FUNCTIONAL RESPONSE TRAITS AND PLANT COMMUNITY STRATEGY INDICATE THE STAGE OF SECONDARY SUCCESSION

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Abstract

Changes of species composition, plant community strategy and functional response trait turnover were studied in a succession from dry pastures to a forest community (oak-hornbeam forests). The following question was asked: are functional response traits and plant community strategies indicators of TAA (time since agricultural land use abandonment), thus of a specific succession stage.

Indirect gradient analysis (DCA) was used in order to observe the position of the relevés along the axis and to correlate it with TAA. It was found that the position of relevés on DCA axis 1 is our proxy for TAA. Correlations (Spearman's *rho*) between the occurrence of plant functional traits and TAA were performed.

Low-growing herb species with scleromorphic leaves and green or red flowers are the predominant plant type on grassland areas, while plant species with digitate, hydro or mesomorphic leaves and white flowers typically prevail in forest. The proportion of chamaephytes increases immediately after land abandonment (afforestation). In a closed forest stand, there are many more herb species with vegetative propagation (bulbils). Herbal species in those stands most often reward pollinators with pollen. The ecological strategy of the entire plant community changes with spontaneous afforestation. On grassland, stress-tolerant species are dominant. After 10 years, the community is defined as CS and after 200 years as a community with a C-CS strategy.

Key words: plant functional traits, land use transformations, secondary succession, Bela krajina, Slovenia.

Izvleček

Raziskava se ukvarja s spreminjanjem funkcionalnih rastlinskih znakov, ekoloških značilnosti vrst in ekološke strategije združbe skozi posamezne stadije zaraščanja pašnikov v odvisnosti od časa opustitve kmetijske rabe (TAA).

V raziskavi smo uporabili multivariatno DCA analizo in opazovali položaj florističnih popisov v DCA prostoru in jih korelirali s TAA. Izračunali smo Spearmanov korelacijski koeficient med pojavnostjo posameznega rastlinskega funkcionalnega znaka in TAA.

Nizkorastoče zeliščne vrste s sklerofilnimi listi in cvetovi rumenih in rdečih barv so prevladujoč tip rastlin na pašnikih. V gozdovih prevladujejo vrste z deljenimi, hidro ali mezomorfnimi listi in s svetlejšimi (belimi) cvetovi.

Delež hamefitov se v združbi po opustitvi kmetijske rabe močno poveča (proces zaraščanja). V sklenjenem gozdnem sestoju je opazen večji delež zeliščnih vrst, ki se razmnožujejo vegetativno (zarodni brstiči ipd.). Omenjene zeliščne vrste privabljajo opraševalce največkrat s cvetnim prahom.

Ekološka strategija celotne združbe se preko sekundarne sukcesije spreminja. Na pašnikih prevladujejo stres-toleratorji. Po desetih letih ima združba strategijo kompetitor/ stres tolerator, po dvesto letih pa kompetitor-kompetitor/ stres tolerator.

Ključne besede: funkcionalni rastlinski znaki, sprememba krajinske zgradbe, sekundarna sukcesija, Bela krajina, Slovenija.

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1. INTRODUCTION

Changes in biodiversity are most commonly evaluated through changes in the species composition. Many studies provide a precise assessment of the influence of land use transformations on vegetation composition and ecosystemic structure (at regional and global levels). That has led to new attempts to measure plant functional traits and establish which plant strategies reflect ecological and morphological adaptations (Pärtel & Zobel 1999, Garnier et al. 2001, Cousins & Eriksson 2002, Garnier et al. 2004, Castro et al. 2010, Saatkamp et al. 2010, Catorci et al. 2011, Prévosto et al. 2011, Vitasović Kosić et al. 2011).

The change from grassland to forest as a consequence of the absence of human disturbance results in potential natural vegetation (Odum 1980). That is the final, stable stage resulting from the climatic and edaphic conditions in the area. Many studies have shown that during the afforestation process, the appearance of communities, ecological and morphological species turnover (Castro et al. 2010, Řehunková & Prach 2010, Saatkamp et al. 2010, Latzel et al. 2010).

Řehunková & Prach (2010) analysed the role of local site and landscape factors in the course of spontaneous succession in disused gravel-sand pits over a broader geographical area. They recognised plant functional traits as a powerful tool for predicting the colonization success of plants available in the local species pool. The next important study of secondary succession with functional response traits was by Castro et al. (2010). The authors assessed the response of species richness, composition and functional traits to decreasing land use intensity. They found changes in community strategy and species composition through the secondary succession.

In our study, we observed the changes in species composition, in functional response traits and in plant community strategy that occurred subsequent to the abandonment of agricultural land use. We were particularly interested in the ecological and morphological changes in the plant communities during the process of spontaneous afforestation (secondary succession).

We tried to complete a detailed study of the afforestation stages that result in the potential natural vegetation of the region. Our aims were (1) to study the species turnover process between different succession stages, (2) to understand the process of functional trait and species habitat preference turnover between individual succession stages and (3) to study the appearance of a particular functional response trait in each succession stage and to correlate it with the time, since the agricultural land use was abandoned (TAA).

Our hypothesis: (A) specific functional response traits may be related to TAA and may therefore be strongly linked to plant species growing in a specific succession stage, (B) functional response traits and ecological plant characteristics are a good indicator of the succession stage and therefore of TAA.

2. METHODS

STUDY AREA

The research took place in the region of Bela krajina in SE Slovenia (Figure 1). This is a karst solution plain formed mainly by calcareous rocks, limestone and dolomites. On the surface, these rocks weather into chromic cambisols and luvisols, which sporadically even completely cover them. Annual precipitation in this part of Slovenia is 1300 mm and mean annual air temperature is 10.9 °C (ARSO 2011).

An area of ca. 1000 ha was selected (45.514535° – 45.539406° N and 15.209397° – 15.246939° E) for the purpose of this research. The region lies on a Pleistocene karst corrosion plain, at an altitude between 160 and 420 metres and is fairly homogeneous in terms of geomorphology and climate.

