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Original Research Article

Do environmental predictors affect the regeneration capacity of sandy habitats? A country-wide survey from Hungary

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A B S T R A C T

European countries are far from the 15% restoration target to be reached by 2020, partly due to the lack of large-scale studies at the national level that would help prioritise restoration efforts. We investigated the regeneration capacity and the determining environmental factors at the national level for three Pannonian sandy habitat types. The analysis was based on the Hungarian Vegetation Mapping database that includes a three-level regeneration capacity estimate of semi-natural habitats based on expert judgments after local vegetation mapping. We have selected fifteen environmental predictors that could possibly influence regeneration, including proxies for landscape naturalness, landscape context and abiotic factors. Using the decision tree method, we found that the local regeneration of open and closed steppes is primarily determined by habitat naturalness. For juniper-poplar stands the seasonality of the precipitation is the most important predictor and Natural Capital Index of sandy habitats, as a proxy for landscape naturalness, is the second. In case of neighbouring areas and abandoned fields, the regeneration is primarily affected by the sand content of the soil and the total local extent of habitats. Furthermore, grasslands and agricultural areas represent a potential for regeneration after abandonment. Our results show that in addition to habitat adequacy, proxies for landscape naturalness are the most important predictors of regeneration capacity. This implies that the future dynamics of habitats – and consequently ecosystem health and integrity – are determined primarily by the conservation of remnant natural and semi-natural areas and active restoration to increase the area or improve the state of semi-natural habitats.

1. Introduction

The EU Biodiversity Strategy by 2020 (European Commission, 2011) and the Aichi Biodiversity Targets of the Convention on Biological Diversity (CBD, 2010) prescribed 15% of all degraded land to be restored by 2020. Unfortunately, little has been achieved regarding the restoration target (Cortina-Segarra et al., 2016), only a few member states have started to develop their prioritization strategies in time to delay ecosystem degradation by 2020 (Tolvanen and Aronson, 2016) or evaluated the total area restored (Aradóttir et al., 2013; Török et al., 2019). These efforts are far from the targeted 15%, and realising this, new

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restoration goals are planned for the next decade (UN Decade on Ecosystem Restoration 2021–2030: UNEP/FAO, 2020; COM, 2019; GBO5, 2020). In this new period, restoration costs need to be considered in the different member states as these severely influence prioritization (Kotiaho et al., 2016; Tolvanen and Aronson, 2016). For the restoration of large areas, apart from fine-scale studies, large-scale research projects are also needed (Ormerod, 2003) to obtain a country-wide overview of regeneration capacity and naturalness (Seregélyes et al., 2008). Ways to implement cost-effective country-level restoration projects include relying on spontaneous regeneration, developing indicators and monitoring results.

According to our interpretation, regeneration capacity is an indicator of healthy ecosystems and their services, that can also provide information about the future dynamics of habitats under human pressure (Seregélyes et al., 2008). Studying the regeneration capacity of landscapes, which is one of the main functional indicators of habitat quality regarding the future, can help achieve conservation and restoration objectives (Hirst et al., 2005). Diverse and stable ecosystems promote resistance to disturbances (Schulcze and Mooney, 1993) and are capable of rapid recovery after extreme events (Hoover et al., 2014). Land degradation reduces resilience, making the ecosystems more vulnerable, and decreasing their capacity to recover from disturbance (Eckert et al., 2015), therefore elongating the process to restabilize degraded ecosystems (Tilman, 1989; Milchunas and Laurenroth, 1995).

Quantifying habitat regeneration capacity and assessing the mechanisms underlying recovery is currently a major challenge for ecologists (Hoover et al., 2014). Local and regional studies have evaluated the success of spontaneous and active restoration and shown the regeneration capacity of dry grasslands (Erdős et al., 2017; Csecserits and Rédei, 2001; Csecserits et al., 2007, 2011; Halassy, 2004, Sengl et al., 2017; Rédei et al., 2014), but national evaluation has not yet been carried out. The factors that influence the recovery can vary, and are dependent on environmental variables, moreover these are inter-correlated, thus the relationships are difficult to untangle (Fagan et al., 2008). The recovery process is dependent on – for example – changes in soil chemistry, soil seed bank, structure and function characteristics or dispersal limitation (Halassy, 2001; Hirst et al., 2005; Karlík and Poschlod, 2019; Wagner et al., 2019).

One of the most diverse and species rich plant communities in Europe are temperate grasslands with a high number of endemic, rare and endangered species (Butaye et al., 2005; Csecserits et al., 2011; Janišová et al., 2014; Poschlod and WallisDeVries, 2002; Török and Dengler, 2018; Török et al., 2018). Protecting, maintaining (Dicks et al., 2019) and successfully restoring dry temperate grasslands (Dicks et al., 2019) are key objectives of the European conservation policy and of evidence-based conservation management in general. The extraordinarily high species richness is due to the combined effect of natural processes and traditional human activities, especially on grasslands with long management histories such as extensive pastures and meadows (Biró, 2003; Biró et al., 2008; Hájková et al., 2011; Janišová et al., 2014; Poschlod and WallisDeVries, 2002). Due to changes in human land-use, such as the intensification of agriculture practices (Biró et al., 2013a; Dicks et al., 2019), the abandonment of traditional grazing (Butaye et al., 2005; Hegedüšová and Senko, 2011) and use of non-native species in forest management (Szilassi et al., 2017), the extent of temperate grasslands has decreased dramatically. The remaining areas are strongly fragmented (Butaye et al., 2005; Biró et al., 2013a) and threatened by the spread of invasive plant species (Botta-Dukát, 2008; Csecserits et al., 2016).

