Česká zemědělská univerzita v Praze

Fakulta lesnická a dřevařská

Katedra ochrany lesa a entomologie

Vliv antropogenní fragmentace porostů na společenstva bezobratlých v lesních ekosystémech v různých podmínkách prostředí

Disertační práce

Autor: Ing. Strahinja Mladenović

Školitel: doc. Ing. Jakub Horák, Ph.D.

2019

Prohlašuji, že jsem disertační práce na téma **Vliv antropogenní fragmentace porostů na společenstva bezobratlých v lesních ekosystémech v různých podmínkách prostředí** vypracoval samostatně s použitím uvedené literatury a na základě konzultací a doporučení školitele.

Souhlasím se zveřejněním disertační práce dle zákona č. 111/1998 Sb. o vysokých školách v platném znění, a to bez ohledu na výsledek její obhajoby.

V Praze, dne 07. 05. 2019

Podpis autora

Poděkování

Děkuji svému školiteli doc. Jakubu Horákovi za odborné vedení disertační práce, za odborné vedení terénních prací, konzultace k metodice a za pomoc při sestavení disertační práce a trpělivost. Velice děkuji všem spoluautorům odborných publikací především mgr. Tereze Loskotové. Také bych chtěl poděkovat prof. Jaroslavu Holušovi, vedoucímu katedry ochrany lesa a entomologie za trpělivost a podporu.

Dále bych rád poděkoval za pomoc, rady a zázemí dr. Janu Maternovi (KRNAP), za pomoc při terénních práci v Krkonoších a cenné rady a konzultace, a také za vstřícnost.

Ing. Kristýně Braumové děkuji za pomoc při jazykové korektuře a podporu. Svým nejbližším, bratrovi Stefanovi, matce Slađaně a otcovi Radomírovi pak děkuji za velkorysost, trpělivost a podporu.

Disertační práce byla podpořena především projektem CIGA 20154301 - Vliv velikosti izolovaných ostrovů polopřirozených bučin na saproxylické brouky a lesní ptáky.

Abstrakt

Degradace nebo ztráta stanovišť je spojena se zánikem druhů a je považována za dominantní hrozbu pro biodiverzitu. Fragmentace lesa je často způsobena antropogenní činností, zejména rozšiřováním zemědělských ploch, dopravní infrastruktury a měst. Evropské lesy čelí řadě disturbancí, například těžbě dřeva. To je rostoucí hrozbou především pro organismy závislé na dřevě. Na druhou stranu se s rostoucí plochou středoevropských lesů (neboť okrajová zemědělská půda a pastviny jsou často opuštěny) zvýšil počet druhů některých organismů, a to především těch, které jsou přizpůsobeny k životu na stanovištích mladých porostů.

Cíle práce byly následující: (i) Jakým způsobem jsou vybrané vysoce diverzifikované čeledi brouků ovlivněny disturbancemi na úrovni porostu, které reflektují fragmentaci lesů, a také charakteristikou vnitroporostní úrovně, která reflektuje mikroklima a světelné podmínky; (ii) Jaký je vliv původních a nepůvodních dřevin na biotu v hospodářských lesích sledovaného pomocí osmi skupin organismů s různými dispersními schopnostmi, taxonomickou příslušností a ekologickými požadavky; (iii) Jaké jsou nejdůležitější environmentální faktory ovlivňující larvěnku obrovskou na krajinné úrovni; (iv) Jaká je role přírodních horských bukových lesních ostrovů a jejich topografických a vnitřních charakteristik pro distribuci různých skupin organismů.

V nížinných hospodářských lesích vliv disturbance porostů ukázal, že dominance nepůvodních smrků a velké plochy porostů neovlivnily většinu studovaných taxonů tak, jak bylo očekáváno. Dále i druhové složení šesti z osmi studovaných skupin směřovalo spíše k vyššímu podílu smrku ve druhové skladbě dřevin. Rostoucí zastoupení smrku negativně ovlivňoval pouze brouky a ptáky. V horských lesích larvěnka obrovská byla výrazně pozitivně ovlivněna přítomností smrku na úrovni krajiny. Hmyz byl ovlivněn vzrůstající nadmořskou výškou a není tak přímo ohrožován vyvíjejícím scénářem klimatických změn, oproti tomu lišejníky ano. Taxony hmyzu byly ovlivněny především ploškovou strukturou. Smrk negativně ovlivňoval pouze brouky. Pozitivní byl vliv otevřenosti zápoje.

Nejvhodnějším praktickým řešením z pohledu studovaných organismů a budoucí stability porostů by mohlo být například selektivní kácení smrků. Kromě snížení podílu smrku by tato možnost zvýšila otevřenost zápoje a množství mrtvého dřeva. Tento typ managementu by měl být proveden především s ponecháním padlého bukového a dubového mrtvého dřeva. Přirozená mortalita smrku v budoucnu je také jednou z možných opatření, která mohou být využita například u bezzásahových bukových ostrovů. Lesní hospodaření napodobující přirozené disturbance by měly posílit heterogenitu porostu, což by zároveň mělo zvýšit i biologickou rozmanitost.

Klíčová slova: biodiverzita, disturbance, fragmentace, lesní hospodářství, saproxylické organismy, smrk, buk, dub

Abstract

Degradation or loss of habitat is associated with species extinction and is considered a dominant threat to biodiversity. Fragmentation of the forest is often due to anthropogenic activities, in particular by expanding agricultural areas, transport infrastructure and cities. European forests face a number of disturbances, such as tree logging. This is a growing threat especially for wood-dependent organisms. On the other hand, with the growing area of Central European forests (as marginal agricultural land and pastures are often abandoned), the number of species of some organisms, especially those adapted to live on the stands of young stands, has increased.

The objectives of the work were as follows: (i) How selected highly diversified beetle families are affected by tree level disturbances that reflect fragmentation of forests, as well as the characteristics of an intra-level level that reflects the microclimate and light conditions; (ii) What is the impact of native and non-native trees on biota in farm forests monitored through eight groups of organisms with different dispersal capacities, taxonomy and ecological requirements; (iii) What are the most important environmental factors affecting the Giant springtail on the landscape level; (iv) What is the role of natural mountain beech forest islands and their topographic and internal characteristics for the distribution of different groups of organisms.

In lowland commercial forests, the impact of stand disturbance showed that the dominance of non-native spruce and large areas of stands did not affect most of the studied taxa as expected. In addition, the species composition of six of the eight studied groups was rather directed towards higher share of spruce in the species composition of tree species. Growing representation of spruce negatively affected only beetles and birds. In the mountain forests the giant springtail was significantly influenced by the presence of the spruce at the landscape level. Insects have been affected by increasing altitudes and are not so threatened by a developing climate change scenario; on the contrary, lichens are threatened by a developing climate change scenario. Insect taxa were mainly influenced by the patch structure. Spruce was negatively affected only by beetles. The influence of openness of the canopy was positive.

The most suitable practical solution from the point of view of the studied organisms and the future stability of the stands could be, for example, selective cutting of spruce trees. In addition to reducing the share of spruce, this option would increase the openness of the canopy and the amount of deadwood. This type of management should be done primarily with the keeping of fallen beech and oak deadwood in the stand. The natural mortality of the spruce in the future is also one of the possible measures that can be used, for example, in the nocturnal beech islands. Forest management simulating natural disturbance should enhance plant heterogeneity, which should also increase biodiversity.

Key words: biodiversity, disturbance, fragmentation, forest management, saproxylic organisms, spruce, beech, oak

Obsah

1. ÚVOD

Zájem o zachování biologické rozmanitosti (dále v textu jako biodiverzita) vzrostl v posledních desítiletích a zachování biodiverzity se stalo důležitým cílem multifunkčního a trvale udržitelného lesního hospodářství (Druhá ministerská konference o ochraně lesů v Evropě, 1993). Degradace nebo ztráta stanovišť je spojena se zánikem druhů a celosvětově je považována za dominantní hrozbu pro všechny druhy (Sala et al., 2000 Nejen organismy závislé na mrtvém dřevu, ale i lidé soutěží o zdroje dřeva již tisíce let a stále existuje konkurenční boj mezi člověkem a volně žijícími organismy (např. saproxylickými brouky) o dřevo v krajině (Speight, 1989, Grove, 2002a). Fragmentace je způsobena zejména neustálým rozšiřováním zemědělských ploch, dopravní infrastruktury a měst. Může být také dočasné a využitelné v lesních podmínkách, jako je kácení. Mozaikovitost krajiny a její změny jsou důležité, protože ovlivňují stav lesů a poskytují ekosystémové služby, jako je zajištění stanovišť a regulace vlivů disturbance. Zároveň ovlivňují ekologické procesy, např. genový tok, opylení, disperzi divokých zvířat a invazi škůdců různými způsoby (Forest Europe, 2015).

Dlouhá historie lidských vlivů vedla ke změně využívání půdy, která pak vedla ke změnám krajiny, ekosystémů a životního prostředí a pouze 0,2% středoevropských listnatých lesů zůstává v relativně přirozeném stavu. (Perlin, 1988; Hannah et al., 1995). Evropské lesy čelí řadě disturbancí (např. těžba dřeva, fragmentace stanovišť) a rostoucí hrozbě pro saproxylické organismy (převážně produkci palivového dřeva). Zachování saproxylických brouků v rozmanité evropské krajině vyžaduje lepší pochopení požadavků na stanoviště saproxylických biotopů. Specializovaní bezobratlí, kteří jsou závislí na mrtvém dřevu, představují mimořádně druhově bohatou ekologickou skupinu, zároveň ale patří mezi nejrychleji kvantitativně klesající část evropské biodiverzity (Nieto & Alexander, 2010).

Lesy v Evropě jsou především ve věku mezi 20 a 80 let. 12% lesů je mladších než 20 let, 40% je ve věku 20 až 80 let a 18% je starších 80 let. Téměř třetina evropských lesů je nerovnoměrného věku (Forest Europe, 2015). Hospodářské lesy (monokultury) zahrnují většinu lesních ploch v mnoha zemích po celém světě. Například 12% půdního krytu ve Velké Británii tvoří lesy a 68% lesa jsou monokultury (FAO, 2007). Evropské hospodářské lesy, které jsou určeny k produkci dřeva, se často skládají z druhů dřevin, které nejsou specifické pro určitý region (Bauhus et al., 2010). Přírodní lesy (s minimálním antropogenním vlivem) mají zpravidla vyšší druhovou diverzitu a strukturální stabilitu a jsou kvalitnější než hospodářské lesy (monokultury) s ohledem na produkci a ekologické funkce (Sargent and Bass, 2013). V Evropě jsou bukové lesy (*Fagus sylvatica* L.) zvláště důležité pro biologickou rozmanitost. Příloha 1 směrnice o stanovištích (92/43/EHS) obsahuje seznam osmi typů stanovišť charakteristických bukovými lesy, které jsou chráněny. Současná hrozba pro bukové ekosystémy zahrnuje také i klimatické změny (Gessler et al., 2007; Bonan, 2008; Di Filippo et al., 2012). Největší hrozbou je přeměna velkých ploch smíšených listnatých lesů v minulosti (převážně bukových a dubových) na monokultury jehličnatých dřevin (Spiecker et al., 2004). Smrk ztepilý (*Picea abies* L.) není původní dřevina v mnoha oblastech střední Evropy, a současný pokles plochy smrkových monokultur v regionu České republiky je způsoben nevhodnými abiotickými a geografickými podmínkami prostředí (Holuša, 2004). Od 16. století byl smrk ztepilý preferovanou dřevinou na obnovu degradovaných lesních ploch a zalesnění nových lesů ve střední Evropě díky svému vynikajícímu růstovému potenciálu, vysoké kvalitě dřeva a minimálním nárokům v místních podmínkách. Tato vlastnost měla za následek rozšíření stanoviště smrku ztepilého daleko za své přirozené hranice vegetačních stupňů (Spiecker, 2000; von Teuffel et al., 2003).

Jako jeden ze standardních ukazatelů byl historicky používán objem mrtvého dřeva pro biologickou rozmanitost lesních druhů a je stále široce využíván k hodnocení vlivů hospodaření v lesích nebo politiky ochrany prostředí. Poměr objemu mrtvého dřeva a druhového bohatství spojeného s mrtvým dřevem se zdá být nižší v opadavém listnatém lese mírného pásma než ve srovnání s boreálními lesy (Lassauce et al., 2011). Mrtvé dřevo je důležitým substrátem pro velké množství lesních druhů, včetně obratlovců, bezobratlých, řas, mechorostů, cévnatých rostlin, hub a lišejníků. Mrtvé dřevo přispívá ke strukturální stabilitě půdy, např. na svazích a pomáhá při zadržování organických látek, uhlíku, dusíku a vody. Mrtvé dřevo lze považovat za řadu mikrohabitátů, které se postupně vyvíjí v průběhu času zvýšením rozpadu, přičemž každá fáze se rozlišuje na základě druhů závislých na mrtvém dřevě. Množství mrtvého dřeva v přírodních lesích závisí na mnoha faktorech, jako je složení a struktura druhů dřevin, stupeň sukcese, druh a četnost přirozených disturbancí v daném regionu, typ hospodaření a charakteristiky půdy a klimatu (Forest Europe, 2015).

Pohledem různých skupin s vazbou na lesní prostředí lze konstatovat, že například saproxyličtí brouci mají velmi zvláštní požadavky a využívají mrtvé dřevo mnoha způsoby. Jsou mezi prvními organismy, které se objeví na odumřelém lesním porostu, přičemž řada druhů se vyskytuje až do konečných fází rozpadu dřeva (Alexander, 2008). Rozsáhlé změny v krajinné struktuře ovlivňují rozmanitost jak pozitivně, tak i negativně. Otevírání krajiny lidskou činností pravděpodobně vedlo k větší rozmanitosti v prehistorických a historických časech, i když změny v tomto období vedly především ke ztrátám rozmanitosti. Například mnoho druhů přizpůsobených na otevřené spásané lesy zmizelo. Existují však výjimky. Počet druhů ptáků, především těch, které byly přizpůsobeny k životu v zakrslých stanovištích, se dočasně zvýšil, neboť okrajová zemědělská půda a pastviny byly opuštěny a postupovaly směrem k vysokým lesům (Bengtsson et al. 2000). Organismy, jako jsou saproxyličtí brouci a houby, poskytují klíčový vztah v lesním potravinovém řetězci (tzv. ang. forest wood web) a podporují vyšší trofické úrovně, jako jsou malí savci a ptáci spojovaní s mladými i starými lesy (Lehmkuhl et al., 2004). To platí i pro ptačí společenstva, kde Bütler et al. (2004) zjistil jednoznačnou souvislost mezi výskytem datlíka trojprstého a množstvím mrtvého dřeva ve švýcarských a skandinávských smrkových lesích.

Cíle práce

Konkrétní cíle práce byly najít odpovědi na tyto čtyři otázky:

(i) Jakým způsobem jsou vybrané vysoce diverzifikované čeledi brouků ovlivněny disturbancemi na úrovni porostu za využití dvou charakteristik, které reflektují fragmentaci lesů – tj. dominantní druh dřevin (tj. dub vs. smrk) a plocha porostu, také na vnitroporostní úrovni, konkrétně korunovým zápojem;

(ii) Jaký je vliv původních a nepůvodních dřevin na biotu v lesních monokulturách sledovaný pomocí osmi skupin organismů s různými disperzními schopnostmi, taxonomickou příslušností a ekologickými požadavky;

(iii) Jaké jsou nejdůležitější environmentální faktory ovlivňující larvěnku obrovskou na krajinné úrovni, a jak je její populační hustota ovlivněná stromovými faktory na úrovni izolované lokality;

(iv) Jaká je role přírodních horských bukových lesních ostrovů a jejich topografických a vnitřních charakteristik pro distribuci různých skupin organismů.

2. LITERÁRNÍ REŠERŠE

Biologická rozmanitost je popisována jako kruh, který obsahuje geny, jedince, druhy, populace, společenstva, ekosystémy a samozřejmě interakce mezi nimi a neživým prostředím. To jsou velmi důležité faktory k pochopení, jak ekosystémy fungují (Lindenmayer & Franklin 2002; Scherer-Lorenzen et al. 2005). Předvídá se, že v následujících sto letech budou změny ve využívání krajiny (společně s klimatickou změnou) jedny z hlavních problémů úbytku globální biodiverzity. Většina výzkumů týkajících se změn biodiverzity je založena na druhovém bohatství a fungování ekosystémů (Chapin III et al. 2000). Co se týče lesních ekosystémů, tak dle Winter (2012) je hlavním problémem fakt, že degradace lesů nemusí být dostatečně rychle identifikována lesníky. Proto by se ztráta biologické rozmanitosti mohla nepozorovaně zvýšit. Jak uvádí Siitonen (2001), odstranění přibližně 90% mrtvého dřeva z lesů by mohlo vést k poklesu všech saproxylických druhů o 25-50%. V případě, že by byla součástí negativního procesu i fragmentace stanovišť, snížení počtu druhů by mohlo být ještě vyšší.

Takzvaná teorie ostrovů (nebo ostrovní biogeografie), kterou popsali MacArthur & Wilson (1967), říká, že větší plocha ostrova vede k vyššímu druhovému bohatství. Z tohoto pohledu se v lesnické praxi doporučuje ponechat určité plochy pro druhy, které jsou závislé na lesích pralesního typu a vytvořit mozaiku těchto ostrovů včetně menších nášlapných kamenů (Janssen et al. 2009; Horak 2014). Stanoviště o větší rozloze mohou pomoci početnějším populacím v delším časovém horizontu, což vede k nižšímu riziku jejich vyhynutí (MacArthur & Wilson 1967). Stanoviště, která jsou blíže k větší zdrojové populaci, budou pravděpodobně kolonizována v kratším časovém období (Moilanen & Hanski, 1998).

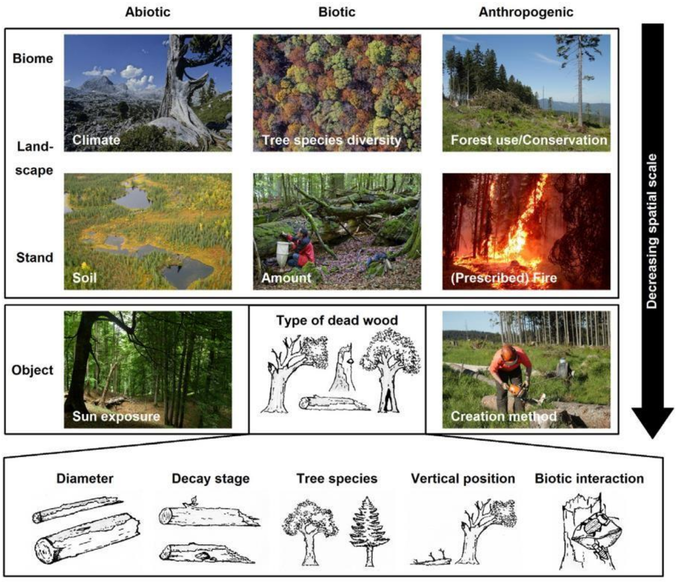
Antropogenní vliv na fragmentaci

Antropogenní disturbance změnily ekosystémy po celém světě, což vedlo ke ztrátě stanovišť a vyhynutí druhů u širokého spektra biomů (Butchart et al., 2010). Antropogenní vliv, jako je těžba palivového dřeva a management ochrany přírody, představují extrémy gradientu intenzity využívání lesa a také hrají důležitou a dominantní roli při ovlivňování množství, rozmanitosti a distribuce hmoty v celé krajině (Gossner et al., 2013). Fragmentace lesů může být definována jako proces, při kterém se kontinuální lesní plošky postupně rozdělují na menší a izolované fragmenty (Lord and Norton, 1990). Fragmentace lesů může být způsobena různými faktory (viz Obrázek 1), včetně přírodních procesů, jako jsou požáry a napadení hmyzem anebo už zmíněnou antropogenní činností, jako je těžba dřeva a výstavba infrastruktury (Linke et al., 2007). Bez antropogenního vlivu přírodní disturbance také silně ovlivňují časovou a prostorovou dynamiku lesů a mrtvého dřeva (Seidl et al., 2014). Lesní ekosystémy jsou jedny z nejcitlivějších habitatů na Zemi a jsou nejčastěji ovlivněny fragmentací. V minulosti byly lesy nejčastěji přeměněny na plochy využívané pro zemědělství, každopádně lesy byly káceny i z důvodu rozšiřovaní měst a budovaní infrastruktury. Dnes je střední Evropa jednou z nejhustěji zalidněných oblastí na světě s největší fragmentací lesů způsobenou člověkem, kde lze pralesy nalézt jen stěží. Biodiverzita je spojována se ztrátou biotopů, fragmentací a nadměrným využíváním způsobující zvýšené obavy mezi správci přírodních zdrojů a ochranáři (Forman, 1995, Wilcove et al., 1998, Spiecker, 2003, Wade a kol., 2003, Parviainen, 2005). Proces fragmentace lesů vznikl v důsledku lidské činnosti, jako je těžba dřeva či přeměna lesů na zemědělské plochy a suburbanizace (Forman 1995). Termín fragmentace měl odkazovat především na ztrátu stanovišť a konfiguraci zbývajícího prostředí po nějaké události, ale fragmentace sama o sobě, tj. rozdělení kontinuálního prostředí do většího počtu menších plošek se může lišit v identických stupních ztráty biotopu (Fahrig, 1997).

