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Habitatové preference, stanovištní dynamika a management hmyzu vázaného na staré stromy

Disertační práce

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Anotace

Tato práce se zabývá habitatovými preferencemi a stanovištní dynamikou hmyzu vázaného na staré a volně rostlé stromy a na management středoevropských nížinných světlých lesů. Práce poukazuje na současné problémy v ochraně hmyzu vázaného na staré stromy. Na příkladu brouka specializujícího se výhradně na staré stromy popisuje jeho ekologické nároky v rámci jednotlivých starých stromů a zároveň poukazuje na rozdíly ve využívání starých stromů na stanovištích s rozdílnými podmínkami prostředí. Práce se dále věnuje vlivu ořezávání stromů na tvorbu stanovišť s mrtvým dřevem a na vliv aktivního managementu na společenstva organismů středoevropských nížinných lesů.

Annotation

The thesis presents studies on habitat preferences of beetles associated with senescent, open-grown trees and on dynamics and management of saproxylic habitats. It presents a brief insight into the current issues in the conservation of insects dependent on old trees. It presents the patterns of exploitation by a veteran tree specialist within old open-grown trees and the local patterns of tree exploitation by the same species at sites with different characteristics. Further, it presents a study of the effect of a prunning technique on formation of deadwood microhabitats, and also the importance of active interventions in closed-canopy forests for the communities in temperate lowland woodlands.

Prohlášení

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

Vsetín, 5. 8. 2019

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Mgr. Michal Plátek

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I. Albert, J., **Plátek, M.** & Čížek, L., 2012. Vertical stratification and microhabitat selection by the Great Capricorn Beetle (*Cerambyx cerdo*) (Coleoptera: Cerambycidae) in open-grown, veteran oaks. *European Journal of Entomology* 109: 553–559. (IF = 0,918)

M. Plátek se významně podílel na zpracování výsledků a jejich interpretaci, analyzoval data a podílel se na psaní manuskriptu s L. Čížkem; design studie byl sestaven L. Čížkem a data sbíral J. Albert.

II. Šebek, P., Altman, J., **Plátek, M**. & Čížek, L., 2013. Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows. *PLoS One* 8, e60456. (IF = 3,23)

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Vyjádření spoluautorů

Lukáš Čížek, vedoucí této disertační práce a spoluautor všech předložených studií prohlašuje, že Michal Plátek je prvním autorem manuskriptu IV. a korespondenčním autorem manuskriptu I. a že se na jejich vypracování podílel zásadní měrou.

Pavel Šebek, první a korespondenční autor manuskriptu II. a III., prohlašuje, že souhlasí s jejich zařazením do této disertace a že podíl M. Plátka na jeho vypracování odpovídá výše stanovenému popisu.

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Obsah

Úvod

Data z poslední doby dokládají rapidní trend ochuzování diverzity i početnosti hmyzu na evropském kontinentu. Nemizí přitom jen ohrožené druhy hmyzu, ale klesají i populace běžných druhů (van Swaay et al. 2013; Habel et al. 2015; Hallmann et al. 2017). Dramaticky klesly populace lučních motýlů (Nilsson et al. 2008; van Swaay et al. 2013), žahadlových blanokřídlých (Goulson et al. 2008; Winfree et al. 2009; Potts et al. 2010; Ollerton et al. 2014; Woodcock et al. 2016) nebo nočních motýlů (Conrad et al. 2002; Conrad et al. 2006; Fox 2013; Fox et al. 2014).

Příčiny poklesu jsou přičítány hlavně ničení přirozených stanovišť a intenzivnímu průmyslovému zemědělství (Morecroft et al. 2002; Biesmeijer et al. 2006; Nilsson et al. 2008; Winfree et al. 2009; Potts et al. 2010; Ollerton et al. 2014; Fox et al. 2014), v lesích je přičítán intenzivnímu lesnickému hospodaření (Bergman, 2001; Beneš et al. 2006; van Swaay et al. 2006; Agnoletti, 2007; Brockerhoff et al. 2008; Nieto & Alexander, 2010; Kopecký et al. 2013). Ochuzování biodiverzity ale pokračuje i přes to, že jsou vyhlašována nová chráněná území, která jsou od intenzivního hospodaření ušetřena (Winter, 2012; Schultze et al. 2014).

Jednou z nejpočetnějších a nejvíce zkoumaných skupin organismů v lesích je saproxylický hmyz, tj. hmyz vázaný na mrtvé nebo rozkládající se dřevo a na staré stromy (bližší definice popsána v dalších kapitolách). Za klíčová stanoviště, jež hostí podstatnou část spektra saproxylických organismů lze považovat staré a velké stromy (Šebek et al. 2016). V dnešní krajině však dochází k úbytku starých stromů (Read, 2000; Andersson & Östlund 2004) a s tím spojenému vymírání saproxylických organismů (Miklín et al. 2018).

V následujících kapitolách popisuji význam starých stromů pro biodiverzitu saproxylického hmyzu, příčiny jejich úbytku, mizení na ně vázané biodiverzity a možnosti, jak tomu zamezit.

Staré a velké stromy

Pro organismy vázané na mrté dřevo jsou významné zejména stromy s velkým průměrem kmene a stromy staré (Ranius, 2000; 2001; 2002; Buse et al. 2008; Harvey & Gange 2011; Harvey et al. 2011; Gouix et al. 2015; Foit et al. 2016; Kostanjsek et al. 2018; Kašák et al. 2019). Některé druhy jsou na takové stromy vysloveně specializovány, mnohé další se na nich pravidelně vyskytují, protože na nich často nacházejí vhodná stanoviště (viz. níže). Velikost a stáří jsou ale relativní pojmy. Někde je strom stoletý dub mohutným velikánem s průměrem kmene přes metr, jinde má stejně starý strom kmen jen 15 cm silný. Starý nebo mohutný strom není proto snadné definovat. Read (2000) navrhuje definovat staré stromy podle několika kritérií - jsou zajímavé svým stářím biologicky, esteticky nebo kulturně; jsou v rámci svého života ve fázi stáří; jsou staré v porovnání se stromy stejného druhu. Definice starého stromu je závislá na typu ekosystému a specifických podmínkách prostředí v jakých roste (Lindenmayer et al. 2012). Není přitom striktně stanovena nejnižší hranice, v jakém věku je strom starý (Horák, 2017). Na rozdíl od menších a mladých stromů je však jejich ekologická role unikátní. Velikost a místo, kde tyto stromy rostou, totiž ovlivňují typické charakteristiky vzhledu, což staré stromy odlišuje od těch menších a mladších (Lindenmayer et al. 2012; Šebek et al. 2016). Poskytují širší variabilitu, dlouhodobou přítomnost a objem tzv. „mikrostanovišť" s mrtvým dřevem. V rámci jednoho stromu mohou tato mikrostanoviště po dlouhou dobu sloužit jako potrava, úkryty či rozmnožovací substrát pro širokou škálu organismů (Warren & Key 1991; Irmler et al. 1996; Siitonen et al. 2000; Lindhe & Lindelöw 2004; Radu, 2006; Hartel et al. 2013; Horák et al. 2014; Šebek et al. 2016).

Staré stromy ve středoevropských nížinných lesích

Důležitou otázkou je, kde staré stromy přirozeně rostly. V současné době tyto stromy ve volné krajině téměř nenajdeme, rostou hlavně v městských parcích, alejích kolem cest, na hrázích rybníků, část jich roste jako tzv. výstavky v mladších lesích ponechané po těžbě (Bouget et al. 2014; Horák, 2017), zbytek stromů dožívá zastíněn uvnitř hospodářských lesů nebo v rezervacích, které podléhají bezzásahovému managementu (Miklín & Čížek 2014).

Ve střední Evropě automaticky dělíme krajinu na les a bezlesí. Bezlesí je rozděleno na velká pole nebo pastviny téměř bez dřevin. Každého logicky napadne, že místem, kde by staré stromy měly přirozeně růst, je les. Současné lesy jsou však většinou vysokokmenné, často monokulturní plantáže s plným zápojem korun případně tmavé rezervace. Jakýkoliv přechod mezi těmito dvěma extrémy je vzácný. Odpověď na otázku, jak vypadá les nebo krajina, kde přirozeně rostou staré velké stromy, však není jednoznačná. Je proto nutné podívat se do historie vývoje středoevropských lesů od konce doby ledové a příchodu člověka až do současnosti.

Na základě pylových analýz z půdních sedimentů a výzkumem složení uhlíků z raně neolitických sídlišť je přibližně známo, že se lesy skládaly převážně ze světlomilných dřevin – dubů, lísek, lip (Bakels, 1992; Salavert et al. 2014). Bengtsson et al. (2000) a Vera (2000) přišli s hypotézou, že lesy byly spíše světlé a mnohem více otevřené, protože dub a líska vyžadují pro svůj růst místa s otevřenou strukturou lesa. Vera (2000) tak popisuje podobu středoevropské krajiny jako mozaiku různě zapojených lesů a parkové krajiny. Strukturu takových lesů ovlivňovaly nejen abiotické faktory jako vítr, oheň, voda (Bradshaw, 1997; Bengtsson et al. 2000; Niklasson et al. 2010; Whitehouse & Smith 2010; Adámek et al. 2015), ale také biotické faktory. Podle Very (2000) totiž omezovala růst a regeneraci stromů pastva a činnost velkých savců – zubra, pratura, divokého koně, jelena, ale i bobra (Nolet & Rosell 1998). Rozptýlené křoviny, které tato zvířata nespásla, poskytly úkryt a ochranu pro semena světlomilných dřevin, které měly možnost regenerovat a vyrůst. Takto se mohla udržet parková krajina s novými solitérními stromy (Vera, 2000). Lokální vliv, kromě velkých býložravců, měl už v té době také člověk (Clark et al. 1989; Tinner et al. 1999).

V období neolitu byl již vliv člověka na nížinné lesy nepopiratelný (Szabó, 2009). Lidé káceli lesy a měnili je na ornou půdu a pastviny. Dřevo zužitkovali jako stavební materiál nebo jako palivo. Během středověku dále docházelo k silné redukci a změně struktury zbylých nížinných lesů (Szabó, 2009). Otázkou tak zůstává, kde v tak člověkem ovlivněné krajině zůstaly staré a velké stromy.

Tam, kde se více páslo, osekávali lidé vhodné stromy a opakovaně tak mohli během relativně krátké doby získávat z jednoho stromu dostatek paliva nebo letniny (větví na palivo a/nebo s listím pro dobytek) po velmi dlouhou dobu (Buckley, 1992; Rackham, 1998; Rackham, 2003; Petit & Watkins 2003; Kirby & Watkins 2015; Plieninger et al. 2015; Čížek et al. 2016). Osekávání stromů se provádělo různými způsoby. Častou formou zřejmě bylo tzv. „vrškové“ hospodaření, někde známé jako ořez „na hlavu“ (v angl. pollarding), při němž se větve stromů stínaly zpravidla ve výšce 1,5 až 3 m nad zemí a kmeny byly ponechány, aby regenerovaly tvorbou pňových výmladků (Čížek et al. 2016). Další způsob, v angličtině známý jako „shredding“, byl tradiční způsob získávání letniny, při němž se osekávaly větve na hlavním kmeni a na vrcholu se ponechala malá koruna (Rackham, 1998). Pokud se strom nepokácel, umožnil ořez přežívat starým stromům po staletí, při čemž se zachovávala kontinuita stanovišť s mrtvým dřevem (Rackham, 1998; Read, 2000; Siitonen & Ranius 2015).

Strukturu lesních biotopů, ve kterých rostly staré a mohutné stromy, silně ovlivňovala pastva dobytka nebo chov zvěře v loveckých oborách (Rackham, 1998; Rackham, 2003; Bergmeier et al. 2010; Hartel et al. 2013; Hooke, 2013; Kirby & Watkins 2015; Fletcher, 2015; Plieninger et al. 2015). Historicky byla pastva dobytka v lese velmi rozšířená a provozovala se již v době, kdy došlo k domestikaci zvířat na začátku neolitu (Szabó, 2009). Do jisté míry tak pastva domestikovaných zvířat v lese nahradila činnost divokých zvířat a jejich ekologickou roli (Vera, 2000; Szabó, 2009; Jirků & Dostál 2015). Krajina byla srovnatelná spíše s dnešními parky s více méně roztroušenými starými stromy (Bütler et al. 2013; Siitonen & Ranius 2015). Druhové složení, míra a způsob vypasení vegetace se lišilo tím, jaký druh dobytka se v lese pásl (Vera, 2000; Jirků & Dostál 2015). V pastevních lesích bylo zároveň možné získávat dřevo, aniž by se staré stromy likvidovaly.

Další, historicky velmi rozšířený způsob hospodaření, nahrazující přirozenou otevřenou strukturu lesů, bylo výmladkové hospodaření (pařezení) (Szabó, 2009; Müllerová et al. 2014). Tímto způsobem se získávalo hlavně palivové dříví tak, že se stromy osekaly a po nějaké době z pařezu zregenerovaly vegetativní výmladností. Pařezení mělo několik forem, včetně výše zmíněných způsobů ořezu stromů, které se používalo převážně tam, kde se více páslo. Tyto formy lesa představovaly dynamickou mozaiku v různých fázích sukcese, od zcela otevřených ploch, po hustě zapojené porosty a umožňovaly zachovat kontinuitu různě otevřených lesních stanovišť s mrtvým dřevem (Buckley, 1992; Joys et al. 2004). Není divu, že takové lesy hostily bohatá společenstva živočichů, rostlin a dalších organismů (Warren & Thomas 1992; Bengtsson et al. 2000; Beneš et al. 2006; Spitzer et al. 2008; Bergmeier et al. 2010; Hédl et al. 2010; Bugalho et al. 2011; Vodka & Čížek 2013; Hartel et al. 2014). Přítomnost starých a velkých stromů v pařezinách je však diskutabilní (blíže Šebek, 2016). Ekologickou roli starých stromů tak nahrazovaly spíše mohutné osluněné pařezy (Harvey et al. 2011).

Výše zmíněné způsoby hospodaření v lesích střední Evropy převládaly minimálně dlouhá staletí. Ke změně využívání lesů začalo docházet v posledních 200 letech, v České Republice pak ještě dramatičtěji po nástupu komunismu. Mizely formy tradičního hospodaření, stejně jako byly potlačovány přirozené disturbance (Bergmeier et al. 2010; Müllerová et al. 2014; Müllerová et al. 2015). Světlé lesy začaly razantně ubývat a převáděly se na lesy vysoké, aby poskytly kvalitní sortimenty dřeva (Müllerová et al. 2014). Intenzifikace zasáhla nejen lesnictví, ale i zemědělství a s ním pastevní hospodaření (Bürgi 1999; Szabó, 2013; Savill, 2015). Dobytek začal být chován pod střechou a roztroušené stromy bývalých pastevních lesů byly záměrně odstraňovány, ať už z důvodu zvýšení produktivity intenzivních luk a pastvin nebo jako nebezpečné či možné zdroje nákazy pro mladší a zdravé stromy v okolí (Bürgi, 1999; Plieninger & Bieling 2013). Tato praxe přetrvává dodnes. Pokud nebyly otevřené lesy zalesněny, podlehly sekundární sukcesi. Postupný proces zhoustnutí lesů pak bez přirozených disturbancí postihl plošně i hospodářsky nevyužívaná chráněná území a rezervace, kde došlo k expanzi zapojených lesů na úkor světlých lesů s mohutnými stromy (Miklín & Čížek 2014). Staré stromy nebyly schopny konkurovat o světlo s mladými a postupně usychaly (Rackham, 1998). Posledními místy, kde se udržely otevřené lesy s mohutnými stromy, jsou obory se zvěří, ovocné sady, městské parky, aleje a hráze rybníků (Alexander, 2008b; Bergmeier et al. 2010; Horák, 2017).

Nejdůležitější faktory určující diverzitu saproxylického hmyzu na starých stromech

Saproxylický hmyz tvoří významnou část biodiverzity, podle některých odhadů tvoří dokonce třetinu hmyzu v lesních ekosystémech (Stokland et al. 2012; Ulyshen & Šobotník 2018). Saproxylický hmyz lze stručně definovat jako organismy, které jsou v určité fázi svého životního cyklu vázány na mrtvé dřevo, rozkládající se dřevěnou hmotu nebo stojící či padlé mrtvé stromy. Svou činností umožňují rozkládat dřevní hmotu a navracet rozložené látky zpět do lesních ekosystémů (Speight, 1989; Dajoz, 2000). Saproxylický hmyz lze rozdělit do několika funkčních skupin: floemofágy, xylofágy, fungivory, či predátory (Hövemeyer & Schauermann 2003; Bouget et al. 2005; Krivosheina, 2006; Stokland et al. 2012; Ulyshen & Šobotník 2018). Někteří autoři řadí mezi saproxylický hmyz i skupiny hmyzu živící se mízou stromů (Alexander, 2008a), blanokřídlé hnízdící v dutinách stromů (Bogusch & Horák 2018) nebo dokonce vodní hmyz žijící ve stromových dendrotelmách (Ulyshen & Šobotník 2018).

Saproxylický hmyz lze najít napříč taxonomickými skupinami, přesto jsou druhově nejbohatší skupinou brouci (až 25 %) (Stokland et al. 2012). Brouci jsou zároveň nejvíce prozkoumanou a také ekologicky nejvýznamnější skupinou saproxylického hmyzu (Speight, 1989; Stockland et al. 2012; Horák, 2017; Ulyshen & Šobotník 2018).

Co tedy určuje druhovou bohatost saproxylického hmyzu na starých stromech v nížinných listnatých lesích střední Evropy? Z předešlé kapitoly je patrné, že složení společenstev saproxylických organismů bylo po tisíciletí adaptováno na lesy, které měly odlišnou podobu a strukturu než ty dnešní.

Světelné podmínky

Jako jeden z nejdůležitějších faktorů se tedy jeví otevřenost porostů, dostupnost a míra slunečního záření (Jonsell et al. 1998; Ranius & Jansson 2000; Franc & Götmark 2008; Vodka et al. 2009; Bergmeier et al. 2010; Bugalho et al. 2011; Hartel et al. 2013; Horák & Rébl 2013; Vodka & Čížek 2013; Bouget et al. 2014; Plieninger et al. 2015). Dřevo exponované ke slunci se totiž lépe vyhřeje a zvyšuje se tak šance na vývoj larev (Horák et al. 2014; Siitonen & Ranius 2015). Otevřenost porostů také usnadňuje dospělcům větších druhů prohřátí a let (Harvey et al. 2011). Teplejší podmínky umožňují dokonce přežívat organismům i ve stromech, které májí menší objem mrtvého dřeva (Müller et al. 2015).

Velikost stromu

Otevřenost porostu a světelné podmínky ovlivňují také samotný růst stromu. Volně rostlé stromy totiž mají větší korunu a kmeny s velkým objemem dřeva v porovnání se stromy rostoucí v zapojeném lese (Šebek et al. 2016). Další klíčovou charakteristikou starých stromů je tedy velký průměr kmene, respektive objem dřeva (Warren & Key 1991; Irmler et al. 1996; Siitonen et al. 2000; Lindhe & Lindelöw 2004; Radu, 2006; Horák, 2017). Stromy s kmeny o velkých průměrech vytváří pestrá mikrostanoviště – dřevo v různé fázi rozkladu a fyziologickém stavu, velké mrtvé větve, dutiny, praskliny, části kmenů bez kůry, hnijící kořeny, plodnice dřevokazných hub, epifytické mechy a lišejníky a místa s výrony mízy (Winter & Möller 2008; Vuidot et al. 2011; Bütler et al. 2013; Siitonen & Ranius 2015; Kraus et al. 2016). Tyto stromy vyhovují velkým a ohroženým druhům saproxylických brouků (Stokland et al. 2012). Nejznámější zástupce, kteří zároveň figurují jako druhy deštníkové, najdeme téměř výhradně na velkých stromech. Patří mezi ně páchník hnědý (*Osmoderma barnabita*) (Ranius, 2000; 2001; 2002), roháč obecný (*Lucanus cervus*) (Harvey & Gange 2011; Harvey et al. 2011), tesařík obrovský (*Cerambyx cerdo*) (viz níže), ale i další, méně studované druhy jako tesařík drsnorohý (*Aegosoma scabricorne*) (Foit et al. 2016), kovařík fialový (*Limoniscus violaceus*) (Gouix et al. 2015) nebo horské druhy jako rýhovec pralesní (*Rhysodes sulcatus*) (Kostanjsek et al. 2018) a roháček jedlový (*Ceruchus chrysomelinus*) (Kašák et al. 2019). Každý z těchto druhů vyhledává v rámci velkých stromů různá mikrostanoviště, jejich přítomnost je ovlivněna interakcemi rozdílných faktorů, někteří z nich se dokonce dokáží vyvíjet v menších stromech (Harvey et al. 2011; Chiari et al. 2013; blíže také Kapitola I.). I přes tento fakt je velikost stromu klíčovou charakteristikou neboť, v souvislosti s populační dynamikou, hostí obrovské stromy daleko větší populace saproxylického hmyzu, které jsou méně náchylné na vymření (Hanski, 1998).

Stáří stromu

V úvodu této práce jsem definoval starý a velký strom. Velikost i stáří stromu je ovšem, s ohledem na environmentální faktory, relativní. Výše jsem popsal, že strom s velkým objemem kmene je i velmi starý a vytváří širokou škálu mikrostanovišť s mrtvým dřevem. Ukazuje se však, že i stromy s obrovským průměrem kmene nevytváří vždy pro saproxylické organismy vhodná mikrostanoviště (Horák, 2017). Relativitu stáří dokumentují obrovské duby v České Republice rostoucí na půdách s bohatým zdrojem živin, dostatečnou vlhkostí substrátu a s dostatečným osluněním. V dřívějších studiích se uvádělo, že jsou staré 400 až

800 let (Vrška et al. 2006). Novější práce ovšem odhadují věk těchto stromů maximálně na 400 let (Altman et al. 2016). To dokazuje, že i přes úctyhodný věk mají solitérní stromy mnohem rychlejší radiální růst, než se dříve předpokládalo. Problematika stáří stromu, jako charakteristiky určující biodiverzitu saproxylických organismů, je proto poměrně složitá (Horák, 2017). Přesto faktu, že stromy dokážou dorůst velkých rozměru v relativně nízkém věku lze, za určitých podmínek a pomocí vhodných nástrojů, využít k poměrně rychlému vytváření vhodných mikrostanovišť s mrtvým dřevem (tomuto tématu se věnuji v Kapitole III.).

Vertikální stratifikace

Z předchozích kapitol vyplývá, že složení společenstev saproxylických bezobratlých a jejich populace ovlivňuje míra oslunění stromu. Nabízí se otázka, zda v hustě zapojeném lese jsou druhově bohatší místa v podrostu či v korunách stromů a zda korunové patro případně nabízí podmínky k životu specialistům vyžadujícím osluněná stanoviště. Několik prací dokazuje, že složení společenstev bezobratlých v korunách stromů a v jejich podrostu se prokazatelně liší (Wermelinger et al. 2007; Floren & Schmidl 2008; Ulyshen, 2011; Vodka & Čížek 2013; Weiss et al. 2016). Výstupy z jednotlivých studií se však rozcházejí (Weiss et al. 2016). Rozdíly můžou být přičítány různým typům lesů, míře otevřenosti porostů, převládajícímu druhovému složení stromů nebo způsobu managementu (Vodka & Čížek 2013). Není tedy vertikální stratifikace saproxylických bezobratlých pouze funkcí otevřenosti porostů nebo míry oslunění měnící se s rostoucí vzdálenosti od země (Gossner, 2009)?

