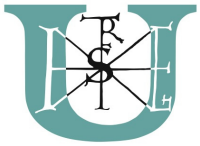

SZENT ISTVÁN UNIVERSITY

Farmstead abandonment in the Duna-Tisza Interfluve: landscape ecological and conservation effects

PhD thesis

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1. BACKGROUND AND OBJECTIVES

1.1 The significance of the research topic

Agricultural extensification and associated land abandonment and rural depopulation can be observed worldwide (Bazzaz 1975, Pascarella et al. 2000, Hölzel et al. 2002, Gellrich and Zimmermann 2007). While succession on arable lands following abandonment has been widely documented (Harmer et al. 2001, Chinea 2002, Howard és Lee 2003, Mottet et al. 2006), abandoned residential areas (villages, farmsteads) have generally been overlooked.

Land-use change is a major phenomenon in Hungary as well, especially in the Duna-Tisza Interfluve, due to a decline in the water table and socioeconomic changes (Pálfai 1994). In the Great Hungarian Plain, the number of people living outside cities and villages declined from 1.1 million after the World War II to 200,000 in 1990 (Duró 2004). A decline in the rural population and small-scale farming, as well as an associated land and farmstead abandonment, started after the World War II, accelerated in the 1960s and 1970s, and continues today. Between 1990 and 2005, 10,000–12,000 farmsteads were abandoned in this region (Csatári and Kanalas 2006), and a further 20,000-25,000 may be abandoned in the near future (Czene and Jávor 2006).

We hypothesize that abandoned farmsteads are heavily transformed unique habitats characterised by a vegetation and successional development that are different from those of the surrounding landscape.

The Duna-Tisza Interfluve region provides an excellent setting for studying the effects of changing land use and rural depopulation due to its changing agriculture and rapidly disappearing rural farmsteads. Many of these abandoned farmsteads are still identifiable elements in the landscape based on their remains (buildings, walls, piles of collapsed buildings). Different times since farmstead abandonment makes it possible to study the importance of time since abandonment for vegetation recovery. Furthermore, the contrasting land-use types in the region such as active agricultural areas and natural grasslands provide a nice setting for assessing the importance of surrounding landscape.

While vegetation of abandoned agricultural fields has previously been explored in the region (Csecserits and Rédei 2001, Csecserits et al. 2007, Ruprecht et al. 2007, Csecserits et al. 2011), no study so far has documented the vegetation of abandoned farmsteads.

1.2 Aims

The objective of our work was to assess the present state and vegetation of farmsteads abandoned in the past decades in Duna-Tisza Interfluve. In three

independent research projects we investigated (1) the persistence and landscape-scale spread of cultivated plants following abandonment, (2) the effect of time since abandonment and the surrounding landscape on the vegetation of abandoned farmsteads, and (3) the vegetation of special microhabitats of abandoned farmsteads (ruins, yards, oldfields), and how this is affected by black locust (*Robinia pseudoacacia*) invasion.

2. METHODS

2.1 Present state and cultivated species of abandoned farmsteads and the spread of cultivated species in the surrounding landscape

In the first study, we examined the current state of abandoned farmsteads and the persistence of planted cultivated plants on 240 farmsteads abandoned between 1956 and 2005 in the Duna-Tisza Interfluve, and the spread of these species in the surrounding landscape.

Four study sites (Tázlár, Soltvadkert, Orgovány, Fülöpháza; 36 km^2 each), were selected in the centre of the region. Sites include all major habitat types of the region (natural grasslands, natural forests, old fields, forest plantations, and arable lands) in each site.

The earliest map that showed individual farmsteads from 1956 was used as a starting point to locate once existing farmsteads in the landscape. Of these farmsteads, we identified those that were abandoned by 2005 using high-resolution aerial photos taken in 2005, and subsequently ground truthed their status in 2007.

To assess the time of abandonment for each farmstead, we checked archive maps and aerial photos between 1956 and 2005. Based on these maps (1956, 1978, 1989) and aerial photos (2005), we determined the number of active farms at each of these 4 years, and estimated the time of abandonment for each of the surveyed farmstead. This resulted in three age classes for abandoned farmsteads:

(1) abandoned between 1956 and 1978 (old farmsteads);
(2) abandoned between 1978 and 1989 (medium-aged farmsteads);
(3) abandoned between 1989 and 2005 (young farmsteads).