The region experienced the gradual formation of a cultivated landscape, which began to change intensively at the beginning of the 20th century. This was a result of a period of migration of the local inhabitants out of Bela krajina. There were three major migration flows, with the first at the beginning of the 20th century, when people migrated to Western Europe and North and South America. The second wave of migration took place during WWII and the third wave resulted from delayed industrialisation in the 1960s, when the local inhabitants emigrated to larger industrial hubs (Orožen-Adamič et al. 1995). Today, the area is forested or under the process of secondary succession, as a consequence of land use abandonment.
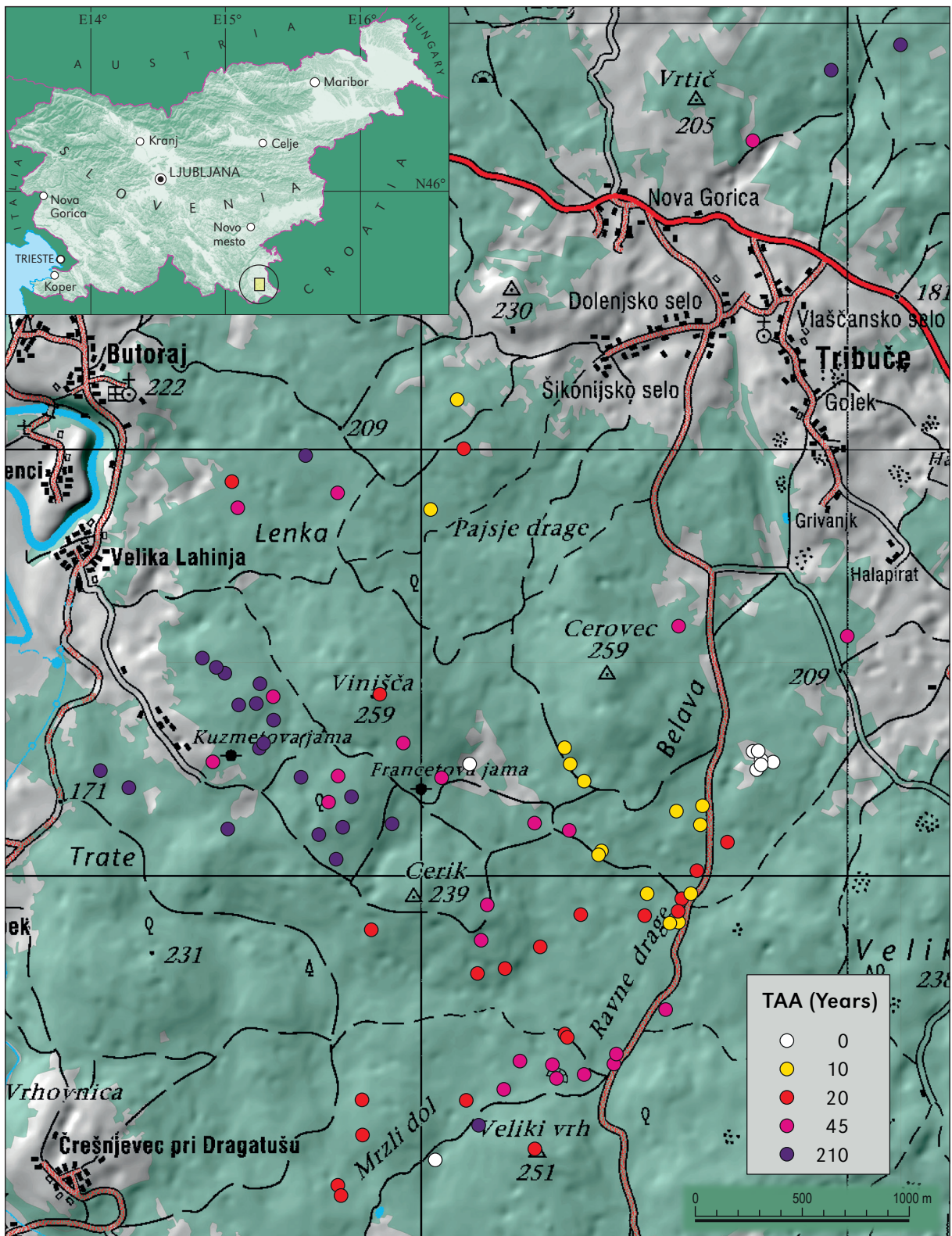
Figure 1: Study area in Bela krajina (SE Slovenia). The dots represent relevé plots with attached TAA attribute.
Slika 1: Območje raziskav v Beli krajini. Prikazane so lokacije popisov s podatkom o času od opustitve kmetijske rabe oz. paše (TAA).

VEGETATION

Eighty-nine randomised plots (10 × 10 m) were selected on flat terrain away from depressions or sinkholes, in order to get samples with similar geomorphologic characteristics. The plots were located in different stages of forest succession (illyrian oak-hornbeam forests). The minimum distance between sample plots was 100 meters (less for plots of the stage A, since there were not enough appropriate sites to be included in the study). The period of time since agricultural land use abandonment of each plot (the TAA) was estimated by overlaying different digitalized old cadastral maps (1790, 1823 and 1913) and digital orthophotos (1954, 1975, 1986, 1999 and 2009) (Paušič & Čarni 2012 b). If a pasture was clearly recognizable on a cadastral map of the year 1823, but abandoned in the next observed time interval (year 1913), we assumed that the time since agricultural land use was abandoned can be considered to be approximately 100 years (since we do not have information about the exact year that agricultural land use was abandoned). All the studied plot sites were abandoned once; therefore no anthropogenic influences were present after the land use was abandoned on these sites.

Communities were sampled according to the Central European method (Braun-Blanquet 1964). Data were stored in the Turboveg programme (Hennekens & Schaminée 2001).

Taxa nomenclature cited in the text is in agreement with Flora Europaea (Tutin et al. 1964–1993).

PLANT FUNCTIONAL TRAITS

We analyzed functional response traits and habitat preferences (Table 1), divided into five groups. The traits were chosen from those proposed by Weiher et al. (1999) as indicators linked to the main plant population processes: dispersal, establishment and persistence.

Using the BIOLFLOR database (Klotz et al. 2002) and data on habitat preferences (Ellenberg et al. 1992), the species (249 recorded taxa) were attributed selected functional response traits, ecological strategy of species and data on habitat preferences of species for each selected plot in turn. As a result, a table was worked out for each plot, presenting the occurrence of each particular trait (number of taxa) in the plot (relevé) as for the whole cluster group.

STATISTICAL ANALYSIS AND DATA PROCESSING

Based on TWINSPAN (Hill 1979) classification analysis, the relevés were classified into 5 groups (A, B, C, D and E), using Juice 6.5 software (Tichý 2002). TWINSPAN pseudospecies cut levels for species abundances were set to 0–5–25 percentage scale units. Initially, six division levels were chosen. Later, different levels of division were accepted, resulting in 5 groups of relevés interpretable in terms of ecology. Using a fidelity index (Chytrý et al. 2002, Tichý 2002) for each species, we were able to calculate the diagnostic species of each of the five cluster groups.

In the next step, we investigated the actual TAA of each relevé site with the help of old cadastral maps.

Indirect gradient analysis (DCA) of floristic data from relevé plots was performed with the Canoco program (ter Braak and Šmilauer 2002), in order to observe the position of the relevés along axes and to calculate their projection values along axis 1.