Jakákoliv rozsáhlá disturbance korunového zápoje může mít vliv na další vývoj lesa, z tohoto důvodu je důležité rozlišovat aktivity na území lesa či jeho blízkosti, pokud se jedná o antropogenní narušování (např. za účelem vybudovaní infrastruktury), které je pro les mnohem škodlivější pro lesní ekosystémy. Například les, jehož porost je smíšeného věku a který je více či naopak méně otevřený (osvětlený), muže také byt důsledkem dobrého lesního hospodaření, což může způsobit pouze dočasnou změnu v lesní fragmentaci. Snížení počtu a fragmentace lesních porostů vlivem člověka způsobuje mimo jiné i ztrátu biologické rozmanitosti, zvyšuje výskyt invazních rostlin, škůdců a patogenů a dalších environmentálních hazardů. Fragmentace zvyšuje izolaci mezi lesními společenstvy a zvyšuje takzvané okrajové efekty (Knight et al., 2014, Newbold et al., 2015). Okrajový efekt je klíčovým faktorem pro pochopení vlivu krajiny na kvalitu stanovišť (Varasteh Moradi a Zakaria, 2009).

V závislosti na cílech lesního hospodářství a souvisejících intenzitách hospodaření se dynamika přírodních procesů posunula do různých rozměrů, což způsobilo zhoršování půdy, ničení stanovišť, změnu a fragmentaci a posun ve věkové struktuře a složení druhů, což má vliv na biologickou rozmanitost (Rosson and Amundsen, 2004). Urbanizace přináší řadu faktorů a každý z nich může odlišným způsobem ovlivnit různorodost dřevní skladby. Ačkoli lesy představují významnou niku pro mnoho druhů rostlin a živočichů, dopad urbanizace na rozmanitost různých taxonů se může lišit od jeho vlivu na rozmanitost dřevin (Polyakov et al. 2008).

Obrázek 1 - Systematický seznam faktorů ovlivňujících biodiverzitu v mrtvém dřevu a manipulovaný v experimentálních studiích mrtvého dřeva (S. Seibold et al. / Biological Conservation 191 (2015) 139-149)



Fragmentované ostrovy lesa

Principy odvozené z ostrovní biogeografie (MacArthur and Wilson, 1976) byly použity pro řízení velikosti, tvaru, disperze atd. zbývajících lesních plošek, kde nebyla provedena těžba, a o nichž se má předpokládat, že fungují jako rezervy biologické rozmanitosti pro bioty charakterizující předtěžební podmínky v lesním ekosystému. Kapacita rozptýlení, šíře niky a reprodukční potenciál, jsou klíčovými determinanty druhového přetrvávání ve fragmentované krajině (Ewers & Didham, 2006).

Studie z České republiky, Šálek et al. (2013) ukazuje, že okraje hospodářských lesů mají žádoucí atributy starého lesa a zároveň vykazují uspokojivou schopnost přirozené obnovy lesa do budoucna. Neobhospodařované okraje lesů mohou být také důležité pro další funkce lesa, jako jsou úkryty pro lesní organismy, které jsou vylepšeny zelenou oponou oddělující lesy od jiného využití půdy.

Albuquerque & Rueda (2010) zkoumali, že variace lesních druhů je podmíněna především prostorovou konfigurací biotopu. Zejména se jedná o zásadní výsledek pro řízení biologické rozmanitosti, protože opatření by měla být zaměřena hlavně na zachování prostorové struktury lesních patchů.

Saproxylické organismy jako ilustrace problému

Fragmentace lesů je klíčovým aspektem rozsahu a distribuce ekologických systémů. Mnoho lesních druhů je přizpůsobeno buď okrajovým, nebo vnitřním stanovištím. Změny stupně nebo struktury fragmentace mohou ovlivnit kvalitu stanovišť pro většinu druhů savců, plazů, ptáků a obojživelníků nacházejících se v lesních stanovištích (Fahrig, 2003). Pro saproxylické organismy (například brouky nebo houby), je velice důležité mít klíčové složky pro přežití (tj. mrtvé dřevo) jakožto stanovištní ostrovy na jednom místě (Schiegg 2000a). Konkrétně by měly být při péči o lesní ekosystémy v ochranářsky významných územích některé porosty vyčleněny tak, aby jednotlivé stromy mohly dokončit svůj přirozený cyklus – tj. včetně odumření a následného rozkladu. Menší ostrovy starších porostů o velikosti jednotek hektarů je vhodné ponechat samovolnému vývoji tak, aby vytvořily nášlapné kameny mezi většími lesními celky. Také se doporučuje, aby jednotlivé stromy mohly i zde dokončit přirozený cyklus (Kraus & Krumm 2013). Konkrétně je dle Speighta (1989) saproxylický hmyz ohrožen komerčním lesním hospodařením, a to především proto, že tento způsob hospodaření ovlivňuje množství a kvalitu mrtvého dřeva v porostu. Například roháčovití (Lucanidae) jsou považováni jako jeden z vhodných bioindikátorů ukazující kvalitu stanoviště z pohledu množství mrtvého dřeva (Lachat et al. 2012). Roháči jsou navíc závislí na vhodných klimatických podmínkách a indikují i časoprostorovou kontinuitu stanoviště. Například populace roháče obecného (*Lucanus cervus*) obvykle neopustí stanoviště (poloměr cca. 1 km) po dobu více než 30 let. Tento nápadný druh je také velmi závislý na stanovištích, které obsahují prvky typické pro přirozené lesy (Müller et al 2005; Thomaes 2009). Podobná situace, jako se saproxylickými organismy, je s lesními ptačími společenstvy, které patří mezi nejvíce studované skupiny organismů. Přestože řada druhů ptáků bývá specializovaná na konkrétní lesní mikro-stanoviště (např. dutiny), celkové druhové složení je spíše závislé na podobnosti určitých stanovištních charakteristik, a to zpravidla až do úrovně porostu (Müller et al. 2007). Prostorové uspořádání většiny druhů ptáků uvnitř lesních fragmentů bylo vhodně vybaveno modelem, který zahrnoval jak vzdálenost k okraji lesa, tak i velikost fragmentu lesa jako vysvětlující proměnné, na rozdíl od modelů založených pouze na vzdálenosti k okraji lesa nebo velikosti fragmentu lesa. Proto bylo prostorové rozložení společných lesních druhů ptáků často postiženo pouze vzdáleností od okraje lesa, méně často pouze velikostmi lesních fragmentů a nejčastěji oběma těmito faktory (Hofmeister et al., 2017). Vogel et al. (2017) ukazují, že živé plodnice troudnatce pásovaného (*Fomitopsis pinicola*) se objevily již po prvním roce po invazi lýkožroutem smrkovým a byly stejně hojné o 11 a 21 let později. F. pinicola je tedy jeden z prvních druhů hub, který využívá smrk po invazi lýkožrouta a přetrvává po celá desetiletí. Toto zjištění naznačuje, že je troudnatec silným konkurentem v rozkladu smrkového mrtvého dřeva.

V severní Evropě vedla rozsáhlá lesní těžba ke snížení množství a kvality hrubé dřevní hmoty, což vedlo k lokálnímu vyhubení některých saproxylických druhů brouků (Siitonen, 2001). Nejvýznamnějším hmyzím škůdcem v Evropě je doposud lýkožrout smrkový (*Ips typographus*). Ve Střední Evropě poškozuje až 2,9x10^6 m^3 smrku evropského (*Picea abies*) ročně (Schelhaas et al., 2003).

Vztahy s typologií mrtvého dřeva byly pozorovány také u tesaříkovitých (Cerambycidae) a kovaříkovitých (Elateridae), zvláště u pařezů a stojících mrtvých stromů, a proto by měly být upřednostňovány při vývoji alternativních hospodářských plánů a ochranných přístupů ke zvyšování množství mrtvého dřeva a zlepšovaní biodiverzity lesů (Parisi et al., 2016).

Lesní hospodářství

Intenzivní lesní hospodaření dramaticky snižuje množství a rozmanitost dřevní hmoty, která je rozhodující pro koloběh lesních živin a slouží jako základní struktura biodiverzity (Harmon et al., 1986).

Retenční lesnictví (anglicky *retention forestry*) lze definovat jako přístup ke správě lesů založený na dlouhodobé retenci struktur a organismů, jako jsou živé a mrtvé stromy a malé plochy nedotčeného lesa, v době lesní těžby (Lindenmayer et al., 2012). Ve své studii Lee et al. (2015) ukazuje, že po desetileté izolaci dokonce i centra malých lesních plošek úspěšně udržovaly společenství saproxylické brouků, které původně kolonizovaly mrtvé dřevo smrku sivého (*Picea glauca*). Taková společenstva brouků byla ve vytěžených plochách zřetelně nepřítomna. Vliv okrajů však byl zjištěn u patchů menších než 3 ha, což naznačuje, že větší plochy (3-6 ha) jsou dostatečné pro minimalizaci negativních okrajových účinků (Mladenović et al., 2018). Informace o tom, jak jsou saproxylické organismy spojené s mrtvým dřevem v retenčních ploškách, jsou stále poměrně omezené. Rozsáhlá a trvalá selektivní těžba může negativně ovlivnit růstové rysy, ale dopad je potlačován rozsáhlým proudem genů u několika druhů, které byly vystaveny této praxi, jako je smrk ztepilý a borovice lesní (Geburek & Myking, 2018).

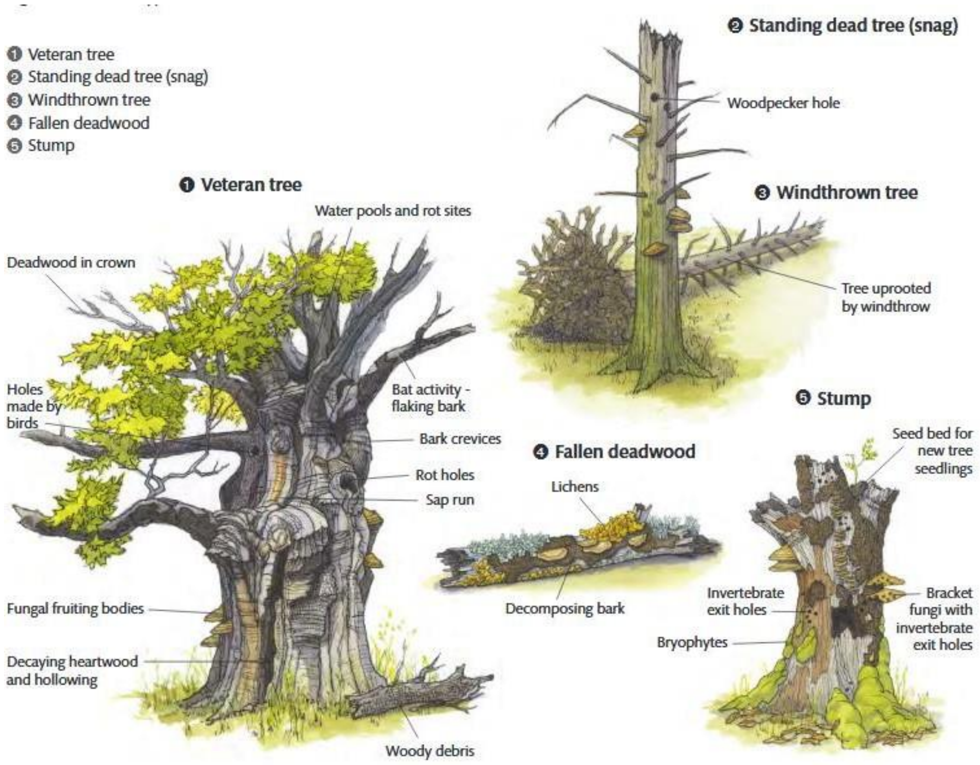
Expanze lesní plochy byla jednou z nejvýraznějších nedávných změn ve využívání půdy a krajiny v mnoha evropských zemích. Výměna dřeva za fosilní paliva jako hlavní zdroje energie a spontánní obnova lesa po ukončení zemědělské činnosti byly spojeny s rozvojem komerčního lesního hospodářství, vývojem legislativy na ochranu lesů a záměrným zalesněním (Mather, 2001). Je politickým záměrem převodu využívání půdy ze zemědělství do lesního hospodářství s cílem zvýšit produkci surového dříví a snížit nadprodukci zemědělských komodit, a některé země používají zalesňování, aby se zabránilo erozi půdy a snížení odtoku vody (Weber, 2005).

Stanovení závislosti starých lesů na saproxylických druzích vyžaduje další studie v celé řadě lesních stanovišť, včetně narušených, těžených a zalesněných travních porostů (Horák et al., 2012).

Poměrně značných zisků pro biologickou rozmanitost lze v krajině dosáhnout zvýšením a udržováním objemu mrtvého dřeva (viz Obrázek 2.) ve všech typech lesů, včetně jehličnatých monokultur (hospodářských lesích). Výhody jsou nejvíce zřejmé u běžných a rozšířených druhů závislých na mrtvém dřevě (důležité pro fungování ekosystému), ale také u některých vzácnějších a specializovanějších druhů. Navzdory tomu, že se zvýšila plocha lesních porostů, u několika druhů saprofytického hmyzu, které byly dříve považovány za druhy s nízkými disperzními schopnosti, bylo zaznamenáno jejich rychlé rozšíření v krajině (Humphrey a Bailey, 2012).

Management mrtvého dřeva má zároveň důležitý význam pro udržitelné lesní hospodaření a podporu biodiverzity, protože mrtvé dřevo je klíčovým prvkem funkce lesních ekosystémů a poskytuje jedinečné strukturální a ekologické vlastnosti, které jsou rozhodující pro přetrvání různých saproxylických druhů (Langor et al., 2008, Grove, 2002b; Della Rocca et al., 2014).

Obrázek 2 - Různé typy mrtvého dřeva nalezeného v lesích (www.forestry.gov.uk)



3. METODIKA

Studované oblasti

Krkonoše

Studovaná oblast o velikosti téměř 454 km^2 se nachází v lesích Krkonošského národního parku. Jedná se o nejstarší a nejznámější národní park v České republice (zal. 1963). Přinejmenším až do středověku byla oblast Krkonoš pokryta listnatými a smíšenými lesy s převahou buku lesního (*Fagus sylvatica*) (Neuhauselova et al. 2001).

Orlické hory

Oblast Bukačka v Orlických horách je velmi starý horský smrko-bukový les. Tento les má více než 50 ha a nachází se přibližně v nadmořské výšce cca 1000 m. Oblast Bukačka je ponechána v bezzásahovém režimu, s výjimkou nahodilé těžby v posledních desetiletích kvůli invazi kůrovců.

Choceňsko-hradecké lesy

Studované lesy zahrnovaly téměř 6500 ha v prostorově souvislé ploše východočeských lesů. V minulosti byla tato oblast pokryta listnatými lesy, v nichž dominuje dub zimní (*Quercus petraea*). Velká část studované plochy byla vysázena před více než dvěma stoletími s rychle rostoucím nepůvodním smrkem ztepilým (*Picea abies*), který je původní pouze ve vyšších polohách střední Evropy.

Studované taxony

Hmyz (Insecta)

Kovaříkovití (Elateridae)

Druhy této čeledi jsou vysoce diverzifikovány s ohledem na jejich chování a požadavky na stanoviště. Většina druhů je spojena s lesními porosty (Laibner, 2000). Kovaříkovití jsou z hlediska druhové bohatosti středně bohatou čeledí (Bouchard et al., 2009).

Tesaříkovití (Cerembycidae)

Druhy této čeledi mají střední až vysoké druhové bohatství (Bouchard et al., 2009), a většina druhů mírného pásma je spojovaná s lýkem a dřevem dřevnatých rostlin (Sláma, 1998).

Drabčíkovití (Staphylinidae)

Drabčíkovití jsou čeledí druhově velmi bohatou (Bouchard et al., 2009). Většina druhů této čeledi je považována za predátory-generalisty nebo se živí rozkládajícím materiálem (Boháč & Matějíček, 2003).

Blanokřídlí (Hymenoptera)

Blanokřídlí byly studováni jako taxony bezobratlých s relativně dobrými schopnostmi disperze a jsou také známi tím, že vykazují dobrou reakci na změny biotopů. Tato čeleď je jedním z nejvíce druhově bohatých taxonů na světě. Aculeata Hymenoptera byla vzorkována během vegetačního období v roce 2011.

Chvostoskoci (Collembola)

Larvěnka obrovská (*Tetrodontophora bielanensi*)

Larvěnka obrovská obývá převážně v hrabance společně s vyššími vrstvami půdy. Uvedený druh je poměrně známý svou chemickou obranou (Dettner et al., 1996). Tento slepý členovec obvykle stoupá na stromových kmenech při hledání potravy, ale pouze tehdy, když je dostatečná vlhkost. Rovněž preferuje nižší teplotu, ideálně mezi 8-11ºC. To je hlavní důvod, proč je jeho přirozeným stanovištěm hlavně pohoří. Žije také v nížinách, ale pouze v těsné blízkosti vodních toků, kde je voda přiváděna z horních oblastí a kde lze v údolích nalézt vhodné životní podmínky (Materna, 2006).

Ptáci (Aves)

Ptáci jsou ve vědecké literatuře široce využíváni jako ukazatele biologické rozmanitosti kvůli své obecné citlivosti na změny životního prostředí, ale všeobecně je málo známo o rozdílech v biologické rozmanitosti ptáků v hospodářských lesích ve srovnání s přírodními lesy (Stephens and Wagner, 2007). Ptáci spojení s jehličnatými lesy jsou i generalisté a specialisté; a tudíž mohou těžit z jiných typů lesa, jako jsou například přírodní listnaté lesy (Aronson et al., 2014). Druhy lesních dřevin a jejich složení jsou významné faktory, které ovlivňují výběr stanoviště ptáky. Ptáci byli vzorkováni jako taxony, které mají obecně relativně dobré schopnosti rozptýlení. Údaje o ptácích byly shromážděny na jaře v roce 2014.

Houby (Fungi)

Saproxylické houby jsou úzce spojeny s mrtvým dřevem a mohou být citlivé na těžbu dřeva. kloboukaté mykorrhizní houby jsou poměrně dobře známé a jsou většinou symbiotické s lesními dřevinami, což je předurčuje k závislosti na lese. Vzácné druhy hub byly nacházeny v blízkosti stromů s větším průměrem, zatímco často se vyskytující druhy měly obecně málo nebo žádnou spojitost s určitými průměry (Kruys et al., 1999, Lindhe et al., 2004). Všechny skupiny hub byly vzorkovány během podzimu v roce 2014.