The main aim of the present study is to evaluate the regeneration capacity of sandy habitats at the national level and to identify the key environmental predictors that determine it. Besides local regeneration after a potential partial degradation, which describes resilience, we also evaluate the colonisation ability of remnant grasslands to neighbouring areas and to abandoned fields, that represent a potential for passive restoration (Prach et al., 2020). Our questions are as follows: (i) What is the regeneration capacity of Pannonian sandy habitat types at the national scale? (ii) Which environmental predictors determine the regeneration capacity in a landscape? (iii) Is there a difference in the predictors that determine the regeneration capacity on spot (existing patches), on neighbouring spots and on nearby abandoned fields?

2. Materials and methods

2.1. Studied habitats

We investigated three endemic Pannonian sandy habitat types at the national scale (Bölöni et al., 2011), which are, according to the EU Habitat Directive (92/43/EEC, I. Appendix: 6260, 2340, 91N0), integrated into the European Union Natura 2000 network (Romão, 1996). The species composition of studied habitats overlaps substantially.

Open sand steppes (further referred to as open steppes, Fig. 1a) and b) belong partly to Pannonic inland dunes (code 2340) and partly to Pannonic sand steppes (code 6260). These habitats are dominated by the bunch grasses *Festuca vaginata* and *Stipa borysthenica*. The total vascular plant cover is less than 75%, the remaining surface can be either bare or covered by mosses and lichens. Open steppes are most common in the driest parts of Hungary, occupying poor sandy soils with low humus content. The total actual area is 10,700 ha. Black-locust plantations pose the main threat, destroying the habitat and opening the soil for further alien colonisation (Csecserits et al., 2016). Open steppes can spread in sandy areas at the expense of the other forest-steppe components due to groundwater drainage, deforestation and heavy grazing (Máté, 2014; Molnár et al., 2011b).

Closed sand steppes (further referred to as closed steppes, Fig. 1c) also belong to Pannonic sand steppes (code 6260). The habitat is dominated by *Festuca wagneri*, *Festuca rupicola* and *Stipa capillata*. Closed steppes develop on more humus rich soils, and have once occupied almost every sandy region in the country. Their total area is around 28,000 ha. Main threats to these habitats include habitat loss and fragmentation due to agriculture and forestry, overgrazing and invasion. As groundwater levels fall, closed steppes retreat from drier areas, but can spread to former wet grasslands (Molnár et al., 2011c).

Fig. 1. Pannonian sandy habitat types in Hungary. a) Open sand steppes: Pannonic inland dunes (code 2340) in Kiskunság, Fülöpháza, b) open sand steppes: Pannonic sand steppes (code 6260) in South Nyírség, Martinka c) closed sand steppes: Pannonic sand steppes (code 6260) in Kiskunság, Kunpeszér, d) poplar-juniper sand dune forests and thickets: Pannonic inland sand dune thickets (code 91N0) in Kiskunság, Fülöpháza. Photos by Á. Molnár.

Poplar-juniper sand dune forests and thickets (further referred to as juniper-poplar stands, Fig. 1d) belong to Pannonic inland sand dune thickets (code 91N0). The habitat is dominated by *Juniperus communis*, *Populus alba* and *Populus × canescens*. Their stands often form mosaics with open sand grasslands. They are only found in the calcareous sand region in the central part of the country with a total cover of 3000 ha. The main threats to these habitats are overgrazing, logging, spread of *Robinia pseudoacacia* and fire. Juniper-poplar stands can naturally spread to open and closed steppes (Molnár et al., 2011a).

2.2. Estimation of regeneration capacity

We used the Hungarian Vegetation Mapping Database (MÉTA – Horváth et al., 2008; Molnár et al., 2007) to estimate the regeneration capacity of the three sandy habitats. The MÉTA database is the result of a large-scale vegetation mapping project conducted between 2003 and 2006 on the whole territory of Hungary. 86 different types of natural and semi-natural habitats were distinguished according to the National Habitat Classification System (Á-NÉR; Bölöni et al., 2007, 2011) and surveyed by 200 experts. The database is built from 5.5 × 6.5 km (35 km^2) rectangular landscape units (2813 quadrats) according to the grid system of Central European Flora Mapping Units (FMUs) that are further divided into 267,813 hexagonal grid cells (the area of each cell is 35 ha) (Horváth et al., 2008, Molnár et al., 2007). Occurrence of habitats and habitat quality attributes were estimated at the quadrat and/or hexagon level based on field surveys. All field surveyors participated in preliminary trainings where the coding methodology was substantially standardised. The experts spent 2–3 days on average in each quadrat, where they were instructed to look for regenerating stands of all habitat types, after which they sorted all habitats of the quadrat into 4 different pre-set categories of regeneration capacity (Molnár et al., 2007).

Three different types of regeneration capacity are included in the MÉTA database based on expert judgments at the quadrat level (Seregélyes et al., 2008): (i) on spot: the capability of an existing stand to return to its natural state after a possible partial degradation; (ii) on neighbouring spots immediately adjacent to the studied habitat: the capability of the habitat to spread to and restore itself in adjacent areas without human intervention; (iii) on old fields: the capability of the habitat to colonise left-over open areas, in our case abandoned agricultural land. A four-level ordinal scale was used (Table A1) to estimate the potential of each regeneration capacity type (Seregélyes et al., 2008) from good to low (1–3), plus lack of suitable spaces (4).

