UNIVERZA V LJUBLJANI
BIOTEHNIŠKA FAKULTETA

Andrej PAUŠIČ

SPREMEMBA KRAJINSKE ZGRADBE, FLORISTIČNE SESTAVE IN EKOLOŠKIH RAZMER V JUGOVZHODNI SLOVENIJI V ZADNJIH 200 LETIH

DOKTORSKA DISERTACIJA

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DOKTORSKA DISERTACIJA

CHANGES OF LANDSCAPE STRUCTURE, FLORISTIC COMPOSITION AND ECOLOGICAL CONDITIONS IN SOUTHEASTERN SLOVENIA IN LAST 200 YEARS

DOCTORAL DISSERTATION

Ljubljana, 2013

Na podlagi Statuta Univerze v Ljubljani ter po sklepu Senata Biotehniške fakultete in sklepa 20. seje Komisije za doktorski študij Univerze v Ljubljani z dne 21. 9. 2011 je bilo potrjeno, da kandidat izpolnjuje pogoje za opravljanje doktorata znanosti na Interdisciplinarnem doktorskem študijskem programu Bioznanost, znanstveno področje biologija. Za mentorja je bil imenovan doc. dr. Andraž Čarni.

Doktorsko delo je bilo opravljeno na Biološkem inštitutu Jovana Hadžija ZRC SAZU v Ljubljani.

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Doktorsko delo je rezultat lastnega raziskovalnega dela. Podpisani se strinjam z objavo svoje naloge v polnem tekstu na spletni strani Digitalne knjižnice Biotehniške fakultete. Izjavljam, da je naloga, ki sem jo oddal v elektronski obliki, identična tiskani verziji.

Andrej PAUŠIČ

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JI sl/en
AI Delo obsega spremembo krajinske zgradbe, floristične sestave in ekoloških razmer v jugovzhodni Sloveniji v zadnjih 200 letih. Disertacijo sestavljajo štiri raziskave, katere med seboj povezuje spreminjanje krajinske zgradbe v obdobju 200 let. Prva raziskava se ukvarja s spreminjanjem krajinske zgradbe na območju Bele krajine v zadnjih 220 letih, druga in tretja raziskava obsegata spreminjanje funkcionalnih rastlinski znakov, ekoloških značilnosti vrst in ekološke strategije združbe v posameznih stadijih zaraščanja pašnikov v odvisnosti od časa opustitve kmetijske rabe. V zadnji raziskavi smo izdelali na osnovi funkcionalnih rastlinskih znakov, Ellenbergovih ekoloških vrednosti in edafskih značilnosti tal štiri modele iz skupine GAMM in ocenjevali njihovo napovedno moč o času od opustitve kmetijske rabe tal. Rezultati prve raziskave kažejo, da je bila do leta 1913 Bela krajina značilna kmetijska krajina. Po prvem emigracijskem valu (pred in po koncu 1. svetovne vojne) se začne območje postopoma zaraščati z gozdom. Druga svetovna vojna je regiji prinesla številne spremembe: začel se je drugi val izseljevanja prebivalcev, spremenila pa se je tudi krajinska zgradba. Zaradi intenzivnega opuščanja kmetijske rabe in zaraščanja kmetijskih zemljišč dobi Bela krajina značaj gozdnate krajine. Leta 1980 raziskovano območje že popolnoma porašča gozd. Današnja krajinska zgradba Bele krajine je precej drugačna kot v preteklosti in je odraz ekonomskih in socialnih sprememb v pokrajini. Druga in tretja raziskava obsegata raziskavo premene funkcionalnih rastlinskih znakov in ekoloških značilnosti vrst med sekundarno sukcesijo. Rezultati druge in tretje raziskave kažejo, da so nizko rastoče zeliščne vrste s sklerofilnimi listi ter cvetovi rumenih in rdečih barv 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 zaradi procesa zaraščanja. V sklenjenem gozdnem sestoju je opazen večji delež zeliščnih vrst, ki se razmnožujejo vegetativno. Takšne zeliščne vrste privabljajo opraševalce največkrat s cvetnim prahom. Ekološka strategija celotne združbe se med sekundarno sukcesijo spreminja. Na pašnikih prevladujejo stres-toleratorji. Po desetih letih ima združba strategijo kompetitor/stres tolerator, po dvesto letih pa kompetitor/kompetitor-stres tolerator. Rezultat četrte raziskave kaže, da je informacija o starosti posamezne rastlinske združbe v sekundarni sukcesiji »shranjena« v spremembi merjenih funkcionalnih rastlinskih znakov, horotipov in Ellenbergovih bioindikatorskih vrednostih, a je najbolj vidna iz edafskih značilnosti. Izbrane edafske značilnosti dajejo najboljše rezultate za izdelavo napovedovalnih modelov GAMM za obdobje od opustitve kmetijske rabe.

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AB The dissertation deals with changes in the landscape structure, floristic composition and ecological conditions in south-eastern Slovenia in the last 200 years. The dissertation consists of four studies that elaborate land use changes during this period. In the first study, changes in land use, landscape structure and heterogeneity in Bela krajina were compared over a time interval of 220 years and linked to socio-economic factors. The second and third studies are about changes in species composition, plant community strategy and functional response trait turnover. In the fourth study, four models based on selected trait groups (plant functional traits, plant chorotypes, Ellenberg bioindicator values and soil properties) were built and their predictive power for the time since land use was abandoned (TLA) in Bela krajina was compared. The results from the first study show a significant increase of forested areas in the past 220 years. Until 1913, the landscape was agricultural. After human emigration at the beginning of the 20th century and during World War I, the land was partly abandoned. During and after the World War II, local inhabitants migrated from the region. The land structure changed and became of a transitional type. The third wave of emigration started in the 1960s. By around 1980, the study area had become completely forested. After 1981, the number of inhabitants again increased in settlements near traffic routes but people were employed in other economic activities. This trend had no significant impact on the landscape. The study shows that the present landscape structure is substantially different from those in the past and reflects the current social and economic features. The second and third study investigated the changes in functional response traits and species ecological preferences over the period of 220 years. The results show that 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 such 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. The fourth study shows that information about the process of abandonment of traditional land use is stored within changes of plant functional response traits, chorotypes and Ellenberg bioindicator values of the study area, but is best reflected in soil properties. Soil properties provide the most reliable basis for the elaboration of a prediction model for the time since land use was abandoned.

KAZALO VSEBINE

KAZALO ZNANSTVENIH DEL

1 PREDSTAVITEV PROBLEMATIKE IN HIPOTEZE

Doktorska disertacija celovito obravnava problematiko opuščanja kmetijske rabe prostora in spremembe, ki se pojavijo v obdobju, ko se začno procesi zaraščanja krajine, torej med sekundarno sukcesijo. V disertaciji so zajeti trije pogledi na prostor; najprej smo se dotaknili sprememb, ki nastopijo po opuščanju kmetijske rabe v krajinsko-ekološkem pogledu. V nadaljevanju proučujemo spremembe v prostoru z vidika sprememb floristične sestave in ekologije združb med sekundarno sukcesijo. V zadnji raziskavi ovrednotimo spremembe v prostoru, ki so posledica antropogenih vplivov s pomočjo izbranih rastlinskih znakov in ekoloških značilnosti, ki nakazujejo nekdanjo rabo prostora.

Bela krajina je z vidika raziskav krajinsko-ekoloških sprememb in sprememb v vegetacijski strukturi primerno območje raziskav, saj se je zaradi postopnega izseljevanja prebivalstva (začetek 20. stoletja, med drugo svetovno vojno in v 60. letih) postopoma preoblikovala (Josipovič, 2007). Zato se je celoten prostor zaraščal postopoma, s tem pa smo dobili možnost v vpogled ekoloških in krajinsko-ekoloških razlik med območji, ki so bila opuščena v različnih časovnih obdobjih.

1.1 SPREMEMBA KRAJINSKE ZGRADBE V BELI KRAJINI V ZADNJIH 200 LETIH

Najprej smo raziskali spremembe v krajinski zgradbi, ki so posledica opuščanja kmetijske rabe zaradi izseljevanja prebivalcev. Tukaj smo se ukvarjali predvsem s hitrostjo spreminjanja krajine ter opazovali smer teh sprememb.

Krajino največkrat opredelimo kot določeno geografsko območje, ki ga označuje preplet različnih ekosistemov, agroekosistemov, kmetijskih zemljiških kategorij in antropogenih območij (Turner in sod., 2001). Nekateri avtorji dojemajo koncept krajine kot socialno-prostorsko enoto, drugi spet kot geografsko enoto ter dajejo v ospredje njene naravne elemente. Sprememba (po)krajine, izginjanje habitatov in drobljenje njenih elementov so značilen proces, ki poteka danes v Sloveniji.

Po Formanu (1995) označujejo krajinsko zgradbo pestrost tal, naravne motnje ali disturbance in antropogeni vplivi. Slednji lahko velikokrat celo pozitivno vplivajo na pestrost rastlinskih in živalskih vrst v prostoru, torej na biodiverziteto (Farina, 1995; Mršić, 1997). Številne študije opisujejo spremembo krajinske zgradbe kot posledico človekovega delovanja v okolju v določenem časovnem obdobju. Zaradi pomanjkanja natančnih prostorskih podatkov pa take študije največkrat ne obravnavajo časovnega intervala, daljšega od 50 ali 60 let (Lira in sod., 2012). Kako pa se krajinska zgradba v opuščeni pokrajini spreminja skozi daljše časovno obdobje, recimo po 150 letih? So te spremembe premo sorazmerne s časom od opustitve kmetijske rabe? Kako hitro poteka sprememba krajinske zgradbe? Zaradi spreminjanja krajinske zgradbe se spreminja tudi krajinska pestrost. Termin krajinska pestrost se neposredno nanaša na informacijo o pestrosti pojavov, oblik in prvin v krajini. Je torej rezultat, preplet nekaterih ali vseh spodaj navedenih sestavin (Matičič, 2006):

- pestrost reliefa (gore, vrhovi, polja, vrtače, skalne stene),
- pestrost vodnega prostora in vodnih tokov (jezera, reke, poplavne ravnice, meandri, vodni izviri),
- pestrost vegetacijskih oblik v strukturnem smislu (gozd, mejice, zaplate gozda),
- pestrost kulturnega preoblikovanja prostora (kmetijska raba in oblika poselitve),
- biodiverziteta (število živalskih in rastlinskih vrst, število cenoz) in
- številčnost ter preplet vseh omenjenih oblik in pojavov.

Matičič (2006) ter nekatere druge študije omenjajo visoko stopnjo krajinske pestrosti na območjih Nature 2000 in zavarovanih območjih. Nas pa je zanimala predvsem sprememba krajinske pestrosti v tipični kmetijski krajini.

Dinamika sprememb v kmetijski krajini je povezana s spremembami v krajinski zgradbi in v odnosu posameznih krajinskih elementov ter njihovo prostorsko povezanostjo (Wagner in sod., 2000; Arx von in sod., 2002). Velikokrat se kmetijska intenzifikacija odraža v površini posamezne zemljiške kategorije in s prisotnostjo linijskih elementov ali koridorjev v krajini.

Prvi del disertacije opisuje raziskavo sprememb krajinske zgradbe in krajinske pestrosti v Beli krajini, ki je nastala kot posledica izseljevanja in opuščanja obdelave kmetijskih zemljišč. Osnova za raziskavo so stari katastrski načrt, vojaške karte, letalski posnetki in digitalni ortofoto posnetki ter statistični podatki o številu ovac in prebivalcev na izbranem območju med opazovanim obdobjem.

S pomočjo prekrivanja digitaliziranih kartografskih virov smo ocenili stanje, krajinsko zgradbo in pestrost po posameznih obdobjih ter rezultate povezali s številom prebivalcev in demografskimi procesi, ki so se odvijali v obravnavanem časovnem obdobju. Tako smo dobili vpogled v krajinsko zgradbo, pestrost in ugotovili vzroke za takšno stanje v posameznem obdobju.

Pašna živinoreja (ovčereja, govedoreja) ima pomembno vlogo pri vzdrževanju krajinske zgradbe in pestrosti, kakor tudi pri ohranjanju biotske pestrosti posameznega območja (Papanikolaou in sod., 2011; Louhaichi in sod., 2012). Kako pa se spremeni krajinska zgradba 200 let po prenehanju pašne živinoreje? V raziskavi nas je zanimal vpliv pašne živinoreje na krajinsko pestrost in zgradbo predvsem z vidika sprememb krajinske zgradbe ter značilnosti krajine, ki bi nakazovale na nekoč prisotno pašništvo. Število drobnice (ovac) v posameznih opazovanih obdobjih smo povezali s spreminjanjem (zmanjševanjem) pašnih površin in tako dobili vpogled v vlogo pašne živinoreje za značilnost krajinske zgradbe v opazovanem obdobju.

V prvi raziskavi smo izhajali iz naslednjih hipotez:

A) Izseljevanje in demografske spremembe so imele v Beli krajini pomembno vlogo pri spremembi krajinske zgradbe in krajinske pestrosti. Takoj po opuščanju kmetijske obdelave se na območju začne proces zaraščanja, torej sekundarna sukcesija. Zaraščanje površin z gozdom vpliva na manjšo razdrobljenost gradnikov, elementov krajine ter s tem na poenotenje celotnega prostora. Zato se manjša tudi krajinska pestrost.

B) Predpostavljamo, da se krajina zarašča premo sorazmerno s hitrostjo opuščanja obdelovanih območij.

C) Pašništvo ima v krajini pomembno vlogo pri ohranjanju prostora (pašnik, polje, mejica, njiva). Poleg tega pašništvo povečuje biotsko pestrost posameznega območja, saj zmanjšuje homogenost prostora in dodatno poskrbi za obstoj novih habitatov (pašniki).

1.2 SPREMEMBA FUNKCIONALNIH RASTLINSKIH ZNAKOV IN EKOLOŠKE STRATEGIJE ZDRUŽB V BELI KRAJINI MED SEKUNDARNO SUKCESIJO V OBDOBJU 200 LET

V drugem delu disertacije o spremembah krajine v časovnem obdobju 200 let obravnavamo krajino v luči florističnih, morfoloških in ekoloških sprememb rastlinskih združb in premene posameznih vrst, ki so posledica spreminjanja kmetijske krajine v gozdno. Drugi del disertacije obsega dve raziskavi, ki opisujeta proces sekundarne sukcesije, torej zaraščanje kmetijske krajine kot posledico prenehanja motnje (kmetijske obdelave območja).

V tej raziskavi izpostavljamo sekundarno sukcesijo, proces, ki je korenito spremenil videz obravnavanega območja v zadnjih 200 letih. Z raziskavo želimo podati celovito študijo posameznih faz sekundarne sukcesije, ekoloških sprememb združbe ter izbranih funkcionalnih rastlinskih znakov med različnimi fazami sekundarne sukcesije.

Raziskava prikazuje spremembe floristične in ekološke zgradbe združb in vrst na prehodu med pašniki (*Genisto-Callunetum*) in hrastovo-gabrovimi gozdovi (*Abio albae-Carpinetum betuli*). Spremembe ekoloških značilnosti združbe, ki so nastale zaradi opuščanja kmetijske rabe območja, najlažje ovrednotimo z analizo sprememb v vrstni sestavi združb (Shao in sod., 2003; Wild in sod., 2004).

Sekundarna sukcesija je niz sprememb rastlinske združbe, ki se pojavijo v času po prenehanju motnje (paša, košnja, vetrolom). Proces zmeraj vodi v ekološko stabilnejše stanje. Končni stadij sekundarne sukcesije danes pojmujemo kot trenutno potencialno vegetacijo (ang. current potential vegetation) (Biondi, 2011).

Številne študije navajajo metode za oceno vpliva sprememb v krajini na spremembo vrstne sestave združb, tako na regionalni kot tudi globalni ravni. Poskus ocenjevanja in merjenja sprememb v krajini s pomočjo ekoloških sprememb in vrstne sestave rastlinskih združb je sprožil uvajanje metod merjenja funkcionalnih rastlinskih znakov in ocenjevanja ekoloških strategij vrst in združb, ki so neposreden odraz sprememb v okolju (Campetella in sod., 2011; Wellstein in sod., 2011).

Da bi lahko razumeli odziv posamezne rastlinske vrste, rastlinske združbe ter celotnega ekosistema na okoljske spremembe (ki so posledica človekove dejavnosti), še posebej na spremembe rabe tal, moramo meriti funkcionalne rastlinske znake (De Bello in sod., 2010; Webb in sod., 2010; Walck in sod., 2011).

Metoda raziskav funkcionalnih in ekoloških sprememb vrst in rastlinskih združb med sekundarno sukcesijo obravnava posamezne vrste in tudi celotno rastlinsko združbo s pomočjo različnih bioloških atributov, ki predstavljajo specifičen odgovor vrste in združbe na biotske in abiotske spremembe v okolju, krajini. Zato je v tak pristop vključenih veliko različnih bioloških panog: taksonomija, funkcionalna ekologija, filogenija, ekologija.

V skladu s splošno sprejetim konceptom analize sprememb s funkcionalno-ekološkimi znaki (Lavorel in Garnier, 2002) smo v naši raziskavi izdelali analizo ekoloških in funkcionalnih sprememb vrst in združb. Ekološki in funkcionalni znaki odražajo torej spremembe v krajini. Raziskava funkcionalne diverzitete (ang. functional diversity) je definirana kot vrednost in razpon izbranih funkcionalnih znakov, zastopanih v združbi (Tilman, 2001).

Že nekatere podobne raziskave (Řehunková in Prach, 2010) ugotavljajo velik pomen funkcionalnih rastlinskih znakov pri analizi dolgoročnih sprememb v prostoru in poudarjajo velik pomen takšnih analiz.

Celoten sukcesijski niz od začetnega stadija (*Genisto-Callunetum*) do trenutne potencialne vegetacije, hrastovo-gabrovih gozdov (*Abio albae-Carpinetum betuli*), sestavljajo v Beli krajini naslednji stadiji:
A- stadij *Calluna*,
B- stadij *Pteridium−Frangula*,
C- stadij *Betula*,
D- stadij *Epimedium−Carpinus* in
E- končni stadij *Carpinus−Quercus*.

V raziskavi smo vsaki vrsti pripisali izbrane funkcionalne rastlinske znake in ekološke značilnosti (bioindikatorsko vrednost). Med sekundarno sukcesijo se spreminja tako ekološka adaptacija kot tudi morfologija same združbe, v združbi pa pride do premene vrst s spremenjenimi morfološkimi in ekološkimi prilagoditvami.

Danes vemo, da se rastlinska združba spreminja zaradi staranja in premene vrst ter zaradi postopnega naseljevanja novih vrst in spreminjanja ekoloških razmer v združbi (edafske razmere, spremembe temperature tal, osvetljenosti rastišča ipd.) (Koniak in Moy-Meir, 2009). Čeprav so omenjene spremembe danes dokazane, pa so procesi med sekundarno sukcesijo (recimo spreminjanje fenofaz vrst, premena oblike in barve cvetov) danes še zmeraj slabo poznani, vpliv sprememb na spremenjene ekološke razmere pa nejasen (Shipley in sod., 2006; Westoby in Wright, 2006). Študije, ki bi obravnavale holističen pristop k poznavanju dolgoročnih sprememb v združbi med sekundarno sukcesijo, pa tako rekoč ne obstajajo.

Še do nedavnega je veljalo pravilo, da procese, ki potekajo v spreminjajoči se združbi, opazujemo in analiziramo izključno s pomočjo premene vrstne sestave, to je premene vrst v združbi v opazovanem časovnem obdobju. Menimo, da je poznavanje premene vrst, floristične sestave pomemben podatek o ekoloških spremembah združbe. Vendar pa z dodatno informacijo, rastlinskimi znaki in ekološkimi značilnostmi vrst dobimo vpogled v procese, česar pa zgolj samo s preučevanjem premene vrst ne bi dosegli.

Tako na primer podatki o spreminjanju oblike in fiziognomije listov vrst v spreminjajoči se združbi nakazujejo na spremenjene ekološke značilnosti na ravni krajine (Dahlgren in sod., 2006) kot tudi na globalni ravni (Wright in sod., 2004). Zato poznavanje sprememb rastlinskih znakov in ekoloških značilnosti rastlin med sekundarno sukcesijo ponuja vpogled v številne (čeprav še ne popolno razumljive) ekološko funkcionalne spremembe in omogoča boljše poznavanje ekoloških procesov v združbi (Lavorel in sod. 1997; Kahmen in Poschlod, 2008).

V naši raziskavi smo smiselno razdelili funkcionalne rastlinske znake in ekološke značilnosti ali poteze vrst v pet skupin: (1) znaki ki opisujejo vegetativno morfologijo vrst, (2) znaki ki opisujejo morfologijo in zgradbo listov, (3) znaki ki opisujejo obliko cvetov ter reprodukcijsko biologijo vrst, (4) podatki o razširjenosti in ekologiji vrst in (5) podatki o ekološki strategiji vrst.

Pri vsaki takšni vrsti raziskav je pomembna pravilna izbira popisnih ploskev, ki morajo zaradi natančnosti analize ležati na ekološko podobnih, homogenih legah, sicer lahko dobimo heterogene rezultate, ki jih ne moremo analizirati. Dodaten problem predstavlja nabor izbranih funkcionalnih rastlinskih znakov in nabor osnovnih geografskih in geomorfoloških podatkov, ki so dosegljivi za vsako posamezno popisno ploskev.

Čas od opustitve kmetijske rabe je podatek, ki velikokrat ni natančen, še posebej, če obravnavamo vmesne sukcesijske stadije zaraščanja. Zato je ključno, da razpolagamo s kvalitetnimi prostorskimi viri o stanju vegetacije in krajinski zgradbi za vsak časovni interval v opazovanjem obdobju. V naši raziskavi smo podatke o krajinski zgradbi ter podatke o stanju združbe za obdobje 200 let pridobili iz starih katastrskih načrtov, letalskih posnetkov različnih starosti ter digitalnih ortofoto posnetkov.

V drugi raziskavi izhajamo iz naslednjih hipotez:

A) Med sekundarno sukcesijo se bistveno spremenijo ekološke in morfološke značilnosti celotne združbe. Le-te so v začetnih stadijih sukcesije odraz spremenjenih svetlobnih razmer na rastišču (z zaraščanjem je v zeliščnem sloju čedalje manj svetlobe), spremenjenih razmer v hidričnem režimu (gostejši je zastor, več vlage je v tleh zaradi zmanjšanega izhlapevanja iz zgornjih horizontov tal) in zaradi spremenjenih ekoloških razmer rastišča (ni disturbance, paše). V kasnejših fazah sukcesije pa so ekološke in morfološke spremembe vrst in združbe odraz predvsem spremenjenih edafskih značilnosti rastišča, spremenjenih ekoloških razmer združbe (spremenjene ekološke strategije posameznih vrst) ter pojavljanja vrst iz zaloge vrst (ang. *species pool*) v prostoru (semenska banka, naselitev vrst iz drugih lokacij).

B) Predpostavljamo, da je razvoj sukcesijskih stadijev v začetku najočitnejši, trajanje in formiranje posameznega stadija ali faze združbe pa najkrajša ravno na začetku (prvih nekaj let po opustitvi paše). Ker prav paša ohranja negozdne površine pred zaraščanjem, se po opustitvi le-te združba spremeni. Zgolj v nekaj letih negozdni sestoj naselijo prve grmovne in drevesne vrste, ki prej zaradi specifičnih ekoloških razmer na rastišču (stalne motnje) ne bi mogle uspevati. Predpostavljamo, da stadij *Pteridium−Frangula*, ki nasledi stadij *Calluna* traja na rastišču zgolj nekaj let. Tega nato nasledi stadij *Betula*. Tukaj se začne formirat sklenjen gozdni sestoj, hitrost premene vrst in spremembe ekoloških razmer ter floristične sestave združbe pa se upočasnijo. Po naši hipotezi traja formacija zadnjih dveh stadijev sekundarne sukcesije; stadija D, *Epimedium−Carpinus* in stadija E (*Carpinus−Quercus*) najdlje, ekološke razlike med obema stadijema in floristična sestava združbe pa so veliko manjši, kakor med prvimi stadiji (na primer med stadijem *Pteridium−Frangula* in *Betula).*

C) Med sekundarno sukcesijo se spreminja tudi vrstna sestava v posameznem stadiju združbe. Tako prevladujejo v sklenjenih pašnikih zeliščne vrste, prilagojene na močno osončenje ali insolacijo. V sklenjenem gozdnem sestoju (kasnejši stadiji sukcesije) travniške vrste zamenjajo senčne - skiofilne vrste, ki so tako ekološko kot tudi morfološko prilagojene novim razmeram (drugačne morfološke poteze, fenofaza, trajanje cvetenja, ekološka strategija).

D) Z zaraščanjem nekoč odprtih, pašnih površin se spremeni ekološka strategija vrst in zato tudi strategija celotne združbe. Izhajamo iz predpostavke, da bodo v prvih stadijih zaraščanja prisotne vrste z razvito življensko strategijo stres tolerator. V zadnjih stadijih zaraščanja pa bodo prevladovale vrste, pri katerih bo življenjska strategija temeljila na tekmovalnosti oz. kompeticiji.

E) Morfološko-ekološke spremembe vrst in celotne združbe so odraz dejanskih razmer na rastišču v posamezni fazi sekundarne sukcesije. Zato predpostavljamo, da funkcionalni rastlinski znaki vrst ter celotne združbe odražajo dejansko obdobje, od katerega je bila na določeni popisni ploskvi kmetijska dejavnost (pašništvo) prekinjena. Torej drugače: po naboru rastlinskih znakov in ekoloških značilnosti združbe bi lahko ugotovili, da znaša starost gozdnega sestoja 50 let.

1.3 DOLOČANJE STAROSTI SESTOJA S POMOČJO IZBRANIH FUNKCIONALNIH RASTLINSKIH ZNAKOV, EKOLOŠKIH ZNAČILNOSTI VRST TER EDAFSKIH ZNAČILNOSTI RASTIŠČA

Zadnja raziskava je vsebinsko povezana s prvima dvema raziskavama oz. s prvimi tremi objavljenimi znanstvenimi deli. Rdeča nit, ki povezuje omenjeni raziskavi z zadnjo, je spreminjanje krajinske zgradbe v povezavi s spreminjanjem ekoloških in morfoloških značilnosti združbe in rastlinskih vrst. V zadnji raziskavi smo ocenjevali spremembe območja s pomočjo izbranih rastlinskih znakov in ekoloških in edafskih značilnosti, ki nakazujejo nekdanjo rabo prostora. V raziskavi smo izdelali štiri modele iz skupine GAMM (ang. generalized additive mixed models), v katere smo vključili izbrane skupine funkcionalnih rastlinskih znakov, ekoloških značilnosti vrst (Ellenbergove bioindikatorske vrednosti), horotipov vrst in edafskih parametrov. Izračunali smo napovedno moč štirih generaliziranih aditivnih mešanih modelov (GAMM) za čas od opustitve kmetijske rabe, rezultate pa primerjali med seboj.

S to študijo smo želeli zaključiti celotno raziskavo spreminjanja krajinske zgradbe in pestrosti med sekundarno sukcesijo.

Raziskava predstavlja metodologijo za ocenjevanje starosti stadijev sekundarne sukcesije (torej oceno časa od opustitve kmetijske rabe prostora). Metodologija izhaja iz dejstva, da analize sprememb v vegetaciji temeljijo na spremembah vrstne pestrosti. Kljub temu pa se je ravno zaradi potrebe po ocenjevanju vpliva sprememb krajinske zgradbe na vegetacijo pojavila potreba po prepoznavanju funkcionalnih rastlinskih znakov in povezav le-teh s spremembami v krajini (Lavorel S. in Garnier E., 2002; Campetella in sod., 2011).

Raziskave, ki temeljijo na morfoloških, fizioloških, fenoloških ali ekoloških rastlinskih znakih, so omogočile vpogled v številne, do sedaj manj znane odnose med vrsto (osebkom) in okoljem ali odnose med vrstami. Analiza izbranih funkcionalnih značilnosti ali edafskih značilnosti rastišča omogoča pridobitev veliko bolj posplošenih rezultatov.