We randomly selected 60 farmsteads per site (a total of 240) that were abandoned between 1956 and 2005. In each farmstead we classified their state as (1) building remains (buildings, walls), (2) mounds of collapsed buildings, and (3) converted to some other land-use type (ploughed). In total, 190 were scored as categories 1 and 2, and 50 were ploughed and converted to vineyards, cropland, or forest plantations (category 3).

We recorded all cultivated alien species, including agricultural, ornamental, amenity species at all the 190 unploughed farmsteads in 2007.

To assess the occurrence of cultivated species outside farmsteads, we used vegetation plots from a previous study (Csecserits et al. 2011) sampled at the same four sites, that covered all major non-arable habitat types (natural grasslands, natural forests, old fields, forest plantations).

We tested if the number of cultivated species in vegetation plots was related to nearby farmstead density, distance to the nearest village, or distance to the nearest road, as these landscape elements may be sources of spreading cultivated species.

We used generalized linear mixed models (GLMM), χ^2-test and Tukey's post hoc test in statistical analyses.

2.2 Vegetation of abandoned farmsteads in relation to the time since abandonment and the surrounding landscape

In the second study we surveyed the vegetation of 72 abandoned farmsteads and paired control sites in relation to the time since abandonment and the surrounding landscape. We focused on three farmstead types: (1) abandoned recently (1989-2005) in agricultural landscapes, (2) abandoned recently (1989-2005) in natural landscapes, and (3) abandoned long ago (1956-1978) in natural landscapes.

In 2008, we recorded all species and estimated their cover in 20 m × 20 m plots centered on the farmstead yard, which could be identified in the field based on buildings, ruins, or piles of loam from the adobe walls. Next to each farmstead, a paired control plot was chosen and sampled the same way in the most natural adjacent habitat (Németh and Seregélyes 1989), 20 m distance from the farmstead boundary. In natural landscapes paired control plots were sampled in primary or secondary grasslands, whereas in agricultural landscapes in vineyards or arable lands (*Medicago sativa*, *Panicum miliaceum*).

We used analysis of variance (ANOVA), permutational multivariate analysis of variance (PERMANOVA), generalized linear models (GLM), and Tukey's post hoc test in statistical analyses.

2.3 Vegetation of microhabitats on abandoned farmsteads, and the effects of black locust (*Robinia pseudoacacia*) invasion

In the third study, we compared the vegetation of microhabitats (ruins, yards, oldfields) on 60 farmsteads abandoned between 1956 and 1978, including 30 treeless abandoned farmsteads (covered only by herbaceous vegetation) and 30 invaded abandoned farmsteads, overgrown by the invasive black locust (*Robinia pseudoacacia*).

In 2009, we recorded all species and estimated their cover in 5 m × 3 m plots centered on the farmstead ruin. Next to each ruin, the yard plot was sampled the same way on the farmstead yard, 1 m distance from the ruin. Oldfield plot was chosen and sampled the same way in the farmstead oldfield, 20 m distance from the ruin.

Three soil samples were collected and mixed within each plot. Soil samples were analyzed for texture (percent sand, silt, and clay), pH-H_2O, H%, humus content (%), ammonium lactate soluble available phosphorus (Al-P_2O_5, mg kg^{-1}), potassium (Al-K_2O, mg kg^{-1}), available nitrate (NO_3-N, mg kg^{-1}) and ammonium (NH_4-N, mg kg^{-1}), and $CaCO_3$ (%) content according to the

standards of the Magyar Szabványügyi Testület (1978, 1999).

We used linear mixed effects models (LME) and Tukey's post hoc test in statistical analyses.

3. RESULTS

3.1 Present state and cultivated species of abandoned farmsteads and the spread of cultivated species in the surrounding landscape

The rate of farmstead abandonment

We examined the number of active farmsteads through time (1956-2005) on the four study sites. We found that farmstead density varied considerably among sites, but decreased steadily through time at all sites, with the average density decreasing from 8.1/km^2 in 1956 to 3.8/km^2 in 2005.