Instead of the TAA attribute, we decided to correlate the values from DCA axis 1 with functional response traits, since some older cadastral maps give inaccurate attributions and using this method minimised errors in our study. The position on DCA axis 1 is therefore our proxy for TAA.

The correlations (Spearman's *rho*) between TAA and selected functional response traits (Table 1) were calculated in Statistica 8.0 (Statsoft Inc. 2007).

The average ecological strategy of the entire community (stage) at a specific succession stage was calculated from the ecological strategy of each sample, with the C-S-R Signature Calculator 1.2 program (Hunt et al. 2004). The program consists of conversion and comparator tools. The conversion of floristic data into a C-S-R signature is carried out automatically by the first, or 'calculator', part of the new spreadsheet tool. The user pastes-in a data matrix containing quantitative records from one vegetation sample. The tool calculates the percentage abundance of each functional type. The second, or 'comparator', part of the tool accepts a selection of C-S-R signatures transferred manually from the 'calculator' part. The positions of all of these signatures are then plotted in C–S–R space. The direction and magnitude of any differences between samples with respect to C, S and R components are reported (Hunt et al. 2004).

Table 1: Selected plant functional traits and ecological characteristics.
Tabela 1: Izbrani funcionalni rastlinski znaki in ekološke značilnosti vrst.

TRAITS USED IN STUDY	DESCRIPTION	% of missing data
A) Traits describing the vegetative morphology of the species		
1. Life form (Raunkiaer 1934)	Life form refers to the vertical position of vegetative buds (as an adaptation to adverse seasons)	0
2. Method of vegetative propagation	We distinguished runners, propagation with bulbils, fragmentation, rhizome and bulbs.	5.2
B) Traits describing the shape and morphology of photosynthesising leaves		
1. Leaf form (Günther 1987)	Plants with grass-like, simple, full, digitate, pinnate and needle were found.	0
2. Leaf anatomy (Frank and Klotz 1990)	We distinguished helomorphic, hygromorphic, mesomorphic and scleromorphic leaves.	0
C) Traits describing the flower shape and reproductive biology of the species:		
1. Flower shapes (Müller 1881)	Müller classified insect pollinated flowers into 9 classes. The main aim was to achieve a grouping of pollinators. Nectariferous flowers were grouped according to the depth of nectar display (flowers with open, partly hidden and hidden nectar).	0
2. Flower shapes according to Kugler (Kugler 1970)	Kugler distinguished 10 major flower types: disk- and bowl- shaped flowers, funnel flowers, bell-shaped flowers, stalk disc flowers, lip flowers, flag blossoms, flower heads, spike flowers, brush flowers and trap flowers.	0
3. Flower colour	We observed flowers with blue, brown, green, red, violet, white and yellow flowers.	0
4. Beginning of flowering	We selected three months in which most of the species start to bloom (March, April and May).	0
5. Duration of flowering	Most of the species in the study area have a flowering duration from 2 to 4 months.	2.8
6. Fruit type (Bässler et al. 1996; Strasburger et al. 1998)	The fruit is defined here only as the fruit at the time of seed ripening. The remaining parts of the flower are treated as "additional structures" and are identified with germinules. Fruits are categorized according to characteristics of seed maturation, pericarp or arrangement of the pericarp.	2.8
7. Diaspore type	Generative diaspores (units of dispersal) may be seeds or can be imbedded in additional structures or an additional structure can be attached to them (fruit with appendage, infructescense, seed, spore, vegetative).	3
8. Diaspore weight (mg)	We set three investigated weight classes: diaspores with weight up to 1 mg, from 1 to 50 mg and above 50 mg	15.2
9. Floral rewards for pollinators (Ayasse et al. 2000; Gumbert and Kunze 2001)	The plant species were distinguished in 3 groups according to the floral reward offered to pollinators (nectar, pollen and deceit).	10.8
D) Data on distribution areas and species ecology		
1. Species continentality (Meusel & Jäger 1992)	Continentality characterizes the range of a plant species from the coasts to the centres of continents.	0
2. Ellenbergs indicator values for individual plant species (Ellenberg 1992)	Simple ordinal classes of organisms (initially plants) with a similar realized ecological niche along a gradient. The latest edition of Ellenberg's indicator values contains values on a 9 point scale for soil acidity, productivity/nutrients, soil humidity, continentality, soil salt content and light.	3.2
E) Ecological strategy of the species		
1. C-S-R (Grime et al. 1997)	Description of plant ecological strategies. Grime distinguishes 3 major - extreme groups (stress tolerators, ruderals and competitors) and a combination of those groups.	18
2. Species life span	The life span refers not only to the actual life span of species (annuals, biennials, perennials).	0

3. RESULTS

Twinspan classification divided the relevés into 5 separate groups, corresponding to the TAA.

We calculated median values for the TAA of each cluster group individually. The results are: group A – 0 years, B – 10 years, C – 20 years, D – 45 years and E – 210 years abandoned plots.

Vegetation on grasslands was classified into group A. The largest proportion of heliophilous species (highest fidelity; Phi coefficient) occurs in this group (*Genista germanica*, *Leontodon hispidus*, *Potentilla erecta*, *Calluna vulgaris*). This stage can be described as *Calluna* stage.

The following stage is the *Pteridium–Frangula* stage (group B), in which *Pteridium aquilinum* and shrub species (*Frangula alnus*) prevail. This is the initial phase of the secondary succession process.

Stage C is the *Betula* stage. In this stage of secondary succession, a dense forest formation is visible, with species such as *Betula pendula* and *Populus tremula*.

Stage D is a forest stage, in which *Carpinus betulus* is the dominant tree species. This stage is dominated by *Carpinus betulus* and heliophilous herbs disappear. The herb layer is dense, consisting of typical forest species. *Epimedium alpinum*, *Fragaria moschata* and *Aremonia agrimonoides* are characteristic herb species of this stage. Such a

stage of secondary succession occurs 45 years after land abandonment. Stage D is considered to be the *Epimedium–Carpinus* stage.

Stage E is forest with a characteristic herb layer composed of sciophilous forest species (e.g., *Pulmonaria officinalis*, *Anemone nemorosa*, *Galium sylvaticum*). The forest is two-layered, with *Quercus petraea* as the characteristic tree species in the upper tree layer and *Carpinus betulus* in the lower tree layer. We consider stage E to be the *Carpinus–Quercus* stage, the end stage of secondary succession.

The relevés indicate species abundance in relation to the TAA (Figure 2). Species such as *Frangula alnus* and *Calluna vulgaris* soon disappear in the afforestation process, due to the changed ecological conditions. *Pteridium aquilinum* is abundant in stages A, B and C and disappears completely in the final stage E. *Betula pendula* in the tree layer has the highest abundance in stage C.