Odnos med merjenimi ekološkimi in morfološkimi značilnostmi vrst ali rastlinskih združb, opazovano premeno rastlinskih znakov in ekoloških značilnosti v obravnavanem časovnem obdobju lahko analiziramo s pomočjo linearne regresije. Prav metoda linearne regresije je ena najstarejših tehnik za izdelavo napovednih modelov. Razlog tega je enostavnost analize in izdelave prognostičnih modelov (Faraway, 2005; Wood, 2006). Čeprav je napovedna moč modelov, izdelanih s pomočjo linearne regresije največkrat precej velika, pa je uporaba takih napovednih modelov neprimerna, kadar razpolagamo s podatki, ki niso v linearnem odnosu (Wood, 2006).

Že Castro in sod. (2010) so v svoji študiji raziskovali premeno izbranih funkcionalnih rastlinskih znakov v odvisnosti od spremembe krajine v Montadu. Avtorji opozarjajo na problematiko izdelave modelov z nelinearnimi spremenljivkami. Na podoben problem opozarja tudi Wood (2006). Saatkamp in Römermann (2010) v svoji študiji raziskujeta odnos med funkcionalnimi rastlinskimi znaki in pašništvom. V študiji uporabljata generalizirane aditivne modele (GAM modele). Do danes so se podobne raziskave dotaknile največkrat zgolj na odnos med spreminjanjem opazovanih rastlinskih znakov ter spreminjanjem krajine v določenem časovnem obdobju.

Z našo raziskavo pa obravnavamo problematiko spreminjanja krajine in vegetacije iz drugega zornega kota. Zanima nas, ali lahko uporabimo funkcionalne rastlinske znake, horotipski spekter vrst, Ellenbergove bioindikatorske vrednosti ali edafske značilnosti kot vir informacij za čas od opustitve rabe tal (v nadaljevanju TLA- time since land use abandonment) v določenem stadiju sekundarne sukcesije.

V raziskavo smo vključili funkcionalne rastlinske znake, horotipe vrst, Ellenbergove bioindikatorske vrednosti in merjene edafske značilnosti popisnih ploskev ter opazovali njihovo spreminjanje med sekundarno sukcesijo v Beli krajini. Iz omenjenih skupin smo izdelali napovedne modele GAMM in jih testirali glede njihove napovedne moči za TLA.

V raziskavi smo želeli ugotoviti, v katerih izmed štirih izbranih skupin rastlinskih znakov je informacija o TLA najbolje »shranjena«. Še posebej nas je zanimalo, ali lahko razvijemo metodo, ki nam bo omogočala izračun TLA iz omenjenih skupin podatkov za določeno območje v Beli krajini.

Za samo ovrednotenje rezultatov smo potrebovali popisne ploskve, na katerih natanko poznamo čas od opustitve kmetijske rabe. Podatke smo pridobili s pomočjo prekrivanja starih katastrskih načrtov, vojaških kart, letalskih posnetkov in digitalnih ortofoto posnetkov.

Odločili smo se za izdelavo modelov iz skupine GAMM, saj nam le-ti omogočajo kombinirano vključevanje tako linearnih kot nelinearnih spremenljivk.

V tretji raziskavi izhajamo iz naslednjih hipotez:

A) Informacija o TLA, torej o starosti sestoja (stadiju sekundarne sukcesije), je shranjena bodisi v kombinaciji funkcionalnih rastlinskih znakov, horotipskem spektru vrst, Ellenbergovih bioindikatorskih vrednostih ali edafskih značilnostih rastišča.

B) Napovedne moči štirih modelov o TLA se med seboj razlikujejo.

2 ZNANSTVENA DELA

2.1 SPREMEMBE KRAJINE NA OBMOČJU BELOKRAJNSKEGA NIZKEGA KRASA V ZADNJIH 220 LETIH

Landscape transformation in the low karst plain of Bela krajina (SE Slovenia) over the last 220 years, Paušič A., Čarni A., Acta geographica Slovenica, 2012, 52, 1, 35−60.

Izvleček

Raziskava se ukvarja s spreminjanjem krajinske zgradbe na območju Bele krajine v zadnjih 220 letih.

Do leta 1913 je bila Bela krajina značilna kmetijska krajina. Po prvem emigracijskem valu (po koncu 1. svetovne vojne) se začne območje postopoma zaraščati z gozdom. Druga svetovna vojna je regiji prinesla številne spremembe: začel se je drugi val izseljevanja prebivalcev, spremenila pa se je tudi krajinska zgradba.

Zaradi intenzivnega opuščanja kmetijske rabe tal in zaraščanja kmetijskih zemljišč dobi Bela krajina značaj gozdnate krajine. Po letu 1960 se začne v Beli krajini tretji val izseljevanja prebivalstva. Leta 1980 raziskovano območje že popolnoma porašča gozd. Krajina postane gozdna. Po letu 1981 opazimo rahel porast prebivalstva, še posebej v naseljih ob glavnih prometnicah in v večjih naseljih. Ta trend pa ni imel vpliva na spremembo krajinske zgradbe.

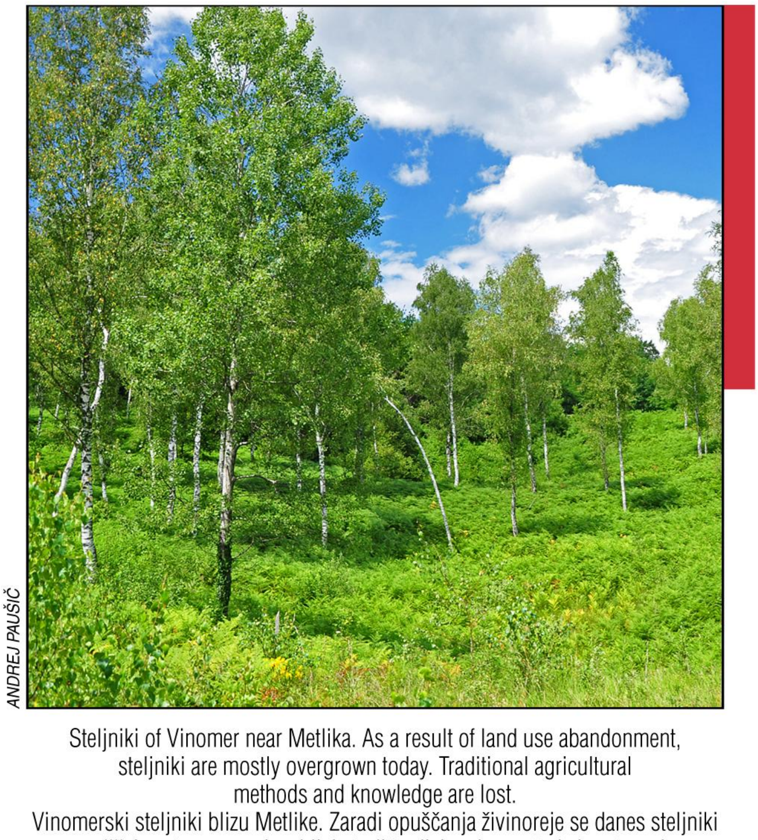
Današnja krajinska zgradba Bele krajine je precej drugačna kot v preteklosti in je odraz ekonomskih in socialnih sprememb v pokrajini.

Acta geographica Slovenica, 52-1, 2012, 35–60

LANDSCAPE TRANSFORMATION IN THE LOW KARST PLAIN OF BELA KRAJINA (SE SLOVENIA) OVER THE LAST 220 YEARS

SPREMEMBE KRAJINE NA OBMOČJU BELOKRAJNSKEGA NIZKEGA KRASA V ZADNJIH 220 LETIH

Andrej Paušič, Andraž Čarni



Steljniki of Vinomer near Metlika. As a result of land use abandonment, steljniki are mostly overgrown today. Traditional agricultural methods and knowledge are lost.
Vinomerski steljniki blizu Metlike. Zaradi opuščanja živinoreje se danes steljniki zaraščajo, s tem pa se izgubljajo tudi tradicionalne metode kmetovanja.

Landscape transformation in the low karst plain of Bela krajina (SE Slovenia) over the last 220 years

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UDC: 504.61:630*23(497.434Bela krajina)
COBISS: 1.01

ABSTRACT: The changes in land use, landscape structure and heterogeneity in Bela krajina were compared over a time interval of 220 years and linked to the socioeconomic factors. A significant increase of forested areas in the past 220 years is evident, which has led to forestation of open pastures. Until 1913, the landscape was agricultural. After human emigration at the beginning of the 20th century and World War I, the land was partly abandoned. During and after the World War II local inhabitants migrated from the region. The land structure changed and became of a transitional type. The third wave of emigration started in the 1960s. By around 1980, the study area had become completely forested. After 1981, the number of inhabitants again increased in settlements near traffic routes but people were employed in other economic activities. This trend had no significant impact on the landscape. The study shows that the present landscape structure is substantially different from those in past and reflects the current social and economic features.

KEYWORDS: geography, landscape heterogeneity, landscape structure, landscape change, afforestation, Slovenia, Bela krajina

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Contents

1 Introduction

Intensive clearing, burning and the formation of the open landscape of Bela krajina dates to time between the late prehistoric and medieval periods. Palynological research suggests that human impact was significant and contributed to increasing biodiversity (Andrič 2007b). The human impact on vegetation in Bela krajina was much stronger than in other parts of Slovenia (Andrič and Wallis 2003; Andrič 2007). This is an indication that the region was not unpopulated, as it has been in the recent period. Bela krajina became part of the Krain Region (nowadays an integral part of Slovenia) in the 15th century. In the 16th century, the so-called Vojna Krajna (War March) was formed in Croatia and Serbia, and Turkish incursions ceased to be a threat to the country. Areas of forest were already small at that time and were the property of feudal lords. After the first agrarian reform (beginning of 19th century), the local peasants were free from taxes and could posses their own land. As a consequence, the land was divided among the people (Kos 1991). The region thus experienced the gradual formation of a cultural landscape, which began to change intensively at the beginning of the 20^{th} century. This was a result of a period of migration of the local inhabitants away from 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 the delayed industrialisation in the 1960s, when the local inhabitants emigrated to larger industrial hubs (Orožen Adamič et al. 1995). During and after the emigration waves landscape vas abandoned and the process of afforestation was going on. As a consequence, the structure and heterogeneity had changed.

Many studies have been conducted in Europe that have attempted to understand and evaluate changes in landscape (Skanes and Bunce 1997; Aničić and Perica 2003; Eetvelde and Antrop 2004; Urbanc et al. 2004; Kaligarič et al. 2006; Schneeberg et al. 2006; Sirami et al. 2010; Persson et al. 2010; Tempesta 2010; Ignacio-Diaz et al. 2011, Paušič and Čarni 2012). These studies have also dealt with the landscape indicators that drive changes in land use and landscape structure and even determine the appearance of the landscape as a whole, therefore the spatial heterogeneity that indicates the variability of the system's properties in spatial terms (the landscape structure) (Calvo-Iglesias et al. 2006; Sirami et al. 2010).

In our study we investigated the landscape structure change and its indicators. We observed the following landscape characteristics (Farina 2001, 2007): a) the proportion of major land use (forest, meadows, pastures, fields, vineyards and urban areas); b) heterogeneity (homogenous space, heterogeneous fine-grained, heterogeneous coarse-grained, heterogeneous mixed; c) landscape type (agricultural, transitional or wooded and forested) (Anko 1982).

The main aims of this study were: (A) to determine (and evaluate) changes in the landscape in the area of SE Slovenia in the past 220 years, (B) to relate landscape changes to demographic changes and (C) to identify the rate of modification of the landscape during the process of population migration and abandonment of agricultural land use.

Additionally we were keen to answer the following sub-questions: (1) how important is sheep grazing (main grazers in study area) for the landscape structure and heterogeneity, what happens to the landscape structure if such disturbance is eliminated from the area?

The changing of the human population was also studied in detail. Our second (2) objective was to establish whether the changes of human population could be associated with increased land afforestation.

2 Methodology

2.1 Study area

The research took place in the south eastern part of Bela krajina, near Črnomelj. To the south and east Bela krajina is bordered by the Kolpa River, to the north by the slopes of the Gorjanci mountain range, and to the west by the Poljanska Gora and Kočevski Rog mountain ranges. From the Bela krajina plain (190–220 m), the surface rises to Slovenia's high Dinaric karst in the northwest of Bela krajina between the Kočevski Rog and Gorjanci mountain ranges (Gams et al. 2011). Northeastern part of Bela krajina consist of the peaks (576 and 626 meters above sea level), the upper edge of the vineyard belt is around

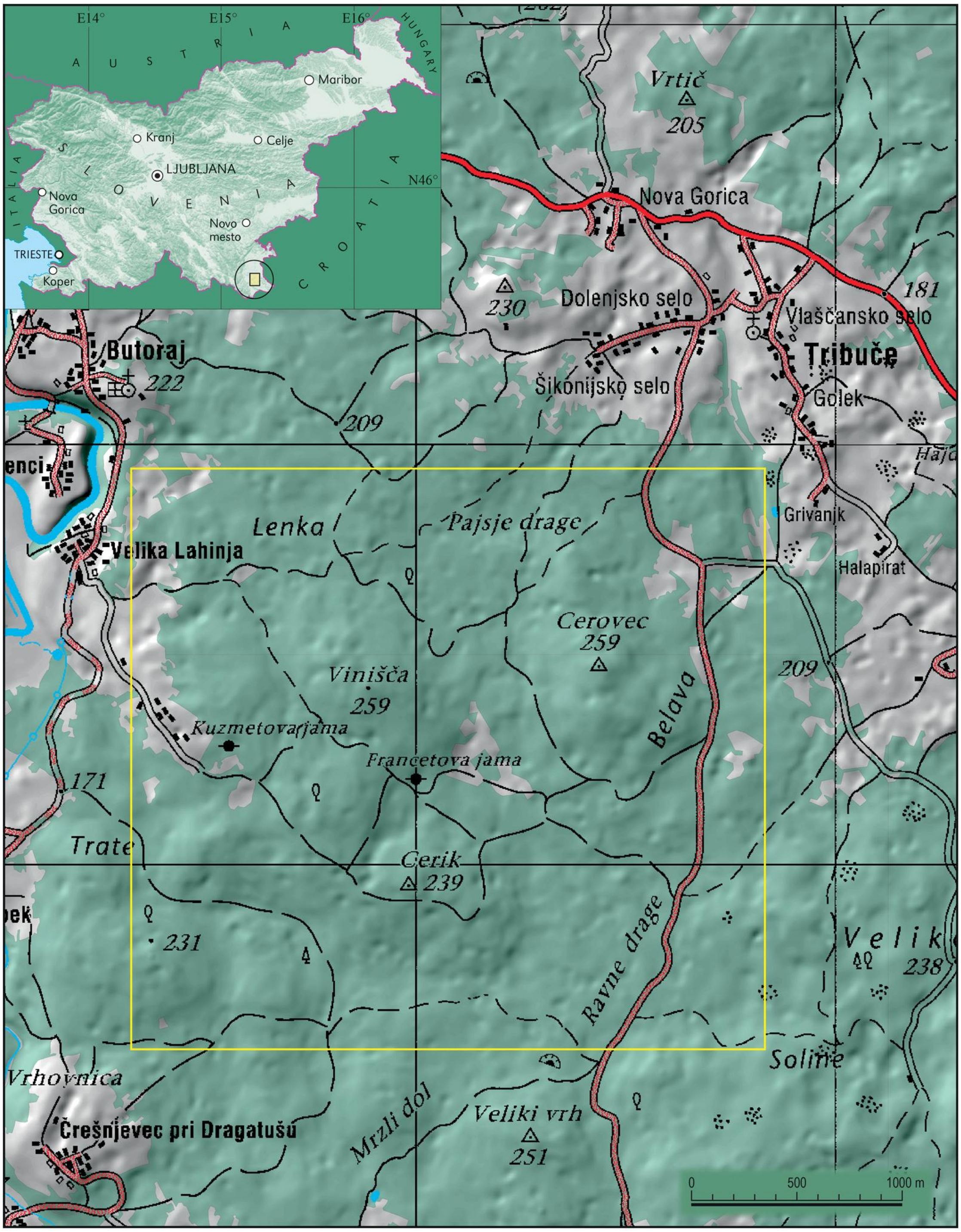


Figure 1: Study area in SE Slovenia.

400 meters, and the transition to the Črnomelj plain at the lower edge of the slope lies at an altitude of around 220 meters.

The study area is located on 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 ranges between 900 and 1200 mm and mean annual air temperature is 10.2°C (Internet). The potential natural vegetation of the area is *Quercus-Carpinus* forest (Čarni et al. 2007).

An area of 1000 ha was selected for the research (45.514535°–45.539406°N and 15.209397°–15.246939°E) (Figure 1), with an altitude between 160 and 420 metres and fairly homogeneous in terms of geomorphology and climate.

2.2 Data sources – historical land-cover data

The first information about land use that can be geo-referenced is from Josephine military maps (1 : 28.000), which were prepared for military purposes at the end of the 18th century (1784–1790) (Rajšp and Ficko 1996; Rajšp et al. 1997) and were used as the information layer for 1790.

Another reliable source of information is the Franciscan land cadastre (1 : 1440 and 1 : 2880), which provides exact information about land use in 1823 (Petek and Urbanc 2004).

A military map (1 : 75.000; Militärgeographisches Institut 1913) was used for 1913, from which we obtained information about detailed land use in the study area.

In year 1918, a new state, the Kingdom of Yugoslavia, was established, which invested considerable resources in the southern parts of the country. For the territory of Slovenia only a special military map (1 : 25.000) from 1937 (V.G.I. 1937) exists.

From 1954 on, cyclic aerial photos of the land exist and were used as information layers (1954, 1975, 1986, 1999 and 2009). They were provided by the Surveying and mapping authority of the Republic of Slovenia (GURS 2009).

Since not all data were available for each time sequence for the same area, we decided to include an L-shaped study area, which covers the data of all layers.

2.3 Analysis of land-cover data

Land cover data were digitalized and geo referenced using ArcInfo 9.2 programme (ESRI 2008). Digitalised military map and cadastral maps (1790 and 1823), digitalised topographic maps (1913 and 1937) and aerial photos (1954, 1975, 1986, 1990, 2009) provided a relatively good insight into the dynamics of changes that have taken place in the study region. The Josephine military map (1 : 28.000) provides just an approximation of the real land use of that time since the map is rather imprecise. Another problem these map has is the determination of land use types (eg. pasture – meadow, meadow – field) since those categories were not clearly marked.

Franciscan land cadastre (1 : 1440 and 1 : 2880) on the other hand is reliable and accurate material to use. The land use types are well described and marked with the parcel number in the descriptive part of the cadastre.

The material from younger age (after 1823), used for the study, is accurate enough to distinguish the basic land use categories and to fulfil the precise study.

Data on the rate of spontaneous afforestation are of considerable importance in terms of the dynamics of landscape transformation and also provide an insight into the fundamental rules of interrelation and transition between individual land use categories (forest, field, meadow, pasture). It can be therefore determined which of these categories have been subject to change, which of them have expanded the most and how the landscape structure used to appear (and also enable a presentation of the results).

We analysed the appearance of forest areas, pastures, meadows, fields, vineyards and urban areas in the above-mentioned time interval and transformations of one land use into another. We selected for that purpose 200 equidistant plots, at the distance of 150 meters within the study area. The plots were located in different land use types. Information about the land use dynamics and afforestation was extracted by overlaying old cadastral maps, military maps and digital orthophotos.

In the next stage a diagram of landscape structure transformation was prepared along with a matrix for transformations of individual land use during selected time periods. The matrix facilitates understanding of the processes taking place during the observed periods and provides information on the conservation status of an individual land use (Reger et al. 2007).

Based on the information obtained through all the analyses performed, a diagram of landscape structure transformation was prepared.

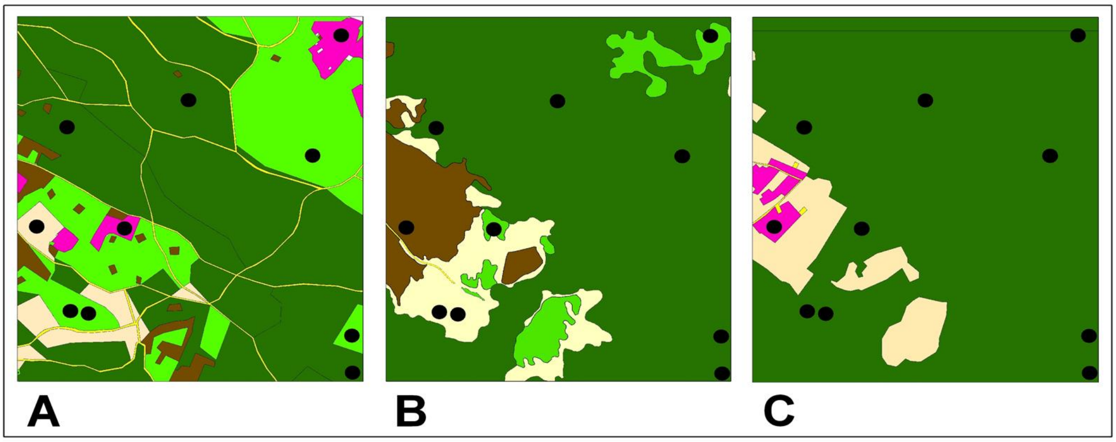


Figure 2: Landscape fragmentation of the studied area. In situation A (1823), there are 9 polygon groups (the randomised point fell in nine different plots). In situation B (1954) 5 groups appear. In situation C (2009) there are just two groups (attrition process).

2.4 Human population data; data on sheep number

Changes in the number of inhabitants and the number of sheep in the study area are indicators that facilitate better understanding of landscape transformations. Spontaneous afforestation is often described as a delayed phenomenon that follows population migration (Scozzafava et al. 2004). The total sheep number provides good information about land use. This, in turn, has an influence on the landscape mosaic pattern (Lang and Blaschke 2007).

Data on the number of inhabitants was collected from available sources provided by SURS (2012) (Internet) and Šifrer (1969). We obtained data on the number of sheep for 1823 (Franciscan land cadastre for Kranjska 1823–1869), 1913 and 1931 (Local Lexicon of the Drava Banovina 1937), 1971, 1981, 1991, 2002 (SURS 2012).

Data on the number of inhabitants and the number of sheep were collected for four villages in the close vicinity of the study area (Tribuče, Butoraj, Dragatuš and Bojanci) and the result obtained was presented as the sum of these values.

2.5 Analysis of the landscape fragmentation process

We set 300 randomized points in our study area and extracted the land use type for them for selected years (1790, 1823, 1913, 1954, 1986 and 2009). A table (Table 1) was prepared from the results, that shows (1) the mean surface (ha) of the land use category within which the points lie and (2) the number of (all) points, that lie in the same land use surface (same patch!). Two points that lie in the same land use area (polygon) but were separated in a previous time set therefore indicate the rate and manner of the landscape defragmentation process (Figure 2).

According to Anko (1982) and Pirnat (2000), a forested landscape is a landscape in which the proportion of forest exceeds 85% of the total surface area (interior area of the forest matrix) and a transitional landscape means a landscape in which the proportion of forest ranges between 40 and 85%. Forest cover in an agricultural landscape is 20–39% in the impact area (interior area of agricultural and urban areas).

Heterogeneity of a landscape structure implies that landscape elements are distributed unevenly and non-randomly (Farina 2007). It is described by the size (and combination) of individual landscape elements in a mosaic. The optimum is a coarse-grained landscape structure (Lang and Blaschke 2007; Ahlqvist and Shortridge 2010) that includes some fine-grained areas. Such a structure should provide a habitat for the existence of species associated with interior as well as edge areas (Farina 2007). We distinguish between a) an entirely homogeneous environment, b) a homogeneous environment with a small proportion of other land use types (between 1 and 5%), c) larger grains, d) finer grains and e) shape combinations (Lang and Blaschke 2007).

3 Results and Discussion

By overlaying various cadastral maps and recent aerial orthophotos, we obtained information on how the landscape changed between 1790 and 2009 (Figure 3), as proportions of different land-use categories. The changes in human population and in the number of sheep between 1823 and 2002 in study area in Bela krajina are represented in Figure 4.

The diagram describing the changes in proportions (%) of land use types in Bela krajina between 1790 and 2009 (Figure 5). It gives an insight into the dynamics of land structure change, since it clearly demonstrates the fast transformation of the landscape structure (by the changing proportion of observed land categories). On the basis of transformation of an individual land use type to another during the elaborated period, the process of landscape change can be divided into three segments:

- A characteristic of the period between 1790 and 1913 is that land use remained the same. More than 80 % of land was thus used in the same way during the period (with the exception of arable land, which became subject to spontaneous afforestation in 1913).
- The period between 1913 and 1954 was characterised by transformation of most categories into forest area.
- After 1954 there was an intensive trend toward afforestation of all observed land categories (the land-use conversion rate to forest was 60% or more of all observed areas).

3.1 Landscape structure between 1790 and 1913

In 1790, the study region had the characteristics of an agricultural landscape. The prevalent land-use type was pasture, indicating that sheep grazing was an important economic activity at that time. Forested areas were scarce and did not exceed a third of the study area. At that time, the area of forest had been reduced to its minimum extent.

The next periods for which information is available are 1823 and 1913. The total area of pastures was already declining in 1823 (and even more in 1913), while the total arable area was increasing. The total area of vineyards was below 2% of the whole area. It is evident that the landscape structure in this period remained more or less stable.

In this period, the landscape was an agricultural one, with extremely few urban areas (Figure 3). There were more urban settlements (grouped villages and villages along roads) in the westernmost part. The structure of the landscape mosaic was characterised by a combination of finer grains in the west and a homogeneous, coarse-grained structure in the east (Figure 3). Generally, small forest patches prevailed. There were no hedgerows or non-forest patches in the forested areas. The common straight forest edge was either un-fragmented or little fragmented. Based on the landscape matrix analysis, it can be said that it was a typical agricultural landscape type.

3.2 Period between 1913 and 1954

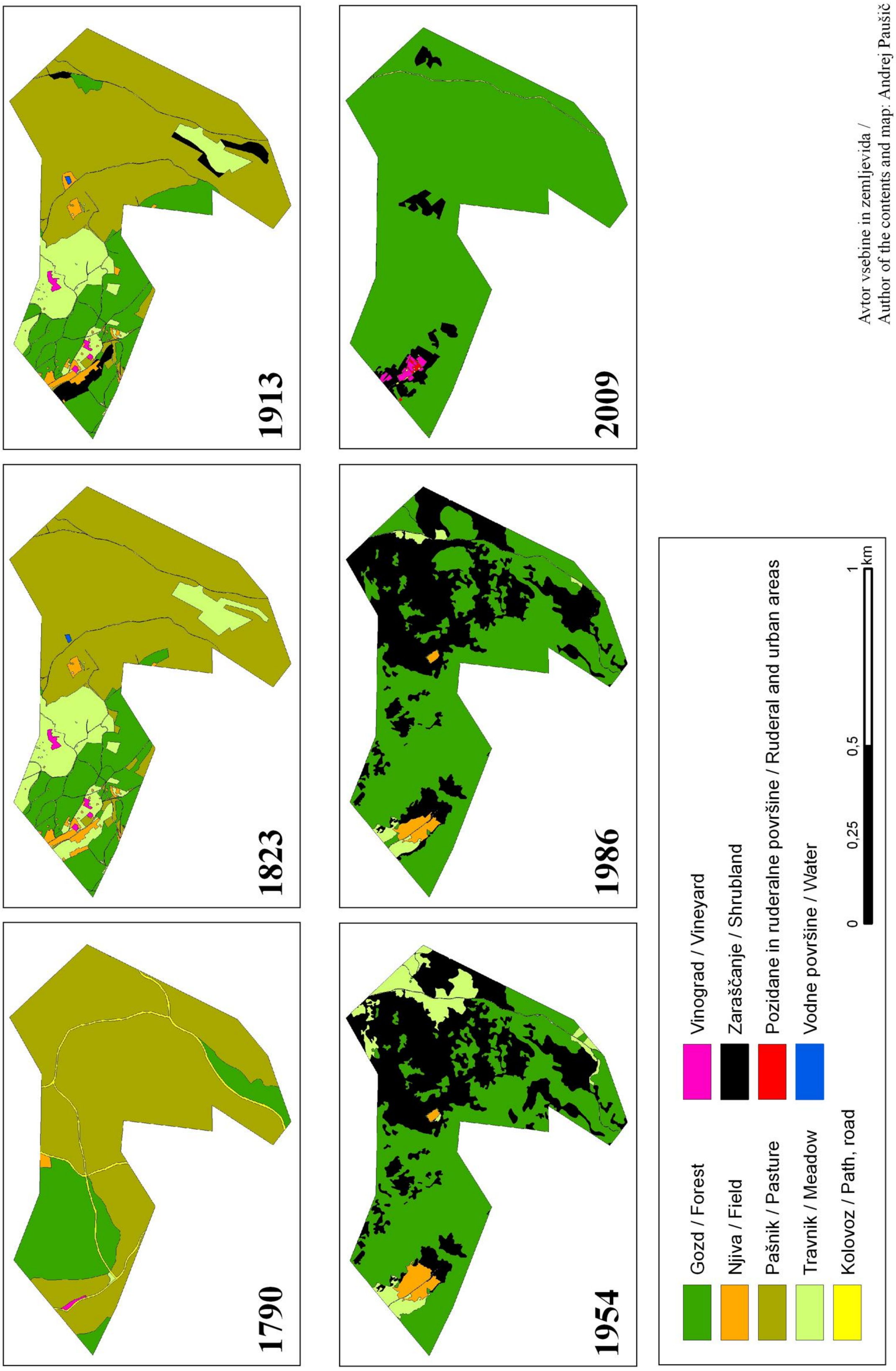
In 1913, forests already formed around one third of the total study area. The area of pasture had declined and was subject to afforestation (total scrubland had already doubled in extent). In 1954, however, the proportion of forest had risen to more than half of the total area. The proportion of arable land was almost the same as in 1937.