Lišejniky (Lichen)

Předmětem studie byly také lišejníky, jejichž vzorkování probíhalo v průběhu podzimu 2014. Většina druhů lišejníků je závislá na veteránských stromech (Uliczka & Angelstam, 1999), které jsou důležitým prvkem biologicky rozmanitých lesů (Horák, 2017). Je známo, že je druhové bohatství lišejníků vyšší v případě větší heterogenity lesní krajiny (Horák et al., 2014). Možnosti disperze lišejníků jsou velmi omezené. Jedinou šancí na jejich přežití se zdají být posuny v ekologických požadavcích jednotlivých druhů, které nejsou až tak běžné, ale byly pozorovány u druhů blížících se vyhynutí (Horák, 2016).

Ostatní organismy

Vzorkovány byly dvě skupiny cévnatých rostlin. První z nich se skládala z bylin a keřů. Hlavním důvodem vzorkování těchto organismů bylo, že lesy měly poměrně málo keřů většího vzrůstu a že mnoho z těchto keřů jsou spíše polokeře, jako je brusnice borůvka (*Vaccinium myrtillus*), která má podobné požadavky jako celoroční rostliny. Byliny a keře patří mezi taxony se střední rozptýleností. Druhá skupina rostlin sestávala ze stromových sazenic produkovaných prostřednictvím přirozené regenerace. Semena většiny lesních stromů mají poměrně vysoké rozptýlení. Hlavním důvodem pro studium sazenic byl ten, že distribuce sazenic ve starších porostech jen nepatrně ovlivněna lidským disturbancemi a protože sazenice přesně odrážejí vliv dubu a smrku na budoucí druhovou skladbu porostů. Rostliny byly shromažďovány na létě a podzimu v roce 2014.

Jednotlivé proměnné

Byly testovány proměnné na charakteristické bázi porostu, které reflektují antropogenní disturbanci a fragmentaci – vliv dominantních druhů dřevin, celková plocha porostu v hektarech a proměnná na bázi plošky (patch) a reflektovala disturbanci zápoje a mikroklimatu.

Dále byly testovány hierarchické prostorové úrovně prostředí: topografie byla popsána výškovým gradientem; struktura plošek byla popsána otevřeností zápoje, množstvím mrtvého dřeva a pokrytým smrku ztepilého (*Picea abies*); a úroveň stromu byla popsána podle druhů vzorkovaného stromu a jeho průměru.

Množství mrtvého dřeva bylo měřeno jako odraz přirozených disturbancí a udržitelného rozvoje lesů. Otevírání zápoje bylo měřeno jako odraz gradientu disturbancí, které ovlivňují mikroklima nezávisle na nadmořské výšce.

Proměnné, jako je celkový počet druhů a exkluzivních druhů, byly analyzovány s ohledem na dominantní druhy dřevin (smrk vs. dub). Druhová kompozice a individuální odezvy druhů byly analyzovány jako matrice přítomnosti / nepřítomnosti, která dala lepší konečné srovnání mezi různými taxony. Pečlivě byly vybrány čtyři prediktory, které podle nejlepších znalostí popsaly environmentální podmínky lesních porostů: vliv smrku na druhové složení porostu, pařezy mladší než 5 let v poloměru 40 m, otevřenost zápoje, okrajový efekt a efekt odlesněné půdy.

4. VÝSLEDKY

Základem výsledků předkládané disertační práce jsou 4 články (3 publikované a 1 manuskript). Články jsou přiloženy jednotlivě v této kapitole a zabývají se antropogenním vlivem na fragmentaci krajiny a hlavně lesních ekosystému a hospodářských lesích.

Publikováno - *Bulletin of Entomological Research* (IF: 1.721):

Mladenović, S., Loskotová, T., Boháč, J., Pavlíček, J., Brestovanský, J., & Horák, J. (2018). The effects of within stand disturbance in plantation forests indicate complex and contrasting responses among and within beetle families. *Bulletin of Entomological Research,* **108 (6)**, 750-764.

Online: doi:10.1017/S0007485317001304.

Publikováno - *Forest Ecology and Management* (IF: 3.169):

Horak, J., Kout, J., Halda, J., Zasadil, P., Bogusch, P., **Mladenović, S.,** & Loskotová, T. (2019). Green desert?: Biodiversity patterns in forest plantations. *Forest Ecology and Management* **433**, 343–348.

Online: doi.org/10.1016/j.foreco.2018.11.019

Publikováno - *Scientific Reports* (IF: 4.122):

Horák, J., Materna, J., Halda, J.P., **Mladenović, S.**, Bogusch, P., Pech, P. (2019). Biodiversity in remnants of natural mountain forests under the conservation-oriented management. *Scientific Reports* **9**, 89.

Online: doi:10.1038/s41598-018-35448-7

Manuskript před odesláním do časopisu - *Insect Conservation and Diversity* (IF: 2.091):

Mladenović, S., Materna, J., Loskotova, T., & Horak, J. What are the most important factors influencing the Giant Springtail? The effect of tree level characteristics could differ at different spatial scales.

Efekty narušení porostů v hospodářských lesích naznačují složité a odlišné reakce mezi a uvnitř čeledí brouků

The effects of within stand disturbance in plantation forests indicate complex and contrasting responses among and within beetle families

Strahinja Mladenović, Tereza Loskotová, Jaroslav Boháč, Josef Pavlíček,
Jiří Brestovanský a Jakub Horák

2018

Bulletin of Entomological Research

Publikováno

Bulletin of Entomological Research, Page 1 of 15
doi:10.1017/S0007485317001304

The effects of within stand disturbance in plantation forests indicate complex and contrasting responses among and within beetle families

S. Mladenović[1], T. Loskotová[1,2], J. Boháč[3], J. Pavlíček[1], J. Brestovanský[1] and J. Horák[1]*

[1]Department of Forest Protection and Entomology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 1176, CZ-165 21 Prague, Czech Republic: [2]Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Květnové náměstí 391, CZ-252 43 Průhonice, Czech Republic: [3]Department of Plant Production and Agroecology, Faculty of Agriculture, University Of South Bohemia, Studentská 13, CZ-37005 České Budějovice, Czech Republic

Abstract

Plantation forests with timber production as the major function are highly fragmented and disturbed regarding the tree species composition and stand area. Their closed canopies also have different microclimatic conditions compared with better studied conservation areas. We studied three beetle families (click, longhorn, and rove beetles) with different ecological demands in lowland plantation forests dominated by Sessile oak and Norway spruce in the Czech Republic. Our main interest was how their species richness, abundance, diversity, body length, rarity, red-list status, species composition and individual species were driven by the main tree species, stand area and canopy openness. We analyzed 3466 individuals from 198 beetle species and the results revealed complex and contrasting responses of the studied beetle families – click beetles mostly preferred sun-exposure and spruce as the dominant tree species, longhorn beetles mainly preferred large stands, whereas rove beetles were mostly influenced by oak as the dominant tree species and increasing area. We also observed that some species had different preferences in plantation forests than is known from the literature. The main conclusions of our results are that the dominance of non-natural spruce plantations and a large stand area (both originating from artificially replanted large clear-cuts) did not affect the majority of the studied taxa as we expected. On the other hand, our results might have been influenced by other factor, such as the current small total area of the former vegetation, which in the past might have led to extinction debt; or a large area of other conifers in the surroundings that might have promoted conifer-associated fauna.

Keywords: biodiversity, canopy openness, forest ecology, Norway spruce, Sessile oak, stand area

(Accepted 5 December 2017)

---

*Author for correspondence:
Phone: +420 777 83 82 84
E-mail: jakub.sruby@gmail.com

Introduction

European forest plantations, which are intended for timber production, are often composed of tree species that are non-native to a particular site (Bauhus *et al.*, 2010). In Europe, the tree composition generally consists of natural beech and oak stands and large areas are given over to commercial coniferous monocultures, whereas more than three-quarters of the central European forests are managed (Hannah *et al.*, 1995). The usual method of recent forest management is still clear-cutting, when the biomass of a mature forest is completely removed from the stand, followed by replanting of the same stand (Magura *et al.*, 2003). Nevertheless, forest management is mostly restricted by law – e.g. in the Czech Republic, the maximum permitted area that can be clear-cut is 1 ha and the minimum age is 80 years.

Some of the most sensitive taxa to modifications by the management of plantation forests (e.g., changes in canopy openness, tree species alterations, or clear-cutting) are arthropods, of which insects are among the most studied taxonomical groups (Horak, 2013). Beetles belong to one of the four most abundant and species-rich taxa of insects and are an important part of the forest ecosystem food chain. The intensive management of plantation forests can affect the composition of species for some beetle families.

Some authors have discussed the response of particular beetle families in forest ecology and management (Niemelä *et al.*, 1993; Sebek *et al.*, 2012; Horák & Rébl, 2013) and others have also dealt with the foraging and functional ecology of particular families (e.g., ground, rove, or bark beetles) and have demonstrated that particular species of beetle families exist in several different habitats (Lövei & Sunderland, 1996; Bussler *et al.*, 2011; Přikryl *et al.*, 2012). Some studies have investigated different aspects of ecology (e.g., habitats) of particular families or species and have concluded that variations in habitat loss and heterogeneity play a huge role in their sensitivity in terms of distribution and life cycles (Niemelä *et al.*, 1993; Driscoll & Weir, 2005). Furthermore, changes in habitat complexity can shift species richness at certain local sites (Tews *et al.*, 2004). Nevertheless, several management activities that influence beetle diversity are well known – e.g., habitat diversification and an increase in the habitat area, together with improvements in habitat connectivity via the creation of stepping stones and corridors (Kuuluvainen *et al.*, 2002; Horak, 2014).

Functional or conservation traits are still not often used for evaluation of the effect of forest management. Experiments on ecological traits have been performed regarding the invertebrates (e.g., Nota *et al.*, 2013 for springtails, Kunieda *et al.*, 2006 for Hymenopterans and Dipterans). Dupont & Nielsen (2006) suggest that body length is a proxy for body size, which is an important functional trait. Saproxylic beetles are an example of complexity in the food chain and are commonly affected by habitat fragmentation (Horak, 2014), and therefore, are at a high risk of extinction. Conservation traits could be evaluated using more approaches. Red lists serve as a useful mechanism to establish a system for the potential extinction probability of species in different geographical locations (Rodrigues *et al.*, 2006). Seibold *et al.* (2015) tested the red-list status for a phylogenetic signal and for some beetle families (e.g., Elateridae, Tenebrionidae, Melandryidae, and Buprestidae) and almost half of all species were considered to be threatened, whereas, e.g., Nitidulidae, Pselaphidae, and Staphylinidae contained a very low number of threatened species.

The stand and patch structure of plantation forests might be changed from year to year and furthermore, in more extensive and different ways than changes that are caused by natural disturbances (Horak, 2015). We were interested to understand how selected beetle families are driven by stand-level disturbance using two characteristics that reflect forest fragmentation – dominant tree species (i.e., oak vs. spruce) and stand area, and also by one patch-level characteristic that reflects microclimate – canopy light conditions. In this study, we focused on the response of three beetle families: click beetles (Elateridae), as representatives of a highly diversified group in terms of habitat requirements; longhorn beetles (Cerambycidae), as representatives of a group associated with dead wood; and rove beetles (Staphylinidae), as a highly species-rich and abundant group with a low number of specialists.

Methods

Study area

The study area consisted of more than 6000 ha of forest and was situated in the southern half of a spatially continuous area of the eastern Bohemian woodlands (Pardubice Region, Czech Republic). The area was in the past mainly covered by deciduous forests dominated by Sessile oak (*Quercus petraea*) (Neuhauselova & Moravec, 2001). For more than two centuries, most of the area has been planted by conifers (Scots pine, *Pinus sylvestris*) and Norway spruce (*Picea abies*), of which the latter is non-native in the studied area.

Study families and trapping method

We used non-attractive crossed-panel window traps. The height of the center of the trap was 1.3 m. Traps were fixed using two iron sticks and were located in the center of the stand (Loskotová & Horák, 2016). All of the traps were activated at the beginning of March and were deactivated at the end of September 2011. Traps were regularly emptied and cleaned in 2–3 week intervals.

We studied the response of three selected families; firstly, we selected a family of click beetles (Elateridae), which is intermediate in terms of species richness (Bouchard *et al.*, 2009) and its species are highly diversified with respect to their foraging behavior (predators, herbivores, saprophages, etc.), habitat requirements (soil-dwelling, hollow trees, phytophages, etc.), and a majority of species are associated with woodlands (Laibner, 2000). The second family consisted of longhorn beetles (Cerambycidae), which is a family with a medium to high species richness (Bouchard *et al.*, 2009) and the majority of species in temperate zones are associated with bast and wood of woody plants (Sláma, 1998). The third family consisted of rove beetles (Staphylinidae), which is a highly species-rich family (Bouchard *et al.*, 2009) and the majority of its species are generalist predators or feeders of decaying material (Boháč & Matějíček, 2003).

Study environment

We studied the influence of three important forest characteristics on mature stands (i.e., older than 80 years) in plantation forests.

The first variable was a stand-based characteristic that reflects anthropogenic disturbance and fragmentation – namely, the effect of dominant (i.e., main) tree species. This focused on the origin of the tree species, which is a potentially important factor for beetles (e.g., Bertheau *et al.*, 2009). Norway spruce (*P.*

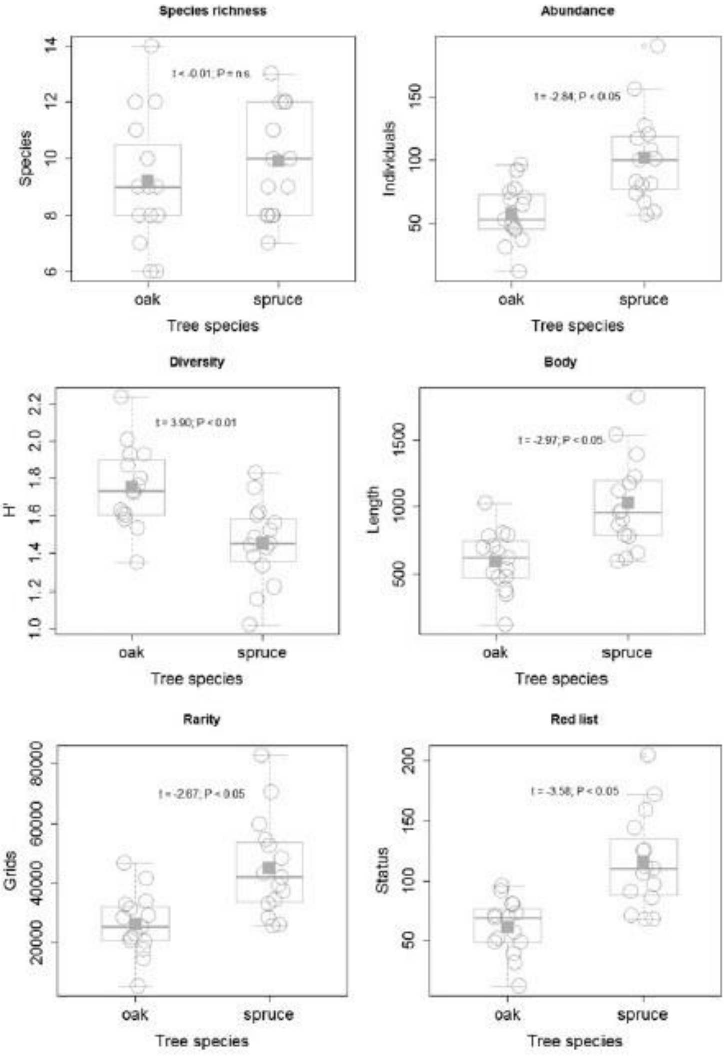


Fig. 1. Results for the comparison of species richness, abundance, Shannon diversity, body length, rarity, and red-list status of click beetles (Elateridae) between stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests – the *t* and *P* values are derived from a linear mixed-effects model (table 1); open circles show the actual values, filled squares represent the means, and thick lines show the median values.

abies), as the non-native tree to our study area (especially its intensive plantations), covered approximately the same area as native sessile oak (*Q. petraea*), which was one reason to choose spruce (instead of the widespread Scots pine) to compare the effect of dominant tree species. An additional reason was that Scots pine was potentially distributed in the study area in the past – even if only as a relict species (Neuhauselova & Moravec, 2001) and thus, it is native to the area. The final reason was that relatively few pine stands were mature in age and most were spatially clumped.

The second variable was again stand-based. Namely, the total area of the stand in hectares (mean = 2.06 ± SE = 0.15;

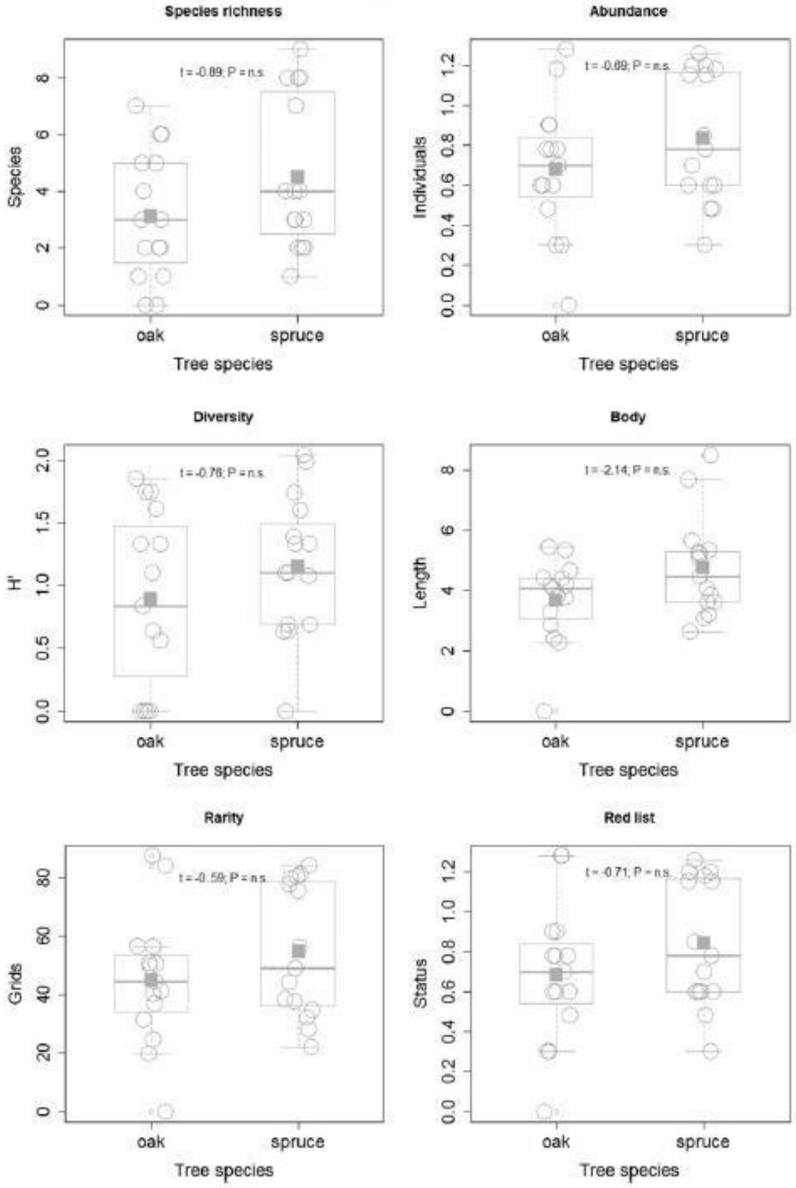


Fig. 2. Results of the comparison of species richness, abundance, Shannon diversity, body length, rarity, and red-list status of longhorn beetles (Cerambycidae) between stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests – *t* and *P* values are derived from a linear mixed-effects model (table 2); open circles show the actual values, filled squares show the means, and thick lines show the medians. Note that the length and grids are root-square-transformed, and individuals and status are log-transformed.

