to extreme habitats, such as heavily polluted sites, where wild plants cannot establish, or for emergency cases when large ecosystems must be quickly restored to prevent land degradation (Breed et al. 2018).

Local provenancing

The most common alternative to using cultivars in ecological restoration is the use of seeds of native plants that originate from wild populations, preferentially from local genotypes (Kiehl et al. 2014), i.e. *local provenancing*. This strategy is based on the observation that almost all plants show genetic and phenotypic differentiation among populations (Linhart and Grant 1996; Bossdorf et al. 2005; Jay et al. 2012), which often reflects adaptation to local environmental conditions such as soil, climate or biotic interactions (e.g. Keller et al. 1999). As a result, local plants on average perform better and have a higher fitness than plants of foreign origin (Oduor et al. 2016). This does not necessarily mean that a local provenance will always perform better than any particular foreign one at a given site. Provenance trials in forestry have shown that at individual planting sites, foreign provenances may grow better than the local ones (e.g. Gray et al. 2011; Gellie et al. 2016). However, when searching for a general, average pattern across all provenances, planting sites and/or across many species, local adaptation is the general pattern in woody and herbaceous plants (Oduor et al. 2016; Bucharova et al. 2017a). Moreover, many provenance trials of trees use growth in the first few years as a proxy of overall performance (e.g. Gray et al. 2011; McLane and Aitken 2012; Schreiber et al. 2013; Lu et al. 2014). Such growth-oriented measures of fitness can be problematic because populations likely possess conservative legacy of adaptation to extreme events, which may not be recognizable as intrinsically advantageous within few decades of early tree

life if extreme events do not occur during that time (Whittet et al. 2016).

Despite the general evidence for local adaptation, seeds from a local population may also not be ideal for restoration in some cases. Local plants are adapted to past environmental conditions and may lack a sufficient amount of genetic variability to adapt to rapidly changing climatic conditions (Lesica and Allendorf 1999; Sgrò et al. 2011). Additionally, in modern landscapes with fragmented habitats, local populations might sometimes be small, genetically impoverished and/or inbred (Leimu et al. 2006). Consequently, it has been argued that seeds from such populations may be of low quality, and that the resulting offspring may fail to establish and to persist (Breed et al. 2013).

Matching future climate

A number of alternative seed-sourcing strategies has been suggested, which put greater emphasis on preadaptation to climate change and/or an enhanced genetic diversity (Fig. 1).

Predictive provenancing (Crowe and Parker 2008; Sgrò et al. 2011) recommends the use of genotypes from areas that have similar climates as the one predicted for the target locality, whereas *climate-adjusted provenancing* (Prober et al. 2015) suggests introduction of several non-local ecotypes sourced along a climatic gradient to include higher genetic diversity and introduces genotypes adapted to future climate. The main aim of these strategies is to maximize population performance in the future under global change.

While these alternative seed-sourcing approaches are intuitive, the available evidence they are based on should be carefully considered. Some studies in fully controlled environments like growth chambers suggest that plants from drier and warmer origins are better adapted to heat and drought than plants from colder and wetter regions (e.g. Fernández et al. 1999; Matías et al. 2014; Dounavi et al. 2016; Varone et al. 2016; Taïbi et al. 2017). Experiments that are more realistic used a space-for-time approach, i.e. they simulated climate change by transplanting plants to warmer areas. This approach is also used in provenance