In that period, landscape heterogeneity in Bela krajina was at its peak. In year 1954 it is evident that the surface of forest patches increases already.

Figure 3 and figure 5 show the land transformation dynamics. It is evident that forest areas (unlike other land use categories) increased on account of pastures, that were rapidly becoming overgrown, which is why the proportion of forest had increased to such an extent (similar to other regions in Europe) (Poldini 1989; Antrop 2004; Morgan and Gergel 2010).

An important factor affecting the appearance and structure of the landscape in this period was World War II. During this period, there was a considerable increase in population emigration from the region

Figure 3: Sequence of digitalised cadastral maps and aerial photos (for 1790, 1823, 1913, 1954, 1986 and 2009). ➤



Avtor vsebine in zemljevida /
Author of the contents and map: Andrej Paušič

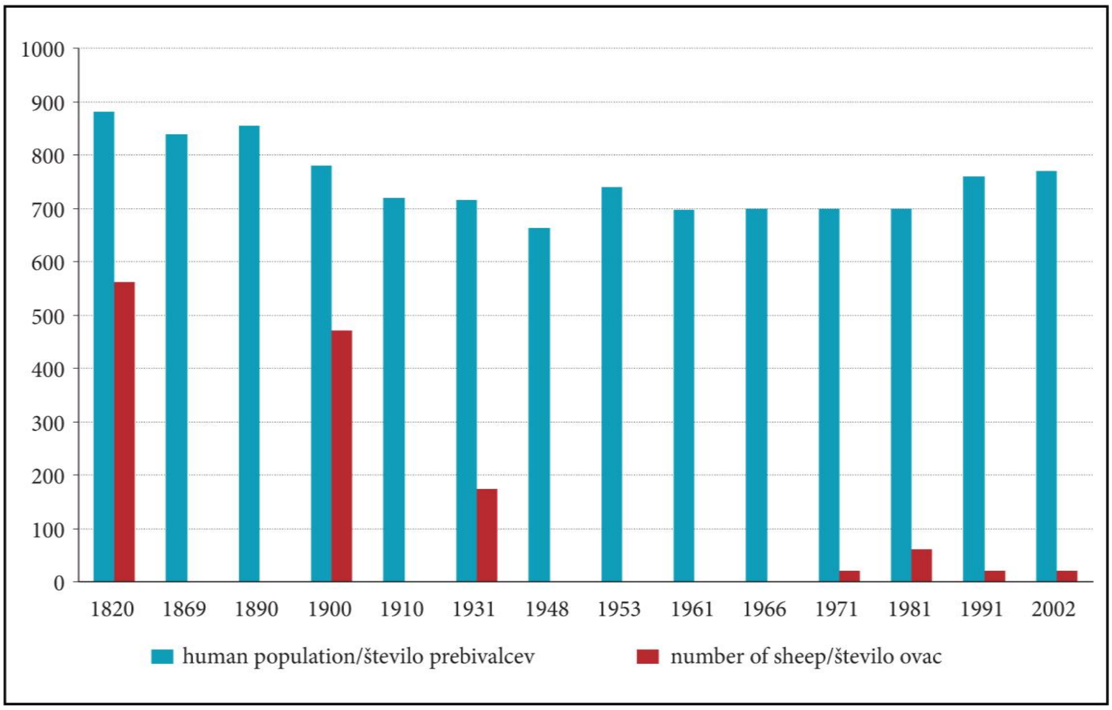


Figure 4: Changes in human population and in the number of sheep (data available for 1820, 1900, 1931, 1971, 1981, 1991 and 2002) between 1823 and 2002 in study area in Bela krajina.

of Bela krajina (the number of inhabitants was lowest in 1948), with some 60% of the area being afforested (Figure 4).

With a proportion of forest of 27,5 % in 1937, it can be described as a transitional landscape type. A heterogeneous landscape structure prevailed, sporadically larger grains and a homogeneous combination of larger and finer grains in the SE part of the region. Forest patches were common and mostly medium in size. There were frequent non-forest patches (meadows or pastures within the forest). A rounded and fragmented forest edge prevailed. The landscape structure in 1954 was transitional. In the central part, a transitional landscape can be seen, while in the east, a mosaic of grazing areas and meadows under spontaneous afforestation formed a characteristic transitional landscape (Figure 3).

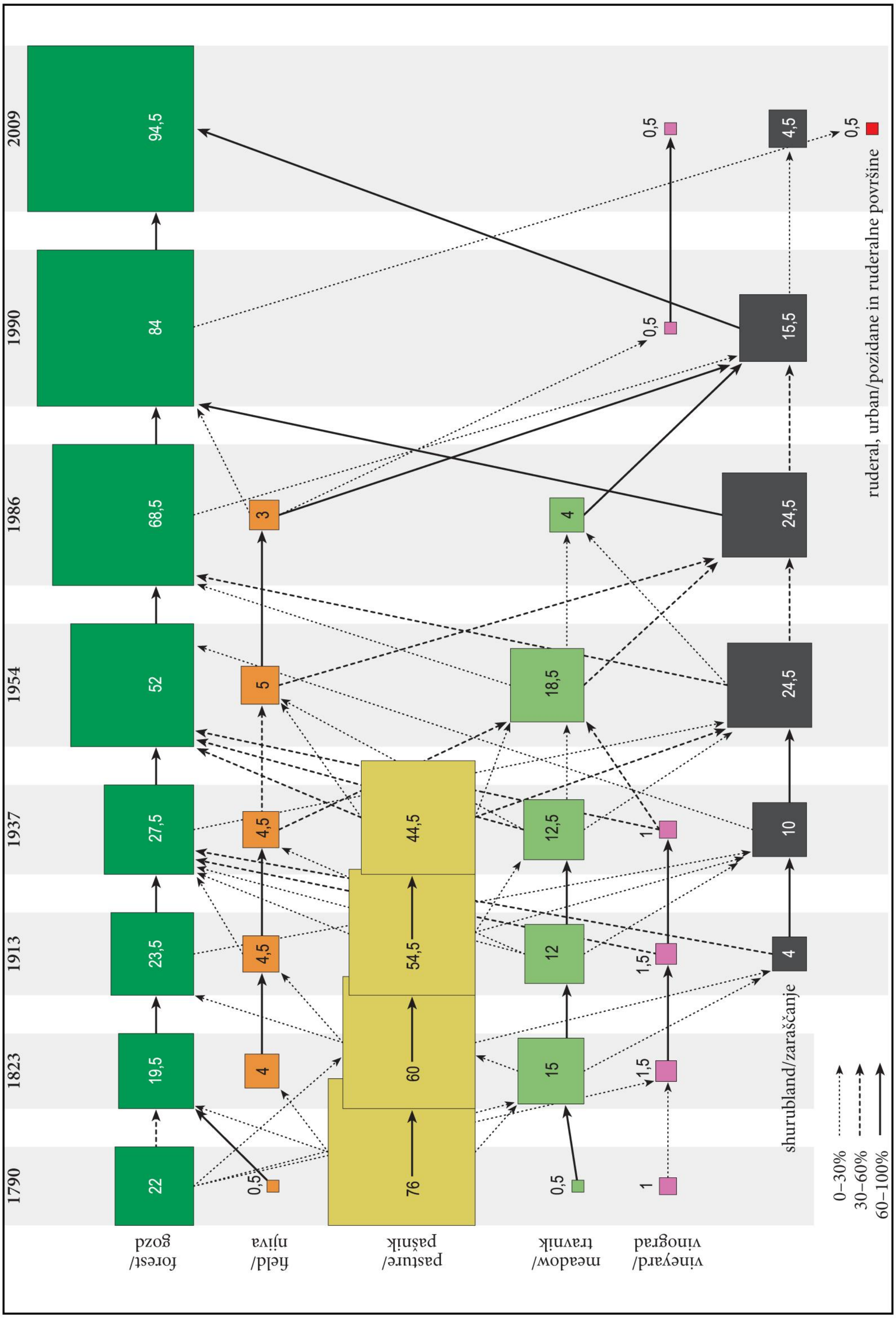
3.3 Landscape structure from 1954 to the present (2009)

In the most recent period, one third of the entire area being scrubland (in 1986). Fields, pastures and meadows have a very limited extent and have not existed in the study area since 1986 (since the landscape have even more abandoned). In comparison with the two previously described periods, this is a time in which the landscape lost its diversity (Topole et al. 2006).

By 1990, forest already covered 84 % of the area and 15.5 % was subject to spontaneous afforestation. Consequently, after 1990, the region features only 3 land use categories (out of 6 in 1937), which once again indicates the downward trend in the structural diversity of the landscape.

The studied region is currently (2009) dominated by a characteristic forested landscape type (with forest cover over 90%). Only the westernmost part of the region, near the village of Dragatuš, features an agricultural landscape. The characteristic structure is homogeneous, with a combination of finer and medium grains only in the west; there are few non-forest patches (pastures under spontaneous afforestation),

Figure 5: Changing landscape structure in Bela krajina (Slovenia) between 1790 and 2009. The diagram shows the observed land-use categories with added proportions of the area covered (%) and the conversion trend for individual categories during the observed time periods. ➤


1790
1823
1913
1937
1954
1986
1990
2009
forest/
gozd
field/
njiva
pasture/
pašnik
meadow/
travnik
vineyard/
vinograd
shurubland/zaraščanje
ruderal, urban/pozidane in ruderalne površine
0–30%
30–60%
60–100%

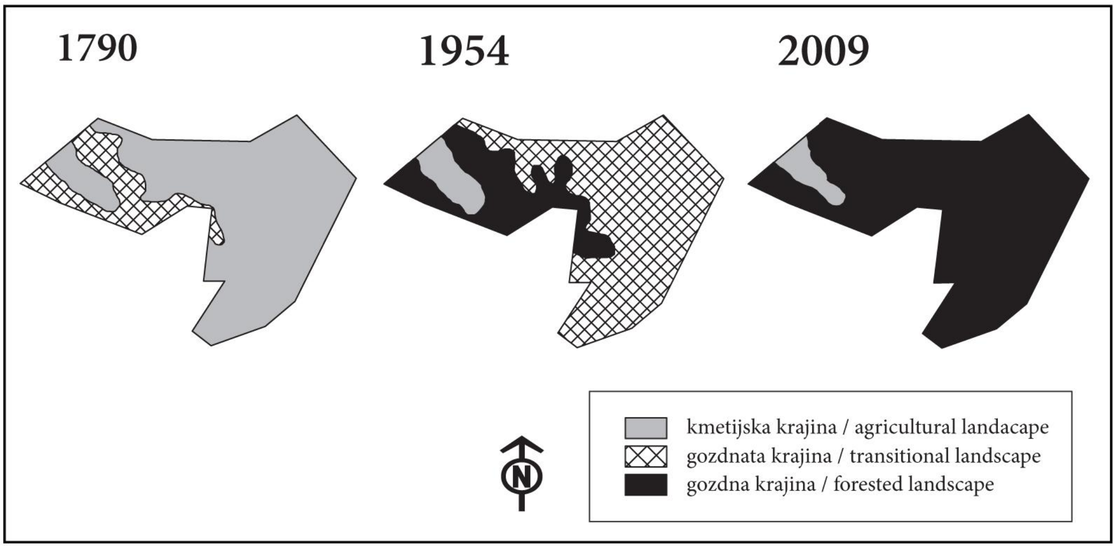


Figure 6: Changing landscape structure in Bela krajina in the period between 1790 and 2009. Presented are comparisons of the landscape structure in 1790, 1954 and 2009.

no hedgerows but a fairly homogeneous landscape structure. The proportion of basic land use categories (Figure 5) is small (only 4 categories), a notable impoverishment of landscape structure diversity.

Even though the number of inhabitants in the analyzed region has not changed very much from year 1900 on (Figure 4), despite the described demographic changes, the population is no longer as strongly agriculture or forestry-dependant as in the past. Most of the inhabitants today are employed in the tertiary economic sector in larger settlements (Črnomelj) or are engaged in supplementary activities (farm tourism, organic food and sheep production) that do not affect the structure and appearance of the landscape to the extent that traditional management did. This situation resulted in quick afforestation process and even more abandoned land.

3.4 Landscape fragmentation process

The mean patch size measured in year 1790 was 40.44 ha (Table 1) and there were 24 different land use parcels, where the randomised points lie. In 1823, the number of parcels rose to 170 and the mean patch size measured 2,287 ha. In 1954, we counted 197 point groups (parcels), the mean patch size measured just 0,238ha. Due to the attrition process (Forman 2006), in 2009 just 37 different parcels included all our randomized points. The mean patch size measured 43,873 ha.

The method used is represented in Figure 2, on an example of the part of study area. The observation and counting of randomized points in a changing landscape with the regard to patch size seems an efficient method for observation of the landscape fragmentation process.

Table 1: Landscape fragmentation process between 1790 and 2009.

Time interval	1790	1823	1913	1954	1986	2009
Number of points that coincide with the same patch	24	170	181	197	162	37
Mean patch size (ha)	40.44	2.287	1.782	0.238	5.321	43.873

Sheep grazing used to have a significant role in the appearance and structure of the landscape (Nagashima et al. 2002; Thomson and Simpson 2005; Wehn 2008; Carmona et al. 2010; Pipenbaher et al. 2011). We tried to link the decreasing number of sheep, the main grazers in the past (Local Lexicon of the Drava Banovina 1937) in the study area, (the villages of Bojanci, Butoraj, Dragatuš and Trubuče) with changes in the landscape structure.

We found a significant correlation between the decrease in the number of sheep and spontaneous afforestation (Figure 4, figure 5). The highest number of sheep in the region was in 1820 (562 animals). In 1931, the number had plummeted to 173. The trend continued until 1990, when the number was 20. In 2002, there were only 21 animals left. Grazing activity therefore used to have a key role in maintaining the landscape structure (Poldini and Feoli 2006; Morgan and Gergel 2010). After grazing was abandoned and spontaneous afforestation took place, this in turn changed the appearance of the landscape and its structure.

Our study has shown that the studied region in Bela krajina used to be an agricultural (partly also transitional), fairly evenly heterogeneous, medium-grained landscape (Figure 3), the structure of which became subject to rapid change. Although these changes were only minor in the first observed periods (1790, 1823, 1913), by 1913 this region was already considerably transformed. Today, this is a homogeneous forested landscape with large patches.

4 Conclusion

Similar studies conducted in Europe (Antrop 2004; Bender et al. 2005; Reger et al. 2007; Linden et al. 2008), show a similar pattern in the afforestation of abandoned agricultural regions. These studies also highlight the change in the demographic structure, reflected in land use practices, as the reason for the change in the landscape structure and demonstrate a similar pattern of change in the landscape structure through the observed period of time.

Our results show an extremely dramatic change in the landscape structure around 1954. Spontaneous afforestation of the landscape after WWII was faster than in other European regions (Čarni et al. 1998; Linden et al. 2008; Garcia-Feced et al. 2011). Our results also not only indicate the significance of human interventions in the appearance of the traditional landscape in Europe but also signal the threat to these landscapes by a changed land use regime.

Numerous studies have explored the afforestation of post-agricultural landscapes (Skanes and Bunce 1997; Čarni et al. 1998; Seabrook et al. 2006; Linden et al., 2008; Zomeni et al. 2008) but rarely cover

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Figure 7: Silver Birch (*Betula pendula*) is a characteristic species occurring in the early stage of forestation.

Figure 8: Two sessile oaks (*Quercus petraea*) near the village of Tribuče with well developed lateral branches indicate the landscape was open (pasture) 10 years ago.

Figure 9: A vineyard in Vinišča in Bela krajina that was abandoned 40 years ago.

the long time span available in the area of Bela krajina. This is primarily due to the lack of reliable and comparable data on the spatial patterns of land-cover types in other regions. This study provides an insight into changes in land cover over a period of more than two centuries.

In terms of the preservation of landscape diversity (if landscape is considered to be a system of ecosystems with individual structures, functioning and changes (Farina 2001; Garcia-Feced et al. 2011), we can confirm impoverishment at the landscape structural level as well as at the level of impoverishment of landscape elements (forests, hedges, hedgerows, meadow and pasture complexes).

Landscape evaluation based on landscape heterogeneity and structure is considered sufficient for a general evaluation of biodiversity at the landscape level.

With severely decreasing ecosystem (ecotope) diversity in recent years, it is again possible to speak of landscape impoverishment or fast change of an agrarian and transitional landscape into a forested one (Bela krajina). The present homogeneous forested landscape of Bela krajina is certainly very different as the diverse landscape structure from the period before 1954.

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Spremembe krajine na območju belokrajnskega nizkega krasa v zadnjih 220 letih

DOI: 10.3986/AGS52102
UDK: 504.61:630*23(497.434Bela krajina)
COBISS: 1.01

IZVLEČEK: Raziskava se ukvarja s spreminjanjem krajinske zgradbe na območju Bele krajine v zadnjih 220 letih. Do leta 1913 je bila Bela krajina značilna kmetijska krajina. Po prvem emigracijskem valu (po koncu 1. svetovne vojne) se začne območje postopoma zaraščati z gozdom. Druga svetovna vojna je regiji prinesla številne spremembe: začel se je drugi val izseljevanja prebivalcev, spremenila pa se je tudi krajinska zgradba. Zaradi intenzivnega opuščanja kmetijske rabe in zaraščanja kmetijskih zemljišč dobi Bela krajina značaj gozdnate krajine. Po letu 1960 se začne v Beli krajini tretji val izseljevanja prebivalstva. Leta 1980 raziskovano območje že popolnoma porašča gozd. Krajina postane gozdna. Po letu 1981 opazimo rahel porast prebivalstva, še posebej v naseljih ob glavnih prometnicah in v večjih naseljih. Ta trend pa ni imel vpliva na spremembo krajinske zgradbe. Današnja krajinska zgradba Bele krajine je precej drugačna kot v preteklosti in je odraz ekonomskih in socialnih sprememb v pokrajini.

KLJUČNE BESEDE: geografija, krajinska heterogenost, krajinska zgradba, spreminjanje krajine, zaraščanje, Slovenija, Bela krajina

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Vsebina

1 Uvod

Človeški posegi v prostor (požigalništvo, sečnja gozdov in oblikovanje odprte krajine) so v Beli krajini opazni že v času med prazgodovino in srednjim vekom. Palinološke raziskave opozarjajo na vpliv človeka v tistem času, tako na prostor kakor tudi na dvig biodiverzitete (Andrič 2007b). Človek je s svojim delovanjem v preteklosti v Beli krajini spreminjal gozd veliko bolj, kot v drugih delih Slovenije, zato so bile tudi spremembe pokrajine (kot posledica človekovega delovanja) v Beli krajini največje (Andrič in Wallis 2003; Andrič 2007). To je tudi dokaz, da regija od prazgodovine do srednjega veka ni bila nikoli neposeljena.

Bela krajina postane del Kranjske vojvodine v 15. stoletju, v 16. stoletju pa jo ogrožajo turški vpadi. Površina gozdnih območij je bila v tem času majhna in last plemiških družin. Po prvi kmetijski reformi konec 18. stol. dobi takrat svoboden belokranjski kmet pravico nakupa lastne posesti, od katere še zmerom plačuje dajatve plemstvu. Iz tega obdobja je opazna večja razdrobljenost nekoč homogene kmetijske posesti (Kos 1991).

Zato se širše območje Bele krajine oblikuje v mozaično krajino, v začetku 20. stoletja pa prične intenzivnost obdelave zemljišč naglo upadati.

Poglavitni vzrok za opuščanje obdelave zemljišč v Beli krajini v 20. stoletju je izseljevanje prebivalcev. Potrebno je omeniti tri pomembnejša obdobja izseljevanja. Najprej v začetku 20. stol. (pred prvo svetovno vojno), ko se prebivalstvo izseli v države zahodne Evrope ter v obe Ameriki. Temu valu izseljevanja je med 2. svetovno vojno sledil drugi val. V 60. letih pa omenjamo še tretji val izseljevanja prebivalstva, ki je posledica zakasnele industrializacije, ko se lokalno prebivalstvo preseli v večja industrijska središča (Orožen Adamič in ostali 1995).

Zato se je pokrajina med in po obdobjih izseljevanja postopno zaraščala zaradi prenehanja kmetijske obdelave zemljišč, s tem pa se je spremenila tudi krajinska zgradba in raznolikost.

Številne raziskave v evropskem prostoru opisujejo spremembe pokrajin v času opuščanja kmetijske rabe v odvisnosti od izseljevanja prebivalstva (Skanes in Bunce 1997; Aničić in Perica 2003; Eetvelde in Antrop 2004; Urbanc in ostali 2004; Kaligarič in ostali 2006; Schneeberg in ostali 2006; Sirami in ostali 2010; Persson in ostali 2010; Tempesta 2010; Ignacio-Diaz in ostali 2011; Paušič in Čarni 2012). Omenjene študije analizirajo dejavnike, ki določajo izrabo prostora ter izgled pokrajine kot celote, torej krajinske zgradbe (Calvo-Iglesias in ostali 2006; Sirami in ostali 2010).

Naša raziskava preučuje spreminjanje krajinske zgradbe, heterogenosti in strukture skozi izbrano časovno obdobje. Obravnavali smo spremembo naslednjih značilnosti pokrajine (Farina 2001; 2007):

- spreminjanje deleža obdelovanih in nekmetijskih površin v obravnavanem obdobju (gozd, travnik, pašnik, njiva, vinograd in poseljena območja);
- spreminjanje heterogenosti v pokrajini (homogen prostor, heterogen drobno deljen; heterogen z večjimi zaplatami; heterogen mešan), spreminjanje krajinskih tipov skozi opazovano časovno obdobje (kmetijska ali agrarna, gozdnata in gozdna krajina) (Anko 1982).

Raziskava je imela naslednje cilje:

- določiti (in ovrednotiti) prostorske spremembe v Beli krajini v zadnjih 220 letih, ki so posledica demografskih sprememb,
- povezati spremembe krajinske zgradbe z demografskimi spremembami in
- ugotoviti raven sprememb v pokrajini med procesom emigracije lokalnega prebivalstva ter opuščanja kmetijske dejavnosti.

Dodatno so nas zanimali odgovori na naslednja vprašanja:

- Kako vpliva pašništvo (ovčereja) na spreminjanje krajinske zgradbe in krajinske heterogenosti, oz. kakšen vpliv ima opustitev pašništva na krajinsko zgradbo in strukturo.

Raziskali smo nihanje števila prebivalstva na raziskanem območju in želeli ugotoviti

- ali obstaja povezava med nihanjem števila prebivalstva in stopnjo gozdnatosti pokrajine.

2 Metodologija

2.1 Območje raziskav

Raziskava je potekala v Beli krajini, jugovzhodno od mesta Črnomelj. Proti jugu razdvaja Belo krajino od Hrvaške reka Kolpa, na severu južna pobočja Gorjancev in na zahodu Kočevski Rog s Poljansko Goro.

Pokrajina je odprta prozi vzhodu in jugovzhodu. Belokrajnski ravnik je s svojo povprečno nadmorsko višino med 190 in 220 metri najzahodnejši del nizkega krasa (Gams in ostali 2011) v zaledju Karlovca. Proti severovzhodu Bela krajina polagoma prehaja v gričevnat svet z vrhovi do 626 metrov. Zgornji višinski pas gojenja vinske trte dosega tukaj 400 metrov (Gams in ostali 2011).

Območje raziskav se nahaja na kraškem ravniku, katerega grade večinoma karbonatne kamnine, apnenci in dolomiti. Na površju omenjene kamnine preperevajo v kromičen kambisol in luvisol, ki velikokrat popolnoma prekrivata matično podlago.

Povprečna letna količina padavin v Beli krajini znaša med 900 in 1200 mm, povprečna letna temperatura zraka pa znaša 10.2 °C (Internet). Potencialna vegetacija območja je gozd hrasta in gradna (Čarni in ostali 2007).

Za območje raziskav smo izbrali 1000 ha velik predel med Bojanci, Tribučami, Dragatušem in Butorajem (45.514535°–45.539406° N in 15.209397°–15.246939° E) (slika 1), kjer znaša povprečna nadmorska višina terena med 160 in 420 m. n. v.

Slika 1: Območje raziskav v Beli krajini.
Glej angleški del prispevka.

2.2 Viri podatkov – prostorski podatki

Jožefinska vojaška karta (1 : 28.000), izdelana za vojaške namene konec 18. stoletja (1784–1790) (Rajšp in Ficko 1996; Rajšp in ostali 1997) je služila kot vir prostorskih podatkov za leto 1790. Naslednjo informacijo smo pridobili iz Franciscejskega katastra (1 : 1440, 1 : 2880), ki je dober vir podatkov o krajinski zgradbi, heterogenosti in izrabi tal za leto 1823 (Petek in Urbanc 2004). Vojaška karta (1 : 75.000; Militärgeographisches Institut, 1913) pokriva območje Bele krajine za leto 1913.

Leta 1918 pride do formiranja Jugoslavije, ki je vlagala veliko truda v izdelavo specialnih kart in načrtov, Belo krajino pa zajema posebna vojaška karta (1 : 25.000) iz leta 1937 (V.G.I. 1937).

Od leta 1954 do danes uporabljamo posnetke cikličnih letalskih snemanj slovenskega ozemlja. Letalski posnetki kakor tudi digitalizirani ortofoto (DOF) posnetki so dober vir informacij o izrabi tal in krajinski zgradbi. V raziskavo smo vključili letalske posnetke in DOF-e iz let 1954, 1975, 1986, 1999 in 2009 (GURS 2009).

Kljub temu pa prostorski viri iz omenjenih obdobij ne zajemajo celotnega območja Bele krajine. Zato smo se odločili za območje raziskave v obliki črke L, za katero so zbrani prostorski podatki iz vseh navedenih obdobij.

2.3 Analiza in obdelava prostorskih podatkov

Katastrske načrte, vojaške karte in letalske posnetke smo digitalizirali in georeferencirali s programskim paketom *ArcInfo 9.2* (ESRI 2008). Omenjeni prostorski viri so dali dober vpogled v dinamiko sprememb krajinske heterogenosti in zgradbe med leti 1790 in 2009.

Jožefinski katastrski načrt (1 : 28.000) je po sami izdelavi kakor tudi obsegu razpoložljivih prostorskih informacij precej nenatančen, zato je tudi georeferenciranje le-tega težavno. Načrt ima priložen kratek pisni del, zato je natančna določitev kmetijske rabe tal (travnik ali pašnik, njiva ali travnik) težavna in nenatančna. Omenjen vir prostorskih podatkov je zgolj približek dejanskega stanja iz tistega časa.

Franciscejski zemljiški kataster (1 : 1440, 1 : 2880) je zanesljiv vir informacij o krajinski zgradbi in kmetijski izrabi tal iz 1823. Katastru je dodan opisni del, kjer so opisane posamezne parcele skupaj s kmetijsko rabo tal. Številne meje parcel so ostale do danes skorajda nespremenjene in so v veliko pomoč pri georeferenciranju samega katastra.

