

UNIVERZA V LJUBLJANI
BIOTEHNIŠKA FAKULTETA

Špela ČONČ

**VPLIV GEOMORFOLOŠKIH OBLIK NA RABO
PROSTORA PRI EVRAZIJSKEM RISU (*Lynx lynx*) IN
EVROPSKI DIVJI MAČKI (*Felis silvestris*)**

DOKTORSKA DISERTACIJA

Ljubljana, 2025

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**IMPACT OF GEOMORPHOLOGICAL FEATURES ON USE OF SPACE
BY EURASIAN LYNX (*Lynx lynx*) AND EUROPEAN WILDCAT (*Felis
silvestris*)**

DOCTORAL DISSERTATION

Ljubljana, 2025

Posvetilo

“We know the sap which courses through the trees as we know the blood that courses through our veins. We are part of the earth and it is part of us. The perfumed flowers are our sisters. The bear, the deer, the great eagle, these are our brothers. The rocky crests, the dew in the meadow, the body heat of the pony, and man all belong to the same family.

The shining water that moves in the streams and rivers is not just water, but the blood of our ancestors. If we sell you our land, you must remember that it is sacred. Each glossy reflection in the clear waters of the lakes tells of events and memories in the life of my people. The water's murmur is the voice of my father's father.

The rivers are our brothers. They quench our thirst. They carry our canoes and feed our children. So you must give the rivers the kindness that you would give any brother.

If we sell you our land, remember that the air is precious to us, that the air shares its spirit with all the life that it supports. The wind that gave our grandfather his first breath also received his last sigh. The wind also gives our children the spirit of life. So if we sell our land, you must keep it apart and sacred, as a place where man can go to taste the wind that is sweetened by the meadow flowers.

Will you teach your children what we have taught our children? That the earth is our mother? What befalls the earth befalls all the sons of the earth.

This we know: the earth does not belong to man, man belongs to the earth. All things are connected like the blood that unites us all. Man did not weave the web of life, he is merely a strand in it. Whatever he does to the web, he does to himself.”

(Chief Seathl, 1854)

Na podlagi Statuta Univerze v Ljubljani ter po sklepu Senata Biotehniške fakultete in sklepa Komisije za doktorski študij Univerze v Ljubljani z dne 5. 7. 2022 je bilo potrjeno, da kandidatka izpolnjuje pogoje za opravljanje doktorata znanosti na Interdisciplinarnem doktorskem študijskem programu Bioznanosti, znanstveno področje Varstvo naravne dediščine. Za mentorja je bil imenovan doc. dr. Miha Krofel, za somentorico je bila imenovana doc. dr. Mateja Breg Valjavec.

Doktorska disertacija je rezultat raziskovalnega dela, ki je bilo opravljeno v okviru interdisciplinarnega doktorskega študija Bioznanosti, znanstveno področje Varstvo naravne dediščine na Oddelku za gozdarstvo in obnovljive gozdne vire, Biotehniška fakulteta, Univerza v Ljubljani in v okviru programa usposabljanja mladega raziskovalca na Geografskem inštitutu Antona Melika, Znanstvenoraziskovalni center Slovenske akademije znanosti in umetnosti.

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KLJUČNA DOKUMENTACIJSKA INFORMACIJA

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SA	KROFEL, Miha (mentor), BREG VALJAVEC, Mateja (somentorica)
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IN	VPLIV GEOMORFOLOŠKIH OBLIK NA RABO PROSTORA PRI EVRAZIJSKEM RISU (<i>Lynx lynx</i>) IN EVROPSKI DIVJI MAČKI (<i>Felis silvestris</i>)
TD	Doktorska disertacija
OP	X, 140 str., 9 sl., 4 pril., 207 vir.
IJ	sl
JI	sl/en
AI	Razgiban teren in izstopajoče reliefne oblike pogosto privlačijo prostoživeče mačke, vendar se je večina dosedanjih raziskav osredotočala le na splošne topografske značilnosti (npr. naklon). V tej raziskavi smo na podlagi GPS-telemetričnih podatkov preučevali vplive različnih reliefnih in mikrohabitatnih značilnosti na izbiro habitata pri evrazijskem risu (<i>Lynx lynx</i>) in evropski divji mački (<i>Felis silvestris</i>), pri čemer smo upoštevali različna vedenja in faze aktivnosti. Na podlagi LiDAR podatkov smo z avtomatskimi metodami zaznali reliefne oblike in primerjali vzorce izbire habitata med obema vrstama, pri risih pa tudi glede na njihov izvor (preseljeni v okviru okrepitve populacije in nepreseljeni) in stopnjo izkušenosti z območjem (čas od preselitve; naivni in izkušeni preseljeni risi). S primerjavo dveh (bio-)geografsko različnih območij v Evropi smo preverili, ali pri izbiri habitata risa prihaja do funkcionalnega odziva. Pri obeh vrstah smo opazili pomemben vpliv reliefnih oblik na rabo prostora, vendar z različnimi vzorci izbire. Ugotovili smo, da je na izbiro habitata divjih mačk bolj vplivala bližina gozdnih robov in človeške infrastrukture kot pa reliefne značilnosti. Risi so izbirali razgiban, skalnat in strm teren ter bližino različnih reliefnih oblik, pri čemer je bil vpliv reliefnih značilnosti večji podnevi kot ponoči. Tudi vpliv človeške infrastrukture na izbiro habitata risa se je razlikoval glede na del dneva; podnevi so se izogibali rekreacijskih poti, ponoči pa so jih poleg gozdnih in glavnih cest izbirali. Pri preseljenih risih smo opazili močnejše vzorce izbire/izogibanja kot pri nepreseljenih, medtem ko so bile razlike v izbiri glede na stopnjo izkušenosti z območjem manjše. Opazili smo funkcionalni odziv pri izbiri skalnatih in razgibanih območij, saj se je izbira takih habitatov pri risih povečala z manjšanjem njihove razpoložljivosti. Naša raziskava poudarja pomen vključevanja tehnik daljinskega zaznavanja in podatkov o abiotičnih mikrohabitatnih značilnostih v analize pri preučevanju prostorske ekologije divjih živali in poudarja pomen varstva geodiverzitete za ohranjanje biodiverzitete.

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AA KROFEL, Miha (supervisor), BREG VALJAVEC, Mateja (co-advisor)
PP SI-1000 Ljubljana, Jamnikarjeva 101
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AB Many wild felids are attracted to rugged terrain and conspicuous relief features, but most previous studies have been limited on effects of general topographic characteristics (e.g. slope). In this study, we used GPS-telemetry data to investigate the effects of various relief and microhabitat features on the habitat selection by Eurasian lynx (*Lynx lynx*) and the European wildcat (*Felis silvestris*), considering different behavioural states and phases of activity. Using automatic methods for relief features detection based on LiDAR data, we compared selection patterns between two felids and among lynx also based on their origin (lynx translocated within population reinforcement and lynx from the remnant population) and experience level with the area (time since the translocation; naïve and experienced translocated lynx). Using two (bio-)geographically-contrasting areas in Europe, we tested whether lynx exhibit functional responses in habitat selection. We observed a significant influence of relief features on space use by both species, with distinct selection patterns. Wildcat habitat selection was more influenced by forest edges and human infrastructure than by relief features. Lynx preferred rugged, rocky and steep terrain and vicinity of various relief features, but selection of topographic features was stronger during the day than at night. Time phase also affected lynx selection of human infrastructure; during the day they avoided recreational paths but selected them beside forest and main roads at night. We observed stronger selection/avoidance patterns for the translocated lynx than for the lynx from the remnant population, while the differences in experience levels with the area were less pronounced. We also observed a functional response in the selection of rocky and rugged areas, as lynx selection of such habitats increased with their lower availability. This study highlights the potential of integrating remote sensing techniques and abiotic microhabitat features in studying wildlife spatial ecology and emphasizes the importance of protection of geodiversity for the conservation of biodiversity.

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Čonč Š., Oliveira T., Portas R., Černe R., Breg Valjavec M., Krofel M. 2022. Dolines and cats: remote detection of karst depressions and their application to study wild felid ecology. *Remote Sensing*, 14, 3: 656, <https://doi.org/10.3390/rs14030656>

Čonč Š., Oliveira T., Hočevár L., Černe R., Breg Valjavec M., Krofel M. 2024. Integrating geodiversity in animal spatial ecology: microhabitat selection of Eurasian lynx (*Lynx lynx*) and European wildcat (*Felis silvestris*) in a karst landscape. *Global Ecology and Conservation*, 54: e03138, <https://doi.org/10.1016/j.gecco.2024.e03138>

Čonč Š., Oliveira T., Belotti E., Bufka L., Černe R., Heurich M., Breg Valjavec M., Krofel M. 2024. Revealing functional responses in habitat selection of rocky features and rugged terrain by Eurasian lynx (*Lynx lynx*) using LiDAR data. *Landscape Ecology*, 39: 121, <https://doi.org/10.1007/s10980-024-01923-y>

KAZALO SLIK

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OKRAJŠAVE IN SIMBOLI

DMV	Digitalni model višin
GAM	Posplošeni aditivni modeli (<i>Generalized additive models</i>)
GLMM	Posplošeni linearni mešani modeli (<i>Generalized linear mixed models</i>)
GPS	Globalni sistem pozicioniranja (<i>Global Positioning System</i>)
LiDAR	Lasersko skeniranje površja (<i>Light Detection And Ranging</i>)
MCP	Minimalni konveksni poligoni (<i>Minimum convex polygons</i>)

1 UVOD

Širok spekter neživih oz. abiotskih dejavnikov, pogosto imenovanih tudi geodiverziteta, vpliva na biotski del narave in pogojuje oblikovanje habitatov ter razširjenost vrst (Huggett, 2004; Gordon in sod., 2022). Habitati se med seboj razlikujejo glede na obliko in velikost, od mikrohabitatov do zelo velikih megahabitatov, v katerih biota, pokrajinski elementi in geomorfni procesi medsebojno vplivajo na habitate in vedenje živali na različnih prostorskih ravneh (Johnson, 1980; Huggett, 2004; Gordon in sod., 2022). Prav tako pa se na različnih prostorskih ravneh pojavljajo tudi geomorfološke oz. reliefne oblike različnih velikosti, od majhnih oz. mikro- (npr. skalni bloki) do makro (npr. gorske verige) reliefnih oblik.

Geodiverziteta omogoča razpoložljive ekološke niše za različne organizme in v splošnem pozitivno vpliva na biotsko raznovrstnost (Tukiainen in sod., 2023; Maliniemi in sod., 2024). Vključevanje geodiverzitete oz. elementov geodiverzitete (npr. reliefne oblike in mikoreliefne značilnosti površja) v ekološke raziskave zato lahko izboljša naše razumevanje vzorcev in dinamike biotske raznovrstnosti ter ekologije vrst (Tukiainen in sod., 2023). Vplivi splošnih abiotskih dejavnikov (npr. podnebje, geologija in nadmorska višina) na habitate in razširjenost vrst so dobro poznani in raziskani (Huggett, 2004). Poleg tega, da raznolike reliefne oblike zagotavljajo habitate in predstavljajo zavetišča za različne vrste (Bouchet in sod., 2015; Fitzsimons in Michael, 2017; Dorph in sod., 2021; Čarni in sod., 2022), lahko vplivajo tudi na ekologijo in osnovne vedenjske vzorce prostoživečih živali. Npr. velike reke lahko delujejo kot ovire, doline v gorovjih pa kot koridorji in vplivajo na premikanje živali (Bouchet in sod., 2015). Stene in jame pticam ter netopirjem služijo kot gnezdišča in nudijo zaščito pred plenilci (Gordon in sod., 2022). Tovrstna raba reliefnih oblik lahko vpliva na preživetje in razmnoževalni uspeh vrste. Pri plenilcih pa lahko vplivajo na uspešnost lova, saj jim zagotavljajo kritje pri zalezovanju in plenjenju, upočasnijo plen ali predstavljajo fizično oviro in plenu onemogočijo pobeg (Andersson in sod., 2009; Bouchet in sod., 2015). Živali uporabljajo reliefne oblike, ki očitno izstopajo iz okolice (npr. skalni bloki), kot markirna mesta za označevanje teritorija in delujejo kot komunikacijska središča, ki pomagajo ohranjati socialno-prostorsko organizacijo populacij (Allen in sod., 2017; Melzheimer in sod., 2020).

Povezave med topografijo in reliefnimi oblikami so še posebej izrazite pri prostoživečih mačkah (Felidae). Pretekle raziskave o pumah (*Puma concolor*), leopardih (*Panthera pardus*), snežnih leopardih (*Panthera uncia*), rdečerjavih (*Lynx rufus*) in evrazijskih risih (*Lynx lynx*) so pokazale, da te mačke pogosto izbirajo razgiban, skalovit in težko dostopen teren, grebene ter podobne izstopajoče reliefne oblike za različna vedenja, kot so gibanje, lov, markiranje in počitek (Dickson in Beier, 2007; Bouchet in sod., 2015; Abouelezz in sod., 2018; Ironside in sod., 2018; Farhadinia in sod., 2020; Mohorović in Krofel, 2020; Hočevár in sod., 2021). Evrazijski ris (v nadaljevanju ris) in evropska divja mačka (*Felis silvestris*; v nadaljevanju divja mačka) na primer za označevanje teritorija pogosto uporabljata izdanke kamnin in stene (Allen in sod., 2017; Krofel in sod., 2022), medtem ko risi pogosto izbirajo te reliefne oblike tudi za dnevni počitek (Signer in sod., 2019; Hočevár in sod., 2021).

Raziskovalci in naravovarstveniki vse bolj prepoznavajo pomen vključevanja različnih mikoreliefnih značilnosti in oblik (geodiverzitete) v ekološke raziskave in naravovarstvene

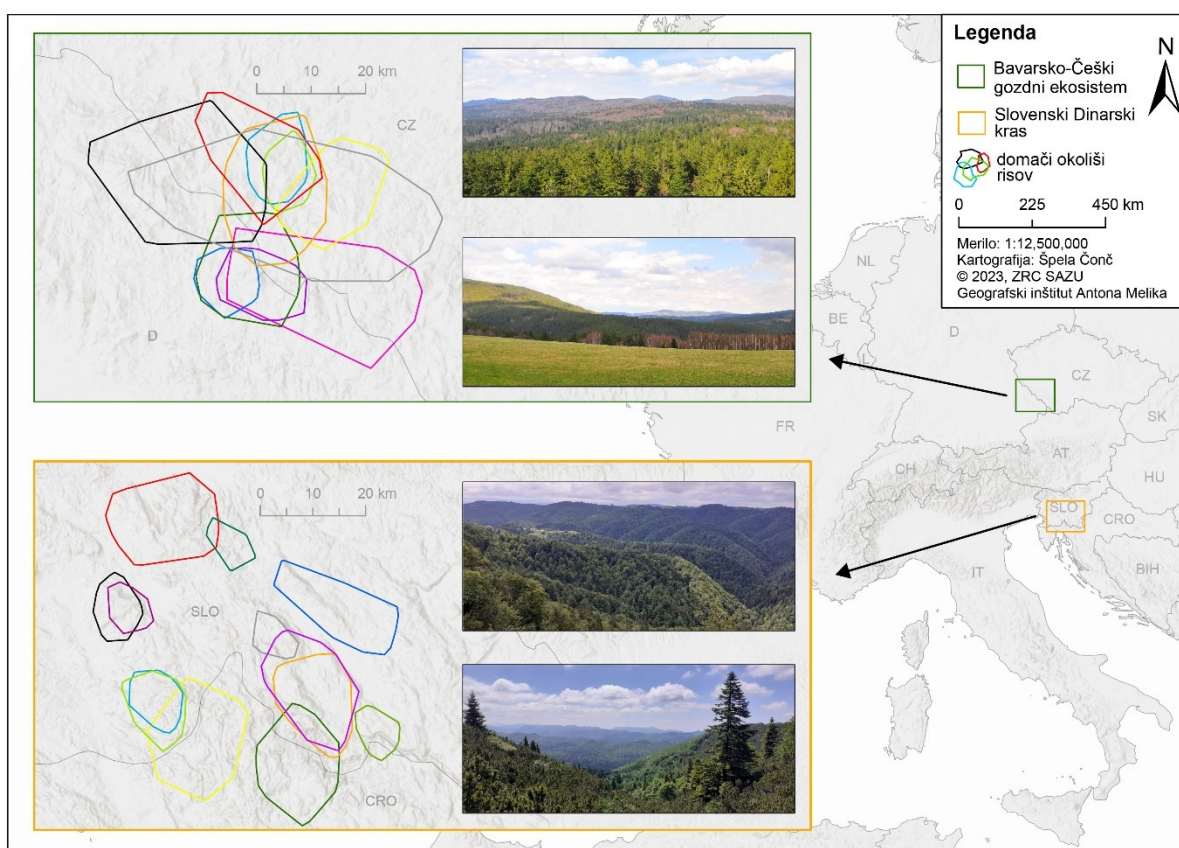
smernice (Albano, 2015; Anderson in sod., 2015; Bailey in sod., 2018; Crofts, 2019; Čonč, 2020; Bátori in sod., 2023; Maliniemi in sod., 2024), vendar se kljub temu soočajo z različnimi izzivi. Velike prostoživeče mačke imajo navadno obsežne domače okoliše. Posledično tudi prostorske analize, ki se nanašajo npr. na njihovo rabo prostora ali povezanost habitatov, obsegajo velika naravna območja (npr. Dickson in Beier, 2007), države (npr. Potočnik in sod., 2020) ali celo kontinente (npr. Ripari in sod., 2022). V tako obsežnih prostorskih analizah so bile v dosedanjih raziskavah topografske spremenljivke pogosto omejene le na splošne značilnosti terena (npr. nadmorska višina, ekspozicija, naklon, razgibanost) in so posledično prezrle učinke mikro- in mezoreliefnih značilnosti. Ta vrzel je povezana predvsem z omejeno razpoložljivostjo visokoločljivostnih digitalnih modelov višin (DMV) in podrobnih slojev s podatki o reliefnih oblikah na tako obsežnih območjih. Posledično so se pretekle raziskave, ki so v analize izbire habitatov vključevale značilnosti mikoreliefa, navadno zanašale na tradicionalne metode, kot sta terensko kartiranje (npr. Hočevár in sod., 2021) ali ročna digitalizacija reliefnih oblik (npr. Signer in sod., 2019). Uporaba tradicionalnih metod je zamudna in draga, pogosto pa je natančnost in kakovost podatkov slabša. Zato se na področju geomorfologije in drugih ved razvijajo različne metode in tehnologije za daljinsko ter stroškovno učinkovito kartiranje in zaznavanje reliefnih oblik ter analize reliefnih značilnosti površja (Bishop, 2013; Smith, M.J. in sod., 2013; Tarolli in Mudd, 2020; Ciglič in sod., 2022). Napredek na področju zajema in obdelave visokoločljivostnih podatkov daljinskega zaznavanja (npr. LiDAR, ang. *Light Detection And Ranging*) omogoča preučevanje mikoreliefnih značilnosti tudi na večjih, odročnih, z vegetacijo poraslih in težko dostopnih območjih (Höfle in Rutzinger, 2011; Triglav Čekada, 2011; Davies in Asner, 2014; Breg Valjavec in sod., 2018; Ciglič in sod., 2022).

V preteklih raziskavah ekologije prostoživečih mačk je bilo interpretaciji geomorfoloških značilnosti in procesov ter analizam LiDAR DMV-jev, ki zahtevajo posebna znanja in spretnosti, namenjene manj pozornosti. To je bilo delno povezano tudi s pomanjkanjem slojev, ki vsebujejo informacije o reliefnih značilnosti za večja območja in z omejeno razpoložljivostjo visokoresolucijskih LiDAR DMV-jev. Za popolno in učinkovito uporabo visokoločljivostnih LiDAR podatkov je v ekologiji živali pogosto potrebno sodelovanje med raziskovalci s področja geo- in bioznanosti. Glede na to, da le maloštevilne raziskave v ekoloških analizah zajemajo tudi podatke o mikro- in mezoreliefnih značilnostih habitatov, je naše znanje o njihovem vplivu na ekologijo prostoživečih mačk in tudi drugih vrst še vedno precej omejeno. Po našem vedenju je raziskava v okviru te doktorske disertacije ena prvih, ki se pri ugotavljanju podrobnih in natančnih informacij o mikoreliefnih značilnostih habitatov na tako velikem območju opira predvsem na podatke daljinskega zaznavanja. Zato je eden izmed ciljev te doktorske disertacije tudi prikazati uporabnost daljinskega zaznavanja reliefnih oblik za raziskave s področja ekologije živali, kar je možno na podlagi kombiniranja pridobivanja podatkov o mikro- in mezoreliefnih značilnostih z metodami daljinskega zaznavanja ter podatkov o rabi prostora prostoživečih živali pridobljenih z GPS-telemetrijo.

1.1 RELIEFNE OBLIKE

1.1.1 Reliefne oblike in splošne geografske značilnosti slovenskega Dinarskega krasa

Kras je poseben tip površja, ki ga opredeljujeta skalovitost in pestrost površinskih ter podzemeljskih geomorfoloških oblik. Območje lahko opredelimo kot kraško oziroma zakraselo, kadar deluje odnašanje snovi v raztopini, vertikalni odtok padavinskih voda, akumulacija raztopljenega materiala pa je zanemarljiva (Ford in Williams, 2007; Veress, 2020). V Sloveniji kras pokriva 49,7 % celotnega ozemlja. Od tega je približno 50 % krasa razvitega v apnencih in 25 % krasa v dolomitih, ki sta prostorsko najbolj razširjena v zahodni in južni Sloveniji, na območju slovenskega Dinarskega krasa (Gostinčar in Stepišnik, 2023). Preostalih 25 % krasa je razvitega v različnih karbonatnih kamninah, kot so npr. klastične karbonatne kamnine, karbonatni peski, fino-zrnati sedimenti in fliši (Gostinčar in Stepišnik, 2023). Slovenski Dinarski kras (Slika 1) delimo na visoki dinarski kras (z nadmorsko višino med 800 in 1700 m; 66,8 % celotnega slovenskega Dinarskega krasa), za katerega so značilne visoke kraške planote, in nizki dinarski kras (33,2 % celotnega slovenskega Dinarskega krasa), kjer prevladujejo nizke kraške planote, korozijske uravnave in kraška polja. V zahodnem delu se vode izlivajo v Jadransko morje, v osrednjem in južnem delu pa odtekajo proti Črnemorskemu povodju (Perko in Ciglič, 2020; Zorn in sod., 2020).



Slika 1: Zemljevid in primeri slik pokrajine na območju Bavarsko-Češkega gozdnega ekosistema in slovenskega Dinarskega krasa z domačimi okoliši risov

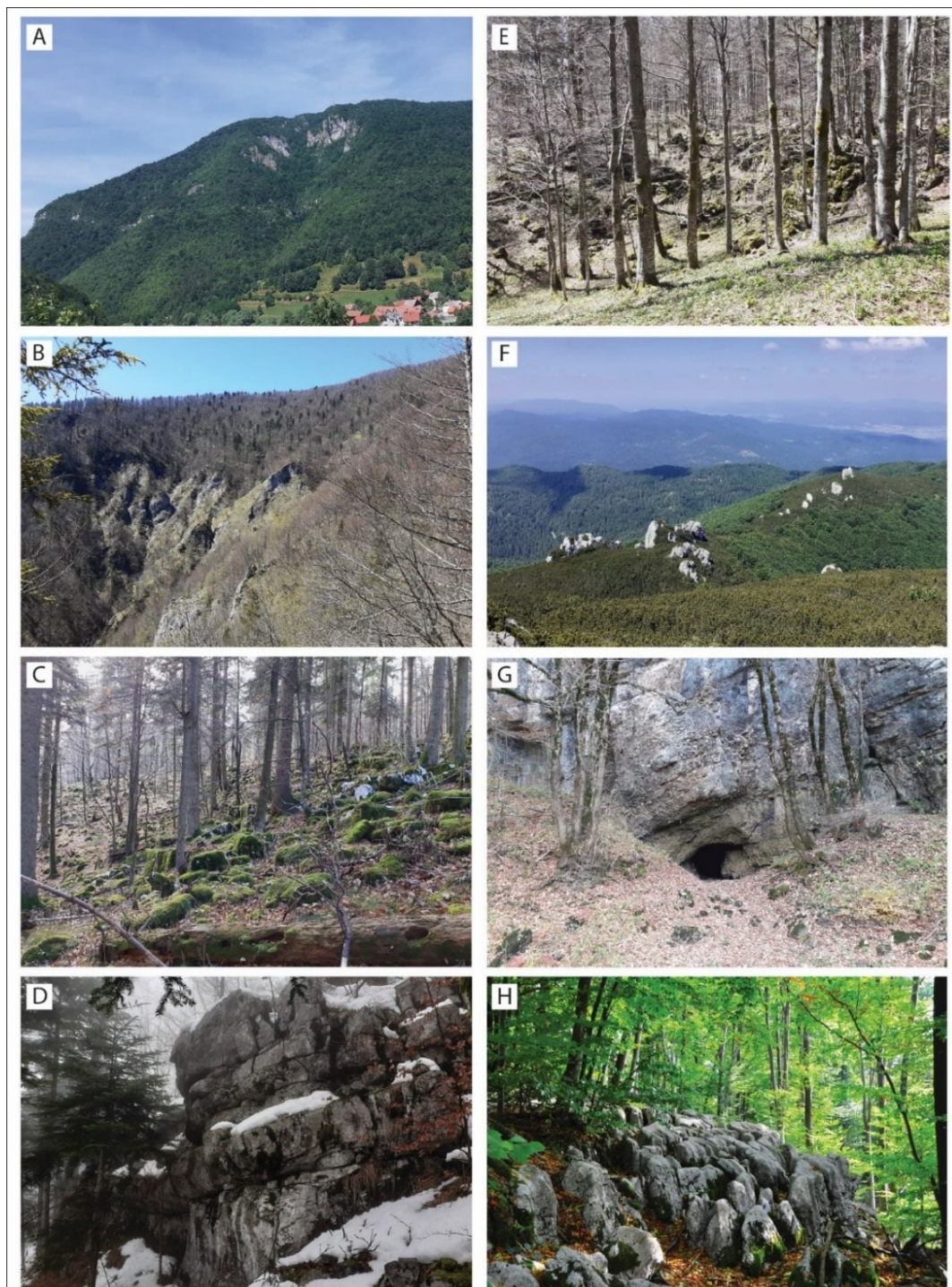
Geografsko in geološko je območje slovenskega Dinarskega krasa del Dinarskega gorstva, približno 650 km dolge in 150 km široke mlado nagubane gorske verige, ki poteka v značilni

dinarski smeri od severozahoda proti jugovzhodu. Dinarsko gorstvo na severu meji na Alpe, na vzhodu na Panonsko kotlino, na zahodu ga omejuje Jadransko morje, na jugu pa Šarsko-pindsko gorstvo (Mihevc in sod., 2010). Z geološkega vidika ga delimo na zunanje in notranje Dinaride. Notranji del poteka na severovzhodu ob Panonski kotlini. Gradijo ga magmatske ter metamorfne kamnine, zato prevladuje fluvialni geomorfni sistem. Ker jugozahodni oziroma zunanji del gradijo večinoma karbonatne kamnine (apneneci in dolomiti), prevladuje kraški tip reliefa, zato območje zunanjih Dinaridov imenujemo tudi Dinarski kras (Mihevc in sod., 2010; Glavaš in Stepišnik, 2019). Osrednji del slovenskega Dinarskega krasa gradijo predvsem mezozojske in kvartarne kamnine, med katerimi prevladujeta apnenec in dolomit. Proti jadranski obali se nadmorska višina znižuje, med območji apnenca pa se pojavljajo pasovi eocenskega fliša (Mihevc in sod., 2010; Zorn in sod., 2020).

Za kraška območja je značilna pestrost površinskih in podzemnih pojavov in procesov, ki nastajajo kot posledica različne litologije in dinamike mehanskega preperevanja kamnin (Mihevc in sod., 2010; Zorn in sod., 2020). Součinkovanje oziroma prevlada posameznih procesov lahko vpliva na delovanje krasa, posledično so kraški procesi lahko zavrti ali spremenjeni. To se odraža kot pestrost različnih tipov krasa in tudi nastajanja oziroma preoblikovanja kraških geomorfoloških oblik (Stepišnik, 2020, 2024; Veress, 2020). Glede na Stepišnikovo (2024) procesno-geomorfološko sistematizacijo krasa v Sloveniji, kraški geomorfni sistem razvrščamo v štiri tipe: globoki kras, plitvi kras, fluviokras in glaciokras. V Sloveniji globoki kras obsega 48 % celotnega površja krasa, fluviokras 39 %, glaciokras 11,3 % in plitvi kras 1,8 % (Stepišnik, 2024). Na preučevanem območju so prisotni vsi štirje tipi z značilnimi reliefnimi oblikami (Slika 2).

S terminom globoki kras opredeljujemo območja krasa, kjer je gladina podzemne vode oz. piezometrični nivo globoko pod površjem (Gams, 2004; Stepišnik, 2024). Na oblikovanje površja vplivajo geomorfni procesi, ki potekajo na površju in v podzemlju. Dominantni proces je raztapljanje, zato prevladuje kemična denudacija. Za globoki tip krasa so značilna večja uravnana območja (npr. kraške planote in ravniki), ki jih opredeljujemo kot korozijske uravnave (Stepišnik in Ferk, 2024). Zaradi neenakomernega raztapljanja in denudacije pa je kraško površje močno razčlenjeno s številnimi kopastimi vzpetinami, uvalami in korozijskimi vrtačami. Udorne vrtače in brezstope jame se zaradi denudacije preslikajo na površje, podzemni tokovi pa s spodjedanjem v jamah povzročajo nastanek udornic na površju (Stepišnik, 2024). Globoki kras glede na pokritost s sedimentom delimo na goli in pokriti kras. Termin goli kras uporabljamo za območja, kjer je kraško površje izrazito skalovito, brez ali z zelo malo sloja preperine. Površje, ki ga le delno prekriva preperina in kjer matična kamnina izdanja le mestoma, imenujemo polgoli kras (Stepišnik, 2024). Kraško površje poleg tipičnih večjih kraških reliefnih oblik razčlenjujejo tudi številne manjše reliefne oblike. Na območjih golega in polgolega krasa na kamninah nastajajo oblike v velikosti od nekaj milimetrov do več deset metrov. Na (pol)golem krasu so poleg škavnic, kotličev, škrapelj in ostalih mikroreliefnih oblik pogoste tudi škraplje in škrapljišča, skalni bloki ter skalni samotarji (Gams, 2004; Veress in Vetési-Foith, 2021; Stepišnik, 2024). Golo kamnino in druge skalne oblike, ki so razkrite na površju, lahko imenujemo tudi izdanki kamnin. Izdanki kamnin nastanejo z erozijo okoliškega materiala oz. preperine, ki je mehansko manj odporna (Twidale, 2000). Za izdanke kamnin, ki

nastajajo v različnih tipih kamnin in so pestrih oblik ter velikosti, je značilen predvsem velik naklon in prostorska izoliranost (Fitzsimons in Michael, 2017). Zaradi skalovitosti, številčnosti in gostote najrazličnejših mikro- in mezoreliefnih kraških oblik, ki razčlenjujejo površje, lahko kras opredelimo tudi kot enega najbolj skalovitih in razgibanih geomorfoloških sistemov na našem planetu (Day in Chenoweth, 2013).



Slika 2: Primeri različnih reliefnih oblik na območju slovenskega Dinarskega krasa: A) Stene nad kanjonom reke Kolpe, B) stene nad fluviokraško dolino, C) apnenčasti skalnati bloki na pobočju, D) stena oz. večji izdanek kamnine, E) vrtača s skalovitim robom, F) skalni čoki ter kopasti vrhovi z vmesnimi uvalami v ozadju, G) jamski vhod, H) škrapljišče

Območja krasa, na katerih gladina podzemne vode sega nad površje in se na površju oblikujejo stalna ali občasna vodna telesa, opredeljujemo kot plitvi kras (Gams, 2004; Stepišnik, 2024). Plitvi kras nadaljnjo delimo na dve okolji: okolje stoječih voda in okolje tekočih voda. Za okolje stoječih voda so značilne stalno ali občasno ojezerjene kraške kotanje kot so vrtače, uvale in udornice. Večje občasno ali stalno ojezerjene kraške kotanje zaradi dimenzij uvrščamo med kraška polja. Prevladujoč geomorfni proces v kraških jezerih je kemična denudacija, ki deluje predvsem lateralno in jih širi. V okolju tekočih voda so kanjoni najznačilnejša kraška reliefna oblika, ki se poglobljajo z mehansko in kemično denudacijo (Stepišnik, 2024).

Fluviokras in glaciokras se od globokega in plitvega krasa razlikujeta glede na dominantne procese preoblikovanja površja, ki so tipični za druge (nekraške) geomorfne sisteme. Fluviokras se pojavlja na pobočjih pokritega krasa, najpogosteje na območjih dolomita, ki je bolj podvržen mehanskemu preperevanju. Na teh območjih je zaradi debelejšje plasti preperine vertikalni odtok padavinskih voda zavrt. Posledično se na takem kraškem površju pojavijo površinski tokovi, ki povzročijo fluvialno premeščanje materiala. Najbolj značilne fluviokraške oblike so erozijski žlebovi, nasipni stožci, erozijski jarki, dolki, fluviokraški vršaji, fluviokraške doline in pritočna kraška polja (Komac, 2004, 2006; Stepišnik, 2024).

Dinarsko gorstvo je bilo v pleistocenskih ledenih dobah preoblikovano z delovanjem posameznih manjših ledenikov, ki so prekrivali najvišje predele visokih kraških planot. Na območju Slovenije sta bili v Dinarskem gorstvu poledeneli le najvišji kraški planoti: Snežnik (Veliki Snežnik, 1796 m) in Trnovski gozd (Mali Golak, 1495 m) (Žebre in Stepišnik, 2015, 2018; Kodelja in sod., 2018). Območja, ki imajo podedovane površinske in podzemne oblike nekdanjega poledenega krasa ter oblike nekdanje poledenitve imenujemo glaciokras (Veress, 2020; Stepišnik, 2024). Najbolj tipične oblike glaciokrasa, ki so nastale na območju ledeniške erozije so jame, kotlički, kotličaste vrtače, konte, ledeniške grbine in lašti, na območju ledeniške akumulacije pa bočno-čelni morenski kompleksi, predledeniška kraška polja, ledeniški vršaji in korita (Stepišnik, 2024).

Nadmorska višina se na območju slovenskega Dinarskega krasa razteza med približno 200 in 1800 m. Dinarsko gorovje predstavlja pomembno orografsko pregrado, ki vpliva na količino padavin. Zaradi izrazite razlike v nadmorski višini in orografske pregrade so znotraj slovenskega Dinarskega krasa opazne podnebne razlike. Na splošno je za slovenski Dinarski kras značilno zmerno celinsko podnebje, za najvišje vrhove pa je značilno gorsko podnebje (Komac in sod., 2020; Ogrin in sod., 2023). Glede na vertikalno conacijo ločujemo tri glavne pasove: dolinska dna, termalno ali toplo območje in gorsko območje (Gams, 1972). Za dna dolin in kraških depresij je značilna temperaturna inverzija, kar povečuje število dni z meglo in onesnaženost zraka. Sledi termalni oz. toplotni pas, ki je ob močni inverziji lahko tudi do 10 °C toplejši od nižje ležečega pasu, v povprečju pa je toplejši za približno 1 °C. Hribovito območje (400–800 m) je primerljivo z območjem temperaturne inverzije. Sledijo mu nižje gorsko območje (800–1200 m), višje gorsko območje (1200 m–zgornja drevesna meja), subalpinsko območje (nad zgornjo drevesno mejo) in alpsko območje (Gams, 1972; Ogrin, 2004; Komac in sod., 2020). Na območjih visokega dinarskega krasa (nad 800 m) je povprečna letna temperatura med 2 in 8 °C, na območjih nizkega dinarskega krasa (pod 800 m) pa med 8

in 10 °C. Povprečna letna količina padavin je med 1200 in 1800 mm, ki upada od zahoda proti vzhodu, z izjemo najvišjih vrhov (npr. Snežnik), kjer je povprečna letna količina padavin med 1700 in 3000 mm. Snežna odeja je pogosta v januarju in navadno traja od 20 do 60 dni. Največ snega pa zapade februarja, v povprečju pa v zimi zapade 60–100 cm snega (vsota dnevnih količin novozapadlega snega) (Komac in sod., 2020; Ogrin in sod., 2023).

Prevladujoč tip gozdov slovenskega Dinarskega krasa so bukovi gozdovi, ki predstavljajo pomemben življenjski prostor za velike zveri. Na kraških planotah je najbolj značilna združba dinarskih jelovo-bukovih gozdov (*Omphalodo-Fagetum*) z glavnima vrstama navadna bukev (*Fagus sylvatica*) in navadna jelka (*Abies alba*). Dopolnjujeta ju navadna smreka (*Picea abies*), katere razširjenost je posledica človekovega poseganja v sestoje, in gorski javor (*Acer pseudoplatanus*). Na južnih ekspozicijah dolomitnih pobočjih prevladuje termofilna združba bukve in črnega gabra (*Ostryo-Fagetum*). Z naraščanjem nadmorske višine in v kraških kotanjah, kjer prihaja do vegetacijskega obrata, uspevajo gozdovi, v katerih prevladuje navadna smreka, sledi pas ruševja (*Pinetum mugi croaticum*) in floristično bogata travišča (*Seslerietalia caeruleae*). Na občasno ali stalno ojezerjenih kraških poljih so pogosto travišča z združbami, ki jih sestavlja navadni trst (*Phragmites australis*) in različni šaši (Čarni in sod., 2002; Šilc in sod., 2020).

Poleg tipične slemenitve, prevlade zakraselega sveta in kraških pojavov so temeljne značilnosti slovenskega Dinarskega krasa velika namočenost in gozdnatost, ekstenzivna živinoreja, gozdarstvo, redka poselitev in ekološka ranljivost, območje pa je tudi osrednji življenjski prostor velikih zveri ter ostalih vrst živali, med katerimi so številne endemične (Belec in sod., 1998; Mihevc in sod., 2010; Perko in Ciglič, 2020; Šilc in sod., 2020). Površinska vodna mreža je razvita le na območjih plitvega krasa in fluviokrasa. Za območje je značilna redka poselitev s povprečno gostoto 17,2 prebivalca na km². Poselitev je razpršena, prevladujejo manjša naselja, ki so večinoma na večjih uravnanih območjih, kot so kraška polja ali nizke kraške planote (Perko in Ciglič, 2020).

Obsežni dinarski bukovo-jelovi gozdovi predstavljajo habitat treh velikih zveri, risa, volka (*Canis lupus*) in rjavega medveda (*Ursus arctos*). Poleg teh vrst pa na območju najdemo tudi druge srednje velike in velike sesalce kot so npr. zlati šakal (*Canis aureus*), divja mačka, jazbec (*Meles meles*), lisica (*Vulpes vulpes*), srnjad (*Capreolus capreolus*), jelenjad (*Cervus elaphus*) in divji prašič (*Sus scrofa*) (Šilc in sod., 2020). Zaradi visoke bio- in geodiverzitete so na slovenskem Dinarskem krasu vzpostavljena številna zavarovana območja z različno stopnjo varovanja. Večja zavarovana območja so Notranjski regijski park, Regijski park Škocjanske jame, Krajinski park Pivška presihajoča jezera, sega pa tudi na obronke Krajinskega parka Ljubljansko barje in Krajinskega parka Radensko polje. Pragozdova Krokari in Snežnik–Ždrolc sta vpisana na UNESCO-v seznam svetovne dediščine, Cerkniško jezero pa je skupaj z Rakovim Škocjanom in Križno jamo vpisano med Mednarodno pomembna mokrišča kot eno od treh Ramsarskih območij v Sloveniji (Šilc in sod., 2020). Velik del slovenskega Dinarskega krasa obsega tudi območja Natura 2000 (npr. Kočevsko, Javorniki-Snežnik) in spada tudi pod številna Ekološko pomembna območja (npr. Osrednje območje življenjskega prostora velikih zveri) (Šilc in sod., 2020; Naravni parki ..., 2023). Po podatkih Katastra jam (2024) je bilo v

Sloveniji do sredine leta 2022 (4. 7. 2022) registriranih 14.853 kraških jam (Kataster jam, 2024). Poleg jam med naravne vrednote uvrščamo tudi druge biotske in abiotske naravne pojave, ki so opredeljeni kot naravne vrednote državnega ali lokalnega pomena. Gostota podzemnih naravnih vrednot oz. jam je zelo visoka na dinarskih planotah (130,4 jam/100 km²) in dinarskih podoljih (109,9 jam/100 km²), celotno območje pa ima tudi visoko raznolikost in gostoto ostalih abiotskih naravnih vrednot (Perko in Tičar, 2020).

1.1.2 Reliefne oblike in splošne geografske značilnosti Bavarsko-Češkega gozdnega ekosistema

Bavarsko-Češki gozdni ekosistem (Slika 1) je s približno 5000 km² eno največjih zavarovanih gozdnih območij v srednji Evropi. Območje obsega štiri zavarovana območja: narodni park Bavarski gozd (240 km²) in naravni park Bavarski gozd (3007 km²) v Nemčiji, ter narodni park Šumava (690 km²) in naravni park Češki gozd (~ 1000 km²) na Češkem (Heurich in sod., 2015). Približno 130 km dolgo in 60 km široko območje, ki se razteza od severozahoda proti jugovzhodu, je grudasto gorovje in je geografsko ter geološko del Češkega masiva. Glavni greben gorovja tvori mejo med Nemčijo in Češko ter ločuje severnomorsko (reka Laba) in črnomorsko (reka Donava) povodje. Jugovzhodni del gorovja sega v Avstrijo (Heurich in sod., 2010; Krause in Margold, 2019). Gorovje se razteza od nadmorske višine 370 m do vrhov z nadmorsko višino okoli 1450 m (Großer Rachel – 1453 m, Großer Arber – 1456 m). Velik del območja (več kot 350 km²) je nad 1000 m nadmorske višine (Heurich in sod., 2010).

Današnji relief Bavarskega gozda in Šumave je odraz dolgotrajnega geološko-geomorfološkega razvoja, ki se je začel z variskično orogenezo, sledila pa je erozija in oblikovanje uravnanega planotastega površja (Mentlík, 2016). Na območju najdemo dva tipa večjih tektonskih prelomov. Starejše prelome, ki potekajo v smeri od severa proti jugu, je poglobila rečna in ledeniška erozija. Ob mlajših prelomih, ki potekajo v enaki smeri kot glavni grebeni gorovja (severozahod-jugovzhod), pa se je gorovje dvignilo na sedanjo nadmorsko višino (Finger in sod., 2007; Mentlík, 2016). Območje gradijo več kot 300 milijonov let stare magmatske, metamorfne in kristalinske kamnine, predvsem gnajs in granit. Na območju so prisotni tudi paragnajsi, migmatiti, kvarciti, filiti in sljudni skrilavci. V času variskične orogeneze so bile kamnine močno deformirane (Babůrek in sod., 2006).

Površje se je sčasoma dvigovalo, hkrati pa sta na preoblikovanje vplivali rečna in ledeniška erozija. Osrednji del gorovja (1000 – 1200 m) je planotast in uravnan. Zaradi velike količine padavin in slabega sistema odvodnjavanja so se razvila številna visoka šotna barja (Mentlík, 2016). Na nemški strani se relief iz uravnanih vrhov strmo spusti preko ledeniških krnic in preide v razmeroma hribovito površje s položnejšimi pobočji, ki jih razčlenjujejo številni erozijski jarki, rečne doline in grebeni. Na češki strani se relief počasneje spušča in prehaja v ostanke dvignjenega uravnanega površja v obliki večjih planot (Šumavske ravnice), kjer se prepletajo barja in travniki. Na severozahodnem in jugovzhodnem robu Šumave je površje razrezano z dolinami večjih rek (Weisse Regen, Úhlava, Vltava). Na tem območju se kažejo največje višinske razlike, do 600 m relativne višine med dnem dolin in najvišjimi okoliškimi vrhovi (Mentlík, 2016).

Poleg rečne erozije pa so na izoblikovanost površja močno vplivali tudi ledeniški in periglacialni geomorfni procesi. Območje je bilo v hladnih pleistocenskih obdobjih poledenelo, ledeni pokrov je glede na ocene obsegal približno 650 km². Po koncu zadnje ledene dobe se je gozd razširil in prekril takrat neaktivne ledeniške (npr. krnice, ledeniške doline, ledeniška jezera, morene) in periglacialne reliefne oblike (npr. eratični bloki, balvani, deflacijske kotanje, geliflukcijske terasice, »blockmeer« oz. polja blokov) (Slika 3). Pred tem je na izoblikovanje pobočij vplivala predvsem geliflukcija, ki je pustila številne razpršene bloke in balvane (Mentlík, 2016; Hauner in sod., 2019; Krause in Margold, 2019). Na podlagi terenskih raziskav in pregleda visokoločljivostnih LiDAR podatkov so na območju identificirali 12 večjih krnic, večino danes zapolnjujejo ledeniška jezera (npr. Grosser Arbersee, Prášilské jezero, Rachelsee). Najštevilčnejša ledeniška reliefna oblika so čelni klifi oz. stene, ki so najpogostejše oblikovani na območju krnic in večjih dolin (Hauner in sod., 2019; Krause in Margold, 2019).

Od umika ledenikov je površje podvrženo predvsem fluvio-glacialnim procesom (Hauner in sod., 2019). Zaradi neprepustnih kamnin voda odteka površinsko. Fluvialni procesi vplivajo na premeščanje gradiva in prenašanje preperine iz višjih v nižje lege. Površinska voda, ki se na površju združuje v vodotoke, erodira površja in vpliva na oblikovanje tipičnih fluvialnih reliefnih oblik kot so soteske, rečne doline, grebeni, aluvialne ravnice, slapovi in kaskade ter izdanki kamnin različnih velikosti in oblik (npr. stene, kamniti bloki, ipd.). Izdanki kamnin (Slika 3D–H) so ena najbolj značilnih reliefnih oblik v Bavarsko-Češkem gozdnem ekosistemu. Na območjih, ki jih gradijo metamorfne kamnine (npr. gnajs), kamnina izdanja na površje predvsem v obliki skalnatih grebenov, kamnitih plošč, plastovitih sten in previsnih izdankov kamnin. Na obliko izdankov vplivajo predvsem naklon, plastovitost in primesi mineralov oz. kamnin, kot je na primer kremen (Mentlík, 2016). V primerjavi z metamorfnimi kamninami, so magmatske kamnine (gnajs) manj odporne na mehansko preperevanje. Zaradi ohlajevanja in strjevanja magme globoko pod površjem se kamnina krči in lomi, kar ustvarja razpoke. Granitna kamnina doseže površje, ko se okoliško površje erodira. Voda in korenine rastlin prodirajo po razpokah, postopno mehansko delovanje postopoma ločuje celotne skalne bloke drug od drugega, njihove oblike in velikosti pa se ujemajo z razporeditvijo sistema razpok. Na območju granita je posledično več izdankov kamnin, ki lahko dosežejo tudi večje dimenzije (Mentlík, 2016). Poleg površinske vode na višjih nadmorskih višinah še danes na oblikovanje površja vplivajo tudi periglacialni geomorfni procesi kot posledica sezonskega taljenja in zmrzovanja (Hauner in sod., 2019).

Zaradi razlik v nadmorski višini so na območju Bavarsko-Češkega gozdnega ekosistema izoblikovani trije različni podnebni oz. bioklimatski višinski pasovi – nižinski, gorski in subalpski pas. Povprečna letna temperatura in količina padavin se razlikujeta tako znotraj posameznih pasov kot tudi med pasovi (Röder in sod., 2010). Trajna snežna odeja na vrhovih gora traja od oktobra do maja, v dolinah pa od novembra do aprila (Heurich in sod., 2015). Subalpski pas (nad 1150 m) je s povprečnimi letnimi temperaturami med 3,9 in 4,9 °C najhladnejše območje. Letna količina padavin v tem pasu znaša 1505–1860 mm, pri čemer lahko v najvišjih predelih padavine v obliki megle prispevajo tretjino celotne količine padavin (Heurich in sod., 2010; Röder in sod., 2010).



Slika 3: Primeri različnih reliefnih oblik na območju Bavarsko-Češkega gozdnega ekosistema: A) Položno nerazčlenjeno pobočje, B) potok, C) ledeniško jezero, D) stene nad rečno dolino, E) ledeniški balvani, F) ledeniška krnica, G) balvansko ali kamnito polje oz. »blockmeer«, H) izdanki kamnine

Prevladujoča gozdna združba subalpinskega pasu je gorski smrekov gozd, za katerega je v naravnem stanju značilna skoraj izključno navadna smreka, ki jo dopolnjujeta navadna jerebika (*Sorbus aucuparia*) in gorski javor (Heurich in sod., 2010; van der Knaap in sod., 2019). V gorskem pasu (650–1150 m) je povprečna letna temperatura med 4,7 in 6,7 °C, povprečna letna količina padavin znaša 1085–1815 mm (Röder in sod., 2010). Zaradi razmeroma ugodnih podnebnih razmer je to območje gorskega mešanega gozda, kjer so glavne drevesne vrste bukev, jelka in smreka. Te gozdove lahko razdelimo na dva tipa: na revnih tleh je acidofilni

bukov gozd s praprotnjo (*Luzulo luzuloides-Fagetum*), na bogatejših tleh pa bazofilni bukov gozd z jelko (*Galion odorati-Fagetum*) (Heurich in sod., 2010; van der Knaap in sod., 2019). V nižinskem pasu (pod 650 m) je povprečna letna temperatura med 6,0 in 8,6 °C, povprečna letna količina padavin pa znaša 965–1565 mm (Röder in sod., 2010). Topografsko so to ravna območja in dna rečnih dolin, v katerih se zadržuje hladen zrak, ki se spušča z višjih nadmorskih višin. Za ta pas so značilne pogoste, zgodnje in pozne zmrzali ter vlažna tla, kar določa spodnjo mejo razširjenosti bukve. Klimaksna gozdna združba na dnu dolin je vlažen smrekov gozd (*Calamagrostio villosae Piceetum bazzanietosum*), v katerem prevladuje smreka. Dopolnjujeta jo navadna (*Betula pendula*) in puhasta breza (*Betula pubescens*) (Heurich in sod., 2010; van der Knaap in sod., 2019).

NP Bavarski gozd je bil ustanovljen leta 1970 kot prvi narodni park v Nemčiji. Leta 1991 je bil na češki strani ustanovljen NP Šumava. V evropskem kontekstu oba narodna parka (Bavarsko-Češki gozdni ekosistem) predstavljata eno največjih sklenjenih in zavarovanih gozdnih površin v Srednji Evropi. Za območje je značilna nizka gostota prebivalstva, z 2 osebama na km² v osrednjem območju parkov in 30–70 oseb na km² na obrobni območjih (Heurich in sod., 2015). Medtem ko sta narodna parka večinoma porasla z gozdovi, je v podeželski okolici pokrajina bolj mozaična. Na območju širših zavarovanih območij se prepletajo manjši gozdovi, travniki, obdelovalne površine in vasi. Zaradi varstva narave in ekstenzivne rabe tal sta za območje značilni visoka bio- in geodiverziteti, kar se odraža v pestrosti habitatov ter živalskih in rastlinskih vrst, hkrati pa privablja tudi številne turiste (Heurich in sod., 2010; Navrátil in sod., 2014). Območje predstavlja habitat risa in volka, med manjšimi zvermi pa je najpogostejša lisica. Med parkljarji prevladujejo srnjad, jelenjad in divji prašič (Belotti in sod., 2013).

1.1.3 Daljinsko zaznavanje reliefnih oblik

Geomorfološke oz. reliefne oblike so eden izmed ključnih elementov zemeljskega površja, ki v različnih geomorfnih sistemih (npr. kraški, rečni, ledeniški) nastajajo kot posledica različnih interakcij med geološkimi procesi, podnebjem in tektonskim delovanjem (Strahler A. H. in Strahler A. N., 1992; Gutiérrez in Soldati, 2018). Reliefne oblike so različni elementi z izrazitimi morfološkimi značilnostmi, ki sestavljajo pokrajine. Znanstveno vedo, ki na sistematičen način preučuje reliefne oblike, njihove pokrajine ter procese, ki jih ustvarjajo, imenujemo geomorfologija (Strahler A. H. in Strahler A. N., 1992; Sack in Orme, 2013; Gutiérrez in Soldati, 2018).

Pri preučevanju, interpretaciji, analizi in vizualizaciji reliefnih oblik ter značilnosti površja imajo grafični popisi oz. geomorfološke karte izjemen pomen. V preteklosti so bile geomorfološke karte predvsem ročno izdelane in so temeljile na podlagi terenskih popisov (Otto in Smith, 2013). Napredek v tehnologiji zajema (npr. natančni satelitski in zračni posnetki ter podatki laserskega skeniranja površja) in obdelave podatkov (npr. geografski informacijski sistemi oz. GIS), omogoča vse bolj podrobne analize zemeljskega površja (Tarolli in Mudd, 2020). Na področju geomorfologije in drugih ved se zato razvijajo številne metode in tehnologije za daljinsko ter stroškovno učinkovito kartiranje in zaznavanje reliefnih oblik ter analize reliefnih značilnosti površja (Bishop, 2013; Smith in sod., 2013; Tarolli in Mudd, 2020). Digitalne vizualne interpretacije reliefa (npr. senčenje oz. *Hillshade*, *Red relief image*, 3D

prikazovanje), različni reliefni koeficienti (npr. razgibanosti površja, naklon, *Sky-view* faktor) ter metode za polavtomatsko ali avtomatsko zaznavanje in omejevanje reliefnih oblik (npr. objektno ali pikselno usmerjene metode, topografski pozicijski indeks, zaznavanje vrtač) vse pogosteje nadomeščajo stroškovno in časovno potratno terensko kartiranje (npr. Weiss, 2001; Chiba in sod., 2008; Zakšek in sod., 2011; Drăguț in Eisank, 2012; Telbisz in sod., 2016; Syzdykbayev in sod., 2020).

Daljinsko zaznavanje je definirano kot »znanost pridobivanja informacij o površju Zemlje, ne da bi z njo prišli v neposredni stik. Pri tem zaznavamo in zapisujemo odbito ali sevano elektromagnetno valovanje, ga obdelujemo, analiziramo in uporabimo v različnih aplikacijah« (Oštir, 2006). S procesom klasifikacije podob iz daljinsko zaznanih podatkov ustvarimo kvantitativne sloje, ki omogočajo prostorske analize. Glavni namen klasifikacije je torej prepoznavanje pojavov na zemeljskem površju (Oštir, 2006).