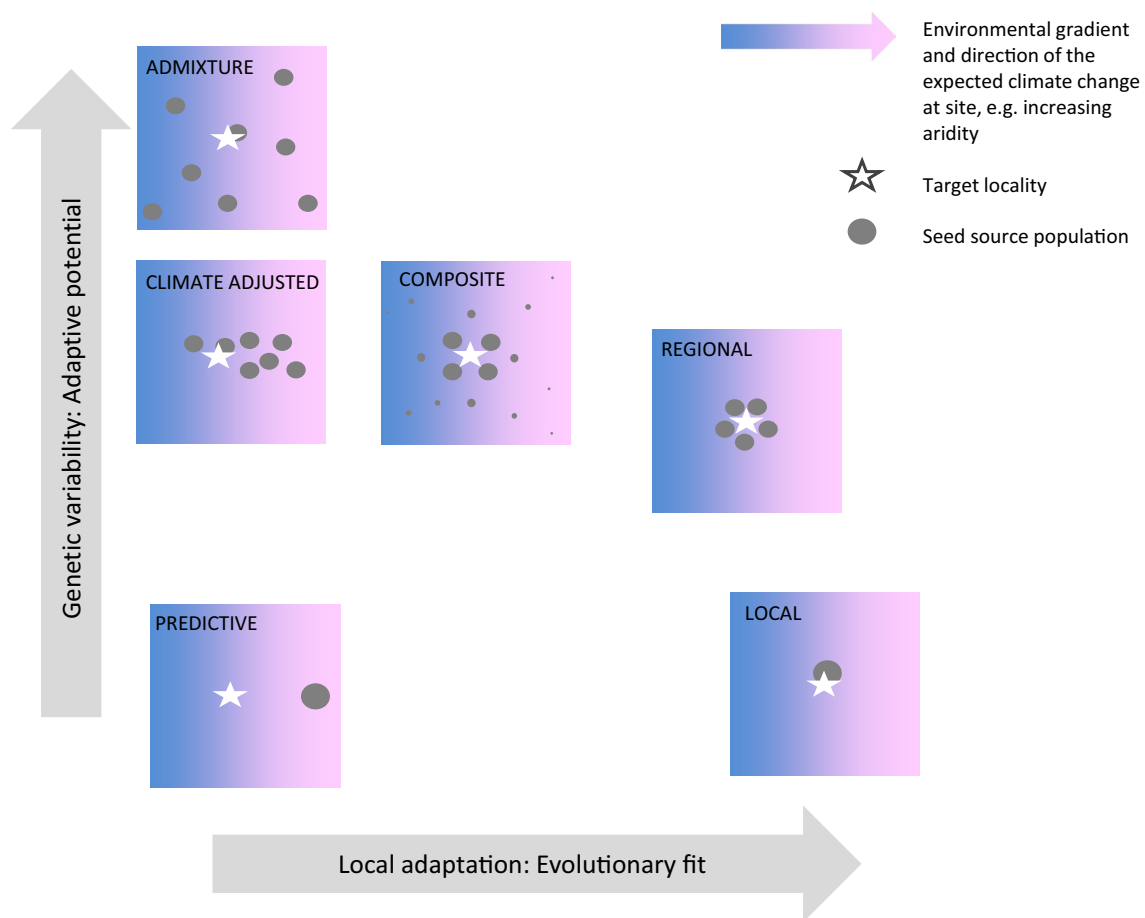


Fig. 1 The position of different seed-sourcing strategies within the inevitable trade-off between increasing local adaptation versus providing genetic variability. The different size of the seed-source pop-

ulations reflects their relative contributions; the colour of the background represents an environmental gradient; modified after Prober et al. (2015) and McDonald et al. (2016). (Color figure online)

trials in forestry, and it partly supports the results from controlled environments (e.g. Etterson 2004; Lu et al. 2014; Taïbi et al. 2016). Although the space-for-time approach is more realistic than growth-chamber experiments, its results must still be interpreted with caution since it exaggerates effect sizes compared to real climatic change (Elmendorf et al. 2015).