Prostorski viri, nastali leta 1913 in kasneje, so dober vir informacij o kmetijski izrabi tal in krajinski zgradbi, kakor tudi letalski posnetki iz leta 1954 in viri iz novejšega časa.

V študijo smo vključili prav tako spremembe, dinamiko zaraščanja gozdnih površin, pašnikov, travnikov, njivskih površin, vinogradov ter dinamiko razvoja urbanih območij med leti 1790 in 2009. V ta namen smo izbrali 200 med seboj enako oddaljenih točk (150 m). Točkam smo v nadaljevanju s pomočjo prekrivanja prej navedenih digitaliziranih prostorskih virov pripisali rabo tal v določenem obdobju in sklepali na čas opustitve kmetijske rabe (primerjava med prostorskimi viri različne starosti).

V nadaljevanju smo izdelali diagram premene krajinske heterogenosti (in zgradbe) skupaj z matriko premene posamezne točke (obdelovalne parcele). Diagram nam nudi natančen vpogled v hitrost in dinamiko spreminjanja krajinske zgradbe med letoma 1790 in 2009 ter omogoča analizo krajinske zgradbe v določenem, izbranem časovnem obdobju (Reger in ostali 2007).

2.4 Demografski podatki, podatki o številu ovac

Sprememba števila prebivalcev na opazovanem območju kot tudi števila drobnice (ovac) je podatek, ki olajša razumevanje vzrokov in procesov sprememb v prostoru. Spontano zaraščanje je v literaturi velikokrat opisano kot zakasnel pojav, ki sledi izseljevanju ali migracijam prebivalcev v lokalnem okolju (Scozzafava in ostali 2004). Skupno število krav ali drobnice v določenem časovnem obdobju odraža izrabo tal ter narekuje krajinsko zgradbo in heterogenost (Lang in Blaschke 2007).

SURS (2012) (Internet 1) in Šifrer (1969) ponujata podatke o številu prebivalcev na raziskanem območju. Podatke o številu ovac kot glavne pašne vrste na območju pa povzemamo za leto 1823 iz opisnega dela Franciscejskega katastra (Franciscan land cadastre for Kranjska 1823–1869) za leto 1913 in 1931 (Local Lexicon of the Drava Banovina 1937), in za leta 1971, 1981, 1991, 2002 iz SURS 2012 (Internet 1).

Podatke o številu prebivalcev kakor tudi o številu ovac na opazovanem območju smo prikazali kot skupno število prebivalcev in ovac, zbranih iz štirih okoliških vasi (Tribuče, Butoraj, Dragatuš in Bojanci).

2.5 Analiza sprememb krajinske strukture

Izbrali smo 300 naključno določenih točk po celotnem območju raziskav ter le-tem pripisali atribut kmetijske izrabe za vsako časovno obdobje (1790, 1823, 1913, 1954, 1986 in 2009). Izdelali smo preglednico (preglednica 1), ki prikazuje (1) povprečno površino zemljišča z enako kmetijsko rabo, na kateri točka leži, in (2) število vseh skupin točk, ki ležijo na zemljišču z enako kmetijsko rabo (poligonu).

Tako dve točki, ki ležita na območje enake rabe tal (skupnem poligonu), a sta bili ločeni v predhodnem opazovanem časovnem obdobju, jasno kažeta na novo, (bolj homogeno) manj mozaično stanje (slika 2).

Slika 2: Primer analize sprememb krajinske zgradbe. Stanje A (1823) prikazuje 9 skupin točk (naključno ležeče točke ležijo v devetih poligonih). Stanje B (1954): zaradi spremenjene krajinske zgradbe (opuščanja kmetijske rabe) imamo le 5 skupin točk (na petih različnih poligonih). Stanje C (2009): točke ležijo znotraj 2 poligonov, torej imamo dve skupini točk. Opazen je trend zaraščanja prostora in povečanja homogenosti krajinske zgradbe.

Glej angleški del prispevka.

Krajino obravnavamo kot prostorski izraz funkcionalnega sklopa ekosistemov in njihovega anorganskega okolja, ki je sicer odprt, vendar sposoben lastne samoregulacije (odvisno od intenzitete človekovih vplivov). Ločimo naravno in kulturno krajino (Anko 1982).

V študiji smatramo za gozdno krajino tisto, kjer površina gozda dosega 85 % celotne površine območja. Gozdnata krajina je krajina, kjer delež gozda obsega med 40 in 85 % njene celotne površine. V kmetijski ali agrarni krajini pa gozd porašča 20 do 39 % celotnega območja, krajina pa je preplet kmetijskih in urbanih območij) (Anko 1982; Pirnat 2000).

Heterogenost krajinske strukture razumemo kot neenakomerno in naključno razporeditev njenih elementov (Farina 2007). Označuje jo velikost (in kombinacija) posameznega elementa krajine znotraj celote, mozaika. Iz ekološkega vidika je optimalna heterogena krajina z večjimi zaplatami, ki pa vsebuje tudi drobno mozaična območja (Lang in Blaschke 2007; Ahlqvist in Shortridge 2010). Taka struktura naj bi po raziskavah zagotavljala primerne habitate za številne rastlinske in živalske vrste, njihove migracijske koridorje, kakor tudi pravilno postavitev kmetijskih površin v prostoru (Farina 2007).

Pogosto je ocena (heterogenosti) krajinske zgradbe subjektivna. Ločimo med a) homogeno krajinsko strukturo, b) homogeno krajinsko strukturo z majhnim deležem drugih krajinskih tipov (rabe tal) med 1–5 % celotne površine, c) zgradbo, ki jo grade večje površine in zaplate, d) mozaično krajinsko strukturo in e) prehodi omenjenih tipov (Lang in Blaschke 2007).

3 Rezultati in diskusija

S pomočjo analize digitaliziranih prostorskih podatkov smo pridobili podatke o krajinski heterogenosti, strukturi in deležih posamezne kategorije kmetijske rabe tal in stanju krajinske zgradbe na območju raziskave med letoma 1790 in 2009 za vsako opazovano obdobje posebej (slika 3).

Sprememba in dinamika števila prebivalcev ter glav ovac med leti 1823 in 2002 na območju raziskav sta predstavljeni s sliko 4.

Slika 3: Sekvence digitaliziranih katastrskih načrtov, vojaških kart in letalskih posnetkov (za leta 1790, 1823, 1913, 1954, 1986 in 2009).
Glej angleški del prispevka.

Slika 4: Spremembe v številu prebivalcev in glav ovac (razpoložljivi podatki za leta 1820, 1900, 1931, 1971 in 1981) med leti 1823 in 2002 na območju med Bojanci, Butorajem, Tribučami in Dragatušem.
Glej angleški del prispevka.

Diagram (slika 5) prikazuje spreminjanje deleža posamezne rabe tal na opazovanem območju med leti 1790 in 2009. Diagram prikazuje dinamiko spreminjanja krajinske zgradbe (spremembe posamezne kategorije kmetijske rabe tal). Na osnovi premene posamezne kategorije kmetijske rabe tal (v drugo) skozi opazovano časovno obdobje ločimo 3 stopnje spreminjanja krajinske zgradbe (in funkcije):

- krajinska zgradba se med leti 1790 in 1913 skorajda ni bistveno spremenila. 80 % površin ima skozi obravnavano obdobje enako rabo tal. Izjema so zgolj njivske površine, ki jih do leta 1913 prerase gozd.
- krajino med leti 1913 in 1954 zaznamuje premena oz. začetno zaraščanje večine kmetijskih površin in s tem ekspanzija gozdnih površin.
- letu 1954 je jasen trend zaraščanja pokrajine. Nad 60 % vseh negozdnih površin iz obdobja B se v tem obdobju zarase z gozdom.

Slika 5: Spreminjanje krajinske strukture na območju Bele krajine med leti 1790 in 2009. Diagram prikazuje premeno kmetijske rabe tal s prikazanim odstotkom površine posamezne kategorije kmetijske rabe tal glede na celotno območje. Dodan je tudi trend premene rabe tal.
Glej angleški del prispevka.

3.1 Krajinska zgradba, struktura in krajinski tip v obdobju med leti 1790 in 1913

V obdobju med leti 1790 in 1913 predstavljajo pašniki prevladujoč tip izrabe tal, kar jasno nakazuje na gospodarsko pomembnost pašništva v tem času. Gozdnih površin je leta 1790 malo in po površini ne presegajo ene tretjine celotnega območja. Leta 1790 je bil gozd izkrčen na najmanjši obseg.

Naslednje obdobje sta leti 1823 in 1913. Pašne površine se začno po letu 1823 manjšati (še intenzivneje leta 1913), v nasprotju pa se skupna površina obdelovalnih površin (njive) povečuje. Skupna površina vinogradov je leta 1823 ter 1913 znašala pod 2 % celotne površine. Gozdnih površin je več kakor leta 1790. Med letoma 1823 in 1913 se krajinska zgradba in krajinski tip skorajda nista spreminjala, krajina je še zmeraj značilna kmetijska z majhnim deležem urbanih površin (slika 3). Urbane površine, naselja se v prostoru pojavljajo na zahodnem delu območja raziskav. Krajinsko strukturo v opisanem obdobju označuje značilen mozaični preplet območja z manjšimi zaplatami ter nekoliko bolj homogenega prostora na vzhodnem delu (slika 3). V splošnem prevladujejo manjše, sklenjene zaplate gozda. Gozdni rob je v tem obdobju jasen in nefragmentiran, kar nakazuje intenzivnejšo obdelanost kmetijskih zemljišč. Leta 1790 je tip krajine med Bojanci, Butorajem, Dragatušem in Tribučami značilen kmetijski (agraren).

3.2 Krajinska zgradba, struktura in krajinski tip v obdobju med leti 1913 in 1954

Leta 1913 predstavljajo gozdne površine že tretjino celotnega območja. Območja pašnikov se začno zaraščati (površina zaraščenih kmetijskih površin se je po letu 1913 podvojila).

Leta 1954 površina gozdnih površin doseže polovico celotnega območja, površina kmetijskih površin (njiv) pa ostaja enaka kot leta 1937. Pašne površine do leta 1954 popolnoma zaraste gozd. Travnikov je bilo leta 1954 18.5 % celotnega območja (slika 5).

V obdobju med leti 1913 in 1954 (leta 1937) doseže strukturiranost krajine svoj višek. Sliki 3 in 5 prikazujeta dinamiko premene krajinske zgradbe in strukture. Opazen je trend večanja gozdnih površin (52 % celotne površine območja leta 1954) na račun drugih tipov rabe tal, predvsem pašnikov in travnikov. To je eden izmed vzrokov hitre rasti gozdnih površin v 40. in 50. letih ne le v Beli krajini, ampak tudi drugod v Evropi in poteka na območju raziskav še danes (Poldini 1989; Antrop 2004; Morgan in Gergel 2010). Pospešen proces transformacije krajinske zgradbe je opazen prvih nekaj let po koncu 2. svetovne vojne.

Pomemben družbeni dejavnik, ki je vplival na krajinsko zgradbo v tem obdobju, je druga svetovna vojna. Med in po končani vojni se namreč številni prebivalci izselijo iz Bele krajine (2. val migracij), migracija pa je imela vpliv tudi na opuščanje kmetijskih površin in obdelanost tal. Število prebivalcev je bilo na območju raziskav najnižje leta 1948 (slika 4).

Krajinska struktura je bila leta 1913 značilno heterogena z občasno večjo zrnatostjo in kombinacijo homogenega območja z večjimi zaplatami gozdov na jugovzhodnem delu in osrednjem delu. Govorimo o krajinskem tipu gozdnate krajine (Anko 1982). Prevladuje fragmentiran gozdni rob (zaraščanje). Krajina je leta 1954 gozdnata, v osrednjem območju že gozdna. Na vzhodu se pojavlja mozaik pašnih površin in travnikov v stanju zaraščanja.

3.3 Krajinska zgradba, struktura in krajinski tip od leta 1954 do danes (2009)

Leta 1999 gozdne površine predstavljajo 84 % celotne površine območja, 15.5 % pa površine v zaraščanju (slika 5). Po letu 1990 se pojavljajo na območju raziskave zgolj 3 različne kategorije kmetijske rabe tal (leta 1937 še 6), kar je ponovno dokaz hitrega procesa zaraščanja ter zmanjševanja raznolikosti krajinske strukture. Danes je območje med Bojanci, Butorajem, Dragatušem in Tribučami krajina z 90 % deležem gozdnih površin na celotnem območju. Za območje raziskav je značilna homogena krajinska struktura s kombinacijo večje zrnatosti ter z nekaterimi negozdnimi zaplatami na zahodu (pašniki v fazi zaraščanja). Število kategorij kmetijske rabe tal na območju je znašalo leta 2009 4 (slika 5). Diverziteta in strukturiranost krajine sta nizki.

V zadnjem opazovanem obdobju prevladuje na območju krajina gozdnega tipa (Topole in ostali 2006) z grmišči (zaraščajočimi se površinami), ki leta 1986 predstavljajo tretjino celotnega območja (slika 5). Pašne površine, njive in travniki so se močno skrčili na račun gozdov, po letu 1986 pa zaradi hitrega procesa zaraščanja krajine teh površin na območju raziskav na najdemo več.

Večina prebivalcev območja je danes zaposlenih v sekundarnem in terciarnem gospodarskem sektorju, predvsem v večjih mestih. Kmetijstvo predstavlja le še dopolnilno dejavnost. Zato prebivalstvo nima vpliva na krajinsko podobo in strukturo kot nekoč, kar se odraža tudi v stopnji gozdnatosti prostora.

3.4 Spreminjanje krajinske strukture

V obdobju 1790–2009 se je pokrajina spremenila; iz homogene (1790) do mozaično fragmentirane (1954) in nazaj v homogeno (2009) (slika 3). Skozi opazovano obdobje se število skupin točk, ki ležijo znotraj istega poligona, poveča s 24 na 197 ter naposled zmanjša na 37. Leta 1790 je bilo tako vseh 300 naključno postavljenih točk deljenih v zgolj 24 poligonov. Povprečna velikost parcele je bila 40.44 ha (preglednica 1). Leta 1823 se število poligonov poveča na 170, leta 1954 pa na 197. Po letu 1954 se je začela homogenizacija krajinske strukture, s tem pa pride do »združevanja« parcel (Forman 2006). Leta 2009 je bilo tako vseh 300 točk deljenih zgolj v 37 različnih parcel (prostor se zarašča, mozaičnost pa zmanjša).

Izbrano metodo predstavljamo s sliko 2, ki zajema zgolj del celotnega območja raziskav. Opazovanje in štetje skupin točk v spreminjajoči se pokrajini (v odvisnosti od povprečne površine kategorije kmetijske rabe tal) se je izkazalo za učinkovito metodo analize sprememb krajinske strukture skozi izbrano obravnavano obdobje.

Slika 6: Spreminjanje krajinskih tipov v Beli krajini v letih 1790, 1954 in 2009.
Glej angleški del prispevka.

Ker ima pašništvo velik vpliv na videz pokrajine in vpliva na krajinsko zgradbo (kakor tudi strukturo), smo v študiji raziskali odnos med upadom števila ovac na območju Tribuč, Bojancev, Dragatuša

Preglednica 1: Spreminjanje krajinske strukture med leti 1790 in 2009.

obdobje	1790	1823	1913	1954	1986	2009
število zemljišč, kjer se točke nahajajo	24	170	181	197	162	37
povprečna površina zemljišča (ha)	40.44	2.287	1.782	0.238	5.321	43.873

in Butoraja kot glavne pašne vrste v Beli krajini nekoč (Local Lexicon of the Drava Banovina 1937). Upad števila drobnice smo nato povezali s spreminjanjem krajinske zgradbe in strukture. Številne raziskave kažejo, da je ovčereja ključen faktor, ki narekuje poteze pokrajine (Nagashima in ostali 2002; Thomson in Simpson 2005; Wehn 2008; Carmona in ostali 2010; Pipenbaher in ostali 2011), po opustitvi paše pa se spremenita tako krajinska struktura kot tudi njena zgradba. Podoben proces smo ugotovili tudi v naši raziskavi; še posebej po postopnem zmanjšanju števila ovac na območju raziskave (po letu 1931) (slika 4; slika 5).

Ovac je bilo na območju štirih vasi največ leta 1820 (562 glav). Leta 1931 je število živali strmo padlo na 173, trend upadanja pa se je nadaljeval vse do leta 1990 (20 glav) oziroma 2002 (21 glav).

Raziskava kaže na ključno vlogo pašništva pri ohranjanju odprte kulturne krajine in mozaične krajinske strukture (Poldini in Feoli 2006; Morgan in Gergel 2010). Po ukinitvi ali opustitvi pašne dejavnosti se odprt prostor zaraste z gozdom, kar se hitro odrazi v spremenjeni krajinski zgradbi in strukturi. Pokrajina se spremeni iz mozaične v homogeno – sklenjeno (slike 3, 4 in 5).

Rezultati raziskave kažejo, da je bila krajina na območju Bele krajine nekoč kmetijskega tipa, enakomerno heterogena, struktura pa srednje zrnata (slika 3). Le-ta se je skozi opazovano obdobje zaradi opuščanja pašništva, kmetijske dejavnosti ter kot posledica izseljevanja hitro spremenila v homogeno krajino gozdnega tipa.

Podoben potek transformacije prostora prikazujejo tudi druge raziskave, ki pa ne zajemajo tako dolgega časovnega intervala (Antrop 2004; Bender in ostali 2005; Reger in ostali 2007; Linden in ostali 2008). Omenjene raziskave obravnavajo problematiko zaraščanja prostora po opustitvi kmetijske rabe in zajemajo tudi spremembe v demografski strukturi ter gospodarski dejavnosti, ki se kažeta v spremembah videza pokrajine.

4 Sklep

Naša raziskava prikazuje izjemno hitro spremembo krajinske strukture in zgradbe v obdobju med leti 1790 in 2009. Zaraščanje prostora kot posledica opuščanja kmetijske rabe je v Beli krajini veliko hitrejše kot v drugih delih Slovenije in Evrope (Čarni in ostali 1998; Linden in ostali 2008; Garcia-Feced in ostali 2011). Rezultati raziskave na primeru Bele krajine kažejo močan vpliv človeka na strukturo in funkcijo pokrajin v Sloveniji ter poudarjajo hkrati človekovo dejavnost kot močno gonilo pri samem vzdrževanju in ohranjanju krajine danes.

Slika 7: Breza (*Betula pendula*) je drevesna vrsta, značilna za zgodnjo fazo zaraščanja kmetijskih zemljišč.
Glej angleški del prispevka.

Številne študije obsegajo problematiko zaraščanja prostora v opuščeni kmetijski krajini (Skanes and Bunce 1997; Čarni in ostali 1998; Seabrook in ostali 2006; Linden in ostali 2008; Zomeni in ostali 2008), a le redke zajemajo spremembe, nastale v daljšem časovnem obdobju. Vzrok so največkrat slabi ali nenatančni prostorski podatki. Naša raziskava opisuje spremembe v prostoru kot posledico demografskih in ekonomskih sprememb v daljšem časovnem obdobju, v obdobju 220 let.

Če pokrajino razumemo kot del ekosistema z lastnimi zakonitostmi in delovanjem (Farina 2001; Garcia-Feced in ostali 2011), lahko v kontekstu ohranjanja le-tega potrdimo na primeru Bele krajine zmanjšanje krajinske zgradbe, kakor tudi spremembo, nastalo v njeni zgradbi, spremembe v elementih krajine (število in oblika travnikov, gozdnih robov, pašnikov).

Ocenjevanje in opis pokrajine, ki temelji na poznavanju krajinske strukture in zgradbe, je lahko zadosten kriterij o splošni oceni diverzitete pokrajine.

Slika 8: Široka krošnja in razrast dveh gradnov (*Quercus petraea*) pričata o njunem nekoč precej bolj odprtem rastišču (pašnik), ki se je zaradi prenehanja paše pred desetimi leti zaraslo. Danes razen redkih travniških vrst zeli v sestoju in debeline drevesnih debel skorajda ni dokazov, ki bi nakazovali na do nedavnega odprto krajino.
Glej angleški del prispevka.

Slika 9: Opuščen vinograd, Vinišča. Nekoč obdelane terase danes prerašča sklenjen gozdni sestoj, star približno 40 let.
Glej angleški del prispevka.

5 Zahvala

Za tehnično pomoč se zahvaljujemo g. Iztoku Sajku. Zahvaljujemo se g. Iztoku Vraničarju (Geodetska uprava RS, geodetska pisarna Črnomelj) za pomoč pri zbiranju prostorskih podatkov. G. Martin Cregeen je lektoriral angleško verzijo.

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6 Literatura

Glej angleški del prispevka.

2.2 RASTLINSKE ZDRUŽNE IN GRADIENTI

Plant communities in gradients, Čarni A., Juvan N., Košir P., Marinšek A., Paušič A., Šilc U., Plant Biosystems, 2011, 145, 45−64.

Izvleček

Raziskava opisuje dva pristopa raziskav vegetacije, ki izvirata že iz začetka prejšnjega stoletja; ordinacijo in klasifikacijo. V raziskavi smo testirali razporejenost vzorčnih ploskev glede na izbran gradient z ozirom na individualistični ali integrativni koncept. V raziskavo smo vključili gradiente različnih študij: sukcesijski gradient, višinski gradient, gradient antropogenih vplivov na okolje, fenološki gradient, makro-ekološki in fitogeografski gradient. V raziskavi smo želeli določiti najpomembnejši gradient, s pomočjo direktne in indirektne ordinacijske metode.

V raziskavo smo vključili analizo sekundarne sukcesije iz Bele krajine, analizo sekundarne sukcesije gozdov *Pinus brutia* iz Turčije, višinsko distribucijo združb na silikatnih skalnih stenah v Sloveniji, gradient naseljevanja smreke v bukove gozdove, vpliv uvajanja neavtohtonih drevesnih vrst v gozdne sestoje na primeru uvajanja smreke v bukove gozdove, makroekološki in fenološki razvoj segetalne vegetacije v Evropi in vzorec razširjenosti plemenitih listavcev ob Jadranskem morju.

Rezultat raziskave je pokazal, da je razporeditev vrst po kateremkoli gradientu posledica medvrstnih odnosov. To dejstvo nam omogoča določanje in opisovanje rastlinskih združb po vzoru srednjeevropske Braun-Blanquetove metode.

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Plant communities in gradients

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Abstract

The work deals with the confrontation of two approaches in vegetation science, which already had their origins at the beginning of the past century: gradient analysis and classification of communities. We tested whether samples are arranged along gradients according to the individualistic or the integrative concept. We studied gradients in several case studies – successional, altitudinal, gradient of human impact, phenological, macroecological, (phyto)geographical – and tried to detect the main gradient (by direct or indirect ordination methods) and arrange the plant assemblages along the gradient. We then applied different classification methods to test whether it is possible to detect discrete plant communities. We analyzed the secondary succession of birch forests in Slovenia, the process of autosuccession of *Pinus brutia* in Turkey, the altitudinal distribution of communities in rock crevices on silicate bedrock in Slovenia, the gradient of spruce planting in beech forest, the influence of the introduction of non-native tree species into forests, the macroecological and phenological development of weed vegetation in Europe, and the circum-Adriatic pattern of broadleaved ravine forests. The results show that, in most cases, the turnover of species composition along the gradient, according to the integrative concept, is due to species interactions. This enables us to detect and describe discrete plant communities in terms of the central European Braun-Blanquet method.

Keywords: *Classification, gradient, ordination, phytosociology, syntaxonomy, vegetation*

Introduction

This year marks 100 years since the Botanical Congress accepted a definition of association that is defined by floristic composition, physiognomy, and ecological circumstances (Flahault & Schröter 1910). Abroad development of methods dealing with the classification of plant communities (Braun-Blanquet 1964) and successional processes (Clements 1916) then followed. The basis of these methods is the re-occurrence of plant assemblages (phytocoenon, communities) in the landscape, which enables the definition of abstract units, termed syntax. Debate about the true nature of these species assemblages has been the main issue in theoretical, sometimes even philosophical discussions during the past century (Wilson 1991; Mucina 1997; Wildi & Orloci 2009).

There are two main approaches to understanding vegetation. The above-described approach, termed the integrated (or community unit) concept, considers communities as a real functional system in which populations of plant species are integrated both by the environment and by interactions among and within plant populations. Plant species do not reach their potential (physiological) optimum in communities, but the optimum of their appearance may be shifted due to plant interactions and so they possess the so-called real (ecological) optimum nature (Moravec 1989). This is one of the reasons for discontinuity along gradients. We can detect certain species that are diagnostic for a group of samples along a gradient, which can be determined by the statistical fidelity measure (Barkman 1989; Chytrý et al. 2002). The method is widely accepted in Eurasia and also used on other continents (e.g. Casavecchia & Biondi 2001; Duarte et al. 2005).

The opposite view is the individualistic concept of plant communities. This means that species possess their own pattern of dynamics. This approach thus rejects the idea of the re-occurrence of species

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combinations; compositional patterns are seen merely as transient phenomena on a space–time continuum. This is the main idea of Anglo-American plant ecology (Gleason 1926, 1939; Ewald 2003).

Two main analytic approaches exist in vegetation science. One is gradient analysis. Samples are arranged along a gradient and this approach (termed ordination) enables an understanding of plant communities, their relation to one another and to the changing environment. Either a gradient is measured (direct ordination) or axes of diversity are derived from the samples themselves (indirect ordination). This approach originates from the concept of vegetation being a continuum (Bray & Curtis 1957; van der Maarel 1975). The second approach is classification of communities with the aim of finding common features of communities and assigning them to various syntaxa (community types), which have a common floristic composition, community characteristics, and ecological circumstances (Braun-Blanquet 1964).

The aim of this study was to test whether species are distributed along gradients according to the integrative (community unit) or the individualistic concept in various gradients and, as a consequence, whether we can detect distinct community types (syntaxa) with common features.

Methods

We used the standard methods for vegetation elaboration. Relevés were sampled and elaborated by the standard Braun-Blanquet method (Braun-Blanquet 1964). Data were elaborated using various program packages TWINSPAN (Hill 1979), SYN-TAX (Podani 2001), CANOCO 4.5 (Ter Braak & Šmilauer 2002), JUICE program (Tichý 2002), PC-ORD 5.0 (McCune & Mefford 1999), and Statistica 8.0 (StatSoft 2007).

Results

Succession

Succession is a series of changes in communities that occur over time after disturbance. It can be primary succession, when there is a new substrate with no existing vegetation (e.g. after eruption of a volcano); secondary succession, when the substrate has sustained vegetation (e.g. after the abandonment of grazing); or autosuccession, when all species are present throughout the time (e.g. recovery of Mediterranean forests after fire).

Secondary succession. The first case study is a typical secondary succession of oak–hornbeam forests (*Abio albae-Carpinetum betuli*) in SE Slovenia (Bela

Table I. The synoptic table showing the turnover of species in the time gradient. Clusters are indicated by capital letters, as A – grasslands, B – stage of *Pteridum aquilinum-Frangula alnus*, C – *Betula pendula* dominating, young *Carpinus betulus*, D – young *Carpinus betulus* forest, herb layer dominated by *Epimedium alpinum*; E – old *Carpinus betulus* forest with many forest species.

		A	B	C	D	E
Age					1 2 2 11	21 1 212 2222 2 2212222
			1 3 11111	11222323222233	5343611213436235333317653538 37	02672722274222237272252222
		70004007	02036655505	55000005880000	0050580250555030520500000500000	000505000550000000800000000
Calluna vulgaris	6	+334344+	++.....+.+.	+.1...........	....	....
Frangula alnus	6	+++++++.	+++22.+1+.+	+.+.+.++1...+.	++.....+........+..+..........	...+......................
Betula pendula	3	....	12	2131++...+....	.................+......2.....	....
Epimedium alpinum	6	..+.+.11	.2....+.21.	..........2...	224.++.++1344312134.2331.43433	3+2424++121.++..122+14.++.
Carpinus betulus	3	....	....	....+.1.+.122.	443453333511+44344355454345353	55544455544554335425341313
Pulmonaria officinalis	6	....	....	....	+.............................	+.++..++++.++.+....+.+++..