Ključni dejavnik pri uporabi daljinsko zaznanih podatkov je ločljivost pridobljenih podatkov (Campbell in Wynne, 2011). Na globalni ravni so se topografski podatki s kilometrsko ločljivostjo leta 1996 (*GTOPO30*) povečali na podatke z ločljivostjo 5 m v letu 2018 (*ALOS World 3D*). Številni produkti so prosto dostopni (npr. *TanDEM-X-DEM* z ločljivostjo 12 m) in omogočajo analizo površja območij večjih dimenzij na državni, kontinentalni ali globalni ravni (Mudd, 2020). Vzporedno z ostalimi metodami daljinskega zaznavanja se je razvilo tudi lasersko skeniranje oziroma LiDAR, ki omogoča zbiranje podatkov z zelo visoko natančnostjo, tudi centimetrsko (Tarolli in Mudd, 2020). Letalski ali terestrični zajem LiDAR podatkov je metoda daljinskega zaznavanja, s katero lahko na podlagi merjenja časa povratnega potovanja laserskega pulza od senzorja do odbojne površine (npr. drevesnega lista) in spet nazaj določimo razdaljo, iz znanega položaja senzorja pa lahko izračunamo tudi 3D koordinato vsakega odboja (Fernandez Diaz in sod., 2013). LiDAR se pogosto uporablja za obdelavo in analizo podatkov visoke ločljivosti na različnih znanstvenih, inženirskih in drugih področjih (Höfle in Rutzinger, 2011; Fernandez Diaz in sod., 2013). Natančno lasersko skeniranje površja zagotavlja vpogled v 3D fizično strukturo ekosistemov, od vegetacijskih struktur do reliefa (Davies in Asner, 2014). Uporaba LiDAR podatkov je še posebej primerna v geomorfologiji, saj omogoča preučevanje reliefnih značilnosti na večjih, odročnih, z vegetacijo poraslih in težko dostopnih območjih, kot sta npr. slovenski Dinarski kras in Bavarsko-Češki gozdni ekosistem (Höfle in Rutzinger, 2011; Triglav Čekada, 2011; Davies in Asner, 2014; Breg Valjavec in sod., 2018; Ciglič in sod., 2022).

GIS-i ponujajo različne tehnike in metode za digitalno interpretacijo in analizo daljinsko pridobljenih podatkov, ki omogočajo prepoznavanje in/ali merjenje lastnosti preučevanih linijskih, točkovnih ali ploskovnih objektov (Oštir, 2006). Ena izmed tehnik interpretacije je vizualizacija reliefa, ki služi predvsem kot podlaga za digitalizacijo reliefnih oblik in oblikovanje kartografskih prikazov (Smith in Clark, 2005; Chiba in sod., 2008). Z izbiro tehnike vizualizacije (npr. barvni ton oz. psevdobarvni prikaz, vzorec, tekstura, senčenje) lahko vplivamo na kartografske prikaze, ki omogočajo lažjo interpretacijo in pridobivanje podatkov o preučevanih oblikah ali območjih (Oštir, 2006; Chiba in sod., 2008). Najpogostejša vizualizacijska tehnika je senčenje reliefa oz. *Hillshade* (Kraak in Ormeling, 2020). Pri

vizualizaciji in interpretaciji značilnosti površja si lahko pomagamo tudi z reliefnimi koeficienti, ki jih na podlagi izračuna osnovnih aritmetičnih operacij ali kompleksnejših indeksov pridobimo iz digitalnega modela višin (DMV) (Oštir, 2006). Iz DMV-ja lahko izračunamo naklon, ukrivljenost, indeks razgibanosti, odprtost površja, ipd. (Sappington in sod., 2007; Zakšek in sod., 2011; Saleem in sod., 2019).

Reliefne oblike lahko zaznamo ali omejimo na podlagi različnih polavtomatskih in avtomatskih metod. S klasifikacijo lastnosti vhodnih podatkov DMV-ja pridobimo kvantitativni sloj, ki v GIS-ih omogoča nadaljnje prostorske analize (Oštir, 2006). Metode za polavtomatsko in avtomatsko zaznavanje reliefnih oblik temeljijo na izračunu reliefnih koeficientov, dodatnih prostorskih analizah ali osnovnih aritmetičnih operacijah in strojnem učenju. Pri polavtomatskih metodah lahko reliefne oblike zaznamo in omejimo na podlagi klasifikacije reliefnih koeficientov v razrede. Na primer, stene in izdanke kamnin lahko omejimo z enostavno določitvijo vrednosti naklona (npr. Loye in sod., 2009; Smith in Mullins, 2022). Grebene, doline (npr. Weiss, 2001), kraške kotanje, kraške vzpetine (npr. Bauer, 2015; Telbisz, 2021) ali območja grbinastih travnikov (Stefanovski in Lampič, 2022) pa lahko omejimo na podlagi kombinacije različnih reliefnih koeficientov z dodatnimi prostorskimi ali računskimi analizami.

Z napredkom programske opreme se razvija vse več metod na področju strojnega učenja, ki omogočajo kvantitativno in avtomatsko klasifikacijo reliefnih oblik (Tarolli in Mudd, 2020). Preprostejše avtomatske metode so pikselno ali objektno usmerjene metode. Pikselno usmerjene metode so primerne predvsem za analizo in klasifikacijo podatkov z nizko in srednjo ločljivostjo. V analizi posamičen piksel razvrstimo v najprimernejši razred na podlagi njegovih podatkovnih (spekter, tekstura, nadmorska višina, ipd.) lastnosti (Oštir, 2006; Veljanovski in sod., 2011). Za klasifikacijo podatkov z večjo prostorsko ločljivostjo (npr. LiDAR) so primernejše objektno usmerjene metode, ki temeljijo na segmentaciji preučevanih elementov oz. objektov (Blaschke, 2010; Veljanovski in sod., 2011). V postopku segmentacije semantična klasifikacija objekte razdeli na homogene skupine pikslov oz. segmente, ki jih nato klasificira v razrede na podlagi njihovih lastnosti (Oštir, 2006; Veljanovski in sod., 2011; Drăguț in Eisank, 2012). Objektno usmerjene metode in njihove modifikacije so se izkazale kot uspešne pri razvrščanju topografskih značilnosti površja v posamezne razrede kot so npr. uravnave, gričevja, hribovja in gorovja (npr. Drăguț in Eisank, 2012) in prepoznavanju reliefnih oblik kot so npr. ravnina, vrh, greben, vzpetina, pobočje in dolina (npr. Jasiewicz in Stepinski, 2013). Naprednejše metode za zaznavanje reliefnih oblik uporabljajo metodo globokega strojnega učenja. Na primer, za zaznavanje vrtač sta Mihevc, A. in Mihevc, R. (2021) razvila metodo, ki temelji na strojnem učenju z U-net konvolucijskimi nevronskimi mrežami.

Napredek na področju geoprostorskih tehnologij je torej omogočil tudi napredek na področju geomorfologije. Z uporabo tehnik in metod daljinskega zaznavanja ter GIS-ov so morfološke in morfometrične analize značilnosti površja in posameznih reliefnih oblik hitrejša in natančnejša (Smith in sod., 2013). Natančna sistematizacija reliefnih oblik in procesov je ključnega pomena pri reševanju izzivov in izkoriščanju priložnosti, saj omogoča razumevanje razvoja pokrajine, procesov ter interakcij med človekom in okoljem. Še posebej pa je

sistematizacija uporabna pri upravljanju okolja, varovanju pred naravnimi nesrečami, prostorskemu načrtovanju, geomorfoloških raziskavah (Bishop, 2013), vpliva pa tudi na razumevanje prostorskih vzorcev biodiverzitete in njeno varovanje (Tukiainen in sod., 2019; Čonč, 2020).

1.2 BIOLOGIJA IN EKOLOGIJA EVRAZIJSKEGA RISA IN EVROPSKE DIVJE MAČKE

Ris in divja mačka sta danes edina avtohtona predstavnika družine mačk v Sloveniji. Risa uvrščamo v rod *Lynx*, divjo mačko pa v rod *Felis* (Mattern, 2000). Kot specializirana plenilca imata za lov prilagojeno zobovje in druge morfološke značilnosti (Van Valkenburgh, 1989; Kitchener, 1998; Kos in sod., 2005). Obe vrsti sta na rdečem seznamu ogroženih vrst IUCN na globalnem nivoju trenutno uvrščeni v kategorijo »vrste zunaj nevarnosti« (*Least Concern*) (Breitenmoser in sod., 2015; Gerngross in sod., 2023). Kljub temu, da vrsti globalno gledano nista ogroženi, so med posameznimi populacijami izrazite razlike v stopnji ogroženosti (von Arx in sod., 2021; Gerngross in sod., 2023). Na primer, le 3 od 11 evropskih populacij risa so opredeljene kot »zunaj nevarnosti«, medtem ko so pri ostalih populacijah potrebni stalni ohranitveni ukrepi za zagotavljanje ohranitve ali obnove populacij (Fležar in sod., 2021; von Arx in sod., 2021). Dinarska populacija risa je opredeljena kot kritično ogrožena (von Arx in sod., 2021). Največje grožnje obema vrstama predstavljajo izguba habitatov zaradi fragmentacije (Gil-Sanchez in sod., 2020; Premier in sod., 2021), smrtnost zaradi človeka (npr. lov, nezakoniti lov, trki z vozili) (Andrén in sod., 2006; Heurich in sod., 2018; Bastianelli in sod., 2021), pri divji mački je velik problem hibridizacija z domačo mačko (*Felis catus*) (Mattucci in sod., 2016; Urzi in sod., 2021), pri risu pa za mnoge populacije, vključno z dinarsko, parjenje v sorodstvu (Sindičić in sod., 2013; Mueller in sod., 2022). Varovanje in ohranjanje risa in divje mačke je pomembno tudi zaradi vlog obeh vrst v ekosistemi (Lozano in sod., 2006; Odden in sod., 2006; Krofel in sod., 2011; Apostolico in sod., 2016).

1.2.1 Morfološke značilnosti

Evrazijski ris (Slika 4) je največja evropska mačka in največji predstavnik rodu *Lynx*. Telesna masa odraslega risa se giblje med 12 in 35 kg, v višino meri približno 65 cm, v dolžino pa 70–130 cm (Breitenmoser in sod., 2000). Po podatkih ustreljenih risov v Sloveniji je teža samcev $21,5 \pm 3,3$ kg, samic pa $17,9 \pm 3,0$ kg (Kos in sod., 2005). Kljub nekoliko manjši velikosti, risa uvrščamo med velike zveri, saj ima več fizioloških, ekoloških in etoloških značilnosti, ki so značilne zanje (npr. dolgoživost, velik teritorij, nizke populacijske gostote, tehnika lova in plenjenje plena velikega vsaj polovico njegove teže) (Sundquist, M. E. in Sundquist, F. C., 1989). Za risa je značilno tipično mačje telo s kratko lobanjo in zverskim zobovjem, kratkim repom (10–30 cm), ušesa s čopki, krajše sprednje noge od zadnjih in pegast ali lisast vzorec na kožuhi, ki je po številu in razporejenosti peg individualno specifičen (Kos in sod., 2005).



Slika 4: Evrazijski ris

Evropska divja mačka (Slika 5) sodi med male mačke (Kitchener, 1998; Mattern, 2000) in v povprečju tehta med 3 in 8 kg, telo je dolgo med 45 in 80 cm, dolžina repa pa je približno 30 cm (European wildcat, b. l.). Dlaka divje mačke je sivorjave barve z dobro izraženim vzorcem prog na glavi, vratu in okončinah ter z izrazito hrbtno črto. Izrazit je tudi košat rep s črno topo konico in več sklenjenimi črnimi obroči (Ragni in Possenti, 1996).



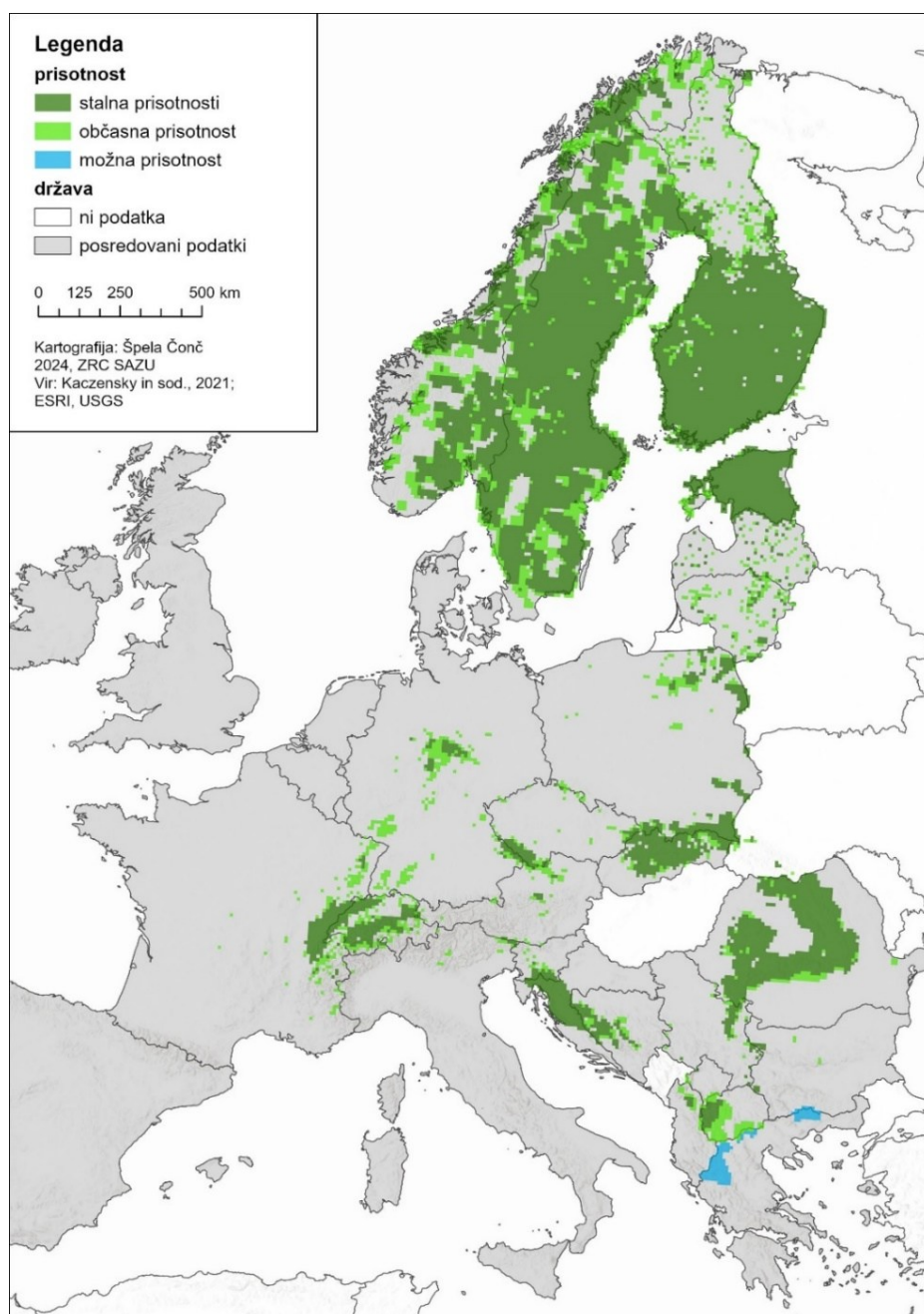
Slika 5: Evropska divja mačka

1.2.2 Življenjski prostor in razširjenost

Ris je vrsta mačke z eno najširših razširjenosti na svetu (Slika 6). Na območju Evrope in Rusije (Sibirija) naseljuje predvsem gozdne habitate, v severnih geografskih širinah jih najdemo lahko tudi v tundri, v Srednji Aziji pa naseljujejo bolj odprta, z gozdom neporaščena območja, polpuščave in območja nad gozdno mejo (Breitenmoser in sod., 2000). Ris v srednji in zahodni Evropi večinoma naseljuje območja strnjenih gozdov. Na izbiro habitata vpliva več dejavnikov, med katerimi so najpomembnejši odsotnost človeka in njegovih dejavnosti, gozdnatost, razpoložljivost plena in težka dostopnost terena (Filla in sod., 2017; Ripari in sod., 2022).

V prejšnjih stoletjih so rise, tako kot ostale velike zveri, sistematično preganjali in lovili, njihovi habitati so bili podvrženi uničevanju (krčenje gozdov, izraba gozda), hkrati pa je človek zaradi pretiranega lova povzročil upad ali celo lokalna izumrtja populacij risovega plena (Breitenmoser, 1998). Gozdni prostor je postal vse bolj fragmentiran in prehransko osiromašen, posamezne populacije risov so postajale vse bolj izolirane, populacijska gostota in reprodukcija sta bili nizki, kar je bilo usodno za rise v večini Evrope. Ris je do začetka 20. stoletja praktično izumrl po celotni zahodni Evropi (Breitenmoser, 1998; Kos in sod., 2005). V 20. stoletju se je pritisk na naravo nekoliko zmanjšal, saj je bila v ospredju industrializacija, posamezne populacije parkljarjev so se obnovile in lov nanje je postal reguliran. V 60. in 70. letih 20. stoletja so se začele tudi večje pobude za zaščito velikih zveri in njihovo ponovno naselitev na območja, kjer so bile iztrebljene (Breitenmoser, 1998; Treves in Karanth, 2003; Kos in sod., 2005; Heurich in sod., 2018).

Po ocenah evropske populacije risa (brez Rusije in Belorusije) štejejo med 8000 in 9000 osebki, ob upoštevanju območja iz Rusije zahodno od gorovja Ural, pa se število risov giba med 17,000 in 18,000 (Breitenmoser in sod., 2015; von Arx in sod., 2021). Najštevilčnejše populacije so skandinavska (1300–1800 osebkov), karelijska (2500 osebkov) in karpatska (2100–2400 osebkov). Kljub temu, da je ris strogo zaščiten z državnimi in mednarodnimi zakonodajami, so populacije v srednji in zahodni Evropi redke, majhne in nepovezane (Linnell in sod., 2008). Najbolj kritično ogrožena je balkanska podvrsta risa, ogrožene pa so tudi ponovno naseljene populacije v zahodni in srednji Evropi (alpska, vogejsko-palatinska, jurska, češko-bavarsko-avstrijska in dinarska), z nizkim številom osebkov (1–163 osebkov) (von Arx in sod., 2021). V doktorski disertaciji smo se osredotočili na preučevanje rabe prostora pri dinarski in češko-bavarsko-avstrijski populaciji risa.



Slika 6: Zemljevid razširjenosti evrazijskega risa v Evropi (Kaczensky in sod., 2021)

V začetku 70. let prejšnjega stoletja se je na pobudo gostujočega švicarskega lovca Karla Webra porodila ideja o ponovni naselitvi risa kot lovne vrste v Slovenijo. Leta 1973 so v kočevske gozdove izpustili tri samce in tri samice, ki so bili ujeti v slovaškem delu Karpatov in nato nastanjeni v karanteni v živalskem vrtu Ostrava na Češkoslovaškem (današnja Češka) (Čop, 1994). Populacija je v naslednjih letih rastla in se prostorsko širila po Sloveniji, na severozahodu tudi proti Italiji in Avstriji, na jugovzhodu pa vse do Bosne in Hercegovine (Čop, 1994; Kos in sod., 2005). Z letom 1986 se je začela kampanja za sproščen odstrel risa na t.i. nerajoniziranem območju, kar je vplivalo na ustavitev nadaljnjega širjenja v druge primerne dele Slovenije in na upad števila risov (Kos in sod., 2005). Populacija risa v Sloveniji se sooča s problemom parjenja v sorodstvu zaradi prostorske izoliranosti in onemogočenega pretoka genov ter majhnega števila naseljenih živali, med katerim so bile nekatere v sorodu (Kos in

sod., 2005, 2012). Z namenom reševanja Dinarsko-JV alpske populacije risa pred izumrtjem ter njeno dolgoročno ohranitvijo so v okviru projektov *LIFE Lynx* in *ULyCA2* v Slovenijo, Italijo in na Hrvaško med letoma 2019 in 2023 doselili 22 risov iz Švice, Slovaške in Romunije (Slika 7). Od 22 preseljenih risov se je 15 risov uspešno vključilo v populacijo (Krofel in sod., 2024). Pred naselitvijo je bila gostota risov v dinarski populaciji ocenjena na 0,51 risov/100 km² (Fležar in sod., 2023), po naselitvi pa na $1,27 \pm 0,15$ risov/100 km² oz. 156 ± 19 odraslih osebkov (Krofel in sod., 2024). Po naselitvi pa se je izboljšala tudi genska slika populacije in zabeležen je bil precejšen upad sokrvja (Krofel in sod., 2024).



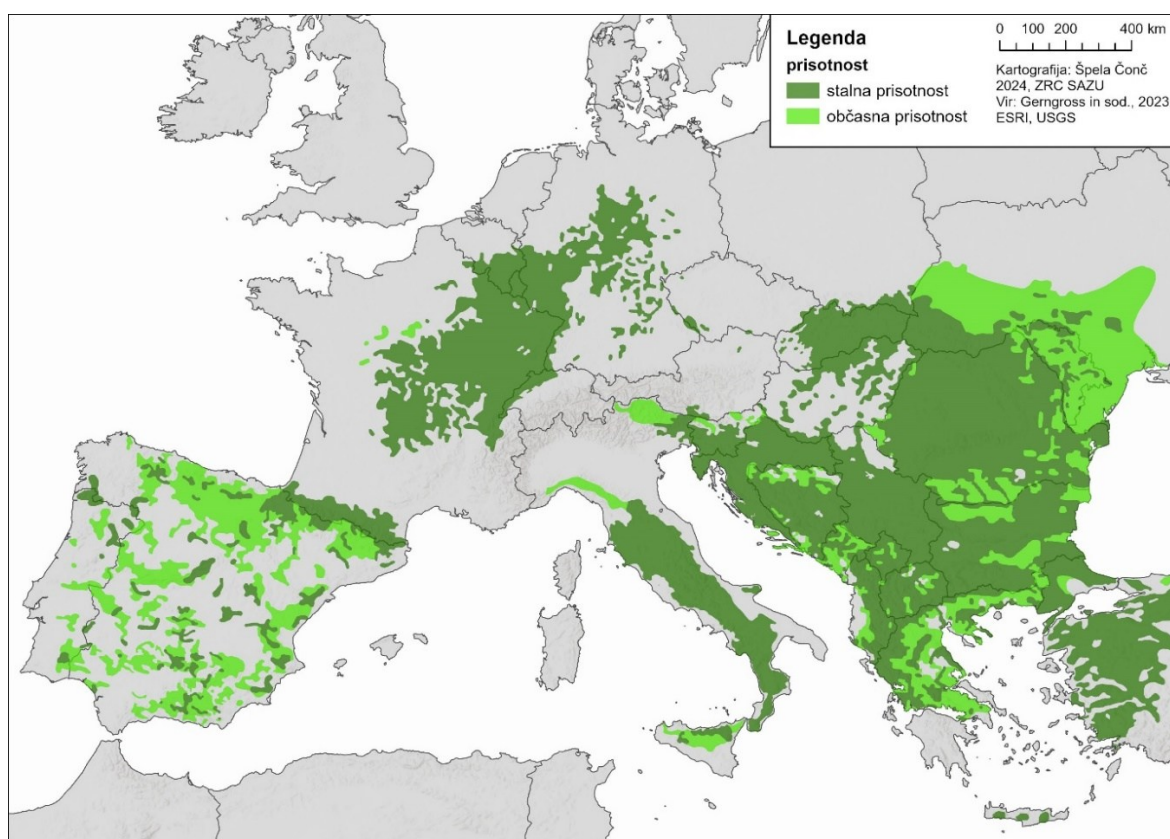
Slika 7: Izpust risa Bliska iz prilagoditvene obore na območju Snežnika

Na območju Bavarsko-Češkega gozdnega ekosistema je bila med letoma 1970 in 1974 izvedena prva ponovna naselitev risa v srednji Evropi (5–10 osebkov), ki pa je bila neuspešna, domnevno zaradi nezakonitega lova (Festetics, 1980). Ponovna naselitev je bila izvedena med letoma 1982 in 1989, ko so na češki strani izpustili 18 risov iz Karpatov (Červený in sod., 1996). Po izpustitvi se je populacija povečala na približno 60–69 osebkov in se do konca 90. let prejšnjega stoletja razširila tudi na območje Avstrije in Bavarske v Nemčiji (Červený in sod., 2012; Heurich in sod., 2018). Trenutna populacija risa je močno vezana na zavarovana območja ob nemško-češki meji (Müller in sod., 2014). Gostota populacije risa je bila leta 2018 ocenjena na 1,33 risa/100 km² (Palmero in sod., 2021). V zadnjih desetletjih je bilo dokazanih več primerov nezakonitega lova, zlasti v obdobju tik pred vstopom Česke republike v Evropsko unijo leta 2004, ko je nezakonit lov na risa postal hudo kaznivo dejanje. Domneva se, da je nezakoniti lov najpomembnejši dejavnik dinamike risje populacije na tem območju (Heurich in sod., 2018).

Divja mačka je razširjena po večini Evrope, od Iberskega polotoka do vzhodne Evrope, najdemo pa jo tudi v Turčiji in na Kavkazu (Slika 8). V Evropi je območje razširjenosti divje mačke razdeljeno na dve otoški (Škotska in Kreta) in štiri celinske metapopulacije: 1) zahodna in srednja Evropa, 2) Apeninski polotok in Sicilija, 3) vzhodno-srednja, vzhodna in jugovzhodna Evropa, ter 4) Iberski polotok (Gerngross in sod., 2023). Največji sklenjeni

območji razširjenosti sta v osrednji (osrednji in severovzhodni del Francije ter jugozahodni del Nemčije) in vzhodni Evropi (Gerngross in sod., 2023). Po ocenah evropske populacije divje mačke obsegajo približno 140,000 osebkov. Posamezne populacije so bile precej izolirane, sedaj pa se ponekod že povezujejo (Gerngross in sod., 2023). Podatki o številčnosti, smrtnosti in regionalni razširjenosti so omejeni, kar je večinoma posledica prezrtosti zaradi udomačene oblike (domače mačke), skrivnega življenja in nizke populacijske gostote (Potočnik, 2006; Otgontamir in sod., 2024).

Divja mačka na območju Evrope naseljuje različne tipe habitatov. Najdemo jo v večjih strnjjenih gozdovih (Potočnik, 2006; Klar in sod., 2008), naseljuje pa tudi bolj mozaično pokrajino, kjer manjši gozdovi povezujejo bolj odprta območja, travnike, mejice, grmišča, kmetijska zemljišča in pašnike (Jerosch in sod., 2017; Oliveira in sod., 2018; Otgontamir in sod., 2024).



Slika 8: Zemljevid razširjenosti evropske divje mačke v Evropi (Gerngross in sod., 2023)

Podobno kot rise in ostale velike zveri so tudi divje mačke v zadnjih nekaj stoletjih sistematično preganjali in lovili, zaradi krčenja gozdov in širjenja poselitve pa so bili njihovi habitatni podvrženi uničevanju (Mueller in sod., 2020). Kljub temu, da se vrsta še vedno sooča s številnimi grožnjami, kot so npr. intenziviranje rabe pokrajine (Jerosch in sod., 2018), povozi na cestah (Bastianelli in sod., 2021) in križanje z domačimi mačkami (Urzi in sod., 2021), so se nekatere populacije v zadnjih nekaj desetletjih obnovile, k čemer je najverjetneje prispevalo pogozdovanje, selitev ljudi v mesta ter varovanje vrste in njenih habitatov (Pereira in Navarro, 2015; von Thaden in sod., 2021).



Slika 9: Opremljanje divje mačke z ultralahko GPS ovratnico

V Sloveniji sta razširjenost in številčnost divje mačke razmeroma slabo raziskani. Leta 1977 je bila številčnost ocenjena na 1000 osebkov (Potočnik in Kos, 2000). Glede na podatke odvzema živali se divja mačka najpogosteje pojavlja v južnem delu države na dinarskem in submediteranskem območju (Kryštufek, 1991; Potočnik, 2006), podatki spremljanja s fotopastmi in GPS-telemetrijo v okviru projektov *LIFE Lynx*, *InterMuc* in *ExtremePredator* pa kažejo tudi na stalno prisotnost na območju Julijskih Alp (Krofel, 2024). Po preliminarnih analizah podatkov iz fotopasti je gostota divjih mačk na območju slovenskega Dinarskega krasa ocenjena na 20,3 divje mačke/100 km² (Krofel, 2024). Rezultati raziskav s področja genetike kažejo, da je stopnja hibridizacije v Sloveniji nižja v primerjavi z drugimi državami (Urzi in sod., 2021). Obsežnejša raziskava ekologije divjih mačk s poudarkom na značilnostih rabe prostora ter njihove aktivnosti v Sloveniji je bila opravljena v okviru doktorske disertacije, ki je temeljila na VHF radiotelemetričnem spremljanju 12 osebkov na območju Goteniške in Velike gore (Potočnik, 2006). V okviru temeljnega raziskovalnega projekta *InterMuc* je bilo med letoma 2020 in 2023 z ultralahkimi GPS ovratnicami opremljenih 11 divjih mačk na območju slovenskega Dinarskega krasa in Julijskih Alp (Slika 9), kar bo omogočilo prve raziskave na divjih mačkah v Sloveniji z uporabo GPS-telemetrije (Krofel in sod., 2022).

1.2.3 Ekologija, specifična vedenja in reliefne oblike

Podatki različnih načinov spremljanja risov in divjih mačk (zimsko sledenje v snegu, GPS in VHF telemetrija, fotopasti) kažejo določene vzorce, ki pri obeh vrstah nakazujejo povezanost med rabo prostora, reliefnimi oblikami in mikroliefnimi značilnostmi. To je še posebej izrazito na kompleksnem kraškem površju Dinarskega gorovja, kjer pretekle raziskave pri obeh vrstah nakazujejo povezavo med rabo prostora v različnih fazah aktivnosti (noč, dan) in specifičnimi vedenji (npr. gibanje, označevanje teritorija, počivanje, plenjenje) ter določenimi

kraškimi reliefnimi oblikami, kot so skalni bloki, jame, spodmoli, skalnati previsi, stene, grebeni in zaprte kraške kotanje (Krofel in sod., 2006, 2007, 2013, 2022; Potočnik, 2006; Krofel, 2010; Allen in sod., 2017; Mohorović in Krofel, 2020; Hočevnar in sod., 2021).

1.2.3.1 Teritorialnost in markiranje

Za obe vrsti je značilno teritorialno vedenje in pretežno samotarski način življenja, izjema so samice z mladiči ter pari v času parjenja. Zaradi razlik v velikosti domačih okolišev, običajno na območju enega para risov živi več deset divjih mačk. Pri obeh vrstah se domači okoliši istega spola navadno izključujejo, domači okoliši samcev pa se lahko prekrivajo z enim ali več domačimi okoliši samic (Schmidt in sod., 1997; Jerosch in sod., 2017). Velikost domačih okolišev obeh vrst se v Evropi zelo razlikujejo. Velikost pa se razlikuje tudi med spoloma, saj so domači okoliši samic manjši od domačih okolišev samcev (Herfindal in sod., 2005; Anile in sod., 2017; Jerosch in sod., 2017). Pri risu je v srednjih zemljepisnih širinah povprečna velikost domačega okoliša samca približno 250 km², samic pa približno 100 km² (Herfindal in sod., 2005). V Sloveniji je velikost domačega okoliša samcev divjih mačk ocenjena med 5,73 in 18,76 km², samic pa med 2,64 in 12,75 km² (Potočnik, 2006).

Za prostorsko razporejanje in vzdrževanje teritorialnosti je bistvenega pomena kemična komunikacija preko označevanja oz. markiranja z uriniranjem, iztrebljanjem in drgnjenjem z ličnicami ter telesom (Kos in sod., 2005; Ruiz-Olmo in sod., 2013; Allen in sod., 2017). Samci risa markirajo pogosteje kot samice, najintenzivnejše pozno pozimi, v času paritve, manj intenzivno pa je markiranje poleti, ko samice skrbijo za mladiče (Vogt in sod., 2014; Krofel in sod., 2017). Vrsti za markiranje uporabljata predvsem pokončne objekte ali predmete, ki od okolice izstopajo, saj jih bodo drugi osebk preje opazili, hkrati pa markiranje navpične površine označbo zaščiti pred vremenskimi vplivi (Kos in sod., 2005; Ruiz-Olmo in sod., 2013; Allen in sod., 2017; Mohorović in Krofel, 2020; Krofel in sod., 2022). Raziskave na območju Dinarskega gorovja v Sloveniji kažejo, da risi za markiranje z urinom najpogosteje označujejo skalne bloke, skalne oblike in stene, majhne smreke in drevesne šore na višini med 0.5 in 1 m. Med skalnimi oblikami prevladujejo take oblike, ki jih prerašča mah, kar lahko izboljša vpojnost urina in dlje trajajoče oddajanje vonja, in so oblikovane kot previsi, kar zaščiti urin pred vremenskimi vplivi (Allen in sod., 2017; Mohorović in Krofel, 2020). Rezultati raziskav tudi kažejo, da risi pogosteje markirajo objekte med hojo po gozdnih cestah in vlakah kot pa pri hoji po naravnem okolju (Krofel in sod., 2017).

1.2.3.2 Gibanje in plenjenje

Zaradi zakraselosti je površje slovenskega Dinarskega krasa ponekod izrazito skalovito. Na teh območjih so najpogostejše reliefne oblike škrapljišča in skalni bloki, ki jih pogosto prerašča mah. Ris za gibanje pogosto uporablja skalovito površje, saj mu omogoča kritje in tišje gibanje (Krofel in sod., 2007). Za obe vrsti je značilna podobna strategija lova, saj plenita tako, da se plenu približata z zalezovanjem, in nato napadeta iz presenečenja, zato sta tehnika zalezovanja in tih pristop toliko bolj pomembna. Pri risu praviloma sledi krajši pregon (do 50 m), medtem ko divja mačka plena ne preganja, ampak navadno plen naskoči (Kos in sod., 2005, 2007; Potočnik, 2006).

Na območju slovenskega Dinarskega krasa srnjad predstavlja 80 % risovega plena, s sedmimi odstotki sledijo navadni polhi (*Glis glis*), ki so še posebej pomemben del prehrane samic in mladostnih risov, preostanek predstavljajo jelenjad, gamsi (*Rupicapra rupicapra*) in drugi kopenski vretenčarji (Krofel in sod., 2011), občasno pa lahko upleni tudi divjo mačko (Krofel in sod., 2021a). Prehranjevalne navade in prehrana divje mačke v Sloveniji še niso bile celostno raziskane. Na območju srednje Evrope se divje mačke prehranjujejo predvsem z glodavci (Lozano in sod., 2006; Ruiz-Villar in sod., 2023), predvsem pozimi je bilo opaženo tudi prehranjevanje s kadavri parkljarjev (Ruiz-Villar in sod., 2020; Krofel in sod., 2021b), hranjenje z mrhovino pa je bilo opaženo med drugim tudi pri hranjenju z ostanki plena risov (Krofel, 2024).

Med večjimi površinskimi kraškimi reliefnimi oblikami so najbolj pogoste in opazne zaprte kraške kotanje različnih dimenzij (vrtače, udornice, brezstrobe jame ...) (Mihevc, A. in Mihevc, R., 2021). Poleg gibanja po skalovitem površju ter markiranja skalnih blokov, sten in reliefnih previsov, so pri risu ugotovili tudi povezavo med plenjenjem in vrtačami (Krofel in sod., 2006, 2007; Krofel, 2010). V preliminarni študiji, ki se je nanašala na topografske in vegetacijske značilnosti lokacij plena risa, so ugotovili, da je 39 % lokacij plena na dnu vrtač (Krofel in sod., 2007). Večina lokacij plena se je nahajala na razgibanem reliefu in strmih pobočjih, kar bi lahko povezali tudi s tem, da plen na takem terenu ne uspe razviti maksimalne hitrosti, ris pa izkoristi svojo agilnost. Poleg tega se pozimi na dnu vrtač akumulira sneg, kar še dodatno upočasni plen (Krofel in sod., 2007).

Zimsko sledenje kaže tudi na to, da risi pogosto obiskujejo vrtače, v katerih se nahajajo jamski vhodi (Krofel, 2010). Jamski vhodi in špranje med skalnimi bloki oz. izdanki kamnin pogosto predstavljajo primeren prostor za hibernacijo navadnega polha (Polak, 1997), ki je na območju slovenskega Dinarskega krasa drugi najpomembnejši vir hrane za risa, prav tako so polhi in ostali manjši glodavci glavni vir prehrane tudi pri divjih mačkah (Lozano in sod., 2006; Potočnik, 2006; Krofel, 2010; Krofel in sod., 2011). Poleg vrtač in jam pa risi obiskujejo tudi udornice, v katerih se nahajajo večje in strmejše stene, ki so habitat gamsa, ki je prav tako risov plen (Krofel in sod., 2011).

1.2.3.3 Počivanje

Na izbiro habitata obeh vrst vpliva izogibanje področjem prisotnosti človeka podnevi, ponoči pa izbirajo področja, kjer lahko ujamejo plen (Klar in sod., 2008; Filla in sod., 2017). Preko dneva izbirata predvsem težko dostopna, strma, razgibana in poraščena območja, ki nudijo varnostno kritje (Potočnik, 2006; Klar in sod., 2008; Signer in sod., 2019; Hočevár in sod., 2021), v nočnem času se pogosteje nahajata tudi na odprtih območjih, kar je povezano s prisotnostjo plena (Potočnik, 2006; Klar in sod., 2008; Jerosch in sod., 2010; Filla in sod., 2017).

V raziskavi na območju Bavarsko-Češkega gozdnega ekosistema, so ugotovili, da risi izbirajo lokacije za dnevni počitek v bližini ali na območju večjih izdankov kamnin in sten (Signer in sod., 2019). Prav tako so v raziskavi na območju slovenskega Dinarskega krasa ugotovili, da risi izbirajo lokacije za dnevni počitek na grebenih ter na območjih s strmejším naklonom in

nižjo vidljivostjo, kot pomembna pa so se izkazala tudi območja z visoko razgibanostjo reliefa, južno ekspozicijo in višjo skalovitostjo (Hočevvar in sod., 2021). Raziskave v Nemčiji, kjer je teren manj razgiban, kažejo na to, da divje mačke za dnevna počivališča izbirajo lokacije z dobrim kritjem, gosto vegetacijo, visokim deležem odmrle lesne mase in južno ekspozicijo (Klar in sod., 2008; Jerosch in sod., 2010). Na območju slovenskega Dinarskega krasa pa ima poleg vegetacije in južne ekspozicije na izbiro počivališč velik vpliv tudi naklon, razčlenjenost in skalovitost površja (Potočnik, 2006).

1.3 CILJI RAZISKAVE IN RAZISKOVALNE HIPOTEZE

Zgoraj opisane povezave med reliefnimi oblikami in rabo prostora pri specifičnih vedenjih risa in divje mačke predstavljajo okvirna izhodišča, ki pa doslej še niso bila celostno raziskana in v nekaterih primerih tudi ne znanstveno potrjena. Na izbranih preučevanih območjih smo poskušali preveriti nekatera dosedanja opažanja in zastavljene hipoteze, ki izhajajo iz izkušenj pri terenskem preučevanju ekologije obeh vrst. Glavni namen doktorske disertacije je ugotoviti vpliv reliefnih oblik na rabo prostora pri risu in divji mački, pri čemer so upoštevane različne faze aktivnosti (dan in noč) in specifična vedenja (npr. počivanje, plenjenje, hranjenje, gibanje, markiranje). S tem namenom smo zasnovali natančnejšo kvantitativno prostorsko-ekološko interdisciplinarno raziskavo, ki je celostno obravnavala tako reliefne oblike kot tudi rabo prostora pri specifičnih vedenjih in različnih obdobjih aktivnosti dveh vrst prostoživečih mačk. Zadal si naslednje raziskovalne cilje:

- **Identifikacija reliefnih oblik, morfografska analiza na podlagi (pol-)avtomatskih metod za zaznavanje reliefnih oblik ter analiza okoljskih in antropogenih značilnosti na izbranih območjih.** V okviru tega cilja smo kot območje preučevanja izbrali območja domačih okolišev (MCP – minimalni konveksni poligoni) risov in divjih mačk, za katere smo imeli na voljo podatke GPS telemetričnih ovratnic v Sloveniji, Nemčiji in na Češkem. Na podlagi literature, terenskega pregleda in vizualizacij digitalnega modela višin (DMV) smo na preučevanih območjih identificirali glavne reliefne oblike in v geografskih informacijskih sistemih na podlagi visokoločljivostnih LiDAR podatkov pripravili sloje za analizo. Identificirane reliefne oblike smo zaznali na podlagi že razvitih (pol-)avtomatskih metod (npr. vrtače), razvili svojo metodo (izdanki kamnin) in uporabili že obstoječ prostodostopen sloj z lokacijami jamskih vhodov. Pridobili in pripravili smo tudi različne sloje za analizo okoljskih (npr. naklon, ekspozicija, razgibanost) in antropogenih (npr. oddaljenost do cest in naselij) značilnosti preučevanega območja.
- **Pridobivanje podatkov o gibanju na podlagi metode zimskega sledenja in analiza podatkov pridobljenih z GPS-telemetrijo risov ter divjih mačk.** Analizirali smo GPS-telemetrične podatke in na podlagi izbranih metod ter pristopov za divje mačke identificirali nočne lokacije, za rise pa poleg nočnih lokacij tudi lokacije uplenitev in dnevnih počivališč. Pri identifikaciji dnevnih počivališč risov smo, kjer so bili na voljo, upoštevali tudi podatke s senzorjev aktivnosti (merilniki pospeškov). S klasifikacijo lokacij smo ločili različna vedenja (npr. počivanje, plenjenje, gibanje) in faze dneva (dan, noč). Z namenom pridobivanja znanja o ekologiji risov in divjih mačk smo v zimskem času v snegu na

območjih domačih okolišev iskali prisotnosti sledi obeh vrst in s hojo po sledi pridobili podatke o gibanju, markiranju, plenjenju in izbiri dnevnih počivališč.

- **Analiza vpliva reliefnih oblik na rabo prostora pri risih in divjih mačkah.** S statističnim modeliranjem, natančneje z metodo posplošenih linearnih mešanih modelov (GLMM - *generalized linear mixed models*), smo ovrednotili vpliv reliefnih oblik na izbiro prostora pri specifičnih vedenjih risov in divjih mačk. Na podlagi posplošenih aditivnih modelov (GAM - *generalized additive models*) pa smo testirali tudi, ali v primeru izbire habitata risa prihaja do funkcionalnega odziva glede na razpoložljivost izdankov kamnin, razgibanega in skalovitega površja na območjih raziskave. Poleg reliefnih oblik smo v analizah upoštevali tudi druge potencialno pomembne okoljske in antropogene spremenljivke.
- **Primerjava rabe prostora risa na kraškem (Dinarsko gorovje) in fluvialnem reliefu (Bavarsko-Češki gozdni ekosistem).** V okviru tega cilja smo izbrali dve (bio)geografsko in geološko različni preučevani območji, slovenski Dinarski kras in Bavarsko-Češki gozdni ekosistem, kjer je bila na voljo enaka struktura podatkov (topografske in antropogene spremenljivke ter GPS-telemetrija risov). Razvili smo metodo za avtomatsko zaznavanje izdankov kamnin in v analizo vključili tudi nekatere druge okoljske in antropogene spremenljivke. Primerjali smo izbiro habitata risa za dnevne in nočne lokacije ter testirali, ali v primeru izbire habitata risa prihaja do funkcionalnega odziva glede na razpoložljivost razgibanega in skalovitega površja.

Glede na izhodišča, ki so opisana v poglavju 1.2.3, ter zastavljene cilje smo opredelili naslednje raziskovalne hipoteze:

- Hipoteza 1 (H1): Obe vrsti selektivno izbirata notranjost ali rob kraških kotanj, v primeru risa pa imajo kraške kotanje pomembno vlogo tudi pri plenjenju (poglavji 2.1 in 2.2).
- Hipoteza 2 (H2): Obe vrsti selektivno izbirata območja v bližini različnih reliefnih oblik ter strmo, razgibano in skalovito površje (poglavja 2.1, 2.2 in 2.3).
- Hipoteza 3 (H3): Pri risih je izbira topografskih in izogibanje antropogenih elementov bolj izrazita podnevi kot ponoči (poglavje 2.3).
- Hipoteza 4 (H4): Risi, ki izvirajo iz okolja s fluvialnim reliefom in so bili preseljeni na kraško območje, kažejo podobne vzorce izbire habitata kot risi, ki so celo življenje preživeli na kraškem reliefu (poglavje 2.2).
- Hipoteza 5 (H5): Na fluvialnem reliefu, kjer je površje manj skalovito in razgibano kot na kraškem reliefu, ris še pogosteje izbira skalovita in razgibana območja, izdanke kamnin oz. njihovo bližino glede na njihovo razpoložljivost, torej prihaja do funkcionalnega odziva pri rabi prostora glede na razpoložljivost razgibanega in skalovitega površja (poglavje 2.3).

2 ZNANSTVENA DELA

2.1 VRTAČE IN MAČKE: DALJINSKO ZAZNAVANJE KRAŠKIH KOTANJ IN NJIHOVA UPORABA PRI PREUČEVANJU EKOLOGIJE PROSTOŽIVEČIH MAČK

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Avtomatske metode za identifikacijo in zaznavanje reliefnih oblik omogočajo oddaljeno in stroškovno učinkovito kartiranje, kar ima izjemen potencial pri preučevanju ekologije divjih živali in podobnih raziskav. Vrtače in druge kraške kotanje na razgibanem terenu Dinarskega gorovja v Sloveniji smo zaznali z uporabo metode zapolnjevanja digitalnega modela višin (»filled-DMV«) na podlagi LiDAR-skih podatkov (Light Detection and Ranging). S tem pristopom smo odkrili 9.711 kraških kotanj na 137 km² velikem preučevanem območju in izračunali njihove osnovne morfometrične značilnosti, kot so obseg, površina, premer, globina in naklon. Na podlagi senčenega reliefa smo izvedli vizualno validacijo metode, ki je pokazala 83,5-odstotno uspešnost pri zaznavanju kraških kotanj. Čeprav ima metoda nekaj pomanjkljivosti, se je izkazala za primerno pri zaznavanju, splošnih prostorskih analizah in izračunu morfometričnih značilnosti kraških kotanj na velikem, odročnem in gozdnatem območju. Da bi dokazali njeno uporabnost pri raziskavah prostoživečih živali, smo jo uporabili v preliminarni študiji v kombinaciji z GPS-telemetričnimi podatki za oceno izbire kraških kotanj pri dveh prostoživečih vrstah mačk, evrazijskem risu (*Lynx lynx*) in evropski divji mački (*Felis silvestris*). Potrdili smo, da sta obe vrsti izbirali bližino kraških kotanj, med katerimi sta izbirali predvsem večje kotanje. V bližini teh reliefnih oblik so risi tudi pogosto uplenili parkljarje, saj smo več kot polovico ostankov risovega plena našli znotraj kraških kotanj ali v njihovi neposredni bližini. Rezultati kažejo, da bi lahko imele kraške reliefne oblike pomembno vlogo v ekologiji prostoživečih mačk in upravičujejo nadaljnje raziskave z uporabo metod daljinskega zaznavanja reliefnih oblik.

Ključne besede: geografski informacijski sistemi, digitalni model višin, LiDAR, kraške kotanje, geomorfologija, telemetrija, prostorska ekologija, prostoživeče mačke



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Article

Dolines and Cats: Remote Detection of Karst Depressions and Their Application to Study Wild Felid Ecology

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Abstract: Automatic methods for detecting and delineating relief features allow remote and low-cost mapping, which has an outstanding potential for wildlife ecology and similar research. We applied a filled-DEM (digital elevation model) method using LiDAR (Light Detection and Ranging) data to automatically detect dolines and other karst depressions in a rugged terrain of the Dinaric Mountains, Slovenia. Using this approach, we detected 9711 karst depressions in a 137 km² study area and provided their basic morphometric characteristics, such as perimeter length, area, diameter, depth, and slope. We performed visual validation based on shaded relief, which indicated 83.5% accordance in detecting depressions. Although the method has some drawbacks, it proved suitable for detection, general spatial analysis, and calculation of morphometric characteristics of depressions over a large scale in remote and forested areas. To demonstrate its applicability for wildlife research, we applied it in a preliminary study in combination with GPS-telemetry data to assess the selection of these features by two wild felids, the Eurasian lynx (*Lynx lynx*) and the European wildcat (*Felis silvestris*). Both species selected for vicinity of karst depressions, among which they selected for larger karst depressions. Lynx also regularly killed ungulate prey near these features, as we found more than half of lynx prey remains inside or in close vicinity of karst depressions. These results illustrate that karstic features could play an important role in the ecology of wild felids and warrant further research, which could be considerably assisted with the use of remote detection of relief features.

Keywords: geographic information systems; digital elevation model; LiDAR; karst depressions; geomorphology; telemetry; spatial ecology; wild felids



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1. Introduction

Recent advances in accurate satellite and aerial imagery, as well as laser scanning data, enable increasingly detailed analyses of the earth's surface [1]. Geographic information systems (GIS) allow the creation of various thematic maps from satellite and aerial imagery, most commonly for land use or land cover [2]. However, field mapping and digitizing relief features and other landscape elements is often inaccurate, time-consuming, and costly [3]. Therefore, various methods, such as visual interpretations of relief and semi-automatic or automatic methods for detecting and delineating features are being developed in the field of remote sensing for non-contact and low-cost mapping (e.g., [4–10]).

LiDAR (Light Detection and Ranging) is a remote sensing method which uses electromagnetic energy to detect an object and determine its distance to the instrument, as well as ascribe its physical properties based on the radiation [11]. LiDAR is widely used for high-resolution data processing and analysis in scientific, engineering, and natural hazard management fields, among others [11,12]. LiDAR can also be applied to ecological

research, as it provides insights into the 3D physical structure of ecosystems, from relief to vertical vegetation structures [13] and allows the study of relief features even under vegetation [11,14]. High-resolution LiDAR data and automatic or semi-automatic methods for relief features detection are especially useful for relief analysis in large, remote, and hard-to-access areas [3,13,15].

Karst landscape is known as one of the most rugged terrains on our planet and exhibits high density of various geomorphological features [16]. It differs from many other geomorphological systems by dissolution and removal of material in solution, negligible accumulation, and predominant vertical water flow are predominant processes, resulting in the formation of surface and subsurface geomorphological features [17–20]. These features include karst depressions, which are primarily understood as concave relief forms on an ideally levelled or smooth surface where the material at the surface is more exposed to erosion or corrosion due to discontinuity, cracks, or porosity [17–22].

Dolines (also known as sinkholes, e.g., [23]) are the most common and characteristic feature of karst depressions and are therefore considered as a diagnostic karst form. Dolines are defined as circular or elliptical depressions of different sizes and are generally wider than deeper. Their diameter and depth range varies from a few meters to more than a hundred meters [17,21,24,25]. Due to their importance and abundance, karst depressions have been subject of various scientific studies for decades. Besides geomorphology and karstology, which are mainly focused on morphometric, morphological, and morphogenetic studies, dolines are also subject of other research fields, such as geology, biogeography, forestry, botany, animal ecology, and nature conservation (e.g., [26–32]). Until the advanced development of remote sensing technology and the availability of remote sensing data, tasks such as mapping, morphometric and morphogenetic analyses of karst depressions were mostly done in the field or based on topographic maps. However, these approaches were often time-consuming and resulted in low accuracy, poor data quality and were affected by the subjectivity of the perception of the size of depressions [22], which limited their use for further research. Several authors have recently initiated development and application of methods for automatic detection of karst depressions (e.g., [15,22,23,25,27,28,31,33–37]). The methods are based on various approaches, generally divided into three groups: delineation of depressions based on the outermost closed contour line, watershed-based depressions delineation, and filled-DEM (digital elevation model) based depressions delineation [34].

Relief characteristics are often included in studies of animal spatial ecology, but they are usually limited to general terrain characteristics, such as elevation, terrain ruggedness, or slope (e.g., [38–43]). On the other hand, the influence of micro- and meso-relief features, such as karst depressions, are rarely considered in these studies, despite their potential importance (e.g., [44]). This was partially connected to the lack of methodology developed for remote detection of specific relief features on a larger scale, which is needed for many large-bodied species with large home ranges, as well as to limited availability of high-resolution LiDAR DEM. In the previous studies on micro-habitat use, the focus was mainly on the evaluation of land-cover (e.g., [45]) and other biotic elements of studied micro-habitats. Less attention was given to geomorphology, specific relief features, geomorphic processes, and LiDAR DEM analyses, which require specific skills and interdisciplinary cooperation between bio- and geo-scientists is often necessary to take full advantage of high-resolution LiDAR DEM data use in animal ecology. On the other hand, many recent studies exist on detailed geomorphometric characteristics derived from high-resolution LiDAR DEM, and diverse methods were developed for automated extraction of micro- and meso-relief features, including dolines (e.g., [7–10,15,22,23,25,27,28,31,33–37]). Therefore, combining automatized identification of relief features with GPS-telemetry data could provide novel insights into ecology of elusive and wide-roaming animals, such as carnivores.

The main goal of this study was to remotely detect karst depressions based on LiDAR data and to demonstrate the applicability of remote detection of relief features for further ecological research by investigating potential importance of karst depressions for two native

carnivores. Specifically, we aimed to (1) detect dolines and other karst depressions larger than 10 m in diameter and 2 m in depth, (2) calculate their geomorphometric characteristics, (3) compare our model with visually detected karst depressions based on a shaded relief, and (4) assess the selection of these features by two wild felids: the Eurasian lynx (*Lynx lynx*; hereafter lynx) and the European wildcat (*Felis silvestris*; hereafter wildcat). Additionally, we conducted a preliminary case study on importance of karst depressions for lynx hunting behavior. We selected felids as a model group due to their general attraction to rugged and rocky terrain, as well as previous studies documenting the importance of micro-habitat characteristics for their ecology (e.g., [26,40,44–52]). Previous studies on these felids almost exclusively relied on assessing micro-habitat characteristics in the field, which demanded considerable effort to obtain a relatively limited amount of data. Our study on wild felids in Dinaric Mountains is one of the first that primarily relies on remote sensing data to detect micro-habitat characteristics on a large scale. We used GPS-telemetry data of both felids, as well as distribution of lynx kill sites, to understand whether felids select for karst depressions in their habitat use and, in case of the lynx, hunting behavior. We also tested whether lynx or wildcats select for certain karst depressions in respect to their morphometric characteristics. Finally, we discuss the suitability and applicability of remote detection of specific relief features for further large-scale ecological studies.