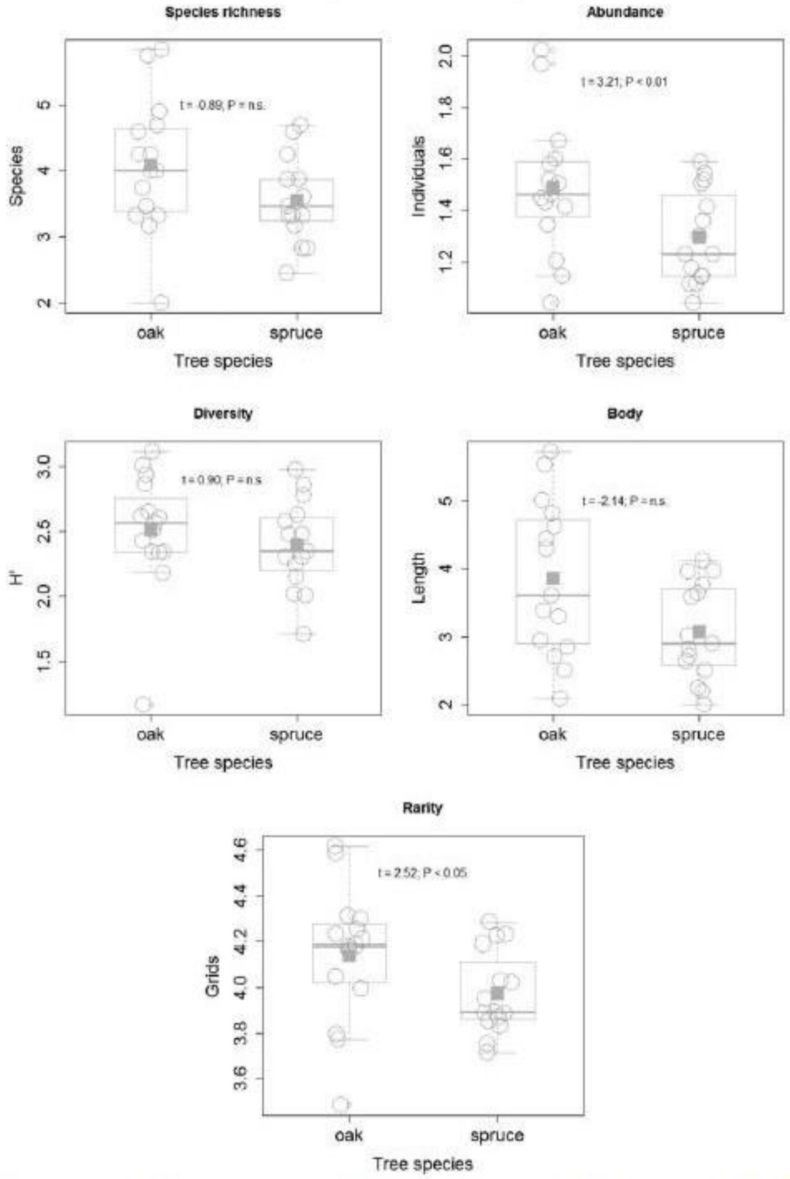


Fig. 3. Results of comparison of species richness, abundance, Shannon diversity, body length, and rarity of rove beetles (Staphylinidae) between stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests – *t* and *P* values are derived from a linear mixed-effects model (table 3); open circles show actual values, filled squares show means, and thick lines show medians. Note that species and length are root-square-transformed, and individuals and grids are log-transformed.

Table 1. Results of linear mixed-effect models on the species richness, abundance, Shannon diversity, body length, rarity, and red-list status of click beetles (Elateridae) in lowland plantation forests; significant variables appear in bold.

Name	Variable	AIC	*t*	*P*
Species richness	Tree (spruce)	133.77	<0.01	n.s.
	Canopy openness		2.31	0.0395
	Area		0.96	n.s.
Abundance	**Tree (spruce)**	271.69	2.84	0.0149
	Canopy openness		2.36	0.0359
	Area		−1.58	n.s.
Diversity	**Tree (spruce)**	18.06	−3.89	0.0021
	Canopy openness		1.08	n.s.
	Area		1.48	n.s.
Body	**Tree (spruce)**	390.95	2.97	0.0116
	Canopy openness		2.03	n.s.
	Area		−1.50	n.s.
Rarity	**Tree (spruce)**	589.22	2.67	0.0203
	Canopy openness		2.45	0.0308
	Area		−1.67	n.s.
Red list	**Tree (spruce)**	276.24	3.58	0.0038
	Canopy openness		1.92	n.s.
	Area		−1.75	n.s.

Table 2. Results of linear mixed-effect models on the species richness, abundance, Shannon diversity, body length, rarity, and red-list status of longhorn beetles (Cerambycidae) in lowland plantation forests; significant variables appear in bold.

Name	Variable	AIC	*t*	*P*
Species richness	Tree (spruce)	145.51	0.89	n.s.
	Canopy openness		1.37	n.s.
	Area		0.69	n.s.
Abundance	Tree (spruce)	35.68	0.69	n.s.
	Canopy openness		1.71	n.s.
	Area		2.22	0.0462
Diversity	Tree (spruce)	76.09	0.76	n.s.
	Canopy openness		0.67	n.s.
	Area		0.31	n.s.
Body	Tree (spruce)	115.53	2.14	n.s.
	Canopy openness		0.46	n.s.
	Area		2.34	0.0373
Rarity	Tree (spruce)	255.27	0.59	n.s.
	Canopy openness		1.69	n.s.
	Area		2.27	0.0421
Red list	Tree (spruce)	35.58	0.71	n.s.
	Canopy openness		1.70	n.s.
	Area		2.35	0.0369

min = 1.00; max = 3.81 ha). This variable was measured based on actual forest management plans and was confirmed by our observations in the field and by actual aerial photographs. The relationship of area to disparate biological variables is often studied (Horák, 2016), but its use in forest insect ecology is, to the best of our knowledge, relatively limited (Webb *et al.*, 2008).

The final variable was patch-based and reflected the disturbance of canopy and microclimate. Namely, the canopy light conditions of the environment, which is very important for insects (Vodka *et al.*, 2009). Canopy openness was measured as a percentage (9.44 ± 0.36; 6.74–14.46%) during the same weather conditions in the peak of vegetation season (i.e., under the full canopy). We used a Nikon COOLPIX 995 with a Nikon FC-E8 Fish Eye converter. Each photograph of 180° was taken at the top of the trap, 1.55 m above the ground. All photographs were then evaluated using Gap Light Analyzer 2.0.

In these conditions, we found and studied 15 pairs of spruce and oak tree-dominated stands.

Statistical analyses

We used three dependent variables that are traditionally analyzed regarding biodiversity: species richness (the number of species trapped), abundance (the number of individuals trapped), and diversity (the Shannon diversity index). We also used one dependent variable that is used in functional ecology: body length (the mean of maximum and minimum value published in the entomological literature), and two dependent variables that reflected conservation traits, i.e., rarity (the total number of unoccupied grids in the Czech Republic based on Sláma, 1998; Dušánek & Mertlik, 2015 and the personal database of J. Boháč) and the red-list status (the species rank values based on the red-list index using IUCN criteria LC = 1, NT = 2, VU = 3; EN = 4 from Farkač *et al.*, 2005). Some dependent variables were transformed to reach normality (abundance of longhorn and rove beetles, click beetles' red-list value and rove beetles' rarity were log-transformed; rarity and body length of longhorn beetles, species richness of rove beetles, and their body length were square-root transformed).

To compute the relationship between the dependent variables and the variables that reflected the study environment, we used linear mixed-effect models in R (package nlme). Three independent variables we treated as fixed factors. Numbers of pairs of stands (spruce vs. oak, from 1 to 15) were used as a random factor. The species composition and the responses of individual species were analyzed in CANOCO. We used redundancy analyses (RDA) for click beetles (Detrended correspondence analysis length of gradient = 2.697) and canonical correspondence analyses for longhorn (8.460) and rove beetles (4.475). We used 9999 randomizations with pairs of stands as a split-plot design.

Results

In total, 2388 individuals from 31 species of click beetles, 194 individuals of longhorn beetles from 36 species, and 884 individuals from 131 species of rove beetles were trapped during the research in the lowland plantation forests.

The results showed that there was no significant difference in species richness between oak- and spruce-dominated stands (figs 1, 2 and 3), although the number of click beetle species significantly benefited from increasing canopy openness (table 1). The number of individuals of click and rove beetles (figs 1 and 3) was significantly positively influenced by spruce and oak, respectively. The abundance of click beetles, furthermore, was positively influenced by canopy openness (table 1), where longhorn beetles were positively influenced only by the increasing area of the stand (table 2). The diversity of click beetles was significantly higher in oak than in spruce stands (fig. 1) and the diversity of rove beetles was significantly positively influenced by the increasing stand area (table 3). Spruce stands hosted click beetles with a higher body length than oak stands (fig. 1). The body length of longhorn and rove beetles was positively significantly influenced by an increasing stand area (tables 2 and 3). Rare click beetles were significantly more abundant in spruce than in oak stands (fig. 1) and

Table 3. Results of linear mixed-effect models on the species richness, abundance, Shannon diversity, body length, and rarity of rove beetles (Staphylinidae) in lowland plantation forests; significant variables appear in bold.

Name	Variable	AIC	*t*	*P*
Species richness	Tree (spruce)	145.51	0.89	n.s.
	Canopy openness		1.37	n.s.
	Area		0.69	n.s.
Abundance	**Tree (spruce)**	18.85	−3.21	0.0075
	Canopy openness		1.37	n.s.
	Area		−0.13	n.s.
Diversity	Tree (spruce)	46.04	−0.90	n.s.
	Canopy openness		0.15	n.s.
	Area		2.33	0.0380
Body	Tree (spruce)	115.53	2.14	n.s.
	Canopy openness		0.46	n.s.
	Area		2.34	0.0373
Rarity	**Tree (spruce)**	23.09	−2.52	0.0271
	Canopy openness		1.36	n.s.
	Area		0.77	n.s.

were also positively influenced by increasing canopy openness (table 1). Rare rove beetles were more frequent in oak than in spruce stands (fig. 3) and the rarity of longhorn beetles significantly increased with an increase in area (table 2). Spruce stands hosted significantly more red-listed click beetles than oak stands (fig. 1), whereas the red-list index of longhorn beetles was positively influenced by increasing area (table 2). We did not trap red-listed rove beetles.

The analyses of the species composition of click beetles showed that there was significant discrimination between species preferences for oak- and spruce-dominated stands (fig. 4), similar to for longhorn beetles (fig. 5). Analyses of the species composition of rove beetles showed that there was no significant discrimination between species preferences for oak- and spruce-dominated stands ($R^2 = 3.17\%$; $F = 0.92$; $P = \text{n.s.}$). Species composition analyses of click beetles also showed that the species that were associated with spruce stands were more influenced by canopy openness and area than those associated with oak-dominated stands, which is demonstrated by a higher clustering of spruce associates to the second axis in RDA visualization (fig. 4). Species of longhorn beetles showed a higher preference for spruce or oak stands, which is illustrated by more color-pure pies (fig. 5).

Two species (*Agriotes acuminatus* and *Athous haemorrhoidalis*) and four species (*Athous subfuscus*, *A. zebei*, *Ectinus aterrimus*, and *Sericus brunneus*) of click beetles were significantly associated with oak- and spruce-dominated stands, respectively (table 4). Two longhorn beetles (*Prionus coriarius* and *Pyrrhidium sanguineum*) preferred oak stands, whereas one (*Stenocorus meridianus*) preferred spruce stands (table 5). Three rove beetles (*Gabrius breviventer*, *Liogluta granigera*, and *Oxytelus rugosus*) preferred oak stands (table 6). Two click beetles (*A. acuminatus* and *Athous vittatus*) were negatively affected by, and four species (*Ampedus balteatus*, *Ampedus nigrinus*, *A. subfuscus*, and *S. brunneus*) thrived on canopy openness (table 4). Five longhorn beetles significantly responded to canopy openness (table 5). Four longhorn species preferred open stands (*Molorchus minor*, *Paracorymbia maculicornis*, *Rhagium mordax*, and *Stenurella melanura*), whereas *Oplosia cinerea* was more abundant in shaded stands. Three rove beetles (*Atheta fungi*, *L. granigera*, and *O. rugosus*) preferred conditions of low canopy openness (table 6). Three species of click beetles responded to the area of the stand (table 4) – *A. vittatus* and *Melanotus castanipes* preferred an increasing area of mature stands, whereas *Dalopius marginatus* showed the opposite relationship. Only one longhorn beetle responded to the area of the stand (table 5) – *S. melanura* was more abundant in large stands. Four rove beetles (*Amarochara umbrosa*, *Atheta celata*, *Atheta elongatula*, and *Omalium rivulare*) were negatively affected by an increasing stand area (table 6).

Discussion

Our results revealed several different and contrasting responses among three studied beetle families: click beetles responded mainly to the dominant tree species and insolation of stands, whereas longhorn beetles were influenced by the stand extent and rove beetles were most influenced by the dominant tree species and stand area.

We also observed that the responses of individual species within the studied beetle families in plantation forest stands dominated by oak and spruce were in many cases complex and highly diverse and that some species indicated contrasting patterns compared to the literature (e.g., the preference of *S. meridianus* for conifer-dominated stands).

The response of click beetles as a highly diverse family

Click beetles revealed relatively interesting and partly contrasting responses regarding the dominant tree species. Even when their species richness did not show a significant response, the number of individuals, their length, rarity value, and red-list status was higher in spruce plantations than in oak stands. This appears to be a surprising result that might be explained by the positive influence of increasing openness in canopies (Vodka *et al.*, 2009; Horák & Rébl, 2013) in the case of abundance, but not for the other studied variables. From this point of view, it appears that click beetles represent a group that is more adaptable than is mentioned in the literature (Laibner, 2000). On the other hand, one of the factors that potentially influenced our results might be the long-term presence of Scots pine in our study area – even if this fact is questionable (Neuhauselova & Moravec, 2001). The higher adaptability of click beetles to conifer vs broadleaved tree stands rather than to particular tree species might also be relevant. Further explanations might reside in the species composition, i.e., species that were associated with oak stands were more significantly bound to it than species that preferentially occurred in spruce plantations. Another potential explanation might be that the current presence and extent of mature oak stands is below the threshold area and fragmentation caused by isolation that is acceptable for the successful development of populations of oak-associated click beetles (Alexander, 2002). This appears to be well reflected in the fact that only two relatively common species (Loskotová & Horák, 2016) significantly preferred oak stands, whereas four species were associated with spruce plantations. The opposite relationship was observed for diversity and, thus, we concluded that tree species that is not native in the studied area can negatively influence the diversity of the family; however, why the other traits responded differently remains unclear (Loehle, 2003).

The response of *Limonius poneli* that preferred closed oak stands is different to the literature – this species prefers steppes and forest steppes where adults occur on vegetation (Mertlik, 2008). This contrasts with species such as *M. castanipes*, which prefer spruce-dominated stands (Laibner, 2000). This

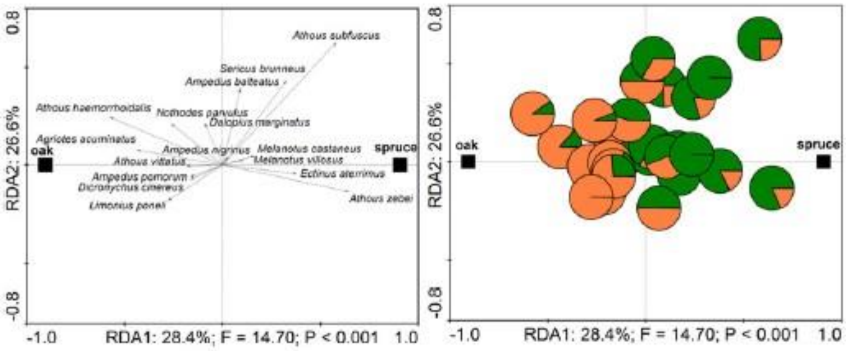


Fig. 4. Visualization of individual click beetle (Elateridae) species preferences for stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests using redundancy analysis. The explained variance, *F* and *P* values are derived from redundancy analysis; species with fewer than ten individuals were suppressed in the left species-environmental biplot; light-brown represents individuals on oak trees and green represents individuals captured in spruce-dominated stands in the right pie plot.

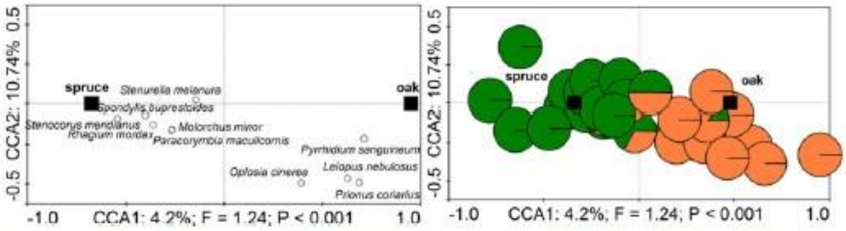


Fig. 5. Visualization of individual longhorn beetle (Cerambycidae) species preferences in stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests by canonical correspondence analysis. The explained variance, *F* and *P* values are derived from canonical correspondence analysis; species with fewer than five individuals were suppressed in the left species-environmental biplot; light-brown represents individuals on oak trees and green represents individuals captured in spruce-dominated stands in the right pie plot.

preference was also observed for *S. brunneus*, which mostly prefers pine stands (Laibner, 2000). Thus, this relationship might indicate that species that are associated with disparate conifer stands might use stands containing different conifer tree species as a supplementary habitat. The species *E. aterrimus* might represent an example of contrasting preferences to those known in the literature. This click beetle prefers broad-leaved forests (Laibner, 2000), but in this study, was significantly associated with spruce stands. As mentioned above, most of the studied click beetle traits were favored by the insolation of stands. However, we observed some species that were associated with a closed canopy (e.g., *A. acuminatus*). An open canopy was preferred by two *Ampedus* species (*A. balteatus* and *A. nigrinus*) that are known to be associated with conifer stands, whereas *A. nigrinus* is also associated with mountainous areas (Laibner, 2000). The stand area was not one of the most important variables in determining the distribution of click beetles, although some species showed a significant relationship with stand area – e.g., *D. marginatus* showed a negative relationship and *M. castanipes* a positive relationship to increasing area of stand. A positive response is unsurprising, but the negative response of *D. marginatus* appears to be difficult to interpret, because this species is a typical forest-dwelling species.

Longhorn beetles as representatives of a saproxylic family

Except for the species composition and the individual species, the group of longhorn beetles did not change according to the dominant tree species. This is on one hand surprising, because many species are specialized either on the wood of conifer or deciduous trees and Japanese research has shown that longhorn beetles were negatively affected by the conversion of deciduous forest stands to conifer plantations (Makino *et al.*, 2007). On the other hand, our results might have been influenced by the fact that the stands were not absolutely pure in terms of tree species and this might also be influenced by the surrounding stands. The species composition and particularly, the abundance of three species were influenced by the dominant tree in the tree species composition. The explained variance in the tree species composition was relatively low, but the majority of species were present only in one type

Table 4. Individual click beetle (Elateridae) species preferences for stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*), canopy openness and area in lowland plantation forests; t and P values ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$) are derived from species response curves; species with fewer than ten individuals were not analyzed.

Species	Individuals	Oak	Spruce	Canopy openness	Area
Adrastus rachifer	1				
Agriotes acuminatus	44	0.18*		−0.07*	
Agriotes obscurus	1				
Agriotes pilosellus	1				
Agrypnus murinus	9				
Ampedus balteatus	167			10.67**	
Ampedus erythrogonus	1				
Ampedus nigrinus	17			5.15***	
Ampedus pomorum	49				
Ampedus sanguineus	5				
Ampedus sanguinolentus	6				
Anostirus castaneus	2				
Anostirus purpureus	2				
Athous haemorrhoidalis	212	0.86*			
Athous subfuscus	1068		2.32*	10.89*	
Athous vittatus	21			−4.19*	4.25*
Athous zebei	257		0.89*		
Cardiophorus nigerrimus	6				
Cardiophorus ruficollis	4				
Dalopius marginatus	134				−0.05*
Denticollis linearis	6				
Dicronychus cinereus	15				
Ectinus aterrimus	137		0.41*		
Limonius poneli	40				
Melanotus castanipes	19				3.10*
Melanotus villosus	101				
Nothodes parvulus	16				
Paraphotistus nigricornis	1				
Pheletes aeneoniger	6				
Selatosomus aeneus	1				
Sericus brunneus	39		0.13*	5.82*	

of stand. With respect to the individual species, the preference of *P. coriarius* and *P. sanguineum* for oak trees is not surprising, whereas the preference of *S. meridianus* for spruce plantations is difficult to explain. This species is known to be associated with broadleaved trees in lowland forests (Sláma, 1998). Furthermore, this species was present in nine stands and thus, this result cannot be influenced by a clumped distribution in one or a few spruce stands, due to the circumstantial presence of a piece of oak dead wood.

