An example of fast old field succession in a traditionally managed rural landscape on the Slovenian Karst

Andraž Čarni[1,2,*] , Zita Zimmermann[3,4] , Nina Juvan[5], Andrej Paušič[6] , Gábor Szabó[4] & Sándor Bartha[3,4]

Abstract

We report an exceptionally fast grassland recovery process from a karst plateau in SW Slovenia. Vegetation of old fields with different ages was sampled using a chronosequence of fields abandoned 1, 3, 6, 9, 13, 15 and 100 years ago. We prepared dendrogram dividing the data set into 9 clusters that were further analyzed: diagnostic species, ecological conditions and life forms were evaluated. The initial stage of succession was characterized by segetal weeds and indicated high levels of soil nutrients. The second stage was dominated by dense patches of perennial forbs (most of them ruderal species) preferring also high levels of soil nutrients. The third stage was dominated by caespitose hemicryptophyte grasses, many of them of sub-Mediterranean origin. The first two stages took 13 years and both could be considered as early successional stages developing on nutrient rich soils. These stages were switched to late successional stage characterized by seminatural grassland species. The quick succession can probably be attributed to the rich species pool of natural grassland flora, the small size and annual mowing of abandoned agricultural fields and the close proximity of seed sources.

Izvleček

Prispevek obravnava hitro zaraščanje opuščenih kmetijskih površin na kraški planoti v jugovzhodni Sloveniji. Na podlagi kronosekvece smo vzorčili površine, ki so bile opuščene pred 1, 3, 6, 9, 13, 15 in 100 leti. Na podlagi dendrograma smo pridobljene podatke razdelili v 9 snopov, ki smo jih nadalje analizirali: diagnostične vrste, ekološke razmere in življenjske oblike. Za prvi stadij zaraščanja (sukcesije) je značilno pojavljanje plevelnih vrst in visoka vsebnost hranil v tleh. V drugem stadiju prevladujejo goste zaplate trajnih zelišč (večinoma ruderalnih vrst), ki dobro uspevajo na tleh z visoko vsebnostjo hranil. V tretjem stadiju prevladujejo rušnate, trajne trave, od katerih mnoge izvirajo iz submediteranskega območja. Prva dva stadija trajata 13 let in jih lahko oba obravnavamo kot zgodnja sukcesijska, ki se razvijeta na s hranili bogatih tleh. Potem se razvije pozen sukcesijski stadij, kjer prevladujejo travnate vrste. Hiter potek sukcesije povzročijo: velika zaloga vrst polnaravnih travišč, majhna površina opuščenih površin, vsakoletna košnja in neposredna bližina virov semen.

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Introduction

Old field succession is a process of natural regeneration of vegetation after the cessation of cultivation (Cramer et al. 2008). Secondary grasslands recovering after the abandonment of agricultural fields provide habitats for many grassland species and partially compensate for the general loss of grasslands. However, the rate of spontaneous old field succession might vary greatly between habitats due to various factors (Pywell et al. 2002, Walker et al. 2004, Török et al. 2011a, Halassy et al. 2016). In early stages of succession, high concentrations of soil nutrients (as legacy from cultivation) and the dominance of invasive aliens are considered as major factors limiting spontaneous regeneration (Cramer & Hobbs 2007, Cramer et al. 2008). In middle stages of succession, several species (both native and invasive alien) form nearly monodominant patches suppressing other species and preventing the colonization of native species (Bartha et al. 2003, 2014, Házi et al. 2011, Szentes et al. 2012). Spontaneous succession might be limited also by the lack of available propagules (Donath et al. 2003, Öster et al. 2009, Halassy et al. 2016).

Patterns learnt about vegetation development in old field succession (Pickett et al. 1987, Osbornová et al. 1989, Cramer & Hobbs 2007) contributed to ecological theory and supported restoration practice (Török & Helm 2017). Case studies describing patterns of spontaneous successions in different habitats provide indispensable background for ecological restoration (Prach et al. 1999, 2001). Despite to the large number of related studies (for bibliography see Rejmánek & van Katwyk 2005, http://botanika.bf.jcu.cz/suspa/pdf/BiblioOF.pdf), generalizations about old field succession are still limited due to the paucity of comparable data (Prach & Walker 2019). Following recommendations and the related framework of Prach & Walker (2019), we intend to collect data comparable to other studies. Therefore, we have estimated the ecological circumstances by Ellenberg bioindicator values and assessed the presence of invasive alien species and the spatial heterogeneity of dominant species. We have also evaluated the success of succession (i.e. the time required for recovering some desirable target community with natural or semi-natural species composition) and the temporal pattern of species richness. For assessing the patchwork of midsuccessional dominants (Bartha et al. 2014) we have sampled long transects that able to cross several vegetation patches within a particular stand estimating their diversity and heterogeneity (Bartha et al. 2004).