2. Material and Methods

2.1. Study Area

The Menišija plateau (hereafter Menišija) and the Logatec-Begunje plain (hereafter Ravnik) are located in the northern part of the Dinaric Mountains, Slovenia (Figure 1). The study area covers 137.0 km², where the average elevation is 627 m, and the highest peak is 998 m. The area is dominated by the karst relief type, numerous karst relief features, and underground water flow. Menišija is defined as a high karst plateau and Ravnik as a karst plain, on which the deep karst has developed [19]. Carbonate rocks predominate in the area and follow in belts from west to east: Cretaceous limestones, Jurassic dolostone with Jurassic limestones, Triassic dolostone, and Holocene deposits of rivers and streams [53,54]. Due to the bedrock types and karstification, the relief is very rugged. The most common of many karst features are caves, karrens and karst depressions, which include dolines, collapse dolines, denuded caves, uvalas, karst poljes, and dells [17,19,33]. The rock layers are approximately 10 km deep and therefore relatively resistant to tectonic deformation. The piezometric level of groundwater is at depths between 300 and 400 m below the surface. Since the deepest karst depressions do not reach the groundwater level, the area is defined as deep karst [17,33,55,56]. The area lies at the junction of two climate subtypes, the temperate continental climate of western and southern Slovenia and the temperate continental climate of central Slovenia with average annual precipitation of 1587 mm [57,58]. The study area is characterized by dense forest cover, along with extensive livestock farming, logging, and scattered small human settlements on the periphery of the study area [59]. Most of the area is covered by forest, mainly of Dinaric fir-beech associations (*Omphalodo-Fagetum*) [60]. It is also known for its high biodiversity and, besides the two species of felids, the local carnivore guild includes grey wolves (*Canis lupus*), brown bears (*Ursus arctos*), and several species of small carnivores [59]. The main prey of lynx in the study area are wild ungulates, which together represent 88% of biomass consumed by lynx, with roe deer (*Capreolus capreolus*) being the main prey species (79% of consumed biomass) [61].

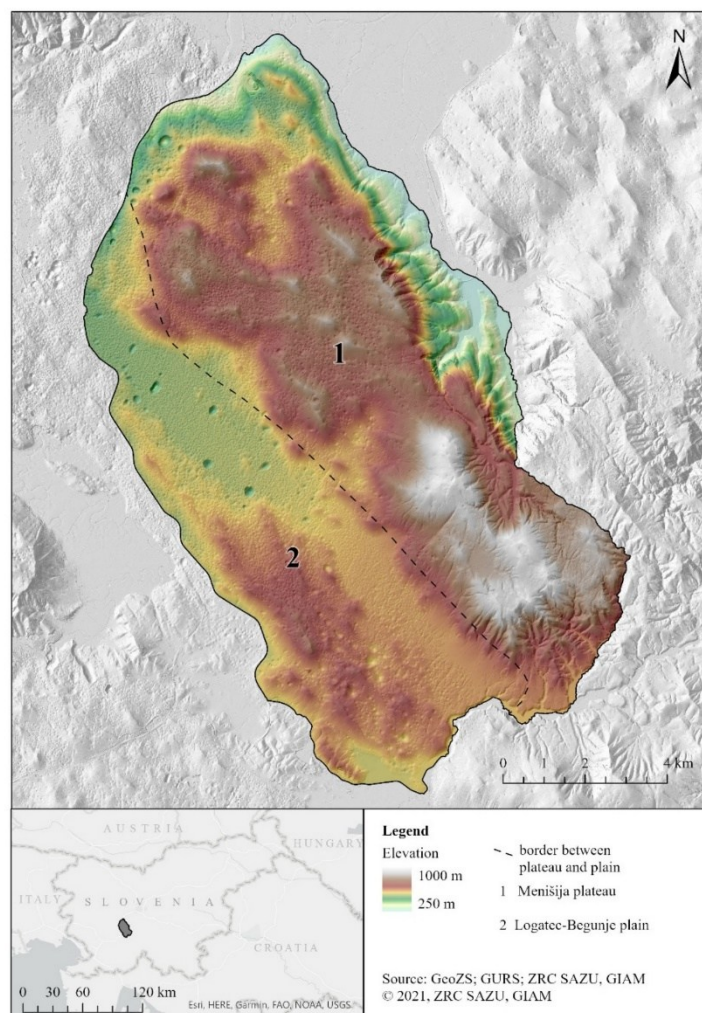


Figure 1. Map of the study area and location of the two regions considered (1—Menišija plateau; 2—Logatec-Begunje plain/Ravnik).

2.2. Detection of Karst Depressions

We used the filled-DEM method for karst depression detection [33,62]. Similar to previous authors who used this method (e.g., [15,28,34]), we used its adapted phases (Figure 2). We used a data cloud of ground points from aerial laser scanning conducted in 2011, 2014, and 2015 to create a raster layer of DEM with a cell resolution of 1×1 m; the estimated density of ground points in forested areas is 0.5 per m^2 [63,64]. To detect karst depressions and calculate of their geomorphometric characteristics, we used ESRI software ArcGIS Pro 2.8.2. Based on LiDAR-derived DEM, we first calculated the watersheds and delineated the karst depressions. Next, we calculated the morphometric characteristics of the karst depressions and eliminated depressions that were smaller according to the size criteria (see Section 2.2.2) or had non-karst origin.

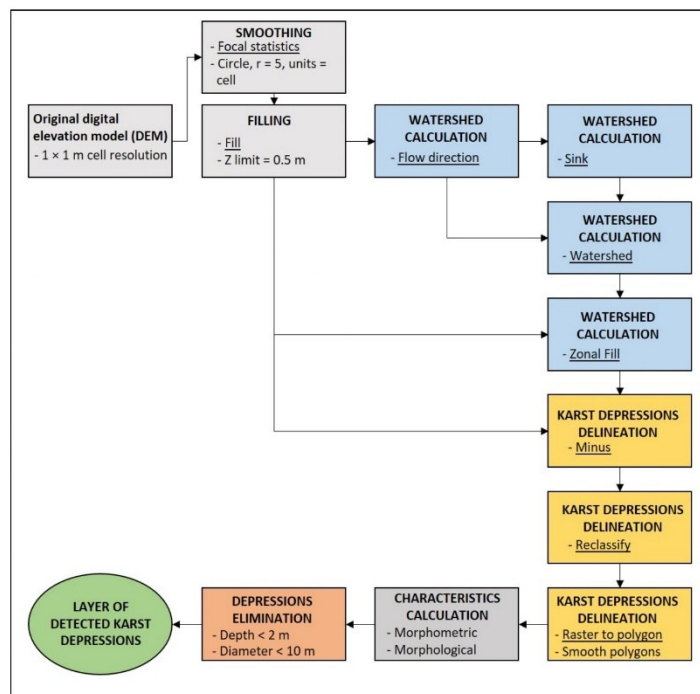


Figure 2. Flowchart of karst depressions detection.

2.2.1. Calculation of Watersheds and Karst Depressions Delineation

Apparent depressions may occur as errors or noise in the input data due to DEM creation and laser scanning over areas with dense vegetation [15,33]. The input raster data layer of the DEM was pre-processed in two ways following Telbisz et al. [15] in order to remove any potential noise in the data. The following tools were used: (1) Focal statistics—smoothing using a 5-cell circular radius filter; (2) Fill—filling the depressions that were shallower than 0.5 m. The Focal statistics tool undertakes a calculation for each cell and ascribes to it an average value of all the surrounding cells in a certain radius. Following Telbisz et al. [15], we also used a 5-cell radius for relief smoothing. The Fill tool detects the cells that are encircled by cells with a higher elevation on all sides and therefore represent a theoretical sink. This kind of depression is filled up to the depth of the z-limit parameter. In our case, the depressions were filled further up to 0.5 m.

The smoothed and filled input DEM was used to simulate the flow direction for individual cells using the D8 method, which calculates the direction of the steepest fall in the local 3×3 window (for 8 surrounding cells). Based on the flow direction, we used the Sink tool to identify sinks, which occur when all adjacent cells are higher than the mean or when two adjacent cells merge. Next, we used the Watershed tool to calculate watersheds based on the flow direction and sink raster layers, which resulted in a layer with the entire drainage area flow for a given sink. We delineated the karst depressions by determining the lowest rim cell in the karst depression where water would theoretically overflow from depression, using the Zonal Fill tool based on the watersheds and the input DEM. The Minus tool was used to subtract the input DEM from the Zonal Fill layer. Using the Raster Calculator, we determined the karst depressions as all areas with a subtraction value greater than 0. We vectorized the detected karst depressions and used the Simplify Polygons option during vectorization, which generalizes the vector representation of polygons from a cell

representation to a smoothed line. We used the tools available in ArcGIS Pro [65] to perform these calculations.

2.2.2. Morphometric Characteristics and Size Criteria

We calculated the basic morphometric characteristics: area, perimeter, diameter, depth, elongation, length, width, orientation, and slope of all the karst depressions, as well as elevation of the karst depression rims, using tools Zonal Statistics, Calculate Geometry Tool, Slope and Calculate Field Tool. For each characteristic, we present its minimum and maximum values, as well as the median along with the interquartile range (IQR), respectively. Values of orientation were converted to degrees between 0 and 180°, where a value of 0° represents east and a value of 180° represents west. We calculated the elongation of the depressions as the ratio between the length and the width of a depression [28]. Depending on the elongation values (Re: ratio between the length and the width), we classified the depressions into 4 groups: circular or sub-circular ($Re \leq 1.21$), elliptical ($1.21 < Re \leq 1.65$), sub-elliptical ($1.65 < Re \leq 1.8$), or elongated ($Re > 1.8$) [28]. In the last phase, we calculated the slope using the Slope tool, and classified values into 5 classes based on the activity of slope processes following Obu [62] and Stepišnik [56]: 0–3° (plains), 3–10° (gentle slopes), 10–25° (balanced slopes), 25–60° (active slopes), and > 60° (cliffs).

In accordance with previous research, we defined dolines and other karst depressions as having at least 2 m depth and 10 m diameter [17,28,33,62]. We excluded all depressions that did not fit these criteria.

2.2.3. Comparison of Automatic-Detection Method with Visual Recognition

We created a 500 × 500 m grid, which comprised a total of 372 polygons including at least 1 detected karst depression, and randomly selected 10% ($n = 37$) to compare results of the automatic-detection method with visual recognition. We created shaded relief from a LiDAR-based DEM for visualization of a surface and marked with a single point each karst depression we visually recognized from shaded relief (example shown in Figure S1). Then, we overlapped manually marked karst depressions recognized visually with the layer of automatically detected karst depressions (including those eliminated according to size criteria) and determined (1) the proportion of manually marked karst depressions, but that were missed by the automatic method (i.e., false negatives), and (2) the proportion of karst depressions automatically detected but not manually marked (i.e., false positives).

Karst depressions are of various sizes and shapes and, despite occurring mostly as independent relief units, sometimes two dolines become connected, which is called a compound doline. When a series of dolines is connected, it is called a series of dolines [19]. When a compound doline or a series of dolines were automatically detected as one feature, we manually marked more than one point and counted each point as a successfully recognized karst depression.

2.3. Felid Space Use and Lynx Kill-Site Distribution in Respect to Karst Depressions

We used GPS-telemetry data ($n = 2143$ GPS fixes) from 2 lynx (both males) and 2 wildcats (1 male, 1 female) inhabiting the study area to understand the influence of karst depressions on their space use. We used standard protocols for capturing, collaring, and tracking of lynx and wildcats [41,66]. Wildcats were captured within the study area, while lynx were released in Dinaric Mountains as part of a reinforcement project [67]. We used GPS-GSM collars (Vectronic Aerospace GmbH, Germany) for lynx and remote-download GPS collars (e-obs GmbH, Germany) for wildcats. Lynx collars were scheduled to obtain 2 fixes/night, and wildcat collars 3 fixes/night, both with an interval of 4 h between fixes.

We investigated the selection of karst depressions at the 3rd order of selection [68] under a use-availability approach, by comparing GPS locations within the 95% minimum convex polygons of tracked animals (use) with an equal number of random points sampled within each home range (availability). As the home ranges for both lynx included areas outside the study area, we considered only the locations within the study area where data

of distribution of karst depressions was available. Because felids are known to regularly use local gravel forestry roads [69], we also considered the effects of forestry roads on lynx and wildcat movement. We estimated the Euclidean distance from each used and random point to the nearest karst depressions and forestry road, and then used generalized linear models (GLMs) to understand the patterns of selection of these features, for each species separately. Prior to this step, we checked for a correlation between the two covariates using Spearman rank correlation. Since the two variables showed low correlation (0.22), we kept both covariates in the model. Additionally, we ran two species-specific null models and compared the Akaike's information criteria (AIC) with the respective full model [70]. We used k-fold cross-validation to assess model fit, using the same approach as presented in Hočvar et al. [52]. We also tested if lynx or wildcats select for certain karst depressions in respect to their morphometric characteristics, namely the area and depth. We used the Wilcoxon rank sum test with continuity correction to compare the sizes of karst depressions used by lynx and wildcats with those available within their home-ranges.

Because lynx in our study area are known to often kill their prey near or inside dolines and other karst depressions [44], we also estimated the proportion of kill sites located inside or in the vicinity of karst depressions, and compared it with randomly distributed points within the home range of each animal. Because of a smaller sample size, and due to potential underrepresentation of the available resources, we generated random points 10 times the number of kill sites [71]. To test the selection of karst depressions for lynx kill sites, we ran a GLM for this dataset using the same procedure as described above. Lynx kill sites were identified with the use of GPS-locations cluster analysis [66] and then confirmed in the field, when we also noted whether the kill site was located inside or on the edge of a karst depression. This also enabled us to compare accordance of identifying karst depressions based on automatic method described above (see Section 2.2) with field-checking during the kill site location surveys. We calculated the proportion of GPS locations of kill sites that would be considered located in or near karst depression identified with automatic method in respect to the field-checked kill sites that were found in or at the edge of a karst depression. To account for the kills located at the edge of a karst depression, as well as for potential error of hand-held GPS [72] when noting position of the kill site in the field, we created a buffer of 15 m around each karst depression.

All analyses were conducted using R version 4.1.0 (R Core Team 2021). GLMs and respective k-fold cross validation were developed using lme4 v1.1–21 R-package [73].

3. Results

3.1. Detection of Karst Depressions and Their Morphometric Characteristics

We identified 9711 karst depressions within the study area (area size: 137.0 km²) with an average density of 70.9 karst depressions/km². In Ravnik, we detected a total of 5720 (58.9%) karst depressions, with average density of 110.0 karst depressions/km² and in Menišja 3911 (41.1%) with average density 46.0 karst depressions/km² (Figure 3). Most karst depressions were located in the western and north-western part of study area, which is consistent with the bedrock types. The highest number ($n = 8016$) and average density of karst depressions (117.0 depressions/km²) was recorded in the limestone area (68.5 km², 50.0% of the study area), compared to parts with predominate dolostones (63.4 km², 46.2% of the study area) where number ($n = 1686$) and average density (26.6 depressions/km²) of karst depressions was considerably lower. Only nine karst depressions were detected in parts with alluvial deposits (3.7 km², 2.7% of the study area) and no karst depressions were detected in the areas with boxite (1.4 km², 1.1% of the study area).

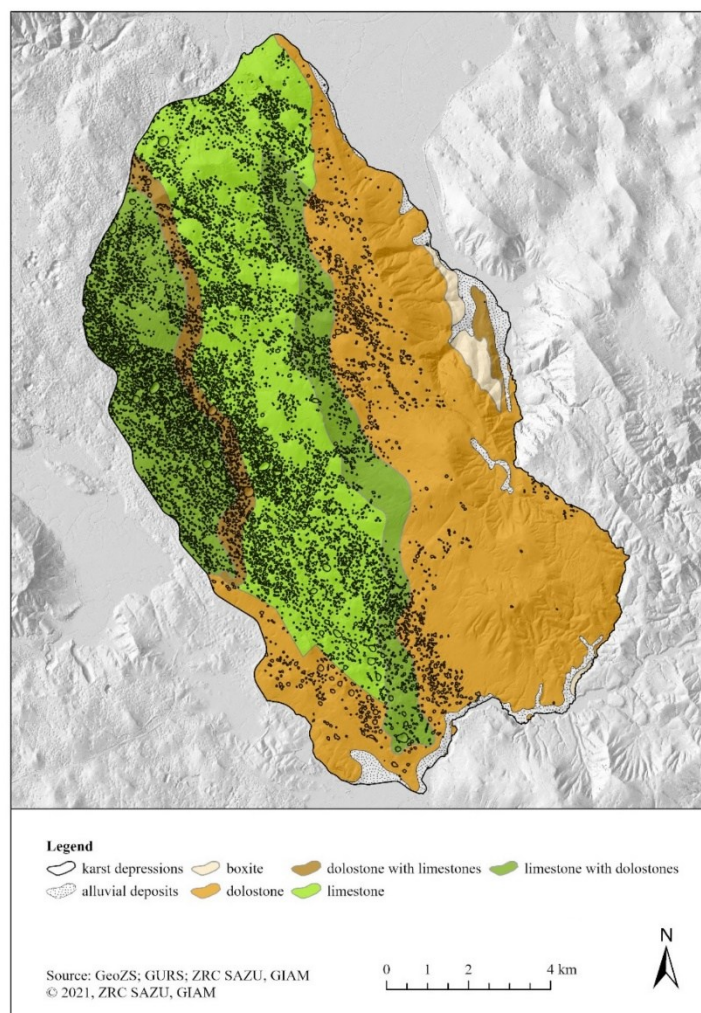


Figure 3. Detected karst depressions and geological map of the study area.

The measurements of morphometric characteristics obtained from automatically detected karst depressions are presented in Table 1. The median value $\pm$ IQR for the area of the karst depressions was $765.6 \pm 713.6 \text{ m}^2$ and total area of all detected karst depressions was estimated to be 10.7 km^2 , which corresponds to 7.8% of the entire study area. We observed that the depressions in Ravnik are slightly larger than in Menišija (Table 1). Most of the karst depressions had similar morphometric characteristics, however, some of these features displayed very large areas and depths (see maximum values in Table 1). The average orientation of depressions was 98.9° , which coincides with the bedrock inclination (northwest to southeast). Most depressions (59%, $n = 5733$) had an axis orientated between 90° and 180° (northwest), followed by 0° to 90° orientation (northwest; 41%, $n = 3976$), while depressions with other orientations were almost non-existent ($n = 2$). The most common shapes were circular or sub-circular depressions (48.5%, $n = 4715$), followed by

elliptical depressions (47.3%, $n = 4598$), while sub-elliptical and elongated ones were rare (2.1%, $n = 199$ each) (Figure S2). The majority (73.4%) of the detected karst depressions had balanced slopes, followed by gentle slopes (13.4%) and active slopes (11.9%), while plains and cliffs were rare (less than 1.5%; Figure S3).

Table 1. Estimated minimum (Min) and maximum (Max) values for each morphometric characteristic considered, as well as median and interquartile range (Median $\pm$ IQR). Values are presented for the entire study area, and then separately for Ravnik and Menišija.

	Area (m ²)	Perimeter (m)	Diameter (m)	Depth (m)	Length (m)	Width (m)	Elevation (m)
Study area (area = 137 km², n_{depressions} = 9711)							
Min	102.4	37.8	11.4	2.0	6.2	5.0	299.9
Max	54,965.8	907.2	264.6	80.9	168.5	127.6	942.3
Median $\pm$ IQR	765.6 $\pm$ 713.6	102.6 $\pm$ 46.1	31.2 $\pm$ 14.0	3.6 $\pm$ 2.3	17.4 $\pm$ 8.0	14.0 $\pm$ 6.3	587.6 $\pm$ 98.8
Ravnik (area = 52 km², n_{depressions} = 5720, %depressions = 58.9%)							
Min	102.4	38.1	11.4	2.0	6.6	5.0	482.8
Max	54,965.8	907.2	264.6	80.9	168.5	127.6	697.6
Median $\pm$ IQR	788.8 $\pm$ 699.1	104.2 $\pm$ 44.7	31.7 $\pm$ 13.5	3.5 $\pm$ 2.2	17.6 $\pm$ 7.7	14.3 $\pm$ 6.2	554.8 $\pm$ 65.8
Menišija (area = 85 km², n_{depressions} = 3991, %depressions = 41.1%)							
Min	102.7	37.8	11.4	2.0	6.2	5.3	299.9
Max	48,146.5	794.8	247.6	68.0	132.4	115.8	942.3
Median $\pm$ IQR	722.9 $\pm$ 725.4	100.5 $\pm$ 47.7	30.3 $\pm$ 14.5	3.6 $\pm$ 2.4	17.1 $\pm$ 8.3	13.4 $\pm$ 6.6	642.1 $\pm$ 112.3

3.2. Comparison of Automatic-Detection Method with Visual Recognition

Within the 37 polygons randomly selected to compare our model with visually recognized karst depressions, we marked 2186 karst depressions based on shaded relief, while the automatic method detected 1988 karst depressions. A total of 1826 (83.5%) manually marked karst depressions matched with automatically detected karst depressions. The model identified 162 (8.2%) of karst depressions that were not manually detected (false positives), while 360 (16.5%) of the manually marked karst depressions were not automatically detected (false negatives) (example shown in Figure S1).

3.3. Felid Space Use and Lynx Kill-Site Distribution

We used lynx ($n = 1161$) and wildcat ($n = 982$) GPS fixes to assess felid selection for karst depressions and forestry roads within their home ranges. When compared to random points within the tracked animals' home ranges, we observed a selection for karst depressions by the lynx, especially when rims of karst depressions are also considered, while for the wildcats only slight selection for karst depressions with rims was observed (Figure 4, Table 2). In respect to distances to the closest feature, both species selected vicinity of karst depressions, while vicinity of roads was selected by lynx but avoided by wildcats (Tables 2 and S1). Among the karst depressions available within their home ranges, both lynx and wildcats selected those with larger areas (median_{area_lynx} = 852.7 $\pm$ 799.2, $W_{lynx} = 3,246,031.0$, $P_{lynx} = 0.0002$; median_{area_wildcat} = 1315.1 $\pm$ 1584.8, $W_{wildcat} = 139,528.0$, $P_{wildcat} < 0.0001$) and greater depth (median_{depth_lynx} = 3.9 $\pm$ 2.8, $W_{lynx} = 3,254,652$, $P_{lynx} = 0.0001$; median_{depth_wildcat} = 4.9 $\pm$ 3.8, $W_{wildcat} = 138,131.0$, $P_{wildcat} < 0.0001$), when compared to karst depressions available within their respective home ranges (median_{area_avail_lynx} = 746.9 $\pm$ 679.1, median_{depth_avail_lynx} = 3.5 $\pm$ 2.2; median_{area_avail_wildcat} = 902.3 $\pm$ 947.0, median_{depth_avail_wildcat} = 3.9 $\pm$ 3.1).

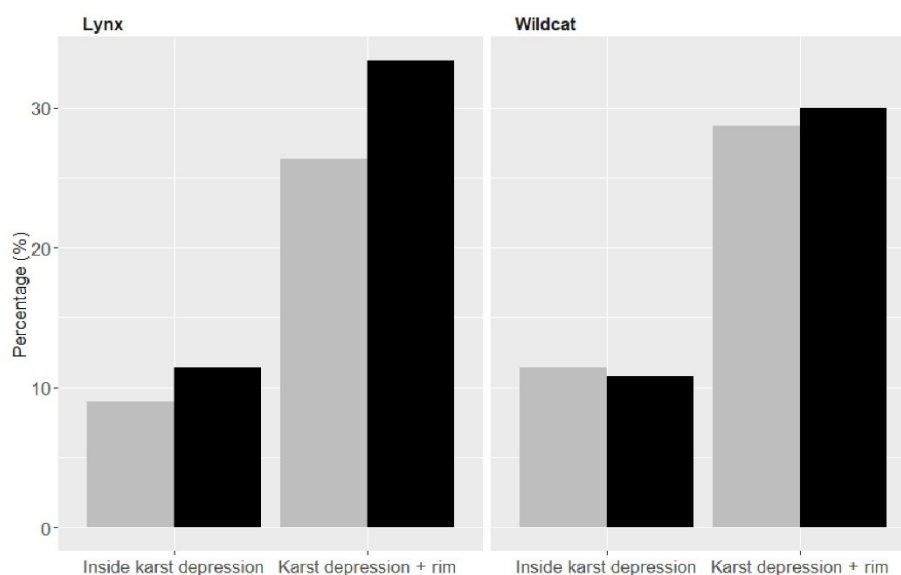


Figure 4. Selection of karst depressions by lynx (left) and wildcats (right), indicated by comparison of random points inside the tracked animals' home ranges (availability; grey) and felid GPS points (use; black). 'Inside karst depression' refers to areas inside karst depressions, while 'Karst depression + rim' includes also a 15 m buffer to account for the rims of these depressions, as well as GPS-error of telemetry collars.

Table 2. Generalized linear models for habitat selection of Eurasian lynx and European wildcats in respect to their GPS locations, as well as locations of lynx kill sites. Covariate depressions and roads represent the distance to the nearest karst depression and forestry road, respectively. k—number of model variables; AIC—Akaike's information criterion; ρ —Spearman rank correlation; CI—confidence interval.

Dataset	Model	k	AIC	Δ AIC	ρ	Model Coefficients	
						Dist_Depressions [95% CI]	Dist_Roads [95% CI]
Lynx_GPS	Use ~ depressions + roads	4	3241.6	0.0	0.9	−0.8 [−0.9; −0.7]	−0.2 [−0.3; −0.1]
	Null	2	3374.6	133.0	0.5	-	-
Wildcat_GPS	Use ~ depressions + roads	4	2818.2	0.0	0.4	−0.7 [−1.2; −0.1]	0.5 [0.34; 0.7]
	Null	2	2854.9	36.7	0.5	-	-
Lynx_kills	Use ~ depressions + roads	4	155.5	0.0	0.3	−0.1 [−0.3; 0.0]	−0.0 [−0.2; 0.1]
	Null	2	155.7	0.1	0.5	-	-

We found 40 lynx kill sites in the study area, among which 58% ($n = 23$) were noted during the field survey as being located within or nearby a karst depression. When compared to automatically detected karst depressions, 35% ($n = 14$) of kills were located inside or on the rim of a karst depression ($\text{median}_{\text{dist}} = 29.1 \pm 72.1$). In respect to availability, this is higher compared to the proportion of random points located inside or on the rim of the automatically detected karst depressions (27%, $n = 111$), although model coefficients do not indicate significant selection of these features (Table 2). We did not observe selection nor avoidance towards roads (Table 2).

4. Discussion

4.1. Remote Large-Scale Detection of Geomorphic Features

Use of an automatic method to analyze remote sensing high-resolution topography data (LiDAR) enabled us to efficiently detect and measure a very large number (almost 10,000) of studied relief features (karst depressions) in a rugged karstic landscape of the Dinaric Mountains. This highlights the potential of such methodology for large-scale ecological research, which we applied to study habitat selection by wild felids. Such task would be nearly impossible or would require enormous effort, if done using traditional methods to detect landscape features and obtain their morphometric and morphological characteristics in the field or visually using topography maps with much lower resolution.

Nevertheless, the method also had some drawbacks. When compared to manually marked karst depressions recognized visually from shaded relief, 16.5% of the karst depressions were not detected by the automatic method. Comparison between the automatically generated layer and visually recognized karst depressions from the shaded relief suggests that discrepancy is largest on sloped surfaces. This causes larger areas of some depressions to be missed (i.e., not defined as part of depressions), because the rim of a karst depression is assigned to the entire depression at the same elevation of the lowest rim cell where theoretical water would overflow from the karst depression. This is particularly noticeable in karst depressions with a pronounced rim, such as collapse dolines. This problem has been recognized before and is also connected to a lack of clear consensus in karstological and geomorphological literature on what represents the rim of a karst depression, particularly when located on a slope [74]. Until this issue is resolved, it may be difficult to better approximate the state of nature using existing methods for detecting and delineating karst depressions. Nevertheless, the method has shown its usefulness and the data obtained for density of karst depressions and their morphometric and morphological characteristics are comparable to previously reported estimates [25]. The medians of the diameter and depth of karst depressions in the study area are slightly lower than the Slovenian average (42 and 9 m, respectively; [25]). The average elevation where karst depressions occur is 592.7 m, which is consistent with the average elevation of Ravnik and the majority of the karst depressions occur in this area [25]. The orientation of the karst depressions, as expected, coincides with the bedrock inclination and has northwest–southeast direction typical for Dinaric mountains.

4.2. Selection of Karst Depressions by the Wild Felids

We used the layer of karst depressions together with their morphometric and morphological characteristics to perform the first large-scale analysis of felid habitat selection in respect to these relief features. Felids are known to be attracted to rugged terrain, rocky areas, and conspicuous relief features, for example for resting, scent-marking, and hunting [26,44,46,49,51,52], but lack of detailed GIS layers containing information on such features over larger scales had so far often prevented more advanced studies, because the amount of data was often limited by logistic and economic constraints to conduct fieldwork. Our study demonstrates the potential of combining GPS-telemetry data and methods involving automatic detection of relief features for wildlife research. This approach enabled us to confirm attraction of wildcat and, especially, lynx to karst depressions. While GPS-error inherent to GPS-telemetry data limits our ability to discern which parts of the depressions are most attractive to felids, our results suggest that rims of karst depressions might be especially interesting. This is not unexpected given that lynx and other felids are known to use elevated vantage points that provide them with a good overview of the surroundings to easily detect incoming prey or potential danger [52]. Cave entrances are often found in karst depressions [75], which are used by felids for foraging and scent-marking [26].

In the interpretation of results, we need to consider that our study area is characterized by a very high density of karst depressions (on average over 70 depressions/km²), which could reduce their attractiveness to felids in respect to availability. In the future, it would be therefore interesting to extend research also to areas with lower availability of these

relief features to test for potential functional response (i.e., variation in habitat selection as a function of habitat availability; [76]) in selection of karst depressions by both felids. Our results also need to be treated with caution, since telemetry data was obtained from only four individuals. Felids like lynx are known for their relatively stereotypical behavior, universal habitat use, and homogeneous responses between sexes, especially when it comes to habitat selection at finer scales [77], which was also the focus of this study. Although this allows for certain generalizing, we recommend further studies using larger number of tracked individuals.

Incorporation of data on morphometric characteristics of karst depressions suggests that felids might be especially attracted to larger features, which could again be connected with better vantage points and presence of caves. Furthermore, large collapse dolines with vertical cliffs can be very conspicuous in the landscape, which could make them attractive as scent-marking sites [49] or hunting of certain prey, like chamois (*Rupicapra rupicapra*) [26]. A large proportion of lynx prey remains found at the bottom or near the rim of karst depressions (58% of all kills) suggest that these landscape features could have an important role in hunting behavior of this predator. This confirms previous anecdotal observations [44], which suggested that dolines with rocky terrain can make hunting more successful because of easier stalking for lynx and escape impediments to ungulates. In contrast to previous research, use of automatic detection of karst depressions across the entire study area enabled us to generate data on availability of karst depressions in the landscape, which indicates that lynx may be actively selecting karst depressions for hunting. However, the relatively small sample of field-checked kill sites at present limits the reliability of our conclusions (95% confidence interval of model coefficients slightly overlapped with zero) and more data on distribution of predator kill sites is needed to better understand role of karst depressions in foraging behavior of lynx and other large carnivores.

These findings improve our understanding of wildcat and lynx microhabitat characteristics and in the case of lynx also hunting behavior. They can contribute to the improvement of management and conservation of both protected species, for example, for implementation of monitoring. Our results indicate that rims of karst depressions might be especially suitable for deploying camera-traps for estimating population densities or box-traps for capturing and collaring the animals [67]. Overall, our results provide further evidence of the importance to protect geomorphological features (geodiversity) for biodiversity conservation [29,30,32,51,78,79].

5. Conclusions

We showed that method of karst depressions detection based on the filled-DEM approach is suitable for detection, general spatial analysis, and calculation of morphometric and morphological properties of depressions. The process is partially automated and allows easy and inexpensive application to other areas, including over large scales. The method thus provides several advantages over manual mapping, especially when time investment and field costs are considered, as well as when study areas are difficult to access and forested. However, the method also has some drawbacks, such as difficulties in assigning the rim of the karst depression on sloped surfaces and consequent failure to detect part of depressions in such areas. Nevertheless, we believe the method has considerable potential for application in large-scale analyses in many fields besides geomorphology and karstology, including geology, botany, zoology, tourism, spatial planning, nature conservation, creation of new geoparks, and development of national or local action plans for the protection of geodiversity. Our study case on habitat selection of wild felids in karstic landscapes demonstrates such potential application. Results suggest that both, lynx and wildcats, are attracted to karst depressions, especially those of larger dimensions, and that lynx often capture their prey inside such depressions or in their vicinity. This suggests that relief features could play an important role in the ecology of wild felids and warrants further research.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/rs14030656/s1>, Figure S1: Comparison of automatic-detection method with visual recognition based on shaded relief. Eliminated karst depressions did not fit to size criteria, i.e., depth was <2 m and diameter < 10 m; Figure S2: Shape of depressions according to elongation values: circular or sub-circular (A), elliptical (B), sub-elliptical (C), elongated (D); Figure S3: Map of geomorphological characteristics of karst depressions based on slope; Table S1: Range of values [Min-Max] and associated median [median $\pm$ IQR] for each covariate per species, for both used and available points.

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Informed Consent Statement: Not applicable.

Data Availability Statement: Data available on request due to restrictions (nature conservation).

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Dolines and cats: remote detection of karst depressions and their application to study wild felids' ecology

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Supplementary file - List of figures and tables.

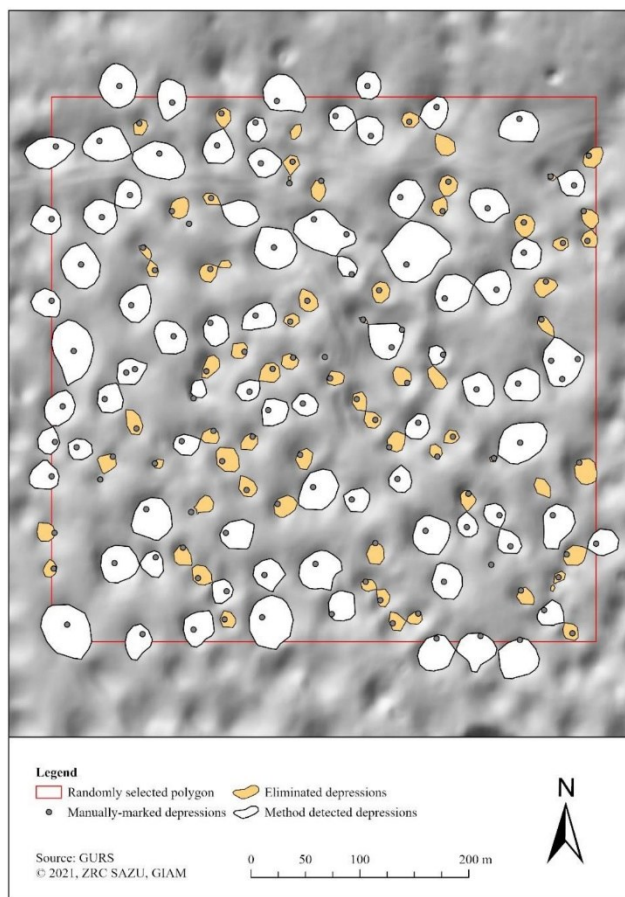


Figure 1 S1: Comparison of automatic-detection method with visual recognition based on shaded relief. Eliminated karst depressions did not fit to size criteria, i.e. depth was < 2 m and diameter < 10 m.

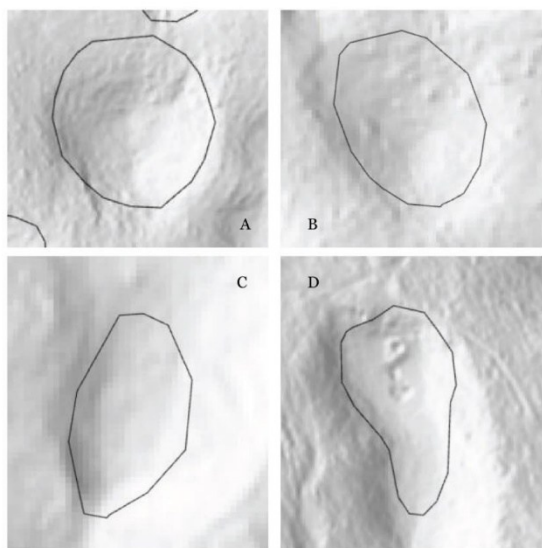


Figure 2 S2: Shape of depressions according to elongation values: circular or sub-circular (A), elliptical (B), sub-elliptical (C), elongated (D).

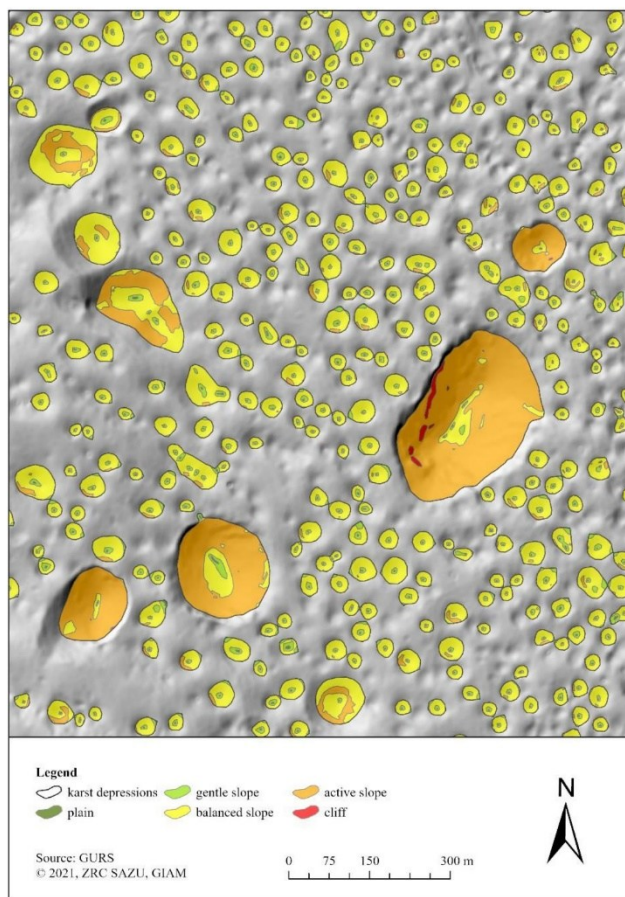


Figure 3 S3: Map of geomorphological characteristics of karst depressions based on slope.

Table 1 S1: Range of values [Min-Max] and associated median [median $\pm$ IQR] for each covariate per species, for both used and available points.

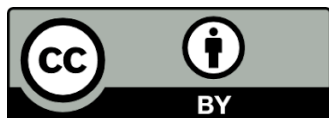
Lynx				
	Dist_depressions (used)	Dist_depressions (available)	Dist_roads (used)	Dist_roads (available)
Min – Max	0.0 – 960.0	0.0 – 1504.8	0.4 – 913.5	0.3 – 1006.3
Median $\pm$ IQR	25.0 $\pm$ 50.0	39.0 $\pm$ 113.8	180.1 $\pm$ 209.5	170.6 $\pm$ 242.1
Wildcat				
	Dist_depressions (used)	Dist_depressions (available)	Dist_roads (used)	Dist_roads (available)
Min – Max	0.0 – 277.8	0.0 – 298.3	< 0.1 – 637.8	0.6 – 678.2
Median $\pm$ IQR	32.2 $\pm$ 58.3	37.71 $\pm$ 66.2	217.0 $\pm$ 255.2	185.2 $\pm$ 228.6

2.2 VKLJUČEVANJE GEODIVERZITETE V PROSTORSKO EKOLOGIJO ŽIVALI: IZBIRA MIKROHABITATA EVRAZIJSKEGA RISA (*LYNX LYNX*) IN EVROPSKE DIVJE MAČKE (*FELIS SILVESTRIS*) V KRAŠKI POKRAJINI

Čonč Š., Oliveira T., Hočevar L., Černe R., Breg Valjavec M., Krofel M. 2024. Integrating geodiversity in animal spatial ecology: microhabitat selection of Eurasian lynx (*Lynx lynx*) and European wildcat (*Felis silvestris*) in a karst landscape. *Global Ecology and Conservation*, 54: e03138, <https://doi.org/10.1016/j.gecco.2024.e03138>

Geodiverziteta, ki zajema različne geofizikalne elemente, lahko pomembno vpliva na razširjenost vrst in na vedenjske vzorce živali. Čeprav razgiban teren in izstopajoče reliefne oblike privlačijo številne velike zveri, se je večina dosedanjih raziskav osredotočala le na splošne topografske značilnosti (npr. naklon ali razgibanost terena) in le redko raziskovala vplive specifičnih mikrohabitatnih značilnosti. Ta vrzel je predvsem posledica omejene razpoložljivosti visokoločljivostnih digitalnih modelov terena (DMT) in podatkov o reliefnih oblikah na večjem prostorskem nivoju. LiDAR DTM-ji se lahko v kombinaciji z različnimi avtomatskimi metodami uporabljajo za zaznavanje reliefnih oblik, kar omogoča brezkontaktno in natančno kartiranje velikih, odročnih in gozdnatih območij. V tem članku smo na območju Dinarskega gorovja v Sloveniji raziskali vzorce izbire različnih kraških reliefnih oblik, topografskih, antropogenih in vegetacijskih značilnosti pri dveh vrstah prostoživečih mačk, evrazijskem risu (*Lynx lynx*) in evropski divji mački (*Felis silvestris*). Na podlagi LiDAR DTM-ja smo izračunali topografske značilnosti in avtomatsko zaznali kraške reliefne oblike. Med risi in divjimi mačkami, opremljenimi z GPS ovraticami, smo na podlagi pristopa rabe in razpoložljivost (*»use-availability«*) primerjali izbiro habitata. Raziskali smo tudi razlike v izbiri habitata pri risih glede na njihov izvor (nepreseljeni in preseljeni) in stopnjo izkušenosti (naivni in izkušeni preseljeni). Pri obeh vrstah smo opazili pomemben vpliv reliefnih oblik na rabo prostora, vendar z različnimi vzorci izbire. Risi so izbirali razgiban teren in bližino jam, sten, kraških kotanj, grebenov, majhnih izdankov kamnin in cest, izogibali pa so se naseljem in gozdnim robovom. Divje mačke so izbirale območja z manjšim naklonom, bližje glavnim cestam, gozdnim robovom, jamam in grebenom, vendar so se izogibale stenam, gozdnim cestam in naseljem. Pri preseljenih risih smo opazili močnejše vzorce izbire/izogibanja kot pri nepreseljenih risih, medtem ko so bile razlike v izbiri glede na stopnjo izkušenosti manjše. Naša raziskava dokazuje potencial vključevanja tehnik daljinskega zaznavanja in informacij o geodiverziteti v raziskave prostorske ekologije živali. Poleg tega naši rezultati kažejo, da specifične reliefne oblike predstavljajo pomembne abiotске mikrohabitate za prostoživeče mačke in da lahko vplivajo na ločevanje habitatov med podobnimi vrstami. Naše ugotovitve so dodaten dokaz o pomenu ohranjanja geodiverzitet in potrebi po vključevanju abiotских mikrohabitatnih značilnosti v raziskave o izbiri habitata pri prostoživečih živalih.

Ključne besede: LiDAR, reliefne oblike, geomorfologija, daljinsko zaznavanje, prostorska ekologija, velike zveri



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Integrating geodiversity in animal spatial ecology: microhabitat selection of Eurasian lynx (*Lynx lynx*) and European wildcat (*Felis silvestris*) in a karst landscape

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ABSTRACT

Geodiversity, encompassing various geophysical elements, can have an important impact on species distribution and affect animal behaviour patterns. Although many wild felids are attracted to rugged terrain and conspicuous relief features, most previous research was limited to general topographical characteristics (e.g., slope or terrain ruggedness) and rarely considered the effects of specific microhabitat characteristics. This gap is primarily due to the limited availability of high-resolution digital terrain models (DTMs) and relief features data at larger scales. However, LiDAR DTMs can be used in combination with various automatic methods to detect relief features, enabling non-contact and accurate mapping of large, remote and densely-forested areas. Here, we investigated the selection patterns of various karstic relief features, as well as topographic, anthropogenic and vegetation characteristics, by two sympatric felids, the Eurasian lynx (*Lynx lynx*) and the European wildcat (*Felis silvestris*), in the Dinaric Mountains, Slovenia. We used LiDAR DTM to calculate topographic characteristics and detect karst relief features based on automatic methods. We compared the selection of these features between the GPS-collared lynx and wildcats under a use-availability approach. We also investigated the differences in the selection of these features by lynx based on their origin and experience (remnant vs. translocated and naive vs. experienced, respectively). We observed significant impact of relief features on space use by both felids and detected distinct selection patterns between the two species. Lynx selected rugged terrain and proximity of caves, cliffs, karst depressions, ridges, small rocky outcrops, and roads, but avoided human settlements and forest edges. Wildcats selected areas with lower surface slope, closer to main roads, forest edges, caves and ridges, but avoided cliffs, forest roads and human settlements. We observed stronger selection/avoidance patterns among the translocated compared to the remnant lynx, while the differences in experience levels were less important. Our study demonstrates the potential of integrating remote sensing techniques and information on geodiversity into the study of animal spatial ecology. Furthermore, our results indicate that specific relief features provide important abiotic microhabitats for felids and may influence habitat segregation between sympatric species. Our findings provide further evidence

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for the importance of geodiversity conservation and the need to incorporate abiotic microhabitat features in wildlife habitat selection studies.

1. Introduction

Various abiotic factors, often termed as geophysical diversity or geodiversity, influence animal communities and shape their habitats (Huggett, 2004; Gordon et al., 2022). Certain links between geodiversity and biodiversity are well established, such as the influence of general abiotic factors (e.g., climate, geology or general topography) on habitats and the distribution of species (Huggett, 2004). However, scientists and conservationists are increasingly recognising the importance of including various microhabitat components of geodiversity, such as specific relief features (landforms) and micro-relief characteristics into the ecological research and biodiversity conservation efforts (Albano, 2015; Anderson et al., 2015; Bailey et al., 2018; Crofts, 2019; Čonč, 2020; Gordon et al., 2022; Maliniemi et al., 2024). Specific relief features within the landscapes, ranging from large-scale topographic characteristics (e.g., mountain ranges) to microhabitat elements (e.g., rocky outcrops), play a vital role in providing habitat and/or shelter for a variety of species (Bouchet et al., 2015; Fitzsimons and Michael, 2017; Dorph et al., 2021; Čarni et al., 2022; Bátori et al., 2023). Additionally, relief features can also influence the basic animal behavioural patterns, which are essential for the survival and functioning of populations. For example, relief features can act as barriers (e.g., a large river) or corridors (e.g., a valley in a mountain range) that influence the movement paths of animals and provide protection from predators (e.g., cliffs and caves as breeding and nesting grounds for birds and bats; Bouchet et al., 2015; Gordon et al., 2022). Furthermore, terrain characteristics and specific relief features can determine hunting success, for example by providing cover for stalking predators, slowing down prey or providing a physical barrier against which they can corner their prey (Andersson et al., 2009; Bouchet et al., 2015). Conspicuous relief features also attract animals to use them for scent-marking and thus function as communication hubs that help maintain socio-spatial organisation of populations (Allen et al., 2017; Melzheimer et al., 2020). At the same time, in human-dominated landscapes rocky, rugged and hard-to-access areas often correlate with lower levels of human disturbance and potentially influence the use of such areas by more elusive species (Basille et al., 2009; Nickel et al., 2021; Oeser et al., 2023).

Connections between topography or specific relief features are particularly pronounced in felids. Previous studies on pumas (*Puma concolor*), leopards (*Panthera pardus*), bobcats (*Lynx rufus*) and Eurasian lynx (*Lynx lynx*) have shown that these felids select rugged and inaccessible terrain, rocky areas, ridges and conspicuous relief features for various behaviours, such as movement, hunting, scent-marking and resting (Dickson and Beier, 2007; Bouchet et al., 2015; Abouelezz et al., 2018; Ironside et al., 2018; Farhadinia et al., 2020; Hočevar et al., 2021). For example, Eurasian lynx and European wildcats (*Felis silvestris*) use rocky outcrops/cliffs for scent-marking (Allen et al., 2017; Krofel et al., 2022), while lynx often select such features for day-resting and movement (Signer et al., 2019; Hočevar et al., 2021; Čonč et al., 2024). Because these predators typically occupy extensive home ranges, studies on their space use or habitat connectivity often cover larger areas (e.g. Dickson and Beier, 2007; Bojarska et al., 2020; Potočnik et al., 2020; Ripari et al., 2022). However, for large-scale studies, topographic predictor covariates are often limited to general terrain characteristics (e.g., altitude, exposure, slope, ruggedness) and therefore they usually do not consider the effects of fine-scale terrain characteristics and various relief features, despite their potential importance for the ecology of wild felids (Ironside et al., 2018; Čonč et al., 2022b; 2024; Schmidt et al., 2023). This gap is primarily related to the limited availability of high-resolution digital terrain models (DTM) and detailed large-scale GIS layers with data on relief features. Furthermore, the limited amount of research that incorporated micro-relief characteristics in habitat selection studies usually relied on manual collection of geomorphic data in the field (e.g., Hočevar et al., 2021) or based on digitising relief features (e.g., Signer et al., 2019), which was time-consuming and costly, and resulted in lower accuracy and data quality (Ciglić et al., 2022; Čonč et al., 2022b; 2024). With the advances in the field of remote sensing, high-resolution data such as LiDAR (Light Detection and Ranging) based DTM, combined with various automatic methods for the detection of relief features, enable non-contact, cost-effective and accurate mapping of such features in remote and densely forested areas at large spatial scales (Davies and Asner, 2014; Ciglić et al., 2022; Čonč et al., 2022b; 2024).

Karst landscapes are one of the most diverse geomorphological systems on Earth, due to their unique surface and subsurface features (Márton and Vetési-Foith, 2021). In addition to high geodiversity, karst landscapes can also be defined as one of the rockiest and rugged geomorphologic systems on the planet due to the abundance and density of micro- and meso-relief features that dissect the karst surface (Day and Chenoweth, 2013; Čonč et al., 2022b). The karst surface is mainly characterised by circular concave and convex relief features such as conical hills, dolines, uvalas and poljes (Ford and Williams, 2007; Mihevc et al., 2010; Zorn et al., 2020). While these large relief features can be easily detected with a number of already developed automatic detection methods (e.g., Bauer, 2015; Grlj and Grigillo, 2014; Telbisz et al., 2016; Mihevc and Mihevc, 2021; Stefanovski and Repe, 2021), smaller features consisting mainly of numerous rocks of different shapes and sizes are difficult to detect (Čonč et al., 2024).

We selected Dinaric Karst region in southern Slovenia as a study area to investigate the fine-scale selection of various karstic relief features and topographic characteristics by two sympatric felids: an apex predator, Eurasian lynx (hereafter lynx), and a mesopredator, the European wildcat (hereafter wildcat). We considered these two species due to their widespread and overlapping distribution, their selection of rugged and rocky terrain and the importance of several relief features for various behavioural states (e.g., Potočnik, 2006; Krofel et al., 2007; Jerosch et al., 2010; Krofel, 2010; Allen et al., 2017; Signer et al., 2019; Ruiz-Villar et al., 2023b; Čonč et al., 2024). First, we used high-resolution LiDAR DTMs to calculate topographic characteristics and detect karstic relief features across the Slovenian Dinaric Mountains based on automatic methods. Next, we assessed the selection of these features and anthropogenic infrastructure by lynx and wildcat under a use-availability approach and compared the selection patterns between the two species. We

predicted that both species select areas with high ruggedness, steep slopes and vicinity of relief features, such as caves, cliffs and rocky outcrops. Based on previous research on lynx, we also predicted selection of gravel forest roads (e.g., for scent-marking; Křofel et al., 2017) and avoidance of human settlements (Ripari et al., 2022). Finally, because part of the lynx population consisted of animals translocated from a different landscape (i.e., non-karst; Carpathian Mountains), we compared the selection of these features based on their origin (remnant vs. translocated). Although translocated lynx are faced with a largely unfamiliar environment, previous studies have shown that they adapt to their new environment very quickly (Topličanec et al., 2022), but they can adjust their habitat selection over time (Nagl et al., 2022). They were also observed to exhibit a functional response in the selection of rocky and rugged areas, as lynx' selection of such habitats increases in regions with lower availability of these habitats (Čonč et al., 2024). Thus, we predicted that translocated lynx show similar selection patterns as the remnant lynx, but that their selection would be more pronounced. We also tested if behaviour of the translocated lynx changed with experience level (naive translocated vs. experienced translocated lynx; Oliveira et al., 2023).

2. Materials and methods

2.1. Study area

The Slovenian Dinaric Karst (hereafter SDK; Fig. 1) encompasses a karst landscape in the western and southern part of Slovenia, developed on Mesozoic and Cenozoic rocks, primarily limestones and dolomites (Gostinčar and Stepišnik, 2023). Geographically and geologically, it is part of the Dinaric Mountains, wide young folded mountain range that stretches from the Alps in the north to the Sar-Pindus Mountains in the south and from the Adriatic Sea in the west to the Pannonian Basin in the east (Mihevc et al., 2010; Zorn et al., 2020). The altitudes in the SDK range from around 200–1800 m and area is characterised by various levelled areas, such as high and low corrosion plains, lowlands and poljes, running in a typical Dinaric direction, from the northwest to the southeast (Mihevc et al., 2010; Zorn et al., 2020; Stepišnik and Ferk, 2023). Due to the different lithology and dynamics of mechanical weathering of the rocks that make up the SDK, the karst surface exhibits a wide range of surface and subsurface relief features (Fig. S1) such as conical hills, karst depressions (e.g., dolines, collapse dolines, denuded caves) and caves (Mihevc et al., 2010; Zorn et al., 2020). In addition to meso-relief features, the surface is also dissected by numerous smaller scale features of different shapes and sizes such as rocky

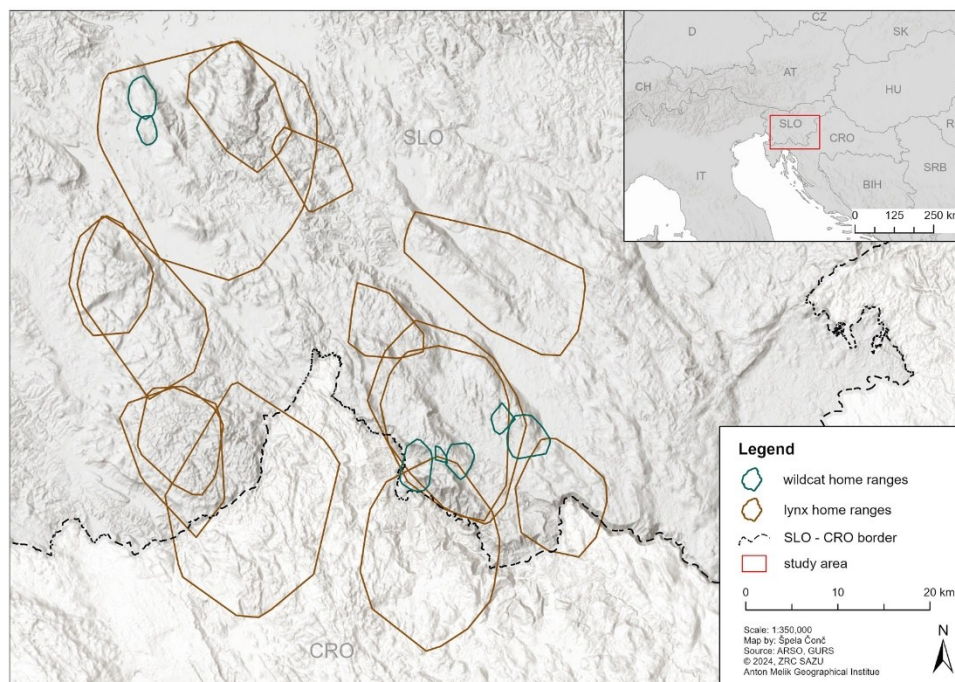


Fig. 1. Map of the lynx (brown) and wildcat (green) home ranges in the study area of the Slovenian Dinaric Karst (SDK). Because some of the home ranges included areas that were outside the study area, where LiDAR data were not available (i.e., Croatia), we included only the parts of the home ranges within the study area (Slovenia) in the analysis.

outcrops, karrenfields, grikes and rocky blocks (Fig. 2 and Fig. S1; Gams, 2004; Mihevc et al., 2010; Márton and Vetési-Foith, 2021).

