

RESEARCH ARTICLE

Seed transfer zones based on environmental variables better reflect variability in vegetation than administrative units: evidence from Hungary

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To preserve the natural genetic pattern of species and to avoid the introduction of nonadapted ecotypes during restoration, seed transfer should be spatially restricted. Instead of applying administrative borders in the absence of species-specific empirical data, biogeographical knowledge can be used as a proxy. Hungary was used as a suitable test region for this approach. The aims of the study were (1) to produce an evidence-based seed transfer zone (STZ) map applying the Multiple Potential Natural Vegetation model; (2) to assess the uncertainty of the resulting STZ map; and (3) to compare the present seed transfer regulation based on administrative regions with the evidence-based STZ map. The analysis was based on a floristic map, a vegetation map, and a landscape map of Hungary. Intersected polygons of the three maps were filled with Multiple Potential Natural Vegetation data and clustered to produce seven contiguous units that can serve as STZs. The uncertainty analyses provided a numerical comparison between the two approaches and demonstrated the inadequacy of defining administrative regions as STZs. The practical result of the study is the production of an evidence-based STZ map that could replace the administrative map currently used for regulation in Hungary. Moreover, this map helps to develop native seed propagation and to enhance ecological restoration. We conclude that field-based potential vegetation models, similar to the Multiple Potential Natural Vegetation, are suitable for STZ development in countries lacking an evidence-based system for seed transfer.

Key words: biogeographical information, herbaceous species, local adaptation, native seed propagation, potential natural vegetation, seed transfer regulation

Implications for Practice

- Biogeographic maps are used as proxies for developing seed transfer zones (STZs) for restoration. It is suggested to link these maps to potential vegetation models to improve reliability.
- Administrative regions are unsuitable for guiding seed transfer. To convince legislators to avoid this option, evidence-based comparison with ecologically sound approaches should be offered.
- The evidence-based STZ map fills the gap between science and policy and paves the road to a certification system for quality seed transfer to support restoration at a large scale, sufficient to cope with the ambition of green infrastructure development in Europe and elsewhere.

Introduction

Ecological restoration is a more and more important public issue as there are concerns about land degradation even at a high political level (Scholes et al. 2018). In case of severe degradation, restoration activities are often based on reintroducing seeds of native species (Merritt & Dixon 2011; Gibson et al. 2016). During such seed introductions, there is a risk of using germplasm

maladapted to the local environment that may result in low survival and the introduction of nonlocal genetic material threatening the integrity of the natural genetic structure of populations (Bischoff et al. 2008, 2010). There is a remarkable amount of literature attempting to find scientific support for using local versus nonlocal seeds in restoration (McKay et al. 2005; Breed et al. 2013; Bischoff 2014; Bucharova et al. 2017a). The debate is still ongoing (Schröder & Prasse 2013; Breed et al. 2018), but there is a general agreement that seed provenance has to be guided by the best available knowledge and should be regulated

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(Gibson & Nelson 2017; Giencke et al. 2018; León-Lobos et al. 2020).

The basis for regulating seed transfer is the use of seed transfer zones (STZs), i.e. geographically distinct areas within which seeds can be introduced with low risk of maladaptation (Bower et al. 2014; Breed et al. 2018), and minimal loss of biodiversity (Malaval et al. 2010). The development of STZs for herbaceous plants in Europe is motivated by a directive of the European Commission on the marketing of seed mixtures intended for ecological restoration (EC 2010). Once established, STZs constitute the units for seed propagation and transfer: authorization is provided only to activities carried out within the particular region, including seed collection, propagation certification, and restoration interventions.

For native tree species, such delineations are well established, and the resulting regulations have been used for some decades in many countries (Johnson et al. 2004; Breed et al. 2018). However, as the necessary analyses on genetic differentiation and fitness of many species are costly, STZs have been empirically tested for only a few herbaceous species (Bower et al. 2014; Durka et al. 2017; Bucharova et al. 2017a). Due to the lack of species-specific knowledge, provisional (Bower et al. 2014; PCA 2015; Gibson & Nelson 2017) or generalized (Bucharova et al. 2019) STZs have been developed in many countries.