Longhorn beetles appear to be more connected to the forest environment, because of their dependence on dead wood biomass for larval development (Sláma, 1998). However, recent research has shown that adults are more abundant in forest edges and open forests or larvae can even develop on solitary trees (Wermelinger *et al.*, 2007; Vodka *et al.*, 2009). Thus, their dependency on dead wood does not necessarily mean that this taxon is associated with forests and it is relatively surprising that longhorn beetles did not respond to canopy openness. Nevertheless, four out of five species that significantly responded to canopy openness were more associated with an increasing canopy openness. Only *O. cinerea* was associated with very shaded stands (for thresholds, see, e.g., Müller *et al.*, 2010), which contrasts with the known preference for avenues and solitary trees from the literature (Sláma, 1998). This suggests that plantation forests are still an understudied habitat type and might lead to different results than traditionally studied forest habitats such as old-growth forests or ancient woodlands (Vodka *et al.*, 2009; Horák & Rébl, 2013).

Stenurella melanura also showed a high preference for large open stands. This species is widespread throughout most of central Europe, which might be consistent with the occurrence of this species on blossoms (Sláma, 1998). Nevertheless, its distribution might be different in southern Europe, where *S. melanura* was found to be more abundant in oak forests, which generally have closed canopy (Peris-Felipo *et al.*, 2011). This difference is probably because insects can find a suitable ambient temperature in warmer climates, even under the closer canopy.

The effect of isolation caused by fragmentation in forests is understudied in comparison to non-forest habitats (Krauss *et al.*, 2004; Webb *et al.*, 2008; Horák, 2015) – and when studied, isolated forest fragments are usually only compared with different land uses (Pavuk & Wadsworth, 2013). In this study, the abundance, body size, rarity, and red-list status of longhorn beetles all increased with an increase in the area of the stand. Our results indicate that larger mature stands are highly significant not only for the total number of individuals, but also for indices that are important from the point of view of conservation biology (i.e., rare and threatened beetles) and functional ecology – larger and thus, more conspicuous longhorn beetles are associated with large stands (note that the mean value of our stand area was approximately 2 ha). The habitat area of saproxylic organisms is often characterized by the amount of dead wood or the diameter of the studied tree (Horak *et al.*, 2014; Buse *et al.*, 2016). However, the amount of dead wood in plantation forests is generally low (Kirby *et al.*, 1998); thus,

Table 5. Individual longhorn beetle (Cerambycidae) species preferences for stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*), canopy openness and area in lowland plantation forests; t and P values ($^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$) are derived from species response curves; species with fewer than five individuals were not analyzed.

Species	Individuals	Oak	Spruce	Canopy openness	Area
Acanthocinus griseus	1				
Alosterna tabacicolor	1				
Anaglyptus mysticus	1				
Callidium aeneum	2				
Clytus arietis	4				
Clytus lama	1				
Cortodera femorata	1				
Cortodera humeralis	1				
Gaurotes virginea	4				
Leiopus nebulosus	6				
Leptura quadrifasciata	2				
Menesia bipunctata	1				
Molorchus minor	13			2.66**	
Obrium brunneum	1				
Oplosia cinerea	5			−1.72*	
Oxymirus cursor	1				
Paracorymbia maculicornis	5			2.65*	
Pedostrangalia revestita	1				
Phymatodes testaceus	2				
Pogonocherus fasciculatus	3				
Pogonocherus hispidus	1				
Prionus coriarius	14	0.60*			
Pyrrhidium sanguineum	8	0.62*			
Rhagium bifasciatum	4				
Rhagium inquisitor	3				
Rhagium mordax	6			2.39*	
Saphanus piceus	1				
Spondylis buprestoides	10				
Stenocorus meridianus	12		0.47*		
Stenostola dubia	3				
Stenurella bifasciata	1				
Stenurella melanura	70			1.13***	0.03*
Tetropium castaneum	2				
Tetropium fuscum	1				
Tetropium gabrieli	1				
Xylotrechus antilope	1				

we conclude that the stand area could easily contribute to the amount of dead wood available for saproxylic organisms in studies on plantation forests.

What was the response of a rove beetle family?

Rove beetles are one of the families with the highest species richness and also one of the most complicated groups for identification to the species level (Brunke *et al.*, 2012). Previous studies have identified them as potential indicators (Boháč, 1999); although recent findings have indicated that they are probably generalists at the habitat level, at least in semi-natural forests (Parmain *et al.*, 2015).

The generalist habitat state of rove beetles appeared to be confirmed by the absence of threatened species in this study. However, we observed significantly more rare species in oak stands. We predicted that oak stands promote most of the studied dependent variables, but this was only true for the diversity of click beetles. Therefore, the greater number of rare species and total abundance of rove beetles was relatively unexpected, especially because the hypothesis concerning higher biodiversity values in stands with prevailing native vegetation was confirmed by the taxon that is currently considered to be that with the greater number of generalists or opportunists. Setting aside the problems outlined above concerning generalist taxa, rove beetles occasionally responded positively to oak stands mainly because they avoid conifer plantations (Buse & Good, 1993). Another reason might be because even if they do not appear to show habitat preferences in general (Parmain *et al.*, 2015), it is known that individual species occupy a relatively large number of microhabitats (Caballero *et al.*, 2007) – and disparate microhabitats are mostly more common in stands with native vegetation (Winter & Möller, 2008).

Rove beetles did not respond to the canopy openness gradient; however, their diversity and body length increased with increasing stand area, which was a similar response to that of longhorn beetles. Nevertheless, considering individual species responses, we found that three species were promoted by the native vegetation, three species were negatively influenced by canopy openness and four species were affected by an increasing stand area. On the other hand, the species that showed a response (e.g., *A. fungi*, *G. brevicenter* or *O. rugosus*) are mostly associated with non-specific habitats, in leaf litter or decaying plant, fungal or animal residues (Boháč & Matějíček, 2003).

Potential implications for management

Oaks that were dominant in the study territory in the past (Neuhauselova & Moravec, 2001) are mostly no longer present

Table 6. Individual rove beetle (Staphylinidae) species preferences for stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*), canopy openness and area in lowland plantation forests; t and P values ($^{*}P < 0.05$; $^{**}P < 0.01$) are derived from species response curves; species with fewer than ten individuals were not analyzed.

Species	Individuals	Oak	Spruce	Canopy openness	Area
Acidota crenata	1				
Acidota cruentata	1				
Aleochara bipustulata	1				
Aleochara sparsa	4				
Aloconota sulcifrons	3				
Amarochara umbrosa	24				−0.07*
Amischa analis	67				
Anotylus nitidulus	5				
Anotylus rugosus	5				
Anotylus tetracarinatus	15				
Atheta aeneicollis	1				
Atheta amicula	3				
Atheta celata	11				−2.60*
Atheta crassicornis	3				
Atheta elongatula	11				−0.05*
Atheta fungi	91			−5.05*	
Atheta livida	2				
Atheta malleus	2				
Atheta melanocera	6				
Atheta nigripes	2				
Atheta pittionii	1				
Atheta ravilla	3				
Atheta subtilis	1				
Atheta triangulum	3				
Atrecus affinis	3				
Autalia rivularis	2				
Bibloporus minutus	3				
Bisnius fimetarius	3				
Bythinus burrelli	5				
Bythinus macropalpus	3				
Carpelimus bilineatus	2				
Carpelimus elongatulus	7				
Carpelimus obesus	2				
Carpelimus rivularis	5				
Elonium striatulum	1				
Euplectus decipiens	2				
Euplectus karsteni	1				
Euplectus punctatus	21				
Gabrius breviventer	12	2.32**			
Gabrius nitritulus	8				
Gabrius osseticus	1				
Gabrius splendidulus	1				
Gyrophaena boleti	1				
Haploglossa puncticollis	4				
Heterothops dissimilis	2				
Kenothus laevicollis	5				
Lathrobium laevipenne	1				
Lathrobium terminatum	1				
Leptusa pulchella	7				
Lesteva longoelytrata	48				
Liogluta granigera	15	0.47**		−3.20*	
Lordithon lunulatus	4				
Lordithon trimaculatus	1				
Meotica exilis	8				
Mycetoporus corpulentus	4				
Mycetoporus erichsonanus	1				
Mycetoporus lepidus	19				
Mycetoporus splendidulus	1				
Ocalea badia	1				
Ocalea picata	1				
Omalium caesum	10				
Omalium rivulare	17				−2.82*
Oxypoda abdominalis	1				
Oxypoda acuminata	1				

Continued

Table 6. (*Cont.*)

Species	Individuals	Oak	Spruce	Canopy openness	Area
Oxypoda brevicornis	2				
Oxypoda opaca	4				
Oxypoda vicina	2				
Oxypoda vittata	1				
Oxyporus rufus	1				
Oxytelus insecatus	4				
Oxytelus migrator	2				
Oxytelus rugosus	20	2.78**		−2.50*	
Philhygra elongatula	2				
Philonthus atratus	7				
Philonthus carbonarius	34				
Philonthus cognatus	23				
Philonthus decorus	6				
Philonthus fumarius	1				
Philonthus laevicollis	6				
Philonthus laminatus	11				
Philonthus quisquiliarius	3				
Philonthus rectangulus	1				
Philonthus rotundicollis	2				
Philonthus tenuicornis	2				
Philonthus umbratilis	1				
Philonthus varians	12				
Phleopora testacea	2				
Phloeonomus planus	1				
Phloeonomus pusillus	1				
Phloeopora testacea	43				
Plataraea interurbana	1				
Platydracus fulvipes	1				
Platystethus nitens	7				
Plectophloeus fischeri	32				
Plectophloeus nitidus	3				
Quedius boopoides	1				
Quedius boops	2				
Quedius fuliginosus	3				
Quedius nitipennis	1				
Quedius xanthopus	1				
Rugilus mixtus	4				
Rugilus rufipes	2				
Rugilus scutellatus	2				
Scaphisoma agaricinum	11				
Scaphisoma assimile	3				
Scaphisoma boleti	9				
Scopaeus cognatus	1				
Scopaeus laevigatus	7				
Scopaeus minutus	1				
Sepedophilus pedicularius	1				
Staphylinus erythropterus	1				
Stenus clavicornis	1				
Stenus comma	1				
Stenus fossulatus	1				
Stenus humilis	2				
Syntomium aeneus	1				
Tachinus subterraneus	1				
Tachinus corticinus	1				
Tachinus signatus	2				
Tachyporus chrysomelinus	7				
Tachyporus hypnorum	34				
Tachyporus nitidulus	3				
Tachyporus obtusus	3				
Tachyporus solutus	5				
Trimium brevicorne	2				
Trimium carpathicum	1				
Tyrus mucronatus	2				
Xantholinus linearis	6				
Xantholinus longiventris	16				
Zyras cognatus	2				
Zyras limbatus	4				

as a dominant species (Loskotová & Horák, 2016). One potential reason why oak stands did not lead to the expected promotion of the majority of the studied taxa was that total area of broadleaved stands was relatively low and isolation was high compared with in conifer plantations (Loskotová, 2013). Therefore, one recommendation for forest management is to at least preserve indigenous broadleaved tree species, which would help to regenerate, create, and connect new islands of deciduous trees (Webb *et al.*, 2008). Although the natural regeneration of oak trees is occasionally considered complicated (Annighöfer *et al.*, 2015), it is preferred for the maintenance of beetle diversity.

Another important point for management is that legal forestry restrictions appear to be strict in most countries in central Europe. For example, clear-cuts in the Czech Republic can be performed in most cases only up to 1 ha, whereas some beetle families and their studied traits responded to an increasing area of the forest stand in our research area and the largest stand exceeded 3 ha. In Scandinavia, clear-cuts of a larger area are allowed, although with particular conservation-oriented amendments (e.g., the retention of green trees and dead wood), which might protect biodiversity (Vanha-Majamaa & Jalonen, 2001). This also appears to be important in the context of the first-mentioned management implication – i.e., an increase in the total area of broadleaved islands. To conserve the initial insect fauna, it is necessary to increase size of the broadleaved stands (Webb *et al.*, 2008), including the fragmented patches of native oaks, which are generally found in the lowland forests of the central Europe (Neuhauselova & Moravec, 2001). On the other hand, conifer plantations also supported several beetle species of conservation interest and therefore, specific forest management applications (such as support of diversified tree species composition) should be applied to avoid the loss of biodiversity and also to conserve rare and threatened species (Roder *et al.*, 2010). This is also highly connected to the fact that the majority of large forest plantations were subjected to the forest management of closed canopy stands, which is predicted to be more resistant to wind breaks (Vicena *et al.*, 1979). Therefore, larger scales of present and future harvesting with veteran tree retention (Alexander *et al.*, 1996) might also introduce a level of mosaic structure to the stands. Moreover, if natural regeneration is applied to the new clear-cut area, beetle diversity indices and traits can benefit from the newly created ecosystem heterogeneity, as has been observed for other insects (Véle *et al.*, 2016).

One of the well-known patterns in biogeography is that a large surface area of suitable habitats (i.e., stands, in this case) also means a higher species richness. Even if in this case it is rather a patch-matrix model than application of theory of island biogeography, the implication for management remains the same. The above-mentioned legal acts are oriented toward sustainable management (e.g., Gossner *et al.*, 2013); however, they might limit the further biodiversity-oriented management implications in the plantation forest stands. When we consider the maximal nature regeneration, one of the important issues regarding the future of clear-cut stands is the fact that the heterogeneity of tree species composition would be potentially higher in larger areas compared with in small cuts (Yasuhiro *et al.*, 2004).

The positive effect of spruce monocultures on certain families and species of click beetles was relatively surprising. This was probably because abundance of two native conifers of Scots pine and Silver fir together with Norway spruce in our research area could promote abundance of click beetles. The study area in total had a very low level of canopy openness (a mean light penetration of only 9%), which possibly negatively affected the final number of captured beetle species. Another explanation for the positive response to Norway spruce is that conifer plantations were more disturbed by abiotic factors in the past (spruce mainly by wind), which increased the insolation of stands compared with undisturbed oak-dominated stands. Regarding the improvement of conditions in native vegetation, any type of forest management of oak stands (e.g., the thinning of young trees or the intermediate felling of older and shelterwood cuttings in mature stands) can lead to a more open site canopy, to which many beetle species react positively (Vodka *et al.*, 2009), since the temperature of the stand is increased by the amount of sunlit space (e.g., Iverson *et al.*, 2008).

Acknowledgements

The authors would like to thank to all landowners and their managers. Jan Matějíček contributed to the data on the distribution of rove beetles. The study was supported by the project of the Ministry of Agriculture NAZV KUS QJ1520197 and CULS Prague CIGA 20174307.

References

Alexander, K.N.A. (2002) The invertebrates of living and decaying timber in Britain and Ireland – a provisional annotated checklist. *English Nature Research Reports*, **467**, 142 pp.

Alexander, K.N.A., Green, E.E. & Key, R.S. (1996). The management of over mature tree populations for nature conservation – the basic guidelines. pp. 122–135 in Read, H.J. (*Ed.*) *Pollard and Veteran Tree Management*, vol. **2**. London, Corporation of London.

Annighöfer, P., Beckschäfer, P., Vor, T. & Ammer, C. (2015) Regeneration patterns of European oak species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. *PLoS ONE* **10**(8), e0134935.

Bauhus, J., Van der Meer, P. & Kanninen, M. (2010) *Ecosystem Goods and Services from Plantation Forests*. Earthscan, Oxon, pp. 1–240.

Bertheau, C., Salle, A., Rossi, J.P., Bankhead-Dronnet, S., Pineau, X., Roux-Morabito, G. & Lieutier, F. (2009) Colonisation of native and exotic conifers by indigenous bark beetles (Coleoptera: Scolytinae) in France. *Forest Ecology and Management* **258**, 1619–1628.

Boháč, J. (1999) Staphylinid beetles as bioindicators. *Agriculture, Ecosystems & Environment* **74**, 357–372.

Boháč, J. & Matějíček, J. (2003) *Katalog brouků Prahy, svazek IV, Drabčíkovití – Staphylinidae*. Flóra, Praha, 256 pp.

Bouchard, P., Grebennikov, V.V., Smith, A.B. & Douglas, H. (2009) Biodiversity of Coleoptera. *Insect Biodiversity: Science and Society*. Willey Interscience.

Brunke, A., Klimaszewski, J. & Anderson, R.S. (2012) Present taxonomic work on Staphylinidae (Coleoptera) in Canada: progress against all odds. *ZooKeys* **186**, 1–5.

Buse, A. & Good, J.E.G. (1993) The effects of conifer forest design and management on abundance and diversity of rove beetles (Coleoptera: Staphylinidae): implications for conservation. *Biological Conservation* **64**, 67–76.

Buse, J., Entling, M.H., Ranius, T. & Assmann, T. (2016) Response of saproxylic beetles to small-scale habitat connectivity depends on trophic levels. *Landscape Ecology* **31**(5), 939–949.

Bussler, H., Bouget, C., Brustel, H., Brändle, M., Riedinger, V., Brandl, R. & Müller, J. (2011) Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. *Forest Ecology and Management* **262**, 1887–1894.

Caballero, U., Leon-Cortés, J.L. & Moron-Ríos, A. (2007) Response of rove beetles (Staphylinidae) to various habitat types and change in Southern Mexico. *Journal of Insect Conservation* **13**, 67–75.

Driscoll, D.A. & Weir, T. (2005) Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology* **19**, 182–194.

Dupont, Y.L. & Nielsen, B.O. (2006) Species composition, feeding specificity and larval trophic level of flower-visiting insects in fragmented versus continuous heathlands in Denmark. *Biological Conservation* **131**, 475–485.

Dušánek, V. & Mertlik, J. (2015) Elateridae. Click beetles of the Palearctic region. http://www.elateridae.com

Farkač, J., Král, D. & Škorpík, M. (2005) *Red List of Threatened Species in the Czech Republic. Invertebrates.* AOPK ČR, Prague.

Gossner, M.M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brandl, R., Weisser, W.W. & Müller, J. (2013) Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conservation Biology* **27**(3), 605–614.

Hannah, L., Carr, J.L. & Landerani, A. (1995) Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity Conservation* **4**, 128–155.

Horak, J. (2013) Effect of site level environmental variables, spatial autocorrelation and sampling intensity on arthropod communities in an ancient temperate lowland woodland area. *PLoS ONE* **8**, e81541.

Horak, J. (2014) Fragmented habitats of traditional fruit orchards are important for dead wood-dependent beetles associated with open canopy deciduous woodlands. *Naturwissenschaften* **101**(6), 499–504.

Horak, J. (2015) What is happening after an abiotic disturbance? Response of saproxylic beetles in the Primorsky Region woodlands (Far Eastern Russia). *Journal of Insect Conservation* **19**, 97–103.

Horák, J. (2016) Suitability of biodiversity-area and biodiversity-perimeter relationships in ecology: a case study of urban ecosystems. *Urban Ecosystems* **19**(1), 131–142.

Horák, J. & Rébl, K. (2013) The species richness of click beetles in ancient pasture woodland benefits from a high level of sun exposure. *Journal of Insect Conservation* **17**, 307–318.

Horak, J., Vodka, S., Kout, J., Halda, J.P., Bogusch, P. & Pech, P. (2014) Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. *Forest Ecology and Management* **315**, 80–85.