U saproxylických brouků se ukazuje, že druhová diverzita je vyšší spíše v podrostu a že společenstva žijící v korunách stromů nejsou pouze podskupinou žijící v podrostu (Hjältén et al. 2007; Wermelinger et al. 2007; Ulyshen & Hanula 2009; Bouget et al. 2011; Floren et al. 2014). Preference pro místa, která jsou níže na stromech, může být vysvětlena tím, že je zde větší pestrost mikrostanovišť a obecně více mrtvého dřeva (Weiss et al. 2016). Vodka et al. (2009) však prokázali, že druhová pestrost tesaříkovitých a krascovitých brouků vyvíjejících se v dubech byla sice vyšší v podrostu, ale spíše v osluněných částech stromu. Vodka & Čížek (2013) rozšířili studium vertikální stratifikace saproxylických bezobratlých o horizontální rozměr. Gradient slunečního záření byl významný pro distribuci bezobratlých jak vertikálně, tak i horizontálně. Přesto byla vyšší diverzita na okraji zapojeného lesa a vertikální stratifikace měla na diverzitu a složení společenstev spíše menší vliv. Šebek et al. (2016) dále studovali vertikální stratifikaci uvnitř zapojených dubových lesů a mezi solitérními duby a prokázali, že vertikální stratifikace měla na složení společenstev bezobratlých (včetně saproxylických brouků) menší vliv než míra oslunění. Důležitým výstupem z této studie však bylo, že přežívání specializovaných společenstev bezobratlých nelze nahradit tím, že část přežije v korunách stromů v zapojeném lese nebo jeho podrostu. Společenstva žijící na stromech uvnitř zapojeného lesa byla druhově chudší a tvořena většinou generalisty. Navíc byla jen podmnožinou toho, co lze najít na solitérních stromech. Staré solitérní stromy totiž hostily mnohem více specializovaných druhů vyžadující osluněná mikrostanoviště. Znovu se tak dostávám k významu volně rostlých a starých stromů.

Otázce, jak ovlivňuje vertikální stratifikace přítomnost a velikost populací tesaříka obrovského právě na solitérních dubech, se věnuji v Kapitole II.

Ostatní faktory

Další charakteristikou, jež ovlivňuje složení společenstev saproxlických bezobratlých je druhové složení stromů. Ze všech evropských druhů stromů hostí nejvíce druhů saproxylických brouků duby (*Quercus* sp.) (Brändle & Brandl 2001). Druhy vázané na staré stromy také často vyžadují těsnou návaznost na kvetoucí louky a pastviny. Larvy řady druhů potřebují k vývoji dřevo statných stromů, ale dospělci vyhledávají kvetoucí byliny s nektarem (Fayt et al. 2006; Müller et al. 2008; Lachat et al. 2013).

Neméně důležitou charakteristikou ovlivňující populační dynamiku specializovaných druhů saproxylických bezobratlých je hustota (tedy celkové množství) starých stromů (Ranius, 2000). Stromy by od sebe neměly být příliš vzdálené, protože se tím snižuje pravděpodobnost osídlení hmyzem z původně obsazených stromů (Buse et al. 2007).

Modelový druh – tesařík obrovský – specialista žijící na starých stromech

Předložená práce se z velké části věnuje studiu habitatových preferencí tesaříka obrovského (*Cerambyx cerdo* Linnaeus, 1758) – jednoho z největších evropských brouků úzce specializovaného na velké a staré stromy (blíže Kapitola I. a II.). Tento brouk je rozšířen na většině území Evropy až po Kavkaz (Sláma, 1998). Na většině území Evropské unie však téměř vymizel (Sláma, 1998; Ehnström & Axelsson 2002; Starzyk, 2004; Jurc et al. 2008) a je legislativně chráněn (Council of the European Communities, 1992). Přesto je v oblasti mediteránu poměrně běžný a dokonce je zde považován za škůdce (Torres-Vila et al. 2017).

Larvy tesaříka obrovského se vyvíjí převážně ve dřevě velkých a silně osluněných dubů (Buse et al. 2007), ale i dalších druzích stromů (Sláma, 1998). Preferují staré a oslabené, ale stále žijící stromy (Buse et al. 2007). Larvy brouka hrají důležitou ekologickou roli, protože dokáží vytvářet mikrostanoviště v mrtvém dřevě pro další ohrožené organismy vázané na staré stromy. Proto je nazýván tzv. ekosystémovým inženýrem (Buse et al. 2008).

Managementu a ochraně populací tesaříka obrovského se podrobně věnuji v Kapitole I. a II. K návratu populací na vhodná místa a zvýšení lokální míry biodiverzity lze, krom vhodného managementu, přispět reintrodukcí (Buse et al. 2008). Což dokládá i práce Draga & Čížka (2015), v níž popisují úspěšnou reintrodukci tesaříka obrovského do jižních Čech.

U tesaříka obrovského byla studována i míra disperze. U specializovaných saproxylických druhů hmyzu vázaných na staré stromy se totiž předpokládá, že disperze je spíše slabá (Feldhaar & Schauer 2018) a tomu je přizpůsoben i následný management stanovišť. Domněnku stálosti populací a slabé disperze tesaříka obrovského sice dokládají Torres-Vila et al. (2017), přesto Drag & Čížek (2018) ve své práci prokázali, že brouk je mnohem mobilnější a je schopen překonat i větší vzdálenosti, čímž přináší jiný pohled na ekologii a strategii ochrany tesaříka obrovského.

Management a ochrana hmyzu na starých stromech

V předešlých kapitolách jsem nastínil, jakou podobu měly středoevropské nížinné lesy od konce doby ledové po současnost a kde a za jakých podmínek rostly staré velké stromy. Struktura lesů byla utvářena po tisíciletí přirozenými činiteli i člověkem. Na takové lesy se adaptovaly organismy s různými životními strategiemi. Kdysi druhově bohaté lesy se specializovanými světlomilnými organismy dnes hostí pouze generalisty schopné přežít v zastíněných a na živiny bohatších stanovištích (van der Werf, 1991; van Calster et al. 2008; Hédl et al. 2010; Kopecký et al. 2013; Vild et al. 2013). Pochopení toho, jak různé ekologické faktory a jejich kombinace spolu se znalostí historického vývoje nížinných lesů ovlivňují diverzitu (nejen) bezobratlých, nám umožní navrhnout ochranářská opatření, která mohou zpomalit stále pokračující ztráty biodiverzity evropských lesů (EEA, 2009).

Představa historické podoby středoevropských lesů jako neproniknutelného zapojeného hvozdu byla a je široce rozšířená u ekologů, lesníků i veřejnosti. V ochranářské praxi stále přetrvává doktrína, že les jsou stromy, které vyrostou v zapojený porost, a když zahynou či jsou pokáceny, musí se přirozeně vrátit podoba lesa zpět ke stabilnímu tmavému hvozdu (Hédl & Szabó 2010). Tato představa vychází z konceptu tzv. ekologické stability, podle níž jsou „stabilní" biotopy považovány za hodnotnější, než tzv. biotopy nestabilní. Za biotopy stabilní jsou považovány zapojené lesy blízko tzv. klimaxu, k němuž podle zastánců této teorie stability po disturbanci směřuje veškerá sukcese a který je rovnovážným, přirozeným stavem přírody (Čížek et al. 2016). V rezervacích a chráněných oblastech proto stále převládá tzv. bezzásahový režim, který je postaven na představě, že v ochranářsky cenných lesích ponechaných bez zásahu vznikne člověkem nedotčená divočina nebo prales.

V nížinných lesích je bezzásahový režim pro biodiverzitu organismů vázaných na světlé lesy, vzhledem k historickému vývoji a způsobu využívání (viz výše), spíše kontraproduktivní. Většina ploch současných lesů je určena k hospodářskému využívání a produkci kvalitních sortimentů dřeva. Porosty ponechané samovolnému vývoji jsou zase příliš malé, aby v nich probíhala přirozená vegetační dynamika (Schultze et al. 2014), chybí v nich větší zvířata a oheň (Vera, 2000; Götmark et al. 2015).

Vliv aktivního managementu na biodiverzitu je velmi dobře zdokumentován (Horák et al. 2013; Horák et al. 2014; Miklín & Čížek 2014; Šebek et al. 2016; Miklín et al. 2018). Aktivní management se dokonce nevylučuje s představami zastánců divočiny a přirozených procesů, jen je doplňuje o prvky, které zastánci bezzásahového způsobu hospodaření buď neakceptují, nebo neznají. Je však nutné brát v potaz historii využívání krajiny na daném místě (Foster et al. 2003; Jamrichová et al. 2013).

V současnosti existuje několik podrobných manuálů, jak vhodně postupovat při vytváření lesních stanovišť s vysokou mírou biodiverzity (např. Read, 2000; Konvička et al. 2005; Jirků & Dostál 2015; Čížek et al. 2016). Autoři navrhují návrat k tradičním způsobům hospodaření jako je pastva v lese nebo různé formy pařezení (včetně ořezu starých stromů). V hospodářských lesích České Republiky jsou ovšem tyto způsoby hospodaření legislativně omezeny (Čížek et al. 2016).

Klíčovým zásahem pro vznik nebo záchranu starých stromů je tedy prosvětlení porostů. Prosvětlením lze totiž docílit vzniku tzv. „biotopových stromů“. V rozvolněném porostu dopadá na mrtvé dřevo biotopových stromů sluneční světlo a ty jsou pak atraktivní pro mnoho druhů ohrožených organismů (Vodka et al. 2009; Seibold et al. 2015; Šebek et al. 2016). Stromy rostoucí volně nebo v otevřených porostech mají rozložitou korunu a poskytují mnoho mikrostanovišť. Je prokázáno, že vznik komplexní koruny je podmíněn růstem mimo zapojený les, protože uvnitř hustého porostu nemá strom možnost takovou korunu vytvořit. Naopak v hustém lese rostou stromy co nejrychleji do výšky, aby uspěly v konkurenčním boji. Na vrcholu vytvoří korunu, která s ostatními stromy vytvoří neproniknutelný zápoj. Zároveň nejsou velké staré stromy, které jsou většinou pozůstatky hospodaření z minulosti, schopny konkurovat mladším a vyšším jedincům a usychají (Rackham, 1998; Šebek et al. 2016).

Volně rostlé stromy mají i rychlejší radiální růst než stromy rostoucí v hustém lese. Rychlým radiálním růstem lze poměrně snadno a rychle docílit vzniku mohutných stromů a zachovat jejich kontinuitu v čase a prostoru (Altman et al. 2016). Je ovšem nutné znovu sázet nové stromy, protože generace velkých solitérů rychle mizí (Miklín & Čížek 2014; Altman et al. 2016; Miklín et al. 2018). Vznik většího počtu habitatových stromů s rozmanitými mikrostanovišti ze stromů mladších lze urychlit ořezem (viz také Kapitola III.). U starých stromů zase ořez může prodloužit jejich věk. Pokud je totiž strom rostoucí mimo zapojený les pravidelně ořezáván a nepodléhá konkurenčnímu boji s ostatními stromy v hustém lese, může se dožít i několika stovek let (Rackham, 1998; Read, 2000; Lonsdale, 2013). Odstraňováním větví se sníží těžiště stromu a tím dojde k jeho stabilizaci. Klesá tak riziko, že se strom rozpadne v důsledku velké váhy přerostlých větví (Rackham, 1998; Read, 2000; Siitonen & Ranius 2015). Ořezávaný strom tak může poskytovat mrtvé dřevo a vhodná mikrostanoviště mnoha druhům organismů po velmi dlouhou dobu (Lonsdale, 2013; Čížek et al. 2016).

Příčiny úbytku starých stromů a biodiverzity na ně vázané jsou poměrně dobře zdokumentované. K jejich záchraně je klíčové porozumění historického vývoje středoevropské krajiny, porozumění přirozených disturbancí a vliv člověka nahrazující přirozenou disturbanční dynamiku. Existuje poměrně mnoho nástrojů a manuálů, jak úbytku biodiverzity zabránit. I přes snahu odborníků a organizací zabývající se ochranou přírody se nedaří zabránit úbytku řady ohrožených a specializovaných saproxylických druhů organismů. Existují další nástroje, jak zamezit mizení starých stromů se specializovanými druhy? Je možné studiem habitatových preferencí jednoho klíčového druhu saproxylického brouka pomoci před ochuzováním biodiverzity? V následujících kapitolách se pokusím na tyto otázky odpovědět.

Cíle práce

Předložené práce se snaží poukázat na význam starých a velkých stromů ve světlých nížinných lesích a vliv aktivního managementu na biodiverzitu saproxylického hmyzu v podmínkách střední Evropy. První dvě studie rozšiřují znalosti o habitatových preferencích ohroženého a deštníkového druhu saproxylického brouka – tesaříka obrovského – specialisty žijícího na starých stromech. Další práce doplňují předešlé studie a poukazují na význam aktivních managementových zásahů podporující populace ohrožených organismů vázaných na světlé lesy.

Kapitola I. poukazuje na překvapivou variabilitu nároků různých populací brouka specializovaného na staré duby, které obývají rozdílná stanoviště. Na modelovém druhu, tesaříkovi obrovském, který je považován za druh žijící převážně na velkých starých dubech se ukazuje, že za určitých podmínek je schopen využívat mladší stromy o malých průměrech kmene. Cílem studie bylo zjistit, jak parametry stromů a okolí ovlivňují populace tesaříka obrovského na stanovištích s rozdílnými podmínkami. První populace obývala velké duby v nížinné oblasti bohaté na živiny a vodu, další obývala duby střední velikosti, rostoucí na písčitých půdách a třetí obývala duby malých rozměrů rostoucí na kamenitých svazích říčního kaňonu. Porozumění mechanismů, proč a za jakých podmínek jsou tesaříci obrovští schopni využívat menší stromy, může být užitečné v ochraně celého spektra ohrožených druhů vázaných na staré stromy. Velké stromy totiž z krajiny rapidně mizí a často je nutné hledat jejich dočasné náhrady, než dorostou nové generace. Ve studii jsou komentovány možná ochranářská opatření na podporu populací specializovaných saproxylických organismů a způsoby, jak zamezit úbytku starých stromů.

Kapitola II. popisuje faktory ovlivňující výskyt tesaříka obrovského v rámci jednotlivých mohutných stromů. Tesařík obrovský patří k deštníkovým druhům reprezentující rozmanitou a ohroženou faunu starých dubů. Cílem této studie bylo zjistit, jak parametry stromu (výška nad zemí, zastínění, orientace ke světovým stranám a tloušťka kmene) ovlivňují počty výletových otvorů (nepřímo velikost populace) tesaříka obrovského. Průzkum byl proveden na dvou lokalitách, kde rostou duby s velkým průměrem kmene – v Hluboké nad Vltavou a v Lánské oboře. Ve studii jsou komentována ochranářská opatření na podporu populací tesaříka obrovského.

Kapitola III. popisuje vliv vrškového ořezu na vznik dutin ve stromech. Vrškový ořez byl historicky široce rozšířená metoda, při níž se pravidelně ořezávaly větve v takové výšce nad zemí, aby na regenerující se větve nedosáhl dobytek. Tímto ořezem bylo možné opakovaně z jednoho stromu získat palivové dřevo nebo krmivo pro dobytek. Stromy ořezané tímto způsobem hospodaření jsou zajímavé tím, že vytvářejí v místech ořezu dutiny. Cílem studie je popsat, zda pravidelný ořez podporuje tvorbu dutin a zda je možné využívat tuto metodu v ochraně saproxylických druhů organismů.

Kapitola IV. popisuje efekt korunového zápoje na společenstva cévnatých rostlin, plazů, denních motýlů, saproxylických brouků a florikolních brouků v Národním parku Podyjí, který byl do 50. let minulého století obhospodařován pařezením a pastvou dobytka. Od té doby došlo k opuštění tradičního hospodaření a území zarostlo lesem. Většina ploch světlých lesů zmizela během posledních 60 let. Design studie spočíval ve vytvoření 12 experimentálních ploch uvnitř národního parku. Rostliny a vybrané skupiny živočichů byly sledovány na nově vytvořených pasekách a na kontrolních stanovištích (řídký les, lesní okraj a nivní louka). Ve studii jsou komentovány ohrožené druhy vybraných skupin organismů a vliv propojenosti vytvořených pasek na otevřená stanoviště.

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Kapitola I.

When is a tree suitable for a veteran tree specialist? Variability in the habitat requirements of the great capricorn beetle (*Cerambyx cerdo*) (Coleoptera: Cerambycidae)

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Abstrakt

Large veteran trees are key structures sustaining biodiversity in wooded landscapes. Many organisms associated with such trees are, however, also able to inhabit suitable trees with smaller diameters or other surrogate habitats. Understanding the mechanisms behind the importance of veteran trees and the conditions enabling veteran tree specialists to exploit smaller trees might help conservation efforts targeted at the diverse and highly endangered biota associated with veteran trees. To investigate this, we studied local patterns in the exploitation of trees by a veteran tree specialist, the great capricorn beetle (*Cerambyx cerdo*), at three sites with different soil characteristics, namely floodplain, dry-sandy and dry-rocky sites, where this beetle exploits oaks of large (~1.5 m), medium (~0.75 m) and small (~0.25 m) diameters, respectively. We recorded the presence and number of exit holes made by *C. cerdo* on each tree and related these to the characteristics of the trees: their diameters, openness of the canopy around them and their state of health. The probability of occurrence and the number of exit holes increased with tree diameter, canopy openness, and decreasing tree health, but these relationships differed considerably among the study sites. In dry conditions, trees of small diameters were more likely to be exploited by the beetle than in the floodplain. The number of exit holes, on the other hand, was a function of tree diameter, with large trees sustaining more beetles and thus acting as larger habitat patches. The species of oak affected the probability of exit hole presence as the sessile oak (*Quercus petraea*) and pedunculate oak (*Q. robur*) were preferred over Turkey oak (*Q. cerris*). The slope orientation also affected the presence of exit holes as trees on slopes with either an eastern or northern orientation were not exploited by the beetle. This study revealed a high level of between-site variability in the tree characteristics relevant to predicting the occurrence of *C. cerdo,* mainly with respect to diameter. Therefore, while the general patterns of habitat use and the fundamental niche of this beetle are well known, survival and protection of local populations is dependent on site-specific characteristics. The realized niche of this beetle must therefore be carefully considered when planning conservation management for a particular site. The results also signify that at some sites, small trees can, at least temporarily, substitute for scarce large trees if the state of their health is managed using proper conservation measures.

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ORIGINAL ARTICLE

When is a tree suitable for a veteran tree specialist? Variability in the habitat requirements of the great capricorn beetle (*Cerambyx cerdo*) (Coleoptera: Cerambycidae)

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Key words. Coleoptera, Cerambycidae, saproxylic beetles, deadwood, conservation management, old trees, veteran trees, habitat requirements, realized niche, site-specific patterns, great capricorn beetle, *Cerambyx cerdo*

Abstract. Large veteran trees are key structures sustaining biodiversity in wooded landscapes. Many organisms associated with such trees are, however, also able to inhabit suitable trees with smaller diameters or other surrogate habitats. Understanding the mechanisms behind the importance of veteran trees and the conditions enabling veteran tree specialists to exploit smaller trees might help conservation efforts targeted at the diverse and highly endangered biota associated with veteran trees. To investigate this, we studied local patterns in the exploitation of trees by a veteran tree specialist, the great capricorn beetle (*Cerambyx cerdo*), at three sites with different soil characteristics, namely floodplain, dry-sandy and dry-rocky sites, where this beetle exploits oaks of large (~1.5 m), medium (~0.75 m) and small (~0.25 m) diameters, respectively. We recorded the presence and number of exit holes made by *C. cerdo* on each tree and related these to the characteristics of the trees: their diameters, openness of the canopy around them and their state of health. The probability of occurrence and the number of exit holes increased with tree diameter, canopy openness, and decreasing tree health, but these relationships differed considerably among the study sites. In dry conditions, trees of small diameters were more likely to be exploited by the beetle than in the floodplain. The number of exit holes, on the other hand, was a function of tree diameter, with large trees sustaining more beetles and thus acting as larger habitat patches. The species of oak affected the probability of exit hole presence as the sessile oak (*Quercus petraea*) and pedunculate oak (*Q. robur*) were preferred over Turkey oak (*Q. cerris*). The slope orientation also affected the presence of exit holes as trees on slopes with either an eastern or northern orientation were not exploited by the beetle. This study revealed a high level of between-site variability in the tree characteristics relevant to predicting the occurrence of *C. cerdo*, mainly with respect to diameter. Therefore, while the general patterns of habitat use and the fundamental niche of this beetle are well known, survival and protection of local populations is dependent on site-specific characteristics. The realized niche of this beetle must therefore be carefully considered when planning conservation management for a particular site. The results also signify that at some sites, small trees can, at least temporarily, substitute for scarce large trees if the state of their health is managed using proper conservation measures.

INTRODUCTION

Large veteran trees provide deadwood and a wide range of deadwood-related microhabitats, such as hollows, bare wood and fungal fruiting bodies, which offer feeding opportunities for highly diverse assemblages of biota (Siitonen & Ranius, 2015). Due to this, veteran trees are key structures for sustaining biodiversity in wooded landscapes (Buse et al., 2008; Lindenmayer et al., 2014). Large veterans occur primarily in open places that have escaped intensive forestry or agricultural practices, such as savannas, wood pastures, avenues, hedgerows, orchards, game reserves or parks (Manning et al., 2006; Siitonen & Ranius, 2015; Horák, 2017; Miklín et al., 2018). Open woodlands support rich communities of animals including many light-demanding species that cannot be found under closed canopies (Ranius & Jansson, 2000; Sebek et al., 2016; Horák et al., 2018; Parmain & Bouget, 2018). Open conditions also help trees to attain large dimensions and age slowly, due to the absence of competition from younger trees (Drobyshev et al., 2008; Miklín et al., 2018). Large old trees are especially important for saproxylic (i.e. deadwood dependent) organisms (Siitonen & Ranius, 2015; Horák, 2017). By slowly ageing, living veteran trees provide deadwood and associated microhabitats for decades, therefore creating temporal continuity in the availability of deadwood resources. This is in contrast with already dead trees, which can offer such habitats only temporarily before they decay.

However, there has been a rapid global decline in the abundance of large veteran trees (Irmler et al., 1996; Read, 2000; Andersson & Östlund, 2004; Lindenmayer et al., 2012, 2014) and this has led to their associated specialists becoming highly endangered (Ranius, 2002; Siitonen & Ranius, 2015). In areas with numerous large old trees there is often a lack of young trees (Alexander, 1998; Bergmeier et al., 2010; Miklín & Čížek, 2014), leading to a potential gap in availability of old trees in the future, and thus to a temporal discontinuity in this precious habitat. Hence, bridging this gap in the availability of veteran trees is currently one of the main problems in the conservation of biodiversity in temperate regions (Gibbons et al., 2008; Miklín et al., 2018).

In order to propose conservation recommendations for overcoming the lack of veteran trees, knowledge of the fundamental demands of veteran tree specialists is needed. Trees or deadwood of large diameter are often mentioned as an important resource for many endangered saproxylic species (Gossner et al., 2013; Seibold et al., 2015; Eckelt et al., 2018; Kostanjsek et al., 2018), but many insects are at least occasionally able to exploit other habitats, such as younger and thinner trees or accumulated plant matter. For example, a model saproxylic beetle, the hollow specialist *Osmoderma* s.l. *eremita* mainly inhabits large hollow trees, but occasionally it is recorded in small trees with diameters of around 25 cm (Ranius et al., 2005; Barnouin et al., 2017). Deadwood of small diameter (around 20 cm) and even wood chips may serve as a habitat for larvae of another model beetle, the stag beetle *Lucanus cervus* (Harvey et al., 2011). In addition, the great capricorn beetle, *Cerambyx cerdo*, can also complete its development in large branches or occasionally in trees with a diameter less than 20 cm (Schwenke, 1974; Kimoto et al., 2006). It is still unclear as to what extent such marginal habitats may facilitate the long-term survival of organisms generally associated with large veteran trees. Furthermore, there is limited knowledge about the conditions that facilitate the exploitation of such marginal habitats (Ranius, 2007; Harvey et al., 2011; Macagno et al., 2015). Moreover, since habitat requirements may vary with biotic and/or abiotic conditions (Freese et al., 2006; Strausz et al., 2012), information on the requirements obtained in one part of a species' distributional range, or habitat type, may not be relevant elsewhere, thus hampering conservation efforts (Cromsigt et al., 2012).

The great capricorn beetle, *Cerambyx cerdo* Linnaeus 1758 (Cerambycidae), develops in the subcortical zone of trunks, branches and roots of open-grown old or weakened oaks (*Quercus* spp.) (Buse et al., 2007). Inhabited trees can be identified by typical oval exit (emergence) holes up to a width of 20 mm (Ehnström & Axelsson, 2002; Buse et al., 2007). This beetle is distributed throughout the Mediterranean region, Central Europe and the Caucasus (Bily & Mehl, 1989; Sláma, 1998; Sama, 2002). It is rare and declining in the northern parts of its European range (Sláma, 1998; Starzyk, 2004; Ellwanger, 2008; Jurc et al., 2008). Due to this, the beetle is listed as near threatened in the European Red List of saproxylic beetles (Cálix et al., 2018) and is also included in Appendix II and IV of the EU's Habitats Directive (Council of the European Communities, 1992), which specifies species of special conservation interest. It is considered to be an ecosystem engineer; the damage to trees caused by its larvae creates favourable conditions for many other saproxylic insects (Buse et al., 2008). Although closely associated with large trees (Buse et al., 2007; Albert et al., 2012), *C. cerdo* occasionally develops in small trees (Sláma, 1998). Therefore, it is a good model for investigating the variability in habitat requirements of saproxylic insects. Understanding the conditions that enable this beetle to exploit small trees might help to bridge a future gap in availability of veteran trees at currently inhabited sites, and thus increase the effectiveness of conservation measures aimed at this beetle and possibly also other veteran tree specialists.