The development of STZs may rely on geographical distance (Mortlock 2000), but this is unlikely to be a good predictor of adaptive differentiation unless it correlates well with environmental distance (Breed et al. 2018). Several genetic analyses showed that ecological similarity is more important for restoration success than geographical proximity (Malaval et al. 2010; Bower et al. 2014). Similar environmental variables result in similar vegetation as a cumulative response of species fitness (Moravec 1998), and thus environmental factors may constitute a basis for the delineation of vegetation or ecoregions (Miller et al. 2011). These vegetation regions have been used as proxies for developing provisional or general STZs in a number of countries (SKEW 2009; Prasse et al. 2010; Kirmer et al. 2012; FCBN 2014; Krautzer et al. 2018). The suitability of this approach has been proven in transplant and genetic experiments for a few species (Bower et al. 2014; Durka et al. 2017; Gibson & Nelson 2017; Bucharova et al. 2017b). In Hungary, the directive on the marketing of seed mixtures for restoration (EC 2010) was applied by using the seven administrative-territorial units (NUTS2) as STZs in the absence of scientifically based zonation (VM 2012). However, administrative borders have little relevance to ecological differences (De Vitis et al. 2017). Therefore, the regulation should be revised, based on the best available ecological knowledge.

In Europe, the description and mapping of vegetation units are well established (Mucina et al. 2016), and this is valid for Hungary as well (Fekete & Varga 2006; Borhidi et al. 2012). Flora, vegetation, and landscape regions have been delineated for the country (Hajdú-Moharos & Hevesi 2002; Molnár et al. 2008; Kocsis & Schweitzer 2011), and the respective maps can serve as inputs for STZ development. The borders of vegetation maps were partly based on expert judgment and personal experience, and the scale of their validity may differ from region

to region. This bias might be reduced by using large databases with extensive field vegetation data and environmental variables. The combined application of traditional eco-region borders and environmental databases can be more accurate as proxies for the development of STZs. Predictions made by Potential Natural Vegetation (PNV) models can serve this approach. For their development, field data on contemporary natural vegetation remnants and environmental parameters are modeled to obtain the potential vegetation of any area, even in places where vegetation was destroyed.

A novel development of PNV provides multiple potential vegetation types for a given area with different probabilities (Multiple Potential Natural Vegetation, MPNV; Somodi et al. 2017). The MPNV model for Hungary is based on climatic, hydrologic, topographic, and edaphic patterns linked to the present-day remnant (semi)natural vegetation data. The high resolution of environmental and vegetation information within the MPNV model is appropriate to aggregate biogeographic map polygons to an operational number of units for STZ. The model predicts potential vegetation type probability composition for given polygons that can be compared to that of neighboring polygons. Polygons of similar composition can be merged to reach the number of zones that can be handled at the country level as STZs.

The aims of our study were (1) to produce an evidence-based STZ map using the MPNV model; (2) to assess the uncertainty of the resulting STZ map; and (3) to compare the present seed transfer regulation based on administrative regions with the evidence-based STZ map.

Methods

Development of an Evidence-Based STZ Map

The three biogeographic input maps used as initial geometry (i.e. polygons) for the development of the evidence-based STZ map were: floristic regions (33 polygons, simplified to 24; Molnár et al. 2018), vegetation-based landscape regions (109 polygons; Molnár et al. 2008), and the Hungarian subset of the Carpathian-Pannonian landscape regions (71 polygons, simplified to 48; Hajdú-Moharos & Hevesi 2002; digitized by the authors). Floristic and landscape regions were simplified by merging small (<10,000 ha) polygons with the neighboring polygon that shared the longest border. These small polygons either belonged to larger ecoregions outside the country, or in a few cases, they were small inclusion polygons surrounded by other regions.

As none of the maps could be considered best for the purpose to produce an STZ map, all three input maps were taken into consideration. To summarize information on their polygon geometry, polygons of the three input maps were intersected and sliver polygons (<10,000 ha) from the resulting intersected map were eliminated, as described above for input maps. This process (step 1 in Fig. 1) resulted in a base map of 136 polygons used for the development of our evidence-based STZ map.