Cultivated fields have been abandoned due to various reasons (e.g. droughts, natural disasters, political and economic crises or agricultural mismanagement). These problems usually affect large areas, therefore abandoned fields are typically aggregated in space and time. Therefore, in related studies the abandoned fields occupied large part of the landscape after some drastic collapse of local economy followed by drastic change in land use (e.g. Osbornová et al. 1989, Molnár & Botta-Dukát 1998, Palang et al. 2006, Csecserits et al. 2007). In contrast, information about old field succession in traditionally managed landscape with stable land use is still lacking. In this study, we intend to fill this gap. Our study area is located on a Karst plateau in SW Slovenia near the coast of Adriatic Sea. This is a traditional rural landscape with continuous low intensity agriculture since the Roman Era (Vitasović et al. 2012, Kaligarič & Ivanjšič 2014, Batalha et al. 2015, Breg Valjavec et al. 2018). Fields appropriate for cultivation are small and are surrounded by semi-natural forests and grasslands. Field abandonment is rare. Ex-arable fields are small and they are utilized as pastures or meadows.

The aim of the research was to explore some characteristics of secondary succession in this specific traditional rural landscape. We explored temporal and spatial differentiation of vegetation and described patterns of life forms and ecological indicator values. We addressed the following questions: How do diagnostic species, ecological conditions, life-form spectrum and spatial heterogeneity change along the succession? How long does the development of semi-natural grasslands take after land abandonment? How does our research fit with similar research in this field?

Materials and methods

Study site

The study area is located on a karst plateau in the northwest edge of the Dinaric Alps, Slovenia, in the area that is under the influence of the Adriatic Sea. The climate is sub-Mediterranean (Köppen-Type Cfa) with average January temperatures above 0 °C and annual precipitation between 1400 and 1500 mm. The karst plateau consists of karstified Mesozoic limestone, covered predominantly by rendzinas and cambisols (Vršćaj et al. 2017). The zonal vegetation is forest, dominated by *Ostrya carpinifolia* and *Quercus pubescens* (Čarni et al. 2002, 2009). After intensive deforestation that occurred centuries ago (Gams 1993), karstic pastures (*Carex humilis-Centaurea rupestris* community) and karstic meadows (*Danthonia calycina-Scorzonera villosa* community) were established (Kaligarič 1997, Kaligarič et al. 2006). As a consequence of large-scale socio-economic changes, afforestation began and grasslands declined from 82 to 20% and forests pro-

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gressed from 17 to 73% in the last 250 years (Kaligarič & Ivanjšič 2014).

The cultivated surfaces are mainly located in "cultural dolinas", i.e. in enclosed karstic depressions that are filled with soil (Breg Valjavec et al. 2018) and only rarely appear on flat surfaces. Such a flat area was found above the village Podpeč near Črni Kal (45.536° N, 13.900° E, elevation 385 m a.s.l.), where we could find fields of different age after abandonment. These areas are still mown once a year and occasionally grazed (Škornik et al. 2010, Pipenbaher et al. 2011).

Sampling of vegetation

Using the method of improved space for time substitution (Pickett 1989, Molnár & Botta-Dukát 1998, Csecserits et al. 2007), we built a chronosequence representing a succession series in the region (Čarni et al. 2007). Abandoned fields were selected close to each other in order to have the same regional species pool and habitat conditions. We sampled in the area of Podpeč near Črni Kal, where we can find nearly all stages of succession on a small area of 5 ha, only one plot (the 1-year-old-stand) was 3 km apart. The size of individual abandoned fields was small, ranged between 0.03 and 1 ha. We could find fields abandoned 1, 3, 6, 9, 13, 15 and 100 years ago. Age of the fields was determined using a time series of aerial photos and information from local people. Specific transect sampling was used for assessing within-stand heterogeneity of vegetation (Bartha et al. 2004, Supplement S, Figure 1). In each field, the presence of rooted vascular plant species was recorded in 5 cm × 5 cm contiguous microquadrats arranged along a 52 m long belt transect. Transects were positioned in the middle of the individual field to avoid the edge effect. Vegetation patchwork (spatially heterogeneous vegetation mosaic) is typical to these transitional vegetation types (Pickett et al. 2001, Bartha et al. 2004, Szentes et al. 2012). The 52 m long transects were long enough to estimate properly the related spatial heterogeneity at each field. Base-line transect data were resampled by computer (with the method of computerized sampling, Podani 1987, Bartha et al. 2004). During computerized resampling, each transect was subdivided into 1 m long segments and species abundances were calculated in each segment (by summarizing presences of species in the particular segment) (for details, see S, Figure 1). Based on previous analyses of spatial patterns in succession (Bartha et al. 2004, Bartha 2007, Ruprecht et al. 2007, Szentes et al. 2012), we chose the 1 m scale to provide relatively homogeneous segments for further analyses. The transects were sampled in 2012 in late May – early June during the optimal growing period of veg-etation, before the fields were mown. The high resolution transect-based sampling design was chosen because it was effective in several other old field studies (Bartha et al. 2004, Jongepierová et al. 2004, Ruprecht et al. 2007, Szentes et al. 2012).