Both controlled-environment experiments and the space-for-time approach assume that climate is the main driver of plant performance. However, there are many other environmental factors besides climate that affect plant performance, e.g. soil conditions, photoperiod, neighbouring plants, herbivores or pathogens (Laine 2005; Leimu et al. 2012; Kalske et al. 2012; Alexander et al. 2015). In controlled environments these factors are excluded, but in space-for-time experiments the plants are generally planted into novel communities which also differ in soil conditions and harbour different interacting species. Thus, the space-for-time approach confounds climate change with other environmental changes and does not allow robust causal inference. The mismatch between home and target ecological communities can be of crucial importance (Araújo and Luoto 2007). For example, Alexander et al. (2015) showed that survival under climate change depends on the identity of interacting communities. This context-dependence of experimental outcomes together with the uncertainty of future community changes questions the outcome of simple space-for-time experiments. Although the communities of associated organisms are also likely to change under climate change, the resulting community will be always derived from the ones that are currently present (Elmendorf et al. 2015). Thus, we need in situ experiments that compare non-local, climate-adapted plants with the local plants under climate change conditions in a transplant experiment to the target locality.

We thoroughly searched the literature for such in situ experiments. A Web of Knowledge search (3rd July 2017) using “provenance climate change plant” as keywords resulted in 248 studies. From these, we selected experiments that (i) were carried out in common gardens or field sites, (ii) compared the performance of several provenances including a clearly defined local or regional one, and (iii) involved some kind of in situ climate change—through experimental manipulation or a natural climatic event like an extremely dry or hot year. We found only eleven studies that met these criteria, and they had inconsistent results. Two studies supported predictive provenancing (Schreiber et al. 2013; Wilczek et al. 2014), and in three studies the evidence was ambivalent because responses differed for different fitness traits (Thiel et al. 2014; Montwé et al. 2016) or among different climate-adapted provenances (Wellstein and Cianfaglione 2014). The remaining six studies provided evidence against predictive provenancing. In manipulated warmer climates or during natural climate events, provenances

from drier or warmer origin performed equally or worse in comparison with the local provenances in forest trees (Taeger et al. 2013, 2015; Hancock and Hughes 2014; Baudis et al. 2014) and several herbs (Beierkuhnlein et al. 2011; Hancock and Hughes 2014; Bucharova et al. 2016a; Bjorkman et al. 2017). In summary, the available in situ studies so far provide very limited evidence that transplanting of climate-adapted ecotypes will lead to the desired effect of increased plant performance under climate change, probably because plants are adapted also to other environmental conditions and climate adaptation is not enough to predict plant performance (Bjorkman et al. 2017). Any decision on the use of climate-adapted provenances will require further experiments.

Maximizing adaptive potential

There are other seed-sourcing strategies, *composite provenancing* and *admixture provenancing* (Broadhurst et al. 2008; Breed et al. 2013), that do not focus on climate matching but on increasing overall genetic diversity with the idea that a large genetic variability will allow for selection of the best suited genotypes. *Composite provenancing* keeps the benefits and reduces the risks associated with seed transfer by combining the local sourcing approach with materials from more distant sources to mimic natural gene flow, while *admixture provenancing* maximizes the adaptive potential (and heterosis) with little regard for natural gene flow. Both strategies include transfer of plant genotypes, sometimes over considerable spatial scales.

Translocations over large geographic distances entail potential risks because geographic distance frequently correlates with both neutral and adaptive genetic differentiation in plants (de Kort et al. 2013; Sexton et al. 2014). This differentiation is partly because of isolation-by-distance effects, i.e. gene flow is becoming less likely with increasing geographic distance, and partly because geographic distance often correlates with environmental differences and thus is a proxy of adaptive differentiation (De Kort et al. 2013). Indeed, the strength of local adaptation often increases with geographical distance or correlated environmental dissimilarity, for example soil, altitude or climate (Becker et al. 2006; Ellis et al. 2007; Raabová et al. 2007; Volis et al. 2015; Hamann et al. 2016; Bucharova et al. 2017b). Consequently, gene flow between local and distant non-local native populations, as proposed in several seed-provenancing strategies, might result in “dilution” of local adaptation (Hufford and Mazer 2003; McKay et al. 2005; Crémieux et al. 2010). Furthermore, hybridization between genetically dissimilar individuals can cause outbreeding depression (Edmands 2007), especially if there are ploidy or major chromosomal polymorphisms between the provenances (Frankham et al. 2011),

as is often the case in plants from several families commonly used for restoration (Kramer et al. 2018).

