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Štruktúra, dynamika a manažment horských lesov Karpát vo vzťahu s biotopovými nárokmi hlucháňa hôrneho (*Tetrao urogallus*)

Structure, dynamics and management of Carpathian mountain Norway spruce forests in relation to habitat requirements of the capercaillie

*(*Tetrao urogallus*)*

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Prehlasujem, že som dizertačnú prácu na tému „Štruktúra, dynamika a manažment horských lesov Karpát vo vzťahu s biotopovými nárokmi hlucháňa hôrneho (*Tetrao urogallus*)“ vypracoval samostatne s použitím literatúry a na základe konzultácií a doporučení školiteľa. Súhlasím so zverejnením dizertačnej práce podľa zákona č. 111/1998 Zb. o vysokých školách v platnom znení, a to bez ohľadu na výsledok obhajoby.

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Abstrakt

Prudký pokles biodiverzity v súčasnosti je najmä dôsledok straty prirodzených biotopov, ktorá je zvyčajne výsledkom pozmenenia prirodzenej dynamiky ekosystémov. Väčšina suchozemskej biodiverzity prežíva v lesoch a pozmenenie prírodných disturbančných režimov vo forme intenzívneho odlesňovania a obhospodarovania lesov pokračuje v rastúcom tlaku na lesnú biodiverzitu v mnohých častiach sveta. Postupné uvedomovanie si dôležitosti a významu lesov z hľadiska biodiverzity si vyžaduje nové postupy manažmentu lesov, avšak súčasné poznatky v tejto oblasti sú limitované. Hlucháň hôrny patrí medzi ohrozené dáždnikové druhy Európy. Je to druh viazaný na špecifické štruktúry horských lesov, vyžaduje veľké rozlohy vhodných lesných komplexov a je citlivý na fragmentáciu biotopov. V Karpatoch sa nachádza ťažisko výskytu tohto vzácneho druhu v Európe, ale doposiaľ neexistovali pre túto oblasť dostatočné podklady pre jeho ochranu a definovanie vhodných lesníckych manažmentových opatrení. Pre pochopenie štruktúry a dynamiky horských lesov s výskytom hlucháňa hôrneho a následné odvodenie vhodného manažmentu lesov sme tento problém riešili komplexne na niekoľkých priestorových úrovniach s využitím štyroch metodických prístupov – populačný monitoring, modely druhovej distribúcie, analýza genetickej štruktúry, metódy dendroekológie. Základnými cieľmi práce bolo: 1.) Analyzovať vplyv rôznych typov manažmentu lesov na stav biotopov hlucháňa hôrneho, 2.) Analyzovať vplyv manažmentu lesov na početnosť hlucháňa, 3.) Vytvoriť model vhodnosti biotopov hlucháňa hôrneho pre celé Karpaty a analyzovať ako veľkoplošná ťažba ovplyvňuje konektivitu populácie, 4.) Analyzovať vplyv veľkosti biotopov a konektivity územia na genetickú diferenciáciu hlucháňa, 5.) Analyzovať, ako prírodné disturbancie ovplyvňujú štruktúru biotopov hlucháňa hôrneho v smrekových pralesoch Karpát, 6.) Navrhnúť vhodné lesnícke manažmentové opatrenia, ktoré umožnia prežiť hlucháňovi hôrnemu v smrekových lesoch Karpát. Výsledky potvrdzujú, že pralesy a prírodné lesy sú najviac využívanými biotopmi hlucháňa v Karpatoch. Veľkoplošné holiny sú nevhodný biotop pre hlucháňa hôrneho, a preto veľkoplošná ťažba negatívne ovplyvňuje jeho početnosť. Suchý les po napadnutí podkôrnym hmyzom predstavuje podstatne vhodnejší biotop ako veľkoplošne asanované plochy. Na krajinnej úrovni veľkoplošná ťažba 30% vhodných biotopov redukovala počty hlucháňov až o 76%. V posledných desaťročiach došlo v Karpatoch k výrazným stratám vhodných biotopov. Podľa našich výsledkov, len za posledných 20 rokov bolo veľkoplošne vyťažených 1 110 km^2 (približne 15%) potenciálne vhodných biotopov, následkom čoho celková konektivita klesla o 33%. Miera prepojenia ovplyvnila aj genetickú štruktúru. V Karpatoch boli identifikované 2 geneticky vzájomne izolované populácie hlucháňa hôrneho - západokarpatská populácia a východokarpatská populácia. Dobre prepojená východokarpatská populácia si udržala vysokú genetickú diverzitu, avšak západokarpatská populácia vplyvom dlhodobej izolácie a vysokej fragmentácie biotopov stráca genetickú diverzitu. Je evidentné, že dostatočná rozloha a prepojenosť vhodných lesných komplexov je kriticky potrebná pre dlhodobé prežitie populácie hlucháňa v Karpatoch. Pre zabezpečenie priaznivého stavu vhodných biotopov je ideálnou formou manažmentu bezzásahový režim. Pôsobenie prírodných disturbancií (vietor a lykožrút) je kľúčovým faktorom pri tvorbe vhodných štruktúr biotopu hlucháňa hôrneho v pralesoch. Podľa výsledkov tejto štúdie hlucháň potrebuje všetky typy severít disturbancií (slabé, mierne, silné) pre tvorbu vhodných biotopových štruktúr. Disturbančný režim zmiešaných severít typický pre smrekové pralesy Karpát vytvára heterogénny les, ktorý poskytuje dôležité štruktúry pre život hlucháňa. Prírodné disturbancie ovplyvňujú regeneráciu, korunový zápoj, mŕtve drevo a taktiež bylinnú vegetáciu. Na obnovenie rozľahlých degradovaných biotopov je možné využiť praktické lesnícke opatrenia. Dynamika skúmaných pralesov nám môže slúžiť ako príklad, ktorého napodobovaním dosiahneme vhodné cieľové štruktúry biotopu tohto vzácneho druhu. Tento prístup je možné považovať za tzv. ekologické lesníctvo, ktoré má za cieľ okrem ťažby dreva zabezpečiť plnohodnotné ekosystémové služby vrátane zachovania vysokej biodiverzity. Táto práca poskytuje komplexné informácie o štruktúre a dynamike horských lesov s výskytom hlucháňa hôrneho v Karpatoch a bude slúžiť ako podklad pre oblasť lesníctva a ochrany prírody na udržanie populácii tohto emblematického druhu v karpatských horských lesoch.

Kľúčové slová:
ekologické lesníctvo, disturbancie, biodiverzita, fragmentácia biotopov, konektivita, genetická štruktúra

Abstract

Species assemblages have evolved under natural disturbance regimes. Currently, biodiversity loss is greater than ever documented, mainly due to the rapid loss of natural habitats and alteration of disturbance regimes. Forests harbour most global terrestrial biodiversity, and deforestation and forest management continue to exert pressure on forest biodiversity in many parts of the globe. The increasing awareness of the importance of forests for biodiversity requires new managemenmet strategies, however information is limited. The capercaillie (*Tetrao urogallus*) is an increasingly threatened umbrella species. It is a forest dwelling species with relatively low dispersal abilities, complex habitat requirements, and it is sensitive to habitat fragmentation. The Carpathians are one of the remaining strongholds of capercaillie in Europe, yet sufficient information for its preservation and definition of suitable forest management are missing. To inform an effective conservation strategy, we studied capercaillie habitat at different spatial scales using four methodological approaches including population monitoring, species distribution modeling, genetical analyses and dendroecology. The results of this study show, that old-growth spruce forests are the most suitable habitat for capercaillie in the Carpathians. Large-scale logging negatively affected the capercaillie numbers, implying that large-scale clearcuts are unsuitable habitats for the capercaillie. Forest attacked by bark-beatle represented a more suitable habitat compared to sanitary felling areas. On the landscape level, the clearcuts of size 30 % reduced the capercaillie numbers by 76 %. Recently, large areas of suitable habitat were lost across the Carpathians. During the last 20 years 1,110 km^2 (ca. 15 %) of suitable habitats were destroyed by logging, followed by a decline in the connectivity by 33 %. The connectivity also affected the genetic structure of the capercaillie population. We identified two genetically isolated populations – Western Carpathians and Eastern Carpathian populations. The abundant Eastern Carpathian populations share alleles with populations from the boreal forest suggesting a common origin of these populations since the last glaciation. Genetic evidence suggests the Western Carpathian populations have been isolated over a long period with only a few migrants from the east, thereby it is loosing genetical diversity and becoming differentiated from the eastern and northern populations. It is evident, that sufficient size and high connectivity of suitable forest complexes is critically important for long-term survival of capercaillie in the Carpathians. Allowing natural events and natural disturbance processes across multiple scales is likely to benefit capercaillie conservation in European mountain forests. Natural disturbances (wind and barkbeatle) are the factors that create suitable habitat structures of capercaillie in the old-growth forests. According to our results, a wide range of disturbance severities is required to maintain capercaillie populations in natural habitats. The mixed-severity disturbance regime created a heterogeneous and complex environment for capercaillie. Natural disturbance regimes were tightly linked with structural characteristics of forest, including ground vegetation, age structure, density of standing dead wood, and tree density. Dynamics of the studied old-growth forests might be emulated in order to restore suitable habitats. This study provides information about the structure , dynamics and management of capercaillie inhabited mountain spruce forests, which is necessary for conservation and forest management for capercaillie relevant areas in the Carpathians.

Key words:

ecological forestry, forest management, disturbances, biodiversity, habitat fragmentation, connectivity, genetic structure

Obsah

1. Úvod

Prudký pokles biodiverzity prebieha v súčasnosti najmä ako dôsledok straty prirodzených biotopov, ktorá je zvyčajne výsledkom pozmenenia prirodzenej dynamiky ekosystémov. Väčšina suchozemskej biodiverzity prežíva v lesoch a pozmenenie prírodných disturbančných režimov vo forme intenzívneho odlesňovania a obhospodarovania lesov pokračuje v rastúcom tlaku na lesnú biodiverzitu v mnohých častiach sveta (Gustafsson et al. 2012). Postupné uvedomovanie si dôležitosti a významu lesov z hľadiska biodiverzity si vyžaduje nové postupy manažmentu lesov, avšak súčasné poznatky v tejto oblasti sú limitované.

V Európe sa plocha lesov významne zvýšila, ale taktiež sa zvýšila aj intenzifikácia ťažby, ktorej výsledkom je vznik hustých homogénnych lesov a nárast fragmentácie, ktoré predstavujú nové výzvy pre ochranu a manažment lesov (UNECE/ and FAO 2000; Böttcher et al. 2012; Levers et al. 2014). Jedny z najrozsiahlejších lesných ekosystémov Európy sú Karpaty. V Karpatoch sa nachádzajú najväčšie rozlohy pralesov a prírodných lesov, ktoré sú domovom mnohých vzácnych a ohrozených druhov. Práve rôznorodosť štruktúry a substrátov v nich vytvára množstvo ekologických ník. Pre početné náročné, vzácne a ohrozené druhy poskytujú vhodné stanovištia, ktorých je nedostatok v lesoch obhospodarovaných bežným spôsobom. Patria medzi ne machy, lišajníky, slimáky, huby, veľa vtákov a druhov netopierov, a na mŕtve drevo viazané druhy hmyzu (Bütler & Lacha 2009).

Pre manažment lesov s cieľom udržať vysokú biodiverzitu sú často vyberané ako predmet ochrany tzv. dáždnikové druhy, ktoré reprezentujú konkrétny prirodzený ekosystém a ich ochrana akoby vytvára ochranný dáždnik nad radou ďalších vzácnych a ohrozených druhov. Medzi typické a významné dáždnikové druhy prirodzených horských lesov Karpát patrí ohrozený hlucháň hôrny (*Tetrao urogallus*). Hlucháň hôrny je druh veľmi náročný na kvalitu a rozlohu vhodného prírodného prostredia a jeho prežitie doslova závisí na vhodnej štruktúre a veľkej rozlohe lesných komplexov. Znižovanie početnosti hlucháňa je spôsobené vysokou úmrtnosťou juvenilných jedincov, ktoré sú veľmi citlivé na stratu a fragmentáciu starých lesov (Lakka & Kouki 2009). Intenzívne lesné hospodárenie spojené s fragmentáciou vhodných biotopov sú hlavným dôvodom poklesu populácie hlucháňa hôrneho vo svete (napr. Leclerq 1987, Rolstand & Wegge 1987, Klaus et al. 1989, Storch 2000, Obeso & Bañuelos 2003, Sachot et al. 2003, Saniga 2013). Karpaty sú obývané druhou najväčšou populáciou hlucháňa v Európe (pokiaľ nepočítame Škandináviu a Rusko), dosahujúcou početnosť až

11 000 jedincov. Všetky ďalšie európske populácie okrem Škandinávie, Ruska a Álp majú nižšiu početnosť (obvykle do 1 000 jedincov) (napr. Čierny les, Bavorský les, Kantabríske pohorie atď.). Preto možno Karpaty považovať za jedno z hlavných útočísk tohto druhu v Európe. Doposiaľ však neboli vytvorené komplexné materiály potrebné pre ochranu a manažment horských lesov s výskytom hlucháňa pre toto hodnotné územie, i keď z hľadiska dlhodobého prežitia populácie sú nevyhnutné. Preto bolo hlavnou úlohou tejto práce poskytnúť komplexné informácie o štruktúre a dynamike horských lesov s výskytom hlucháňa hôrneho v Karpatoch a vytvoriť podklad, ktorý bude slúžiť pre oblasť lesníctva a ochrany prírody ako návod na udržanie populácii tohto emblematického druhu v karpatských horských lesoch.

2. Literárna rešerš

2.1 Zaradenie druhu a rozšírenie

Hlucháň hôrny (*Tetrao urogallus* Linnaeus 1758) patrí podľa taxonomickej nomenklatúry do triedy vtákov *(Aves)*, radu hrabavce *(Galliformes)*, čeľade tetrovovité *(Tetraonidae)*. V červenom zozname IUCN je hlucháň hôrny zaradený v kategórii najmenej ohrozených taxónov (LC – *Least Concern*) z dôvodu stále početných populácii v Škandinávii a v Rusku. Avšak na území západnej, strednej a južnej Európy došlo v posledných desaťročiach k vyhynutiu alebo výraznému poklesu lokálnych populácii tohto druhu a preto je v mnohých krajinách zaradený do kategórie silne ohrozených taxónov. Priestorová distribúcia hlucháňa hôrneho v Európe nie je súvislá (Obr. 1). Fragmentácia pôvodného areálu vyústila k vytvoreniu 11 poddruhov hlucháňa, identifikovaných na základe morfologických charakteristík. Od 50-tych rokov 20. storočia došlo v Európe vplyvom nepriaznivých antropických zmien k zmenšeniu výmery vhodných biotopov, k zníženiu až strate konektivity, k fragmentácii, k zhoršeniu kvality biotopov, k zníženiu hustoty populácií, k vyhynutiu viacerých lokálnych populácií a k zmenšeniu areálu druhu (Storch 2000).

Obr. 1 *Rozšírenie hlucháňa hôrneho (Tetrao urogallus) v Európe (Coppes et al. 2016)*

2.2 Biologické a ekologické nároky

Hlucháň hôrny (Obr. 2) sa vyznačuje nápadným pohlavným dimorfizmom, tak v sfarbení peria, ako aj vo veľkosti. Kohút je hnedočierny, so zeleným leskom peria na prsiach. Má výraznú bielu škvrnu pri koreni krídel a lysé polmesiačikovité sýtočervené „ruže" nad očami. Perie na brušnej časti aj koncové časti chvostových pier bývajú viac alebo menej bielo fŕkané. V zaokrúhlenom chvoste je 18, niekedy 20 – 22 pier. Pod zobákom má predĺžené peria tvoriace „bradu“. Sliepka je nápadne menšia, tmavo hrdzavohnedá s nápadnou jasno hrdzavou škvrnou na prsiach. Za letu sa dá rozpoznať od podobnej sliepky tetrova hôľniaka podľa zaokrúhleného chvosta. Kuriatka sú hrdzavo-žlté, na čele majú dva tmavohnedé pozdĺžne pruhy, nadočný prúžok, prúžok pod okom, chrbát hnedo až čierno škvrnitý, brucho bledo okrovo žlté, oko namodralo šedé, zobák zhora tmavej a zospodu svetlej farby, prsty s pazúrmi žlté (Kněžourek 1912).

Hlucháň sa najčastejšie zdržiava na zemi, nocuje na stromoch a kohút na strome aj toká. Kohút meria v rozpätí krídel asi 1,40 m, sliepka len 0,95 – 1,05 m. Hmotnosť kohútov kolíše od 3,0 po 6,5 kg (priemer 4,1 kg), ale aj sezónne – pred tokaním sa zvyšuje a počas tokania klesá takmer o 0,5 kg. Sliepka dosahuje hmotnosť 1,5-2,5 kg. Naše populácie hlucháňa patria k európskej geografickej rase *Tetrao urogallus major*. Vek kohúta sa odhaduje podľa hmotnosti, zobáka, ryhy na zobáku, prípadne veľkosti paletkových pierok. Všeobecne, kohúty do hmotnosti 3,5 kg sú nedospelé (jednoročné), s hmotnosťou 4 – 4,2 kg sú priemerné, 4,5 kg možno považovať za silné a vyše 5 kilogramové za kapitálne. Pri druhom znaku sa posudzuje dĺžka chvostových pier. Staré kohúty majú zvyčajne na hornom zobáku zjavnú ryhu, mladé ho majú hladký a menej zohnutý. Tieto údaje však nemusia platiť všeobecne (Klaus et al. 1989).

***Obr.* 2** *Hlucháň hôrny, vzadu kohút, vpredu sliepka. Foto: Martin Mikoláš*

2.3 Hlucháň hôrny, lesníctvo a druhová ochrana

Hlucháň hôrny je pre svoje vysoké a špecifické nároky na kvalitu biotopu považovaný za dáždnikový druh horských lesov. Jeho ochrana vytvára "ochranný dáždnik" nad radou ďalších vzácnych a ohrozených druhov horských lesov (Suter et al. 2002). Stav a vývoj jeho populácie je zároveň indikátorom stavu lesných ekosystémov, v ktorých sa prirodzene vyskytuje. Hlucháň je kvôli obrovským priestorovým nárokom veľmi citlivý na fragmentáciu lesa. Telemetrické údaje ukázali, že hlucháne počas roka využívajú plochu 132 ha – 1 207 ha, priemerne 550 ha (Storch 1995). Prepojené biotopy tokaniskových jednotiek by nemali byť menšie ako 1400 ha a takéto ostrovy vhodných biotopov by nemali byť od seba vzdialené viac ako 5-10 km (Bollmann et al. 2011). Pre minimálnu životaschopnú populáciu by takto prepojené biotopy mali dávať spolu 250 – 500 km^2 (Grimm & Storch 2000, Braunisch & Suchant 2013).

Uprednostňovaný biotop hlucháňa je charakterizovaný ihličnatými hlboko zavetvenými stromami, otvorenými štruktúrami s miernym zápojom 50 – 60 % a bohatou pozemnou vegetáciou tvorenou brusnicou čučoriedkovou (*Vaccinium myrtillus*) a inými krami z čeľade vresovcovité (*Ericaceae*) (Storch 2002). Čučoriedka zohráva dôležitú úlohu v biotope hlucháňa, poskytuje letnú potravu pre adultov, bezstavovce pre kuriatka a krycí a tepelný úkryt v jednom (Storch 1995). Ihličím sa prevažne kŕmia na stromoch s redukovanou živicou, ale zvýšeným obsahom energie. Sú to často stromy napadnuté chorobou, poranené, alebo rastúce na nevhodných pôdach (Lindén 1984). Výber biotopu v zimnom období je podobný jesennému. Výber biotopu podľa ročného obdobia je ovplyvnený časovou a priestorovou dostupnosťou potravy, klimatickými podmienkami a možnosťami úkrytov a hradovacích stromov, charakteristickým správaním počas jarného a jesenného obdobia toku (Saniga 2004). Sliepky môžu využívať čistiny obzvlášť v období neskoršieho leta a počas jesene kvôli dostatku potravy. Hlucháne upredností̌ujú staré lesy a vyhýbajú sa mladým lesom. Ak je ale štruktúra a vegetácia v mladých porastoch vhodná, môžu využívať aj takéto lesy (Rolstand & Wegge 1987). Pomocou telemetrie a pozorovaní z rokov 1988 - 1992 v Bavorských Alpách – Teisenberg opisuje Storch (1994) biotop sliepok s kuriatkami. Hniezda a neskôr aj mláďatá sa najčastejšie vyskytovali v lesoch s bohatou pozemnou vegetáciou. Ukrytie hniezda bolo pravdepodobne hlavným faktorom pre úspešné vyliahnutie kuriatok. Využívaný areál jednej rodinky bol priemerne 148 ha od vyliahnutia po neskoré leto. Preferované boli staré lesy s bohatou pozemnou vegetáciou a s vysokým zastúpením bezstavovcov, pričom dôležitou súčasťou je čučoriedka. Naopak, Wegge et al. (1992) na základe telemetrických výskumov v Nórsku tvrdí, že sliepky potrebujú na hniezdenie 20 - 30 ha. Rodinka po vyliahnutí potrebuje až 1000 ha vhodného biotopu kvôli pohybu počas 4 - 6 týždňov.

Štruktúra lesa ovplyvňuje dokonca aj rýchlosť celkového pohybu. V nórskom Varaldskogen, Fjella študovali Wegge et al. (2007) sliepky zo štyroch rodiniek. Zistili, že keď bola rodinka vo vnútri starého prírodného lesa, nepresúvala sa do hospodárskeho lesa. Keď bola vo vnútri hospodárskeho lesa, nerozlišovala medzi vstúpením do starého prírodného lesa alebo zotrvaním v hospodárskom lese. Vo vnútri hospodárskeho lesa sa rodinky pohybovali rýchlejšie ako v starých lesoch, čo môže súvisieť s vyššou dostupnosťou potravy a úkrytových možností v starých lesoch. Priemerná rýchlosť pohybu rodinky je 83,2 m za hodinu. Suaréz-Seoane & García-Rovéz (2004) sa snažil zistiť, či ľudské vyrušovanie v plochách obklopujúcich pralesovité lesné plochy ovplyvňujú jadrové populácie kantábrijského hlucháňa v severozápadnom Španielsku viac ako štruktúra a kompozícia biotopu. Zistil, že miesta, ktoré si hlucháne vybrali na tok, boli charakteristické väčšími plochami starého lesa s väčšou relatívnou druhovou bohatosťou stromov, väčšou nadmorskou výškou a vzdialenosťou od riek. Tieto vhodné plochy boli pod menším vplyvom ľudských aktivít, nachádzali sa vo väčšej vzdialenosti od ciest a domov. Hluchánie tokaniská zanikli v nižších nadmorských výškach bližšie k domom a poľovníckym oblastiam.

2.4 Rozmnožovanie a význam štruktúry lesa pre úspešnosť reprodukcie - letný biotop

Hlucháň žije v polygamii. Kohúty sa združujú v blízkosti sliepok iba v čase tokania, inak tvoria malé kŕdliky. Vo februári až marci sa kŕdliky rozpadávajú a kohúty začnú navštevovať staré tokaniská, ktoré využívajú po mnoho rokov, prípadne aj tokajú na tom istom strome. Tokanie sa začína zvyčajne v prvej polovici apríla, vrcholí v druhej polovici mája. V závislosti od nadmorskej výšky a poveternostných podmienok sa môže pretiahnuť až do konca mája – začiatku júna. Tokanie sa začína pri svitaní a predstavuje charakteristický ceremoniál sprevádzaný v jednotlivých fázach osobitými hlasovými prejavmi označovanými ako klepanie, trilkovanie, lusknutie a brúsenie. Vo fáze brúsenia má hlucháň zníženú schopnosť prijímať z okolia podnety, najmä zvukové. Postupne kohúty zletujú na zem, kde pokračujú v tokaní a medzi blízkymi jedincami dochádza k súbojom. V čase plného tokania sa kompletná toková strofa opakuje 200 – 300 ráz. Sliepky vábia kohúty nosovým zvukom „gok –gok". Po krátkom krúžení okolo sliepky nasleduje párenie, ku ktorému dáva podnet sliepka zaujatím charakteristickej pričupenej pózy. Sliepky zvyčajne navštevujú niekoľko tokanísk, kde sa pária iba s dominantným kohútom. Tokaniská bývajú v nenarušených podmienkach vzdialené priemerne 2 km od seba. Po spárení opúšťajú sliepky tokanisko a upravujú si hniezda, zvyčajne pri pni alebo pri kmeni stromu, prípadne pod vývratom. Koncom apríla znášajú priemerne 8 (5 – 12) žltkastých a tmavohnedo škvrnitých vajec. Inkubácia trvá 26 dní.

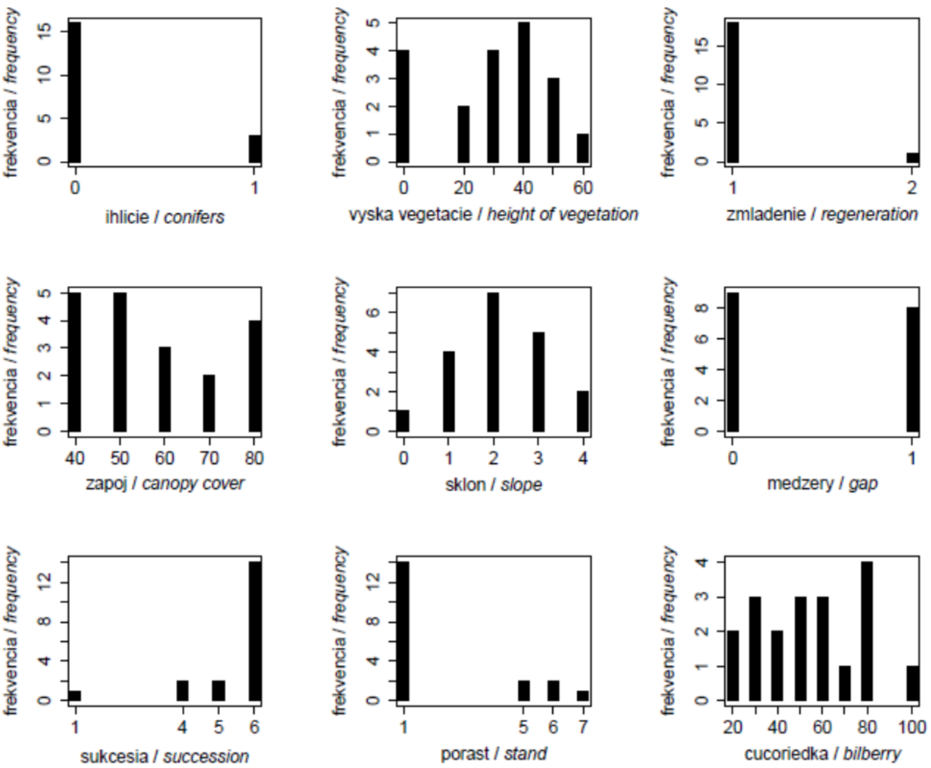
Hlavný dôvod poklesu populácie hlucháňa je nízka reprodukcia. Vhodná štruktúra a dostatočná rozloha lesov zohráva najvýznamnejšiu úlohu pre prežitie juvenilných jedincov (Obr. 3). Už 24 hodín po vyliahnutí sliepka odvádza kuriatka z hniezda do vhodných porastov, kde je dostatok potravy, ktorú im odkrýva hrabaním. V prípade nebezpečenstva dokáže reagovať odvádzaním nepriateľa, alebo kuriatka priamo brániť. Mláďatá sa pomerne rýchlo vyvíjajú, za 10 dní sa operujú a za 2 týždne vedia lietať. V druhom mesiaci sa úplne operia, ale až do jesene sa držia matky. Ekológia mláďat v Nemecku bola študovaná tak, že bolo odchytených 16 sliepok, ktoré boli následne vybavené telemetrickými vysielačmi. Boli pozorované počas obdobia kladenia vajec, sedenia na vajciach a výchovy mláďat. Všetky dospelé sliepky inkubovali, dve tretiny hniezd sa vyliahli a iba jedna pätina kuriatok prežila do jesene (Storch 1994).

Hmyz tvorí dominantnú časť potravy hlucháních mláďat prvých 28-29 dní. Bezstavovce tvoria viac ako 50 % potravy kuriatok v prvom týždni života. V prvom rade sú to húsenice motýľov, ktoré sú najdôležitejšou zložkou potravy hlucháních kuriatok a ich hustota determinuje pohyb hlucháních rodiniek (Wegge at al. 2005). Dostupnosť húseníc závisí najmä na štruktúre porastu- konkrétne na hustote porastu a na pokryvnosti a výške bylinnej vegetácie (predovšetkým čučoriedky) (Obr. 4). Pokiaľ je les príliš tmavý, húsenice (a ďalší hmyz) sa v ňom nevyskytujú. Pokiaľ je les riedky s dostatkom dopadajúceho svetla na zem, avšak výška čučoriedok presahuje 40-50 cm, húsenice vylezú na vrchol čučoriedok, kuriatka na ne nedočiahnu a tým prichádzajú o základnú zložku potravy potrebnú pre ich prežitie. Preto je ideálna výška čučoriedkových kríčkov pre biotopy hlucháních kuriatok 30 - 40 cm (Mikoláš et al. 2013). Dostatok mikrostanovíšť vo forme vývratov a mŕtveho dreva zvyšuje heterogenitu prostredia a tým aj možnosť dosiahnuť potrebnú potravu na miestach s vysokou výškou čučoriedok. Dôležité je spomenúť aj vplyv depozície dusíka, ktorý mení spoločenstvá a výšku bylinnej vegetácie a môže mať zásadný vplyv na úspešnosť prežitia kuriatok hlucháňa. Ďalšími zložkami potravy juvenilných jedincov sú mravce s ich kuklami, rozličný hmyz žijúci na zemi, jeho larvy a kukly, pavúky, kosce, mnohonôžky, menšie mäkkýše a pod. (Ferianc 1964).

Obr. *3 Kuriatko hlucháňa a jeho biotop - prirodzený les s korunovým zápojom do 50% a vysokou pokryvnosťou čučoriedky. Nízka reprodukcia je hlavný dôvod poklesu populácií tetrova hlucháňa v Európe, do jesene umrie viac ako 80 % kuriatok (Storch 1994). Foto: Artur Tabor (vľavo), Erik Baláž (vpravo)*

Kuriatka sa po siedmych týždňoch života živia takmer výlučne rastlinnou potravou. Z toho 85 % tvoria čučoriedky. Ďalšou významnou zložkou ich potravy môžu byť kvety -

napríklad vresovca štvorradového (*Erica tetralix)* a čermeľa lúčneho (*Melampyrum pratense)*. Pozorovaný pokles v proporcii skonzumovaného hmyzu nie je výsledkom poklesu jeho abundancie (Spidsø & Stuen 1988).



Obr. 4 *Histogramy základných premenných vyplývajúcich s charakterizujúcich habitat juvenilných jedincov podľa HSI (Storch 2002). Vysvetlenie jednotlivých premenných: ihličie (prítomnosť preferovaných kŕmnych stromov), výška vegetácie – výška bylinnej etáže (v triedach 1: 1–10 cm, 2: 11–20 cm, 3: 21–30 cm atď.), zmladenie (pokryvnosť drevinného zmladenia: v triedach 1: < 25 %, 2: 26–50 %, 3: 51–75 %, 4: >75 %), zápoj (korunový zápoj (%), sklon svahu (v triedach 0: < 5°, 2: 6–15°, 3: 26–35°, 4: 36–45°, 5: >45°), medzery – prítomnosť medzier v poraste, sukcesia (sukcesná štádium porastu: 1: mladina, 2: žrďkovina, 3: žrďovina, 4: kmeňovina, 5: starý porast, 6: vekovo rôznorodý porast, 0: žiadny les), drevinové zloženie – v triedach (1. Picea abies, 2. Picea abies + Pinus sp., 3. Picea abies + Abies alba, 4. Picea abies + Larix decidua, 5. Picea abies + Fagus sylvatica, 6. Picea abies + Sorbus aucuparia, 7. Picea abies + iné listnaté stromy, 8. Pinus sp., 9. Abies alba + iné listnaté stromy, 10. Fagus sylvatica, 11. Fagus sylvatica + Picea abies, 12. Fagus sylvatica + Abies alba), čučoriedka – pokryvnosť čučoriedky Vaccinium myrtillus (%).*

V severozápadnom Rusku sa Wegge et al. (2005) snažili identifikovať kľúčové prvky pri výbere biotopu sliepok s kuriatkami. Počas siedmych týždňov monitorovali pohyb desiatich rodiniek. Porovnali abundanciu hmyzu a pokryvnosť kríkov v priľahlých kontrolných plochách. Lokality, na ktorých sa rodinka vyskytovala, boli bohatšie na hmyz ako kontrolné plochy. Najväčší rozdiel bol v hustote húseníc motýľov (*Lepidoptera*), ktoré determinovali výber biotopov sliepok s kuriatkami. Takýto výber biotopu prebiehal počas celých 7 týždňov. Aj keď sa v porovnaní s distribúciou hmyzu pokryvnosť čučoriedky javila menej dôležitým faktorom pri výbere biotopu rodinky, bola na lokalitách výskytu vyššia. Kríky čučoriedok poskytujú hlucháňom okrem potravy aj úkryt pred predáciou.

Moderné lesníctvo môže mať škodlivý vplyv na kvalitu habitatu kuriatok redukciou potravných zdrojov. Rodinka sa pohybuje rýchlejšie v hospodárskych plantážach ako v starých prirodzených lesoch. V prirodzených lesoch má viac kvalitnejšej potravy a lepšie úkrytové možnosti. Aj vo Fínsku sa počas posledných desaťročí značne znížili stavy hlucháňov. Lakka a Kouki (2009) študovali, ako rôzne manažované typy lesov ponúkajú zdroje na prežitie hluchánich kŕdlikov. Čučoriedka pozitívne korelovala s biomasou lariev a všetkých bezstavovcov. Preukázalo sa, že vývojové štádiá nasledujúce po holoruboch vážne znižujú dostupnosť potravy pre kuriatka a tiež úkrytové priestory. To isté zaznamenal aj Steuen (1988) pri porovnaní odťažených a neodťažených plôch v Nórsku. Hustota bezstavovcov a špeciálne lariev je značne redukovaná holorubmi (80 %) a o niečo menej v monokultúrach. Veľkým nebezpečenstvom pre prežitie kuriatok je aj použitie pesticídov. Pesticídy používané na boj s podkôrnym hmyzom sú založené na báze cyklických pyretroidov. Účinnou látkou použitých prípravkov je zväčša cypermetrín. Táto látka pôsobí v priebehu niekoľkých týždňov, navyše neselektívne, teda usmrcuje aj hmyz, ktorý tvorí potravu hlucháňa hôrneho. Keďže sa pesticídy používajú v čase rojenia lykožrútov (obyčajne máj - august) zasahujú najcitlivejšiu fázu v ročnom cykle života hlucháňa – vyvádzanie mláďat (Mikoláš et al. 2013). Extrémne teplotné výkyvy v počasí spôsobené klimatickou zmenou prispievajú k zvýšenej úmrtnosti kuriatok (Schröder et al. 1982). Počasie počas obdobia liahnutia kuriatok môže mať vysoký význam - chladné počasie a sneh ovplyvňuje najmä rýchlosť pohybu kuriatok a tým zvyšuje zraniteľnosť voči predácii.

2.5 Štruktúra zimných biotopov

V zime sa hlucháne na Slovensku zdržiavajú prevažne v smrekovom pásme, kde nachádzajú vhodnú potravu a to v blízkosti tokanísk, v lesoch s hlboko zavetvenými stromani a rozvoľneným korunovým zápojom (Obr. 5) (Stroch 1997). Počas zimy sa živia iba ihličím, ktoré je chudobné na energiu. Preto hlucháne musia počas obdobia zimy energiu šetriť, takmer vôbec nelietajú a aj chôdzu obmedzujú na iba krátke vzdialenosti. Časté plašenie preto spôsobuje významnú stratu energie v tomto období. Pri výbere druhov stromov, ktorými sa kŕmia, preferujú ihličie jedle a borovice pred smrekom. Vyhľadávajú si často práve zranené stromy s vyšším obsahom živice. Hlucháne zväčša zimujú samostatne, alebo v malých skupinkách (2-4 jedince).

***Obr.* 5** *Štruktúra zimného biotopu: medzernatý zápoj, bohatý podrast, stromy zavetvené po zem. Nemusia to byť pralesy, no musia to byť lesy s vhodnou štruktúrou, t.j. lesy rozvoľnené. Foto: Miroslav Svoboda*

2.6 Potravné nároky druhu (kvalita, kvantita potravy, spôsob výživy, získavanie potravy)

V skorom jarnom období sa hlucháň živí predovšetkým vetvičkami a výhonkami smreku (*Picea abies*), ale pokiaľ sú dostupné, preferovanými kŕmnymi stromami sú jedľa (*Abies alba*) a borovica (*Pinus spp.*) (Saniga 1998, Zawadzka 2014, Obr. 21) a na hranici lesa aj kosodrevina (*Pinus mugo*). V nižšie položených biotopoch (dnes už vzácnych) postupne v jeho potrave prevládnu púčiky buka. V máji začína byť významným zdrojom potravy čučoriedka (*Vaccinium myrtillus*). V lete konzumuje listy, púčiky, kvety a bobule rôznych bylín a kríkov. Prevažne ide o čučoriedku a malinu (*Rubus ideaus*), ale aj ďalšie vresovcovité rastliny ako napr. brusnica obyčajná (*Vaccinium vitis-idaea*) (Saniga 1998). Okrem rastlinnej potravy sa hlucháne v lete živia aj hmyzom a inými drobnými živočíchmi z rastlín, prípadne ich vyhrabávajú spod lístia (Bakoš & Hell 1999). Na jeseň sa v potrave opäť zvyšuje podiel ihličia, čučoriedka však naďalej zostáva dôležitou zložkou. V zimnom období je hlavnou zložkou hluchánej potravy ihličie, výhonky a púčiky ihličnatých stromov (Saniga 2005). Pre ľahšie mechanické spracovanie potravy zbierajú hlucháne gastrolity, ktorých majú v žalúdku asi 30 – 40 g.

2.7 Vzdialenosť preletov

Hlucháň hôrny je stály vták, existuje však niekoľko málo zdokumentovaných prípadov sezónnej migrácie. Napríklad na Urale sa celé populácie presúvajú medzi letným biotopom v listnatom lese a zimným v ihličnatom (Kirikov 1947). Dôvodom je pravdepodobne priestorové oddelenie letnej a zimnej potravy (Stroch 2007). Hlucháň je relatívne bežne schopný preletov do 5 – 10 km (Bollman et al. 2011). Práve tieto presuny umožňujú komunikáciu a výmenu genetickej informácie medzi jednotlivými populáciami. Preto je dôležité, aby vhodné biotopy neboli od seba vzdialené viac než 10 km. V opačnom prípade sa naruší prepojenosť metapopulácie, ktorá sa následne rozpadne na viacero malých izolovaných populácií. U takto izolovaných populácii je pravdepodobnosť postupného zániku oveľa vyššia. Areál jednotlivcov však nie je v priebehu roka stály. V zime a na jar využívajú samce areály najbližšie k tokanisku, starší sú k nemu bližšie než mladší (Wegge & Larssen 1987, Storch 1995). Koncom jari sa presúvajú do letného habitatu, ktorý môže byť od tokaniska vzdialený až 7,3 km. Samice vo všeobecnosti využívajú väčší areál a ďalej od tokaniska než samci (Storch 1995). Wegge & Rolstad (1986) v Nórsku preukázali, že veľkosť využívaných areálov je nepriamo úmerná ploche starých lesov v ňom – čím ich je viac, tým menší areál jedinec potrebuje.

2.8 Príčiny ohrozenia

2.8.1 Strata vhodných lesných komplexov

Intenzívne lesné hospodárenie spojené s fragmentáciou vhodných biotopov sú hlavným dôvodom poklesu populácie hlucháňa hôrneho vo svete (napr. Leclerq 1987, Rolstand & Wegge 1987, Klaus et al. 1989, Rolstand & Wegge 1989a, 1989b, Gjerde 1991, Wegge et al. 1992, Ménomi & Bougerol 1993, De Franceschi 1994, Klaus & Bergman 1994, Ménomi 1994, Moss 1994, Saniga 1994, Kurki et al. 2000, Storch 2000, Obeso & Bañuelos 2003, Sachot et al. 2003, Bučko et al. 2011, Štefančík et al. 2011, Tesák 2011, Saniga 2012, Mikoláš et al. 2013, Saniga 2013, Mikoláš et al. 2015). Nízka reprodukcia spôsobená priamym a nepriamym vplyvom lesného hospodárstva je hlavný dôvod poklesu populácií hlucháňa hôrneho v Európe (Wegge et al. 2005), pretože vývojové štádiá nasledujúce po veľkoplošnej ťažbe značne znižujú potravnú ponuku a úkrytové možnosti pre juvenilné jedince (Lakka & Kouki 2009). Telemetrické údaje ukázali, že hlucháne počas roka využívajú plochu 132 ha – 1 207 ha, priemerne 550 ha vhodných biotopov (Storch 1995). Hlucháň je kvôli obrovským priestorovým nárokom veľmi citlivý na fragmentáciu lesa (Storch 1997, Kurki et al. 2000). V porovnaní so súvislými lesnými celkami je vo fragmentovaných oblastiach vplyvom zvýšeného predačného tlaku významne vyššia mortalita kuriatok (Wegge & Storaas 1990).

2.8.2 Malá veľkosť vhodných lesných komplexov a ich vzájomná izolácia

Kľúčový význam má silná geografická izolácia spolu s nízkou početnosťou populácií, čo má za následok inbreeding (príbuzenské kríženie) a stratu genetickej variability, čo zvyšuje pravdepodobnosť vymretia danej populácie (Segelbacher et al. 2003, Storch 2007, Zawadzki & Zawadzka 2012). Schopnosť adaptácie populácie je v priamom vzťahu s jej genetickou diverzitou (Frankham et al. 2010). Informácie o genetických a demografických faktoroch majú zásadný význam pre úspešnú ochranu druhu. Stupeň inbreedingu sa zvyšuje s tým, ako početnosť populácie klesá. Vysoký stupeň príbuzenského kríženia vedie ku zníženiu životaschopnosti – k tzv. inbrednej depresii (Frankham et al. 2002).

Pre dlhodobú udržateľnosť populácií hlucháňa hôrneho je veľmi dôležité zachovať pôvodné biotopy. Maximálna vzdialenosť medzi biotopmi o veľkosti minimálne 14 km^2 obsadenými hlucháňom by mala byť 10 km (Bollmann et al. 2011). Spolu by tieto biotopy mali zaberať plochu 250-500 km^2 vhodných biotopov, aby bola zabezpečená dostatočná rozloha pre minimálnu životaschopnú populáciu o veľkosti minimálne 500 jedincov (Grimm & Storch 2000, Braunisch & Suchant 2013). Pokiaľ sú splnené tieto podmienky, ďalšie negatívne faktory (napr. predácia, vplyv výkyvov počasia) neohrozia dlhodobé prežitie populácie.

2.8.3 Predácia

Dôležitým faktorom, ktorý ohrozuje prežitie najmä malých a izolovaných populácií je predácia. Zhrnutie problematiky predácie prináša Storch (2007). Predácia predstavuje prirodzený proces. Interakciu medzi predátorom a jeho korisťou chápeme ako druh súťaže, kde inovácia zo strany predátora vedie k odpovedi zo strany koristi. Hovoríme o koevolúcii, vlastnosti predátora a jeho koristi nie sú izolované a majú zmysel, len ak o nich uvažujeme ako o súčasti jedného systému. Hlucháne získali súbor morfologických, fyziologických a behaviorálnych adaptácií, ktoré im umožňujú vyrovnať sa s predáciou. Bez predátorov by sa evolúcia hlucháňa odvíjala inou cestou a práve vďaka predácii sú tým druhom, ktorý poznáme. Napriek tomu je predácia v mnohých Európskych krajinách vnímaná ako vážne ohrozenie pre populácie hlucháňa. Tento názor nie je neopodstatnený, existujú presvedčivé doklady, že výrazná redukcia predátorov vedie k lepšiemu prežívaniu hlucháňov. Na druhej strane, časť odborníkov zastáva názor, že predácia sotva dokáže zlikvidovať populáciu hlucháňa, ak je jeho habitat nedotknutý.

Ak odhadujeme relatívny význam faktorov, ktoré môžu ovplyvniť veľkosť a dynamiku populácie, je užitočné rozoznávať *proximálne* (blízke) a *ultimátne* (konečné) príčiny. Populácie predátorov nepochybne vzrástli a predácia môže viesť k vyhynutiu malej a izolovanej populácie. Nejedna hluchánia populácia žije na „ostrovoch“ vhodného prostredia obklopených „morom“ hustého hospodárskeho lesa a kultúrnej krajiny. Kultúrna krajina hostí početné populácie predátorov, čo síce nebol ľudský zámer, predačný tlak je však vďaka tomu omnoho silnejší. Predácia je teda *proximálnou* príčinou. *Ultimátnou* príčinou je strata a fragmentácia prostredia v dôsledku ľudských aktivít. V tejto situácii tlmenie predátorov jednoducho potláča príznaky a nerieši príčinu nežiaduceho stavu (Storch 2007).

Jeden zo spôsobov, akým sa vtáky vyrovnávajú s predáciou je počet vajec v znáške. Vysoký počet vajec v znáške hlucháňa (5-12 vajec) a možnosť zniesť aj druhú znášku v prípade zničenia prvej teda môžeme považovať za evolučnú adaptáciu na silnú predáciu. Hlucháne sú síce náchylné stať sa korisťou predátorov, vysokú mieru predácie však kompenzujú vysokou natalitou.

V tomto kontexte sa ako kľúčový faktor javí práve možnosť rozmnožovať sa, t.j. mimoriadnu dôležitosť má prítomnosť tokanísk, hniezdísk a dostupnosť potravy pre kuriatka. V súlade s tým z nášho územia nemáme doklady o tom, že by predácia ohrozila populáciu hlucháňa. Napr. populácia hlucháňov v Západných Tatrách zostáva dlhodobo stabilná a zároveň tu nedošlo k zásahom do jeho prostredia. Naopak, v Nízkych Tatrách existovala pred lesníckymi zásahmi (v nadväznosti na veternú kalamitu v r. 2004) najsilnejšia populácia hlucháňa na Slovensku. V súvislosti so zánikom vhodného prostredia klesla početnosť hlucháňa. Zároveň neexistujú pozorovania, ktoré by potvrdili nárast predátorov v tom istom čase.

Fragmentácia prostredia však silne zvyšuje predáciu, a to kuriatok i dospelých jedincov (Wegge & Storaas 1990, Wegge et al. 1992). Tým, že po náhlej strate biotopu sa hlucháne vyskytnú vo väčšom počte na menšej výmere lesa, stávajú sa magnetom pre predátorov. Následný vývoj holorubov – vznik husto zapojenej homogénnej mladiny predstavuje úplnú stratu habitatu pre hlucháňa. V hustom lese hlucháň nedokáže lietať (je to veľký vták a nedokáže dobre manévrovať), nenachádza v ňom potravu a taktiež stráca výhľad potrebný na únik pred predátormi. Predačný tlak môžeme eliminovať aj nepriamo - znižovaním výmery (resp. zabraňovaním vzniku nových) rozsiahlych odťažených plôch a v prípade už vzniknutých holín zabrániť vzniku homogénnych hustých porastov.

Žiadny z druhov, ktoré lovia hlucháňa sa nešpecializuje na vyhľadávanie hniezd, ale ničí znášky príležitostne. Pri výskumoch prirodzených znášok v Nórsku sa zistilo, že najväčšie škody spôsobila líška a krkavcovité vtáky (Storaas & Wegge 1987). V našich podmienkach zo 75 kontrolovaných hniezd bolo zničených až 65 %. Najvyšší podiel na tom mali líšky, kuny a iné lasicovité (spolu 22 %), ďalej diviaky (9 %), medveď (3 %) a z vtákov hlavne sojka a krkavec (až 18 %) (Saniga 2002). V Poľsku spôsobila predácia líšok 77 % z 22 prípadov usmrtenia hlucháňa (Zawadzka & Zawadzki 2008). Vo Fínsku tvorili 7 % potravy jastraba lesného práve sliepky hlucháňa (Tornberg 2001). Dospelé jedince netvoria základnú potravu žiadneho z predátorov. Predačný tlak je rozdielny pre obe pohlavia. Veľké kohúty sa stávajú korisťou ťažšie ako malé a na zemi hniezdiace sliepky, prípadne sliepky vodiace mláďatá.

Zhrnutie: hlucháň hôrny je ako druh evolučne dobre adaptovaný na silný predačný tlak. Predácia zohráva významnú úlohu, len ak dôjde k zmene prostredia vplyvom ľudských aktivít, napr. fragmentácii prostredia. Predácia je preto iba príznakom, skutočnou príčinou nežiaduceho stavu sú človekom navodené zmeny prostredia. Či je kontrola predátorov akceptovateľnou a udržateľnou formou ochrany hlucháňa je však otázkou ľudských hodnôt, nie ekológie (Storch 2007).

2.8.4 Ľudské vyrušovania

Turistické centrá môžu predstavovať prekážku v komunikácii medzi populáciami. Turizmus má taktiež vplyv na zvýšenie predačného tlaku na hlucháne. Horské chaty a miesta navštevované ľuďmi totiž prispievajú k zvýšeniu nosnej kapacity prostredia pre významné predátori hlucháňov (napr. čeľaď Corvidae) (Storch & Leidenberger 2003). Ďalším významným negatívnym vplyvom je plašenie. Pre hlucháňa je vyrušovanie kritické najmä v zimných a jarných (obdobie toku) biotopoch a biotopoch rodiniek s kuriatkami počas letných mesiacov - najmä máj, jún a júl (Ménomi & Magnani 1998). Pri porovnaní obsahu stresového hormónu kortikosterónu v truse jedincov v blízkosti rekreačných zimných aktivít v smrekových lesoch Thiel et al. (2011) zistili jeho rastúci obsah smerom od miest s nízkym a stredným vyrušovaním až k miestam s vysokou turistickou intenzitou.

Okrem turizmu významne vtáky vyrušujú aj lesné práce (ťažba, odvoz dreva, pestovné práce ...). Vyplašené jedince majú málo času na kŕmenie a odpočinok, a vďaka zníženej zdatnosti sa ľahšie stanú korisťou predátorov. Priebeh ťažby počas celého roka nepriamo pôsobí na kondíciu, väčšiu zraniteľnosť a nižší úspech liahnutia (Zawadzka 2014).

Opakované alebo pretrvávajúce zvýšenie kortikosterónu v súvislosti s vyrušovaním, môže ovplyvniť celkovú zdatnosť jedincov - telesnú kondíciu, imunitu, reprodukciu a prežívanie jedincov (Wingfield et al. 1997). Preto lokality s vysokou kvalitou biotopu nemusia byť obývané hlucháňmi, ak je lokalita pod vplyvom iných negatívnych faktorov (napr. intenzívny turizmus) pôsobiacich zo širšieho okolia (Storch 2002), čo sa prejavilo aj vo výsledkoch mapovania v Nízkych Tatrách (Mikoláš et al. 2013).