The fate of abandoned farmsteads

Over half of the recently abandoned (after 1989) farmsteads had building remains in 2007, whereas few (2.2%) old farmsteads (abandoned before 1978) had building remains. Only about 30% of the old farmstead sites were ploughed following abandonment and thus subject to major land-use change, with all the others being simply set aside and not used intensively.

The number of persisting cultivated species as a function of time of abandonment

The number of cultivated species on abandoned farmsteads was negatively related to the time since abandonment, with more cultivated species occurring at young (abandoned in 1989-2005) and medium-aged (abandoned in 1978-1989) farmsteads compared to old ones (abandoned in 1956-1978). Old farmsteads harboured an average of seven species compared to about ten species at young and medium-aged abandoned farmsteads which did not differ in the number of cultivated species. We found a total of 77 cultivated species at the 190 abandoned farmsteads, including 56 woody species. A total of 39 species occurred at farmsteads abandoned at least 30 years ago.

Spreading of cultivated species

Eleven cultivated species were observed to occur outside farmsteads, in plots sampled in the surrounding landscape. These were *Morus alba, Ribes aureum, Juglans regia, Persica vulgaris, Ailanthus altissima, Armeniaca vulgaris, Gleditsia triacanthos, Acer negundo, Eleagnus angustifolia, Parthenocissus inserta,* and *Hedera helix.* All these species occurring outside farmsteads were woody.

The number of cultivated species found in the surrounding landscape differed among major habitat types, with the highest numbers found in forest plantations, and lowest numbers in old fields and grasslands. The number of cultivated species in forest plantations was positively related to the number of farmsteads within 500 m, but was not related to the distance from the nearest village and distance from the nearest road.

The survival and persistence of cultivated species at abandoned farmsteads

We found many (77) cultivated species that survived the cessation of cultivation, but they form a heterogeneous group that can be subdivided based on survival time following abandonment and spreading ability.

First, species that are confined to young abandoned farmsteads (e.g. *Malus domestica, Pyrus communis, Tulipa gesneriana, Narcissus poeticus, Iris germanica*). These species constitute only the short-term legacy of human habitation.

Second, species that are confined to farmsteads, but are still there decades after abandonment (old farmsteads) (e.g. *Syringa vulgaris, Prunus domestica, Yucca filamentosa, Spirea × vanhouttei*). After the deterioration of buildings, these species may, in fact, serve as the only remaining marker or ‘‘memento’’of once existing farmsteads.

Third, species that also occurred outside farmsteads, within habitats that they had not been planted, have reached the final invasion stage: landscape spread (Theoharides and Dukes 2007), and pose the greatest threat (e.g.: *Morus alba, Juglans regia, Ailanthus altissima, Gleditsia triacanthos*).

3.2 Vegetation of abandoned farmsteads in relation to the time since abandonment and the surrounding landscape

The effect of surrounding landscape and time of abandonment on the fate of abandoned farmsteads

Less than half (41%) of the farmsteads abandoned in 1956-1978 in agricultural landscapes remained unplowed by 2007, while the vast majority (91-98%) of recently abandoned farmsteads in agricultural landscape and recently abandoned and long-ago abandoned farmsteads in natural landscapes were just set aside and remained unplowed.

Woody and herbaceous species at abandoned farmsteads

The cover of woody species was higher in farmsteads than in neighboring control plots. Woody cover was also affected by farmstead type, with the recently abandoned farmsteads in natural landscapes having higher woody cover than long-ago abandoned farmsteads in natural landscapes. The most abundant woody species of abandoned farmsteads were *Robinia pseudoacacia, Morus alba,* and *Ailanthus altissima.*

In farmsteads abandoned in 1989-2005, the cover of herbaceous species was higher than in control plots in both agricultural and natural landscapes. In farmsteads abandoned in 1956-1978, herbaceous cover did not differ between farmsteads and controls. The cover of herbaceous species was similar in each farmstead type. The most abundant herbaceous species of

abandoned farmsteads were *Elymus repens, Bromus sterilis,* and *Poa angustifolia.*

Non-native species at abandoned farmsteads

In natural landscapes, the cover of non-native species was much higher on abandoned farmsteads than in control plots for both long-ago and recently abandoned farmsteads. In agricultural landscapes, there was no significant difference between farmsteads and control plots. The cover of non-native species was higher in farmsteads abandoned in 1989-2005 compared to those abandoned in 1956-1878. The most abundant non-native species of abandoned farmsteads were *Robinia pseudoacacia*, *Bromus sterilis,* and *Morus alba*.