Subsequently, the polygons of the base map were filled with potential natural vegetation data (step 2 in Fig. 1) obtained from

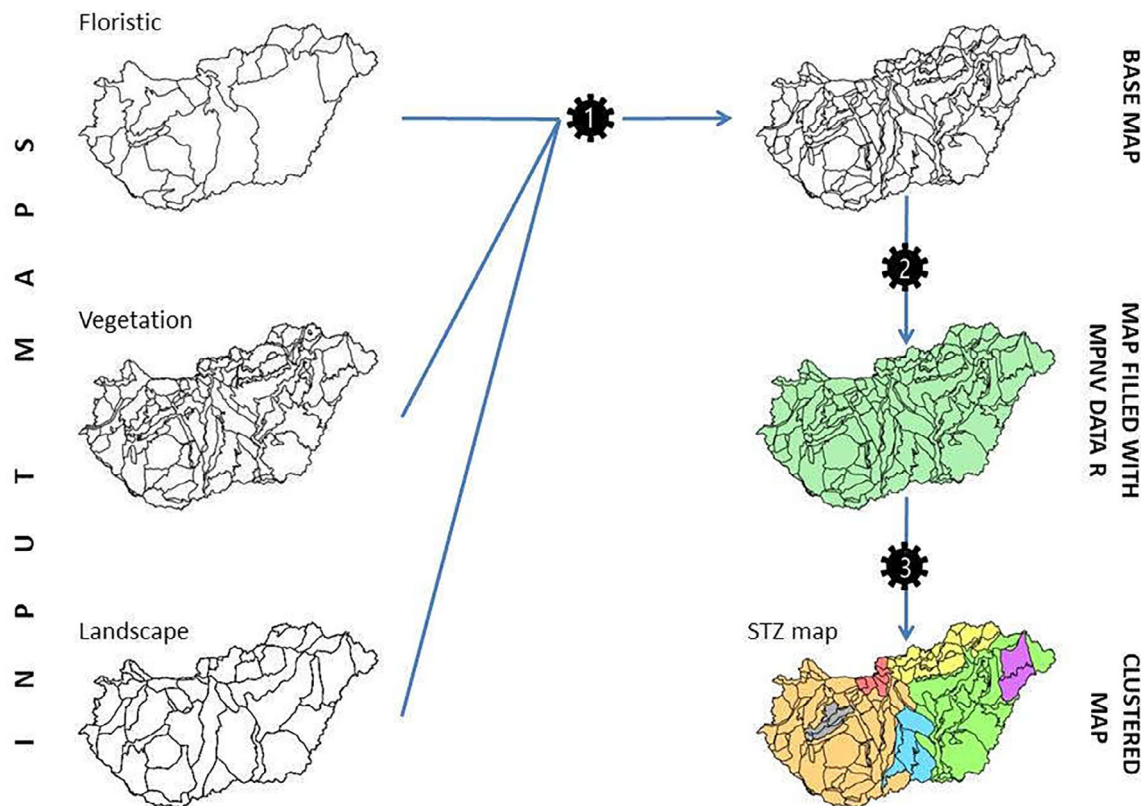


Figure 1. Workflow of the development of the seed transfer zone map based on the intersection of the floristic, vegetation, and landscape maps. Steps are as follows: (1) intersection of the geometries of the three input maps; (2) filling the resulted base map polygons with Multiple Potential Natural Vegetation data; and (3) clustering of the polygons to form seven clusters (equal to the number of administrative regions).

the prediction of the MPNV model (Somodi et al. 2017). MPNV describes the probability of occurrence of 39 climax and subclimax habitats (Bölöni et al. 2011), rescaled to a 5-level ordinal scale (0–4, where 4 is the most probable) in a grid of 35 ha hexagons for the whole country, based on existing natural vegetation, and climatic, topographic, edaphic, and hydrologic predictors. For all the polygons of the base map, the hexagons with their center situated within the given polygon were included in the analyses. The process resulted in a table where the rows represented the polygons and the columns the 39 habitat types. In the cells of the table, the number of hexagons indicated where the occurrence of a given habitat type had either medium or high probability (ranks 2, 3, or 4), divided by the total number of hexagons within the polygon. This table was used for the distance calculation in the cluster analysis, detailed below (step 3 in Fig. 1).