Iverson, L.R., Hutchinson, T.F., Prasad, A.M. & Peters, M.P. (2008). Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern US: 7-year results. *Forest Ecology and Management* **255**, 3035–3050.

Kirby, K.J., Reid, C.M., Thomas, R.C. & Goldsmith, F.B. (1998) Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology* **35**(1), 148–155.

Krauss, J., Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2004) Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodiversity Conservation* **13**(8), 1427–1439.

Kunieda, T., Fujiyuki, T., Kucharski, R., Foret, S., Ament, S.A. & Toth, A.L. (2006) Carbohydrate metabolism genes and pathways in insects: insights from the honey bee genome. *Insect Molecular Biology* **15**, 563–576.

Kuuluvainen, T., Aapala, K., Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J. & Tukia, H. (2002) Principles of ecological restoration of boreal forested ecosystems: Finland as an example. *Silva Fennica* **36**(1), 409–422.

Laibner, S. (2000) *Elateridae of the Czech and Slovak Republics.* Kabourek Nakladatelstvi, Praha. ISBN-13: 978-8090146624.

Loehle, C. (2003) Competitive displacement of trees in response to environmental change or introduction of exotics. *Environmental Management* **32**(1), 106–115.

Loskotová, T. (2013) *The importance of the forest continuity and fragmentation as a variable determining the diversity of beetles.* MSc. thesis. Charles University, Prague.

Loskotová, T. & Horák, J. (2016) The influence of mature oak stands and spruce plantations on soil-dwelling click beetles in lowland plantation forests. *PeerJ* **4**, e1568.

Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* **41**, 231–256.

Magura, T., Tóthmérész, B. & Elek, Z. (2003) Diversity and composition of carabids during a forestry cycle. *Biodiversity Conservation* **12**, 73–85.

Makino, S., Goto, H., Hasegawa, M., Okabe, K., Tanaka, H. & Takenari, I. (2007) Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by conversion from broad-leaved to man-made conifer stands of *Cryptomeria japonica* (Taxodiaceae) in central Japan. *Ecological Research* **22**, 372–381.

Mertlik, J. (2008) Species of genus *Limonius* Eschscholtz, 1829 from the Czech and Slovak Republics (Coleoptera: Elateridae). *Elateridarium* **2**, 156–171.

Müller, J., Noss, R.F., Bussler, H. & Brandl, R. (2010) Learning from a 'benign neglect strategy' in a national park: response of saproxylic beetles to dead wood accumulation. *Biological Conservation* **143**, 2559–2569.

Neuhauselova, Z. & Moravec, J. (2001) *Map of Potential Natural Vegetation of the Czech Republic*. Academia, Praha.

Niemelä, J., Langor, D. & Spence, J.R. (1993) Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conservation Biology* **7**, 551–561.

Nota, B., de Korte, M., Ylstra, B., van Straalen, N.M. & Roelofs, D. (2013) Genetic variation in parthenogenetic collembolans is associated with differences in fitness and cadmium-induced transcriptome responses. *Environmental Science & Technology* **47**, 1155–1162.

Parmain, G., Bouget, C., Müller, J., Horak, J., Gossner, M.M., Lachat, T. & Isacsson, G. (2015) Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests? *Bulletin of Entomological Research* **105**, 101–109.

Pavuk, D.M. & Wadsworth, A.M. (2013) Longhorned beetle (Coleoptera: Cerambycidae) diversity in a fragmented temperate forest landscape. *F1000Research* **1**, 25.

Peris-Felipo, J.F., Falcó-Garí, J.V. & Jiménez-Peydró, R. (2011) The diversity of Cerambycidae in the protected Mediterranean landscape of the Natural Park of Carrascal de La Font Roja, Spain. *Bulletin of Insectology* **64**, 87–92.

Přikryl, Z.B., Turčani, M. & Horák, J. (2012) Sharing the same space: foraging behaviour of saproxylic beetles in relation to dietary components of morphologically similar larvae. *Ecological Entomology* **37**, 117–123.

Röder, J., Bässler, C., Brandl, R., Dvořak, L., Floren, A., Goßner, MM., Gruppe, A., Jarzabek-Müller, A., Vojtech, O., Wagner, C. and Müller, J. (2010) Arthropod species richness in the Norway Spruce canopy along an elevation gradient. *Forest Ecology and Management* **259**, 1513–1521.

Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M. & Brooks, T.M. (2006) The value of the IUCN Red List for conservation. *Trends in Ecology & Evolution* **21**, 71–76.

Sebek, P., Bamouin, T., Brin, A., Brustel, H., Dufrêne, M., Gosselin, F., Meriguet, B., Micas, L., Noblecourt, T., Rose, O., Velle, L. & Bouget, C. (2012) A test for assessment of saproxylic beetle biodiversity using subsets of 'monitoring species'. *Ecological Indicators* **20**, 304–315.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. & Müller, J. (2015) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology* **29**(2), 382–390.

Sláma, E.F. (1998) *Cerambycidae of the Czech and Slovak Republics (Beetles-Coleoptera)*. Milan Sláma, Krhanice.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92.

Vanha-Majamaa, I. & Jalonen, J. (2001) Green tree retention in Fennoscandian forestry. *Scandinavian Journal of Forest Research* **16**, 79–90.

Véle, A., Holuša, J. & Horák, J. (2016) Ant abundance increases with clearing size. *Journal of Forest Research* **21**, 110–114.

Vicena, I., Pařez, J. & Konopka, J. (1979) *Ochrana Lesa Proti Polomům*. SZN, Praha.

Vodka, S., Konvicka, M. & Cizek, L. (2009) Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *Journal of Insect Conservation* **13**(5), 553–562.

Webb, A., Buddle, C.M., Drapeau, P. & Saint-Germain, M. (2008) Use of remnant boreal forest habitats by saproxylic beetle assemblages in even-aged managed landscapes. *Biological Conservation* **141**(3), 815–826.

Wermelinger, B., Flückiger, P.F., Obrist, M.K. & Duelli, P. (2007) Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *Journal of Applied Entomology* **131**, 104–114.

Winter, S. & Möller, G.C. (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. *Forest Ecology and Management* **255**(3), 1251–1261.

Yasuhiro, K., Hirofumi, M. & Kihachiro, K. (2004) Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, southern Japan. *Journal of Ecology* **92**, 230–240.

Zelená poušť? Vzorce biodiverzity v hospodářských lesích

Green desert?: Biodiversity patterns in forest plantations

Jakub Horak, Tereza Loskotová, **Strahinja Mladenović,** Jiri Kout, Petr Bogusch,
Josef Halda, Petr Zasadil

2019

Forest Ecology and Management

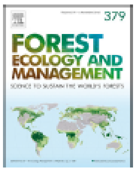
Publikováno

Forest Ecology and Management 433 (2019) 343–348

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Green desert?: Biodiversity patterns in forest plantations

Jakub Horák[a,*], Tereza Brestovanská[a], Strahinja Mladenović[a], Jiří Kout[b], Petr Bogusch[c], Josef P. Halda[c], Petr Zasadil[d]

[a] *Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Department of Forest Protection and Entomology, Kamycka 1176, CZ-165 00 Prague, Czech Republic*
[b] *University of West Bohemia, Faculty of Education, Department of Biology, Geosciences and Environmental Education, Klatovska 51, CZ-306 19 Plzen, Czech Republic*
[c] *University of Hradec Kralove, Faculty of Science, Department of Biology, Rokitanskeho 62, CZ-500 03 Hradec Kralove, Czech Republic*
[d] *Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Department of Ecology, Kamycka 1176, CZ-165 00 Prague, Czech Republic*

ARTICLE INFO

Keywords:
Biological desert
Forest management
Native vegetation
Multi-taxa approach
Nonnative tree
Threatened species

ABSTRACT

Forest plantations represent a globally important land use, and their growth is expected to triple by the end of the century. Therefore, they could represent an important habitat remnant to support the survival of species. We measured the impact of forest plantations on biodiversity with a focus on eight groups of biota including saproxylic and ground mycorrhizal fungi, lichens, herbs together with shrubs, tree seedlings, aculeate hymenopterans, beetles and birds, in patches with formerly continuous vegetation dominated by native oak and in patches in spruce plantations (reflecting spatiotemporal discontinuity) in the East-Bohemian woodlands of the Czech Republic.

We found that species richness and numbers of obligate species were higher in native than in nonnative forests, but there was no significant difference in red-listed species. Nevertheless, the species of three of the eight forests, but there was no significant difference in red-listed species. Nevertheless, the species of three of the eight studied groups profited from increasing proportion of spruce in the tree composition; only beetles and birds were negatively affected.

The results revealed more highly contrasting and often complex responses among the groups than what might be expected theoretically. The first key issue in the management of plantation forests in terms of biodiversity is the partial retention and restoration of islands of native vegetation. The second issue is that the impact of a nonnative tree species is not always negative.

1. Introduction

The conservation and maintenance of biodiverse forest ecosystems is a crucial issue worldwide. Importantly, the current global tree plantation area (excluding palm oil plantations) is approximately 7% of the forested area of the world, and this value is expected to grow to more than 20% over the next century (Brockerhoff et al., 2013; Hansen et al., 2013). At least one-quarter of the global commercial plantations consist of nonnative and fast-growing tree species (FAO, 2010). Moreover, natural forests will likely become fragmented and smaller with an accompanying decrease in their native biodiversity (McGill et al., 2015). The maintenance of biodiversity is not only an issue for conservation hot spots; it also applies to the harvested forests of Europe, North America and East Asia (Hansen et al., 2013; Hannah et al., 1995). Many of the old-growth beech and oak forests in central Europe have been transformed into plantations of coniferous trees, but the forest cover area in Europe is constantly increasing. The problem is that the increase in forest cover is mainly attributable to the establishment of commercial plantation forests on former agricultural land (Forest Europe UN & FAO, 2011).

Plantation forests are often characterized by the public, journalists and, frequently, conservation biologists, as “biological deserts” or “green deserts” (Acosta, 2011; Qiu, 2014). Recently, it was estimated that biological deserts constitute 40% worldwide, and this value continues to increase (e.g., Polovina et al., 2008). The alteration of tree species in commercial plantation forests, especially through the introduction of nonnative trees, is predicted to hinder the survival of native organisms. Thus, the biodiversity of these forests is often considered to be very low, and it is claimed that they leave no place for rare or endangered species (Acosta, 2011; Graves, 2015). However, recent studies suggest that plantation forests are not necessarily green deserts (Carnus et al., 2006; Brockerhoff et al., 2008; Graves, 2015).

Indeed, biodiversity in forest plantations is not necessarily low relative to other systems. Changes to spatiotemporal heterogeneity (e.g.,

---

* Corresponding author.
E-mail address: jakub.sruby@gmail.com (J. Horák).

https://doi.org/10.1016/j.foreco.2018.11.019
Received 4 July 2018; Received in revised form 9 November 2018; Accepted 10 November 2018

opening canopies or establishing an even-aged structure matrix) together with natural disturbances in forest plantations (e.g., leaving dead wood materials within the stands) at the landscape scale may help restore forest biodiversity (Lindenmayer et al., 2010; Horak et al., 2014). Leaving natural or seminatural patches within plantations to function as biodiversity islands may also be a useful strategy (As, 1993), and scattered veteran trees can be enormously important for retaining biodiversity (Horák, 2017).

Forest management may affect populations of species directly through logging and indirectly through changes in habitat heterogeneity and prey availability (Brunet et al., 2010). From the perspective of biodiversity, studying taxa with different life characteristics and strategies (Jackson and Fahrig, 2015) appears to be crucial, especially for plantation forests. Even when focusing on a particular taxa, different species require variety of habitat types (Horak et al., 2014), and plantation forests may represent an important habitat remnant to support the survival of such species. Plantation forests, therefore, should also be included in discussions of biodiversity-promoting natural disturbances (Lindenmayer et al., 2010).

We measured the impact of commercial forest plantations on biodiversity with a focus on multiple groups of biota. We used eight groups of organisms with disparate dispersal abilities, taxonomic affiliations and ecological requirements that we organized according to the disparate environmental characteristics that, to the best of our knowledge, reflect the conditions of plantation forests globally.

1.1. *Objectives*

We were interested in the effects of native vs. nonnative tree species on the biota in plantation forests. Our particular questions were:

(i) Are there differences between native oak stands and nonnative spruce plantations in terms of species richness and the number of obligate and threatened species?
(ii) What is the response of the species composition to the studied environmental variables?
(iii) What is the response of individual species to the studied environmental variables?

2. Materials and methods

2.1. *Study area*

The studied forests comprised nearly 6500 ha in a spatially continuous area of the East-Bohemian woodlands in the Czech Republic (GPS of centroid: 50.0260N, 16.1260E). In the past, this area was covered by temperate broadleaved forests dominated by sessile oak (*Quercus petraea*), but a large area has been planted for more than two centuries with the fast-growing, nonnative Norway spruce (*Picea abies*) that is only native to the highest mountains in central Europe. The oak stands served as isolated islands and represented the former dominant vegetation in the landscape, whereas the spruce plantations are nonnative trees and represented spatial and temporal discontinuity of former vegetation. In total, thirty mature stands distributed throughout the entire East-Bohemian woodlands were studied using a paired design with the minimal distance between sampling points and the distance from sampling points to the woodland edge set as 50 m.

2.2. *Sampling*

We used equal-stratified sampling (Hirzel and Guisan, 2002). Eight groups of organisms were selected for this study including two groups of fungi. Saproxylic fungi (i) are strictly associated with dead wood and may be sensitive to logging. Ground mycorrhizal fungi (ii) are relatively well known and mostly symbiotic with particular forest tree species, which mostly restricts them to forest habitat. We also sampled lichens (iii) as specialized and sedentary symbiotic organisms. All the groups of fungi and lichens were collected during early autumn in 2014. We also sampled two groups of vascular plants, the first of which consisted of herbs and shrubs (iv) which were pooled together because forests had relatively few larger shrubs and many of these shrubs were low shrubs, such as Bilberry (*Vaccinium myrtillus*), with requirements similar to those of perennial plants. Herbs and shrubs belong to taxa with medium dispersal abilities. The second group of plants consisted of tree seedlings (v) produced via natural regeneration; the seeds of most forest trees have relatively high dispersal. We primarily studied this group because we predicted that the distribution of tree seedlings in mature stands would only be slightly affected by human disturbances and because seedlings accurately reflect the influence of oak and spruce on the future species composition of the stands. The plants were collected during late summer and early autumn in 2014. Hymenoptera (vi) were studied as invertebrate taxa with relatively good dispersal abilities, and they are also known to exhibit good responses to habitat alterations. Beetles (vii), along with hymenopterans, constitute one of the most species-rich taxa in the world, but their dispersal abilities are predicted to be lower than those of the hymenopterans. Aculeata Hymenoptera (excl. Formicidae) and Coleoptera (excl. Nitidulidae, Anobiidae, Chrysomelidae, Hydrophilidae, Leiodidae, Scirtidae and Throscidae) were collected during the vegetation growing season in 2011 and then identified to the species level. Birds (viii) were sampled as taxa that generally have relatively good dispersal abilities during spring 2014.

All of the studied insects were sampled using standard crossed panel window traps fixed to two iron sticks, which enabled the traps to move in the wind (Loskotová and Horák, 2016). All of the fungi, lichens, plants and birds were sampled within a 40-m radius surrounding the center of the stand (marked by the window trap) via a time-limited survey with 15 min as the limit for sampling (e.g., Horák et al., 2018a). In the case of fungi, lichens and plants, we used direct species observations; birds were also surveyed aurally (Horák et al., 2018a, 2018b).

2.3. *Variables*

We studied the total number of species. Obligate species were those that were only found in oak or spruce stands. We used obligate species instead of rare or infrequent species, which are more commonly analyzed, because rare species have a high potential to only be tourists. We also analyzed species listed on actual Czech red lists. All of these dependent variables were first analyzed with respect to the dominant tree species (spruce vs. oak). The species composition and individual species responses were then analyzed as a presence/absence matrix, which enabled a better final comparison among the different taxa.

We carefully selected four predictors that described the environmental conditions of the plantation forests. Not all stands were of regular shape, the same area, or pure spruce plantations or oak stands, so we measured (i) the percentage of spruce and oak within a 40-m radius (i.e., a circular patch) of the overstory. Spruce coverage exhibited collinearity with that of the oak (VIF = 2.26), meaning that an increasing amount of spruce reflected a decreasing amount of oak. Thus, the oak coverage was not analyzed further. We then analyzed the influence of spruce in the tree species composition. Additionally, (ii) we counted in detail all stumps less than five years old (reflected by the presence of bark) within a 40-m radius. Because we studied mature plantations of nearly the same age, the stumps had the same relative dimensions, and this predictor reflected the actual management intensity, which simply cannot be found in the management plans (e.g., due to sanitary cuttings). (iii) The third predictor was canopy openness, which reflected the microclimatic and light conditions of the individual patch being studied. Canopy openness was measured under the full foliage using fish-eye photographs from the center of a particular patch. (iv) The last predictor was chosen with respect to the potential edge effect and the effect of deforested land and measured as a percentage of nonforest area within a 40-m radius.

2.4. Statistical analyses

All of the statistical analyses were performed in R 3.0.2 and CANOCO 4.5. The distribution of the dependent variables was tested with Shapiro-Wilk and chi-square tests, and the influence of the spatial autocorrelation was tested using Geary's C test under randomization (package spdep). The potential bias caused by the multicollinearity of the predictors was detected using the variance inflation factor (package HH). The Wilcoxon paired test was used to analyze the difference in the number of obligate and red-listed species between oak and spruce stands, and a canonical correspondence analysis (CCA) was used to investigate the species composition. The coordinates and their crossed and quadratic products were treated as continuous covariables for taxa that were significantly influenced by spatial autocorrelation (lichens and hymenopterans). A global permutation test was set at 9999 permutations under the full model; the permutation type was restricted for a split-plot design, and the whole plot was freely exchangeable. Because of the presence of empty samples for some taxa, we added one species present in all samples (Horak et al., 2014), and to estimate the response of the species richness gradient, we used the t-value of the correlated axis. We used generalized linear mixed-effect models (GLMM) with binomial distributions to analyze the response of individual species with site incidences exceeding 10. The pairs of plots were used as a random factor (package MASS). Each fish-eye photograph was evaluated on canopy openness using Gap Light Analyzer 2.0.

3. Results

We identified 789 species among the eight studied groups including 523 species of beetles, 71 bees and wasps, 50 saproxylic fungi, 49 herbaceous plants and shrubs, 37 birds, 21 lichens, 20 mycorrhizal fungi and 18 trees.

3.1. Species richness

We found that the number of species was significantly higher in native oak stands (76.81% of the total species) than in nonnative spruce stands (68.57%), and the number of obligate species in a particular group was also higher for oak (31.43%) than spruce (23.19%) stands (Fig. 1). In total, 30 species were listed on country red-lists, but we found no significant difference in the incidences of red-listed species between oak and spruce stands ($z = 0.94$; $P = 0.35$).

3.2. Species composition

The species composition of five of the eight studied groups responded significantly to the set of the studied independent predictors (Table SI 1). Beetles, hymenopterans, and birds exhibited the highest P-value significance followed by mycorrhizal fungi and tree seedlings. Wood-inhabiting fungi, lichens and plants were the only groups that did not respond to the studied environment.

Beetles, as medium-dispersing taxa, and birds, which are good dispersers, were negatively affected by increasing proportions of spruce in the tree composition (Table 1). Beetles also exhibited a complex pattern in response to the environment. In addition to the tree species composition, they also responded negatively to increasing canopy openness and were positively influenced by the surrounding deforested areas. Surprisingly, three groups benefited from an increasing percentage of spruce cover (Table 1) in contrast to previous results (Fig. 1). Namely, the number of species of mycorrhizal fungi that preferred spruce-dominated stands was higher than the number of species that were promoted by native oak. Tree seedlings constituted the second group that was positively influenced by spruce dominance, and bees and wasps responded positively to increases in the proportion of spruce and canopy openness (Table 1).