Negatívny vplyv turizmu je možné minimalizovať. V niektorých krajinách (napr. Rakúsko, Francúzsko, Nemecko, Švajčiarsko) boli vyvinuté programy opatrení na obmedzenie ľudského vyrušovania (Zeitler & Glanzer 1998).

2.8.5 Kolízie s oplotkami

Hlucháne v rýchlom lete nevidia ploty a podobné konštrukcie pokiaľ nie sú dostatočne označené. Preto v lokalitách výskytu, pokiaľ je nutné tieto konštrukcie umiestňovať, musia byť dostatočne označené.

2.9 Efekt lesníckeho manažmentu na hlucháňa hôrneho

V Európe prežívajú hlucháne v rôznych typoch lesov. V strednej Európe sú to prevažne lesy s dominanciou smreka obyčajného, v boreálnych lesoch Škandinávie sú významným biotopom typické boreálne borovicovo-smrekové lesy, v južnej Európe v Albánsku prežívajú hlucháne v borovicových lesoch ovplyvnených pastvou a napríklad v Španielsku v Kantabrískom pohorí sa hlucháne vyskytujú v špecifických brezovo dubových lesoch (Quevedo et al. 2006). Rôzne typy lesov vyžadujú odlišný lesnícky manažment, ktorý musí byť prispôsobený špecifickým podmienkam danej oblasti a v prístupoch pre konkrétne oblasti sú patričné rozdiely. V oblasti Strednej a Západnej Európe boli jasne preukázané negatívne vplyvy rozsiahlej holorubnej ťažby na populácie (Storch 2007). Hlucháne prežívajú najmä v starých prirodzených lesoch alebo v lesoch kde sa cielene udržiava otvorený korunový zápoj a vysoká pokryvnosť čučoriedky podľa špecializovaných lesníckych postupov (tzv. hlucháňovi priateľský manažment lesov). Údaje z oblasti Bavorského lesa a Šumavy poukazujú aj na to, že hlucháňe môžu prežívať aj v mladých lesoch vzniknutých po prírodnej disturbancii, pokiaľ nedošlo k asanačnej ťažbe (Rössner et al. 2014). V Škandinávii sú taktiež považované staré lesy ako hlavný typ biotopu hlucháňa a po dlhé roky bola veľkoplošná ťažba starých lesov pokladaná ako hlavný dôvod poklesu populácie (Wegge et al. 1992). I keď ťažba dočasne odstránila biotopy hlucháňa, paradoxne však v boreálnej oblasti z dlhodobého hľadiska nebol preukázaný negatívny vplyv veľkoplošných holorubov na populáciu hlucháňa. Výsledky štúdie z Nórska a Fínska poukazujú na to, že hlucháň je relatívne tolerantný voči týmto zásahom a populácia dokáže z dlhodobého hľadiska prežiť aj v krajine kde došlo k rozsiahlej holorubnej ťažbe a po približne 30 rokoch znova začínajú osídľovať tieto mladé porasty (Miettinen 2009; Wegge & Rolstad 2011). Tieto výsledky však nie je možné aplikovať na územie Strednej a Západnej Európy , ktoré sú mimo boreálneho pásma, pretože dynamika regenerácie boreálnych lesov je odlišná od horských lesov v miernom pásme a na vyťažených plochách umožňuje vznik mladých a rozvoľnených lesov s hlboko zavetvenými stromami, s dominanciou borovice lesnej (*Pinus silvestris*) a s vysokou pokryvnosťou čučoriedky. Ďalej, v boreálnych lesoch je výskyt hlucháňa kontinuálny a hlucháne majú po dorastení lesa (približne 30 rokov po ťažbe) odkiaľ územie znova osídliť.

Hlucháne žijúce v oblastiach mimo boreálneho pásma prežívajú v malých metapopuláciach viazaných na horskú krajinu (Storch 2007). Vo fragmentovaných podmienkach strednej a západnej Európy je veľmi náročné udržať životaschopnú populáciu, ktorá vyžaduje minimálne 250 km^2 vhodných biotopov a približne 470 komunikujúcich jedincov hlucháňa (Grimm & Storch 2000). Vysoká prepojenosť územia je veľmi dôležitá pre metapopulačnú dynamiku. Pokiaľ dôjde k strate nášľapných kameňov a konektivita je narušená veľkoplošnou ťažbou na veľkých plochách, migrácia jedincov medzi populáciami je limitovaná a prežitie populácie je ohrozené, pretože malé a izolované populácie sú neodolné a ich dlhodobé prežitie je nepravdepodobné (Segelbacher et al. 2003). Tie isté faktory vedú k extinkčnému dlhu aj pri malých a izolovaných populáciach iných druhov (Pullin 2002). Ďalším dôvodom prečo v lesoch mimo boreálneho pásma nie je možné prežitie hlucháňa po holorubnej ťažbe, je vznik tmavých a hustých lesov s takmer žiadnou bylinnou etážou a nízkou pokryvnosťou čučoriedky (*Vaccinium myrtillus*), ktorá je základným faktorom ovplyvňujúcim vhodnosť biotopu hlucháňa a poskytuje potravu pre dospelé jedince, bezstavovce pre kuriatka a úkryt pred predáciou (Bollmann et al. 2005, Hancock et al. 2011; Storch 1993). Vznik vhodných štruktúr je možný v týchto podmienkach iba vplyvom pôsobenia prirodzených procesov v dlhodobom horizonte alebo pomocou upravených lesníckych postupov hlucháňovi priateľského manažmentu lesov.

V Karpatoch ešte v 90-tych rokoch hlucháne bežne obývali aj zmiešané lesy, v súčasnosti však prežívajú už len v “úzkych pásoch” prirodzených ihličnatých lesov, ktoré sú umiestnené medzi vrcholmi hôr a listnatými lesmi v nižších nadmorských výškach. Tieto lesy neboli dlhodobo sprístupnené cestami, a neprebiehal tu intenzívny manažment minimálne niekoľko desaťročí. V minulosti mohli byť ovplyvnené napríklad pastvou alebo selektívnou ťažbou, ale podstatné je to, že si zachovali svoju prirodzenú štruktúru – tzn. rozvoľnenosť porastu, hlboko zavetvené stromy a vysokú pokryvnosť bylinnej vegetácie. Posledné desaťročia ale dochádza k neusmernenej veľkoplošnej ťažbe biotopov v Karpatoch a je zrejmé, že bezzásahové územia (prírodné rezervácie) nie sú v súčasnosti dostatočne veľké pre poskytnutie dostatku vhodného prírodného prostredia pre životaschopné karpatské populácie z dlhodobého hľadiska (Grimm & Storch 2000). Tieto požiadavky zreteľne ukazujú, že ochrana hlucháňa je možná v Karpatoch iba vo vzájomne sa dopĺňajúcej sieti systému bezzásahových rezervácii a lesov osobitého určenia, v ktorých bude aplikovaný hlucháňovi priateľský manažment lesa (Bollmann & Müller 2012). Doposiaľ však pre Karpaty neboli vytvorené komplexné materiály potrebné pre ochranu a manažment horských lesov s výskytom hlucháňa, preto bolo hlavnou úlohou tejto práce poskytnúť komplexné informácie o štruktúre a dynamike horských lesov s výskytom hlucháňa hôrneho v Karpatoch a vytvoriť podklad pre lesnícky manažment karpatských horských lesoch s výskytom hlucháňa.

3. Ciele práce

Hlucháň hôrny patrí medzi ohrozené dáždnikové druhy. Je to druh viazaný na špecifické štruktúry lesa, vyžaduje veľké rozlohy vhodných lesných komplexov a je citlivý na veľkoplošnú ťažbu. V Karpatoch prežíva ťažisko tohto vzácneho druhu v Európe, ale doposiaľ neexistovali pre túto oblasť dostatočné podklady pre jeho ochranu. Pre pochopenie štruktúry, dynamiky a následné odvodenie manažmentu horských lesov s výskytom hlucháňa hôrneho sme tento problém riešili komplexne na niekoľkých priestorových úrovniach s využitím štyroch metodických prístupov – populačný monitoring, modely druhovej distribúcie, analýza genetickej štruktúry, metódy dendroekológie.

Základnými cieľmi práce bolo:

1.) Analyzovať vplyv rôznych typov manažmentu lesov na stav biotopov hlucháňa hôrneho

2.) Analyzovať vplyv manažmentu lesov na početnosť hlucháňa

3.) Vytvoriť model vhodnosti biotopov hlucháňa hôrneho pre celé Karpaty a analyzovať ako veľkoplošná ťažba ovplyvňuje konektivitu populácie

4.) Analyzovať vplyv veľkosti biotopov a konektivity územia na genetickú diferenciáciu hlucháňa
5.) Analyzovať, ako prírodné disturbancie ovplyvňujú štruktúru biotopov hlucháňa hôrneho v smrekových pralesoch Karpát
6) Navrhnúť vhodné lesnícke manažmentové opatrenia, ktoré umožnia prežiť hlucháňovi hôrnemu v smrekových lesoch Karpát

4. Metodika

4.1 Študovaná oblasť

Dizertačná práca bola vypracovaná v oblasti Karpát, ktoré pokrývajú celkovo 220,400 km^2 a sú najrozsiahlejším lesným komplexom v miernom pásme Európy. Nadmorská výška Karpát stúpa zo 100 m do maximálne 2655 m nad morom. Klíma je mierna až kontinentálna (UNEP 2007) s nižšími teplotami a vyššími zrážkami vo vyšších nadmorských výškach a na severe. Listnaté lesy dominujú v nižších nadmorských výškach Karpát, pozostávajú najmä z buka lesného (*Fagus sylvatica* L.) s prímesou hraba obyčajného (*Carpinus betulus* L.), duba letného (*Quercus robur* L.), javora horského (*Acer pseudoplatanus* L.), a jaseňa štíhleho (*Fraxinus excelsior* L.). V podhorských lesoch dominujú dreviny ako buk lesný zmiešaný s jedľou bielou (*Abies alba* Mill.) a smrekom obyčajným (*Picea abies* (L.) Karst.). Smrekové lesy dominujúce vo vyšších nadmorských výškach sú hlavným biotopom hlucháňa hôrneho v Karpatoch. Tieto lesy môžu rásť s prímesou jedle bielej, borovice limby (*Pinus cembra* L.), smrekovca opadavého (*Larix decidua* Mill.) alebo i buka lesného v niektorých oblastiach (Bohn et al. 2004). Horná hranica lesa kolíše od približne 1600 m na severozápade Karpát do približne 1850 v Južných Karpatoch.

V obhospodarovaní a manažmente lesov od roku 1990 došlo k významným zmenám. Ťažba holorubným spôsobom v niektorých regiónoch bola redukovaná, hlavne v západných Karpatoch (napr. na Slovensku z 85 % na 29 %; Green Report, Ministry of Agriculture of the Slovak Republic, 2010), a využívanie metód prírode blízkeho hospodárenia vzrástlo ako dôsledok zmeny legislatívy zabraňujúcej holorubnej ťažbe. Ale v iných krajinách, prinavrátenie štátnych lesov súkromným vlastníkom spôsobilo zvýšenie rozsahu ilegálnej ťažby dreva. Okrem toho, vo všetkých krajinách dochádza k rozsiahlym asanačným ťažbám, ktoré sú v súčasnosti pravdepodobne hlavným dôvodom veľkoplošných ťažieb v Karpatoch (Merganičová et al. 2013; e.g. Kuemmerle et al. 2009; Knorn et al. 2012a,b; Griffiths et al. 2014). Hlavne vďaka nedostupnosti terénu a dlhodobo nesprístupneným dolinám sa v Karpatoch zachovali najrozsiahlejšie komplexy prírodných lesov a pralesov v rámci Európskej únie.

4.2 Zber dát a analýza dát

Pre splnenie konkrétnych cieľov boli prispôsobené metódy zberu a analýzy dát. Práca bola vykonaná na celom území Karpát pre splnenie cieľov 3 a 4, pre ciele 1, 2, a 5 boli vybrané konkrétne územia spĺňajúce parametre na prevedenie požadovaného zberu dát a analýz. Informácie získané na základe zodpovedania cieľov 1-5 boli použité na formuláciu manažmentových opatrení (cieľ č. 6).

1.) Analyzovať vplyv rôznych typov manažmentu lesov na stav biotopov hlucháňa hôrneho

Pre splnenie tohto cieľa bolo vybrané územie národného parku Nízkych Tatier, pretože sa nachádza v jadre výskytu hlucháňa a zároveň sa na území nachádzajú všetky typy manažmentu smrekových lesov od najintenzívnejšie využívaných až po územie bez dlhodobých zásahov, tzv. pralesy. Terénny prieskum sa uskutočnil v letnom období (júl – september), kedy je plne vyvinutá pozemná vegetácia. Celkovo bolo zmapovaných 666 plôch na 132 km dlhom transekte. Pre hodnotenie kvality habitatu hlucháňa bola zvolená metodika HSI podľa Storch 2002. Územie bolo mapované v transektoch, každých 200 m boli priradené súradnice bodu, na ktorom boli na kruhovej ploche s polomerom 20 m odčítané a podrobne zaznamenané všetky kľúčové charakteristiky habitatu hlucháňa podľa metodiky na výpočet indexu vhodnosti habitatu (HSI, Storch 2002): sklon svahu (v triedach 0: < 5°, 2:6–15°, 3: 26–35°, 4: 36–45°, 5: >45°), pokryvnosť čučoriedky (%), výška bylinnej etáže (v triedach 1: 1–10 cm, 2: 11–20 cm,3: 21–30cm atď.), pokryvnosť dreviného zmladenia (v triedach 1: < 25 %, 2:26– 50 %, 3: 51–75 %, 4: >75 %), sukcesné štádium porastu (1: mladina, 2: žrďkovina,3: žrďovina, 4: kmeňovina, 5: starý porast,6: vekovo rôznorodý porast, 0: žiadny les), korunový zapoj (%), drevinové zloženie, prítomnosť medzier v poraste a prítomnosť preferovaných kŕmnych stromov (*Abies alba, Pinus sylvestris, Pinus mugo, Pinus cembra*). Pobytové znaky (trus, perie, škrupiny, prachovisko atď.) sme hľadali po dobu 10 minút na výskumnej ploche každého bodu. Pokiaľ to bolo možné určiť, zaznamenali sme pohlavie, ako aj sezónu nálezu (podľa druhu konzumovanej potravy). Okrem toho sme na každej ploche určili, či ide o suchý les, odťaženú plochu alebo prales. Tieto informácie sme následné použili k porovnaniu vhodnosti habitatu a využívania habitatu pri rôznych typoch manažmentu. Na vyhodnotenie vplyvu asanačných opatrení a na vyhodnotenie rozdielov HSI medzi jednotlivými typmi stanovišťami sme použili neparametricky Kruskal-Wallisov test.

2.) Analyzovať vplyv manažmentu lesov na početnosť hlucháňa

Holorubná ťažba bola široko dokumentovaná ako jedna z hlavných príčin vedúcich k lokálnym zánikom populácii (Storch 2007). Našim cieľom nebolo dokumentovať pokles populácie, ale identifikovať lesnícke opatrenia, ktoré dovolia prežiť hlucháňovi hôrnemu. Preto sme zbierali dáta na plochách, ktoré reprezentovali širokú škálu manažmentu - žiadny manažment, čiastočný manažment až po intenzívny manažment lesov na území zodpovedajúcom veľkosti areálu využívaného hlucháňom. Pomocou máp distribúcie hlucháňa poskytnutých Lesným výskumným inštitútom v Rumunsku (ICAS), lokality s najvyššími hustotami hlucháňa boli vybrané v 11 pohoriach Rumunska, ktoré boli následne intenzívne prehľadávané na ploche 314 ha. Táto plocha zodpovedá priemernému areálu, ktorý hlucháne využívajú počas obdobia toku (Storch, 1995). Takto sme identifikovali 21 tokanísk v pohoriach Făgăraş (n = 4), Rodnei (n = 4), Harghita (n = 3), Maramureş (n = 3) Piatra Craiului (n = 1), Bucegi (n = 1), Diham (n = 1), Prisciu (n = 1), Hâşmaş (n = 1), Călimani (n = 1), and Piatra Mare (n = 1).

Kohúty hlucháňa sa schádzajú v období párenia na tokaniskách, kde súperia o sliepky. Teritória kohútov počas ranného toku sú vzdialené 50 m od seba. Počítanie kohútov na tokaniskách je široko využívaná metóda na monitoring populačných trendov (Miettinen et al. 2005; Picozzi et al. 1992; Saniga 2003). Počas dňa sa hlucháne zdržujú približne 1 km od tokaniska (Storch 1995). Lokalizácia výskumnej plochy bola definovaná pozíciou alfa kohúta, GPS koordináty boli zaznamenané potom, ako hlucháne ukončili tok. Tieto tokaniská sú umiestnené každoročne na tom istom mieste a môžu byť využívané po desaťročia (Klaus et al. 1989). Hľadanie tokanísk sme prevádzali od Marca do Mája počas rokov 2009-2011. Na každom tokanisku boli minimálne 2 návštevy v ranných hodinách od 03:00 do 09:00, počas ktorých boli zaznamenané počty jedincov. Pri analýzach boli brané do úvahy maximálne zistené počty kohútov. V letných mesiacoch boli tokaniská znova navštívené a následne odobrané dáta na vybrané charakteristiky štruktúry lesa a ďalších faktorov, ktoré by mohli mať vplyv na početnosť druhu. Vzťah medzi početnosťou hlucháňa a environmentálnymi charakteristikami bol analyzovaný pomocou zovšeobecnených lineárnych modelov (McCullagh & Nelder 1989).

3.) Vytvoriť model vhodnosti biotopov hlucháňa hôrneho pre celé Karpaty a analyzovať ako veľkoplošná ťažba dreva ovplyvňuje konektivitu populácie

Dáta o výskyte hlucháňa sme zbierali 150 dní v štyroch sezónach 2010-2013 na celom území Karpát. Celkovo sme nazbierali 447 údajov o výskyte hlucháňa na 725 km transektov v 29 pohoriach; Južné Karpaty (n = 8), Východné Karpaty (n =10), and Západné Karpaty (n=11). Cieľom tejto štúdie bolo zmapovať celkový areál rozšírenia, kvantifikovať vhodnosť biotopov a zhodnotiť ich priestorovú konektivitu a zmenu konektivity spôsobenú veľkoplošnou ťažbou. Potenciálne vhodný biotop bol modelovaný pomocou metódy maximálnej entropie na základe výskytových dát a vybraných environmentálnych premenných. Na vyhodnotenie funkčného prepojenia mozaiky vhodných biotopov sme použili index pravdepodobnosti konektivity vychádzajúci z teórie grafov a potenciálnych migračných koridorov.

Nálezové dáta, ako jeden zo základných vstupov pre tvorbu modelu rozšírenia, tvorili GPS záznamy o výskyte hlucháňa získané počas celého roka, v období 2010-2013. Za výskyt bolo považované priame pozorovanie, nález trusu, peria či stôp. V rámci kontroly nálezových dát boli najskôr odstránené duplicitné záznamy. Kvôli zmierneniu negatívneho dopadu silnej priestorovej závislosti (autokorelácie), spôsobenej rôznymi metódami zberu dát, boli záznamy ešte priestorovo filtrované. V konečnom dôsledku tak boli zaradené iba záznamy, ktoré sa od seba nachádzali najmenej 300 m. Táto vzdialenosť bola zvolená ako vhodný kompromis medzi maximálnym možným znížením autokorelácie dát a zároveň dostatočným počtom záznamov pre tvorbu modelu rozšírenia. Druhý typ dát, nevyhnutný k modelovaniu rozšírenia druhu, tvorili environmentálne podmienky prostredia (ďalej iba prediktory), majúce pre oba druhy ekologický význam. Prediktory, ktoré vyjadrovali topografické podmienky prostredia (nadmorská výška, svahovitosť, orientácia k svetovej strane a topografický index), boli odvodené z digitálneho výškového modelu SRTM (NASA). Dáta o klimatických podmienkach územia, reprezentované priemerom mesačných zrážok za rok a priemernou teplotou, pochádzali z projektu WorldClim (Hijmans et al. 2005). Prediktory vyjadrujúce vplyv (euklidovskej) vzdialenosti či plošného zastúpenia vybraných krajinných prvkov (napr. komunikácie, sídla, lúky, orná pôda) na výskyt oboch druhov boli vytvorené na základe dát z európskeho programu Corine Land Cover (EEA 2007). V rámci tohto programu prebehla v roku 2012 v EU inventarizácia typov krajinného pokryvu analýzou leteckých snímok. K podrobnejšiemu hodnoteniu významu fragmentácie lesa v našom modely, sme pomocou softwaru Guidos (Vogt 2015) vytvorili prediktor, v rámci ktorého bol každý pixel reprezentujúci les rozlíšený medzi niektorou z nasledujúcich kategórií: jadro lesa, vonkajší alebo vnútorný okraj lesa a ostrovček lesa. Špeciálnym prípadom bol kategoriálny prediktor vyjadrujúci členitosť lesa. Prediktor zemepisnej šírky a dĺžky bol do modelu zahrnutý pre prípad, že by bola distribúcia hlucháňa ovplyvnená inými faktormi, s týmito úzko spojenými. Vybrané prediktory boli upravené na zhodný priestorový rozsah, rastrový formát a rozlíšenie (100 × 100 m) v programe ArcGIS 10.3 (ESRI Inc. USA).

Pred samotnou tvorbou modelu bolo nutné vybrať len tie prediktory, ktoré spĺňali nasledovné kritériá: (1) prijateľná miera ich vzájomnej priestorovej závislosti, (2) dostupnosť vo forme vektorových alebo GIS dát pre celé územie a (3) schopnosťou prispieť k vysvetleniu variability nálezových dát. Prijateľná miera priestorovej závislosti prediktorov bola zohľadnená výberom iba tých prediktorov, medzi ktorými bola hodnota Pearsonovho korelačného koeficientu < ±0,6 (Montoya et al. 2009). Najproblematickejším kritériom sa ukázala obmedzená dostupnosť prediktorov vo forme GIS dát. Na stanovenie významu daného prediktoru k vysvetleniu celkovej variability nálezových dát sme použili jacknife test, ktorý testoval zmeny v presnosti predikcie medzi modelom, v ktorom bol tento prediktor zahrnutý a modelom bez tohto prediktoru.

Tvorba habitatového modelu

Potenciálne vhodný biotop hlucháňa bol modelovaný pomocou metódy maximálnej entropie implementovanej v programe MaxEnt verzia 3.3.3e (Phillips et al. 2006, dostupné na http://www.cs.princeton.edu/~schapire/maxent/). Táto v súčasnosti najrozšírenejšia modelovacia metóda (Ahmed et al. 2015) poskytuje v porovnaní s ostatnými metódami (napr. bioklimatické modely, regresia, neurónové siete) porovnateľné alebo lepšie výsledky (Gastón & García-Viñas 2011, Elith et al. 2011). Veľkou výhodou tejto metódy je jej schopnosť pracovať výhradne s prezenčnými nálezovými dátami, ktoré sú v súčasnosti najčastejšie dostupné. Program MaxEnt využíva princíp maximálnej entropie k odhadu súboru štatistických funkcií, ktoré aproximujú rozšírenie druhu z dát o ich výskyte a environmentálnych premenných (Phillips et al. 2006). Výsledkom modelovacieho procesu je teda model vymedzujúci ekologickú niku hlucháňa v geografickom priestore (Franklin 2009). Viac o tejto metóde píšu Phillips & Dudik (2008) alebo Elith et al. (2011).

V našom prípade boli parametre modelu nastavené s ohľadom na odporučenie (Elith et al. 2011, Merow et al. 2013). Pre zaistenie robustnejších výsledkov bol výsledný model priemerom jeho 7 opakovaní, založených na metóde krížového overovania a súčasne maximum 2 000 iterací výpočtu. K dosiahnutiu optimálneho výsledku sme použili 10 000 náhodne vybraných pseudoabsencií, ktorých generovanie sme (vzhľadom k biotopovým nárokom oboch druhov) obmedzili len na územie nad 600 m.n.m. V snahe minimalizovať možné nadhodnotenie modelu sme pre jeho výpočet použili východiskovú hodnotu parametra regularizácie (Phillips and Dudik 2008) a len „linear, quadratic a hinge features“ (Merow et al. 2013).

Úspešnosť predikcie výsledného modelu bola kvantifikovaná pomocou nezávislej diskriminačnej hladiny AUC (Area Under the ROC Curve), ako základnej metriky pre popis grafu ROC (Receiver Operating Characteristic curve) krivky (Phillips and Anderson 2006; Elith et al. 2011). Táto neprahová metrika meria úspešnosť modelu rozlíšiť medzi skutočnou prezenciou druhu a jeho absenciou v danom území (Hanley & McNeil 1982). Hodnota AUC predstavuje obsah plochy pod ROC krivkou, ktorá môže nadobúdať hodnoty od 0,5 do 1, pričom hodnoty 0,5 možno považovať za náhodnú predpoveď a hodnoty vyššie ukazujú výsledky lepšie než náhodné. AUC hodnoty 0,5-0,7 indikujú zlý výkon modelu; 0,7 – 0,9 priemerný výkon a hodnoty > 0,9 vysoký výkon modelu (Pearce & Ferrier 2000).

Hlavným výsledkom predikčného modelu je mapa indexu vhodnosti biotopu (HSI – habitat suitability index). Tento index, s rozsahom hodnôt 0-1 (resp. 0-100%), reprezentuje potenciálnu vhodnosť biotopu pre hlucháňa. Pre potreby ďalších analýz je však nutné identifikovať najcennejšie biotopy (ďalej len „jadrové územia“). K tomu je potrebné stanoviť zodpovedajúce prahové hodnoty HSI („threshold“), ktoré rozdelia škálu vhodnosti biotopu do dvoch kategórií: vhodný a nevhodný. Na tento účel bola vybraná hranica reprezentujúca súčet maximálneho počtu správne určených prezencií („senzitivita“) a absencií („špecificita“) modelom. Táto hranica zaisťuje v porovnaní s inými typmi robustnú predikciu, nezávislú na vzájomnom pomere prezencií a pseudoabsencií (Liu et al. 2013) a je vhodná hlavne na ochranárske účely (Liu et al. 2005).

Hodnotenie fragmentácie

Vzhľadom k roztrúsenej mozaike vhodných biotopov a zložitej sieti ich vzťahov sme k hodnoteniu funkčného prepojenia použili index pravdepodobnosti konektivity, vychádzajúci z teórie grafov (Saura & Pascual-Hortal 2007). Grafom sa v tomto prípade myslí súbor “uzlov“ a „prepojení,“ existujúcich medzi dvoma susednými uzlami. Uzol v našom prípade reprezentuje identifikované jadrové územie, zatiaľ čo prepojenie symbolizuje schopnosť druhu šíriť sa medzi nimi.

Vybraný index upravuje vlastnosti klasických krajinných indexov, lepšie zohľadňuje aktuálne zmeny v krajine (napr. stratu biotopu alebo jeho prepojenie) a to bez ohľadu na priestorovú mierku ich posúdenia (Blazquez-Cabrera et al. 2014). Je možné ho definovať ako pravdepodobnosť, s ktorou sa dva jedince (náhodne rozmiestnené v krajine) nachádzajú vo vzájomne prepojených lokalitách výskytu, vzhľadom k ostatným lokalitám a ich prepojeniu. Význam každého vhodného územia, v rámci ich celkového prepojenia, bol získaný z rozdielu hodnôt indexu spočítaného pre všetky jadrové územia spolu a indexu, do ktorého výpočtu nebolo toto čiastkové územie zahrnuté. Zvolený index nadobúda hodnoty od 0 po 1, spolu so zvyšujúcou sa prepojenosťou jadrových území stúpa a jeho výpočet bol vykonaný v programe CONEFOR 2.6 (Saura & Thorne 2009, Conefor 2015).

Na kvantifikovanie vplyvu veľkoplošnej ťažby na veľkosť biotopov hlucháňa a konektivitu medzi rokmi 1985-2010 sme premenili HSI mapu na binárnu mapu vhodných a nevhodných biotopov. Následne sme využili vrstvu disturbancií od Griffithsa et al. 2014, ktorou sme celý model pre jednotlivé obdobia orezávali a porovnávali konektivitu pre meniace sa rozlohy a priestorové usporiadanie biotopov.

4.) Analyzovať vplyv veľkosti vhodných lesných celkov a konektivity územia na genetickú diverzitu druhu

Dôležitým problémom ohrozených druhov je genetická izolácia. Prebiehajúci populačný pokles hlucháňa hôrneho v Karpatoch sa vzťahuje predovšetkým k zmenšovaniu plochy a fragmentáciu komplexov starých horských lesov. Ako sa prejavuje konektivita územia na genetickej štruktúre je možné dokumentovať pomocou analýzy genetickej štruktúry. V Západných, Východných a Južných Karpatoch sme zozbierali celkom 209 vzoriek trusu a peria hlucháňa hôrneho. Pri každej vzorke boli zaznamenané geografické koordináty. Trus je najľahšie získateľná vzorka, ktorú môžeme nájsť na miestach výskytu počas rozmnožovania, odpočinku a získavania potravy. Najlepšie je zbierať trus za prítomnosti snehovej pokrývky. Trus zbierame čerstvý a nevystavený slnečnému žiareniu. Perie sa taktiež často používa ako dobrý zdroj DNA. DNA z peria môže byť získaná aj z malej časti poškodeného pera. DNA je väčšinou izolovaná z 1–1,5 cm bazálnej časti brka alebo z krvnej zrazeniny nachádzajúcej sa vo vnútornej časti brka na rozhraní s kostrnkou. Zber peria prebieha po celý rok, najmä v období preperovania.

Laboratórne analýzy

Vzorky boli zhromaždené v priebehu roka, hlavne počas toku a uložené v skúmavkách alebo papierových vreckách naplnených silikagélom. Na extrakciu DNA bol použitý DNA EXTRACTION KIT. Trus v dĺžke 2– 3 cm sa umiestnil do 15 ml skúmaviek a počas noci sa nechal vylúhovať v ASL roztoku pri izbovej teplote. Významom tohto lúhovania je, že sa z trusu uvoľnia epitely čreva zachytené na truse. Nasledujúci deň sa 1,6 ml roztoku prenieslo do nových skúmaviek s InhibitEX tabletou. Ostatné postupy boli vykonané podľa protokolu uvedeného výrobcom.

Alelická bohatosť a počet privátnych alel boli vypočítané v programe HP-RARE 1.0 (Kalinowski 2005). Miery genetickej diverzity, diferenciácie a odchýlka od 12 Hardy-Weinbergovej rovnováhy boli určené v programe GENETIX 4.05 (Belkhir et al. 2004). Interval spoľahlivosti (CI 95%) bol definovaný na základe 10 000 permutácií. Pre jasnú identifikáciu jadrovej populácie na základe alelickej bohatosti sme využili nástroj SINGLE SPECIES DIVERSITY TOOL implementovaný v programe pre ArcGIS, GENETIC LANSCAPE GIS TOOLBOX. Pre vyhodnotenie potenciálnych migrácií jedincov prvej generácie sme použili softvér GENECLASS2 (Piry et al. 2004). Softvér počíta pravdepodobnosť pôvodu jedinca z danej populácie. Miera spoľahlivosti P je určená na základe 10.000 opakovaní. Genetickú štruktúru populácií Západných Karpát sme určili v softvéri STRUCTURE 2.3.3 (Pritchard et al. 2000). Pravdepodobnosť priradenia jedinca do 1–10 populácií sme testovali 100.000 MCMC repetícií vylučujúc prvých 10.000 (burn-in period) s 10 replikáciami. Súbor dát sme testovali za pravdepodobnosti možnosti migrácie medzi populáciami (admixture model).

Vzorky boli analyzované na Katedre fytológie na Lesníckej fakulte vo Zvolene.

5.) Analyzovať ako prírodné disturbancie ovplyvňujú štruktúru biotopov hlucháňa v smrekových pralesoch Karpát.

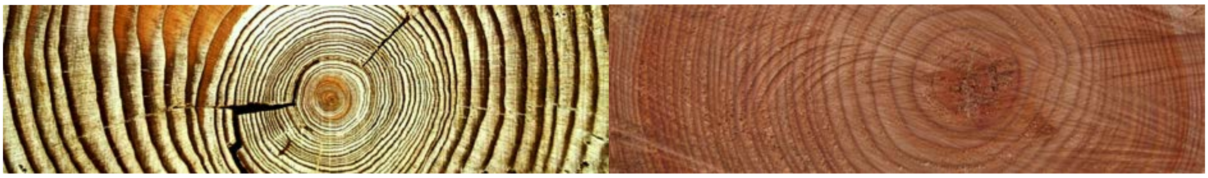
Pre splnenie tohto cieľa boli vybrané dva pralesy v Rumunsku, ktoré sa nachádzajú v jadre výskytu hlucháňa hôrneho vo Východných Karpatoch. Dáta boli odobrané na 104 kruhových výskumných plochách (1000 m^2), ktoré boli rozmiestnené pomocou náhodného rozdelenia opísaného v práci Svobodu et al. 2014. Plochy celkovo reprezentujú územie pralesov o rozlohe 182 ha (v Calimani 60 ha a v Giumalau 122 ha).

Na každej výskumnej ploche boli všetky živé a mŕtve stromy s priemerom ≥ 10 cm v prsnej výške zmerané a bol zapísaný druh stromov. Hustota zmladenia bola zaznamenaná v troch výškových triedach (0.5-1.3 m, 1.3-2.5 m, a > 2.5 m). Bylinná vegetácia bola popísaná pomocou priemernej výšky a pokryvnosti čučoriedky (*Vaccinium myrtillus*), ktorá je dôležitým zdrojom potravy pre hlucháňa (Storch 2002). Vzdialenosť k najbližšej porastovej medzere bola vyhodnotená zo satelitných snímkov, veľkosť porastových medzier bola overená pomocou GPS v teréne.

Prítomnosť a neprítomnosť pobytových znakov hlucháňa bola určená pomocou celkového prehľadávania plochy počas dĺžky 15 minút. Pobytové znaky boli hľadané v jarnom období, kým bol na zemi sneh.

História režimu disturbancií a veková štruktúra

Veková štruktúra a história disturbancií bola analyzovaná pomocou metód dendroekológie. Pre každú plochu boli použité krížovo dátované letokruhové série z 25 náhodne vybraných žijúcich uvoľnených stromov. Pre zistenie vekovej štruktúry pri vývrtoch, ktoré nedosiahli priamo do stredu, bol počet chýbajúcich letokruhov dopočítaný pomocou Duncanovej metódy (1989). Pre každú plochu sme vypočítali priemerný vek, medián veku, minimálny a maximálny vek 5 najstarších stromov. História disturbancií bola rekonštruovaná na základe dvoch princípov: (i) uvoľnenie – prudký nárast stromu nasledujúci po odstránení zápoja okolitých tieniacich stromov, (ii) rýchly počiatočný rast, ktorý je prejavom toho, že strom rástol od začiatku svojho rastu v otvorenom zápoji (Obr. 6) (Frelich & Lorimer 1991). Sila disturbancií bola hodnotená ako súčet uvoľnení a rýchlych počiatočných rastov v každej dekáde, prevedené na % korunového zápoja (Svoboda et al. 2014).



Obr. 6 *Letokruhy znázorňujúce odlišné typy rastu indikujúce narušenie okolitých stromov a) vľavo: (i) uvoľnenie – prudký nárast stromu nasledujúci po odstránení zápoja tieniacich stromov v hornej etáži, b) vpravo: (ii) rýchly počiatočný rast, ktorý je prejavom toho, že strom rástol od začiatku svojho rastu v otvorenom zápoji.*

Z týchto dát sme vytvorili premenné charakterizujúce históriu disturbancií pre jednotlivé plochy: a) maximálna severita disturbancií, b) čas od maximálnej disturbancie, c) diverzita severít disturbancií reprezentovaná disturbančným indexom (Svoboda et al. 2014).

Disturbančný index reprezentuje celkovú severitu disturbančného režimu na plochu charakterizovanú pomocou bežne používaného Shannonovho indexu. Nízke hodnoty (minimum dosahuje približne -3) indikujú disturbancie s nízkou severitou, ktoré sa diali frekventovane na časovej osi. Maximálna teoretická hodnota je 0 a indikuje 100 % korunového zápoja, ktorý bol narušený počas jednej dekády. Najvyššia diverzita disturbancií je reprezentovaná strednými hodnotami indexu. Viac informácii je možné nájsť v práci Svoboda et al. 2014.

Efekt disturbancií na štruktúru lesa bol hodnotený pomocou viacnásobných lineárnych modelov. Pre pochopenie vzťahu medzi disturbanciami, štruktúrou pralesa a výskytom hlucháňa sme využili jednoduché logistické modely, parsimónny GLM model (McCullagh & Nelder 1989) a PLS-DA analýzu (Barker & Rayend 2003).

5. Výsledky

5.1 Mikoláš M., Kalafusová I., Tejkal M., Černajová I., Michalová Z., Hlásny T., Barka I., Zrníková K., Bače R. & Svoboda M., (2013). Stav habitatu jadrovej populácie hlucháňa hôrneho (Tetrao urogallus) v Západných Karpatoch: Je ešte pre hlucháňa na Slovensku miesto? Sylvia 49, 79–98.

Stav habitatu jadrovej populácie hlucháňa hôrneho (*Tetrao urogallus*) v Západných Karpatoch: Je ešte pre hlucháňa na Slovensku miesto?

Habitat conditions of the core population of the Western Capercaillie (Tetrao urogallus) *in the Western Carpathians: Is there still place for the species in Slovakia?*

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Mikoláš M., Kalafusová I., Tejkal M., Černajová I., Michalová Z., Hlásny T., Barka I., Zrníková K., Bače R. & Svoboda M. 2013: Stav habitatu jadrovej populácie hlucháňa hôrneho (*Tetrao urogallus*) v Západných Karpatoch: Je ešte pre hlucháňa na Slovensku miesto? *Sylvia 49: 79–98.*

Územie Nízkych Tatier a Veľkej Fatry predstavuje jadrovú populáciu hlucháňa hôrneho (*Tetrao urogallus*) v Západných Karpatoch. Po veternej smršti v roku 2004 tu došlo k významným zásahom do jeho habitatu. Pre záchranu tohto vtáčieho druhu sú kľúčové ucelené informácie o kvalite a rozlohe habitatu, ktoré sme spracovali v tejto štúdii, pomocou dvoch metodických prístupov. V rokoch 2011–2012 sme v uvedených pohoriach vykonali hodnotenie prostredia a výskytu tetrova hlucháňa na 666 bodových transektoch umiestnených na línii o dĺžke 132 km. Na posúdenie vhodnosti habitatov na úrovni porastu sme použili index vhodnosti habitatu (HSI). Na vytvorenie modelu vhodného habitatu na úrovni krajiny sme využili komplexný model MaxEnt. HSI na plochách suchého lesa bolo štatisticky významne vyššie v porovnaní s asanovanou plochou. HSI bol najvyšší pre prales, nižší pre hospodársky les a najnižší pre holiny. Z aplikácie modelu MaxEnt vyplynulo, že na úrovni krajiny najlepše vysvetľovali prítomnosť hlucháňa premenné: priemerná ročná teplota, priemerné júlové zrážky, krajinná pokrývka, nadmorská výška (m n. m.), druhové zloženie porastu a zakmenenie porastu. Potenciálne vhodné územie pre výskyt hlucháňa malo rozlohu 180 km^2 (16 % lesných porastov modelového územia). Táto rozloha je pre minimálnu životaschopnú populáciu hlucháňa nedostatočná. Dochádza k fragmentácii habitatu vykonanými lesohospodárskymi zásahmi. Ohrozenie zdrojovej populácie hlucháňa predstavuje ohrozenie celoslovenskej populácie. Je potrebné zabrániť ďalšej strate vhodných porastov a zmeniť spôsob manažmentu.

The area of the Nízke Tatry and Veľká Fatra Mts. is considered a core population habitat of the Western Capercaillie (Tetrao urogallus) *in the Western Carpathians. Considerable interventions occurred in this habitat after the windstorm in 2004. We provide complex information about the quality and size of the suitable habitat – representing key data for successful conservation of this species – obtained by two methodological approaches. Habitat characteristics were recorded at 666 points on a 132 km transect during the years 2011–2012. To assess habitat suitability at the level of forest stands, we used the habitat suitability index (HSI). To create a habitat suitability model at the landscape level, we used the complex MaxEnt model. HSI was significantly higher in unmanaged forests affected by bark-beetle, compared to managed areas. The highest HSI values were obtained in primary forests, lower in managed forests and lowest in clear-cuts. Application of the MaxEnt model showed that Capercaillie presence is best explained by the following variables: mean annual temperature, mean July precipitation, type of land cover, altitude, tree species composition, and canopy closure. The potential suitable habitat was 180 km^2 in size (16% of the forests in the study area). However, this area is not sufficient for a minimum viable population. Furthermore, the suitable habitat is being fragmented by salvage logging practices. The threat to the source population represents a threat to the entire Slovak population of the species. It is crucial to stop further loss of Capercaillie habitats through changes in forest management.*

Keywords: endangered species, forest management, habitat assessment, habitat loss, minimum viable population

ÚVOD

Hlucháň hôrny (*Tetrao urogallus*) je dôležitým elementom prírodného dedičstva Karpát. Populácia hlucháňa najmä v strednej a západnej Európe prudko ustupuje (Storch 2001). Hlucháň je zaradený v prílohe 1 Európskej Smernice o ochrane vtáctva a je na zozname v červenej knihe väčšiny krajín západnej, strednej a juhovýchodnej Európy (Storch 2000). Nízka reprodukcia spôsobená priamym a nepriamym vplyvom lesného hospodárstva je hlavný dôvod poklesu populácií tetrova hlucháňa v Európe (Wegge et al. 2005), pretože vývojové štádiá nasledujúce po veľkoplošnej ťažbe značne znižujú potravnú ponuku a úkrytové možnosti pre juvenilné jedince (Lakka & Kouki 2009). Na Slovensku boli podľa Sanigu (1994) hlavné príčiny poklesu hlucháních populácií lesohospodárska činnosť (velkoplošné holoruby a následný vznik tmavých monokultúr a chemizácia pesticídmi), znečisťovanie ovzdušia, ktoré priamo ovplyvňuje zdravotný stav jedincov a taktiež znižuje potravinovú ponuku hmyzu a rastlín (Porkert 1982), nadmerný lov, vyrušovanie inými ľudskými aktivitami a prirodzené negatívne faktory (napr. predácia). Telemetrické údaje ukázali, že hlucháne počas roka využívajú plochu 132–1207 ha, priemerne 550 ha (Storch 1995). Hlucháň je kvôli obrovským priestorovým nárokom veľmi citlivý na fragmentáciu lesa (Storch 1997, Kurki et al. 2000).

V roku 1972 poľovnícka štatistika uvádzala pre územie Slovenska 3700 kohútov, v roku 1992 bol na Slovensku odhadovaný počet jedincov 1100–2000 (Saniga

1992). Na základe pozorovaní z rokov 1981 až 2003 zaznamenal Saniga (2003) vo Veľkej a Malej Fatre, Kremnických vrchoch, Starohorských vrchoch a Nízkych Tatrách zánik tokanísk a značný pokles početnosti – na 22,1 % u kohútov a na 13,3 % u sliepok z pôvodného stavu. Je jednoznačné, že početnosť hlucháňa na Slovensku klesá. Dnes žije vo fragmentovaných a vzájomne izolovaných populáciách približne 300–600 kohútov (Saniga in litt.). Vážnosť situácie si pre záchranu hlucháňa na Slovensku vyžaduje podrobný plán manažmentu, na ktorý sú potrebné jasné ukazovatele životaschopnosti populácie. Plošný podiel vhodného habitatu vo fragmentovanej krajine je považovaný za dobré meritko životaschopnosti metapopulácie (Hanski 1998).

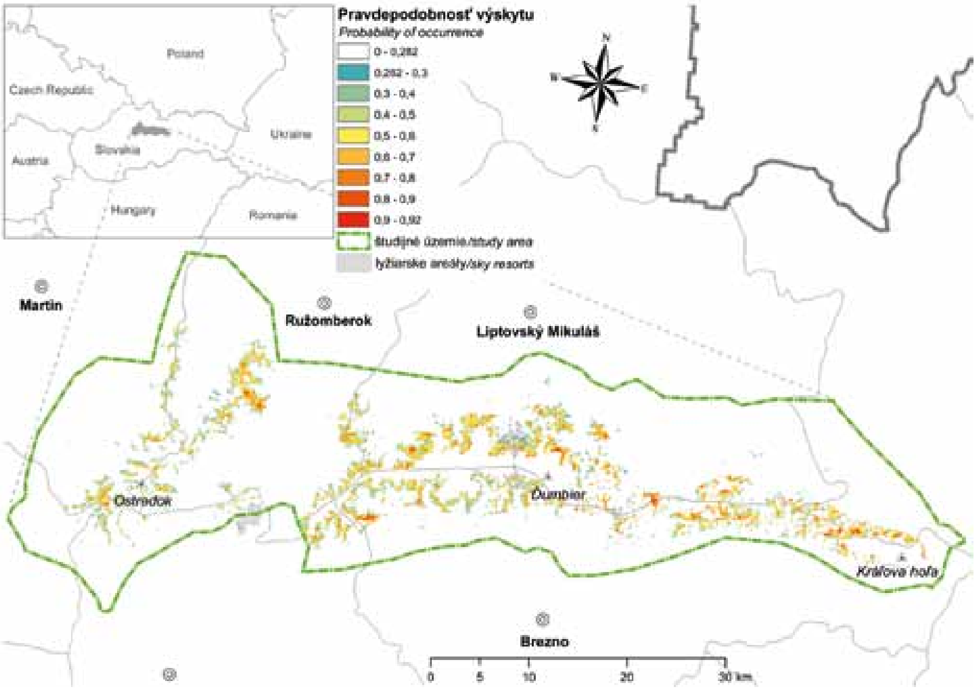
Grimm & Storch (2000) vytvorili stochastický populačný model, ktorého cieľom bolo zistiť, aká veľká je minimálna životaschopná populácia hlucháňa, ak pravdepodobnosť vyhynutia v priebehu 100 rokov má byť nižšia ako 1 %. Model predpovedá minimálnu životaschopnú populáciu s počtom okolo 470 jedincov, vyžadujúcu vhodný habitat s rozlohou až 250 km^2. Vychádzajúc z týchto parametrov, v podmienkach Slovenska je pre dosiahnutie takejto rozlohy habitatu nutné zachovať prepojenie minimálne medzi Nízkymi Tatrami a Veľkou Fatrou, ktoré by mali slúžiť ako zdrojová populácia. Vetrová smršť z 19. 11. 2004 zasiahla rozsiahlu plochu lesných porastov v študovanej oblasti, najmä v národnom parku Nízke Tatry. Následne došlo ku gradácii podkôrneho hmyzu a spracovaniu kalamity. Celkovo v Nízkych Tatrách od roku 2004 došlo k vzniku odťažených plôch s rozlohou viac ako 10 000 ha. Na väčšine územia ešte stále dochádza k spracovaniu kalamity, preto je základnou otázkou prežitia hlucháňa na Slovensku, akým spôsobom sa bude vyvíjať manažment týchto oblastí.

Cieľom tejto štúdie je predložiť komplexné informácie potrebné k záchrane tohto ohrozeného druhu v Západných Karpatoch. Cieľom je (i) vyhodnotiť vplyv kalamitných asanačných opatrení na kvalitu habitatu a výskyt hlucháňa, (ii) zistiť geografické rozšírenie a celkovú rozlohu vhodného habitatu zdrojovej populácie hlucháňa v Západných Karpatoch na úrovni krajiny a (iii) overiť použiteľnosť metodiky indexu vhodnosti habitatu podľa Storch (2002) na území Slovenska pre plánovanie manažmentu na úrovni porastu. Výsledky budú slúžiť ako podporný nástroj pri rozhodovaní o manažmente území s výskytom hlucháňa hôrneho.

METODIKA

Študovaná oblasť

Lokality výskumu sa nachádzajú v dvoch orografických celkoch – Nízkych Tatrách a Veľkej Fatre, pričom sa študovaná oblasť rozkladá na ploche 1717 km^2 (obr. 1). Obe pohoria spadajú do Fatransko-tatranskej oblasti (Miklós et al. 2006). Nadmorské výšky stúpajú od 900 do 1550 m n. m. Klíma je charakteristická krátkym letom bohatým na zrážky. Priemerná teplota v júli je 14.5 °C a v januári 5.5 °C. Priemerné zrážky sa pohybujú medzi 1000–1400 mm. V študovanej oblasti dominujú spoločenstvá smrekových lesov čučoriedkových na podzolových typoch pôd, na ne nadväzujú jedľovo-smrekové lesy a jedľové lesy, prípadne na minerálne bohatšom podloží smrekové lesy vysokobylinné (Michalko et al.1986). Prirodzené lesné spoločenstvá sú v súčasnosti v značnej miere premenené na hospodárske lesy, často s pozmenenou druhovou skladbou porastotvorných drevín. Rozsiahle plochy lesov aj na hornej hranici lesa sú ovplyvnené asanačnou kalamitnou ťažbou a chemickými postrekmi.



Obr. 1. Mapa potenciálneho rozšírenia tetrova hlucháňa v študovanom území hodnotená pomocou modelu MaxEnt. Farebná škála vyjadruje pravdepodobnosť výskytu tetrova hlucháňa. Územia, ktoré vyhodnotil model ako nevhodné (<0,282), sú reprezentované bielou farbou.
Fig. 1. *Map of potential distribution of the Capercaillie in the studied area based on the MaxEnt model. The colour scale indicates probability of Capercaillie occurrence. Areas predicted by the model as unsuitable (<0.282) are shown in white.*

TERÉNNE PRÁCE A ZBER DÁT

Porasty s lokalitami boli vybrané na základe predpokladaného výskytu hlucháňa hôrneho. Terénny prieskum sa uskutočnil v letnom období (júl – september) v rokoch 2011–2012, kedy je plne vyvinutá pozemná vegetácia. Celkovo bolo zmapovaných 666 plôch na 132 km dlhom transekte. Pre hodnotenie kvality habitatu hlucháňa bola zvolená metodika HSI, pretože je to finančne nenáročný nástroj, ktorý je jednoduché použiť aj pre praktický manažment. Územie bolo mapované v transektoch, každých 200 m boli priradené súradnice bodu, na ktorom boli na kruhovej ploche s polomerom 20 m odčítané a podrobne zaznamenané všetky kľúčové charakteristiky habitatu hlucháňa podľa metodiky na výpočet indexu vhodnosti habitatu (HSI, Storch 2002): sklon svahu (v triedach 0: < 5°, 2: 6–15°, 3: 26–35°, 4: 36–45°, 5: >45°), pokryvnosť čučoriedky (%), výška bylinnej etáže (v triedach 1: 1–10 cm, 2: 11–20 cm, 3: 21–30cm atď.), pokryvnosť drevinného zmladenia (v triedach 1: < 25 %, 2: 26–50 %, 3: 51–75 %, 4: >75 %), sukcesné štádium porastu (1: mladina, 2: žrďkovina, 3: žrďovina, 4: kmeňovina, 5: starý porast, 6: vekovo rôznorodý porast, 0: žiadny les), korunový zápoj (%), drevinové zloženie, prítomnosť medzier v poraste a prítomnosť preferovaných kŕmnych stromov (*Abies alba, Pinus sylvestris, Pinus mugo, Pinus cembra*). Pobytové znaky (trus, perie, škrupiny, prachovisko atď.) sme hľadali po dobu 10 minút na výskumnej ploche každého bodu. Pokiaľ to bolo možné určiť, zaznamenali sme pohlavie, ako aj sezónu nálezu (podľa druhu konzumovanej potravy). Okrem toho sme na každej ploche určili, či ide o suchý les, odťaženú plochu alebo prales. Tieto informácie sme následne použili k porovnaniu vhodnosti habitatu a využívania habitatu na jednotlivých stanovištiach. Či sa daná výskumná plocha nachádza v pralese/pralesnom spoločenstve, sme určili podľa mapy pralesov Slovenska pochádzajúcou z podrobného mapovania v roku 2009–2010 (www.pralesy.sk). Ako prales je chápaný relatívne nedotknutý les (znaky po bývalej ľudskej činnosti nie sú evidované, alebo sú ťažko identifikovateľné a málo evidentné) s prirodzeným drevinovým zložením, s výskytom typických druhov ekosystému, zachovalou prirodzenou vekovou, vertikálnou, horizontálnou a priestorovou štruktúrou, s primeranou prítomnosťou mŕtveho dreva (stojaceho a ležiaceho) v rôznych štádiách rozkladu a s prítomnosťou jedincov drevín, ktorých vek sa blíži fyzickému veku. Za prales sa považujú aj mladšie vývojové štádiá lesa, ktoré vznikli po prírodnej disturbancii (Jasík et al. 2009).