2.3. Environmental predictors

We included three groups of environmental predictors that potentially influence the regeneration capacity of sandy habitats in the studied quadrats: proxies for landscape naturalness, landscape composition and abiotic factors. We used the following proxies for landscape naturalness based on the MÉTA database (Molnár et al., 2003): (i) area, i.e. the quantity of natural and semi-natural habitats, which means the total local extent of habitats within the quadrat; (ii) habitat naturalness, i.e. the quality of the habitat estimated at the hexagon level, based on expert judgement (1–5 scale from totally degraded habitats without any natural or semi-natural vegetation to habitats with a high number of specialist and rare species without weeds and invasive species; Table A2) (Bölöni et al., 2008), (iii) and the previous two approaches combined in the Natural Capital Index (NCI) calculated based on the ecosystem quantity (area) and ecosystem quality (naturalness) (Czúcz et al., 2008, 2012; Szilassi et al., 2017). Two types of NCI were queried: NCI of sandy habitats and NCI of all the habitats within the hexagon.

To calculate landscape context, we used CORINE Land Cover 2006 database, which is the closest in time to the MÉTA survey. The CLC map uses a uniform methodology for the countries of the European Union (EEA, 2013). Its scale is 1:100,000. The minimum mapping unit was 25 ha for habitat patches and 100 m width for linear landscape elements (EEA, 2017). We merged the CLC classes into six categories according to land cover types: (AS) artificial surfaces; (AA) agricultural areas; (F) forests; (GL) grasslands; (WL) wetlands; (W) water bodies. The area of all CLC classes was calculated within the studied quadrats using the ArcGIS 10.2 (ESRI, 2013) software.

In addition, we selected abiotic factors that were good predictors for sandy vegetation at the country level in multiple potential natural vegetation models (MPNV; Somodi et al., 2017). These were as follows: (i) maximum sand fraction ratio in the upper 0–30 cm soil layer; (ii) mean level of groundwater; (iii) standard deviation of Topographic Position Index (TPI; Gallant and Wilson, 2000; Weiss, 2001); (iv) thirty-year average of temperature seasonality and (v) thirty-year average of precipitation seasonality. Soil properties were obtained from the DOSoReMI.hu soil database (Pásztor et al., 2015). TPI was calculated with a 3 × 3 focal matrix with the 'raster' package (Hijmans, 2015) of the R statistical software (R Core Team, 2019). Elevation data for the TPI calculation were acquired from the SRTM digital terrain model (USGS, 2004) that has 90 m horizontal and cca. 16 m vertical resolution (SRTM, 2015). Raw climatic data was obtained from the CarpatClim-Hu database (Szalai et al., 2013) for the 1977–2006 period at daily temporal and 0.1° (approx. 10 km) horizontal resolution. All the abiotic predictors were downscaled to the hexagon level and aggregated by Somodi et al. (2017). A summary of environmental predictors is given in Table A3.

2.4. Data analysis

Since regeneration capacity data was available at the quadrat level, we had to aggregate hexagonal data to this level. We calculated the sum of the area; the weighted average of habitat naturalness where the weight was the extent of sandy habitats within the quadrat; the average of NCI values and soil, topographic and climatic data. The extraction of CLC categories within MÉTA sandy quadrats and all predictor datasets were managed using ArcGIS and MS Excel (Microsoft Corporation, 2016).

The relationship between regeneration capacity and environmental predictors was analysed by the decision tree method (also known as classification tree). It is a non-parametric statistical method that can handle nonlinear relationships of large sets of categorical and continuous predictors, and expressively interpret the significant differences between classes (Csecserits et al., 2016; Crawley, 2007). A further advantage of the method is that it handles the predictors separately, therefore it is free of problems caused by multicollinearity (Csecserits et al., 2016; Hothorn et al., 2006). Decision tree analyses were carried out with the R statistical software (R Core Team, 2019) using the 'party' package (Hothorn et al., 2020). The Bonferroni-corrected significance of the split was $p < 0.05$ ($r = 0.95$) and the maximum depth of internal nodes was 4. The models were evaluated using accuracy measure and Cohen's κ (Cohen, 1960), calculated with the 'caret' package (Kuhn, 2020). Spatial autocorrelation of the model residuals according to Moran's I and its significance were studied with packages 'sf' (Pebesma, 2018) and 'spdep' (Bivand et al., 2013; Bivand and Wong, 2018).

3. Results

3.1. General success of regeneration

The regeneration capacity of the three sandy habitat types at the national level were as follows; Juniper-poplar stands had the best on spot regeneration capacity among the studied habitat types: in 90% of quadrats the estimated regeneration capacity was good, in 4% moderate and in 6% low. The regeneration capacity of open steppes on spot was mostly good (48%), moderate in 29% and low in 24%, whereas closed steppes had the lowest overall regeneration capacity, with good in 39%, moderate in 46% and low in 16% of the quadrats. The regeneration capacity for neighbouring spots declined compared to on spot regeneration. Juniper-polar stands still had the best regeneration capacity, since in 65% of quadrats it was good. For open steppes the good regeneration capacity decreased to 9% and for closed steppes it decreased to 10%. Closed steppe habitat had again the lowest regeneration capacity (58% low regeneration), meanwhile for open steppes the regeneration was low in 45%, and for juniper-poplar stands it was low in 10% of the quadrats. The old fields had the worst regeneration capacity in all habitat types. The regeneration capacity of juniper-poplar stands was mostly moderate (42%), low in 8%, and good in 23%, while the regeneration capacity of open steppes was moderate in 25%, low in 47%, and good only in 9%. The regeneration capacity of closed steppes was moderate in 10%, low in 55% and similarly good in 9% of the quadrats (Table A4).

3.2. Regeneration capacity on spot and its predictors

In the fitted decision tree for regeneration capacity of open steppes on spot (accuracy = 0.54; $\kappa = 0.25$; I = 0.14; $p < 0.01$), habitat naturalness was the only important predictor variable ($p < 0.001$). The regeneration capacity was better if naturalness was higher than 3.15, namely more than 60% of the observations showed good regeneration capacity in that case. If naturalness was lower, good regeneration capacity observations were under 30% and low regeneration capacity was dominant (ca. 40%) (Fig. 2a).