In the study area the average temperature in January is between 0 and -3°C and in July between 16 and 20°C . The average annual precipitation is between 1300 and 2500 mm (Komac et al., 2020; Ogrin et al., 2023). The snow cover is common in January, with the highest amount in February. This area receives on average a total (the sum of the daily depths of new snow) of 60–100 cm of snow, and the snow cover lasts from 20 to 60 days (Komac et al., 2020).

The SDK is known for high forest cover, dominated by the Dinaric fir-beech association (*Omphalodo-Fagetum*), extensive livestock farming, logging, and hunting, with scattered small human settlements mostly located in larger levelled areas such as karst poljes or low karst plateaus. Area is also known for its high biodiversity and ecological fragility (Gams, 2004; Mihevc et al., 2010).

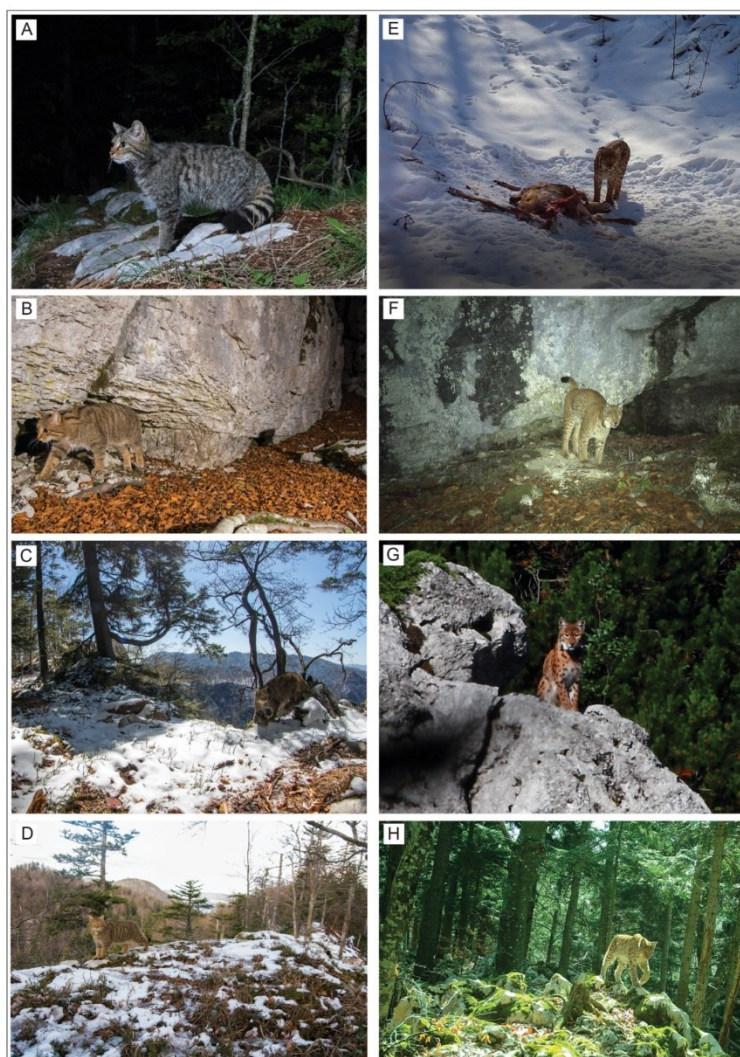


Fig. 2. Examples of various relief features used by wildcat (from A to D) and lynx (from E to H): A) Wildcat on a rocky ridge, B) wildcat next to a rocky outcrop that served as a scent-marking site, C) wildcat on the edge of a cliff, D) wildcat on the ridge/edge of a cliff, E) lynx with a kill at the bottom of a karstic depression, F) lynx scent-marking on a rocky outcrop, G) lynx resting on a rocky outcrop, H) lynx moving along a rocky ridge. Photos by Lan Hočevár (A-E), LIFE Lynx project (F and H), and Miha Krofel (G).

2.2. Study species

In the beginning of the 20th century, lynx was exterminated, but reintroduced in 1973. Due to increasing inbreeding levels, the population reinforcement was initiated in 2019 with translocation of 12 lynx from the Carpathian to the Dinaric Mountains (Fležar et al., 2021). Before translocations from the Carpathians, the population density was estimated to 0.51 adult lynx/100 km² in 2019–2020 (Fležar et al., 2023). The main prey of the lynx are wild ungulates, which account for 88% of the biomass consumed by the lynx, with roe deer (*Capreolus capreolus*) being the main prey species (Krofel et al., 2011). In contrast to studies from other regions, lynx in the SDK also frequently feed on the edible dormouse (*Glis glis*), which generally accounts for 7% of the biomass consumed, but frequency of consumption is 27% and 50% for subadults and females, respectively (Krofel et al., 2011).

The distribution and abundance of the wildcat in Slovenia is poorly studied. According to the hunting statistics from the 20th century, the majority of the population seems to be located in the southern part of the country in the Mediterranean and Dinaric Karst region (Kryštufek, 1991; Potočnik, 2006), possibly with recent expansion into the Alps (pers. obs.). The hybridization rate in Slovenia appears to be lower compared to other countries (Urzi et al., 2021). Their feeding habits and diet have not been studied in Slovenia, but in the temperate distribution range they mainly feed on rodents while lagomorphs are mostly absent (Lozano et al., 2006; Ruiz-Villar et al., 2023c). Especially in winter, wildcats also scavenge on ungulate carcasses (Krofel et al., 2021a; Ruiz-Villar et al., 2020), including the prey remains of lynx (pers. obs.).

2.3. Telemetry data

We used GPS-telemetry data from 13 lynx (eight males and five females) tracked between 2007 and 2023 and seven wildcats (six males and one female) tracked between 2020 and 2023 (Table S1) in the Slovenian Dinaric Karst. Animals were captured, collared, and tracked according to standardized protocols (Krofel et al., 2013; Fischer et al., 2024). Nine lynx and all wildcats were captured in the study area, while four lynx were released as part of a reinforcement project (Table S1; Topličanec et al., 2022; Fležar et al., 2021). Lynx

Table 1
Characteristics of predictor covariates used for the analysis of habitat selection by lynx and wildcat.

Covariate	Range (min–max)		Description	Data source
	Lynx	Wildcat		
Topographic (geodiversity)				
Caves	2–4395 m	5–2975 m	Euclidean distance to cave entrances locations. Only the caves whose locations were spatially confirmed by GPS, GPS-RTK, LiDAR or theodolite method were used.	Data from National Cave registry (Cave registry, 2024) provided by the Ljubljana Cave Exploration Society (DZRJL).
Cliffs	0–916 m	0–431 m	Euclidean distance to cliffs (height ≥ 3 m) detected based on the surface slope values (cliffs ≥ 54°; Loye et al., 2009).	LiDAR data (1 × 1 m cell resolution) provided by the Slovenian Environment Agency (ARSO).
Karst depressions	0–2351 m	0–1536 m	Euclidean distance to different types of karst depressions (e. g., dolines, collapse dolines, denuded caves) detected based on the filled DTM method (Čonč et al., 2022b).	LiDAR data (1 × 1 m cell resolution) provided by the Slovenian Environment Agency (ARSO).
Ridges	0–890 m	0–182 m	Euclidean distance to ridges detected based on the Topographic Position Index (TPI) values (ridges ≥ 1; Weiss, 2001).	LiDAR data (1 × 1 m cell resolution) provided by the Slovenian Environment Agency (ARSO).
Small rocky outcrops	0–843 m	0–646 m	Euclidean distance to different types of small rocky outcrops (e.g., rock boulders, karrens, grikes, rocky ridges) with height ≤ 3 m detected based on the approach developed by Čonč et al. (2024) .	LiDAR data (1 × 1 m cell resolution) provided by the Slovenian Environment Agency (ARSO).
Slope	1–56°	3–52°	Mean value of steepness of the slope in the 25 m radius around each location.	LiDAR data (1 × 1 m cell resolution) provided by the Slovenian Environment Agency (ARSO).
Vector Ruggedness Measure (VRM)	0–0.05	0–0.03	Mean value of the terrain ruggedness as the variation in 3-D orientation (Sappington et al., 2007) in the 25 m radius around each location.	LiDAR data (1 × 1 m cell resolution) provided by the Slovenian Environment Agency (ARSO).
Anthropogenic-vegetation				
Forest roads	0–3001 m	0–2985 m	Euclidean distance to (gravel) forest roads.	Data provided by the Surveying and Mapping Authority of the Republic of Slovenia (GURS).
Main roads	0–6270 m	0–3012 m	Euclidean distance to (paved) main roads.	Data provided by the Surveying and Mapping Authority of the Republic of Slovenia (GURS).
Human settlements	0–4276 m	0–2742 m	Euclidean distance to human settlements. To create the layer, we aggregated the floor plans of the buildings into polygons, subject to a maximum distance of 100 m between buildings. Polygons with area less than 300 m² (i.e., scattered buildings) were eliminated.	Data provided by the Surveying and Mapping Authority of the Republic of Slovenia (GURS).
Forest edges	0–2744 m	0–1513 m	Euclidean distance to forest edges. The forest edges are anthropogenic, therefore the variable was included in this group.	Data provided by the Ministry of Agriculture, Forestry and Food (MKGP).

were equipped with GPS-GSM collars (Vectronic Aerospace GmbH, Germany, and TVP Positioning AB, Sweden) and transmitted their locations over a period of 58–1350 days (Table S1), with a frequency of 3–8 GPS locations/day (variable between individuals and time periods; Krofel et al., 2013; Topličanec et al., 2022). The collars of four lynx were programmed to collect only night locations (Čonč et al., 2024). Some individuals were captured multiple times and re-collared to extend the tracking period. Wildcats were equipped with remote-download GPS collars (e-obs GmbH, Germany) and tracked over a period of 21–462 days (Table S1), with a frequency of 1–3 GPS locations/day. The GPS collars of the wildcats were programmed to collect mainly night locations (the GPS collars of three wildcats collected just night locations and four collars collected one location between 7:00 and 10:00 a.m.).

Lynx and wildcat are mainly active during night and twilight and usually rest in the middle of the day (Klar et al., 2008; Jerosch et al., 2010; Krofel et al., 2013; Podolski et al., 2013; Heurich et al., 2014; Filla et al., 2017). Since the lynx day-resting sites selection was already studied (Hočevár et al., 2021; Čonč et al., 2024) and the sample size was too small for wildcats, we only included night locations (from 7:00 p.m. to 7:00 a.m.) in the analyses in order to focus on the active behavioural states (e.g. feeding, movement or foraging).

To consider the selection of features within the areas familiar to the lynx and wildcats, we removed the initial dispersal excursions for translocated lynx (i.e., before the settlement, which was defined as a polygonal movement with the decrease and stabilisation in distance from the release site; Topličanec et al., 2022), and the periods for long-distance mating excursions for lynx and wildcats (when they temporarily leave their territory to find additional mates; Oliveira et al., 2023). We also removed the denning periods of female lynx (birth date and the following 60 days; Dalpiaz, 2023), as their movements during this period are restricted to a smaller area (maternal home range) and could therefore bias our results. For each animal, only the data from the time when it showed site fidelity and settled in a specific area were used to define home ranges and for further analysis.

2.4. Predictor covariates

We considered 11 predictor covariates reflecting topographic characteristics (geodiversity), anthropogenic and vegetation characteristics (Table 1). ESRI software ArcGIS Pro 3.0.3 (ESRI, Redlands, CA, USA) was used to calculate and process the predictor covariates.

Digital terrain model (DTM) with a cell resolution of 1×1 m provided by the Slovenian Environment Agency (ARSO) was used to remotely detect relief features (i.e., cliffs, karst depressions, ridges, and rocky outcrops), and to calculate topographic characteristics (i.e., slope and Vector Ruggedness Measure).

The description of each covariate along with range and data source is provided in Table 1. Their median values with interquartile ranges (IQR) for lynx (all, remnant and translocated individuals) and wildcats are shown in Table S2.

2.5. Data analyses

To investigate how lynx and wildcat select or avoid topographic and anthropogenic features, we applied a use-availability approach at the 3rd order of selection (home range level; Johnson, 1980). We considered as “use” the sample of the GPS night-time locations within the home range, defined as the 90% minimum convex polygons (MCP; Mohr, 1947). We generated twice the number of random locations within the home range for each tracked individual (available sample; Koper & Manseau, 2012). We removed the areas that fell across the Slovenian border (i.e., data in Croatia) from the analyses, because LiDAR-based DTM was only available for Slovenia (see Fig. 1 and Table S1 for details).

To reveal selection patterns by remnant and translocated lynx, we considered a subset of the primary dataset. We classified individuals by their origin (remnant and translocated; Table S1). We also tested if the behaviour of the four translocated lynx changed after they gained experience in the novel environment. For this, we classified them as “naive” (translocated lynx up to one year since they established their new territory after the translocation) and “experienced” (more than a year of living in the new territory; Oliveira et al., 2023). The periods of lynx monitoring are listed in Table S1.

We used RStudio version 2023.09.0 (R Core Team 2023) for evaluating the selection of topographic and anthropogenic features. We first built several generalized linear mixed-effect models (GLMMs) implemented in the package “lme4” v.1.1–30 (Bates et al., 2014), for each species separately. We created a binary response variable, where 0 represents the available sample and 1 represents the used sample. To account for inter-individual variation and unequal sample sizes, we included lynx and wildcat individual ID as random effects (Gillies et al., 2006). We created models with different groups of covariates: topographic predictors only, anthropogenic predictors only, and a combination of topographic and anthropogenic predictors (Table 2). We followed the same procedure to investigate potential differences in selection patterns among different lynx groups (Table 2). We also built null models to evaluate whether the covariates included represented substantial information gain. We ranked the models based on the Akaike’s information criterion (AIC), calculated the Δ AIC per model, and considered the models with lowest AIC value as the best models (Burnham and Anderson, 2004). Before modelling, we rescaled continuous covariates into z-scores by subtracting their mean and dividing by 2 standard deviations (Gelman, 2008) and checked for collinearity between covariates using the variance inflation factor (VIF). If the VIF was above 3 for a given covariate, we did not include it in the model (Zuur et al., 2010). We employed k-fold cross-validation to evaluate model fit (Boyce et al., 2002), with the data randomly split into 80% for modelling and 20% for testing. This process was iterated five times. The Spearman rank correlation was then used to evaluate the relationships between the model ranks and the withheld subsample of data. A strong correlation ($\rho > 0.80$; Boyce et al., 2002) is expected from a well-performing model. To estimate the significant effects (selection or avoidance) of predictor covariates on lynx and wildcat habitat selection, we used the package “sjPlot” v.2.8.15 to plot coefficients with 95% confidence intervals for the best-fit models (Lüdtke, 2023).

Additionally, to find out how frequently lynx and wildcat were in the close vicinity of topographic and anthropogenic features, we compared the percentages of used and available samples within 50 m radius of each feature (Fig. S2).

3. Results

3.1. Lynx and wildcat habitat selection

We considered a total of 14,755 GPS night-time locations from 13 lynx (nine remnant and four translocated) and 3540 GPS night-time locations from seven wildcats (Table S1). For both species, the model that best explained the selection of topographic and anthropogenic-vegetation features included both groups of predictor covariates (Table 2). For models of both species, the cross-validation revealed a very high model fit ($p_{lynx,all} = 0.99$ and $p_{wildcat,all} = 0.97$; Table 2).

Estimated coefficients for the best-fit model for lynx selection indicate that the forest roads and ruggedness (VRM) had the strongest effect. They also selected for vicinity of caves, cliffs, karst depressions, ridges, small rocky outcrops and main roads, but avoided human settlements and forest edges (Fig. 3).

We observed the strongest selection by wildcats for main roads and forest edges. They also selected lower slopes and locations closer to caves and ridges, but avoided cliffs, forest roads and human settlements (Fig. 3).

When comparing the proportions of used and available locations within 50 m of each feature (Fig. S2 and Table S2), for lynx, we found higher proportion of used locations within 50 m of caves, cliffs, karst depressions, ridges, small rocky outcrops and forest roads, with the highest proportions for ridges (83.3%), small rocky outcrops (72.5%) and cliffs (45.0%). Wildcats were mostly near ridges (43.3%), small rocky outcrops (23.6%) and karst depressions (21.1%), but the proportions of used locations were lower for all features compared to the availability (Fig. S2).

Table 2

Generalized linear mixed-effect models explaining lynx and wildcat selection of topographic and anthropogenic features ranked by AIC (Akaike information criterion) values, as well as remnant and translocated lynx. k —number of model covariates, ΔAIC —delta AIC, p —Spearman rank correlation.

Model	Formula	k	AIC	ΔAIC	p
Lynx vs. wildcat					
All lynx					
Topographic and anthropogenic-vegetation	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + 8 + 9 + 10 + 11 + (1 animal_id)$	13	53,738.72	0.00	0.99
Topographic only	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + (1 animals_id)$	9	54,527.36	788.64	0.96
Anthropogenic-vegetation only	used $\sim 8 + 9 + 10 + 11 + (1 animal_id)$	6	54,652.63	913.91	1.00
Null model	used $\sim (1 animals_id)$	2	56,354.60	2615.88	0.52
Wildcat					
Topographic and anthropogenic-vegetation	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + 8 + 9 + 10 + 11 + (1 animal_id)$	13	13,087.46	0.00	0.97
Anthropogenic-vegetation only	used $\sim 8 + 9 + 10 + 11 + (1 animal_id)$	6	13,122.73	35.27	0.94
Topographic only	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + (1 animal_id)$	9	13,365.12	277.66	0.87
Null model	used $\sim (1 animal_id)$	2	13,523.56	436.10	0.52
Remnant vs. translocated lynx					
Remnant lynx					
Topographic and anthropogenic-vegetation	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + 8 + 9 + 10 + 11 + (1 animal_id)$	13	27,458.49	0.00	0.95
Anthropogenic-vegetation only	used $\sim 8 + 9 + 10 + 11 + (1 animal_id)$	6	27,603.66	145.17	0.65
Topographic only	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + (1 animal_id)$	9	27,670.28	211.79	0.72
Null model	used $\sim (1 animals_id)$	2	27,917.69	459.20	0.52
Translocated lynx					
Topographic and anthropogenic-vegetation	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + 8 + 9 + 10 + 11 + (1 animal_id)$	13	25,351.18	0.00	1.00
Anthropogenic-vegetation only	used $\sim 8 + 9 + 10 + 11 + (1 animals_id)$	6	26,115.14	763.96	0.99
Topographic only	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + (1 animal_id)$	9	26,563.32	1212.14	1.00
Null model	used $\sim (1 animal_id)$	2	28,440.91	3089.73	0.52
Naive vs. experienced translocated lynx					
Naive translocated lynx					
Topographic and anthropogenic-vegetation	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + 8 + 9 + 10 + 11 + (1 animal_id)$	13	9628.31	0.00	0.96
Anthropogenic-vegetation only	used $\sim 8 + 9 + 10 + 11 + (1 animals_id)$	6	9900.90	272.59	0.94
Topographic only	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + (1 animal_id)$	9	10,106.12	477.81	1.00
Null model	used $\sim (1 animal_id)$	2	10,804.37	1176.06	0.52
Experienced translocated lynx					
Topographic and anthropogenic-vegetation	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + 8 + 9 + 10 + 11 + (1 animal_id)$	13	15,693.95	0.00	0.98
Anthropogenic-vegetation only	used $\sim 8 + 9 + 10 + 11 + (1 animals_id)$	4	16,205.26	511.31	0.98
Topographic only	used $\sim 1 + 2 + 3 + 4 + 5 + 6 + 7 + (1 animal_id)$	6	16,427.95	734.00	1.00
Null model	used $\sim (1 animal_id)$	2	17,640.53	1946.58	0.52

1—slope, 2—VRM (Vector Ruggedness Measure), 3—caves, 4—cliffs, 5—karst depressions, 6—ridges, 7—small rocky outcrops, 8—forest roads, 9—main roads, 10—human settlements, 11—forest edges

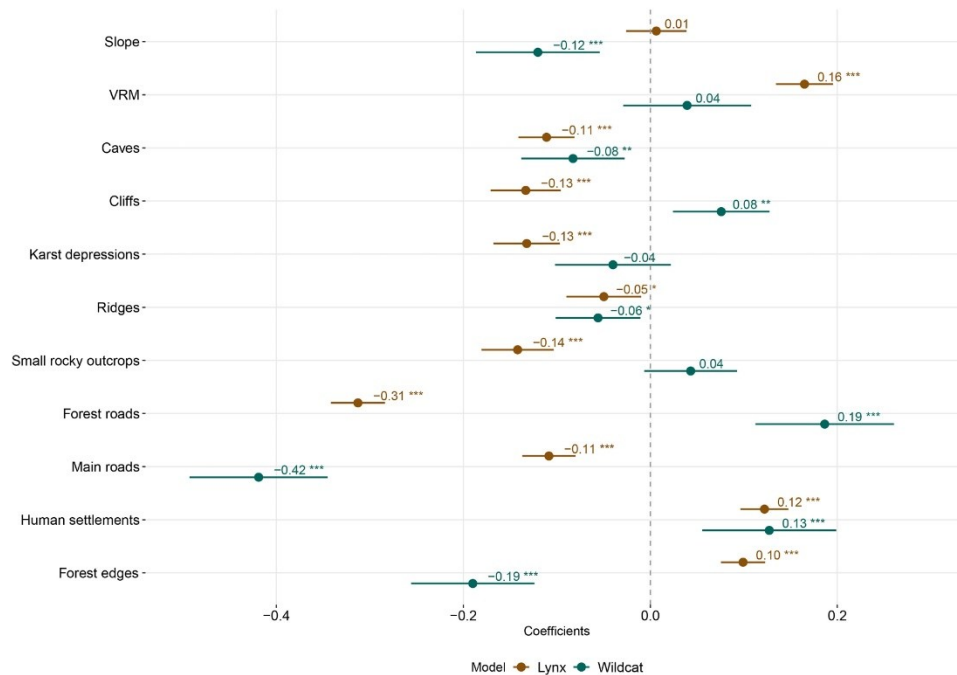


Fig. 3. Estimated coefficients with 95% confidence intervals for the best-fit models for lynx (brown) and wildcat (green) (Table 2). The coefficients indicate either selection or avoidance of a given covariate, where confidence intervals that do not overlap zero (vertical dashed line) indicate significant effects. All covariates except slope and VRM are distance-based, where negative values indicate selection and positive values indicate avoidance.

3.2. Remnant and translocated lynx habitat selection

In order to compare the selection patterns by lynx based on their origin, we considered 7309 GPS night-time locations of nine remnant and 7446 GPS night-time locations of four translocated lynx (Table S1). For both groups, the model that best explained the selection of topographic and anthropogenic-vegetation features included both groups of predictor covariates (Table 2). Cross-validation revealed a very high model fit for remnant ($p_{\text{remnant}} = 0.95$) and translocated lynx ($p_{\text{translocated}} = 1.00$; Table 2).

Overall, we observed similar selection patterns by the remnant and translocated lynx and generally more pronounced selection by the translocated lynx (Fig. 4). The strongest selection by the remnant lynx was for the vicinity of caves, forest roads and main roads. They also selected areas with higher ruggedness, and closer to small rocky outcrops and forest edges, but avoided human settlements. Predictors slope, cliffs, karst depressions and ridges were not statistically significant (Fig. 4). For the translocated lynx, we observed the strongest selection for forest roads and rugged areas. They selected the vicinity of caves, cliffs, karst depressions, small rocky outcrops and main roads, but avoided human settlements and forest edges (Fig. 4).

When comparing the proportions of used and available locations within 50 m of each feature, we observed the similar general patterns between both lynx groups, but again with more pronounced selection among the translocated lynx (Fig. S2 and Table S2).

When comparing selection patterns over time for the translocated lynx, we considered 2828 GPS night-time locations of four naive translocated lynx and 4618 GPS night-time locations of three experienced translocated lynx (for details see chapter 2.5 Data analyses). We did not observe major differences in selection patterns between naive and experienced translocated lynx (Fig. S3). However, the selection pattern was somewhat more pronounced in the experienced lynx for selection for steeper slopes, cliffs, karst depressions, small rocky outcrops and avoidance of human settlements, but less pronounced for selection of rugged areas and forest roads, and avoidance of forest edges (Fig. S3).

4. Discussion

By using automatic methods to analyze high-resolution LiDAR data, we were able to show that lynx selected not only the generally rugged terrain, but also several specific relief features, i.e. geodiversity elements, including caves, cliffs, karst depressions, ridges and small rocky outcrops. We also detected a significant effect of human infrastructure on lynx habitat selection, although with the

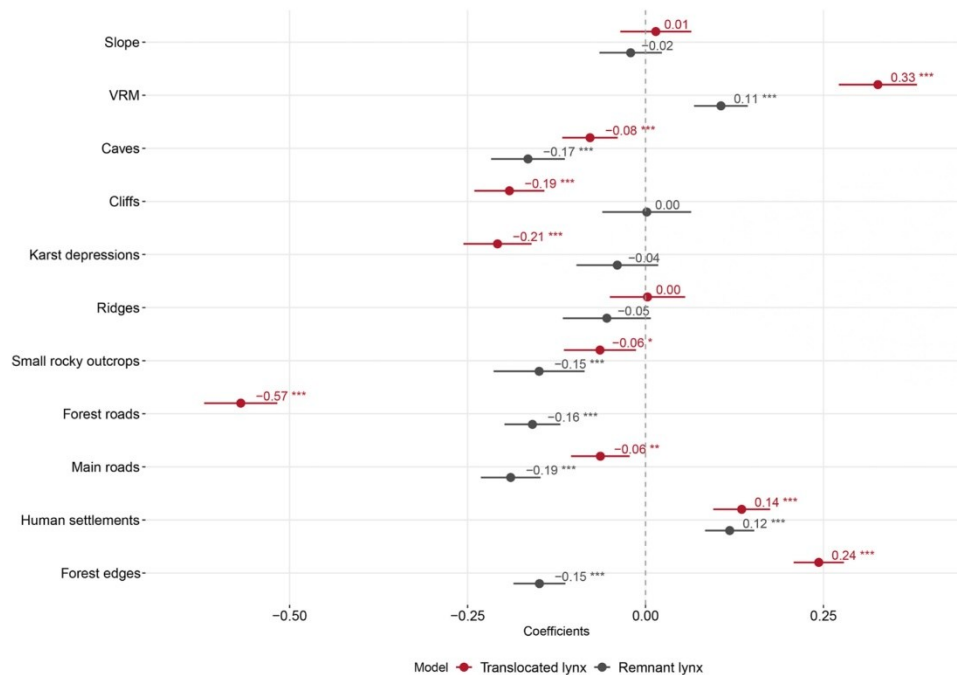


Fig. 4. Estimated coefficients with 95% confidence intervals for the best-fit models for the translocated (red) and the remnant (black) lynx. The coefficients indicate either selection or avoidance of a given covariates, where confidence intervals that do not overlap zero (vertical dashed line) indicate with non-overlapping intervals with zero indicate significant effects. All covariates except slope and VRM are distance-based, where negative values indicate selection and positive values indicate avoidance.

contrasting impact of linear transportation infrastructure (forest and main roads) and human settlements/forest edges. At the same time, this study represents one of the first studies of wildcat habitat selection focused on effects of topography. Although wildcats are generally considered to select similar features as lynx (Potočník, 2006; Čonč et al., 2022b) and sometimes use the same scent-marking sites (Krofel et al., 2022), we observed marked differences in habitat selection between the two species. Our results thus confirm the importance of karst phenomena and other relief features for lynx and wildcat ecology and demonstrate the importance of considering such covariates in habitat selection studies.

Our approach efficiently identified and delineated a large number (>1 million) of studied relief features, such as caves, cliffs, karst depressions, ridges and small rocky outcrops in the study area (Table S3). This underscores the potential of such methodology for conducting large-scale ecological research, as exemplified in our study on habitat selection by wild felids. Undertaking such a task using traditional methods to detect relief features in the field or through manual interpretation of lower-resolution topographic maps would be nearly impossible or would require enormous field efforts. Using this approach in a combination with GPS-telemetry enabled us to conduct one of the first studies on felid habitat selection in respect to fine-scale geodiversity data.

4.1. Lynx habitat selection and geodiversity

Lynx is a stalking and ambush predator, therefore rugged and rocky terrain with abundant and diverse relief features, in addition to the biotic microhabitat characteristics (i.e., vegetation), can provide concealment needed for successful hunting, as well as escape obstacles for ungulate prey (Sunquist and Sunquist, 1989; Krofel et al., 2007; Podgórski et al., 2008; Podolski et al., 2013; Belotti et al., 2013; Čonč et al., 2022a, 2022b). As indicated by snow-tracking, lynx in the Slovenian Dinaric Karst (SDK) while moving frequently step on smaller rocks and rocky surfaces, which are often covered with moss in this area (unpublished data). This enables silent approach and may be particularly relevant in dry weather, when stepping on the leaf-covered ground makes much more noise. Besides, using the top of the cliffs and ridges can provide hunting lynx with easier approach and a good view of the surroundings, which facilitates detection of potential prey or approaching danger (Hočevar et al., 2021). Karst depressions, which are often associated with high terrain ruggedness, rocky outcrops, smaller cliffs, caves and other karst features, appear especially relevant for lynx predation, as almost 60% of lynx prey remains in the SDK were found at such sites (Čonč et al., 2022b). Besides the advantages listed above, snow accumulates at the bottom of dolines during the winter, which further slows down the ungulates during the chase and prevents them to

develop maximum speed (Krofel et al., 2007; 2022a, 2022b). Furthermore, kills located in the dolines might have a lower chance of being detected and removed by kleptoparasites, such as bears, who incur important food losses for the lynx (Krofel and Jerina, 2016). Vertical cliffs in large collapse dolines and on the edges of fluvio-karst river valleys are also preferred habitats of the Alpine chamois (*Rupicapra rupicapra*), which could make them attractive for hunting (Krofel, 2010; Čonč et al., 2022b). Selection of caves could be partly explained by predation on edible dormice, which represents the second most important prey for lynx in the SDK, and is frequently consumed especially by females and subadult lynx (Krofel et al., 2011). At least during the winter period, lynx apparently hunt the dormice while they are hibernating in caves and crevices between rocky outcrops, which are abundant in the rugged and rocky karst landscape (Table S3; Polak, 1997; Krofel, 2010; Krofel et al., 2011).

Relief features, such as rocky outcrops, bases of cliffs, cave entrances and rock shelters also feature prominently among the preferred scent-marking locations of felids (Allen et al., 2017; Mohorović and Krofel, 2020). This is partly explained by their conspicuousness in the landscape, which attracts animal attention and thus increases the probability that scent-marking signal will be detected by the conspecific (Gosling and Roberts, 2001; Vogt et al., 2014). Furthermore, such relief features are often covered with moss, which improves absorption of urine, and include overhangs that provide protection from the weather. Both of these were shown to substantially increase the persistence of the scent and thus improve the efficiency of chemical communication in felids (Mohorović and Krofel, 2020). This suggests that abundance and availability of relief features could also impact the distribution of communication hubs in the landscape and thus influence felid spatio-social systems.

In addition to topographic features, a strong selection was observed for the forest roads. While lynx avoid human infrastructure during the day, at night, when human use of forest roads is negligible, lynx use them selectively for easier movement (Filla et al., 2017; Hočevar et al., 2021; Čonč et al., 2024). In addition, forest roads appear to function as communication hubs, as scent-marking frequency considerably increases, when lynx are walking along these roads (Krofel et al., 2017).

Familiarity with the home range can influence movement and predation by predators, as it was shown also for lynx (Oliveira et al., 2023). We compared habitat selection between the remnant lynx born in the SDK and lynx translocated from the Carpathian Mountains. We observed stronger selection and avoidance patterns among the translocated compared to the remnant lynx. These lynx mainly originated from the landscape with fluvial relief developed in crystalline and metamorphic rocks and flysch bands (De Martonne, 1917; Mráz and Ronikier, 2016). The fluvial relief is characterised by the features such as gorges, river valleys, ridges, and flat slopes, with rocky outcrops generally occurring on river banks and on the edges of larger river valleys and ridges. However, compared to karst landscapes, the fluvial relief is less rugged and rocky, which could make karst relief features and rocky terrain even more suitable and attractive for lynx originating from such terrain (Čonč et al., 2024). The same applies to forest roads, which are less available in the areas from where lynx originated. This is not unexpected, as the study area has a dense network of established human trails (mainly for logging activities) with an average density of about 2 km of forest roads per km² of forest (Krofel et al., 2017), while the density in Romania is 0.62/km² (Cretu and Rusnac, 1996). However, the observed differences might be also related with lower availability of some of the analysed features in home ranges of translocated lynx compared to remnant lynx (Fig. S2), which could partly explain their stronger selection by the translocated lynx, as functional responses in habitat selection have been reported for this species (Oeser et al., 2023; Čonč et al., 2024). We also observed differences in the selection of forest edges, which might be connected with human avoidance (human encounters are probably higher closer to forest edges) and/or hunting (forest edges are preferred habitat for roe deer, which is the main prey for lynx in SDK; Morellet et al., 2011). Overall, lynx are flexible species that inhabit a wide variety of landscape types across their range (von Arx et al., 2021). Also, results on behaviour in the initial post-release period show that translocated lynx establish their new territories on average 23 days after release, suggesting that they familiarise themselves very quickly with new environments (Topičanec et al., 2022).

4.2. Wildcat habitat selection and geodiversity

While lynx clearly selected for rugged areas and features like cliffs, small rocky outcrops and forest roads, wildcats were mostly avoiding them. Wildcats selected for lower slopes, main roads, vicinity of forest edges, caves and ridges. In contrast to lynx, which mostly hunt ungulates (Krofel et al., 2011), wildcats in temperate climates predominantly feed on rodents, especially voles and mice, and other small prey (Lozano et al., 2006; Ruiz-Villar et al., 2023c). There is limited knowledge on the distribution of voles and mice in the SDK, but avoidance of steep terrain and rocky features might be linked with higher rodent abundance in more productive habitats with deeper soil (Niedziałkowska et al., 2010). The second potential explanation for the observed habitat segregation between the two species could be avoidance of intra-guild predation. Lynx are considerably larger than a wildcat and they were occasionally observed killing wildcats (Krofel et al., 2021b; 2022). Thus, by avoiding landscape features selectively used by lynx, wildcats could be reducing risk of predation.

Although wildcats regularly used also cliffs and small rocky outcrops (Fig. S2) and might even select them for specific behaviours (e.g. scent-marking) as indicated by snow-tracking and camera-trapping (Krofel et al., 2022), this study revealed that during their general night activity they avoided them in respect to availability. Our results somewhat differ from previous wildcat study in southeastern Slovenia based on VHF-telemetry (Potočnik, 2006), where selection for steeper slopes and rocky terrain was reported. This could be partly explained by different methodology including lower precision of VHF-telemetry and topographical maps used in the previous study compared to GPS-telemetry and LiDAR DTM that were available here. Additionally, our study area was larger and also included large high karst plateaus, which resulted in different habitat availability that could potentially lead to functional responses in habitat selection. Finally, habitat selection can differ among seasonal and circadian cycles. Our study focused on the active (night) period while data from Potočnik (2006) mostly contained daytime locations, when habitat selection for rocky and rugged areas was more pronounced, which probably reflects needs for security during the resting period (Jerosch et al., 2010). During the winter,

wildcats were also reported to change habitat preferences and more strongly select steeper southwest slopes, where snow cover melts faster (Potočnik, 2006). In such areas small prey could be more easily available as its food is mostly determined by snow cover and temperature which affect its abundance (Trilar, 1991; Strbenc, 2001). As wildcat GPS collars were programmed to mostly collect night-time locations, when wildcats were active, our sample did not allow us to test for potential differences in habitat selection between day and night locations. Thus, wildcat habitat selection warrants further research as selection patterns might considerably vary if accounting for seasonality, activity phases and different behavioural states (e.g. resting, moving, marking), similarly to what was already observed in lynx (Čonč et al., 2024).

In line with the results of previous studies in other European countries (Klar et al., 2008; Jerosch et al., 2018), we observed the selection for the vicinity of forest edges and avoidance of human settlements. This could be explained by the fact that wildcats often hunt rodents on open habitats (i.e., meadows and pastures), along the forest edges and avoid vicinity of human settlements due to various disturbance factors (Klar et al., 2008; Beutel et al., 2017; Jerosch et al., 2018; Ruiz-Villar et al., 2023c). We also observed strong selection for main roads. Unlike in some European countries where they avoided main roads (Klar et al., 2008; Jerosch et al., 2018), the same selection pattern was observed in the Cantabrian Mountains, where wildcats spent significantly more time hunting closer to paved roads (Ruiz-Villar et al., 2024) and potentially also scavenging on road-kills (Ruiz-Villar et al., 2020). Conversely, strong avoidance of forest roads by the wildcats could be connected with avoidance of predation risk, as these anthropogenic linear features are frequently used by the lynx and other large predators (Krofel et al., 2017; Bojarska et al., 2020). However, further studies are needed to clarify to what extent wildcats adapt their habitat use to avoid larger predators (e.g. by comparing habitat selection in areas with and without apex predators). Further research should also include a higher number of females, as our male-biased wildcat sample did not allow us to test for potential for sex-specific differences in wildcat habitat selection, which was observed elsewhere (Oliveira et al., 2018; Ruiz-Villar et al., 2023a).

5. Conclusions

Our study demonstrates the potential of integrating remote sensing techniques and information on geodiversity into wildlife ecology and conservation research. By combining GPS-telemetry data, high-resolution LiDAR DTMs and automatic methods for relief features detection, we were able to confirm species-specific differences in habitat selection among felids in the Slovenian Dinaric Karst and to some degree also between the remnant and translocated individuals.

Furthermore, our results indicate that specific relief features are a crucial part of abiotic microhabitat characteristics and may affect the suitability of a given area for felids, as well as facilitate spatial segregation among sympatric species. Our study highlights the importance of integrating such microhabitat characteristics in habitat selection analyses not only for understanding animal ecology, but also for guiding conservation efforts and decision-making in spatial planning. This includes, for example, introducing restrictions on introducing new infrastructure for transportation and green energy (e.g., wind turbines) or limiting human recreation activities (e.g., hiking, mushroom picking) to already established and marked paths in the felid distribution areas. Our results are also relevant for wildlife management, as they establish that certain relief features might be especially suitable for deploying camera-traps for monitoring or box-traps for capturing animals.

Finally, our study provides further evidence for the importance of protecting relief features (geodiversity) for biodiversity conservation, as various relief features provide important structures for specific felid behaviours (e.g. hunting, scent-marking and movement) and can be also essential habitat for numerous other threatened species (Fitzsimons and Michael, 2017; Tukiainen et al., 2017; Bailey et al., 2018; Signer et al., 2019; Hočevar et al., 2021; Čonč, 2020; Carni et al., 2022; Čonč et al., 2022b; 2024; Gordon et al., 2022; Smith and Mullins, 2022).

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Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03138](https://doi.org/10.1016/j.gecco.2024.e03138).

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SUPPLEMENTARY MATERIALS

Global Ecology and Conservation

Integrating geodiversity in animal spatial ecology: microhabitat selection of Eurasian lynx (*Lynx lynx*) and European wildcat (*Felis silvestris*) in a karst landscape

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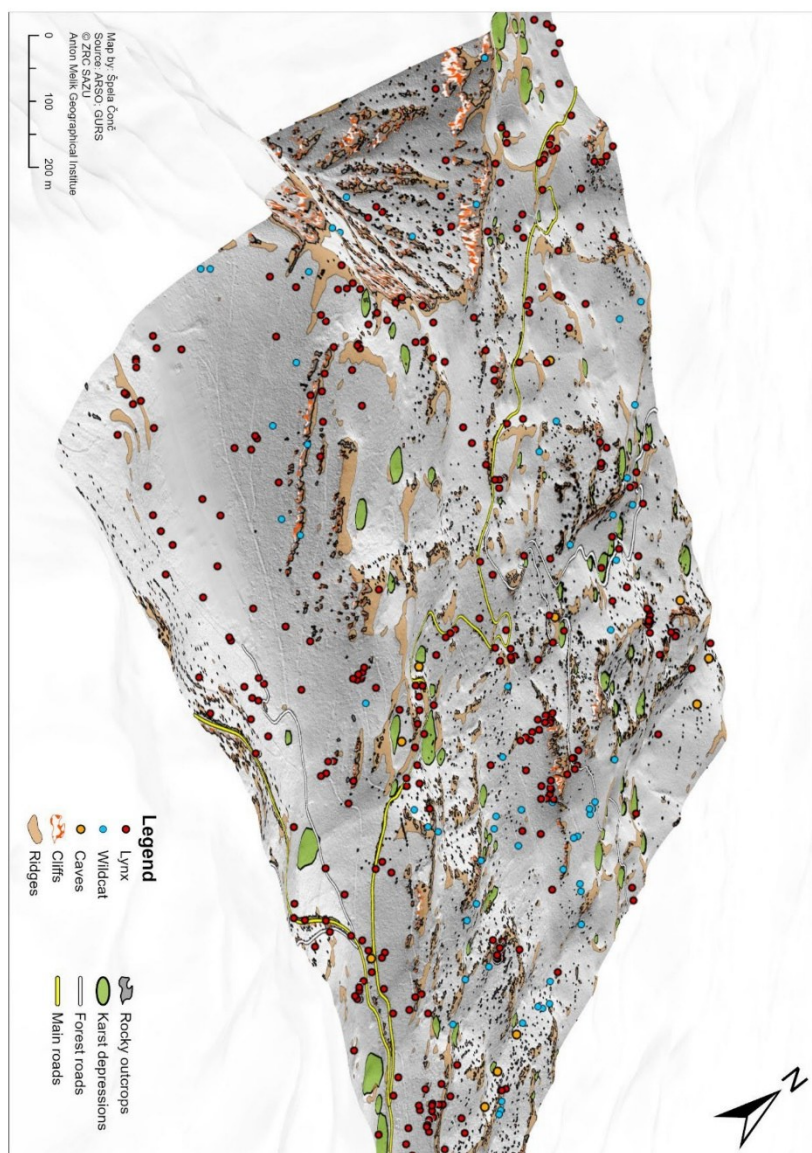


Fig. S1. Example of a 3D scene of lynx and wildcat night locations in Kočevsko region, Slovenia in comparison with geodiversity (caves, cliffs, ridges, rocky outcrops, karst depressions) and anthropogenic features (forest roads and main roads). Based on the map it can be seen that lynx locations are close to cliffs and ridges, as well to karst depressions and main roads. Wildcat locations are more common on flat slopes, further from relief and anthropogenic features.

Table S1. Details on data of 13 lynx and seven wildcats used in this study, * at the beginning of the monitoring, ** area reported for the whole 90% MCP (also for cross-border home ranges), *** was monitored during two non-sequential time periods.

	Lynx/wildcat	Age/sex class*	Origin	Cross-border	Night locations period (no. of days)	No. of night locations	90% MCP area [km] ² **
Lynx	Dina	adult female	remnant	yes	2007/01/02 - 2007/06/05 (154)	80	323.66
	Sneška***	adult female	remnant	yes	2008/02/10 - 2008/10/02 (235) 2010/12/28 - 2011/03/30 (92)	784	121.85
	Mihec	sub-adult male	remnant	no	2011/05/01 - 2011/10/09 (161)	167	85.27
	Maja	adult female	remnant	no	2012/01/28 - 2012/05/26 (119)	213	46.79
	Goru	adult male	translocated (Romania)	no	2019/06/01 - 2022/08/24 (1.180)	2,418	177.85
	Bojan	adult male	remnant	yes	2019/12/01 - 2020/09/16 (290)	56	231.26
	Catalin	adult male	translocated (Romania)	no	2020/04/16 - 2023/12/27 (1,350)	3,196	455.36
	Petra	adult female	remnant	yes	2021/03/01 - 2023/12/19 (1,023)	2,274	198.18
	Bor	sub-adult male	remnant	yes	2022/05/01 - 2023/12/10 (588)	1,365	92.81
	Kliff	adult male	remnant	yes	2022/02/04 - 2023/12/29 (693)	2,209	254.09
	Igi	adult male	remnant	no	2022/02/18 - 2022/04/17 (58)	161	46.12
	Blisk	adult male	translocated (Romania)	yes	2022/06/15 - 2023/12/24 (557)	1,354	164.31
	Sneška	adult female	translocated (Slovakia)	yes	2023/07/01 - 2023/12/28 (180)	478	97.53
	Total					14,755	
Wildcats	Soštica	adult female	remnant	no	2020/12/21 - 2021/09/08 (261)	490	5.04
	Tekumseh	adult male	remnant	yes	2021/03/10 - 2021/08/24 (167)	329	14.63
	Patron	adult male	remnant	no	2021/03/11 - 2022/03/14 (368)	695	8.52
	Xo	adult male	remnant	no	2021/03/16 - 2022/06/21 (462)	1,031	10.34
	Pacho	adult male	remnant	no	2022/08/16 - 2022/09/06 (21)	41	1.50
	Falko	adult male	remnant	no	2022/08/23 - 2022/10/04 (42)	92	4.96
	Rubinho	adult male	remnant	no	2022/09/01 - 2023/10/08 (402)	862	16.90
Total						3,540	

Table S2. Median values with IQR of covariates for available (white) and used (grey) locations for lynx (all, remnant and translocated) and wildcats.

		LYNX						WILDCAT	
		Available - all	Used - all	Available - remnant	Used - remnant	Available - translocated	Used - translocated	Available	Used
Caves (m)		597.73 ± 660.50	495.12 ± 542.50	574.91 ± 587.51	518.70 ± 512.42	621.32 ± 764.09	469.78 ± 565.39	505.44 ± 494.12	563.11 ± 551.83
Cliffs (m)		66.73 ± 93.00	57.23 ± 78.23	50.92 ± 69.65	49.07 ± 67.90	89.11 ± 114.15	66.70 ± 86.50	76.88 ± 102.83	87.35 ± 111.07
Karst depressions (m)		97.11 ± 222.05	84.13 ± 157.67	85.69 ± 163.03	78.25 ± 136.05	116.40 ± 294.56	91.84 ± 179.91	62.41 ± 110.60	65.49 ± 121.12
Ridges (m)		21.15 ± 35.66	16.99 ± 32.85	16.69 ± 27.81	14.41 ± 27.97	27.15 ± 44.64	20.35 ± 38.30	17.27 ± 28.36	19.05 ± 28.27
Small rocky outcrops (m)		32.69 ± 64.46	23.80 ± 44.41	23.17 ± 44.54	20.24 ± 38.03	44.32 ± 85.67	27.60 ± 50.11	35.28 ± 88.05	55.95 ± 132.16
Slope (°)		15.82 ± 10.25	16.92 ± 9.27	17.69 ± 10.07	17.88 ± 9.29	13.96 ± 9.54	15.94 ± 9.07	15.99 ± 8.47	14.63 ± 7.71
VRM		0.0043 ± 0.0042	0.0052 ± 0.0042	0.0053 ± 0.0046	0.0056 ± 0.0044	0.0036 ± 0.0035	0.0048 ± 0.0038	0.0043 ± 0.0035	0.0042 ± 0.0031
Forest roads (m)		235.61 ± 366.60	152.52 ± 274.31	223.43 ± 343.47	186.11 ± 314.99	248.98 ± 386.01	122.46 ± 235.86	217.19 ± 289.97	258.89 ± 292.99
Main roads (m)		729.56 ± 1,152.43	885.05 ± 1,136.96	785.84 ± 1,127.80	770.89 ± 1,035.58	669.15 ± 1,173.77	1,024.59 ± 1,213.27	640.79 ± 800.26	453.44 ± 636.40
Human settlements (m)		923.80 ± 994.82	1,111.20 ± 921.14	1,056.60 ± 1,037.26	1,106.00 ± 970.53	803.00 ± 934.21	1,116.60 ± 874.40	1,140.00 ± 925.20	1,036.40 ± 861.84
Forest edges (m)		225.97 ± 397.71	306.43 ± 474.97	259.99 ± 428.30	240.66 ± 420.15	194.35 ± 366.16	374.09 ± 512.96	357.46 ± 514.38	242.65 ± 436.07

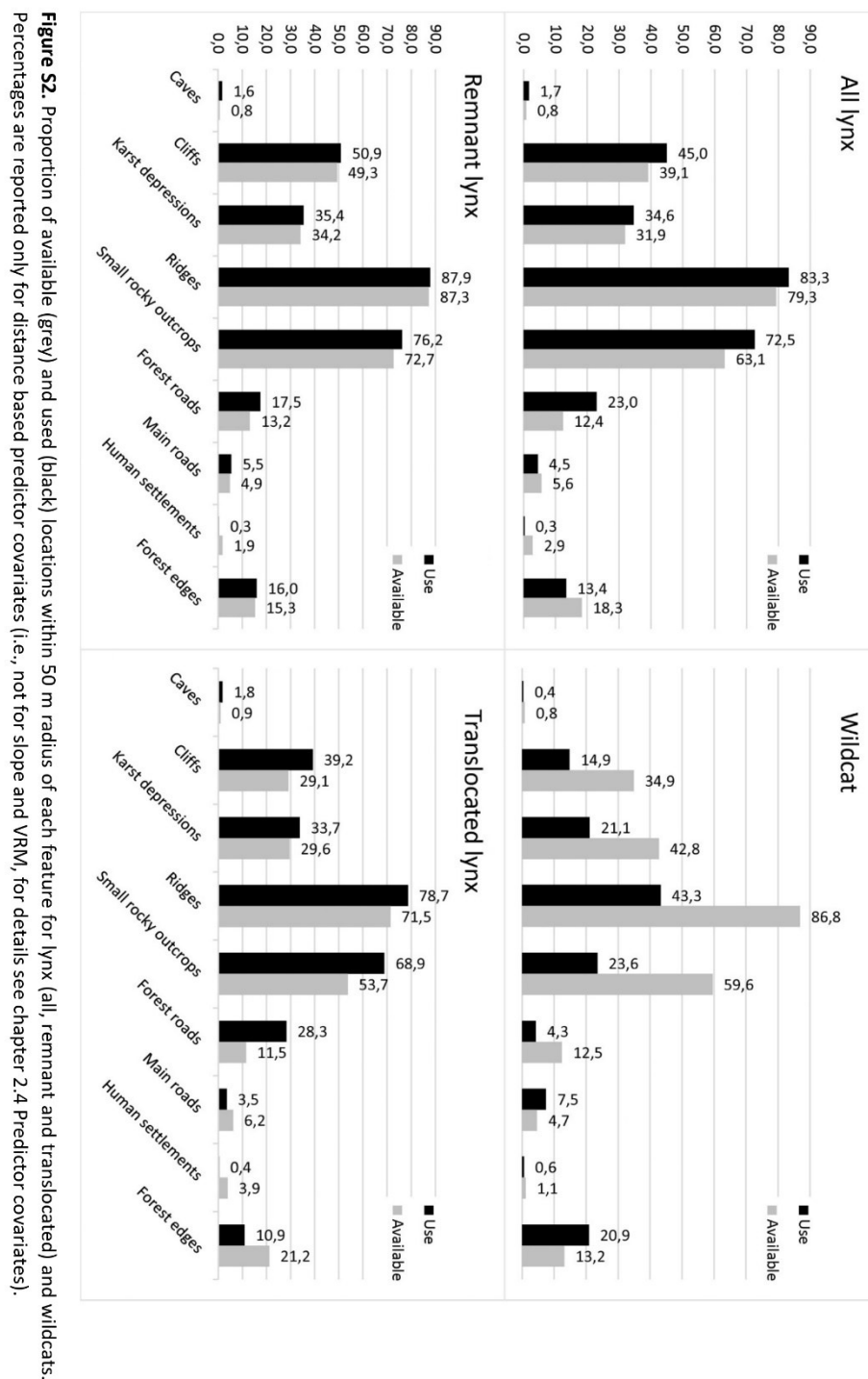


Table S3. Total number and average density of automatically detected relief features in lynx (all, remnant, translocated) and wildcat home ranges in SDK study area.