To address the above issues, we recorded the parameters of trees locally exploited by three populations of *C. cerdo*. One population inhabits large trees growing on a floodplain, another inhabits medium-sized trees growing on dry sandy deposits, and the last population depends solely upon small trees growing on steep, rocky slopes of a river canyon. In order to reveal general and site-specific patterns in the exploitation of trees, we tested (i) whether the relationship between the probability of *C. cerdo* occurrence on trees and the characteristics of trees or their surroundings (diameter, canopy openness and state of tree health) differs among the sites, (ii) whether the relationship between the number of *C. cerdo* exit holes on a tree and the tree's characteristics differs among the sites, and (iii) whether species of oak or slope orientation affect the probability of *C. cerdo* occurrence and the number of its exit holes on trees.

MATERIAL AND METHODS

Study sites

This study was conducted at three sites inhabited by *C. cerdo* populations in South Moravia, Czech Republic. Each site is covered with a different type of woodland because of the abiotic conditions, such as terrain, humidity and substrate (Fig. 1).

The sampling included:

(i) Floodplain site covered by woodlands growing on mostly humid, nutrient rich soils in the Soutok game reserve (48°43′N, 16°55′E; 150 m a.s.l.; mean annual temperature 9.5°C; mean annual rainfall ~600 mm). There are large (diameters mostly > 1 m) and mostly open-grown, veteran pedunculate oaks (*Quercus robur*) in meadows at this site. For detailed information on the area and its woodland cover see Miklín & Čížek (2014).

(ii) Dry-sandy site covered by a thermophilous oak woodland on nutrient poor, dry sands of a river terrace in the Rendezvous National Nature Monument (48°45′N, 16°47′E; ~200 m a.s.l.; mean annual temperature 9.5°C; mean annual rainfall ~500 mm). There are semi-open stands of mostly old (up to 270 years) and mainly formerly coppiced Turkey oak (*Q. cerris*), pedunculate oak (*Q. robur*) and sessile oak (*Q. petraea*) of medium size (trunk diameters < 1 m) at this site.

(iii) Dry-rocky site covered by a xeric, dry woodland on nutrient poor, shallow soils on the steep, rocky slopes of the Dyje River canyon in the eastern part of the Podyji National Park (48°49′N, 15°58′E; 250–350 m a.s.l.; mean annual temperature 8.8°C; mean annual rainfall ~560 mm). There are mostly semi-open, formerly coppiced sessile oak (*Q. petraea*) stands both small in height and diameter (diameters mostly < 40 cm) at this site. The absence of large trees inhabited by *C. cerdo* in the wider

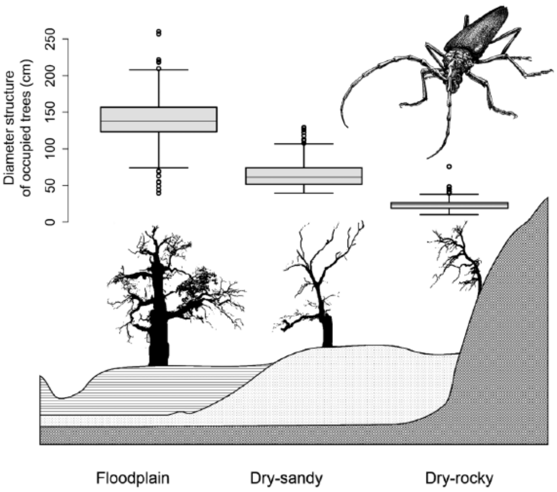

Fig. 1. Characteristic forms of the oaks that are potentially exploitable by *Cerambyx cerdo* at the three sites studied and the structure of the diameter of the trees occupied by this beetle (DBH in cm).

surroundings of this site demonstrates the ability of this beetle to survive without large trees. For detailed information on this site, see Miklín et al. (2016).

The dry-sandy site is seven km from the floodplain site and five km from the nearest floodplain woodland inhabited by the beetle. The dry-rocky site is > 60 km from both of the other two sites. Molecular genetic analysis indicates that the populations at the floodplain and dry-sandy sites are connected (Drag & Cizek, 2015), while the population inhabiting the dry-rocky site is most likely isolated.

Sampling strategy

At each site, oaks occupied by or potentially suitable for the great capricorn beetle were inspected for the presence of typical, up to 20 mm wide, oval-shaped exit holes of *C. cerdo*. For each tree, the presence/absence of exit holes and the number of exit holes were recorded. On the lower parts of the trunk, from 0 to 2.5 m above ground, we counted all the exit holes, higher up on the trunk, the number of exit holes was checked visually using binoculars and counted, or if too numerous to count the number was estimated. The number of exit holes up to 2.5 m and higher were then summed. Although estimating the number of exit holes higher up on the trunk may increase observation bias, we consider it negligible, as it is mostly the lower part of trunk that is used by the beetle (Albert et al., 2012). Moreover, we recorded the characteristics of each tree and its surroundings, such as the diameter at breast height (DBH), the tree's state of health (a gradient from healthy to nearly dead) and the openness of the canopy around the tree (a gradient from fully closed to fully open) (Table 1). At the dry-sandy site, we also recorded the species of oak and at the dry-rocky site, we recorded the orientation of the slope as the terrain there is hilly.

At (i) the floodplain site, the inventory included oaks in mostly open and semi-open conditions with DBH > 40 cm within a selected area of ~600 ha in July 2006. At the two dry sites, the forest canopy is generally more open. At (ii) the dry-sandy site, details of all the oaks with DBH > 40 cm were recorded within the selected area of ca. 6.5 ha in July 2015, and at (iii) the dry-rocky site, the information for trees with DBH > 10 cm was recorded along 44 transects of 10 × 50 m, in an area covering 2.2 ha in July 2010. The different size of the sampling areas reflects the low density of the trees sampled at the floodplain site and the limited area of suitable habitat at the other sites. We did not include standing dead trees in this study (Table 1) as such trees are unsuitable for the beetle; although in recently dead trees larvae can finish their development, females of the beetle do not lay eggs in dead trees. We inspected altogether 198, 515 and 353 trees at the floodplain, dry-sandy and dry-rocky sites, respectively, i.e. 1,066 trees in total (Table 2). The threshold DBH values were set following preliminary surveys carried out at each site in order to determine the minimum DBH values of trees locally used by the beetle (Fig. 1).

The position of each tree measured was located using GPS, except for the dry-rocky site, where only 176 trees out of 353 were located. This was because the distance between trees was often lower than the GPS precision, and the trees were thus recorded along transects. Based on GPS coordinates, we created a distance matrix of all trees with their spatial position marked (altogether 889 trees). For each of these trees we recorded the shortest distance to a measured tree occupied by *C. cerdo*, and thus created a variable representing distance to the *nearest occupied tree*. We included this variable in the statistical analysis (see below) but using a smaller dataset containing only trees with GPS locations.

To further describe the sites, we determined the radial growth of oaks. At each site, 4–17 randomly selected trees were cored using a steel increment borer (Mora™, Sweden). All cores were dried, glued onto a wooden lath, cut using a razor blade and inspected for injuries, reaction wood and other aberrant features. Tree rings were counted from pith to bark and their widths meas-

Table 1. Environmental variables measured for each of the trees inspected.

Variable	Description	Type
Health	State of health of tree on a scale 0–4 (according to percentage of dead crown: 0 = healthy tree, 4 = nearly dead). Dead trees were not included in this study.	Continuous
Openness	Visual estimation of the openness of the canopy in immediate surroundings of the measured tree (the degree to which the tree is shaded by crowns of surrounding trees or shrubs), on a scale 0–10 (0 = fully closed, 5 = half open, 10 = fully open)	Continuous
Diameter	Diameter of trunk at breast height (1.3 m above ground; DBH) (in cm)	Continuous
Site	Site affiliation: Floodplain, Dry-sandy, Dry-rocky	Categorical
Slope orientation	Cardinal direction of the slope (exposed to North, East, South, West; or flat); only recorded at the dry-rocky site.	Categorical
Tree species	*Quercus cerris*, *Q. petraea* or *Q. robur*; only recorded at the dry-sandy site.	Categorical
Nearest occupied tree*	Distance to the nearest measured tree occupied by *Cerambyx cerdo*. Computed from the distance matrix of all trees whose GPS coordinates were located.	Continuous

* At the dry-rocky site, not all the trees were located using GPS and therefore the distance to the nearest occupied tree was only included and tested in analyses on a smaller dataset with all the trees from the other sites, but only 176 trees from the dry-rocky site. See Materials and Methods and Supplementary Material.

ured to the nearest 0.01 mm using a TimeTable device and PAST4 software (SCIEM, 2012). Mean tree ring widths (and standard deviation) were: 3.13 mm per year (0.76) at the floodplain, 1.02 mm per year (0.18) at the dry-sandy and 0.87 mm per year (0.28) at the dry-rocky site.

Statistical analysis

We tested the effect of tree characteristics on the occurrence and number of *C. cerdo* exit holes on trees. In order to compare general and site-specific patterns in the exploitation of trees by *C. cerdo*, we fitted two types of regression models: generalized linear and generalized linear mixed-effect models. Presence/absence data (occurrence) and number of exit holes (count data) served as dependent variables in specific models.

In order to filter out the effect of site and thus reveal general patterns, we fitted generalized linear mixed-effect models using a binomial distribution (*logit* link) and Poisson distribution (*log* link) for presence/absence data and for number of exit holes, respectively. In both models, diameter, health and openness were explanatory variables and site a random factor variable. The models were built using forward selection procedure; only significant terms were left in final models. The models were fitted using the Generalized Estimating Equations algorithm (Hojsgaard et al., 2006).

To test whether the effect of tree characteristics differed among the sites studied, we fitted generalized linear models using a binomial distribution (*logit* link) and quasi-Poisson distribution (*log* link) for presence/absence data and number of exit holes, respectively. In both models, diameter, health, openness and site were explanatory variables. After fitting the models using forward selection procedure, we also tested the interaction terms of diameter, health and openness with site and included them in final models if significant.

To test the potential effect of distance to the nearest occupied tree, we then repeated the procedure but with a smaller dataset containing only the 889 trees with GPS locations. The variable *nearest occupied tree* was included in the forward selection procedure together with the other three variables.

Moreover, as we had the information on the species of oak at the dry-sandy site and information on slope orientation at the dry-rocky site, we tested to what extent these might affect the results at a particular site. We created separate models for each of the sites, firstly testing the effects of diameter, health, openness and tree species on the occurrence and the number of exit holes on trees for the dry-sandy site, and secondly testing the effects of diameter, health, openness and slope orientation on the occurrence and the number of exit holes on trees for the dry-rocky site.

All the analyses were carried out using R 3.3.3 (R Core Team, 2017); generalized linear mixed-effect models were performed using the *geepack* package (Hojsgaard et al., 2006).

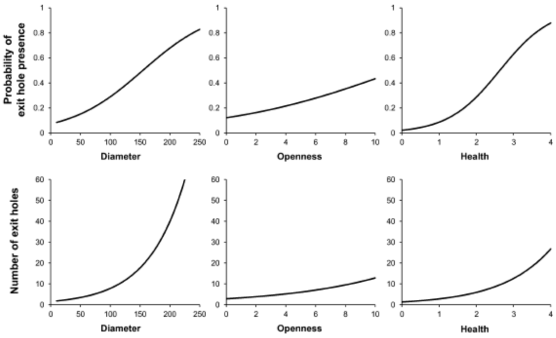

Fig. 2. Predicted probability of occurrence (top row) and number of *C. cerdo* exit holes (bottom row) in relation to three significant variables: diameter, openness, state of health of tree; based on generalized linear mixed-effect models with binomial and Poisson distributions, respectively.

RESULTS

Altogether, 1,066 oaks were inspected at the three sites. In total, 15,424 *C. cerdo* exit holes were recorded on 307 trees (see Table 2 for the summary of field data).

General patterns

All three variables, diameter, openness and tree health, had a significant effect on the occurrence of *C. cerdo* exit holes on trees (diameter: $\chi^2_{(1)} = 26.9$, $P < 0.0001$; openness: $\chi^2_{(1)} = 46$, $P < 0.0001$; health: $\chi^2_{(1)} = 48.8$, $P < 0.0001$). Similarly, all three variables had a significant effect on the number of exit holes on trees (openness: $\chi^2_{(1)} = 107$, $P < 0.0001$; health: $\chi^2_{(1)} = 54.4$, $P < 0.0001$; diameter: $\chi^2_{(1)} = 33.9$, $P < 0.0001$). Coefficient estimates of model parameters are shown in the Table 3. The probability of occurrence as well as the number of exit holes increased with the diameter of a tree, with greater canopy openness around a tree and with decreasing state of health of a tree (Fig. 2).

Site-specific patterns

The models testing differences among the study sites showed that all three variables, tree health, diameter and openness, had a significant effect on the occurrence of *C. cerdo* exit holes on trees (health: $\chi^2_{(1)} = 379$, $P < 0.0001$; diameter: $\chi^2_{(1)} = 127$, $P < 0.0001$; openness: $\chi^2_{(1)} = 24$, $P < 0.0001$) and site proved to have a significant effect ($\chi^2_{(2)} = 20$, $P < 0.0001$). Moreover, interaction terms of health

Table 2. Summary of the field data for the three sites studied, Soutok (floodplain), Rendezvous National Nature Monument (dry-sandy) and Podyjí National Park (dry-rocky), located in South Moravia, Czech Republic.

	Floodplain	Dry-sandy	Dry-rocky
Number of inspected trees	198	515	353
Number of trees with exit holes	116	85	106
Percentage of trees inhabited by *C. Cerdo*	0.59	0.17	0.30
Mean DBH (in cm)	139	64	24
Mean DBH of trees with exit holes (in cm)	152	69	27
Mean height (in m)	18.3	18.8	7.5
Number of exit holes recorded	14 337	579	508
Number of exit holes up to 2.5 m	4783	218	422
Percentage of exit holes found up to 2.5 m	0.33	0.38	0.83
Mean number of exit holes per tree	72.4	1.1	1.4
Mean number of exit holes per inhabited tree	123.6	6.8	4.8

and diameter with site also had significant effects on the occurrence of exit holes (health : site : $\chi^2_{(2)} = 33$, $P = 0.002$; diameter : site : $\chi^2_{(2)} = 19$, $P = 0.023$).

Diameter, tree health and openness also had a significant effect on the number of exit holes on a tree (diameter: $F_{(1,1064)} = 1651$, $P < 0.0001$; health: $F_{(1,1063)} = 413$, $P < 0.0001$; openness: $F_{(1,1062)} = 128$, $P < 0.0001$), and again, site also proved to have a significant effect ($F_{(2,1060)} = 37.21$, $P < 0.0001$). Regarding interaction, only the interaction between health and site was significant ($F_{(2,1058)} = 3.84$, $P = 0.022$). Coefficient estimates of model parameters are shown in Table 3.

The distance to the nearest occupied tree did not have a significant effect, either on the probability of occurrence of *C. cerdo* in trees ($\chi^2_{(1)} = 0.3$, $P = 0.58$), or on the number of exit holes ($F_{(1,882)} = 3.71$, $P = 0.054$) (see Table S1 of the Supplementary Material for more details).

Table 3. Estimates of the parameters of the (A) generalized linear mixed-effects models with binomial and Poisson distributions and for (B) generalized linear models with binomial and quasi-Poisson distributions, with standard errors, test statistics (Wald statistic, z-value, t-value) and significance (*P*). Only significant variables were included in the final models (see Results section for details).

(A) General patterns

Occurrence (binomial distribution)

Model parameter	Estimate	SE	Wald statistic	*P*
(Intercept)	–5.368	0.389	190.3	<0.0001
Diameter	0.016	0.002	65.2	<0.0001
Openness	0.171	0.052	10.9	0.001
Health	1.445	0.207	48.8	<0.0001

Number of exit holes (Poisson distribution)

Model parameter	Estimate	SE	Wald statistic	*P*
(Intercept)	–1.227	0.878	1.95	0.16
Openness	0.151	0.016	89.54	<0.0001
Health	0.754	0.058	170.56	<0.0001
Diameter	0.016	0.003	33.94	<0.0001

(B) Site-specific patterns

Occurrence (binomial distribution)

Model parameter	Estimate	SE	z value	*P*
(Intercept)	–7.726	0.854	–9.05	<0.0001
Health	1.179	0.149	7.94	<0.0001
Diameter	0.122	0.023	5.28	<0.0001
Openness	0.284	0.044	6.43	<0.0001
Site Dry-sandy	0.622	1.179	0.53	0.598
Site Floodplain	–1.278	1.507	–0.85	0.396
Health : Site Dry-sandy	1.206	0.283	4.26	<0.0001
Health : Site Floodplain	0.642	0.326	1.97	0.049
Diameter : Site Dry-sandy	–0.103	0.025	–4.09	<0.0001
Diameter : Site Floodplain	–0.091	0.025	–3.70	0.0002

Number of exit holes (quasi-Poisson distribution)

Model parameter	Estimate	SE	t value	*P*
(Intercept)	–2.940	0.859	–3.42	0.0006
Diameter	0.013	0.001	11.12	<0.0001
Health	0.874	0.246	3.55	0.0004
Openness	0.148	0.018	8.05	<0.0001
Site Dry-sandy	–0.517	1.022	–0.51	0.613
Site Floodplain	2.255	0.883	2.55	0.011
Health : Site Dry-sandy	0.425	0.307	1.38	0.167
Health : Site Floodplain	–0.079	0.251	–0.31	0.753

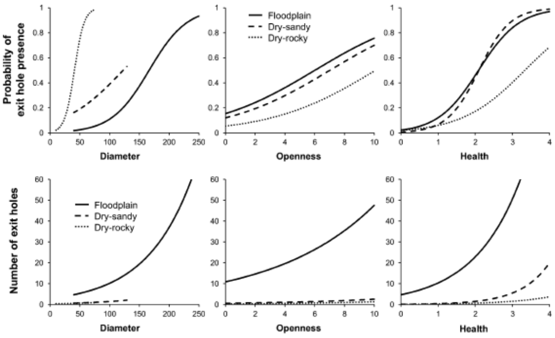

Fig. 3. Predicted probability of occurrence (top row) and number of *C. cerdo* exit holes (bottom row) in relation to three significant variables, site as a factor variable and their interactions; based on generalized linear models with binomial and quasi-Poisson distributions, respectively. Solid line – floodplain site, dashed line – dry-sandy site, dotted line – dry-rocky site.

At all sites, the probability of occurrence and the number of exit holes increased with the diameter of a tree, with a more open canopy around a tree and with decreasing state of health of a tree, but the shapes of the relationship differed considerably among the sites studied (Fig. 3). For instance, at the dry-rocky site, the probability of occurrence exhibited a sharp increase at small diameters; at a DBH of 50 cm the probability was already higher than 0.50. In contrast, at the floodplain site, the increase with diameter was very slow, reaching a probability of 0.50 at ca. DBH of 160 cm. On the other hand, at the dry-rocky site, the probability of occurrence in relation to openness and state of health was lower or less steep than at the dry-sandy and floodplain sites. Regarding the number of exit holes, at the floodplain site there was a higher number of exit holes and constant increase with diameter, openness, and poorer state of health; the two dry sites had a comparatively lower number of exit holes (Fig. 3).

Within-site effects

In a separate analysis of data from the dry-sandy site, where there were three species of oaks, tree species proved to have a significant effect on both the occurrence and number of exit holes on a tree after all other significant variables; Analysis of occurrence – health: $\chi^2_{(1)} = 210$, $P < 0.0001$; openness: $\chi^2_{(1)} = 28$, $P = 0.0001$; diameter $\chi^2_{(1)} = 4.4$, $P = 0.036$; species: $\chi^2_{(2)} = 6.5$, $P = 0.039$. Analysis of the number of exit holes – health: $F_{(1,513)} = 569$, $P < 0.0001$; openness: $F_{(1,512)} = 174$, $P < 0.0001$; diameter: $F_{(1,511)} = 52.7$, $P < 0.0001$; species: $\chi^2_{(2,509)} = 10.8$, $P < 0.0001$. On average, the probability of the occurrence of exit holes was greater on *Quercus petraea* (0.24) and *Q. robur* (0.29) than on *Q. cerris* (0.10), and similarly, the mean number of exit holes was greater on *Q. petraea* (1.7) and *Q. robur* (2.4) than on *Q. cerris* (0.5), indicating that *Q. cerris* is less exploited by the beetle in this area.

In a separate analysis of data from the dry-rocky site, slope orientation proved to have a significant effect on both occurrence and number of exit holes together with health and diameter, whereas openness did not have a significant effect at this site. Analysis of occurrence – slope: $\chi^2_{(4)} = 128.5$, $P < 0.0001$; health: $\chi^2_{(1)} = 45.6$, $P < 0.0001$; diameter

Table 4. The results of the generalized linear models with binomial and (quasi-)Poisson distributions testing (A) the effect of species of oak (*Quercus cerris*, *Q. petraea*, *Q. robur*) on the probability of occurrence and the number of *Cerambyx cerdo* exit holes on trees at the dry-sandy site, and (B) the effect of slope orientation (East, North, South, West, flat) on the probability of occurrence and the number of *C. cerdo* exit holes on trees at the dry-rocky site. The table gives estimates of the coefficients of model parameters with their standard errors, test statistics (z-value, t-value) and significance (*P*). Only significant variables were included in the final models (see the Results section for details).

(A) Dry-sandy site (effect of species of oak)

Occurrence (binomial distribution)

Model parameter	Estimate	SE	z value	*P*
(Intercept)	–8.85	1.1187	–7.91	<0.0001
Health	2.47	0.273	9.05	<0.0001
Openness	0.44	0.087	5.02	<0.0001
Diameter	0.03	0.0109	2.77	0.006
Species *petraea*	1.17	0.4853	2.4	0.016
Species *robur*	0.73	0.4283	1.71	0.088

Number of exit holes (Poisson distribution)

Model parameter	Estimate	SE	z value	*P*
(Intercept)	–5.57	0.34536	–16.14	<0.0001
Health	1.34	0.06422	20.81	<0.0001
Openness	0.31	0.02593	11.91	<0.0001
Diameter	0.03	0.00332	8.48	<0.0001
Species *petraea*	0.74	0.18957	3.88	0.0001
Species *robur*	0.68	0.16636	4.08	<0.0001

(B) Dry-rocky site (effect of slope orientation)

Occurrence (binomial distribution)

Model parameter	Estimate	SE	z value	*P*
(Intercept)	–24.13	1633.62	–0.01	0.99
Slope flat	16.68	1633.62	0.01	0.99
Slope north	–0.05	2218.327	0	0.99
Slope south	18.78	1633.62	0.01	0.99
Slope west	21.34	1633.62	0.01	0.99
Health	1.04	0.1593	6.53	<0.0001
Diameter	0.10	0.0248	4.16	0.00003

Number of exit holes (quasi-Poisson distribution)

Model parameter	Estimate	SE	t value	*P*
(Intercept)	–20.60	887.00	–0.02	0.98
Slope flat	16.40	887.00	0.02	0.99
Slope north	0.10	1210.00	0	1
Slope south	18.30	887.00	0.02	0.98
Slope west	18.70	887.00	0.02	0.98
Health	0.72	0.05	14.73	<0.0001
Diameter	0.04	0.00	10.54	<0.0001

$\chi^2_{(1)} = 20$, $P < 0.0001$; openness: $\chi^2_{(1)} = 0.7$, $P = 0.42$. Analysis of the number of exit holes – slope: $F_{(4,348)} = 41.7$, $P < 0.0001$; health: $F_{(1,347)} = 82.6$, $P < 0.0001$; diameter: $F_{(1,346)} = 27.2$, $P < 0.0001$; openness: $F_{(1,345)} = 0.01$, $P = 0.91$. On average, the probability of the occurrence of exit holes was greater for trees on slopes oriented to the West (0.92) and South (0.48) than for trees on flat ground (0.09); no exit holes were found on trees on slopes oriented to the North and East. Similarly, the mean number of exit holes was greater on trees on slopes oriented to the West (3.92) and South (2.45) than on trees on flat ground (0.22). These results indicate that in hilly terrain, trees are more prone to be exploited by the beetle if they grow on sun-facing and thus warmer slopes.