Data analysis

Spatiotemporal differentiation of species composition at the scale of 1 m long segments was analysed by classification and ordination of the full data set. For finding the most appropriate classification method (distance measures between samples and method for construction of clusters), the OptimClass program was applied (Tichý et al. 2010). Classification was then carried out by the PC-ORD software (McCune & Mefford 1999), run in the JUICE 7.0 program. Non-metric multidimensional scaling (NMDS) was also performed by the vegan program package run in R environment (Oksanen et al. 2017, R Core Team 2018). Diagnostic species of each cluster were determined in JUICE 7.0 program by calculating the fidelity, using the phi-coefficient as fidelity measure on basis of presence of species within and beyond each cluster (Sokal & Rohlf 1995). In these calculations, each cluster was compared with the other samples in the data set, which were taken as single, undivided group. Species with phi > 0.4 were considered as diagnostic for individual clusters, but species whose occurrence concentration in the plots of a particular cluster was not significant at p < 0.05 (Fisher´s exact test) were excluded (Chytrý et al. 2002, Tichý & Chytrý 2006).

Patterns of life forms and ecological indicator values (EIV, called also Ellenberg bioindicator values) were assessed according to Pignatti et al. (2005). Dry grasslands specialist species have been determined by a local monograph (Kaligarič 1997) and a wider European list (Mucina et al. 2016), all species considered as diagnostic for *Festuco-Brometea* dry grasslands were considered as target species. Soil nutrient content was estimated by abundance-weighted mean ecological indicator values at the scale of 1 m segments of transects. Ecological indicator values were tested for significant differences between coenostate clusters (vegetation patch types) found by classification. For this analysis we used Zelený's methods (Zelený 2018) to account for potential biases.

We tested temporal trends in succession using years since abandonment as predictor variable. We used nitrogen indicator values, number of all species and number of specialist species as response variables. Years since abandonment was fitted with log transformation. We used a linear model with polynomial terms in case of nitrogen indicator values and number of species, while we used

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GLM ('glm' function with Gaussian family) in case of specialist species. We fitted the models with polynomials because of the non-linearity of our variables. We chose cubic model because it had lower AIC values and higher R^2 values than a linear model. Figures were created using 'ggplot2' package in R (Wickham 2016).