	All lynx (1,941.1 km ²)		LYNX Remnant lynx (1,046.0 km ²)		Translocated lynx (895.1 km ²)		WILDCAT Wildcats (61.9 km ²)	
	No.	Density (no./km ²)	No.	Density (no./km ²)	No.	Density (no./km ²)	No.	Density (no./km ²)
Caves	1,703	0.9	889	0.8	926	1.0	88	1.4
Cliffs	703,458	362.4	444,885	425.3	281,041	314.0	61,277	989.9
Karst depressions	45,742	23.6	20,543	19.6	26,820	30.0	2,515	40.6
Ridges	210,471	108.4	114,966	109.9	108,644	121.4	10,742	173.5
Small rocky outcrops	1,066,402	549.4	767,829	734.1	364,826	407.6	57,138	923.1

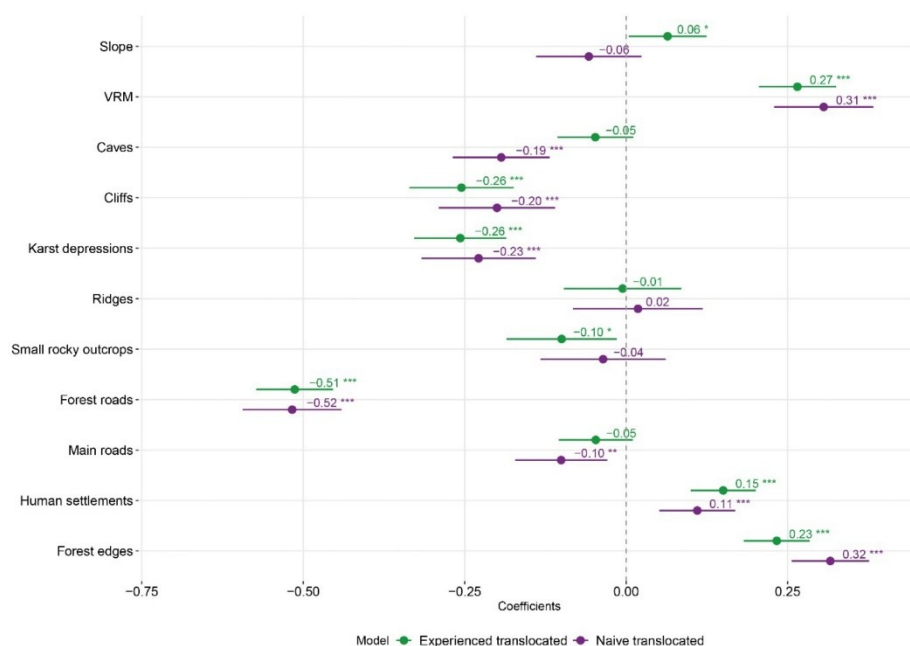


Figure S3. To test if translocated lynx show different selection patterns over time, we compared the selection/avoidance of features for two experience levels. We expected they select relief features even more once they become more familiar with their spatial distribution in their new territories (i.e. category “experienced” - after one year of translocation from the Carpathians to the Dinarics). Results show that experienced lynx avoided a bit more forest roads, human settlements and rugged areas than naive lynx. As well experienced lynx selected less the vicinity of caves, but selected more steep areas and vicinity of cliffs, karst depressions and small rocky outcrops.

2.3 ODKRIVANJE FUNKCIONALNIH ODZIVOV PRI IZBIRI HABITATA EVRAZIJSKEGA RISA (*LYNX LYNX*) GLEDE NA RAZŠIRJENOST IZDANKOV KAMNIN IN RAZGIBANEGA TERENA S POMOČJO LIDAR PODATKOV

Čonč Š., Oliveira T., Belotti E., Bufka L., Černe R., Heurich M., Breg Valjavec M., Krofel M. 2024. Revealing functional responses in habitat selection of rocky features and rugged terrain by Eurasian lynx (*Lynx lynx*) using LiDAR data. *Landscape Ecology*, 39: 121, <https://doi.org/10.1007/s10980-024-01923-y>

Razgiban teren, skalovita območja in izrazite reliefne oblike privlačijo številne zveri. Kljub temu je večina dosedanjih raziskav omejena na vključevanje splošnih topografskih značilnosti habitata in le redke upoštevajo vplive mikrohabitatnih značilnosti. Da bi natančneje raziskali vpliv mikrohabitatnih značilnosti in človeške infrastrukture na izbiro habitata pri velikih zvereh, smo na podlagi letalskih LiDAR podatkov razvili nov pristop za zaznavanje izdankov kamnin in kot modelno vrsto uporabili evrazijskega risa (*Lynx lynx*). V kombinaciji z drugimi tehnikami daljinskega zaznavanja in GPS-telemetričnimi podatki smo ovrednotili izbiro habitata in funkcionalne odzive risa na dveh geološko raznolikih območjih v Evropi. Preverili smo tudi, ali pri izbiri habitata prihaja do funkcionalnega odziva znotraj velikega razpona razpoložljivosti habitata. Zaznali smo več kot milijon izdankov kamnin in potrdili, da jih risi močno izbirajo. Risi so izbirali tudi strma, razgibana in skalovita območja, še posebej pri izbiri dnevnih počivališč. Poleg tega so se risi podnevi izogibali človeškemu potem, ponoči pa so te poti in drugo linearno človeško infrastrukturo izbirali, kar kaže na vedenjsko specifičen vpliv človeške infrastrukture. Opazili smo tudi funkcionalni odziv pri izbiri skalnatih in razgibanih območij, saj se je izbira teh habitatov povečala z manjšanjem njihove razpoložljivosti. To poudarja pomen ohranjanja takšnih območij, zlasti če so v pokrajini redka. Naši rezultati poudarjajo pomen vključevanja tehnik daljinskega zaznavanja in podatkov o mikrohabitatnih značilnosti v raziskave o izbiri habitata pri živalih. Priporočamo tudi pazljivost pri načrtovanju nove infrastrukture za rekreacijo ali spodbujanju njene uporabe v bližini geomorfoloških značilnosti in na razgibanem terenu.

Ključne besede: daljinsko zaznavanje, LiDAR, izdanki kamnin, relief, raba prostora, zveri



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Revealing functional responses in habitat selection of rocky features and rugged terrain by Eurasian lynx (*Lynx lynx*) using LiDAR data

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Abstract

Context Many carnivores are attracted to rugged terrain, rocky areas, and conspicuous relief features. However, most of the previous research is limited to general topographical habitat characteristics and rarely consider the effects of microhabitat characteristics.

Objectives We used the Eurasian lynx (*Lynx lynx*) as a model species to investigate the effects of

microhabitat characteristics and human infrastructure on habitat selection. We also tested whether there is evidence for a functional response in habitat selection across a large gradient of habitat availability.

Methods We developed a new approach for detecting rocky outcrops from airborne LiDAR data. In combination with other remote sensing techniques and GPS-telemetry data, we assessed lynx habitat selection and functional responses across two geologically contrasting areas in Europe.

Results We detected > 1 million rocky outcrops and confirmed their strong selection by lynx. Lynx also

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selected steep, rugged, and rocky areas, especially for day-resting sites. Furthermore, lynx avoided paths during the day but selected them and other linear anthropogenic infrastructure during the night, indicating the behaviour-specific impact of human infrastructure. We also observed a functional response in the selection of rocky and rugged areas, as lynx' selection of such habitats increased with their lower availability. This highlights the importance of preserving such terrains, especially when they are rare in a landscape.

Conclusions Our results highlight the importance of incorporating remote sensing techniques and data on microhabitat features in animal habitat selection research. We also recommend caution when developing new infrastructure for human recreation or promoting its use near geomorphological features and in rugged terrain.

Keywords Remote sensing · LiDAR · Rocky outcrops · Relief · Space use · Carnivores

Introduction

Animal communities and their habitats are shaped by a wide spectrum of biotic and abiotic factors and processes (Hugget 2004; Gordon et al. 2022). Habitats vary in shape and size, ranging from microhabitats to very large megahabitats, in which biota, landscape elements, and geomorphic processes interact and drive animal behaviours at various spatial scales (Johnson 1980; Huggett 2004; Gordon et al. 2022). Besides providing habitat and refugia for plants and animals, microtopography and specific relief features (i.e., geodiversity) may influence the ecology and various behaviours of wild animals, such as their foraging, movement, dispersal, breeding, and resting, which are essential for the survival and persistence of populations (Podgórski et al. 2008; Bouchet et al.

2015; Fitzsimons and Michael 2017; Bailey et al. 2018; Hočevár et al. 2021; Čonč et al. 2022; Smith and Mullins 2022). Large-bodied apex predators require extensive home ranges with good habitat connectivity, which is also important for dispersal that allows gene flow within and among different populations (Premier et al. 2020). Consequently, most studies relating to habitat use, habitat-suitability modelling or habitat connectivity focus on spatial analysis at a large scale: large contiguous natural areas, entire countries or even continents (e.g., Bouchet et al. 2015; Muhly et al. 2019; Ripari et al. 2022; Oeser et al. 2023; Tucker et al. 2023).

Previous research has shown that felids, such as cougars (*Puma concolor*), lions (*Panthera leo*), leopards (*Panthera pardus*), snow leopards (*Panthera uncia*), bobcats (*Lynx rufus*), and Eurasian lynx (*Lynx lynx*) are attracted to rugged and inaccessible terrain, rocky areas, mountain ridges, and conspicuous relief features (Jackson 1996; Dickson and Beier 2007; Bouchet et al. 2015; Abouelezz et al. 2018; Ironside et al. 2018; Farhadinia et al. 2020; Hočevár et al. 2021; Schmidt et al. 2023). However, these studies were usually restricted to single study areas. Consequently, our capacity of understanding the functional responses in habitat selection (i.e., how an individual adjusts their use of a particular habitat characteristic with changes in its availability) is limited (Mysterud and Ims 1998; Holbrook et al. 2019; Oeser et al. 2023). Furthermore, topographical predictor covariates are often limited to general terrain characteristics, such as elevation, ruggedness, and slope. Thus, large-scale studies typically do not consider the impact of microhabitat characteristics, like various relief features (Bailey et al. 2018; Ironside et al. 2018; Čonč et al. 2022). This is mainly due to the lack of detailed GIS layers containing information on such features across larger areas. Until the development of advanced remote sensing techniques, tasks, such as field mapping, digitising relief features, and the quantification of vegetation availability, were time consuming and costly, which resulted in low accuracy and poor data quality (Čonč et al. 2022; Ciglič et al. 2022; Sergeyev et al. 2023). High-resolution data, such as satellite images or LiDAR (Light Detection and Ranging)-based digital terrain models (hereafter DTM), combined with various (semi-)automatic methods for detecting and delineating relief and vegetation features, now enable no-contact, low-cost,

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and accurate mapping of large, remote, and densely forested areas (Bailey et al. 2018; Oeser et al. 2020; Ciglič et al. 2022; Čonč et al. 2022).

Besides the terrain characteristics, anthropogenic impacts can also have an important influence on animal behaviour and habitat selection, especially in human-dominated landscapes (Filla et al. 2017; Muhly et al. 2019; Ripari et al. 2022; Tucker et al. 2023). Although many large carnivores inhabit remote and/or protected natural areas, human recreational activities and infrastructure development have also increased in such areas during the past decades (Belotti et al. 2012, 2018; Muhly et al. 2019). Human infrastructure can have a positive or negative impact on animals. Specifically, during the day, when human disturbance is generally higher, animals tend to avoid human infrastructure. However, at night, when the disturbance is reduced, carnivores may be attracted to anthropogenic features, for example for scent marking, looking for prey or moving through the territories (Filla et al. 2017; Krofel et al. 2017; Muhly et al. 2019; Tucker et al. 2023). Additionally, animals often use abandoned human-modified areas, for example old quarries or artificial tunnels (Davis 1979; Marchewka and Postawa 2022); thus, human infrastructure could also be understood or interpreted as anthropogenic landforms (Li et al. 2017).

In the past, conservation and wildlife research focused primarily on biotic elements or general topographical characteristics, which limited our understanding of the importance of fine scale geodiversity (Albano 2015; Bailey et al. 2018; Gordon et al. 2022). However, microhabitats can facilitate carnivore adaptation to human pressure, providing cover for resting, and hosting prey species (Podgórski et al. 2008; Oeser et al. 2023). Understanding the relationship between spatial patterns, landscape heterogeneity, and ecological processes is crucial (Turner and Gardner 2015; Hersperger et al. 2021). Therefore, microhabitat characteristics, as well as specific relief features, should be incorporated in studies focusing on habitat selection, habitat connectivity and habitat suitability modelling, by including microhabitat data at finer scales.

To investigate the impact of rocky relief features (i.e., cliffs, rocky blocks, rocky ridges, karrens, and similar rocky features; hereafter 'rocky outcrops'), as well as other abiotic microhabitat characteristics and human infrastructure on the Eurasian lynx

(hereafter lynx) habitat selection, we selected two geologically and (bio-)geographically contrasting areas in Europe: the Slovenian Dinaric Karst (carbonate karst) and the Bohemian Forest Ecosystem (fluvial, glacial, and periglacial relief). We used the lynx as a model species due to their widespread distribution, general attraction to rugged and rocky terrain, and the importance of several relief features for their behavioural ecology (Krofel et al. 2007, 2017; Allen et al. 2017; Signer et al. 2019; Hočevár et al. 2021; Čonč et al. 2022; Schmidt et al. 2023). Similar to research on most other large carnivores, the majority of these studies on lynx habitat use have relied almost exclusively on a limited amount of data on microhabitat characteristics obtained in the field or by digitising relief features. Our main goals were to explore lynx selection of rocky outcrops as well as rugged and rocky terrain and to test for evidence of a functional response in lynx selection across a large gradient of availability of such terrain. To our knowledge, our study is one of the first that primarily relies on remote sensing data to identify detailed and accurate information on the microhabitat characteristics and studied relief features over a large area.

To examine how lynx select rocky outcrops and other abiotic microhabitat characteristics, as well as human infrastructure within their home ranges, we (1) developed a semi-automatic approach for identifying and delineating rocky outcrops from high-resolution LiDAR data and (2) evaluated the selection of these features by lynx in respect to their availability. To account for different behavioural states of lynx activity, we evaluated the selection under a used-available approach for two different behavioural states: day-resting sites, when lynx are typically resting on daybeds, and night locations, when lynx are engaged in various active behaviours (e.g., movement, foraging, territorial marking; Heurich et al. 2014; Hočevár et al. 2021). We tested the following hypotheses:

H1 Lynx select rocky outcrops, rugged terrain, and rocky surfaces during the day and at night.

H2 Lynx avoid the vicinity of human infrastructure (e.g., forest roads, paths, scattered buildings, and roads) for day-resting sites but select it during the nighttime.

H3 The selection of topographic features and avoidance of anthropogenic features is more pronounced during the day than at night.

H4 Lynx exhibit a functional response in selecting rocky outcrops, rugged terrain, and surface rockiness, with a stronger selection when availability is lower.

Study area

Dinaric Karst (Slovenia)

The Slovenian Dinaric Karst (hereafter SDK) is a karst landscape in the west and south of Slovenia (Fig. 1) formed on Mesozoic and Cenozoic rocks, mainly limestone and dolomite. Geographically

and geologically, it is part of the Dinaric Mountains (Mihevc et al. 2010). The SDK is characterised by high and low karst plateaus, corrosion plains, and karst poljes running in a distinctive Dinaric direction (NW–SE), as well as by diverse surface and subsurface features (Mihevc et al. 2010; Zorn et al. 2020). In terms of lithology, karst types are divided into limestone karst and dolomite karst. Limestone karst exhibits a high density of caves, conical hills, karrens, and karst depressions (e.g., solution and collapse dolines). Dolomite karst, or fluviokarst, is characterised by dry shallow valleys, or delts, while other typical (sub)surface karst features are less common than in limestone karst (Zorn et al. 2020). The elevation in the study area ranges from about 200 to 1800 m.

The SDK is known for dense forests, mainly Dinaric fir-beech associations (*Omphalodo-Fagetum*),

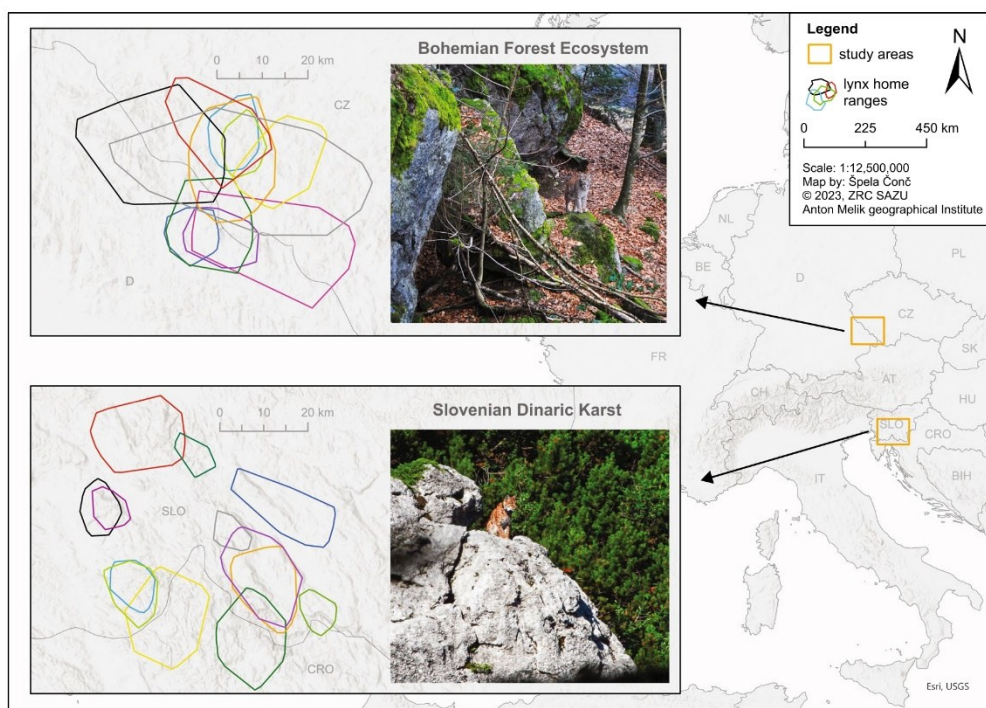


Fig. 1 Map of the lynx home ranges in two selected study areas: the Slovenian Dinaric Karst (SDK) and Bohemian Forest Ecosystem (BFE) with lynx on rocky outcrops. Because some of the home ranges of lynx in the SDK included areas

that were outside the study area, where LiDAR data were not available (i.e., Croatia), we included only the locations within the study area (Slovenia) in the analysis. Photos by ŠČ and MK

extensive livestock farming, logging, hunting, and scattered small human settlements usually located in larger levelled areas, such as karst poljes or low karst plateaus (Mihevc et al. 2010). Around 20% of all hiking paths in Slovenia are located in the SDK region (Cigale and Gosar 2018), with the area around Snežnik being particularly popular. An average of 10 crossings/day (peaking at 161 crossings/day) were observed on the educational path, with the highest intensity on weekends and during the summer (Koželj et al. 2021). The area also has a dense network of forest roads (approximately 2 km of forest roads/km²) that were primarily established for logging activities (Krofel et al. 2017), but this infrastructure is frequently used for tourism and recreation as well (Potočnik 1996). In the Snežnik area, an average of 39 vehicles/day crossed the main roads, while the crossing on the forest roads was lower with an average of 10 vehicles/day. The intensity of traffic is highest on weekends and in the summer months (Koželj et al. 2021). Other human recreation activities are concentrated in and around famous tourist areas and natural landmarks (Cigale and Gosar 2018), mostly located on karst poljes.

Lynx were exterminated at the beginning of the twentieth century, but were reintroduced in 1973 and their current density is estimated to be 0.51 lynx/100 km² (Fležar et al. 2023a). The main prey of the lynx are wild ungulates, which account for 88% of the biomass consumed by lynx, with roe deer (*Capreolus capreolus*) being the main prey species (Krofel et al. 2011).

Bohemian forest ecosystem (Germany and Czech Republic)

The Bohemian Forest Ecosystem (hereafter BFE) encompasses the Bavarian Forest National Park (240 km²) and a surrounding Bavarian Forest Natural Park (3007 km²) in Germany, and the Šumava National Park (690 km²) and the Bohemian Forest Protected Landscape Area (~ 1000 km²) in the Czech Republic (Fig. 1). It is one of the largest strictly protected forest areas in Central Europe (Navrátil et al. 2014; Heurich et al. 2015).

The BFE encompasses a fault-block mountain range on the border between Germany and the Czech Republic. Geographically and geologically, the BFE is part of the Bohemian Massif, which consists of Variscan

igneous and metamorphic rocks, mainly gneiss and granite (Baburek et al. 2006; Krause and Margold 2019). The BFE mountains were glaciated during the Pleistocene cold periods, resulting in the development of glacial features, such as cirques, cliffs, short glacial valleys, moraines, erratic blocks, and glacial lakes (Hauner et al. 2019; Krause and Margold 2019). It is also characterised by a fluvial relief, resulting in features such as gorges, river valleys, ridges, alluvial plains, cascades, and different sizes and shapes of rocky features. The elevation in the study area ranges from 600 to 1450 m.

The most common tree species at higher elevations is Norway spruce (*Picea abies*), complemented by mountain ash (*Sorbus aucuparia*). At lower elevations Norway spruce, European beech (*Fagus sylvatica*), and silver fir (*Abies alba*) are most common (van der Knaap et al. 2020).

The area is characterised by extensive land use and a low population density with <2 people per km² in the core area and 30–70 people per km² in the peripheral areas (Heurich et al. 2015). In the national parks, the main human activities are related to recreation (e.g., hiking, cycling, horse-back riding, mushroom picking). In their core zones, such activities are only permitted on marked paths (Belotti et al. 2018). Recreation intensity is highest at weekends, peaks in July–August, and is concentrated during light hours. A maximum of around 5300 visitors/day and a total of around 1,840,000 people/year were counted at the main recreation sites of the national parks. The number of daily visits varies considerably between sites (Seibold and Shao 2014; Porst et al. 2020). Recreation in the peripheral areas is less intensive and human activities are more strongly associated with transportation, forestry and agriculture (Seibold and Shao 2014; Belotti et al. 2018).

In 2018, the density of the lynx population in BFE was estimated to be 1.33 lynx/100 km² (Palmero et al. 2021). Roe deer accounts for up to 80% of the animals killed by lynx (Belotti et al. 2015).

Materials and methods

Rocky outcrops detection

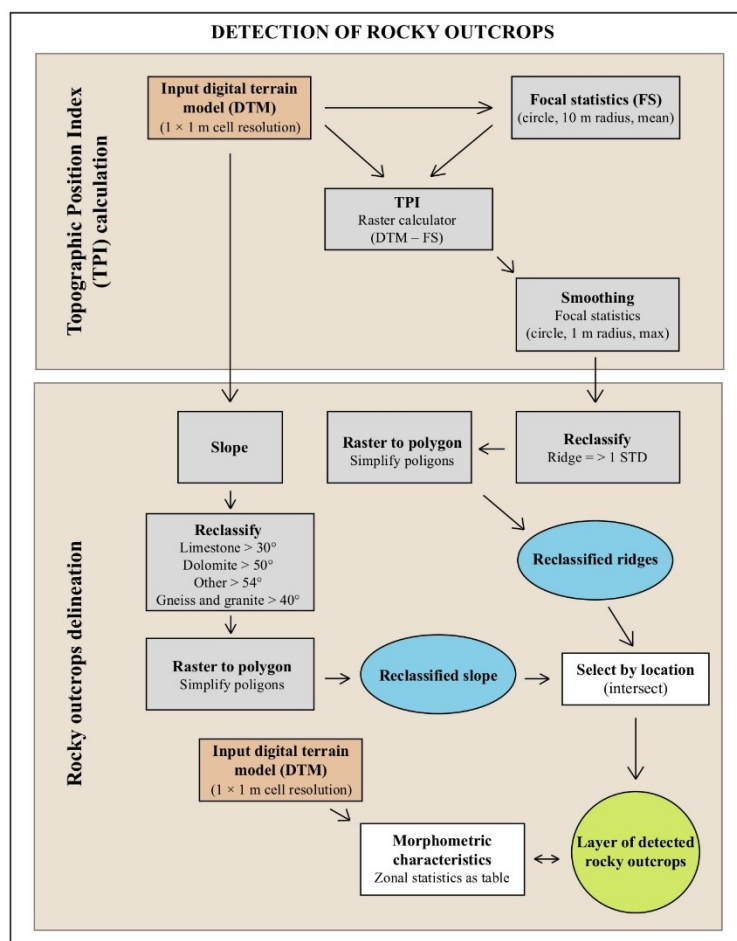
Geological features that protrude above the surface of the surrounding land are defined as rocky outcrops (Twidale 2000). They are characterised by higher

steepness, spatial isolation, and in many cases represent relatively undisturbed natural habitats. They occur in different bedrock and landscape types and form landscape features that vary in size and shape (examples shown in Fig. S1; Fitzsimons and Michael 2017; Smith and Mullins 2022).

Existing methods for the automatic detection of rocky outcrops are mostly based on satellite images (Kwok et al. 2018), which can cause rocky outcrops under forest canopy to be overlooked, or on the delineation from DTM based only on slope values (Smith and Mullins 2021), which can miss small outcrops on flat areas or misinterpret rocky outcrops as

steep (soil-)covered slopes. Therefore, we developed a new two-step approach for the quantitative detection of rocky outcrops (Fig. 2) based on the spatial analysis of a high-resolution DTM (1 m × 1 m) and field measurements of the morphographic and morphometric characteristics of rocky outcrops. To create a DTM, we used LiDAR data from aerial laser scanning that was available in the form of a cloud of ground points (LAS files) provided by the Slovenian Environment Agency, the Bavarian Land Survey, and the administrations of Šumava National Park and Bavarian Forest National Park. The estimated density of the ground points in BFE is 55 points/m², while the

Fig. 2 Flowchart of rocky outcrop detection. The grey boxes represent tools for raster analyses and raster layers, and the blue ovals represent vector layers



density in the SDK is considerably lower with an estimation of 0.5 per m² in forested areas, respectively (Triglav Čekada and Bric 2015; Krzystek et al. 2020). We used ESRI software ArcGIS Pro 3.0.3 (ESRI, Redlands, CA, USA) to detect the rocky outcrops.

The *Topographic Position Index* (TPI; Weiss 2001) can be used to determine flat, concave (valleys), and convex (ridges) areas. Since rocky outcrops protrude above the surface of the surrounding land and are convex in shape, we identified all the convex-shaped areas in the first step. To calculate the TPI, we used the elevation for each cell (input DTM) and subtracted it by the mean elevation of the neighbouring cells (calculated by the *Focal Statistics* tool; Weiss 2001; Fig. 2). We tested different thresholds (5 m, 10 m, 15 m, 20 m, and 25 m) and found the 10 m search radius to be the most suitable for detecting convex features of different sizes (Čonč and Breg Valjavec 2023). Bigger ridges tend to be missed at lower thresholds, while smaller ridges are missed at higher thresholds (Weiss 2001). In the next step, we used the slope values of the rocky outcrops measured in the field as an additional criterion for rocky outcrop detection. Specifically, we measured the slope values between the lower and upper part of the rocky outcrops to determine the average slope values at which bedrock protrudes from the surface. In the SDK, the bedrock in areas with limestone outcropped at a lower surface slope (30°) than in areas with dolomite (50°) or other bedrock types (54°). In BFE (gneiss and granite), the bedrock outcropped at a surface slope of 40°. Based on the DTM (1 m × 1 m), we calculated *Slope* and assigned it to the slope categories determined in the field. We used the *Select by Location* tool to delineate the ridges (i.e., convex relief features) in each geological unit (limestone, dolomite, other, gneiss and granite) that overlapped with the determined slope values as rocky outcrops. In the final step, we calculated the heights of the rocky outcrops.

To assess the accuracy of the developed approach for rocky outcrop detection, we compared the results of the semi-automatically detected rocky outcrops with the *Sky-View Factor* layer for surface visualisation, created from a DTM (Zakšek et al. 2011), topographic maps, and field-mapped rocky outcrops (164 mapped in the SDK and 133 in BFE).

Lynx habitat selection in respect to rocky outcrops

Telemetry data

We used GPS-telemetry data from a total of 22 lynx (14 males and eight females; Table S1), with 12 lynx (eight males and four females) captured and collared between 2006 and 2023 in the SDK and 10 lynx (six males and four females) from the BFE captured between 2005 and 2012 (Table S1). Standardized protocols were used to capture, collar, and track the lynx (Heurich 2011; Krofel et al. 2013; Belotti et al. 2015). In both study areas, the animals were equipped with GPS-GSM collars (Vectronic Aerospace GmbH, Germany and TVP Positioning AB, Sweden; for details, see Heurich 2011; Krofel et al. 2013 and Topličanec et al. 2022). The GPS collars had an accuracy of 4–16 m, depending on habitat type (Stache et al. 2012). Some individuals were captured multiple times and recollared to prolong the tracking period.

In the SDK, nine residential lynx were captured in the study area and three lynx were released as part of a reinforcement project (Topličanec et al. 2022; Fležar et al. 2023b). The collars transmitted the lynx' locations over a period of 1.9 to 38.1 months (Table S1) and were scheduled to obtain 3–8 GPS locations per day (variable among individuals and time periods) (Krofel et al. 2013; Topličanec et al. 2022).

The collars in the Bohemian Forest Ecosystem transmitted locations over a period of 3.5–18 months (Table S1) and were scheduled to store two locations daily. In addition, the collars recorded one location per hour every second week from 15:00 to 7:00 the following day, and two additional locations per day were recorded at dusk and dawn for a period of one month in each season of the year (Belotti et al. 2015; Filla et al. 2017). Prior to the analyses, we performed quality controls and scanned all the GPS data. Specifically, we detected and removed locations that indicated the collar malfunctioning, such as duplicated locations, locations falling in impossible places (e.g., large water bodies), or locations with a low degree of reliability (e.g., a very large distance between two consecutive points in a short amount of time).

Detection of behavioural states

The dataset contained 19,230 GPS locations, with each individual contributing between 61 and 2583

locations (Table S1). To differentiate between the behavioural states (e.g., resting, feeding, moving, searching for food) and phases (night and day) of lynx activity, we divided the data into two different categories: day-resting sites and night locations. A two-step approach was used to define the day-resting sites. Specifically, since lynx are primarily active during the night and twilight and generally rest in the middle of the day (Podolski et al. 2013; Heurich et al. 2014; Filla et al. 2017), we defined the daytime locations (9:00 a.m. to 3:00 p.m.) as potential day-resting sites. To confirm inactivity, we used activity data from built-in accelerometers for 14 lynx as a second criterion (Signer et al. 2019; Hočevár et al. 2021). Activity data with values of 0–11% of maximum activity were considered as corresponding to the resting behaviour (Heurich et al. 2014; Hočevár et al. 2021). In cases where multiple locations were recorded for the same individual during the daytime period on the same day, the location with the lowest activity value was included in the analysis, and in cases where no activity data was available, we considered the GPS location with the closest time to noon as a day-resting site. We classified GPS locations during the high-activity phase as night locations (from 7:00 p.m. to 7:00 a.m.) (Heurich et al. 2014).

To account for lynx selection of familiar habitat (i.e., within their home ranges – 95% MCP), we removed the periods of long-distance mating excursions (i.e., the period when they temporarily left their territory to find additional mates; Oliveira et al. 2023) and periods for females during the denning period (birth date and the following 60 days; Mattisson et al. 2022; Dalpiatz 2023). Furthermore, we removed the periods of the initial exploratory excursions for translocated lynx (i.e., the period before they established their territories; Topličanec et al. 2022).

Predictor covariates

We used 11 predictor covariates to test for the selection or avoidance of habitat features by lynx and categorised them into two groups: topographical and human infrastructure (Table 1). All the covariates were mapped and processed in ArcGIS Pro. The data for calculating the predictor covariates were provided by the Slovenian Environment Agency (ARSO-Agencija RS za okolje), the administrations of Šumava National Park and Bavarian Forest National Park,

the Bavarian Land Survey (Bayerisches Vermessungsamt), OpenStreetMap (<https://www.openstreetmap.org>), the State Administration of Land Surveying and Cadastre (ZABAGED, ČÚZK-Český úřad zeměměřický a katastrální), and the Surveying and Mapping Authority of the Republic of Slovenia (GURS-Geodetska uprava RS; Table 1).

Within the topographical features, we obtained elevation data with a cell resolution of 1×1 m in the form of a LiDAR-DTM. Based on the DTM, we further calculated the aspect, rocky outcrops, slope, Topographic Position Index (TPI; Weiss 2001), and Vector Ruggedness Measure (VRM; Sappington et al. 2007). For the aspect, slope, and VRM, we calculated the mean values of the raster layers within a 25 m buffer of each point. We used a 25 m buffer to account for the GPS measurement error (Stache et al. 2012) and to consider the characteristics of the close proximity of lynx locations. We considered rocky outcrops as two different predictor covariates: the distance to the closest rocky outcrop (with a height ≥ 3 m; Signer et al. 2019) and surface rockiness based on the calculation of the share of area of (all) rocky outcrops within a 25 m buffer around each location.

Since lynx habitat selection is known to be influenced by the presence of human activities (Filla et al. 2017; Ripari et al. 2022; Oeser et al. 2023), we also included covariates describing human infrastructure in the analysis. We calculated the distances from scattered buildings and transportation infrastructure. Scattered buildings (e.g., forest cabins, which are regularly used for scent-marking by lynx; Allen et al. 2017) included buildings within categories 3–5 of the Corine Land Cover (CLC) data provided by the European Environment Agency that are at the same time at least 200 m away from the 1st and 2nd category of CLC. We divided transportation infrastructure into three categories: forest roads, paths, and transport infrastructure (Table 1). We grouped paths used for hiking, cycling, horse riding, and similar as paths, while the transport infrastructure layer included all other major roads and railways. The mean values with a standard deviation and the median values with interquartile ranges of covariates for used and available locations by both study areas are shown in Table S2.

Table 1 Characteristics of predictor covariates used for the analysis of habitat selection by lynx in the SDK and BFE

Covariate	Type	Range or categories of all locations		Description and *data source
		Slovenian Dinaric Karst	Bohemian Forest Ecosystem	
Topographical characteristics				
Altitude	Continuous	194–1796 m	474–1455 m	Elevation above the sea level ^{a,c}
Aspect	Categorical	North: 315–45° East: 45–135° South: 135–225° West: 225–315°		Mean value of the aspect in a 25 m buffer around each location indicating the compass direction the surface faces at that location ^{a,c}
Rocky outcrops	Continuous	0–497.73 m	0–1392.30 m	Distance to different types of rocky relief features, such as cliffs, rock boulders, karrens, rocky ridges with a height ≥ 3 m ^{a,c}
Slope	Continuous	1.66–51.24°	0.02–43.85°	Mean value of steepness of the slope in a 25 m buffer around each location ^{a,c}
Surface rockiness	Continuous	0–68.16%	0–58.51%	Share of area of (all) rocky outcrops in a 25 m buffer around each location ^{a,c}
Topographic Position Index (TPI)	Continuous	– 57.79 to 56.32	– 14.19 to 18.21	Terrain classification of features, such as flat area (value around 0), valley (large negative value), ridge (large positive value) ^{a,c}
Vector Ruggedness Measure (VRM)	Continuous	0–0.30	0–0.10	Terrain ruggedness as the variation in 3-D orientation of grid cells within a neighbourhood calculated as mean value in a 25 m buffer around each location (0 represents flat and 1 represents most rugged) ^{a,c}
Human infrastructure				
Forest roads	Continuous	0–3001.09 m	0–708.95 m	Distance to forest roads ^{a,b,c}
Paths	Continuous	0–6949.03 m	0–4371.46 m	Distance to hiking, cycling, horse riding, and similar paths ^{a,b,c}
Scattered buildings	Continuous	34.29–6408.89 m	1.18–6009.61 m	Distance to scattered buildings ^{a,c,c}
Transport infrastructure	Continuous	0–6596.92 m	0.90–5274.34 m	Distance to major roads and railways ^{a,b,f}

^aSlovenian Environment Agency (ARSO-Agencija RS za okolje)

^bThe administrations of Šumava National Park and Bavarian Forest National Park

^cBavarian Land Survey (Bayerisches Vermessungsamt)

^dState Administration of Land Surveying and Cadastre (ZABAGED, ČÚZK-Český úřad zeměměřický a katastrální)

^eSurveying and Mapping Authority of the Republic of Slovenia (GURS-Geodetska uprava RS)

^fOpenStreetMap (<https://www.openstreetmap.org>)

Data analyses

We analysed lynx selection of topographical features and human infrastructure at the 3rd order of habitat selection, i.e., the home-range level (Johnson 1980). Specifically, we used a use-availability approach to compare a used sample (i.e., day -resting sites and night locations) with the available habitat (sample of random locations, see below for details) within 95% minimum convex polygon (MCP) home ranges for each individual lynx. As the home ranges of some lynx in the SDK included areas outside the study area (their home ranges extend across the Slovenian-Croatian border), we considered only the locations within the study area for which LiDAR-based topographical data were available.

We estimated the availability using a systematic approach (Benson 2013), by sampling points at a 100×100 m resolution, created with ArcGIS Pro 3.0.3. We set a value of 100 m based on the GPS locations resolution (see Sect. "Telemetry data" and "Detection of behavioural states") and a high density of rocky outcrops, especially in the SDK study area (Benson 2013).

To test the first three hypotheses (H1–3), we built generalized linear mixed-effect models (GLMMs) implemented in the R (R Core Team 2023) package "lme4" v.1.1–30 (Bates et al. 2015) with a binary (0=available, 1=used) response variable (Table 2). Lynx IDs were included as random effects to account for interindividual variation and the uneven sample size (Gillies et al. 2006). We built models with different groups of covariates considering their potential influence on the selection of topographical features and human infrastructure by lynx for both behavioural states (Table 2). We ranked the models based on the Akaike information criteria (AIC) and calculated the ΔAIC per model. We considered the models with ΔAIC values < 2 as the best models (Burnham and Anderson 2002). We also included a null model to test the strength of our hypothesis and the importance of the chosen covariates. We used *k*-fold cross-validation to assess model fit (Boyce et al. 2002) and randomly split the data into 80%/20% for modelling and testing, respectively. We repeated this procedure five times (*k*=5) and then used the Spearman rank correlation to evaluate the relationships between the model ranks and the withheld subsample of the data. A well-performing model is expected to demonstrate

Table 2 Logistic regression models explaining the habitat selection of day-resting sites and night locations. *k*—number of model covariates, AIC—Akaike information criterion, ΔAIC —delta AIC, *p*—Spearman rank correlation

Model description	Formula ^a	<i>k</i>	AIC	ΔAIC	<i>p</i>
Day-resting sites (habitat selection—H1, H2, H3)					
All the covariates affect lynx day-resting site selection	Used ~ 1 + 2 + 3 + 4 + 5 + 6 + 7 + 8 + 9 + 10 + 11 + (1 lynx ID)	13	25,836.36	0.00	0.97
Only topography affects lynx day-resting site selection	Used ~ 1 + 2 + 3 + 4 + 5 + 6 + 7 + (1 lynx ID)	9	25,857.91	21.55	0.92
Only human infrastructure affects lynx day-resting site selection	Used ~ 8 + 9 + 10 + 11 + (1 lynx ID)	6	27,390.91	1554.55	0.05
None of the covariates affect lynx day-resting site selection	Used ~ (1 lynx ID)	2	27,433.46	1597.10	0.52
Night locations (habitat selection—H1, H3)					
All the covariates affect lynx night location selection	Used ~ 1 + 2 + 3 + 4 + 5 + 6 + 7 + 8 + 9 + 10 + 11 + (1 lynx ID)	13	105,638.50	0.00	0.73
Only human infrastructure affects lynx night location selection	Used ~ 8 + 9 + 10 + 11 + (1 lynx ID)	6	106,493.30	854.80	– 0.90
Only topography affects lynx night location selection	Used ~ 1 + 2 + 3 + 4 + 5 + 6 + 7 + (1 lynx ID)	9	106,716.20	1077.70	0.54
None of the covariates affect lynx night location selection	Used ~ (1 lynx ID)	2	107,637.50	1999.00	0.52

^a1: altitude, 2: slope, 3: distance to rocky outcrops, 4: surface rockiness, 5: aspect, 6: TPI, 7: VRM, 8: distance to forest roads, 9: distance to scattered buildings, 10: distance to paths, 11: distance to major transport infrastructure

a robust correlation ($\rho > 0.80$; Boyce et al. 2002). Prior to modelling, we checked for collinearity between covariates using a variance inflation factor (VIF), and we kept all predictor covariates since the VIF value was < 3 (Zuur et al. 2010). We rescaled the continuous covariates to z-scores to improve model convergence by subtracting their mean and dividing by 2 standard deviations (Gelman 2008).

To test for a functional response in habitat selection according to the availability of rocky outcrops, rugged, and rocky terrain within home ranges (H4), we created three different generalised additive models (GAMs), i.e., one per covariate. We first included random slopes for these three covariates in the two best ranked GLMM models for day-resting sites and night locations (Table 2), and then we extracted individual-level coefficients. These coefficients were then included as a response variable in the GAMs. We included the mean distance (rocky outcrops) or value (surface rockiness and VRM) of each covariate across the home range of each lynx as the predictor variable. These means represented the availability of the habitat variable to the individual lynx in question. We specified predictor variables as non-parametric smooth functions in the GAMs to allow non-linear relationships (Wood 2017). We used the R package “mgcv” v.1.8–33 (Wood 2015) to build GAMs.

Results

Rocky outcrops detection

We identified 984,833 rocky outcrops within the lynx home ranges in the SDK study area (area size: 1184.1 km²) with an average density of 831.7 rocky outcrops/km². The highest number ($n=881,895$) and average density (1115.2 rocky outcrops/km²) was recorded in the limestone area (790.8 km², 66.8% of the study area), compared to the dolomite area (308.1 km², 26.0% of the study area) where the number ($n=89,436$) and average density (290.3 rocky outcrops/km²) of rocky outcrops was considerably lower. Only 14,546 rocky outcrops were detected in parts with other bedrock types (85.3 km², 7.2% of the study area), with an average density of 17.1 rocky outcrops/km².

In the BFE study area (area size: 1914.7 km²), we identified 80,590 rocky outcrops within lynx home ranges with an average density of 42.1 rocky outcrops/km². The highest number ($n=63,427$) of rocky outcrops with an average density of 45.4 rocky outcrops/km² was recorded in the gneiss area (1396.5 km², 72.9% of the study area), followed by a considerably lower number ($n=10,658$) and average density (28.3 rocky outcrops/km²) of detected rocky outcrops in areas with granite (376.5 km², 19.7% of the study area). Even though the areas with other bedrock types encompass the smallest area and proportion of the BFE (141.9 km², 7.4% of the study area) and that we detected the lowest number of rocky outcrops ($n=6790$) there, the average density was the highest here with 47.9 rocky outcrops/km².

Additionally, we compared the results of the detected rocky outcrops with layers for surface visualisation (*Hillshade* and *Sky View Factor* created from a DTM), topographic maps, and field-mapped rocky outcrops (164 mapped in the SDK and 133 in BFE). A total of 153 (93.3%) in the SDK and 111 (83.5%) in BFE of field-mapped rocky outcrops matched with the automatically detected ones. By comparing automatically detected rocky outcrops with digitised ones ($n=627$) from topographic maps in BFE that were used by Signer et al. (2019), a total of 620 (98.9%) rocky outcrops matched.

Lynx habitat selection

Day-resting sites

We used 2841 day-resting sites from 18 lynx (eight from the SDK and 10 from BFE; GPS collars of four lynx from the SDK were programmed to collect only night locations; Table S1) to assess the selection of topographic characteristics and human infrastructure by comparing them to available locations ($n=226,117$). According to the AIC values, the model that best explained lynx day-resting site selection included both covariate groups: topographical and human infrastructure (Table 2). The k -fold cross-validation revealed a very high model fit ($p=0.97$; Table 2). All the topographical covariates except aspect were statistically significant (Fig. 3). Specifically, we observed that for day-resting sites, lynx selected the vicinity of rocky outcrops, steeper slopes, areas with higher ruggedness, higher rockiness, and

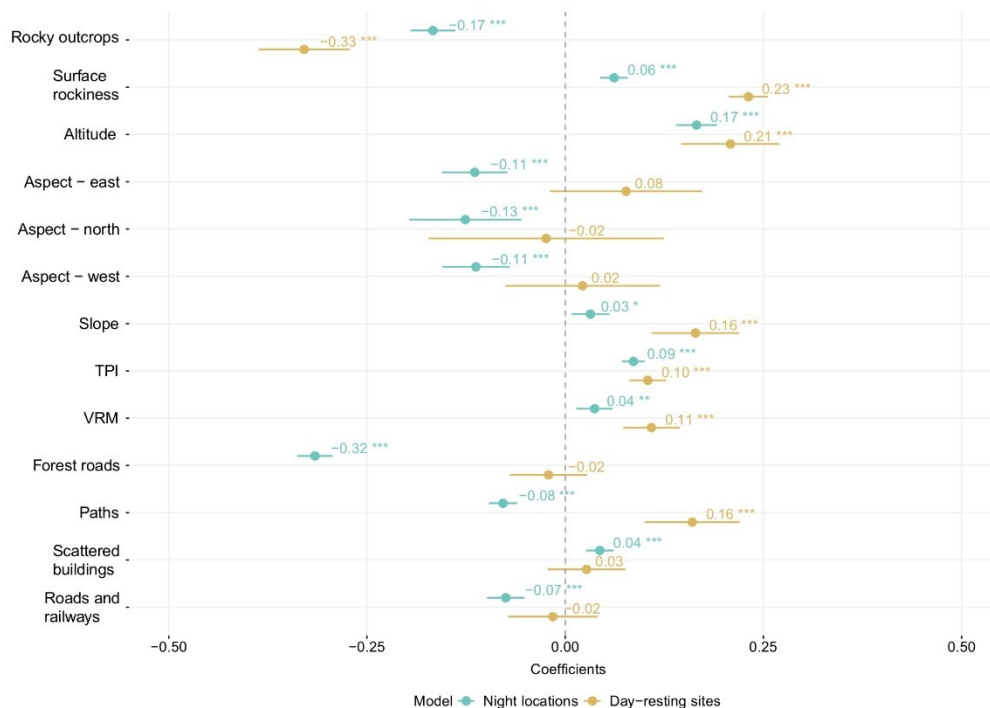


Fig. 3 Estimated coefficients with 95% confidence intervals for the models with the best fit for lynx night locations (green) and day-resting sites (brown). The coefficients indicate the selection/avoidance of the target covariates and intervals that

do not overlap with zero, indicating significant effects. Rocky outcrops, forest roads, paths, scattered buildings, roads, and railways are distance-based covariates (negative values indicate selection and positive avoidance)

higher altitudes than available. The TPI showed that they selected areas where the index had higher values than what was available. The strongest selection was observed for the proximity to rocky outcrops and surface rockiness (Fig. 3). In the SDK, 73.2% of lynx resting sites and 51.2% of available locations were within a 50 m buffer of rocky outcrops, while in the BFE, the values were 31.1% for resting sites and 8.5% for available locations.

Only distance to paths had a statistically significant effect among human infrastructure, indicating that lynx avoided paths when resting. Distance to forest roads, scattered buildings, and major transport infrastructure did not influence day-resting site selection (Fig. 3).

Night locations

We used GPS locations from 22 lynx (12 from the SDK and 10 from BFE; Table S1) to assess their habitat selection during the night by comparing used night locations ($n=16,389$) to available locations ($n=226,117$). According to the AIC values, the model that best explained habitat selection for night locations also included both covariate groups—topographical and human infrastructure (Table 2). The k -fold cross-validation revealed a moderate model fit for the best model ($p=0.73$; Table 2). All the topographical covariates were statistically significant. We observed that during the night, lynx selected the vicinity of rocky outcrops, steeper slopes, more rugged and rocky surfaces, steeper slopes and higher altitudes, as well as areas with a higher TPI than

available, but the values of the coefficients for continuous variables were lower than for day-resting site selection. Compared to southern exposures, they avoided other orientations (Fig. 3). In contrast to day-resting sites, the proportion of used locations within a 50 m buffer of rocky outcrops was lower than available in both study areas (43.9% of used vs. 51.2% of available locations in SDK and 0.6% of used vs. 8.5% of available locations in BFE).

All the covariates of the human infrastructure group were statistically significant. During the night, lynx avoided scattered buildings, but selected the vicinity of forest roads, paths, and major transport infrastructure. The strongest selection was observed for the proximity to forest roads, followed by the proximity to rocky outcrops and altitude (Fig. 3).

Functional response

We observed a functional response in the selection of rocky and rugged surface for day-resting sites and night locations. Specifically, lynx exhibited a stronger selection for rocky and rugged surfaces where such habitats were less available (particularly in the Bohemian Forest Ecosystem; Fig. 4). As the availability increased, we observed a general trend of avoidance of rocky and rugged surface. The main exception was at higher availability of rocky surfaces, where the lynx did not exhibit strong selection/avoidance patterns (Fig. 4). On the other hand, we did not detect a functional response in the selection of rocky outcrops at night or daytime periods, as their selection did not change with increased availability (Fig. 4). The AIC values, Δ AIC, and degrees of freedom of functional response models are reported in Table S3.

Discussion

Rocky outcrops detection and high-resolution LiDAR-DTM

The use of a semi-automatic approach to analyse high-resolution DTM (LiDAR) enabled us to efficiently detect and measure a very large number (more than 1 million) of studied relief features (i.e., rocky outcrops) in two densely forested, large (> 1000 km²), and remote landscapes of the Slovenian Dinaric Mountains (SDK) and the Bohemian

Forest Ecosystem (BFE). Such a task would be nearly impossible or would require enormous effort if done by traditional methods, such as field mapping or a visual digitisation of features based on different layers (e.g., topography maps with a much lower resolution or *Hillshade* derived from the DTM).

In the BFE, Signer et al. (2019) used a layer of digitalised rocky outcrops from topographic maps (1:25,000) that contained merely 627 polygons of rocky outcrops, while we identified 80,590 rocky outcrops in the same study area. In addition to fewer detected features, the previously-used digitised layer was spatially inaccurate as some polygons were mapped at the wrong locations, many outcrops were missing, and the shapes of polygons did not match with feature shapes (examples shown in Figs. S2 and S3). This highlights the potential of LiDAR-DTMs for large-scale ecological research, as they can be a useful and more reliable source of information for efficient detecting and studying the spatial patterns and morphometric settings of rocky outcrops, other landforms, or vegetation characteristics (Čonč et al. 2022; Smith and Mullins 2022; Sergeyev et al. 2023). Our study also showed that the abundance and spatial distribution of the rocky outcrops is closely related to the geology of the study areas. Rocky outcrops are much denser and more numerous on limestones than on dolomites, gneiss, and granites. We also found that they often occur on certain relief features, e.g., on the slopes of dolines and other karst depressions, valleys, cirques, or on ridges.

Nevertheless, the method had some drawbacks. When compared to field-mapped rocky outcrops, 6.7% of the rocky outcrops in the SDK and 16.5% in the BFE were not detected by the automatic method. The proportion of missed rocky outcrops could be caused by manual errors when placing the outcrops on the map or because some of the mapped rocky outcrops were too small (personal observations from the field) and were consequently not detected by the method (the search radius of the method was 10 m). By comparing automatically detected rocky outcrops with digitised ones from topographic maps in BFE, 98.9% automatically detected rocky outcrops matched with digitised ones. Those that did not match were mapped on the topographic maps on the wrong locations (i.e., there are no rocky outcrops there), which could be connected to the mapping of rocky outcrops on a small scale (example shown in Figs. S2 and S3).

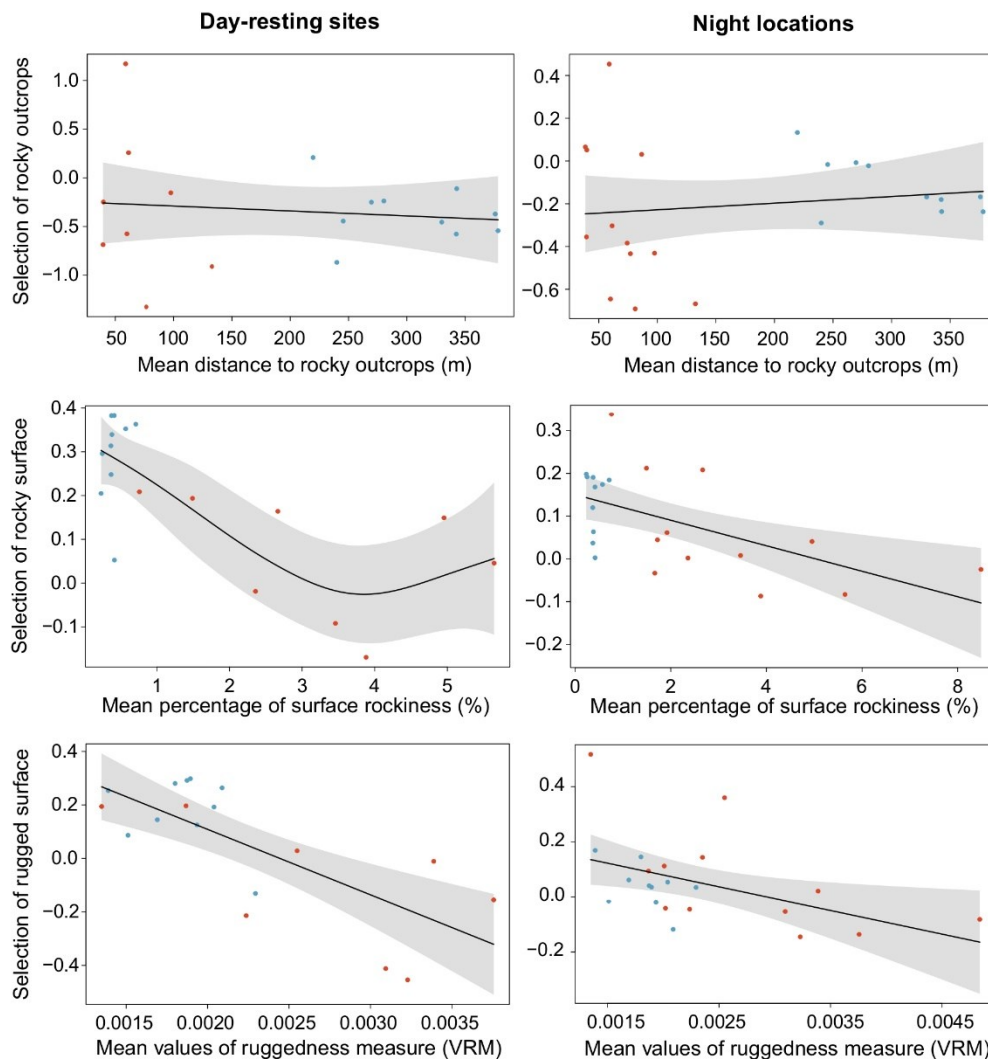


Fig. 4 Selection of rocky outcrops, surface rockiness, and ruggedness by individual lynx as a function of the availability of the same covariates as predicted by generalized additive models. Each point indicates the value per individual lynx coloured by study areas (Slovenian Dinaric Mountains (SDK)—red and

Bohemian Forest Ecosystem (BFE)—blue). Note that for the distance-based parameter (i.e., distance to rocky outcrops), the negative values represent selection and the positive values avoidance

In addition to the remote sensing of specific relief features, high-resolution DTMs can provide more realistic and accurate information about abiotic microhabitat characteristics for covariates derived

from DTMs. While high-resolution LiDAR data is not available everywhere, our approach can also be applied to lower resolution data, such as TanDEM-X (12×12 m) provided by German Aerospace Center

(DLR; <https://tandemx-science.dlr.de/>), available worldwide; this would allow extending the analysis to more countries or even continental scales and enable faster processing. On the other hand, low resolution DTMs pose challenges, risking the loss of microhabitat details. The evaluation of the differences between input DTMs warrants further research.