Coefficient estimates of model parameters for analyses of both dry-sandy and dry-rocky sites are shown in Table 4.

DISCUSSION

The present study extends the knowledge on habitat use of the great capricorn beetle, an endangered saproxylic beetle regarded as a specialist feeder on veteran trees (Buse et al., 2007). It corroborates the main findings of previous studies, such as that decreasing health state of a tree, its increasing diameter and sunlight availability (herein represented by the openness and slope orientation) favour the presence of *C. cerdo* in trees (Buse et al., 2007; Albert et al., 2012). More importantly, however, it reveals a high between-site variability in characteristics of trees exploited by this beetle, principally the variability in their diameter. This implies that although we can well describe the general patterns in habitat use and describe the beetle's fundamental niche, for the survival of local populations the local conditions and the beetle's realized niche are what is important and thus should be considered in conservation management planning. Below, we discuss the findings and their implications for the conservation of *C. cerdo* and potentially other veteran tree specialists.

Diameter of inhabited trees and the importance of large trees

The probability of the presence of exit holes on a tree with respect to its diameter differed substantially among the sites. The number of exit holes on a tree, on the other hand, was affected mainly by tree diameter, rather than locality, as suggested by the positive relationship between tree diameter and the number of exit holes (Fig. 3).

We consider the local soil and humidity conditions as the most likely factors behind the differences in the diameter of trees exploited by *C. cerdo*. The floodplain and the dry-rocky sites represent extreme oak habitats. At the former site, nutrient rich, deep soils and a high water table offer optimal conditions for rapid growth, resulting in trees of large dimensions (Altman et al., 2016). The dry-rocky site, on the other hand, is characterized by stressful conditions due to nutrient poor, shallow and desiccating soils, which result in slow growth and low vitality of the trees, allowing for colonisation of small trees by *C. cerdo*. Due to differences in the rate of growth between the two sites, the trees may reach the same probability of occupancy at a similar age (estimated by dividing the DBH of a tree with a particular probability of occurrence by average ring width), but the trees at the dry-rocky site are just smaller. At the dry-sandy site, tree growth was nearly as slow as at the dry-rocky site. The conditions at that site are, however, relatively stable. The trees thus remain vigorous for longer; they are likely to grow larger and become suitable for *C. cerdo* later than trees at the dry-rocky site.

The positive relationship between tree diameter and the number of exit holes (Fig. 3) indicates that tree diameter limits the number of *C. cerdo* exit holes via the amount of substrate suitable for larval development. There were about 30 times more exit holes on a large tree (~150 cm DBH) than on a small tree (~30 cm DBH). Although the number of exit holes may not be a direct measure of the number of beetles that developed in a tree, the two numbers are rather closely related. Moreover, at the dry-rocky site, trees were shorter in height and most of the exit holes (83%) were found up to 2.5 m above the ground, whereas at the dry-sandy and floodplain sites only one-third (33–38%) of all exit holes were found up to 2.5 m above the ground.

As substantially more individuals of *C. cerdo* develop in large trees these represent larger habitat patches than small trees. Regarding the metapopulation theory (Hanski & Ovaskainen, 2003), we hypothesize that the dimensions of trees may have an effect on population dynamics. It implies that the number of trees needed for the survival of *C. cerdo* populations is lower at sites with large trees than at sites with small trees. On large trees, individuals of *C. cerdo* are more likely to encounter a mate without moving to another tree. Thus, the need for dispersal may be higher in populations living on small trees (Clobert et al., 2004; Bowler & Benton, 2005). Some authors even suggest that insect populations occupying small habitat patches may have a greater tendency to disperse in order to avoid inbreeding (Pusey & Wolf, 1996; Feldhaar & Schauer, 2018), because in small patches the chance that individuals are closely related may be higher than in large patches. However, this theory seems to have limited support in the case of *C. cerdo*. On very small trees, only a single individual per year may emerge, whereas on large trees the probability of two emerging adults originating from the same hatch, and therefore closely related, may be higher. But in any case, if the small dimensions of trees drive the beetle to disperse more frequently, the populations inhabiting small trees are probably more likely to be susceptible to the effects of habitat fragmentation and isolation (Clobert et al., 2001; Ranius, 2006), because dispersal always increases the risk of predation and abandoning a suitable habitat.

Published data indicate the existence of a relationship between diameter of inhabited trees and the incidence of dispersal for another veteran tree specialist, the hermit beetle (*Osmoderma eremita*). In Sweden, an average inhabited tree (with DBH of 130 cm) hosted ~11 beetles and the population structure was described as a metapopulation with low dispersal between trees (Ranius, 2000, 2007; Hedin et al., 2008). In Italy, where the inhabited trees were smaller (mean DBH of 65 cm) an average tree hosts only 0.5–2 individuals (Chiari et al., 2013) and the incidence of dispersal was higher (Chiari et al., 2012). Although these differences in dispersal rate were attributed to differences in the climate at the northern and southern edges of the beetle's distributional range, they might also reflect relatively low numbers of beetles per tree, determined by the parameters of the available trees. This needs to be studied further, by comparing the mobility of beetles from populations that exploit large and small trees growing in areas with the same climate.

Although most of the saproxylic species associated with large, veteran trees are also at least occasionally able to utilize small trees (Sláma, 1998; Harvey et al., 2011; Chiari et al., 2013), it is the large trees that are likely to host the bulk of their populations and increase the probability of their survival. This is probably one of the main reasons for the great importance of large trees for *C. cerdo* (Buse et al., 2007; Albert et al., 2012) and probably also saproxylic biodiversity as a whole (Eckelt et al., 2018; Parmain & Bouget, 2018).

Effect of species of oak

The presence of exit holes is also associated with the species of oak, as the Turkey oak (*Quercus cerris*) was less exploited by *C. cerdo* than the sessile and pedunculate oaks. Within the genus *Quercus*, the Turkey oak is distantly related to the sessile and pedunculate oaks (Oh & Manos, 2008; Denk & Grimm, 2010) and its wood differs from that of most other oaks by its lower durability and tendency to split (Ferrari et al., 2013). Such wood properties may have a potentially adverse effect on *C. cerdo*, as is also proposed for the red oak (*Quercus rubra*) (Oleksa & Klejdysz, 2017). This agrees with observations from Slovakia and Hungary, where this beetle is rather rare in stands of Turkey oak and even senescent, large Turkey oaks often lack any signs of the presence of *C. cerdo* (L. Cizek, pers. obs.). We attribute the observed pattern rather to the avoidance of Turkey oak by *C. cerdo* than to a lower detectability of old exit holes due to the faster decay of its wood, as larval galleries of *C. cerdo* reach deep into the wood and are detectable for decades. Turkey oak made up about 60% of the oaks inspected at the dry-sandy site and the lower occupancy of Turkey oaks probably has partially affected the results for this site. Similar occupancy, wood properties and the relatedness of pedunculate and sessile oaks, however, justify neglecting species of oak in data analyses of the two other study sites.

Distance to the nearest occupied tree

In contrast to Buse et al. (2007) or Oleksa & Klejdysz (2017), we did not find any effect of distance to the nearest occupied tree on the probability of occurrence or on the number of exit holes of *C. cerdo* on trees. While traditionally the dispersal capacity of saproxylic insects was considered to be limited, recent studies show that dispersal may be strongly dependent on the life history of the species or group studied and is often greater than thought in the past (Feldhaar & Schauer, 2018; Schauer et al., 2018). This is also the case for *C. cerdo*, for which a radio-tracking study (Drag & Cizek, 2018) revealed dispersal over greater distances than reported in a previous mark-recapture study (Torres-Vila et al., 2017). Therefore, the size of our three study sites might have been too small to reveal the dispersal limitations of *C. cerdo*.

Implications for conservation

Our findings indicate that site conditions affect occupancy and potentially population dynamics, and therefore must be taken into consideration in developing management strategies for the conservation of *C. cerdo*. At inhabited sites, an inventory of all available oaks should be performed, specifying how many trees are occupied by the beetle, what is their state and diameter, and also what are the trees potentially suitable for *C. cerdo* there. As long-term planning is necessary for efficient conservation of the organisms associated with veteran trees, it is also important to record the numbers and diameters of young trees in order to identify potential gaps in the future availability of suitable trees.

Since mortality of veteran trees exceeds their recruitment in the long term (Siitonen & Ranius, 2015), there is a need to bridge the temporal gap in their availability (Gibbons et al., 2008; Miklín & Čížek, 2014). Ensuring the continuity of large veteran trees is always the most desirable, though rarely an available option, simply because it is impossible to manipulate tree diameter and volume in the short term. Our results, nevertheless, indicate that even small (or young) trees may be utilized by *C. cerdo* beetle if they are exposed to sunshine and in poor health. Both exposure to sun and tree health can be manipulated. Thus, it is possible to bridge the gap in the availability of large veteran trees by creating large numbers of small trees that are exposed to sunshine and in poor health. In stands occupied by *C. cerdo*, opening the canopy by partial cutting or thinning should be followed by practices like, e.g. pollarding, grazing, bark-stripping, partial bark-ringing or fire (Smith & Sutherland, 1999; Helm et al., 2011; Gruebler et al., 2013; Sebek et al., 2013; Reichmuth et al., 2018).

At sites where *C. cerdo* inhabits small trees that sustain fewer beetles, greater areas of habitat and higher densities of suitable trees are needed to sustain these local populations. At sites where *C. cerdo* occupies large old trees, management should primarily focus on sustaining such trees to keep them alive as long as possible (Read, 2000; Lindenmayer, 2017) but also on taking care of other oaks in the surroundings. Increased canopy closure is a common problem in European woodlands (Altman et al., 2013; Miklín & Čížek, 2014; Chudomelová et al., 2017). It decreases the suitability of the existing veteran trees for *C. cerdo* and compromises their survival (Miklín et al., 2018) and also hinders the establishment of new generations of veteran trees. Maintenance of open oak woodlands is thus the key for the conservation of *C. cerdo* in temperate climates. There are several options for keeping or restoring the open structure of woodlands, such as grazing, significant thinning, coppicing, or prescribed burning (Vera, 2000; Lindbladh et al., 2003; Hédl et al., 2010; Hanberry & Abrams, 2018). The canopy of large open-grown oaks that are currently in closed-canopy conditions should be freed from the rest of the canopy by gradually and carefully clearing a circle or partial circle around them, a technique called "haloing" (Lonsdale, 2013). The lifespan of old trees can be prolonged by crown reduction, which reduces the risk of trunk collapse, such as pollarding or shredding (Lonsdale, 2013; Sebek et al., 2013). Moreover, in hilly areas where *C. cerdo* is present, conservation effort should target primarily South- and West-facing slopes, and in stands composed of several species of oak, the sessile and pedunculate oaks should be of a primary interest.

It is important to stress that the above-mentioned recommendations apply principally to woodlands in the temperate zone, where *C. cerdo* is considered to be a threatened species. In Mediterranean regions of Europe, the requirements of this beetle may differ significantly. Firstly, *C. cerdo* there usually exploits other species of oak, mostly holm oak (*Quercus ilex*) and cork oak (*Q. suber*) (Sallé et al., 2014; Torres-Vila et al., 2017). Secondly, in a warm climate, even trees on East- and North-facing slopes may be utilized. Finally, in some parts of the Mediterranean, *C. cerdo* is considered a pest, being one of the principal insect species responsible for oak decline (Sallé et al., 2014; Duque-Lazo & Navarro-Cerrillo, 2017) and thus not a species in need of protection.

Study limitations

With respect to the different rates of growth of trees recorded at different sites, it would be interesting to relate the exploitation of trees by *C. cerdo* directly to tree age, not their diameter (Horák, 2017). However, this approach would require coring and analysing hundreds of trees, which is beyond the scope of this study. And it is, unfortunately, a general limitation in most studies relating habitat use of woodland biota to the diameter of trees growing under different conditions or managements (Jüriado et al., 2009; Nascimbene et al., 2013; Horák, 2017; Nordén et al., 2018). Based on the average ring widths (growth rate) measured for our sites, the trees at dry sites grew about three times slower than at the floodplain site and the trees on floodplains thus reach large dimensions sooner than those on the dry sites. But when comparing particular occurrence probabilities divided by average ring width, trees at the dry-rocky and the floodplain sites may have a similar occupancy by *C. cerdo* at a similar age, and trees at the dry-sandy site reach such probabilities later.

Further, it would be interesting to compare data from more sites. The dry-sandy and dry-rocky sites are, however, the only such sites hosting populations of *C. cerdo* in the Czech Republic, the closest similar sites being further east in Slovakia or Hungary. Although there are sites with *C. cerdo* inhabiting smaller trees in Southern Europe, they are occupied also by other large species of *Cerambyx* (*C. miles*, or *C. welensii*) with exit holes indistinguishable from those of *C. cerdo*. Most studies on the ecology of large saproxylic beetles are based on data collected at smaller spatial scales and less intensive in terms of the number of trees sampled (Ranius, 2001; Buse et al., 2007), indicating that a larger, continental-wide, approach is necessary. Such an approach is especially important for the saproxylic beetles listed in the EU's Habitat Directive (Council of the European Communities, 1992), which serve as focal species for conservation in most European countries.

CONCLUSIONS

The present study revealed that the habitat requirements of *C. cerdo* differ significantly among sites. Management aimed at conservation of its populations thus has to respect the local requirements of the beetle. Further, the study showed that large oaks are very important for *C. cerdo* because they represent large patches of suitable habitat. At the same time, however, it showed they are not a necessary condition for the survival of *C. cerdo*. It is principally exposure to sunshine and the state of health of the trees that is important for this beetle. Therefore, a tree becomes suitable for *C. cerdo* once it contains wood suitable for the development of its larvae, regardless of its diameter or age. This knowledge has important implications for the effective conservation of this species and possibly also other veteran tree specialists. It indicates that although focusing on ensuring the presence of large veteran trees is crucial, efforts might also be directed towards active creation of suitable conditions in smaller trees, especially if there are a low number of large trees at the site.

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Supplementary material

Test of distance to the nearest tree

The following table shows results of the generalized linear models performed on a smaller dataset of 889 trees whose GPS coordinates were located. For each of these trees, we recorded the shortest distance to a measured tree occupied by *Cerambyx cerdo* (referred to as Nearest tree). This variable was included in the forward selection procedure together with, openness, diameter, state of health, site and their interactions with site, to assess their effect on occurrence of *C. cerdo* exit holes (model with binomial distribution) and number of exit holes on trees (model with quasi-Poisson distribution). For the details, see Material and Methods in the original article.

Results of the models performed on the smaller dataset showed that the distance to the nearest occupied tree did not have an effect on the occurrence ($\chi^2_{(1)} = 0.3$, P = 0.58) or the number of exit holes of *C. cerdo* on trees ($F_{(1,882)} = 3.71$, P = 0.054). See Table S1 for the test statistics.

Table S1. Test statistics for the parameters of the generalized linear models with binomial and quasi-Poisson distributions (χ^2 test or F test), with degrees of freedom (d.f.) and significance level (P).

Occurrence (binomial distribution)			
Model parameter	d.f.	χ^2	P
Health	1	450.64	<0.0001
Diameter	1	63.7	<0.0001
Openness	1	22.63	<0.0001
Site	2	13.99	0.0009
Nearest tree	1	0.3	0.581
Health : Site	2	13.39	0.001
Diameter : Site	2	9.43	0.009
Openness : Site	2	5.25	0.072
Nearest tree : Site	2	1.54	0.463
Number of exit holes (quasi-Poisson distribution)			
Model parameter	d.f.	F	P
Diameter	1,887	1320.74	<0.0001
Health	1,886	375.03	<0.0001
Openness	1,885	111.72	<0.0001
Site	2,883	27.44	<0.0001
Nearest tree	1,882	3.71	0.054
Health : Site	2,880	3.19	0.041
Openness : Site	2,878	2.81	0.061
Nearest tree : Site	2,876	2.06	0.128
Diameter : Site	2,874	0.82	0.443

Kapitola II.

Vertical stratification and microhabitat selection by the Great Capricorn Beetle (*Cerambyx cerdo*) (Coleoptera: Cerambycidae) in open-grown, veteran oaks

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Abstrakt

The great capricorn beetle or Cerambyx longicorn (*Cerambyx cerdo*, Linnaeus, 1758) is an internationally protected umbrella species representing the highly diverse and endangered fauna associated with senescent oaks. For the conservation and monitoring of populations of *C. cerdo* it is important to have a good knowledge of its microhabitat requirements. We investigated determinants and patterns of *C. cerdo* distribution within individual old, open-grown oaks. Trees inhabited by this species were climbed, and the number of exit holes and environmental variables recorded at two sites in the Czech Republic. Distribution of exit holes in relation to height above the ground, trunk shading by branches, orientation in terms of the four cardinal directions, diameter, surface and volume of inhabited tree parts were investigated. This study revealed that the number of exit holes in the trunks of large open-grown oaks was positively associated with the diameter of the trunk and openness and negatively with height above the ground, and the effects of diameter and openness changed with height. The number of exit holes in the surface of a trunk was also associated with the cardinal orientation of the surface. Approximately half of both *C. cerdo* populations studied developed less than 4 m and approximately a third less than 2 m above the ground. This indicates that most *C. cerdo* develop near the ground. Active management that prevents canopy closure is thus crucial for the survival of *C. cerdo* and searching for exit holes is an effective method of detecting sites inhabited by this species.

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Vertical stratification and microhabitat selection by the Great Capricorn Beetle (*Cerambyx cerdo*) (Coleoptera: Cerambycidae) in open-grown, veteran oaks

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Abstract. The great capricorn beetle or Cerambyx longicorn (*Cerambyx cerdo*, Linnaeus, 1758) is an internationally protected umbrella species representing the highly diverse and endangered fauna associated with senescent oaks. For the conservation and monitoring of populations of *C. cerdo* it is important to have a good knowledge of its microhabitat requirements. We investigated determinants and patterns of *C. cerdo* distribution within individual old, open-grown oaks. Trees inhabited by this species were climbed, and the number of exit holes and environmental variables recorded at two sites in the Czech Republic. Distribution of exit holes in relation to height above the ground, trunk shading by branches, orientation in terms of the four cardinal directions, diameter, surface and volume of inhabited tree parts were investigated. This study revealed that the number of exit holes in the trunks of large open-grown oaks was positively associated with the diameter of the trunk and openness and negatively with height above the ground, and the effects of diameter and openness changed with height. The number of exit holes in the surface of a trunk was also associated with the cardinal orientation of the surface. Approximately half of both *C. cerdo* populations studied developed less than 4 m and approximately a third less than 2 m above the ground. This indicates that most *C. cerdo* develop near the ground. Active management that prevents canopy closure is thus crucial for the survival of *C. cerdo* and searching for exit holes is an effective method of detecting sites inhabited by this species.

INTRODUCTION

Organisms associated with old trees and dead wood are among the most diverse and endangered elements of European biodiversity (Berg et al., 1994; Davies et al., 2008). Many highly endangered species are associated with senescent, open-grown trees of large diameter, especially oaks (e.g. Ranius & Jansson, 2000; Ranius, 2002; Buse et al., 2008a; Skarpaas et al., 2011). Such trees used to be common and an indispensable element in European landscapes in the past, e.g., open pasture woodlands and coppices with standards. Modern intensification of land use, however, has resulted in the loss of such trees from the landscape due to increased canopy closure in commercial as well as protected woodlands and removal of old trees from farmed areas (e.g. Warren & Key, 1991; Rackham, 1998; Vera, 2000).

The great capricorn beetle (*Cerambyx cerdo*, Linnaeus, 1758) is one of the largest longhorn beetles living in Europe. It acts as an ecosystem engineer (Buse et al., 2008b) and, together with the stag beetle (*Lucanus cervus* Linnaeus, 1758) serve for the general public and legislature as umbrella species representing a diverse and highly endangered fauna associated with old oaks (Buse et al., 2008a; Ducasse & Brustel, 2008). Apart from being protected and/or red-listed in many European countries (Jäch, 1994; Geiser, 1998; Witkowski et al., 2003; Farkač et al., 2005; Jurc et al., 2008), *C. cerdo* is explicitly protected under the EU Habitats Directive (Council of the European Communities, 1992), classified as globally vulnerable according to the IUCN Red List of Threatened Species (IUCN, 2007) and is nearly a threatened species in Europe (Nieto & Alexander, 2010). *C. cerdo* occurs in most of Europe, the whole Mediterranean region and the Caucasus (Bílý & Mehl, 1989; Sláma, 1998; Sama, 2002). It is common in the south but rare and rapidly declining in the northern part of its range (e.g. Sláma, 1998; Ehnström & Axelsson, 2002; Starzyk, 2004; Jurc et al., 2008; Ellwanger, 2009). It is extinct in the United Kingdom (Alexander, 2002).

Larvae of *C. cerdo* develop mainly in the trunks, but also branches and roots of oaks (*Quercus* spp.); other species of trees are occasionally used, including e.g. chestnut (*Castanea sativa*), and probably also elm (*Ulmus* spp.) and common walnut (*Juglans regia*) (Sláma, 1998). Larval development takes three or more years (Sama, 2002). Adults are 24 to 53 mm long and active from May to August, peaking in June and early July, when the beetles are most active at dusk feeding on the sap of old trees (Heyrovský, 1955; Sláma, 1998). Occupied trees can be identified by typical oval exit holes up to 20 mm wide on the trunk or thick branches; typical signs of recent activity include wood meal and fresh exit holes the interior walls of which are a red colour (Buse et al., 2007). This beetle prefers old, sun exposed trees (Sláma, 1998; Buse et al., 2007). Tree vitality, age, thickness of bark, trunk diameter, distance to the next colonized tree and trunk insolation increase the probability of the occurrence of *C. cerdo* (Buse et al., 2007).

Whereas the determinants of the distribution of *C. cerdo* in a landscape and among trees are described (Buse et al., 2007; 2008b) little is known about the factors affecting its distribution within individual trees. Such information is, however, crucial for the conservation of this species and for monitoring its populations. If the beetle prefers tree tops, it is likely to survive in closed canopy oak stands, often undetected. If, on the other hand, the majority of a population inhabits the lower parts of trunks, the presence of *C. cerdo* would be easy to detect and inhabited sites would need to be actively managed. We therefore investigated the distribution of *C. cerdo* exit holes in old open-grown oaks in relation to: (i) Height above the ground, (ii) shading, (iii) cardinal orientation and (iv) diameter of the parts of the trunk inhabited.

METHODS

Study sites

This study was conducted in southern and central Bohemia (western part of the Czech Republic) in parkland-like woodlands with old, open-grown oaks. Two sites were surveyed, Hluboka nad Vltavou and the Lanska Game Reserve. The Hluboka site is located in south-western Czech Republic, 115 km S of Prague (49°2′N, 14°26′E, 380 m a.s.l.) in the Budejovicka Basin, near the river Vltava. The bedrock consists of sandstone, puddingstone and clay-stone. Mean annual temperature is 7.1°C and mean annual rainfall nearly 659 mm. The study took place in system of alleys of trees and wooded meadows (recently converted into a golf-course) with open-grown oaks of up to 200 years old (max DBH ~160 centimetres) (Hauck & Cizek, 2006). The locality is protected as a Site of Community Importance (total area: 67.2 ha), with *C. cerdo* as one of its target species. It hosts numerous saproxylic species associated with old oaks. The second site, the Lanska Game Reserve, is located 40 km W of Prague (50°5′N, 13°55′E; 300–461 m a.s.l.) in the Krivoklatsko Protected Landscape Area and UNESCO Biosphere Reserve. This is an upland area with deep valleys with bedrock consisting of slate mainly covered by cambisol and partly by gley. Mean annual temperature is 8.2°C and mean annual rainfall nearly 590 mm. The game reserve (total area 3,000 ha) mostly consists of beech and oak-hornbeam forests, patches of planted conifers and several meadows and pastures with scattered old oaks (*Quercus robur*). The site is a local saproxylic biodiversity hot-spot (Horák & Rébl, 2012).