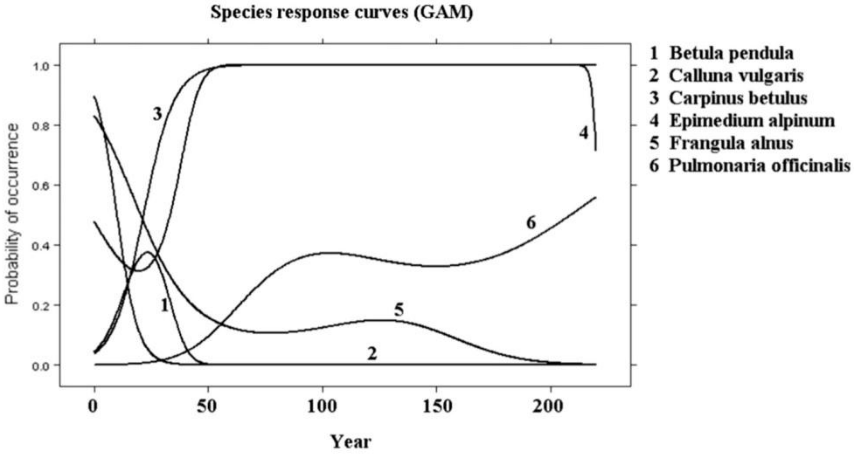

Figure 1. Species response curves demonstrate the occurrence of selected species during secondary succession (JUICE, generalized additive models). Only the most characteristic species are shown.

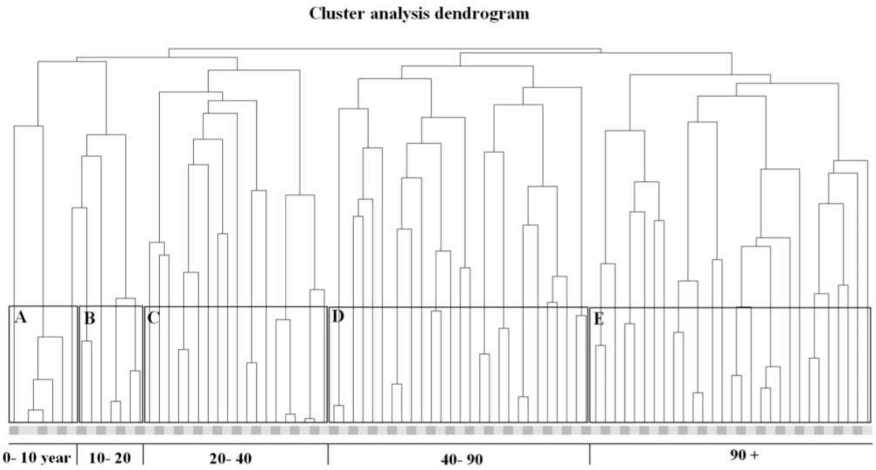

Figure 2. Hierarchical cluster classification of relevés (PC-ORD, Ward method, Bray–Curtis). Five clusters correspond to Table 1 and Figure 1.

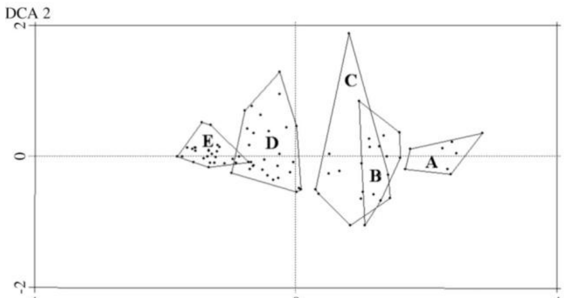

Figure 3. Indirect gradient analysis (DCA). Five groups correspond to those in Table 1 and Figure 2.

krajina). We constructed a chronosequence of vegetational development over the last 220 years. Cadastral maps and aerial photographs were used as the source of information about previous land use (Čarni et al. 2007).

The synoptic table (Table I) shows the species turnover in time, also indicated by species response curves (Figure 1). Grassland species (*Agrostis capillaris*, *Brachypodium rupestre*, *Calluna vulgaris*, *Potentilla erecta*) are present at the beginning. After the land has been abandoned, a stage of *Pteridium aquilinum-Frangula alnus* appears, followed over the course of about 30 years by well-established birch forest. Such forest contains young samples of *Carpinus betulus*, which take over the dominant role in about 50 years. We then detected two stages in the development of *Carpinus* forest; the first is characterized by the decay of birch and other heliophilous species, the herb layer is dominated by *Epimedium alpinum* and, finally, typical forest species such as *Pulmonaria officinalis* appear.

Succession does not run smoothly; distinct clusters (Figures 2 and 3) can be detected, which are the result of events and processes that are abrupt (and coincide with time stages). For instance, (a) when grazing and moving is abandoned, *Pteridium* and shrub species overgrow the surface; (b) when these species are shaded by birch trees, they disappear; (c) when birches pump enough cations from lower soil horizons, faster decay of litter begins that makes the soil more fertile, which gives hornbeam the opportunity to develop. It can be seen that species are distributed according to the integrative concept along the time gradient.

Autosuccession. In the research of the recovery of *Pinus brutia* stands (Kavgaci et al. 2010b), we tried to detect distinct community types (syntaxa) in the autosuccession process. Two extreme cases describe the turnover of species in the succession process: *relay floristic*, in which the area under the succession process is overgrown by waves of species that come from outside; and *initial floristic composition*, in which all species are present on the surface the whole time and only differences in dominance occur. The extreme situation is rarely found, but it seems that recovery of *Pinus brutia* forest may be closer to the latter: i.e. initial floristic composition; the process is often termed autosuccession or direct recovery (Eggler 1954; Buhk et al. 2006).

The recovery of *Pinus brutia* forests was studied in SW Anatolia. These forests are often burnt by fire, which is considered to be a natural factor in the Mediterranean region (Pausas et al. 2008). In this area, the chronosequence of forest recovery after fire has been established. Vegetation was sampled on 1, 2, 3, 4, 7, 12, 20, 40 and more than 50-year-old sites (treated as mature) of *Pinus brutia* forests.

Ordination diagrams (Figure 4) show that the process is autosuccession. In the diagram in Figure 4a, which is the result only of presence/absence data, only samples from the first year built a distinct group, while others form fairly unique groups characteristic of the autosuccession process. Individual syntaxa can only be detected with difficulty. The diagram in Figure 4b was prepared also taking into consideration the structure (i.e. cover of species and distinct layers). Three distinct groups of samples can be detected here. The same pattern is also shown in the classification diagram (Figure 5). Since the structure also has an important role in vegetation classification (e.g. Pignatti et al. 1995), the separation of samples as indicated in the lower diagram (Figure 4b) and in the dendrogram (Figure 5) can be accepted.

The initial stages of succession are classified within the class of annual, nitrophilous species (weeds) of *Stellarietea mediae*. In the third year, communities appear with a dominance of chamaephytic shrubs, above all from the genus *Cistus* sp. div. (Čarni et al. 2010). This vegetation is termed garrigue and is classified within the class *Cisto-Micromerietea*. The next cluster is dominated by shrub species (e.g. *Arbutus andrachne, Myrtus communis, Pistacia terebinthus*), which build a vegetation termed macchia and is classified within the order *Pistacio-Rhamnetalia alaterni* (class *Quercetea ilicis*) – within this group, two subgroups can be detected, one dominated by sclerophyllous shrub and the

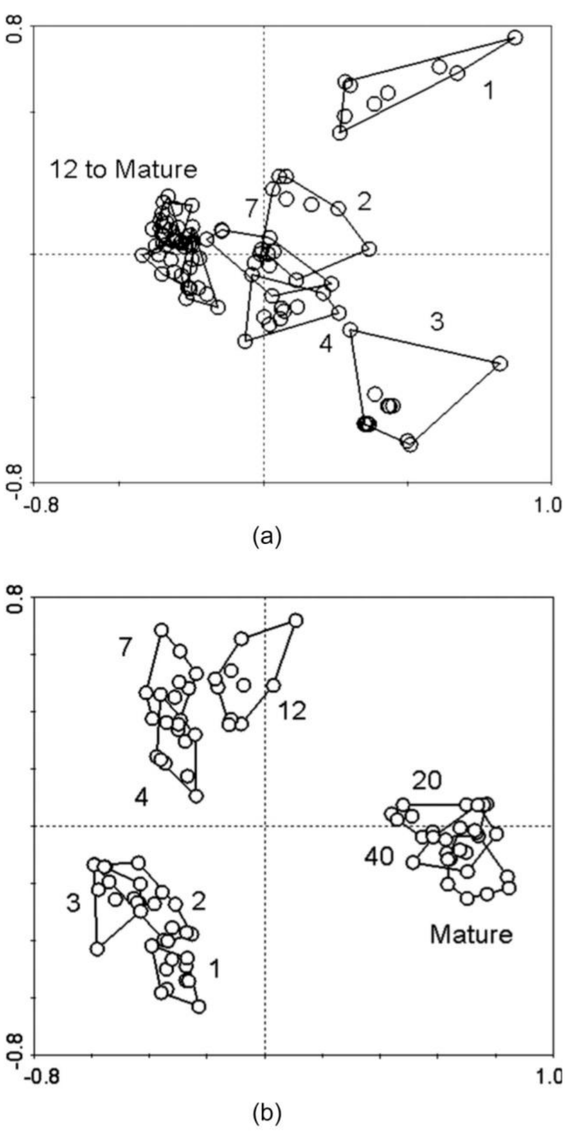

Figure 4. Indirect gradient analysis (PCA) of floristic data from plots of different age after fire; 4a. Only presence/absence data were used, 4b. Floristic and structural characteristics of plant communities (different layers and cover of species) on the right.

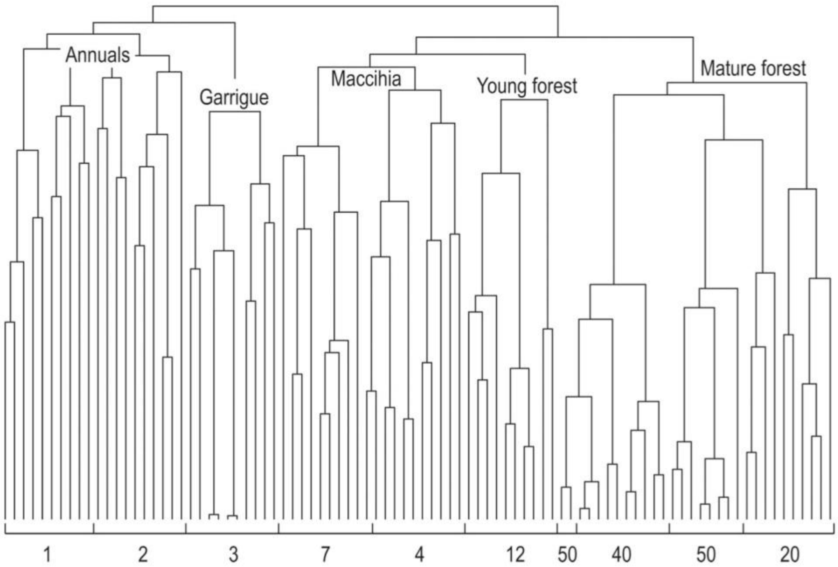

Figure 5. Classification of relevés (PC-ORD, correlation, flexible beta –0.25). The age of the stands is given below the graph.

other of a transitional type, in which a forest species (e.g. *Pinus brutia*) gradually overgrows the macchia species and represents young forest. The last group in the diagram is composed of samples dominated by *Pinus brutia*, classified within the class *Quercetea ilicis* (Kehl 1995; Rodwell et al. 2002; Ketenoglu et al. 2010).

It can be concluded that even in a process of autosuccession, in which the majority of species are present throughout the process, we can detect plant communities but, in this case, information about the structure of the vegetation must also be taken into consideration.

Altitudinal gradient

The altitudinal gradient was studied on vegetation thriving in rock crevices on silicate bedrock (order *Androsacetalia vandellii*, class *Asplenietea trichomanis*). This vegetation appears under extreme site conditions (high radiation, oscillation of temperature and humidity, and lack of nutrients). The altitude does not influence the vegetation directly but through changes of ecological factors (Mucina 1993; Valachovič 1995; Chytrý 2009). The vegetation was sampled from lowland to high altitudes (400–1700 m a.s.l.) (Juvan 2008).

The ordination of relevés shows a distribution along the first axis which could be understood as altitudinal gradients (Figure 6). This is also confirmed by the passively projected values of altitude. Cluster analysis indicated three clusters, which are significantly differentiated by altitude (Figure 7), and which is also reflected in the diagnostic species of the clusters (Table II). At higher altitudes,

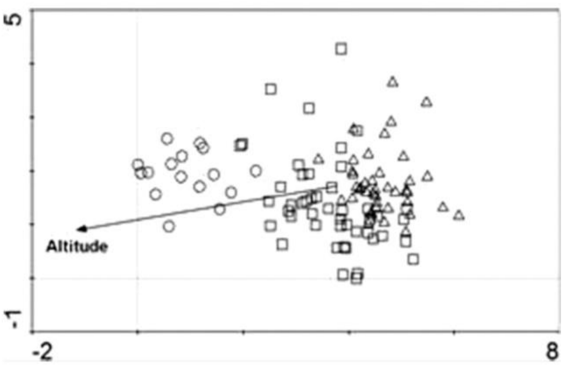

Figure 6. Indirect gradient analysis (DCA) of floristic data from plots from different altitudes. Legend: □ highest altitude, ○ medium altitude, Δ low altitude.

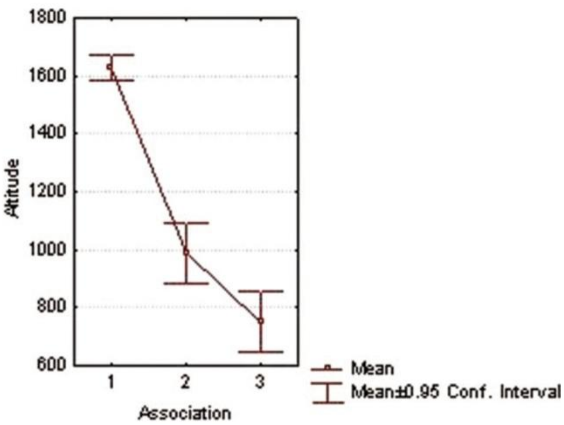

Figure 7. Box–Whiskers diagram presents altitudes of the three clusters. Legend: 1 – subalpine and altimontane cluster, 2 – montane cluster, 3 – lowland cluster.

altimontane and subalpine species can be found, such as *Primula villosa* or *Pederota lutea*; lower down, there are species that have optimum distribution in the montane belt (e.g. *Calamagrostis villosa*) and in the lowlands more thermophilous species, such as *Polypodium vulgare*, *Asplenium trichomanes* and *Hypnum cupressiforme*.

It was found that the vegetation forms distinct syntaxa along the altitudinal gradient, as had already been established (Hemp 2006; Kavgaci et al. 2010a).

Gradient of spruce planting in a beech forest

Forest management creates ecological differences that strongly affect plant species composition (Burrascano et al. 2009). We estimated the changes of species composition under the influence of different proportions of planted spruce in a beech forest. For various reasons, spruce (*Picea abies*) was a promoted tree species in the past, even on sites unsuitable for its growth. This problem is encountered all over Central Europe, where 6–7 million hectares of pure spruce stands have been estimated to be outside its natural area of distribution. Introduced spruce causes various changes in the stand, such as microclimate, a decrease in the natural pH value, and it hinders rejuvenation and the processes of litter decomposition (Klimo et al. 2000; Anon. 2005).

In the study of submontane beech forest (*Hacquetio-Fagetum*), we tried to discover whether forest management (artificial introduction of spruce) causes changes in plant composition to such an extent that another plant community is formed. We selected sample plots in homogeneous mature stands with different proportions of spruce in the tree layer. We divided them into five classes in relation to the proportion of spruce basal area. Stands with 0–5% of spruce were considered to be natural beech forest and stands with 95–100% of spruce, to be spruce monoculture. The other three classes contained 5–30%, 30–60% and 60–95% of spruce. It can be seen in the classification diagram (Figure 8) that stands with a proportion of spruce up to 60%, still maintain the floristic composition of beech forest. When the proportion of spruce is higher, the community changes dramatically and the species composition resembles that of spruce forest. Characteristic plants species of beech forests disappear (e.g. *Carex pilosa*, *Pulmonaria officinalis*) and are replaced by acidophilous species, such as *Thuidium tamariscinum*, *Gentiana asclepiadea*, etc. (Table III).

It can be concluded that a certain proportion of spruce initiates a significant species turnover, which enables the recognition of two different syntaxa.

Table II. Synoptic table of diagnostic species of groups on the altitudinal gradient of crevice communities. Classification is made by modified TWINSPAN (JUICE, fidelity for a group exceeds 0.5).

	1111111111111111	01000111111000100111100110111111111101111000000	000000000011000000000001100110111101011111
	6666666655536666	42466001101666565600176556121153153165110565566	44444645550044454544554531546151121515111110
Altitude	8588786644588857	35022665552222126667652012606500508525267726402	566665946005535665668080055306066575587566 5
	0000000000000000	00000000000000000000040000000050050000000000000	000005000000000000000005070007544040909669 0
Primula villosa	++++11++....+++1	....	....
Festuca varia	11.+2.22....112.	....	....
Grimmia ovalis	.++1....++..++++	.................+.....+.......................	....
Thymus praecox ssp. polytrichus	.1....1+.+.2.+1+	....	....
Festuca ovina	..1++1.11212++12	.................+....++12.+..+..+..+1.......+	.++.+......1...................................
Campanula cochleariifolia	.1..1++.+1..111.	...............2..1......1.....................	....
Paederota lutea	1..1..11....++..	....	....
Calamagrostis arundinacea	....	1....+.1..1.1..1+.+11..11..+1111222+..11..+.+..	........+..1...1......1...........1....+...
Hieracium murorum	....	.....1+.1++.....+.++.+....++.+.1+++.....+2.+1+.	.....+.........+..................+........
Polypodium vulgare	....	....1..+.....1..++.....+.1+.1.+.........1.....++	2+...++..+1111+11+111+1+1++1+++2.2.11+1+++1
Asplenium trichomanes	..........+.....	..................1........++.........1..+.1+.+1.	+21111+13+1.+2+2.2+.22....+.++1.1.++++.1++.
Hypnum cupressiforme	.......+........	.......13.......1..1......1..+..+.1...........1	2..1...222131..2.....343.33..22322332212.11
Cluster	1	2	3

Macroecology and phenology of weed vegetation

Another gradient in relation to the change of plant communities that has puzzled researchers is the pattern of weed vegetation along the climatological gradient in Europe and the seasonality of weed vegetation (Kropáč et al. 1971; Holzner 1978).

The syntaxonomy of weed vegetation changes in the macroecological gradient from south toward north. Along this long gradient, substantial

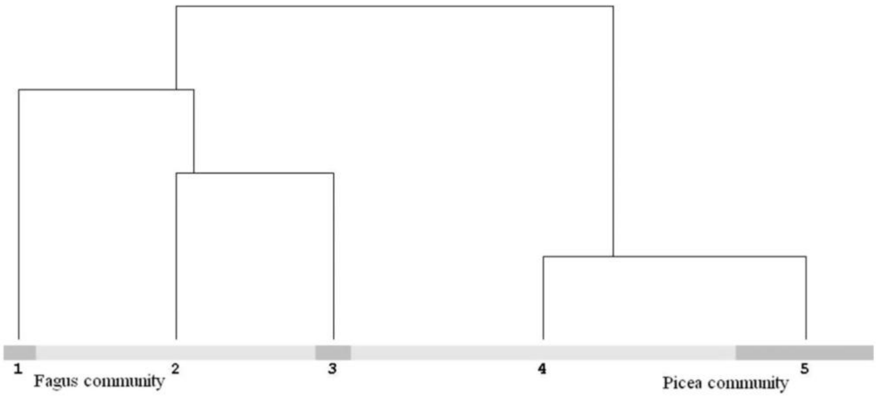

Figure 8. Classification of relevés of natural beech forests. The matrix was divided into five classes in relation to the proportion of spruce (C1 = 0–5% of spruce, C2 = 5–30%, C3 = 30–60%, C4 = 60–95%, C5 = 95–100% of spruce). (PC-ORD, Ward's method, Euclidean distance).

Table III. Diagnostic plant species of communities on the gradient between natural beech forest and monoculture of spruce.

Percent of spruce	0–5%					5–30%					30–60%					60–95%					95–100%				
Releve number	5	9	25	27	37	4	14	18	22	24	6	12	21	26	28	7	19	20	38	39	3	29	30	34	35
Fagus sylvatica	5	5	5	5	5	5	3	3	4	4	2	3	3	4	4				2	2		+			
Carex pilosa	1	+	3	+	3	2	3	3	4			2			+			+	1						
Pulmonaria officinalis		+				+	+	+		+		+			1										
Picea abies							2	2	2	1	3	2	3	3	2	4	4	4	4	4	5	4	4	4	4
Thuidium tamariscinum					+				+	+	+	+	+				+	+			+	3	1	+	+
Rubus hirtus			+			+			+	+			+				+	+			1	+	+	+	+
Luzula pilosa							3				+			+	+	+		+	+		1	1	+	+	+
Eurhynchium angustirete						+	+	+			+	+	+				+		+			3	1	4	2
Gentiana asclepiadea													+					+		+		+		+	+
Mycelis muralis																+		+			+	+	+	+	+
Galium rotundifolium																						+		+	

Table IV. Ranking of different factors influencing species composition of weed vegetation along the large macroecological gradient.

NW Balkans Šilc et al. (2009)	France Fried et al. (2008)	Hungary Pinke et al. (2009)	Slovenia Šilc (2007)	Czech Republic Lososova et al. (2004)	Sweden Hallgren et al. (1999)
Phytogeography	Crop	Aspect (seasonal changes)	Climatic district	Altitude	Geographical region
Crop	Preceding crop	Soil pH	Crop	Season	Soil type
Year	Soil pH	Precipitation	Phytogeography	Year	Crop
Season	Rainfall	Soil texture	Year	Crop	Time (Year)
Altitude	Altitude	Temperature	Precipitation		
	Longitude	Altitude	Temperature		
	Soil texture		Altitude		
	Latitude				
	Landscape				
	Sowing date				

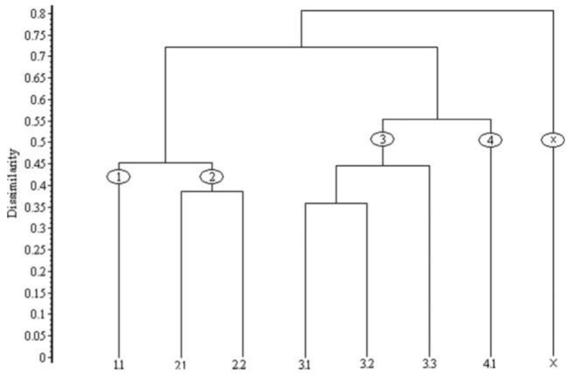

Figure 9. Cluster analysis of the eight TWINSPAN groups of relevés (sub-clusters) of broad-leaved ravine forests in SE and central Europe, resulting in four clusters; Cluster 1 (1.1) Central European xerothermophilous forests, Cluster 2 (sub-clusters 2.1, 2.2) Apennine and Balkan xerothermophilous forests, Cluster 3 (sub-clusters 3.1, 3.2, 3.3) Central European mesophilous forests, Cluster 4 (4.1) Balkan (Illyrian) mesophilous forests (after Košir et al. 2008).

differences occur in summer temperatures and the length of the vegetation period, which are crucial for the development of weed vegetation. Use of large databases and statistical methods has enabled us to rank the various factors influencing species composition of weed vegetation along a large macroecological gradient. The results show an increasing importance of crops toward the south (Hallgren et al. 1999; Lososová et al. 2004; Šilc & Čarni 2007; Fried et al. 2008) (Table IV). Floristical differences between plant communities in cereals and root crops are therefore less significant in Northern and Central Europe (Tüxen 1950), and the classification within a single class *Stellarietea mediae* is supported. The main reason is that the short vegetation period does not allow the development of floristically distinct plant communities within different crops. Historically, weed vegetation in the south of Europe was classified within two classes on the basis of different crops (*Secalietea* and *Chenopodietea*), and Oberdorfer (1993) upheld this approach even for southern Germany. Nevertheless, the principle of a single class of weed vegetation was also adopted in SE Europe (Šilc et al. 2008) but with different diagnostic species (Kropáč 2006).

As stated, the annual cycle of weed vegetation is more pronounced in the south of Europe, since the vegetation period is longer, allowing species with different phenological spectra to develop in even up to three different assemblages within a single year on the same field. These species do not grow together at the same time and are not therefore in competition with each other (Kropáč et al. 1971; Holzner 1978). This caused researchers dealing with vegetation in the southern part of Europe to accept these

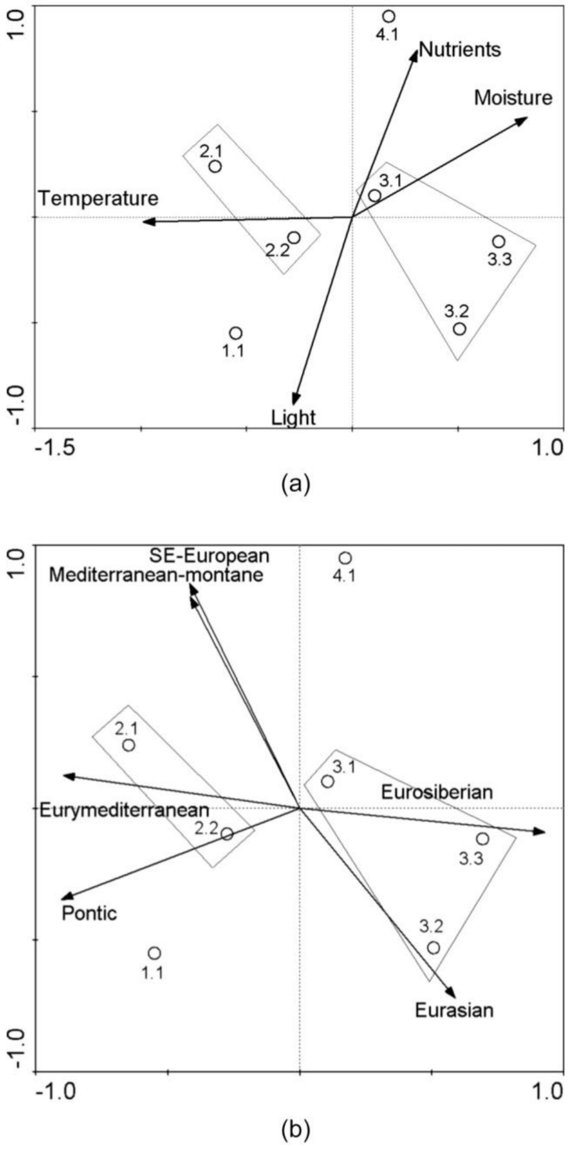

Figure 10. Indirect gradient analysis (PCA) of sub-clusters: 10a. Pignatti indicator values; 10b. Proportion of geoelements in sub-clusters, plotted as supplementary data on the diagram. Sub-clusters are numbered as in Figure 9 (after Košir et al. 2008).

assemblages as associations (Slavnić 1951; Oberdorfer 1954; Holzner 1973). They correspond to the so-called aspects (Schubert & Mahn 1968) oragroecophases (Kropáč et al. 1971) of northern and central European authors. In recent years, these two similar concepts were adopted in large scale surveys, which made classification more synecologically sound (Kropáč 2006; Šilc et al. 2009).

Different treatments of syntaxa can be detected, which reflect many of the differences in macroecological circumstances. Differences in syntaxa because of seasonal development (periodicity) can also be detected, so the temporal component (seasonality) has also to be taken into consideration in syntaxonomy.

Phytogeography

Many authors have also investigated syntaxa along the (phyto)geographical gradient. It is widely accepted that vegetation changes along the geographical gradient (Knollová & Chytrý 2004; Tsiripidis et al. 2007; Košir et al. 2008; Čarni et al. 2009; Šilc et al. 2009; Landi & Angiolini 2010). Geographical position affects vegetation through changes of global climate and different distribution of species due to vegetation history and it has therefore the largest effect on zonal vegetation.

The question is whether different syntaxa of the same type of azonal forest vegetation can be distinguished (in which the main effect of global climate is substituted by another ecological factor) along the geographical gradient? We tried to answer this question on the case of broad-leaved ravine forests in SE Europe (Apennine and Balkan Peninsula).