Certain challenges are also posed by the GPS-telemetry data inaccuracies (estimated errors are 4–16 m, depending on habitat type; Stache et al. 2012). To account for GPS error, we would usually use buffers around the GPS locations and calculate the average values of covariates within the buffers (e.g., average slope). However, such a data generalisation can misrepresent the actual situation. For example, if a day-resting site is located in a flat area between rocky outcrops with a TPI value indicating “flat”, the calculation of the average value in a 50 m buffer may incorrectly result in the “upper slope” category, which does not correspond to reality. At the same time, these values can be misleading because the day-resting site might be on a flat area (e.g., rocky shelf) between or under a rocky outcrop (example shown in Fig. S4) and not necessarily on an (open) flat area. Therefore, the appropriate approach is to use distance-based covariates or the proportion of studied features in a given search area, as done in this study.

Lynx habitat selection and functional responses

Our results showed that lynx generally selected the vicinity of rocky outcrops, steep slopes, and areas with high ruggedness, rockiness, topographic position index, and altitudes for day resting in both study areas (H1 supported). These results are in line with the findings of previous studies. Specifically, in the Slovenian Dinaric Mountains, Hočevar et al. (2021) revealed a preference for lynx to rest on the top of mountain ridges or hilltops, as well as on steep slopes and microhabitats with good cover. These areas also provide concealment for the lynx, as well as a good view of the surrounding area to detect potential incoming danger or prey. Similarly, Signer et al. (2019) observed that lynx tend to select rocky outcrops when resting, 12.3% of day-resting sites were located within a 50 m buffer around these features. Our study improved the detection of rocky outcrops (i.e., using LiDAR DTM) and day-resting sites (i.e., incorporating accelerometer data), allowing us to observe that

31.1% of day-resting sites were located within a 50 m buffer around rocky outcrops in the same study area as in Signer et al. (2019). This comparison suggests that more detailed and accurate information on the studied features and lynx behaviour may have important implications for understanding lynx ecology.

During the night, when lynx are generally active (Heurich et al. 2014), we observed a similar selection of topographical covariates, which supports our first hypothesis. However, in line with our third hypothesis, the values of the coefficients were lower compared to the day-resting sites, indicating a weaker selection during nighttime (Table S2, Fig. 3). The selection of the vicinity of rocky outcrops, as well as rugged, steep and rocky terrain during the night may indicate that lynx select such terrain for scent-marking (Allen et al. 2017) or hunting (Krofel et al. 2007; Čonč et al. 2022). Felids often seek out features that serve as communication hubs (Melzheimer et al. 2020). Previous studies (Vogt et al. 2016; Allen et al. 2017; Mohorović and Krofel 2020) showed that lynx most often scent mark rocks and juvenile conifers, and among rocks, they often select those that are covered with moss (better absorption of urine and longer persistence) and shaped as overhangs (protection from the weather). As lynx are a stalking and ambush predator, their hunting may be more successful in rugged, rocky terrain and around rocky outcrops, which are often covered with moss. This enables a quieter approach and provides cover for the lynx, as well as escape impediments to ungulates (Krofel et al. 2007; Podgórski et al. 2008; Belotti et al. 2013; Čonč et al. 2022; Schmidt et al. 2023).

Beside the topographical characteristics, lynx were also influenced by anthropogenic factors. Our results indicated that, during the daytime, lynx avoided paths used for human recreation. This was expected, given that people mainly use these paths during the day, which is also when lynx are most vulnerable due to their lower alertness during sleeping periods. Therefore, they require safer (i.e., less accessible and less disturbed) locations (Belotti et al. 2012, 2018; Filla et al. 2017; Hočevar et al. 2021) while resting. Although metric data on the intensity of the recreational use of paths were not available for our study areas, further research incorporating such data would be important to understand the thresholds at which lynx start avoiding such infrastructure. In contrast to the day-resting sites, we observed that lynx selectively

use linear human infrastructures (roads, paths) during the nighttime, when human use is reduced and lynx are more active. These findings support our second and third hypothesis. By using linear features, lynx may benefit from easier movement and the increased efficiency of scent-marking (Krofel et al. 2017). We observed that lynx avoid scattered buildings during the night, even though they regularly use them for scent-marking, especially abandoned or less used cabins (Allen et al. 2017; Krofel et al. 2017).

Finally, by considering a large gradient of availability of the microhabitats used by the lynx, we were able to test whether lynx exhibit functional responses within two regions in Europe, as hypothesised in previous local studies (Hočevár et al. 2021). Our analyses confirmed the functional response in the selection of rugged and rocky terrain during two behavioural states (day-resting sites and night locations). Indeed, lynx exhibited a stronger selection towards rugged and rocky terrain when the availability was lower. As the availability of such features increases, lynx might not show a particular selection pattern (no selection/avoidance), although they would still regularly use them. Our findings partially confirm our fourth hypothesis, as we did not detect a functional response in the selection of rocky outcrops. Despite the unknown ecological importance of these features, it is important to have in mind that we only considered rocky outcrops higher than 3 m. Therefore, our results do not reflect the selection towards smaller rocky outcrops, which could be equally important for different lynx behaviours. Furthermore, we observed a high individual variability, especially in the selection of rocky outcrops and rocky surface in both study areas, indicating that these features might be particularly relevant for some individuals. Such variability may rise from different reasons, such as intrinsic (sex, age) or external factors (such as seasonality, presence of conspecifics, prey type and availability). Moreover, the general increase of human recreational activities (e.g., hiking, geocaching, mushroom picking, and climbing, among others) in natural areas during the past decades might negatively affect lynx, especially during the daytime (Belotti et al. 2012, 2018). Thus, it would not be surprising if lynx increasingly select habitats that are less accessible to people, especially in areas where the availability of such terrain is limited. On the other hand, in areas with abundant rugged and rocky surfaces, their selection might not be

so obvious or lynx might even avoid them in some behaviours (e.g., when moving through the landscape for the ease of movement).

Conclusions and management implications

The use of remote sensing methods and lynx GPS-telemetry data from two geographically and geologically contrasting study areas enabled us to show that lynx select the vicinity of rocky outcrops, as well as rugged and rocky terrain. This pattern was particularly pronounced when selecting day-resting sites and in areas with a lower availability of the preferred microhabitats. We also showed that lynx avoid paths during the day (i.e., while resting), while they are attracted to linear human infrastructure at night. This highlights the importance of evaluating habitat selection among different behavioural states, as the selection patterns might change considerably among activity phases.

Our results indicate that specific relief features may increase the suitability of a given area for lynx and possibly other felids. Furthermore, this study emphasises the importance of including such microhabitat characteristics in habitat selection analyses and landscape ecology in general. The results provided by such research can also be used for guiding conservation efforts and decision-making in spatial planning (Dickson and Beier 2007; Podgórski et al. 2008; Abouelezz et al. 2018; Bailey et al. 2018; Signer et al. 2019; Farhadinia et al. 2020; Čonč et al. 2022). For example, as human populations grow, disturbance of natural habitats and habitat fragmentation increases, with transportation infrastructure being among the main problems (Meijer et al. 2018). The approach used in our study to detect microhabitat characteristics could contribute to identifying the most suitable micro-sites for the placement (Huck et al. 2010; Potočník et al. 2020), structure, and design of wildlife crossings over fragmentation barriers (Brennan et al. 2022). In addition, the results could also be useful for the selection of micro-sites for the deployment of camera-traps and box-traps to increase the efficiency of population monitoring and animal capture for research purposes (Fležar et al. 2023). Furthermore, our results indicate that rocky and rugged areas should be avoided whenever possible when planning new

recreation infrastructure in lynx habitat (e.g., hiking paths, geocaching locations, and climbing routes). This appears to be especially important where such areas are rare in the landscape.

We draw special attention to the construction of new paths (e.g., for hiking, cycling, and horse-riding), towards which lynx seem to be particularly sensitive during the daytime. Lynx' avoidance of paths appears to be stronger compared to forestry roads, indicating the importance of separating these types of linear human infrastructure in wildlife ecology and behavioural studies. However, it should first be mentioned that regulations in the use of forestry roads can differ among different regions, and second, the use of forestry roads for recreational purposes is generally increasing, especially with the recent availability of map applications.

In conclusion, our study provides further evidence for the importance of protecting geomorphological features (geodiversity) for biodiversity conservation, as rocky outcrops and other relief features provide an important habitat for lynx, as well as for numerous other endangered animals, plants, and fungi (Fitzsimons and Michael 2017; Bailey et al. 2018; Signer et al. 2019; Čonč 2020; Čarni et al. 2022; Čonč et al. 2022; Gordon et al. 2022; Smith and Mullins 2022).

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Data availability Data supporting the findings of this study are not included due to conservation concerns. Data may, however, be available from the authors upon reasonable request and with permission of Administrations of NP Bayerischer Wald, NP Šumava, BF UL and SFS.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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SUPPLEMENTARY INFORMATION

Landscape Ecology

Revealing functional responses in habitat selection of rocky features and rugged terrain by Eurasian lynx (*Lynx lynx*) using LiDAR data

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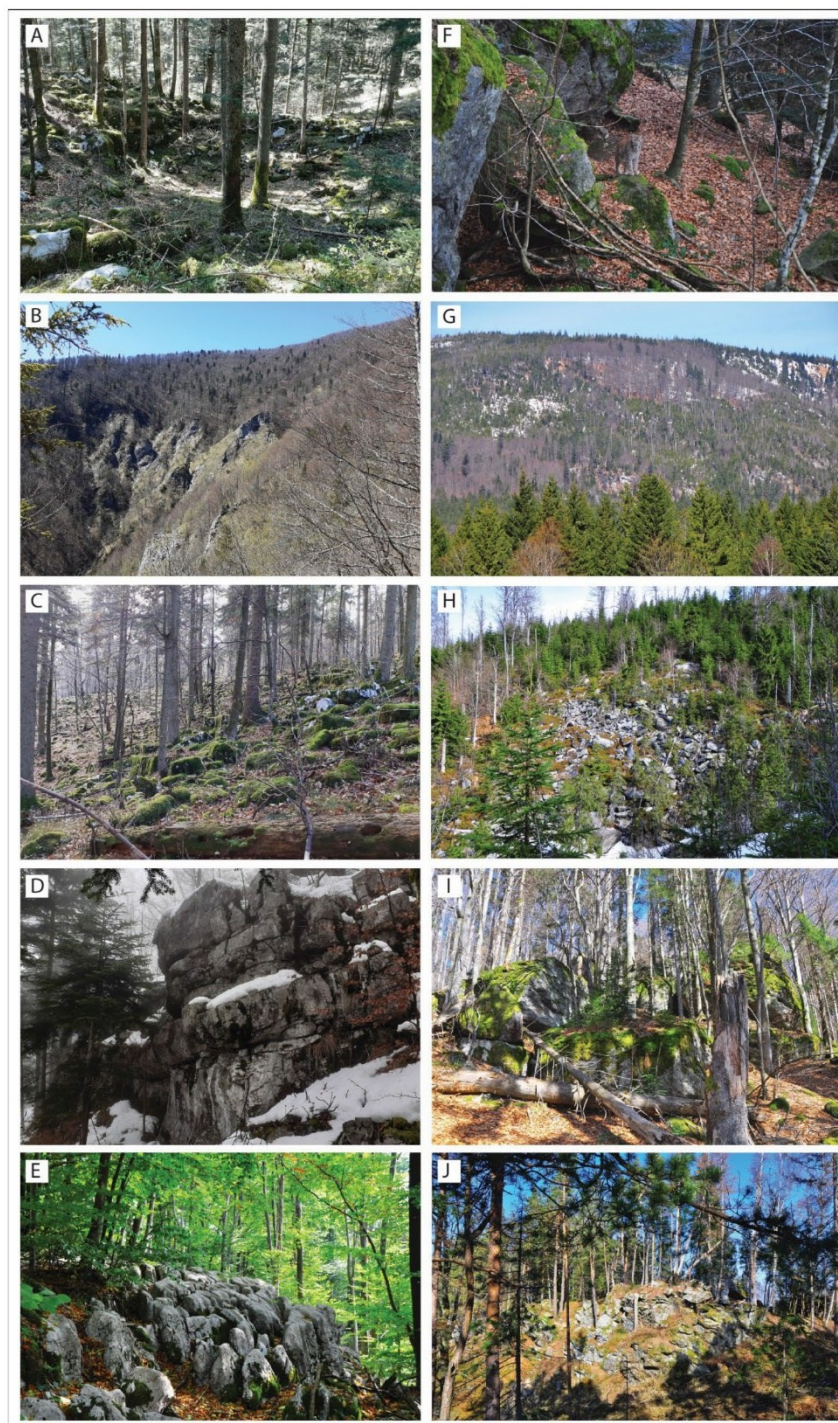


Fig. S1: In both study areas, the surface is dissected by small natural features consisting mainly of numerous rocks such as smaller-scale rocks, rocky boulders, rocky ridges, cliffs, cirques, rock shelters. Due to the different lithology composing the SDK (limestone, dolomite) and BFE (gneiss, granite) and the different dynamics of mechanical weathering of the bedrock, rocky outcrops have different morphographic and morphometric characteristics. In both study areas, they reach heights of up to several metres and lengths of about 10 metres. In BFE, where fluvial terrain predominates, the surface is less rugged and rocky than in the SDK.

Examples of different rocky outcrops in the SDK (photographs from A to E) and BFE (photographs from F to J): A) Rocks on a rim of a doline, B) cliffs in fluviokarst valley, C) rock boulders on a limestone slope, D) cliff in a limestone, E) karrenfield in a limestone, F) lynx on rocky boulders, G) cliffs in a cirque, H) "blockmeer" or block field, I) rock boulders, J) cliff on the edge of a river valley. Photos by ŠČ.

Table S1: Details on the capturing and monitoring of 12 lynx in the Slovenian Dinaric Karst and 10 lynx in the Bohemian Forest Ecosystem used in this study; ¹at the beginning of lynx monitoring; ²GPS collars programmed to send just night locations; ³translocated individuals; ⁴cross-border lynx (Slovenia-Croatia); ⁵was monitored during two non-sequential time periods; therefore information for 95% MCP is reported as range.

Lynx ID	Age/sex class ¹	Monitoring period	No. of GPS fixes	No. of day-resting sites	No. of night locations	95% MCP [km ²]
Dina ⁴	sub-adult female	2006/12/29 - 2007/09/02	81	10	71	303.17
Snežka ^{4, 5}	adult female	2008/02/10 - 2008/10/04 2010/12/28 - 2011/03/30	880	65	815	90.12-126.05
Mihec	sub-adult male	2011/05/01 - 2011/10/09	243	72	171	86.79
Maja	adult female	2012/01/28 - 2012/07/10	277	51	226	51.67
Goru ³	adult male	2019/06/01 - 2022/08/24	2583	34	2549	218.31
Bojan ²	adult male	2019/12/01 - 2021/03/03	61	0	61	255.97
Catalin ³	adult male	2020/04/16 - 2022/07/26	2086	71	2015	287.55
Petra ⁴	adult female	2021/03/01 - 2022/10/30	1592	91	1501	215.05
Bo ^{2,4}	sub-adult male	2022/05/01 - 2022/10/31	432	0	432	60.20
Kili ⁴	adult male	2022/02/04 - 2022/10/29	1205	31	1174	265.95
Igi	adult male	2022/02/17 - 2022/04/17	171	0	171	52.05
Blisk ^{2,3}	adult male	2022/06/15 - 2022/11/03	326	0	326	60.01
Milan	adult male	2005/03/07 - 2010/02/13	764	101	663	601.49
Nora	adult female	2007/01/17 - 2008/03/12	211	26	185	168.65
Patrik ⁵	adult male	2007/02/19 - 2007/10/31 2010/03/11 - 2011/03/20	970	211	759	321.37-1066.88
Kubicka	adult female	2010/03/17 - 2011/11/08	1258	344	914	144.66
Matylda	sub-adult female	2010/03/17 - 2012/08/03	1715	490	1225	101.86
Emmanuel	adult male	2010/03/27 - 2010/07/13	216	55	161	266.23
Čitrad	sub-adult male	2011/01/15 - 2012/05/20	1178	301	877	413.68
Tessa	adult female	2011/02/27 - 2012/03/11	818	229	589	115.00
Kika	adult male	2011/03/22 - 2012/11/01	1248	392	856	312.21
Nimo	adult male	2012/03/11 - 2013/09/13	915	267	648	632.74
Total			19,230	2841	16,389	/

Table S2: Mean values with standard deviation (grey) and median values with interquartile range (white) of covariates for used and available locations by both study areas. Aspect is a categorical variable and is reported as the proportion of locations in each category.

	Slovenian Dinaric Karst (SDK)			Bohemian Forest Ecosystem (BFE)		
	Available	Day-resting sites	Night locations	Available	Day-resting sites	Night locations
Rocky outcrops (m)						
	77.85 ± 87.92	40.58 ± 49.68	69.94 ± 69.55	321.49 ± 273.90	206.89 ± 229.86	263.14 ± 222.43
	53.20 ± 82.49	22.78 ± 46.60	50.38 ± 79.06	245.73 ± 337.30	127.92 ± 286.06	214.52 ± 293.18
Surface rockiness (%)						
	2.98 ± 6.61	6.78 ± 9.56	3.22 ± 6.51	0.41 ± 2.51	4.00 ± 9.26	1.07 ± 4.45
	0.25 ± 2.67	2.43 ± 8.34	0.47 ± 3.21	0.00 ± 0.00	0.00 ± 0.84	0.00 ± 0.00
Altitude (m)						
	776.63 ± 265.47	900.01 ± 222.67	762.85 ± 218.30	902.23 ± 176.17	870.52 ± 155.07	845.87 ± 160.14
	729.22 ± 377.27	914.55 ± 334.57	724.27 ± 331.51	889.04 ± 271.16	854.14 ± 222.91	823.58 ± 205.68
Aspect (%)						
	North: 4.84 East: 26.29 South: 45.00 West: 23.88	North: 6.59 East: 28.71 South: 41.41 West: 23.29	North: 5.47 East: 26.84 South: 46.83 West: 20.87	North: 8.14 East: 26.38 South: 38.61 West: 26.88	North: 8.98 East: 28.15 South: 36.59 West: 26.28	North: 8.91 East: 24.63 South: 40.18 West: 26.28
Slope (°)						
	15.32 ± 7.58	19.56 ± 6.74	15.24 ± 6.42	8.76 ± 4.71	11.66 ± 7.22	9.76 ± 5.43
	13.93 ± 9.14	18.95 ± 9.31	14.00 ± 7.96	7.84 ± 6.03	10.00 ± 8.12	8.56 ± 6.51
TPI						
	0.00 ± 0.50	0.06 ± 0.55	0.05 ± 0.49	0.13 ± 0.25	0.34 ± 0.78	0.19 ± 0.41
	0.01 ± 0.35	0.02 ± 0.43	0.05 ± 0.37	0.10 ± 0.21	0.16 ± 0.35	0.11 ± 0.27
VRM						
	0.0026 ± 0.00233	0.0041 ± 0.0029	0.0027 ± 0.0022	0.0019 ± 0.0017	0.0031 ± 0.0037	0.0021 ± 0.0021
	0.0020 ± 0.0020	0.0034 ± 0.0026	0.0022 ± 0.0019	0.0015 ± 0.0017	0.0019 ± 0.0025	0.0015 ± 0.0018
Forest roads (m)						
	323.25 ± 339.55	268.43 ± 247.29	223.53 ± 253.27	110.42 ± 107.21	132.09 ± 109.52	105.58 ± 97.93
	219.21 ± 323.65	209.66 ± 207.61	147.08 ± 251.13	79.24 ± 115.71	98.60 ± 132.36	79.38 ± 110.43
Paths (m)						
	1,214.04 ± 1,200.46	988.73 ± 895.73	1,143.59 ± 1,135.29	351.41 ± 390.31	380.92 ± 321.63	311.39 ± 333.19
	816.67 ± 1427.92	740.68 ± 1114.37	785.06 ± 1,326.29	219.05 ± 385.17	311.25 ± 389.46	212.93 ± 332.05
Scattered buildings (m)						
	2,261.13 ± 1,205.10	2,180.69 ± 1,208.72	2,230.61 ± 1,186.31	1,330.98 ± 870.19	1,507.39 ± 959.49	1,485.22 ± 1,000.72
	2,113.22 ± 1,704.94	1,966.29 ± 1,722.70	2,121.34 ± 1,850.00	1,150.74 ± 1,154.52	1,234.23 ± 1,410.63	1,257.20 ± 1,539.29
Roads and railways (m)						
	1,201.40 ± 1,099.66	1,521.72 ± 1,199.86	1,092.06 ± 885.36	1,026.76 ± 1,095.40	1,050.10 ± 930.60	927.56 ± 965.43
	887.12 ± 1,330.17	1,193.28 ± 1,481.14	916.97 ± 1089.60	619.86 ± 1,208.62	783.00 ± 1,025.34	589.68 ± 948.46

Table S3: Akaike's Information Criteria (AIC), differences between AIC (ΔAIC), and degrees of freedom (df) of functional response models for the day-resting sites and night locations selection by lynx.

	Day-resting sites			Night locations		
	AIC	ΔAIC	df	AIC	ΔAIC	df
Distance to rocky outcrops	-167.95	0.00	3.00	-233.27	0.00	3.00
Surface rockiness	-76.02	91.93	4.31	-103.93	129.34	3.00
VRM	214.11	382.06	3.00	252.70	485.97	3.00

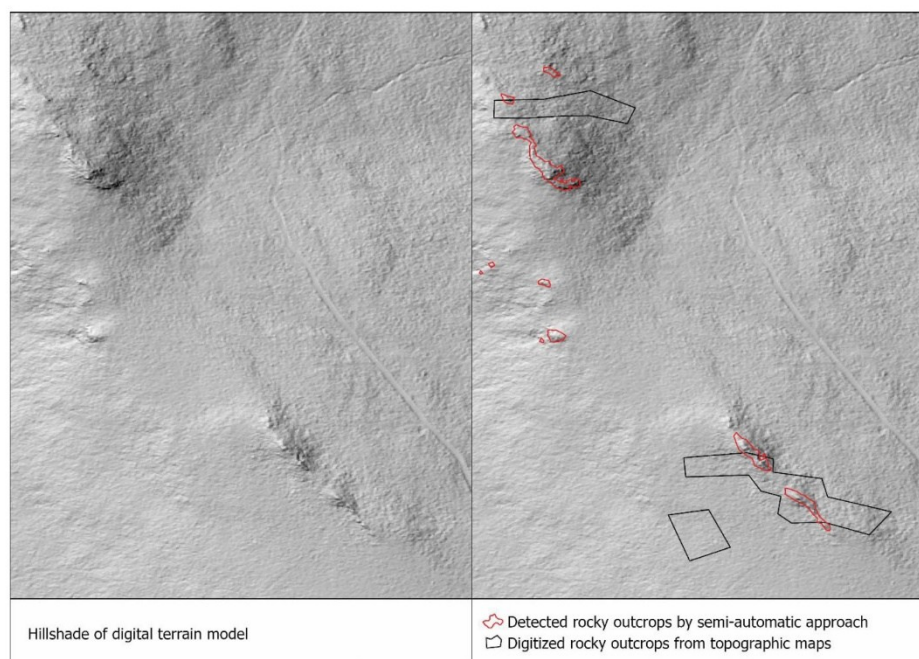


Fig. S2: Comparison of detected rocky outcrops by semi-automatic approach and digitized rocky outcrops from topographic maps in Bohemian Forest Ecosystem study area. Based on the hillshade of the digital terrain model we can see that on the map on the right lower left digitized polygon is mapped on the wrong location (i.e., there are no rocky outcrops). We can also see there are some rocky outcrops detected by semi-automatic approach but were not mapped on topographic maps. Both cases could be connected to the mapping of rocky outcrops on a high scale of the topographic maps (1:25,000). As seen on the both maps, shapes and locations of rocky outcrops detected by semi-automatic approach are more accurate compared to digitized rocky outcrops.

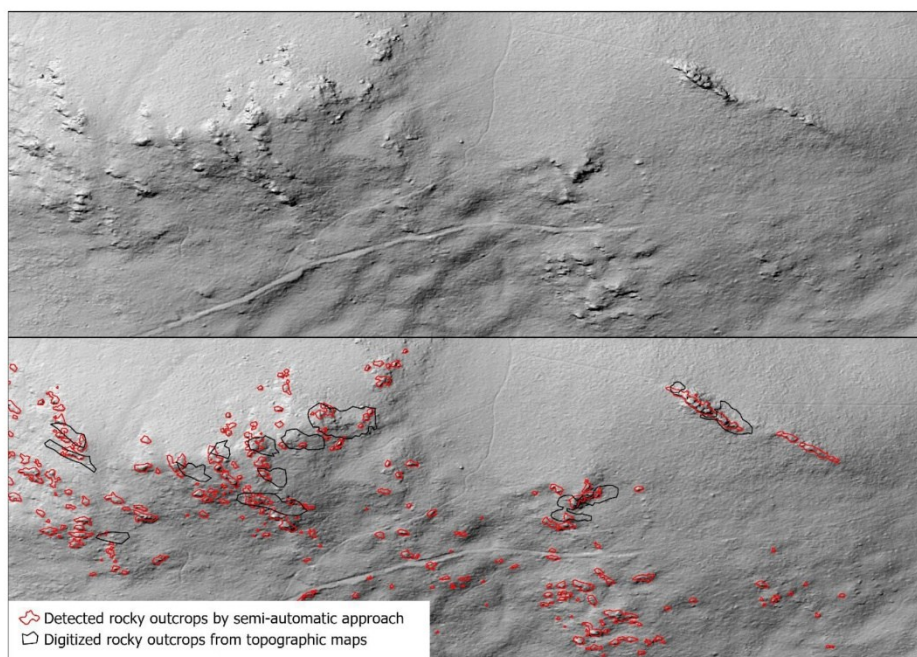


Fig. S3: Another example of comparison of detected rocky outcrops by semi-automatic approach and digitized rocky outcrops from topographic maps in Bohemian Forest Ecosystem study area. We can see there are many rocky outcrops detected by semi-automatic approach but were not mapped on topographic maps. Again, this could be connected to the mapping of rocky outcrops on a high scale (1:25,000) of the topographic maps. As seen on the both maps, shapes and locations of rocky outcrops detected by semi-automatic approach are more accurate compared to digitized rocky outcrops.

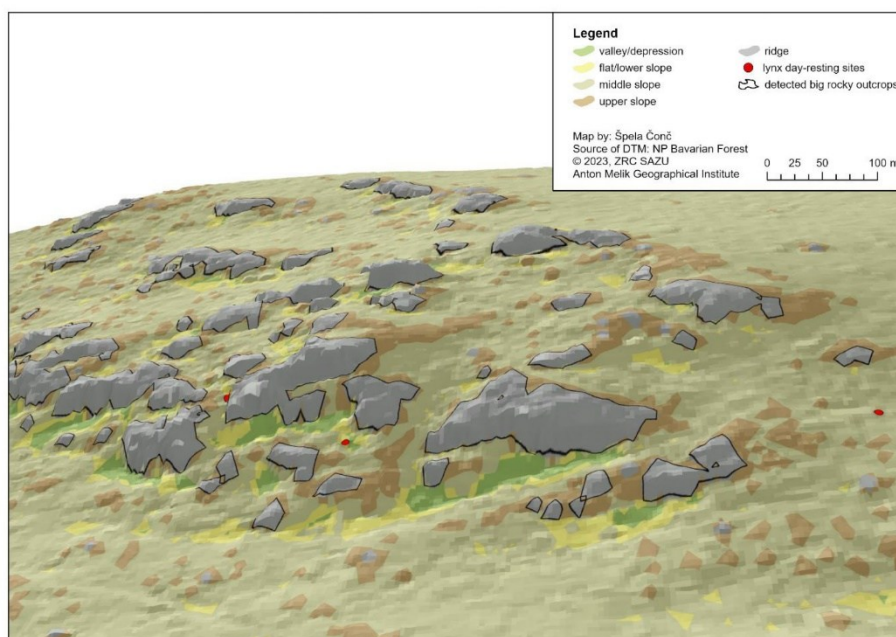


Fig. S4: Example of a 3D scene of lynx day-resting sites in Bohemian Forest Ecosystem study area. Lynx' day-resting site in the middle is on the flat area between rocky outcrops where TPI value represents the category "flat". Calculating the average value in a 50 m buffer would give a TPI value of category "upper slope", which is not the real situation. At the same time, such actual values can be misleading in terms of interpretation of results, because the day-resting site is not necessarily really on the (open) flat area, but on the flat area (e.g., rocky shelf) between or under the rocky outcrops. Thus, the best estimation of the situation is to include in the analysis distance-based covariates or the share of studied features in a specified search area.

3 RAZPRAVA IN SKLEPI

3.1 RAZPRAVA

Pretekle raziskave o ekologiji prostoživečih mačk nakazujejo, da je interpretacija vpliva mikrohabitatnih značilnosti pomembna tako za boljše razumevanje njihove ekologije kot tudi za njihovo varovanje in ohranjanje (Podgórski in sod., 2008; Belotti in sod., 2013; Bouchet in sod., 2015; Ironside in sod., 2018; Jerosch in sod., 2018; Signer in sod., 2019; Schmidt in sod., 2023). Vendar je bil v preteklosti pri analizi vpliva mikrohabitatnih značilnosti na rabo prostora poudarek predvsem na vrednotenju biotskih (npr. pokrovnost in tip vegetacije) in antropogenih elementov, manj pozornosti pa je bilo namenjeno abiotskim elementom (npr. reliefne oblike, reliefne značilnosti površja).

Kljub temu, da poleg biotskih in antropogenih elementov na ekologijo in specifična vedenja risa in divje mačke vplivajo tudi reliefne oblike in mikroreliefne značilnosti, so jih doslej vključevale le maloštevilne raziskave (Potočnik, 2006; Krofel in sod., 2007; Signer in sod., 2019; Hočevar in sod., 2021). Te raziskave so se večinoma opirale na podatke pridobljene na podlagi terenskega kartiranja (npr. Hočevar in sod., 2021) ali ročne digitalizacije reliefnih oblik (npr. Signer in sod., 2019) in so bile navadno omejene le na manjša raziskovalna območja, posledično je bila naša sposobnost razumevanja funkcionalnih odzivov pri izbiri habitata omejena (tj. kako posamezna žival prilagodi rabo določenih habitatnih značilnosti glede na spremembe v njegovi razpoložljivosti) (Myrsterud in Ims, 1998; Holbrook in sod., 2019; Oeser in sod., 2023). Zaradi omenjenih vrzeli v znanju s področja ekologije risa in divje mačke, smo se v okviru doktorske disertacije osredotočili na preučevanje vpliva reliefnih oblik in mikroreliefnih značilnosti površja na izbiro habitata pri obeh vrstah.

Raziskava v okviru te doktorske disertacije je ena prvih, ki na področju preučevanja ekologije prostoživečih mačk poleg vpliva antropogenih in biotskih elementov vključuje tudi podrobne in natančne informacije o mikroreliefnih značilnostih in se opira predvsem na podatke daljinskega zaznavanja. Zato imajo izsledki te raziskave pomemben doprinos na področju metodološkega pristopa preučevanja ekologije obeh preučevanih vrst (in ostalih vrst), hkrati pa raziskava naslavlja tudi nove ugotovitve s področja njune ekologije, kar je pomembno predvsem z vidika ohranjanja in varovanja.

3.1.1 Daljinsko zaznavanje reliefnih oblik

Napredek v tehnologiji zajema in obdelave podatkov omogoča vse bolj podrobno preučevanje zemeljskega površja, posledično se na področju daljinskega zaznavanja razvijajo različne metode in tehnologije, ki omogočajo stroškovno učinkovito kartiranje reliefnih oblik in analiziranje značilnosti površja (Bishop, 2013; Smith in sod., 2013; Tarolli in Mudd, 2020). Na preučevanih območjih (domači okoliši risov in divjih mačk) smo na podlagi literature, lastnih terenskih izkušenj, terenskega pregleda in vizualizacij DMV-ja identificirali glavne reliefne oblike in v GIS-ih na podlagi visokoločljivostnih LiDAR podatkov pripravili sloje za nadaljnje analize. Za zaznavanje identificiranih reliefnih oblik smo uporabili že razvite (pol-)avtomatske metode (npr. za vrtače), razvili svojo metodo (za izdanke kamnin) ali uporabili že obstoječe

prosto dostopne sloje (npr. lokacije jamskih vhodov). Pridobili in pripravili smo tudi različne sloje za analizo topografskih (npr. naklon, ekspozicija, razgibanost), okoljskih (npr. oddaljenost od gozdnega roba) in antropogenih (npr. oddaljenost do cest in naselij) značilnosti preučevanega območja. Po našem vedenju je raziskava v okviru te doktorske disertacije ena prvih, ki se pri ugotavljanju podrobnih in natančnih informacij o mikroreliefnih značilnostih habitatov na tako velikem območju opira predvsem na podatke daljinskega zaznavanja.

Za zaznavanje kraških kotanj smo uporabili prilagojeno metodo zapolnjevanja DMV-ja (Obu in Podobnikar, 2013), ki je temeljila na treh fazah dela: 1) izračun porečij kraških kotanj, 2) omejevanje kraških kotanj, 3) izračun morfometričnih in morfoloških značilnosti ter izločanje kraških kotanj, ki ne ustrezajo velikostnemu kriteriju (globina večja ali enaka 2 m in premer večji ali enak 10 m). Z metodo smo lahko učinkovito prepoznali zelo veliko število kraških kotanj (9.711 v znanstvenem delu 2.1.1 in 45.742 v znanstvenem delu 2.1.2) in določili tudi njihove značilnosti. Kljub temu ima metoda tudi nekaj pomanjkljivosti. V postopku preverjanja natančnosti metode, kjer smo primerjali avtomatsko zaznane kraške kotanje z ročno označenimi na podlagi sloja senčenega reliefa, 16,5 % kraških kotanj ni bilo zaznanih z avtomatsko metodo. Relativno visok delež nezaznanih kraških kotanj je morda povezan s predprocesiranjem oz. glajenjem vhodnega DMV-ja, kjer so manjše kotanje zglažene in jih posledično metoda za avtomatsko zaznavanje ni zaznala (Ciglič in sod., 2022). Primerjava med slojema kaže tudi, da je neskladje največje na pobočjih, saj z metodo nekatere kotanje na pobočjih niso bile zaznane. Problem metode je tudi, da rob kraške kotanje pripiše celicam na tisti nadmorski višini, kjer bi se ob teoretičnem zapolnjevanju voda prelila preko roba. Posledično so lahko robna območja kraških kotanj izpuščena, kar je še posebej vidno pri udornicah in udornih vrtačah, ki imajo zelo izrazit rob. Ta težava je bila prepoznana že prej in je povezana s pomanjkanjem jasnega soglasja v krasoslovni in geomorfološki literaturi o tem, kaj predstavlja rob kraške kotanje, zlasti če se ta nahaja na pobočju (Šegina in sod., 2018; Novljan, 2021). Dokler to vprašanje ne bo rešeno, se bo z uporabo obstoječih metod za zaznavanje kraških kotanj težko bolje približati naravnemu stanju. Kljub nekaterim pomanjkljivostim se je metoda izkazala za uporabno, saj so pridobljeni podatki o lokaciji, gostoti in morfometričnih ter morfoloških značilnostih kraških kotanj primerljivi s predhodno objavljenimi raziskavami (Mihevc, A. in Mihevc, R., 2021).

Medtem ko je večje okroglaste konkavne reliefne oblike mogoče zaznati z obstoječimi metodami daljinskega zaznavanja, predstavlja zaznavanje izdankov kamnin zaradi raznolikosti oblik in velikosti izziv za avtomatizirane metode. Posledično so metode za zaznavanje izdankov kamnin maloštevilne in temeljijo na satelitskih posnetkih (Kwok in sod., 2018) ali na omejevanju na podlagi vrednostih naklona (Smith in Mullins, 2022). Na podlagi satelitskih posnetkov ni možno zaznati izdankov kamnin pod gozdnimi krošnjami, zaznavanje na podlagi naklona pa lahko spregleda manjše izdanke kamnin na ravnih območjih oz. napačno interpretira druge reliefne oblike kot izdanke kamnin (npr. strma, s prstjo prekrita pobočja). Zato smo v okviru doktorske disertacije razvili nov dvostopenjski pristop za kvantitativno zaznavanje izdankov kamnin, ki temelji na prostorski analizi visokoločljivostnega LiDAR DMV-ja in terenskih meritvah morfometričnih značilnosti izdankov kamnin (poglavje 2.3). Uporaba metode nam je omogočila učinkovito prepoznavanje in računanje značilnosti zelo velikega števila (skoraj 1 milijon) izdankov kamnin na dveh geološko in (bio-)geografsko različnih

območjih, slovenskem Dinarskem krasu in Bavarsko-Češkem gozdnem ekosistemu. Največje število in gostoto izdankov kamnin smo zaznali na apnencih in dolomitih ($n = 984.833$, povprečje $831,7$ izdankov kamnin/ km^2). V gnajskih in granitih, ki gradijo Bavarsko-Češki gozdni ekosistem, sta bila število in gostota občutno nižja ($n = 80.590$, povprečje $42,1$ izdankov kamnin/ km^2). To potrjuje, da je kraški geomorfni sistem eden izmed najbolj skalovitih in razčlenjenih geomorfoloških sistemov na našem planetu (Day in Chenoweth, 2013). Ugotovili smo tudi, da se izdanki kamnin pogosto pojavljajo na določenih reliefnih oblikah, npr. na pobočjih in robovih kraških kotanj, rečnih dolin ali na grebenih.

Rezultate zaznanih izdankov kamnin smo primerjali s sloji za vizualizacijo površja (senčen relief in *Sky View Factor*), slojem izdankov kamnin terenskega kartiranja (164 iz slovenskega Dinarskega krasa in 133 iz Bavarsko-Češkega gozdnega ekosistema) in slojem digitaliziranih izdankov kamnin na podlagi topografskih zemljevidov (Signer in sod., 2019). Skupaj se je 153 (93.3 %) terensko kartiranih izdankov kamnin na slovenskem Dinarskem krasu in 111 (83.5 %) iz Bavarsko-Češkega gozdnega ekosistema ujemale z avtomatsko zaznanimi. Delež zgrešenih izdankov kamnin je lahko posledica nepravilne lokacije pri terenskem kartiranju ali kartiranju premajhnih izdankov kamnin (osebna opažanja s terena), posledično pa jih metoda ni zaznala. V primerjavi z digitaliziranim slojem ($n = 627$) se je 98,9 % avtomatsko zaznanih izdankov kamnin ujemale z digitaliziranimi. Tisti, ki se niso ujemale, so bili na topografskih kartah prikazani na napačnih lokacijah (tj. tam ni izdankov kamnin), kar je najverjetneje povezano z majhnim merilom topografskih kart (1:25.000). Poleg slabše prostorske natančnosti (poligoni kartirani na napačnih lokacijah in neujemanje oblik z oblikami izdankov kamnin) digitaliziranega sloja, ima sloj tudi nizko število poligonov, ki predstavljajo izdanke kamnin ($n = 627$). Na enakem območju (Bavarsko-Češki gozdni ekosistem) smo namreč z avtomatsko metodo zaznali 80.590 izdankov kamnin. To kaže na velik potencial uporabe visokoločljivostnih LiDAR podatkov za obsežne ekološke raziskave, saj so lahko koristen in zanesljivejši vir informacij za učinkovito zaznavanje in preučevanje prostorskih vzorcev in morfometričnih značilnosti izdankov kamnin in drugih reliefnih oblik.

Poleg kraških kotanj in izdankov kamnin, smo na podlagi LiDAR podatkov zaznali še druge reliefne oblike (stene, grebeni) in izračunali reliefne značilnosti površja (naklon, razgibanost, usmerjenost) (Weiss, 2001; Sappington in sod., 2007; Loye in sod., 2009). Podatke o lokacijah jamskih vhodov smo pridobili iz zbirke podatkov Katastra jam (Kataster jam, 2024). Uporaba (pol-)avtomatskih metod za zaznavanje reliefnih oblik in izračun reliefnih značilnosti omogoča ponovitev tudi na drugih območjih. Poleg tega pa imajo take metode več prednosti pred terenskim kartiranjem ali digitalizacijo, zlasti če upoštevamo časovni napor in stroške terenskega dela, še posebej pa so uporabne na obsežnih, z rastlinstvom poraslih, težko prehodnih in odročnih območjih. Uporaba visokoločljivostnega LiDAR DMV-ja nam je zagotovila natančnejše prostorske podatke o reliefnih oblikah in mikoreliefnih značilnostih kot v predhodnih raziskavah, kjer so bili podatki o reliefnih oblikah pridobljeni s tradicionalnimi metodami (kartiranje ali digitalizacija) in reliefni koeficienti izračunani na podlagi vhodnih podatkov z manjšo ločljivostjo.

3.1.2 Izbira habitata pri evrazijskem risu in evropski divji mački

Risi in divje mačke so aktivni predvsem ponoči in v mraku, podnevi pa običajno počivajo (Klar in sod., 2008; Jerosch in sod., 2010; Krofel in sod., 2013; Podolski in sod., 2013; Heurich in sod., 2014; Filla in sod., 2017). Na aktivnost in različna vedenja obeh vrst vplivajo mnogi dejavniki, tako intrinzični (npr. spol) kot tudi zunanji oz. okoljski (npr. del dneva, letni časi) (Nielsen, 1984; Schmidt, 2006; Heurich in sod., 2014; Migli in sod., 2021). Poleg tega na aktivnost in vedenje obeh vrst pomembno vpliva tudi razpoložljivost in aktivnost plena (Podolski in sod., 2013; Filla in sod., 2017; Migli in sod., 2021). Ponoči, v času večje aktivnosti, so vedenja pri obeh vrstah povezana z aktivnostmi, kot so npr. gibanje, markiranje in vzdrževanje teritorija, iskanje hrane in partnerjev, podnevi pa s počivanjem (Mahoney in sod., 2016; Allen in sod., 2017; Jerosch in sod., 2017; Oliveira in sod., 2018, 2023; Signer in sod., 2019; Ruiz-Villar in sod., 2023, 2024).

Z integracijo daljinskega zaznavanja in uporabo GPS-telemetričnih podatkov se je izboljšala naša sposobnost podrobnega preučevanja in razumevanja ekologije risov in divjih mačk. Rezultati analiz izbire habitata na podlagi posplošenih linearnih mešanih modelov (GLMM) so pokazali, da risi na splošno znotraj svojih domačih okolišev izbirajo strma, razgibana in skalovita območja ter bližino kraških kotanj, jam, izdankov kamnin, grebenov in sten. V različnih fazah aktivnosti (noč, dan) risi v splošnem kažejo podobne vzorce izbire reliefnih značilnosti, vendar pa imajo ponoči reliefne značilnosti manjši vpliv na izbiro habitata kot podnevi. Drugačne rezultate smo pridobili pri analizi vplivov človeške infrastrukture, ki so se razlikovali glede na del dneva. Podnevi so se risi izogibali bližine rekreacijskih poti, ostala človeška infrastruktura pa ni imela vpliva na izbiro lokacij za dnevna počivališča. Nasprotno so v času največje aktivnosti (ponoči) risi izbirali bližino rekreacijskih poti, gozdnih in glavnih cest; še vedno pa so se izogibali stavbam, gozdnim robovom in naseljem. Pri primerjavi izbire habitata med nepreseljenimi (risi, ki so celo življenje preživeli na območju slovenskega Dinarskega krasa) in preseljenimi risi (risi, ki so bili preseljeni in se ustalili na območju slovenskega Dinarskega krasa) smo opazili bolj izrazite vzorce izbire in/ali izogibanja pri preseljenih risih, medtem ko so bile razlike pri izbiri habitata med risi z različnimi stopnjami izkušenosti (izkušeni in naivni risi) manj izrazite. V nasprotju z našimi predvidevanji smo ugotovili, da na izbiro habitata divje mačke znotraj njihovih domačih okolišev v času največje aktivnosti (ponoči) bolj vplivata človeška infrastruktura in vegetacija kot pa reliefne značilnosti. Divje mačke so izbirale bližino glavnih cest in gozdnih robov, bolj položna pobočja ter lokacije bližje jamam in grebenom. Izogibale so se stenam, gozdnim cestam in naseljem. Kljub temu, da določenih reliefnih oblik niso izbirale (npr. kraške kotanje, izdanki kamnin), pa so jih še vedno redno uporabljale, čeprav manj v primerjavi z njihovo razpoložljivostjo znotraj domačih okolišev.

Izbiro habitata smo ovrednotili na podlagi GLMM-jev, ki temeljijo na linearni kombinaciji parametrov, pri čemer pa odzivi odvisnih spremenljivk vzdolž gradienta neodvisne spremenljivke niso nujno linearni (npr. logistični odziv pri logit povezavi). Kljub tej možnosti rezultati GLMM-jev ne kažejo jasnega vzorca odziva odvisne spremenljivke na spremembe neodvisne spremenljivke vzdolž celotnega gradienta. Nekatere spremenljivke lahko vplivajo na izbiro habitata le v krajšem intervalu oz. do določene razdalje (npr. oddaljenost od prometne

infrastrukture), z nadaljnjim naraščanjem neodvisne spremenljivke pa odvisna še vedno variira, vendar je to rezultat drugih faktorjev, ki so povezani z neodvisno (npr. razgibanost površja). Da bi se izognili morebitni napačni interpretaciji in natančneje ovrednotili vpliv neodvisne spremenljivke vzdolž njenega celotnega gradienta, smo izbiro habitata naknadno preverili še s posplošenimi aditivnimi modeli (GAM), ki omogočajo nelinearne odnose med odvisnimi in neodvisnimi spremenljivkami. Za vse spremenljivke uporabljene v poglavjih 2.1, 2.2 in 2.3, ki temeljijo na razdalji, smo pripravili bivariatne (parne) GAM-e za analizo vrednosti odvisne spremenljivke v gradientu neodvisne (Priloga A, B in C). V veliki večini primerov (59 od 66) so rezultati ostali nespremenjeni, pri sedmih primerih pa se je trend med rezultati GLMM-jev in GAM-ov razlikoval, zato smo v sledečih poglavjih v teh primerih zaključke ovrednotili nekoliko previdnejše. Do razlik pri izbiri oz. izogibanju je prišlo pri naslednjih primerih: »oddaljenost od cest« v primerih izbire habitata pri vseh risih, preseljenih risih in naivnih preseljenih risih (poglavje 2.2, Priloga B2, B8 in B10), »oddaljenost od naselij in jam« pri divjih mačkah (poglavje 2.2, Priloga B3 in B4) ter »oddaljenost od razpršenih stavb, cest in železnic« za nočne lokacije risov (poglavje 2.3, Priloga C2).

V primerih, kjer pri GAM-ih in GLMM-jih prihaja do razlik v izbiri oz. izogibanju pri posameznih spremenljivkah, je potrebna previdnost pri vrednotenju rezultatov, saj se učinek lahko spreminja glede na razdaljo. Prav tako pa je lahko rezultat drugačen, če modeli upoštevajo kombinirane učinke različnih spremenljivk ali ločeno testirajo vplive samo ene spremenljivke. To lahko razložimo na primeru izbire oz. izogibanja bližine naselij pri divji mački. Pri grajenju GLMM modelov smo sprva izpustili spremenljivko »razdalja do gozdnih robov«, saj se na preučevanem območju (slovenski Dinarski kras) večina travnikov nahaja v okolici razpršenih naselij. Rezultati modela so pokazali, da divja mačka izbira bližino naselij, kar pa je lahko dejansko povezano z izbiro travnikov, ki se nahajajo v bližini naselij. Ko smo v GLMM vključili tudi spremenljivko »razdalja do gozdnih robov«, se je trend obrnil in so rezultati napovedali, da divje mačke izbirajo bližino gozdnih robov, naselij pa se izogibajo. Ob preverjanju porazdelitve spremenljivke »razdalja do naselij« na podlagi GAM-a, ki temelji le na bivariatni analizi, rezultati kažejo, da divja mačka izbira bližino naselij. Razlike v trendih je mogoče pripisati dejstvu, da je GAM obravnaval spremenljivko, ki temelji na razdalji, ločeno, medtem ko jo je GLMM obravnaval skupaj z drugimi spremenljivkami in je upošteval kombinirane učinke drugih spremenljivk, ki lahko spremenijo navidezno smer razmerja..

3.1.2.1 Nočna aktivnost

Na podlagi GPS-telemetričnih podatkov in analize visokoločljivostnih LiDAR podatkov smo analizirali vpliv reliefnih oblik, reliefnih značilnosti in človeške infrastrukture na izbiro habitata pri risih in divjih mačkah. Potrdili smo, da so reliefne oblike in reliefne značilnosti v nočnem času, ko sta obe vrsti najbolj aktivni, pomembno vplivale na izbiro habitata, vendar so se vzorci izbire med obema vrstama razlikujejo (poglavji 2.1 in 2.2). Rezultati kažejo, da so risi izbirali razgiban teren in bližino jam, sten, kraških kotanj, grebenov, izdankov kamnin in gozdnih cest; na splošno so izbirali tudi bližino glavnih cest, izogibali pa so se naseljem in gozdnim robovom. Divje mačke so izbirale manj strma območja, bližino glavnih cest, gozdnih robov in grebenov, vendar so se izogibale sten in gozdnih cest. Rezultati kažejo, da so na splošno izbirali tudi bližino jam, izogibali pa so se naselij. Kljub temu, da so nekatere oblike uporabljali manj

pogosto od njihove razpoložljivosti v prostoru, so jih vseeno absolutno gledano redno uporabljali (poglavje 2.2, Supplementary materials, Figure S2). Take reliefne oblike morda izbirajo le za določena vedenja (npr. markiranje ali gibanje), kar je bilo ugotovljeno tudi na podlagi sledenja v snegu in spremljanja s fotopastmi (Krofel in sod., 2022). Razlike v izbiri habitata pa bi lahko bile tudi posledica tega, da se divja mačka prostorsko izogiba dominantni vrsti (risu), ki jo občasno pleni (Krofel in sod., 2021a, 2022).

Reliefne oblike, kot so izdanki kamnin, stene, jamski vhodi in spodmoli, lahko služijo kot pomembna komunikacijska mesta za markiranje teritorijev (Allen in sod., 2017; Melzheimer in sod., 2020; Mohorović in Krofel, 2020). Ker je za obe vrsti značilno teritorialno vedenje in pretežno samotarski način življenja (Schmidt in sod., 1997; Jerosch in sod., 2017), je kemična komunikacija preko označevanja oz. markiranja z uriniranjem, iztrebljanjem in drgnjenjem pomembna za prostorsko razporejanje in vzdrževanje teritorija (Kos in sod., 2005; Ruiz-Olmo in sod., 2013; Allen in sod., 2017). Izbiro preučevanih reliefnih oblik je deloma mogoče pojasniti z njihovo opaznostjo v pokrajini, kar lahko pritegne pozornost živali in s tem poveča verjetnost, da bo lokacijo markiranja zaznal osebek iste vrste (Gosling in Roberts, 2001; Vogt in sod., 2014). Poleg tega so predvsem izdanki kamnin pogosto poraščeni z mahom, kar izboljša vpojnost urina, ali so oblikovani kot previsi, kar zagotavlja zaščito pred vremenskimi vplivi. Za oboje se je izkazalo, da poveča obstojnost vonja in s tem izboljša učinkovitost kemične komunikacije pri mačkah (Mohorović in Krofel, 2020). Naši rezultati nakazujejo, da bi lahko številčnost in razpoložljivost raznolikih reliefnih oblik oz. geodiverziteta vplivala tudi na razporeditev komunikacijskih mest znotraj domačih okolišev in s tem vplivala na socialno-prostorsko organiziranost prostoživečih mačk. Poleg reliefnih oblik risi v nočnem času, ko je človeška prisotnost manjša, selektivno izbirajo tudi linearno človeško infrastrukturo, predvsem gozdne ceste in rekreacijske poti, kar lahko izkoristijo za lažje gibanje in večjo učinkovitost markiranja (Krofel in sod., 2017). Nasprotno pa bi lahko bilo močno izogibanje gozdnih cest s strani divjih mačk povezano z izpostavljenostjo nevarnostim srečanj s plenilci, saj jih pogosto uporabljajo tako risi, kot tudi ostale velike zveri (Krofel in sod., 2017; Bojarska in sod., 2020).

Poleg kemične komunikacije je izbira razgibanega in skalovitega terena, različnih reliefnih oblik in linearne človeške infrastrukture pri risu lahko povezana tudi z gibanjem in lovom. Zaradi zakraselosti je površje slovenskega Dinarskega krasa ponekod izrazito skalovito. Na teh območjih so najpogostejše reliefne oblike izdanki kamnin (npr. škrapljišča, skalni bloki), ki jih pogosto prerašča mah. Takšen teren risu omogoča kritje in tih pristop oz. gibanje, kar je lahko še posebej pomembno v suhem vremenu, ko hoja po z listjem pokritih tleh povzroča hrup, ki lahko izda plenilca potencialnemu plenu. Dodatno gibanje po izstopajočih reliefnih oblikah, npr. izdankih kamnin, grebenih, robovih sten in kraških kotanj omogoča dober pregled nad okolico in zaznavanje morebitnega plena ali nevarnosti (Hočevár in sod., 2021). Ris pleni tako, da se plenu približa z zalezovanjem in nato napade na presenečenje. Zato lahko razgiban in skalovit teren z raznolikimi reliefnimi oblikami poleg vegetacije zagotavlja kritje, hkrati pa plenu onemogoča lažji pobeg (Sunkuist, M. E. in Sunkuist, F. C., 1989; Krofel in sod., 2007; Podgórski in sod., 2008; Belotti in sod., 2013). Naše rezultate o izbiri (pri risu) oz. rabi (pri divji mački) izdankov kamnin dodatno podpirajo tudi podatki sledenja v snegu in spremljanja

s fotopastmi (poglavje 2.2, Figure 2), ki nakazujejo, da obe vrsti pogosto uporabljata skalovito površje, ki je pogosto poraščeno z mahom.