Variables with different age (years since abandonment) were compared with Kruskal–Wallis-H-test, followed by Dunn-test as post hoc test. Significant differences between years were plotted with 'FSA' (Ogle 2018) and 'rcompanion' (Mangiafico 2000) packages in R.

Results

Classification of plots revealed nine clusters representing different vegetation patch types, i.e. plots with similar species composition (Appendix, Figure 2). Each cluster had specific dominant and diagnostic species (Table 1). NMDS ordination showed further structure: three main distinct groups with overlapping subgroups (Figure 1). The main groups represented temporal differentiation in

vegetation (three stages in succession) while clusters within the main groups represented spatial heterogeneity of stands. High compositional similarity was found between clusters of 15 years old and 100 years old fields (clusters 8 and 9). *Plantago major, Trifolium repens* and weeds typical to cultivated fields dominated in the first main group of clusters (clusters 1–2): *Cirsium arvense* and many annual species (e.g. *Anagallis arvensis, Cerastium brachypetalum, Chenopodium album*) (Table 2). Within this stage, some small differences were found between two clusters: with more *Chenopodium album* in cluster 1 and more *Cynodon dactylon* in cluster 2. The second main group of clusters (clusters 3–7) represented the period in succession with fields of ages between 2 and 13 years. These fields had ruderal weeds (e.g. *Bromus sterilis, Pastinaca sativa, Melilotus officinalis, Elymus repens, Taraxacum officinale*) and species typical of mesic and eutrophic meadows (e.g. *Dactylis glomerata, Festuca pratensis, Verbena officinalis, Leucanthemum liburnicum, Brachypodium rupestre*). The terminal main group (clusters 8 and 9) was characterized by *Bromus erectus, Chrysopogon gryllus, Scorzonera villosa, Thymus longicaulis, Festuca rupicola* and many other spe-
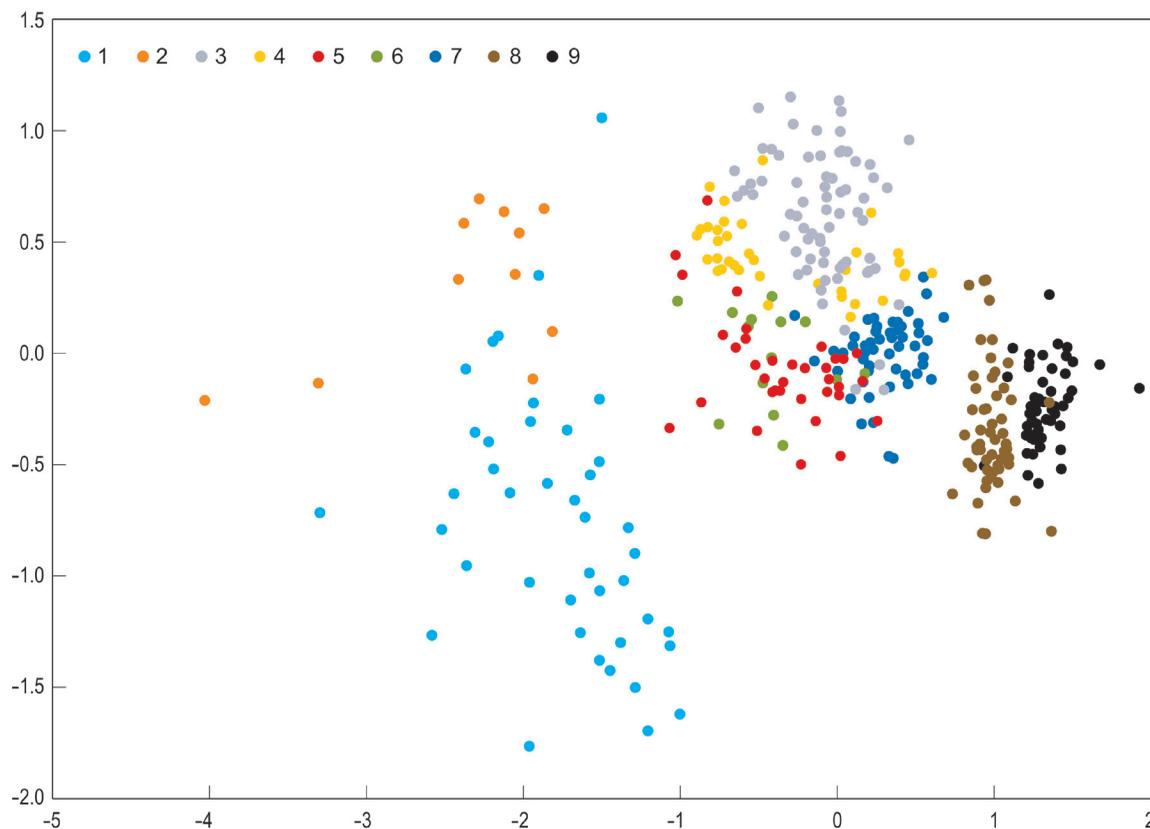
Figure 1: Bray-Curtis based non-metric multidimensional scaling (NMDS) plot of all samples. NMDS plot (stress 0.14) shows that samples were divided into three main groups: initial (clusters 1 and 2), early successional (clusters 3, 4, 5, 6 and 7) and late successional main group (clusters 8 and 9).
Slika 1: Nemetrično multidimenzionalno lestvičenje (*NMDS*) vseh vzorčnih ploskev na podlagi Bray-Curtisove podobnosti (stres 0,14) kaže, da so vzorci razdeljeni v tri glavne skupine: inicialno (snopa 1 in 2), zgodnje sukcesijsko (snopi 3, 4, 5, 6 in 7) in pozno skucesijsko skupino (snopa 8 in 9).