Clustering was performed on the filled polygons of the base map. Since clusters formed by isolated polygons are not relevant for STZs, Spatial 'K'luster Analysis by Tree Edge Removal (SKATER) algorithm was used, which, due to the applied constraint, resulted in contiguous clusters formed by adjacent polygons (Assunção et al. 2006). The algorithm builds a minimum spanning tree of the connectivity graph according to the neighborhood relationship and the Euclidean distance (i.e. cost of the edges) between the polygons and then removes the edges

iteratively to gain the desired number of clusters. The algorithm cannot choose the optimal cluster number since it is acquired as an input parameter. Seven clusters were formed to get an interpretable and applicable result that can be compared to the seven regions of the administrative units.

Uncertainty Analysis

To test the uncertainty (Dong et al. 2015; Retchless & Brewer 2016) of the resulting STZ map in the later phases of the study, an independent map was introduced (Fig. 2) that is the systematic square grid of the MÉTA database (Landscape Ecological Vegetation Database & Map of Hungary; Molnár et al. 2007) with 2,834 quadrats (with the size of geographical longitude $5' \times$ latitude $3' =$ approx. 6.25×5.05 km), where each quadrat contains 100 hexagons of 35 ha. The geometry of these quadrats is completely systematic and is not based on vegetation or administrative borders. The quadrats were filled with MPNV data and then clustered to form seven contiguous clusters in the same way as the base map was (steps 2 and 3 in Fig. 1).

Uncertainty of the STZ map was analyzed and displayed by calculating the agreement between the seven clusters of the map based on the quadrat geometry and the clusters of the evidence-based STZ processed from the base map geometry (step 4 in Fig. 2). This required that the seven clusters of the