Sampling design

Trees with *C. cerdo* exit holes and currently inhabited by the species (i.e. with larval frass on the bark and/or at the base of the tree) were surveyed. For safety reasons and also to avoid the effect of larval activity on the environmental conditions biasing the results, the trees climbed were relatively healthy (most of the tree alive, tree top not completely dead) and probably not inhabited by *C. cerdo* for longer than one or two decades (Klečka & Klečka, 2003). Each tree surveyed was divided into 2 meter long vertical sections (0–2 m above the ground, 2–4 m, 4–6 m, 6–8 m ... up to 14 m). Each vertical section was divided into four trunk segments according to their orientation (North, East, South or West). Trees were climbed using the two-rope climbing technique. Environmental variables and number of *C. cerdo* exit holes were recorded for each segment of trunk. Exit holes were counted; height of each tree, and diameter in the middle of each 2 m vertical section were measured. Estimates of the outer surface and volume of wood in each segment of trunk segment were based on its diameter. Orientation (cardinal direction of the segment) was identified using magnetic compass (North, East, South, West).

Variables

Eight explanatory variables were used: (i) Height – mean vertical height in meters of a 2 m long section of trunk from the ground, ranging from 1 to 13 m (1 – sections 0–2 m above the ground, 3 – 2–4 m, 5 – 4–6 m etc.). Continuous. (ii) Openness – shading of each segment by the branches or crowns of surrounding trees or shrubs on a scale of 1–5 (1 – fully shaded; 2 – mostly shaded, 3 – half shaded, 4 – mostly exposed, 5 – fully exposed). Continuous. (iii) Diameter – diameter in centimetres at the middle of each vertical section of trunk. Continuous, in centimetres. (iv) Surface area – surface of each segment of trunk in square centimetres. Continuous. (v) Volume of wood – volume of each segment of trunk in cubic centimetres. Continuous. (vi) Orientation – cardinal direction of each segment of trunk (North, East, South or West). Categorical: (vii) Tree – serial number of the tree and (viii) Site – location of study area (Lanska obora or Hluboka nad Vltavou).

The response variables were the number and density of *C. cerdo* exit holes in each segment of trunk. The density was the number of exit holes divided by the area of each segment of trunk (in m^2, analysis 2, see below), or volume (in m^3, analysis 3, see below) of each trunk segment. All response variables were continuous.

Analyses

Three analyses were carried out using R 2.7.2 (Maindonald & Braun, 2003), in which the association between the number of exit holes and their density per m^2 and per m^3, and environmental variables was investigated using multiple LME (Linear mixed-effect models) (Crawley, 2007; Zurr et al., 2009). In the first analysis, the number of *C. cerdo* exit holes on each segment of trunk was the response variable. The height, diameter, openness and orientation of each segment of trunk were fixed effect variables and the tree a random effect variable. Surface area ($r_s = 1$) and volume of wood ($r_s = 1$) were not included in the final model because of their strong multicollinearity with diameter (tested using Spearman rank correlation). The final model investigated the association between the number of exit holes and the height, diameter, openness, orientation and interactions of height and diameter, and height and openness. In the second analysis, the density of exit holes per m^2 was the response variable. This was done in order to correct for differences in sampling effort, i.e. the lower segments of trunks have the largest diameter and greatest surface areas. The height, openness and orientation were fixed effect variables and the tree a random effect variable. In the third analysis, the density of exit holes per m^3 was the response variable. The height, openness and orientation were fixed effect variables the tree a random effect variable. In all analyses, the response variable was Poisson distributed as it was transformed using a ln(number of exit holes + 1) transformation in order to achieve the normal distribution required by LME. The best models and order of variables were chosen using AIC (Akaike's Information Criterion, Akaike, 1974). Models were fitted using the ML method (maximum likelihood). The relationships among variables were investigated in order to identify strong correlations between pre-

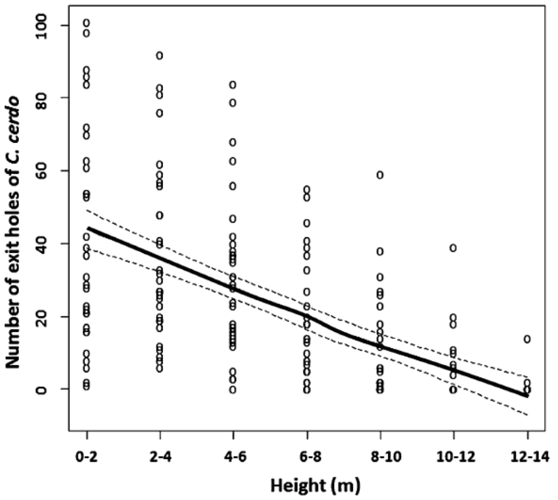

Fig. 1. Vertical stratification of the exit holes of the great capricorn beetle (*Cerambyx cerdo*) on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic (both sites combined). Depicted as number of *C. cerdo* exit holes in 2 m long sections of trunk at particular heights.

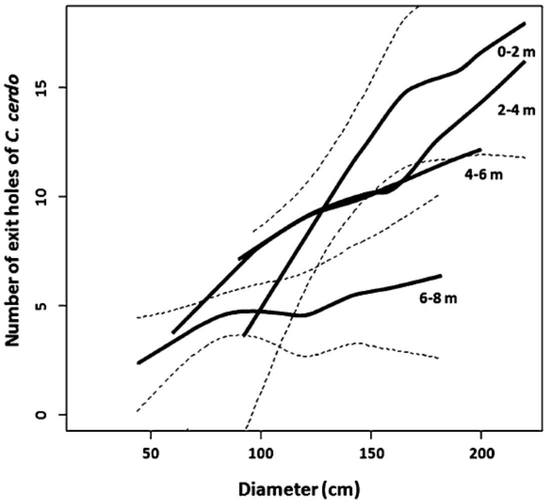

Fig. 2. The effect of trunk diameter on relationship between the number of exit holes of the great capricorn beetle (*Cerambyx cerdo*) at particular heights on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic (both sites combined). Solid lines show the relation between trunk diameter and number of exit holes in 2 m long section of trunk at a particular height; dashed lines show 95% CI for the 0–2 m and 6–8 m heights.

dictors. The final models were fitted using the REML method (restricted maximum likelihood). All the vertical trunk segments measured were included in the analyses.

The association between the number of exit holes and site was tested using LME. The response variable was transformed using a ln(number of exit holes + 1) transformation. The site was the fixed effect variable and tree a random effect variable. The association between height of tree and tree diameter (at a height of 1 m) and site was investigated using ANOVA.

Charts showing the relationships between the number of exit holes of *C. cerdo* and given variables (Figs 1–3) were created using LOESS (locally weighted scatter plot smoothing) function in the R 2.7.2.

RESULTS

In total, 30 oaks were climbed (22 in the Lanska Game Reserve and eight at Hluboka nad Vltavou), data on 169 vertical trunk sections and 676 trunk segments were collected and 4259 exit holes of *C. cerdo* were recorded. Mean height and diameter (at 1 m above the ground) with standard deviation (*SD*) of trees were 10.5 m (± 2.1) and 127 cm (± 10.9), respectively, at the Hluboka site, and 11.5 m (± 2.5) and 142 cm (± 36.1) at the Lány site. Site had no effect on number of exit holes ($F_{1,\ 28} = 0.80$; $P > 0.05$), tree diameter ($F_{1,\ 28} = 1.41$; $P > 0.05$) or tree height ($F_{1,\ 28} = 1.14$; $P > 0.05$). All the trees were taller than 6 m; number of tree sections investigated at a given height, and vertical distribution of exit holes is given for both sites separately and combined (see Table 1). Mean number of exit holes at a given height was calculated as the number of all exit-holes in all the sections at a given height/number of tree sections investigated at that height (Table 1). Density of exit holes at different heights was the number of exit holes in a given 2 m long trunk section divided by the area of bark on that section (Table 1). Numbers of exit holes were similar on East (Mean 27.7; SD ± 26.6) and North (26.9; ± 28.3) facing segments, and also on South (43.1; ± 36.8) and West facing segments (44.3; ± 37.7).

TABLE 1. Vertical distribution of the exit holes of the great capricorn beetle (*Cerambyx cerdo*) on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic. (a – both sites combined, b – Hluboka, c – Lanska). * number of all exit-holes at a given height/number of trees; ** number of exit-holes per m^2 of bark surface at a given height/number of trees.

Meters above the ground	Number of trees (**a**; b; c)	Total (relative) number of exit holes recorded (**a**; b; c)	Mean number* (relative), median and SD of number of exit holes (a)	Mean density**, median and SD of density of exit holes (a)
0–2	**30**; 8; 22	**1253 (29.4%)**; 386 (28.3%); 867 (29.9%)	41.8 (27.9%); 34; 29.4	4.7; 3.8; 3.1
2–4	**30**; 8; 22	**1114 (26.2%)**; 349 (25.6%); 765 (26.4%)	37.1 (24.8%); 28,5; 22.1	4.8; 3.9; 3.1
4–6	**30**; 8; 22	**944 (22.1%)**; 296 (21.7%); 648 (22.4%)	31.5 (21%); 30; 20.3	4.7; 4.2; 3.3
6–8	**29**; 8; 21	**526 (12.4%)**; 140 (10.3%); 386 (13.3%)	18.1 (12.1%); 14; 15.9	3.4; 2.5; 3.1
8–10	**24**; 6; 18	**291 (6,8%)**; 118 (8.7%); 173 (6%)	12.1 (8.1%); 5.5; 11.7	2.9; 1.2; 4.2
10–12	**17**; 3; 14	**115 (2,7%)**; 59 (4.3%); 56 (1.9%)	6.8 (4.5%) 0; 6.8	2.4; 0; 4.4
12–14	**9**; 1; 8	**16 (0.4%)**; 14 (1%). 2 (0.1%)	2.1 (1.4%); 0; 0.7	1.1; 0; 3.2

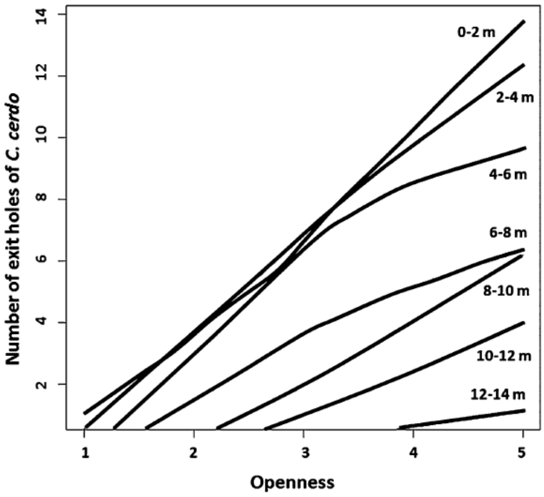

Fig. 3. Effect of openness on the number of exit holes of the great capricorn beetle (*Cerambyx cerdo*) changes with height on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic (both sites combined). This is depicted in terms of the number of exit holes in 2 m long segments of trunk and openness of the environment. 1 – fully shaded; 2 – mostly shaded, 3 – half shaded, 4 – mostly exposed, 5 – fully exposed.

In the first analysis with the number of exit holes as a response variable, the Linear mixed-effect model (LME) (Table 2) revealed that the number of exit holes in a trunk segment was negatively affected by the height of the segment from the ground (Fig. 1), and positively affected by its diameter (Fig. 2) and openness (Fig. 3). The effect of orientation was significant; the effect of diameter and openness on number of exit holes changed with height (Figs 2, 3). In the second and third analyses, the Linear mixed-effect model (LME) (Table 2) revealed that the number of exit holes per m^2 and per m^3 were negatively affected by the height above the ground and positively by openness; the effect of orientation was significant (Table 2).

DISCUSSION

This study revealed that the larvae of *Cerambyx cerdo* occur mainly in sun-exposed parts of large diameter of large, open-grown oaks, especially those near the ground and facing west or south. Previous studies of the habitat preferences of *C. cerdo* at the landscape and between-tree levels indicate that its distribution is affected by tree vitality, age, bark thickness, trunk diameter, insolation and habitat openness (Buse et al., 2007). Similar variables thus influence *C. cerdo* distribution within individual trees and at larger scales.

Table 2. Environmental characteristics affecting the distribution of exit holes of the great capricorn beetle (*Cerambyx cerdo*) on old, open grown oaks at Hluboka nad Vltavou and the Lanska Game Reserve, Czech Republic. Model 1 predicts the association between the number of exit holes and the environmental variables and some of their interactions (Linear mixed-effect model). Model 2 predicts the association between the density of exit holes per m^2 of bark surface and the environmental variables. Model 3 predicts the association between the density of exit holes per m^3 of wood and the environmental variables (Linear mixed-effect model). The final models include all the variables and interactions cited below (Model 1 null deviance = 0.602, residual deviance = 1.007; Model 2 null deviance = 0.524, residual deviance = 0.691; Model 3 null deviance = 0.854, residual deviance = 1.132).

	Regression coefficient *b*	SE	*d.f.*	*F*	*P*
Model 1					
Intercept	–0.902	0.500	1, 638	156.022	< 0.0001
Height	–0.027	0.044	1, 638	276.715	< 0.0001
Diameter	0.380	0.004	1, 638	14.929	< 0.0001
Openness	0.552	0.075	1, 638	114.699	0.0001
Orientation	–	–	3, 638	7.647	< 0.0001
North	0.064	0.085	–	–	–
South	0.248	0.085	–	–	–
West	0.353	0.085	–	–	–
Height : Diameter	0.001	0.001	1, 638	10.092	0.0016
Height : Openness	–0.024	0.010	1, 638	6.485	0.0111
Model 2					
Intercept	0.151	0.180	1, 641	128.939	< 0.0001
Height	–0.072	0.008	1, 641	128.300	< 0.0001
Openness	0.347	0.032	1, 641	122.944	< 0.0001
Orientation	–	–	3, 641	6.284	< 0.0001
North	0.057	0.076	–	–	–
South	0.205	0.076	–	–	–
West	0.293	0.076	–	–	–
Model 3					
Intercept	0.021	0.293	1, 641	138.477	< 0.0001
Height	–0.082	0.013	1, 641	74.835	< 0.0001
Openness	0.594	0.053	1, 641	133.606	< 0.0001
Orientation	–	–	3, 641	4.411	0.004
North	0.079	0.124	–	–	–
South	0.250	0.123	–	–	–
West	0.410	0.123	–	–	–

Trunk diameter is generally recognised as a key determinant of saproxylic beetle diversity (Ranius & Jansson, 2000; Ranius, 2002; Buse et al., 2008b; Foit, 2010) and an important factor affecting the presence of *C. cerdo* at both sites studied (Hauck & Cizek, 2006; Sreiber, 2010). Large trees are old and less vigorous, and offer a wide variety of longer lasting and a greater volume of dead wood microhabitats (Warren & Key, 1991; Irmler et al., 1996; Siitonen et al., 2000; Lindhe & Lindelöw, 2004; Radu, 2006) and thus better conditions for the development of *C. cerdo* larvae.

Effect of solar radiation

Both openness and orientation affect the amount of solar radiation reaching the trunk. The higher number of exit holes on those parts of trunks facing south and west could thus be explained by their higher heat intake. This accords with the fact that *C. cerdo* is a thermophilous species in Central Europe (Buse et al., 2007). Preference of xylophagous and saproxylic insects for sun-exposed wood is common and is discussed elsewhere (Ranius & Jansson, 2000; Kappes & Topp, 2004; Moretti et al., 2004; Lindhe et al., 2005; Vodka et al., 2009; Horak et al., 2011).

The change in effect of openness (i.e. solar radiation) with height does not mean that this beetle exhibited a lower light requirement higher up the trunks of the trees. It is an artifact of this beetle's preference for those parts of the trunk and branches with the greatest diameters. Since the branches and stems near the tops of trees are mostly thin, the numbers of exit holes high in a tree are generally low (see above). In addition, oak branches and stems are rarely fully shaded near tree tops (mostly they were half or not shaded in this study) and, therefore, the openness gradient is shorter.

There is an interesting pattern in the distribution of exit holes in those parts of the trunk facing the four cardinal directions. Numbers of exit holes on the west and south facing sides were similar, although the south facing side receives more heat than the west side (Allen et al., 2006, Zeleny & Chytry, 2007). Also, the numbers of exit holes were similar on the north and the east facing sides, although the latter receive more heat (cf. Zeleny & Chytry, 2007). This may be explained by the fact that the peak activity of *C. cerdo* adults occurs late in the evening in June (Bílý & Mehl, 1989). At this time, the west oriented part of trunks are the warmest as they accumulate heat during most of the afternoon, when even north facing parts are exposed to solar radiation (Allen et al., 2006). Thus *C. cerdo* females might oviposit on those parts of the trunk that are warmest when they are active rather than those parts that receive the highest heat intake during the whole day, which would most benefit the larvae (Sláma, 1998). On the other hand, larvae often migrate under the bark and/or in the inner parts of the trunk for distances of up to several decimetres. Thus an exit hole indicates where pupation rather than ovipositon occurred. The observed pattern is probably a result of the preferences of both ovipositing females and larvae.

Activity of *C. cerdo* larvae often results in the gradual death of the whole or parts of inhabited trees. It is true that larval activity in causing the death of nearby branches is likely to increase the amount of solar radiation reaching the trunk. The observed relation between the number of exit holes and openness thus could be due to larval activity. The effect of the orientation towards cardinal directions and habitat openness at a larger scale (Buse et al., 2007), however, show that the amount of solar radiation affects the distribution of *C. cerdo* exit holes.

Vertical stratification

The number and density of *C. cerdo* exit holes decreased with height. At both study sites, about half of the population developed in those parts of trunks between 0–4 m above the ground and approximately a third in those parts less than 2 m above the ground. This is an important result, indicating that the bulk of the *C. cerdo* population develops near the ground. This is useful information when monitoring and estimating the size of *C. cerdo* populations inhabiting open-grown old oaks.

Lower parts of trunks are of larger diameter with a greater area of bark and a greater volume wood than the upper parts. This, however, does not fully explain the vertical stratification of exit holes, as exit-hole density decreased with height even when bark area and wood volume were accounted for in the analyses. Thus this beetle prefers the lower parts of trunks for reasons other than the resources available to the larvae. Despite the preference for the lower parts of trunks, *C. cerdo* diameter requirements seemed to decrease with height, as indicated by the effect of the interaction. Previous inventories of trees inhabited by this beetle demonstrate that at both the sites studied *C. cerdo* nearly never inhabits trees with DBH <80 cm (Hauck & Cizek, 2006; Sreiber, 2010). We recorded exit holes also on much thinner parts of the trunk high above ground. This agrees with the fact that its larvae feed in the wood of weakened trees (see above) and thus often develop in oaks of much smaller diameters at sites where tree growth is slower.

C. cerdo preference for lower, insolated parts of tree trunks may explain the decrease in the abundance of this species during the last century (Sláma, 1998; Buse et al., 2007, 2008b). Transition of forest pastures, coppices and coppices with standards into high, closed-canopy forests (Warren & Key, 1991; Rackham, 1998; Vera, 2000) affected this beetle in two ways. Firstly, it decreased habitat quality by shading the bases of suitable trees. Secondly it led to gradual disappearance of the habitat, i.e. open-grown oaks that are most likely to reach the trunk diameters required by this species.

C. cerdo prefer the trunks of large, open-grown oaks, especially the sun-exposed parts of the west and south facing sides of the lower parts of the trunks. Our results also suggest that the bulk of the *C. cerdo* populations develop near the ground. Searching for exit holes is thus an effective method of detecting sites inhabited by this species and active management preventing canopy closure is thus crucial for the survival of *C. cerdo*.

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Kapitola III.

Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows

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Abstrakt

Trees with hollows are key features sustaining biodiversity in wooded landscapes. They host rich assemblages of often highly specialised organisms. Hollow trees, however, have become rare and localised in Europe. Many of the associated biota is thus declining or endangered. The challenge of its conservation, therefore, is to safeguard the presence of hollow trees in sufficient numbers. Populations of numerous species associated with tree hollows and dead wood are often found in habitats that were formed by formerly common traditional silvicultural practices such as coppicing, pollarding or pasture. Although it has been occasionally mentioned that such practices increase the formation of hollows and the availability of often sun-exposed dead wood, their effect has never been quantified.

Our study examined the hollow incidence in pollard and non-pollard (unmanaged) willows and the effect of pollarding on incremental growth rate by tree ring analysis. The probability of hollow occurrence was substantially higher in pollard than in non-pollard trees. Young pollards, especially, form hollows much more often than non-pollards; for instance, in trees of 50 cm DBH, the probability of hollow ocurrence was ~0.75 in pollards, but only ~0.3 in non-pollards. No difference in growth rate was found.

Pollarding thus leads to the rapid formation of tree hollows, a habitat usually associated with old trees. It is therefore potentially a very important tool in the restoration of saproxylic habitats and conservation of hollow-dependent fauna. If applied along e.g. roads and watercourses, pollarding could also be used to increase landscape connectivity for saproxylic organisms. In reserves where pollarding was formerly practiced, its restoration would be necessary to prevent loss of saproxylic biodiversity. Our results point to the importance of active management measures for maintaining availability, and spatial and temporal continuity of deadwood microhabitats.

Is Active Management the Key to the Conservation of Saproxylic Biodiversity? Pollarding Promotes the Formation of Tree Hollows

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Abstract

Trees with hollows are key features sustaining biodiversity in wooded landscapes. They host rich assemblages of often highly specialised organisms. Hollow trees, however, have become rare and localised in Europe. Many of the associated biota is thus declining or endangered. The challenge of its conservation, therefore, is to safeguard the presence of hollow trees in sufficient numbers. Populations of numerous species associated with tree hollows and dead wood are often found in habitats that were formed by formerly common traditional silvicultural practices such as coppicing, pollarding or pasture. Although it has been occasionally mentioned that such practices increase the formation of hollows and the availability of often sun-exposed dead wood, their effect has never been quantified. Our study examined the hollow incidence in pollard and non-pollard (unmanaged) willows and the effect of pollarding on incremental growth rate by tree ring analysis. The probability of hollow occurrence was substantially higher in pollard than in non-pollard trees. Young pollards, especially, form hollows much more often than non-pollards; for instance, in trees of 50 cm DBH, the probability of hollow ocurrence was ~0.75 in pollards, but only ~0.3 in non-pollards. No difference in growth rate was found. Pollarding thus leads to the rapid formation of tree hollows, a habitat usually associated with old trees. It is therefore potentially a very important tool in the restoration of saproxylic habitats and conservation of hollow-dependent fauna. If applied along e.g. roads and watercourses, pollarding could also be used to increase landscape connectivity for saproxylic organisms. In reserves where pollarding was formerly practiced, its restoration would be necessary to prevent loss of saproxylic biodiversity. Our results point to the importance of active management measures for maintaining availability, and spatial and temporal continuity of deadwood microhabitats.

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Introduction

In Europe, the intensification of forestry and agriculture and the abandonment of traditional silvicultural practices have resulted in an increase in the size of landscape mosaic grain, increased canopy closure, and a decline in the number of old and open-grown trees in both forested and agricultural landscapes [1–4]. Old trees with hollows (i.e. cavities) are a key feature in sustaining biodiversity in wooded landscapes because they host rich, specialised assemblages of numerous vertebrate and invertebrate species [5–7]. Their walls and wood mould (loose decayed wood that accumulates in hollows) provide a continuous supply of dead wood to wide spectrum of saproxylic (dead wood dependent) invertebrates and fungi that constitute a large part of woodland biodiversity [8,9]. Some, such as the hermit beetle *Osmoderma eremita*, are found only in tree hollows, while others exploit other deadwood microhabitats such as old and dead trees, including the stag beetle *Lucanus cervus*, and the Rosalia longicorn *Rosalia alpina* [10,11].

These key deadwood habitats, such as old trees and hollow trees, are now rare and localised in Europe and most organisms associated with them are thus threatened or declining. Their conservation requires that the continuity of these deadwood habitats is maintained [3,12–14]. Knowledge about the formation of hollows is, therefore, needed. Several works have studied or simulated the occurrence of hollow-bearing trees at the stand or landscape level [15–18]. Because the natural formation of hollows takes a long time, active measures are often required to bridge the gap between current hollow trees and those young trees that will substitute for them in the future. Jansson *et al.* (2009) [19] suggest using special boxes that mimic tree hollows to help preserve endangered populations of hollow-dependent beetles. Bird nest boxes are commonly used to help hollow-nesting birds overcome the same problem. Such artificial hollows, however, are only able to support a small proportion of tree hollow organisms and their effect is relatively short-term. A simple method designed to speed up the formation of hollows is therefore needed.