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Table 1: Diagnostic and dominant species of different successional stages according to nine clusters (coenostate clusters). Species with phi > 0.4 were considered as diagnostic (associated) for individual clusters. Among them species with >50% abundance in the 1 m quadrats were considered as dominant.

Tabela 1: Diagnostične in dominantne vrste različnih sukcesijskih stadijev glede na devet snopov (cenostatski snopi). Vrste z phi > 40 smo opredelili kot pridružene (diagnostične) za posamezen snop. Med njimi smo vrste z abundanco večjo od 50% na ploskvah 1 m smatrali kot dominantne.
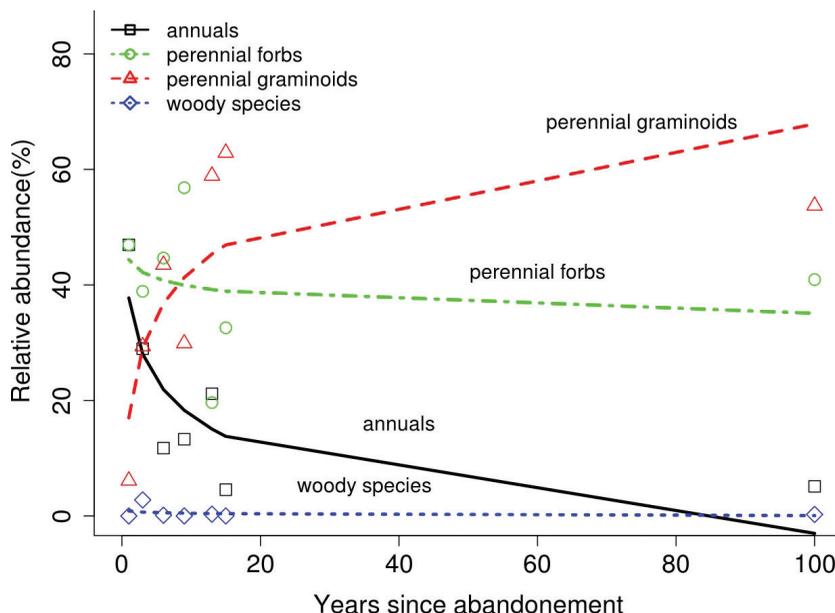
Successional stage	Cluster	Age of old fields	Diagnostic species	Dominant species
Initial stage	1	year 1	*Anagallis arvensis, Chenopodium album, Cirsium arvense, Crepis taraxacoides, Plantago major, Polygonum aviculare, Veronica persica*	*Anagallis arvensis, Chenopodium album, Cirsium arvense, Plantago major, Polygonum aviculare*
	2	year 1	*Cerastium brachypetalum, Cynodon dactylon, Lolium perenne, Plantago major, Poa annua, Trifolium repens*	*Cerastium brachypetalum, Convolvulus arvensis, Cynodon dactylon, Lolium perenne, Plantago major, Poa annua, Taraxacum officinale, Trifolium repens*
Early stage	3	year 6 year 9 year 13	*Lotus corniculatus, Medicago sativa, Poa bulbosa, Poa sylvatica*	*Brachypodium rupestre, Convolvulus arvensis, Dactylis glomerata, Elytrigia repens, Lotus corniculatus, Medicago sativa, Pastinaca sativa, Plantago lanceolata, Poa sylvicola, Taraxacum officinale, Trifolium pratense*
	4	year 9	*Pastinaca sativa, Trifolium pratense*	*Convolvulus arvensis, Elytrigia repens, Linaria vulgaris, Medicago lupulina, Medicago sativa, Pastinaca sativa, Plantago lanceolata, Taraxacum officinale, Trifolium pratense*
	5	year 3 year 13	*Festuca pratensis, Medicago lupulina, Setaria pumila*	*Convolvulus arvensis, Elytrigia repens, Medicago lupulina, Plantago lanceolata, Setaria pumila, Taraxacum officinale, Trifolium pratense*
	6	year 3	*Filipendula hexapetala, Leucanthemum platylepis, Melilotus officinalis, Setaria pumila*	*Brachypodium rupestre, Convolvulus arvensis, Dactylis glomerata, Elytrigia repens, Filipendula hexapetala, Melilotus officinalis, Plantago lanceolata, Poa sylvicola, Setaria pumila, Taraxacum officinale*
	7	year 3 year 13		*Brachypodium rupestre, Dactylis glomerata, Elytrigia repens, Medicago lupulina, Medicago sativa, Plantago lanceolata, Trifolium pratense*
Terminal stage	8	year 15 year 100	*Betonica serotina, Bromopsis erecta, Festuca rupicola, Filipendula hexapetala, Galium lucidum, Salvia pratensis, Scorzonera villosa, Thymus longicaulis*	*Betonica serotina, Brachypodium rupestre, Bromopsis erecta, Plantago media, Scorzonera villosa, Thymus longicaulis*
	9	year 15 year 100	*Anthyllis vulneraria, Bromopsis erecta, Carex flacca, Carex montana, Chrysopogon gryllus, Festuca rupicola, Hippocrepis comosa, Onobrychis tommasiniana, Potentilla tommasiniana, Rhinanthus major, Scorzonera villosa, Thymus longicaulis*	*Anthyllis vulneraria, Bromopsis erecta, Chrysopogon gryllus, Festuca rupicola, Rhinanthus major, Scorzonera villosa, Thymus longicaulis*

cies typical for dry and oligotrophic grasslands. Clusters represented vegetation differentiation both in space (spatial heterogeneity) and time (asynchrony). Spatial heterogeneity was obvious as different clusters appeared within a particular field. Some clusters appeared in different fields, i.e. these vegetation patch types were present over several years (Table 2).

Table 2: Number of individual plots of each age in clusters divided according to OPTIMCLASS proposal.

Tabela 2: Število posameznih ploskev določenega časovnega obdobja razdeljenih v snope s postopkom OPTIMCLASS.

| Cluster | Age | | | | | | | Dominant age |
	1	3	6	9	13	15	100	
1	41							1
2	11							1
3			52	15	6			6
4				37				9
5		36			2			3
6		14						3
7		2			44			13
8						51	3	15
9						1	49	100