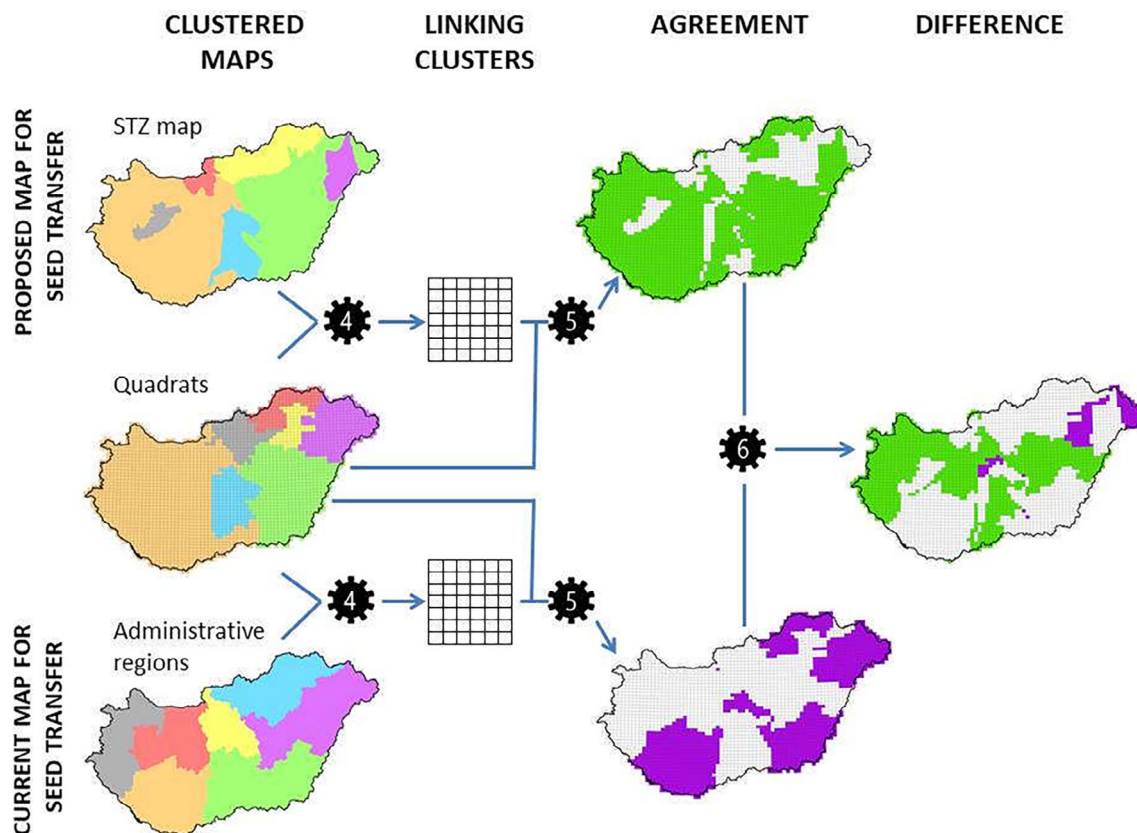


Figure 2. Workflow of the uncertainty analyses of the seed transfer zone map and that of the administrative regions. Both maps are compared to the clustered landscape ecological vegetation database (MÉTA) quadrats. Steps are as follows: (4) linking each of the seven clusters of the seed transfer zones and the administrative regions to quadrat clusters based on maximum area shared; (5) estimating agreement of seed transfer zones (and administrative regions) with the clusters of the quadrats at quadrat level; and (6) subtraction of the two agreement maps to produce the difference map. Green color in the agreement and difference maps indicates polygons where seed transfer zones and quadrat clusters agree, white means no difference between seed transfer zones and administrative borders; purple shows the polygons where the administrative regions agree with quadrat clusters.

quadrats were linked to the seven STZs in advance. The linking was done algorithmically by iterating through all the possible permutations ($7! = 5,040$) of the cluster-cluster linkages, and selecting the permutation that maximizes the summed area of the intersection of the linked clusters, i.e. maximizes resemblance. Then, for all MÉTA quadrats, we studied whether the two clustered maps were in agreement, i.e. the quadrat is placed in the clusters linked previously (step 5 in Fig. 2). If a quadrat was not entirely within a cluster, the one with which it shared the largest area was selected.

Comparison Between Administrative Regions and Evidence-Based STZs

To compare the evidence-based STZ map with that of the administrative regions presently serving as the basis for the regulation of seed transfer, we repeated the uncertainty analysis detailed above, with STZs replaced with the administrative regions. Thus, the agreement of the administrative regions with the clusters of the independent quadrats was produced. Following that, we calculated the difference between the two agreement maps by a simple subtraction (step 6 in Fig. 2).

Calculations and visualization were done in ESRI ArcGIS (10.2) and R statistical software (R Core team 2018), and the R packages “sf” (Pebesma 2018b), “gttools” (Warnes et al. 2018), “lwgeom” (Pebesma 2018a), and “tidyverse” (Wickham 2017).

Results

The Evidence-Based STZ Map

The clustering of the base map based on the most probable potential natural vegetation types of the polygons resulted in the map shown in Figure 3A (see Supplement Data S1 for ESRI shapefiles and Rdata format). The zonation separated two large regions: a cluster in the Transdanubia was formed including the small cluster of the Balaton Uplands, and the Great Plain including the Nyírség region (region names in Fig. 3B). In between the two large clusters, the Mid-Danube-Tisza sandy region was formed as a zone. The surroundings of the Pilis-Visegrád-Börzsöny region were clustered separately from the North Hungarian Mountains. The pattern of the STZ map greatly differs from that of the administrative regions (NUTS2) (Fig. 3C).