The D stage has characteristic herb species; *Aremonia agrimonoides*, *Fragaria moschata and Epimedium alpinum,* which show the highest abundance and fidelity values (Phi coefficient).

In older forest stands (E) dominated by *Quercus petraea*; *Anemone nemorosa, Polygonatum multiflorum, Pulmonaria officinalis* and *Tamus communis* have the highest fidelity coefficient values (Figure 2) and could justifiably be considered to be indicator species for forest stands older than 200 years.

Figure 2: Synoptic table showing the turnover of species in the time gradient. Clusters (stages) are indicated by capital letters: A – *Calluna* stage, B – *Pteridium–Frangula* stage, C – *Betula* stage, D – *Epimedium–Carpinus* stage and E – *Carpinus–Quercus* stage. The layers are indicated as: 1 upper tree layer, 3 lower tree layer, 4 shrub layer and 6 herb layer.

Slika 2: Sinoptična tabela florističnih popisov iz Bele krajine. Jasno je vidna premena vrst skozi stadije sekundarne sukcesije. Različni stadiji so označeni kot: A– stadij *Calluna*, B – stadij *Pteridium–Frangula*, C – stadij *Betula*, D – stadij *Epimedium–Carpinus* in E – stadij *Carpinus–Quercus*.
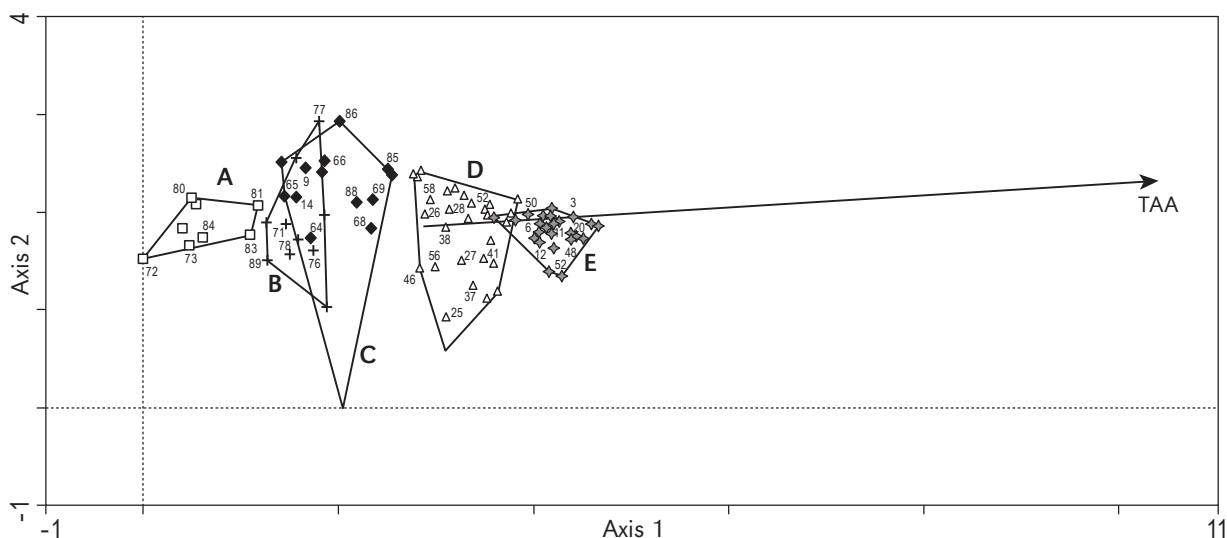
Figure 3: DCA ordination diagram with 89 relevés shows the separation of relevés into five groups (A–E), which correspond to the passive projection of the TAA.

Slika 3: DCA ordinacija prikazuje razporeditev florističnih popisov v pet skupin (A–E)(kot so bile določene po Twinspan klasifikaciji) po stadijih sekundarne sukcesije.

DCA diagram analysis shows the position of 89 relevés, divided into five distinct groups (Figure 3). The distinction corresponds to groups made by Twinspan analysis. The relevés are arranged in groups according to the TAA and are along axis 1 (eigenvalue 0.636) in DCA. Axis 2 has a much lower eigenvalue of 0.261.

We subsequently performed a correlation statistical test and calculated Spearman's (*rho*) correlation coefficients for each measured functional plant trait to TAA; these are shown in Table 2.

Table 2: Correlation (Spearman *rho*) of selected plant traits and ecological characteristics with TAA. Legend: * p<0.05, ** p<0.01, n.s. non significant

Tabela 2: Spearmanov koeficient korelacije (*rho*) izbranih funkcijskih rastlinskih znakov in ekoloških značilnosti s TAA.
Legenda: * p<0.05, ** p<0.01, n.s. ni korelacije.

Traits describing vegetative morphology of the species

VEGETATIVE PROPAGATION

bulb	0.19	n.s.
Bulbil	0.31	(*)
fragmentation	-0.05	n.s.
rhizome	-0.09	n.s.
runner	-0.59	(**)

Traits describing leaf form and morphology

LEAF FORM (Raunkiaer 1934)

digitate	0.41	(**)
full	0.16	n.s.
grass-like	-0.68	(**)
needle	-0.30	(*)
pinnate	-0.17	n.s.
simple	0.14	n.s.

LEAF ANATOMY (Frank & Klotz 1990)

helomorphic	-0.16	n.s.
hygromorphic	-0.51	(**)
mesomorphic	-0.02	n.s.
scleromorphic	-0.64	(**)

Traits describing flower shape and reproductive biology of the species

Flower classes according to MÜLLER (Müller 1881)

flowers with open nectar	-0.03	n.s.
flowers with totally hidden nectar	0.33	(*)
flower associations with totally hidden nectar	0.69	(**)
butterfly flowers	-0.17	n.s.
bee flowers	-0.31	(*)

Flower types according to KUGLER (Kugler 1970)

pollen flower	-0.21	n.s.
disc flowers with nectar open	-0.01	n.s.
disc flowers with nectar ± hidden nectaries at base of stamens	0.58	(**)
funnel, tube flowers (large)	-0.26	(*)

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funnel, tube flowers (small)   -0.13 n.s.
bell shaped flowers with sticky pollen   0.08 n.s.
true lip flowers   0.05 n.s.
lip flowers, *Orchidaceae* type   -0.18 n.s.
flower heads, *Asteraceae*   -0.40 (**)

FLOWER COLOUR

blue	-0.14	n.s.
brown	-0.02	n.s.
green	-0.38	(**)
red, purple	-0.50	(**)
violet	-0.08	n.s.
white	-0.30	(*)
yellow	-0.08	n.s.