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Figure 2: Changes of the main life form categories (annuals, perennial forbs, perennial graminoids and woody species) during succession.
Slika 2: Spremembe glavnih življenskih oblik (enoletnice, trajna zelišča, trajne trave in lesnate vrste) med sukcesijo.
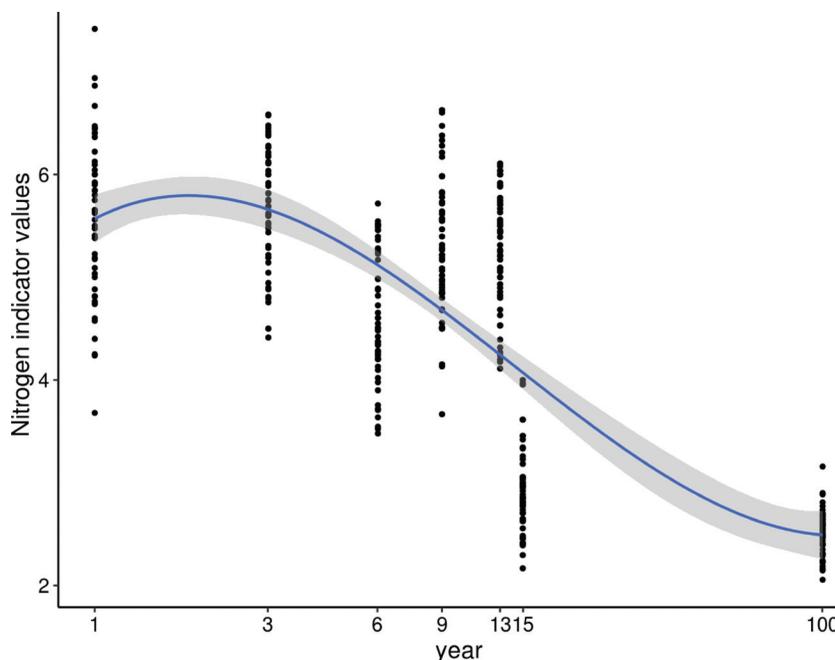
Perennial forbs dominated the first stages in succession then perennial grasses became dominant from the 13th year (Figure 2). Annuals were abundant only in the initial stage. Woody species (*Pinus nigra, Prunus mahaleb* and *Rosa gallica)* appeared as early as in the 3rd year of succession with ca. 3% relative abundance. However, abundance of woody species decreased and remained negligible in subsequent years due to annual mowing.
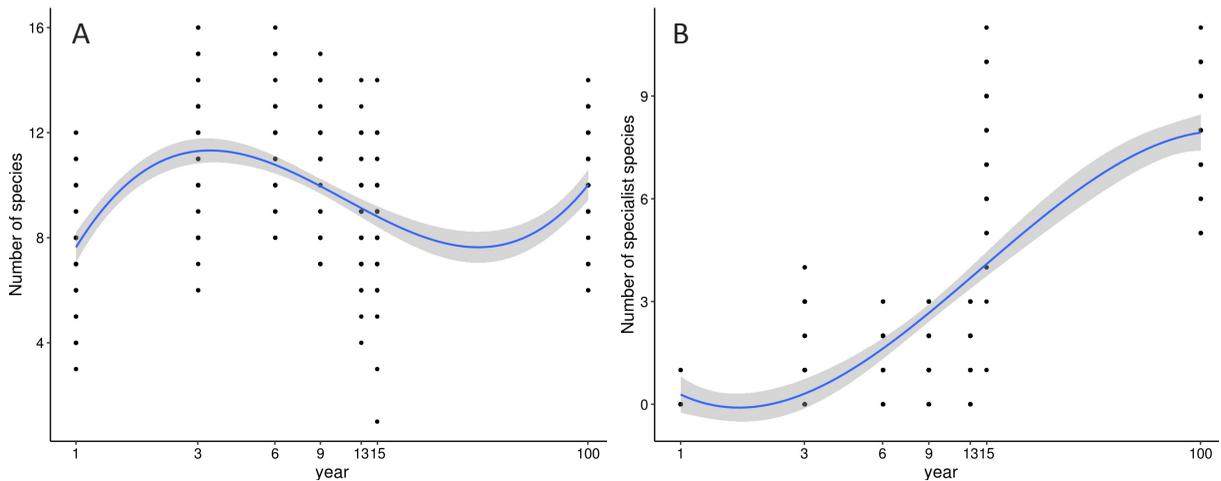
Ecological indicator values for nutrients showed non-linear decrease over time (Figure 3, Appendix, Table 3)

indicating mesotrophic conditions in early succession and oligotrophic conditions in the 15-year-old and 100-year-old stands. In our study, the ecological indicator values for nutrients were higher in initial and early successional stages than in the 15-year-old and the 100-year-old stands (Appendix, Figure 3a). Total species richness reached a local maximum early in succession in the 3rd year and the fitted cubic relationship predicted a minimum between the 15 and 100-years (Figure 4a, Appendix, Table 3). Due to the high within-stand variation at 1 m plot scales (cf.

Figure 3: Relationship between nitrogen indicator values and years since abandonment in old fields in SW Slovenia (p < 2.2e-16, adj R^2 = 0.572, y = 5.56 + 0.55x − 0.36x^2 − 0.03x^3). The 95% confidence level interval for predictions from the linear model is marked with gray envelop. Individual points represent nitrogen indicator values estimated in 1 m long segments. Note the strong spatial heterogeneity represented by variability within particular years.

Slika 3: Odnos med indikatorsko vrednostjo za dušik in leti od opustitve starih polj v JZ Sloveniji (p < 2,2e-16, adj R^2=0,572, y = 5,56 + 0,55x − 0,36x^2 − 0,03x^3). Interval zaupanja (95%) za napovedi z lineranim modelom je prikazan s sivo. Posamezne točke predstavljajo indikatorske vrednosti za dušik ocenjene na 1 m odsekih. Opazna je močna prostrska heterogenost zaradi variabilnosti med posameznimi leti.

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Figure 4: Relationship (A) between the number of all species and years since abandonment ($p < 2.2e\text{-}16$, adj $R^2 = 0.22$, $y = 7.63 + 4.77x - 1.89x^2 + 0.17x^3$) and (B) between the number of specialist species and years since abandonment ($p < 2.2e\text{-}16$, adj $R^2 = 0.616$, $y = 0.28 - 1.06x + 0.79x^2 - 0.06x^3$) in old fields in SW Slovenia. The 95% confidence level interval for predictions from the linear model is marked with gray envelop. Individual points represent species richness estimated in 1 m long segments. Note the strong spatial heterogeneity represented by variability within particular years.