Výpočet indexu vhodnosti habitatu HSI – habitat suitability index (podľa Storch 2002)

Pre každú zo zaznamenaných premenných Storch (2002) zostavila funkciu pre výpočet indexu vhodnosti (suitability index, SI). SI nadobúda hodnoty medzi 0 (nevhodný) a 1 (optimálny). Indexy vhodnosti sú následne skombinované do rovníc určujúcich hodnoty HSI. HSI sa počíta samostatne pre zimný a letný habitat, ktoré sa následne kombinujú do celoročného HSI. HSI, rovnako ako SI, nadobúda hodnoty od 0 do 1.

Z pôvodného modelu na výpočet HSI sme vynechali nadmorskú výšku, ktorá vyjadrovala vzdialenosť od poľnohospodársky využívaných dolín. Dôvodom bolo, že všetky hodnotené plochy sa vyskytovali vo výške nad 900 m n.m., kde je hodnota tohto SI konštantná.

HSI pre zimný habitat sa počíta na základe sukcesného štádia porastu, korunového zápoja, prítomnosti preferovaných kŕmnych stromov a sklonu svahu:

$$\text{HSI}_{\text{zima}} = (\text{SI}_{\text{sukcesia}} \times \text{SI}_{\text{korun. zápoj}}) \times \sqrt{}(\text{SI}_{\text{kŕmne stromy}} \times \text{SI}_{\text{sklon}})$$

Najdôležitejšou zložkou HSI_{zima} je štruktúra stanovišťa, vyjadrená pomocou sukcesného štádia porastu a korunového zápoja. Oboje môžu byť limitujúce, ich nulové hodnoty vedú k nulovému HSI_{zima}. Sklonu svahu a prítomnosti preferovaných kŕmnych stromov je pridelená nižšia váha. SI_{sklon} je vždy >0. $\text{SI}_{\text{kŕmné stromy}}$ je nulový len v prípade bezlesia.

HSI pre letný habitat kombinuje sukcesné štádium porastu, korunový zápoj, pokryvnosť čučoriedky, pokryvnosť drevinného zmladenia, výšku bylinnej etáže a sklon svahu:

$$\text{HSI}_{\text{leto}} = 0{,}25 * \{(\text{SI}_{\text{sukcesia}} * \text{SI}_{\text{korun. zápoj}}) + (2\text{SI}_{\text{čučoriedka}} * \text{SI}_{\text{zmladenie}}) + \text{SI}_{\text{byliny}}\} * \text{SI}_{\text{sklon}}$$

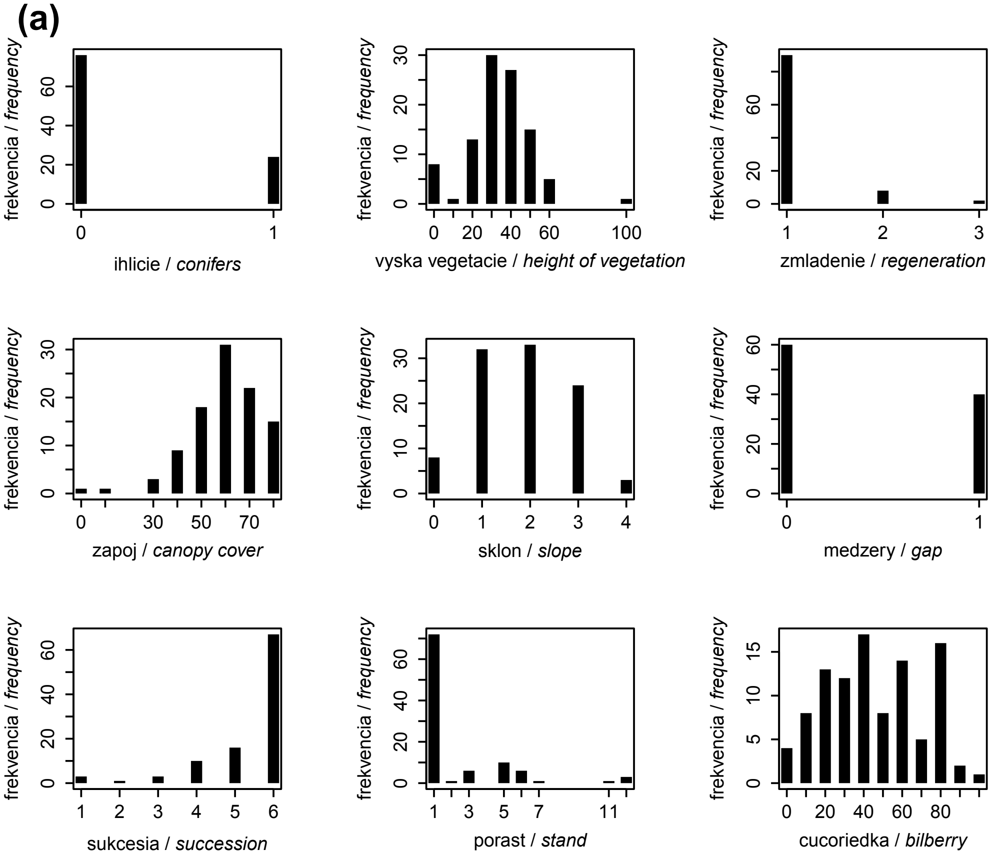
Štruktúra stanovišťa, typ vegetácie – vyjadrený pomocou pokryvnosti čučoriedky a pokryvnosti drevinného zmladenia a výška bylinnej etáže majú vzájomne kompenzujúci efekt. Najväčšia váha je prikladaná typu vegetácie. Sklon svahu môže opäť znížiť vhodnosť habitatu.

Celoročný HSI je geometrickým priemerom HSI_{leto} a HSI_{zima}:

$$\text{HSI}_{\text{rok}} = \sqrt{}\ (\text{HSI}_{\text{zima}} * \text{HSI}_{\text{leto}})$$

Oba HSI sa teda vzájomne kompenzujú, ten s nižšou hodnotou je však limitujúci.

Pre podrobnejšie informácie k výpočtu HSI pozri Storch (2002).



Obr. 2. Histogramy jednotlivých premenných: a) charakterizujúcich habitat s pozitívnym záznamom hlucháňa hôrneho; b) charakterizujúcich habitat s pozitívnym záznamom juvenilných jedincov. Vystetlenie jednotlivých premenných: ihličie (prítomnosť preferovaných kŕmnych stromov), výška vegetácie – výška bylinnej etáže (v triedach 1: 1–10 cm, 2: 11–20 cm, 3: 21–30 cm atď.), zmladenie (pokryvnosť drevinného zmladenia: v triedach 1: < 25 %, 2: 26–50 %, 3: 51–75 %, 4: >75 %), zápoj (korunový zápoj (%), sklon svahu (v triedach 0: < 5°, 2: 6–15°, 3: 26–35°, 4: 36–45°, 5: >45°), medzery – prítomnosť medzier v poraste, sukcesia (sukcesné štádium porastu: 1: mladina, 2: žrďkovina, 3: žrďovina, 4: kmeňovina, 5: starý porast, 6: vekovo rôznorodý porast, 0: žiadny les), drevinové zloženie – v triedach (1. *Picea abies*, 2. *Picea abies* + *Pinus* sp., 3. *Picea abies* + *Abies alba*, 4. *Picea abies* + *Larix decidua,* 5. *Picea abies* + *Fagus sylvatica*, 6. *Picea abies* + *Sorbus aucuparia,* 7. *Picea abies* + iné listnaté stromy, 8. *Pinus* sp., 9. *Abies alba* + iné listnaté stromy, 10. *Fagus sylvatica*, 11. *Fagus sylvatica* + *Picea abies*, 12. *Fagus sylvatica* + *Abies alba*), čučoriedka – pokryvnosť čučoriedky *Vaccinium myrtillus* (%).

Štatistické vyhodnotenie vhodnosti a využívania habitatu

S využitím popisnej štatistiky sme skonštruovali histogramy pre jednotlivé premenné prostredia, aby sme ukázali vhodné vlastnosti habitatu pre výskyt druhu.

Na testovanie vzťahu medzi hodnou HSI a zaznamenanými pobytovými znakmi, teda na overenie funkčnosti HSI v podmienkach Západných Karpát, sme použili všeobecný lineárny model (GLM) kvazibinomickej rodiny so spojovacou

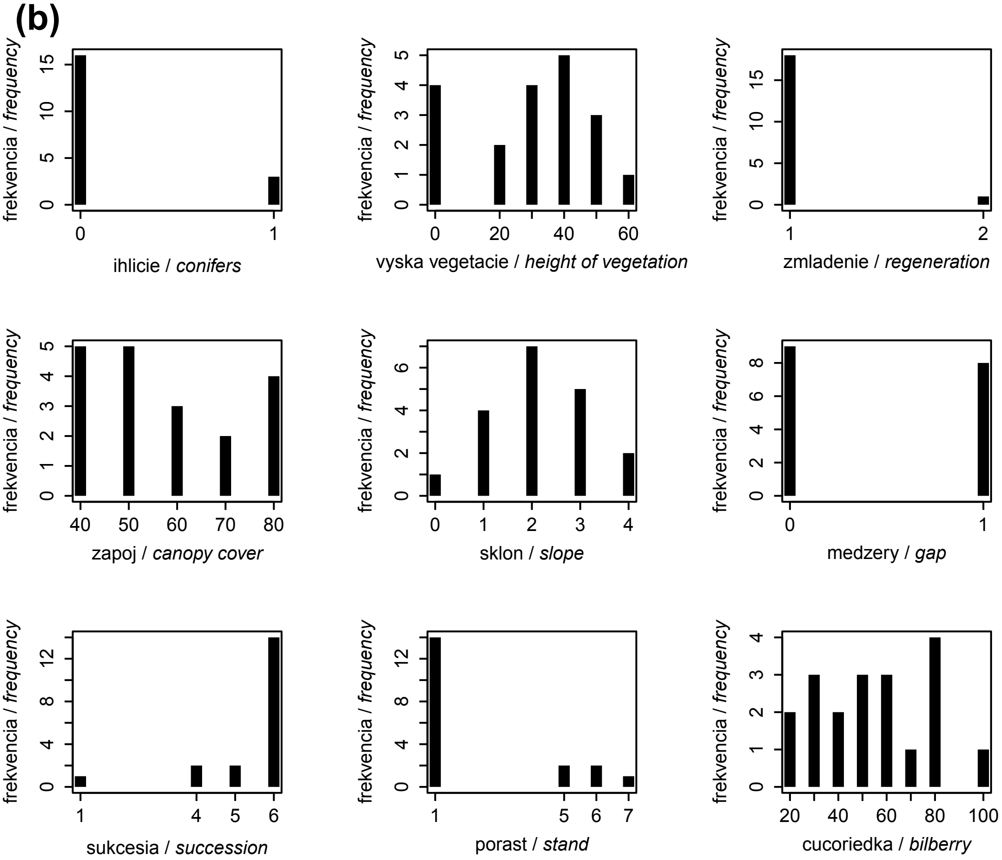


Fig. 2. *Histograms of particular habitat variables: a) characterising a habitat with confirmed Capercaillie presence; b) characterising a habitat with confirmed presence of Capercaillie juveniles. Legend: conifers – presence of prefered feeding trees, height of herb vegetation (in categories: 1: 1–10 cm, 2: 11–20 cm, 3: 21–30 cm etc.), regeneration (coverage of rejuvenated woody plants: in categories 1: < 25 %, 2: 26–50 %, 3: 51–75 %, 4: >75 %), canopy cover (in %), slope – slope inclination (in categories: 0: <5°, 2: 6–15°, 3: 26–35°, 4: 36–45°, 5: >45°), gaps – presence of gaps in the stand, succession – succession stages (1. thicket , 2. pole timber, 3. stake wood, 4. mature forest, 5. old stand, 6. age-heterogeneous stand, 0: forest-free area), type of stand – species composition of the stand (in categories – 1. Picea abies, 2. Picea abies +* Pinus *sp., 3. Picea abies + Abies alba, 4. Picea abies + Larix decidua, 5. Picea abies + Fagus sylvatica, 6. Picea abies + Sorbus aucuparia, 7. Picea abies + other deciduous trees, 8. Pinus* sp.*, 9. Abies alba + other deciduous trees, 10. Fagus sylvatica, 11. Fagus sylvatica + Picea Abies, 12. Fagus sylvatica + Abies alba), bilberry – bilberry cover (Vaccinium myrtillus) (in %).*

funkciou logit. Na vyhodnotenie vplyvu asanačných opatrení a na vyhodnotenie rozdielov HSI medzi jednotlivými typmi stanovíšť sme použili neparametrický Kruskal-Wallisov test.

Pre každý z desiatich intervalov HSI (1 = nevyhovujúci, 10 = excelentný) sme vypočítali percento plôch s pobytovým znakom a Ivlevov index I (Krebs 1989) na základe relatívnej dostupnosti plochy (A – percento zo všetkých plôch) a relatívneho využívania (U – percento zo všetkých nájdených pobytových znakov):

I = (U – A)/(U + A).

Ivlevov index nadobúda hodnoty od –1 do +1, pozitívne hodnoty naznačujú preferenciu a negatívne vyhýbanie sa plochám daného intervalu.

Dáta boli spracované v programoch Microsoft Excel a R 2.15.2 (R Core Team, 2011). Hladiny významnosti boli stanovené na $\alpha = 0{,}05$. Všetky analýzy boli počítané na základe celoročného HSI.

Modelovanie rozšírenia hlucháňa hôrneho

Pre plánovanie manažmentu je potrebné mať ucelený obraz o stave habitatu na úrovni krajiny a identifikovať izolované plochy habitatu. Keďže počas dvoch rokov mapovania HSI nebolo možné zozbierať dostatok dát z terénu pre utvorenie komplexného modelu HSI, potenciálne rozšírenie hlucháňa hôrneho na území Nízkych Tatier a Veľkej Fatry bolo modelované pomocou SDM modelu MaxEnt (Phillips et al. 2006), ktorý je v súčasnosti považovaný za jednu z najspoľahlivejších metód predikcie geografickej distribúcie najmä u druhov, u ktorých je k dispozícii iba obmedzené množstvo dostupných dát o ich výskyte (Elith et al. 2006; Pearson et al. 2007; Franklin 2009, Elith et al. 2011). Pre modelovanie bolo použitých 113 záznamov výskytu (pôvodných 100 záznamov získaných počas HSI mapovania bolo obohatených o 13 ďalších záznamov pochádzajúcich z monitoringu ŠOP SR) a z environmentálnych premenných. Pracovali sme v rastrovom formáte s priestorovým rozlíšením 100×100 m.

Pre modelovanie bolo vybraných z pôvodných 39 len 6 prediktorov: priemerná ročná teplota vzduchu (°C; medzi rokmi 1950–2000), priemerné júlové zrážky (mm; medzi rokmi 1950–2000), krajinná pokrývka (Corine Land Cover 2006; 16 kategórií), nadmorská výška (m n. m.), druhové zloženie porastu (20 kategórií;) a zakmenenie porastu (0–1).

Vzhľadom k silnej väzbe hlucháňa na lesné porasty a zároveň ich intenzívnej ťažbe v posledných rokoch, bolo potrebné vymedziť plochy odťažených lesných plôch (holín) a vyňať ich z analýzy. Boli použité satelitné snímky Landsat ETM+ za rok 2012 s rozlíšením 30×30 m. Použitá kompozícia bola vhodná pre odlíšenie ihličnatých a listnatých lesov, miest bez vegetácie – kanály 4,5,3 (blízky infračervený, stredný infračervený, červený). Pre klasifikáciu defoliácie (straty asimilačných orgánov), boli stanovené hodnoty tried defoliácie podľa %, tj. trieda 1: 0–10 %, trieda 2: 11–20 % atď., pričom trieda 11 znamená vyťažený les (Bucha et al. 2000). Geografické rozšírenie hlucháňa hôrneho tak bolo modelované v lesných porastoch o celkovej rozlohe 1132 km^2 (66 % rozlohy územia).

Pre overenie výsledkov modelu bol model 100× opakovaný a to na náhodne vybranej trénovacej množine dát (70 % záznamov o výskyte) a následne testovaný (zvyšné dáta). Predpovedacia schopnosť výsledného (spriemerovaného) modelu bola odhadnutá pomocou nezávislej diskriminačnej hladiny AUC (Area Under the ROC Curve) zodpovedajúce metriky pre popis grafu ROC krivky (Receiver Operating Characteristic curve; Fielding & Bell 1997). Výsledná hodnota AUC je navyše priemerom 100 opakovaní, pri ktorom boli záznamy o výskyte vždy náhodne rozdelené do trénovacej a testovacej sady.

Pre určenie celkovej rozlohy rozšírenia tetrova hlucháňa v skúmanom území bolo potrebné stanoviť hranicu („treshold“) pravdepodobnosti, podľa ktorého bol výsledný raster pravdepodobnosti (0–100 %) rozdelený na binárny (ne/výskyt). Podľa Liu et al. (2005) a Bean et al. (2012) sme použili hranicu určenú zhodným pomerom správne určených presencií („senzitivita") a absencií („špecificita") druhu („Equal training sensitivity and specificity"). Podrobnejšie informácie o použití modelu MaxEnt opisujú Phillips & Dudík (2008) a Elith et al. (2011).

VÝSLEDKY

Vzťah medzi skúmanými faktormi a zaznamenaným výskytom druhu

Najčastejšie zaznamenané pobytové znaky boli perie (45 %), trus (36 %), priamo videné jedince (16 %) a škrupiny vajec (3 %). Iba 19 zo 100 záznamov výskytu hovorí o reprodukcii hlucháňa. Jednotlivé premenné prostredia na plochách s pozitívnym výskytom druhu (n = 100) a na plochách s pozitívnym záznamom juvenilných jedincov (n = 19) sú zobrazené pomocou histogramov (obr. 2).

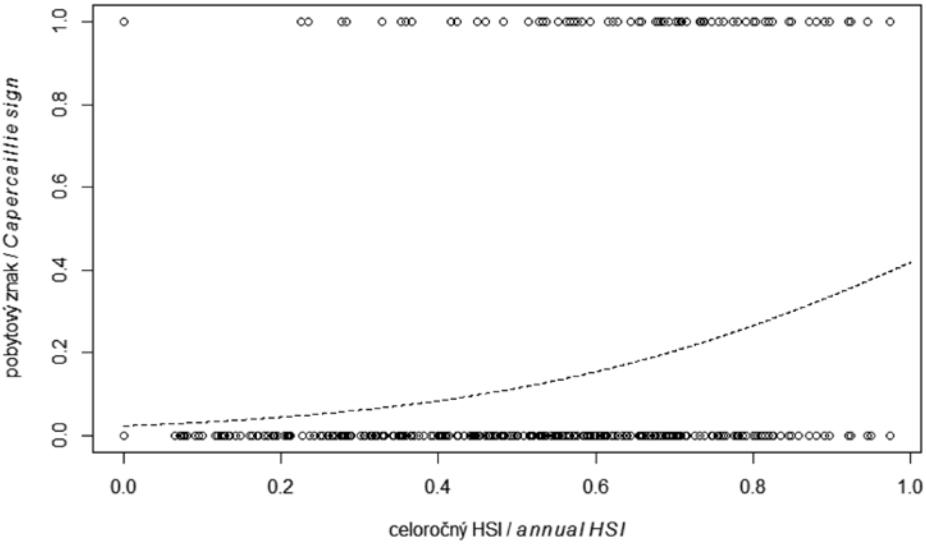
Overenie funkčnosti modelu HSI

Výsledok GLM potvrdil pozitívnu závislosť medzi indexom HSI a výskytom pobytových znakov (p < 0,0001, nulová deviancia = 563,40 na d.f. = 665, reziduálna deviancia = 510,54 na d.f. = 664, disperzný parameter = 0,9992). Vzťah zobrazuje obrázok obr. 3. Rozloženie mapovaných plôch v HSI intervaloch a počet plôch s nájdenými pobytovými znakmi zobrazuje Tabuľka 1.

Lineárna regresia potvrdila závislosť Ivlevovho indexu na intervale HSI (F = 50,47, d.f. = 1 a 8, p < 0,0001, adj. R^2 = 0,85, (obr. 4). Tento vzťah vyjadruje, že plochy s vyšším HSI sú hlucháňom využívané častejšie. Na základe týchto výsledkov považujeme HSI podľa Storch (2002) za vhodný nástroj na predikciu výskytu hlucháňa v Západných Karpatoch.

Vplyv kalamitných asanačných opatrení

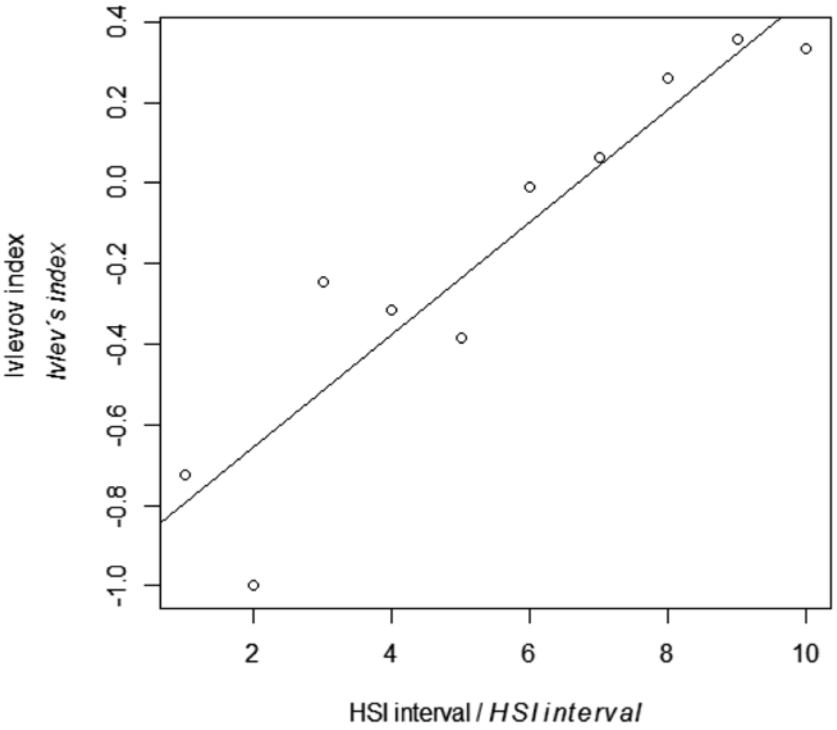
Kruskal-Wallisov test ukázal štatisticky signifikantný rozdiel medzi HSI_{rok} na



Obr. 3. Vzťah medzi indexom vhodnosti celoročného habitatu a výskytom pobytových znakov.
Fig. 3. *Relationship between the annual habitat suitability index (HSI) and occurence of Capercaillie signs.*

Tab. 1. Počet plôch s pobytovými znakmi v kategóriách ročného indexu vhodnosti habitatu.
Table 1. Number of plots with Capercaillie signs in categories of the annual habitat suitability index (HSI).

trieda HSIrok *HSI category*	1	2	3	4	5	6	7	8	9	10
počet plôch *number of plots*	83	33	44	51	75	88	100	86	76	30
% zo všetkých plôch *% of all plots*	12	5	7	8	11	13	15	13	11	5
počet bodov so zistenými pobytovými znakmi *number of plots with Capercaillie signs*	2	0	4	4	5	13	17	22	24	9



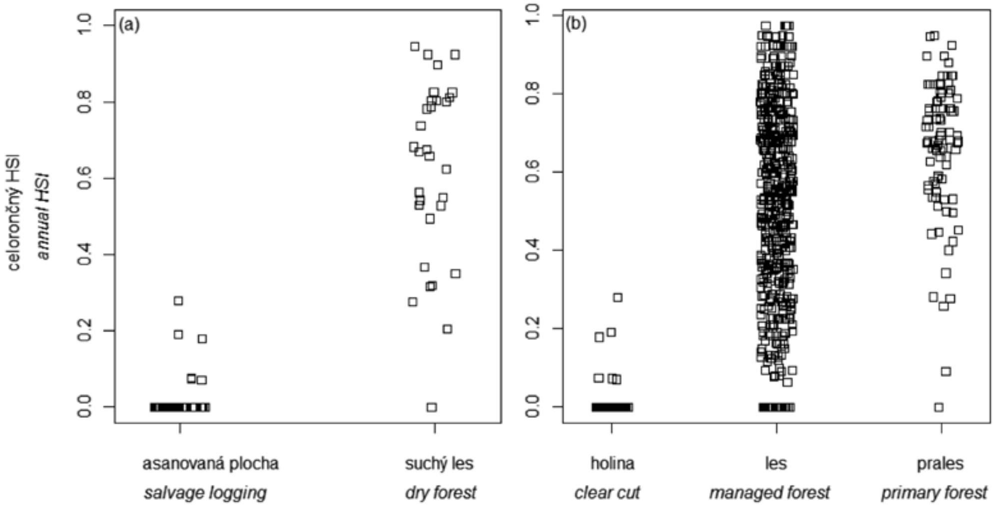
Obr. 4. Vzťah ročného indexu vhodnosti habitatu a Ivlevovho indexu.
Fig. 4. *Relationship between the annual habitat suitability index (HSI) and the Ivlev's index.*

plochách s vyťaženou (priemerné HSI 0,016) a ponechanou drevnou hmotou (0,62) po lykožrútovej kalamite (chi^2 = 65,92, d.f. = 1, p < 0,0001). HSI na plochách s nespracovanou kalamitou je významne vyšší (obr. 5a).

HSI sa tiež líšil aj medzi holinou (priemerne 0,016), lesom (0,534) a pralesom (0,664) a to medzi všetkými úrovňami (chi^2 = 149,74, d.f. = 2, p < 0,0001, obr. 5b).

Modelovanie rozšírenia hlucháňa hôrneho

Priemerná hodnota AUC hlavných modelov bola na hranici strednej a vysokej predikčnej presnosti, podobný výsledok



Obr. 5. a) Index vhodnosti celoročného habitatu na asanovaných plochách (holina) a na plochách s nespracovanou kalamitou (suchý les) b) Index vhodnosti celoročného habitatu v závislosti na type stanovišťa (holina, les, prales).
Fig. 5. *a) Annual habitat suitability index (HSI) on managed (clear-cut) and unmanaged (dry forest) plots after the bark beetle outbreak. b) Annual habitat suitability index in different habitat types (clear-cut, managed forest and primary forest).*

bol získaný z testovacích modelov. Na základe tejto hodnoty bola pre rozdelenie výsledného rastru pravdepodobnosti do binárnej podoby (výskyt hlucháňa / absencia hlucháňa) určená hodnota 0,282, tzn. územie s nižšími hodnotami bolo považované za nevhodný biotop pre hlucháňa a naopak.

Klasifikáciou výsledného rastra pravdepodobnosti do binárnej podoby bolo ako vhodné územie pre výskyt hlucháňa označených 180 km^2 (16 % lesných porastov), ako nevhodné územie rozloha 952 km^2 lesných porastov (obr. 1).

DISKUSIA

Základným predpokladom pre úspešnú ochranu hlucháňa hôrneho je zabezpečenie dostatočnej rozlohy vhodného prírodného prostredia (Rolstad & Wegge 1987, Storch 2002, Quevedo et al. 2006). Jasný obraz o tom podáva napríklad neúspech projektov záchrany hlucháňa zameraných na vypúšťanie jedincov z odchovní v Nemecku, kde bolo od roku 1950 vypustených viac ako 4800 hlucháňov bez viditeľného úspechu (Siano 2008). Vo väčšine prípadov nebol odstránený hlavný dôvod vyhynutia pôvodnej populácie.

Zhodnotenie rozlohy a kvality habitatu

Hlucháň hôrny je druh veľmi náročný na kvalitu a rozlohu vhodného prírodného prostredia a preto manažment životaschopnej populácie hlucháňa musí vyplývať zo širších vzťahov na úrovni krajiny (Storch 1997, Graff et al. 2005, Bollmann et al. 2011). Z dôvodu nedostatku dát z terénneho mapovania sme pre určenie celkovej rozlohy vhodného habitatu ma úrovni krajiny využili model druhovej distribúcie (Elith & Leathwick 2009). Aj keď je model menej presný ako výsledky terénneho mapovania, sme pomocou neho schopní na úrovni krajiny identifikovať oblasti, kde dochádza k fragmentácii populácie, kde nie je zastúpený vhodný habitat v dostatočnej miere a vyčleniť územia určené na pasívny alebo aktívny manažment.

V Nízkych Tatrách došlo k rozsiahlej strate vhodného habitatu hlucháňa. Oslabením populácie v Nízkych Tatrách a Veľkej Fatre, ktorá je pokladaná za zdrojovú populáciu na Slovensku, dôjde k poklesu menších populačných jednotiek v priľahlých pohoriach (Slovenský raj, Stolické vrchy, Muránska planina, Veporské vrchy atď.). Preto je pre prežitie hlucháňa jednoznačne potrebné usmernenie manažmentu tohto územia. Pre spresnenie konkrétnych lesníckych opatrení v hospodárskych lesoch v oblastiach určených na aktívny manažment je potrebné identifikovať faktory, ktoré znižujú kvalitu stanovišťa na úrovni porastu – jednou z možností je v tejto práci použitá metodika HSI (Storch 2002). Výsledky našej štúdie potvrdzujú, že metodika HSI je dobrým ukazovateľom využívania habitatu hlucháňom na území Nízkych Tatier a Veľkej Fatry, a preto je použiteľná ako praktický nástroj pre plánovanie manažmentu s cieľom zachovať hlucháňa na tomto území. HSI počíta „perfektný“ hluchání les, ktorý na mnohých lokalitách výskytu ani nemusí existovať, obzvlášť ak stanovištné podmienky (napr. pôda, pH) nedovoľujú rast čučoriedky. Ak sa na lokalite nevyskytuje čučoriedka, HSI nebude nikdy vyššie ako 0,5. Čučoriedkové plochy, ktoré sú mimo lesa (napr. pasienky), nebudú viesť k zvýšeniu hodnoty HSI, pretože kód lesného typu by bol nulový. Takže v lese bez čučoriedky HSI nedosiahne nikdy vyššiu triedu ako 3 (Storch in litt.). Ak by HSI nebol na niektorých špecifických lokalitách funkčný, je ho možné kalibrovať pomocou logistickej regresie alebo ENFA na špecifické modely pre jednotlivé lokality. V našej štúdii metodika HSI prejavuje určité nedostatky na vápencovom podloží alebo v lesoch s prevahou buka. Ale aj v týchto prípadoch zväčša platí, že hlucháň využíva plochy s vyššou hodnotou HSI, preto nebolo potrebné model kalibrovať. Čučoriedka obyčajná ako potravný zdroj môže byť nahradená v iných vegetačných stupňoch napríklad ostružinou malinovou (*Rubus ideaus*) alebo ostružinou černicovou (*Rubus fructicosus*). Keďže metodika bola vytvorená v hospodárskych lesoch v Alpách, bolo by zaujímavé podrobnejšie preskúmať význam mŕtveho dreva pre hlucháňa v karpatských podmienkach. Hovorí o tom aj výsledok, že pralesy, ktorých významnou súčasťou štruktúry je stojace i ležiace mŕtve drevo, sú preferovaným habitatom hlucháňa. V Karpatských podmienkach je vyšší počet druhov predátorov hlucháňa (Saniga 2002) v porovnaní s Alpami (Storch 2005) a mŕtve drevo by mohlo mať podstatný význam pre zvyšovanie úkrytových možností pred predátormi, najmä počas obdobia hniezdenia.

Fragmentácia habitatu a genetická izolácia

Na základe predikčného modelu je zjavné, že habitat hlucháňa je viditeľne fragmentovaný na 2 miestach (Čertovica, Donovaly) a zároveň časť významných biotopov hlucháňa je pod silným vplyvom turistického ruchu. Rozsiahle odťažené plochy a následný vznik husto zapojených lesov sú jedným z hlavných dôvodov, ktorý tvorí bariéru v úspešnej komunikácii medzi jednotlivými populačnými jednotkami hlucháňa. Fragmentácia habitatu môže mať negatívne účinky na genetiku populácie hlucháňa, pretože vytvára malé populácie s limitovaným tokom génov medzi populáciami a zvyšuje genetický drift, inbríding (Pullin 2002). V záujme udržania životaschopnej populácie by malo byť zachovaných čo najviac habitatových plôch a malo by sa predchádzať ďalšej strate veľkosti a kvality týchto plôch. Je dôležité sústrediť sa na ochranu nielen silnejších (zdrojových) populácií, ale aj na zachovanie menších okrajových lokálnych populácii, pretože ich zánikom nenávratne strácame genetickú informáciu (Segelbacher 2003).

Fragmentácia habitatu a predačný tlak

Často je diskutovaná otázka vplyvu predácie na početnosť hlucháňa. V porovnaní so súvislými lesnými celkami je vo fragmentovaných oblastiach vplyvom zvýšeného predačného tlaku významne vyššia mortalita kuriatok (Wegge & Storaas 1990, Wegge 1992). Rozsiahle odľažené plochy predstavujú pre hlucháňa veľké nebezpečenstvo (Swenson & Angelstam 2003). Tým, že po náhlej strate biotopu sa hlucháne vyskytnú vo väčšej hustote na menšej výmere lesa, stávajú sa zraniteľnejšie voči predátorom z dôvodu otvorenosti priestoru. Následný vývoj porastu – vzniku husto zapojenej homogénnej mladiny predstavuje úplnú stratu vhodného habitatu pre hlucháňa. V premenenom hustom lese hlucháň nedokáže lietať, nenachádza v ňom potravu a taktiež stráca výhľad potrebný na únik pred predátormi (Finne et al. 2000). Predačný tlak môžeme eliminovať aj nepriamo – znižovaním výmery (resp. zabraňovaním vzniku nových) rozsiahlych odľažených plôch a v prípade už vzniknutých holín zabrániť vzniku homogénnych hustých porastov.

Turistický ruch

Napriek vysokým hodnotám HSI v okolí turistických areálov (Chopok Juh, Chopok Sever, Donovaly), lokality nie sú využívané hlucháňmi. V týchto oblastiach môžu turistické centrá predstavovať barierový prvok (najmä počas zimy) v komunikácii. Turizmus má vplyv na zvýšenie predačného tlaku na hlucháne. Horské chaty a miesta navštevované ľuďmi totiž prispievajú k zvýšeniu nosnej kapacity prostredia pre významné predátory hlucháňov (napr. čeľaď Corvidae) (Storch & Leidenberger 2003). Ďalším významným negatívnym vplyvom je plašenie. Pre hlucháňa je vyrušovanie kritické v zimných a jarných (obdobie toku) biotopoch a biotopoch rodiniek s kuriatkami počas letných mesiacov – najmä máj, jún, júl (Ménomi & Magnani 1998). Pri porovnaní obsahu stresového hormónu kortikosterónu v truse jedincov v blízkosti rekreačných zimných aktivít v smrekových lesoch Thiel et al. (2011) zistili jeho rastúci obsah smerom od miest s nízkym a stredným vyrušovaním až k miestam s vysokou turistickou intenzitou. Opakované alebo pretrvávajúce zvýšenie kortikosterónu v súvislosti s vyrušovaním, môže ovplyvniť celkovú zdatnosť jedincov – telesnú kondíciu, imunitu, reprodukciu a prežitie jedincov (Wingfield et al. 1997). Preto lokality s vysokou kvalitou habitatu nemusia byť obývané hlucháňmi, ak je lokalita pod vplyvom negatívnych faktorov pôsobiacich zo širšieho okolia (Storch 2002), čo sa prejavilo aj vo výsledkoch mapovania. Negatívny vplyvy turismu je možné minimalizovať. V niektorých krajinách (napr. Rakúsko, Francúzsko, Nemecko, Švajčiarsko) boli vyvinuté programy opatrení na obmedzenie ľudského vyrušovania (Zeitler & Glanzer 1998).

Význam bezzásahových území v sieti habitatu hlucháňa

Početné štúdie preukázali význam neobhospodarovaných lesov pre biodiverzitu (Bouget & Duelli 2004, Müller et al. 2008, Bässler et al. 2012, Lehert et al. 2013). Výsledky našej štúdie potvrdzujú, že pralesy sú do veľkej miery využívané hlucháňmi, a preto predstavujú významný prvok v zostávajúcej sieti habitatu hlucháňa. Napriek tomu, že pralesy predstavujú najcennejšie lesné ekosystémy, od roku 2010 bolo vyťažených v Nízkych Tatrách cca 64 ha pralesov a tlak na ne stále rastie (na Slovensku bolo identifikovaných iba 122 pralesových lokalít s celkovou výmerou 10 104 ha, čo predstavuje len 0,47 % slovenských lesov, ich rozloha sa naďalej zmenšuje (www.pralesy.sk)). V pralesoch a prírodných lesoch prírodné disturbancie, ako napríklad premnoženie podkôrneho hmyzu v prípade ponechania drevnej hmoty v lese, môžu v dlhšom časovom merítku pozitívne podporiť populáciu hlucháňa (Teucher et al. 2011). Podľa výsledkov našej štúdie aj „suchý les“ (les s odumretou hornou stromovou vrstvou) vyhovuje nárokom na prírodné prostredie hlucháňa viac ako rozsiahle odťažené plochy. Hlucháň tu nachádza jedinečné úkrytové, ale i potravné podmienky.

Možné riešenia – hlucháňovi-priateľský manažment lesa

Aj keď výsledky tejto štúdie potvrdzujú, že pralesy a prírodné lesy sú najviac využívanými habitatmi hlucháňa, bezzásahové územia (prírodné rezervácie) nie sú v súčasnosti dostatočne veľké pre poskytnutie dostatku vhodného prírodného prostredia pre životaschopnú populáciu (Grimm & Storch 2000). Tieto požiadavky zreteľne ukazujú, že ochrana hlucháňa je možná iba vo vzájomne sa doplňajúcej sieti systému bezzásahových rezervácií a hospodárskych lesov, v ktorých bude aplikovaný hlucháňovi-priateľský manažment lesa (Bollmann 2012). V hospodárskych lesoch môže byť manažment doplnený o praktické lesnícke opatrenia na zachovanie tohto vtáčieho druhu. Konkrétne opatrenia určené na zveľaďovanie habitatu hlucháňa môžeme rozdeliť do troch skupín podľa úrovne, na ktorej budú prevedené – na úrovni krajiny, porastu a stromu. Opatrenia na úrovni krajiny by mali zahŕňať ochranu pralesov a prírodných lesov, obmedzenie fragmentácie vhodného habitatu a zachovanie prepojenia pomocou koridorov, zabránenie veľkoplošnému odlesňovaniu, zabezpečenie optimálnej rozlohy letného a zimného habitatu (Suchant 2003, Braunisch & Suchant 2007). Je všeobecne známe, že biotopové nároky hlucháních rodiniek s kuriatkami sa mierne odlišujú od dospelých jedincov (Summers et al. 2004). Čiastočne to zachytávajú aj výsledky tejto štúdie (obr. 2), rozdiel je viditeľný najmä v korunovom zápoji – rodinky s kuriatkami využívajú porasty s nižším korunovým zápojom a vyššou pokryvnosťou čučoriedky. Je potrebné klásť dôraz na ochranu a zachovanie dostatočnej rozlohy reprodukčných lokalít, pretože sú zásadné pre prežitie druhu (Wegge et al. 2005).

Na úrovni porastu vylepšenie hluchánieho habitatu znamená hlavne výchovu presvetlenejších lesných porastov a zvýšenie rôznorodosti štruktúry porastov. Hlavné ťažisko manažmentu má byť sústredené na prerezávkové až prebierkové porasty (najdlhšie trvajúci efekt), príp. na kmeňoviny, ktoré pôsobia ako barierový prvok v hlucháních stanovištiach. V dospelých porastoch je odporúčaná maloplošná ťažba (skupinový clonný rub do 0,2 ha). Ďalšie opatrenia zahŕňajú udržiavanie a vytváranie čistín, zdokonaľovanie lesných okrajov, ponechávanie mŕtveho dreva a pod. Na úrovni stromu je vhodné podporovať výsadbu jedle, hlboko zavetvené stromy na lesných okrajoch, ponechávať prirodzené zmladenie, podporovať jarabinu a iné pionierske dreviny (Suchant & Braunish 2008). Obzvlášť v čisto smrekových porastoch významnú úlohu zohráva stojace mŕtve drevo, ktoré je s obľubou hlucháňom využívané na odpočinok (Mollet 2001). V dnešnej situácii je nutné aplikovať vhodné opatrenia smerom von z plôch aktuálneho výskytu, tzn. nie v lokalite aktuálneho výskytu, ale na jej hranici. Je potrebné tieto kroky uskutočniť, kým je prirodzená populácia dostatočne veľká (MacMillan & Marshall 2003). Konkrétne opatrenia by mali byť využité najmä pre naliehavú reštauráciu už značne človekom poznačených a degradovaných lesných ekosystémov (tzn. na rozsiahlych odťažených plochách).

Veľkým nebezpečenstvom pre prežitie kuriatok je použitie pesticídov. Pesticídy používané na boj s podkôrnym hmyzom sú založené na báze cyklických pyretroidov. Účinnou látkou použitých prípravkov je zväčša cypermetrín. Táto látka pôsobí v priebehu niekoľkých týždňov, navyše neselektívne, teda usmrcuje aj hmyz, ktorý tvorí základnú potravu juvenilných jedincov v prvom mesiaci života (Lakka & Kouki 2009). Keďže sa pesticídy používajú v čase rojenia lykožrútov (obyčajne máj – august) zasahujú najcitlivejšiu fázu v ročnom cykle života hlucháňa – vyvádzanie mláďat, preto by ich použitie v národných parkoch malo byť trestné. V žiadnom prípade nesmú byť aplikované podobné prostriedky v oblastiach s výskytom hlucháňa.

Je ohrozená slovenská populácia hlucháňa hôrneho?

Nízke Tatry a Veľká Fatra by vzhľadom na svoju rozlohu lesov (cca 1132 km^2) mali niesť zdrojovú populáciu hlucháňa hôrneho na Slovensku. Zdrojová („source“) populácia je mimoriadne dôležitá, pretože práve ona je zodpovedná za prežívanie druhu v krajine a je zdrojom nadpočetných jedincov, ktoré môžu obsadzovať vhodné, novovzniknuté plochy. Okrajové („sink“) populácie sú naopak existenčne závislé od zdrojovej. Pri narušení takejto zdrojovej populácie dochádza k poklesu v počte okolitých populačných jednotiek („source-sink model“) (Pullin 2002). V študovanej oblasti sme zaznamenali výrazné lokálne poklesy počtu hlucháňa na konkrétnych lokalitách. Vykonanými zásahmi (ťažba dreva, výstavba ciest, použitie pesticídov) došlo v rámci skúmanej oblasti k priamemu zničeniu biotopov hlucháňa, následne došlo k poklesu počtu hlucháňov. Aktuálna rozloha vhodného habitatu podľa výsledkov tejto štúdie nepostačuje pre životaschopnú populáciu a naviac došlo k fragmentácii zdrojovej populácie, ktorá môže časom viesť k úplnemu vyhynutiu tohto druhu na území Slovenska v budúcnosti. Je potrebné zabrániť ďalšej strate vhodných porastov a zmeniť spôsob manažmentu na min. 250 km^2. Znižovaniu stavu populácie hlucháňa sa dá zabrániť jedine zastavením všetkých negatívnych zásahov do ich biotopov, vrátane kalamitnej ťažby dreva, budovania ciest, používania chemikálií a výstavby zjazdoviek. Na novovzniknutých holinách, v mladinách a porastoch určených na prebierku je potrebné aplikovať hlucháňovi-priateľský manažment, a tým prinavrátiť štruktúry lesa vhodné pre prežitie hlucháňa.

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SUMMARY

The area of the Nízke Tatry and Veľká Fatra Mts. is inhabitated by the core population of the Western Capercaillie in the Western Carpathians. Large-scale forestry interventions led to a rapid decline in the Capercaillie numbers after the windstorm in 2004. To stop the rapid decline, complex information about the quality and extent of suitable habitat is required, which we provide in this study using two methodological approaches.

During the years 2011–2012 we conducted a systematic survey of the Capercaillie habitat suitability. The subject of the statistical analysis was the presence/absence data obtained at 666 study sites in the model area. To consider habitat suitability at the level of forest stands, we used the habitat suitability index (HSI) (Storch 2002). It was necessary to verify the HSI concept in the Carpathian conditions – to test the relationship between the HSI values and Capercaillie presence data we used the general linear model (GLM) quasibinomial family with logit link function. The HSI values were divided into 10 intervals (1 = unsuitable, 10 = excellent). For each interval we calculated the percentage of plots with Capercaillie signs and the Ivlev's index (Krebs 1989), based on the relative availability of the plots and their relative use. We used linear regression to evaluate the relationship between the percentage of plots with Capercaillie signs and the intervals of HSI. We used the non-parametric Kruskal-Wallis test to evaluate the impact of sanitary logging (clear-cut and unmanaged forest) on the quality of Capercaillie habitat (expressed by HSI). We used a post-hoc pair comparison in the case of different types of sites (clear-cut, managed forest, primary forest).

Because of the lack of HSI data from the field, we used a complex SDM model MaxEnt (Phillips et al. 2006) to create a habitat suitability model at the ladscape level. Out of the original 39 variables, the application of the MaxEnt model showed that the Capercaillie presence is best explained by the following ones: mean annual temperature, mean precipitation during July, type of land cover, altitude, tree species composition, and canopy closure. The recently created clear-cuts were excluded from the analyses using the Landsat ETM+ data from the year 2012, because according to the results of a field survey, Capercaillies use clear-cuts only within 50 m from the forest edge.

The most frequent Capercaillie signs included feathers (45%), droppings (36%), directly observed individuals (16%) and broken egg shells (3%). Only 19 out of 100 capercaillie signs were assigned to juveniles. Single habitat variables on plots with Capercaillie presence (n = 100) and on plots with juvenile presence (n = 19) are showed using histograms (Fig. 2).

The GLM results showed a positive correlation between the HSI index and Capercaillie signs ($p < 0.0001$, zero deviance = 563.4 on d.f. = 665, residual deviance = 510.54 on d.f. = 664, dispersion parameter = 0.9992) (Fig. 3). Linear regression showed the dependence of the Ivlev's index on the HSI interval ($F = 50.47$, d.f. = 1 a 8, $p < 0.0001$, adj. $R^2 = 0.85$) (Fig. 4). The Kruskal-Wallis test showed a statistically significant differ-

ence between the HSI_{year} in the managed (mean HSI 0.016) and unmanaged (0.62) bark beetle affected stands (dry forest) ($chi^2 = 65.924$, d.f. = 1, $p < 0.0001$). The HSI value in the unmanaged forest is significantly higher (Fig. 5a). The HSI values differ between the clear-cut (mean 0.016), managed forest (0.534) and the primary forest (0.664) ($chi^2 = 149.74$, d.f. = 2, $p < 0.0001$, Fig. 5b).

Based on the application of the MaxEnt model, the area predicted to be suitable for the Capercaillie was 180 km^2 (16% of all forest stands in the study area), while 952 km^2 of the forest stands were predicted to be unsuitable (Fig.1).

The results of our study show that primary forests represent very important habitat patches for the Capercaillie in its habitat network. Even the unmanaged bark beetle affected stands (dry forest) meet habitat requirements of the Capercaillie better than the large-scale clear-cuts.

Direct destruction of the Capercaillie habitat is a result of forestry measures (salvage logging, building of new forest roads, and application of pesticides) in the studied area, and consequently, Capercaillie numbers have been declining rapidly. The current size of the suitable habitat is predicted to be 180 km^2, which is insufficient for a minimum viable population; furthermore, the suitable habitat of a potential source population is being fragmented. The threat of the core population represents a threat for the whole Slovak population of the species. A complex management plan for the Capercaillie areas is highly needed.

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Evaluating forest management intensity on an umbrella species: Capercaillie persistence in central Europe

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ABSTRACT

Deforestation and fragmentation of forests worldwide are negatively impacting biodiversity. The capercaillie (*Tetrao urogallus*) is an endangered umbrella species of montane forests in central Europe. Despite its status, it has largely been overlooked in forest management planning in the Carpathian Mountains, a biodiversity hotspot within the European Union. Previous investigations of timber management effects on capercaillie have shown contradictory results within Europe; habitat loss and fragmentation due to intensive forest management have been implicated in population declines, while other studies have suggested neutral or positive effects. In Romania, recent changes in forest management have shifted from extensive, selective logging to intensive clearcutting; this change provides the opportunity to assess the effects of harvesting on capercaillie numbers across a full range of forest management intensities, thereby addressing discrepancies in the literature. Across the Southern and Eastern Carpathian mountains from 2009–2011, we used spring counts of capercaillie males at leks to evaluate the impact of forest management, other human activities, and habitat at two spatial scales – stand (~2 ha) and landscape (~300 ha). At the landscape level, the proportion of forest clearcuts and intensity of tourism had significant negative effects on the number of capercaillie males in the lek. In contrast, low intensity selective logging had a positive effect at the local stand (lek) level. Large scale (landscape level) forest clear-cutting had a negative effect on the capercaillie population – areas comprised of clearcuts of 30% reduced male lek counts by 76%. The protection of intact mature and old-growth forests, and forest management practices that emulate natural disturbance processes are recommended to support habitat of this critical umbrella species and associated biodiversity.

1. Introduction

Over the past century, global declines in mature forested area (Hansen et al., 2013) and biodiversity related to habitat loss, fragmentation, and overexploitation are causing increased concern among natural resource managers and conservationists (Wilcove et al., 1998). Large-scale clear-cutting of forested landscapes has driven the vast majority of forest species losses (Lamberson and McKelvey, 1992; Wallenius et al., 2010) and much attention has been devoted to alternative harvest strategies and associated management to retain forest species within landscapes (e.g. Franklin and Johnson, 2012). In areas such as central Europe that historically have been heavily forested but now have limited and increasingly fewer areas of old-growth forest cover (Mackey et al., 2014), identifying management impacts and alternatives is a priority. Here, we use the capercaillie, *Tetrao urogallus*, to evaluate the effects of logging old forests on mating habitat selection. The capercaille is considered an umbrella species within the region and an indicator of structurally rich forest conditions (Suter et al., 2002). Capercaillie populations in central Europe have declined rapidly in recent decades (Storch, 2007a). Identifying

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forestry practices that may aid in maintaining viable population levels of this species within forested landscapes are vital to ensure their persistence in the landscape alongside many other species commonly represented in these habitat types.