Probably the most important objection against the transfer of ecotypes over large spatial scale are the possible effects on interacting biota (Bucharova 2017). Since plants are the main primary producers in terrestrial ecosystems, a myriad of other organisms depends on them. These organisms frequently differentiate between plant genotypes, so that their performance will be influenced by plant origin (Leger and Forister 2005; Hull-Sanders et al. 2007; Abdala-Roberts and Marquis 2007; Herrera et al. 2011; Bischoff and Trémulot 2011; Laukkanen et al. 2012; Sinclair et al. 2015; Bucharova et al. 2016b). The current relationships between host plants and their interacting organisms are shaped by coevolutionary processes (Toju and Sota 2006; Garrido et al. 2012; Leimu et al. 2012), and introduction of foreign provenances will likely disrupt these relationships, with unpredictable consequences. However, there is a lack of long-term experiments that investigated the effects of translocations on biotic interactions.

Apart from microevolutionary processes such as selection and adaptation, intraspecific variation is also strongly influenced by historical processes, mainly Pleistocene climatic changes. This phenomenon is best known from the northern hemisphere, where glaciations and subsequent colonization of flora and fauna caused distinct patterns of within-species genetic differentiation, i.e. phylogeographic structure (Taberlet et al. 1998). However, Pleistocene glaciations had major imprints also on biota in the southern hemisphere. For example, Australia experienced extreme drought during Pleistocene glacial cycles and parts of the continents were covered by sand dunes. After retraction of the dunes in the interglacial, unsuitable habitats became suitable and were recolonized, resulting in phylogeographic patterns similar to those from the northern hemisphere (Byrne et al. 2008). Pleistocene climatic change also affected genetic structure of plant populations in Africa (Kebede et al. 2007; Kadu et al. 2013) and South America (Turchetto-Zolet et al. 2013). Together, these historical genetic patterns are an important part of global biodiversity and have intrinsic value (Ghilarov 2000). So far, the discussion on seed sourcing strategies did not consider preserving within-species patterns for their intrinsic value, mainly because the focus was on ecosystem services and productivity. However, we believe that within-species diversity is worth preserving similar to species diversity, at least in absence of evidence for conflict between biodiversity protection and maintenance of ecosystem functions. Translocation of seed material that ignores historical gene-flow corridors and barriers will disrupt these patterns.

In summary, the provenancing strategies discussed so far face a dilemma: (1) they either favour natural patterns of genetic structure and local adaptation at the expense of low genetic variability and inbreeding depression, or (2) they

increase genetic variability and evolutionary potential but break up natural genetic patterns, risk outbreeding depression and maladaptation. Given increasing habitat fragmentation and global warming, a new approach that reconciles the two contrasting strategies for ecological restoration is needed.

Regional admixture provenancing

Here we describe a seed-sourcing strategy called *regional admixture provenancing*, which we believe represents a compromise between the existing approaches described above. In contrast to local provenancing, the seeds are collected from several large populations and mixed to provide high genetic variability (Havens et al. 2015; Espeland et al. 2017). In contrast to composite provenancing, simple admixture or climate-adjusted provenancing, the source populations should be located in a defined area ('region') around the target site with similar environmental conditions and a common biogeographical history to preserve regional adaptation and historical intraspecific patterns (Fig. 1).