BEGINNING OF FLOWERING

March	0.30	(*)
April	-0.31	(*)
May	-0.01	n.s.

DURATION OF FLOWERING

2 month	0.29	(*)
3 month	-0.04	n.s.
4 month	-0.63	(**)

FRUIT TYPE (Bässler et al. 1996; Strassburger 1998)

berry	0.31	(*)
capsule	-0.66	(**)
nut	0.33	(*)
schizocarp	0.02	n.s.

DIASPORE TYPE

infructescence	-0.12	n.s.
fruit with appendage	0.31	(*)
seed	-0.33	(*)
spore	0.65	(**)
vegetative	0.07	n.s.

DIASPORE WEIGHT (mg)

0.1 – 1	-0.68	(**)
1 – 50	-0.12	n.s.
50+	-0.37	(**)

FLORAL REWARDS (Ayasse et al. 2000; Gumbert & Kunze 2001)

nectar	-0.02	n.s.
pollen	-0.33	(*)
deceit	-0.32	(*)

Data on distribution areas, species ecology

OCEANITY – CONTINENTALLITY (Mäusel & Jäger 1992)

species of continental climate but ranging
   into sea climate   -0.01 n.s.
species of sea climate   -0.19 n.s.
species missing in extreme continental climate
   and extreme sea climate   0.30 (*)

Habitat preferences – ELLENBERG VALUES
(Ellenberg 1992)

light	-0.83	(**)
temperature	-0.36	(**)
continentallity	-0.15	n.s.
moisture	0.11	n.s.
soil reaction	0.68	(**)
nutrients	0.71	(**)

SPECIES LIFE SPAN

annual	-0.32	(*)
perennial	0.03	n.s.

In the group of traits describing the vegetative morphology of the species (Table 2), the formation of the bulbils trait and runner trait show a significant correlation trend with TAA in the vegetative propagation group. The runner trait has a high negative correlation with the time gradient, while the bulbil trait has a positive one.

In the observed traits describing leaf anatomy, there was a positive correlation between TAA and the hygromorphic leaf trait, while the sclero-morphic leaf trait showed a negative correlation with TAA.

Among the traits describing the flower shape and reproductive biology of the species, the number of flowers with totally hidden nectar in the receptacle and flower associations (inflorescences) with totally hidden nectar increase along the TAA gradient. On the other hand, the bee flower trait negatively correlates with increasing TAA. There is also a strong positive correlation between the category of disc flowers with nectar ± hidden nectaries at the base of stamens and TAA and a negative correlation between the funnel flower trait and TAA.

In the category flower colour, we found that a white colour has a positive correlation with TAA, while on open grassland; plants with red and green flower colours prevail.

The beginning of flowering, in April (on grasslands) and in March (in forests) is also significant. A flowering duration of 2 months correlates positively with TAA, while a flowering duration of 4 months correlates strongly negatively with TAA.

In the fruit type group, berry and nut correlate positively with TAA, which indicates that the number of species with these traits increases with the land use abandonment stage. The capsule trait has a strong negative correlation with TAA.

Within the diaspore group, the spore trait and the fruit with appendage trait have a high posi-

tive correlation with TAA. The seed trait has a negative correlation. The diaspore weight class up to 1 mg correlates negatively with TAA and the class weight more than 50 mg positively.

In the floral rewards category, pollen is the only trait which significantly correlates positively with TAA, the deceit trait shows a negative correlation.

Among data on habitat preferences and species ecology: the trait "species missing in an extreme continental climate" correlates positively with TAA. Ellenberg values of temperature, soil reaction and nutrients correlate with TAA positively, while the Ellenberg value for light trait shows a strong negative correlation.

In relation to plant life form changes (Figure 4), we determined that grassland (*Calluna* stage) was dominated by hemicriptophytes (63.6%), followed by macro phanerophytes with 15.1%, geophytes contributed 7.6% and 6% of all recorded species were nano-phanerophytes. There were 4.2% chamaephytes and 3.2% therophytes. The annual life span trait shows a negative correlation with TAA.
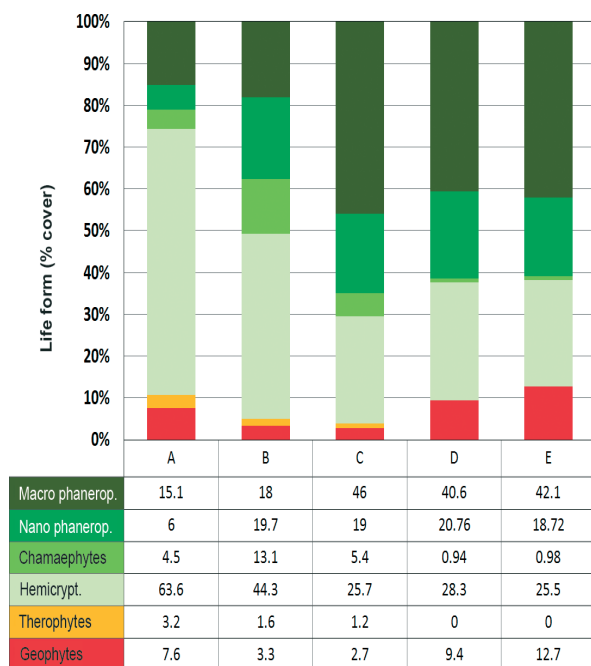
In the first stage of afforestation (*Frangula–Pteridium* stage), 44% of all species were hemicryptophytes, 19.7% of the species were nano-phanerophytes, 18% were macro-phanerophytes, 13.1% chamaephytes, 3.3% geophytes and 1.6% of the recorded species were therophytes.

The *Betula* stage is a forest stand that indicates an already slightly altered state. Groups were represented as follows: macro-phanerophytes 46%, hemicriptophytes 25.7%, nano-phanerophytes 19%, chamaephytes 5.4%, geophytes 2.7% and therophytes 1.2% of all recorded species.

The species composition in young forest with a median TAA of 45 years (*Epimedium-Carpinus* stage) was as follows: macro-phanerophytes predominate with 40.6%, followed by hemicriptophytes with 28.3%, nano-phanerophytes with 20.76%, geophytes with 9.4% and chamaephytes with 0.94%. The species composition in old forests with a median TAA of 210 years (*Carpinus–Quercus* stage) was: macro-phanerophytes 42.1%, hemicriptophytes 25.5%, nano-phanerophytes 18.72%, geophytes 12.7% and chamaephytes 0.98%.

Change of plant community strategy in the TAA gradient.