Capercaillie inhabits forests of Eurasia, and they are associated with extensive natural, old-growth or young open canopy forests, characterized by high levels of structural heterogeneity, particularly, multistoried tree layers and abundant cover of ericaceous understory shrubs (Bollmann et al., 2005; Klaus et al., 1989; Storch, 2002; Suter et al., 2002). Because capercaillie is strongly associated with open canopy forest and has a relatively large home range, it is considered an indicator species for high biodiversity and protection of its habitat will benefit other old-growth forest species as well (Pakkala et al., 2003; Suter et al., 2002).

Lek sites, where males display in spring, are particularly vulnerable to disturbance by humans and may be readily abandoned, as is common with many species of grouse with this mating system (e.g. Hess and Beck, 2012; Klaus et al., 1989). Anthropogenic activities, especially the intensification of forest management, have resulted in the significant loss and fragmentation of suitable capercaillie habitat in many parts of western and central Europe (Storch, 2007a). In many European countries, capercaillie populations are now artificially maintained using release projects, specialized habitat management measures, or predation control (Klaus, 1997; Marshall and Edwards-Jones, 1998; Siano and Klaus, 2013; Storch, 2000). Capercaillie is a red-listed species in Annex I of the EU Birds Directive in most European countries, and it is a specific designated feature of many of the Natura 2000 sites (Storch, 2007a).

One of the remaining strongholds of capercaillie populations in central Europe is the Carpathian Mountains that stretch from the Czech Republic east to Ukraine and extend to southern Romania. The Carpathian Mountains possess one of the largest areas of old-growth and natural forests in Europe with thriving populations of brown bears (*Ursus arctos*), lynx (*Lynx lynx*), grey wolves (*Canis lupus*), european bison (*Bison bonasus*) (Veen et al., 2010), and, historically, a stable and self-sustainig capercaillie population. Historic land uses, such as grazing and selective logging, maintained habitat conditions suitable for capercaillie (Hancock et al., 2011; Klaus et al., 1989). However, management practices have changed in the last few decades, with more large scale clearcuts and associated landscape fragmentation taking place, mainly due to new post-communist forest restitution laws (privatization of forest lands) and increasing accessibility by new forest roads (Knorn et al., 2012a,b).

Habitat loss and fragmentation related to logging activities have been shown to negatively impact the reproductive success of capercaillie in boreal forests (Lakka and Kouki, 2009). Similarly, in western and central Europe, a decline of capercaillie populations also has been linked to habitat loss through fragmentation and logging (Storch, 2007a). In contrast, recent evidence from boreal forests indicates that the capercaillie is relatively tolerant to changes in forest management regimes and populations will persist in the long term, even in landscapes with large-scale clearcutting (Miettinen, 2009; Wegge and Rolstad, 2011). However, capercaillie distribution in boreal forests is continuous and not as fragmented as in other areas of Europe (Storch, 2007a), and boreal forest regeneration patterns and dynamics is different compared to temperate regions of Europe.

Given clear declines of capercaillie associated with intensification of forest management over the last two decades, the main objective of this study was to identify the most important predictors influencing capercaillie male numbers in the leks in the Southern and Eastern Carpathians. We focused on stand and landscape features surrounding lek centres where mating occurs because they are critically important for sustaining local populations (Miettinen et al., 2005; Picozzi et al., 1992; Saniga, 2003). Specifically, we were interested in how human land use, intensity of forest management, habitat fragmentation, and loss of suitable habitat affect capercaillie abundance at the display grounds. Outcomes from this study highlight threats to capercaillie and identify forest management practices compatible with conservation goals.

2. Methods

2.1. Study area

Across the Southern and Eastern Carpathians within Romanaia, we sampled forests of 11 separate mountains. The potential size of suitable habitats (mountain forests with elevation >1000 m above sea level) was estimated on 190,113 ha; total area of all studied lek centres (1 km radius around the lek centres) was 6594 ha. The climate of Romania ranges from temperate to continental, and cold winters and high precipitation are typical for mountainous areas. The mean winter temperature is −5.2 °C with mean winter precipitation of 355 mm, while mean summer temperature is 13.9 °C and summer precipitation of 1095 mm in the study area (Toader and Dumitr, 2005).

2.2. Capercaillie population in the study area

Based on hunting surveys across Romania, the total population of Capercaillie was estimated to be ∼10,000 birds as of 2007 (Storch, 2007b). During our the study period, hunting of capercaillie was legal in Romania; however, since 2012, hunting of capercaillie has been prohibited, although ongoing illegal hunting may still have serious effects on capercaillie populations in some regions. The lek centres studied were located at altitudes ranging from 1320 to 1722 m above sea level. The prevalent vegetation type was Norway spruce (*Picea abies* (L.) Karst.) forest (86%), mixed European larch (*Larix decidua* Mill.)-Norway spruce forest (9.5%), and mixed Norway spruce-Silver fir (*Abies alba* Mill.)-European beech forest (*Fagus sylvatica* L.) (4.5%).

2.3. History of forest management in the study area

The capercaillie habitats in the Carpathians are mostly high elevation natural forests with old-growth characteristics, such as large amounts of dead wood, elevated root plates, and multi-cohort open canopy stands (see the Appendix). Only 9% of the lek centres occurred in areas of naturally regenerated open canopy stands (∼60 years old) resulting from abandonment of grazing of montane pastures. In the past, all stands were difficult to access and forest management was predominantly selective single-tree or group logging made by the shepherds who used the surrounding mountain pastures during the summer (Huband et al., 2010). Forest management practices changed considerably in the studied area after the collapse of communism in 1989. New forest roads were built into formerly inaccessible areas and large areas of state forest were restituted to prior owners resulting in increased forest harvesting at large spatial scales (Griffiths et al., 2014; Knorn et al., 2012a,b). In addition, some forested areas were officially categorized as pastures, thus enabling owners to make large clearcuts without any control, and illegal logging has occurred during the post-communist era. Extensive clearcutting forestry has also occurred in protected areas, such as national parks. Based on remote sensing data (Landsat imagery; Table 1, Griffiths et al., 2014), in our study plots the mean percentage of clearcuts after 1990s in protected areas is higher (24.6%), compared to unprotected areas (16.4%). Based on the forest ownership

Table 1
Forest extent and losses in each study plot ($N = 21$, plot size = 314 ha) with mean values (italicized) representing subregions of the Southern and Eastern Carpathians in Romania 2009–2011. For every study plot the maximum number of capercaillie males lekking in the display ground (centre of the study plot) and maximum number of females recorded during the spring season are reported. The top portion of the table shows the values in study sites with no protection regulations while the bottom portion shows the protected study sites.

1985–1990		1990–2010		1990–2010	1990–2010	Conservation status	Male numbers	Female numbers
Clearcut (ha)	Forest (ha)	Clearcut (ha)	Forest (ha)	Clearcut (%)	Average forest loss			
0	314.1	12.96	301.14	−4.1	16.40%	No protected	7	5
0	239.85	6.3	234.54	−1.7			4	2
0	240.57	33.21	207.36	−10.6			2	2
3.06	304.65	178.47	129.24	−55.8			2	0
0	135.09	9.27	125.82	−3			3	1
0	283.32	45.81	238.23	−14.4			1	2
1.89	267.93	6.48	263.34	−1.5			3	3
1.26	291.42	108.18	184.5	−34			1	1
4.95	253.62	75.51	183.06	−22.5			1	1
1.24	*258.95*	*52.91*	*207.47*	*−16.4*				
21.78	165.69	19.62	167.85	0.7	21.14%	Protected	3	1
0	303.03	135.72	167.31	−43.2			4	2
9	237.42	3.6	242.82	1.7			1	1
1.44	281.34	123.57	159.21	−38.9			3	1
0	266.85	225.81	41.85	−71.6			1	1
0	212.22	119.97	92.61	−38.1			1	2
8.19	224.19	77.04	155.34	−21.9			2	1
0	277.65	5.67	272.88	−1.5			2	1
61.47	200.34	3.06	258.75	18.6			2	3
7.02	130.23	51.39	85.86	−14.1			2	1
17.01	297.36	132.48	181.89	−36.8			6	8
1.08	258.03	27.99	231.12	−8.6			9	4
10.58	*237.86*	*77.16*	*171.46*	*−21.14*				

data (Abrudan, 2012) in our study plots, 43% were private and 57% owned by state. For the whole of Romania (as of early 2013), over 4.4 million hectares of state, public, and private forest lands were administered by state and experimental forest districts, with a further 1.7 million hectares of forest land administered by private forest districts (Marinchescu et al., 2014). It is evident that changes in ownership have resulted in changes in forest management and structure across multiple scales (Griffiths et al., 2014; Knorn et al., 2012a,b)

2.4. Data sampling

2.4.1. Study design

Clearcutting has been widely documented to lead to local extirpation of capercaillie (Storch, 2007b). Our objective was not to document population declines, but rather to identify forest practices that would permit persistence of capercaillie. Therefore, we sampled forest conditions representing a range of no harvest to partial harvest within the known range of capercaillie. Using capercaillie distribution and density maps provided by the Forest Research and Management Institute of Romania (ICAS), localities with the highest capercaillie densities across 11 mountain ranges were intensively surveyd in a 1 km radius area (314 ha), which was considered to be the average territorial area used by capercaillie males during the lekking period (Storch, 1995). We identified 21 lek centres in Făgăraș ($n = 4$), Rodnei ($n = 4$), Harghita ($n = 3$), Maramureş ($n = 3$) Piatra Craiului ($n = 1$), Bucegi ($n = 1$), Diham ($n = 1$), Prisciu ($n = 1$), Hâşmaş ($n = 1$), Călimani ($n = 1$), and Piatra Mare ($n = 1$) (Fig. 1.).

2.4.2. Data collection

Capercaillie males gather in lek centres to display and compete for females; within display grounds, males establish display territories spaced ~50 m apart. Counting of males at lek centres is a widely used technique across many species of grouse to monitor population trends (Miettinen et al., 2005; Picozzi et al., 1992; Saniga, 2003). During the daytime period, they remain within a radius of approximately 1 km of the lek centre (Storch, 1995). Plot locations, defined by lek centres, were determined by the position of the alpha capercaillie male; GPS coordinates recorded after birds finished displaying during each visit. These lek centres are usually located in the same sites annually and may be used for several decades (Klaus et al., 1989). Lek surveys were conducted from March to May during 2009–2011 with two visits per season; the maximum counts were used in the analyses. Surveys were performed from 03:00 to 09:00, and all observed or heard capercaillie males were recorded. During the day we returned to look for signs and display stances, which helped to clarify the capercaillie male numbers in the leks.

2.4.3. Environmental data and scale consideration

To understand drivers of capercaillie abundance we collected data on three principal types of data: habitat, forest management, and human activity, excluding forest management activities (Table A1). Data were restricted to stand scale and landscape scale; stand scale measurements were defined as an 80 m radius circular plot (2.1 ha), and landscape scale as a 1 km radius area (314 ha) to evaluate broader scales impacts, such as forest management and intensity of tourism. Landscape scale considerations were also defined by distance based variables for habitat or human activity variables (e.g. distance to the closest building, water spring, etc.).

2.4.4. Habitat measurements

Habitat characteristics were measured in the lek centres during the summer months. We used an extensive list of site characteristics to evaluate possible lek centre preferences in the under-researched part of the species distribution in Southern and Eastern Carpathians. The variables recorded included topography, surface type, main canopy characteristics, understorey, ground vegetation, dead wood, soil, habitat use by large herbivores, human land use, type of forest management, and the landscape; for a complete listing, see Table A1.

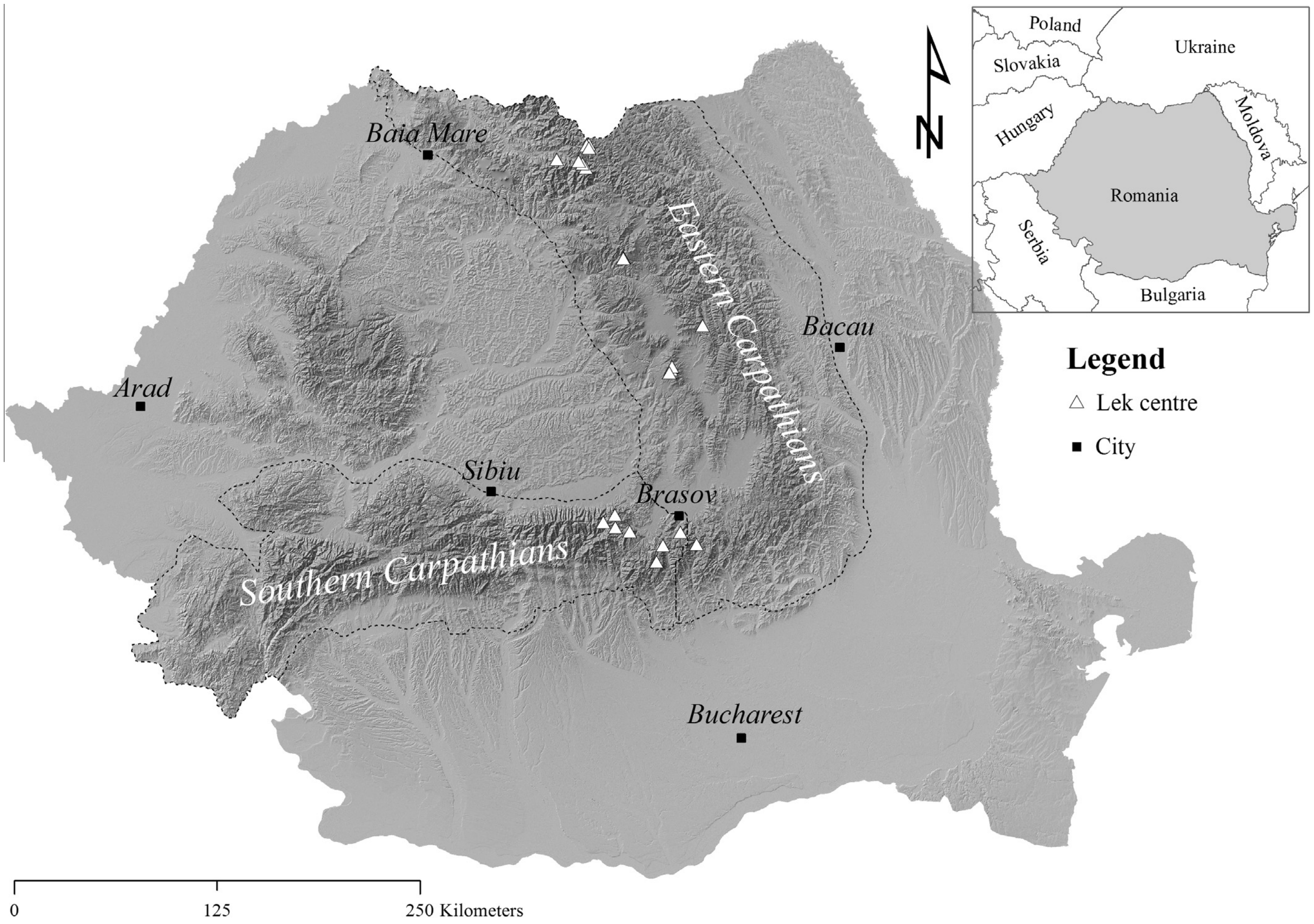

Fig. 1. Locations of the studied lek centres.

2.4.5. Forest management

Forest management activities were evaluated at the stand and landscape levels. At the stand scale, selective logging intensity was measured based on percent canopy removal and presence of forest roads within 80 m plot radius (2.1 ha). At the landscape scale, clearcut estimates were based on the proportion of the 1 km radius (314 ha) plot area that was clearcut within the previous five years (since 2005) and larger than one ha. A detailed list of variables and an explanation of variable scales are provided in Table A1 and Table 2, respectively.

2.4.6. Impact of (non-logging) human activity

To evaluate human land use intensity, activities were defined based on maps and direct enquiries of local and regional experts (administrators of national and natural parks, forestry administrators, and local shepherds), similar to Rösner et al. (2013). Every activity was classified on a scale from 0 to 5 to define intensity, with '0' being the least intensive and '5' being the most intensive (Table 2). The tourist activity was evaluated for the peak tourist period that included weekends during the winter/spring period; it was based on the number of tourists who visited the 314 ha plot.

Table 2
Detailed description of the scales of measured variables.

	0	1	2	3	4	5
Intensity of tourism (314 ha plot)	No tourism	<10 person/day	10–50 people/day	50–100 people/day	100–150 people/day	>150 people/day
Selective logging intensity (2.1 ha plot)	Non-managed forest	Presence of a forest road, no cuttings in the lek centre	Cuttings in the lek centre <1%	Cuttings 1–15%	Cuttings 15–30%	Cuttings >30%
Intensity of grazing (314 ha plot)	No grazing	Grazing of <15 standard livestock units irregularly	Grazing of 15–150 livestock units irregularly	Grazing <15 livestock units regularly	Grazing of 15–150 livestock units regularly	More than 150 livestock units
Intensity of hunting (314 ha plot)	No hunting	Legal hunting of 1 capercaillie per 15 years	Legal hunting of 1 capercaillie per 10 years	Legal hunting of 1 capercaillie per 5 years	Legal hunting of more than 1 capercaillie per 5 years	Illegal hunting
Spatial distribution of vegetation clustering (ID) (2.1 ha plot)	Homogenic matrix	Obscure clusters	Small clear clusters	Large clear clusters	Small orientated clusters	Large orientated clusters

The number of tourists was based on information from administrators of national and natural parks and tourist centre administrators (e.g. ski-lift companies, mountain cottages owners). Distance-based variables, such as distance to the closest buildings, and distance to closest road, were also used to evaluate human activity and presence.

2.5. Statistical analyses

Because a large numbers of explanatory variables were measured for a relatively small sample size ($n = 21$), the number of explanatory variables was reduced prior to analyses to avoid problems with collinearity (Dormann et al., 2013). Principal component analysis (PCA) on correlation matrices of landscape characteristics (12 variables), the cover of individual species in the tree layer (7 variables), the shrub layer (11 variables), and the herb layer (27 variables) was used to reduce the dimensionality. The broken stick model was used to identify the number of non-trivial principal components (Jackson, 1993). This selection process resulted in one principal component (PC) for the landscape characteristics, two PCs for the tree layer, two PCs for the shrub layer, and four PCs for the herb layer (see Table A2).

The relationships between capercaillie numbers and environmental characteristics were analysed using generalized linear models (GLM; McCullagh and Nelder, 1989). In addition to the latent variables described above, the remaining variables (see Tables A1 and A2) were then combined to form a list of candidate predictors. An exhaustive best-subset regression procedure was employed in search of the most parsimonious model (McLeod and Xu, 2009). Poisson distribution and logarithmic link-function were used within GLMs to relate numbers of males in the lek centres with the predictors. The Bayesian information criterion (BIC) was used for model selection. Due to the limiting number of degrees of freedom, only those models with a maximum of 5 explanatory variables were considered in the analyses. Parameters of the final model were tested using likelihood ratio tests (Crawley, 2007), and the model fit was assessed using McFadden's (pseudo) determination coefficient (McFadden, 1973). Standardized regression coefficients were calculated to facilitate direct comparisons across significant predictors, regardless of differences in the scale of the predictors. The relative importance of explanatory variables on capercaillie abundance was assessed by variation partitioning (Borcard et al., 1992). The deviance explained by each variable was expressed as a percentage of the total variation, represented by the deviance of a null model. Partial regression plots and effect plots were constructed to depict partial relationships in the final model (Fox, 2001). Partial regression plots allowed us to visualize the effect of each predictor after adjusting for all the other predictors in the final model. Effect plots display fit for each partial relationship while the other predictors are fixed at mean values. All analyses were performed in R (R Development Core Team 2010) using the *bestglm* (McLeod and Xu, 2011) and *vegan* (Oksanen et al., 2011) packages.

3. Results

Active capercaillie leks were not found within recent clearcuts and they were not detected where clearcutting exceeded 62% of the surrounding landscape (314 ha) (Fig. A1). Almost all lek centres were situated in forests with old-growth characteristics and limited anthropogenic influence (see Table A1). Only two lek centres were situated in younger forests, but these were in fact abandoned pastures and not clearcut areas. The average forest cover in the 314 ha plot was 187 ha (60%), with a range between 79 ha (25%) and 301 ha (96%); the remaining areas were covered by mountain pastures or clearcuts. The average number of capercaillie males counted in the lek centres was 2.9 (SD = 2.15), and the average number of females was 2 (SD = 1.8) (see Table 1.)

The best model to explain the number of male capercaillie at lek centres contained three variables: the proportion of clearcuts at the landscape scale and intensity of tourism negatively influenced male capercaillie numbers, but selective logging intensity at the stand scale had a positive effect (Table 3). The overall model significantly explained 62.8% of the deviance ($\chi^2_{(3)} = 17.27$, $p < 0.001$), and partial regression plots indicated the model provided a reasonable fit to the data (Fig. 2a–c). Based on standardized regression coefficients, the effect size of landscape scale clearcuts was largest. Variation partitioning indicated that >37% of the deviance in male numbers could be explained by the proportion of clearcuts; holding the effect of other variables constant, clearcuts of 30% reduced male lek counts by more than four times (Fig. 2d). The deviance attributable to tourism and selective logging intensity amounted to 31% and 20%, respectively. Differences between no (0) and intensive (5) tourism and selective logging indicated a 4.4-fold decrease and a 3.7-fold increase in male lek counts, respectively, when other factors were held constant (Fig. 2e–f).

4. Discussion

Of all the studied variables, three anthropogenic factors had the highest influence on capercaillie numbers: the proportion of clearcuts, intensity of tourism, and selective logging. Romania has experienced massive socio-economic and institutional change over the past 25 years (Knorn et al., 2012a,b) that has impacted ownership and human land use, such as forestry and tourism. Negative effects of emerging land use (increased forest exploitation and tourism) were evident, while historic forest practices were positively related to capercaillie numbers. The average capercaillie male numbers per lek were similar to numbers detected in other regions, where long term declining population trends were detected (e.g. Zawadzki and Zawadzka, 2012; Saniga, 2012).

4.1. Capercaillie and forest harvesting

The effects of forest harvesting on capercaillies depend on the intensity and extent of harvesting practices (Klaus, 1991). The selective logging intensity in the lek centres had a positive effect on capercaillie male numbers. In dense managed stands, selective logging reduces canopy cover in a manner similar to small-scale natural disturbance processes, which makes the forest canopy more open and increases structural heterogeneity of the stand (Broome et al., 2014; MacMillan and Marshall, 2004). Multistoried tree layers with gaps and abundant cover of ericaceous understory shrubs may improve summer forage and cover from predators for capercaillies. Although our results did not show a significant relationship between number of capercaillie males and bilberry cover, the capercaillie habitats typically contained extensive patches of bilberry; based on other studies, we do know

Table 3

Parameters of the final GLM model showing relationships between the number of capercaillie males in the lek centres and the proportion of clearcuts, intensity of tourism, and intensity of forest management. Standardized regression coefficients (β), regression coefficients (b), standard errors (se), test statistics (χ) and probabilities (p) are displayed.

Parameter	β	b	Se	χ	p
Intercept		2.036	0.187	44.54	<0.001
Proportion of clearcuts	−0.41	−0.048	0.009	14.32	<0.001
Intensity of tourism	−0.22	−0.296	0.071	9.86	0.002
Selective logging intensity	0.24	0.262	0.083	5.35	0.021

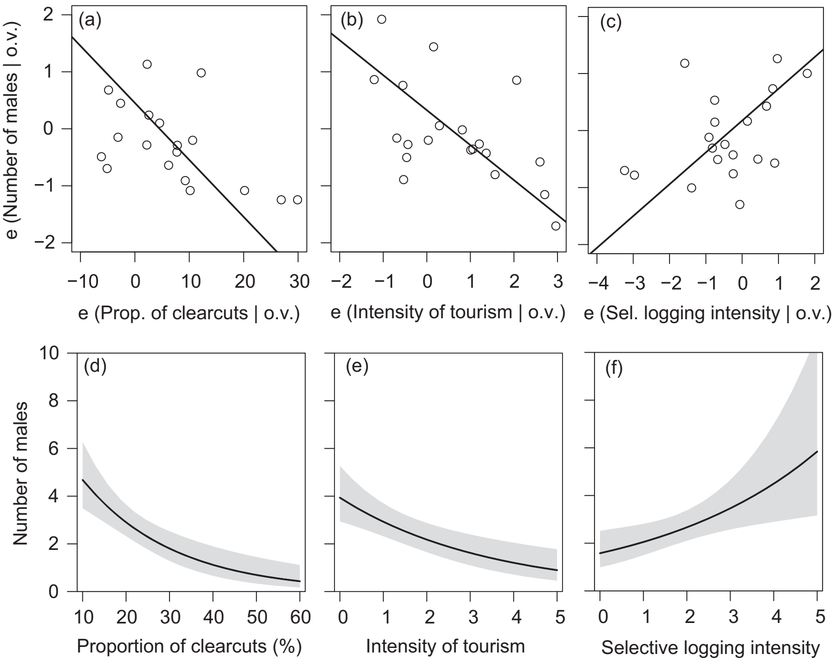

Fig. 2. Partial regression plots (a, b, c) and effect plots (d, e, f) demonstrating the multivariate relationship between number of males in the lek centres and the proportion of clearcuts (a, d), intensity of tourism (b, e) and selective logging intensity (c, f). Lines represent partial regression slopes (a, b, c) and partial fitted relationships holding the other variables (o.v.) constant at their means (d, e, f). Ninety-five percent confidence intervals are shown in grey.

that bilberry is an important habitat component (eg. Wegge and Rolstad, 2011; Hancock et al., 2011; Storch, 2002, 1993).

At the landscape scale, the proportion of clearcuts surrounding the lek centres had an exponential negative effect on capercaillie numbers (Fig. 2d), as suitable habitats are lost and fragmented by clearcuts. The relationship between habitat fragmentation and extinction has been demonstrated to be highly non-linear (Fahrig, 2003), thus, the presence of clearcuts also has broader implications to population and metapopulation dynamics throughout the region.

Our results are in contrast with the findings of studies conducted in the boreal zone (Miettinen, 2009; Wegge and Rolstad, 2011); they observed that capercaillie were tolerant to clearcutting across the landscape because capercaillie were also able to use open canopy middle-aged plantations (>30 years old) with bilberry ground cover. The findings of these studies cannot necessarily be applied to central Europe or the Southern and Eastern Carpathians, which are all outside the boreal zone. Capercaillie distribution in central Europe is very fragmented compared to the boreal zone; capercaillie persist here in patchy populations embedded in a mountainous landscape (Storch, 2007a). In fragmented conditions of central Europe it is very difficult to maintain viable capercaillie populations, which require ca. 250 km^2 and an estimated 470 interacting capercaillie individuals (Grimm and Storch, 2000). Inter-patch dispersal is very important for the persistence of capercaillie, thus, high habitat connectivity is important for metapopulation dynamics. In the Carpathians, suitable capercaillie habitats are a mere small 'habitat band' of coniferous dominated forest situated between mountaintops and the deciduous forests of lower altitudes. In case of intensive clearcutting, alternative forest nearby which represents suitable capercaillie habitat is thereby naturally limited. When stepping stones are lost and habitat connectivity is disrupted by clearcuts on large spatial scales, as in this study, migration of individuals between populations could be severely limited and population persistence may be threatened because small isolated populations are unlikely to survive (Segelbacher et al., 2003). These factors has lead to extinction debt in other small and isolated metapopulations (Pullin, 2002). In addition, the typical management practices in central Europe do not enable creation of open canopy forest structure suitable as capercaillie habitat (Bollmann et al., 2005). Plantation establishment after clearcutting is mandatory in central Europe; the result is very dense forest canopies with very little ground vegetation, particularly critical bilberry cover (*Vaccinium myrtillus* L.), which provides food for adults, invertebrates for chicks, and hiding and thermal cover (Hancock et al., 2011; Storch, 1993).

The negative landscape level effect of large clearcuts on capercaillie numbers was significant and outweighed the positive effects of selective logging intensity. These clearcuts cover large areas and might almost completely remove the narrow spruce forest vegetation belt in some areas. Unlike smaller clearcut patch harvesting that creates fine grain forest fragmentation that may be suitable for capercaillie in the boreal forests (Sirkiä et al., 2011), large clearcuts cause long-term loss of habitat with no alternative options of suitable habitats in the surrounding forests where the birds could migrate. Increased harvesting using clearcuts practices are largely related to restitution laws implemented after the collapse of communism in 1989; forest harvesting increased sharply in two waves around 1995 and 2005 (Knorn et al., 2012a). Clearcuts recorded in our study (younger than 5 years) in the capercaillie habitats coincide with the second wave of harvesting after 2005. The area of suitable habitats is declining and becoming more fragmented as a result of large-scale clearcuts in the Carpathians, with little differentiation in forest management practices between protected or non protected areas (Knorn et al., 2012a).

4.2. Capercaillie and tourism

The negative effect of intensive tourism (e.g. ski resorts) on capercaillie and other bird populations has been reported in many regions (e.g. Moss et al., 2014; Rösner et al., 2013; Thiel et al., 2011). Human disturbance may influence metapopulation dynamics and contribute to genetic impoverishment in small populations (Moss et al., 2014). For example, collisions with ski-lift cables may increase capercaillie mortality. Intensive tourism can negatively influence brood success because it increases levels of the stress hormone corticosterone, which influences reproduction and survival (Thiel et al., 2011). Also, areas frequented by people have increased carrying capacity for a family of avian predators – the *Corvidae*; ravens, crows and jays favour human inhabited areas (Storch and Leidenberger, 2003). Recent increased use of snowmobiles and off-road vehicles concentrated near tourist recreation areas may have the most negative effects, as they may cause serious yearlong disturbances to the capercaillie in many regions. To offset the effects of tourism on capercaillie populations, sufficiently large habitat patches that provide good hiding cover and buffers from touristic areas and roads should be established and maintained (Newsome and Moore, 2012). Increased use of selective harvesting can help to achieve this. Further, by planting dense vegetation bordering frequented tourist paths, the probability of people leaving marked trails and disturbing capercaillies would be reduced (Coppes and Braunisch, 2013).

4.3. Old growth forests as refuge

Old-growth forests are the primary habitats for capercaillies (Klaus et al., 1989) and it was shown already for the Carpathians as the main capercaillie habitat type (Saniga, 2003). The habitat characteristics of most of the studied lek centres were typical of old-growth forests – large amounts of dead wood, elevated root plates, multi-cohort open canopy stands, etc. (Table A1). The structure of these forests is a result of natural disturbance regimes characterized by windthrows and bark beetle outbreaks, which are usually infrequent, moderate- to high-severity disturbances that influence forest structure across all spatial scales – tree, stand, and landscape (Svoboda et al., 2014; Trotsiuk et al., 2014). These disturbances create canopy gaps and forest edges of different sizes (Fraver and White, 2005), which provides suitable habitats for capercaillie. These types of stands are currently just a small fraction of the landscape in central Europe (Wesolowski, 2005), thus, they play a key role for the preservation of capercaillie populations and many other species in the Carpathians. There has been a clear trend in the large-scale destruction of mountain spruce forests, including old-growth and natural forests across the whole Carpathian region over the past few decades (Griffiths et al., 2014; Knorn et al., 2012a,b; Kuemmerle et al., 2009, 2007), and the natural mountain forest community is endangered. The long-term survival of the species is therefore reliant on the viability of core areas to serve as refuges.

5. Conclusions and implications for forest management

Our study indicates that extensive human land use, such as low intensity selection harvesting, can have positive effects on capercaillie, but large-scale clearcutting and intensive tourism can also have very negative effects. Measures to conserve the umbrella species capercaillie will benefit a wide range of other forest species and better preserve a wide range of ecosystem functions and services (Balvanera et al., 2006; Suter et al., 2002). Our results indicate that even protected areas do not ensure the protection of threatened species and their habitats in the Carpathian region (Table 1). This can only be changed if the priority in protected areas is the conservation of biodiversity and prioritization of non-extractive ecosystem services rather than timber production as in typical commercial forests.

Conservation and forest management goals should be based on a multi-scale approach. Commercial forest management in relevant areas should be modified to emulate natural disturbance processes across multiple scales. With single-tree selection, group selection, conversion of spruce to mixed species, increasing large snag densities, and creating a multi-layered canopy at the stand level, foresters can accelerate the development of suitable natural forest habitats (Franklin et al., 2002). Sufficient areas (cca 250 km^2) of quality habitat are necessary foundations for viable capercaillie populations (Grimm and Storch, 2000), thus, management planning for viable populations should be in accordance with broader relationships at the landscape scale to ensure a sufficiently-sized mosaic of suitable habitats and connectivity between habitat patches (Graf et al., 2009; Segelbacher et al., 2003). To ensure the long-term survival of capercaillie populations in the Carpathians, it is necessary to conduct further assessments of the suitability of existing capercaillie habitats (e.g. create a habitat suitability model) and identify the optimal extent of suitable habitat and its connectivity (Braunisch and Suchant, 2008). The habitat suitability model should be adapted regionally, because species – habitat relationships may differ between regions, due to different site conditions, vegetation types, and successional processes (Graf et al., 2005), as exemplified by differences in capercaillie habitat use in Norway and central Europe. Management at the landscape scale should include the protection of old-growth forests, the restriction of fragmentation and large-scale deforestation, to ensure a more ecologically sustainable forestry model in central Europe.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.07.001.

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5.3 Tejkal M., Mikoláš M., Kuemmerle T., Griffiths P., Svoboda M., Hlásny T., Leitão P.J. & Morrisey R.C. Forest management impacts on capercaillie (Tetrao urogallus) habitat distribution and connectivity in the Carpathians (minor revision in Landscape Ecology).

Forest management impacts on capercaillie (*Tetrao urogallus*) habitat distribution and connectivity in the Carpathians

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ABSTRACT

Context

Distribution and connectivity of suitable habitat for species of conservation concern is critical for effective conservation planning. Capercaillie (*Tetrao urogallus*), an umbrella species for biodiversity conservation, is increasingly threatened because of habitat fragmentation.

Objective

We assessed the impact of drastic changes in forest management in the Carpathian Mountains, a major stronghold of capercaillie in Europe, on habitat distribution and functional connectivity.

Methods

We used field data surveys with a forest disturbance dataset for 1985 – 2010 to map habitat suitability, and we used graph theory to analyse habitat connectivity.

Results

Climate, topography, forest proportion and fragmentation, and the distance to roads and settlements best identified capercaillie presence. Suitable habitat area was 7,510 km^2 in 1985; by 2010, clear-cutting had reduced that area by 1,110 km^2. More suitable habitat was lost inside protected areas (571 km^2) than outside (413 km^2). Habitat loss of 15 % reduced functional connectivity by 33% since 1985.

Conclusions

Forest management, particularly the large-scale clear-cutting and salvage logging in the 1990s, have substantially diminished and fragmented suitable capercaillie habitat, regardless of the status of forest protection. Consequently, larger areas with suitable habitat are now isolated and many patches are too small to sustain viable populations. Given that capercaillie protection would benefit many other species, including old-growth specialists and large carnivores, conservation actions to halt the loss of capercaillie habitat is urgently needed. We recommend adopting policies to better protect natural forests, limiting large-scale clear-cutting and salvage logging, implementing nature-based forest management, and restricting road building to reduce forest fragmentation.

Keywords

Forest management, clear-cutting, Carpathian Ecoregion, connectivity, forest disturbance, habitat fragmentation, habitat modelling, umbrella species.

INTRODUCTION

Forests harbour most of the global terrestrial biodiversity, and deforestation and forest management continue to exert pressure on forest biodiversity in many parts of the globe (Gustafsson et al. 2012). In Europe's temperate zone, forest extent has been increasing lately (FAO, 2010), but so has harvesting intensity (UNECE/ and FAO 2000; Böttcher et al. 2012; Levers et al. 2014) and rates of natural disturbances (Schelhaas and Nabuurs 2003; Seidl et al. 2014). Harvesting and large-scale natural disturbances mainly affect mature stands, thus area of older forests are declining despite total forest area inceases (Wallenius et al. 2010). Older forests, particularly old-growth forests, foster high and unique biodiversity, including many endemics, and species of conservation concern (Moning and Müller 2009; Wallenius et al. 2010). Anthropogenic and natural disturbances thus threaten species that depend on mature or old-growth forests (McNeely 1994), as well as many species beyond old-growth forest boundaries (Wilcove et al. 1998; Wallenius et al. 2010). However, the effects of increasing natural and anthropogenic forest disturbances on biodiversity remains poorly understood.

Eastern Europe still possesses extensive areas of natural and old-growth forests, forest types that were converted to intensively managed monocultures in much of Western Europe in the past (Johann 2006; Paillet et al. 2010). As result, Eastern Europe still harbors much forest biodiversity that is of great conservation concern for Europe as a whole, some of it endemic to Eastern Europe (UNEP 2007). Within Eastern Europe, the Carpathian Mountains constitute one of the largest remaining continuous forest ecosystems in Europe (Gurung et al. 2009) and they harbor most of Europe's remaining temperate old-growth and natural forests (Grodzińska et al. 2004; Kuemmerle et al. 2010), thus they are of outstanding conservation value.

Social and political changes that followed the breakdown of socialism in 1990 triggered major changes in Eastern Europe's forest sectors, including forest management approaches (Baumann et al. 2011; Simpson and Prots 2012). In many regions, this has led to a transition from clear-cutting to close-to-nature forestry and a growing interest in the multiple ecosystem services forests provide. However, this period has also been characterized by widespread clear-cutting following ownership changes and privatization, illegal logging, and improper disturbance management following windthrows and insect outbreaks, all of which have disproportionally affected older forests (Schulze 2002; Main-Knorn et al. 2009; Knorn et al. 2012a,b; Griffiths et al. 2012, 2014). Moreover, although the protected area network in the Carpathians has increased substantially since 1990, many protected areas do allow large-scale harvesting inside their boundaries, some areas were logged illegally, and, in many cases, extensive harvesting occurred prior to their designation as protected areas (Kuemmerle et al. 2009; Knorn et al. 2012b). Current rates of natural and old-growth forest loss would further increase pressure on forest biodiversity (Brockerhoff et al. 2008), thus understanding how old-growth forest losses affect the habitat availability and connectivity of species of conservation concern at the landscape scale is important for effective conservation planning (Fahrig 2003; Uezu et al. 2005; Laita et al. 2011; Helm 2015).

To evaluate landscape-level impacts of forest management on biodiversity, we selected the endangered capercaillie (*Tetrao urogallus* L.) as a surrogate for forest biodiversity of old-growth forests (Saniga et al. 2003). Capercaillie, the biggest bird of the grouse family, are associated with natural, open-canopy forests with rich ground vegetation cover (Graf et al. 2005; Graf et al. 2007), habiat requirements shared by many species associated with natural and older forests (Suter et al. 2002; Pakkala et al. 2003). Capercaillie are highly sensitive to habitat loss, disturbance, and fragmentation (Mikoláš et al. 2015). Viable capercaillie populations require a minimum of 250-500 km^2 of connected, suitable habitat with 470 communicating individuals (Grimm and Storch 2000; Braunisch and Suchant 2013), thus functional connectivity beteween habitat patches is critical to the persistence of capercaillie. Capercaillie tend to move only over short distances, rarely exceeding 10 km, with an average dispersal distance of less than 3 km (Hjeljord et al. 2000; Storch 2000), thus, large-scale clear-cutting has the potential to substantially affect connectivity among capercaillie populations. Given their habitat requirements and dispersal patterns, capercaillie are an excellent umbrella species whose conservation would benefit many other species of conservation concern (Suter et al. 2002; Pakkala et al.2003), and they are an ideal model species to assess the effects of habitat loss and fragmentation on functional connectivity across broader scales (Storch 2007; Pascual-Hortal and Saura 2008).

The Carpathian Mountains are occupied by the second largest capercaillie population in the Europe (i.e., outside Scandinavia and Russia) numbering about ~11,000 individuals. All other capercaillie populations outside of the Scandinavia, Russia and Alps (e.g., in the Black Forest, Bavarian Forest, Cantabrian Mountains) are much smaller in size, typically not exceeding 1,000 individuals (Storch et al. 2007). Therefore, the Carpathians are one of the remaining strongholds of capercaillie in Europe, yet the effects of recent intensifying forest harvesting on capercaillie habitat availability and connectivity have not been studied.

Habitat suitability models are widely used to guide capercaillie conservation planning (e.g. Storch 2002; Bollmann et al. 2005; Graf et al. 2005; Braunisch and Suchant 2008), but existing models from different European regions often diverge as a result of different environmental conditions, data sources, spatial scale, or resolution of the modelling exercise. For example, the major determinant of capercaillie habitat selection in the German Alps was bilberry (*Vaccinium myrtillus*, L.) cover (Storch 1993), but, in the nearby Swiss Alps, canopy cover was more important than bilberry cover (Bollmann et al. 2005; Graf et al. 2009). Similarly, in the Black Forest in Germany, habitat suitability corresponded significantly with soil conditions (Braunisch and Suchant 2008), whereas in the Bavarian and Bohemian forests, elevation, deadwood, clear-cut areas, and young coniferous forest were important predictors of capercaillie habitat (Teuscher et al. 2013). In the Spanish Cantabrian Mountains, the proportion of oak forest, which does not occur in other areas inhabited by capercaille, was an important variable explainig habitat selection (Bañuelos et al. 2008). Given these diverse resutls, more assessments of capercaillie habitat are needed, particularly for areas such as the Carpathians where habitat suitability has not been quantified, and evaluations should occur at broad spatial scales and accompanied by connectivity assessments, particularly in fragmented landscapes characterized by low connectivity between habitat patches (Segelbacher et al. 2003; Quevedo et al. 2006).

We used species distribution models, connectivity analyses, and a satellite-based assessment of forest harvesting to evaluate habitat changes for capercaillie across the enire Carpathian Mountains for the period 1985 to 2010. Specifically, we addressed three main research questions:

(1) What factors characterize capercaillie habitat in the Carpathians?

(2) How did spatial patterns of suitable capercaillie habitat in the Carpathians change between 1985 and 2010?

(3) How has forest disturbance affected capercaillie habitat distribution and connectivity for the period of 1985 to 2010?

METHODS

Study area

Our study area encompassed the entire Carpathian Ecoregion (CERI 2001) in the Czech Republic, Hungary, Poland, Romania, Slovakia, and Ukraine, covering ca. 220,400 km^2 (Fig. 3). Elevation ranged from 100 m to 2,655 m above sea level (a.s.l.). The climate is temperate-continental (UNEP 2007) with lower temperatures and higher rainfall at higher altitudes and in the north. Summer precipitation ranges from 600 mm/year in the lowest parts to over 2,000 mm/year at higher elevations, and annual average temperatures range from -2 °C to 10 °C (UNEP 2007). Broadleaved forests dominate forests the lower altitudes of the Carpathians; they are composed of mostly Europen beech (*Fagus sylvatica* L.) mixed with European hornbeam (*Carpinus betulus* L.), pedunculate oak (*Quercus robur* L.), sycamore maple (*Acer pseudoplatanus* L.), and European ash (*Fraxinus excelsior* L.). Forests at higher altitudes in the lower mountain forest zone are predominantly mixed forests composed of mainly European beech mixed with silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.). Spruce forests dominate higher mountain forest zones with admixtures of silver fir, stone pine (*Pinus cembra* L.), or European larch (*Larix decidua* Mill.) in some regions. At the highest elevations, sub-alpine and oro-Mediterranean forests, scrub and dwarf shrub communities occur (Bohn et al. 2004). The timberline varies from approximately 1,600 m in the northwestern Carpathians to about 1,850 m in the Southern Carpathians.

Forest management in the Carpathians has changed substantially since 1990. The use of clearcuts for harvesting timber has declined considerably in some regions, particularly in the Western Carpathians (e.g., in Slovakia from 85 % to 29 %; Green Report, Ministry of Agriculture of the Slovak Republic, 2010), where close-to-nature forestry practises are increasingly used as legislation to limit the extent of cleacutting was adopted. However, forest restitution has also resulted in unsustainable forest management in some regions, particularly in Ukraine, Romania, and Serbia, and salvage logging has increased across the entire Carpathians (Merganičová et al. 2013). Salvage logging is typically employed when natural disturbances (e.g., insect, windthrows) occur; field surveys indicate that naturally disturbed forests are left with no intervention after disturbance in less than 10% of all disturbances (Text S2, Fig S1). Forest cover loss in the Carpathians is primarily attributable to logging, either planned timber harvesting, salvage logging, or illegal logging (e.g. Kuemmerle et al. 2009; Knorn et al. 2012a,b; Griffiths et al. 2014).

Species data

To assess the current capercaillie population sizes for the Carpathians, we summarized data for the year 2015 from capercaillie experts responsible for national censuses. Capercaillie populations of countries within the Carpathian range were estimated to be ~9,000 birds in Romania (O. Ionescu, pers. comm.), ~850 birds in Slovakia (Mikoláš, unpubl.), ~500 birds in Ukraine (A.-T. Bashta, pers. comm.), ~300 birds in Poland (Z. Zurek pers. comm.), and ~20 birds in the Czech Republic (V. Tomasek, pers. comm.).

We also collected capercaillie occurrence data in four field seasons between 2010 and 2013. Details regarding the sampling design are provided in Suppelemtary Material (Text S1, Table S1). In total, we collected 447 occurrence points, which we filtered using a minimum distance of 300 m between presence localities points (i.e., average daily relocation distance of capercaillie; Eliassen and Wegge 2007) to reduce spatial autocorrelation and pseudo-replication. In total, 395 presence points were retained for our capercaillie habitat suitability model, covering an elevation span of 750 m to 1,950 m. Capercaillie were predominantly found in coniferous forests (n=296), particularly Norway spruce stands (n=283), as well as mixed European larch - Norway spruce stands (n=5), Stone pine - Norway spruce - larch stands (n=8), mixed Norway spruce - Silver fir -European beech forest stands (n=31), and beech-fir forests (n=20). Some samples were also found on pastures (n=15), transitional shrubland (n=14), heathlands (n=11), and in natural grasslands (n=8).

Predictor variables

For our habitat suitability model, we initially selected variables that influenced capercaillie in previous studies (Graf et al. 2005; Braunisch and Suchant 2007) and that were available for the entire Carpathians. We checked for collinearity among predictors and if candidate variables had a Pearson correlation coefficient > 0.7 (Dormann et al. 2013), we retained only the variables deemed to be more ecologically relevant. Our full model included nine variables, grouped into four categories (climate, topography, land cover, and human disturbance; Table 1). All variables were generated for a target grid of 100 x 100 m (1 ha in size) and re-projected to the Lambert Azimuthal Equal Area projection.

Climate variables included average annual temperature and precipitation from the WorldClim dataset (Hijmans et al. 2005). For topography, we calculated a terrain ruggedness index (Sappington et al. 2007); we did not include elevation because of high collinearity with our climate variables, and because vegetation belts change markedly with latitude in the study area. Land cover contained cropland, grassland, settlements, and forest and was classified from region-wide, radiometrically consistent, and cloud-free Landsat image composites (30 m resolution, Griffiths et al. 2013); each 1 ha grid cell was classified as the dominant land cover type. Based on this map, we derived the Euclidean distance to cropland and grassland. To assess forest fragmentation, we used morphological image segmentation (Soille and Vogt 2008; Vogt 2015) to categorize each forest pixel as “core” (i.e., only forest neighbors), “edge”, “perforated” (i.e., edge inside larger forest patches), “islet” (i.e., patches consisting of edge forest only) forest, or “background” (i.e., non forest) using a 100-m edge width. We also included the proportion of deciduous, coniferous, and mixed forest cover within each cell (Griffiths et al. 2014). We calculated Euclidean distance to major roads, railways, and settlements to evaluate the role of human disturbance. Human settlements were mapped within a 30 m x 30 m grid within Griffiths et al. (2013) study. All variables were prepared and analysed in ArcGIS 10.2 (ESRI Inc. USA).

Habitat suitability models

To map capercaillie habitat suitability across the Carpathians, we used maximum entropy modeling (MaxEnt) to accommodate our presence-only dataset (MaxEnt, Phillips et al. 2006; Elith et al. 2011). MaxEnt is widely considered as one of the most powerful presence-only species distribution models (Elith et al. 2011; Warren and Seifert 2011); it involves a machine-learning approach based on contrasting the distributions of environmental variables (e.g., climate, topography, land cover) at the presence locations with those at randomly chosen background (i.e., pseudo-absence) locations (Phillips et al.2006; Phillips and Dudik 2008). MaxEnt thus estimates species' distributions given the constraint that the expected value of each environmental variable matches its empirical average derived from the occurrence points (Elith et al. 2011). We used the freely available software Maxent (ver. 3.3.3k; http://www.cs.princeton.edu/~schapire/maxent).

To assess model robustness, we used 10-fold cross-validation with a maximum of 2,000 iterations. We used a randomly selected background sample of 10,000 points. Because our field surveys did not cover all areas in the Carpathians, we restricted background point selection (Phillips and Dudik 2008; Merow et al. 2013) and allowed points only from areas above the minimum elevation (>600 m) where capercaillie were detected in the Carpathians (Saniga 2002), which covered 33% of our study area. Other measures to avoid over-fitting the model included the default regularization (Phillips and Dudik 2008), and using only linear, quadratic, and hinge features (Merow et al. 2013).

To evaluate model fit, we used the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Phillips et al. 2006; Elith et al. 2011). This threshold-independent metric measures the ability of the model to distinguish between true presences and absences (Hanley and McNeil 1982). The AUC metric ranges from 0 to 1, where a score of 1 represents a perfect fit, and values above 0.5 indicate a better fit than a random model. We also assessed variable importance using single-variable models as well as a jackknife procedure that tests AUC drops when a variable is dropped from a model. Finally, we calculated variable response curves that illustrate how a variable relates to habitat suitability. Using our model, we predicted capercaillie habitat suitability across the whole Carpathian region, using a logistic link function to convert the MaxEnt output values to a relative habitat suitability index (HSI) ranging between 0 and 1.

Forest disturbance datasets

To identify forests that were disturbed since 1985, we used a satellite-based forest disturbance map (Griffiths et al. 2014). This map contains all forest disturbances, defined as full or near-full canopy removal, at five-year intervals between 1985-2010 at a resolution of 30 m. Disturbances were mapped across the Carpathians using image composites based on about 1,407 Landsat TM/ETM+ images, an extensive training dataset on disturbances, and a random forests change classification approach (Griffiths et al. 2014). The resulting map captures the past 25 years of forest cover dynamics with a minimum mapping unit of 0.27 ha and an overall accuracy of 86%. While smaller forest disturbances may exist, only clear-cuts larger than one hectare are unsuitable for capercaillie (Storch 2002). We summarized the percentage of disturbed forest per 1 ha gridcell.