The idea of sourcing seeds from a region is not new, and it is established practice, for example, in forestry. The regions for such seed transfers are called 'seed transfer zones'. They are usually regions that share similar environmental characteristics and within which the species (seeds, seedlings, vegetative propagules or adults) can be transferred with no detrimental effects on mean population fitness (Hufford and Mazer 2003). So far, seed sourcing from seed transfer zones has been perceived as somewhat relaxed local provenancing, but did not require mixing of seeds from multiple origins to increase genetic variability (Vergeer et al. 2004; Williams et al. 2014; McDonald et al. 2016; but see Havens et al. 2015). We believe that a clear distinction between *regional admixture provenancing* and (*relaxed*) *local seed provenancing* is important, because the regional admixture provenancing as defined in this paper includes the mixing of seeds from several populations, which solves the main objection against local provenancing, i.e. negative effects of genetic drift and low genetic variability resulting in low adaptability to environmental change.

The main idea behind regional admixture provenancing is that populations within such regions experience similar environmental conditions. Although older meta-analyses of local adaptation did not reveal relationship between geographic distance and strength of local adaptation (Leimu and Fischer 2008), a number of recent, well-designed studies found regional adaptation, i.e. a geographically broader analogue of local adaptation for several species as well for entire communities (Becker et al. 2006; Ellis et al. 2007; Raabová et al. 2007, 2011; Weißhuhn et al. 2012; Volis et al. 2015; Hamann et al. 2016). Patterns of regional adaptation

have also been observed between pathogens or herbivores and their host plants (Laine 2005; Kalske et al. 2016).

Despite regional adaptation, individual populations within the regions are still genetically differentiated on smaller spatial scale because of spatial isolation, habitat fragmentation, physical barriers and restricted gene flow determined by species traits (Michalski and Durka 2012; Reisch and Bernhardt-Römermann 2014). Consequently, the mixing of seeds from different populations within a region will increase genetic variation compared to single seed sources. At the same time, restricting seed transfers to within a region will protect historical genetic patterns that exist on larger spatial scales, especially if the regions are delineated taking the biogeography of a given species into account (Taberlet et al. 1998).

The mixing of seeds will likely reduce inbreeding. In fragmented landscapes, it might be necessary to collect seeds from rather small and possibly inbred populations. Using seeds from individual small populations for restoration may lead to poor plant performance, but the mixing of seed from several populations can reduce inbreeding depression and result in healthy progeny in the next generation (Hufford et al. 2012; Frankham 2015).

Some environmental factors, such as microclimate, soil moisture or nutrient supply, vary locally rather than regionally and are thus often associated with local adaptation at small spatial scales (Lenssen et al. 2004; Gimenez-Benavides et al. 2007). In such cases, seeds should ideally be sourced from natural populations where the conditions match the target locality as closely as possible. This is, however, often unrealistic. Therefore, a mixture of seeds from several populations within a region will likely provide diverse material adapted to a range of environmental factors, and at least some of the seeds will come from a population with an environment not too dissimilar from the target locality. The idea is that such a regional mixture should be useful for the majority of common microenvironments within a region.

The key component of *regional admixture provenancing* is delineating the regions. In principle, the requirements for regions are the same as for seed transfer zones. They share similar environmental characteristics, so that seeds can be transferred with no or negligible detrimental effects on mean population fitness (Hufford and Mazer 2003). The delineation of seed transfer zones has been subject of intense research. Some authors suggest using ecoregions (Miller et al. 2011), others rely on climatic zones (Bower et al. 2014), genecological studies of individual species (Bradley St Clair et al. 2013 and reference therein) or a combination thereof (Gibson and Nelson 2017). The optimal size of a seed transfer zone is of course species-specific. Large seed zones of several hundreds or thousands of square kilometres may be sufficient for species with frequent long-distance

gene flow, such as wind-pollinated or wind-dispersed ones. In contrast, species with short-distance gene flow require much smaller seed zones. In extreme cases of rare, highly specialized species, regional admixture provenancing may not be suitable at all.