Grasslands and grasslands under afforestation are dominated by S-CS strategists (Figure 5). In the course of secondary succession, through abandonment of grazing and mowing, both species and the community as a whole in the C-S-R triangle show an increasing tendency toward the C-CS category (in the last observed succession stage E).
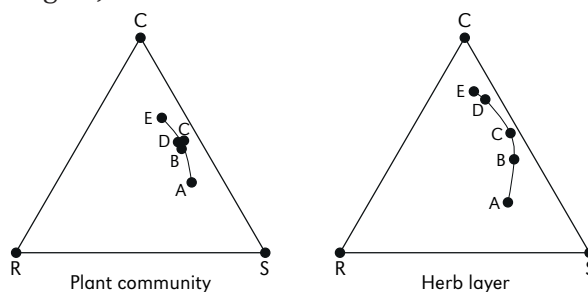

	A	B	C	D	E
Macro phanerop.	15.1	18	46	40.6	42.1
Nano phanerop.	6	19.7	19	20.76	18.72
Chamaephytes	4.5	13.1	5.4	0.94	0.98
Hemicrypt.	63.6	44.3	25.7	28.3	25.5
Therophytes	3.2	1.6	1.2	0	0
Geophytes	7.6	3.3	2.7	9.4	12.7

Figure 4: Life form changes in different succession stages. A – *Calluna* stage, B – *Pteridium-Frangula* stage, C – *Betula* stage, D – *Epimedium-Carpinus* stage and E – *Carpinus-Quercus* stage.

Slika 4: Premena življenjskih oblik rastlin v različnih stadijih sekundarne sukcesije. A – stadij *Calluna*, B – stadij *Pteridium-Frangula*, C – stadij *Betula*, D – stadij *Epimedium-Carpinus* in E – stadij *Carpinus-Quercus*.

Figure 5: Changes in CSR signatures of the whole plant community and herbal layer in secondary succession. A – *Calluna* stage, B – *Pteridium-Frangula* stage, C – *Betula* stage, D – *Epimedium-Carpinus* stage and E – *Carpinus-Quercus* stage.

Slika 5: Premena strategije rastlinske združbe za celotno združbo in zeliščno plast. A – stadij *Calluna*, B – stadij *Pteridium-Frangula*, C – stadij *Betula*, D – stadij *Epimedium-Carpinus* in E – stadij *Carpinus-Quercus*.

Additional analysis was performed for the herb layer change through secondary succession. Grassland herbs mainly possess a stress-tolerator strategy, while in the last stage (state E), forest herbs demonstrate the traits of C-CS strategists (the herb layer is more pronounced than the whole plant community). The turnoff of the whole community life strategy in succession stages B, C and D is very similar to the life strategy turnoff of the herbal layer (Figure 5).

4. DISCUSION

Landscape abandonment has resulted in changes in floristic composition in Bela krajina. Similar results have also been found elsewhere in Europe and the world in general (Sternberg et al. 2000, Vesk & Westoby 2001, Adler et al. 2004, Čarni et al. 2007, Johansson et al. 2010, Řehunková & Prach 2010, Čarni et al. 2011, Paušič & Čarni 2012).

Detailed studies on the early successional patterns of forest species were already carried out in the 1980s. Halpern (1989) studied the interactions of life history traits and disturbance in clear cut and burned *Pseudotsuga* forests in the Cascade Range of Oregon. The detailed study by Lepš & Štursa (1989) on the life history strategies change in secondary succession in the Krkonoše Mountains already included the plant strategy turnover but encompassed a shorter successional interval (20 years). The results of these studies refer to short-term experiments, while the changes documented in our study cover a much longer time period.

The plant community composition co-develops in newly developed ecological conditions, as is also evident from the results of our study: during the first 10 years after land abandonment, grassland alters into shrubland of the *Pteridium–Frangula* stage. After the next 10 years, this stage transforms into the *Betula* stage, which needs an additional 25–30 years (or 50 years in total) to be dominated by *Carpinus betulus* (*Epimedium–Carpinus* stage). The last stage in secondary succession in the study area is the *Carpinus–Quercus* stage, which occurs after 200 years of land abandonment. The course of succession is fast at the beginning, since abandonment results in the increased growth of competitive plant taxa that were unable to grow in the previous disturbed environment.

One of the characteristics of species in a closed stand is an ability to propagate vegetatively via bulbils (*Cardamine bulbifera*). The occurrence of species with such a form of vegetative propagation in older forests is due to the higher proportion of competitors (Grime et al. 1997) in closed forest stands. Runners are plants found mostly on grasslands and shrubland (*Ajuga reptans, Carex pilosa, Fragaria vesca*). Such a form of propagation enables the species to populate a larger distribution area over a relatively short time period (Mony et al. 2010).

Changes in leaf morphology and method of vegetative propagation in relation to TAA

Scleromorphic leaves possess a special cuticle and epidermis. They often comprise additional structures to facilitate water retention or to reduce evapotranspiration (trichomes, specialized sunken leaf stomata, special leaf dyes etc.). Species with scleromorphic leaves are common in grasslands and do usually not appear in closed forest stands (*Dorycnium germanicum, Carlina acaulis, Calluna vulgaris*) (Čarni et al. 2010, Řehunková & Prach 2010).

It has been determined that the number of species with hygromorphic leaves increases with forest stand age (Řehunková & Prach 2010). Hygromorphic leaves have a characteristic soft tissue typical of sciophilous species adapted to high air humidity. The leaf cuticle and epidermis are very thin. Such leaves are characteristic of species from shady forests (*Cyclamen purpurascens, Anemone nemorosa*).

Over the time since abandonment, leaf shape changes greatly. On grasslands, species with grass-like leaves (*Poaceae*) and solid, needle-like leaves (*Juniperus communis*) dominate, while plant species with digitate leaf shapes (*Acer, Crataegus*) occur in forests.

Shape, colour, morphology of reproductive organs and fruits

The general flower shape (Müller 1881) shows a tendency to change along secondary succession phases. On open grasslands, forest edges and shrubland, the prevailing types of flowers are funnel or tube shaped (*Gentiana asclepiadea, Primula vulgaris, Vinca minor, Buphthalmum salicifolium*). According to the Kugler classification (Kugler

1970), through spontaneous afforestation and transformation of areas into forest, flowers assume the characteristics of disc-type flowers with hidden nectar (*Crataegus laevigata*). Flowers with totally hidden nectar are much more frequent in forests than in open grasslands (*Fragaria moschata*).

The colour of the flowers in an individual succession stage certainly has a significant role.