The number of non-native species was higher in abandoned farmsteads than in control plots for all farmstead types. In natural landscapes, non-native species numbers were lower in farmsteads abandoned long ago (1956-1978) than in farmsteads abandoned recently (1989-2005).

Native species at abandoned farmsteads

In agricultural landscapes, the cover of native species was significantly higher in abandoned farmsteads than in the controls, but in natural landscapes there was no difference between abandoned farmsteads and controls. The cover of native species on abandoned farmsteads was similarly high in each farmstead type. The most abundant native species of abandoned farmsteads were *Elymus repens*, *Poa angustifolia,* and *Cynodon dactylon*.

In natural landscapes, farmsteads and control plots had similar number of native species. In agricultural landscape, the number of native species was higher in farmsteads than in control plots. The number of native species in farmsteads was lowest in agricultural landscapes, intermediate in natural landscapes at recently abandoned farmsteads, and highest in natural landscapes at farmsteads abandoned long ago.

Target species (characteristic species of natural habitats in the region)

In agricultural landscapes, the cover of target species was higher in abandoned farmsteads than in the controls, while in natural landscapes it was lower at farmstead than in controls at recently abandoned farmsteads and there was no difference at long-ago abandoned farmsteads. The cover of target species was higher at long-ago abandoned farmsteads compared to recently abandoned ones, irrespective of landscape type.

In agricultural landscapes farmsteads were richer in target species compared to paired control sites, while in natural landscapes recently abandoned farmsteads were poorer in target species than the control plots. Farmsteads adandoned long ago, had similar number of target species as their control sites. The number of target species was highest at long-ago

abandoned farmsteads in natural landscapes, intermediate in recently abandoned farmsteads in natural landsapes, and lowest at recently abandoned farmsteads in agricultural landscapes.

3.3 Vegetation of microhabitats of abandoned farmsteads, and the effects of black locust (*Robinia pseudoacacia*) invasion

Native herbaceous species

In treeless microhabitats the cover of native herbaceous species was highest at ruins, intermediate at yards and lowest at oldfields. No differences were found among woody microhabitats in the cover of native herbaceous species, and it was similar to the treeles oldfields.

Non-native herbaceous species

In treeless microhabitats the cover of non-native herbaceous species was extremely low at ruins and yards, and relatively high at oldfields. No differences were found among woody microhabitats in the cover of non-native herbaceous species, and it was much higher than in treeless microhabitats.

Open sand grassland species

In treeless microhabitats the cover of open sand grassland species was extremely low at ruins, intermediate at yards and high at oldfields. No differences were found among woody microhabitats in the cover of open sand grassland species, and it was as low as at the treeles ruins.

Closed sand grassland species

In treeless microhabitats the cover of closed sand grassland species was very high at ruins, whereas it was much lower, but similar at yards and oldfields. No differences were found among woody microhabitats in the cover of closed sand grassland species, and it was as low as in the treeles oldfields.

3.4 Most important new results

(1) We systematically assessed the present state and vegetation of abandoned farmsteads. We showed that farmstead density declined to less than half between 1956 and 2005 in the Duna-Tisza Interfluve. We found that in natural landscapes the vast majority of farmsteads were still identifiable (remained unplowed), irrespective of time since abandonment. In agricultural landscapes the vast majority of recently abandoned farmsteads were still identifiable, while more than half of

the old abandoned farmsteads were completely destroyed, and were converted to a different land-use.