Regional admixture provenancing aims to provide material for restoration of genetically variable, yet regionally adapted populations of foundation species. Genetic variability is essential for future adaptation to environmental changes including climatic change. Such adaptation from standing genetic variation is likely to take place quickly in herbaceous plants with short generation time. However, in long-lived plants like trees the offspring of the currently planted regional generation will probably be maladapted to the future climate because climate is changing rapidly (Aitken and Bemmels 2016). To some extent, this will be buffered by high phenotypic plasticity of trees (Petit and Hampe 2006). Further, most trees have populations with high within-population genetic diversity and they produce a lot of seeds of which many germinate, but only few reach canopy height (Petit and Hampe 2006). The huge amount of genetically diverse seedlings provides tremendous material for natural selection, and only individuals that are the most suited to the novel environment will survive, allowing for adaptation. However, for the most extreme climate scenarios, it is not clear whether this will be sufficient and predictive provenancing (assisted migration) might be considered necessary. Unfortunately, as discussed above, the direct evidence that predictive provenancing will indeed have the desired effect is limited, probably because plants are adapted not only to climate, but also to other aspects of the environment (Ennos 2015; Kranabetter et al. 2015; Sinclair et al. 2015). Further research is needed to find the optimal seed sourcing strategy for plants with long generation times in the era of climate change.

Regional admixture provenancing in practice

Regional admixture provenancing as described here has been developed for non-woody plants in Germany (Prasse et al. 2010). It consists of two major elements: (1) a map of seed transfer zones (*region of origin*) and (2) seed zone-specific species lists. The system was regularized by the Ordinance on Preservation mixtures (ErMiV 2011) which implements the EU Directive 2010/60, and which has already been adopted in several certified seed production systems (e.g. RegioZert®, VWW-Regiosaat®).

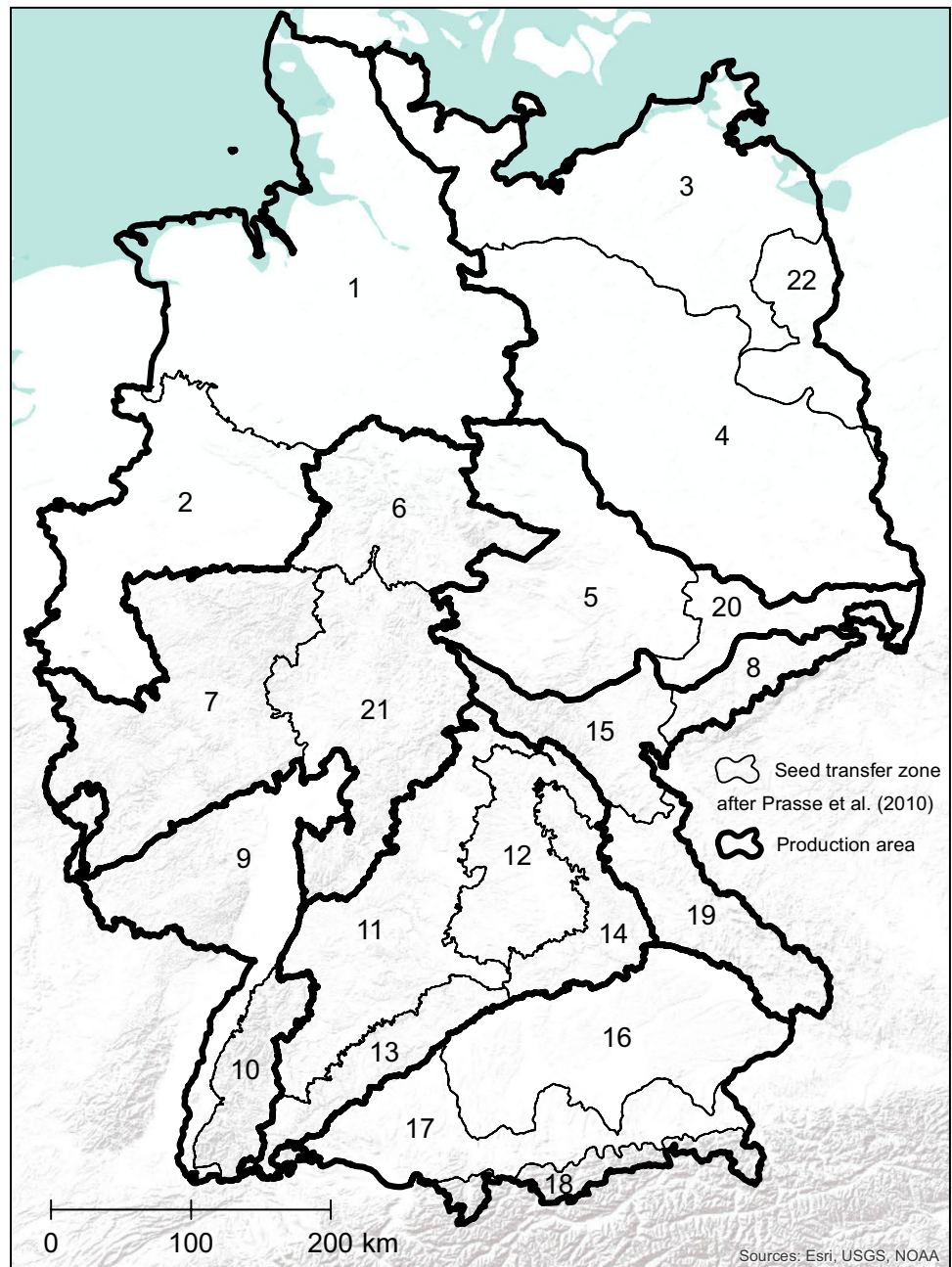
The basis for the delineation of the seed transfer zones was the German system of 89 natural regions (Meynen and Schmithüsen 1953) which have been identified based on geomorphology, geology, hydrology and soil. These natural regions were then grouped together based on pedogenic rock, soil type and climate. For the climate factors,