3.3. Species responses

Three species (the lichen *Lepraria incana*, the beetle *Athous subfuscus*, and the bird *Fringilla coelebs*) should be regarded as generalists because they were represented in all study sites. Additionally, 1 species of fungi, 4 lichens, 2 trees, 5 bees and wasps, 17 beetles and 5 birds responded significantly to some of the studied environmental variables (Table SI 2). The fact that these 34 species responded to the environment suggests that research at the level of individual species could reveal some details about biodiversity that cannot be observed by analyzing groups.

Surprisingly, more species (17 in total) were positively influenced than were negatively affected (10 in total) when the proportion of spruce increased (Table SI 2). Moreover, many species were not affected by the nonnative trees in forests.

Regarding the other plantation forest parameters, most species (especially insects and their predators) responded positively to increasing sunlight in the stands. Indeed, increasing the area without forest cover negatively affected fewer species than the opposite, but the difference was not as large as that observed for canopy openness. More species preferred intermediate felling in the recent past in mature forests (Table SI 2).

4. Discussion

We found that there were differences between native oak stands and nonnative spruce plantations in terms of species richness and the number of obligate species, but this difference was not significant for threatened species. Six studied groups responded significantly to the studied independent variables regarding their species composition. We also found that 34 species responded to the studied environment.

4.1. Biodiversity and the impact of dominants

Based on the ability of oak stands to host higher numbers of unique and total species, the retention and future restoration of fragmented islands of native tree species appear to be highly important within plantation forest matrices (As, 1993; Rodríguez-San Pedro and Simonetti, 2015; Phillips et al., 2018).

4.2. Importance of tree species composition

The results for saproxylic fungi, lichens and plants were quite surprising because these groups are often studied with a number of bioindicators (Hermy et al., 1999; Padoa-Schippoa et al., 2006). Thus, it is difficult to describe plantation forests as green deserts for saproxylic fungi, lichens or plants, but the abilities of these groups to serve as indicators in this type of environment might be limited in comparison with forest reserves (e.g., Horák et al., 2018b).

From the perspective of a multitaxa approach, the impacts of plantation forests on biodiversity were more complex than what might have been expected at first glance. The finding that the representation of nonnative trees negatively impacted only two taxa was relatively surprising (Newbold et al., 2015), and in the case of the complex response of beetles, this effect may be explained by the interconnection of these species with plants and fungi and their dispersal abilities (Jackson and Fahrig, 2015; Müller et al., 2015). The effects on birds were especially surprising because this taxon consists, in general, of mobile animals (especially relative to the other studied taxa), but the dispersal abilities of some bird species might be very low or limited because of habitat specificity. For example, a conspicuous passerine, the Golden oriole (*Oriolus oriolus*), was only observed in oak stands. Trees and hymenopterans preferred large amounts of spruce, and a similar response was interesting in the case of fungi with mycorrhiza because

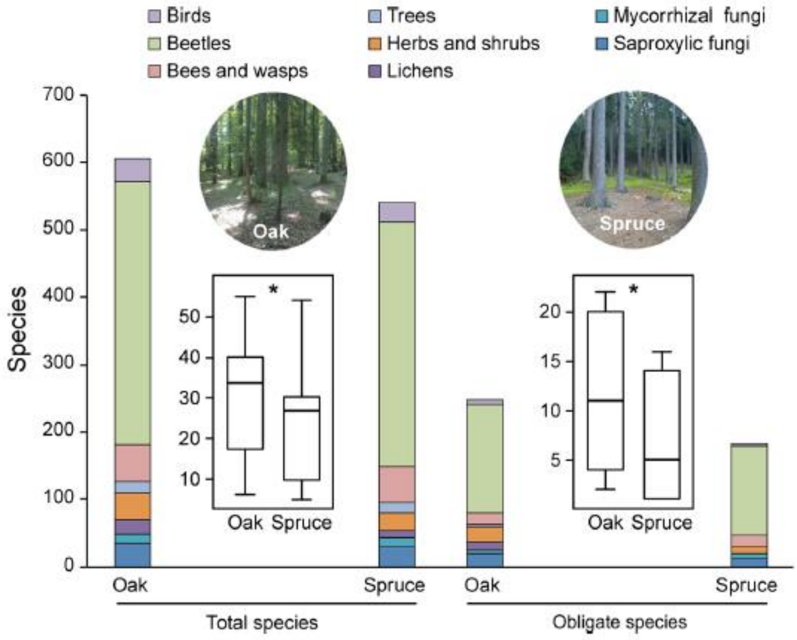


Fig. 1. Differences in the species richness of the studied groups. The differences between forest stands dominated by native (Sessile oak: yellow) and nonnative (Norway spruce: green) trees in temperate plantation forests are presented ($^*P < 0.05$; outliers are not shown). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Responses of five of the studied groups to the environmental variables. The response regarding the number of species was analyzed in temperate plantation forests using the t-value in CCA.

Group	Predictor	R^2 (%)	F	P	Response
Mycorrhizal fungi	Canopy openness	4.05	1.18	0.23	
	No forest	2.53	0.73	0.66	
	Spruce	6.94	2.08	< 0.001	+
	Stumps	4.14	1.21	0.28	
Trees	Canopy openness	4.46	1.28	0.18	
	No forest	3.81	0.96	0.54	
	Spruce	6.47	1.94	< 0.001	+
	Stumps	3.60	0.89	0.53	
Bees and wasps	Canopy openness	5.19	1.53	0.004	+
	No forest	4.39	1.31	0.13	
	Spruce	4.55	1.12	< 0.001	+
	Stumps	3.30	0.92	0.62	
Beetles	Canopy openness	4.42	1.19	0.016	–
	No forest	4.29	1.25	0.001	+
	Spruce	4.73	1.39	< 0.001	–
	Stumps	3.32	0.97	0.64	
Birds	Canopy openness	3.58	0.93	0.60	
	No forest	4.25	1.29	0.18	
	Spruce	7.47	2.27	< 0.001	–
	Stumps	3.94	1.00	0.44	

such fungi should be predicted to have poor dispersal relative to other taxa (Rasmussen and Rasmussen, 2009).

One important issue in nature conservation is natural habitat restoration, including in plantations and degraded forests (Lamb et al., 2005; McFadden and Dirzo, 2018). The higher number of seedlings in spruce stands in our research indicated that plantations of nonnative trees have a high potential for restoration through natural succession; that is, setting aside a few hectares of stands within the plantation matrix by forest managers would lead to the creation of seminatural patches and thus increase the landscape connectivity without incurring additional costs. These plantations have also been described as ecologically unstable (McCann, 2000; Brang et al., 2014; Veldman et al., 2015), but bees and wasps, which were observed to prefer nonnative trees in our study, include a significant number of keystone species including pollinators of commercial plants and predators and parasites that function in pest management (Thies and Tscharntke, 1999). Given that these species were positively influenced by spruce and have relatively high mobility, we can conclude that the future improvement of plantation stability is promising (Cruz-Neto et al., 2018), especially if plantations could be incorporated into a more scattered forest landscape (McCann, 2000).

4.3. Disentangling the contrast

The known beneficial effect of habitat matrices on biodiversity (Horák et al., 2014; Redon et al., 2014; Mortelliti et al., 2015) likely explains why our results appeared to be contrasting and why this factor represents an opportunity to ensure the future of plantation forests (Rodríguez-San Pedro and Simonetti, 2015; Cruz-Neto et al., 2018). We found that stands dominated by native tree species hosted a higher number of species, including those exclusive to native habitats, so we can conclude that the remnants of the former forest vegetation types, even when managed for timber products, promoted biodiversity in plantation forests. Therefore, the maintenance of the former vegetation, at least as habitat islands, is a key opportunity for plantation forests (Hanzelka and Reif, 2016).

Nevertheless, increasing the representation of nonnative conifer species appeared to benefit several groups and species. Thus, we can conclude that mixtures of different species in plantation forests could benefit biodiversity, and whether the mixed species stands are native matters little. Thus, each tree species contributes some spatial and species-specific diversity to the organismal distribution (Müller et al., 2015). Additionally, more heterogeneous plantation forests can be predicted to be more resistant to natural disturbances (Verheyen et al., 2016) and thus more sustainable (e.g., because of diverse forms of carbon sequestration; Jożefowska et al., 2017). For example, spruces are used by many generalists but can also attract specialists from mountainous forests (Röder et al., 2010).

There are two possible approaches for maintaining and improving biodiversity in plantations:

(1) Increasing the heterogeneity of tree species within the stands (i.e., at a spatial scale of a few hectares), which is important for appropriate individual forest management, and
(2) Maintaining native vegetation inside the matrix of plantation forests (i.e., the landscape spatial scale), which is important for global forest management.

4.4. *Implications for promoting biodiverse plantations*

We highlighted the important role of native vegetation as habitat islands within plantations; these fragments could host higher numbers of unique and total species. We also focused on the effect of the representation of nonnative trees in plantations, and despite their poor reputation among nature conservationists, these species appeared to have few negative impacts. Furthermore, some groups even benefited from them. Thus, plantations of nonnative trees are not always green deserts and we can expect similar patterns of biodiversity elsewhere. These conclusions are strengthened by the fact that we studied eight groups with disparate dispersal abilities, taxonomic affiliations and ecological requirements and combined them with diverse environmental characteristics reflecting the conditions of forest plantations worldwide.

The first key issue in promoting the biodiversity of plantation forests during their expected future expansion is the retention and restoration of native vegetation. The second issue is the representation of nonnative trees in various mixtures.

We believe that this study contributes to the knowledge of biodiversity because plantation forests will be a dominant land use type in the future (FAO, 2010). Thus, plantations that are designed to better deliver socioeconomic benefits (e.g., recreation and relaxation activities) and nonproductive forest functions (e.g., dust reduction, and mushroom and fruit production) while providing ecological services (e.g., biodiversity maintenance) will be very important in the future.

Acknowledgments

We wish to thank V. Špidlenová, R. Zachová, V. Ludvíková and J. Brestovanský, who helped us with data collection. We are also grateful for the support of the forest landowners and managers, namely (in alphabetical order), K. Beznoska (Lesy ČR), B. Machata (Městské lesy Vysoké Mýto), J. Marek (Městské lesy Choceň), P. Rolc (Hospodářská a lesní správa Bubna) and P. Starý (Diecézní lesy Hradec Králové), as well as their staff.

Funding

This study was supported by grant no. NAZV KUS QJ1520197 (ENvironmental REsistance of stable FOrest stands fulfilling non-wood-producing roles) and partly by grants no. CIGA ČZU 20144302 (Managed forests in lowlands and their potential from the perspective of two distinct taxa—beetles and birds) and no. IGA FLD B_02_18 (Bark beetles and their antagonists in natural and commercial spruce stands).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.11.019.

References

Acosta, I., 2011. Green Desert' Monoculture Forests Spreading in Africa and South America. The Guardian. http://www.theguardian.com/environment/2011/sep/26/monoculture-forests-africa-south-america.

As, S., 1993. Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. Ecography 16, 219–228. https://doi.org/10.1111/j.1600-0587.1993.tb00212.x.

Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Boncina, A., Chauvin, C., et al., 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry 87, 492–503. https://doi.org/10.1093/forestry/cpu018.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Ferraz, S.F.B., 2013. Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. Forest Ecol. Manag. 301, 43–50. https://doi.org/10.1016/j.foreco.2012.09.018.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17, 925–951. https://doi.org/10.1007/s10531-008-9380-x.

Brunet, J., Fritz, O., Richnau, G., 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. Ecol. Bull. 53, 77–94.

Carnus, J.M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., et al., 2006. Planted forests and biodiversity. J. For. 104, 65–77.

Cruz-Neto, O., Silva, J.L. Se, Woolley, M.M., Tabarelli, M., Lopes, A.V., 2018. Pollination partial recovery across monospecific plantations of a native tree (Inga vera, Leguminosae) in the Atlantic forest: Lessons for restoration. Forest Ecol. Manag. 427, 383–391. https://doi.org/10.1016/j.foreco.2018.06.023.

FAO, 2010. Global forest resources assessment 2010 – main report. FAO Forestry. Rome, Paper 163.

Forest Europe, U.N., F.A.O., 2011. State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe. Forest Europe Liaison Unit, Oslo.

Graves, G.R., 2015. Recent large-scale colonisation of southern pine plantations by Swainson's warbler Limnothlypis swainsonii. Bird Conserv. Int. 25, 280–293. https://doi.org/10.1017/S0959270914000306.

Hannah, L., Carr, J.L., Lankerani, A., 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodivers. Conserv. 4, 128–155. https://doi.org/10.1007/BF00137781.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., et al., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853. https://doi.org/10.1126/science.1244693.

Hanzelka, J., Reif, J., 2016. Effects of vegetation structure on the diversity of breeding bird communities in forest stands of non-native black pine (Pinus nigra A.) and black locust (Robinia pseudoacacia L.) in the Czech Republic. Forest Ecol. Manag. 379, 102–113. https://doi.org/10.1016/j.foreco.2016.08.017.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol. Conserv. 91, 9–22. https://doi.org/10.1016/S0006-3207(99)00045-2.

Hirzel, A., Guisan, A., 2002. Which is the optimal sampling strategy for habitat suitability modelling. Ecol. Model. 157, 331–341.

Horák, J., 2017. Insect ecology and veteran trees. J. Insect Conserv. 21, 1–5. https://doi.org/10.1007/s10841-017-9953-7.

Horák, J., Pavlíček, J., Kout, J., Halda, J.P., 2018a. Winners and losers in the wilderness: response of biodiversity to the abandonment of ancient forest pastures. Biodivers. Conserv. 27, 3019–3029. https://doi.org/10.1007/s10531-018-1585-z.

Horák, J., Rom, J., Rada, P., Šafářová, L., Koudelková, J., Zasadil, P., et al., 2018b. Renaissance of a rural artifact in a city with a million people: biodiversity responses to an agro-forestry restoration in a large urban traditional fruit orchard. Urban Ecosyst. 21, 263–270. https://doi.org/10.1007/s11252-017-0712-z.

Horak, J., Vodka, S., Kout, J., Halda, J.P., Bogusch, P., Pech, P., 2014. Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. Forest Ecol. Manage. 315, 80–85. https://doi.org/10.1016/j.foreco.2013.12.018.

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob. Ecol. Biogeogr. 24, 52–63. https://doi.org/10.1111/geb.12233.

Józefowska, A., Pietrzykowski, M., Woś, B., Cajthaml, T., Frouz, J., 2017. The effects of tree species and substrate on carbon sequestration and chemical and biological properties in reforested post-mining soils. Geoderma 292, 9–16. https://doi.org/10.1016/j.geoderma.2017.01.008.

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–1632. https://doi.org/10.1126/science.1111773.

Lindenmayer, D.B., Likens, G.E., Franklin, J.F., 2010. Rapid responses to facilitate ecological discoveries from major disturbances. Front. Ecol. Environ. 8, 527–532. https://doi.org/10.1890/090184.

Loskotová, T., Horák, J., 2016. The influence of mature oak stands and spruce plantations on soil-dwelling click beetles in lowland plantation forests. PeerJ 4, e1568. https://doi.org/10.7717/peerj.1568.

McCann, K.S., 2000. The diversity-stability debate. Nature 405, 228–233. https://doi.org/10.1038/35012234.

McFadden, T.N., Dirzo, R., 2018. Opening the silvicultural toolbox: a new framework for conserving biodiversity in Chilean timber plantations. Forest Ecol. Manag. 425, 75–84. https://doi.org/10.1016/j.foreco.2018.05.028.

McGill, B.J., Dornelas, M., Gotelli, N.J., Magurran, A.E., 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends Ecol. Evol. (Amst.) 30, 104–113. https://doi.org/10.1016/j.tree.2014.11.006.

Mortelliti, A., Michael, D.R., Lindenmayer, D.B., 2015. Contrasting effects of pine plantations on two skinks: results from a large-scale 'natural experiment. Anim. Conserv. 18, 433–441. https://doi.org/10.1111/acv.12190.

Müller, J., Wende, B., Strobl, C., Eugster, M., Gallenberger, I., Floren, A., et al., 2015. Forest management and regional tree composition drive the host preference of saproxylic beetle communities. J. Appl. Ecol. 52, 753–762. https://doi.org/10.1111/1365-2664.12421.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., et al., 2015.

Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324.

Padoa-Schioppa, E., Baietto, M., Massa, R., Bottoni, L., 2006. Bird communities as bioindicators: the focal species concept in agricultural landscapes. Ecol. Indic. 6, 83–93. https://doi.org/10.1016/j.ecolind.2005.08.006.

Phillips, H.R.P., Halley, J.M., Urbina-Cardona, J.N., Purvis, A., 2018. The effect of fragment area on site-level biodiversity. Ecography 41, 1220–1231. https://doi.org/10.1111/ecog.02956.

Polovina, J.J., Howell, E.A., Abecassis, M., 2008. Ocean's least productive waters are expanding. L03618–LL03618. Geophys. Res. Lett. 35. https://doi.org/10.1029/2007GL031745.

Qiu, L., 2014. Rare southern songbird thrives in 'Biological Deserts'. National Geographic. < http://news.nationalgeographic.com/2014/11/141113-warbler-pines-timber-animals-birds-environment > .

Rasmussen, H.N., Rasmussen, F.N., 2009. Orchid mycorrhiza: implications of a mycophagous life style. Oikos 118, 334–345. https://doi.org/10.1111/j.1600-0706.2008.17116.x.

Redon, M., Luque, S., Gosselin, F., Cordonnier, T., 2014. Is generalisation of uneven-aged management in mountain forests the key to improve biodiversity conservation within forest landscape mosaics? Ann. Forest Sci. 71, 751–760. https://doi.org/10.1007/s13595-014-0371-7.

Röder, J., Bässler, C., Brandl, R., Dvořak, L., Floren, A., Goßner, M.M., et al., 2010. Arthropod species richness in the Norway Spruce (Picea abies (L.) Karst.) canopy along an elevation gradient. Forest Ecol. Manag. 259, 1513–1521. https://doi.org/10.1016/j.foreco.2010.01.027.

Rodríguez-San Pedro, A., Simonetti, J.A., 2015. The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? Landscape Ecol. 30, 1561–1572. https://doi.org/10.1007/s10980-015-0213-5. Acosta.

Thies, C., Tschamtke, T., 1999. Landscape structure and biological control in agroecosystems. Science 285, 893–895. https://doi.org/10.1126/science.285.5429.893.

Veldman, J.W., Overbeck, G.E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G.W., et al., 2015. Where tree planting and forest expansion are bad for biodiversity and ecosystem services. BioScience. BioScience 65, 1011–1018. https://doi.org/10.1093/biosci/biv118.

Verheyen, K., Vanhellemont, M., Auge, H., Baeten, L., Baraloto, C., Barsoum, N., et al., 2016. Contributions of a global network of tree diversity experiments to sustainable forest plantations. Ambio 45, 29–41. https://doi.org/10.1007/s13280-015-0685-1.

Biodiverzita v pozůstatcích přírodních horských lesů v rámci ochraného managementu

Biodiversity in remnants of natural mountain forests
under conservation-oriented management

Jakub Horák, Jan Materna, Josef P. Halda, **Strahinja Mladenović**, Petr Bogusch,
Pavel Pech

2019

Scientific Reports

Publikovano

www.nature.com/scientificreports

SCIENTIFIC REPORTS

Biodiversity in remnants of natural mountain forests under conservation-oriented management

Received: 19 February 2018
Accepted: 6 November 2018

Jakub Horák[1], Jan Materna[2], Josef P. Halda[3], Strahinja Mladenović[1], Petr Bogusch[3] & Pavel Pech[3]

The structure of forests is an important stabilizing factor regarding ongoing global climate and land use change. Biodiverse mountain forests with natural structure are one of the ecosystems most endangered by these problems. We focused on the mountain forest islands of European beech (*Fagus sylvatica*) and their role in the natural distribution of organisms. The study area was situated in the oldest Czech national park, Krkonoše (385 km^2), which is the highest mountain ridge in the country. We studied multi-taxa (lichens, beetles and hymenopterans) responses to three hierarchical spatial levels of the environment: the topography was described by the elevation gradient; the patch structure was described by canopy openness, dead wood amounts, and Norway spruce (*Picea abies*) cover; and the tree level was described by species of the sampled tree and its diameter. Lichens preferred higher elevations, while insect groups responded conversely. Furthermore, insect groups were mainly influenced by the inner patch structure of beech islands. Lichens may be jeopardized due to the predicted future increase in temperatures, since they would need to shift toward higher altitudes. Insects may be mainly threatened in the future by land use changes (i.e., forest management) – as indicated by an interconnection of canopy openness and the amount of dead wood.