Naši rezultati kažejo, da so specifične reliefne značilnosti ključni del mikrohabitatnih značilnosti, ki lahko vplivajo prostorsko ločevanje med risi in divjimi mačkami, hkrati pa vplivajo tudi na primernost določenega območja za obe vrsti. Poleg vrstno specifičnih razlik pri izbiri habitata smo ugotovili tudi, da prihaja do nekaterih razlik pri izbiri habitata med preseljenimi in nepreseljenimi risi ter med preseljenimi risi z različnimi stopnjami izkušenosti oz. poznavanja novega domačega okolisa (naivni in izkušeni preseljeni risi, poglavje 2.2). Kot je pokazala pretekla raziskava, lahko stopnja izkušenosti oz. poznavanje domačega okolisa vpliva na izbiro habitata pri gibanju in plenjenju (Oliveira in sod., 2023). Ob primerjavi izbire habitata med nepreseljenimi in preseljenimi risi, smo opazili podobne vzorce izbire in izogibanja, ki pa so bili nekoliko močnejši pri preseljenih risih (poglavje 2.2). Do razlik pri izbiri habitata lahko prihaja zaradi različne razpoložljivosti preučevanih elementov (npr. reliefne oblike in gozdne ceste) na območju Karpatov, od koder izvirajo preseljeni risi, in slovenskega Dinarskega krasa. Na območju slovenskega Dinarskega krasa je razpoložljivost razgibanega, skalnatega in raznolikost reliefnih oblik večja v primerjavi s fluvialnim reliefom, ki je razvit na območju Karpatov. Prav tako je na območju Slovenije večja gostota gozdnih cest. Večja razpoložljivost mikrohabitatnih značilnosti lahko delno pojasni njihovo močnejšo izbiro s strani preseljenih risov, na kar nakazujejo tudi raziskave s področja funkcionalnih odzivov (poglavje 2.3; Oeser in sod., 2023). Po našem vedenju je to prva raziskava, ki je obravnavala to vprašanje. Ker naši rezultati kažejo, da ni večjih razlik pri vzorcih izbire habitata med risi z različnimi stopnjami izkušenosti (preseljeni in nepreseljeni ter naivni in izkušeni preseljeni risi), to dodatno dokazuje, da so risi na splošno prilagodljiva vrsta, ki ne samo da na območju razširjenosti vrste naseljuje različne pokrajinske tipe (von Arx in sod., 2021), ampak se lahko po preselitvi hitro seznani z novim okoljem in nanj prilagodijo. To je še posebej pomembno v kontekstu ohranjanja te vrste, kjer so ponovne naselitve pomemben del varstvenih strategij.

3.1.2.2 Dnevno počivanje

Pretekle raziskave nakazujejo, da na izbiro habitata risa v dnevnem času vpliva prisotnost človeka in da za dnevna počivališča izbirajo težko dostopna in razgibana območja z nizko vidljivostjo, kar nudi kritje v času počitka in spanja (Filla in sod., 2017; Belotti in sod., 2018; Signer in sod., 2019; Hočevar in sod., 2021). Živali so v tem času najbolj ranljive, posledično je izbira varnega počivališča ključnega pomena za njihovo preživetje (Kusler in sod., 2017; Hočevar in sod., 2021).

Na območju slovenskega Dinarskega krasa so Hočevar in sod. (2021) ugotovili, da risi za počivanje izbirajo lokacije na vrhovih in grebenih ter strma in razgibana območja z manjšo vidljivostjo. Tudi naši rezultati potrjujejo, da risi za dnevno počivanje izbirajo bližino izdankov kamnin ter razgibana, skalovita, strma območja in višje nadmorske višine, izogibajo pa se bližine rekreacijskih poti. Izbira reliefno nedostopnih območij in območij z nizko vidljivostjo jim omogoča dobro kritje, pregled nad okolico in zaznavanje plena ter morebitne nevarnosti. (Hočevar in sod., 2021). Podobno izbiro habitata kažejo tudi rezultati raziskave z Bavarsko-Češkega gozdnega ekosistema, kjer so Signer in sod. (2019) ugotovili, da risi za počitek pogosto

izbirajo izdanke kamnin, saj se je v njihovi neposredni bližini (50-metrski radij) nahajalo 12,3 % dnevnih počivališč. V naši raziskavi smo uporabili sloj izdankov kamnin, ki je temeljil na daljinskem zaznavanju. To nam je omogočilo prostorsko natančnejšo analizo istega preučevanega območja, saj je naš sloj vseboval večje število prepoznanih izdankov kamnin ($n = 80.590$) v primerjavi z uporabljenim slojem v raziskavi Signerja in sod. (2019), ki so lahko vključili precej manjše število izdankov kamnin ($n = 627$). Znotraj posameznih domačih okolišev risov smo zaznali več tisoč izdankov kamnin. Risi, za katere so na voljo podatki o dnevnih počivališčih, so jih redno uporabljali, pri čemer smo na obeh preučevanih območjih opazili individualne razlike v deležu počivališč v bližini izdankov kamnin (poglavje 2.3, Priloga D). Poleg tega smo v naši raziskavi v nasprotju s prejšnjo pri določanju lokacij dnevnih počivališč uporabili tudi podatke o aktivnosti (podatki merilnika pospeškov), kar nam je omogočilo natančnejšo identifikacijo dnevnih počivališč. V preteklih raziskavah so se pri določanju počivališč zanašali le na čas dneva, kar lahko vodi do napačnih rezultatov, ker se risi včasih gibljejo tudi sredi dneva (Heurich in sod., 2014). Z odstranitvijo dnevnih lokacij, za katere so vrednosti merilnika pospeškov kazale na premikanje, smo v naši raziskavi to napako zmanjšali. Uporaba izboljšane sloja izdankov kamnin in natančnejših lokacij dnevnih počivališč je pokazala, da je v neposredni bližini izdankov kamnin 31,1 % dnevnih počivališč. Ta primerjava nakazuje, da imajo lahko podrobnejši in natančnejši podatki o mikrohabitatnih značilnostih pomemben vpliv na rezultate in razumevanje ekologije risov.

Poleg vplivov reliefnih oblik in reliefnih značilnosti površja je na izbiro lokacij za dnevna počivališča vplivala tudi človeška infrastruktura. Naši rezultati kažejo, da so se za razliko od nočnega časa risi pri izbiri dnevnih počivališč izogibali rekreacijskih poti, ostala človeška infrastruktura pa na izbiro lokacij ni imela vpliva. Ljudje rekreacijske poti uporabljajo predvsem podnevi, ko so risi zaradi manjše pazljivosti v času spanja najbolj ranljivi. Zato v času dnevnega počivanja potrebujejo varnejše lokacije, ki so težje dostopnejše in z manjšimi motnjami (Belotti in sod., 2012, 2018; Signer in sod., 2019; Hočevár in sod., 2021).

S primerjavo dveh območij z različno razpoložljivostjo izdankov kamnin, razgibanosti in skalovitosti terena smo v naši raziskavi lahko preverili, ali pri izbiri habitata risa prihaja do funkcionalnih odzivov glede na razpoložljivost takšnih habitatov. Na območju Bavarsko-Češkega gozdnega ekosistema je bila izbira izdankov kamnin pri dnevnih počivališčih močnejša kot na območju slovenskega Dinarskega krasa (Signer in sod., 2019; Hočevár in sod., 2021). Hočevár in sod. (2021) so predvidevali, da bi lahko bila manj izrazita izbira takšnega terena v Sloveniji lahko povezana s funkcionalnim odzivom pri izbiri habitata zaradi večje razpoložljivosti izdankov kamnin na območju slovenskega Dinarskega krasa.

Naše analize so sedaj potrdile funkcionalni odziv pri izbiri razgibanega in skalnatega terena tako za dnevna počivališča kot tudi za nočne lokacije. Risi so pokazali močnejšo izbiro razgibanega in skalnatega terena, ko je bila razpoložljivost takšnih mikrohabitatov manjša. Funkcionalnega odziva pri izbiri izdankov kamnin pa nismo potrdili niti ponoči niti podnevi. Opazili smo veliko individualno variabilnost, zlasti pri izbiri in rabi izdankov kamnin ter skalnatega terena na obeh preučevanih območjih, kar kaže na to, da so te značilnosti lahko za nekatere osebe še posebej pomembne (poglavje 2.3, Priloga D). Variabilnost je lahko

posledica različnih razlogov, kot so intrinzični (npr. spol, starost, reproduktivno stanje) ali zunanji dejavniki (npr. sezonskost, prisotnost sovratnikov, razpoložljivost plena).

Naši rezultati tudi nakazujejo, da bi lahko povečanje rekreacijskih dejavnosti (npr. pohodništvo, »geocaching«, gobarjenje in plezanje) in vse pogostejše umeščanje infrastrukture (npr. ceste, obnovljivi viri energije) v naravna območja, negativno vplivala na rise v dnevnem času, ko se izogibajo bližine človekovih dejavnosti (Belotti in sod., 2012, 2018). Zato ne bi bilo presenetljivo, če bi risi vse pogostejše izbirali habitate, ki so ljudem manj dostopni, zlasti na območjih, kjer je razpoložljivost takšnega terena manjša oz. omejena. Da bi bolje razumeli kako vpliva povečanje rekreacijskih dejavnosti in umeščanje infrastrukture na morebitno skupno spremembo kakovosti habitata za risa ali morda celo vitalnost osebkov, bi bile potrebne nadaljnje raziskave, ki bi poleg teh pritiskov upoštevale tudi kombinacije z drugimi neodvisnimi negativnimi dejavniki, s katerimi se soočajo risi (npr. parjenje v sorodstvu, krivolov). Glede na to, da naši rezultati kažejo, da so skalovita in razgibana območja pomembna za risa, bi se bilo iz načela previdnosti smiselno izogibati bližini takšnih habitatov pri umeščanju nove infrastrukture, zlasti v primeru, ko je teh malo, s tem bi preprečili potencialno slabšanje ali celo izgubo habitata za risa.

3.1.2.3 Plenjenje

Plenjenje je temeljna ekološka funkcija plenilcev, lovna uspešnost pa je dejavnik, ki pomembno vpliva na fitnes oziroma zmožnost preživetja osebkov (Pyke in sod., 1977; Belotti in sod., 2013; Walton in sod., 2016). Na plenjenje in uspešnost lova vplivajo številni dejavniki. Ključnega pomena je razpoložljivost plena (»hipoteza o razpoložljivosti plena«), na uspešno uplenitev pa med drugim vplivajo tudi značilnosti habitata in mikrolokacije (»pokrajinska hipoteza«) (Hopcraft in sod., 2005). Pri plenjenju je pomembno, da habitat plenilcu zagotavlja tako kritje kot tudi dober pregled nad območjem in plenom (Sunkvist, M. E. in Sunkvist, F. C., 1989; Krofel in sod., 2007; Podgórski in sod., 2008; Belotti in sod., 2013).

Poleg drugih vedenj so tudi v preteklih raziskavah pri risu ugotovili povezavo med plenjenjem in določenimi reliefnimi oblikami in značilnostmi (Krofel in sod., 2006, 2007; Krofel, 2007; Krofel, 2010). V preliminarni študiji na slovenskem Dinarskem krasu, ki se je nanašala na topografske in vegetacijske značilnosti lokacij plena risa, so ugotovili, da je 39 % lokacij plena na dnu vrtač, poleg tega pa se je večina lokacij plena nahajala tudi na razgibanem reliefu in strmih pobočjih (Krofel in sod., 2007). Tudi naši rezultati kažejo, da imajo kraške kotanje v primeru risa pomembno vlogo pri plenjenju, saj se je glede na terenski popis v kraških kotanjah ali njihovi neposredni bližini nahajalo 58 % risovih plenov. V primerjavi z avtomatsko zaznanimi kraškimi kotanjami je bilo v kraških kotanjah ali njihovi neposredni bližini 35 % plenov, kar je višje, kot bi pričakovali ob naključnem plenjenju glede na razpoložljivosti. To bi lahko povezali s tem, da plen na tako razgibanem vrtačastem in skalnatem terenu ne uspe razviti maksimalne hitrosti, risi pa izkoristijo svojo agilnost in lažje ujamejo plen. Poleg tega se pozimi na dnu kraških kotanj akumulira sneg, kar še dodatno upočasni plen (Krofel in sod., 2007). Prav tako pa obstaja možnost, da risi svoj plen po uplenitvi odvedejo na dno kraških kotanj, saj je tam verjetno manjša možnost, da ga odkrijejo kleptoparaziti, npr. medvedi, ki risom povzročajo pomembne izgube hrane (Krofel in Jerina, 2016). Naši rezultati kažejo tudi na to, da so risi

glede na razpoložljivost izbirali kraške kotanje z večjo površino in globino. V udornicah in tudi na robovih fluviokraških dolin se nahajajo večje stene, ki so priljubljen habitat gamsa, ki je prav tako risov plen, zaradi česar bi lahko bila izbira teh reliefnih oblik risom privlačna za lov (Krofel, 2010).

V kraških kotanjah se pogosto nahajajo tudi jamski vhodi (Čonč in Tičar, 2024). Izbiro jam bi lahko deloma pojasnili s plenjenjem polhov, ki na območju slovenskega Dinarskega krasa predstavljajo drugi najpomembnejši vir hrane pri risu. Pogosto jih uživajo predvsem samice in mladi risi v času osamosvajanja (Krofel in sod., 2011). Vsaj v zimskem obdobju risi očitno lovijo polhe, ko ti prezimujejo v jamah in razpokah med izdanki kamnin (Polak, 1997; Krofel, 2010; Krofel in sod., 2011).

Kaže se, da na splošno tudi divje mačke izbirajo jame in uporabljajo kraške kotanje. V nasprotju z risi, katerih glavni plen so parkljarji (Krofel in sod., 2011), se divje mačke v zmernem podnebju večinoma prehranjujejo z glodavci, zlasti voluharicami in mišmi, pa tudi polhi (Lozano in sod., 2006; Potočnik, 2006; Ruiz-Villar in sod., 2023). Kot omenjeno, so jame in razpoke med izdanki kamnin pogost habitat polha (Polak, 1997; Krofel, 2010; Krofel in sod., 2011). O razširjenosti voluharic in miši na območju slovenskega Dinarskega krasa je na voljo malo podatkov, vendar bi bilo izogibanje strmemu in razgibanemu terenu pri divjih mačkah lahko povezano z večjo številčnostjo teh glodavcev v produktivnejših habitatih z globljimi prstmi (Niedziałkowska in sod., 2015). Druga možna razlaga za opažene razlike pri izbiri habitata med obema vrstama bi lahko bila povezana z medvrstnimi interakcijami. Ris je precej večji od divje mačke in jih občasno tudi upleni (Krofel in sod., 2021a, 2022). Tako bi lahko divje mačke z izogibanjem določenim mikrohabitatom, ki jih selektivno uporabljajo risi, zmanjšale tveganje plenjenja.

Skladno z ugotovitvami preteklih raziskav, da divje mačke na odprtih habitatih (travniki in pašniki) ob gozdnih robovih pogosto lovijo glodavce in se izogibajo bližini naselij zaradi različnih motečih dejavnikov (Klar in sod., 2008; Beutel in sod., 2017; Jerosch in sod., 2018; Ruiz-Villar in sod., 2023), tudi naši rezultati na splošno kažejo na enake vzorce izbire gozdnih robov in izogibanja naseljem. V nasprotju z opažanji v nekaterih drugih evropskih državah, kjer so se divje mačke glavnim cestam izogibale (Klar in sod., 2008; Jerosch in sod., 2018), so pri nas divje mačke izbirale njihovo bližino. Enak vzorec izbire so opazili tudi v Kantabrijskem gorovju, kjer so divje mačke porabile bistveno več časa za lov v bližini glavnih cest (Ruiz-Villar in sod., 2024) in morda tudi za hranjenje s kadavri na in ob cestah (Ruiz-Villar in sod., 2020). Nasprotno so se divje mačke izogibale gozdnim cestam, kar je morda povezano z izogibanjem nevarnostim srečanj s plenilci, saj te ceste pogosto uporabljajo risi in ostale velike zveri (Krofel in sod., 2017; Bojarska in sod., 2020).

3.1.3 Omejitve

Kljub temu, da smo uspešno naslovili nekatera področja povezana s preučevanjem vpliva abitoskih mikrohabitatnih značilnosti na izbiro habitata pri prostoživečih mačkah, pri naslavljanju te tematike ostaja nekaj izzivov, povezanih predvsem s pridobivanjem podatkov in metodami.

LiDAR predstavlja zanesljiv vir informacij za preučevanje abiotičnih mikrohabitatnih značilnosti površja, kjer do večjih sprememb v reliefu prihaja le ob antropogenih posegih ali obsežnejših geomorfnih procesih, ki pustijo vidne posledice na površju (Triglav Čekada, 2011). Poleg tega pa je LiDAR uporaben tudi pri preučevanju vegetacije (Davies in Asner, 2014; Sergeyev in sod., 2023). Lasersko skeniranje površja Slovenije je bilo izvedeno v letih 2011, 2014 in 2015 (Triglav Čekada in Bric, 2015). V naši raziskavi smo uporabili podatke z GPS-telemetričnih ovratnic risov in divjih mačk, ki so bili spremljani v različnih časovnih obdobjih (2006-2008, 2010-2012, 2019-2023). Čeprav je vegetacija eden ključnih dejavnikov, ki lahko vpliva na izbiro habitata obeh vrst, saj nudi kritje med počivanjem, gibanjem in plenjenjem (Krofel in sod., 2007; Podgórski in sod., 2008; Jerosch in sod., 2010; Jerosch in sod., 2018; Hočevár in sod., 2021), podatkov o strukturi (mikro)vegetacije v analize nismo mogli vključiti. Med časom spremljanja obeh preučevanih vrst (celo leto) ter med LiDAR podatki (skeniranje pozimi, ko je olistanost vegetacije najmanjša) prihaja do prevelikih razlik, zato bi tako velika časovna in sezonska razlika med podatki lahko vplivala na napačno interpretacijo rezultatov. Za pravilno razumevanje ekologije je namreč pomembno, da so podatki spremenljivk v čim bližjem časovnem okviru podatkom pridobljenim z GPS-telemetričnih ovratnic (Belotti in sod., 2013).

V času raziskave v okviru te doktorske disertacije za Hrvaško še ni bilo na voljo javno dostopnih LiDAR podatkov. Domači okoliši nekaterih risov in divjih mačk so obsegali območja zunaj Slovenije (njihovi domači okoliši so bili čezmejni in so segali čez slovensko-hrvaško mejo). Posledično smo v analizah lahko upoštevali le lokacije na območju Slovenije, kjer so bili za izračun topografskih spremenljivk na voljo LiDAR podatki, del domačih okolišev tistih osebkov, ki so segali na Hrvaško, pa smo morali iz raziskave izpustiti. Od začetka leta 2024 so tudi za Hrvaško na voljo javno dostopni LiDAR podatki, kar bo v prihodnjih raziskavah omogočilo raziskovanje vpliva mikroreliefnih značilnosti tudi na takšnih čezmejnih območjih.

GPS-telemetrične ovratnice, s katerimi so bile opremljene divje mačke, so bile zaradi varčevanja z baterijami programirane tako, da so skoraj izključno zbirale GPS lokacije le ponoči (ovratnice treh divjih mačk, ki so bile vključene v analize, so zbirale samo nočne lokacije, štirih divjih mačk pa še eno dodatno lokacijo med 7.00 in 10.00). Premajhen vzorec podatkov tako ni omogočal analize izbire habitata za dnevne lokacije.

Na rezultate bi lahko vplivala tudi uspešnost beleženja GPS lokacij, če bi bila le-ta pomembno drugačna v določenih habitatih glede na ostale (Frair in sod., 2004). Vendar je bila v našem primeru uspešnost beleženja lokacij GPS-telemetričnih ovratnic na območju Slovenije zelo visoka (>98 %), zato ne pričakujemo pomembnega vpliva manjkajočih podatkov na rezultate o izbiri habitata. Določene omejitve predstavljata slabša prostorska natančnost GPS-telemetričnih podatkov (ocenjene napake so 4-16 m, odvisno od vrste habitata) (Stache in sod., 2012). Boljša natančnost GPS lokacij bi omogočila bolj točno in natančno interpretacijo vpliva mikroreliefnih značilnosti na rabo prostora pri obeh vrstah. Zaradi upoštevanja napake GPS, se pogosto okoli GPS lokacij uporabi določen radij in znotraj radija izračuna povprečne vrednosti spremenljivk (npr. povprečni naklon). Takšno posploševanje podatkov lahko napačno prikaže dejansko stanje. Če je na primer lokacija za dnevno počivanje na ravnem območju med izdanki

kamnin, kjer je kategorija glede na vrednost TPI opredeljena kot »ravnina«, lahko izračun povprečne vrednosti v določenem radiju napačno privede do druge kategorije, npr. »zgornje pobočje«, kar ne ustreza realnem stanju. V primeru, da upoštevamo le vrednost spremenljivke na lokaciji GPS, je lahko tudi to zavajajoče. Npr. lokacija dnevnega počivališča risa je lahko na ravnem območju (npr. skalnata polica) med izdanki kamnin ali pod njimi. Z napačno interpretacijo rezultatov bi lahko sklepali, da risi za dnevni počitek izbirajo (odprta) ravna območja. Zato je najbolj ustrezen pristop uporaba spremenljivk, ki temeljijo na razdalji ali deležu preučevanih značilnosti v iskanem radiju.

Rezultati analiz (poglavje 2.3) kažejo, da se risi pri izbiri habitata za dnevna počivališča, izogibajo predvsem različnih poti namenjenih rekreacijskim dejavnostim (npr. pohodništvo, kolesarjenje, jahanje). V zadnjih desetletjih je rekreacija na prostem vedno bolj priljubljena, kar je okrepilo prisotnost človeka v naravnih habitatih. Človeške motnje lahko negativno vplivajo na vedenje živali in povzročijo upad populacij, zato je razumevanje vplivov rekreacije na zavarovane vrste temeljnega pomena (Belotti in sod., 2018; Ripari in sod., 2022). Na žalost je težko kvantitativno opredeliti in primerjati ravni rekreacije, saj za nobeno od preučevanih območij ni bilo na voljo uradnih merskih podatkov o uporabi poti. Zavedamo se, da se danes v ta namen uporabljajo metrični podatki iz različnih športnih aplikacij kot je npr. Strava (Corradini in sod., 2021), vendar ti podatki niso na voljo za vsa obdobja, ko so bili z GPS-telemetričnimi podatki opremljeni risi. Poleg tega pa se intenzivnost rekreacijskih dejavnosti med različnimi leti, letnimi časi in deli preučevanih območij lahko precej razlikuje. Nadaljnje raziskave, ki bi vključevale take podatke, bi bile pomembne za razumevanje mejnih vrednosti, pri katerih se risi začnejo izogibati takšni infrastrukturi.

3.1.4 Perspektive

Raziskava v okviru te doktorske disertacije je doprinesla pomembne napredke na področju metodologije in razumevanja ekologije obeh preučevanih vrst. S kombiniranjem metod za daljinsko zaznavanje reliefnih oblik in mikroreliefnih značilnosti ter GPS-telemetričnih podatkov smo pokazali, da lahko interdisciplinaren pristop pripomore k izboljšavam pri preučevanju ekologije živalskih vrst. Čeprav so tudi pretekle raziskave vključevale podatke o abitoskih mikrohabitatnih značilnostih, so se opirale predvsem na tradicionalne metode, kot so terensko kartiranje in digitalizacija reliefnih oblik, izračuni reliefnih značilnosti pa so temeljili na digitalnih modelih višin s slabšo ločljivostjo. Po našem vedenju je raziskava v okviru te doktorske disertacije ena prvih, ki v habitatne analize vključuje tudi podatke o specifičnih reliefnih oblikah in mikroreliefnih značilnostih ter se pri pridobivanju teh informacij opira predvsem na metode daljinskega zaznavanja na podlagi visokoločljivostnih LiDAR podatkov. Ob upoštevanju različnih dejavnikov v analizah rabe prostora (topografski, antropogeni, vegetacijski) se je izkazalo, da so reliefne oblike in mikroreliefne značilnosti pomemben dejavnik, ki vpliva na izbiro habitata risov in divjih mačk. Poleg tega pa pestrost reliefnih oblik in reliefnih značilnosti lahko poveča primernost določenega območja za obe vrsti in vpliva na različna vedenja.

Naše ugotovitve kažejo, da bi bilo v prihodnjih analizah potrebno upoštevati tudi takšne abiotске mikrohabitatne značilnosti, saj vključevanje večjega števila relevantnih spremenljivk

izboljša habitatne modele in vpliva na rezultate. Rezultati, ki jih zagotavljajo takšne raziskave, se lahko uporabijo tudi za usmerjanje varstvenih prizadevanj in sprejemanje odločitev pri prostorskem načrtovanju, pri pisanju smernic za upravljanje živalskih vrst, gozdnogospodarskih načrtov, prostorskih načrtov in ostalih smernic.

Pripravljen sloje reliefnih oblik lahko poleg geomorfologije v prihodnje uporabimo tudi za raziskave na drugih področjih, kot so na primer geologija, botanika, zoologija, gozdarstvo, turizem, varstvo narave, načrtovanje in odločanje o vzpostavitvi novih geoparkov ter izdelava državnih ali lokalnih akcijskih načrtov za varovanje geodiverzitete. S povečevanjem števila prebivalstva prihaja do naraščanja motenj v naravnem okolju in do drobljenja oz. fragmentacije habitatov (Haddad in sod., 2015). Največji problem fragmentacije oz. razdrobljenosti habitatov predstavlja transportna infrastruktura, pomembno pa k temu prispeva tudi širjenje urbanih območij in umeščanje obnovljivih virov energije v prostor. Rezultati naše raziskave lahko pripomorejo k določanju najprimernejših mikrolokacij za umeščanje prehodov za prostoživeče živali oz. zelenih mostov (ekoduktov) preko ovir, ki jo na primer predstavljajo avtoceste. Ker risi za počivanje izbirajo skalnat in razgiban teren, izogibajo pa se rekreacijskih poti, je potrebno pri načrtovanju potrebno posebno pozornost nameniti umeščanju nove rekreacijske infrastrukture (npr. pohodniške poti, plezalne smeri, »geocaching«) na takšna območja, kar je zaradi opaženih funkcionalnih odzivov vrste še posebej pomembno tam, kjer so ta v pokrajini redka. Ker obe vrsti izbirata določene reliefne oblike, bi bile te še posebej koristne pri izbiri mikrolokacij za postavitve fotopasti ali pasti za odlov za potrebe monitoringa populacij in opremljanja s telemetričnimi ovraticami.

Kljub doprinosu naše raziskave k metodološkemu pristopu in razumevanju ekologije obeh vrst, nekatera področja potrebujejo dodatne izboljšave, kar bi omogočilo odgovore na nerazrešena ekološka vprašanja, ki so povezana predvsem z omejitvami, s katerimi smo se srečali. Zato menimo, da bi morale prihodnje raziskave nasloviti naslednje vidike:

- Na daljinsko zaznavanje rastlinskih združb v podrasti vplivajo gozdne krošnje, ki zaradi gostote zaprejo pogled na podrast. Kljub temu se na tem področju razvija vse več pristopov za prepoznavanje vegetacijske strukture (Davies in Asner, 2014; Sergeyev in sod., 2023; Yang in sod., 2023). Pri preučevanju ekologije živali je pomembno, da upoštevamo tiste mikrohabitatne značilnosti, ki v čim bolj enakem časovnem obdobju lahko potencialno vplivajo na njihovo rabo prostora (Belotti in sod., 2013). Kot omenjeno v poglavju 3.1.3, je bila v naši raziskavi časovna in sezonska razlika med podatki LiDAR in GPS-telemetričnimi podatki zelo velika, kar bi ob vključevanju podatkov o vegetaciji, pridobljenih z laserskim skeniranjem površja, lahko vplivalo na napačno interpretacijo rezultatov. Ena izmed rešitev je sezonsko spremljanje podrasti s pomočjo daljinskega zaznavanja za prepoznavanje podrasti na podlagi satelitskih posnetkov, ki so bili posneti v istem časovnem obdobju, kot so bili spremljani preučevani osebki, vendar je postopek daljinskega zaznavanja zahteven (Yang in sod., 2023). Poleg satelitskih posnetkov pa bi tudi zaporedno lasersko skeniranje površja tekom več let omogočilo vpogled v hitrost rasti vegetacije in vključitev interpolirane spremenljivke o višini vegetacije v analize o rabi prostora pri prostoživečih živalih.

- Dokazali smo, da je metodološki pristop, ki temelji na analizi visokoločljivostnih LiDAR podatkov in GPS-telemetričnih podatkov primeren za analize izbire habitata živali, ki poseljujejo velika območja. Naši rezultati kažejo, da bi bil tak pristop verjetno možen tudi na večji, kontinentalni ravni. To bi omogočilo, da bi pridobili širše znanje o vplivu reliefnih oblik in mikroreliefnih značilnosti na rabo prostora pri vrstah s širšega območja Evrope ali drugih kontinentov. Večje število vhodnih podatkov posameznih osebkov iz različnih populacij bi pripomoglo tudi k znižanju vpliva individualne variabilnosti pri analizah izbire habitata. Od začetka leta 2024 so za Hrvaško na voljo prosto dostopni LiDAR podatki, kar bi omogočilo izboljšanje analiz izbire habitata pri tistih osebkih, katerih domači okoliši segajo na čezmejno območje med Slovenijo in Hrvaško. Ker pa visokoločljivostni LiDAR podatki (še) niso na voljo v vseh državah, bi kot alternativo LiDAR podatkom lahko uporabili digitalni model višin z nekoliko slabšo ločljivostjo, npr. TanDEM-X (12×12 m; German Aerospace Center, DLR), ki je na voljo po celem svetu. To bi omogočilo razširitev analize na več držav oz. celoten kontinent in tudi hitrejšo obdelavo v primerjavi z LiDAR podatki. Po drugi strani pa bi z uporabo nizkoločljivostnih digitalnih modelov višin izgubili na natančnosti mikrohabitatnih značilnosti. Ocena razlik o izgubi podatkov z uporabo visoko- in nizkoločljivostnimi digitalnimi modeli višin zahteva nadaljnje raziskave.
- Izbira habitata se lahko razlikuje glede na faze aktivnosti, specifična vedenja, letne čase, spol in ostale intrinzične in zunanje dejavnike. Naša raziskava se je pri izbiri prostora pri divjih mačkah osredotočila na aktivno (nočno) obdobje zaradi pomanjkanja podatkov o dnevnih lokacijah, kar nam je onemogočilo preverjanje morebitnih razlik v izbiri habitata med dnevnimi in nočnimi lokacijami. Zato bi bilo potrebno zbrati več podatkov o dnevnih lokacijah in z njimi ponoviti analize.

3.2 SKLEPI

- Potrdili smo, da risi izbirajo bližino kraških kotanj, zlasti ob upoštevanju njihovih robov. Glede na razpoložljivost izbirajo kraške kotanje z večjo površino in globino (H1 delno podprta).
- Potrdili smo, da imajo kraške kotanje v primeru risa pomembno vlogo pri plenjenju, saj smo v kraških kotanjah ali njihovi neposredni bližini našli več plenov, kot bi pričakovali glede na razpoložljivost teh reliefnih oblik (H1 delno podprta).
- Rezultati preliminarne raziskave na manjšem območju (poglavje 2.1) so pokazali, da divja mačka izbira bližino kraških kotanj, vendar je izbira manj izrazita kot pri risu. Raziskava, ki vključuje večje število osebkov divjih mačk na širšem območju slovenskega Dinarskega krasa (poglavje 2.2) ne kaže, da bližina kraških kotanj kakorkoli vpliva (spremenljivka ni statistično značilna) na izbiro habitata (H1 delno podprta).
- Dokazali smo, da risi ne izbirajo le splošno razgibanega terena, temveč tudi različne reliefne oblike oz. elemente geodiverzitete (H2 podprta).
- Potrdili smo, da risi za počivanje (podnevi) izbirajo bližino izdankov kamnin ter razgibana, skalovita, strma območja in višje nadmorske višine (H2 podprta).

- Risi v času največje aktivnosti (ponoči) izbirajo razgibana, skalovita in strma območja, bližino jam, sten, kraških kotanj, grebenov in izdankov kamnin ter območja z južnimi ekspozicijami (H2 podprta).
- V nasprotju z našimi predvidevanji smo ugotovili, da na izbiro habitata divje mačke znotraj domačih okolišev v času največje aktivnosti (ponoči) bolj vplivata človeška infrastruktura in vegetacija kot pa reliefne značilnosti. Divje mačke izbirajo bližino glavnih cest, gozdnih robov in grebenov ter bolj položna pobočja, izogibajo pa se stenam in gozdnim cestam. Na splošno se kaže tudi, da izbirajo bližino jam in se izogibajo naseljem (H2 delno podprta).
- Na podlagi primerjave rabe prostora smo potrdili vrstno specifične razlike v izbiri habitata med prostoživečima mačkama na območju slovenskega Dinarskega krasa.
- Ponoči in podnevi risi kažejo podobne vzorce izbire topografskih elementov, vendar imajo ponoči topografski elementi manjši vpliv na izbiro habitata v primerjavi z dnevnimi lokacijami. Obratno pa velja za linearne antropogene elemente, ki se jih risi podnevi izogibajo, ponoči pa jih izbirajo (H3 podprta).
- Potrdili smo, da se risi v času počivanja (podnevi) izogibajo bližini rekreacijskih poti (npr. pohodne, kolesarske in jahalne poti), medtem ko ostala človeška infrastruktura ni imela pomembnega vpliva na izbiro lokacij za počivanje (H3 delno podprta).
- Potrdili smo, da risi v času največje aktivnosti (ponoči) izbirajo bližino rekreacijskih poti in gozdnih cest, izogibajo pa se gozdnih robov in naselij. Kaže se tudi, da na splošno izbirajo bližino glavnih cest, izogibajo pa se razpršenim stavbam (H3 delno podprta).
- Razlike v izbiri habitata v različnih delih dneva kažejo, da je v takšnih raziskavah za boljšo interpretacijo potrebno razlikovati med različnimi vedenji (npr. počivanje, gibanje, plenjenje) in fazami aktivnosti (dan, noč).
- Potrdili smo, da preseljeni in nepreseljeni risi kažejo podobne vzorce izbire habitata, vendar so bili vzorci izbire oz. izogibanja nekoliko močnejši pri preseljenih risih, kar nakazuje na plastičnost in prilagodljivost vrste (H4 podprta).
- Stopnja izkušenosti (čas po izpustu preseljenih risov) nima večjega vpliva na izbiro habitata, saj pri vzorcih izbire habitata med naivnimi in izkušenimi preseljenimi risi ni bilo statistično značilnih razlik.
- Risi bolj izrazito izbirajo skalovita in razgibana območja, kjer je razpoložljivost takšnih habitatov manjša (H5 podprta).
- Potrdili smo, da pri risu pri izbiri kamnitih in razgibanih območjih podnevi in ponoči prihaja do funkcionalnega odziva, medtem ko funkcionalnega odziva pri izbiri izdankov kamnin nismo potrdili (H5 delno podprta).
- Metode za daljinsko zaznavanje reliefnih oblik in značilnosti površja so v kombinaciji s podatki o lokacijah pridobljenih z GPS-telemetrijo zelo uporabne za raziskave s področja ekologije prostoživečih živali.
- Dokazali smo, da imajo različne reliefne oblike oz. elementi geodiverzitete, vključno z jamami, stenami, kraškimi kotanjami, grebeni in izdanki kamnin, pomemben vpliv na izbiro habitata pri risu in divji mački, kar bi lahko vplivalo na primernost prostora za obe vrsti.

- Naša raziskava nakazuje, da je lahko varovanje reliefnih oblik in reliefnih značilnosti površja (geodiverzitete) pomembno za ohranjanje biotske raznovrstnosti, saj predstavljajo pomemben habitat za mnoge ogrožene živali, rastline in glive.

4 POVZETEK (SUMMARY)

4.1 POVZETEK

Neživi oz. abiotiski dejavniki, pogosto imenovani tudi geodiverziteti, vplivajo na biotski del narave in pogojujejo oblikovanje habitatov ter razširjenost vrst. Vplivi splošnih abiotiskih dejavnikov (npr. podnebje, geologija in nadmorska višina) na habitate in razširjenost vrst so dobro poznani in raziskani. Poleg tega, da raznolike reliefne oblike zagotavljajo habitate in predstavljajo zavetišča za različne vrste, lahko vplivajo tudi na ekologijo in osnovne vedenjske vzorce prostoživečih živali. Povezave med topografijo in reliefnimi oblikami so še posebej izrazite pri prostoživečih mačkah (npr. pri pumah, leopardih, risih), kjer so pretekle raziskave o rabi prostora pokazale, da pogosto izbirajo razgiban, skalovit in težko dostopen teren ter različne izstopajoče reliefne oblike za različna vedenja, kot so gibanje, lov, markiranje in počitek. Ker imajo te živali običajno zelo velike domače okoliše, se tudi prostorske in ekološke analize osredotočajo na obsežna območja. Posledično so topografske spremenljivke pogosto omejene le na nekatere splošne značilnosti terena (npr. naklon), medtem ko so vplivi specifičnih reliefnih oblik in mikroreliefnih značilnosti običajno prezrti. V preteklih raziskavah, povezanih z rabo prostora pri prostoživečih mačkah, je bilo interpretaciji geomorfoloških značilnosti ter analizam LiDAR DMV-jev, ki zahtevajo posebna znanja in spretnosti, namenjene malo pozornosti. Posledično je naše znanje o vplivu mikro- in mezoreliefnih značilnostih habitatov na rabo prostora teh živali še vedno precej omejeno.

Glavni namen te doktorske disertacije je bil ugotoviti vpliv reliefnih oblik na rabo prostora pri evrazijskem risu (*Lynx lynx*; v nadaljevanju ris) in evropski divji mački (*Felis silvestris*; v nadaljevanju divja mačka). Zasnovali smo kvantitativno prostorsko-ekološko raziskavo, ki je celostno obravnavala tako reliefne oblike kot tudi rabo prostora znotraj domačih okolišev risov in divjih mačk pri specifičnih vedenjih (npr. počivanje, hranjenje, gibanje, markiranje) ter različnih fazah aktivnosti (podnevi in ponoči). Doktorska disertacija je razdeljena na tri glavna poglavja. Prvi dve poglavji se osredotočata na preučevanje rabe prostora pri risu in divji mački na območju slovenskega Dinarskega krasa, tretje poglavje pa obravnava izbiro habitata pri risu na dveh (bio-)geografsko različnih območjih v Evropi, slovenskem Dinarskem krasu in Bavarsko-Češkem gozdnem ekosistemu.

V prvi raziskavi smo na primeru kraških kotanj prikazali uporabnost visokoločljivostnih LiDAR podatkov in metod za avtomatsko zaznavanje reliefnih oblik za ekološke analize ter preučili izbiro kraških kotanj pri obeh vrstah, v primeru risa pa tudi ovrednotili pomen preučevanih oblik pri plenjenju (poglavje 2.1). Sledi raziskava, v kateri smo primerjali vzorce izbire različnih kraških reliefnih oblik ter topografskih, antropogenih in vegetacijskih značilnosti pri risu in divji mački, raziskali pa smo tudi ali prihaja do razlik v izbiri pri risih glede na njihov izvor (nepreseljeni in preseljeni) ter stopnjo izkušenosti (naivni in izkušeni preseljeni risi) (poglavje 2.2). V tretji raziskavi smo razvili nov pristop za avtomatsko zaznavanje izdankov kamnin in na dveh preučevanih območjih v Evropi ocenili vpliv teh reliefnih oblik, topografskih in antropogenih značilnosti na izbiro habitata pri risu glede na faze

aktivnosti (dan in noč), ter preverili, ali pri izbiri habitata prihaja do funkcionalnih odzivov glede na razlike v razpoložljivosti habitata (poglavje 2.3).

Za analize smo uporabili GPS-telemetrične podatke. Za divje mačke smo uporabili nočne GPS lokacije, za rise pa poleg nočnih lokacij tudi lokacije uplenitev in lokacije dnevnih počivališč. Pri identifikaciji dnevnih počivališč risov smo upoštevali tudi podatke s senzorjev aktivnosti. S klasifikacijo lokacij smo zajeli različna specifična vedenja (npr. počivanje, plenjenje, gibanje) in faze aktivnosti (dan, noč). V analizah smo uporabili raznolike podatke, ki odražajo topografske, antropogene in vegetacijske značilnosti domačih okolišev risov in divjih mačk. Identificirali smo glavne reliefne oblike in v geografskih informacijskih sistemih na podlagi visokoločljivostnih LiDAR podatkov pripravili sloje za nadaljnje analize. Reliefne oblike smo zaznali na podlagi že razvitih (pol-)avtomatskih metod (npr. vrtače), ali pa smo razvili svojo metodo (izdanki kamnin), za nekatere oblike pa smo uporabili že obstoječe prosto dostopne sloje (npr. jamski vhodi). Pridobili in pripravili smo tudi različne sloje topografskih (npr. razgibanost), antropogenih (npr. oddaljenost od cest) in vegetacijskih (npr. oddaljenost od gozdnega roba) značilnosti preučevanega območja.

Da bi ugotovili kakšen je vpliv reliefnih oblik in ostalih habitatnih značilnosti na izbiro habitata pri risih in divjih mačkah, smo uporabili pristop, ki temelji na primerjavi uporabljenih in razpoložljivih lokacij (*»use-availability«*). Izbiro habitata smo nato ovrednotili na podlagi statističnega modeliranja, natančneje z metodo posplošenih linearnih mešanih modelov (GLMM). Na podlagi posplošenih aditivnih modelov (GAM) smo preverili, ali v primeru izbire habitata risa prihaja do funkcionalnega odziva glede na velik razpon razpoložljivost habitatov med dvema preučevanima območjema. GAM-e pa smo uporabili tudi za dodatno preverjanje vpliva značilnosti na izbiro habitata pri tistih spremenljivkah, ki so temeljile na oddaljenosti.

Na podlagi avtomatske metode za zaznavanje kraških kotanj smo preučili njihovo izbiro pri obeh vrstah, v primeru risa pa tudi ovrednotili pomen pri plenjenju. Uporaba metode nam je omogočila učinkovito prepoznavanje in računanje značilnosti zelo velikega števila (skoraj 10.000) kraških kotanj. Kljub nekaterim pomanjkljivostim (tj. uspešnost metode pri zaznavanju je 83,5 %), se je metoda izkazala za primerno pri identifikaciji kotanj in izračunu njihovih morfometričnih značilnosti. Za uporabno se je izkazala tudi pri preučevanju ekologije divjih živali, saj smo potrdili, da obe vrsti izbirata bližino kotanj, vendar je izbira pri divjih mačkah manj izrazita kot pri risu. Glede na razpoložljivost, sta obe vrsti izbirali globlje in večje kotanje. Čeprav slabša natančnost GPS-telemetričnih podatkov omejuje možnost, da bi ugotovili, kateri deli kotanj so najbolj privlačni za obe vrsti, naši rezultati kažejo, da bi bili lahko robovi še posebej zanimivi. Znano je, da risi in druge mačke uporabljajo izstopajoče reliefne oblike, kar jim omogoča dober pregled nad okolico in lažje zaznavanje plena ali potencialne nevarnosti. Poleg tega so v kraških kotanjah pogosto tudi jamski vhodi in stene, ki jih mačke uporabljajo za iskanje hrane (npr. polhov, drugih manjših sesalcev, v primeru risa pa tudi gamsov) in označevanje z vonjem. Potrdili smo tudi, da imajo kraške kotanje v primeru risa pomembno vlogo pri plenjenju, saj se glede na terenski popis v kraških kotanjah ali njihovi neposredni bližini nahaja 58 % risovih plenov. Plenjenje v kotanjah ali njihovi neposredni bližini je lahko

uspešnejše zaradi boljšega kritja in lažjega zasledovanja, razgiban vrtačast in skalnat teren pa predstavlja parkljarjem ovire pri lažjem pobegu.

Za nočne lokacije (faza največje aktivnosti) smo na območju slovenskega Dinarskega krasa primerjali tudi vzorce izbire drugih kraških reliefnih oblik ter topografskih, antropogenih in vegetacijskih značilnosti pri obeh vrstah. Prav tako smo raziskali, ali prihaja do razlik v izbiri habitata pri risih glede na njihov izvor in stopnjo izkušenosti. Primerjali smo izbiro habitata med nepreseljeni in preseljenimi risi ter izbiro glede na stopnjo izkušenosti preseljenih risov (glede na čas od vzpostavitve novega teritorija po naselitvi). Rise do enega leta po vzpostavitvi teritorija smo opredelili kot naivne, rise po več kot enem letu po vzpostavitvi teritorija pa smo opredelili kot izkušene. Pri obeh vrstah smo opazili pomemben vpliv reliefnih oblik na rabo prostora, vendar z različnimi vzorci izbire, kar kaže na vrstno specifične razlike v izbiri habitata. Risi so izbirali razgiban teren, bližino jam, sten, kraških kotanj, grebenov, majhnih izdankov kamnin, gozdnih in glavnih cest, izogibali pa so se naselij in gozdnih robov. Divje mačke so izbirale bližino glavnih cest in gozdnih robov, bolj položna pobočja ter lokacije bližje jamam in grebenom. Izogibale so se stenam, gozdnim cestam in naseljem. Čeprav podatki zimskega sledenja in spremljanja s fotopastmi kažejo, da divje mačke pogosto uporabljajo iste reliefne oblike in lokacije kot risi (npr. za markiranje), lahko do razlik pri izbiri habitata divje mačke prihaja zaradi izogibanja risov. Ris je večji in divjo mačko občasno tudi upleni, zato se morda divje mačke izogibajo mikrohabitatom, da zmanjšajo tveganje plenjenja. Do razlik pa lahko prihaja tudi zaradi prehranjevanja z različnim plenom. Divja mačka lovi manjše sesalce (predvsem glodavce, kot so voluharice in miši). Izogibanje strmega, skalovitega in razgibanega terena bi bilo lahko povezano z večjo številčnostjo glodavcev v produktivnejših habitatih z globljo prstjo in v bližini gozdnih robov. Preseljeni in nepreseljeni risi so kazali podobne vzorce izbire habitata, vendar je bila izbira nekoliko izrazitejša pri preseljenih risih. Stopnja izkušenosti ni imela večjega vpliva na izbiro habitata, saj so bili vzorci izbire habitata med naivnimi in izkušenimi preseljenimi risi podobni. Do izrazitejših vzorcev pri izbiri habitata med preseljenimi in nepreseljenimi risi lahko prihaja zaradi različne razpoložljivosti preučevanih elementov med Karpati, od koder izvirajo preseljeni risi, in slovenskim Dinarskim krasom. Na območju slovenskega Dinarskega krasa je razpoložljivost razgibanega, skalnatega in raznolikost reliefnih oblik večja, prav tako je na območju Slovenije večja gostota gozdnih cest. Manjša razpoložljivost (v izvornem habitatu) lahko delno pojasni njihovo močnejšo izbiro s strani preseljenih risov, na kar nakazujejo tudi raziskave s področja funkcionalnih odzivov. Na splošno majhne razlike v izbiri habitata pri risih glede na izvor in stopnjo izkušenosti kažejo, da so risi prilagodljiva vrsta, ki se po preselitvi hitro seznani z novim okoljem. To je še posebej pomembno v kontekstu ohranjanja in varovanja te vrste, kjer poizkušajo s ponovnimi naselitvami ali doselitvami ohraniti in rešiti populacije pred izumrtjem.

V zadnjem poglavju smo na dveh preučevanih območjih v Evropi na podlagi avtomatsko zaznanih izdankov kamnin ocenili vpliv teh reliefnih oblik, kakor tudi topografskih in antropogenih značilnosti na izbiro habitata pri risih glede na različne faze aktivnosti (dan in noč). Preverili smo tudi ali pri izbiri prihaja do funkcionalnih odzivov glede na velike razlike v razpoložljivosti habitata. Na podlagi novo razvitega pristopa smo prepoznali skoraj milijon izdankov kamnin in potrdili njihovo izbiro pri risih. Potrdili smo tudi izbiro strmih, razgibanih

in skalnatih terenov, zlasti za dnevna počivališča. Ponoči in podnevi so risi kazali podobne vzorce izbire topografskih elementov, vendar so imeli ponoči topografski elementi manjši vpliv na izbiro habitata v primerjavi z dnevnimi lokacijami. Poleg reliefnih značilnosti je imela na izbiro habitata velik vpliv tudi človeška infrastruktura, vendar z nasprotnim vplivom linearne prometne infrastrukture glede na faze aktivnosti. V času počivanja (podnevi) so se izogibali bližini rekreacijskih poti (npr. pohodne, kolesarske in jahalne poti), medtem ko ostala človeška infrastruktura na izbiro lokacij za počivanje ni vplivala. Ponoči, v času največje aktivnosti, pa so izbirali bližino rekreacijskih poti, gozdnih in glavnih cest, izogibali pa so se razpršenih stavb. Izbira linearne prometne infrastrukture je verjetno povezana z lažjim gibanjem in bolj učinkovitim markiranjem. S primerjavo dveh območij z različno razpoložljivostjo izdankov kamnin, razgibanega in skalnatega terena smo potrdili funkcionalne odzive pri izbiri razgibanega in skalnatega terena tako za dnevna počivališča kot tudi za nočne lokacije. Izbira je bila večja, ko je bila razpoložljivost takšnih mikrohabitatsov manjša. Funkcionalnega odziva pri izbiri izdankov kamnin pa nismo potrdili v primeru nobene faze aktivnosti. Opazili smo veliko individualno variabilnost, zlasti pri izbiri izdankov kamnin in skalnatega terena na obeh preučevanih območjih, kar kaže na to, da so te značilnosti lahko za nekatere osebe še posebej pomembne.

Raziskava v okviru te doktorske disertacije je ena prvih, ki v habitatne analize pri velikih zvereh vključuje tudi podatke o specifičnih reliefnih oblikah in mikroreliefnih značilnostih ter se pri pridobivanju teh informacij opira predvsem na metode daljinskega zaznavanja na podlagi visokoločljivostnih LiDAR podatkov. Uporaba LiDAR podatkov nam je zagotovila natančnejše prostorske podatke o reliefnih oblikah in mikroreliefnih značilnostih, na podlagi katerih smo lahko v kombinaciji z GPS-telemetričnimi podatki celostno preučili njihov vpliv na izbiro habitata pri risih in divjih mačkah. Ob upoštevanju različnih topografskih, antropogenih in vegetacijskih dejavnikov v analizah rabe prostora se je izkazalo, da so reliefne oblike in mikroreliefne značilnosti zelo pomemben dejavnik, ki vpliva na izbiro habitata in različna vedenja pri obeh vrstah. To nakazuje, da bi bilo potrebno abiotske mikrohabitatne značilnosti upoštevati tudi v prihodnjih analizah, saj vključevanje več ključnih spremenljivk izboljša habitatne modele in vpliva na rezultate. Tak metodološki pristop pa ni koristen le pri preučevanju izbire habitata pri risih in divjih mačkah, vendar bi bilo verjetno smiselno abiotski del narave upoštevati tudi pri raziskavah na ostalih vrstah. Poleg izboljšanja znanja s področja ekologije lahko naši rezultati pripomorejo tudi k uspešnejšem ohranjanju obeh preučevanih vrst. Uporabni so predvsem pri usmerjanju varstvenih prizadevanj in sprejemanju odločitev pri pisanju smernic za upravljanje obeh (in ostalih) vrst, gozdnogospodarskih načrtov, prostorskih načrtov in ostalih smernic, ki lahko vplivajo na njuno nadaljnje ohranjanje. Sloje reliefnih oblik lahko poleg geomorfologije v prihodnje uporabimo tudi za raziskave na drugih področjih, kot so na primer geologija, botanika, zoologija, gozdarstvo, turizem, varstvo narave, načrtovanje in odločanje o vzpostavitvi novih geoparkov ter izdelava državnih ali lokalnih akcijskih načrtov za varovanje geodiverzitete.

Kljub doprinosu naše raziskave k razvoju metodoloških pristopov in razumevanju ekologije obeh vrst, bi bilo potrebno v prihodnje izboljšati še nekatera področja. V analize rabe prostora bi bilo potrebno vključiti tudi podatke o vegetaciji, predvsem na mikronivoju (tj. o podrašti), ki

bi morali biti v čim bližjem časovnem okviru kot GPS-telemetrični podatki. Metodološki pristop uporabljen v tej raziskavi je mogoče prenesti tudi na večjo, kontinentalno raven, kar bi omogočilo, da bi pridobili splošno znanje o vplivu reliefnih oblik in mikroreliefnih značilnosti na izbiro habitata pri obeh vrstah s širšega območja Evrope. Večje število vhodnih podatkov posameznih osebkov iz različnih populacij bi tudi pripomoglo k znižanju vpliva možne individualne variabilnosti pri analizah izbire habitata. Kot kažejo naši rezultati, prihaja pri risu do razlik v izbiri habitata v različnih delih dneva, zato je za interpretacijo potrebno razlikovati med različnimi vedenji, fazami aktivnosti in letnimi časi. To je lahko pomembno tudi za upravljanje in ohranjanje vrst, kot smo opazili pri vplivu rekreacijskih poti na risa. Pomanjkanje podatkov o dnevnih lokacijah divjih mačk nam je onemogočilo preverjanje morebitnih razlik v izbiri habitata med dnevnimi in nočnimi lokacijami. Ker je to področje še neraziskano, bi bilo potrebno zbrati in analizirati tudi podatke o dnevnih lokacijah.

4.2 SUMMARY

Non-living or abiotic factors, often termed as geodiversity, influence the biotic part of nature and shape habitats and the distribution of species. The effects of general abiotic factors (e.g. climate, geology and altitude) on habitats and the distribution of species are well known and studied. Various relief features not only provide habitat and shelter for many species, but can also influence the ecology and basic behavioural patterns of wildlife. Connections between topography and relief features are particularly pronounced in wild felids (e.g. pumas, leopards, lynx). Previous studies on space use have shown that these animals often select rugged, rocky and inaccessible terrain and various conspicuous relief features for different behaviours such as movement, hunting, scent-marking and resting. As these animals require extensive home ranges, spatial and ecological analyses also focus on large areas. Consequently, topographic variables are often limited to general terrain characteristics (e.g. slope), and therefore usually do not take into account the effects of fine-scale terrain characteristics and various relief features. Previous studies on space use by wild felids have paid less attention to the effects of geomorphological features and the analysis of LiDAR-DEMs, which require specific skills. Because only few ecological analyses also include data on micro- and mesorelief habitat characteristics, our knowledge of their influence on space use by these animals is still very limited.

The main aim of this doctoral dissertation was to determine the influence of relief features on space use by the Eurasian lynx (*Lynx lynx*; hereafter lynx) and the European wildcat (*Felis silvestris*; hereafter wildcat). We designed a detailed quantitative spatial-ecological study that comprehensively addressed impact of relief features on habitat selection during specific behaviours (e.g. resting, feeding, movement, marking) and different phases of activity (day and night). The doctoral dissertation is divided into three main chapters. The first two chapters focus on the study of habitat selection by lynx and wildcat in the Slovenian Dinaric Karst, while the third chapter focus on habitat selection by lynx in two (bio-)geographically-different regions in Europe, the Slovenian Dinaric Karst and the Bohemian Forest Ecosystem.