Broad-leaved ravine forests grow on spatially restricted sites with specific soil conditions. They occur on slopes, at the foot of slopes, in sinkholes, gorges and hollows with colluvial, skeletal and primarily unstable soil, which allow broad-leaved trees *Acer platanoides, Acer pseudoplatanus, Fraxinus excelsior, Tilia cordata, Tillia platyphyllos* and *Ulmus glabra* to replace otherwise competitively stronger tree species, above all beech, *Fagus sylvatica*. The analysis was made on the basis of the collection of relevé material from central and southeastern Europe (Košir et al. 2008).

Cluster analysis of SE European and central European broad-leaved ravine forests has suggested that broad-leaved ravine forests in SE Europe form a separate group within European broad-leaved ravine forests (Figure 9). Xerothermophilous and mesophilous forests divide at the first level. At the second level, the two groups also divide geographically into a group of SE European and a group of central European forests, resulting in four main clusters (Figure 9). The clusters (with sub-clusters) can be interpreted ecologically (Figure 10a) and geographically (Figure 10b); they are defined by groups of geographical differential species, as well as by many other species that reflect their different ecological affinities.

In the case of azonal forests, ecological influence prevails over geographical, although the latter is still very important. On the basis of numerical analysis, two sub-alliances of broad-leaved ravine forests in SE Europe have been proposed, both belonging to the central European alliance *Tilio-Acerion*: an amphi-Adriatic xerothermophilous sub-alliance *Ostryo-Tilienion platyphylli* (cluster 2) and an illyrian mesophilous sub-alliance *Lamio orvalae-Acerenion* (cluster 4). These sub-alliances are parallel to the already established central European sub-alliances *Lunario-Acerenion* (cluster 3) and *Tilienion* (cluster 1).

It can be concluded that associations of broad-leaved ravine forests from southeastern Europe build separate groups (sub-alliances) within the framework of the European alliance *Tilio-Acerion*.

Conclusion

We found that we can detect the integrated (community unit) concept along the gradients, which enables us to recognize individual community types (syntaxa). The research concentrated only on the elaboration of gradients, ignoring other parameters that could possibly also influence the results, such as sampling design, method of sampling, or elaboration of data (Chiarucci 2007; Roleček et al. 2007; Dengler 2009). These topics are discussed within cited references within an individual case study.

Although ordination and classification were treated as antagonistic in the past, they were found to be complementary for the elaboration of vegetation. As has already been established by Whittaker (1973), a comparison of the results of classification and ordination allows better understanding of vegetational processes and the interrelation between plants in communities.

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2.3 FUNKCIONALNI RASTLINSKI ZNAKI IN EKOLOŠKA STRATEGIJA ZDRUŽBE OZNAČUJEJO POSAMEZEN STADIJ SEKUNDARNE SUKCESIJE

Functional response traits and plant community strategy indicate the stage of secondary succession, Paušič A., Čarni A., Hacquetia, 2012, 11, 2, 209−225.

Izvleček

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

V raziskavi smo uporabili multivariatno DCA analizo. Opazovali smo položaj florističnih popisov v DCA ordinaciji, rastlinskim vrstam in opisanim stadijem sekundarne sukcesije pa smo pripisali izbrane funkcionalne rastlinske znake in ekološke poteze. Izračunali smo *Spearmanov* koeficient korelacije med pojavnostjo posameznega funkcionalnega rastlinskega znaka in TLA.

Nizkorastoče vrste zelišč 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 (polgrmičkov) 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 med sekundarno sukcesijo spreminja. Na pašnikih prevladujejo stres toleratorji. Po desetih letih ima združba strategijo kompetitor-stres tolerator, po dvesto letih pa kompetitor/kompetitor-stres tolerator.

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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.

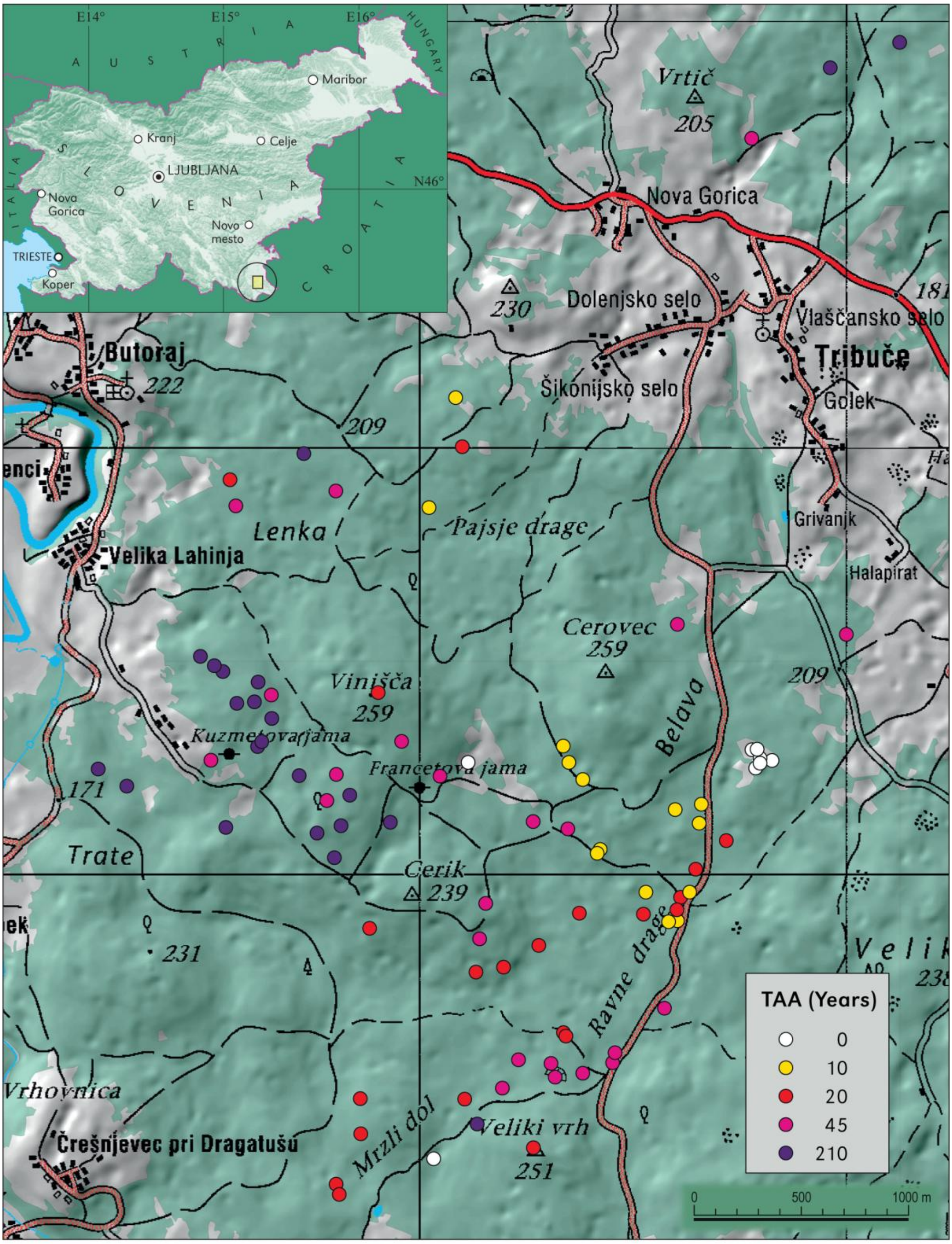

Figure 1: Study area in Bela krajina (SE Slovenia). The dots represent relevé plots with attached TAA attribute.
Slika 1: Območje raziskav v Beli krajini. Prikazane so lokacije popisov s podatkom o času od opustitve kmetijske rabe oz. paše (TAA).

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

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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.

Stage: A, B, C, D, E
TAA: 0, 10, 20, 45, 210

Percentage synoptic table with fidelity (Phi coeff. C)

Species	layer	Relevés (Age: 1 2 2 11 21 1 212 2222 2 2212222 / 1 3 11111112222323222233534361121343623533331765353837026727222742222372722252222 / 70004007020366555055500000588000000505802505550305205000050000000050500055000000080000000)	A	B	C	D	E
Leontodon hispidus	6	..1+1+++..	84.0	---	---	---	---
Hypochaeris radicata	6	..+1++1+..	84.0	---	---	---	---
Genista germanica	6	+.++.+1+..	84.0	---	---	---	---
Viola canina	6	++++++....+...	77.8	---	---	---	---
Dorycnium germanicum	6	+++.+++........+..	77.8	---	---	---	---
Calluna vulgaris	6	+334344+++.....+.+..+.1...	76.1	6.8	---	---	---
Pteridium aquilinum	6	51221325544552333443414422333223 1+.+++2+1..11211213++11+121+2.+..12......+1.+..+1..+.+++.	20.3	20.3	20.3	1.2	---
Brachypodium rupestre	6	23+.+++13.311+22112+1.1.....+..1..	45.1	48.6	---	---	---
Agrostis capillaris	6	1211..121+122+11.++++..1+..+++........+...............+..................+........	29.8	45.8	4.7	---	---
Betula pendula	4	+.............11+.+1++.+..	---	40.5	7.6	---	---
Clinopodium vulgare	6	.............+++....................+...	---	44.1	---	---	---
Dactylis glomerata	6	...+.........+.+++.........+..	2.1	39.9	---	---	---
Frangula alnus	4	........+.+++1+1111222211+2221112....++1....++.+...+.........++...................	---	46.8	56.0	---	---
Betula pendula	1	.............+..+3333.3431.21123..2..11...+......3+...1.3.......................	---	8.9	55.8	---	---
Populus tremula	1	.................1+...+11.+23.2....11.1.......2.....33..........................	---	---	52.8	3.6	---
Teucrium scorodonia	6	+...........+.........113+...2+...1...	---	---	50.9	---	---
Quercus petraea	3	......................1++2.323321........+......................................	---	---	79.2	---	---
Thuidium tamariscinum	9	..................................+........+.+...+....+....+..................+..	---	---	---	35.7	---
Aremonia agrimonoides	6	.................................+++....+..+.+...+.....+..........++..+..........	---	---	---	35.8	7.3
Fragaria moschata	6	........+................+...+++.++++++...++1+.+...............+....+.++..+.........+..	---	---	---	39.1	7.8
Epimedium alpinum	6	..+.+.11.2....+.21............2...224.++.++1344312134.2331.434333+2424++121.++..122+14.++.	---	---	---	34.5	28.6
Carpinus betulus	3	......................+.1.+.122.443453333511+4434435545434535355544455544554335425341313	---	---	---	51.4	51.4
Quercus petraea	1	..............+...2.......+3....2.1.332..+11.2..1122.....1...11.1322222221.15.1114233	---	---	---	16.2	52.9
Polygonatum multiflorum	6	..................................++......+.........+.+.....+..+.+++.++.++++++.+++1++++.+	---	---	---	---	75.6
Tamus communis	6	..................................+.+.......................+..+++++1++++++.++.++++	---	---	---	---	78.0
Galium sylvaticum	6	....+..+++++.+..++.+..+1++	---	---	---	---	69.5
Anemone nemorosa	6	...............+..........+1+.+..+...2....................+1.12223+.++.1+..223333++3.	---	---	---	2.3	67.5
Pulmonaria officinalis	6	..............................+.........................+.++..++++.++.+....+.+++..	---	---	---	---	66.6

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.*

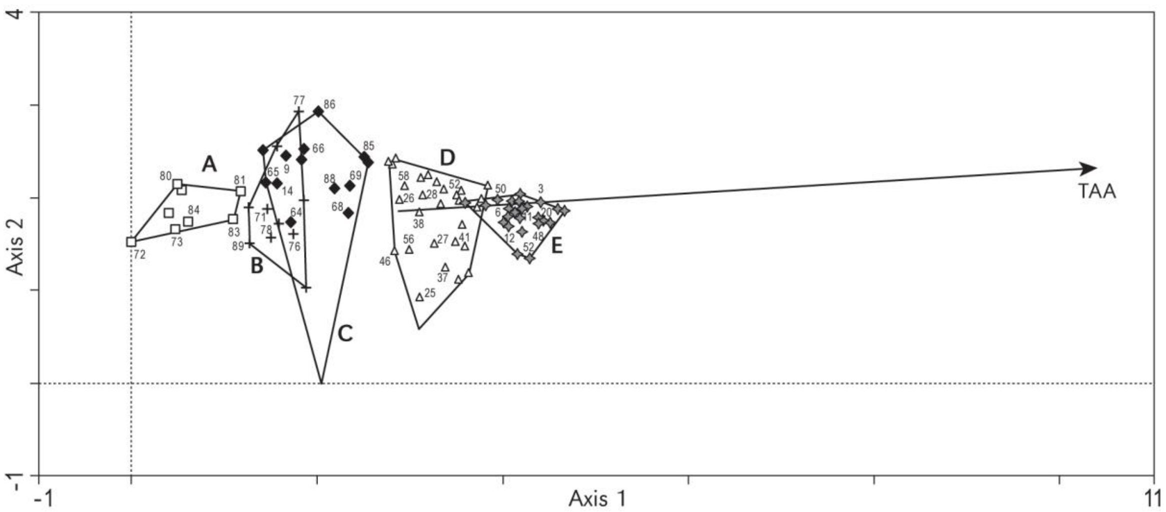


Figure 3: DCA ordination diagram with 89 relevés shows the separation of relevés into five groups (A–E), which correspond to the passive projection of the TAA.

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	(*)

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 scleromorphic 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.

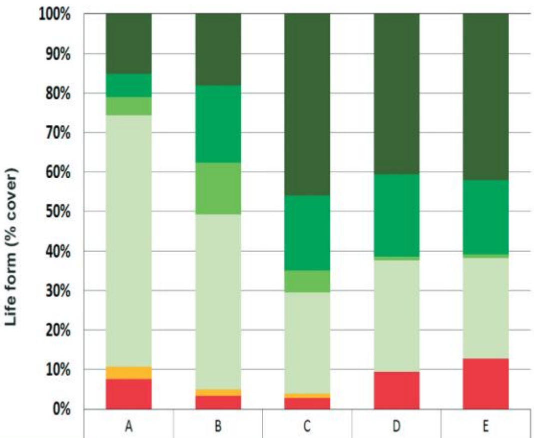
In the fruit type group, berry and nut correlate positively with TAA, which indicates that the number of species with these traits increases with the land use abandonment stage. The capsule trait has a strong negative correlation with TAA.

Within the diaspore group, the spore trait and the fruit with appendage trait have a high positive 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.



	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*.

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).

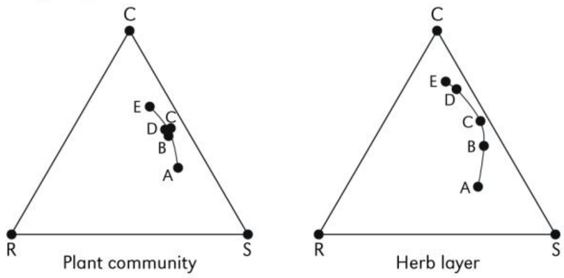


Figure 5: Changes in CSR signatures of the whole plant community and herbal layer in secondary succession. A – *Calluna* stage, B – *Pteridium-Frangula* stage, C – *Betula* stage, D – *Epimedium-Carpinus* stage and E – *Carpinus-Quercus* stage.

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.

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2.4 PODATKI O NEKDANJI RABI SE NAJBOLJE ODRAŽAJO V EDAFSKIH ZNAČILNOSTIH.

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Izvleček

Raziskava je potekala v Beli krajini. V raziskavi smo izdelali štiri generalizirane aditivne mešane modele (GAMM) s pomočjo izbranih funkcionalnih rastlinskih znakov, rastlinskih horotipskih pripadnosti, Ellenbergovih bioindikatorskih vrednosti in edafskih značilnosti popisnih ploskev. Testirali smo napovedno moč izdelanih modelov za čas od opustitve kmetijske rabe zemljišča (TLA). Raziskava obravnava pristop, pri katerem s pomočjo izbranih skupin parametrov napovedujemo TLA.

V raziskavi smo uporabili stare katastrske načrte, letalske posnetke in digitalne ortofoto posnetke območja. Omenjene prostorske vire smo digitalizirali. S pomočjo prekrivanja uporabljenih virov o rabi prostora smo določili dejanski čas, po katerem je bila kmetijska raba na obravnavanih popisnih ploskvah prekinjena. Podatek je v analizi služil kot odvisna spremenljivka in kot kontrola samih rezultatov pri modeliranju.

Raziskava je pokazala, da se podatek ali informacija o času opustitve kmetijske rabe tal odraža v edafskih značilnostih tal, funkcionalnih rastlinskih znakih, horotipih vrst in Ellenbergovih bioindikatorskih vrednostih vrst na popisnih ploskvah.

Izbrane edafske značilnosti so najboljši vir informacij za napovedovanje TLA.

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Records of past land use are best stored in soil properties

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Abstract

Four models from selected trait groups (plant functional traits, plant chorotypes, Ellenberg bioindicator values and soil properties) were developed, and their predictive power for the time since land use was abandoned in Southeastern (SE) Slovenia was compared. The analysis highlights an approach that determines the age of forest using ecological, chorological and pedological attributes. The aim of the study was to develop a tool, a combination of functional response traits, chorotypes, ecological characteristics and soil properties, which allows calculation of the time since land use abandonment (TLA) for a particular secondary succession stage. Using old cadastral maps and orthophotos and employing an overlapping technique, the actual TLA for the sample plots was determined, which served as a dependent variable in modelling, as well as a control for modelling accuracy. The predictive power of four different ecological models was compared. The study shows that information about the process of abandonment of traditional land use is stored within the changes of plant functional response traits, chorotypes and Ellenberg bioindicator values of the study area, but is best reflected in soil properties. Soil properties provide the most reliable basis for the elaboration of a prediction model for TLA.

Keywords: *chorology, functional response traits, land use abandonment, Slovenia, secondary succession, soil properties*

Introduction

Vegetation change has traditionally been described by changes in species composition. However, the need to predict the effects of land use change on vegetation structure and composition on regional and global scales has led to an ongoing effort to identify plant functional traits and types that relate to land use change (Díaz & Cabido 1997; Castro et al. 2010). The study of morphological, physiological, phenological and ecological plant traits overall has yielded deep insight into many plant–environment and plant–plant relations (Saatkamp & Römermann 2010). The trait-based approach aims at generalization of vegetation patterns beyond specific sites or taxa and at prediction of species composition. This approach also extends the identification of changes to ecosystem association level (Violle et al. 2007; Castro et al. 2010; Saatkamp & Römermann 2010; Jose-Maria et al. 2011; Vassilev et al. 2011).

The relationship among the ecological characteristics of plant communities, measured plant traits and their changes over time is usually analysed by means of linear regression, which is one of the oldest and most frequently used techniques for developing prognostic models, because it is simple to use and produces results that can be successfully interpreted (Curt et al. 2001; Pykala et al. 2005; Seynave et al. 2005; Pueyo & Alados 2007; Aertsen et al. 2010). Although this method is exceptionally accurate when applied correctly, it is practically impossible to develop models by means of linear regression when the observed variables are nonlinear (Aertsen et al. 2010; Saatkamp & Römermann 2010).

This study is about the investigation of functional response traits, chorotypes, Ellenberg bioindicator values and soil properties turnover during spontaneous afforestation (secondary succession) of former pastures in SE Slovenia and evaluation of their predictive value for time since land use abandonment (TLA). During secondary succession, vegetation develops towards the potential natural vegetation (Mucina 2010; Čarni et al. 2011; Hegedusova & Senko 2011). Only plant species that are adapted to the new (forest) conditions survive and are preserved; otherwise, new species

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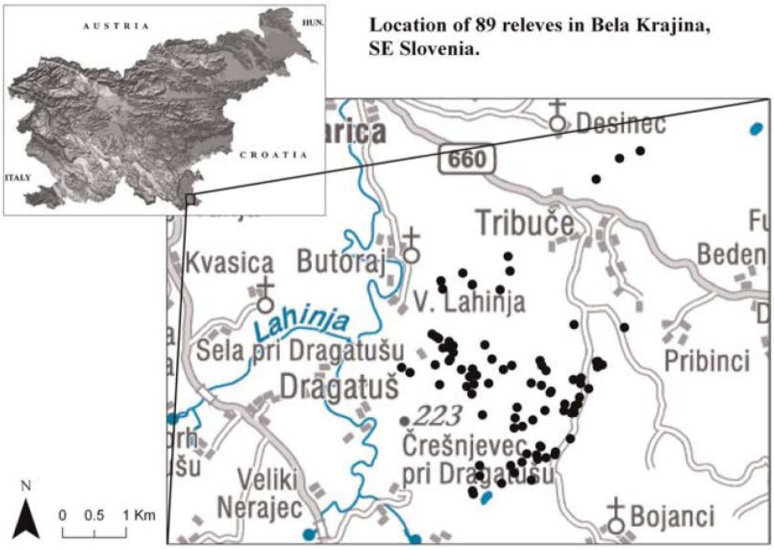

Figure 1. Study area in Bela Krajina (SE Slovenia).

appear and this process also changes the ecological characteristics of the community (Castro et al. 2010; Johansson & Cousins 2010; Latzel et al. 2010; Řehunková & Prach 2010; Saatkamp & Römermann 2010), which proceeds towards a more stable condition, the current potential vegetation (Biondi et al. 2004; Loidi et al. 2010; Biondi 2011). The concept of "current potential vegetation" is an expression of the type of vegetation that will come into an area as long as human activities are evident in that area, obviously excluding major and sudden climate change events (Biondi 2011).

Various studies have linked land use changes to changes of functional response traits. Castro et al. (2010) studied the turnover of plant functional response traits in relation to land use change in Montado. A study by Saatkamp and Römermann (2010) examines plant functional traits and their nonlinear response to grazing. The authors used generalized additive models (GAMs) for data treatment and studied the response of each particular trait to grazing activity. Most studies to date have been linked to the studies of trait response or the trait group turnover process during land use change.

However, can we use plant functional response traits, chorotypes, Ellenberg bioindicator values or soil properties as information sources about the time since traditional land use abandonment? Is information about the secondary succession stages in some way "stored" in these trait groups? We were particularly interested in developing a method that will allow us to calculate TLA precisely (in years) for any forest stand in the study area.

Many methods, of course, provide forest stand age quite accurately, with the help of cadastral maps, with aerial photo images, by which one can estimate the development stage of a studied forest patch, with the help of soil samples, interviewing local people, etc. However, we were interested in what information about TLA is carried by plant chorotype characteristics, Ellenberg bioindicator values, soil properties and functional response traits.

The analysis includes generalized additive mixed models (GAMMs), since they allow combined analysis of both linear and nonlinear variables in a single model. By means of the models, we tried to simplify the expression of the process of agricultural abandonment change in such a way so as to give the process real attributes and to study them over a specific area.

The aim of the study was to develop models from selected trait groups (plant functional traits, chorotypes, bioindicator values and soil properties) and to compare their predictive power for TLA. The specific objectives of the study were to rank the four chosen trait groups according to their predictive performance on TLA and compare their predictive power. Our hypothesis was that TLA for each secondary succession stage is "stored" in plant traits and soil properties. With the right combination of different variables within a trait group, one can elaborate a formula that is powerful enough to calculate the TLA for a forest stand.

Materials and methods

Study area

The research took place in the region of Bela Krajina in SE Slovenia (Figure 1). This is a Pleistocene karst corrosion plain at an altitude between 150 and 320 m, formed mainly by calcareous rocks (limestone

Table I. The following groups of variables were foreseen for developing the models representing the agricultural abandonment process (TLA).

Soil analysis	
• pH ($CaCl_2$) value	
• Organic matter	
• C	
• C/N ratio	
• N	
• Ca^{2+}	
• Mg^{2+}	M1 – Model 1
• K^+	
• Na^+	
• Total exchangeable acidity (h)	
• Sum of base cations (s)	
• Cation exchange capacity (t)	
• Proportion of base cations (v)	
Traits describing the vegetative morphology of species	M2 – Model 2
The method of vegetative propagation (Grime et al. 1997; Mony et al. 2010)	
Traits describing the shape and morphology of photosynthesising leaves	
Leaf anatomy (Klotz et al. 2002)	
Traits describing the flower shape and reproductive biology of species	
1. Flower colour	
2. Diaspore weight (mg)	
Three weight classes were used: diaspores with weight <1 mg, 1–50 mg and >50 mg	
Data on ecology	M3 – Model 3
1. Ellenberg bioindicator values for plant relevés (Ellenberg 1992)	
2. Species chorotypes	M4 – Model 4

and dolomites). On the surface, these rocks weather into chromic cambisols, which sometimes even completely cover them. The potential natural vegetation of the area is illyrian oak-hornbeam forest (Čarni et al. 2007). The actual vegetation of the study area consists of various successional stages, from pastures to *Quercus petraea–Carpinus betulus* forest: *Calluna* stage, *Pteridium – Frangula* stage (initial stage of secondary succession, in which *Pteridium aquilinum* and the shrub species *Frangula alnus* prevail), the *Betula* stage, the *Epimedium–Carpinus* forest stage (*C. betulus* is the dominant tree species). The *Carpinus – Quercus* stage is the end stage of secondary succession in the study area (Čarni et al. 2011).

Annual precipitation in this part of Slovenia ranges between 900 and 1000 mm, and mean annual air temperature is between 9.3 and 12.9°C (Environmental Agency of the Republic of Slovenia – ARSO 2010). The climate of the study area is strong subcontinental (Rivas-Martínez et al. 2011).

An area of ca. 7000 ha was selected (45.467189–45.585940°N and 15.149351–15.361001°E) for the purpose of this research.

Vegetation and soil analysis

In order to obtain samples with similar geomorphologic, pedological and ecological characteristics, 89 plots (10 m × 10 m) were selected on flat terrain away from depressions or sinkholes. The plots were located in different stages of secondary succession, from pastures to the *Carpinus – Quercus* stage. The minimum distance between sample plots was 100 m.

The communities were sampled and elaborated by the modified standard Braun-Blanquet method (Braun-Blanquet 1964; Tüxen 1974; Géhu 1997; Géhu 2006; Blasi et al. 2011; Blasi & Frondoni 2011; Pott 2011). Data were stored in the Turboveg program (Hennekens & Schaminee 2001).

Using the BiolFlor database (Klotz et al. 2002), the species (249 recorded taxa) were attributed selected functional response traits and data on habitat preferences of species (bioindicator values; Ellenberg et al. 1992) for each selected plot in turn. The selected traits were subsequently analysed along the succession gradient, and the changes were evaluated.

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

Representative compound soil samples (depth 0–10 cm) of all 89 plots were taken in order to analyse the chemical soil properties. The samples were treated in accordance with ISO 11464, and the following characteristics were measured: the pH value of $CaCl_2$ was determined in accordance with ISO 10390 and organic carbon was determined in accordance with ISO 14235; the total nitrogen (N) content was determined according to the modified

Table II. Descriptive statistics of the studied variables.