Slika 4: Odnos med (A) številom vseh vrst in leti od opustitve ($p < 2,2e\text{-}16$, adj $R^2=0,22$, $y = 7,63 + 4,77x - 1,89x^2 + 0,17x^3$) in (B) številom specialistov in leti od opustitve ($p < 2,2e\text{-}16$, adj $R^2=0,616$, $y = 0,28 - 1,06x + 0,79x^2 - 0,06x^3$) starih polj v JZ Sloveniji.). Interval zaupanja (95%) za napovedi z lineranim modelom je prikazan s sivo. Posamezne točke predstavljajo indikatorske vrednosti za dušik ocenjene na 1 m odsekih. Opazna je močna prostrska heterogenost zaradi variabilnosti med posameznimi leti.

Figure 4a), the total number of species did not differ between the initial and early successional (years 1–13) and the other stands (year 15 and year 100) (Appendix, Figure 3b). Dry grassland specialist species were present in all stands including the initial stage (Appendix, Table 1) with increasing number of specialists along the successional gradient (Figure 4b). Number of grassland specialist species at 1 m plot scale did not differ between the 15-year-old and the 100-year-old stands. However, these stands had higher number of specialists than earlier stages (Appendix, Figure 3c).

Besides overall trends of temporal vegetation differentiation, using the method suggested by Zelený we found significant spatial heterogeneity of ecological indicator values within-fields (between different clusters; F = 227.965, adjusted p < 0.05).

Discussion

Fast and successful secondary succession

In our study we found an example of fast and successful secondary succession on abandoned agricultural fields in a traditional rural landscape. Species richness and composition become similar to target grasslands on a field that was abandoned only 15 years ago.

According to general models of succession (Cramer & Hobbs 2007) and previous studies in the region (Čarni & Kaligarič 1991, Kaligarič 1997, Kaligarič et al. 2006, Kaligarič & Ivanjšič 2014) local spontaneous succession should terminate in forest after ca. 50 years. Successional stages on unmanaged abandoned fields consist of ruderal communities, mesic perennial grasslands and shrublands with increasing cover of woody components. In contrast, annual mowing may alter the successional pathway to the direction of dry semi-natural grasslands (Čarni & Kaligarič 1991, Kaligarič & Ivanjšič 2014). This type of dry semi-natural grasslands (dominated by *Bromus erectus* and *Chrysopogon gryllus*) can be considered as target vegetation in our study area (Čarni & Kaligarič 1991, Kaligarič & Ivanjšič 2014). We found low abundance of woody species. Although some seedlings and saplings of woody species appeared early after 3 years, their colonization remained unsuccessful with negligible contribution of woody species in subsequent years.

After 15 years, old fields could develop into semi-natural grasslands in our study area. Note that spontaneous succession would reach forest stage only after 50 years (Čarni & Kaligarič 1991, Kaligarič 1997). In contrast to other studies that reported the lack or minor development of weedy stages in fast successions (Jongepierová et al. 2004, Török et al. 2011b), we found distinct early successional ruderal stages. These early stages with the dominance of ruderal species reflect land use legacy, i.e. the

presence of specific seed bank composition and increased nutrient content of soil (Cramer et al. 2008, Halassy et al. 2016, Török et al. 2018). In our study, the ecological indicator values for nutrients were higher in initial and early successional stages than in the 15-year-old and the 100-year-old stands. In vegetation patches (clusters) dominated by ruderal species, the mean Ellenberg N indicator values varied between 4 and 6 indicating medium levels of nutrients. This medium level of soil nutrients most probably is a legacy of the cultivation. Our results suggest that nutrient stocks have been depleted after ca. 15 years. Annual mowing probably enhanced this process. Invasive alien species often dominate early stages in old field succession and might slow down or prevent further regeneration (Prach & Pyšek 1999, Matus et al. 2003, Csecserits et al. 2011, Bartha et al. 2014). It is important to note that invasive alien species did not appear in this succession. The lack of invasive aliens is probably typical in landscapes with traditional extensive land use and with high cover of natural and semi-natural vegetation types (Jongepierová et al. 2004, Ruprecht 2006).

Rate of succession is often limited by the lack of available propagules (Molnár & Botta-Dukát 1998, Pywell et al. 2002, Török et al. 2011a) and diversity of developing semi-natural grasslands is under the influence of surrounding habitats (Janišová et al. 2014). In our study, the surrounding species pool was rich in mesic and xeric grassland species. Hedgerows, dry semi-natural grasslands, forests and shrublands providing these species were present in the close vicinity (within 50 m) or often adjacent to abandoned fields. As a consequence, the total number of species increased fast in succession and reached maximum already in the third year. Specialists appeared in the first year and their number increased continuously along the successional gradient. Therefore, we can conclude that dispersal limitation had minor role here.

Species of mesic grasslands also colonized and some of them became abundant in the early stage of succession (e.g. *Dactylis glomerata*, *Festuca pratensis*). However, after 15 years, these species were replaced by dry grassland species.

Temporal patterns of life forms in secondary succession at the karst plateau of SW Slovenia are similar to patterns described in other studies from Central Europe (Prach et al. 2007). Succession starts with the dominance of perennial forbs then perennial grasses become dominant after ca. 10 years. This early period is very similar to spontaneous succession in other mesic habitats (Prach et al. 2007, 2014). However, annual mowing modifies the subsequent patterns preventing the development of woody stages and promoting the emergence of semi-natural dry grasslands. Contribution of perennial forbs is high in all stages while annuals are abundant only in the initial stage.