Although our satellite dataset cannot distinguish the cause of forest loss (i.e., logging vs. natural disturbances), the vast majority of the disturbances mapped correspond to logging activities (planned fellings, salvage logging, illegal logging) (Text S2, Figure S1, Figure S2), all of which are detrimental to capercaillie (Storch 2000). It should be noted that natural disturbances (such as barkbeetle outbreaks) without post-disturbance logging may have a positive effect on capercaillie (Mikoláš et al. 2013; Teuscher et al. 2013; Rösner et al. 2014; Beudert et al. 2015). Without salvage logging, typically more than 30% of the canopy remains (Svoboda et al. 2014; Trotsiuk et al. 2014), thus creating open, mature forest conditions that capercallie benefit from (Mikoláš et al. 2013). Thus, natural disturbances may create favourable habitat for capercaillie, but as salvage logging is carried out in almost all cases, this effect is negligable (Figure 1.).

Assessing the effect of forest harvesting on capercaillie habitat

To quantify the impact of clearcutting on capercaillie habitat availability and connectivity between 1985 and 2010, we converted our relative HSI into a binary map of suitable and unsuitable habitat based on a suitability threshold of 0.2 (where the sum of sensitivity and specificity was maximized). Compared to alternative thresholds, this threshold produces robust predictions because it is not sensitive to the prevalence of occurrence (Liu et al. 2013), and it is therefore particularly attractive in conservation planning whereby errors of omission are often of greater concern than errors of commission (Liu et al. 2005; Jiménez-Valverde and Lobo 2007).

We then compared our capercaillie habitat map with the area of forest disturbances mapped by Grifffiths et al. (2014). We considered three types of habitat change scenarios based on assumptions about how disturbances would affect capercaillie habitat change from 1985 to 2010. In the first scenario (scenario 1), we assumed neither clear-cutting, which typically result in the full canopy removal, nor afforestation, which typically leads to dense, monoculture stands, would create open-canopy forest suitable for capercaillie (Storch 2002). All areas of disturbed forest between 1985 and 2010 were thus considered unsuitable for capercaillie and masked from our habitat map. Based on our experience and the literature, this represents a realistic scenario. To assess the potential impact of changes in forest management following clear-cutting, we also assessed two alternative scenarios, which assume that disturbed forests would be managed in a capercaillie-friendly way. In the case of natural disturbances with no intervention, sites would be naturally regenerated. In the case of clearcutting, trees would be planted in a pattern that creates interconnected gaps 20-30 m wide. Scenario 2 assumes post-disturbance development into capercaillie-friendly habitat after a period of five years, and scenario 3 assumes a period of ten years for the development of capercaillie-friendly habitat. In our experience, neither of these regeneration models is widespread in the Carpathians. As with scenario 1, we masked the area of disturbed forest from the habitat suitability map, but we added the area of regenerating forests for each time period and cell.

We then used the resulting habitat maps to assess changes in capercaillie habitat connectivity from 1985 to 2010. We considered only habitat patches larger than 2 km^2, which is approximately the minimum capercaillie home range size (132 ha) identified in telemetry studies (Storch 1995). To evaluate the importance of individual habitat patches for overall connectivity in the habitat network, we used the Probability of Connectivity (PC) Index (Saura et al. 2011), calculated using the Conefor 2.6 software (Saura and Torné 2009; www.conefor.org). This graph-based index quantifies functional connectivity at the landscape scale, ranging from 0 (low) to 1 (high). PC is defined as the probability that two individuals randomly placed within the landscape fall into habitat areas that are connected, given a set of *n* habitat patches and links among them (Saura and Pascual-Hortal 2007). PC is computed as:

$$PC=(\Sigma ni=1\Sigma nj=1\ a_i a_j p_{ij}*)/A2L \qquad (1)$$

where a_i and a_j are the areas of habitat patches *i* and *j*, respectively; p_{ij}* is the maximum product probability of all possible paths between patches *i* and *j*, and *AL* is the area of the study region. The relative importance of each habitat patch, expressed as dPC, is then obtained from a percentage change of PC computed for a graph with and without this patch (Saura and Torné 2009). We evaluated the importance of individual habitat patches at different dispersal distances using the average dispersal (2.5 km) and maximum (10 km) distances of adult capercaillie in intervals of 2.5 km (Hjeljord et al. 2000; Storch and Segelbacher 2000).

We also quantified changes in overall capercaillie habitat connectivity from 1985 to 2010 using the Equivalent Connected Area (ECA) index, which compliments the PC index well and is easier to interprete (Saura et al. 2011). ECA is defined as the area of a single patch that would provide the same value of the PC metric as the habitat pattern of a given area (Saura et al. 2011), and is computed as:

$$ECA=\sqrt{}(\Sigma n_i=1\Sigma n_j=1\ a_i a_j p_{ij}*) \qquad (2)$$

We also assessed how much capercaillie habitat was lost within Protected Areas (PAs), or Special Protection Areas (SPAs). PAs are protected areas at the national level (such as national parks or natural park), whereas SPAs are conservation areas designated in accordance with EU criteria on species and habitats of conservation concern, and they may partly overlap the PAs. A layer of PAs came from the Carpathian Environment Outlook database and a layer of SPAs from European Environment Agency.

RESULTS

Distribution of suitable capercaillie habitat

The AUC value for our best Maxent model was 0.942 (with a standard error of ±0.014), which indicates a strong fit and high predictive ability (Pearce and Ferrier 2000). Based on our variable importance tests, climate and land cover were the most important variable groups in our model. Based on our model, average annual temperature and precipitation, proportion of forest, and forest fragmentation were the most important predictors determining capercaillie habitat suitability in the Carpathians, with a combined relative contribution of > 87%. Response curves (see Fig. 2) indicated that habitat suitability for capercaillie increased with an increasing proportion of forest. Capercaillie preferred core and perforated forests compared to forest islets, and avoided areas with intensive human pressure (i.e., areas close to settlements, roads, railways, cropland, or grassland). Terrain ruggedness had the lowest relative contribution to the habitat suitability model, with capercaillie preferring more rugged areas.

Predicting capercaillie habitat suitability across the Carpathians showed large areas of suitable habitat at higher elevations (Fig. 3). Four large patches of highly suitable habitat were identified in the Western, Eastern, Southern Carpathians, and Western Romanian Carpathians (Apuseni Mountains), respectively. Only two of the identified habitat patches were of sufficient size to potentially allow for a viable capercaillie population (250-500 km^2, Grimm and Storch 2000; Braunisch and Suchant 2013). None of the habitat patches was larger than 500 km^2 at any time during 1985 to 2010. Based on our threshold (i.e. sum of sensitivity and specificity), we found 7,509 km^2 to be suitable for capercaillie in the year 1985 (3.4% of the area of the entire Carpathians, Table 2). Most of this area was located in Romania, followed by Slovakia, and Ukraine; no suitable habitat patches were found in Hungary (Fig. 3).

The area of suitable habitat decreased over time, from approximately 3.4% of the total Carpathians area in 1985 to about 2.6% in 2010, a decrease of 1,110 km^2 (15%). Affected habitat was more widespread in the Western and Eastern Carpathians, especially in the Low and High Tatra Mountains (Slovakia and Poland; Fig. 4, inset A), and the Maramures and Rodna Mountains (Northern Romania; Fig. 4, inset B). The impact of forest disturbances on capercaillie habitat differed considerably between countries (Table. 2). The biggest loss of suitable habitat occurred in Romania, particularly along the Ukrainian border. Although the area of capercaillie habitat in Ukraine and Slovakia were similar, almost twice as much habitat was lost in Slovakia; the Czech Republic and Poland did not experience much habitat loss.

A substantial portion of suitable capercaillie habitat occurred within PAs (46%) or SPAs (39%), especially in Romania and Slovakia. The largest areas of suitable habitat within PAs occurred in Slovakia, which strongly contrasted with Ukraine, where a similar amount of capercaillie habitat was found, but they were predominantly in unprotected sites. Surprisingly, our results showed that habitat loss in some countries was higher inside protected areas than outside (Table. 2). This was most evident for Slovakia by PAs (79% inside versus 5.5% outside) or SPAs (65% inside versus 5.5% outside); the opposite scenario was true for Ukraine (27% inside versus 73% outside).

Connectivity of capercaillie habitat

Our connectivity analyses identified four distinct capercaillie habitat networks in the Western, Eastern, Southern, and Western Romanian Carpathians (Apuseni Mountains). The total number of habitat patches and their relative importance for connectivity varied substantially between 1985 and 2010 (Fig. 5). According to our results, importance of many habitat patches, as defined by dPC, continuously decreased from 1985 to 2010 due to the decline in total capercaillie habitat available (Fig. 5); this was most evident in the Western and Eastern Carpathians. For example, the area of capercaillie habitat with very high (dPC > 30) connectivity importance declined from 996 km² in 1985 to 282 km² in 2005, and we did not find any habitat patch with such a high importance value in 2010. Conversely, the area of weakly connected capercaillie habitat patches increased from 2,360 km² in 1980 to 2,750 km² in 2010. The importance of individual habitat patches also increased with dispersal distances from 2.5 km to 7.5 km, but increasing the dispersal distance further to 10 km had only a minimal effect (Fig. 6a). Increasing dPC values here indicate higher capercaillie habitat connectivity.

Assessing overall trends in habitat connectivity since 1985 using the ECA metric confirmed that connectivity declined in all scenarios until 2010 (Fig. 6b), thus indicating a loss of functional connectivity of capercaillie habitat in the Carpathians. The biggest loss (-10.6%) occurred between 2005 and 2010 (Fig. 6c). The result of a continued and marked decrease in overall connectivity of the capercaillie habitat network during the last 25 years was also persistent across all dispersal distances considered (Fig. 6d).

DISCUSSION

Protecting species that are reliant on old-growth forests is a key conservation challenge as forest management intensifies across the globe. Capercaillie are a primary target for conservation because they are endangered in many parts of their range and protecting them will benefit a host of other species of conservation concern. We assessed, for the first time, capercaillie habitat suitability and connectivity in the Carpathians in Europe, where broad-scale habitat assessments to guide conservation planning are desperately needed in a period of changing climate, social, and economic pressures. Our analyses revealed that capercaillie habitat in the Carpathians was fairly abundant, however, the habitat is also highly fragmented. Capercaillie will therefore likely only persist as meta-populations, thus making functional connectivity between habitat patches critically important. Our findings suggest that a large proportion of suitable habitat has been lost since 1985 due to logging, even inside protected areas, and that this has resulted in a substantial decline in functional connectivity of the capercaillie habitat network. In the Carpathians, safeguarding the remaining areas that harbor capercaillie and many co-occurring species that depend on large areas of natural and old-growth forest will require a profound shift in forest management practices. This could include adopting policies that better protect natural forests inside protected areas, limit large-scale clear-cutting and salvage logging, implement nature-based forest management, and restrict forest fragmentation by new roads.

Although the Carpathians (220,400 km^2) harbor one of the largest capercaillie populations in Europe, there have been no prior capercaillie habitat assessments for the region. Our results generally agree with prior capercaillie research from other regions. Capercaillie habitat suitability at the landscape scale was related to climate conditions (i.e., average annual precipitation around1000 mm, average annual temperature around 3 °C), as Graf et al. (2005) observed in the Swiss Alps. Capercaillie avoided areas with intensive human pressure (e.g. settlements, roads, railways, or cropland), factors that have negatively affected capercaillie elsewhere as well (Storch and Leidenberger 2003; Braunisch and Suchant 2007; Thiel et al. 2011). Habitat suitability improved with an increasing proportion of forest, and capercaillie preferred core and perforated forests rather than small forests islets, both of which are consistent with prior work (Graf et al. 2005; Bollmann et al. 2011). Many prior assessments (e.g. Graf et al. 2005; Pascual-Hortal and Saura 2008; Braunisch et al. 2010; Bollmann et al. 2011) have largely focused on small areas using fine-scale data on forest structure (e.g. LiDAR, forest inventories), however, the importance of broad-scale studies to evaluate spatial and temporal dynamics of capercaillie habitat is increasingly recognized.

Capercaillie habitat in the Carpathians was highly fragmented, and it is unlikely any habitat patches were sufficiently large to maintain a minimum viable population (i.e., 250 – 500 km^2, with 470 – 500 communicating individuals, Grimm and Storch 2000; Braunisch and Suchant 2013). In addition, our findings suggest that logging has further eroded connectivity and that capercaillie habitat has progressively shifted to higher elevations and became more isolated and fragmented. For example, in the Western Carpathians, the connectivity of the core capercaillie population decreased significantly due to massive salvage logging after a 2004 storm event (Fig. 4, inset A), thus threatening this geographically isolated population (Saniga 2003; Mikoláš et al. 2013). Similarly, on the Romanian-Ukrainian borders, intensive harvesting, at least in part related to forest privatization and illegal logging, has decreased the connectivity of capercaillie habitat substantially (Fig. 4, inset B). A recent genetic study indicated that gene flow between the Western and Eastern Carpathian capercaillie populations has ceased due to low connectivity, as detected in our study, yet, gene flow between the southern (i.e. Romanian) and eastern (i.e. Ukrainian) populations may still persist (Klinga et al. 2015). However, logging continues unabated in the Southern and Eastern Carpathians (Knorn et al. 2012 a, b; Mikoláš et al. 2013; Mikoláš et al. 2015), which will likely continue to decrease connectivity in the region and limit gene flow between existing populations.

The rate of habitat loss and fragmentation inside protected areas is particularly alarming (Table. 2). In fact, many protected areas in the Carpathians allow logging inside their boundaries, and suitable capercaillie habitats are being harvested in EU-designated Special Protected Areas (SPA) where capercaillie is a priority species. Not surprisingly, capercaillie populations have already disappeared in some SPAs in the Western Carpathians, and populations in other SPAs will be threatened as habitat loss and fragmentation increase. We suggest three key drivers of these trends. First, all Carpathian countries mandate that salvage logging follow natural disturbances (e.g., storms), even in PAs and SPAs, thus potentially suitable capercaillie habitat (i.e., post-disturbance habitat without interventions) may be converted into unsuitable habitat. Second, corruption and illegal logging remain a problem in some Carpathian regions (Irland 2008; Irland and Kremenetska 2009; Schoukens and Bastmeijer 2014; Křenová and Kindlmann 2015), which contributes to the loss of mature and old-growth forests inside formally protected zones (Bouriaud 2005; Kuemmerle et al. 2009; Knorn et al. 2012a). Finally, EU investments to foster rural development support road building into larger forest complexes (Křenová and Kindlmann 2015), thus increasing human disturbance, fragmentation, and access for logging operations (Knorn et al. 2012a,b).

While our habitat model and connectivity analyses relied on established approaches and generally performed very well, model uncertainty warrants discussion. MaxEnt results may be biased due to unequal sampling effort across the study area (Araújo and Guisan 2006). Although we restricted background points to areas above 600 m to limit sampling bias and suitable capercaillie habitat areas above the timberline are rather limited for the Carpathians as a whole, we cannot fully rule out any potential remaining sampling bias. A more intensive sampling of the study area would address this issue (Fourcade et al. 2014), but given our already substantial field work efforts, this would require considerably more funding and time. Our model did not explicitly include fine-scale variables of forest structure (e.g. canopy closure, bilberry cover, coarse woody debris, forest types, shrub cover, selective logging, forest grazing, etc.), which are important predictors of capercaillie occurrence at fine scales (Storch 2002; Graff et al. 2009). Including such fine-scale data (e.g. area-wide LiDAR data) would improve our models (e.g. Rolstad and Wegge 1987; Storch 2002; Bollmann et al. 2005, Mikoláš et al. 2015), but no such maps currently exist for the entire Carpathians region. If more detailed variables are not included in such models, Ehrbar et al. (2011) have recommended that stand-level conservation plans and field-based habitat assessments should also be included to improve management plans. Third, our connectivity index analyses was based on a maximum dispersal distance of 10 km, however, it is well documented that young birds or birds living in highly fragmented habitats may have larger home range sizes, although they may also have lower survival rates (Gjerde and Wegge 1989; Moss et al. 2006). Some limited interactions may exist even when patches occupied by capercaillie are further than 10 km distance, although this may still not ensure sufficient gene flow among populations (Segelbacher at al. 2003).

There are several important management implications that arise from our work. It suggest that a landscape-scale perspective is critical for ensuring capercaillie persistence across the Carpathians; establishing and protecting a viable capercaillie metapopulation requires collaboration across national boundaries, a situation that is challenging with five countries involved, one (Ukraine) of which is not a member of the EU. A priority of conservation efforts should focus on the protection of the remaining patches of suitable habitats, especially those that facilitate functional connectivity among populations (see Figure 5.). The loss of these connectors may result in genetic isolation, smaller gene pools, and an erosion of the capacities of the Carpathian capercaillie population to adapt in the face of climate change (Segelbacher et al. 2003, Braunisch et al. 2014). We therefore recommend a combination of non-intervention and active management measures, specific to the Carpathians, which should positively affect mountain biodiversity in general (Bollmann et al. 2012).

Non-intervention schemes should be established in capercaillie sites with lower forest productivity, where natural succession will result in suitable habitat following disturbance. Ideally, these sites should be larger than 1,400 ha and distances between sites should not exceed 5-10 km (Bollmann et al. 2011). In particular, salvage logging, specifically after bark beetle outbreaks, should not be employed because salvage logging, not the natural disturbance, renders the area unsuitable for capercaillie habitat (Figure 1., Mikoláš et al. 2013; Rösner et al. 2014; Beudert et al. 2015). As suggested by several national legislations in the

Carpathians, national parks could establish core zones with no management interventions, yet this has still not been implemented in most national parks in Slovakia and Romania. Protecting core sites may also require the creation of new protected areas, especially in Romania, Ukraine, and Slovakia, where key capercaillie areas are unprotected.

It is important to recognize that not all forest management activities negatively impact capercaillie. For example, specialized management measures (e.g. group selection) or low-intensity forest grazing may create open forest conditions that benefit capercaillie (Klaus et al. 1989). We identified large areas of clearcuts and young stands in the Carpathians that are currently not suitable capercaillie habitat, but, if managed properly, they could potentially be suitable habitat in a shorter time frame. Managing for open stands with canopy closure around 50% and a rich ground cover of bilberry, they might provide quality capercaillie habitat within 30 to 50 years (Mac Millan and Marshall 2004; Wegge and Rolstad 2011; Broome et al. 2014). To increase connectivity and gene flow among suitable habitat patches, a system of stepping-stones using patches greater than 50 ha in size (Bollmann et al.2011) that serve to connect habitats are critically important (Segelbacher and Höglund 2003); in addition the permeability of the matrix, topography, and landscape structure should be considered in planning, as all of these may be important determinants for habitat connectivity as well (Graff et al. 2007).

Although our study focused on capercaillie as a model species, our findings are relevant to the conservation of many other species. Capercaillie require large areas and are considered an important indicator of high structural diversity in mountain forest ecosystems (Grimm and Storch 2000). Protecting capercaillie may benefit Carpathian biodiversity in general in at least four ways, thus helping safeguard biodiversity in Europe as a whole. First, biodiversity associated with old-growth forests is in peril across Europe because these forests are decreasing in many regions. The Carpathians still contain widespread natural and old-growth forest, many of which are unprotected, and managing for capercaillie populations would thus benefit many species of conservation concern (Rössner et al. 2013, Suter et al. 2002; Pakkala et al. 2003). Second, our results indicates that the long-term persistence of capercaillie in the Carpathians will depend on establishing functioning corridors among populations, and thus metapopulations of other large-bodied species of conservation concern may also benefit (Kuemmerle et al. 2010). The Carpathian Mountains are a biodiversity hotspot for mammals and birds in Europe, including brown bears (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), grey wolf (*Canis lupus*), European bison (*Bison bonasus*), and capercaillie populations (Storch 2007; Kuemmerle et al. 2010; Chapron et al. 2014). All these species are sensitive to habitat fragmentation and human disturbances (Trombulak and Frissell 2000; Houle et al. 2010; Walpole et al. 2012; Dorresteijn et al. 2014; Litvaitis et al. 2015); they depend on large, unfragmented blocks of forest and functioning corridors between them, thus they would also benefit from landscape-scale conservation planning for capercaillie persistence across the Carpathians (Courbin et al. 2009). Third, roads fragment habitat decrease connectivity, and facilitate disturbance via logging, and hunting, poaching, and tourism for many species (Selva et al. 2011). Funding from the EU currently support hundreds of kilometers of new forest roads in the Carpathians, even within protected areas. To enhance conservation efforts to sustain viable capercaillie populations, identifying and limiting access to existing roads and increasing broader participation for planning of new road constructions would greatly improve habitat connectivty and benefit many other species also. Finally, our study suggests that the current policy of protected areas does not effectively protect biodiversity within their borders. Networks of large protected forest reserves are crucial for the long-term persistence of biodiversity hotspots such as the Carpathians.

We used a combination of habitat suitability modeling and connectivity analyses to evaluate the impact of logging on taxa of conservation concern at the ecoregion scale. Although rarely implemented, a similar approach can be readily applied to any region where comparable data exist. Our approach could be extended to include, for example, landscape genetics, population viability analyses, or movement data. Our approach allowed us to examine the spatial and temporal dynamics of habitat loss and its effects on functional connectivity. Substantial habitat loss and decreased connectivity, 15% and 30 %, respectively, over a period of only 20 years are worrying trends for capercaillie and other species depending on old, structurally diverse forests (Suter et al. 2002; Pakkala et al. 2003). Our proposed landscape-scale conservation recommendations would help numerous species that are dependent on such mountain forests, including the three-toed woodpecker (*Picoides tridactylus*) and pygmy owl (*Glaucidium passerinum*) (Suter et al. 2002; Pakkala et al.2003), large carnivores (Dorrestein et al. 2014), and saproxylic organisms (Seibold et al. 2015), among many others. We hope our results provide a basis for improving the balance between forest use and the protection of forest biodiversity.

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Table 1. Environmental variables used to model capercaillie habitat suitability in the Carpathians

Variable category	Description	Unit	Data source
Climate	Average annual precipitation	mm	WorldClim
	Average annual temperature	°C	WorldClim
Topography	Terrain ruggedness	index (0-1)	Calculated from DEM according to Riley et al. (1999)
Land cover	Distance to cropland	m	Calculated from land cover data created in Griffiths et al. (2013)
	Distance to grassland	m	Calculated from land cover data created in Griffiths et al. (2013)
	Proportion of forest	% of area	Griffiths et al. (2014)
	Morphological spatial pattern of forest	5 classes	Calculated as in Vogt et al. (2015) from land cover data created in Griffiths et al. (2013)
Human disturbance	Distance to settlements	m	Calculated from land cover data created in Griffiths et al. (2013)
	Distance to roads and railways	m	Derived from OpenStreetMap

Table 2. Area (km^2) of available suitable capercaillie habitat in 1985 and the impact of forest disturbance on suitable habitat until 2010 in the Carpathians. PAs refers to Protected Areas, and SPAs refers to Special Protection Areas; PAs and SPAs can overlap.

	Suitable capercaillie habitat (km²)				**Loss of suitable capercaillie habitat (km²)**			
	PAs	SPAs	Unprotected	Total (%)	PAs	SPAs	Unprotected	Total (%)
Czech Republic	9	9	0	9 (1)	1	1	0	1 (0)
Hungary	0	0	0	0 (0)	0	0	0	0 (0)
Poland	305	97	32	350 (5)	33	10	4	39 (4)
Romania	1,142	1,469	1,964	3,720 (49)	233	273	260	565 (51)
Slovakia	1,483	1,380	133	1,797 (24)	256	211	18	325 (29)
Ukraine	498	---	1,135	1,633 (21)	48	---	131	180 (16)
Total	**3,437**	**2,955**	**3,264**	**7, 509**	**571**	**495**	**413**	**1,110**

Figure 1. Photographs documenting the effect of leaving naturally disturbed forests (A) and large-scale salvage logging (B) on capercaillie occurrence (Photos: Karol Kaliský). Capercaillie inhabit forest with dead canopy because of the bark beetle outbreak (A), but they do not find suitable habitats in the large-scale clearcuts (B).

Figure 2. Variable response curves for capercaillie (*Tetrao urogallus*) in the Carpathians based on our maximum entropy model (sorted from high to low importance reading left to right and top to bottom). The relative habitat suitability index (HSI) ranges from 0 (low) to 1 (high), while the range of environmental variables is shown on the *x*-axis. Spatial pattern of forest consists of five components: background (i.e., non forest) (0), core (i.e., only forest neighbors) (1), islet (i.e., patches consisting of edge forest only) (2), perforation" (i.e., edge inside larger forest patches) (3), and forest edge (4).

Figure 3. Capercaillie habitat suitability map for the Carpathians.

Figure 4. Forest disturbance patterns between 1985 and 2010, which almost exclusively represent clearcutting and post-disturbance salvage logging, compared to capercaillie habitat in the Carpathians. Frames A and B focus on the Low and High Tatra Mountains and the Maramures region in Romania, respectively.

Figure 5. Change in the importance of individual capercaillie habitat patches between 1985 and 2010, measured by importance of habitat patch based on Probability of Connectivity index (dPC) based on the first (realistic) scenario and a dispersal distance of 2.5 km. The importance of the habitat patches is classified into five levels based on dPC value: 0-1 (Very Low); 1-3 (Low); 3-9 (Medium); 9-27 (High); >27 (Very High).

Figure 6. Connectivity of capercaillie habitat patches in Carpathians between 1985 and 2010. a) Results of importance of habitat patch based on Probability of Connectivity index (dPC) at various dispersal distances and time periods; b) change in overall connectivity of suitable capercaillie habitat across different post-disturbance forest recovery scenarios; c) loss of capercaillie habitat connectivity measured by importance of habitat patch based on Equivalent Connected Area index dECA (difference in Equivalent Connected Area index (ECA) values between time period); d) ECA dynamics across different dispersal distances and time periods.

Figure 1.

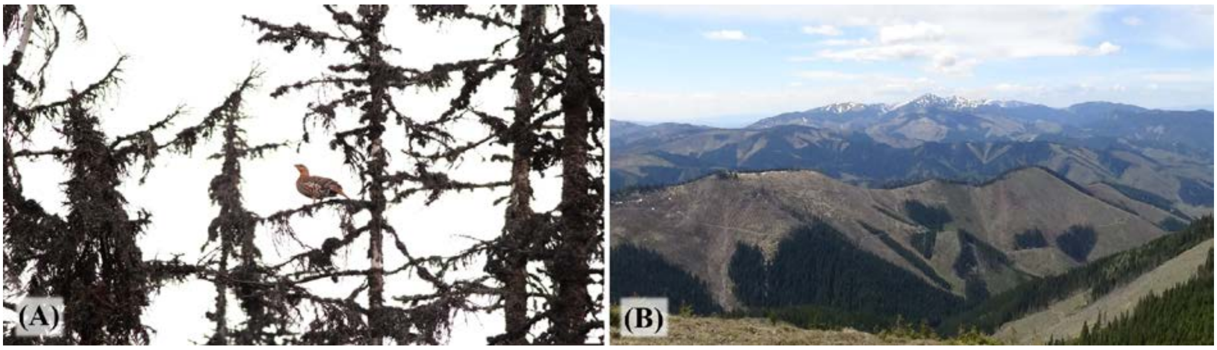
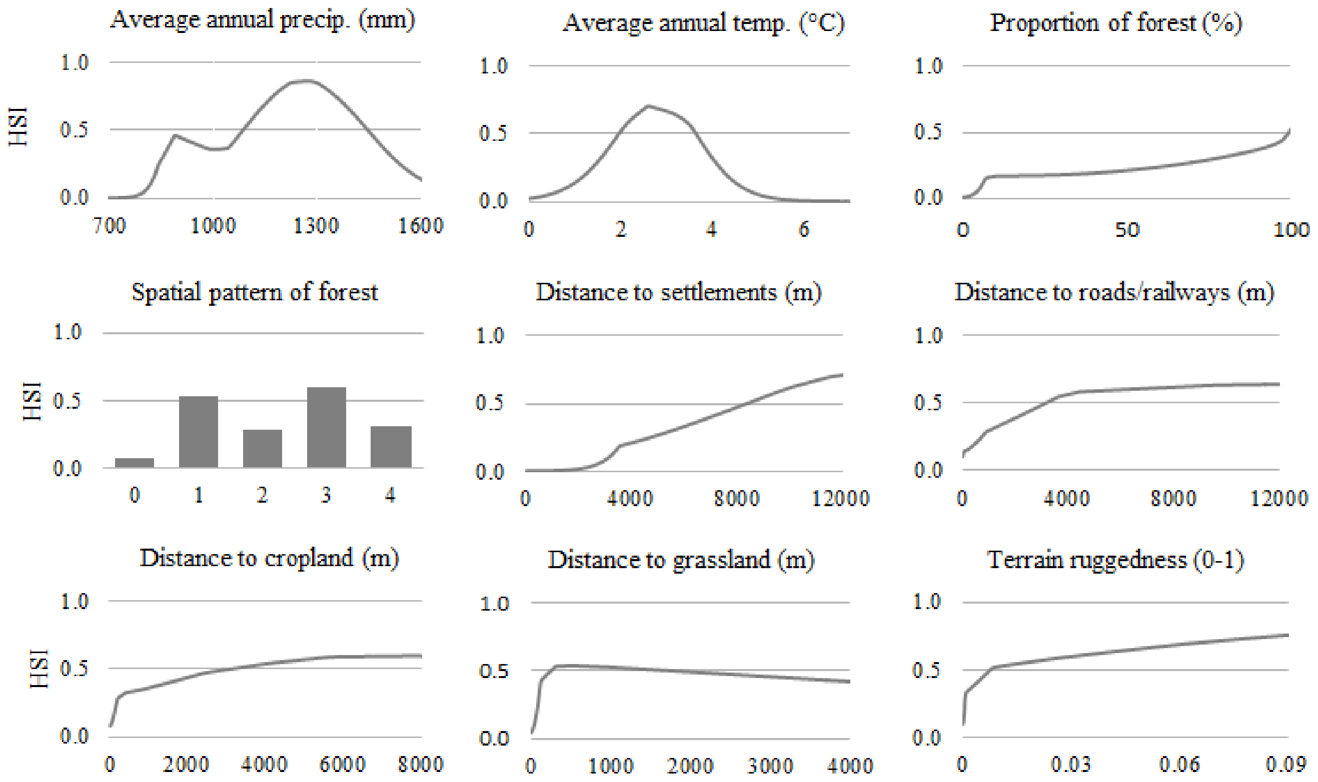


Figure 2.



Average annual precip. (mm)

Average annual temp. (°C)

Proportion of forest (%)

Spatial pattern of forest

Distance to settlements (m)

Distance to roads/railways (m)

Distance to cropland (m)

Distance to grassland (m)

Terrain ruggedness (0-1)

Figure 3.

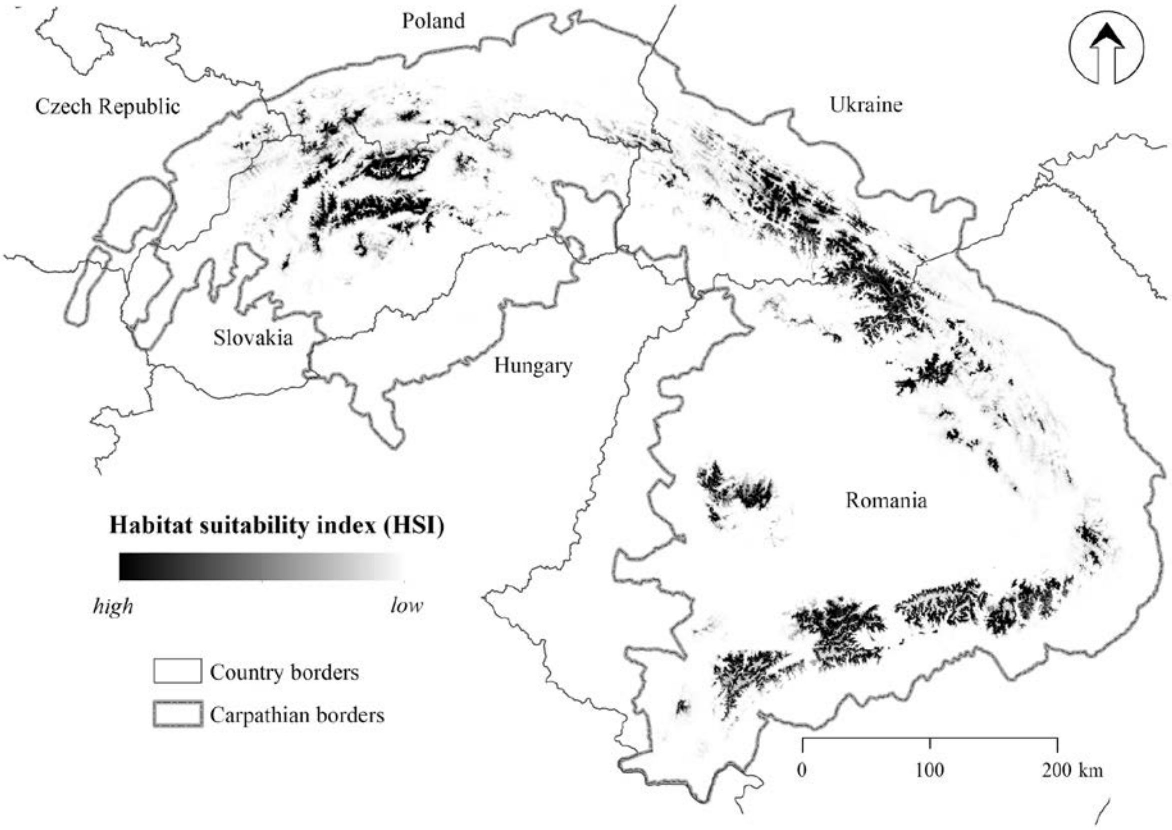

Poland
Czech Republic
Ukraine
Slovakia
Hungary
Romania
Habitat suitability index (HSI)
high
low
Country borders
Carpathian borders
0
100
200 km

Figure 4.

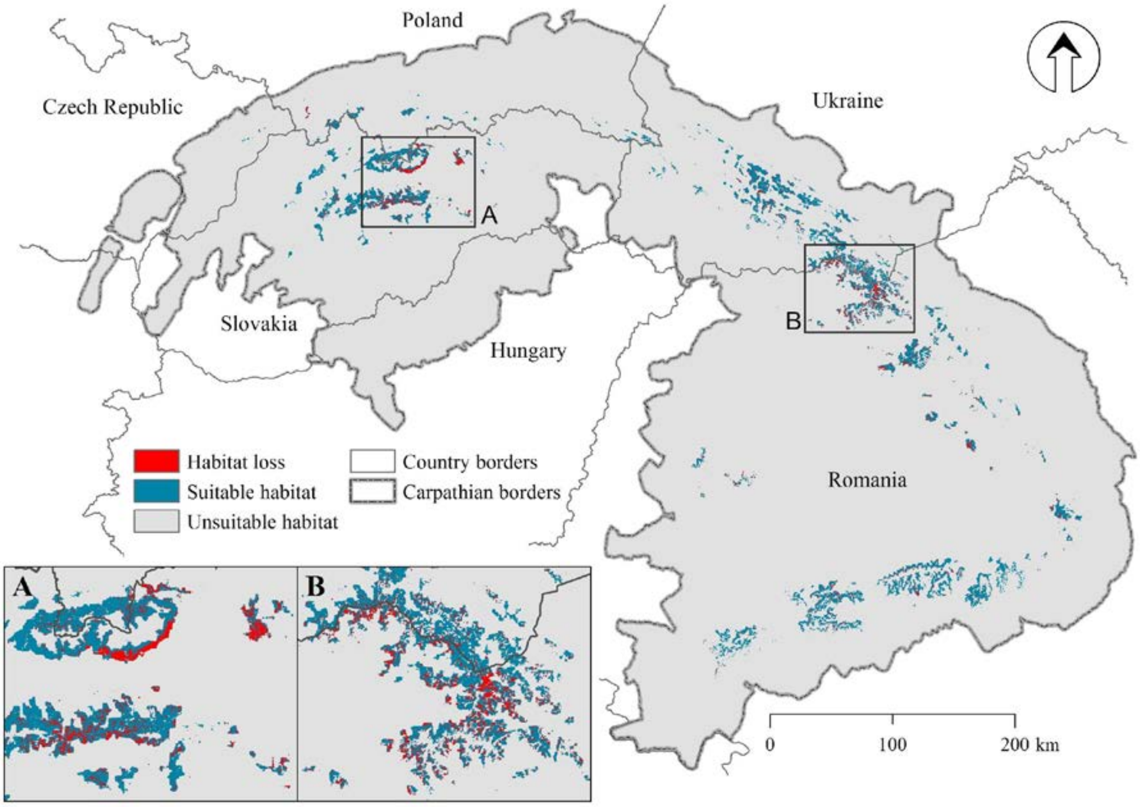

Poland
Czech Republic
Ukraine
Slovakia
Hungary
Romania
A
B
Habitat loss
Suitable habitat
Unsuitable habitat
Country borders
Carpathian borders
0
100
200 km
A
B

Figure 5.

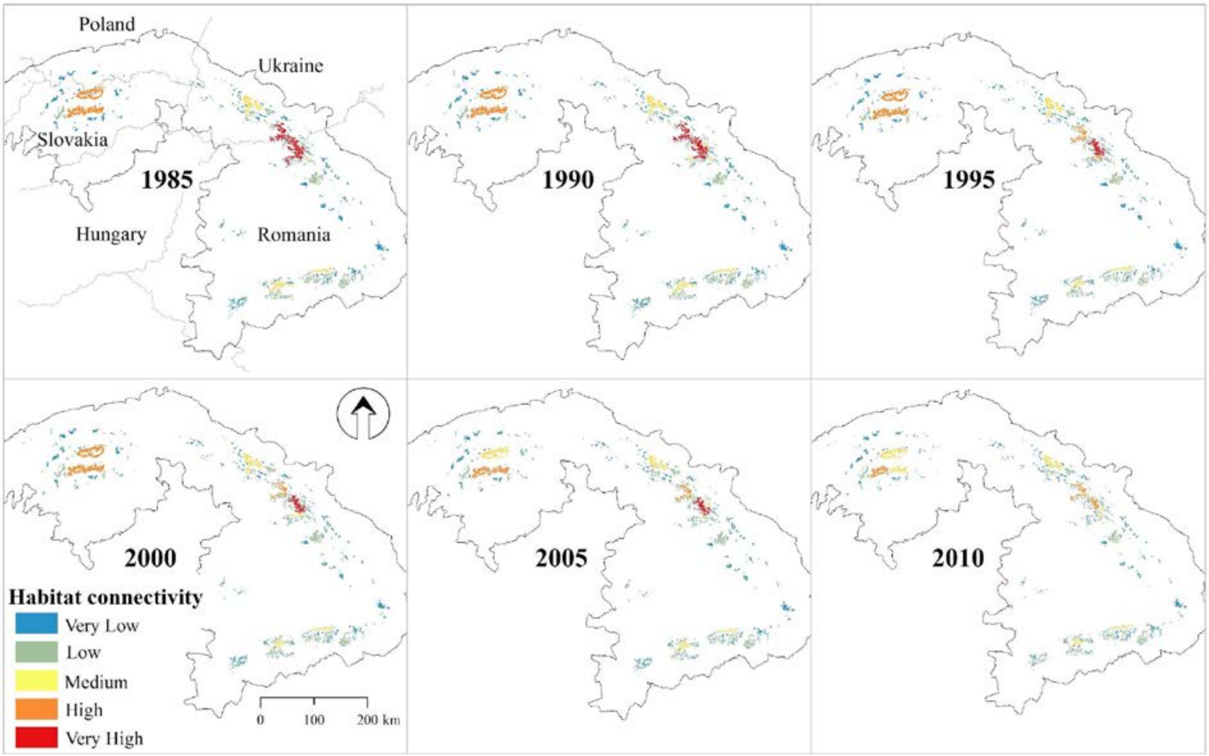
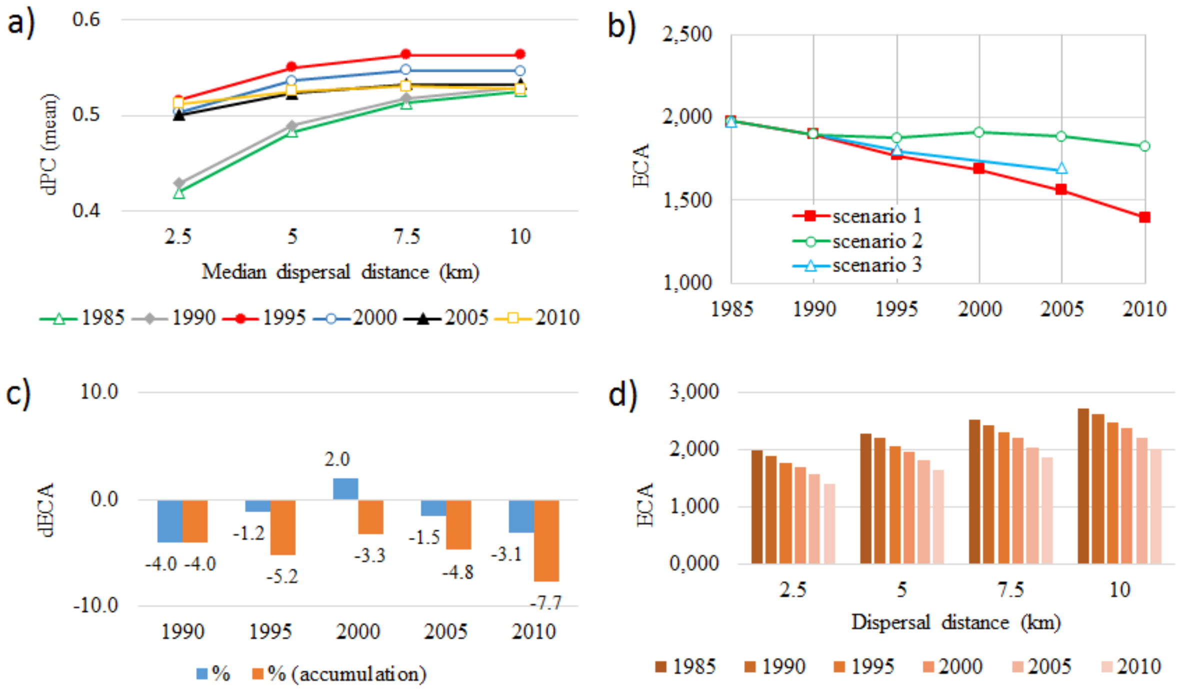

Poland
Ukraine
Slovakia
Hungary
Romania
1985
1990
1995
2000
2005
2010
Habitat connectivity
Very Low
Low
Medium
High
Very High
0
100
200 km

Figure 6.


a)
0.6
0.5
0.4
dPC (mean)
2.5
5
7.5
10
Median dispersal distance (km)
1985
1990
1995
2000
2005
2010
b)
2,500
2,000
1,500
1,000
ECA
scenario 1
scenario 2
scenario 3
1985
1990
1995
2000
2005
2010
c)
10.0
0.0
-10.0
dECA
-4.0
-4.0
-1.2
-5.2
2.0
-3.3
-1.5
-4.8
-3.1
-7.7
1990
1995
2000
2005
2010
%
% (accumulation)
d)
3,000
2,000
1,000
0,000
ECA
2.5
5
7.5
10
Dispersal distance (km)
1985
1990
1995
2000
2005
2010

5.4 Klinga P., Mikoláš M., Zhelev P., Höglund J., & Paule L., 2015. Genetic differentiation of western capercaillie in the Carpathian Mountains: the importance of post glacial expansions and habitat connectivity. Biological Journal of the Linnean Society 116, 873–889.

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Biological Journal of the Linnean Society, 2015, **116**, 873–889. With 5 figures.

Genetic differentiation of western capercaillie in the Carpathian Mountains: the importance of post glacial expansions and habitat connectivity

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Population structure and barriers to gene flow are important components for understanding the evolutionary history of a species. Here we study population structure and differentiation in the western capercaillie (Aves: Phasianidae) along the Carpathian Mountains. Further, we compared the levels of population differentiation among capercaillie from the Carpathian Mountains, Balkans (Bulgaria) and the boreal forest (Russia and Sweden) in order to reveal past and current processes which may influence population structure. Tissue samples, non-invasive faeces and feathers and toe pads from museum specimens were used for genetic analyses of mitochondrial (mtDNA) sequences and allelic variation at nine nuclear DNA (nDNA) microsatellite loci. Analyses of mtDNA sequences revealed a southern subclade within the northern clade. Within the northern clade, microsatellite data distinguished two groups: (1) Western Carpathian populations; and (2) Eastern Carpathian and boreal forest populations. Bulgarian populations constituted a third cluster corresponding to the southern phylogenetic subclade. The Western Carpathian populations showed a heterozygote deficiency. The analyses indicate that the abundant Eastern Carpathian populations share alleles with populations from the boreal forest suggesting a common origin of these populations since the last glacial period. On the other hand, the Western Carpathian populations have been isolated over a long period with only a few migrants from the east, thereby becoming differentiated from the eastern and northern populations. The southern populations have been isolated from the northern populations since the last glacial maximum. The molecular analyses did not support the currently recognised taxonomy at the subspecies level. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **116**, 873–889.

ADDITIONAL KEYWORDS: genetic structure – phylogeography – refugia – *Tetrao urogallus*.

INTRODUCTION

The western capercaillie (*Tetrao urogallus*) has received significant attention mainly as a game species and can be considered a useful umbrella species for much of avian biodiversity inhabiting upper montane and subalpine forests in central Europe (Suter, Graf & Hess, 2002). According to BirdLife International (2012), the western capercaillie is classified as least concern among bird species. However, in many areas of Europe, population abundance has decreased, local populations are endangered or have even disappeared (Klaus *et al.*, 2008). Due to fragmentation and habitat loss during the recent decades, the populations in Western and Central Europe have rapidly declined (Storch, 2007) and, currently in such areas, capercaillie persists in isolated population units (Segelbacher, Manel & Tomiuk, 2008).

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The intraspecific taxonomy of the western capercaillie is rather complicated. Twelve subspecies have been described based on morphological differences (Couturier & Couturier, 1980) (Supporting Information, Fig. S1) but the differences tend to be clinal and may reflect local ecotypes instead of genetically different units (Segelbacher, Höglund & Storch, 2003). In Finland, Liukkonen-Anttila *et al.* (2004) did not find any clear evidence of genetic differentiation between *T. u. major, T. u. urogallus, T. u. uralensis* and *T. u. karelicus*. Nonetheless, Segelbacher & Piertney (2007) provided evidence of genetically different subspecies of capercaillie within Europe and in Cantabrian capercaillie populations. Alda *et al.* (2011) found low genetic diversity and significant genetic differentiation when comparing Cantabrian capercaillie with other subspecies. Significant differences in skeletal traits and body size have been found for *Tetrao urogallus rudolfi* (Eastern Carpathians) and *Tetrao urogallus major* (Western Carpathians) (Kohl & Štollmann, 1968, 1971) that, if having a genetic basis, would suggest a basis for subspecies classification. According to *The Clements Checklist of Birds of the World* (Clements *et al.*, 2013), the range of the *T. u. rudolfi* is localized to both the Carpathian and Rhodope Mountains, while the range of *Tetrao urogallus major* is spread from Germany to the SW Baltic countries and to the Balkan peninsula. This statement is rather imprecise, since the occurrence of capercaillie in Bulgaria is not only confined to the Rhodopes (about 80% of the Bulgarian population, Petrov, 2008), but it also occurs in the Rila and Pirin mountains as well as in the western part of Stara Planina. We thus hypothesize a contact zone for both subspecies in the Eastern Carpathians.

The capercaillie is known to disperse only short distances and the average dispersal distance rarely exceeds 10 km (Storch, 2000) in suitable habitat. There are, however, migration records of longer distances (max. 140 km, Nappée & Douhéret, 2004). Previous microsatellite studies in Europe have shown a correlation between genetic differentiation and Euclidean geographical distance suggesting isolation by distance (IBD) pattern of population structure (Segelbacher *et al.*, 2003). Latitudinal and altitudinal range shifts of the most species during the cold glacial and warmer interglacial phases produced contrasting distribution dynamics, forming geographically restricted distribution patterns but also panmictic distributions, strongly dependent on the ecologic demands of the species (Louy *et al.*, 2014). Currently the major role in explaining genetic and morphological divergence between southern and northern European capercaillie is attributed to habitat modifications which occurred during the Quaternary, whose climatic fluctuations led to many cycles of contraction and expansion of species geographical ranges (Hewitt, 1996). Historically, the Quaternary glaciations resulted in the isolation of the northern and the southern capercaillie populations or lineages allowing for divergence in both genetic and morphological traits. The southern lineage consists of the closely related Pyrenean–Cantabrian and Balkan (Pirin and Rhodopes mountains) populations (Duriez *et al.*, 2007), showing a smaller body size compared to the northern lineage (Couturier & Couturier, 1980). Populations of the southern lineage form a genetically distinct unit due to strong differentiation from other Eurasian populations (Duriez *et al.*, 2007; Segelbacher & Piertney, 2007). The populations belonging to the northern lineage are spread throughout the rest of the Eurasian capercaillie habitats (Duriez *et al.*, 2007). Segelbacher & Piertney (2007) hypothesized glacial refugia in Iberia for the southern lineage and postglacial colonization of Europe by northern lineage birds from East European refugia. Duriez *et al.* (2007) suggested that before the last glacial maximum (LGM), the southern lineage, represented by *Tetrao urogallus aquitanus,* formed a continuous population throughout Europe from the Iberian peninsula to Romania and during the LGM, two refugia could be presumed: in the Balkans and in the Iberian peninsula, respectively. The northern lineage could expand in Asia and North-Eastern Europe assuming LGM refugia placed in southern Asia or Beringia (Duriez *et al.*, 2007). Bajc *et al.* (2011) assigned a glacial refugium to the Rhodope – Rila – Pirin mountain chain for the southern lineage. In addition, the current density of both the Rhodope and Rila populations remains stable in contrast to the declining populations of Eastern and Central Europe (Petrov, 2008) although stability of current population does not necessarily indicate it was a refugium during LGM.

The capercaillie from southern Norway are distinct from birds in Russia and more related to birds in the Black Forest and Alps (Segelbacher *et al.*, 2003), which may indicate a south-western colonization route from Iberia to Scandinavia and a north-eastern colonization route from the southern Asian glacial refugia to Russia (Duriez *et al.*, 2007). A contact zone between the southern and northern lineages was identified in Dinarides in the Balkan peninsula (Bajc *et al.*, 2011) as well as in the Pyrenees for the Cantabrian subgroup (Rodríguez-Muñoz *et al.*, 2007). Bajc *et al.* (2011) suggested an evolutionary scenario where a northern lineage could have evolved from the southern lineage in the Balkans during the period of major glaciations. Thus previous studies have produced mixed results and no clear pattern of the post glacial expansion and how genetic diversity is structured within the European range has yet emerged. There is thus a need for further genetic studies of this species especially in areas where the postulated southern and northern lineages are predicted to meet.

From a biogeographic point of view the Carpathians is an interesting and little explored area with plenty of diverse forest habitats. The Carpathians is the second longest mountain chain in Europe possibly creating a dispersal barrier between northern European plain and Balkan mountain ranges. The genetic studies of several amphibian species (Fijarczyk *et al.*, 2011; Zieliński *et al.*, 2013; Wielstra, Babik & Arntzen, 2015) suggest Carpathians as area where 'refugia within refugia' scenario (Gómez & Lunt, 2007) played an important role in within species genetic differentation. It is not known if the western capercaillie in the Carpathians belongs to the northern or southern lineage. Within the Carpathians, a continuous range in the Eastern Carpathians encompassing Romania and Ukraine is assumed to be occupied by *T. u. rudolfi* which seems to be isolated from the highly fragmented populations in the Western Carpathians which is assumed to be occupied by *T. u. major* (Slovakia and southern Poland) (Supporting Information, Fig. S1).