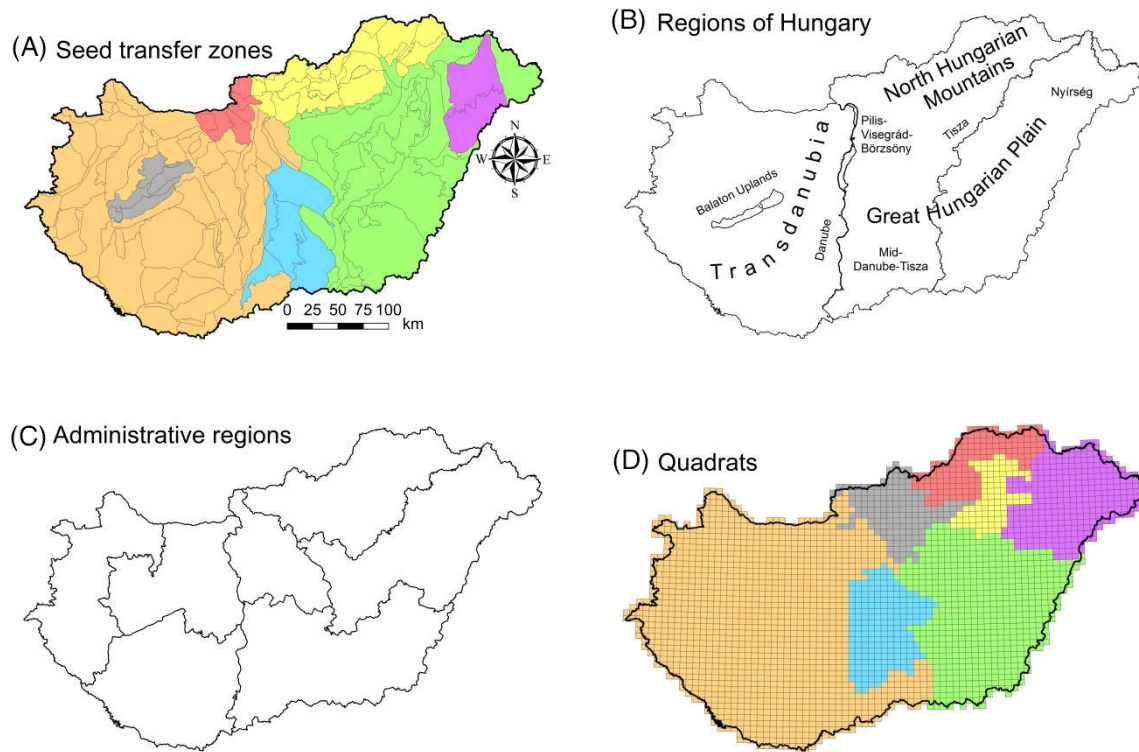


Figure 3. (A) Clustered map of the base map as seed transfer zones, (B) the map of administrative regions; (C) region names in Hungary used in the text; and (D) clustered landscape ecological vegetation database (MÉTA) quadrats, used for the uncertainty analyses. Different colors indicate separate clusters. The figures also show the original geometries of the base map in gray outlines. For quadrats the geometry is a systematic grid of about 35 km².

Uncertainty Analysis of the STZ Map

As a comparison, the clustering of the quadrats was performed with the same approach as for the STZs (Fig. 3D). The two clustered maps show similarities regarding the division of the Great Hungarian Plain into three zones, but they are different in the partition of the North-Hungarian Mountain region and the separation of the Balaton Uplands.

Uncertainty was measured by comparing the agreement between STZs and the zones gained as a result of the clustering of the quadrats (Fig. 2). Polygons where the two approaches resulted in similar clustering are shown in green. Most of the territory of the Transdanubian region and that of the Great Plain match well, whereas the Balaton Upland and the North-Hungarian Mountains differ. The area clustered similarly reached 76% of the territory of Hungary.

Difference Between the Uncertainty of the STZs and Administrative Regions

Similar to the STZ uncertainty test, the agreement of the administrative regions with the quadrat clusters was calculated (Fig. 2; agreements are shown in purple). Only part of Southern Transdanubia, parts of Southern and Eastern Great Plain, and parts of the North-Hungarian Mountains were clustered similarly, with an agreement of 42% of the area. The comparison of the two agreement maps demonstrates how differently the STZ and the administrative regions are supported by the independent

quadrat clusters (Fig. 2). The STZs provided better agreement (40.2%) than administrative regions in the Northern Transdanubian region, the Mid-Danube-Tisza region, and the Northern Great Hungarian Plain. The administrative regions were better supported by quadrat clustering in a few small areas, mainly in Eastern Great Hungarian Plain, altogether adding up to 6.1% of the area of Hungary.

Discussion

This study provides the first attempt to link traditional biogeographic maps with a Multiple Potential Natural Vegetation model to delineate STZs. The approach consisted of filling the polygons of the composite of different biogeographic maps with potential natural vegetation data, and testing their clustering through assembling polygons of similar most probable potential vegetation to form STZs. The potential natural vegetation was criticized earlier for being often overly bold in advising restoration decisions (Siles et al. 2010). Our approach benefitted from the high resolution of the model (35 ha units) and from the multiple probable vegetation types for a given area, instead of the most probable one, which allowed a more realistic estimate of the variability of vegetation types within the polygons analyzed. This approach is valuable with regards to the high ratio (63.3%) of the greatly modified area of Hungary (Török et al. 2019), where biogeographical zones, in absence of current natural vegetation, are hard to establish.