Most species in open grasslands have red or purple flowers, such as *Calluna vulgaris*, *Centaurea jacea*, *Dianthus barbatus*, *Orchis morio*, *Polygala amara* (Forrest & Thomson 2009). A red flower is black in the UV spectra, in which most insect pollinators sense (Chittka & Raine 2006). It is therefore in strong contrast with the surrounding green area (which remains the same colour in UV). In forest stands, the prevalent flower colour is white (*Anemone*, *Convallaria*, *Galium*, *Polygonatum*). White appears in the UV spectra as a strong blue, which helps plants to be visible when they grow in the (dense) forest herbal layer (Forrest & Thomson 2009, Miller et al. 2011).

Most plants of open grasslands start to flower in April and have a flowering duration of 4 months. In forests, plants already start to flower in March, with an average duration of flowering of about 2 months (Forrest & Thomson 2009, Pellissier et al. 2010). The flowering period of grassland species is thou longer, lasting for almost (depending on the species) the entire vegetation period. Strong winds in spring, however, facilitate the pollination of some wind pollinated (anemogamic) plants in forest from the family *Betulaceae*, such as *Corylus avelana* and *Carpinus betulus*. The sample plots in forest contained several early flowering insect pollinated forest species (*Daphne mezereum*, *Pulmonaria officinalis*, *Vinca minor*, *Primula vulgaris*, *Corydalis cava*).

Other species on grasslands, though, have much more time to develop flowers, since they are clearly visible to pollinators for most of the vegetation season. Grassland species thus tend to have a long flowering period (Debussche et al. 1996, Casado et al. 2004, Peco et al. 2005, Pellissier et al. 2010).

The most prevalent fruit type in pastures (myrmeco, anemochorous) is capsules (*Orchis morio*, *Ophrys sphegodes*) (Lengyel et al. 2010), while in closed forest stands, plant species most often produce nuts (*Fagus sylvatica*, *Corylus avellana*) and berries (*Actaea spicata*, *Berberis vulgaris*, *Convallaria majalis*, *Frangula alnus*, *Polygonatum multiflorum).*

Spore is of the diaspore type, which is mostly bound to old forest stands. Most fern species (*Pteridopsida*) grow in forest (*Asplenium trichomanes*, *Athyrium filix-femina*, *Dryopteris filix-mas),* while they are not so common on (often dry) grasslands, since the prothallium (gametophyte stage) needs a lot of moisture for successful fertilization (Hua et al. 2010). Seed is predominantly of the diaspore type among heliophylus grassland species (*Dianthus barbatus*), while fruit with an appendage characterizes forest phanaerophytic species, such as *Carpinus betulus* or *Betula pendula*. The reason is the different dispersion vector and strategy (Tackenberg et al. 2006). With the beginning of the afforestation process, the diaspore weight increases. A diaspore weight up to 1 mg is typical of (anemochorous, zoohorous) grassland species (*Agrostis capillaris*, *Briza media*, *Clinopodium vulgare*), while forest species have much heavier diaspores, normally more than 50 mg (*Cornus mas*, *Quercus petraea*, *Fagus sylvatica*). Grassland plant species have relatively smaller, lighter seeds (often with pappi or narrow wings), since they are normally spread by anemochory (Vittoz et al. 2009, Řehunková & Prach 2010), while forest ones need to be stronger, bigger and often with an edible appendage, since they are mostly spread by autochory and zoochory (insects, mammals) (Heinken et al. 2006, Řehunková & Prach 2010).

The floral reward for pollination by an insect in forest species is usually pollen (*Convallaria majalis*, *Cyclamen purpurascens*), while a zoochorous plant on open grassland or pasture rewards prospective pollinators with deceit pollination. The latter is especially typical of mimicry species from the family *Orchidaceae* (*Ophrys*, *Orchis*) on dry grassland (Pellissier et al. 2010). We conclude that the land abandonment process increases zoochory and autochory and decreases anemochory (Řehunková & Prach 2010).

Ellenberg values for light and temperature indicate that land abandonment and the afforestation process change the ecological conditions for the plant community. During secondary succession after agriculture land use abandonment, organic matter in the soil increases and some minerals and nutrients drawn up by plants (e.g. *Betula*) from lower soil horizons accelerate decomposition and mineralization by higher decomposition activity. With the decomposition of organic litter,

the concentrations of exchangeable Ca^{2+}, P, Mg^{2+}, as well as other nutrients, increase, as does the soil pH (Čarni et al. 2007, Paušič & Čarni 2012).

Changes of plant life forms, changes in functional response traits and habitat preferences in relation to land use change have previously been observed in other studies (Castro et al. 2010). It has been established that the process of afforestation of (open) grassland areas fundamentally changes the life form of the entire community (Fig. 4).

With agricultural land use change (abandonment), the ecological strategies of both plant species and the entire community change. We were also interested in this change. We observed a change in the species strategy of the entire community and in the herbal layer over the course of secondary succession periods (A, B, C, D and E). Our premise was that the community as a whole and the herb layer change according to a similar pattern.

During the course of secondary succession, from grasslands to forests, a shift from S-CS towards C-CS strategy is evident (i.e., species for which competition is the ecological strategy that dictates the existence of individual species on a specific site, a feature of phanerophytes). This is in fact characteristic of older forest.

Additional analysis was performed only for the herb layer change through secondary succession. The range of changes in the herb layer during secondary succession is slightly more extreme than in the community as a whole. It is evident that the community strategy in succession stages B, C and D is very similar, whereas in the herb layer, the transition from one succession stage to another is also reflected in a change of strategy of the herb layer.

Species of grassland and pastures are far more adapted to stress, to human disturbance. Constant mowing or grazing therefore prevent the occurrence of species other than herb species and occasional trees or shrubs. Spontaneous afforestation also reduces the accessibility of certain essential living resources (such as light, space), so species require another strategy to prosper in such environments. They become competitors.

Our methodological approach permitted the identification of a series of individual attributes that are positively or negatively associated with TAA. There is no doubt that the results from this study are linked to a series of methodological decisions. The choice of the traits used was necessarily pragmatic (Peco et al. 2005), in an attempt to minimise the number of chosen traits and the

effort required for their measurement, while at the same time maximising their functional relationship with secondary succession.

5. CONCLUSIONS

Overall, our study showed that secondary succession in Bela krajina is a result of high species turnover, as well as change in plant functional traits and structural changes of the whole community (Sternberg et al. 2000, Vesk & Westoby 2001, Adler et al. 2004, Čarni et al. 2007, Johansson et al. 2010, Řehunková & Prach 2010).

After human activity has been abandoned, species from the forest edge or from nearby forest areas start migrating to the grassland (a changed ecological regime) due to the changed ecological conditions. Over the course of several years, not only does the species composition change, but also the ecological strategy of the whole community, the manner of propagation, duration of flowering, morphology of the plant habitus, leaf forms (species are replaced by those that are best adapted to the new ecological conditions). After land has been abandoned, around 50 years are needed for the development of *Carpinus* forest and 200 years for the development of two-layered *Quercus-Carpinus* forest, which can be seen as the potential vegetation of the study area.