specific emphasis was given to isotherms (0 °C in January, 18 °C in July), annual rainfall (< 500, 500–700, 700–1000, > 1000 mm), and oceanicity (18 °C difference between mean summer and mean winter temperature as threshold for oceanic versus continental climate). This reduced the number of units to 50, which were then further aggregated based on geomorphology (e.g. mountain ranges, large plateaus) and environmental similarity based on expert opinion, and a rule that, to protect natural patterns of intraspecific biodiversity, a resulting seed zone was not allowed to exceed 400 km extent in either direction. The exact borders of the seed zones were discussed with the administration of the federal

states of Germany to ensure practical feasibility. This procedure resulted in a final number of 22 seed transfer zones (*Herkunftsregionen*, Fig. 2). It is important to note that in this system seed transfer zones are not species-specific, but are, to simplify practical implementation, equally applied to all species.

The developed system of seed transfer zones is used together with a criteria-based ‘species filter’ that selects species suitable for general use in each seed transfer zone. The starting point of species selection is a list of all non-woody species that occur within a given seed zone. From these, the filter excludes all species that are either rare, endangered

Fig. 2 Map of seed transfer zones and production areas in Germany. Thin lines indicate 22 seed transfer zones (‘Herkunftsregion’, i.e. region of origin), thick lines indicate eight production areas (Prasse et al. 2010)



(Red listed), hybrids, neoendemics, taxonomically problematic, or species that have their range edge within the zone (further details in Prasse et al. 2010). The final lists were cross-checked by regional experts and agreed upon with German authorities. To facilitate easy application of the concept, an interactive website allows generating species lists for each seed transfer zone, and provides maps of the borders of seed zones (<http://www.regionalisierte-pflanzenproduktion.de>).