In the fitted decision tree for regeneration capacity of closed steppes on spot (accuracy = 0.57; $\kappa = 0.25$; I = 0.13; $p < 0.001$), habitat naturalness was the most important predictor variable ($p < 0.001$). In the case of naturalness below 3.25, close to 50% of the observations showed medium regeneration capacity. If naturalness was higher than 3.25, the group was further divided according to temperature seasonality ($p < 0.001$). If the temperature seasonality was lower than or equal to 780.84, the habitats with medium regeneration capacity had the highest proportion (more than 60% of the observations). A better regeneration capacity was found if the temperature seasonality was higher than 780.84, when more than 60% of the observations indicated habitats with good regeneration capacity (Fig. 2b).

In the case of the regeneration capacity of juniper-poplar stands on spot (accuracy = 0.90; $\kappa = 0$; I = 0.05; $p = 0.279$), the seasonality of precipitation was the most important predictor variable ($p < 0.001$) in the fitted decision tree. Lower regeneration (less than 60% of the observations were good) was found when precipitation seasonality was lower than or equal to 0.25. In the case of higher precipitation seasonality, the first group was further divided according to NCI values of all the habitats ($p = 0.045$). If the NCI of all the habitats was less than or equal to 14.18, all sandy habitats within each quadrat had good regeneration capacity. When the NCI was higher than 14.18, 70% of observations showed good regeneration capacity (Fig. 2c).

3.3. Regeneration capacity on neighbouring spots and its predictors

In the case of regeneration capacity on neighbouring spots (accuracy = 0.54; $\kappa = 0.23$; I = 0.05; $p = 0.140$) of open steppes, the maximum sand content of the soil was the most important predictor variable ($p < 0.001$) in the fitted decision tree. In the case of a maximum sand fraction ratio lower than 79% in the upper 0–30 cm soil layer, nearly 60% of the observations showed low regeneration capacity. If the sand content was higher than 79%, the first group was further divided according to the extent of the habitat ($p = 0.046$). If the extent of the habitat was less than 1.46 ha, the habitats with low regeneration capacity had the highest proportion, more than 60% of the observations. If the extent of the habitat was higher than 1.46 ha, more than 40% of observations showed medium regeneration capacity, and the habitats with good regeneration capacity approached 20% of all observations (Fig. 3a).

A more complex decision tree was created based on the regeneration capacity analyses of closed steppes on neighbouring spots (accuracy = 0.65; $\kappa = 0.25$; I = 0.18; $p < 0.001$). The most important predictor variable was the extent of habitats ($p < 0.001$), followed by temperature seasonality that split at node 2, 5 and 6 ($p = 0.016$, $p < 0.001$, $p = 0.036$, respectively), habitat naturalness (node 9, $p < 0.001$) and altitude (node 11, $p = 0.002$). The best regeneration, when around 90% of observations revealed good regeneration capacity, was found when the extent of habitats was higher than 120.85 ha, the temperature seasonality was higher than 783.76, the naturalness was higher than 3.6 and the altitude was lower than 105.78 m above sea level. Somewhat lower regeneration (40% of observations good and 40% medium) was found at higher elevations, but similar naturalness and temperature seasonality. The other terminal nodes showed low regeneration capacity or the lack of suitable spaces for colonization (Fig. 3b).

In the fitted decision tree for regeneration capacity of juniper-poplar stands on neighbouring spots (accuracy = 0.65; $\kappa = 0$; I = 0.17; $p = 0.066$), wetlands were the only important predictor variable ($p = 0.017$). The regeneration capacity was better where the extent of wetlands was more than 2.87 ha (Fig. 3c).

3.4. Regeneration capacity on old fields and its predictors

When considering regeneration capacity of open steppes on old fields (accuracy = 0.46; $\kappa = 0$; I = 0.06; $p = 0.089$), maximum sand content of the soil was again the most important and only predictor variable ($p < 0.001$) in the fitted decision tree, while the splitting value was the same (79%) as for neighbouring areas. Low regeneration capacity was found at lower levels of sand content: nearly 60% of the observations showed low regeneration and 30% suitable spaces for colonization. At higher levels of sand content, the proportion of habitats with low regeneration capacity was close to 40% and that of habitats with medium regeneration capacity was 30% of the observations (Fig. 4a).

When analysing the regeneration capacity of closed steppes on old fields (accuracy = 0.61; $\kappa = 0.17$; I = 0.21; $p < 0.001$), the extent of habitats was the most important predictor, followed by land uses (GL and AA) and groundwater depth (all with $p < 0.001$). The best regeneration capacity was found when the extent of the habitat was higher than 117.95 ha, agricultural areas exceeded 203.39 ha and groundwater level was under 2.86 m. The lowest regeneration was found when the extent of the habitat was lower than 117.95 ha with less than 77.05 ha of CLC grasslands in the quadrat (Fig. 4b).

The regeneration capacity of juniper-poplar stands on old fields (accuracy = 0.40; $\kappa = 0$; I = 0.25; $p < 0.05$) could not be interpreted as a decision tree, since no optimal splits were found at the selected ($p < 0.05$) significance level.