(2) By examining farmsteads abandoned between 1956 and 2005 in the Duna-Tisza Interfluve, we showed that the number of cultivated species on abandoned farmsteads depended on the time since abandonment: the young and middle-aged abandoned farmsteads harboured more cultivated species than older ones. At the same time, many planted species occurred in similar frequency in long-ago and recently abandoned farmsteads, which indicates that these species can persist in the long run at abandoned farmsteads.

(3) Furthermore, by analysing vegetation samples from the surrounding landscape, we found that some of these cultivated species also occurred outside farmsteads, in areas where they had not been planted, most often in tree plantations. In addition, the number of escaped cultivated species occurring in tree plantations was positively related to farmstead density, suggesting a prominent role of farmsteads as a source.

(4) We showed that abandoned farmsteads had higher woody cover and higher number of non-native species than control sites irrespective of landscape context and time of abandonment. This indicates that abandoned farmsteads serve as hot spots of non-native species. Long-ago abandoned farmsteads had lower number and cover of non-native species and more native species than recently abandoned farmsteads, which shows a recovery towards natural communities.

(5) Farmsteads in agricultural landscapes had fewer native species than farmsteads in natural landscapes. However, these low numbers were still much higher than that found in the paired control plots (agricultural land), suggesting that in agricultural landscapes, abandoned farmsteads also often provide refuge for the native flora.

(6) By comparing the vegetation of microhabitats (ruins, yards, oldfields) on farmsteads abandoned between 1956 and 1978, we found that soil and vegetation of the treeless farmsteads strongly differed from their surroundings even decades after abandonment: the loamy mounds of collapsed buildings were characterized by the occurrence and even dominance of closed grassland species.

(7) We also showed that although farmstead are strongly transformed habitats of the landscape, the treeless ruins and yards had very low cover of non-native species, and thus had a more natural vegetation than the surrounding oldfields.

(8) However, when farmsteads were covered by the invasive black locust, differences among microhabitats (ruins, yards, oldfields) disappeared, the herbaceous vegetation was a homogeneous layer rich in non-native species.

4. CONCLUSIONS AND RECOMMENDATIONS

4.1 Present state and cultivated species of abandoned farmsteads and the spread of cultivated species in the surrounding landscape

The decline in farmstead density we quantified parallels observed trends of rural depopulation throughout Europe (Csatári and Kanalas 2006, Plieninger 2006). Based on the average abandonment of 4.3 farmsteads/km^2 in the last 50 years, we roughly estimate that there are 30,000 abandoned farmsteads across the 7,400 km^2 of the Duna-Tisza Interfluve region.

Even if some of the abandoned farmstead locations were converted to a different land-use and thus were completely destroyed, most of them – in our study area about 80% of all abandoned farmsteads or 67% of old farmsteads – were still identifiable.

The tens of thousands of abandoned farmsteads scattered throughout the region, each harbouring 7–11 alien plant species that have survived abandonment, provide an ideal setting for both long-term persistence and spread of potentially invasive species.

The presence of species in habitats where they were not planted, combined with the positive relationship documented between farmstead density and the number of cultivated species, suggests that some of these cultivated species do spread in the landscape and farmsteads may be the source. These spreading species may constitute the landscape-scale legacy of declining rural settlements.

4.2. Vegetation of abandoned farmsteads in relation to the time since abandonment and the surrounding landscape

Abandoned farmsteads had much higher cover of woody species than neighboring control areas, which is in agreement with higher woody cover of residential areas recorded in treeless agricultural landscapes (Knapp et al. 2010, Hiron et al. 2013). The high woody cover of farmsteads is due to the survival of intentionally introduced (planted) woody species. This high woody cover at farmsteads is a very different situation compared to abandoned arable lands and pastures, where woody cover is typically very low during the early stages of the succession (Rivera et al. 2000, Harmer et al. 2001, Dahlström et al. 2010).

The number of non-native species was significantly higher in abandoned farmsteads compared with control plots, primarily due to the great number of the intentionally introduced horticultural, ornamental, and amenity species.