Considering potential mechanisms, we suggest that initial and early stages of succession are driven by the moderately increased level of soil nutrients (a minor agricultural legacy effect). The subsequent fast succession to target semi-natural dry grasslands can be explained by the interaction of rich species pool, the good condition for dispersal and the appropriate disturbance regime (annual mowing). The small size of fields, the low ratio of ruderal elements in the surrounding landscape and the lack of invasive aliens contribute also to the success of succession. Tölgyesi et al. (2019) proposed an alternative explanation that the rate of recovery might depend on the plot-scale functional redundancy of the target community, as redundant species come back slower due to a self-organized establishment limitation. Species density is relatively low in our case in the target grasslands in this area. Low species density implies low functional redundancy. Therefore, community assembly can proceed quickly and unhindered by internal establishment limitation.

Succession without middle stage?

In this study, we found evidence that early successional stages can develop quickly to late successional grasslands, i.e. the expected midsuccessional stage(s) described by other studies (Čarni & Kaligarič 1991, Bartha et al. 2014, Prach et al. 2014, Sojneková & Chytrý 2015, Schmid et al. 2017) did not appear. The missing midsuccessional stage is an interesting aspect of this successional series (see also Jongepierová et al. 2004, Török et al. 2011b). One may argue against our interpretation saying that our target community is not a terminal stage but it is the "missing midsuccessional" stage due to deflected (or arrested) succession (sensu Godwin 1929). However, we must reject this alternative. First, because no "later successional" grasslands are known from the region (Kaligarič et al. 2006, Vitasović et al. 2012, Kaligarič & Ivanjšič 2014). Second, because the fine-scale community organization of these fields (the 15 years old and the 100 years old stands in our study) is similar to natural and semi-natural grasslands but differ from typical midsuccessional grasslands. In midsuccessional grasslands low diversity patches are characteristic, formed by species that are subordinate in the terminal community (Bartha et al. 2014). These species become locally and temporally dominant due to stochastic priority effects. The related vegetation structure differs considerably from the structure of terminal community (Bartha 2007) and it arrests or delays colonization of other target species (Prach & Pyšek 1999, Házi et al. 2011, Szentes et al. 2012, Bartha et al. 2014). The grasslands developed after 15 years in secondary succession at the Karst plateau of SW Slovenia

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did not show these features. *Bromus erectus* and *Chrysopogon gryllus* formed vegetation matrix (i.e. the same dominant species as in target semi-natural grasslands), and this matrix did not inhibit the colonization and persistence of other dry grassland species.

Spatial heterogeneity in succession

We identified nine vegetation patch types (called 'coenostate clusters') in this study. Patches occurring in early succession were dominated by ruderal and mesic grassland species (mainly legumes and grasses, e.g. *Lotus corniculatus*, *Taraxacum officinale*, *Dactylis glomerata* and *Elymus repens*). On the 15-year-old abandoned field we found that perennial grasses of target community (*Bromus erectus*, *Chrysopogon gryllus*) became dominant and formed additional patch types. To some degree, these structures were repetitive in space and time as we could find indicator species with significant associations (i.e. preference) to these patch types. Our results are consistent with previous studies reporting spatiotemporal contingencies of vegetation patterns in old field succession (Pickett et al. 2001).

At each field (with one exception) two or three patch types were present and formed spatially heterogeneous vegetation mosaic. Patch types (coenostate clusters) that co-occurred on a field often had significant differences in ecological indicator values or in species richness. These patterns suggest the existence of fine-scale environmental and functional heterogeneity within-stands. Spatial heterogeneity of soil characteristics (Robertson et al. 1988), biomass (Symonides 1985) and vegetation structure (Symonides 1985, Lepš 1989, Ruprecht et al. 2007) has been reported in previous old field studies. However, the number of related studies is limited and generalizations about spatial patterns in succession (similar to generalizations made about temporal patterns) are still missing.

Our results highlight the potential role of spatial patterns in controlling the rate and direction of spontaneous regeneration processes (McCallum et al. 2018), and call for further studies on fine scale spatial heterogeneity in succession.

Conclusion

We report an example of fast vegetation succession on abandoned agricultural fields from a traditionally managed "living rural landscape" where land abandonment is a rare event and restricted to small areas. We found here initial and early successional stages similar to other series. However, we did not found typical midsuccessional stage. In contrast, we found a 15-year-old stand distinct from younger abandoned fields but similar to late-successional

fields (represented by a 100-year-old stand in our data). Our study provides evidence that dry semi-natural grasslands can regenerate with high rate within 15 years in this specific rural landscape. Multiple factors (low intensity agriculture with low fertilizer input, small size of agricultural fields, close proximity of seed sources and the annual mowing of ex-arable lands) are probably generating and controlling this specific pattern of fast and successful old field succession. Assessing the generality of these patterns needs further studies based on permanent plots and experiments with monitoring both vegetation characteristics and environmental factors.

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Conflict of interest

The authors declare that there is no conflict of interests regarding the publication of the manuscript.

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