The aim of this study was to use mtDNA sequences and microsatellites: (1) to investigate the genetic structure of capercaillie populations along the Carpathians and Balkans (Rhodope and Rila Mountains), (2) to elucidate evolutionary phylogeographic processes which have led to the current distribution pattern of genetic variation, and (3) to clarify the taxonomical status of capercaillie from East and South-East Europe.

METHODS

SAMPLING

For mtDNA and microsatellites analyses we analysed in total 326 samples. Within the Carpathian population we sampled $N = 149$ faeces and $N = 60$ feathers for microsatellite analyses and 34 of them were used for sequencing of mtDNA. Within the Western Carpathians toe pad samples from $N = 17$ museum specimens (1940–1960) were collected for microsatellite analyses. From the boreal forests of Norway and Sweden we collected 22 feathers and in Russia 12 tissue samples originating from hunted birds were successfully amplified for microsatellites. For sequencing of mtDNA from the boreal forest region we used 12 samples. We also downloaded a sequence from an Estonian bird (DQ307411) from GenBank. In the southern group we collected and amplified 60 samples from hunted animals within the Rila and Rhodope Mountains in Bulgaria for microsatellites and 17 of them were sequenced for mtDNA. In addition, we downloaded three haplotypes from the Pyrenees (DQ307392, DQ307394, DQ307395) and as outgroup to root phylogenetic tree we downloaded two haplotypes of *Tetrao parvirostris* (DQ307426, DQ307427) (Duriez *et al.*, 2007) from GenBank (Supporting Information, Table S1, Fig. S1).

DNA EXTRACTIONS AND AMPLIFICATIONS

DNA was extracted from feathers, tissues and toe pad samples using a QIAmp Tissue Extraction Kit (Qiagen), following the manufacturer's instructions and modifications described in previous studies (Segelbacher, 2002; Horváth *et al.*, 2005; Speller, Nicholas & Yang, 2011; Johansson *et al.*, 2012). DNA from faeces was extracted using the DNA Stool Mini Kit (Qiagen) with a modified methodology described by Regnaut, Lucas & Fumagalli (2005) and Segelbacher & Steinbrück (2001).

For the phylogenetic study the mitochondrial control region domain I (CR I) sequences were amplified using forward GalF (5′-AGGACTACGGCTTGAA AAGC-3′) and reverse GalRi (5′-GGGGTGTAGGGG GAAAGAA-3′) primers (Duriez *et al.*, 2007). The PCR-mix of 25 μL total contained 1× buffer, 0.2 mM dNTPs, 0.02U Kappa Hot Start polymerase and 0.2 μM of each primer, nanopure H_2O, 30–50 ng DNA. The PCR reaction was performed in an Eppendorf Thermal Cycler with the following steps: enzyme activation within initial denaturation 3 min at 95 °C, followed by 30 cycles of 30 s denaturation at 95 °C, 30 s annealing at 59 °C, 30 s extension at 72 °C. Final elongation was performed for 10 min at 72 °C. PCR products were checked in 1.6% agarose gel. Products were analysed on ABI PRISM 3100 capillary DNA sequencer (Applied Biosystems, USA).

The DNA samples were genotyped at ten microsatellite loci: LEI98 (Gibbs *et al.*, 1997), ADL184, ADL230 (Cheng & Crittenden, 1994), BG15, BG16, BG18 (Piertney & Höglund, 2001), TUT1, TUT2, TUT3 and TUT4 (Segelbacher *et al.*, 2000). A negative control was included in all PCR reactions. PCR reactions were carried out in a 6.5 μL volume of 5.2 μL of mastermix (5× Q-solution, 2× Qiagen Multiplex PCR Kit, nanopure H_2O, 25 μM of each marker) and 1.3 μL extracted DNA. All samples were genotyped at least three times to ensure the reliability of individual genotypes (Taberlet *et al.*, 1996; Segelbacher & Steinbrück, 2001; Jacob *et al.*, 2010). The amplification was performed in an Eppendorf Gradient thermal cycler, under the following condition: 15 min initial denaturation (94 °C) and 35 cycles (or 25 cycles for tissue DNA samples) of 30 s denaturation (94 °C), 2 min annealing (55 °C), 45 s extension (72 °C) with final extension 15 min (60 °C). The PCR fragments were separated on ABI PRISM 3130 capillary DNA sequencer with fluorescently labelled markers.

ALIGNMENT AND STATISTICAL ANALYSES OF MTDNA SEQUENCES

The sequences were aligned using ClustalW (Larkin *et al.*, 2007) and manually edited in BioEdit (Hall, 1999). The total length of the alignment was 413 bp. Intrapopulation genetic characteristics such as number of samples per haplotype N, number of haplotypes N_h, nucleotide diversity π and haplotype diversity H_d were estimated in ARLEQUIN 3.1 (Excoffier, Laval & Schneider, 2005). We divided the populations into different groups based on their geographical ranges and environmental condition where occur: a boreal group (Sweden, Norway, Estonia and Russia) and a Carpathian group (Slovakia – Western Carpathians, Ukraine, Romania – Eastern Carpathians). The southern group encompasses distinct geographical sites (Bulgaria – Rhodopes and Rila, Spain – Pyrenees and Cantabrian Mountains) because, before LGM, capercaillie was expected to form continuous population from the Iberian Peninsula to Bulgaria (Duriez *et al.*, 2007). The matrix of pairwise genetic distances θ_{ST} (Nei & Li, 1979) with their corresponding P-values was computed in ARLEQUIN 3.1 with 10 000 MCMC iterations (Excoffier *et al.*, 2005). To test the statistical significance of genetic differentiation between populations we used Fisher's exact test with 10 100 permutations. The AMOVA implemented in ARLEQUIN 3.1 (Excoffier *et al.*, 2005) was employed with 10 000 permutations.

Phylogenetic analyses were performed on CR I (including *Tetrao parvirostris* haplotypes as an outgroup) using neighbor-joining (NJ), maximum likelihood (ML), maximum parsimonious (MP) and Bayesian trees. Firstly the distance based neighbor-joining (NJ) tree was constructed under Tajima–Nei distance model (Tajima & Nei, 1984) and Gamma distributed rate among sites. Gamma was set to one. The reliability of the NJ tree was assessed by 10 000 bootstrap replicates.

A ML tree was constructed by implementing *HKY + I* model, inferred by the Nearest-Neighbor-Interchange heuristic method (NNI) with default set NJ/BioNJ initial tree and very strong branch swap filter. The phylogeny was tested by 10 000 bootstrap replicates.

The topology of the tree was further investigated by Min-Mini Heuristic MP search method, search level three, max number of trees to retain was set to 10. A MP consensus tree was inferred from 10 000 bootstrap replicates in MEGA 5.2 (Tamura *et al.*, 2011). The substitution model *HKY + I* and model frequencies A = 0.2667, C = 0.2936, G = 0.137, T = 0.3027 were selected in JMODELTEST (Posada, 2008), based on the Akaike information criterion corrected for small sample sizes (AICc). Phylogenetic relationships between haplotypes were inferred by Bayesian inference using 1 000 000 the Markov Chain Monte Carlo (MCMC) starting from random tree and sampling every 1000 generation (four chains, heating = 0.2) implemented in MRBAYES 3.1.2 (Ronquist *et al.*, 2011). Searches were performed using *HKY* model including proportion of invariant sites. The Bayesian 50% majority rule consensus tree was visualized in FIGTREE v1.4.2 (Rambaut, 2014). The most divergent *Tetrao parvirostris* haplotypes were used to place a root in all phylogenetic trees. The genealogical relatedness between haplotypes was represented also through a Median-joining (MJ) algorithm built-in NETWORK 4.6.1 (Bandelt, Forster & Röhl, 1999). A haplotype distribution map was constructed in ARCMAP 10.2 (ESRI, Redlands, CA). A sign of historical population expansion in each of the three groups of populations and the two lineages was tested in ARLEQUIN 3.1 (Excoffier *et al.*, 2005) by calculation of Tajima's D (Tajima, 1989), Fu's Fs (Fu, 1997) and a mismatch distribution analyses (Rogers & Harpending, 1992). Expected distribution according to a sudden demographic expansion model was tested using the sum of squared deviations (Schneider & Excoffier, 1999) and the raggedness index (Harpending *et al.*, 1993) with 10 000 bootstraps in ARLEQUIN 3.1 (Excoffier *et al.*, 2005). We visualized the frequencies of pairwise genetic differences in DnaSPv5 (Librado & Rozas, 2009). In general, the histogram of mismatch distribution shows a pattern of nucleotide differences among haplotypes within each population due to population size changes. The sum of square deviations (SSD) was calculated to test the significance of deviation of observed distribution from expected under the population expansion model.

We calculated Tau (τ) implemented in Rogers & Harpending (1992) model to estimate the time since population expansion in ARLEQUIN 1 (Excoffier *et al.*, 2005). Harris, Birks & Leaché (2014) stated mutation rate for cytochrome 1.2% per site per myr for galliformes. The first domain of CR b evolves approximately ten time faster than the average mtDNA mutation rate. The substitution rate for the CR I $\mu_{\text{CR-I}} = 1.2 \times 10^{-7}$ and in the sequence 413 nucleotides long analysed in this study is calculated as mutation rate ($\mu_{\text{CR-I}}$) multiplied by number of nucleotides in a sequence and it results in 4956×10^{-5}. For calculation of time since population expansion we used (τ) value calculated for the northern lineage and the southern lineage in ARLEQUIN 3.1 (Excoffier *et al.*, 2005).

GENOTYPING AND STATISTICAL ANALYSES OF MICROSATELLITES

Panel for microsatellite analyses excludes samples populations from Spain (Pyrenees and Cantabrian) and from Estonia whose mitochondrial data were downloaded from GenBank. Genotyping was carried out in the GENEMAPPPER 3.7 software (Applied Biosystems). The software GIMLET (Valiére, 2002) was used to construct a consensus multilocus genotype and to estimate genotyping errors such as allelic drop-out. The Microsatellite Excel Toolkit was used to identify samples sharing identical multilocus genotypes. Duplicate genotypes with ≥ 95% matching alleles were excluded from the analyses. The microsatellite marker BG16 was excluded due to the presence of null alleles caused by low amplification success in samples with low concentration of DNA extracted from faeces.

A test for deviation from Hardy–Weinberg equilibrium and linkage disequilibrium at each locus separately and per population was performed by GENEPOP (Raymond & Rousset, 1995). Genetic variation including mean number of alleles per loci (N_A), expected (H_E) and observed (H_O) heterozygosities with 95% level of polymorphism, the inbreeding coefficient F_{IS} (Weir & Cockerham, 1984) in each population and confidence interval by 10 000 bootstraps were calculated in GENETIX 4.05 (Belkhir *et al.*, 1996–2004). Allelic richness and private allelic richness were calculated in HP-RARE 1.0 using rarefaction method (Kalinowski, 2005). The program sampled 17 individuals (34 allele copies) at random from each population to match the smallest population sample size.

Pairwise F_{ST} (Nei, 1978) with corresponding *P*-values was computed between seven population units excluding historical samples in GENETIX 4.05 (10 000 permutations) implementing Bonferroni and sequential Bonferroni correction for multiple testing. The linear geographic distances between sampling site centres were measured using Google Earth (http://www.earth.google.com). The semi matrices of pairwise F_{ST} (Nei, 1978) and geographic distances were run in program Isolde implemented in GENEPOP 4.0 (Raymond & Rousset, 1995) to convert *F* statistic to $F_{ST}/1 - F_{ST}$ (Rousset, 1997) implementing sequential Bonferroni correction (Sokal & Rohlf, 1995). Finally the association between untransformed and log-transformed genetic and geographic distances was performed by a Mantel test (Mantel, 1967) using software IBDWS (Jensen, Bohonak & Kelley, 2005) with 10 000 randomizations.

Genetic relationship between individual genotypes was graphically visualized in two-dimensional space by principal coordinate analysis (PCoA) implemented in R software package POPGENEREPORT (Adamack & Gruber, 2014).

To infer the population structure we used the programs STRUCTURE 2.3.3 (Pritchard, Stephens & Donnelly, 2000) and TESS 2.3.1 (Chen *et al.*, 2007) using Bayesian clustering assignment of individuals based on allele frequencies to populations. In STRUCTURE, 10 runs, 100 000 burn-in, and 1 000 000 MCMC iterations were performed for each *K* from 1 to 8 using the admixture ancestry model assumption of correlated allele frequencies (Falush, Stephens & Pritchard, 2003). The optimum number of clusters was identified by STRUCTURE HARVESTER (Evanno, Regnaut & Goudet, 2005; Earl & von Holdt, 2012). The *Q* coefficients were obtained by averaging 20 runs using CLUMPP 1.1.2 and the 'greedy' algorithm plus the 'all possible input order' options (Jakobsson & Rosenberg, 2007). The results were displayed in figures produced by DISTRUCT 1.1 (Rosenberg, 2004).

In addition, TESS considers distinct geographical locations of each sampled individual genotype. TESS was run 20 times for each *K* from 2 to 8 using a conditional autoregressive (CAR) admixture model with interaction parameter 0.7, 10 000 burn-in and 50 000 sweeps. The most likely number of clusters determined by *K* value was specified when the deviance information criterion (DIC) reached a plateau (Chen *et al.*, 2007). We averaged the results in CLUMPP 1.1.2 (Jakobsson & Rosenberg, 2007). Subsequently the results were visualized with DISTRUCT 1.1 (Rosenberg, 2004). The map of individuals and population assignment was constructed in ARCMAP 10.2 (ESRI).

RESULTS

MTDNA SEQUENCES

We unambiguously resolved 413 bp sequences of the control region CR I in 69 samples, which included 21 distinct haplotypes that were defined by 37 polymorphic sites, 30 of them were parsimony informative. Two haplotypes of *Tetrao parvirostris* were used only for rooting the phylogenetic trees and were excluded from further analyses. Nineteen haplotypes were divided into two main lineages (Table 1). Among all 19 haplotypes, six haplotypes belonged to the boreal group, and seven haplotypes belonged to the Carpathian group. These two groups shared one haplotype found in Russia (the area surrounding Kirov) and in Romania (Eastern Carpathians). In the Balkan–Mediterranean group we found seven haplotypes with five segregating sites including

Table 1 . Genetic diversity indices based on mtDNA control region CRI sequences for the western capercaillie

Population	N	N_h	S	π	H_d
Northern lineage	47	12	20	0.006 ± 0.004	0.867 ± 0.026
Boreal group	13	6	6	0.005 ± 0.003	0.833 ± 0.082
Russia	7	2	2	0.002 ± 0.002	0.476 ± 0.171
Sweden	2	1	NA	NA	NA
Norway	3	2	1	0.002 ± 0.002	0.667 ± 0.314
Estonia*	1	1	NA	NA	NA
Carpathian group	34	7	18	0.006 ± 0.004	0.802 ± 0.040
Romania	8	4	15	0.010 ± 0.006	0.750 ± 0.139
Ukraine	7	2	1	0.001 ± 0.001	0.571 ± 0.120
Slovakia	19	3	4	0.004 ± 0.003	0.649 ± 0.061
Southern lineage	20	7	5	0.004 ± 0.003	0.753 ± 0.079
Bulgaria	17	4	3	0.003 ± 0.002	0.654 ± 0.089
Spain*	3	3	3	0.005 ± 0.005	1.000 ± 0.272

The number of analysed individuals (n), number of haplotypes (N_h), number of segregating sites (S), nucleotide diversity (π) ± standard deviation, and haplotype diversity (H_d) ± standard deviation are given.
*Haplotypes downloaded from GenBank.

four haplotypes in Bulgarian (Rila, Rhodope mountains) samples and three haplotypes from Cantabrians and Pyrenees in Spain. The southern lineage showed lower nucleotide diversity and haplotype diversity, compared with the northern lineage. The highest value of nucleotide diversity was recorded in the Carpathian group, followed by the boreal group as representatives of the northern lineage (Table 1).

PHYLOGENETIC ANALYSES

The evolutionary relationships in NJ, ML, MP and Bayesian trees did not reveal any phylogenetic pattern between sequences from the boreal and Carpathian groups within the northern lineage (Fig. 1). Sequences from Spain and Bulgaria representing the southern linage were placed together in a southern subclade within a northern clade. Support for differentiation was found for the southern subclade (bootstrap support NJ = 86%, ML = 88%, MP = 89%, Bayesian posterior probability = 0.73) and northern clade (bootstraps support: NJ = 89%, ML = 85%, MP = 89%, Bayesian posterior probability = 1.00).

The two clusters formed in NJ, ML, MP and the Bayesian trees were fully confirmed by a Minimum Spanning Network (Fig. 2). The Carpathian and Boreal groups were clustered into a group belonging to the northern lineage. The northern clade is organised around dominant haplotype found in Ukraine and Slovakia. The other northern haplotypes were derived from the dominant haplotype. The southern clade is constituted by two dominant haplotypes sampled in Rhodope and Rila Mountains in Bulgaria. Three minor haplotypes originating in Spain (Pyrenees and Cantabrian Mountains) derived from Bulgarian (Rhodope and Rila) haplotypes. One Romanian haplotype sampled in the Romania (Eastern Carpathians) was also diverged from Bulgarian haplotypes by four mutations.

POPULATION DIFFERENTIATION

In the analysis of molecular variance (AMOVA) we calculated genetic variation among boreal, Carpathian, and the southern groups. The overall fixation index was 0.66 ($P < 0.01$) and 66.57% of the total genetic variation is due to differentiation among boreal, Carpathian and Mediterranean groups. Among populations within the boreal forest, Carpathians and the southern group the fixation index (F_{sc}) was 0.35 ($P < 0.000$) and 11.82% of total variation was due to differentiation among populations (Supporting Information, Table S2). Among the northern and the southern lineage the overall fixation index was 0.75 ($P < 0.03$) and 75.59% of total genetic variation was due to differentiation among populations within the southern and the northern lineages (Supporting Information, Table S3). Genetic distances between pairs of populations (θ_{ST}) confirmed very high differentiation of the Mediterranean group from the other two (0.78–0.84). No genetic differentiation was observed between Carpathian and Boreal groups $\theta_{ST} = 0.05$ ($P < 0.07$) (Supporting Information, Table S4). Significantly high genetic differentiation $\theta_{ST} = 0.79$ ($P < 0.000$) was observed between the northern and southern lineages (Supporting Information, Table S5).

POPULATION DEMOGRAPHIC HISTORY

Significantly negative Tajima's D values ($D = -1.498$; $P < 0.05$) were found for the Carpathian group and for the northern lineage ($D = -1.715$; $P < 0.035$) suggesting historical population expansion. Tajima's D and Fu's Fs index did not have enough power to confirm the population expansion and reject a null hypothesis a stable population in the southern group, but an L-shaped graph of mismatch distribution could suggest a recent expansion (Supporting Information, Fig. S2). The northern lineage composed from the Carpathians and boreal forests had a $\tau = 1.52$, corresponding to expansion of this lineage at $T = 16\,400$ YBP. The southern lineage populations from Rhodope, Rila and Pyrenees

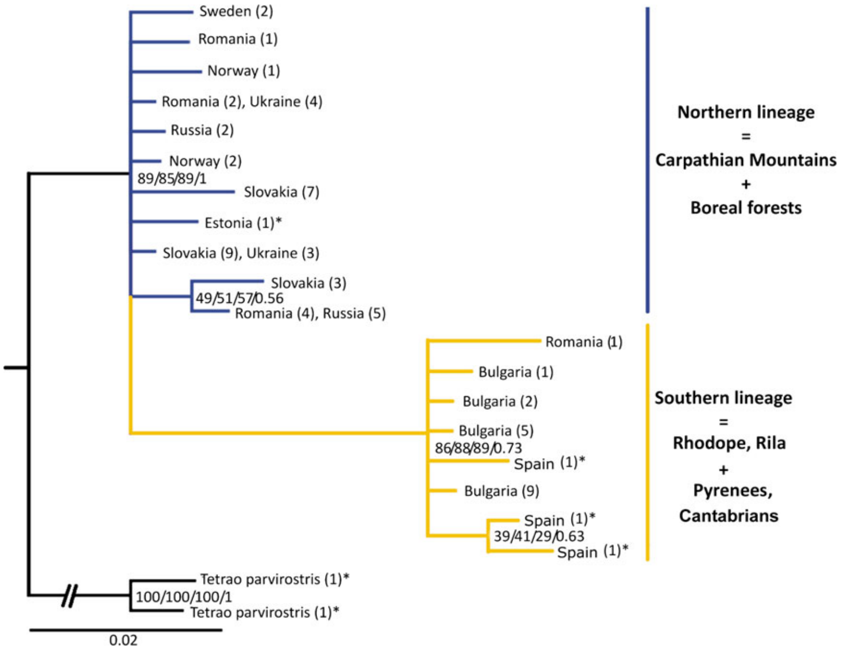

Figure 1. Phylogenetic 50% majority rule consensus tree obtained with Bayesian inference (partitioned by haplotypes) with visualized main interior nodes NJ/ML/MP bootstrap support values and Bayesian posterior probabilities. NJ, ML and MP trees reached the same topology as the phylogenetic 50% majority rule consensus tree. Haplotypes downloaded from GenBank are marked by an asterix. The haplotypes are named according to their country of origin and numbers in brackets indicate the number of samples for each haplotype. Branch lengths are proportional to the number of substitutions per site (scale bar = 0.02 substitutions/site).

had $\tau = 1.89$, corresponding to $T = 20\,800$ YBP (Table 2).

ANALYSES OF MICROSATELLITE VARIATION

Consistent departure from Hardy–Weinberg equilibrium (HWE) at particular loci across all populations and linkage disequilibrium between pairs of loci (LD) was not found by the Markov chain method implemented in GENEPOP. This means that all studied loci were evolved independently in randomly mating populations and at any particular loci was not identified heterozygosity deficiency or excess across all studied populations.

The highest mean number of alleles per locus was found in Eastern and Western Carpathians ($N_A = 6.56 \pm 1.83$, $N = 60$ and 6.67 ± 1.56, $N = 149$ respectively) and the lowest values ($N_A = 5.00 \pm 1.25$) in a group of historical samples of Western Carpathians (WCH) with the lowest sample size ($N = 17$). Expected (H_E) and observed heterozygosities (H_O) varied between $H_E = 0.61 \pm 0.18$ (WCH), $H_E = 0.68 \pm 0.15$ (boreal forests), $H_O = 0.53$ (Western Carpathians) and $H_O = 0.68 \pm 0.2$ (Bulgaria) $H_O = 0.68 \pm 0.18$ (boreal forests). The highest values of allelic richness ($A_R = 5.45 \pm 1.57$), mean number of alleles per locus ($N_A = 7.11 \pm 1.59$), expected heterozygosity $H_E = 0.70 \pm 0.09$, $N = 91$ was calculated in Northern group (Eastern Carpathian and boreal forest populations) as remnant of the northern phylogenetic lineage previously identified by mtDNA in contrary to the lowest values found in Rhodope and Rila populations representing the southern lineage ($AR = 4.42 \pm 1.42$, $N_A = 5.78 \pm 1.87$, $H_E = 0.63 \pm 0.12$, $N = 60$).

The boreal forests population is in HWE as confirmed by CI 95% values from -0.08 to 0.06. The populations of Rhodope and Rila Mountains in Bulgaria representing southern phylogenetic lineage were closer to HWE ($F_{IS} = -0.06$) than remnants of the northern lineage ($F_{IS} = 0.11$) and population of the Western Carpathians ($F_{IS} = 0.15$). The population of Western Carpathians was also in HWE ($F_{IS} = 0.07$, CI 95% = -0.09 to 0.15), but this must be considered with caution sample size were low (Table 3). The matrix of Nei's genetic distances (Nei, 1978) indicates that populations from the Rhodope and Rila Mountains (Bulgaria) are highly differentiated from the Carpathian populations (Romania, Ukraine and Slovakia) and populations of boreal forests (Russia and Sweden). Within the Western Carpathians, fragmented populations in Slovakia are weakly differentiated from populations inhabiting the south of Poland ($F_{ST} = 0.085$, $P < 0.000$) which

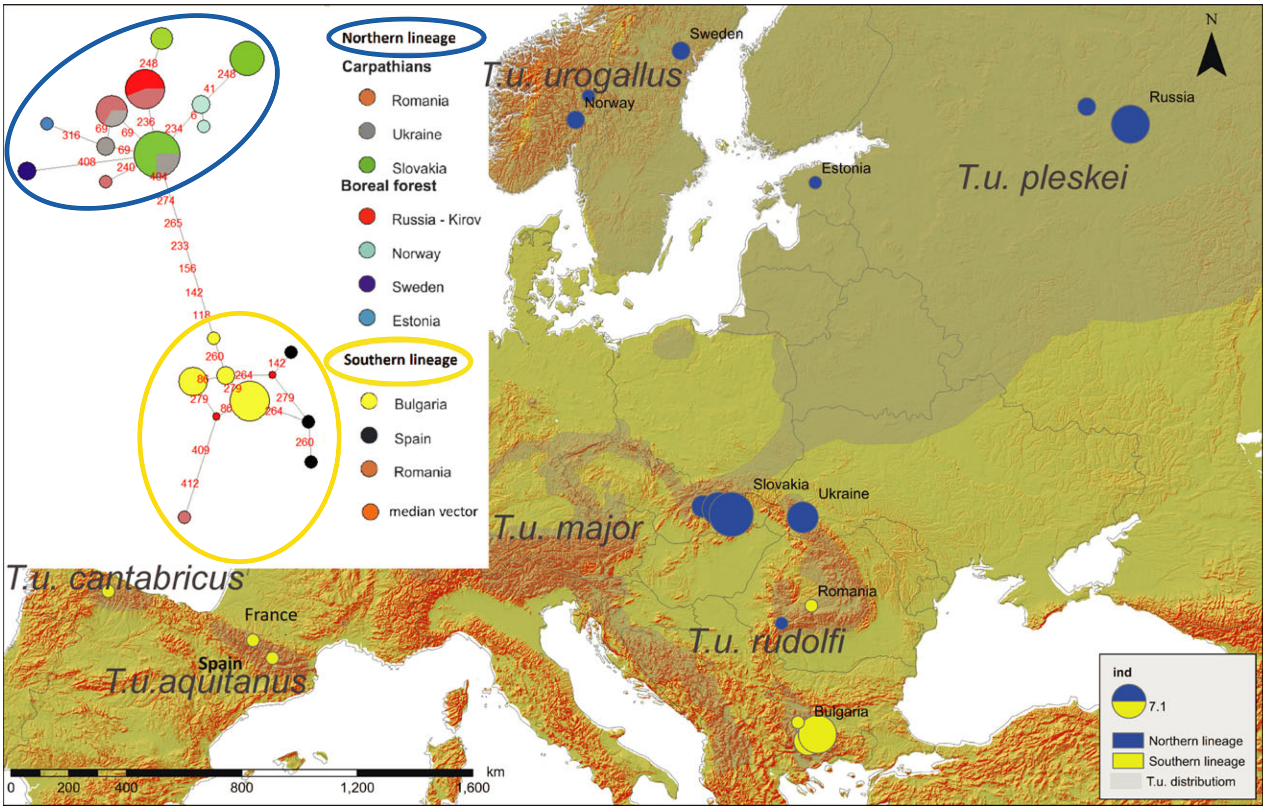

Figure 2. The map of the mtDNA CRI haplotype distribution of two phylogenetic lineages diverged by NJ, ML, MP, and the Bayesian posterior probabilities methods implemented for reconstruction of phylogenetic trees. In the left corner is visualized a Median-joining Network of capercaillie haplotypes. The sizes of the pie charts correspond to the number of individuals restricted to a single haplotype.

Table 2. Population demography history indices of the Northern and Southern lineages as well as the main groups of capercaillie found in the study

Population	Tajima's D	Fu's Fs test	τ	$t = \tau \div 2\mu$	SSD	Raggedness
Northern lineage	−1.715	−2.932	1.5156	16.400	0.020	0.048
	$P < 0.035$	$P < 0.12$			$P < 0.04$	$P < 0.6$
Boreal group	−0.118	−1.314				
	$P < 0.5$	$P < 0.16$				
Carpathian group	−1.498	0.485				
	$P < 0.05$	$P < 0.7$				
Southern lineage	−0.125	−2.172	1.8945	20.800		0.113
	$P < 0.5$	$P < 0.075$			$P < 0.15$	$P < 0.3$

Tajima's D, Fu's Fs, Tau (τ) was to estimate time since population expansion (t), sudden demographic expansion model using the sum of squared deviations (SSD) and the raggedness index was tested with 10 000 bootstraps in Arlequin 3.1. Time (YBP) since population expansion (t).

suggests that the alpine habitats of the High Tatras could slightly limit a gene flow within Western Carpathian population (Supporting Information, Table S6).

The non-significant Mantel test of untransformed distances with 10 000 randomizations excluded IBD effect ($r = 0.54$, $P < 0.05$). But, the Mantel test was significant with log-transformed geographic distance ($r = 0.58$, $P < 0.02$) and the significance increased with log-transformation both genetic and geographic distances ($r = 0.69$, $P < 0.006$). Excluding the population of Rhodope and Rila in Bulgaria the significance of IBD calculation with log-transformed geographic distance increased ($r = 0.6$, $P < 0.007$) (Fig. 3).

The two-dimensional PCoA included all 317 analysed genotypes. We found a clearly differentiated group of birds from Bulgaria, from the most variable group composed of capercaillie sampled in the Eastern Carpathians – Romania, Ukraine and the boreal taiga forests – Sweden and Russia. The third differentiated Western Carpathian group was composed of samples from present and historical genotypes from Slovakia and Poland (Fig. 4).

BAYESIAN ASSIGNMENT

A similar pattern of population clustering as observed by PCoA was found by assignments using a Bayesian approach implemented in STRUCTURE and TESS. In both analyses populations were inferred to $K = 3$ clusters and confirmed the single Western Carpathian group (Slovakia and southern Poland) grouped with the Slovakian historical samples from 1960 to 1940. The second cluster grouped the Eastern Carpathian (Ukrainian and Romanian) samples with boreal forests (Swedish, Russian (Kirov area) samples. The Rhodope and Rila populations in Bulgaria were confirmed as one distinct cluster (Fig. 5). To verify the above observed clustering, we performed an analysis excluding the distinct population of southern individuals originating from Bulgaria and above the mentioned structuring was observed again. The individuals of the Western Carpathian population were inferred to single cluster and those from the Eastern Carpathians and boreal forest were inferred together to the second cluster (Supporting Information, Fig. S3).

DISCUSSION

PHYLOGEOGRAPHY AND REFUGIA

Analyses of mtDNA showed that haplotypes from Bulgaria and Iberia belong to the southern clade and the haplotypes from the Carpathians and boreal forests belong to the northern clade with strong support in the NJ, ML, MP and Bayesian trees. The haplotypes found in the boreal forests and the Carpathian arch did not show any indication of genetic differentiation and were also grouped together within a Minimum Spanning phylogenetic network using the MJ algorithm. Only one sample, originating from the Făgăraș Mountains in southern Romania, shared a haplotype associated with the southern lineage (Fig. 2). Such a pattern could signal a contact zone between the southern and the northern lineage in the past.

Table 3. Genetic diversity indices of microsatellites per population inhabiting seven countries: sample size (*N*), mean number of alleles per locus (N_A/locus), allelic richness (AR), private allelic richness (priv. AR), mean number of alleles per loci (N_A/loci), expected heterozygosity (H_E), observed heterozygosity (H_O), standard deviation (SD), 95% threshold of polymorphism *P* (0.95), and fixation index (F_{IS}) (Weir & Cockerham, 1984) with confidence interval (CI) 95%

Country	*N* samples	AR	Priv. AR	N_A/loci	H_E	H_O	*P* (0.99)	F_{IS}	CI (95%)
Western Carpathians (± SD)	149	4.87 ± 1.21	0.30 ± 0.23	6.67 ± 1.56	0.62 ± 0.19	0.53 ± 0.20	1	0.15	(0.09 to 0.20)
Western Carpathians (historical samples) (± SD)	17	5 ± 1.25	0.30 ± 0.46	5.00 ± 1.25	0.61 ± 0.18	0.59± 0.23	1	0.07	(−0.09 to 0.15)
Northern lineage (± SD)	91	5.45 ± 1.57	0.88 ± 0.44	7.11 ± 1.59	0.70 ± 0.09	0.62 ± 0.13	1	0.11	(0.06 to 0.16)
Eastern Carpathians (± SD)	60	5.24 ± 1.49	0.33 ± 0.29	6.56 ± 1.83	0.67 ± 0.08	0.59 ± 0.11	1	0.13	(0.06 to 0.19)
Boreal forests (± SD)	31	5.19 ± 1.13	0.64 ± 0.63	5.56 ± 1.26	0.68 ± 0.15	0.68 ± 0.20	1	0.01	(−0.08 to 0.06)
Southern lineage (Rila, Rhodope) (± SD)	60	4.42 ± 1.42	0.80 ± 0.5	5.78 ± 1.87	0.63 ± 0.12	0.68 ± 0.18		−0.06	(−0.12 to −0.02)

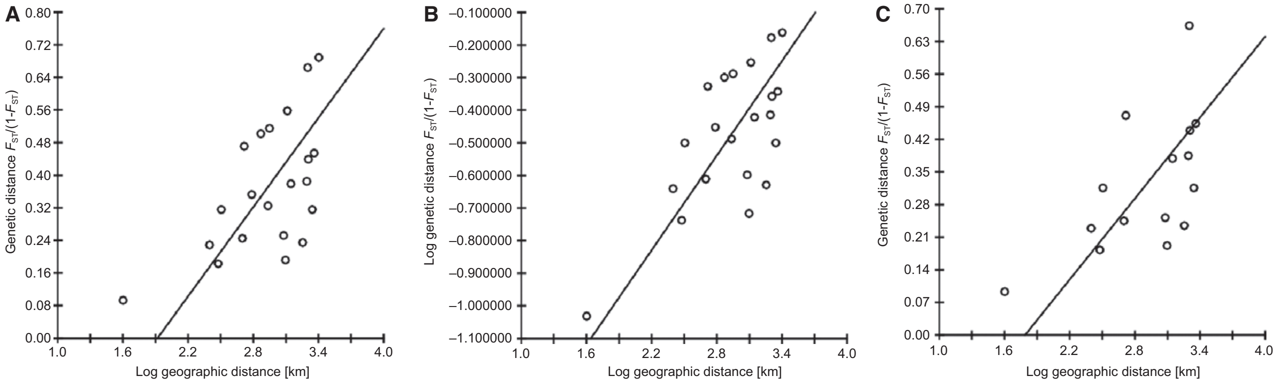

Figure 3. Isolation by distance, the regression of: (A) linear log geographic distance (km) and genetic distance. $F_{ST}/(1-F_{ST})$, $r = 0.58$, $P < 0.02$, (B) log–linear geographic distance (km) and log genetic distance $F_{ST}/(1-F_{ST})$, $r = 0.69$, $P < 0.006$, (A, B) including pairwise distances between all seven populations excluding the historical population from Slovakia (C) log geographic distance (km) and the genetic distance $F_{ST}/(1-F_{ST})$ excluding historical samples and the Bulgarian population $r = 0.6$, $P < 0.007$. The correlation coefficients and their P-values were obtained using the Mantel test (Mantel, 1967) with 10 000 randomizations.

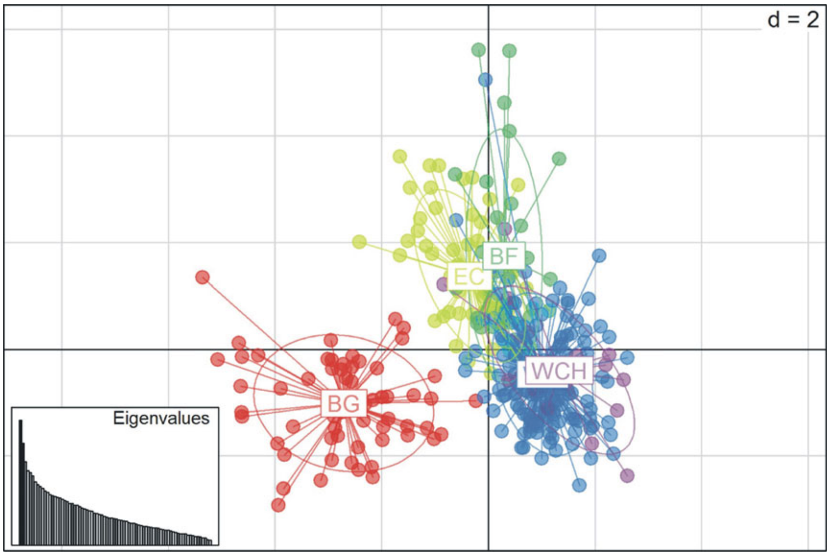

Figure 4. Principal Coordinate Analysis (PCoA) of individual capercaillie microsatellite genotypes and their coordinates performed using the R package PopgeneReport to visualize the three groups: (1) BG (Bulgaria – Rhodope, Rila mountains), (2) BF (boreal forests), EC (Eastern Carpathians), (3) WCH (Western Carpathians historical samples, WC (Western Carpathians present samples) – data overlap. The bar plot shows the proportion of genetic diversity described by principal component (eigenvalues).

In the northern lineage a significant negative Tajima's D value, unimodal mismatch distribution and τ value suggests a population expansion after the LGM 16 400 years BP. In the southern lineage we could not detect any demographic changes (non-significant Tajima's D and Fu's Fs values) but a unimodal mismatch distribution may signal an earlier past demographic expansion of the southern lineage 20 800 years BP. Previously two primary glacial refugia for the western capercaillie populations in Europe were suggested (Segelbacher & Piertney, 2007): one in the Iberian Peninsula for the southern lineage and another one in Eastern Europe for the northern lineage. Our results indicate the Pyrenean, Cantabrian and Bulgarian populations seem to be the remains of the southern lineage and might be considered as a southern lineage of postglacial expansion corroborating conclusions from Duriez *et al.* (2007) and Segelbacher & Piertney (2007). Duriez *et al.* (2007) assumed the glacial refugium of the northern *urogallus* lineage

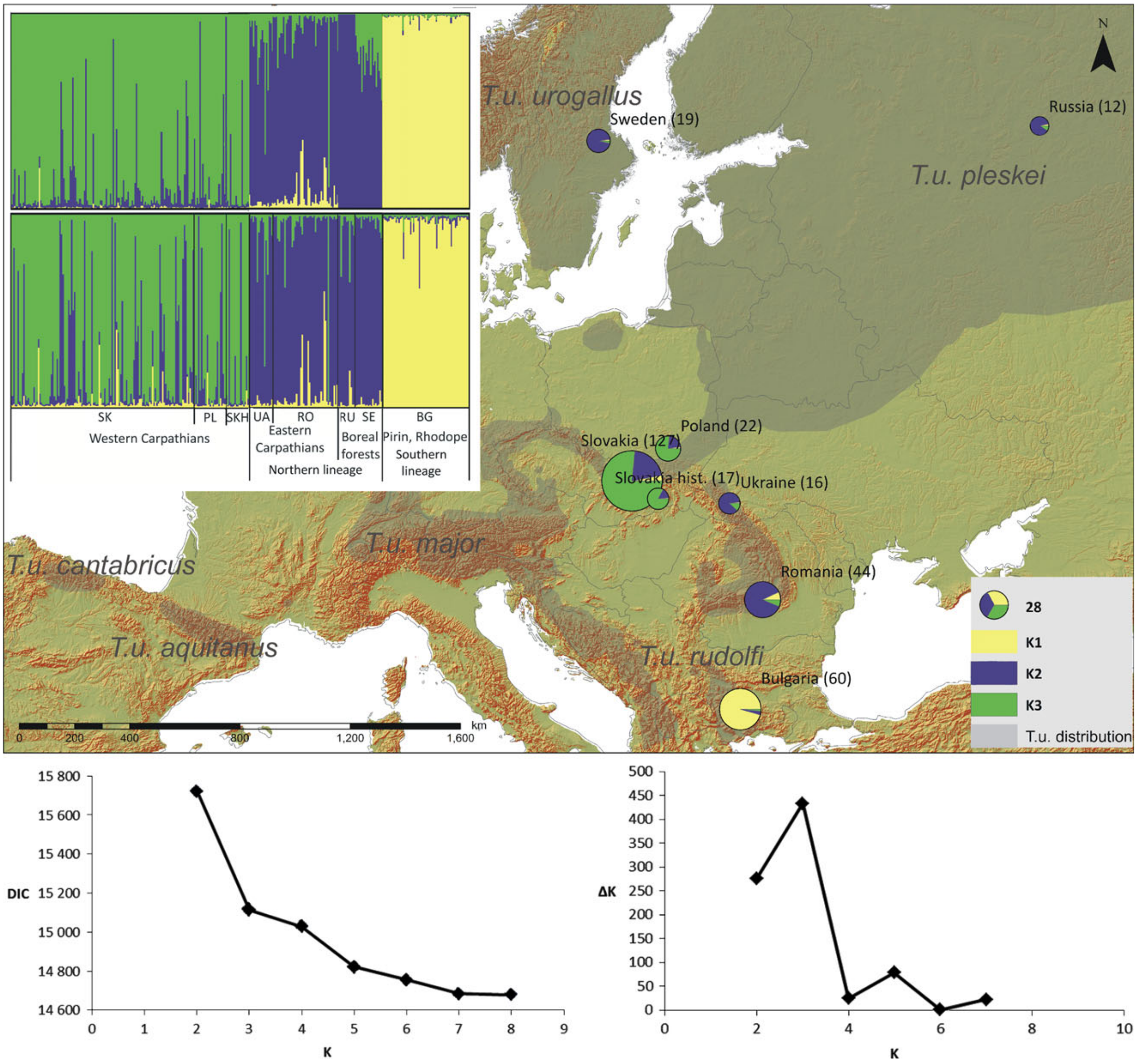

Figure 5. Map of individual and population assignments into three clusters using the TESS (top) and STRUCTURE (bottom) software visualized in the left upper corner. The sizes of the pie charts correspond to the number of individuals per population. The mean values for the deviance information criterion (DIC) vs. K statistics averaged over TESS 20 runs and mean delta K vs. K averaged over STRUCTURE 20 runs are shown.

was in southern Asia. However, the exact location of this refugium is still unknown. It has been suggested that the southern lineage had expanded through Europe before the LGM and during the LGM was forced back to its southern refugia (Duriez *et al.*, 2007; Bajc *et al.*, 2011).

Migration routes and colonization of northern habitats from Iberia, Italy, and the Balkans were suggested by Hewitt (1999) for several mammal, birds and tree species. The western capercaillie is a grouse species adapted to spruce forests, even though sometime inhabiting other coniferous or mixed stands as well. We might thus assume that dispersal and postglacial colonization was tracking the Norway spruce (*Picea abies*) postglacial expansion. Tollefsrud *et al.* (2008) studied the divergence of a southern and northern lineage of spruce expansion during the Holocene and found a single northern lineage spruce refugium in the East European Plain diverged from the southern lineage whose refugia were in the South-western Bulgarian mountains, south-eastern Alps, the southern Bohemian Massif, Western

Carpathians and southern Carpathians (Tollefsrud *et al.*, 2008). The spruce population of the Alps diverged from those of the Hercynic-Carpathian area. Also, spruce populations of the Western Carpathians are differentiated from the Eastern Carpathian populations in quantitative traits (Collignon, van de Sype & Favre, 2002). Our results suggest some correlations with spruce and the postglacial colonization of the capercaillie. We suggest a glacial refugium for the northern lineage birds in the East European Plain in accordance to what has been suggested for spruce. We hypothesize that during the forest recolonization after the LGM, the larger sized northern birds replaced the southern lineage individuals probably inhabiting the above mentioned southern refugia of spruce. The East–West direction of Cantabrian, Pyrenees, Alps, and southern Carpathians with peaks covered by ice interrupted the northern birds' expansion and the southern lineage individuals survived only in Iberia and the Balkan range.

'Long term historical isolation' vs. isolation by distance

Microsatellite analyses of population differentiation and their assignment into clusters suggest that the Western Carpathian population is a single cluster separated from the boreal–Eastern Carpathian population. A pattern of mixed ancestries was shown by the Bayesian analyses of the microsatellite data. Some immigrants from the Eastern Carpathians indicate recent introgression and existence of weak gene flow between the Eastern Carpathian and Western Carpathian populations. It is possible that the Western Carpathian population is derived from the Eastern Carpathian one.

The range of the capercaillie in the Western Carpathians is well separated from that in the Eastern Carpathians (Ukrainian and Romanian Carpathians) by a zone of approximately 200–250 km. This is a zone in which the continuous cover of coniferous forests in higher altitudes is missing. Hence, the observed break in microsatellite genotypes distribution may be due to lack of suitable habitats in this part of the Carpathians, although within a relatively short distance. Straka *et al.* (2012) described a similar pattern of genetic differentiation between the Western Carpathian brown bear (*Ursus arctos*) population and the Eastern one. A study on the Carpathian newt (*Lissotriton montandoni*), combining microsatellite data and ecological niche modelling revealed, consistency of genetically distinct units with the isolated last glacial refugia within the Carpathians. The authors assumed the Western Carpathians as an isolated unit within a major Carpathian refugium. The Western Carpathian newt population was identified by microsatellites as genetically distinct during the LGM and isolated from the refugia in the eastern and the southern Carpathians (Zieliński *et al.*, 2013). We postulate a similar pattern could explain the difference between Western Carpathian and the Eastern Carpathian capercaillie observed in this study. The observed differentiation is likely a consequence of long term isolation since the last glaciation during which the Western Carpathian individuals lost genetic diversity via genetic drift due to environmental and/or demographic stochastic processes occurring in isolated populations. Another possible scenario explaining the genetic differentiation within the Carpathians may be different postglacial recolonization route from the alpine area as revealed by AFLP analyses of the plant *Pritzelago alpina* (Kropf, Kadereit & Comes, 2003). For capercaillie, a microsatellite comparison with neighbouring birds to the west (the Bohemian Forest, Bavarian Forest and the Alps) would make it possible to distinguish among these alternative hypotheses.

Previously a significant IBD has been observed among capercaillie in studies with samples from European populations (Segelbacher & Storch 2002; Segelbacher *et al.*, 2003). We expected that over the whole range of the species, the trend of isolation by distance (IBD) would be weakly significant but that phylogeographic processes such as different recolonization routes for northern and southern habitats may distort the signal. The weak pattern of IBD among capercaillie populations from the boreal forests, Carpathians and Bulgarian Rila and Rhodope are surprising. While there is no significant association between log-untransformed genetic differentiation and geographical distance, the differentiation is significantly associated with the log-transformed geographic distance. This pattern might be explained if the log transformation emphasizes small distance comparisons and de-emphasizes longer distances, which is usually observed in populations where gene flow is more influential on a small scale and genetic drift more important at large distances (Hutchison & Templeton, 1999; Koizumi, Yamamoto & Maekawa, 2006). The pattern of IBD seems to be minimized if the distance separating pairs of populations exceeds 100 km (Barr *et al.*, 2008). Removing the Bulgarian population increased the significance. This may indicate that different refugial populations, colonization routes and long term historical isolation may confound the pattern of IBD.

Assignment of Romanian and Ukrainian (Eastern Carpathian) populations to the cluster with the populations of Sweden and Russia (boreal forests) might be a signal of preserved historical genetic structure due to large population sizes, high quality of habitats as well as good genetic and social structures within the Eastern Carpathian populations.

This study confirms ‘long term historical isolation’ rather than ‘IBD’ at least for the Carpathians. A significant barrier to gene flow exists between Western and Eastern Carpathians based on microsatellite data. Eastern Carpathian birds are genetically more related to geographically remote populations of the boreal forests of Russia and Sweden than to geographically close population of Western Carpathians. A higher differentiation in the case of Balkan (Bulgaria) vs. Eastern Carpathian populations (Romania and Ukraine) might be the result of different historical origins for both populations as was revealed by the phylogenetic analyses. The proposed separation of the Bulgarian population is consistent with a glacial refugium of capercaillie in the Balkans as previously suggested (Duriez *et al.*, 2007; Bajc *et al.*, 2011).

TAXONOMIC COMMENTS

We did not find any evidence of genetic distinction of the subspecies *T. u. pleskei* (in European Russia) and *T. u. urogallus* (in Sweden). However, we suggest that the smaller body size of *T.u. rudolfi* is an adaptation to living in mixed forests while the larger bodied *T. u. major* inhabit the high altitude Norway spruce habitats of the Western Carpathian mountains in Slovakia and Poland. CR I sequence data suggest that the subspecies status of the birds inhabiting the Eastern and Western Carpathians is still not clear (whether they should belong to *T. u. major* or not). Analyses of CR I clearly indicate that *T. u. rudolfi* is not distributed across the Rhodope and Eastern Carpathians as was suggested by Couturier & Couturier (1980), Kohl & Štollmann (1968, 1971) and stated in Clements’ checklist of birds of the world (Clements *et al.*, 2013). CR I differentiation of the Bulgarian Rhodope and Rila populations might indicate presence of different subspecies in each mountain range. However, no genetic differentiation between Eastern and Western Carpathians populations based on CR I indicates that the above mentioned morphological differences could be the result of phenotypic plasticity of capercaillie. Based on the differences among neutral molecular markers such as microsatellites and CR mtDNA we cannot say if the observed differences are due genetic drift, phenotypic plasticity or selection and there is thus scope for further studies using both neutral markers and genetic variation subjected to selection. Contradicting taxonomic classification in subspecies level of another Tetraoninae species was revealed in willow grouse (*Lagopus* sp.) (Höglund *et al.*, 2013).

CONCLUSION

We conclude that based on nDNA and mtDNA analyses abundant Eastern Carpathian populations inhabiting the Romanian and Ukrainian well connected habitats have been able to preserve their genetic structure from the last glaciation period. These populations are genetically similar to populations inhabiting the boreal forests and together they constitute the northern lineage of capercaillie. Present migration among Swedish, Russian and Eastern Carpathian populations is excluded but in spite of this, the genetic structure has been preserved due to both high abundance and habitat connectivity within populations. The Western Carpathian populations are long term isolates with only a few migrants from the Eastern Carpathians, and so became differentiated from the eastern and northern populations. We demonstrated that the Balkan population (Bulgaria) represents a southern lineage of population expansion and should be considered as a genetically distinct unit.

RECOMMENDATIONS FOR THE CONSERVATION MANAGEMENT

Finnish capercaillie lek areas are managed by foresters based on recommendations from Fennoscandinavian grouse experts (Pakkala, Pellikka & Lindén, 2003). It is imperative to develop similar forest management practices in capercaillie areas throughout the entire Carpathian Mountain Range. Proper forest management of wide scale areas taking into account the requirements of capercaillie plays a crucial role in the long term survival of capercaillie populations in Europe’s second largest mountain range – the Carpathians. The revealed genetic constitution should be taken into account in designing supplementation action within the Carpathians.

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AUTHOR CONTRIBUTIONS

PK, LP, JH: Contributed to conception and design. LP, PK, JH, PZ, MM: Contributed to acquisition of data. PK, LP, JH: Contributed to analysis and interpretation of data. PK, LP, JH: Drafted and/or revised the article. PK, LP, JH: Approved the submitted version for publication.