Pollarding, i.e. the periodical removal of the upper branches of a tree by pruning, is an age-old practice [20]. It allows for the harvesting of firewood or fodder from trees without killing them. The branches are usually removed at a height that prevents herbivorous mammals from damaging resprouting shoots, thus allowing pasture and wood production to continue in conjunction. Stands of pollarded trees usually host rich assemblages of saproxylic species, many of which prefer sunny conditions, including endangered hollow specialists (e.g. *Osmoderma eremita*) [21], and other saproxylics (e.g. *Rosalia alpina*) [22,23]. Some authors have mentioned the potential of pollarding for conservation, as pollard trees offer exposed wood and form tree hollows at a smaller diameter than non-pruned trees of the same species [24–27], and pollarding has already found its way into conservation practice [6,22,24,27]. However, the effects of pollarding on the formation of hollows have not been studied yet.

If pollarding substantially increases the probability of hollow formation, it could serve as a key management tool for conserving the often highly endangered biota associated with them. In the present study, the hypothesis that pollarding affects the formation of tree hollows was tested by comparing hollow occurrence in pollards and in unmanaged (unpollarded) trees. To investigate the effects of pollarding on growth rate, patterns in annual ring increments were compared between pollards and unmanaged trees. To quantify the potential effects of pollarding on tree hollow availability, the probability of hollow occurrence in relation to tree diameter was predicted for pollards and unmanaged trees.

Materials and Methods

Study sites and data collection

Data were collected in stands of pollard and unmanaged (i.e. unpollarded) white willows (*Salix alba*) in the catchment area of the Thaya (Dyje) river in South Moravia, Czech Republic. Two stands of pollard trees, Vojkovice (49°3′N, 16°36′E) and Krive jezero (48°51′N, 16°43′E), and two stands of unmanaged willow trees, Kanci obora (48°46′N, 16°52′E) and Pastvisko (48°48′N, 16°47′E), were sampled. Vojkovice and Kanci obora are located on publicly accessible land, two other sites are located within protected areas. Site selection was constrained by the fact that pollarding of willows had been regionally common in the past, but was mostly discontinued after the Second World War. Old willows thus bear the signs of previous pollarding, whereas younger trees were (almost) never pollarded throughout the area. The areas where young trees were pollarded, or where older trees were not pollarded were therefore carefully selected. Trees with trunks higher than 0.5 m, whose upper branches had been pruned at least once were recognized as pollards. They were identified by all the main branches sprouting from single part of the trunk, mostly its swollen top. Trees bearing no signs of management were considered unmanaged (Figure 1). For each tree the diameter at breast height (DBH; 1.3 m above ground) and the presence/absence of hollows were recorded. Any cavity with an entrance hole larger than 5×5 cm and with the inner space larger than the entrance hole was recognized as a hollow. Where hollows were not accessible by ladder (>4 m above ground level), binoculars were used to search for hollows in trunks and branches (following Koch 2008 [28]).

To assess the effects of pollarding on tree growth, pollards and unmanaged trees were cored and their growth rates compared. Cores were taken from 10 unmanaged and 10 pollard trees using a steel increment borer (Mora$^{\text{TM}}$, Sweden) at the Pastvisko site, where one part of the formerly unmanaged willow stand was pollarded in 2003 (once only). All cores were dried, glued onto a wooden lath, cut off by razor blade and inspected for injuries, reaction wood and other aberrant features. One core was badly broken and another one contained rotten sections that did not allow successful ring width measurements. These two cores were removed from further analysis. For the remaining cores (n = 8 for pollard and n = 10 for unmanaged willows), rings were counted from pith to bark and their widths measured to the nearest 0.01 mm using the TimeTable measuring device and PAST4 software [29]. Ring sequences were cross-dated visually using the pattern of wide and narrow rings, and verified using the PAST4 program.

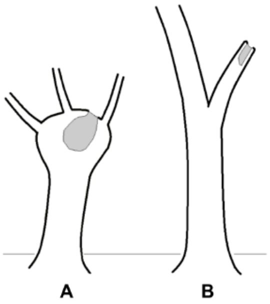

Figure 1. Forms of pollard and unmanaged trees. A pollard (A) and an unmanaged tree (B), shown with their most common type of tree hollows (grey colored): hollows formed in the upper parts of the trunk as a result of bared heartwood after pruning are common in pollards, whereas hollows formed after a branch fall are the most common hollow type in unmanaged trees.
doi:10.1371/journal.pone.0060456.g001

All necessary permits were obtained for the described field studies; the research was conducted under the permit No. 00356/KK/2008/AOPK issued by the Nature Conservation Agency of the Czech Republic. The data are deposited in Dryad, a publicly accessible digital repository [30].

Data analysis

Relationships between DBH, the probability of hollow presence, and the effect of management (pollard/unmanaged) were tested. The data were analyzed using generalized linear regression models with binomial distribution (*logit* link) where presence/absence of hollow in the tree was a dependent variable, DBH (ln-transformed) was an explanatory variable (*lnDBH*), and management type (pollard/unmanaged) was a factor variable (*management*). An interaction between DBH and management type (*lnDBH:management*) was added to the model to assess the differences in slope shape between pollards and unmanaged trees. The second regression model where the interaction parameter was excluded was also tested, and then compared with the full model.

The effects of pollarding on tree growth rate were investigated by detection of radial growth in pollarded and unmanaged trees. Changes in incremental ring width were compared using a regression model with a repeated measures design. Each core sample (8 pollard, 10 unmanaged) was considered as a single subject, its ring widths being longitudinal measurements. In the model, ring width (*ringwidth*) was a dependent variable, subsequent years were equally spaced time points (*time*, continuous explanatory variable), and management type (pollard/unmanaged) was a factor variable (*management*). Firstly, the pattern in ring width increments for the period from 1990 to 2011 was tested, because from 1990 growth information for all the core samples was available. Secondly, the pattern for the period from 2003 to 2011 was tested, 2003 being the year in which trees were pollarded. In both cases, the interaction between *time* and management type (*time:management*) was included in the model. The quadratic effect of *time* was added to the model, and subsequently removed if not significant. The analyses were performed using R 2.14.2 software [31].

Results

Data on 1126 willow trees were collected. Hollows were present in 677 (83%) out of 820 pollard trees, and in 103 (34%) out of 306 unmanaged trees. The number of trees examined and their mean DBH at each site are detailed in Table 1. The proportions of trees with hollows in each DBH class and for each type of management are shown in Figure 2. Six out of eight core samples obtained from pollards (nine years after single pruning), and one out of ten core samples obtained from unmanaged trees of the same age contained signs of wood decomposition (75% and 10%, respectively).

The hollow incidence increased with increasing DBH, and was affected by management as the regression models show (Table 2). Compared to unmanaged trees, the probability of hollow occurrence was higher in pollard trees, and especially in young trees, the increase in probability was steeper when backtransforming DBH to the original scale. The full model explained 23.1% of variance in the data, all three variables had a significant effect (*lnDBH*: $\chi^2 = 172.71$, d.f. = 1, $P<0.001$; *management*: $\chi^2 = 145.34$, d.f. = 1, $P<0.001$; *lnDBH:management*: $\chi^2 = 4.21$, d.f. = 1, $P = 0.04$). The simplified model without the interaction between *lnDBH* and *management* accounted for 22.9% of the total variance.

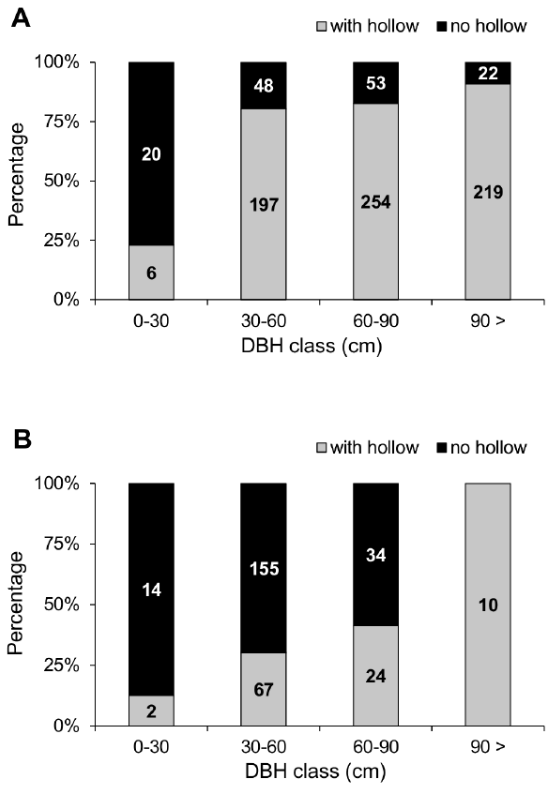

Figure 2. Proportions of hollowed trees in DBH classes. The proportion of hollowed willows in diameter classes (DBH class) for (A) pollards, and (B) unmanaged trees in the Dyje river catchment, Czech Republic. Numbers in bars indicate number of trees measured.
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Growth rate did not differ between pollarded and unmanaged trees, as the results of the regression model for radial growth showed no significant difference in the incremental growth pattern. All effects proved to be non-significant in both the 1990-2011 model (*time*: $F_{1,392} = 0.01$, $P = 0.26$; *management*: $F_{1,392} = 1.27$, $P = 0.98$; *time:management*: $F_{1,392} = 3.31$, $P = 0.07$), and in the 2003–2011 model (*time*: $F_{1,158} = 1.57$, $P = 0.21$; *management*: $F_{1,158} = 2.19$, $P = 0.14$; *time:management*: $F_{1,158} = 0.91$, $P = 0.34$). Quadratic effects of time were not significant. The mean radial growth of pollarded and unmanaged willows in the period 1990–2011 is displayed in Figure 3.

The probability of hollow occurrence in relation to DBH was predicted (Figure 4) using the simplified two-parameter model, because the significance value of the interaction parameter was low in the full model. The prediction showed that hollow occurrence was greater in pollard trees than in unmanaged ones.

Discussion

Study outcome and limitations

Our results show that pollarding increases the probability of hollow formation, especially in young trees (i.e., trees with small DBH). In pollard trees, hollows form more frequently and sooner than in unmanaged trees. For instance, in a stand of 100 willows with DBH of 50 cm, there would be ~75 hollow trees if the trees were pollarded, and only ~30 hollow trees if the trees were unpollarded (see Figure 4). Since pollarding speeds up hollow formation, it substantially increases the hollow density required for survival of hollow specialists [32].

Pollarding also has other positive effects. Firstly, the hollows in pollards occur in stems rather than in branches, while the latter prevail in unmanaged trees [33]. Stem hollows are larger, contain a greater volume of wood mould, and are thus able to host greater numbers of hollow specialists. Secondly, the bare, mostly sunlit heartwood after pruning is open to colonization by xylophages, including numerous threatened and protected species [23]. Pollards thus provide various deadwood microhabitats from a relatively young age. For example, at one of the sites (Vojkovice), larvae of *Osmoderma eremita* were found in a pollard <20 years old [10].

Owing to their lower height, pollard trees are less susceptible to branches breaking and falling due to weight imbalance, as long as pruning is carried out periodically. Pollards thus tend to live longer than unmanaged trees, and a single pollard may provide continuum of various deadwood microhabitats for hundreds of years [25]. On the other hand, if pollarding was discontinued, the increasing weight of overgrown branches often results in serious damage - trunk disintegration and the destruction of the tree. This is the reason why abandoned pollard stands suffer from rapid loss of hollow trees and subsequent loss of associated biodiversity [10].

It's not surprising that hollows are mostly present in trees with larger diameters [18,34,35]. As the tree ages, the heartwood becomes more susceptible to fungal infections and rot due to branch fall or bark loss [36]. Ranius *et al.* (2009) [18] provided data on hollow formation in oaks with regard to DBH. Of oaks with a diameter of 80–100 cm, 20–50% contained hollows. In our study, hollow incidence in both unmanaged and pollard willows of the same diameter is much higher than in oaks, probably due to the

Table 1. Collected data on willows.

Site	Management	Number of trees examined	Percentage of trees with hollow	Mean DBH*		
				All trees	Trees with hollow	Trees with no hollow
Krive jezero	pollard	328	71	99	110	74
Vojkovice	pollard	492	90	64	66	43
Kanci obora	unmanaged	184	40	57	65	52
Pastvisko	unmanaged	122	24	46	49	45
Total		1126				

*Mean DBH = mean diameter in 1.3 m above ground.
Characteristics of pollards and unmanaged willows at four study sites in the Dyje river catchment, Czech Republic.
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fact that faster growth and softer wood make willows more prone to damage and infections [4,37].

During the last century, pollarding was abandoned in most of the study area and also in most of Europe [11,24,25,27,38]. Because of this, it is difficult to separate the effects of pollarding and tree age. Generally, old trees have been pollarded in the past, whereas young trees never have. In the study area, pollarding has continued locally, but is concentrated on predominantly older trees. As a result of this, our sampling was limited by the absence of stands containing both unmanaged and pollard willows of a similar age. This might possibly be a source of some unintended bias and further studies would therefore be needed to ensure sufficient separation of the age effect.

We found no effect of pollarding on radial tree growth. This is in contrast with the documented decrease in growth rate after pollarding in oaks [39]. Willows, however, may respond to pollarding in a different way than oaks. Also, the sampled trees grew in dense stands, and were probably affected by competition. In easily resprouting, light-demanding willows, reduced competition after pruning (pollarding) may have balanced the negative impact of branch removal. Larger sample size would be needed in order to test such a hypothesis. The poor quality or absence of central heartwood in regularly pollarded older trees also prevented us from assessing the potential effects of regular pollarding on tree growth. This question has yet to be addressed.

Table 2. Results of hollow presence analysis.

Coefficient	Estimate	SE	P
A. Full model			
pollard	−4.65	0.90	<0.001
lnDBH	1.48	0.22	<0.001
unmanaged	−6.29	2.23	0.005
lnDBH:unmanaged	1.10	0.55	0.047
B. Interaction excluded			
pollard	−5.44	0.83	<0.001
lnDBH	1.67	0.20	<0.001
unmanaged	−1.87	0.16	<0.001

Pollarding and DBH affect hollow occurrence in willows. Output of generalized linear regression models with binomial distribution (coefficient estimates are on *logit* scale), *lnDBH* = ln-transformed DBH, factor variable *management* is represented by its levels, 'pollard' and 'unmanaged'. Coefficients are displayed for (A) full model with interaction between variables (*lnDBH*: $\chi^2 = 172.71$, d.f. = 1, P<0.001; *management*: $\chi^2 = 145.34$, d.f. = 1, P<0.001; *lnDBH:management*: $\chi^2 = 4.21$, d.f. = 1, P = 0.04) and for (B) restricted model without interaction. For both models n = 1126.
doi:10.1371/journal.pone.0060456.t002

Traditional management as a part of landscape history

Ancient landscape in Europe was strongly influenced by human activities over long periods of time [4]. In the past, traditional pruning techniques like pollarding, shredding or coppicing were used for firewood and fodder production [40–42], and forests were also used for livestock grazing [43,44]. As a result, old, open-grown and hollow trees were common features of the landscape.

Today, the biota associated with old and/or hollow trees finds refuge mainly in orchards, alleys, parks, pasture woodlands and game reserves rather than in intensively managed forest and agricultural landscape, or strict forest reserves [26,45]. The importance of such man-made habitats is especially emphasized for the noble chafer beetle *Gnorimus nobilis* [46,47] and for *Osmoderma eremita* [48]. The latter is among the best known European beetles and serves as an indicator and umbrella species for hollow-dependent invertebrates [49]. Both beetles are thermophilic and rarely occur in natural or semi-natural forests that are too shaded [47,48]. Hollow-dependent invertebrates often have low dispersal abilities, and thus require a high density of microhabitats in space and time [12,13]. Traditional pollard stands, pasture woodlands, and orchards with large aggregations of

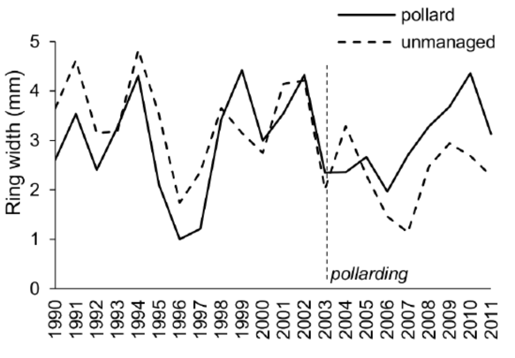

Figure 3. Radial growth of willows. Mean radial growth of pollards (solid line; n = 8) and unmanaged willows (dashed line; n = 10) at the Pastvisko site, Czech Republic. Although pollard willows show increased growth rates after the pollarding event of 2003 (vertical dashed line), the pattern was not significant in our study.
doi:10.1371/journal.pone.0060456.g003

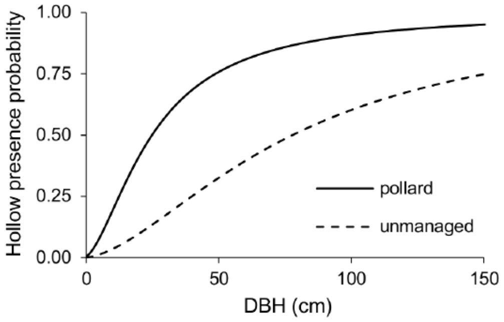

Figure 4. Predicted probability of hollow presence. Model predictions of hollow presence – probability that the tree with any given diameter (DBH) will contain a hollow, for pollards (solid line) and unmanaged willows (dashed line); (the *x*-axis is backtransformed to the original scale).
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sun-exposed hollow trees provide suitable conditions.

Other studies provide evidence for the importance of traditional management practices as they stimulate the formation of open forest features [50]. The cessation of pollarding was found to have negative effects on assemblages of lichens and epiphytic vegetation [25,38,51]. Robles *et al.* (2011) [52] found that the biodiversity of secondary cavity nesting birds was greater in oak forests traditionally managed by extensive grazing and cutting for firewood than in dense forests. Following the same principle as pollarding, coppicing most likely increases the incidence of hollows near the ground, and its cessation thus threatens the violet click beetle *Limoniscus violaceus*, a rare and highly endangered species, which develops in the wood mould of basal cavities. The beetle can mostly be found in formerly coppiced forests [53,54] or ancient forest pastures [55].

In Europe, traditional silvicultural practices have contributed to the creation of today's rare deadwood microhabitats, and therefore they helped to preserve saproxylic species over the years. The discontinuation of such practices not only threatens numerous saproxylic organisms in commercial woodland, but it also leads to a peculiar situation in many protected areas: old trees, that currently host populations of hollow-dependent and other specialised saproxylics, were often subject to pollarding or coppicing, that increased dead wood availability. Young trees, on the other hand, were not treated in this way. This is likely to result in the reduction of suitable deadwood microhabitats in the near future.

Conservation practitioners, therefore, need to acknowledge that extant populations of endangered saproxylic species, many of them preferring sunny conditions, very likely depend on microhabitats created by former management practices, since abandoned [5]. Although the insects are still present at numerous sites, they survive only temporarily, as a part of extinction debt created by past management changes [56,57]. The importance of active management practices is, however, rarely appreciated. Nature conservationists often praise natural, semi-natural and 'old-growth' habitats, and tend to ignore site history and the habitat requirements of endangered organisms. In particular, the 'strict forest reserve' concept [58,59] based on non-intervention management in woodland habitats is especially damaging when applied to traditionally managed sites [3,43,60–62]. In Europe, natural disturbance factors such as large herbivores [63] and fires [64] are mostly lacking. Natural succession thus leads to greater canopy closure and causes a transformation from low competition and sunny conditions to higher competition with shady and cold conditions. Old and veteran trees are not able to adapt to the new conditions and subsequently die [4,5], which leads to the loss of important deadwood microhabitats and therefore to a decline in saproxylic biodiversity associated with these trees.

Future perspectives

The promotion of evidence-based conservation management targeted at saproxylic species is one of the major topics of the currently emerging European Saproxylic Beetle Conservation Strategy [3]. Conservation and retention of hollowed trees as one of the specific habitats are therefore of crucial importance. Creating artificial habitats might be necessary, especially when it takes a long time for the natural production of such habitats [19], or if factors contributing to their formation in the past, e.g. grazing by large herbivores or fires [63,64], are missing. Active management, therefore, should be adopted to prevent the gradual decimation of saproxylic biodiversity. As shown in the present study, pollarding might play an important role in the restoration of saproxylic habitats. If trees along watercourses, roads and other linear structures in the landscape were to be pollarded, they could well become important habitats and corridors connecting refugia of saproxylic fauna.

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Author Contributions

Conceived and designed the experiments: LC PS. Performed the experiments: PS MP. Analyzed the data: PS JA. Wrote the paper: PS JA LC.

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Kapitola IV.

Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests

Forest Ecology and Management 358, 80–89

Abstrakt

Efficient conservation management must be applied in protected areas in order to slow the loss of biodiversity in Europe. Regarding forests, a conservation approach based on minimal intervention prevails in most protected woodlands, thus facilitating the expansion of closed-canopy forests at the expense of open forests. To identify effective conservation strategies for protected forests, the minimal intervention or “hands-off” approach must be compared with active measures to support biodiversity.

We carried out a study in the oak-dominated forests of Podyji National Park (Czech Republic), an historically managed area left for natural succession since 1950. Twelve experimental clearings were created in closed-canopy forests within the core zone of the park; six of these clearings were connected to forest edges and open meadows, the remaining six clearings were isolated from open habitats within closed forest. To assess the importance of minimal intervention and active management measures in protected forests, we compared the richness and composition of insects, reptiles, birds and vascular plants in the clearings and in four reference habitats, including closed forest, forest edge, open forest, and meadow, in the first season following the intervention.

In comparison to closed-canopy forest, the clearings had higher species richness of butterflies, saproxylic and floricolous beetles, reptiles, and vascular plants but lower richness of moths and epigeic beetles, and similar richness of birds. For most groups, the species composition of clearings differed from that of closed forest or even the forest edge, indicating that the latter habitats cannot serve as a sufficient replacements for the conservation of open woodland species. The species richness of isolated clearings was generally lower than that of clearings connected to open habitats, and their communities contained a larger proportion of species associated with closed forest. Most threatened species were associated with clearings or open forest, closed forest and meadow hosted only a few.

The creation of the clearings in closed-canopy forests had a positive effect on overall species richness and supported threatened species in most model groups. It is thus a valuable management tool in the conservation of temperate woodland biodiversity. Our results also point to the importance of connectivity of open habitats in wooded landscapes. Further surveys of the clearings are needed to ascertain the effect of such interventions to see how communities change throughout succession, or alternatively to what extent hindering succession by repeated cutting may alter communities.

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Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests

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ABSTRACT

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The creation of the clearings in closed-canopy forests had a positive effect on overall species richness and supported threatened species in most model groups. It is thus a valuable management tool in the conservation of temperate woodland biodiversity. Our results also point to the importance of connectivity of open habitats in wooded landscapes. Further surveys of the clearings are needed to

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ascertain the effect of such interventions to see how communities change throughout succession, or alternatively to what extent hindering succession by repeated cutting may alter communities.

1. Introduction

Biodiversity conservation has long been a goal of European conservation policy (CBD, 2010; CEC, 1998). However, despite the fact that more than 25% of European land is afforded some level of protection for conservation, biodiversity continues to decline (EEA, 2009). One factor contributing to this decline may be unsuitable management practices in protected areas, or more specifically, the insufficient application of evidence-based conservation recommendations (Sutherland et al., 2004). A major concern involves the selection of efficient strategies for the conservation of biodiversity in forest ecosystems.

Today, most forests in Europe are closed, shady habitats. This contrasts with their past state, which was much more open and dynamic. The open structure was maintained by disturbances such as grazing and fires (Adámek et al., 2015; Bengtsson et al., 2000; Niklasson et al., 2010; Rackham, 1998; Szabó, 2010; Vera, 2000). These disturbances were later substituted by human silvicultural practices such as wood pasturing, controlled burning and coppicing. Wood pasturing and burning prevented full canopy closure and led to the formation of open, park-like habitats with numerous open-grown trees. In coppices, trees were usually cut down every 7–20 years (Szabó, 2010), which maintained a cyclical pattern of extreme changes in ground-level light penetration (Buckley, 1992; Joys et al., 2004). Traditionally managed woodlands were thus open, sunny, heterogeneous mosaics of forest in various stages of succession, which harboured a high richness of animals and vascular plants (Hédl et al., 2010; Benes et al., 2006; Bengtsson et al., 2000; Bugalho et al., 2011; Spitzer et al., 2008; Vodka and Cizek, 2013; Warren and Thomas, 1992).