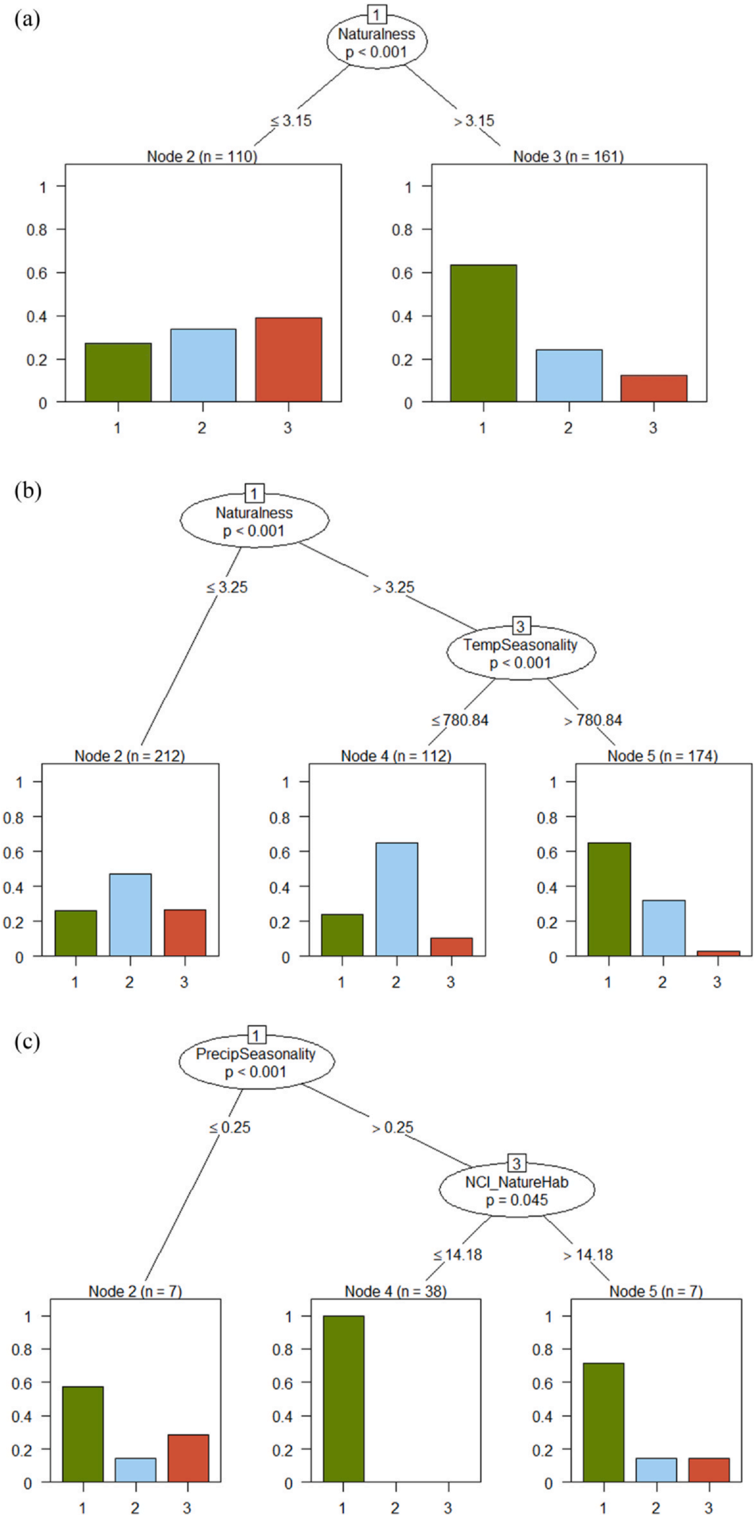

Fig. 2. Classification tree model of regeneration capacity on spot of a) open steppes, b) closed steppes and c) juniper-poplar stands. Green, blue and red colours represent good, moderate and low regeneration capacity, respectively. Each node is described by the splitting variable used at the split, the Bonferroni-corrected significance (p value) of the split and the values at which the split occurs. At each terminal node the number of observations (n) is given. Vertical axes show the percentage of quadrats with good (1), moderate (2) and low (3) regeneration capacity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Regeneration capacity of Pannonian sandy habitat types at the national scale

Country-level research projects are needed to implement cost-effective large-scale restoration projects (Ormerod, 2003). Our study was the first country-level regeneration capacity estimate to our knowledge that investigated environmental predictors as potential indicators of regeneration to help restoration prioritization.

Out of the studied habitat types, juniper-poplar stands had the best regeneration capacity on spot, on neighbouring spots and on old fields as well. This habitat type only occurs in the central part of Hungary and species connected to this habitat have good mobility that enables natural spread to open and closed sand steppes (Molnár et al., 2011a). The regeneration capacity of open steppes was in second place. Open steppes can spread to neighbouring sandy areas in place of other forest-steppe components primarily due to the decreased groundwater level that results in unsuitable conditions for other habitats (Máté, 2014; Molnár et al., 2011b). Regeneration capacity of open steppes decreased towards old fields, where the chance for regeneration is lower as a result of the spread of invasive species, mainly *Robinia pseudoacacia* and *Asclepias syriaca* (Molnár et al., 2011b). Closed steppes occupy almost every sand region in the country, but had the lowest regeneration capacity in all three cases. As groundwater levels fall, this habitat retreats from drier areas, but can spread to former wet grasslands (Molnár et al., 2011c). Characteristic species of closed steppes have a lower capability to spread, therefore their regeneration capacity shows a declining tendency towards old fields. It is the most vulnerable of the three habitat types, particularly threatened by habitat loss and fragmentation as a result of intensive agriculture and forestry, overgrazing and invasion (Molnár et al., 2011c).

Our results correspond to the findings of Albert et al. (2014), who revealed that in Central Europe spontaneous processes can be crucial in the recovery of sand grassland vegetation. Nevertheless, the regeneration capacity of calcareous grasslands compared to mesotrophic grasslands is lower, for instance in Southern England they take more than a century to regenerate after abandonment (Wagner et al., 2019). According to the studies of Fagan et al. (2008), Hirst et al. (2005), Karlík and Poschlod (2019), the reason for this is the low availability of seeds and low soil nutrient content.