Since many of these species survive or persist following abandonment, these farmsteads show the legacy of previous human activities, similar to

other abandoned and regenerating habitats that contain more alien species than undisturbed habitats (Hobbs 1989, Lonsdale 1999, Lugo and Helmer 2004, Colon and Lugo 2006, DeGasperis and Motzkin 2007, Von Holle and Motzkin 2007).

We found that native species and target species were present in remarkable number and abundance in abandoned farmsteads, which suggests a considerable regeneration potential. Although abandoned farmsteads are usually considered as degraded secondary habitats with high abundance of non-native species, our data indicates that they are also potential habitats for the survival and establishment of native species. Abandoned residential areas may recover into valuable secondary ecosystems (Dambrine et al. 2007, Vojta 2007, Hejcman et al. 2013), similar to old-fields (Jongepierová et al. 2004, Ruprecht 2006, Csecserits et al. 2007) and pastures (Aide et al. 1996, Muniz-Castro et al. 2006), although the outcome of this recovery may depend on several factors such as time and the surrounding landscape.

The cover of woody species was lower at long-ago abandoned farmsteads than at recently abandoned ones in natural landscapes, which indicates convergence between these sites and the control plots, consistent with the vegetation of the region (forest-steppe; Zólyomi 1973-1974). Herbaceous species had a similar cover in long-ago and recently abandoned farmsteads, probably because enrichment in soil nutrients is often maintained long after abandonment (Dambrine et al. 2007, Vojta 2007, Muchiru et al. 2009, Hejcman et al. 2013).

Both the number and cover of non-native species were lower at farmsteads abandoned long ago, which is in accordance with observations on old-fields (e. g. Pascarella et al. 2000, Matlack and Schaub 2011). Some non-native species were sensitive to the lack of cultivation and declined sharply following abandonment, while others had similar cover in long-ago and recently abandoned farmsteads. In fact, some of these latter species, such as *Robinia pseudoacacia, Ailanthus altissima, Acer negundo,* are considered invasive alien plants in Europe (Lambdon et al. 2008a) and also in Hungary (Balogh et al. 2004). Accordingly, these species may not decline, but rather expand in the future, and may thus negatively affect or arrest secondary succession The high number and scattered distribution of abandoned farmsteads in the landscape provide a favourable situation for the future spread of these species (Sax and Brown 2000, Lockwood et al. 2005).

While time since abandonment had little influence on native species cover in abandoned farmsteads, cover of target species was significantly higher on long-ago abandoned farmsteads than on younger ones. However, long-ago abandoned farmsteads had higher numbers of native and target species, suggesting a time effect on the number of colonizing species and an increasing ‘naturalness’.

This increasing number of native and target species coupled with the declining cover and number of non-native species through time suggests that these sites are on the way to recovery, and may become similar to natural ecosystems in the long run. These results are in agreement with observations on old-fields, where an increase in native species has often been reported through time (Ruprecht 2006, Csecserits et al. 2007).

Studies on settlements abandoned for several decades (Vojta 2007) or almost two millennia ago (Dambrine et al. 2007) found that human residential areas may become very similar to natural habitats in the long run. On the other hand, our finding that even long-ago abandoned farmsteads support a high amount of non-native cover suggests that these sites are a mixture of native and non-native species, and may thus be considered as novel ecosystems (Hobbs et al. 2006).

Woody and herbaceous cover, as well as the cover of non-native species, were not affected by landscape type (agricultural vs. natural), indicating that these farmsteads are similar habitats with similar productivity and history. Nevertheless, we found clear differences between vegetation cover of non-natives at farmsteads and their surrounding agricultural or natural landscapes. In the agricultural landscape, non-native cover was similar in magnitude at farmsteads and control plots due to the non-native crops in the controls. In contrast, farmsteads in natural landscapes were clearly a hot spot of non-native species compared to their respective controls.

The cover of native and target species was not affected by landscape type (agricultural vs. natural), but the number of native and target species was higher in natural landscapes compared with agricultural landscapes, suggesting a positive effect of natural landscapes as a source of colonizing native species. This is in agreement with reports from many recovering ecosystems (Chinea 2002, White et al. 2004, Pueyo and Alados 2007, Öster et al. 2009).