However, the traditional management practices maintaining these disturbance regimes have largely been abandoned in most of Europe, especially over the last 200 years (Bergmeier et al., 2010; Müllerová et al., 2014, 2015; Tárrega et al., 2009). The formerly common, open woodlands have gradually been transformed into high closed-canopy forests in order to satisfy increased demand for timber or due to secondary succession. Due to the absence of regular disturbances, increases in canopy closure have also occurred in forests in protected areas. For instance, within nature reserves in the south-east of the Czech Republic, the expansion of closed-canopy forest has reduced the cover of open woodlands from 68.5% to 14.1% between 1938 and 2009 (Miklín & Čížek, 2013). Similar reductions have occurred across the European continent (Hartel and Plieninger, 2014; Rackham, 2003). As a result, species composition in forests has shifted from light-demanding and oligotrophic species towards more generalist, mesic and shade-tolerant species (Hédl et al., 2010; Kopecký et al., 2013; Van Calster et al., 2008; Van der Werf, 1991; Vild et al., 2013). Many species associated with open woodlands, including numerous plants, fungi, and animals that were common in the past have thus became rare or endangered.

In commercial forests, the maintenance of high canopy closure is economically justifiable, although even in these forests some forms of management may result in short-term canopy openings (e.g. selection cutting, thinning) (Pawson et al., 2013; Verschuyl et al., 2011). On the other hand, protected areas are mostly dedicated to biodiversity conservation. Management of protected forests therefore must consider the requirements of the species that inhabit those forests, including endangered species. Active management measures restoring or maintaining the open structure of forests in European protected areas are surprisingly rare (but see for instance Plieninger et al. (2015) for the use of wood pasturing), despite the fact that their need is emphasized by many studies concerning biodiversity of temperate forests (Götmark, 2013). Yet while active approaches to forest conservation management are continuously recommended by the scientific community, the "strict forest reserve" concept (Schultze et al., 2014) which prevents intervention is a standard practice applied to over 3 million hectares (or about 1.7% of forested area) in Europe (COST Action E4, 2000). Although traditionally managed open woodlands require a special approach to nature conservation (Götmark, 2013; Lindbladh et al., 2007), policies often consider coppicing or wood pasturing as undesirable disturbances to the "naturalness" of forests (Miklín and Čížek, 2014). Numerous studies compared the biodiversity of unmanaged (minimal intervention approach) and commercially managed forests concluding that minimal intervention favours biodiversity (Lassauce et al., 2013; Martikainen et al., 2000; Paillet et al., 2010). In protected areas, however, the choice is often between active conservation measures and minimal intervention approach rather than between the minimal intervention and commercial management. Yet there is little information comparing the effects of active conservation measures and the minimal intervention (Franc and Götmark, 2008; Götmark, 2013). Managers of protected forests thus lack basic information needed for qualified management decisions.

In order to quantify the effects of minimal intervention and active management approaches on biodiversity of protected forests, we carried out a multi-taxa study in the oak-dominated forests of Podyji National Park (Czech Republic). Twelve experimental clearings were created in unmanaged, closed-canopy forests of the core zone of the park. In the first season after their creation, eight model groups (butterflies, moths, epigeic, floricolous and saproxylic beetles, reptiles, birds and vascular plants) were sampled in the clearings and in adjoining reference habitats (including closed-canopy forest, open forest, forest edge, and meadow). To assess the effect of the active intervention we compared the species richness and the species composition of the model groups among the newly created clearings and the reference habitats. We also assessed the importance of individual habitats for sustaining threatened species in the sampling area.

2. Material and methods

2.1. Study area and design

This study was carried out in Podyji National Park (South Moravia, Czech Republic) (48°50′56″N, 15°53′13″E), an area covering 63 km^2 of the Dyje River canyon (ca 300 m a.s.l.). The canyon is characterised by nutrient poor, shallow soils. Until the Second World War, a large part of the area was managed by livestock grazing and coppicing, which kept the landscape open. After the war, these practices were abandoned, and secondary succession has led to an increase in canopy closure. Today, the area is covered with closed-canopy forests (hereafter referred to as "closed forest"), or more open remnants of the formerly coppiced and pasture forests (hereafter referred to as "open forest") on the upper slopes of the canyon.

Closed forests in the lower part of the river valley belong to Hercynian oak-hornbeam forests (*Melampyro nemorosi-Carpinetum betuli*; *Carpinion betuli*) (Chytrý et al., 2008). The average basal area of the closed forests is 35.4 m^2/ha, the canopy openness is 5.7% (SD = 1.82) (openness was measured by digital hemispherical photographs at 1.3 m above the ground analysed in WinSCANOPY image processing software; Regent Instruments Inc. 2015). These forests are composed of sessile oak (41%), hornbeam (37%), small-leaved lime (18%), and other species (4%). Open forests on the upper slopes belong to open thermophilous oak forests of the association *Sorbo torminalis-Quercetum*, *Genisto pilosae-Quercetum petraeae* (alliance *Quercion petraeae*) (Chytrý et al., 2008). These forests are characterised by a lower mean basal area (25.5 m^2/ha), and higher mean canopy openness (16.9%, SD = 8.25) than the closed forests. The open forests are composed predominantly of sessile oak (90%), with small-leaved lime (5%), hornbeam (4%), and other species (1%) comprising a much smaller component.

At six sites in the core zone of the park (Fig. 1), a pair of small clearings (each ~40 × 40 m) were created. A few trees were left standing in each clearing in order to replicate an open forest environment. The clearings were located near the bottom of the river canyon, close to the alluvial meadow. The clearings were created to support populations of the critically endangered butterfly, the clouded apollo *Parnassius mnemosyne*. One clearing in each pair was always directly connected to the meadow, while the other clearing was isolated from the meadow and from the first clearing by at least 20 m of closed forest (see Fig. 1). After felling, mean canopy openness in the clearings increased to ~22%. Clearings were created at four of the sites (Lipina, Hlubocke louky, Stary Galis, Hardegg) in February 2011, while the remaining two sites (Novy Galis, Siroke pole) were cleared in February 2012. Before felling, the average basal area of the clearings was 40.6 m^2/ha, with composition of sessile oak (36%), hornbeam (39%), small-leaved lime (15%), and others (10%), thus very similar to the closed forests. See also Table A1 in Supplementary material.

Furthermore, at each of the six sites, four reference plots (~40 × 40 m) were established within four types of habitats for comparisons. These reference habitats were: closed-canopy forest, open forest, forest edge, and alluvial meadow (Fig. 1). Therefore, in total there were 12 experimental clearings and 24 reference plots established across six sites.

2.2. Model groups and data collection

Sampling of clearings and reference plots at each site was carried out in the spring and summer following the creation of the clearings. Thus, the four sites cleared in February 2011 were

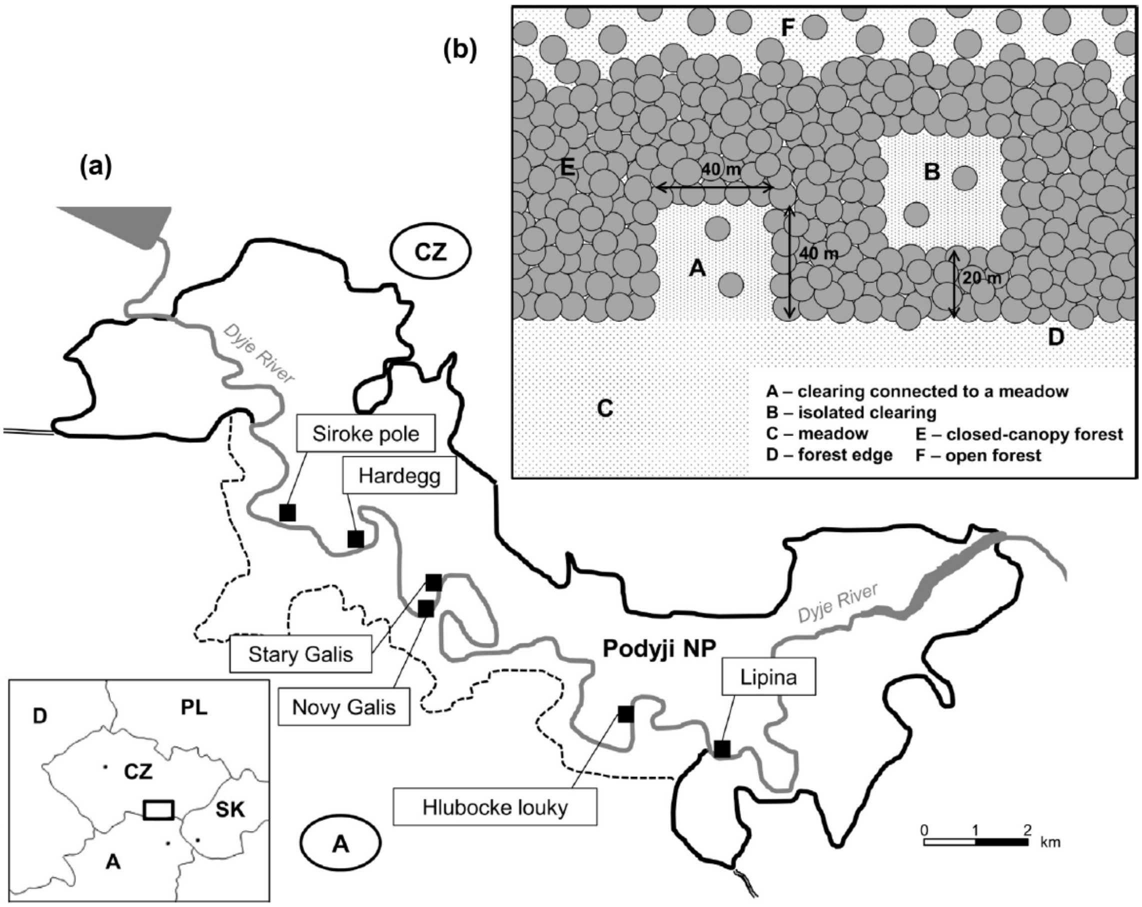

Fig. 1. Study area and design – position of the study sites in Podyji National Park (a). The sites are represented by black squares. The thin dashed line signifies a border of adjoining Thayatal National Park (Austria). A schematic arrangement of the study plots (two types of clearings and four types of reference plots) within each site is displayed in (b). Clearing A was always connected directly to the alluvial meadow C, clearing B was isolated from other open habitats: meadow (C), forest edge (D), open forest (F) and from clearing A by at least 20 m of closed forest (E).

sampled between May and September 2011, while the two sites cleared in February 2012 were sampled between May and September 2012. To cover a wide range of taxa and life strategies, the following groups were sampled: (a) butterflies, (b) moths, (c) epigeic beetles, (d) saproxylic (deadwood dependent) beetles, (e) floricolous beetles, (f) reptiles, (g) birds, and (h) vascular plants.

Day-flying butterflies were recorded by timed records (7 min per each plot), at five times throughout the season (May, June, July, August, September) during suitable weather conditions. Moths were captured using ultra-violet light traps (one trap per plot) on one night each month during the season (May, June, July, August, September). Since the meadow is often a narrow strip between the river and the forest, samples of moths from meadows were omitted to avoid false inclusion of species from neighboring habitats. Epigeic beetles were captured using pitfall traps containing ethylene glycol as a killing agent and preservative. In each plot, five traps were randomly placed and operated from the end of April to the end of July. The traps were emptied every two weeks. Saproxylic beetles were sampled using two window flight interception traps (FITs) in each plot. These traps were placed at 1.5 m above ground level (meadow plots were omitted) and operated from the end of April till the end of July. The samples were collected every two weeks. Floricolous beetles were collected by yellow pan traps filled with salt water (3 traps per each plot) exposed for one day three times in the season (May, June, July). Reptiles were sampled using artificial shelters made from toughened plastic sheets (1 × 1 m). Four such shelters were placed on the ground in each plot and the presence of the reptiles hiding beneath them were recorded each week. Visual observations and bird-song identifications of bird species in each plot were recorded. Because our plot area is smaller than the territories of most birds, all utilizations of the space (including feeding, singing, or nest-building) were recorded. Only those birds that used the plot as an "activity territory" were recorded. Observations were collected over a 30 min period three times during the season (April, June, July; 90 min in total); first 5 min of each observation were not counted to avoid disturbance/attraction effects. Finally, a census of all vascular plants was made in each study plot twice during the year (start of June, start of August). For more information on the species selected for analyses, see Appendix A in Supplementary material.

2.3. Statistical analysis

We focused on the total number of species (species richness), and species composition of sampled habitats.

The differences in species richness among the habitats were analysed separately for each group by generalized linear mixed-effect models with quasi-Poisson distributions, where the habitat represented a fixed effect factor variable, and the site represented a random effect variable (to filter out the effect of site and year of sampling). The models were fitted using the Generalized Estimating Equations algorithm in the *geepack* package (Hojsgaard et al., 2006) in R 2.14.2 (R Development Core Team, 2012), the effect of habitat type being tested by Chi-squared distibution. For all groups $n = 36$ (12 clearings, 24 reference plots), except for moths and saproxylic beetles where $n = 30$ (meadows were not sampled). Post-hoc comparisons among habitat levels were done by setting different treatment contrasts.

Species composition of the habitats was analyzed by multivariate ordination analyses. For each group of organisms, partial Canonical Correspondence Analysis (CCA) was performed based on the abundances of all species in the plots (representing samples); the response data of all groups had a gradient length greater than 1.9 SD units in preliminary DCA analysis. For vascular plants, a presence/absence matrix was used instead of abundance data. The response data were log-transformed and rare species were downweighted. To filter out the effect of site, the site affiliation was used as a covariate. The habitat type represented an explanatory factor variable, differences in species composition were tested by Monte Carlo tests with 999 permutations. The ordination analyses were performed in Canoco 5 (ter Braak and Šmilauer, 2012). We created ordination diagrams based on the analyses of the whole communities but only the preferences of threatened species are emphasized, i.e. centroids representing the highest abundance of particular species, and hence their optimum, were plotted in ordination diagrams. We considered species with a conservation status (IUCN categories RE, CR, EN, VU and NT) in the national red lists as "threatened" (but see also Appendix A in Supplementary material).

3. Results

We recorded 2003 butterflies from 66 species (15 of them threatened), 10,462 moths from 403 species (53 threatened), 6055 epigeic beetles from 89 species (13 threatened), 2927 saproxylic beetles from 293 species (58 threatened), 1039 floricolous beetles from 62 species (7 threatened), 1296 reptiles from 7 species (4 threatened), 806 birds from 49 species (9 threatened), and 449 species of vascular plants (64 threatened). Mean number of threatened species found in particular habitats is displayed in Table 1.

In all the studied groups, analyses revealed significant differences among habitats in species richness (Fig. 2) and in their species compositions (Table 2).

For butterflies, the meadow was the richest habitat ($\chi^2_{(5)} = 23573439$, $P < 0.001$), and closed forest was the poorest. Clearings connected to meadow habitats supported a similar number of species as the forest edge and the open forest, while isolated clearings supported fewer species. The ordination analysis revealed that the species composition of the clearings was most similar to the one of forest edge (Fig. 3A), most threatened species preferring meadow, forest edge and the clearing connected to meadow. No threatened species was associated with the closed forest.

For moths, the highest richness was found in closed forest, then open forest ($\chi^2_{(4)} = 86.1$, $P < 0.001$), and then the clearings connected to a meadow, the forest edge, and lastly the isolated clearings. The forest edge and the clearings connected to meadows had similar species composition, whereas the composition of the isolated clearing tended to resemble the one of closed forests. The open forest harboured distinct species composition from these two groups. The majority of threatened species were, however, associated with the open habitats, mainly the open forest (Fig. 3B), although a few species were associated also with closed forest.

Table 1
Mean number of threatened species in the habitats – mean number of threatened species found in particular habitats (standard deviation, in parentheses).

Habitat	Butterflies	Moths	Epigeic beetles	Saproxylic beetles	Floricolous beetles	Reptiles	Birds	Plants
Clearing connected	2.3 (1.37)	3.8 (2.23)	0.8 (1.17)	5.8 (4.22)	12.8 (5.6)	2 (0.63)	0.3 (0.82)	4.5 (1.97)
Clearing isolated	1.2 (1.17)	2.2 (1.83)	1 (0.89)	4.3 (1.63)	6 (0.89)	1.5 (0.84)	0 (0)	5.5 (2.66)
Forest edge	2 (0.63)	3.2 (2.04)	1.8 (1.33)	4.5 (2.59)	8.2 (2.71)	1.8 (0.41)	0 (0)	2.2 (1.17)
Closed forest	0 (0)	6.3 (4.97)	1.8 (1.17)	4.8 (1.94)	2.7 (1.97)	0.2 (0.41)	0.5 (0.84)	4.8 (2.32)
Open forest	3.5 (0.84)	8.8 (1.47)	0.3 (0.52)	5.8 (3.13)	8.3 (3.08)	3 (0.89)	2.3 (0.82)	13.8 (7.36)
Meadow	3 (1.79)	–	1.5 (1.64)	–	8.7 (2.42)	2.5 (0.55)	0.8 (0.75)	3 (0.89)

For epigeic beetles, the forest edges and meadows had significantly higher species richness than the remaining habitats, with open forest being the poorest ($\chi^2_{(5)} = 118$, $P < 0.001$). The two types of clearings had a similar species composition (Fig. 3C), lying in between of open forest and closed forest with forest edge (at the axis 2). The threatened species associated with wooded habitats generally avoided open forest, but otherwise they mostly did not discriminate among the remaining habitats.

For saproxylic beetles, the greatest species richness was found in the clearings connected to meadows ($\chi^2_{(4)} = 36.74$, $P < 0.001$), followed by the isolated clearings, the open forest and the forest edge, while the closed forest was the least species-rich habitat. The ordination analysis showed three clusters representing differences in compositions, first, the clearings, second, the closed forest and forest edge, third, the open forest. Numerous threatened species were associated with the clearings, the open forest, the closed forest and the forest edge, although many threatened species exploited several, mostly open-canopy habitats (Fig. 3D).

For floricolous beetles, the richness was greatest in the clearing connected to meadow, and lowest in the closed forest; the isolated clearing was less rich than the connected one, and also less rich than the open forest or the edge ($\chi^2_{(5)} = 140.6$, $P < 0.001$). The meadow had different species composition from the other habitats. Regarding the woody habitats, the two types of clearings had a similar species composition which was different from the edge, closed and open forest. Threatened species were approximately evenly distributed among the open habitats, avoiding the closed forest (Fig. 4E).

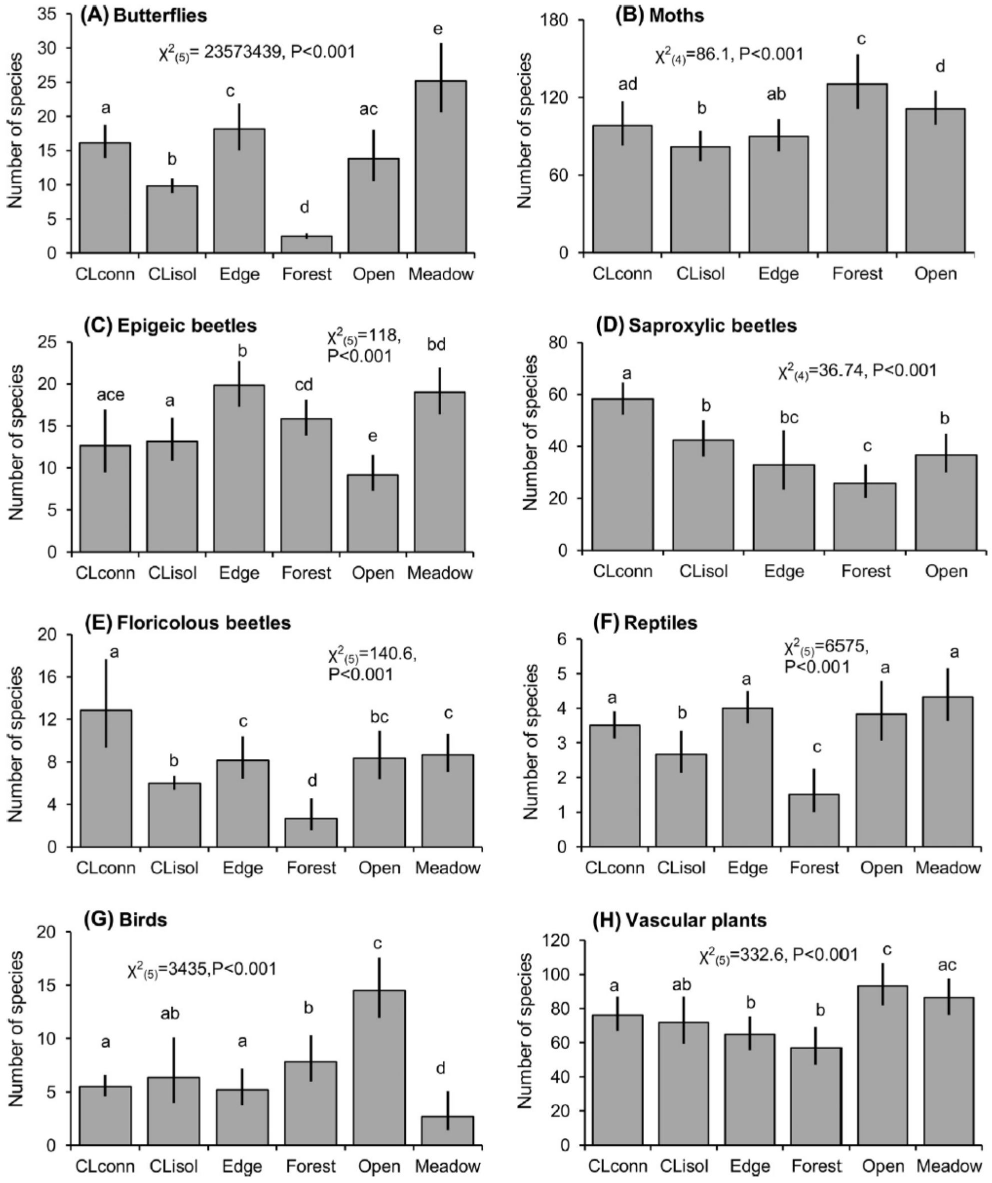

Fig. 2. Species richness – estimated mean (±95% CI) number of species in each habitat type. Estimates were generated by a generalized linear mixed-effect model with a quasi-Poisson distribution, with site as a random factor. The effect of habitat was tested by χ^2 test. Differences between habitat levels are displayed by different letters above the bars. For all groups $n = 36$, except for moths and saproxylic beetles where $n = 30$.

Table 2
Variation explained by partial CCA axes – the effect of the habitats on community composition was tested by partial CCA for each group of organisms. Numbers in the table show the percentage of residual variation (after the effect of site being filtered out) explained by first and second constrained axes (displayed in Figs. 3 and 4). Pseudo-*F* statistics and *P* level were obtained by Monte Carlo tests with 999 permutations.

Group	CCA axis	Explained variation (%)	Pseudo-*F*	*P*
Butterflies	1st	15.45	4.6	0.001
	2nd	13.08	4.6	0.001
Moths	1st	12.49	2.9	0.001
	2nd	6.71	1.7	0.001
Epigeic beetles	1st	23.28	7.6	0.001
	2nd	7.57	2.7	0.002
Saproxylic beetles	1st	9.56	2.1	0.001
	2nd	7.45	1.8	0.001
Floricolous beetles	1st	8.26	2.2	0.003
	2nd	7.01	2.1	0.008
Reptiles	1st	32.29	11.9	0.001
	2nd	18.16	9.2	0.001
Birds	1st	19.49	5.8	0.001
	2nd	5.78	1.9	ns
Plants	1st	20.13	6.3	0.001
	2nd	12.48	4.6	0.001

For reptiles, the closed forest was the poorest habitat in species richness, followed by isolated clearings ($\chi^2_{(5)} = 6575$, $P < 0.001$). The closed forest, the open forest and meadows differed significantly in species composition. The open forest, the edge, and the clearings had a similar species composition, different from the meadow and the closed forest. All the threatened species were associated with open habitats, mainly clearings and open forest (Fig. 4F).