The practical output of the study, the STZ map for Hungary, based on a scientifically sound approach was developed, and could substitute the present regulation using administrative zones for seed transfer control. So far, the scarcity of robust experimental tests of the genetic variability of species is a common drawback of novel seed sourcing strategies (Bucharova et al. 2019; León-Lobos et al. 2020). The vegetation and environmental basis of the zone development empower our approach to be valid for multiple species (SKEW 2009; Prasse et al. 2010; Krautzer et al. 2018).

The introduction of a map with independent geometries (the MÉTA quadrats) enabled the calculation of the credibility of the STZs. The agreement of maps and the difference map between the STZ and the administrative regions discovered the advantage of the STZ map, manifest in a much larger area (about 76% of the country) where the zones overlap with the clusters of quadrats as opposed to the administrative regions (42%). Thus, our study provides an estimation on the level of uncertainty, which has great practical value, and can help convince decision makers that a change in legislation is necessary. Further studies with fewer or more zones, and other types of experiments with species, like a common garden, genetics, etc., are encouraged to fine-tune the system.

The generalized STZs for multiple species might be inadequate for some species, as this approach assumes that plants perform better at their site of origin, and that natural selection is stronger than the homogenizing effect of gene flow (Crow et al. 2018). However, dispersal limitation and the colonization history of species add to the environmental differences resulting in genetic differentiation (Orsini et al. 2013; Durka et al. 2017), and gene flow can occur between biogeographically different regions (Listl et al. 2018). Therefore, for certain species, the validity of generalized STZs can be questioned. Empirical data in the literature on native species of Hungary are scarce; only a few genetic analyses with one to three sampling locations exist, which are not sufficient for testing the seven zones (Sramkó et al. 2014; Mosolygó-L et al. 2016).

The number of STZs in this study (seven) can be considered arbitrary. Our concern was to compare the zones of the present regulation and the evidence-based map, so we used the same number of units. In other countries of Central Europe, the average area of seed zones range from 8,000 to 16,000 km². For example, in Austria 10 zones (Krautzer et al. 2018; average area per zone 8,300 km²), in the Czech Republic five (Ševčíková et al. 2014; 15,700 km²), and in Germany eight production and 22 STZs were delineated (Prasse et al. 2010; 16,200 km²). The average area of 13,300 km² of the Hungarian STZs is of a similar order of magnitude. During further development, fewer or more zones can be tested by the same approach.

The borders in the STZ map should not be considered as lines but rather as broad transition zones. Several authors have stressed the continuous nature of genetic variability instead of discrete units (Bower et al. 2014; Jørgensen et al. 2016; Crow et al. 2018). Therefore, adjacent locations in different regions might be very similar, so seed transport may be acceptable but should be considered on a case-by-case basis (Bucharova et al. 2019). It has to be noted that such a flexible regulation is not part

of current legislation, and new approaches have to be introduced to handle such a system, which is rather unlikely.

The method tested in the study is transferable to other countries looking for developing STZs (León-Lobos et al. 2020), even where no potential vegetation model exists, but detailed vegetation or flora-based subdivision and expert knowledge is available. This approach provides more reliable STZs than using any kind of administrative division. The use of administrative borders for the regulation of seed transfer seems straightforward from the viewpoint of simplifying legislation. However, there are examples where administrative borders were ignored. For instance, the German seed transfer and production zones have no relation to administrative regions but are based on biogeographical zones and expert judgment (Prasse et al. 2010; Bucharova et al. 2017b), just like in Austria (Krautzer et al. 2018). Thus, a change from the administrative borders to the STZs in the legislation of Hungary is advocated. The STZ map can serve the further development of the native seed propagation program in Hungary, which is still in an early stage and cannot meet the demand for seeds necessary for compliance with the Target 2 of restoring 15% of degraded land, aimed as part of the EU Biodiversity Strategy and for the improvement of the green infrastructure (Török et al. 2019). An STZ-based regulation and certification procedure for the propagation and marketing of native herbaceous species seeds could greatly contribute to scaling up the restoration of degraded habitats in countries lagging behind in this regard.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. 1) Seed transfer zones map (basemap); 2) Clustered MÉTA (Magyarország Élőhelyeinek Térképi Adatbázisa) quadrats; 3) Agreement of MÉTA quadrats with Seed Transfer Zone(STZ) map; 4) Agreement of MÉTA quadrats with administrative regions; 5) Difference map between STZ and administrative regions agreement map.

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