Variable	Abbreviation	Unit	Min.	Max.	Mean	Trend	GAMM R^2	F	p-Value	Linear R^2	Trait group – model selection
Potassium content	K content	%	0.18	0.48	0.18	Nonlinear	0.0108	0.222	0.639	0.00634	M1
Magnesium content	Mg content	%	0.2	1.25		Nonlinear	0.0487	4.73	0.0328	0.07143	
C–N ratio	CN ratio	%	2	18.5	8	Nonlinear	0.182	17.26	8.84e−05	0.1885	
Content of organic material	ORGANIC	%	0	9.7	6.5	Nonlinear	0.152	2.679	0.0088	0.05264	
Tree layer cover	Tree.layer	%	2	90	38.7	Decrease	0.18	17.02	9.78e−05	0.1032	M2
Vegetative propagation (fragmentation)	VEG_fragment	Value	2	11	5.82	Decrease	0.0396	4.013	0.0489	0.008174	
Leaf anatomy – mesomorphic	Mesomorphic.leaf	Value	5	32	18.41	Decrease	0.0132	0.047	0.828	0.00985	
Flower colour – white	White flowers	Value	0	12	4.3	Nonlinear	0.0101	0.267	0.607	0.0111	
Diaspore weight (>50 mg)	SEED.3	Value	2	17	9.15	Increase	0.0231	2.726	0.103	0.06313	
Ellenberg value – light	Light	Value	3.76	6.93	5	Nonlinear	0.525	10.24	8.23e−10	0.4068	M3
Ellenberg value – temperature	Temperature	Value	5.3	6.21	6	Nonlinear	0.185	4.344	0.00167	0.1532	
Ellenberg value – moisture	Moisture	Value	4.35	5.62	5	Increasing	0.00937	0.323	0.572	0.01071	
Ellenberg value – soil reaction	Soil react.	Value	3.31	7.55	5.4	Nonlinear	0.336	37.95	3.74e−08	0.3196	
Ellenberg value – nutrients	Nutrients	Value	2.78	5.5	4.25	Nonlinear	0.324	36.03	7.17e−08	0.2899	
Chorotype – Stenomediterranean	STENO	Value	0	10.34	0.158	Nonlinear	0.0573	0.584	0.447	0.00572	M4
Chorotype – Eurimediterranean	EURIMED	Value	0	9.68	1.36	Nonlinear	0.177	2.96	0.00893	0.08457	
Chorotype – Mediterrannean – montane	MED.MONT	Value	0	6.67	0.063	Increasing	0.235	23.43	7.18e−06	0.235	
Chorotype – Atlantic	ATLANTIC	Value	0	6.45	0.23	Nonlinear	0.191	5.23	0.000943	0.1589	
Chorotype – Orophytic – S. European	OROPH.S.EUROP.	Value	0	8.82	0.068	Increasing	0.118	10.78	0.00158	0.1181	
Cosmopolytes	COSMOP.	Value	0	7.27	1.42	Decreasing	0.0649	6.065	0.0162	0.06487	

Note: The variables were selected for the four final models and for describing the TLA.

Kjeldahl method (ISO 11261) and the plant-available phosphorus (P) and potassium (K) were determined by the methods suggested by Hoffman (1991). Exchangeable base cations (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) were analysed using atomic absorption spectrophotometry, and H^{+} was determined using the titrimetric method (ISO 10390).

Land use abandonment and explanatory data

The period of time since agricultural land use was estimated by overlaying different digitalized old cadastral maps and digital orthophotos: Josephine military maps 1784–1790 (Rajšp & Ficko 1996), Franciscan land cadastre 1823 (Petek & Urbanc 2004), military maps from 1913 (Militärgeographisches Institut 1913) and 1937 (Vojnogeografski Institut 1937) and aerial photos (1954, 1975, 1986, 1999 and 2009).

We studied the development of vegetation after land use abandonment, which is reflected in changes in floristic composition on 89 sample plots. The stage of the reforestation process was described with a time variable, i.e. by real TLA of an individual sample plot (Table I).

Statistical data analysis, modelling technique

Detrended correspondence analysis (DCA) was carried out with the Canoco 4.5 program (Ter Braak & Šmilauer 2002) in order to observe the position of the relevés along axis 1. It was established that relevés in DCA have a distinct position in the typical succession (age) continuum, which corresponds to the passive projection of community age.

Axis 1 is therefore considered to be the TLA, and values of axis 1 were used as a dependent variable in the subsequent analyses.

In the second step, we calculated bivariate correlations between different explanatory variables of each trait group. Variables that showed a correlation of $r > 0.70$ with those that explained more information were removed from the analysis, in order to avoid multicollinearity in our models, following Alahuhta et al. (2011) and Sullivan et al. (2011). All the other variables were included in the GAMMs. Twenty of the total of 56 potential explanatory variables were initially selected to be included in our models (Table II).

Since some of the variables in the selected models show a linear response (tested by GAM), the GAMM was chosen as the most suitable analysis method for the explanation of the stage of land use abandonment. GAMMs are an additive extension of generalized linear mixed models (GLMMs) according to Hastie and Tibshirani (1991). This class of models uses additive non-parametric functions to model covariate effects, while accounting for over-dispersion and correlation by adding random effects to additive predictors. GAMMs encompass nested and crossed designs and are applicable to clustered, hierarchical and spatial data (Wood 2006).

A GAMM is therefore simply a GLMM in which part of the linear predictor is specified in terms of smooth functions of covariates (Lin & Zhang 1999; Wood 2006). A GAMM model has a structure something like

$$y_i = X_i\boldsymbol{\beta} + f_1(x_1i) + f_2(x_2i, x_3i) + \cdots + Z_i\boldsymbol{b} + \boldsymbol{e}_i,$$

where y_i is a univariate response; $\boldsymbol{\beta}$ is a vector of fixed parameters; X_i is a row of the fixed effects model matrix; f_j are smooth functions of covariates x_k; Z_i is a row of the random effects model matrix; $\boldsymbol{b} \sim N(0, \psi\theta)$ is a vector of random effects coefficients, with unknown positive definite covariance matrix $\psi\theta$, with parameter θ and $\boldsymbol{e} \sim N(0,\Lambda)$ is a residual error vector, with the ith element e_i, and covariance matrix Λ, which is usually assumed to have some simple pattern (Wood 2006).

The modelling employed the user interface R Studio (R Studio Project 2010). The GAMMs were developed using full stepwise procedures to select relevant explanatory variables. The full stepwise selection procedure utilizes both backward and forward procedures, in which explanatory variables are removed from the model (backward) or added to the empty model (forward). The goal is to achieve maximized residual deviance, without the variables in the model contributing to the residual deviance (Alahuhta et al. 2011).

Once the models had been constructed, the Akaike information criterion (AIC) was examined (Akaike 1974). The AIC provides an effective and objective means for the selection of an estimated "best approximating model" for data analysis (Burnham & Anderson 2002; Sullivan et al. 2011). We also tested other selection algorithms [Bayesian information criterion (BIC) and F], but AIC showed the best prediction accuracy in all four models.

The models were validated using the percentage of explained deviance D^2 (Alahuhta et al. 2011), with the area under the curve (AUC) of a receiver-operating characteristic (ROC) plot and the coefficient of determination R^2 (Pearson 1896). However, a number of authors have concluded that R^2 is not a good measure for comparing different models because it only provides information on how well the model fits the data used to build the model, and not on how well it performs on external data (Cerrato & Blackmer 1990; Aertsen et al. 2010). The model accuracy based on AIC was calculated with the R package tools for visualizing, smoothing and comparing receiver operating characteristic (pROC), and was evaluated with the following classification: low (<0.7), moderate

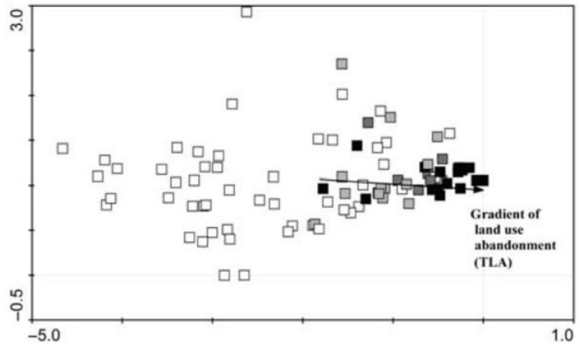

Figure 2. The DCA of 89 relevés shows the arrangement of relevés along the secondary succession gradient, which corresponds to the passive projection of community age (TLA). The brighter relevés are recently abandoned plots, whereas the darker relevés represent more advanced stages of afforestation and black relevés represent the potential natural vegetation.

(0.7–0.8), good (0.8–0.9) and excellent (>0.9) (Swets 1988). In addition, visual validation of the response curves and spatial predictions were conducted according to the standard procedure (Saatkamp & Römermann 2010) (Figure 4).

The predictive power of models was subsequently tested with the actual input of the explanatory variables that explain the stage of land use abandonment or the stage of secondary succession.

Real data for variables were entered into the models. The result was the age of the secondary succession stage in years, calculated by the model. Pearson's correlation coefficient (Pearson's product moment – *r*) was used to compare the accuracy of the model. The correlations between the calculated TLA in R and the real TLA (gained from overlaying cadastral maps and aerial images) were calculated in Statistica 8.0 (Statsoft Inc. 2007; Canullo et al. 2010). Pearson's correlation coefficient ranges from −1 to +1. A value of +1 is the result of a perfect positive relationship between two or more variables (Nie et al. 2011).

The predictive power of each model was presented in a scatter chart that incorporated the TLA of observed land use categories and the results of the models used.

Variables within each model were analysed. We observed the response of an individual variable in a model (linear – nonlinear) and the logic of each variable's response with regard to the relative measured frequency of the dependent variable, the TLA (Figure 4).

Results

The DCA diagram analysis shows the characteristic position of 89 relevés in a distinct gradient of reforestation stages that correspond to the TLA. Since the relevés are arranged according to the time abandonment gradient and are positioned along axis 1 in DCA, axis 1 can be used as a dependent variable, a proxy for TLA. The eigenvalue of axis 1 is 0.636, whereas axis 2 has a lower eigenvalue of 0.261. This shows that axis 1 (proxy for TLA) is the most important factor in the diversification of vegetation in the study (Figure 2).

Variables for four individual models were selected from the full list, excluding those for which the correlation level exceeded 0.70. A set of variables that were included in the model building of the status of secondary cuccession was prepared (Table II).

Our first trait group (M1) encompasses soil properties obtained by the chemical analysis of the samples collected on sample plots. Trait group 2 (M2) encompasses ecological characteristics of plant species and measured functional morphological characteristics, M3 comprises Ellenberg bioindicator values for the plant taxa recorded and trait group 4 (M4) comprises chorological characteristics of the species found on the sample plots (Table II).

By means of the inclusion and exclusion of individual variables from each model, we obtained different results, and decided on the combination of variables for each option that gave the best results for each particular trait group (Supplementary Material). The predictive powers of each trait group are presented in Table III.

As is evident (Figure 3), the four models differ considerably with regard to their predictive power. M1, which contains the variables obtained by soil analyses, came closest to the actual TLA. The group has a Pearson's coefficient value, obtained by comparison of the trait groups result with the real data, of 0.878. This group also has the highest

Table III. Differences in the predictions of TLA in four different trait groups based on calculated Pearson's correlation coefficient (*r*), percentage of explained deviance (D^2), AIC, BIC, AUC of an ROC plot and coefficient of determination (R^2).

Trait group	Trait group description	*R*	D^2	AIC	BIC	AUC	R^2
M1	Soil properties	0.878	89.3	1016.052	1040.934	0.7867	0.811
M2	Plant functional traits	0.812	84.2	1008.020	1030.417	1	0.781
M3	Ellenberg bioindicator values	0.761	81.5	977.143	1002.030	1	0.742
M4	Chorological characteristics	0.656	62.4	985.218	1015.082	0.7738	0.573

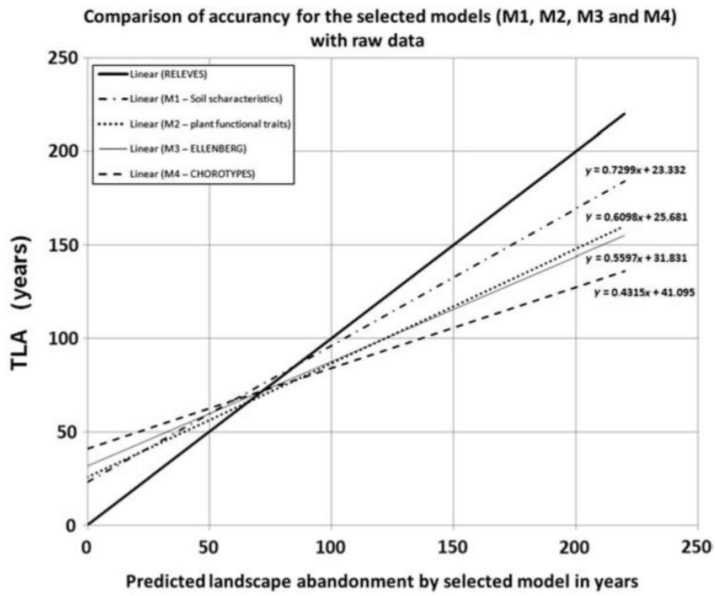

Figure 3. Comparison of predictive power of trait groups for TLA. The thick full line represents the function for real data, to which we added result functions for an individual model. The chart clearly indicates the predictive power of trait groups, presented in the diagram with a function incline (k) by the formula $f(x) = k(x) + n$.

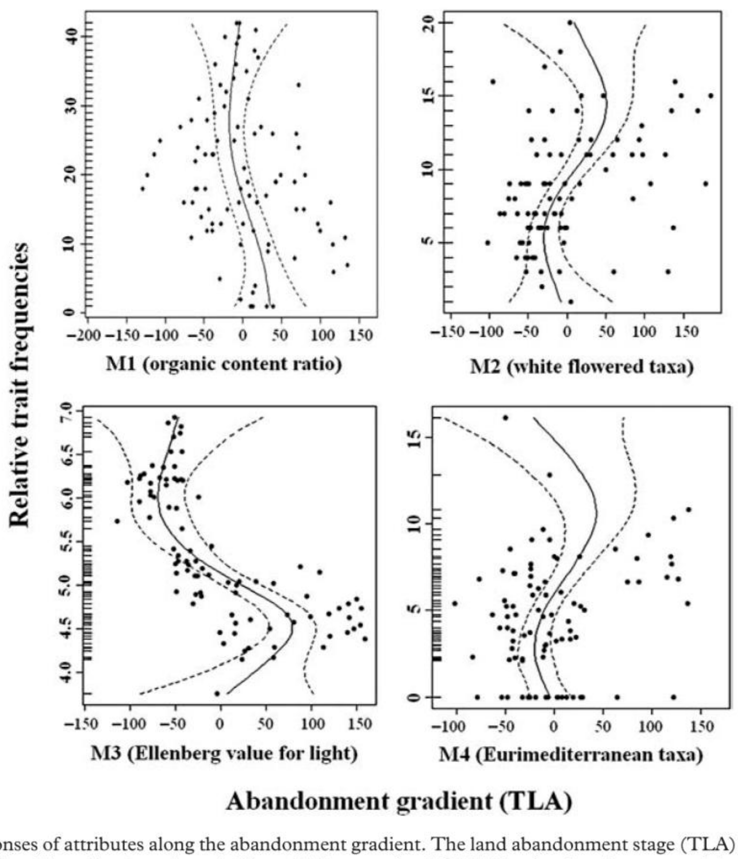

Figure 4. Nonlinear responses of attributes along the abandonment gradient. The land abandonment stage (TLA) was measured as the time since the abandonment of traditional land use (years). The solid lines are fitted GAMMs of each trait group and the broken line areas indicate twofold standard error ranges around the model. The most significant attribute responses are presented, one analysed for each trait group.

proportion of explained deviance (D^2), AIC value and other measured values (Figure 3).

M2 (functional morphological plant trait model) comes the closest to M1. The value of the calculated Pearson's correlation coefficient for this group is 0.812.

Models M3 and M4 have lower predictive power. M3 (Ellenberg bioindicator values) has a higher predictive power than M4 when tested with real data ($r = 0.761$).

M4, which comprises the chorological characteristics of the recorded plant species on the sample plots, is therefore the least accurate predictive model for the evaluation of the level of landscape afforestation ($r = 0.656$).

The estimation of the models' adequacy, i.e. their predictive power, is fairly abstract information, estimated with selected measured statistical coefficients each of which (in turn) describes the power of an individual model. There is therefore, often a dilemma of whether the result is truly satisfactory. In order to provide a more illustrative presentation of the models' predictive power, a scatter diagram was created, in which only the trend of the imputed function was preserved for each model, while, for the sake of clarity, the values for each relevé were excluded (Figure 3).

Throughout the modelling process, we checked the intermediate results (predictive power) for each model in turn. Each variable used in the model was selected according to its response along the TLA gradient (Figure 4). One example is the organic content ratio variable in Model 1 (soil properties), which shows a nonlinear response to TLA. The curve of the organic content ratio along the TLA gradient (Model 1) declines with TLA as a result of land use abandonment. The described variable is strongly related to changes caused as a result of previous agricultural activity (grazing activity, a source of organic substance), and is therefore an appropriate variable to be selected for the model. In Model 2 (plant functional traits), we also included the variable "white flower colour". This variable relates to the number of white-flowered taxa growing in each succession stage. It is evident that forest stands with a TLA between 50 and 100 years containing species that predominately flower white.

Model 3 contains Ellenberg bioindicator values for plant relevés. The value for light was also included and its index is higher in young forest stands and in open landscape. In Model 4 (chorological characteristics), we included a variable of species chorotypes. It is evident that pastures (open landscape overall) are the habitats in which the most Eurimediterranean taxa occur.

Discussion

The results showed that, for all the considered attributes, agricultural land use abandonment causes changes in the species composition and in the ecological properties of the study area (Figure 4). These changes can be well perceived with the study models that describe the soil characteristics of a particular area. Other authors have analysed agricultural land use abandonment versus plant community composition change with the help of various functional attributes (life forms, growth forms; Jose-Maria et al. 2011). Their results showed that agricultural abandonment causes a reduction in species numbers and a general trend of total species reduction.

We tried to go a step further in our study and developed a method of predicting the TLA with the help of Ellenberg bioindicator values, functional response traits, plant chorotypes and soil properties. Soil properties have the strongest predictive power and are a relevant indicator for the TLA in a particular region (Bock et al. 2005; Čarni et al. 2007; Holtkamp et al. 2011). This is evident from the results of this study.

The type of community that overgrows abandoned agricultural land (meadow, field) at a certain stage of secondary succession therefore reflects the C/N ratio, the amount of soil organic matter and the amount of exchangeable cations. Čarni et al. (2007) mention the highest rate of C/N ratio at the stage of secondary forest succession dominated by birch (*Betula pendula*) and aspen (*Populus tremula*); later, with concurrent rapid decomposition, the value of this ratio decreases. Their study also noted that the amount of base cation Na^+ does not change considerably through secondary forest succession. This is also confirmed by our study. Pearson's correlation coefficient (r) for traits used in M1 with the actual forest stand age is very high, so we are of the opinion that M1 is a good and precise tool for the estimation of (forest) stand age (in years).

Many studies have already concluded that there is no general best modelling technique (Thomas & Neil 1991; Aertsen et al. 2010; Saatkamp & Römermann 2010) but, depending on the scope and goal of the study, some of them will probably be better suited than others in particular situations.

In this study, we assume that changes in soil properties in the observed area are a good predictor for the TLA of a particular forest stand in secondary succession.

Our study provides an insight into the strength of the GAMM technique used for modelling the time since traditional land use was abandoned. We propose Pearson's correlation coefficient for trait group comparison and evaluation.

Conclusions

Four models, consisted of different trait groups, were compared and evaluated for their power of predicting TLA. Based on the calculated statistical predictors and calculated predictions for each trait group (model) in the R program, the trait group including soil properties was shown to be the most powerful tool in our study for predicting TLA, followed by functional morphological plant traits and Ellenberg bioindicator values.

Our research findings indicate that information about the TLA is best "stored" in soil properties, which are a powerful predictor of the stage since the abandonment of traditional land use.

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Note

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3 RAZPRAVA IN SKLEPI

3.1 RAZPRAVA

Prva raziskava (1.1) obsega spreminjanje krajinske zgradbe na območju Bele krajine v zadnjih 200 letih.

Rezultat raziskave je pokazal, da se je število prebivalcev na opazovanem območju (vasi Butoraj, Bojanci, Dragatuš in Tribuče) od leta 1820 do 1948 zmanjšalo. Tako je bilo leta 1820 881 prebivalcev, 1948 pa le 662 prebivalcev. Po letu 1948 začne število prebivalcev ponovno naraščati. Leta 1961 je bilo na območju 697 prebivalcev, leta 2002 pa 770 prebivalcev. Spreminjanje števila prebivalcev na opazovanem območju je posledica treh migracijskih tokov. Prvi se je začel v začetku 20. stoletja. Temu valu izseljevanja sledi izseljevanje prebivalcev med 1. sv. vojno (ko se začne kmetijska dejavnost na območju že opuščati) ter zadnji val izseljevanja med in po 2. svetovni vojni (Drnovšek in Brodnik, 2002).

Med časom izseljevanja in po njem sta se spreminjali krajinska zgradba in pestrost. Tak trend prikazuje tudi naša raziskava. V raziskavi sprememb krajinske zgradbe smo uporabili metodo prekrivanja starih katastrskih načrtov, vojaških kart, letalskih posnetkov in digitalnih ortofoto posnetkov. Podobno metodo sprememb krajinske zgradbe uporabljajo tudi druge novejše študije (Drummond in sod., 2012; Parcerisas in sod., 2012; Paudel in Yuan, 2012; Skaloš in Kašparová, 2012; O. Vanwambeke in sod., 2012). Metoda je uporabna in daje točne rezultate prav zaradi načina pridobivanja podatkov o spremembah v krajini.

Raziskava kaže, da se meje zemljiških parcel na območjih od leta 1823 do danes skorajda niso spremenile. Zato lahko uporabimo meje, kote parcel kot denivelacijsko izhodišče pri vpenjanju starejših katastrskih virov na recentne podlage. Pri vojaških kartah, letalskih in ortofoto posnetkih smo kot izhodišče pri vpenjanju uporabili kote ter pomembnejše objekte v krajini (cerkvene zvonike, vrhove, stolpe ipd.) (Forman, 1995; Farina, 2007). Težava nastopi zgolj pri vpenjanju starejših kartografskih virov, recimo Jožefinskega katastra (1784−1790). Gre za katastrske načrte in vojaške karte, ki so po izdelavi precej nenatančni. Zato so tudi informacije, ki jih pridobimo iz omenjenih virov, zgolj informativne narave, a kljub temu pripomorejo k splošnemu razumevanju sprememb krajinske zgradbe.

Rezultat raziskave spreminjanja krajinske zgradbe med leti 1790 in 2009 kaže na homogenizacijo ali poenotenje prostora. Tako se nekoč precej heterogena (kmetijska) krajina zaradi spreminjanja (opuščanja) kmetijske rabe danes zarašča.

Osnovni gradniki krajine, predvsem elementi krajinske matice (mejice, gozdni otok, sklenjene gozdne površine) pa se po površini večajo. Podobne študije omenjajo proces naglega zaraščanja in spremembe krajinske zgradbe tudi za druga območja Slovenije in Evrope (Cocca in sod., 2012; Corbelle-Rico in sod., 2012; Schmitz in sod., 2012).

V našem primeru sta hitrost zaraščanja krajine ter sprememba krajinske zgradbe najhitrejši po letu 1937. Menimo, da je to predvsem posledica skokovitega naraščanja gozdnih površin, predvsem zaradi naglega izginjanja pašnih površin (po letu 1937) in večanja deleža zaraščajočih površin ter gozdnih površin (po letu 1954). Vzrok tako naglega spreminjanja krajinske zgradbe pripisujemo agrarni krizi, ki v Beli krajini nastopi okoli leta 1930 (Dušak in sod., 2012). V omenjenem času je imelo veliko kmetov dolgove, kmetije pa so prehajale na dražbo.

Čeprav splošni trend zaraščanja krajine kaže na zmanjšanje pašnih površin (po letu 1937), pa to ne drži za njivske površine, katerih največji delež na območju opazimo prav v letu 1954. Omenjena obdelovalna zemljišča se leta 1954 nahajajo na območju Sadežev, torej na zahodnem delu območja raziskav.

Predvidevamo, da so porastu deleža njivskih površin botrovale ugodnejše gospodarske razmere po drugi svetovni vojni ter želja nekaterih kmetov, da izkoristijo ugodna kmetijska območja za gospodarsko rast (Dolenjski list, 1954). Očitno je, da so omenjene njivske površine kmetje pridobili iz nekdanjih vinogradov in pašnih površin.

Travniških površin je bilo na opazovanem območju največ leta 1954, predvsem zaradi premene pašnikov (boljše kvalitete) v travniške površine. Tak trend sprememb pripisujemo postopnemu ukinjanju pašništva na območju ter zaraščanju pašnih površin. Potrebno je dodati dejstvo, da smo imeli pri starejših, nenatančnih prostorskih virih težave z opredelitvijo oz. ločevanjem pašnih in travniških površin. V tem primeru smo izhajali iz prejšnjega, znanega stanja. Tako smo vse površine, za katere na vojaški karti iz leta 1913 nismo poznali natančne opredelitve rabe tal (ločevanje pašnik – travnik), le-to povzeli iz zanesljivega vira; Franciscejskega katastrskega načrta. Pri starejših letalskih posnetkih smo to težavo odpravili s pomočjo poznavanja reliefa območja (skalovitost in naklon).

V raziskavi smo se dotaknili tudi raziskave procesa drobljenja oz. fragmentacije krajinske zgradbe, ki je v neposredni povezavi s spreminjanjem krajinske zgradbe. Fragmentacijo oz. drobljenje krajinske zgradbe razlagamo kot drobljenje habitatov in kmetijskih zemljišč na manjše homogene dele. Drobljenju ali fragmentaciji podoben proces v krajini je enostavno deljenje površin na podobne, homogene dele (ang. dissection) (Forman, 1995).
Oba omenjena procesa spreminjanja krajinske zgradbe imata iz ekološkega gledišča podoben učinek; to je drobljenje habitatov, ekotopov ter s tem povezano ločevanje populacij vrst (živalskih in rastlinskih), kar v skrajnem primeru vodi v nastanek

metapopulacij (če med njimi ni povezovalnih koridorjev) ali celo do izumiranja posameznih rastlinskih in živalskih vrst. Krajina postane posledično heterogena ali (enakomerno) heterogena zaradi procesa disekcije (Forman, 1995; Farina, 2007).

Metodo ocenjevanja in ovrednotenja drobljenja ali fragmentacije krajinske zgradbe predstavlja že Forman (1995). Metoda sloni na foto interpretaciji prostorskih podatkov (satelitski posnetki, letalski posnetki), kjer nas zanimajo: (A) površina posamezne zemljiške oz. kmetijske kategorije (za vsako opazovano obdobje posebej), (B) število, premen posameznih kmetijskih kategorij, (C) način in hitrost sprememb, ki jih izračunamo s pomočjo spreminjanja površine posamezne zemljiške kategorije, (D) ocena procesa drobljenja ali poenotenja krajinske zgradbe, za katero potrebujemo matriko sprememb posamezne zemljiške kategorije v drugo (v % ali ha) (Farley in sod., 2012).

V raziskavi smo uporabili nekoliko modificiran pristop. Spremembo krajinske zgradbe smo ocenjevali po metodi, sestavljeni iz postopkov A, B in D. Namesto postopka (C), kjer se ovrednotenje spreminjanja krajinske zgradbe poda z numeričnimi indeksi, smo za potrebe naše raziskave razvili metodo opazovanja in merjenja fragmentacije krajinske zgradbe s pomočjo točk, ki jih naključno razporedimo v opazovan prostor. Z omenjeno metodo preštevamo število točk, ki padejo v določeno zemljiško kategorijo v časovnem obdobju ter spremljamo spreminjanje povprečne površine zemljiških kategorij (ha).

Rezultat metode nam omogoča: A) predstavo o hitrosti drobljenja krajinske zgradbe s pomočjo spreminjanja števila točk v poligonu enake zemljiške rabe med opazovanim obdobjem in B) predstavo o večanju ali manjšanju velikosti posameznih zemljiških kategorij. Tako sta na primer sosednji točki, ki se nahajata v istem poligonu zemljiške kategorije, a sta bili v prejšnjem opazovanem obdobju ločeni, dober indikator za homogenizacijo krajine. Menimo, da je metoda enostavna za uporabo ter omogoča v kombinaciji z uporabo postopkov A, B in D kompleksno analizo spreminjanja in drobljenja krajinske zgradbe.

Nekatere raziskave ocenjujejo fragmentirano krajinsko zgradbo za stabilenjšo kot homogeno krajinsko zgradbo (Farley in sod., 2012; Farina, 2007). Rezultat naše raziskave pa kaže ravno nasprotno. Drži trditev, da fino zrnata krajinska zgradba premore višjo krajinsko ter biotsko pestrost, pestrost ekosistemov in ekotonov. Se pa krajina s fino zrnato krajinsko zgradbo (ob enkratnem prenehanju krajinske rabe) zarašča hitreje kakor homogena krajina. Naša raziskava je pokazala torej veliko občutljivost, krhkost strukturiranih krajin, katerih zgradba je ob prenehanju motenj (kmetijske obdelave tal, paše) hitro podvržena sekundarni gozdni sukcesiji.