For birds, the highest species richness was found in the open forest, and the lowest number of species were recorded in the meadow ($\chi^2_{(5)} = 5330$, $P < 0.001$). There was a difference in composition between meadow and woody habitats, the woody habitats did not differ in the composition (see Table 2). The clearings and the closed forest shared a similar species composition, while the other habitats differed significantly from them and from each other. The majority of threatened species were associated with open wooded habitats, especially the open forest (Fig. 4G).

For vascular plants, the highest species richness was found in the open forest, followed by the meadow. Among the other habitats, species richness decreased from the clearings to the forest edge, and was lowest in the closed forest ($\chi^2_{(5)} = 332.6$, $P < 0.001$). Communities in the meadow and the open forest differed from each other, the closed forest shared a similar composition with clearings. The great majority of threatened species were associated with open forest (Fig. 4H).

Among the six groups for which samples from meadow habitats were included in analyses, there were two partly contrasting responses. Butterflies and reptiles responded mainly to an insolation gradient between fully shaded (closed forest) and sunlit habitats. The epigeic and floricolous beetles, birds and plants, on the other hand were most affected by the gradient between non-wooded (meadow) and wooded habitats, rather than by the insolation gradient within wooded habitats. Of the two groups sampled in the wooded habitats only, moths and saproxylic beetles, the insolation gradient was always a secondary factor, as the first axis differentiated between clearings and other habitats in saproxylic beetles and between open forest and the remaining habitats for moths (Table 2, Fig. 3).

4. Discussion

This is one of the first studies (see also Götmark, 2013; Rancka et al., 2015) to investigate the effect of active interventions in temperate closed-canopy forest that used a large number of model groups with different life histories. The design of the study also allowed for an assessment of the importance of connectivity of open wooded habitats. Other studies show that interventions to closed-canopy forests, like partial cutting, may have positive effect on some groups of organisms (e.g. butterflies, moths, saproxylic beetles) (Bolz, 2008; Fartmann et al., 2013; Götmark, 2013) but also negative effects on another groups (e.g. fungi, molluscs) (Nordén et al., 2008; Rancka et al., 2015).

The clearings had higher richness of butterflies, saproxylic beetles, floricolous beetles, reptiles and vascular plants than the closed forest. By contrast, the richness of moths and epigeic beetles was lower, while the diversity of birds did not differ. The clearings were rarely colonized by meadow species. Instead, they were inhabited mainly by edge and/or open woodland species of butterflies, moths, and reptiles. Among birds and vascular plants, and also for some moths, most species found in clearings were also associated with closed forest habitat. For saproxylic and floricolous beetles, the clearings created new habitat inhabited by highly diverse communities distinct from the other sampled habitats. The isolated clearings were generally poorer in species richness than those connected to open habitats, although the composition of the respective communities was similar.

4.1. Diversity in closed forest

To asses the impact of intervention in the national park's core zone, it is necessary to carefully weigh the subsequent negative and positive effects on biodiversity by comparing the biota of clearings to the previous state of the habitat, i.e. closed forest. Such an assessment must consider not only overall species richness in the two habitats, but also the requirements of threatened species.

With the exception of reptiles, butterflies and floricolous beetles, all the sampled groups contained at least some threatened species with an affinity for closed forest. No genuine closed-forest specialists were detected among the threatened species of moths. Indeed, only the elm-feeding *Cosmia affinis* (Noctuidae) is able to live within closed forest, but it is not restricted to this habitat. Of the few threatened epigeic beetle species, three exhibited some affinity to the closed forest, but all were abundant also in other habitats. All five species of threatened saproxylic beetles that were at least partly associated with closed forest were xylomycetophages. They may thus prefer more humid conditions, which promote the growth of their host fungi (Hulcr et al., 2008). Of the four threatened plant species associated with closed forests, only *Cyclamen purpurascens* (Primulaceae) and *Neottia nidus-avis* (Orchidaceae) are typically found in closed-canopy habitats. The remaining species are generally considered open woodland species (Štěpánková, 2010) and might be relicts of the past state of the habitat.

Although the species richness of groups such as moths and epigeic beetles was highest in the closed forest, in comparison to more open wooded habitats, closed forest supported impoverished communities of most other studied taxa. Further, it supported very few threatened species. This indicates that the conservation value of the closed forests left for succession within our study system is rather limited at present. Since absence of disturbances leads to gradual replacement of light demanding oak by shade tolerant trees (Hédl et al., 2010; Kopecký et al., 2013), and since the diversity of organisms associated with oaks is substantially higher than that associated with its most common shade-tolerant successors (e.g. ash, maple, hornbeam) (Southwood, 1961), it is likely that conservation value of the closed forest will decrease even further in the future.

4.2. The effects of artificial canopy opening

The groups that responded positively to the intervention were generally thermophilous, and thus prefer more open, sunny habi-

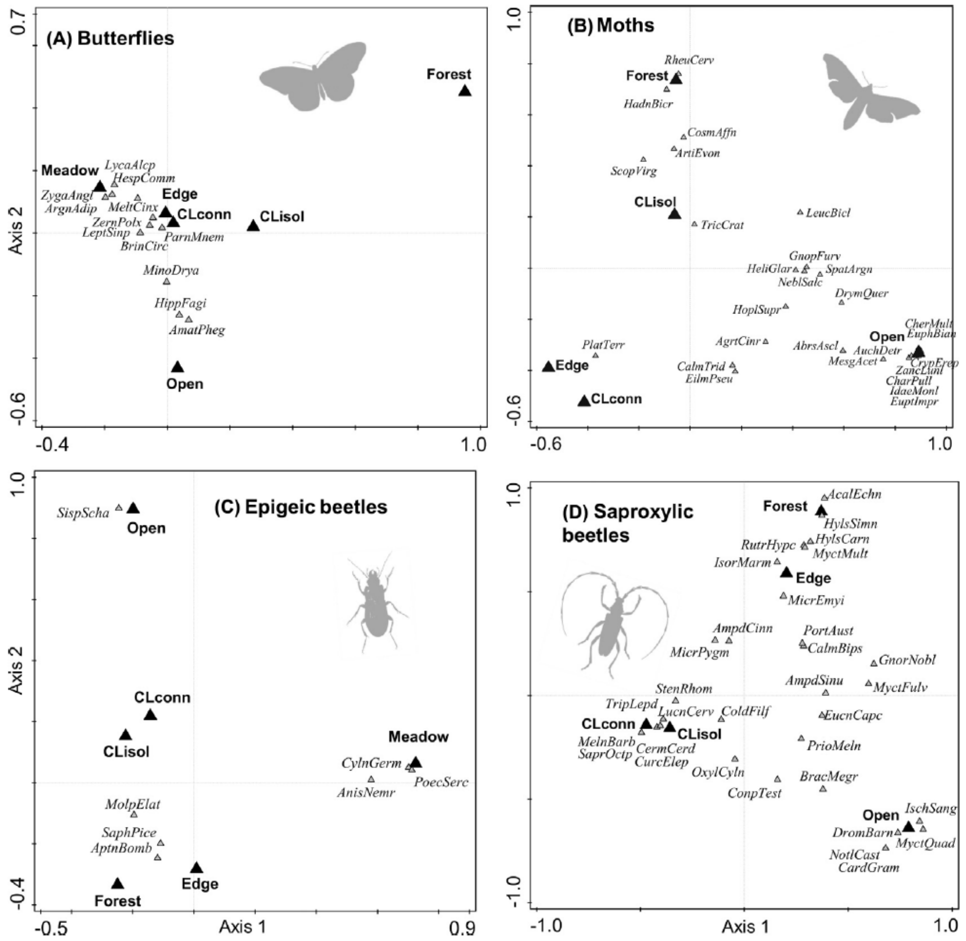

Fig. 3. Species composition and threatened species preferences. Ordination diagrams displaying differences in species composition among habitats, and preferences of threatened species for four groups of insects. The first two axes of the partial Canonical Correspondence Analysis are displayed. Habitats are depicted by full black triangles. The analyses are based on full sets of species, but only best fitting threatened species are depicted (by small grey triangles and abbreviations; for full names, see Appendix A in Supplementary material). See also Table 2 for variation explained by ordination axes.

tats (Benes et al., 2006; Decocq et al., 2004; Fartmann et al., 2013; Hédl et al., 2010; Horak et al., 2014; Kopecký et al., 2013; Ramírez-Hernández et al., 2014; Vodka and Cizek, 2013).

Although bird assemblages are generally richer in gaps than in closed forest, the differences are often small and depend much on the habitat requirements of the species involved (Fuller, 2000). Our clearings were probably too small to be recognized as a distinct habitat by birds. Further, many open-woodland birds, such as the European roller *Coracias garrulus* or the hoopoe *Upopa epops*, are either locally extinct or very rare in the Czech Republic (Šťastný et al., 2009).

The clearings had poorer communities of moth and epigeic beetles than the closed forest. Unlike butterflies, a number of moth species are associated with closed forests. Interestingly, Bolz (2008) found richer moth communities in four year old coppices than in mature forests. The clearings therefore may have been too young for many moth species in this study. The activity of most epigeic beetles increases with humidity (Thiele, 1977). The drier conditions of the clearings and the open forest plots are thus likely to be at least partially responsible for the observed pattern of low species richness of these beetles in these habitats.

Most of our model groups contained threatened species associated with clearings. They were especially numerous among saproxylic beetles, most likely because the clearings contained insolated dead wood in the form of post-logging residues and stumps. Five endangered species that are a focus for conservation efforts in the national park, the clouded apollo *Parnassius mnemosyne*, the great capricorn beetle *Cerambyx cerdo*, the stag beetle *Lucanus cervus*, the European green lizard *Lacerta viridis*, and the Aesculapian snake *Zamenis longissimus*, exhibited clear associations with the clearings (Figs. 3 and 4). All of these species prefer open biotopes such as forest steppes (Buse et al., 2007; Luoto et al., 2001; Mikatova and Vlasin, 2012).

In comparison to the closed forest, the creation of clearings created habitats preferred or even required by numerous threatened species. This result is particularly important as the study occurred in the first season following clearing. It remains to be seen what the longer-term effects of open forest conversion will have on the diversity of native species, and threatened species in particular. Also, study of additional taxa, like molluscs (Rancka et al., 2015), fungi (Nordén et al., 2008) or cryptogams, would be beneficial to allow for wider generalization of the effect of canopy-opening in lowland forests.

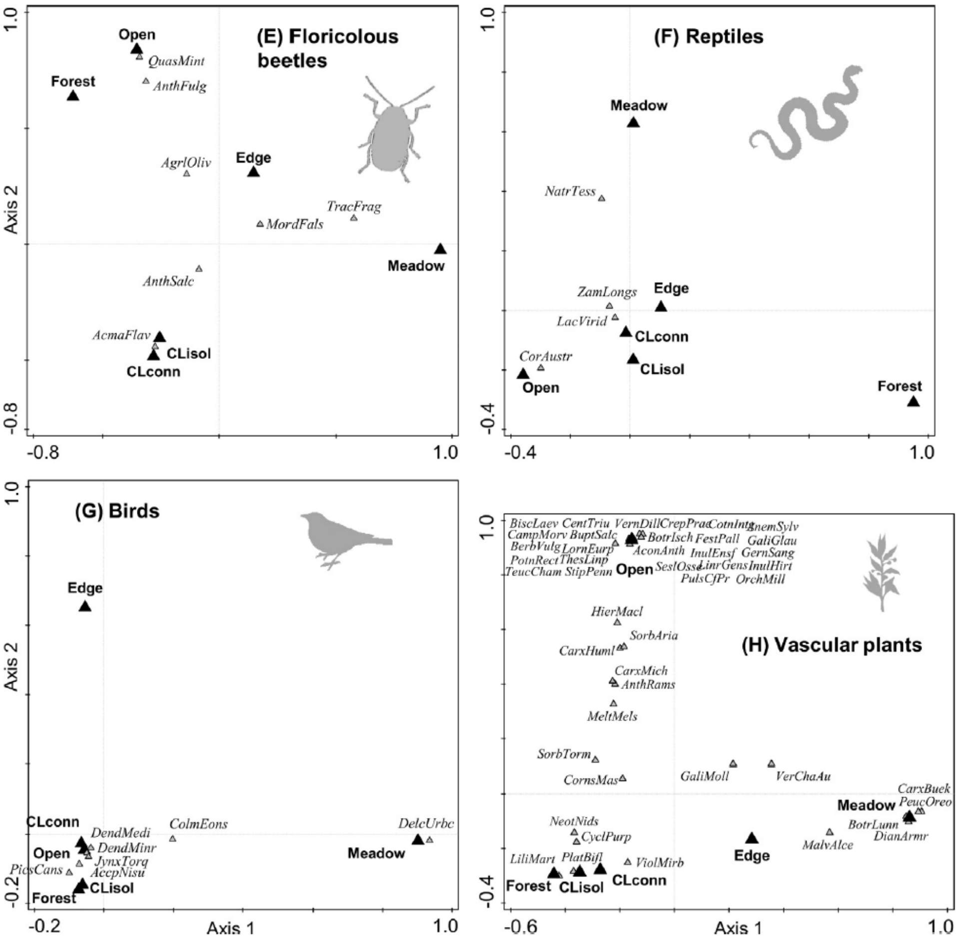

Fig. 4. Species composition and threatened species preferences *(continued)*. Ordination diagrams displaying differences in species composition among habitats, and preferences of threatened species for four groups of organisms. The first two axes of the partial Canonical Correspondence Analysis are displayed. Habitats are depicted by full black triangles. The analyses are based on full sets of species, but only best fitting threatened species are depicted (by small grey triangles and abbreviations; for full names, see Appendix A in Supplementary material). See also Table 2 for variation explained by ordination axes.

4.3. The importance of open forests

The open forest hosted distinct communities (being often on extremes of first or second ordination axes) in most groups. The communities often included a large number of threatened species. Furthermore, for six out of the eight studied groups the open forest supported greater number of species than the closed forest. The open forest is thus a key habitat in the study system. It is also a crucial habitat for biodiversity conservation in Europe. It is, however, also highly threatened. The extent of open forest continues to decrease locally (Miklín and Čížek, 2014; Szabó, 2010), as well as across the continent (Kirby and Watkins, 1998). Substantial effort hence should be put into restoration of open forest habitats in Europe.

At this stage, it is difficult to asses if and when the clearing will resemble open forests. The clearings represent new habitats, and are hardly comparable with old open forest plots that have a well developed herb layer. However, although the species composition of the clearings differed from those in open forests, they were also distinct from those in closed forest, often occupying a transitionary state similar to the forest edge between open and closed forest (Figs. 3 and 4). Longer-term observations are needed to ascertain whether species composition in clearings will gradually move towards the open forest or return to the closed forest in the course of succession.

4.4. Succession and colonization processes

While our results come from the first season after clearing, the species composition of our model taxa is likely to change in the following years depending on their colonisation abilities and the changing availability of resources during succession.

Richness of slow colonizers, such as plants, is likely to increase over time. Plant species richness tends to peak in the second or third year after coppicing (Mason and MacDonald, 2002). In our study, the plant composition of the clearings was very similar to the original composition of the closed forest, but they are likely to diverge as shade-tolerant forest herbs are replaced with light-demanding taxa typical of the early stages of secondary succession (Prach et al., 2014). Vegetation succession is tightly connected with the subsequent turnover of animal assemblages, especially those directly associated with plants such as phytophagous insects

(Warren and Thomas, 1992). The diversity of butterflies and moths in coppices is known to peak 2–5 years after felling (Bolz, 2008; Fartmann et al., 2013). Similarly, for some other butterflies or birds the clearings are not suitable until the shrub-layer develops (Fuller and Henderson, 1992). Conversely, for many early successional specialists that demand open conditions with bare ground (for instance some butterflies, or reptiles), and weak competitors among plants, the clearings may become less suitable after a few years due to increased regrowth and shading. Therefore, it is important to observe the course of succession over a longer period to allow for a more precise quantification of the effect of canopy opening on biodiversity.

Since our clearings were created shortly before the sampling and were not connected to the open forests, they were prone to be colonized mainly by species from adjacent habitats. Indeed, the species composition in the clearings was most similar to the forest edge or closed forest in most groups, indicating that these might serve as the main source of colonizing species. Only for epigeic, floricolous and saproxylic beetles did the clearings have a distinct composition from the other habitats. This is particularly interesting for saproxylic beetles because some threatened species were primarily found in the clearings, perhaps owing to the presence of rare and ephemeral resources such as post-logging wood residues. This also shows that the forest edge, representing an ecotone habitat, cannot serve as a substitute for open-canopy habitats.

Finally, the design of the study allowed us to observe differences in the colonization of two types of clearings. Generally, both types were very similar in terms of species composition. The clearings connected to meadows were however, richer in five of the eight model groups. This illustrates that connectivity in open forest habitat is an important factor affecting colonization by light-demanding species. Therefore, it is important to ensure the connectivity of open habitats within forests in order to facilitate their colonization by plants and animals (Eggers et al., 2010).

5. Conclusions

The present study shows that shortly after intervention, valuable habitats for woodland biodiversity were created in closed-canopy temperate forests. Further research should investigate the importance of such habitats in the longer term. Information on how these communities change throughout secondary succession, or the best policies to maintain the suitability of the habitats for the studied groups (e.g. by repeated cutting after several years) are needed for robust conservation recommendations.

To help slow biodiversity loss, active conservation management strategies should be applied to protected temperate forests. Increasing forest canopy closure in historically open woodlands is often perceived as beneficial for the long-term observation of “natural processes”, despite that the minimal intervention approach commonly applied to reserves and national parks may have a detrimental effect on richness and diversity of most taxa. Active human intervention in protected forests should not be seen as a threat to forest ecosystems, but as an adequate substitution for traditional silvicultural practices, e.g. coppicing or wood pasturing, and natural disturbances, e.g. fires or grazing by large herbivores, that maintained biodiversity in the past (Bugalho et al., 2011; Hédl et al., 2010; Plieninger et al., 2015; Vera, 2000). The conservation management of woodlands should be aimed at the creation and maintenance of a diversified forest vegetation. As demonstrated by this and other studies, opening up the canopy of closed forests is beneficial for woodland biodiversity as it supports light-demanding biota, including numerous threatened species of insects, animals and vascular plants (Franc and Götmark, 2008; Götmark, 2013). It is also important to ensure connectivity of the newly created open woodland structures with other open habitats to facilitate the colonization process.

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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.2015.09.008.

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Shrnutí

V lesních ekosystémech patří saproxylický hmyz a zvláště brouci vázaní na staré a velké stromy k druhově nejbohatším, často úzce specializovaným a zároveň nejohroženějším skupinám organismů. V historii středoevropské krajiny byly velké stromy a světlé lesy mnohem běžnější než dnes. Jejich vznik umožňovaly přirozené disturbance včetně pastvy divokých zvířat. Postupně bylo narušování lesů a vznik starých stromů nahrazeno vlivem člověka. V posledních letech však došlo k rapidní změně ve způsobech zemědělského a lesnického hospodaření a s ním spojený úbytek starých stromů, světlých lesů a organismů na ně vázaných. Výskyt saproxylických organismů na starých a velkých stromech je, krom dlouhodobé koevoluce, ovlivněn několika faktory, z nichž nejvýznamnější je míra oslunění, velikost stromu, pestrost a kontinuita stanovišť s mrtvým dřevem. V současnosti existuje mnoho studií a manuálů, jak pečovat o druhově bohaté lesy, přesto stále dochází k ochuzování lesní biodiverzity.

Studie předložené v této práci přinášejí nové informace o stanovištní dynamice a habitatových preferencích hmyzu vázaného na staré stromy a světlé nížinné lesy ve střední Evropě. Poznatky z předložených studií umožní lépe aplikovat ochranářská opatření na podporu ohrožených druhů organismů.

V **Kapitole I. a II.** demonstrujeme na příkladu modelového druhu saproxylického brouka tesaříka obrovského klíčovou roli starých, velkých a volně rostlých stromů. Tesařík obrovský je některými autory nazýván ekosystémovým inženýrem – tedy klíčovým druhem, který je svou činností schopen vytvářet nová stanoviště s mrtvým dřevem. Ačkoliv existuje několik studií věnující se habitatovým preferencím tesaříka obrovského, žádná z nich uceleně nepopisuje variabilitu ve využívání starých stromů na různých stanovištích, které brouk může využívat. Obě studie znovu potvrzují, že pro výskyt tesaříka obrovského na stanovišti má zásadní vliv míra oslunění, velikost a zdravotní stav stromu. Ukazuje se však, že brouk je schopen využívat mnohem širší škálu stanovišť a na sušších stanovištích je schopen využívat stromy s daleko menším průměrem kmene. Velikost stromu a stanovištní podmínky, kde tyto stromy rostou, mají zásadní vliv na velikost a dynamiku populací nejen tesaříka obrovského, ale i dalších specializovaných druhů saproxylických brouků. Důležitým poznatkem je, že populace tesaříka obrovského ovlivňuje také vertikální stratifikace, tedy místo na stromě v různých výškách, kde se vyvíjí jeho larvy. Většina populací se totiž vyvíjí spíše ve spodních částech kmenů vhodných stromů. Velké stromy tak hrají klíčovou roli pro populace brouka, protože se na nich může vyvíjet více jedinců. Na větší ploše však mohou být velké stromy po nějakou dobu nahrazeny větším počtem vhodných stromů s menším průměrem kmene a tím mohou zajistit kontinuitu stanovišť na místech, kde velké stromy chybí.

Komplexní pochopení mechanismů, jak fungují jednotlivé populace na rozdílných stanovištích i v rámci jednotlivých stromů, tak umožní aplikovat specifická managementová opatření. Tato opatření jsou vhodná jak pro ochranu tohoto mizejícího druhu brouka, tak i pro další specializované organismy vázané na mrtvé dřevo.

Společným jmenovatelem všech předložených studií je vliv aktivního managementu na biodiverzitu. V **Kapitole III.** blíže popisujeme klíčovou roli ořezu stromů na tvorbu dutin, stanoviště, které využívá celé spektrum specializovaných saproxylických druhů hmyzu. Tvorba dutin je přisuzována spíše starým stromům. Aktivním ořezem stromů tzv. na hlavu však prokazatelně vznikají dutiny rychleji, než u stromů ponechaných přirozeným procesům. Na většině takových míst však došlo k opuštění od tradičních metod hospodaření nebo potlačení přirozených disturbancí. Tímto managementovým zásahem tak můžeme snadno a poměrně rychle vytvořit potřebná stanoviště s mrtvým dřevem, jak v přírodních rezervacích, tak i kolem vodních toků nebo komunikací, prostorově propojující stanoviště s mrtvým dřevem. Snadněji tak docílíme vzniku tohoto vzácného stanoviště v místech, kde v současnosti přirozené disturbance chybí.

V **Kapitole IV.** dokumentujeme na několika skupinách organismů, včetně saproxylických brouků, důležitost aktivních managementových zásahů v lesních stanovištích v Národním parku Podyjí. Území bylo historicky ovlivňováno pastvou dobytka a pařezinovým hospodařením, ale od 50. let 20. století podlehlo přirozené sukcesi a tím zhoustnutí korunového zápoje a dnes je chráněno převážně bezzásahovou formou. Na experimentálně vytvořených plochách, připomínající světlé formy lesa, jsme dokázali, že druhová rozmanitost byla vyšší u většiny studovaných skupin organismů. Až na výjimky jsme u většiny studovaných skupin organismů dokázali, že složení společenstev nelze nahradit pouhým přežíváním v zapojeném lese nebo na jeho okraji. Současně jsme potvrdili důležitost propojenosti lesních stanovišť na nelesní, protože experimentální plochy napojené na kvetoucí louky hostily mnohem více ohrožených druhů organismů, než ty izolované uvnitř hustě zapojeného lesa.

Předložené publikace tak pomáhají pochopit, jak nezbytné je aktivní vytváření pestré škály stanovišť s mrtvým dřevem v různé fázi sukcese zavedením dříve běžných metod hospodaření jako je pařezení, lesní pastva, či pravidelný ořez stromů. Dnešní formy lesnictví a tzv. bezzásahový režim v rezervacích totiž prokazatelně vedou k ochuzování biodiverzity. Staré stromy v takových porostech jsou buď odstraněny anebo usychají. V otevřené krajině naopak dožívají poslední jedinci, aniž by se sázely a formovaly stromy nové. V kontextu současného způsobu hospodaření v lesích a chráněných územích jsou lidské zásahy nahrazující přirozenou disturbanční dynamiku nezbytné, abychom zabránili úbytku biodiverzity vázané na světlé lesy a staré stromy.