4.2. Environmental predictors that determine the regeneration capacity of Pannonian sandy habitat types

According to our analysis, the regeneration capacity of sandy habitats is higher in landscapes with higher naturalness. Fagan et al. (2008) and Albert et al. (2014) found that spontaneous regeneration was limited by the distance of natural grassland vegetation and lack of suitable propagules. In landscapes with higher naturalness there is a sufficiently large area for habitats and/or a high species richness, which result in a suitable source of propagules and/or smaller distances between patches.

We found that apart from the proxies for landscape naturalness a few abiotic predictors are also key determinants of regeneration potential, such as the seasonality of precipitation and temperature (parts of the local macroclimate), the sand content of the soil and groundwater level. These environmental factors are the key determinants of dry sandy habitats in Hungary that limit the spread of native and non-native invasive weed and woody species too. Besides these abiotic parameters, other studies highlight the importance of soil chemical composition (Gatica-Saavedra et al., 2017), e.g. nutrient limitation (N:P ratio) (Fagan et al., 2008; Karlík and Poschlod, 2019) and biotic parameters, such as the soil seed bank (Halassy, 2001) and dispersal limitation (Hirst et al., 2005; Albert et al., 2014; Wagner et al., 2019).

Among the proxies for landscape composition based on land cover types, the extent of agricultural areas and grasslands influenced regeneration capacity positively. The presence of agricultural areas might have a positive effect on regeneration in case of less intensive land use with many abandoned arable lands and with significant areas of natural vegetation. Our results correspond to the finding of Vogel et al. (2012) and Gatica-Saavedra et al. (2017), who revealed that extensive land use and species richness contribute to recovery on grasslands and in forest habitats too.

4.3. Differences in the environmental predictors on spot, on neighbouring spots and on abandoned fields

Biotic and abiotic predictors affected regeneration capacity to varying degrees on spot, on neighbouring spots and on abandoned fields according to habitat type. The on-spot regeneration of sandy grasslands is primarily determined by habitat naturalness, supposedly providing a sufficient source of propagules, which corresponds with the studies of Fagan et al. (2008), Hirst et al. (2005), Karlík and Poschlod (2019). Although some abiotic factors – such as the seasonality of temperature and precipitation – were also important predictors for local regeneration, their impact was more pronounced in the regeneration of neighbouring areas and abandoned fields. Additionally, the sand content of the soil primarily affected the regeneration of open grasslands in both neighbouring areas and abandoned fields. Substantially, even in case of suitable propagule sources the species can only establish if habitat conditions and land use are appropriate (Holl and Aide, 2011; Prach et al., 2020). Land cover types appeared as predictors only in case of regeneration on old fields. Agricultural areas in a landscape represent a potential for regeneration after abandonment of cultivation (Prach et al., 2013; Csecserits et al., 2011; Albert et al., 2014), whereas the presence of artificial surfaces hinders regeneration.