In farmsteads in natural landscapes, the number of native and target species was similar to that of control plots, whereas in farmsteads in agricultural landscapes the number of native and target species was far above that in the control plots. In agricultural landscapes, these farmsteads provide the only refuge to the native flora. This indicates that in agricultural landscapes these degraded and secondary habitats can be considered as native diversity hot spots and may have a conservation value, similar to old manor parks (Liira et al. 2012) and sacred sites (Fournier 2011).

4.3 Vegetation of microhabitats of abandoned farmsteads, and the effects of black locust (*Robinia pseudoacacia*) invasion

In case of treeless abandoned farmsteads, the vegetation of microhabitats (ruins, yards, oldfields) strongly differed from each other. The vegetation of

farmstead yards was in intermediate position between ruins and oldfields in every respect, but usually more similar to oldfields. Vegetation of ruins diferred from the other microhabitats due to the differences in soil characteristics. Soil of the ruins (loamy mounds) strongly differed from the other two microhabitats: we found much higher silt, clay, calcium-carbonate, humus, nitrate content in the ruin plots compared to the yards and oldfields. Thus, vegetation of the loamy mounds of collapsed buildings strongly differed from their surroundings even decades after abandonment, probably because altered soil conditions and enrichment in soil nutrients is often maintained long after abandonment. Similar results was reported by Hejcman et al. (2013) in case of abandoned medieval settlement in the Czech Republic and Closset-Kopp and Decocq (2015) on medieval artificial habitats (mounds) in France.

Cover of native herbaceous species was the highest on farmstead ruins, and cover of non-native herbaceous species was very low on ruins and yards compared to the olfields, indicating that although farmsteads are strongly transformed habitats of the landscape, farmstead ruins and yards had a more natural vegetation than the surrounding oldfields.

We found that farmstead ruins had very low cover of open sand grassland species but very high cover of closed sand grassland species compared to the yards and oldfields. This results are interesting because closed sand grasslands are in decline in the region (Biró 2003, Biró et al. 2013), and their regeneration potential is very low (Molnár et al. 2011, Szitár et al. 2014).

We found that in case of farmsteads covered by the invasive black locust (*Robinia pseudoacacia*), the vegetation of microhabitats (ruins, yards, oldfields) did not differ from each other. No differences were found among the woody microhabitats (ruins, yards, oldfields) in herbaceous total cover, native- and non-native herbaceous species cover, open- and closed sand grassland species cover. These results show that the invasion of black locust resulted in deteriorated differences between local habitats, and thus caused biotic homogenisation (Olden 2006, Lambdon et al. 2008b).

The cover of native herbaceous species was lower and the cover of non-native herbaceous species was much higher on woody microhabitats than on treeless microhabitats. Within resistant ecosystems on nutrient-poor soils, the introduction of nitrogen-fixing black locust results in ‘islands of invasion’: non-native species richness and cover are significantly higher under Robinia stands than in native habitats (Von Holle et al. 2006).

In accordance with the decrease of native species, the cover of open and closed sand grassland species was much lower in woody microhabitats than on treeless ones, probably because black locust transforms its habitat considerably (Richardson et al. 2000, Balogh et al. 2004, Botta-Dukát et al. 2004, Pyšek et al. 2004b). Its efficient water intake possibility, increased soil nutrient content, and the allelopathic effects result in low species richness of

the herb layer, which is dominated by nitrophilous plants (Matus et al. 2003, Bartha et al. 2008, Vitková et al. 2017).

In conclusion, abandoned farmsteads are unique habitats that significantly differ from their surroundings. Their scattered distribution in the landscape further increases their importance in hosting and spreading non-native species and providing refuge for native species. As the relative importance of these two parallel processes depends on the landscape context, abandoned farmsteads have contrasting conservation value in different landscapes. Abandoned farmsteads are characterised by a high diversity of microhabitats, which is easily erased and homogenised by spreading invasive species. Overall, our results show that even if the traditional small-scale farming-system is declining in the study region, farmsteads leave a diverse and long-term legacy on the landscape, and contribute to landscape-level biodiversity.

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6. PUBLICATIONS

6.1 Journal articles

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