Po drugi strani rezultat naše raziskave kaže na ključen pomen drobljenja krajinske zgradbe za njeno nadaljnjo homogenizacijo. Protislovje utemeljujemo z dejstvom, da je zaraščanje fino zrnate, heterogene krajine, v kateri so že prisotni elementi krajinske matice (mejice ter manjše zaplate gozda in gozdni koridorji), po opustitvi kmetijske rabe prostora veliko hitrejše kakor zaraščanje homogene, kmetijske krajine. Ta proces pa poteka hitreje, če je »inicialnih« faz več, npr. če v posamezne obdelovalne površine razmejujejo mejice in gozdni otoki (Forman, 1995). Tako je tudi v Beli krajini leta 1790 prevladoval kmetijski tip krajine z relativno velikimi krajinskimi elementi ali gradniki (v našem primeru pašniki). Leta 1954 govorimo o prehodni ali gozdnati krajini, kjer se hitrost zaraščanja prostora naglo poveča. Leta 2009 se krajina spremeni v homogen, gozdni tip krajine.

Raziskava spreminjanja krajinske zgradbe na območju Bele krajine zadnjih 200 letih je pokazala, da je človekovo poseganje v krajino v preučevanem obdobju pustilo močan pečat na krajinski zgradbi. Krajina se je po opustitvi kmetijske rabe in paše postopoma zaraščala. Glavna vzroka za danes pretežno gozdni tip krajine na obravnavanem območju sta opuščanje kmetijske rabe prostora in pašništva (ovčereje).

Menimo, da je ravno pašništvo vplivalo na značilen, odprt tip krajine do leta 1937. Njegov hiter zaton oz. zmanjšanje glav ovac na opazovanem območju pripisujemo splošnemu pomanjkanju, krizi med 1 sv. vojno in svetovni gospodarski krizi leta 1928. Drugi vzrok zmanjšanja števila drobnice na opazovanem območju pa je uvajanje za območje nove pasme ovac (jezersko-solčavske pasme), katero so gojili tudi z namenom prodaje volne, vrsto pa so gojili na manjšem območju (Dolenjski list, 1954).
Spremembe v pašništvu so zato vplivale na spremenjeno krajinsko zgradbo; od heterogene kmetijske (1790) do danes homogene gozde krajine.

V drugi raziskavi (1.2), katere rezultate predstavljamo v znanstvenih delih PLANT COMMUNITIES IN GRADIENTS (2.2) in FUNKCIONALNI RASTLINSKI ZNAKI IN EKOLOŠKA STRATEGIJA ZDRUŽBE OZNAČUJEJO POSAMEZEN STADIJ SEKUNDARNE SUKCESIJE (2.3), smo raziskovali spremembo funkcionalnih rastlinskih znakov in ekoloških strategij združb v Beli krajini med sekundarno sukcesijo.

V začetku raziskave smo izdelane floristične popise (89) analizirali s pomočjo klasifikacije v programu Twinspan. Rezultat analize je združevanje popisov v 5 snopov, ki odražajo starost (TLA) posameznega snopa (popisu pripisan atribut dejanske TLA z namenom kontrole) kakor tudi sukcesijski stadij snopa.

Opisali smo naslednje sukcesijske stadije: A- stadij Calluna, B- stadij Pteridium−Frangula, C- stadij Betula, D- stadij Epimedium−Carpinus in E- Carpinus−Quercus. Povprečna starost sestoja (TLA) za vsak sukcesijski stadij znaša: A - 0 let, B - 10 let, C - 20 let, D - 45 let in E - 210 let.

Že Čarni in sod. (2007) v raziskavi premene brezovih gozdov navajajo pet sukcesijskih stadijev, ki se ločijo tako po ekoloških značilnostih kot tudi strukturnih prilagoditvah združbe in rastlinskih vrst.

Raziskava kaže, da so nekatere rastlinske vrste zastopane zgolj v določenih sukcesijskih stadijih, oz. je njihova pogostost v nekaterih sukcesijskih stadijih veliko višja kot v drugih. Tako so na primer zeliščne vrste navadni otavčič (*Leontodon hispidus*), navadni svinjak (*Hypochaeris radicata*), nemška košeničica (*Genista germanica*), malocvetna španska detelja (*Dorycnium germanicum*) in jesenska vresa (*Calluna vulgaris*) zastopane v prvem sukcesijskem stadiju (A) ali na prehodu iz stadija A v stadij B. Lasasta šopulja (*Agrostis capillaris*), navadna pasja trava (*Dactylis glomerata*) in navadna krhlika (*Frangula alnus*) so vrste, značilne za sukcesijski stadij B. Sukcesijski stadij C označujejo žabljasti vrednik (*Teucrium scorodonia*) in breza (*Betula pendula*). Navadni strček (*Aremonia agrimonoides*) in muškatni jagodnjak (*Fragaria moschata*) sta značilni zeliščni vrsti stadija D. Vrsta navadni vimček (*Epimedium alpinum*) je značilna vrsta zeli v sukcesijskem stadiju D, pogosta pa tudi v sukcesijskem stadiju E. Za zadnji sukcesijski stadij (E) sta značilni zeliščni vrsti podlesna vetrnica (*Anemone nemorosa*) in navadni pljučnik (*Pulmonaria officinalis*).

Opisane rastlinske vrste so tudi približen pokazatelj starosti (TLA) celotne združbe, kakor tudi indikatorji posameznega sukcesijskega stadija.

Vzajemno recipročenje z odstranjenim trendom ali DCA analiza (ang. detrended correspondence analysis) v večrazsežnem prostoru prikazuje jasno razporeditev naših popisov v 5 skupin. Te skupine so prav tako odraz posameznega sukcesijskega stadija. Ugotovili smo, da je položaj skupin popisov po abscisni osi sorazmeren z njihovo povprečno vrednostjo TLA. Zato smo za vsak popis izračunali projekcijo vrednosti na abscisni osi DCA in le-to upoštevali kot nadomestno ali proxy vrednost za TLA.

Menimo, da je tak način korelacije opazovanih funkcionalnih rastlinskih znakov z obdobjem od opustitve kmetijske rabe še najbolj objektiven. Lahko bi sicer izhajali pri analizi kar iz TLA, pridobljenega s pomočjo prekrivanja kartografskega materiala in letalskih posnetkov. Zavedati pa se je treba, da so podatki o starosti posameznega gozdnega sestoja velikokrat nenatančni. To velja še posebej za obdobja, v katerih se sukcesija oz. zaraščanje šele začenjata. S predstavljeno metodo (z vpeljano nadomestno vrednostjo za TLA) lahko zmanjšamo napake, ki izhajajo iz nenatančnih prostorskih podatkov ali v premeru vmesnih posegov v vegetacijo.
Izračunane vrednosti abscisne osi TLA za vsakega izmed 89 popisov smo v nadaljevanju korelirali s pojavnostjo izbranih funkcionalnih rastlinskih znakov in ekološkimi potezami rastlinskih vrst. Izračunali smo *Spearmanov* koeficient korelacije (*Rho*).

Rezultati kažejo, da se z zaraščanjem spreminjajo tako ekološke kot tudi strukturne značilnosti rastlinskih vrst, življenjske oblike vrst in celotna strategija združbe (glej raziskava 1.2).

Rezultate tretje raziskave (1.3), predstavljamo v znanstvenem članku z naslovom: PODATKI O NEKDANJI RABI SE NAJBOLJE ODRAŽAJO V EDAFSKIH ZNAČILNOSTIH (2.4.).

Rezultat tretje raziskave kaže na vpliv opuščanja kmetijske obdelave tal na spremenjene ekološke in morfološke poteze združbe kot tudi na spremenjene edafske značilnosti. Omenjene spremembe se najbolje odražajo v edafskih značilnostih. V raziskavi smo s pomočjo napovednih modelov iz družine GAMM (posplošen adititiven mešan model) računali TLA, napovedno moč posameznega modela pa primerjali z dejanskim oz. izmerjenim TLA na vsakem popisu.

Med seboj smo primerjali napovedno štirih moč modelov. Model M1 je vseboval podatke o izbranih edafskih značilnostih tal na popisnih ploskvah, model M2 ekološke in funkcionalne značilnosti rastlinskih vrst, model M3 je vseboval Ellenbergove bioindikatorske vrednosti ter model M4 horološke značilnosti rastlinskih vrst, najdenih na popisnih ploskvah.

Podatek o času od opustitve kmetijske rabe (TLA) smo pridobili iz prejšnje raziskave (1.2) in nam je služil kot informacija, s pomočjo katere smo ugotavljali zanesljivost štirih modelov.

Ugotovitve kažejo, da ima najvišjo napovedno moč model M1; model izbranih edafskih značilnosti, kar je razvidno tudi iz rezultatov naše raziskave. Tako se podatek o času, po katerem je bilo pašništvo na opazovanem območju prekinjeno, odraža v C/N razmerju, vsebnosti organske mase v tleh in vsebnosti izmenljivih kationov. Čarni s sod. (2007) omenja najvišjo vrednost C/N razmerja v stadiju sukcesije, kjer dominirata breza (*Betula pendula*) in trepetlika (*Populus tremula*). V kasnejših stadijih sekundarne sukcesije, s hitrim procesom dekompozicije, pa se vrednost C/N razmerja nižja. Podoben rezultat je potrdila tudi naša raziskava.

Soodvisnost (izračunan *Pearsonov* koeficient) med izbranimi edafskimi značilnostmi, uporabljenimi v modelu M1, in dejansko starostjo gozdnega sestoja je visoka. Zato menimo, da je metoda ugotavljanja starosti gozdnega sestoja (torej TLA) s pomočjo izbranih edafskih značilnosti tal najbolj natančna.

Za namene merjenja korelacije pri analizah opazovanih funkcionalnih rastlinskih znakov in edafskih značilnosti tal se je zaradi enostavne uporabe izkazal kot primeren *Pearsonov* koeficient korelacije.

3.2 SKLEPI

V prvi raziskavi smo izhajali iz naslednjih hipotez:

A) Demografske spremembe so imele v Beli krajini pomembno vlogo pri spremembi krajinske zgradbe in krajinske pestrosti. Takoj po opuščanju kmetijske obdelave so zemljišča podvržena sekundarni sukcesiji, torej procesu zaraščanja. Zaraščanje površin z gozdom vpliva na manjšo razdrobljenost elementov krajine ter s tem na homogenizacijo ali poenotenje celotnega prostora. Zato se zmanjša tudi krajinska pestrost.

B) Krajina se zarašča premo sorazmerno s hitrostjo opuščanja obdelovanih območij.

C) Pašništvo ima v krajini pomembno vlogo pri ohranjanju heterogenosti prostora ter pri varovanju okolja pred zaraščanjem. Pašništvo povečuje biotsko pestrost posameznega prostora, saj preprečuje zaraščanje krajine.

Naša raziskava prikazuje izjemno hitro spremembo krajinske zgradbe v obdobju med leti 1790 in 2009. Zaraščanje prostora zaradi opuščanja kmetijske rabe je v Beli krajini veliko hitrejše kot v drugih delih Slovenije in Evrope. Rezultati raziskave na primeru Bele krajine kažejo močan vpliv človeka na zgradbo in funkcijo krajin v Sloveniji ter opisujejo človekovo dejavnost kot pomemben dejavnik pri vzdrževanju in ohranjanju krajine danes. Rezultat raziskave kaže na odločilno vlogo demografskih sprememb v Beli krajini pri spreminjanju krajinske zgradbe in krajinske pestrosti. Kmalu po opustitvi kmetijske rabe tal in paše se začne krajina spreminjati. Že leta 1823 je pašnih površin manj. Opazen je proces drobljenja zemljiške posesti. Pokrajina ima še zmeraj značaj kmetijske krajine. Leta 1954 govorimo o krajini gozdnatega tipa, leta 2009 pa o homogeni gozdni krajini.

Najhitrejše spremembe v Beli krajini so se v smislu spreminjanja krajinske zgradbe zgodile po letu 1937. Vzroka sta splošna kriza v obdobju po prvi svetovni vojni ter z njo povezano izseljevanje prebivalstva in svetovna gospodarska kriza (po letu 1928). Zato je viden večji trend opuščanja kmetijskih zemljišč in zaraščanja območja. To je tudi obdobje, ko se na območju med Butorajem, Bojanci, Tribučami in Dragatušem skorajda popolnoma opusti pašništvo, ovčereja. Tako se po letu 1937 krajinska zgradba še hitreje spremeni v smer gozdne krajine.

Raziskava je pokazala, da ima v Beli krajini pašništvo ključno vlogo pri ohranjanju odprte krajine, ki je po svojem videzu vsekakor veliko bolj strukturirana, mozaična, kakor je krajinska zgradba v Beli krajini danes. Ocenjujemo, da je pašništvo tista kmetijska dejavnost, ki je najbolj vplivala na ohranjanje vrstne pestrosti in raznolikosti habitatov na obravnavanem območju. Takoj po opustitvi paše pa je opazen proces poenotenja krajinske zgradbe ter s tem povezan proces izginjanja habitatov, rastlinskih in živalskih vrst ter spreminjanje celotne krajinske zgradbe in krajinske pestrosti.

V drugi raziskavi izhajamo iz naslednjih hipotez:

A) Med sekundarno sukcesijo se spremenijo ekološke in strukturne značilnosti celotne združbe.

B) Razvoj sukcesijskih stadijev je v začetko zaraščanja krajine najhitrejši, trajanje in formiranje posameznega stadija združbe pa v začetku zaraščanja najkrajše.

C) Med sekundarno sukcesijo se spreminja vrstna sestava v posameznem stadiju združbe.

D) Z zaraščanjem nekoč odprtih pašnih površin se pojavijo rastlinske vrste z drugačnimi morfološkimi in ekološkimi potezami. Zato se skozi sekundarno sukcesijo spreminja tudi strategija celotne združbe.

E) Funkcionalni rastlinski znaki in ekološke prilagoditve vrst ter celotne združbe odražajo dejanski čas, po katerem je bila na določeni popisni ploskvi kmetijska dejavnost opuščena.

Rezultat druge raziskave kaže na spreminjanje rastlinskih vrst in vrstne sestave celotne združbe med sekundarno sukcesijo. Ugotovili smo, da združbo na pašnikih sestavljajo heliofilne vrste in jo označujemo kot stadij *Calluna*. Temu stadiju sekundarne sukcesije sledi stadij *Pteridium-Frangula* (TLA = 10). Stadij C imenujemo *Betula*. Stadij D (TLA = 45) je značilen gozdni sestoj, kjer je *Carpinus betulus* dominantna drevesna vrsta, v zeliščni plasti pa prevladuje *Epimedium alpinum*. Stadij imenujemo *Epimedium- Carpinus*. V stadiju E so značilne skiofilne zeliščne vrste, gozd je značilno dvoplasten. V zgornji plasti prevladuje *Quercus petraea,* v spodnji drevesni plasti pa *Carpinus betulus*.

Analiza premene ekološke strategije združbe med sekundarno sukcesijo je pokazala, da je razvoj sukcesijskih stadijev v začetku zaraščanja krajine najhitrejši, trajanje posameznega stadija združbe pa je v začetku zaraščanja najkrajše. Združba na pašnikih ima značilno strategijo stres tolerator, po desetih letih kompetitor/stres tolerator, po dvesto letih pa kompetitor/kompetitor-stres tolerator. Podobno se spreminja tudi strategija zeliščne plasti med stadiji sekundarne sukcesije.

Raziskava je pokazala, da funkcionalni rastlinski znaki in ekološke značilnosti vrst ter celotne združbe odražajo obdobje, po katerem je bila na določeni popisni ploskvi kmetijska dejavnost opuščena. To pa velja tudi za pojavljanje nekaterih, za posamezen stadij sukcesije značilnih rastlinskih vrst, ki so dober pokazatelj starosti sekundarne sukcesije na opazovanem območju.

Rezultati raziskave kažejo na spremembo funkcionalnih rastlinskih znakov in ekoloških značilnosti vrst (kot tudi celotne strategije združbe) med sekundarno sukcesijo, ki je posledica opustitve paše.

V tretji raziskavi izhajamo iz naslednjih hipotez:

A) Informacija o starosti gozdnega sestoja (torej o TLA) je »shranjena« bodisi v funkcionalnih rastlinskih znakih, horološkem spektru vrst, Ellenbergovih bioindikatorskih vrednostih ali edafskih značilnostih rastišča.

B) Napovedne moči generaliziranih aditivnih mešanih modelov (GAMM) o TLA, izdelanih iz štirih skupin znakov se med seboj razlikujejo.

Rezultati tretje raziskave kažejo, da je informacija o starosti gozdnega sestoja zapisana v funkcionalnih rastlinskih znakih, horološkem spektru vrst, Ellenbergovih bioindikatorskih vrednostih in edafskih značilnostih rastišča. Edafske značilnosti rastišča so najboljši pokazatelj TLA, s pomočjo katerih lahko z modeli iz skupine GAMM precej natančno ocenimo čas, po katerem je bila kmetijska dejavnost na določenem območju opuščena.

4 POVZETEK

Doktorsko disertacijo z naslovom Sprememba krajinske zgradbe, floristične sestave in ekoloških razmer v jugovzhodni Sloveniji v zadnjih 200 letih sestavljajo tri ločene raziskave, objavljene v štirih znanstvenih člankih. V disertaciji so zajeti trije pogledi na prostor:

- Najprej smo raziskali spremembe, ki nastopijo po opuščanju kmetijske rabe v krajinsko-ekološkem pogledu.
- V nadaljevanju smo preučili spremembe v prostoru z vidika sprememb, nastalih v floristični sestavi združb, ter ekološke spremembe rastlinskih družb.
- V zadnji raziskavi smo ugotavljali čas od opustitve kmetijske rabe prostora s pomočjo funkcionalnih rastlinskih znakov, ekoloških značilnosti vrst ter edafskih značilnosti, ki smo jih vključili v štiri generalizirane aditivne mešane modele (GAMM).

Naslov prve raziskave je Sprememba krajinske zgradbe v Beli krajini v zadnjih 200 letih. Raziskava je bila objavljena v znanstvenem članku z naslovom Spremembe krajine na območju belokranjskega nizkega krasa v zadnjih 220 letih in je imela naslednje cilje:

- določiti (in ovrednotiti) prostorske spremembe v Beli krajini v zadnjih 220 letih, ki so posledica demografskih sprememb,
- povezati spremembe krajinske zgradbe z demografskimi spremembami in
- ugotoviti raven sprememb v (po)krajini med procesom emigracije lokalnega prebivalstva ter opuščanja kmetijske dejavnosti.

Dodatno so nas zanimali odgovori na naslednji vprašanji:
- Kako vpliva pašništvo (ovčereja) na spreminjanje krajinske zgradbe in krajinske heterogenosti, oz. kakšen vpliv ima opustitev pašništva na krajinsko zgradbo in strukturo.

Raziskali smo nihanje števila prebivalstva na raziskanem območju in želeli ugotoviti, ali obstaja povezava med nihanjem števila prebivalstva in stopnjo gozdnatosti pokrajine.

Raziskava je pokazala izjemno hitro spremembo krajinske zgradbe v obdobju med leti 1790 in 2009. Zaraščanje površin, kot posledica opuščanja kmetijske rabe, je v Beli krajini veliko hitrejše kot v drugih delih Slovenije in Evrope. Rezultati raziskave na primeru Bele krajine kažejo močan vpliv človeka na zgradbo in funkcijo (po)krajin v Sloveniji ter poudarjajo človekovo dejavnost kot močan dejavnik pri vzdrževanju in ohranjanju krajine danes.

Naslov druge raziskave je Sprememba funkcionalnih rastlinskih znakov in ekološke strategije združb v Beli krajini med sekundarno sukcesijo v obdobju 200 let.
Raziskava je bila objavljena v dveh znanstvenih člankih: Rastlinske združbe in gradienti in Funkcionalni rastlinski znaki in ekološka strategija združbe označujejo posamezen stadij sekundarne sukcesije.

Raziskava se ukvarja s spreminjanjem funkcionalnih rastlinski znakov, ekoloških značilnosti vrst in ekološke strategije združb skozi posamezne stadije zaraščanja pašnikov v odvisnosti od časa opustitve kmetijske rabe (TLA). V raziskavi smo uporabili multivariatno DCA analizo in opazovali položaj florističnih popisov v DCA prostoru in jih korelirali s TLA. Izračunali smo *Spearmanov* korelacijski koeficient med pojavnostjo posameznega rastlinskega funkcionalnega znaka in TLA. Raziskava se ukvarja s spreminjanjem opuščenih pašnih površin med sekundarno sukcesijo v gozdni sestoj, torej proti trenutni potencialni vegetaciji. Izhajamo iz dejstva, da so funkcionalni rastlinki znaki in ekološke adaptacije vrst, kot tudi celotne združbe, dober parameter za merjenje in analizo sprememb, ki se dogajajo v vegetaciji po prenehanju človekove obdelave zemljišča.

V raziskavi smo opazovali spremembe v vrstni sestavi združbe ter spremembe izbranih funkcionalnih rastlinskih znakov med stadiji sekundarne sukcesije. Še posebej so nas zanimale ekološke in morfološke prilagoditve združbe kot tudi premena rastlinskih vrst na prehodu med posameznimi stadiji v sekundarni sukcesiji.

Raziskava je imela naslednje cilje: (1) raziskava premene vrst med sekundarno sukcesijo, (B) razumevanje premene izbranih funkcionalnih rastlinskih znakov in ekoloških značilnosti vrst med stadiji sekundarne sukcesije in (3) korelacija izbranih funkcionalnih rastlinskih znakov in ekoloških značilnosti vrst in združbe s časom od opustitve kmetijske rabe prostora.

Raziskava je pokazala, da ima rastlinska združba na pašnikih in pašnikih v zaraščanju značilno ekološko strategijo S-CS. Med sekundarno sukcesijo se rastlinska strategija združbe spremeni v C-CS in je značilna za zadnji stadij, hrastovo- gabrov gozd. Podobna premena ekološke strategije je značilna tudi za zeliščni sloj.

Rezultat raziskave kaže na premeno funkcionalnih rastlinskih znakov vrst, ekoloških potez in strategije vrst kakor tudi celotne združbe v preučevanih stadijih sekundarne sukcesije v obdobju 220 let. Po opustitvi kmetijske rabe se začno gozdne vrste rastlin iz že obstoječih gozdnih zaplat ali mejic preseljevati na opuščena zemljišča zaradi spremenjenih ekoloških razmer (prekinjena antropogena motnja). V obdobju nekaj let se spremeni vrstna sestava združbe zaradi priseljevanja vrst z drugačnimi morfološkimi in ekološkimi potezami in spreminjanja okolja. Zato se spremenijo ekološki in morfološki znaki celotne združbe.

Hitrost zaraščanja je v začetnih stadijih sukcesije izjemno hitra, prav tako premena vrst in spreminjanje ekoloških ter strukturnih značilnosti združbe. Po opustitvi kmetijske rabe je potrebno približno 50 let, da se formira dobro strukturiran gozdni sestoj. Po 200 letih od opustitve pašništva ali kmetovanja pa območje porašča formiran hrastovo-gabrov sestoj.

Tretja raziskava ima naslov Določanje starosti sestoja s pomočjo izbranih funkcionalnih rastlinskih znakov, ekoloških značilnosti vrst ter edafskih značilnosti rastišča. Raziskava je objavljena v znanstvenem delu z naslovom: Records of past land use are best stored in soil properties.

V raziskavi smo izdelali štiri generalizirane aditivne mešane modele (GAMM), s pomočjo izbranih funkcionalnih rastlinskih znakov, horološkega spektra vrst, Ellenbergovih bioindikatorskih vrednosti in edafskih značilnosti popisnih ploskev. Testirali smo njihovo napovedno moč za čas od opustitve kmetijske rabe zemljišča (TLA).

Raziskava obravnava pristop, pri katerem s pomočjo izbranih ekoloških in strukturnih parametrov napovedujemo TLA.

Raziskava je pokazala, da se podatek oz. informacija o času opustitve kmetijske rabe tal odraža v spremembah funkcionalnih rastlinskih znakih, horotipih vrst, Ellenbergovih bioindikatorskih vrednostih in najbolj v edafskih značilnostih tal na popisnih ploskvah.

Izbrane edafske značilnosti so tako najboljši vir informacij za napovedovanje TLA.

4 SUMMARY

The doctoral dissertation entitled Changes of landscape structure, floristic composition and ecological conditions in south eastern Slovenia in last 200 years consists of three independent studies, published in four scientific articles.

Three different approaches toward landscape abandonment are presented in the dissertation. The first study deals with changes in landscape structure, so describes the changes in landscape structure that took place as a consequence of land use abandonment and identifies these changes with the help of a landscape-ecological approach.
The second study is about changes in functional response traits and plant community strategy during secondary succession over the period of 220 years. A phytosociological approach toward the land use abandonment is presented in this study.
The final study highlights method of estimating TLA with the help of selected plant functional response traits and plant community strategy, thus a numerical approach.

In our first study, entitled Landscape transformation in the low karstic plain of Bela krajina (SE Slovenia) over the last 220 years, we investigated landscape structure change and its indicators. We observed the following landscape characteristics: a) the proportions of major land use (forest, meadows, pastures, fields, vineyards and urban areas); b) heterogeneity (homogenous space, heterogeneous fine-grained, heterogeneous coarse-grained, heterogeneous mixed; c) landscape type (agricultural, transitional or wooded and forested).

The main aims of this study were: (A) to determine (and evaluate) changes in the landscape in the area of SE Slovenia over the past 220 years, (B) to relate landscape changes to demographic changes and (C) to identify the rate of modification of the landscape during the process of population migration and abandonment of agricultural land use.
Additionally, we wished to answer the following sub-questions: (1) how important is sheep grazing (main grazers in study area) for the landscape structure and heterogeneity, what happens to the landscape structure if such disturbance is eliminated from the area?
The changing human population was also studied in detail. Our second objective was to establish whether the human population changes could be associated with increased land afforestation.

Our study showed that the studied region in Bela krajina used to be an agricultural (partly also transitional), fairly evenly heterogeneous, medium-grained landscape, the structure of which became subject to rapid change. We found an extremely dramatic change in the landscape structure around 1954. Spontaneous afforestation of the landscape after WWII was faster than in other European regions. Our results also indicate not only the

significance of human interventions in the appearance of the traditional landscape in Europe but also signal the threat to these landscapes by a changed land use regime.

The present homogeneous forested landscape of Bela krajina is certainly very different to the diverse landscape structure from the period before 1954.

Our second study consists of two published scientific articles (2.2 and 2.3). In this study, our goal was to evaluate the landscape changes that are the result of land use abandonment with the help of functional response traits and plant community strategy. We wished to answer the following questions: are functional response traits and plant community strategies indicators of TAA (time since agricultural land use abandonment), thus of a specific succession stage?

In the second study, we observed changes in the 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 ecological and morphological changes in 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 agricultural land use was abandoned TLA.

Our hypotheses: (A) specific functional response traits may be related to TLA 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 TLA.

We found a significant change in selected functional response traits and the ecological preferences of species, as well as of the whole community.

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 this 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 in 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.

Our third study, entitled Records of past land use are best stored in soil properties, was published in the scientific article 2.4. This study reports on the investigation of functional response traits, chorotypes, Ellenberg bioindicator values and changes in soil properties during spontaneous afforestation (secondary succession) of former pastures in SE Slovenia and evaluation of their predictive value for TLA (time since land use abandonment).

In the presented study, we attempted to establish whether the plant functional response traits, chorotypes, Ellenberg bioindicator values or soil properties are appropriate information sources about the time since traditional land use abandonment and whether the information about secondary succession stages is in some way “stored” in these trait groups. We were particularly interested in developing a method that will allow us to calculate TLA precisely (in years) for any forest stand in the study area.

The study includes GAMM models (generalized additive mixed models), since they allow combined analysis of both linear and non-linear variables in a single model. By means of the models, we tried to simplify the expression of the process of agricultural abandonment change in such a way as to give the process real attributes and to study them over a specific area.

The specific objectives of the study were to rank the four chosen trait groups according to their predictive value for TLA and compare their predictive power.

Our hypothesis was that TLA for each secondary succession stage is “stored” in plant traits and soil properties. With the right combination of different variables within a trait group, one can elaborate a formula that is powerful enough to calculate the TLA for a forest stand.

The results showed that, for all the considered attributes, agricultural land use abandonment causes changes in the species composition and in the ecological properties of the study area. Those changes can be well perceived with the study models that describe the soil characteristics of a particular area. On the basis of this study, we conclude that changes in soil properties in the observed area are a good predictor for the TLA of a particular forest stand in secondary succession.

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