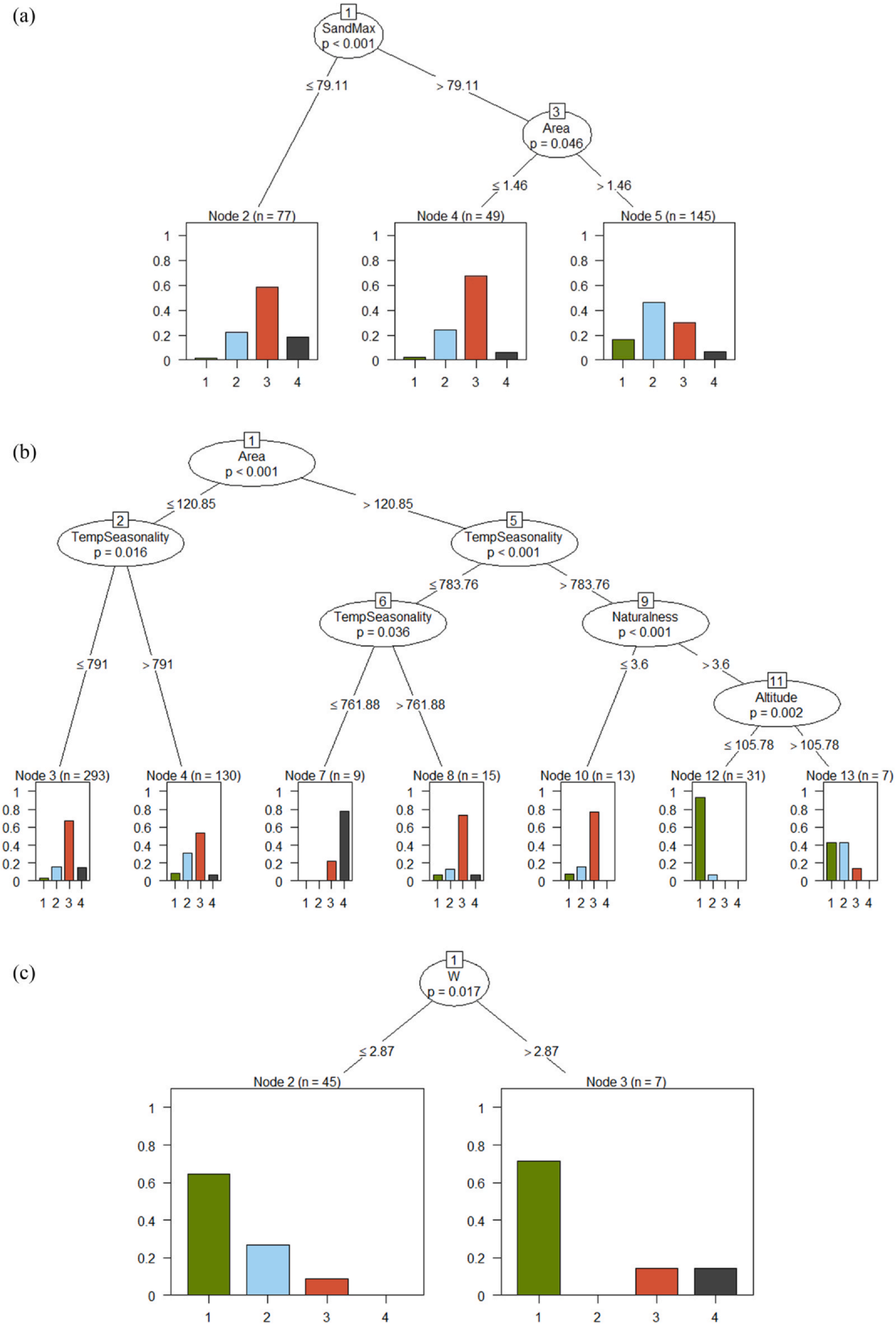

Fig. 3. Classification tree model of regeneration capacity on neighbouring spots of a) open steppes, b) closed steppes and c) juniper-poplar stands. Green, blue, red and black colours represent good, moderate, low and no regeneration capacity, respectively. Each node is described by the splitting variable used at the split, the Bonferroni-corrected significance (p value) of the split and the values at which the split occurs. At each terminal node the number of observations (n) is given. Vertical axes show the percentage of quadrats with good (1), moderate (2) low (3) and no (4) regeneration capacity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

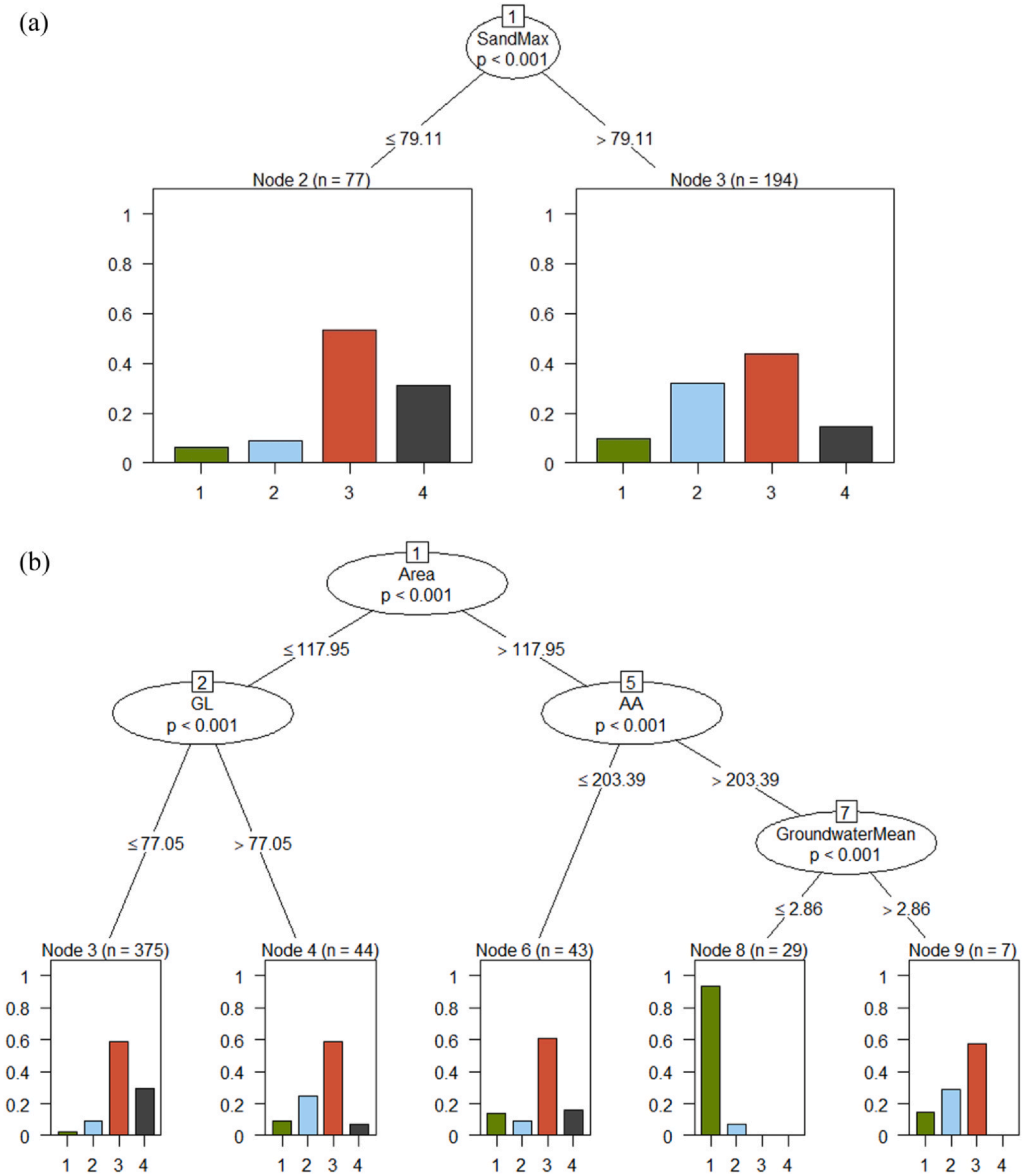

Fig. 4. Classification tree model of regeneration capacity on old fields of a) open steppes and b) closed steppes. Green, blue, red and black colours represent good, moderate, low and no regeneration capacity, respectively. Each node is described by the splitting variable used at the split, the Bonferroni-corrected significance (p value) of the split and the values at which the split occurs. At each terminal node the number of observations (n) is given. Vertical axes show the percentage of quadrats with good (1), moderate (2) low (3) and no (4) regeneration capacity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.4. Limits and possible uses of the study