DATA ACCESSIBILITY

The sequences will be uploaded in GenBank pending acceptance of the paper.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Map of Western capercaillie range (BirdLife International 2012) and subspecies distribution according to (Couturier & Couturier 1980). Sampling sites (circles) and mtDNA haplotypes of control region CRI downloaded from GenBank (squares).
Figure S2. Observed and expected mismatch distributions of pairwise nucleotide differences between 19 capercaillie haplotype frequencies.
Figure S3. Structure graph of Western Carpathians, Eastern Carpathians and Boreal forests populations excluding populations in Rhodope and Rila mountains.
Table S1. Sites and sampling information for microsatellite genotypes and mtDNA sequences of western and blackbilled capercaillie.
Table S2. Analysis of molecular variance AMOVA of mtDNA haplotypes for boreal, Carpathian and southern group. The test of significance was assessed on 10 100 permutations.
Table S3. Analysis of molecular variance AMOVA of mtDNA haplotypes between the northern and the southern lineages, among populations of Sweden, Norway, Estonia, Slovakia, Romania, Ukraine within the northern lineage and Bulgaria, Spain within the southern lineage. The test of significance was assessed on 10 100 permutations.
Table S4. Pairwise genetic distances among population groups θ_{ST}, of mtDNA haplotypes. *P*-values after 10 000 permutations are above the diagonal and θ_{ST}, values are below the diagonal.
Table S5. Pairwise genetic distances among phylogenetic lineages θ_{ST}, of mtDNA haplotypes.
Table S6. Pairwise genetic (Nei 1978) vs. geographic distance matrix [km] all pairwise F_{ST} values $P = 0.000$ after 10,000 permutations.

SHARED DATA

Data deposited in the Dryad digital repository (Klinga *et al.*, 2015).

5.5 Mikoláš M., Svitok M., Janda P., Trotsiuk V., Čada V., Bače R., Morrissey, R. C., Mrhalová H., Theodosiu M., Coppes J. & Svoboda M. Mixed severity disturbance regime critical for survival of endangered umbrella species in the primary forest ecosystems (in prep.).

Mixed severity disturbance regime critical for survival of endangered umbrella species in the primary forest ecosystems

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Summary

1. Currently, biodiversity loss is greater than ever documented, mainly due to alteration of natural disturbance regimes caused by intensive management of biological resources. Species assemblages have evolved under natural disturbance regimes. Detailed information about the relationship between natural disturbance regimes and habitat use of species in their natural settings are missing and are highly essential to halt the rapid biodiversity declines.

2. To understand the effects of long-term multiple disturbance components on species habitat dynamics, we collected dendrochronological data on 104 plots in the primary forests driven by the mixed severity disturbance regime in the largest temperate forest ecosystem in Europe – the Carpathians. Specifically, we studied the relationship between the endangered umbrella species capercaillie (*Tetrao urogallus*) and spatiotemporal dynamics of forest structure and disturbance history.

3. We applied a multi-model approach in combination with predictive modeling, in order to obtain robust answers to following questions: (1) How does the natural mixed severity disturbance regime shape capercaillie habitats? (2) Which disturbance variables and primary forest structures determine the probability of capercaillie occurrence?

4. Natural disturbance-related variables ranked among the best single predictors of capercaillie presence in all models. Natural disturbance regimes were tightly linked with structural characteristics of forest, including ground vegetation, age structure, density of standing dead wood, and tree density. Presence of capercaillie was best explained by the parsimonious GLM with four significant variables (mean diameter of standing dead wood, regeneration cover, and diversity of disturbance severities) and PLS-DA model with distance to the gap, density of living trees, and ground vegetation cover as the variables with the highest importance.

5. Unimodal relationship between historical diversity of disturbance severities and probability of capercaillie occurrence, together with the strong preference of capercaillie to forest stand gaps showed, that wide range of disturbance severities is required to maintain capercaillie populations in natural habitats. The mixed-severity

disturbance regime created heterogeneous and complex environment for an endangered umbrella species, capercaillie.

6. *Synthesis and application*. Protection of ecological processes is likely the most effective way for biodiversity and capercaillie conservation in European mountain forests. To restore capercaillie habitats, management practices that mimic these patterns are recommended to increase structural complexity.

Key words: natural disturbance regime, forest management; predictive modeling, Europe; capercaillie, biodiversity, conservation planning

Introduction

Understanding the role of natural disturbance regimes on species assemblages in their primary habitats is crucial for the effectiveness of conservation strategies (Pickett & White 1985, Willis & Birks 2006, Turner 2010). Species extinctions are occurring at a rapid rate as a consequence of human resource management, particularly the loss of natural habitats due to alteration of disturbance regimes (Chapin *et al.* 2000; Halme *et al.* 2013). From an evolutionary perspective, natural habitats have been shaped by natural disturbance regimes and the disturbance frequency, intensity, and spatial pattern has influenced the habitat structures and consequently the distribution of functional groups across landscapes (Frelich 2002). Despite of long-lasting research on effects of disturbances on biodiversity (eg. Sousa 1984, Angelstam 1998; Survey *et al.* 1999; Fontaine *et al.* 2009), there is still an intense debate about the relation between disturbances and species diversity among the ecologists (Roxburgh *et al.* 2004, Miller *et al.* 2011, Svensson *et al.* 2012). Effects of natural disturbance regimes, characterized by long-term multiple disturbance components under which species assemblages evolved are still poorly understood (Yeboah and Chen 2016).

Many studies on the species diversity-disturbance relationships were focused on effects of either high severity stand replacing disturbances or low severity disturbances (eg. Long 2009, Thorn *et al.* 2016). However, in the primary forests ecosystems (like in many other ecosystems); natural disturbance regimes are comprised of a continuum of disturbances. They are ranging from occasional death of canopy trees caused by pathogens or senescence, to widespread low severity mortality caused by drought or herbivore, or moderate severity or high severity fires, blowdowns, or insect outbreaks, and they are characterized by a variety of patch sizes, frequencies, severity, timing, spatial pattern and extent of natural disturbances. All these often results in mixed severity disturbance pattern that includes all disturbance severities at different spatial scales. However, information about the interactions between species habitat relations under the mixed severity disturbance regimes are very limited in the literature, despite it is currently considered as one of the probably most common disturbance regime types (eg. Perry *et al.* 2011, Halofsky *et al.* 2011, Trotsiuk *et al.* 2014). The disturbance interactions over time yield a countless number of alternate developmental pathways resulting in complex structures of primary forests (Donato, Campbell & Franklin 2012). The complex structure characteristic of primary forests is recognized as critical to the preservation of biodiversity across multiple scales (Halme *et al.* 2013). We refer to “primary forest” as forest without signs of direct human impact which structure, composition and processes resulted from natural disturbances. In these forests a broad range of disturbance severities influence the structure and heterogeneity, providing habitats for diverse functional groups of many forest species (Swetnam, Allen & Betancourt 1999; Kuuluvainen 2002, Seibold *et al.* 2015). Conservation planning often relies on umbrella species as a “coarse filter” approach to preserving biodiversity; umbrella species are typically selected because they confer protection to a wide range of naturally co-occurring species (Branton & Richardson 2014). In the Eurasia, as an important umbrella species is considered the bird species capercaillie (*Tetrao urogallus*), because of its complex habitat and large area requirements (Storch 1995, Suter, Graf & Hesst 2002; Pakkala, Pellikka & Lindén 2003) indicating structurally diverse mountain and boreal forest ecosystems (Cas & Adamic, 1998; Klaus *et al.*, 1989; Storch, 1995). Capercaillie numbers are declining rapidly, especially in central and western Europe, resulting in being red-listed Annex 1 of the EU Birds Directive mainly due to habitat loss (Storch 2007). Extensive studies of capercaillie habitat requirements, mainly in managed forests, found moderate intensities of forest management being beneficial for capercaillie habitat quality (Storch 2002; Graf *et al.* 2005; Bollmann, Weibel & Graf 2005). On the other hand, extensive natural disturbances have affected European forests recently, and have spurred a discussion and management uncertainties due to which large areas of suitable habitats including the primary forest have been harvested by post-disturbance logging on large spatial scales (Mikoláš *et al.* 2013, Knorn *et al.* 2012). However, the impact of natural disturbance regime patterns on capercaillie habitat dynamics in areas without human management has not been evaluated yet.

Therefore, we addressed two main research questions:

(1) How did the natural mixed severity disturbance regime shape capercaillie habitats?

(2) Which disturbance variables and primary forest structures determine the probability of capercaillie occurrence?

Based on the previous studies, we expect that the low to moderate severity disturbances that keep the canopy closure at moderate levels (40-80 %) to be optimal for the capercaillie (e.g. Bollman *et al*., 2005; Graf *et al*., 2009, Mikoláš *et al.* 2015).

In this study, we present the first quantitative analysis of capercaillie habitat requirements in relation to natural forest disturbance history in the primary forests. Instead of relying on a single "best" habitat-requirement model, we adopted multi-model strategy and assessed several models of increasing complexity (simple, parsimonious and complex) in order to prevent discarding any potentially important information and to ensure robustness of the results against the choice of a single analytical method which might be rather subjective. Moreover, we did not restrict ourselves to report statistically significant results of null hypothesis tests, since those might be biologically irrelevant or even misleading (e.g., Berger & Sellke 1987; Johnson 1999; Hurlbert & Lombardi 2009), but we went beyond statistical significance and evaluated predictive performance of the models on out-of-sample data (Shmueli 2010). Stated simply, we were concerned about the real world usefulness of the results and the ability of the models to generalize to out-of-sample situations, such as new sites.

Materials and methods

STUDY AREA

One of the largest remaining continuous forest ecosystems in Europe are the Carpathian Mountains (Gurung et al., 2009), that encompass the largest remaining areas of primary forests in temperate zone of Europe (Veen *et al.* 2010) and the second largest capercaillie population in Europe (when not including Russia or Scandinavia) (Storch 2007). Hence the Carpathians present a unique opportunity to study the effects of natural disturbance regimes on capercaillie in otherwise very urbanized and industrialized European temperate zone. The Carpathian primary forests driven by a mixed severity disturbance regime (Trotsiuk *et al.* 2014, Svoboda *et al.* 2014), provide the opportunity to assess the effects of natural disturbances on capercaillie habitat across a full range of natural disturbance severities, including the moderate severity disturbances.

This study was conducted in the core zone of capercaillie distribution of the Carpathians (in two mountain forest landscapes of Giumalu and Calimani in the Romanian Carpathians (Fig.1.); in each mountain range two primary *Picea abies* (L.) Karst. stands in the core areas of capercaillie distribution were selected. *Picea abies* is the dominant tree species at elevation between 1250 - 1650 m a. s. l. with a lesser admixture (<5%) *of Sorbus aucuparia* L., and *Pinus cembra* L., *Acer pseudoplatanus* L., and *Betula pendula* Roth. These forests have a dense understory dominated by *Vaccinium myrtillus, Calamagrostis villosa, Luzula sylvatica*, and *Avenella flexuosa* (own data). Average annual temperature in the study region varies from 2.4 to ca. 4.0 °C; precipitation varies between 1100 and 1650 mm annually, and increases with altitude (Food and Agriculture Organization (FAO) Local Climate Estimator New_LocCLim v. 1). Snow is present 139–208 days per year, and contributes up to 500 mm of the total annual precipitation.

HABITAT STRUCTURES

We sampled structure and past disturbance history using 104 circular 1000 m2 permanent study plots which were established using stratified random design, as described by (Svoboda *et al.* 2014), that represent an area of 182 ha (in Calimani 60 ha and in Giumalau 122 ha). All live and dead trees ≥ 10 cm diameter at breast height (DBH) were measured and species were recorded. Regeneration density by species was recorded in three height classes (0.5-1.3 m, 1.3-2.5 m, and > 2.5 m). Ground vegetation was described including vegetation height, vegetation cover, and bilberry (*Vaccinium myrtillus*) cover, an important food source for capercaillie (Storch 2002). Distance to the nearest canopy gap (between 0.05 and 0.85 ha, mean 0.23 ha)), was evaluated from aerial images, and later validated during fieldwork.

CAPERCAILLIE DATA

Capercaillie presence and absence was determined by a thorough search of each plot for signs that would indicate capercaillie habitat use (e.g. feathers, droppings, tracks in the snow etc.) during the winter season (2013-2014) before the snow had melted.

DISTURBANCE HISTORY AND AGE STRUCTURE VARIABLES

Age structure and disturbance history reconstruction was based on the study of Svoboda et al. (2014). For each plot, they used crossdated ring-width series from 25 randomly selected living trees that are not underneath the canopy. To get the tree age for cores that did not intersect the pith, the number of missing rings was estimated using Duncan's method (1989) For every plot we calculated mean age, median age, minimum and maximum age, mean age of five oldest trees, interquartile range of age (see Table S1).

The disturbance history was reconstructed based on two patterns of radial growth: (i) abrupt and sustained growth increases related to the mortality of a former canopy tree, classified as "releases", and (ii) rapid early growth rates related to recruitment in canopy gaps, classified as "gap recruitment" (Frelich & Lorimer 1991). Disturbance severity was evaluated by the sum of release and gap recruitment events in each decade, as weighted by the current crown areas, to calculate the proportion of a plot disturbed in each decade. For a more detailed description of the reconstruction of disturbance histories, see Svoboda *et al.* (2014).

We created variables characterizing the disturbance history of individual plots, including the maximum disturbance severity, the time since the maximum disturbance, and diversity of disturbance severities represented by the disturbance index (Svoboda *et al.* 2014). Disturbance index (DI) represents the overall severity of the disturbance regime per plot characterized using the commonly used Shannon index of diversity (Svoboda *et al.* 2014). Low values (minimum reaches ca. -3) indicate low severity disturbances that occurred frequently over time, while the maximum theoretical value, 0, indicates that 100% canopy area was disturbed during a single decade (see Svoboda *et al.* 2014 for more details and justifications). The highest diversity of disturbance severities is represented by the mean values of the DI. All the variables used are summarized in Table S1.

DATA ANALYSIS

EFFECT OF DISTURBANCES ON HABITAT CHARACTERISTICS

The effects of disturbance on habitat characteristics (forest structure) were assessed using multivariate linear models (see Table S1 for an overview of all variables used). Habitat characteristics were standardized to zero means and unit standard deviations to accommodate for different units of measurement across the variables. Our application of multivariate models deviates from traditional MANOVA approaches in two aspects. First, we applied ridge regularization to account for correlation between habitat characteristics; this produces numerically more stable test statistics than the classical approach (Warton 2008). Second, calculation of probabilities was based on randomization of model residuals (10,000 permutations), which does not require multivariate normality (Anderson & Robinson 2001). After significant multivariate tests, we utilized a series of univariate permutation tests (10,000 permutations) to determine which habitat characteristics expressed significant effects. Probabilities in these tests have been adjusted to control the family wise error rate using Holm’s step-down multiple testing procedure (Wang *et al.* 2012)

EFFECT OF DISTURBANCES AND HABITAT CHARACTERISTICS ON CAPERCAILLIE OCCURRENCE

For complete understanding, we did not restrict ourselves to report a single “best” species distribution model, as is usually done, but we rather explored a sequence of models of various complexity.

Simple logistic models with single predictor variables

To ensure we did not exclude potentially important links between environmental settings and capercaillie distribution, we fit a series of simple generalized linear models (GLM) with binomial errors and logit link function (McCullagh & Nelder 1989) relating capercaillie presence/absence to individual habitat characteristics. Because we hypothesized that the highest probability of capercaillie occurrence is associated with moderate levels of disturbance, we fitted the GLM with second-order polynomials to allow for a hump-shaped response along the disturbance gradient. Significance of simple GLMs was tested using permutation of regressor residuals (PRR) with 10,000 permutations (Potter 2005).

Parsimonious GLM model

We built a parsimonious GLM model relating capercaillie occurrence to habitat and disturbance characteristics. To avoid unstable estimates of model coefficients and inflation of their standard errors (multicollinearity problem), we screened correlation matrix of 28 habitat and disturbance characteristics and excluded eight strongly correlated variables until all of the remaining variables had correlation coefficients < 0.75 (Table S2). We verified that the full model did not show considerable multicollinearity patterns using the variance inflation factor (VIF < 10, Quinn & Keogh 2002). We built the most parsimonious GLM via sequential deletion of the non-significant terms ($p > 0.05$) base on PRR tests (10,000 permutations), and relationships between capercaillie occurrence and predictors were displayed as effect plots (Fox 2003).

Because some plots were highly clustered in space, we constructed non-parametric spatial correlograms (Bjørnstad. & Falck 2001) to check for autocorrelation patterns in the residuals of GLM models. Several models showed weak (< 0.3) but significant positive autocorrelation at short lag distances (< 300 m). In these cases, we grouped data into 94 spatial clusters via k-means algorithm and randomly sampled one plot from each group. The new data subset, comprising 90% of the original data, was used to re-build models that showed autocorrelation within the full dataset. After sub-sampling, none of these GLMs showed significant autocorrelation pattern. We report results of these models instead of the models with autocorrelated errors.

Partial least squares discriminant analysis

To evaluate the potential influence of all environmental characteristics simultaneously, we constructed a more complex model. In traditional methods, such a high number of strongly correlated predictors presents limitations for model estimation (Wehrens 2011), therefore partial least squares discriminant analysis was performed (PLS-DA), which effectively handles multicollinearity problems (Barker & Rayend 2003). Based on the original variables

PLS-DA constructs orthogonal components that maximises between-group separation and finds a solution with components maximizing discrimination of capercaillie presence and absence plots. Prior to analysis, habitat and disturbance characteristics were standardized equalizing the weight of dimensionally heterogeneous variables. Cross-validation was used to estimate the optimal number of components that maximized predictive performance. Predictive performance of the final PLS-DA model was assessed using a simple randomization test (Manly 1997) comparing the observed performance of the model with its null distribution generated from randomly reshuffled data (10,000 randomizations). The importance of each environmental variable for discrimination in PLS-DA was calculated using the sum of the absolute model coefficients weighted proportionally to the reduction in the sums of squares by each component (Kuhn 2015).

Model validation and predictive performance

We evaluated capercaillie distribution models using predictive approach (Shmueli 2010), which allows for independent assessment of model performance and may provide useful knowledge about the practical utility of those models. We used sensitivity (Alberg *et al.* 2004), i.e. probability that model correctly detects occurrence of capercaillie, as a measure of predictive performance. To ensure unbiased estimates of predictive performance, sensitivity of each model was calculated from 100-times repeated 10-fold cross-validation (Kuhn & Johnson 2013). Mean sensitivity averaged across validation folds was reported along with bootstrap 95% confidence intervals (10,000 replicates) (Efron & Tibshirani 1986).

All analyses were conducted in R (R Development Core Team 2015) using the packages boot (Davison & Hinkley 1997), caret (Kuhn 2015), effects (Fox 2003), mvabund (Wang *et al.* 2014), and ncf (Bjørnstad 2013).

Results

EFFECTS OF DISTURBANCES ON HABITAT CHARACTERISTICS

Multivariate analyses indicated that disturbances had a significant effect on habitat characteristics, regardless of whether disturbance index (DI), maximum disturbance severity (DIST.max), or time since maximum disturbance (DIST.time) was used as the disturbance measure (Tab. 1). Detailed univariate analysis showed that DI and DIST.max were mainly related to characteristics of tree age and density, both living and dead. For example, maximum age, range of age, and number of large living trees was negatively related to DI and DIST.max, while density of standing dead wood significantly increased with DI and DIST.max. Ground vegetation cover, mean DBH of living trees, and mean and median age were positively related to DIST.time, but density of living trees was negatively related to DIST.time.

EFFECT OF DISTURBANCES AND HABITAT CHARACTERISTICS ON CAPERCAILLIE OCCURRENCE

On 104 circular permanent study plots 41 presences were found; 26 out of 61 in Giumalau (42.6%) and in 15 plots out of 43 in Calimani (35%) were found.

Simple logistic models with single predictor variables

Capercaillie occurrence was significantly related to six habitat and disturbance characteristics based on simple logistic models with single predictor variables (Fig. 2). Presence was negatively related to distance to the nearest canopy gap, density of living trees, whereas positively related to DIST.time, ground vegetation cover and mean DBH of living trees. Interestingly, probability of capercaillie presence showed significant unimodal response to DI (Fig. 3). The highest probability of occurrence was observed at plots with a history of moderate DI (DI = -1.75). Distance to the gap and density of living trees were the best single predictors of capercaillie occurrence (sensitivity ~ 46%), followed by DI (41%), ground vegetation cover (39%), and DIST.time (31%). Predictive performance of the other simple models was no better than random chance.

Parsimonious GLM model

The parsimonious GLM ($\chi^2_{(4)} = 38.65$, $p < 0.001$) involved four significant predictors of capercaillie occurrence: mean DBH of standing dead wood, number of trees in regeneration higher than 2.5 m, distance to the gap, and the second-order polynomial of DI (Fig. 4). In contrast to simple model, the peak of probability of capercaillie presence was shifted more towards disturbances of lower severity (lower DI values), indicating that unimodal relationship with DI was partly captured through incorporating multiple predictors. Predictive performance of the parsimonious GLM (sensitivity ~ 66%) was much higher than the performance of any simple model.

Partial least squares discriminant analysis

We fit the PLS-DA model with all variables combined into three components ($p < 0.001$); distance to the gap, density of living trees, and ground vegetation cover were the variables with the highest importance for discrimination between plots with and without capercaillie (for a complete list see Fig. S1). Cross-validated predictive performance of PLS-DA model only very slightly outperformed parsimonious GLM.

Discussion

Disturbance regime was the main driving factor of capercaillie habitat dynamics. Mixed severity disturbance regime resulted in heterogeneous forest landscape that provided essential habitat structures for this endangered umbrella species. Numerous standing dead wood, low regeneration density, low tree density and high vegetation cover were the main structural predictors (also related to disturbance history) of the capercaillie occurrence in the primary forests.

CAPERCAILLIE DEPENDENT ON NATURAL ECOSYSTEM DYNAMICS

The mixed severity disturbance regime created a dynamic forest landscape and the natural disturbances directly affected whole species assemblage. Natural disturbances did not affect only the tree layer (i.e. age, species deadwood), but also the understory community, most likely due to the significant effect of overstory disturbances on the forest sun light regime (Royo & Carson 2006). The disturbance variables had a significant effect on the bilberry cover, and the total ground vegetation cover which have been shown as the main determinants of capercaillie habitat selection (Storch 2002).

Our results only partially supported the expectations, that moderate severity disturbances will provide higher rates of capercaillie occurrence. The low to moderate disturbance severities together with increasing time since maximum disturbance decreased the tree densities and increased the standing dead wood, basal area, tree age and ground vegetation and particularly the bilberry cover (Tab. 1). This type of disturbances resulted in the old-growth stage of the primary forests. The unimodal relationship between historical diversity of disturbance severities and probability of capercaillie occurrence (Fig 3) showed the importantance of these old-growth forest stages for the capercaillie survival. However, the optimal disturbance regime for the capercaillie could not be simply characterized by combination of frequent moderate to low severity disturbances (Fig. 3). The positive effect of distance to forest gaps on capercaillie that are results of recent high severity disturbances had significant contribution in all three models (Fig. 2, Fig. 4, Fig. S1). This highlights the importance of high severity disturbances that create the early seral stages in form of gaps for the capercaillie (Braunisch *et al.* 2014). The early seral stages sustain high diversity of arthropods and provide higher productivity of plant species (Swanson *et al.* 2010). Arthropods are the main food source of capercaillie chicks and the main food source of adults are the fruits of bilberry during summer (Storch 1993; Wegge *et al.* 2005).

Hence, the early seral stages created by high severity disturbances should be considered as fundamental part of the capercaillie habitat, just like the late seral stages formed by moderate to low severity disturbances. However, the canopy of early seral stages after 40-70 years might get closed, and the structure and composition of the forest might become unsuitable for some time, until another disturbance (low, moderate or high) will open the forest canopy again (Fig. 5). Therefore, capercaillie can be considered a species dependent on disturbances in the range of natural ecosystem dynamics (McElhinny *et al.* 2005).

MULTI-MODEL APPROACH IN COMBINATION WITH PREDICTIVE MODELING

The overriding importance of disturbance regime was supported by multiple modeling techniques, indicating robustness of the results and their independence from analytical method. Disturbance-related habitat characteristics (mean diameter of standing dead wood, regeneration cover), that appeared unimportant in simple (marginal) models, captured significant amount of variation in model with multiple predictors which further underlines the role of disturbances. Therefore, we stress the use of multiple methods and not to rely on a single analytical approach, as is usually done. This will reduce the bias and probability of missing some important variable.

Complex PLS-DA model incorporating 27 habitat characteristics showed only negligibly higher predictive performance than parsimonious GLM with 4 predictors. Apparently, parsimonious GLM (Fig. 4) included the essential predictors of capercaillie distribution. Given high predictive power of parsimonious GLM on out-of-sample data (Fig. 2), we can confidently generalize the results to new sites (Olden & Jackson 2000; Guisan & Zimmerman 2000). Consequently, disturbance severity and related habitat characteristics should be considered of pivotal importance in conservation planning for capercaillie in the Carpathians.

RESTORING HABITATS BY EMULATING NATURAL DISTURBANCE PROCESSES

Thousands of hectares of old-forests are currently destroyed by large-sclae logging in the Carpathians, and the decreasing habitat connectivity threatens the capercaillie population (Tejkal et al. under rev.). Restoration of these habitats is crutial for securing survival of this species. Structures and disturbance history of the studied old-growth forests showed a clear pattern that may be emulated in forest management in order to sustain capercaillie in these stands. Based on our results, forest management should include all disturbance severities (low, moderate and high). Emulating the optimal diversity of disturbance severities (see Fig. S2) for the capercaillie means, that the recommended rotation period for management of capercaillie forests should be planned in time of 150- 200 years. Ideally in the younger stands (to the age 50 years), intervention removing ca 45 % canopy area should be carried out and within next 100-150 years 5-15% of canopy area should be disturbed every 20-40 years to keep the tree densities at moderate level. Low tree densities will enhance the ground vegetation and bilberry cover. Irregularly shaped gaps or patches with sizes of ca 0.25 ha should cover at least 4 % of the total forest area. Long recovery time and natural regeneration should be promoted. Standing dead wood and other disturbance legacies should be left in the forests.

CONCLUSION

In this study we used a novel approach to test the effects of long-term disturbance components on species habitat dynamics. Based on our results we conclude that mixed-severity disturbances created heterogeneous and complex environment for an endangered umbrella species, capercaillie. Natural disturbance regimes can maintain suitable habitat structures of capercaillie. All disturbance severities are required, resulting in a mosaic of different developmental stages, including old-growth (structurally complex forests dominated by large old trees), as well as structurally complex early-seral stands (those following severe canopy-opening disturbances). We stress the importance of maintaining natural disturbance regime and associated structural characteristics in the forest landscapes. Capercaillie is considered an indicator of species rich mountain forest ecosystems (Suter *et al.* 2002), hence we suppose, although we express much of our argument in terms of a single species, conclusions might be applied to other density dependent population interactions (eg. coexistence mechanisms). We therefore suggest conducting multi-taxon analyses in landscapes shaped by mixed severity disturbance regime, to test weather with the offsetting proportions of all disturbance severities the species richness in the landscape will be increasing.

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Figures

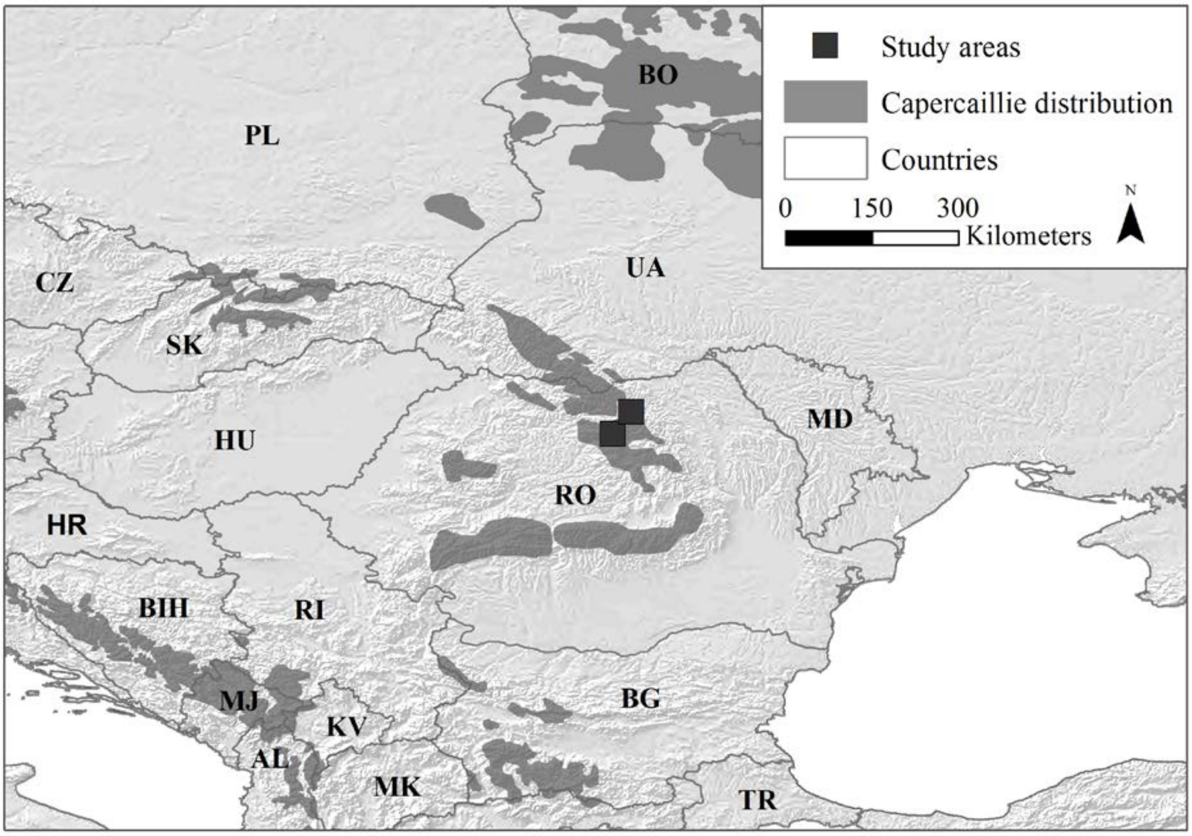


Fig. 1 Location of the study sites

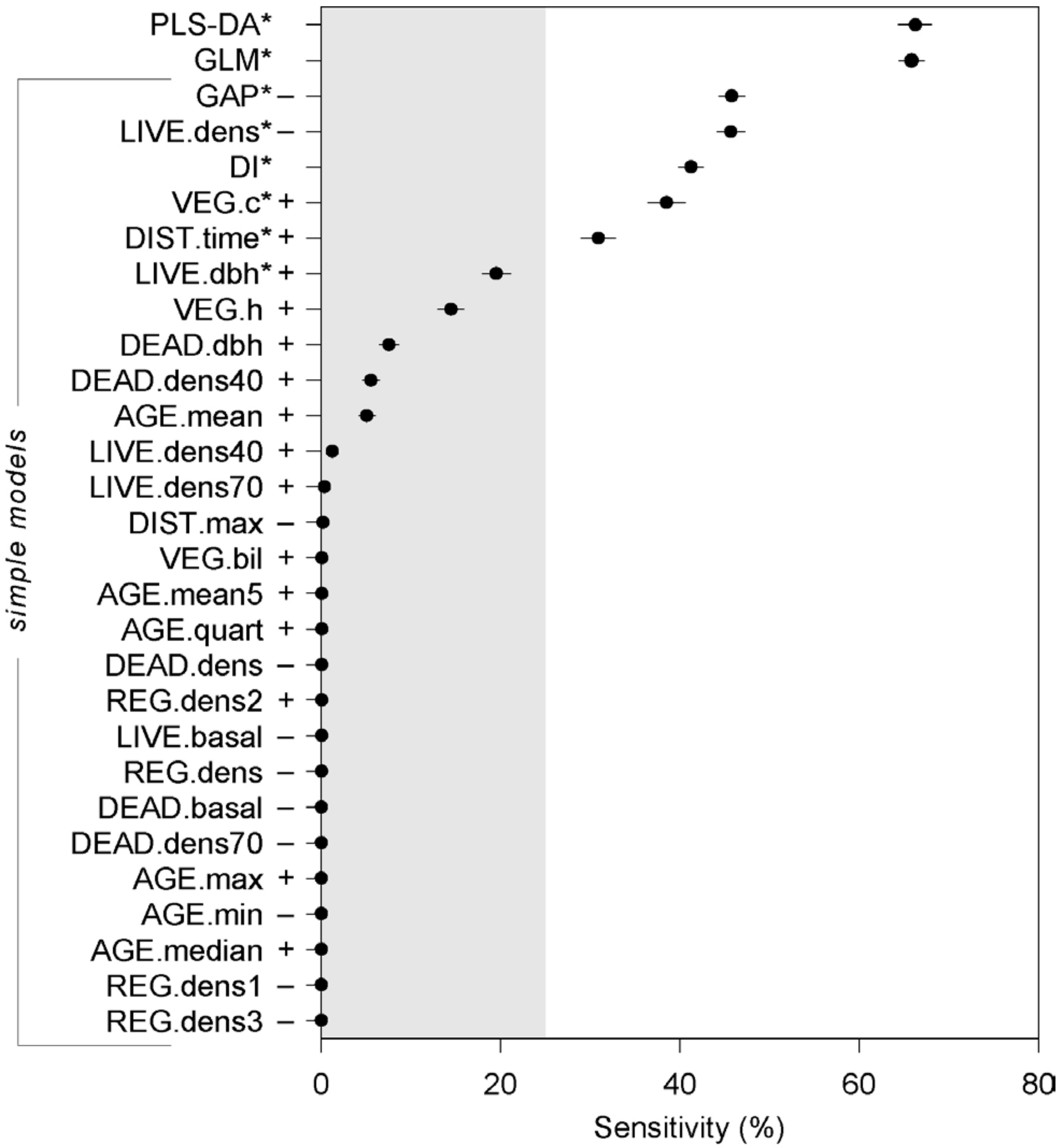


Fig. 2 Capercaillie distribution models ranked according to their predictive performance (sensitivity). Black dots represent average cross-validated sensitivity (± 95% bootstrap confidence intervals). Grey area indicates the range of sensitivity expected by chance (95% randomly reshuffled values). Models significant at $\alpha = 5\%$ are marked with asterisk. Plus and minus signs represent positive and negative relationships with capercaillie presence. Note that model with DI as predictor is polynomial GLM and thus does not have any particular sign.

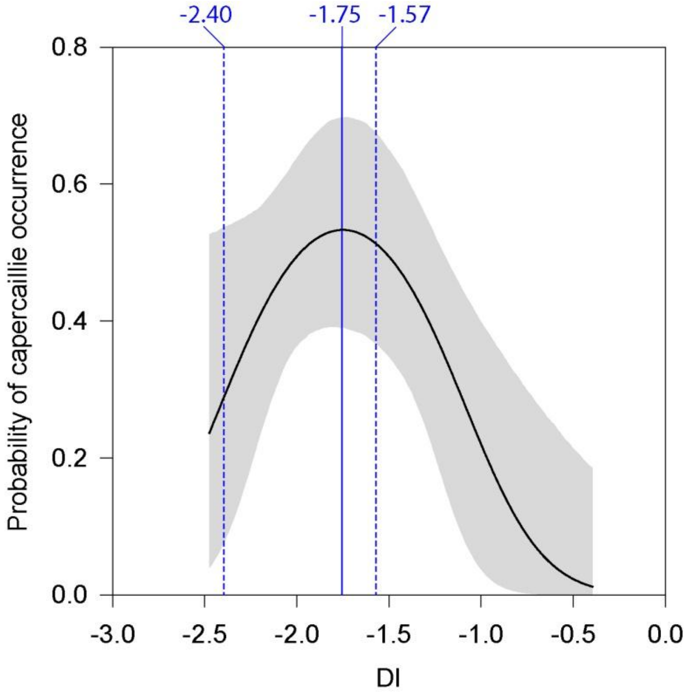


Fig. 3 Unimodal relationship between temporal disturbance diversity characterized by disturbance index (DI) and probability of capercaillie occurrence showing the preference of capercaillie for stands with moderate-severity disturbance histories. The thick line represents polynomial GLM (± 95% bootstrap confidence interval - gray area) and thin blue line is the estimate of optima (± 95% bootstrap confidence interval - dashed lines).

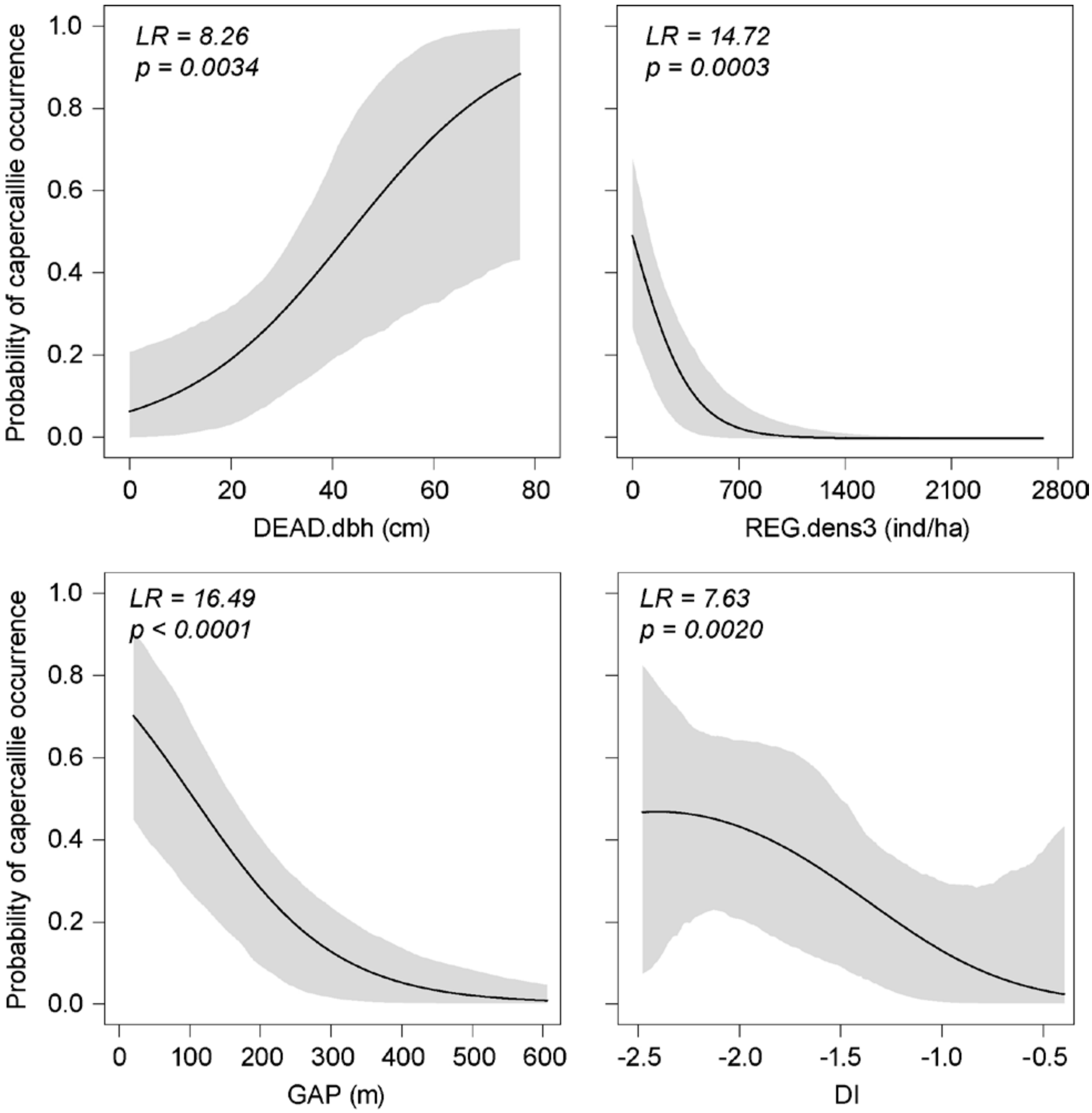


Fig. 4 Effect plots demonstrating the multivariate relationship between probability of capercaillie occurrence and its predictors in the parsimonious GLM. Lines represent partial fitted relationships holding the other variables constant at their means (± 95% bootstrap confidence intervals - gray areas). Results of the tests of model parameters are displayed. Explanation of the variables: DEAD.dbh = DBH of the deadwood, REG.dend 3 = number of trees (≥ 10 cm diameter) in regeneration in the height category > 2.5 m, GAP = distance of the plot to the closes gap (>0.05 ha), DI = disturbance severity index that represent the diversity of disturbance severities in time – the higher the index, the lower the disturbance diversity.

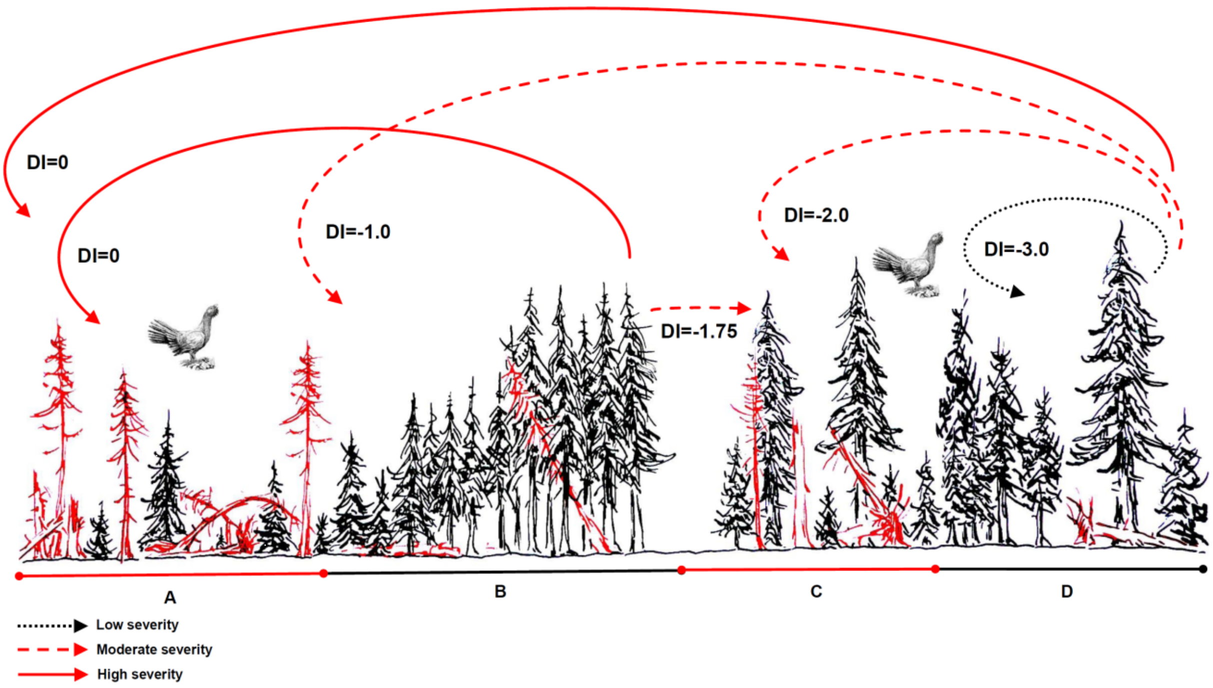


Fig. 5 Mixed severity disturbance regime creates a mosaic of different developmental stages on all spatial scales, living trees are coloured by black and dead trees by red colour. The arrows represent the disturbances to which the values if the disturbance index are attributed. Capercaillie is a disturbance dependent species, it is inhabiting early seral (A) and late seral stages (C, D). However, the stages 40-70 years after the high severity disturbances become too dense for the capercaillie untill next disturbance will open the canopy.

Tables

Tab. 1 Results of multivariate linear modeling of the effect of disturbances on all habitat characteristics. Multivariate analyses are supplemented by the results of univariate analyses of particular habitat characteristics. Standardized regression coefficients (β), test characteristics (F) and permutation probabilities (p) are displayed. Probabilities for univariate test are adjusted for family-wise error (p adj.). Significant results are highlighted in bold.

Disturbance measure:	DI			DIST.max			DIST.time		
Multivariate test:	$F_{(1,102)} = 124.5, p < 0.001$			$F_{(1,102)} = 115.7, p < 0.001$			$F_{(1,102)} = 121.5, p < 0.001$		
Habitat characteristics	β	F	p adj.	β	F	p adj.	β	F	p adj.
AGE.mean	-0.27	7.76	0.070	-0.17	3.05	0.513	**0.59**	**54.59**	**<0.001**
AGE.median	-0.20	4.31	0.283	-0.08	0.58	0.862	**0.57**	**48.57**	**<0.001**
AGE.max	**-0.47**	**29.06**	**<0.001**	**-0.51**	**35.64**	**<0.001**	0.19	3.78	0.467
AGE.min	**0.31**	**10.71**	**0.023**	**0.29**	**9.68**	**0.038**	0.06	0.40	0.961
AGE.mean5	0.03	0.11	0.982	0.12	1.39	0.797	**0.37**	**15.92**	**0.002**
AGE.quart	**-0.54**	**41.69**	**<0.001**	**-0.53**	**39.09**	**<0.001**	**0.35**	**14.34**	**0.004**
VEG.h	-0.10	1.10	0.809	-0.11	1.14	0.818	0.14	2.09	0.725
VEG.c	-0.23	5.57	0.194	-0.21	4.70	0.261	**0.39**	**18.70**	**<0.001**
VEG.bil	**0.28**	**8.57**	**0.049**	0.27	7.77	0.079	0.02	0.03	0.995
LIVE.dbh	-0.04	0.17	0.982	0.06	0.37	0.883	**0.37**	**15.70**	**0.002**
LIVE.basal	0.03	0.09	0.982	0.12	1.40	0.797	0.01	0.02	0.995
LIVE.dens	**0.29**	**9.08**	**0.045**	0.24	6.41	0.137	**-0.41**	**20.62**	**<0.001**
LIVE.dens40	-0.11	1.19	0.809	0.00	<0.01	0.971	0.24	5.97	0.177
LIVE.dens70	**-0.36**	**15.37**	**0.003**	**-0.35**	**14.12**	**0.006**	0.18	3.61	0.468
DEAD.dbh	-0.22	5.32	0.207	-0.23	5.49	0.190	0.17	2.86	0.576
DEAD.basal	0.01	0.01	0.982	0.02	0.06	0.964	0.10	1.07	0.884
DEAD.dens	**0.43**	**22.89**	**0.001**	**0.44**	**24.24**	**<0.001**	-0.19	3.64	0.468
DEAD.dens40	-0.15	2.41	0.589	-0.16	2.53	0.538	0.10	1.05	0.884
DEAD.dens70	-0.11	1.28	0.809	-0.10	1.07	0.818	0.12	1.40	0.844
REG.dens1	-0.20	4.36	0.283	-0.24	6.46	0.137	0.05	0.29	0.961
REG.dens2	**-0.28**	**9.00**	**0.045**	-0.27	8.17	0.070	0.08	0.58	0.937
REG.dens3	-0.15	2.31	0.589	-0.17	3.06	0.513	-0.14	2.14	0.725
REG.dens	-0.25	6.93	0.102	-0.28	8.63	0.059	-0.02	0.04	0.995

Supporting Information

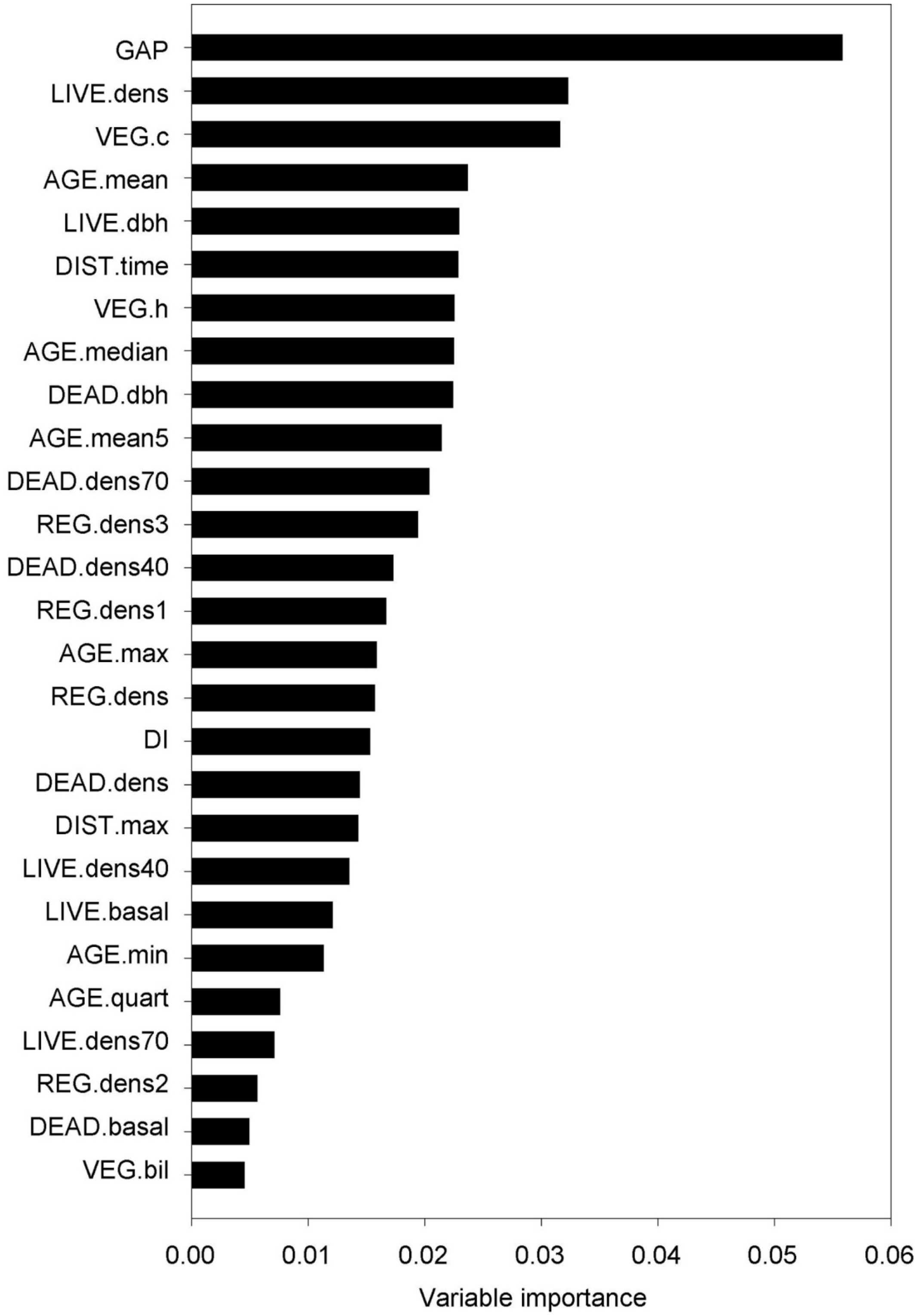
Table S1 Summary of habitat and disturbance characteristics of permanent study plots.