In the first research, we used karst depressions as an example to demonstrate the potential of high-resolution LiDAR data and methods for automatic detection of relief features for

ecological analyses, and examined the selection of karst depressions by both species. In the case of lynx, we also evaluated the importance of the studied features for hunting behaviour (Chapter 2.1). The following research compares the patterns of selection of different karst relief features and topographic, anthropogenic and vegetation characteristics by lynx and wildcat, and investigates whether there are differences in selection by lynx based on their origin (resident and translocated) and experience level (naive and experienced translocated lynx) (Chapter 2.2). In the last research, we developed a new approach for the automatic detection of rocky outcrops and investigated the influence of these relief features, topographic and anthropogenic characteristics on the habitat selection by lynx in two study areas in Europe, taking into account the phases of activity phases (day and night). We also tested whether there is evidence for a functional response in habitat selection across a large gradient of habitat availability (Chapter 2.3).

We used GPS telemetry data, including night locations for both species. In addition, we included also kill sites and day-resting sites for lynx. For the identification of lynx day-resting sites, we took into account activity data from the built-in accelerometers. By classifying the GPS locations, we separated among specific behaviours (e.g. resting, hunting, movement) and phases of activity (day, night). We used different data in our analyses, reflecting the topographic, anthropogenic and vegetation characteristics of the lynx and wildcat home ranges. We identified the main relief features and used geographic information systems to prepare layers for further analyses based on high-resolution LiDAR data. We detected relief features based on already developed (semi-)automatic methods (e.g. karst depressions), developed our own method (rocky outcrops) or used existing freely accessible layers (e.g. cave entrances). We also obtained and produced various layers of topographic (e.g. ruggedness), anthropogenic (e.g. distance to roads) and vegetation (e.g. distance to forest edges) characteristics of the study area.

We determined the influence of relief features and other habitat characteristics on the habitat selection by lynx and wildcats under a "use-availability" approach. Habitat selection was then evaluated based on a statistical modelling, more specifically the generalized linear mixed-effect models (GLMM), and generalized additive models (GAM) were used to test for a functional response in habitat selection by lynx, based on the large variation in habitat availability between the two study areas. GAMs were also used to additionally test the effect of characteristics on habitat selection for distance-based variables.

We used an automatic method for karst depressions detection to study their selection by both species and to evaluate their importance for lynx hunting behaviour. The method allowed us to efficiently identify and calculate the characteristics of a large number (almost 10,000) of karst depressions. Despite some drawbacks (i.e. the detection success rate of the method is 83.5%), the method proved to be suitable for the identification of karst depressions and the calculation of their morphometric characteristics. It also proved applicable for studying the ecology of wild animals, as we confirmed that both species select their proximity, but the selection was less pronounced in the wild cat than in the lynx. In respect to availability, both species selected deeper and larger depressions. While the lower accuracy of GPS telemetry data limited our ability to discern which parts of the depressions are most attractive to both species, our results

suggest that the rims might be of especially interesting. Lynx and other felids are known to use conspicuous relief features, which provide a good view of their surroundings and allow them to more easily detect prey or potential danger. Furthermore, cave entrances and cliffs are often formed in karst depressions and used by felids for foraging (e.g. for dormice, other small mammals and, in the case of lynx, also chamois) and for scent-marking. We also confirmed that karst depressions play an important role in lynx hunting behaviour, as 58% of lynx prey remains were found in or near karst depressions during the field survey. Hunting in or close to depressions may be more successful due to better cover and easier stalking, as well as rugged and rocky terrain may provide escape impediments for ungulates.

For the night locations (phase of maximum activity), we compared the selection patterns of other karst relief features, as well as topographic, anthropogenic and vegetation characteristics for both species in the Slovenian Dinaric Karst. We also investigated whether there are differences in habitat selection by lynx based on their origin and experience level. We compared habitat selection between resident and translocated lynx, and tested if behaviour of the translocated lynx changed with experience level (based on the time since they established new territory after translocation). We classified translocated lynx up to one year since they established their new territory after the translocation as “naïve” and as “experienced” those with more than one year after territory establishment. We observed significant impact of relief features on habitat selection by both felids and detected distinct selection patterns between the two species, indicating on species-specific differences in habitat selection. Lynx selected rugged terrain and proximity of caves, cliffs, karst depressions, ridges, small rocky outcrops, and roads, but avoided human settlements and forest edges. Wildcats selected areas with lower surface slope, closer to main roads, forest edges, caves and ridges, but avoided cliffs, forest roads and human settlements. Although snow-tracking and camera-trapping indicate that wildcats regularly use the same relief features and locations as lynx (e.g., for scent-marking), differences in habitat selection by wildcats could be connected with avoidance of intra-guild predation. Lynx are larger than a wildcat and they occasionally kill wildcats, so the latter may avoid particular microhabitats to reduce the risk of predation. However, observed habitat segregation may also occur due to different feeding with prey. Wildcats predominantly feed on smaller mammals (especially rodents, such as voles and mice). Avoidance of steep, rocky and rugged terrain could be connected with higher rodent abundance in more productive habitats with deeper soil and near forest edges. Translocated and resident lynx showed similar selection and avoidance patterns, with selection being slightly more pronounced in translocated lynx. The experience level did not have a major influence on habitat selection, as selection patterns between naïve and experienced translocated lynx were similar. More pronounced patterns in habitat selection between translocated and resident lynx may be due to the different availability of the studied features between the Carpathian Mountains, where translocated lynx originate, and the Slovenian Dinaric Karst. The availability of rugged, rocky terrain and the diversity of relief features is higher in the Slovenian Dinaric Karst, as well as the density of forest roads. Lower availability (before translocation) may partly explain their stronger selection by translocated lynx, as also indicated by researches on functional responses. In general, small differences in habitat selection by lynx based on their origin and experience level provide further evidence that lynx are plastic species that quickly familiarise themselves with their new

environment after translocation. This is particularly important in the context of the conservation of this species, where reintroductions and reinforcements are often used for establishing and saving the populations.

In the last chapter, we automatically detected rocky outcrops and investigated the influence of these landforms, topographic and anthropogenic features on lynx habitat selection according to two activity phases (day and night) in two study areas in Europe. We also tested whether lynx exhibit functional response in habitat selection according to large differences in habitat availability in these two (bio-)geographically-contrasting study areas. Based on a newly developed approach, we identified almost a million rocky outcrops and confirmed their selection by lynx. We also confirmed the selection of steep, rugged and rocky terrain, especially for day-resting sites. We observed that they showed similar selection patterns of topographic characteristics at night and during the day, but with lower influence of topographic characteristics on habitat selection at night. In addition to topographic features, human infrastructure also had a strong influence on habitat selection, but the influence of linear transportation infrastructure was opposite between the two activity phases. During resting periods (daytime), they avoided the vicinity of recreational paths (e.g. hiking, cycling and horse-riding paths), while other human infrastructure had no influence on the selection of day-resting sites. In contrast, during the highest activity at night, they selected the vicinity of recreational paths, forest roads and main roads, while avoiding scattered buildings. The selection of linear transportation infrastructure is likely related to easier movement and more efficient scent-marking. By comparing two areas with different availability of rocky outcrops, rugged and rocky terrain, we confirmed functional responses in the selection of rugged and rocky terrain for both day-resting sites and night locations. Selection was stronger when the availability of such microhabitats was lower. However, we did not observe a functional response in the selection of rocky outcrops for any activity phase. We observed high individual variability, particularly in the selection of rocky outcrops and rocky terrain in both study areas, suggesting that these characteristics may be particularly important for some individuals.

The research in the framework of this PhD thesis is one of the first that includes information on specific landforms and micro-relief characteristics in habitat selection analyses of large carnivores, and relies mainly on remote sensing methods based on high-resolution LiDAR data to obtain this information. The use of LiDAR data enabled us to gain more detailed spatial data on landforms and micro-relief characteristics, based on which, in combination with GPS-telemetry data, we were able to comprehensively study their impact on habitat selection by lynx and wildcats. Taking into account various topographic, anthropogenic and vegetation features in the habitat selection analyses, it emerged that landforms and micro-relief characteristics are an important factor influencing habitat selection and different behaviours for both species. This suggests that abiotic microhabitat characteristics should be considered in future analyses, as including more of the key variables improve habitat models and provide more robust results. This methodological approach is not only useful for studying habitat selection by lynx and wildcats, but the abiotic part of nature should also be considered for other species. In addition to improving knowledge in the field of ecology, our results can also contribute to the conservation of the two studied species. They might be particularly useful in guiding

conservation efforts and decision-making when writing management guidelines for both (and other) species, forest management plans, spatial plans and other guidelines that may affect their future conservation. In addition to geomorphology, landforms can also be used in the future for research in other fields such as geology, botany, zoology, forestry, tourism, nature conservation, spatial planning and in decision-making on the establishment of new geoparks, and the development of national or local action plans for the protection of geodiversity.

Despite the contribution of our research to the methodological development and understanding of the ecology of both species, there are some fields that could be improved in the future. Vegetation data, especially at the micro-level (i.e. undergrowth), should also be included in habitat selection analyses and should be collected as close in time frame as possible to the GPS-telemetry data. The methodological approach used in this study could also be applied to a larger, continental scale, which would allow us to gain a more general knowledge of the impact of landforms and micro-relief characteristics on habitat selection of both species across a wider area in Europe. A larger number of input data of individuals from different populations would also help to reduce the potential effect of individual variability in habitat selection analyses. As our results show, differences in habitat selection by lynx occur at certain parts of the day, therefore specific behaviours, activity phases and seasons need to be included in studies and considered for the interpretation. In particular, this may have important implications for the conservation of the species. The lack of data on diurnal locations of wildcats prevented us from examining possible differences in habitat selection between day-resting and night locations in this species. Since this field remains unexplored, daytime location data should also be collected and analysed in the future studies.

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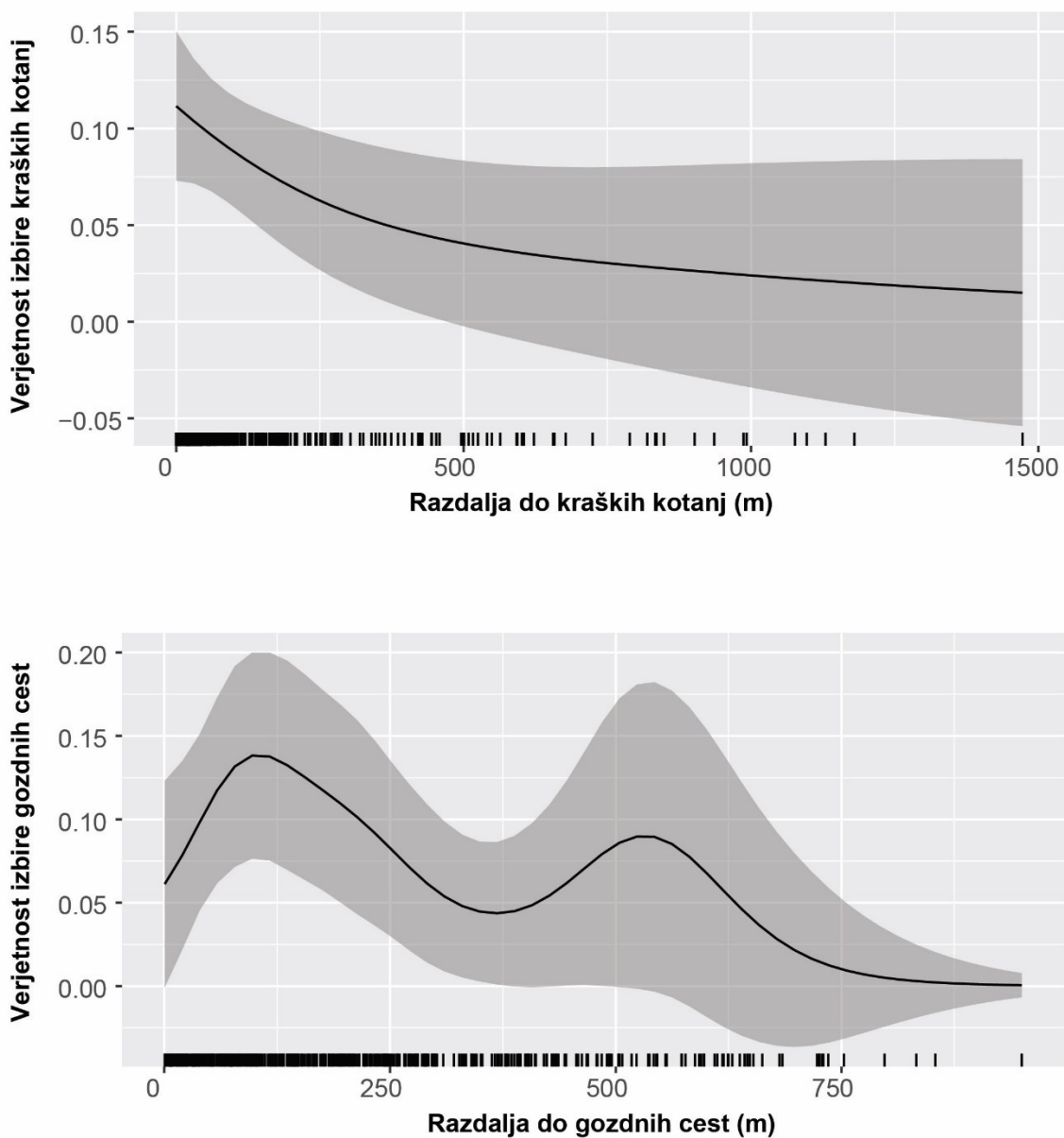
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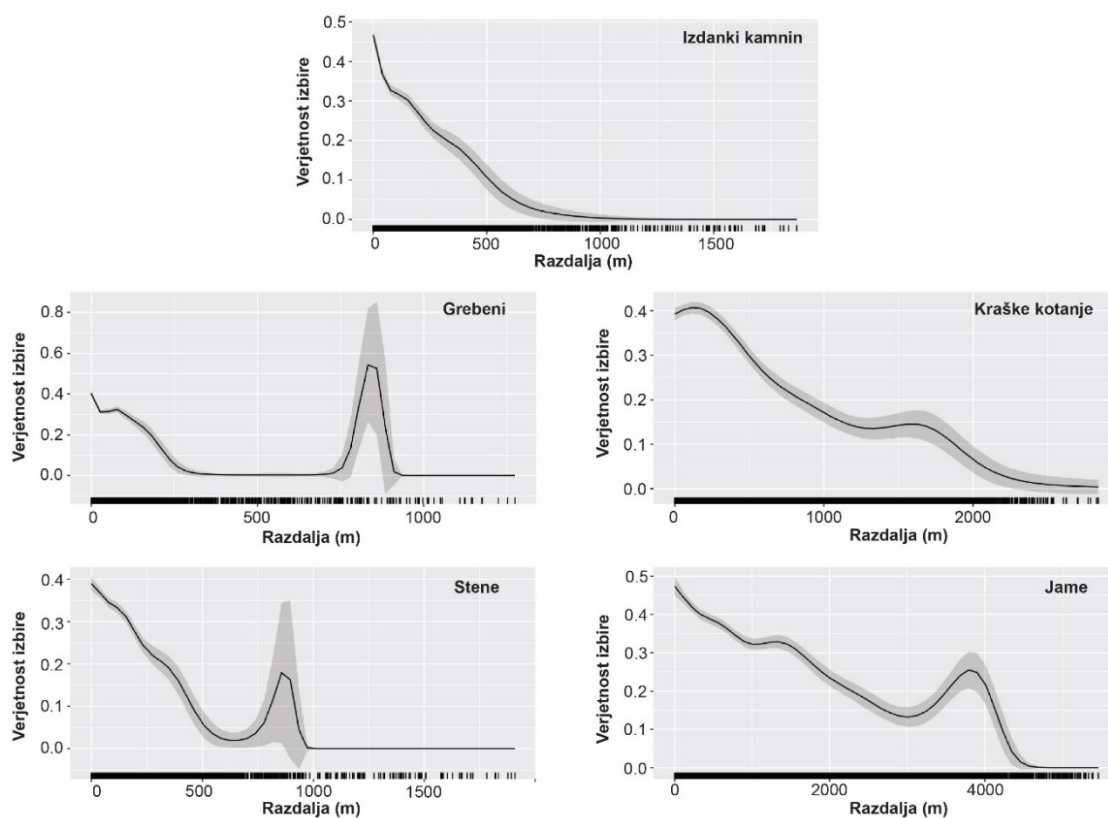
PRILOGE

PRILOGA A: Grafi porazdelitve odvisnih spremenljivk, ki temeljijo na oddaljenosti, na podlagi bivariatnih oz. parnih analiz z GAM-i (posplošenimi aditivnimi modeli) za poglavje 2.1

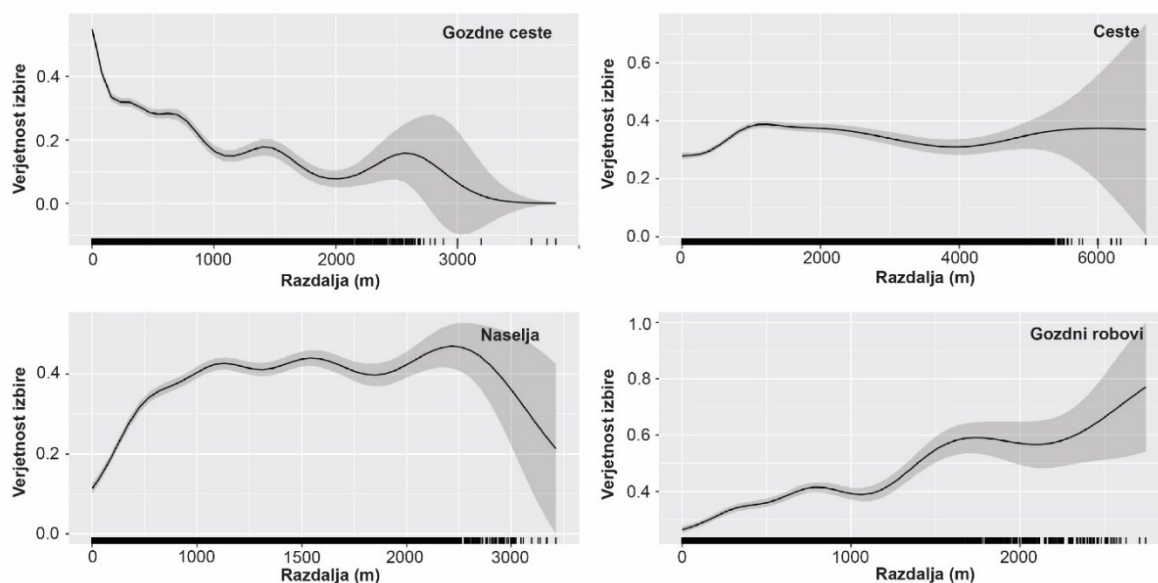


Slika A1: Verjetnost izbire kraških kotanj in gozdnih cest glede na porazdelitev razdalje od lokacij risovih uplenitev na podlagi bivariatnih oz. parnih analiz z GAM-i za poglavje 2.1

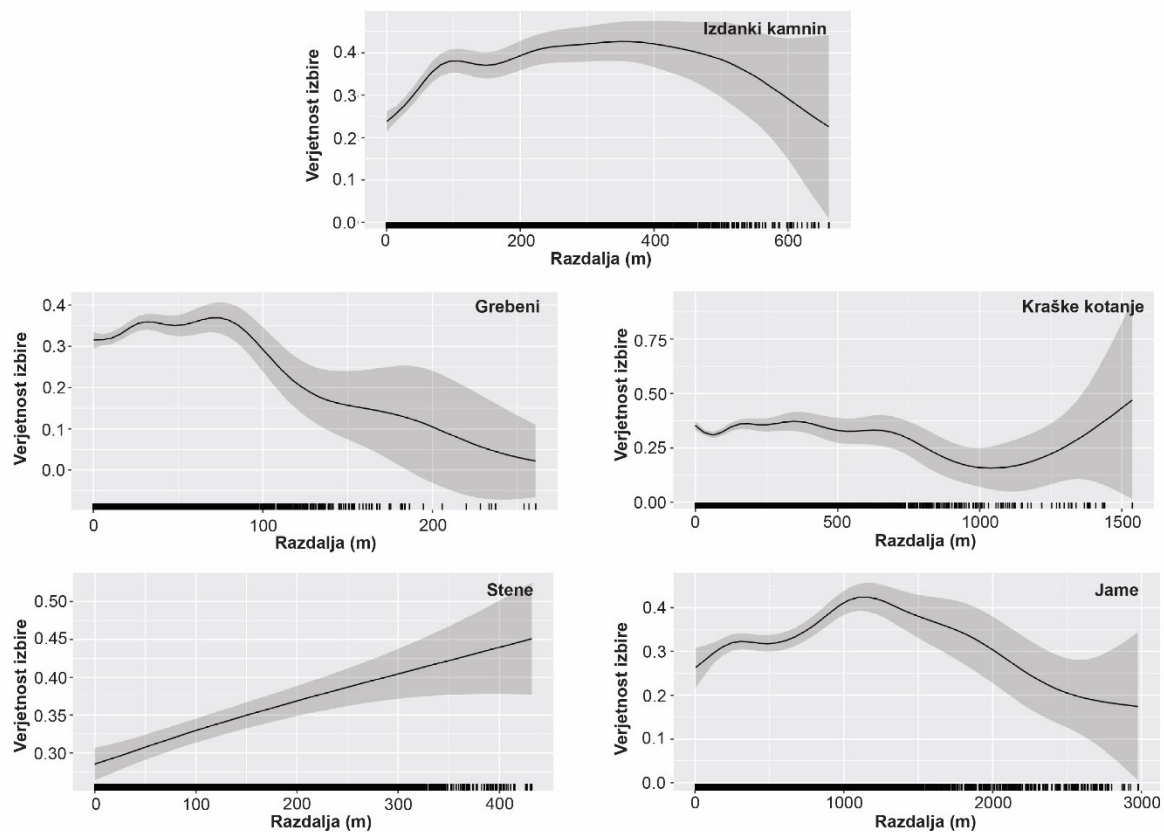
PRILOGA B: Grafi porazdelitve odvisnih spremenljivk, ki temeljijo na oddaljenosti, na podlagi bivariatnih oz. parnih analiz z GAM-i (posplošenimi aditivnimi modeli) za poglavje 2.2



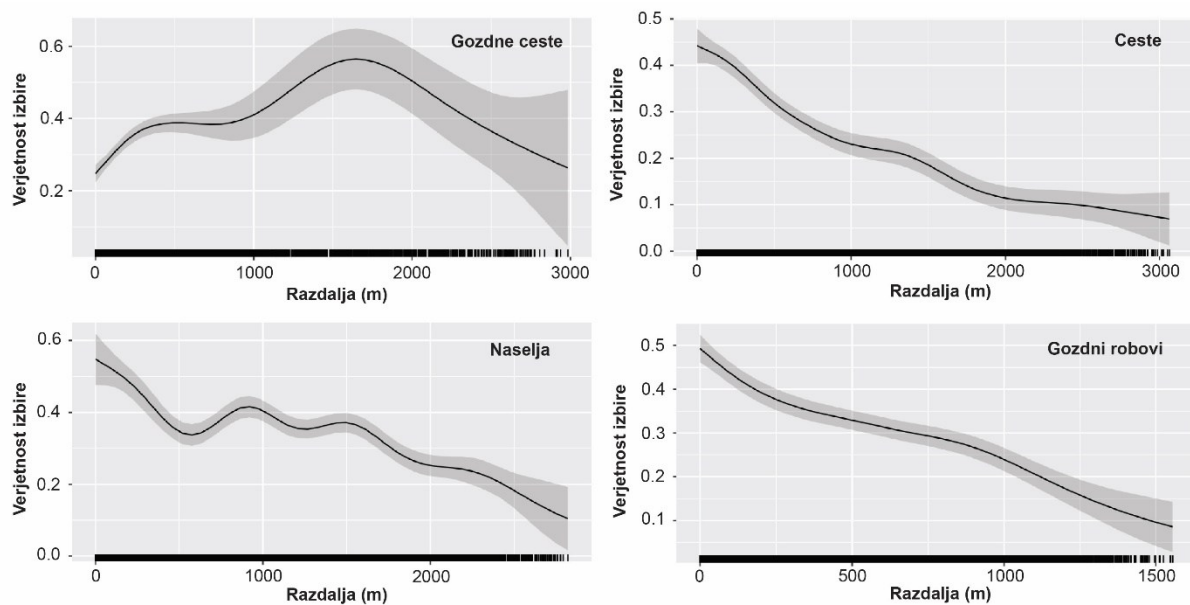
Slika B1: Verjetnost izbire topografskih elementov glede na porazdelitev razdalje od nočnih lokacij risa na podlagi bivariatnih oz. parnih analiz za poglavje 2.2



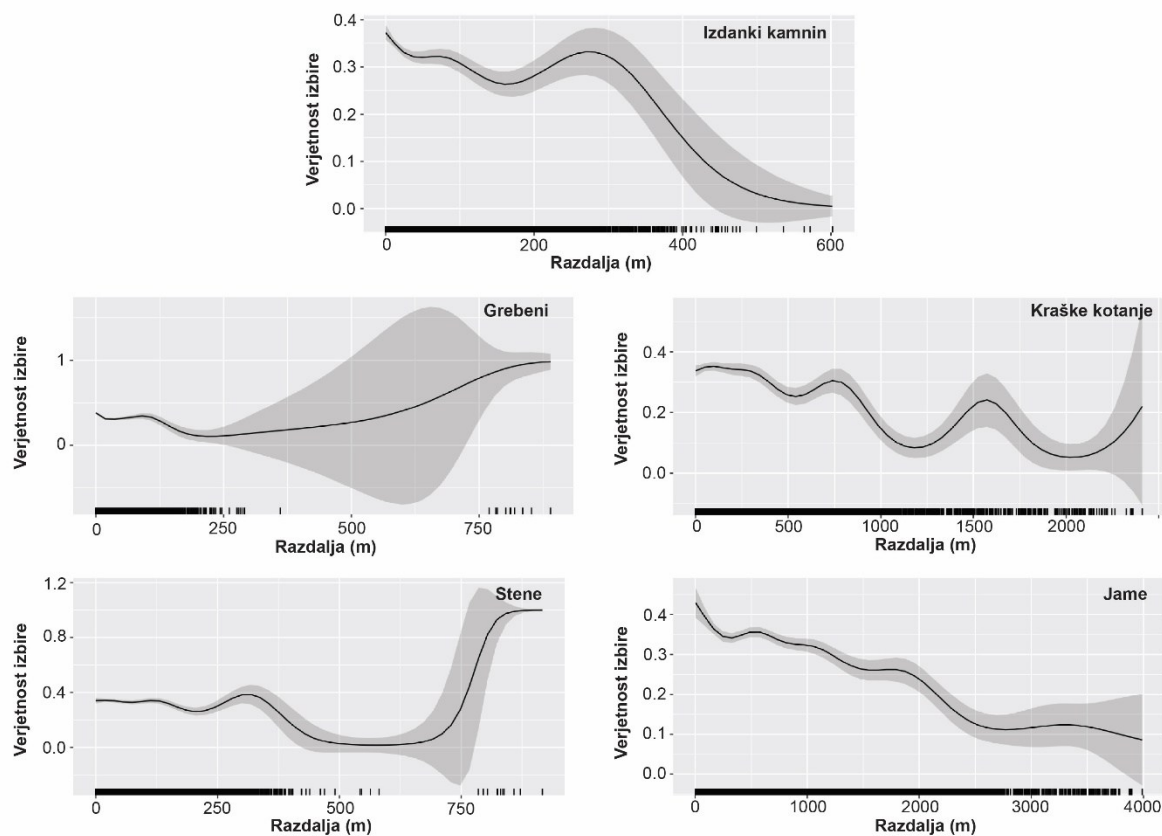
Slika B2: Verjetnost izbire antropogenih in vegetacijskih elementov glede na porazdelitev razdalje od nočnih lokacij risa na podlagi bivariatnih oz. parnih analiz za poglavje 2.2



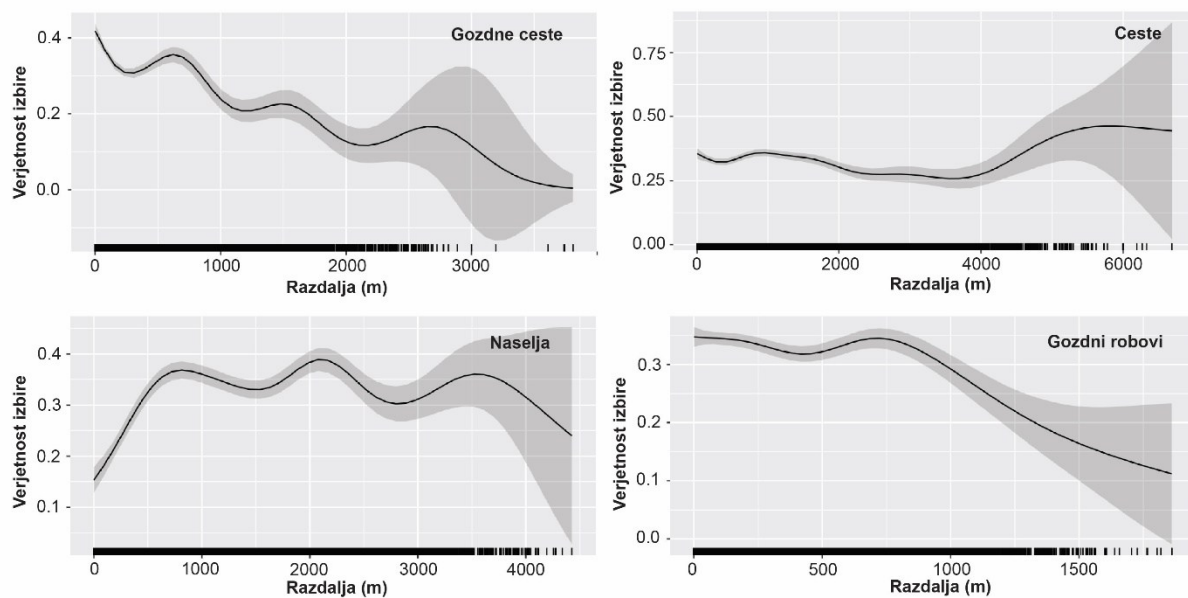
Slika B3: Verjetnost izbire topografskih elementov glede na porazdelitev razdalje od nočnih lokacij divje mačke na podlagi bivariatnih oz. parnih analiz za poglavje 2.2



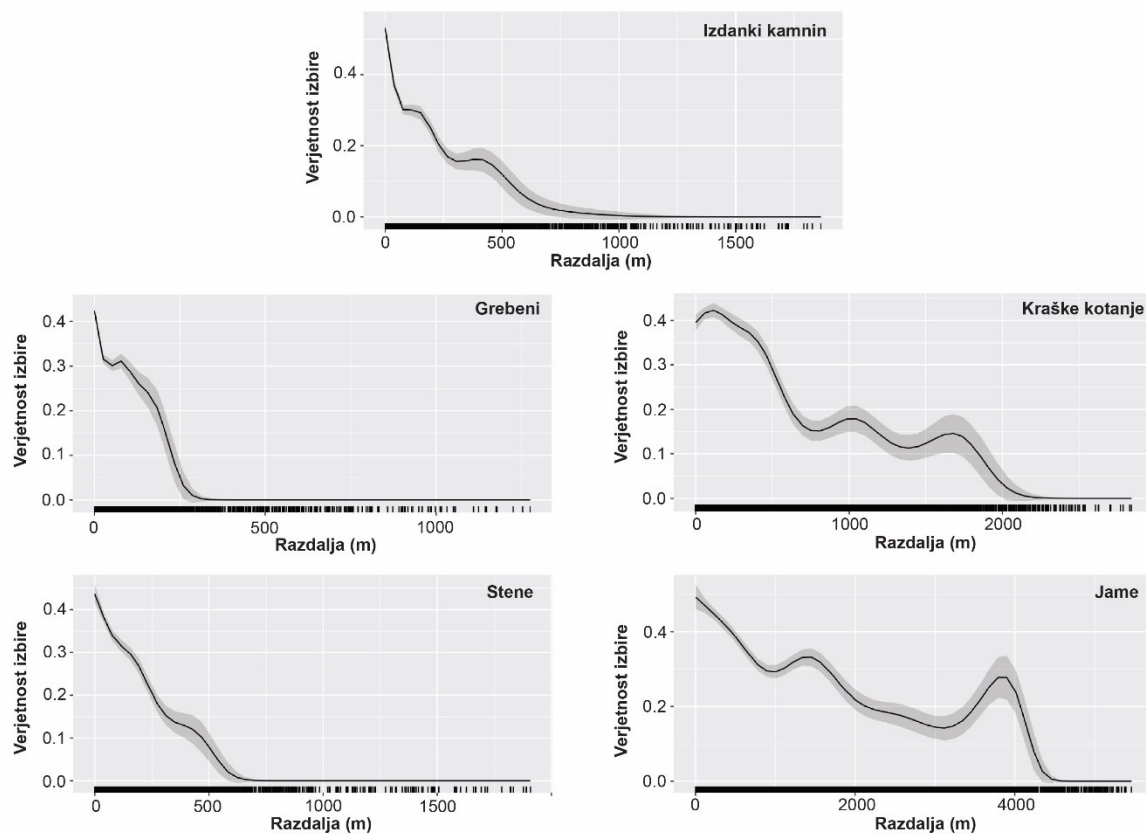
Slika B4: Verjetnost izbire antropogenih in vegetacijskih elementov glede na porazdelitev razdalje od nočnih lokacij divje mačke na podlagi bivariatnih oz. parnih analiz za poglavje 2.2



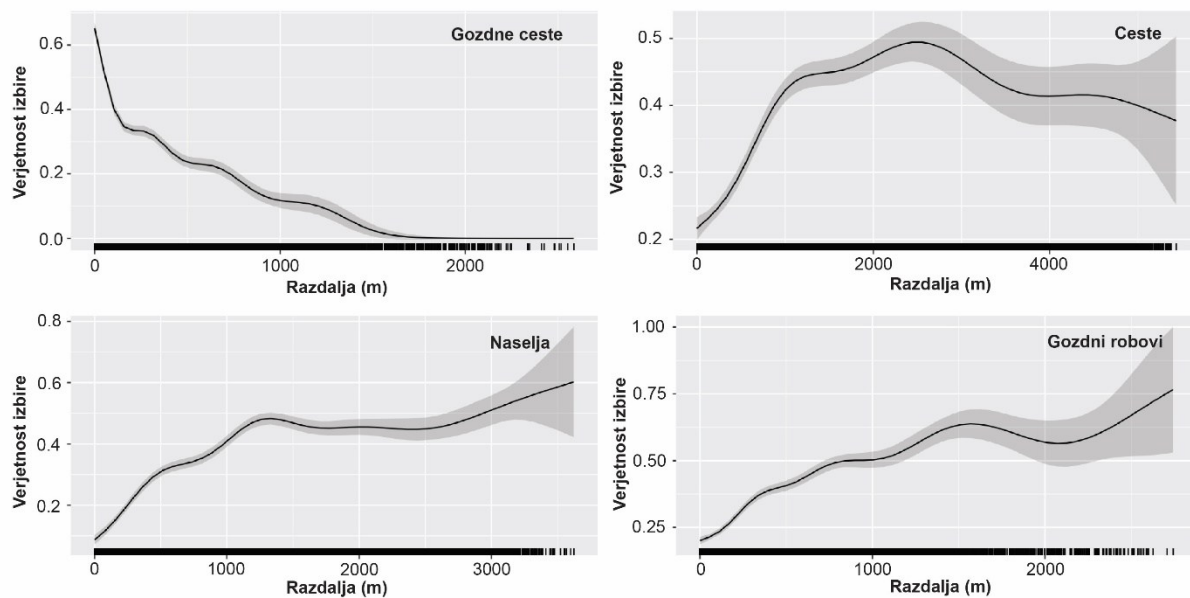
Slika B5: Verjetnost izbire topografskih elementov glede na porazdelitev razdalje od nočnih lokacij nepreseljenih risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.2



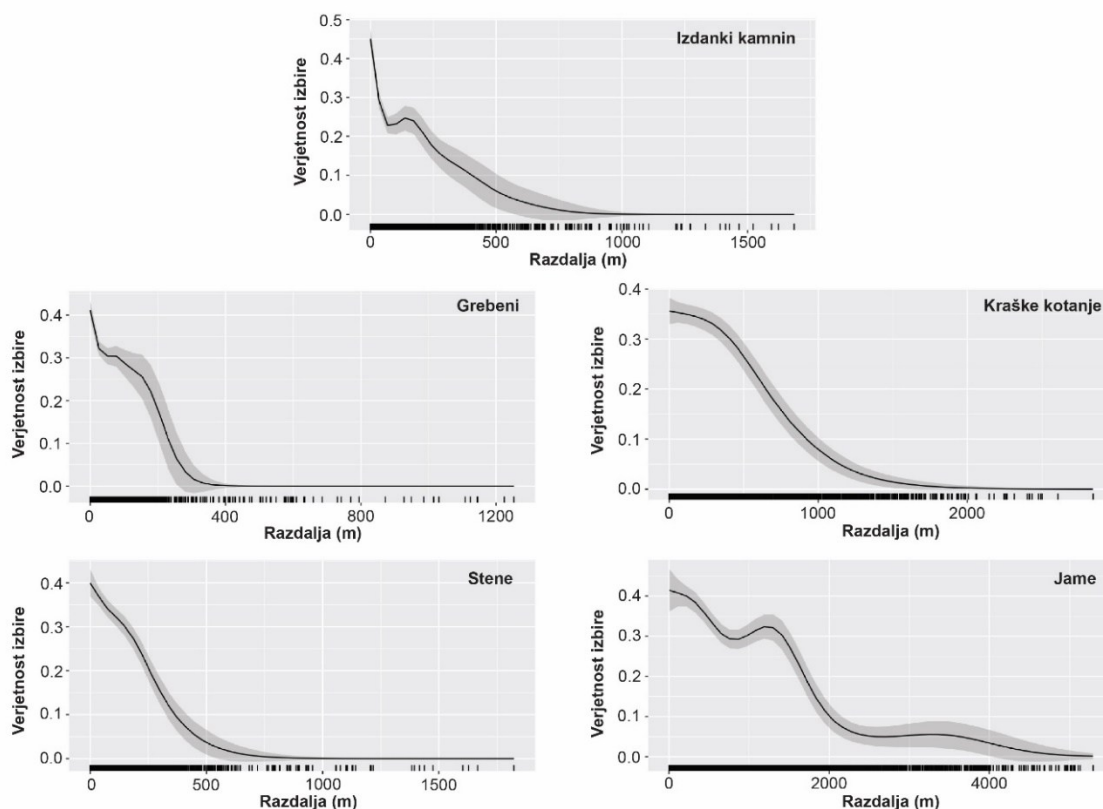
Slika B6: Verjetnost izbire antropogenih in vegetacijskih elementov glede na porazdelitev razdalje od nočnih lokacij nepreseljenih risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.2



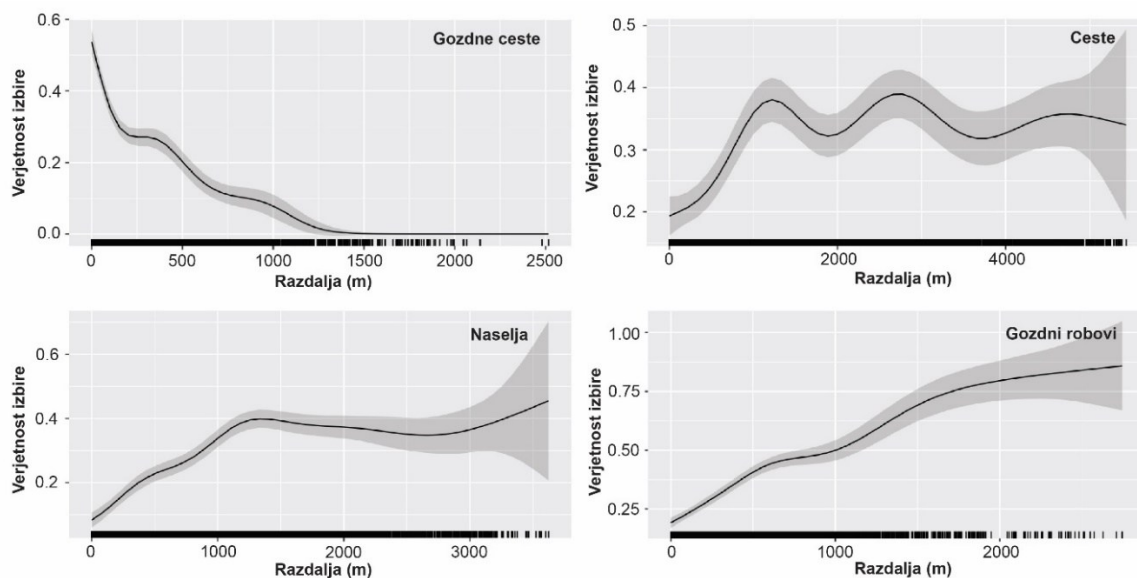
Slika B7: Verjetnost izbire topografskih elementov glede na porazdelitev razdalje od nočnih lokacij preseljenih risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.2



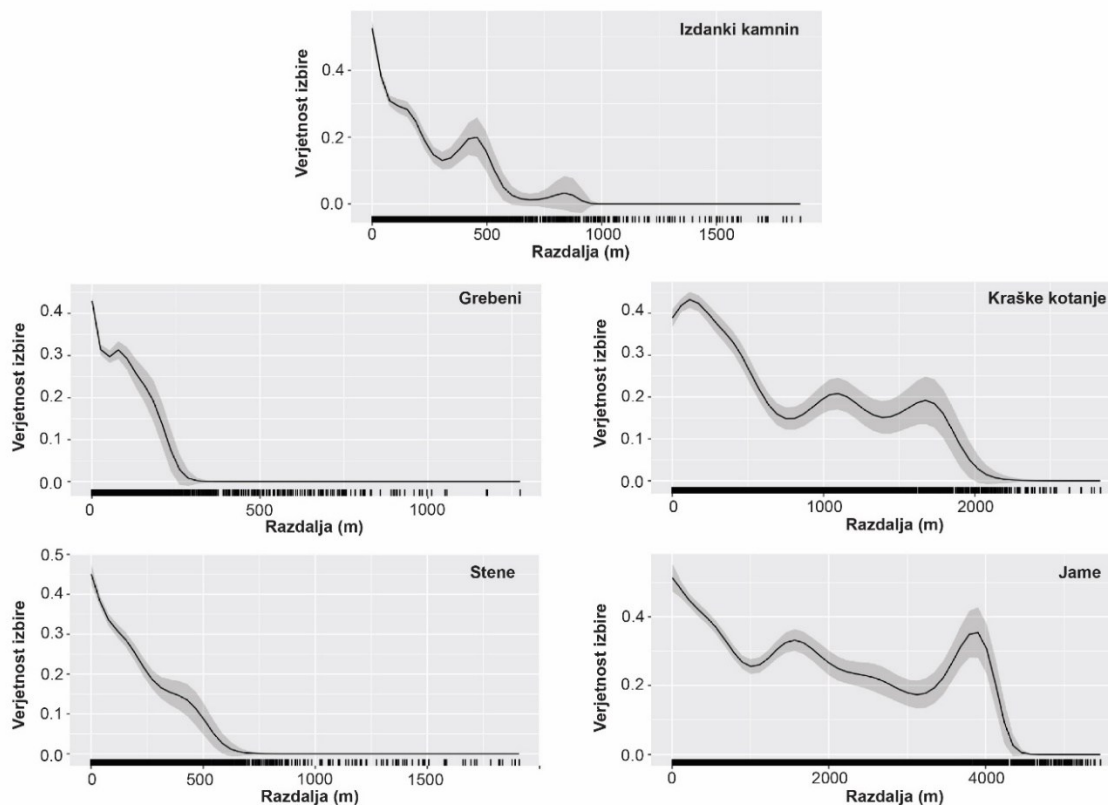
Slika B8: Verjetnost izbire antropogenih in vegetacijskih elementov glede na porazdelitev razdalje od nočnih lokacij preseljenih risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.2



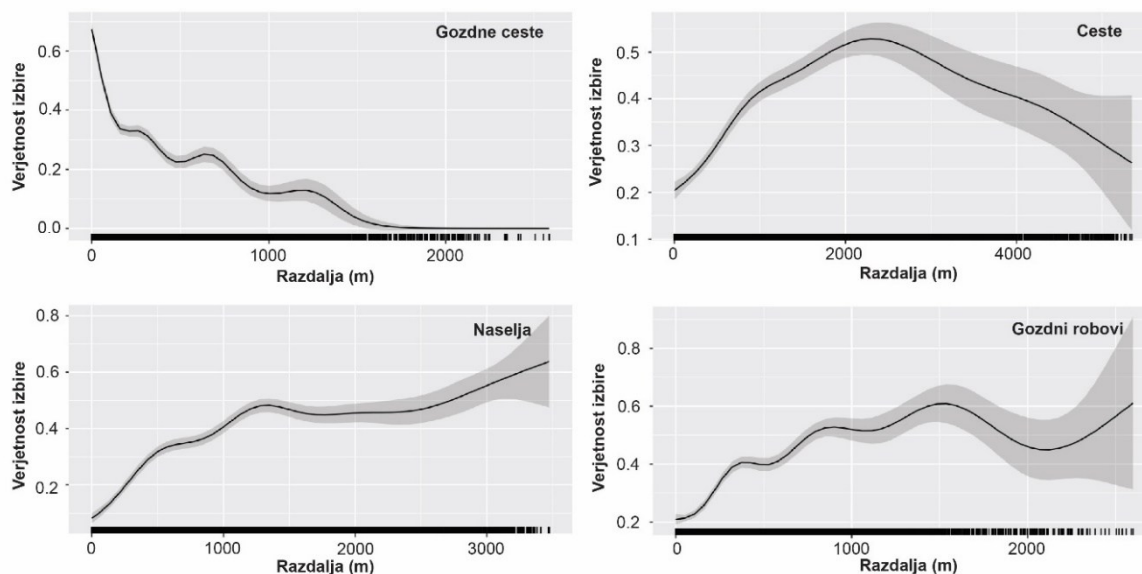
Slika B9: Verjetnost izbire topografskih elementov glede na porazdelitev razdalje od nočnih lokacij naivnih preseljenih risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.2



Slika B10: Verjetnost izbire antropogenih in vegetacijskih elementov glede na porazdelitev razdalje od nočnih lokacij naivnih preseljenih risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.2

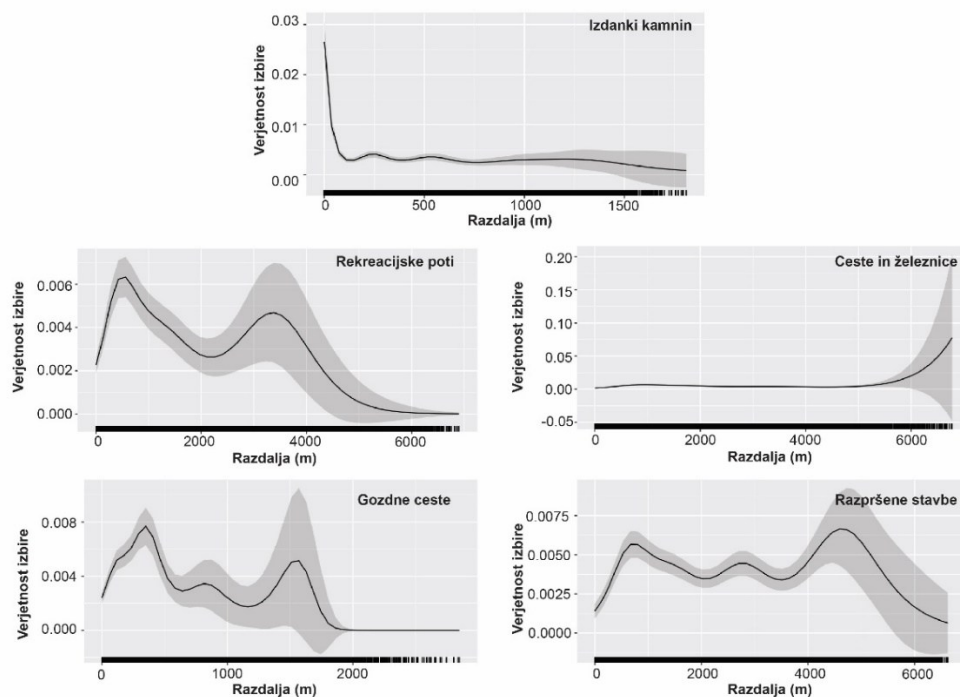


Slika B11: Verjetnost izbire topografskih elementov glede na porazdelitev razdalje od nočnih lokacij izkušenih preseljenih risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.2

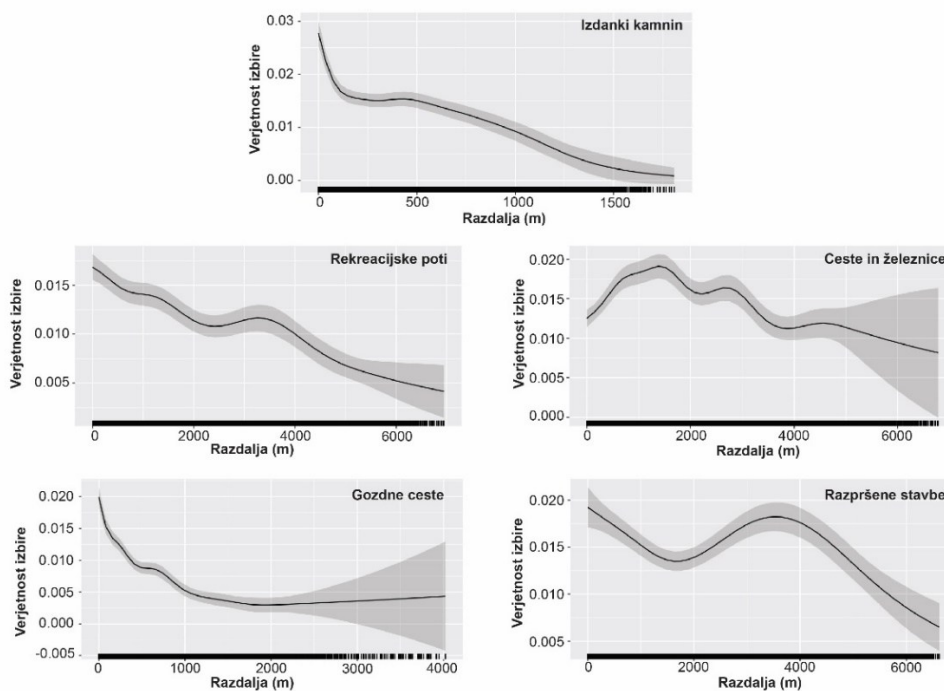


Slika B12: Verjetnost izbire antropogenih in vegetacijskih elementov glede na porazdelitev razdalje od nočnih lokacij izkušenih preseljenih risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.2

PRILOGA C: Grafi porazdelitve odvisnih spremenljivk, ki temeljijo na oddaljenosti, na podlagi bivariatnih oz. parnih analiz z GAM-i (posplošenimi aditivnimi modeli) za poglavje 2.3



Slika C1: Verjetnost izbire topografskih in antropogenih elementov glede na porazdelitev razdalje od dnevnih počivališč risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.3



Slika C2: Verjetnost izbire topografskih in antropogenih elementov glede na porazdelitev razdalje od nočnih lokacij risov na podlagi bivariatnih oz. parnih analiz za poglavje 2.3

PRILOGA D: Preglednica s podatki o razpoložljivih in uporabljenih izdankov kamnin višjih od 3 m v posameznih domačih okoliših risov na območju slovenskega Dinarskega krasa in Bavarsko-Češkega gozdnega ekosistema za poglavje 2.3

Lynx ID	95% MCP [km ²]	Površina izdankov kamnin [km ²]	Št. izdankov kamnin	Št. dnevnih počivališč	Št. dnevnih počivališč v 50 m radiju izdankov kamnin	Št. nočnih lokacij	Št. nočnih lokacij v 50 m radiju izdankov kamnin
Slovenski Dinarski kras							
Dina (470)	303,17	3,76	44.855	10	10 (100 %)	71	55 (77,46 %)
Snežka (471)	90,12-126,05	3,50-4,50	44.508-56.795	65	61 (93,85 %)	815	631 (77,42 %)
Mihec (473)	86,79	0,74	9981	72	53 (73,61 %)	171	83 (48,54 %)
Maja (474)	51,67	0,86	11.166	51	37 (72,55 %)	226	156 (69,03 %)
Goru (475)	218,31	0,94	12.426	34	14 (41,18 %)	2549	893 (35,03 %)
Bojan (519)	255,97	4,45	28.297	/	/	61	34 (55,74 %)
Catalin (522)	287,55	5,80	43.515	71	48 (67,61 %)	2015	916 (45,46 %)
Petra (745)	215,05	6,40	55.818	91	67 (73,63 %)	1501	787 (52,43 %)
Bor (944)	60,20	0,55	5602	/	/	432	221 (51,16 %)
Klif (945)	265,95	6,90	65.197	31	21 (67,74 %)	1174	698 (59,45 %)
Igi (946)	52,05	0,80	6848	/	/	171	84 (49,12 %)
Blisk (1013)	60,01	0,57	7883	/	/	326	172 (52,76 %)
Skupaj	1946,84-1982,77	35,27-36,27	336.096-348.383	425	301 (70,82 %)	9512	4730 (49,73 %)
Bavarsko-Češki gozdni ekosistem							
Milan (1)	601,49	1,35	9812	101	28 (27,72 %)	663	93 (14,03 %)
Nora (2)	168,65	0,62	4792	26	3 (11,54 %)	185	19 (10,27 %)
Parik (720)	321,37-1066,88	0,80-4,00	4715-25.351	211	63 (29,86 %)	759	99 (13,04 %)
Kubicka (722)	144,66	0,39	2377	344	45 (13,08 %)	914	114 (12,47 %)
Matylda (723)	101,86	0,61	3556	490	189 (38,57 %)	1225	208 (16,98 %)
Emanuel (724)	266,23	0,90	5524	55	21 (38,18 %)	161	21 (13,04 %)
Citrad (725)	413,68	1,43	9295	301	111 (36,88 %)	877	156 (17,79 %)
Tessa (3)	115,00	0,42	2844	229	62 (27,07 %)	589	92 (15,62 %)
Kika (4)	312,21	1,16	8314	392	141 (35,97 %)	856	136 (15,89 %)
Nimo (726)	632,74	4,35	27.216	267	154 (57,68 %)	648	185 (28,55 %)
Skupaj	3077,89-3823,40	12,03-15,23	78.445-99.081	2416	817 (33,82 %)	6877	1123 (16,33 %)