The mapping and assessment of regeneration capacity at the national scale becomes more and more important to help prioritise the restoration of large territories. The MÉTA project was a relatively quick but detailed field survey suitable for the estimation of regeneration capacity by expert judgement. The estimation is often burdened by the subjectivity of the experts, but vegetation scientists made an effort to be accurate and standardise judgments (Bölöni et al., 2007; Molnár et al., 2007). In our case a special training and a detailed handbook helped the field experts. One bias might be the correlation between the geographical location and the experts who performed the survey. The limitations of judgement may become apparent especially in smaller regions, such as in the case of juniper-poplar stands in this study. However, the nation-wide survey providing a large number of cases can probably diminish the biases. Since none of the nine models show large and significant spatial auto-correlation of the residuals (the maximum of Moran's I was found to be 0.25 in case of juniper-poplar stands on old fields), we concluded that the used predictors could describe regeneration capacity well without the inclusion of the identity of the experts in the model.

National scale field surveys are labour intensive and time consuming. As a viable alternative, remote sensing can be efficient in habitat mapping on a larger scale (e.g. Eckert et al., 2015; Reis et al., 2019) and it is also more objective compared to expert judgment. However, remote sensing data has varying spatial resolution, works with coarser habitat categories only and requires field validation by experts (Eckert et al., 2015). Despite its advantages, field surveys can only be partially replaced by remote sensing for detecting land degradation and regeneration (Eckert et al., 2015; Hill et al., 1995), because the causes of regeneration can only be understood based on detailed and accurate data on landcover, land-use change and environmental parameters.

Based on our study we suggest that environmental predictors can be used to estimate the regeneration capacity of habitats on a larger scale. Naturalness, abiotic features and landscape context or similar proxies can often be found in national and international databases that can serve as the basis for approximating regeneration capacity. Analysing drivers for assessing regeneration is the key issue for restoration efforts in European countries (Aradóttir et al., 2013; Hagen et al., 2013). We propose to involve many drivers in estimating regeneration capacity, which is the base approach to help prioritise restoration efforts in large areas.

4.5. Prioritization of grassland restoration efforts based on regeneration capacity

Besides local sustainability, remnant habitats provide a source of propagules that enable spontaneous regeneration in neighbouring areas and on abandoned fields. Good colonisation ability of remnant habitats to neighbouring areas and to abandoned fields represents a potential for passive restoration, which offers a cost-effective and natural substitute to active restoration (Prach and Hobbs, 2008). Many examples exist where this potential is realised where both old-fields and natural grasslands are present in a landscape (Ruprecht, 2006; Holl and Aide, 2011; Prach et al., 2013), and this is true also for the studied habitats (Halassy, 2001; Csecserits et al., 2011; Albert et al., 2014; Valkó et al., 2016).

In the case of moderate to low regeneration capacity, active intervention can help to restore and increase the area and naturalness of habitats. Propagule intake is often of primary importance to accelerate the re-establishment of semi-natural habitats (Kiehl et al., 2010; Török et al. 2011; Prach et al., 2013) that was successfully applied also in case of open sand grasslands (Halassy et al., 2019; Kövendi-Jakó et al., 2019, 2020). Besides seeding, mowing could also be a viable restoration treatment (Reis et al. 2021), but its use is more effective in combination with other treatments (Halassy et al., 2016). On sites with low capacity for natural regeneration we suggest seeding followed by low intensity mowing to achieve grassland restoration targets.

If regeneration is not possible due to lack of area, active restoration efforts would be immeasurably expensive and unlikely to be sustainable, therefore not recommended except in priority areas for conservation management.

5. Conclusions

One of the main aims of regeneration capacity estimation is to understand ecological processes to preserve and restore valuable habitats and landscapes for ensuring ecosystem health and integrity. Regeneration studies help better understand the alternating degradative and regenerative stages of habitats and landscape. They can provide information and support decision making in planning green infrastructure, as well as improving ecological networks and habitat connectivity in the future (Butaye et al., 2005; Biró et al., 2013b).

Our study showed that the total extent of semi-natural habitats and their naturalness at the local scale are key factors in ensuring the regeneration capacity of sandy habitats at the national scale. Consequently, the protection of the remaining natural and semi-natural habitats plays a key role in securing the conservation of biodiversity, ecosystem health and integrity. It also implies that increasing the area and naturalness of semi-natural habitats and reducing fragmentation through restorative interventions can strengthen the future sustainability of natural habitats.

We conclude that environmental predictors can be used to estimate regenerative capacity, which can help set priorities for large-scale restorations. We suggest strong protection of still existing natural or semi-natural remnants in the first place, especially in the case of habitats with lower regeneration capacity. While it is possible to rely on spontaneous regeneration in the case of better regenerating habitats, active restoration is required in other cases. Predictors that determine the regeneration capacity can help identify limitations of passive restoration.

Author contributions

MH, ZsM and ECs conceived and designed the study. FH produced queries from the MÉTA database. ÁBF collected environmental data from the MPNV database. ECs and ÁBF analysed the data. ECs and MH wrote the article. All authors reviewed and commented the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

The distribution of quadrats of sandy habitats with regeneration capacity on spot, on neighbouring spots and on old fields within Hungary is demonstrated in Fig. A1–A3. The scale that was used to estimate the potential of each regeneration capacity type is given in Table A1. The scale of habitat naturalness estimates is in Table A2. A summary of environmental predictors is given in Table A3.

Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01547.

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