Code of variable	Description of variable and units	Mean	SD	Min	Max
Age characteristics					
AGE.mean	Mean age of the plot (years)	124	36	37	213
AGE.median	Median age of the plot (years)	116	49	25	226
AGE.max	Maximum age (years)	230	55	84	371
AGE.min	Minimum age (years)	58	35	16	190
AGE.mean5	Mean age of five oldest trees (years)	137	57	25	266
AGE.quart	Interquartile range of age (years)	58	51	2	181
Disturbance measures					
DI	Disturbance severity index	-1.64	0.51	-2.47	-0.39
DIST.max	Proportion of canopy removed by the maximum disturbance, i.e. severity of the maximum disturbance (%)	39	17	13	90
DIST.time	Time from the maximum disturbance (years)	130	60	25	245
Distance to gap					
GAP	Distance to the nearest gap in forest canopy (m)	196	123	21	608
Ground vegetation					
VEG.h	Height of the ground vegetation (cm)	3	1	1	6
VEG.c	Ground vegetation cover (%)	58	26	2	90
VEG.bil	Bilberry cover (%)	19	27	0	90
Living trees					
LIVE.dbh	Mean DBH of living trees with diameter ≥10 cm (cm)	32	8	14	53
LIVE.basal	Basal area of living trees (m^2/ha)	46	16	4	84
LIVE.dens	Density of living trees (ind/ha)	524	243	150	1260
LIVE.dens40	Density of living trees with diameter ≥ 40cm (ind/ha)	132	73	0	340
LIVE.dens70	Density of living trees with diameter ≥ 70cm (ind/ha)	8	16	0	100
Standing dead wood					
DEAD.dbh	Mean DBH of standing dead wood ≥10 cm (cm)	29	14	0	77
DEAD.basal	Basal area of standing dead wood (m^2/ha)	8	7	0	44
DEAD.dens	Density of standing dead wood (ind/ha)	127	113	0	600
DEAD.dens40	Density of standing dead wood with diameter ≥ 40cm (ind/ha)	21	26	0	140
DEAD.dens70	Density of standing dead wood with diameter ≥ 70cm (ind/ha)	2	5	0	20
Regeneration					
REG.dens1	Density of trees in regeneration with height 0.5-1.3 m (ind/ha)	308	361	0	1760
REG.dens2	Density of trees in regeneration with height 1.3-2.5 m (ind/ha)	160	211	0	1020
REG.dens3	Density of trees in regeneration with height >2.5 m (ind/ha)	167	343	0	2700
REG.dens	Density of trees in regeneration (ind/ha)	636	730	0	3260

Table S2 Correlation coefficients (Pearson's r) between habitat and disturbance characteristics of permanent study plots. Collinear variables excluded from statistical modeling are assigned by asterisks.

	VEG.h	VEG.c	VEG.bil	LIVE.dbh	LIVE.basal*	LIVE.dens	LIVE.dens40	LIVE.dens70	DEAD.dbh	DEAD.basal*	DEAD.dens	DEAD.dens40	DEAD.dens70	AGE.mean*	AGE.max	AGE.min	AGE.median	AGE.quart	AGE.mean5*	REG.dens1*	REG.dens2*	REG.dens3	REG.dens	GAP	DI	DIST.time*
VEG.c	0.51																									
VEG.bil	0.27	0.43																								
LIVE.dbh	-0.16	0.26	-0.05																							
LIVE.basal*	-0.41	-0.17	0.07	0.44																						
LIVE.dens	-0.25	-0.45	0.19	-0.57	0.34																					
LIVE.dens40	-0.29	0.06	-0.02	0.69	0.80	-0.13																				
LIVE.dens70	-0.07	0.07	-0.23	0.25	0.29	-0.13	0.15																			
DEAD.dbh	0.05	0.07	-0.42	-0.06	-0.31	-0.25	-0.19	0.28																		
DEAD.basal*	-0.02	-0.07	-0.11	-0.11	-0.24	-0.10	-0.19	0.02	0.47																	
DEAD.dens	-0.15	-0.30	0.26	-0.11	0.15	0.33	-0.11	-0.24	-0.36	0.38																
DEAD.dens40	0.04	0.07	-0.27	-0.08	-0.32	-0.22	-0.17	0.14	0.61	0.82	-0.03															
DEAD.dens70	-0.09	-0.10	-0.22	-0.08	-0.18	-0.10	-0.19	0.12	0.53	0.48	-0.11	0.41														
AGE.mean*	0.02	0.45	0.09	0.76	0.31	-0.46	0.55	0.16	-0.08	-0.15	-0.19	-0.08	-0.05													
AGE.max	0.01	0.24	-0.22	0.28	0.15	-0.29	0.29	0.39	0.14	-0.13	-0.39	0.00	0.06	0.43												
AGE.min	-0.10	0.05	0.23	0.44	0.36	-0.01	0.33	-0.11	-0.30	-0.01	0.34	-0.17	-0.20	0.47	-0.01											
AGE.median	0.02	0.45	0.11	0.71	0.24	-0.44	0.46	0.10	-0.12	-0.15	-0.12	-0.10	-0.06	0.92	0.27	0.36										
AGE.quart	0.07	0.06	-0.26	-0.18	-0.16	-0.19	-0.02	0.29	0.23	-0.05	-0.39	0.06	0.08	0.00	0.29	-0.47	-0.06									
AGE.mean5*	0.04	0.40	0.35	0.65	0.35	-0.31	0.51	-0.03	-0.35	-0.23	0.01	-0.29	-0.17	0.76	0.31	0.41	0.79	-0.18								
REG.dens1*	0.11	0.07	-0.20	-0.10	-0.14	-0.14	-0.05	0.07	0.25	-0.17	-0.37	-0.05	-0.05	-0.06	0.14	-0.29	-0.04	0.24	-0.16							
REG.dens2*	0.12	0.08	-0.19	-0.19	-0.16	-0.04	-0.12	0.05	0.32	-0.11	-0.35	0.00	0.04	-0.15	0.17	-0.45	-0.10	0.17	-0.17	0.69						
REG.dens3	-0.10	-0.28	-0.25	-0.44	-0.18	0.36	-0.23	-0.01	0.33	0.12	-0.22	0.28	0.10	-0.37	0.05	-0.40	-0.34	0.14	-0.44	0.28	0.46					
REG.dens	0.04	-0.07	-0.27	-0.32	-0.20	0.09	-0.17	0.05	0.37	-0.06	-0.39	0.11	0.03	-0.25	0.14	-0.46	-0.21	0.23	-0.33	0.83	0.85	0.74				
GAP	-0.09	-0.11	-0.32	-0.10	0.02	0.03	-0.04	0.29	0.12	0.03	-0.04	0.01	0.21	0.06	0.18	-0.06	0.04	0.19	-0.18	0.10	0.10	0.09	0.12			
DI	-0.10	-0.23	0.28	-0.04	0.03	0.29	-0.11	-0.36	-0.22	0.01	0.43	-0.15	-0.11	-0.27	-0.47	0.31	-0.20	-0.54	0.03	-0.20	-0.28	-0.15	-0.25	-0.21		
DIST.time	-0.14	-0.39	-0.02	-0.37	-0.01	0.41	-0.24	-0.18	-0.17	-0.10	0.19	-0.10	-0.12	-0.59	-0.19	-0.06	-0.57	-0.35	-0.37	-0.05	-0.08	0.14	0.02	-0.02	0.31	
DIST.max*	-0.11	-0.21	0.27	0.06	0.12	0.24	0.00	-0.35	-0.23	0.02	0.44	-0.16	-0.10	-0.17	-0.51	0.29	-0.08	-0.53	0.12	-0.24	-0.27	-0.17	-0.28	-0.17	0.93	0.23

Fig. S1 List of variables in PLS-DA model ordered by the importance scores.



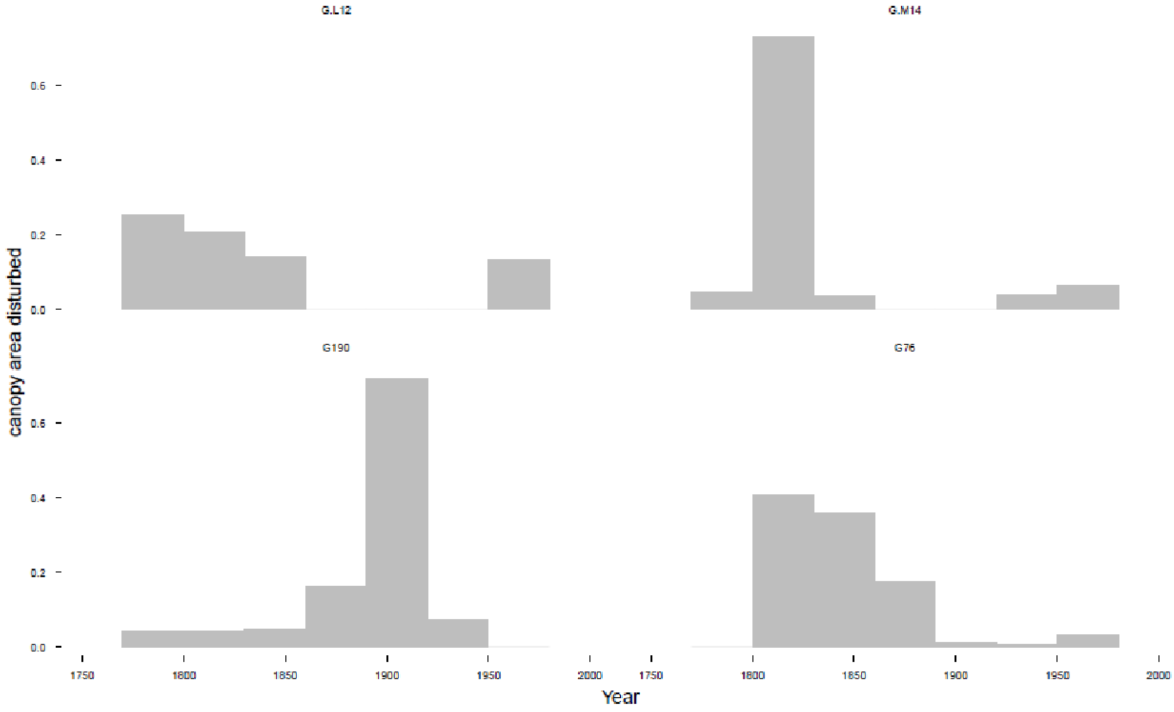


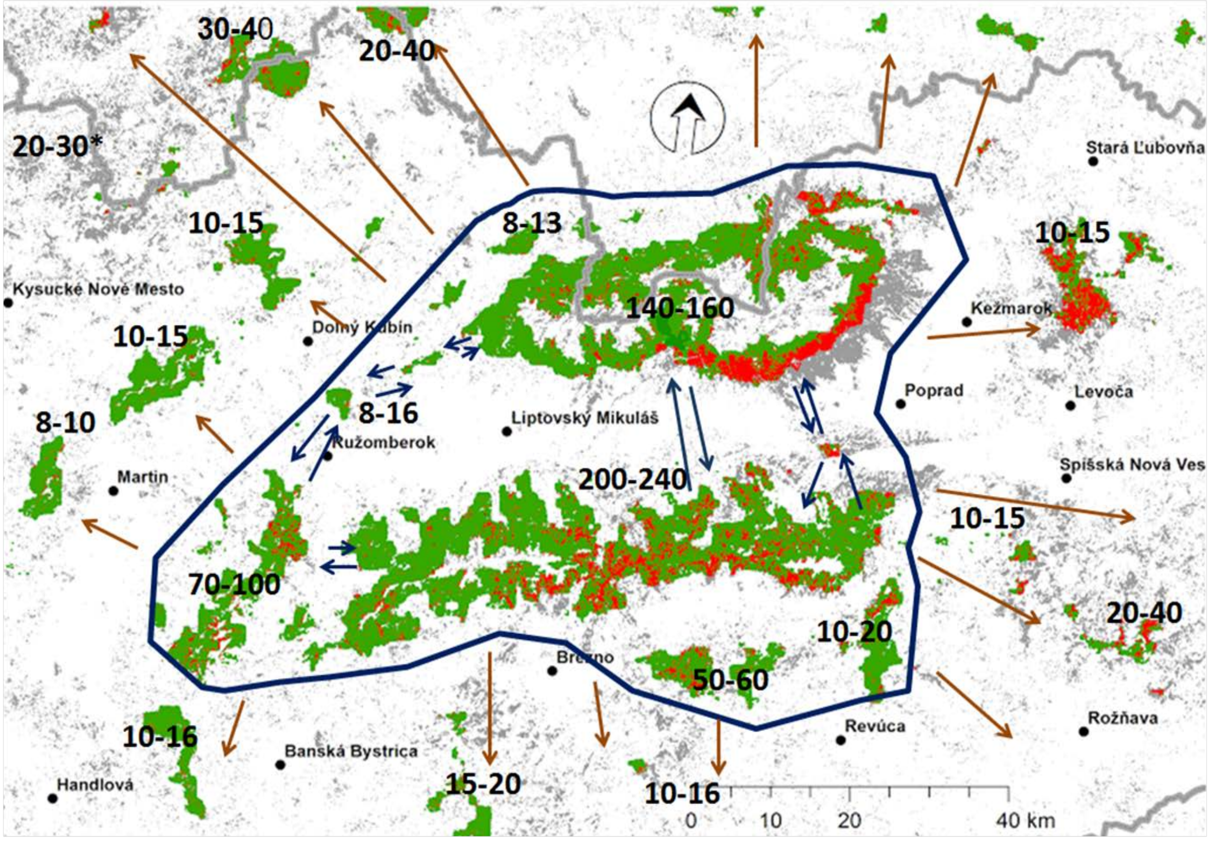
Fig. S2 Disturbance chronology showing the canopy area disturbed per decade in plots with optimal diversity of disturbance severities for the capercaillie, represented by Disturbance index (DI) (optimal DI = -1.75). Every plot experienced different severities of disturbances during the last 200 years. At least one moderate severity disturbance (20-45 % of canopy area disturbed) and 3-5 low severity disturbances (5-15 % of canopy area disturbed) spanning ca 200 years period. DI of plots: GL12 (DI = -1,76); GM14(DI = -1,75), G76 (DI = -1.76), G190 (DI = -1,74).

6. Diskusia a manažmentové opatrenia pre prax

Ochrana druhov, ktorých prežitie je závislé na prirodzených lesoch, je kľúčovou výzvou pre manažment lesov. Hlucháň hôrny je jeden z hlavných cieľových druhov ochrany prírody, pretože je ohrozený v mnohých krajinách a patrí medzi dáždnikové druhy, ktorých ochranou budú prosperovať aj ďalšie vzácne a ohrozené druhy. Pripravili sme komplexné údaje o tomto druhu a stave jeho biotopov pre celé územie Karpát. Vyhodnotili sme vplyv rôznych typov manažmentu lesov na stav biotopov hlucháňa hôrneho a jeho početnosť. Vytvorili sme model vhodnosti biotopov hlucháňa hôrneho pre celé Karpaty a analyzovali ako manažment lesov ovplyvňuje konektivitu populácie. Taktiež prinášame informácie o genetickej štruktúre karpatskej populácie. Pomocou metód dendroekológie sme ukázali, ako prírodné disturbancie formujú štruktúru biotopov hlucháňa hôrneho v smrekových pralesoch Karpát.

Naše analýzy odhalili, že potenciálny biotop hlucháňa v Karpatoch je relatívne veľký, avšak vysoko fragmentovaný. Preto hlucháne v Karpatoch prežijú iba formou metapopulácií, a tým sa zvyšuje význam funkčnej konektivity medzi vhodnými plochami biotopov. Obrovské plochy biotopov boli za posledných 20 rokov veľkoplošne vyťažené. Výsledky našej štúdie poukazujú aj na nelineárnosť vzťahov, ktoré fungujú v prírode a v ekológii. Na krajinnej úrovni veľkoplošná ťažba 30% vhodných biotopov redukovala počty hlucháňov až o 76%. Pri strate 15% biotopov celková konektivita klesla o 33%. Vyššie straty biotopov boli identifikované v chránených územiach, nefunkčnosť chránených území v Karpatoch je teda evidentná. Zachovanie oblastí, kde žijú hlucháne a mnoho ďalších súčasne sa vyskytujúcich druhov, ktorých prežitie závisí na veľkých plochách prírodných lesov a pralesov, si bude vyžadovať významný posun a zmeny v spôsobe manažmentu horských lesov.

Celkový koncept manažmentu lesov s výskytom hlucháňa musí vychádzať z krajinnej úrovne tak, aby bola zabezpečená vysoká konektivita vhodných lesných komplexov a aby metapopulácie ostali prepojené (Grimm and Storch 2000; Braunisch and Suchant 2013). Súvislé celky vhodných lesných komplexov by mali mať rozlohu 1400 ha a nemali by byť vzdialené od seba viac ako 5 – 10 km (Bollmann et al. 2011). Takto prepojená sieť vhodných biotopov by mala spolu dávať rozlohu o veľkosti 250 – 500 km^2 vhodných lesných komplexov s veľkosťou populácie minimálne 470 jedincov hlucháňa (Grimm and Storch 2000, Bollmann et al. 2011, Braunisch and Suchant 2013). Ako veľmi dobrý príklad metapopulácie nám môžu poslúžiť údaje o početnosti a stave biotopov, ktoré sme získali v Západných Karpatoch, kde ani jedno pohorie samostatne nie je schopné splniť minimálne parametre pre dlhodobé prežitie populácie (Obr. 7). Bez celkového plošného konceptu na úrovni krajiny nie je teda možné trvalo udržať populáciu hlucháňa. Podobná je situácia aj v ostatných častiach Karpát a taktiež v iných krajinách strednej a západnej Európy (Storch 2007).



***Obr. 7** Znázornenie súčasného stavu metapopulácie hlucháňa v Západných Karpatoch, vrátane početnosti, koridorov a rozsahu ťažieb v potenciálne vhodných biotopov. Modrá čiara ohraničuje jadrovú (zdrojovú) populáciu pre Západné Karpaty. Zelená farba znázorňuje potenciálny vhodný biotop a červená ťažbu vo vhodných biotopoch hlucháňa medzi rokmi 1990-2010. Modré šípky znázorňujú koridory, ktoré je potrebné udržať a podporiť pre zachovanie komunikácie v rámci jadrovej populácie. Hnedé šípky znázorňujú závislosť prežitia okrajových populácii na funkčnosti zdrojovej populácie. Čísla priradené k jednotlivým pohoriam vyjadrujú počet jedincov. Priaznivý stav celkovej populácie je možné udržať iba zachovaním efektívneho prepojenia na úrovni krajiny.*

Opatrenia na úrovni krajiny (na úrovni metapopulácie) dávajú základný rámec pre plánovanie opatrení na ďalších úrovniach (na úrovni porastu a na úrovni stromu) (Obr. 8) .

Opatrenia *na úrovni krajiny* - metapopulačný manažment

Zásady:
- rozloha súvislých komplexov vhodných lesov = 1400 ha
- vzdialenosť medzi vhodnými komplexmi max. 5-10 km
- prepojená sieť vhodných biotopov má spolu rozlohu 250-500 km^2
- minimálna veľkosť prepojenej populácie je 470 jedincov

Praktické opatrenia:
- ochrana pralesov a prírodných lesov
- obmedzenie fragmentácie
- zachovanie prepojenia pomocou koridorov a nášľapných kameňov
- zabránenie veľkoplošnému odlesňovaniu
- zabezpečenie optimálnej rozlohy letného a zimného biotopu

Opatrenia *na úrovni porastu*

Zásady:
- praktické opatrenia aplikovať smerom von z plôch aktuálneho výskytu, tzn. nie v porastoch aktuálneho výskytu ale na ich hranici
- tvorba presvetlenejších lesných porastov (korunový zápoj 0.4-0.6) s bohatou pokryvnosťou čučoriedky (*Vaccinum myrtillus*)

Praktické opatrenia:
- hlavné ťažisko praktického manažmentu sústredené na prerezávkové až prebierkové porasty
- výchovné zásahy s nerovnomernou intenzitou
- v dospelých porastoch zabezpečiť bezzásahový režim
- pokiaľ nie je možná bezzásahovosť, je nutné prejsť k maloplošnému obhospodarovaniu
- nepretržitá obnovná doba a predĺženie rubného veku na 150-200 rokov
- aplikovať účelový výber jednotlivý, ale aj skupinový

Opatrenia *na úrovni stromu*

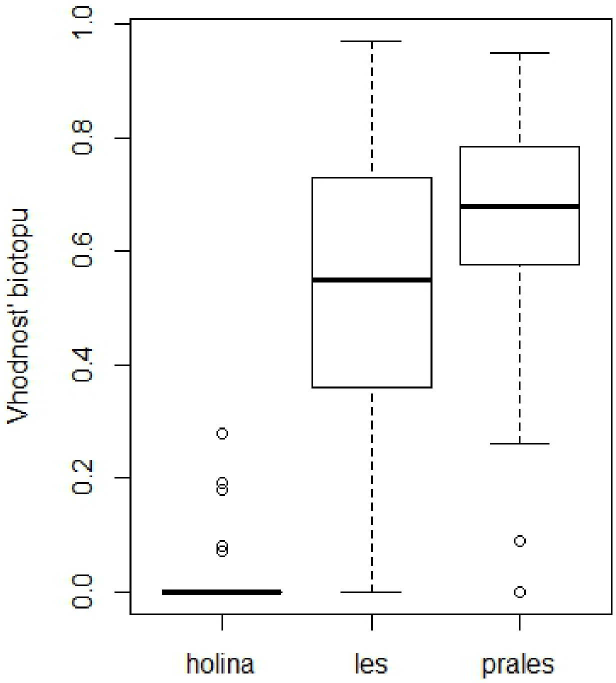
Zásady:
- zvýšenie rôznorodosti štruktúry

Praktické opatrenia:
- podporovať hlboko zavetvené stromy
- ponechávať prirodzené zmladenie,
- prímes borovice limby (*Pinus cembra*), jedle bielej (*Abies alba*),
- podporovať jarabinu (*Sorbus aucuparia*) a iné pionierske dreviny
- ponechávať stojace mŕtve drevo, ktoré je s obľubou hlucháňom využívané na odpočinok
- ponechávať vývraty a ležiace mŕtve drevo

Obr. 8 *Pre úspešný manažment lesov s výskytom populácie hlucháňa je potrebné zohľadniť 3 priestorové úrovne, pričom celkový koncept manažmentu musí vychádzať z krajinnej úrovne.*

Opatrenia na úrovni krajiny by mali zahŕňať prísnu ochranu pralesov a prirodzených lesov, obmedzenie fragmentácie vhodných biotopov a zachovanie prepojenia pomocou koridorov a nášľapných kameňov, zabránenie veľkoplošnému odlesňovaniu a zabezpečenie optimálnej rozlohy letného a zimného biotopu (Braunisch & Suchant 2007). Je potrebné klásť dôraz na ochranu a zachovanie dostatočnej rozlohy reprodukčných lokalít na úrovni krajiny, pretože sú zásadné pre prežitie druhu (Wegge et al. 2005).

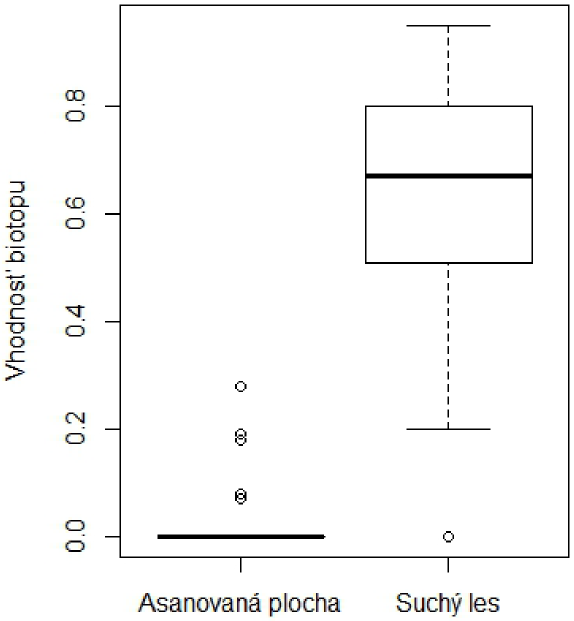
Výsledky tejto štúdie potvrdzujú, že pralesy a prírodné lesy sú najviac využívanými biotopmi hlucháňa (Obr. 9). Bezzásahové územia (prírodné rezervácie) nie sú ale v súčasnosti dostatočne veľké pre poskytnutie potrebnej rozlohy vhodného prírodného prostredia pre životaschopnú populáciu hlucháňa v Karpatoch (Grimm & Storch 2000). Tieto požiadavky zreteľne ukazujú, že ochrana hlucháňa je možná iba vo vzájomne sa dopĺňajúcej sieti systému bezzásahových rezervácií (ochrana existujúcich biotopov) a lesov osobitého určenia, v ktorých bude aplikovaný tzv. hlucháňovi-priateľský manažment lesa (Bollmann & Müller 2012), kde môže byť manažment doplnený o praktické lesnícke opatrenia na zachovanie tohto vzácneho druhu.



Obr. 9 *Index vhodnosti celoročného habitatu v závislosti na type manažmentu (holina, les, prales). Holina predstavuje pre hlucháňa hôrneho nevhodné stanovište. V pralesoch a prírodných lesoch je vhodnosť biotopov najvyššia* (Mikoláš et al. 2013).

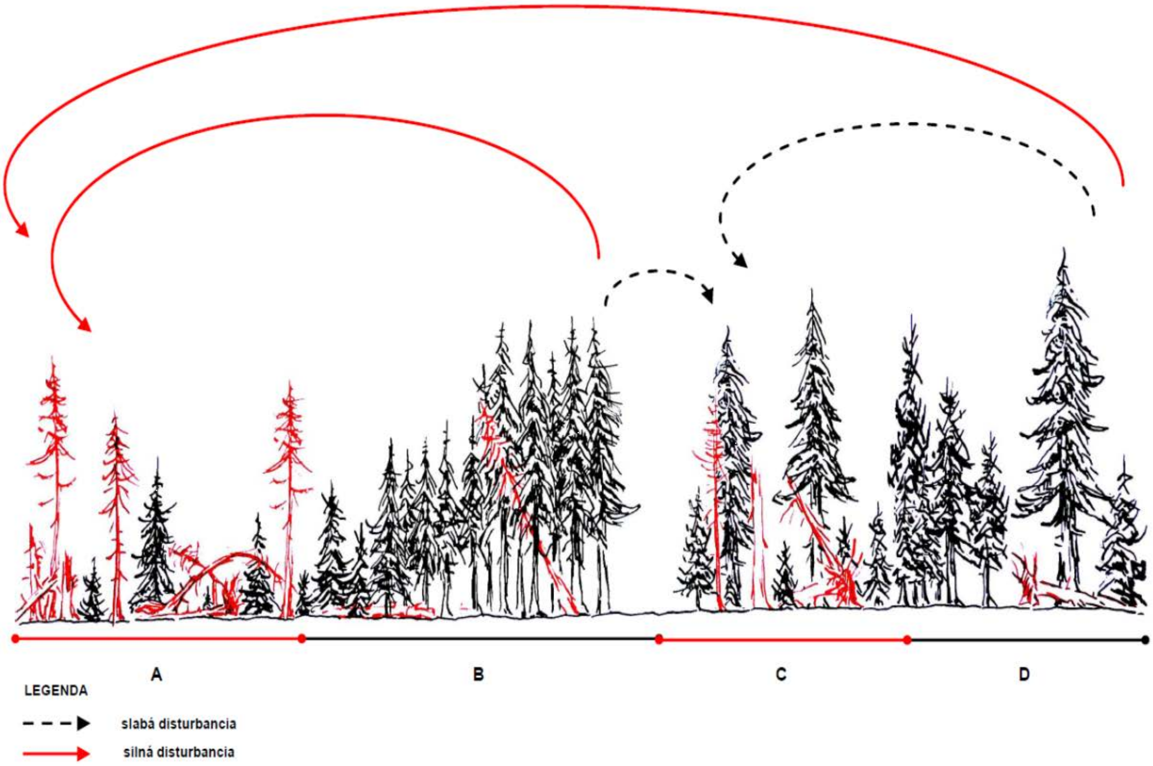
1. Ochrana existujúcich vhodných biotopov

Pre dlhodobé zabezpečenie priaznivého stavu vhodných biotopov je ideálnou formou manažmentu bezzásahový režim. Výskyt prírodných disturbancií (vietor a lykožrút) je kľúčovým faktorom pri tvorbe vhodných štruktúr biotopu hlucháňa hôrneho v prírodných lesoch a pralesoch. Výsledky tejto štúdie potvrdzujú, že veľkoplošné holiny sú nevhodný biotop pre hlucháňa hôrneho, v ktorom tento druh nedokáže prežiť. Naopak prírodné lesy a pralesy najlepšie spĺňajú biotopové nároky hlucháňa hôrneho v Karpatoch (Saniga 2003, Mikoláš et al. 2013). Veľkoplošné holiny v Karpatoch vznikajú v súčasnosti hlavne formou asanačnej ťažby. Je však potrebné poznamenať, že les napadnutý podkôrnym hmyzom bez asanačnej ťažby môže mať na kvalitu biotopu hlucháňa hôrneho pozitívny efekt (Mikoláš et al. 2013; Teuscher et al. 2011; Rösner et al. 2014; Beudert et al. 2015). V prírodných lesoch a pralesoch obvykle aj pri silných prírodných disturbanciách dochádza k narušeniu maximálne 70% korunového zápoja na úrovni porastu (Svoboda et al. 2014; Trotsiuk et al. 2014), obvykle do 50% korunového zápoja. Prírodné disturbancie vytvárajú otvorené lesné štruktúry prospešné pre život hlucháňa (Storch 2002).



***Obr. 10** Index vhodnosti biotopu na asanovaných plochách je nízky. Na plochách s nespracovanou kalamitou (suchý les) je podstatne vyšší (Mikoláš et al. 2013).*

Ako typický prirodzený disturbančný režim pre karpatské smrekové pralesy bol identifikovaný tzv. disturbančný režim zmiešaných severít (z anglického „mixed severity disturbance regime“) (Svoboda et al. 2014, Trotsiuk et al. 2014). Tento typ disturbančného režimu sa javí ako ideálny z pohľadu fungovania hlucháňa (Obr. 11). Podľa výsledkov tejto štúdie (kapitola 5.5), hlucháň potrebuje všetky typy severít disturbancií pre tvorbu vhodných biotopových štruktúr. Práve disturbančný režim zmiešaných severít vytvára heterogénny les, ktorý poskytuje dôležité biotopové štruktúry pre život hlucháňa. Prírodné disturbancie ovplyvňujú regeneráciu, zápoj, mŕtve drevo a taktiež bylinnú vegetáciu.



Obr. 11 *Disturbančný režim zmiešaných severít vytvára v smrekových pralesoch všetky dôležité typy vývojových štádií – od ranných po neskoré vývojové štádiá. Nedochádza k plynulému vývoju a dosiahnutiu dlhodobého rovnovážneho stavu a nedochádza ani k homogenizácií na krajinnej úrovni. Prírodné disturbancie v pralesoch vytvárajú mozaiku vývojových štádií lesa na všetkých priestorových úrovniach, a tým vytvárajú širokú paletu vhodných biotopov pre mnoho, dnes už vzácnych a ohrozených, organizmov.*

Podľa našich výsledkov efekt historických disturbancií, konkrétne slabých až stredne silných narušení, s rastúcim časom od disturbancií znižuje hustotu stromov, zvyšuje kruhovú základňu a zvyšuje pokryvnosť bylinnej vegetácie. Slabé a stredne silné disturbancie formujú starý a rozvoľnený les, kde hlucháň nachádza potravu v bohatej bylinnej vegetácii a dôležitý úkryt pod hlboko zavetvenými stromami. V rozvoľnenom lese môže hlucháň voľne lietať, čo je veľmi dôležité pre únik pred predáciou. Podľa našich výsledkov však pre ideálny biotop hlucháňa iba slabé a stredne silné narušenia lesa nie sú postačujúce. Svoj význam zohrávajú aj disturbancie s vysokou severitou, ktoré vytvárajú porastové medzery rôznych veľkostí (Obr. 12). Ranné vývojové štádiá, nasledujúce po disturbanciách, poskytujú vyššiu produktivitu rastlín a vyššiu diverzitu bezstavovcov (Swanson et al. 2010). Bezstavovce sú hlavným zdrojom potravy hlucháních kuriatok a čučoriedka je hlavným zdrojom potravy pre dospelé jedince (Storch 1993; Wegge et al. 2005). Preto prítomnosť porastových medzier v biotope hlucháňa, ktoré sú výsledkom silných disturbancií, je rovnako dôležitá ako prítomnosť starých rozvoľnených lesov, ktoré vznikajú vplyvom pôsobenia stredne silných a slabých disturbancií.

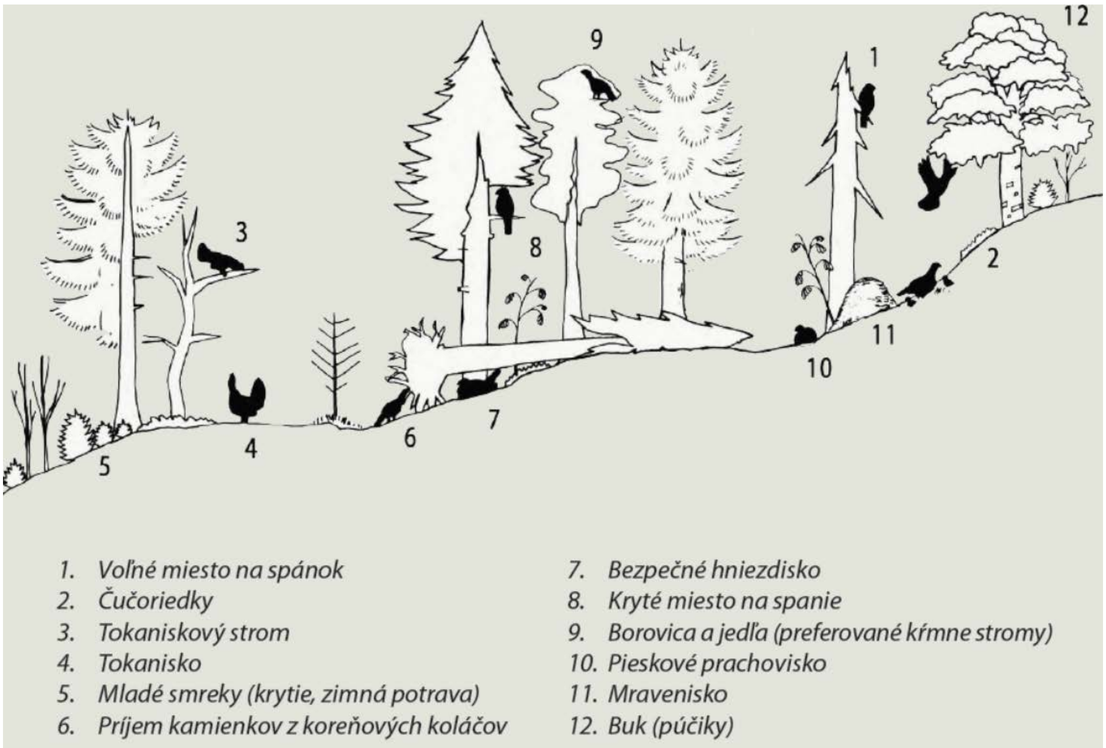
Obr. 12 *Lykožrút presvetľuje tmavé lesy a vytvára vhodné podmienky pre rozmnožovanie hlucháňa hôrneho. V prirodzených lesoch Karpát aj pri silných narušeniach nedochádza zvyčajne k rozpadom väčším ako niekoľko desiatok hektárov. Obvykle dochádza k narušeniu 20 – 50% korunového zápoja najmä kvôli členitému reliéfu (Svoboda et al. 2014, Trotsiuk et al. 2014). Foto: Jozef Fiala/Arolla film*

2. Praktické lesnícke opatrenia

V posledných desaťročiach došlo v Karpatoch k výrazným stratám vhodných biotopov. Podľa našich výsledkov, len za posledných 20 rokov bolo približne 15% (111 000 ha) vhodných lesných biotopov veľkoplošne vyťažených, následkom čoho konektivita klesla o 33%. Pre prežitie karpatskej populácie hlucháňa je potrebné bezodkladne prinavrátiť vhodné štruktúry v degradovaných biotopoch a zvýšiť tým mieru konektivity (Obr. 13).

Obr. 13 *Bývalé vhodné biotopy hlucháňa hôrneho, kde je dnes potrebné aplikovať aktívny manažment. V Karpatoch sa podľa našich výsledkov v súčasnosti nachádza v takomto stave približne 111 000 ha bývalých biotopov hlucháňa.*

Je možné využiť princípy a metódy ekologického lesníctva a vytvoriť praktickými lesníckymi manažmentovými opatreniami vhodné biotopy hlucháňa. Historický prirodzený režim disturbancií nám môže slúžiť ako príklad, ktorého napodobovaním dosiahneme cieľové biotopové štruktúry tohto dáždnikového druhu (Obr. 14). Dendrochronologickým výskumom dynamiky pralesov sme odhalili typické štruktúry a spôsob, akým je potrebné les narúšať tak, aby sme zabezpečili vysokú početnosť populácie hlucháňa.



Obr. 14 *Vhodný biotop hlucháňa podľa Mollet a Marti (2001).*

Napodobovanie prirodzeného disturbančného režimu – ekologické lesníctvo

Ekologické lesníctvo je založené na pochopení a uplatnení prirozených disturbancií a prirozeného vývoja porastu do systému manažmentu lesa (Franklin et al. 2007). Štruktúra pralesov a história disturbancií ukázala jasný vzor, ktorý je možné do značnej miery napodobniť. Cieľom je vytvoriť les s bohatou štruktúrou, rozvoľnený až medzernatý, podľa možností silne diverzifikovaný les, ktorý spĺňa podstatné nároky hlucháňa.

Korunový zápoj je potrebné predčasne a nepretržite narúšať, a tým vytvárať rozvoľnené až medzernaté štruktúry (maximálne korunový zápoj 50 – 70%). Zásadný dôraz je potrebné klásť na výchovu mladých porastov, predovšetkým mladiny a porasty určené na prebierku (Obr. 13). Tento konkrétny typ manažmentu je možné nazývať aj hlucháňovi-priateľský manažment lesa (z anglického „capercaillie-friendly forest management“), ktorý má za cieľ urýchlene vytvoriť biotopy s vhodnou vekovo-druhovo-priestorovou štruktúrou lesných porastov pre hlucháňa.

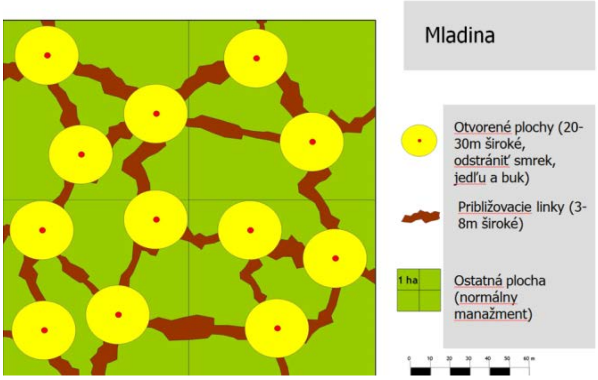
Mladiny

V mladine by existujúce otvorené plochy mali byť zväčšené na plochy s priemerom 20 – 30 m, vzdialené od seba približne 30 – 40 m. Vyrúbané stromy by mali byť z týchto medzier odstránené. Je dôležité, aby tieto malé otvorené plochy boli rozmiestnené nerovnomerne po celých porastoch a musia byť prepojené 3 – 8 m širokými linkami (Obr. 15). Na ostatnej ploche je možné postupovať klasickým spôsobom.

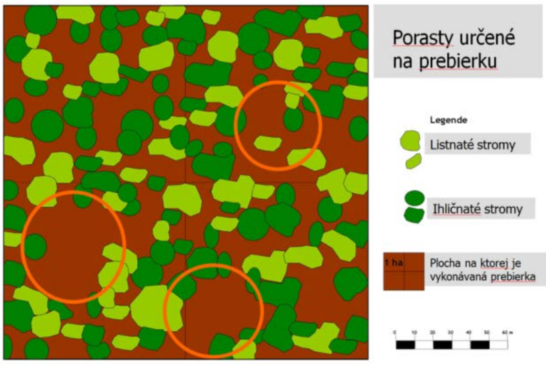
Porasty určené na prebierku

Pri porastoch určených na prebierku je možné vytvoriť a zveľaďovať budúci biotop hlucháňa hôrneho a zároveň sa vyhnúť nadmerným výdavkom. Do veku 40 rokov by intenzívnymi zásahmi malo byť odstránené približne 30 – 45% korunového zápoja. Sú na to vhodné najmä lokality s vekom do 20 – 30 rokov, kde sa ešte dá významne zmeniť štruktúra porastov bez významného vplyvu na ich stabilitu. Taktiež musia mať potenciál pre rýchle vytvorenie priaznivej štruktúry, tzn. po uskutočnených zásahoch musí na otvorených plochách rásť čučoriedka.

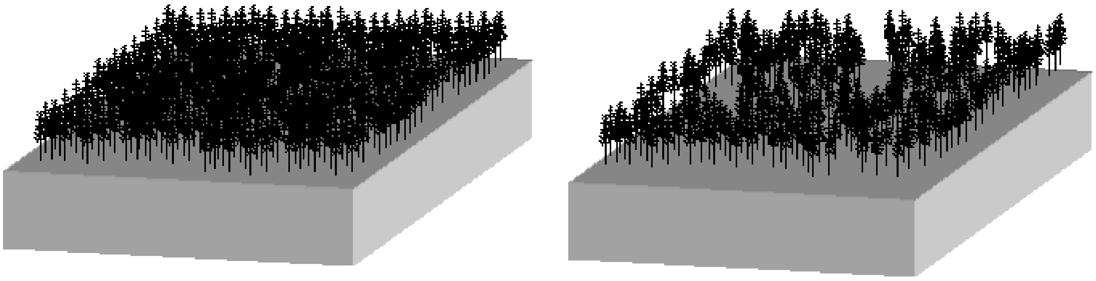
Pri prebierkových zásahoch by mal byť korunový zápoj zredukovaný na 70% a menej. Jedná sa o výchovné zásahy s nerovnomernou intenzitou – prebierka by mala byť rozmiestnená nerovnomerne na celej ploche, ale niektoré plochy by mali byť prebraté viac ako iné tak, aby vznikli malé otvorené plochy – porastové medzery, ktoré by boli prepojené (Obr. 16). Prednostne intenzívnejšia prebierka by mala byť vykonaná v mladších porastoch a na plochách so slabším rastom (napr. na vlhkých plochách). Výsledkom by mala byť mozaika otvorených prepojených medzier a relatívne tmavých hustých plôch (Obr 17, 18).



Obr. 15 *Manažment v porastoch mladín. (podľa Suchant, R. & Braunisch V., 2008)*



Obr. 16 *Manažment porastov určených na prebierku.*



Obr. 17 *Intentzívne prebierky musia byť vykonané nepravidelne, cieľom je vytvárať rozvolnené až medzernaté porasty so stromami zavetvenými až po zem.*

Obr. 18 *Výchovné zásahy s nerovnomernou intenzitou. Cieľom je maximálne napodobniť prirodzené procesy, ktoré prebiehajú v lesných ekosystémoch.*

Dospelé porasty

Na základe údajov z pralesov (kapitola 5.5) je možné odporučiť prechod na maloplošné obhospodarovanie s kontinuálnym udržiavaním starých porastov. Je potrebné prejsť na nepretržitú obnovnú dobu a predĺženie rubného veku na 150 – 200 rokov. Počas nasledujúcich 100 – 150 rokov, zásahy s nižšou intenzitou (5 – 15% narušeného zápoja), by mali byť vykonané niekoľkokrát (tri až štyrikrát) na celej ploche formou výberkového rubu, a tým bude udržiavaná hustota stromov na dostatočne rozvoľnenej úrovni (v prípade rumunských pralesov to bolo priemerne= 423 stromov/ha, max = 840 stromov/ha). Udržanie nízkej hustoty stromov podporí bylinnú vegetáciu a pokryvnosť čučoriedky. Okrem toho počas celej doby je potrebné zabezpečiť dostatočnú rozlohu porastových medzier, tzn. aplikovať účelový výber jednotlivý, ale aj skupinový v rámci jedného porastu. Vzniknuté porastové medzery by mali mať nepravidelný tvar a nemali by prekročiť rozlohu 0.85 ha (minimálna plocha porastových medzier v skúmaných pralesoch bola 0.057 ha; maximálna veľkosť porastových medzier bola 0.85 ha, priemerná plocha bola 0.23 ha). Minimálna plocha porastových medzier v rámci územia by nemala klesnúť pod 4% počas celej doby. Do porastu sa nezasahuje častejšie ako raz za 3 deceniá.

Zmladenie

S prirodzeným zmladením treba narábať dôsledne. Mala by byť podporovaná prirodzená obnova, aby nedošlo k prehusteniu regenerácie. Pokiaľ pokryvnosť zmladenia presiahne 25%, vhodnosť biotopu hlucháňa sa znižuje a pokiaľ prekročí 75%, biotop sa stáva nevhodným (Storch 2002). Preto je potrebné vyhnúť sa veľkoplošnému prehustenému zmladeniu. Lesné čistiny je potrebné udržať otvorené. Ďalej je dôležité vyhnúť sa používaniu oplôtkov. Pokiaľ je ich použitie nutné, oplôtky je potrebné dostatočne označiť, aby do nich hlucháne nemohli naraziť a zahynúť. Podporenie veľkých šeliem je možnosť, ako udržať populáciu raticovej zveri na udržateľnej úrovni.

Obohatenie štruktúry

Naše výsledky zo skúmaných pralesov potvrdzujú, že stojace mŕtve drevo je vhodné v porastoch pre hlucháne ponechať. Stojace mŕtve stromy hlucháne využívajú na odpočinok, pretože takéto stromy sa nekolíšu vo vetre a hlucháne z nich majú dobrý výhľad, potrebný na včasný únik pred predáciou. Dôležitou súčasťou štruktúry vhodného biotopu sú hlboko zavetvené stromy (ide najmä o smrek), ktoré sú dôležité pre hlucháne ako úkryt pred predáciou. Pod hlboko zavetvené stromy sa hlucháň ľahko ukryje, napríklad pred náletom jastraba lesného (*Accipiter gentilis*) alebo orla skalného (*Aquila chrysaetos*). Hlboko zavetvené stromy sa formujú už počas výchovných zásahov dlhodobým udržiavaním otvoreného zápoja na okrajoch liniek a čistín. Štruktúru je taktiež možné obohatiť udržiavaním jarabiny a prímesových drevín (borovica limba, jedľa, javor, buk). Málo produktívne stanoviská je vhodné v poraste ponechať na samovývoj (skalnaté útvary, haldy balvanov, oblasti močarísk a mokradí), pretože prirodzene vytvárajú dôležité porastové medzery, ktoré ostávajú dlhodobo otvorené.

7. Zhrnutie

V Karpatoch sa nachádza ťažisko výskytu hlucháňa hôrneho v Európe, ale doposiaľ neexistovali pre túto oblasť dostatočné podklady pre jeho ochranu a definovanie vhodných lesníckych manažmentových opatrení. V tejto práci sme využili štyri metodické prístupy (populačný monitoring, modely druhovej distribúcie, analýzu genetickej štruktúry, metódy dendroekológie), ktorých výsledky sú plne využiteľné k plánovaniu vhodných lesníckych manažmentových opatrení, ktoré umožnia prežiť hlucháňovi hôrnemu v smrekových lesoch Karpát. Manažment horských lesov Karpát, určený na zveľaďovanie biotopu hlucháňa, môžeme rozdeliť do troch skupín podľa úrovne, na ktorej bude uskutočnený – na úrovni krajiny, porastu a stromu (Obr. 8). Celý koncept manažmentu by mal vychádzať z krajinnej úrovne, pretože len udržaním komunikácie v rámci metapopulácii je možné dlhodobé prežitie tohto druhu v Karpatoch.

Opatrenia ***na úrovni krajiny*** by mali zahŕňať ochranu pralesov a prírodných lesov, obmedzenie fragmentácie vhodného biotopu a zachovanie prepojenia pomocou koridorov, zabránenie veľkoplošnému odlesňovaniu, zabezpečenie optimálnej rozlohy letného a zimného biotopu. Je potrebné klásť dôraz na ochranu a zachovanie dostatočnej rozlohy reprodukčných lokalít, pretože sú zásadné pre prežitie druhu (Wegge et al. 2005). Súvislé celky vhodných biotopov by mali mať rozlohu 1400 ha a nemali by byť vzdialenejšie od seba viac ako 5 – 10 km. Takto prepojená sieť vhodných biotopov by mala spolu dávať rozlohu o veľkosti 250 – 500 km^2 vhodných lesných komplexov, kde veľkosť populácie musí byť minimálne 470 jedincov hlucháňa (Grimm and Storch 2000, Bollamnn et al. 2011, Braunisch and Suchant 2013). ***Na úrovni porastu*** vylepšenie hlucháňieho biotopu znamená hlavne výchovu presvetlenejších lesných porastov a zvýšenie rôznorodosti štruktúry porastov. V dnešnej situácii je nutné aplikovať vhodné opatrenia smerom von z plôch aktuálneho výskytu, tzn. nie v lokalite aktuálneho výskytu. Hlavné ťažisko praktického manažmentu má byť sústredené na prerezávkové až prebierkové porasty (najdlhšie trvajúci efekt). V dospelých porastoch je odporúčané prejsť na bezzásahový režim. Pokiaľ to nie je možné, je potrebné pristúpiť k nepretržitej obnovnej dobe a aplikácii jednotlivého, ale aj skupinového účelového výberu v rámci jednotlivých porastov. Ďalšie opatrenia zahŕňajú udržiavanie a vytváranie čistín, zdokonaľovanie lesných okrajov, ponechávanie mŕtveho dreva a pod. ***Na úrovni stromu*** je vhodné podporovať hlboko zavetvené stromy na lesných okrajoch, v smrekových porastoch prímes borovice limby (*Pinus cembra*), jedle bielej (*Abies alba*), ponechávať prirodzené zmladenie, podporovať aj jarabinu vtáčiu (*Sorbus aucuparia*) a iné pionierske dreviny. Obzvlášť v čisto smrekových porastoch významnú úlohu zohráva stojace mŕtve drevo, ktoré je s obľubou hlucháňom využívané na odpočinok.

V Karpatoch sme preukázali stratu biotopov o 15% a následný pokles konektivity o 30% medzi rokmi 1985 – 2010. Tieto informácie sú veľmi znepokojujúce, nielen pre prežitie populácie hlucháňa v Karpatoch, ale aj pre ďalšie druhy viazané na staré a štruktúrované lesy. Navrhnutá stratégia manažmentu horských lesov s výskytom hlucháňa, vychádzajúca z krajinnej úrovne, by pomohla mnohým ďalším druhom, napríklad ďatľovi trojprstému (*Picoides tridactylus*), kuvičkovi vrabčiemu (*Glaucidium passerinum*) (Suter et al. 2002), veľkým šelmám (Dorrestein et al. 2014), saproxilickým organizmom (Seibold et al. 2015) a mnohým ďalším. Veríme, že výsledky tejto štúdie poskytnú základy pre vytvorenie rovnováhy medzi využívaním lesov a ochranou biodiverzity v Karpatoch.

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