To supply the market with regional seeds adapted to wider range of environmental conditions, the German system demands to collect seeds from at least five large populations across a seed transfer zone (Prasse et al. 2010). The seeds are then mixed and either directly used or, more frequently, propagated as crops on fields and sold for restoration projects (Rieger et al. 2014). To make the propagation practically feasible, the 22 seed transfer zones are currently grouped into eight production areas (Fig. 2), with the idea that while regional seeds can be used only within a given seed transfer zone and must be propagated separately for each, the propagation itself can take place anywhere within the given production area. This enables a single farmer to produce seeds from several seed transfer zones on the same farm and allows development of a profitable business. The farm-produced seeds are available for restoration projects in a given seed zone, or are used for re-establishing another generation of cultivation. This procedure can be repeated for up to five generations, afterwards the seed production must start from a new wild collection (for details see Prasse et al. 2010).

The market with regional seeds ('Regiosaatgut') is now well-established in Germany and it is growing rapidly, with the demand often exceeding the supply (pers. comm. of all major German seed producers). The seed producing companies offer a range of region-specific standard seed mixtures for different habitat types, but they also allow customer-defined mixtures, or sell seeds of individual wild species. Currently, the use of regional seeds is only required in conservation projects or ecological compensation measures, but the seeds are often used for standard greening, too. However, from May 2020 onwards the use of regional seeds will be mandatory for all seeding in the open landscape outside of forests and agriculture. Recent studies indicate that the existing regional seed system in Germany is meaningful. Plants grown from commercially available seeds are indeed often regionally adapted (Bucharova et al. 2017b), their genetic structure often corresponds to the seed transfer zones (Durka et al. 2017), and propagation across several generations does not lead to strong phenotypic or genetic alterations (Nagel et al. unpublished).

The strategy of regional admixture provenancing could be easily applied also in other countries, especially if they already have established systems of seed transfer zones, as

is the case e.g. for the USA, Canada or the UK (e.g. Bower et al. 2014), <http://www.prt.com/products-services/seed-zone-maps>, <http://www.forestry.gov.uk/pdf/FRMGuidelinesRoPmap.pdf>. In these countries, regional provenancing could be adopted with little additional cost as modification of the current system, when seed material from multiple populations within one seed zone will be mixed and the regional mixture will be used for restoration purposes. As regional admixture provenancing relies on seeds from a region, its application in other countries will depend on whether systems for obtaining local or regional seeds exist. In countries where local provenancing is a common practice, regional admixture can be used as simple mixing of seeds from number of local populations (Havens et al. 2015). On the other hand, restoration challenges are sometimes so huge that the demand for seeds vastly exceeds their availability (Merritt and Dixon 2011). For example, in 2017 alone, wild-fires in USA destroyed around 40 million ha (<http://www.nifc.com>), and much of this land would be taken over by invasive species if not actively restored (Mealor et al. 2012). In such cases, lack of regional seeds should not halt restoration projects, and any source of native seeds including native cultivars will help to prevent further land degradation.

Conclusions

We propose regional admixture provenancing as a compromise strategy that reconciles natural adaptation and historical patterns of genetic diversity with the need to provide sufficient genetic variability for populations to be able to adapt to changing environments. The strategy is supported by experimental data, both under current and future conditions (Bucharova et al. 2016a, 2017b). However, so far the data come from one habitat type only—European mesic grasslands—and it is therefore not clear whether the strategy will be successful also in other habitats or on other continents. It is a common problem with novel seed-sourcing strategies that there is a lack of robust experimental tests. So far the only strategy that is supported by data on a global scale is local provenancing, with unambiguous evidence for local adaptation as a general pattern (Oduor et al. 2016). However, theoretical predictions suggest that strict local provenancing may not be suitable under future environmental changes. Consequently, we need to find compromise strategies, and we need in particular well-designed and carefully analysed field experiments (Bucharova et al. 2017a; Breed et al. 2018) and genomic analyses (Durka et al. 2017; Williams et al. 2014) to identify the best seed-sourcing strategies for ecosystem restoration in a changing world.

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