Our research findings indicate that:

1. the rate and direction of development, changes in the plant community (and ecosystem), correlate with abiotic ecological factors (in our case, above all the time gradient) but this impact becomes obvious only after the abandonment of land use (after cessation of the disturbance that hindered the process of secondary succession);
2. changes of anthropogenic activity lead to a change in the floristic inventory of the community. Secondary succession starts when anthropogenic disturbance is absent and the species and the community as a whole show an entirely different morphological-ecological turnover;
3. land use results in an artificially stable system (quasi-equilibrium), which collapses after the land is abandoned and tends toward the natural equilibrium.

Figure 6: Steljniki near the village of Vinomer. Steljniki represent a transition phase between the *Pteridium−Frangula* (B) and *Betula* (C) stages of secondary succesion. The annual removal of litter protect steljniki from overgrowing.

Slika 6: Belokranjski steljniki pri kraju Vinomer. Steljniki predstavljajo prehod med sukcesivnima stadijema *Pteridium−Frangula* (B) in *Betula* (C). Letna košnja in odstranjevanje stelje steljnike varujeta pred zaraščanjem.

Figure 7: Approximately 45 years old forest stand, *Epimedium−Carpinus* stage.
Slika 7: Gozdni sestoj, star približno 45 let. Stadij *Epimedium−Carpinus*.

6. POVZETEK

Funkcionalni rastlinski znaki in ekološka strategija združbe označujejo posamezen stadij sekundarne sukcesije

Raziskava je imela tri cilje: (1) študija premene vrst med sekundarno sukcesijo, (2) razumevanje premene izbranih funkcionalnih rastlinskih znakov in ekoloških značilnosti vrst med stadiji sekundarne sukcesije in (3) študija pojavljanja rastlinskih funkcionalnih znakov v stadijih sekundarne sukcesije in korelacija le-teh s časom od opustitve kmetijske obdelave oz. paše (TAA).

Raziskava je potekala v Beli krajini, na območju med vasmi Bojanci, Butoraj, Dragatuš in Tribuče. Območje je bilo do začetka 20. stoletja še intenzivna kmetijska krajina, nato pa se je zaradi izseljevanja prebivalstva in opuščanja kmetijske dejavnosti krajinska zgradba spremenila. Za območje so značilna tri obdobja izseljevanja prebivalstva; prvo v začetku 20. stoletja (v države Zahodne Evrope in v obe Ameriki), drugo med 2. svetovno vojno in tretje v večja industrijska središča kot rezultat zakasnele industrializacije v 60-tih let. Med in po emigracijskih valovih se je pokrajina zaraščala z gozdom.

Na območju smo izdelali 89 florističnih popisov (Braun-Blanquet 1964), ki so bili med seboj oddaljeni najmanj 100 metrov. Vsi popisi so bili izdelani na območju pašnikov ali pašnikov v različnih fazah zaraščanja. Podatke o času od opustitve kmetijske rabe (TAA) smo pridobili s pomočjo prekrivanja katastrskih načrtov, vojaških kart in letalskih posnetkov iz različnih obdobij (Paušič & Čarni 2012b).

Analizirali smo premeno funkcionalnih rastlinskih znakov in ekoloških značilnosti vrst (Tabela 1), ki smo jih razdelili v pet skupin. Nabor izbranih funkcionalnih rastlinskih znakov povzemamo po Weiher et al. (1999). Vsaki od 249 najdenih rastlinskih vrst smo pripisali funkcionalen rastlinski znak in ekološke značilnosti.

V programu Twinspan (Hill 1979) smo opravili klasifikacijsko analizo popisov. S pomočjo uporabe indeksa navezanosti vrst (Chytrý et al. 2002) smo izračunali diagnostične vrste za vsakega izmed pet snopov.

V naslednjem koraku smo opravili DCA analizo popisov in analizirali položaj popisov v multivariatnem prostoru. Ugotovili smo, da je postavitev skupin popisov po abscisni osi sorazmerna z njihovo povprečno vrednostjo TAA. Zato smo za vsak

popis izračunano projekcijo vrednost na abscisni osi DCA upoštevali kar kot proxy vrednost TAA. Izračunane vrednosti abscisne osi TAA za vsakega izmed 89 popisov smo v nadaljevanju korelirali s pojavnostjo izbranih rastlinskih funkcionalnih znakov in njihovih ekoloških značilnosti. Izračunali smo Spearmanov koeficient (*rho*), Tabela 2.

Na koncu nas je zanimala še premena strategije celotne rastlinske združbe in posebej zeliščne plasti za vsak stadij sekundarne sukcesije.

Klasifikacija v programu Twinspan je naše popise razdelila v 5 snopov, ki so sorazmerni TAA vsakega posameznega popisa. TAA (mediana) za vsak snop posebej znaša: A – 0 let, B – 10 let, C – 20 let, D – 45 let, E – 210 let (Slika 2).

Združbo na pašnikih sestavljajo heliofilne vrste in jo imenujemo stadij *Calluna*. Temu stadiju sekundarne sukcesije sledi stadij *Pteridium-Frangula* (TAA = 10). Stadij C poimenujemo *Betula*. Stadij D (TAA = 45) je značilen gozd, kjer je *Carpinus betulus* dominantna drevesna vrsta, v zeliščni plasti pa dominira *Epimedium alpinum*. Stadij imenujemo *Epimedium – Carpinus*. Stadij E zaznamujejo številne skiofilne vrste v zeliščni plasti, gozd je značilno dvoplasten, kjer v zgornji plasti prevladuje *Quercues petraea*, v spodnji drevesni plasti pa *Carpinus betulus* (Slika 2, Slika 4, Tabela 2). Ostale korelacije opazovanih funkcionalnih rastlinskih znakov s TAA so predstavljene v Tabeli 2.

Analiza premene ekološke strategije združbe med sekundarno sukcesijo (Slika 5) je pokazala, da ima združba na pašnikih značilno strategijo stres tolerator, po desetih letih kompetitor/ stres tolerator, po dvesto letih pa kompetitor- kompetitor/ stres tolerator. Podobno se spreminja strategija zeliščne plasti skozi stadije sekundarne sukcesije.

Rezultati študije kažejo na spremembo funkcionalnih rastlinskih znakov in ekoloških značilnosti, kakor tudi celotne strategije združbe skozi sekundarno sukcesijo kot posledica opustitve paše.

7. ACKNOWLEDGEMENTS

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