Forest structure is an important factor regarding future global changes[1]. Specifically, due to the ability of forests to influence the local climate and their importance as a global carbon stock and in providing biodiversity[2]. Even though some forests benefit from sustainable development policies, many governments are trying to improve their environment using subsidies[3–5].

The situation of forests in Europe appears to be relatively promising with respect to their biodiversity in the future. However, their historical abuse makes their preservation difficult[6] – at least one tenth of the forests of Central Europe consist of plantations dominated by Norway spruce (*Picea abies*)[7]. The main reason for the dominance of spruce plantations in Europe and their preference by foresters is because of their economic value. Forests dominated by this conifer are usually considered to have lower biodiversity than the deciduous forests that once dominated the mainland of Central Europe[8,9]. Thus, one of the most important global actions is the future change of conifer monocultures into stands that support native trees or at least into mixed stands[10,11]. Nevertheless, European beech (*Fagus sylvatica*) forests are still relatively common in the higher elevations of Central Europe[12].

Approximately 10% of the forest area in Europe is in conservation areas[13,14]. Nevertheless, an increase in area of conservation appears not to be the only remedy to protect forest biodiversity. While some authors concluded that conserved forests have higher biological diversity than managed plantations[15,16], others have found that some taxa or species profit from human-managed forests[9,17,18].

Insects and lichens are some of the most-used taxa for the evaluation of forest ecosystem conditions. It is known that most lichens are dependent on veteran trees[19], which are an important element of biodiverse forests[20]. The species richness of lichens is also known to be higher when the forest landscape is more heterogeneous, and a similar situation occurs with insects[21]. In European forest conditions, a long period of time is necessary for

[1]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká, 1176, CZ-165 00, Prague, Czech Republic. [2]Krkonoše National Park, Dobrovského 3, CZ-543 01, Vrchlabí, Czech Republic. [3]University of Hradec Králové, Faculty of Science, Department of Biology, Rokitanského 62, CZ-500 03, Hradec Králové, Czech Republic. Correspondence and requests for materials should be addressed to J.H. (email: jakub.sruby@seznam.cz)

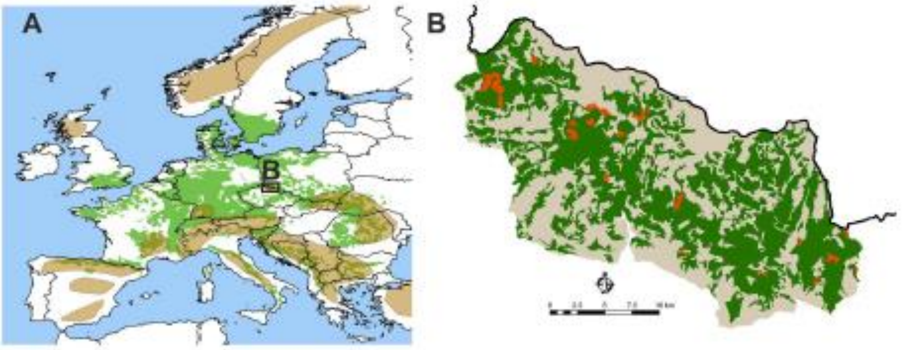


Figure 1. Visualization of the studied area. (**A**) Distribution of mountain beech forests (green) and overlap with highest mountains (brown) in Europe. The study area of Krkonoše (gray) is highlighted by the black frame. (**B**) Distribution of forest cover in Krkonoše is green, studied beech islands are orange.

lichen species to inhabit a suitable area – up to 200 years is suggested to be enough for the creation of a sustainable population of lichens[22,23]. The amount and diversity of dead wood are other important parameters for lichens, as they are known to prefer dead wood in early stages of decay[24,25]. To support threatened lichen species in mountain areas, it is also recommended to enrich spruce stands with broadleaf tree species[26].

Beetles and hymenopterans are among the most species-rich forest taxa. It is often mentioned that managed forests sustain fewer insect species compared to virgin forests[27,28]. One of the most common factors that negatively affects arthropods in forest ecosystems is the total habitat transformation from native tree species to commercial species that are cost effective[29]. It is crucial to obtain more data regarding taxa that are sensitive to different management systems or to abandonment at all[30]. Some of the most important management-sensitive taxa in forest ecosystems are lichens, as they are sedentary organisms with a possible preference for close-to-natural forests, and insects, as they are more mobile taxa with a preference for disturbance.

Our interest was to investigate the role of natural mountain beech (*Fagus sylvatica*) forest islands in the distribution of organisms. We selected three hierarchical levels of the environment that potentially influenced three selected taxa. Specifically, we studied the response of lichens, beetles, and hymenopterans to the topography, forest island patchiness, and individual tree characteristics in the highest mountain ridge in the Czech Republic, Krkonoše. This mountain ridge is part of the oldest Czech national park and is the most isolated within Europe. We also searched for environmental thresholds that may be important for isolated forest islands.

Methods

Study area.

Krkonoše is a 631 km^2 area in the Czech Republic and Poland. It is the oldest national park (est. 1963) and the highest mountain area (Sněžka with 1,603 m a.s.l.) in the Czech Republic, with an area of 385 km^2. Quaternary glaciers influenced its morphology and created extensive plateaus without forest cover specific to the highest mountains in Europe. These plateaus in Krkonoše are partly composed of Dwarf pine (*Pinus mugo*) vegetation at the upper limit of woody vegetation. At the upper tree limit, the vegetation of Dwarf pine is replaced by Norway spruce. The upper limit for forests in Krkonoše is 1,200–1,350 m a.s.l. Forests here are dominated by Norway spruce but also include European beech or mixed forests[31].

This mountain ridge started to be affected by humans at least by the 7th century. From the 14th century, this ridge was mainly affected by extensive deforestation (mainly beech forests) to supply timber for industry in lowlands. The 18th century brought deforestation due to new permanent settlements at high elevations. Forests were then affected by industrial air pollution starting in the middle of the 20th century. This gave rise to the present state of the dominance of Norway spruce stands (79%) partly mixed with the studied natural islands of beech-dominated vegetation[12,31].

Sampling of taxa and environment.

We sampled 128 forest patches (10 m radius surrounding a target tree) inside 16 beech islands (mean = 56.4 ± 5.7 SE ha) distributed in Krkonoše (Fig. 1) using equal-stratified sampling[32] by studying 8 patches per beech island. All beech islands were isolated from each other by forests dominated by Norway spruce. We used a multi-taxa approach; we studied three taxa with different environmental demands. Lichens were visually sampled at 128 target trees at the end of July 2014. Insect taxa of beetles (Coleoptera) and aculeate hymenopterans (Hymenoptera: Aculeata) were sampled using cross-panel trunk tree traps fixed on the south side of each target tree[33]. They were sampled from May to September in 2013 for the 64 patches in the east-central part of Krkonoše and in 2014 for the 64 patches in the west-central part.

We were interested in the influence of the environment at three spatial levels: (i) topographic, (ii) patch, and (iii) tree. Altitude (800.8 ± 12.32 SE; 571.7–1079.4 m a.s.l.) was studied as an important topographical variable reflecting the elevation gradient, which is important for understanding possible shifts in the distributions of species due to climate change[34]. Altitude was not affected by different aspects and the possible effect of gradient inversions, because forests in the Czech part of Krkonoše consist mainly of south-facing slopes.

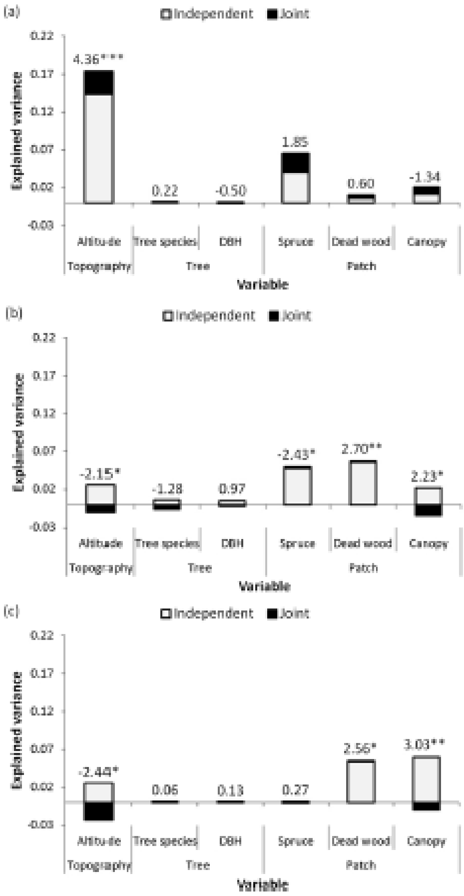


Figure 2. Multi-taxa species richness responses to the environment in Krkonoše National Park in the Czech Republic. The results of hierarchical partitioning (Y-axes) and generalized linear models are visualized for (**a**) Lichenes, (**b**) Coleoptera, and (**c**) Aculeata Hymenoptera; t- or z-values above bars together with significant P-values of GLM are indicated by *For P < 0.05; **For P < 0.01, and ***For P < 0.001. Note that a predictor with a negative shared contribution indicates that other predictors act as its suppressors.

Taxa	Variables	AICc	ΔAICc	P
Lichenes	Altitude + Spruce	565.24	0	—
	Altitude + Spruce + Canopy	565.80	0.56	n.s.
	Altitude	565.94	0.70	n.s.
	Altitude + Canopy	566.87	1.63	n.s.
	Altitude + DBH + Spruce	567.16	1.92	n.s.
	Altitude + Spruce + Deadwood	567.17	1.93	n.s.
Coleoptera	Altitude + Spruce + Deadwood + Canopy	304.42	0	—
	Altitude + Tree + Spruce + Deadwood + Canopy	304.71	0.29	n.s.
	Altitude + DBH + Spruce + Deadwood + Canopy	305.43	1.02	n.s.
	Altitude + Tree + DBH + Spruce + Deadwood + Canopy	305.99	1.57	n.s.
	Spruce + Deadwood	306.29	1.88	n.s.
Aculeata	Altitude + Deadwood + Canopy	453.72	0	—

Table 1. Characteristics of the GLM selection based on data from Krkonoše National Park in the Czech Republic. Best subset GLMs and others with Δ AICc < 2 are listed and ordered by their AICc. P-values are for possible significant drops of Δ AICc.

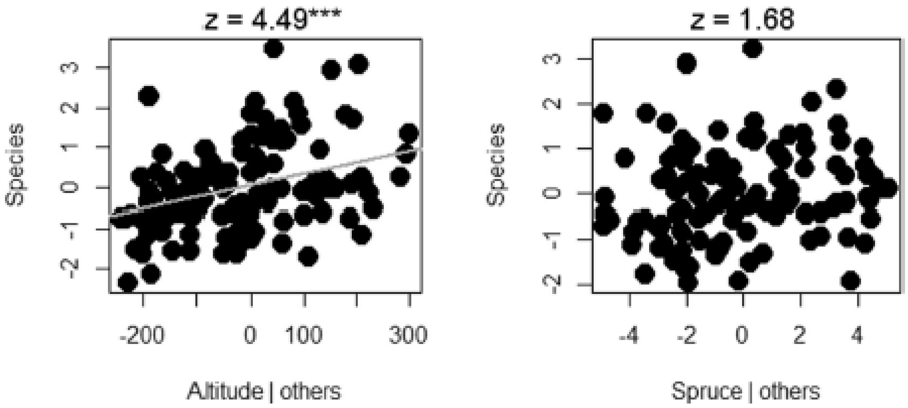


Figure 3. Lichenes species richness response to the environment in Krkonoše National Park in the Czech Republic. The results of partial regression of the best subset of the GLM are visualized by Pearson residuals and gray regression lines for significant responses; z-values together with significant P-values of the GLM are indicated by ***For $P < 0.001$.

Three patch level variables were also studied at a 10-m radius surrounding a target tree[35]. The amount of dead wood (2.2 ± 0.3 SE; 0.1–20.0 m^3) was measured as a reflection of natural disturbances and the sustainable development of forests. Openness in the canopy (12.6 ± 0.5; 4.1–33.8 SE %) was measured as the reflection of gradient of overstory disturbance that influences the microclimate independent of altitude[36]. The canopy was photographed with a Cannon EOS 600D with Sigma circular fish eye DC HSM 4.5 mm 1:2.8 (180° angle) lens at four places in the patch at 1.5 m above the ground. The first two pictures were taken at the top of the trap. The next three pairs of pictures were taken at 5 m from a target tree: the first pair at the north side and the other two pairs at the corners of an equilateral triangle. Pictures were evaluated in GLA 2.0. The cover of spruce (40.3 ± 2.4 SE; 0–100%) in the tree species composition of the overstory was measured as the percentage of this tree species in the crown area of the patch. This was the reflection of artificial plantings and natural regeneration by this conifer tree within beech islands.

We also studied two tree-level characteristics[37] – i.e., the effect of the subject. Specifically, we measured the diameter at breast height (DBH; 49.3 ± 1.1 SE; 28.5–84.6 cm) as a reflection of the potential habitat area for species attracted by the target tree[38,39]. We studied beech (N = 64) and spruce (N = 64) in pairs (i.e., 4 pairs of spruce and beech per forest island). Only mature trees were used as target trees, and we used trees without microhabitats (e.g., tree hollows, conks of fungi or dead limbs).

Statistical analyses. All analyses were done in R 3.0.2.

Dependent variables (species richness of the studied taxa) were first tested for potential spatial bias (using the spdep package) using Moran's I, which was not found for all studied taxa: lichens ($I = -0.01$; $P = 0.71$), beetles ($I = -0.01$; $P = 0.08$) and aculeate hymenopterans ($I = -0.01$; $P = 0.36$).

Independent predictors were tested for potential multicollinearity (package HH) using a criterion of $VIF < 2$, and multicollinearity was not found. The studied beech trees were used for statistical analyses on a semi-quantitative scale and coded as 1, while spruce was coded as 0.

Hierarchical partitioning (package hier.part), a method that informs the explained variance of particular independent variable, was used to compute the independent (by a particular independent variable) and shared explained variance (variance shared with other independent variables).

Initial generalized linear models (GLMs) that included all independent variables were computed with the appropriate distribution (a Poisson distribution for lichen species richness, a Gaussian distribution for square root-transformed beetle species richness, and a quasi-Poisson distribution for aculeate hymenopterans).

Next, GLMs were selected (packages MASS, pgirmess, and nlme) from those that met the criterion of $\Delta AICc < 2$. A χ^2 test was used for the comparison of these models with the best subset model (i.e., the model with the lowest AICc). The differences in AICc did not drop significantly, and thus, the best subset model for each taxon was used for partial regressions.

Partial regressions (package car) of the best subset GLMs were then computed and visualized using Pearson residuals. Visualization illustrates the relationship between dependent and independent variables, with interaction with all other independent variables used in the best subset GLMs.

The conditional inference tree method (package party), from the family of recursive partitioning based on maximally selected rank statistics, was used for the selection of threshold values of independent variables.

Bootstrapping (N = 1000; package boot), a method that allows measures of accuracy to be assigned (defined in terms of confidence intervals) to sample estimates, was used for the computation of 95% confidence intervals of thresholds.

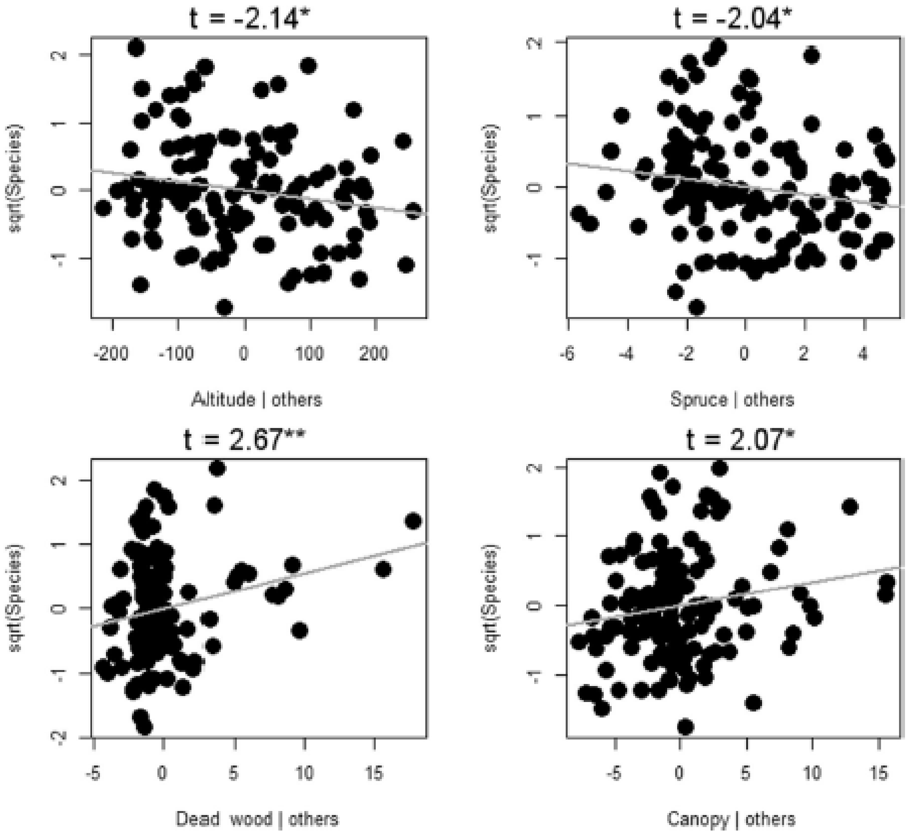


Figure 4. Coleoptera species richness response to the environment in Krkonoše National Park in the Czech Republic. The results of partial regression of the best subset of the GLM are visualized by Pearson residuals and gray regression lines for significant responses; t-values together with significant P-values of the GLM are indicated by *For P < 0.05 and **For P < 0.01.

Results

We observed 37 species of lichens, and trapped 286 species of beetles and 37 species of aculeate hymenopterans.

Variance explained by independent variables. Altitude explained the highest proportion of variance in the case of lichens. This variable was followed by the representation of spruce, but its variance shared with other independent variables was relatively high (Fig. 2a). Spruce and dead wood, followed by altitude and canopy openness, were the independent variables that explained the highest variance in the case of beetles (Fig. 2b). Dead wood and canopy openness were the most influential independent variables regarding the explained variance in the case of aculeate hymenopterans. These two variables were followed by altitude (Fig. 2c). The total and independent effects of other independent variables on species richness were rather low. Canopy openness and altitude were the most negatively influenced by interaction with other independent variables in the case of insect taxa (Fig. 2).

Initial GLMs. Lichens were significantly influenced by topography and increased in species richness toward higher elevations (Fig. 2a). Beetles had the most complex response pattern and were significantly influenced by topography and all studied patch variables. Specifically, their species richness was promoted by increasing the amount of dead wood and openness in the canopy, whereas the effect of an increasing amount of spruce and increasing altitude negatively affected this taxon (Fig. 2b). Aculeate hymenopterans also had a complex response to the environment. They were significantly influenced by topography and some of the patch characteristics, namely, the number of species was negatively affected by rising elevation, while the amount of dead wood and canopy openness had positive effects (Fig. 2c). We did not observe any effect of the subject –, i.e., the target tree on the studied taxa (Fig. 2).

The results of GLM selection. The results of model selection revealed that altitude was the most influential characteristic, included 11 times in the final 12 models selected for all studied taxa. Regarding the patch

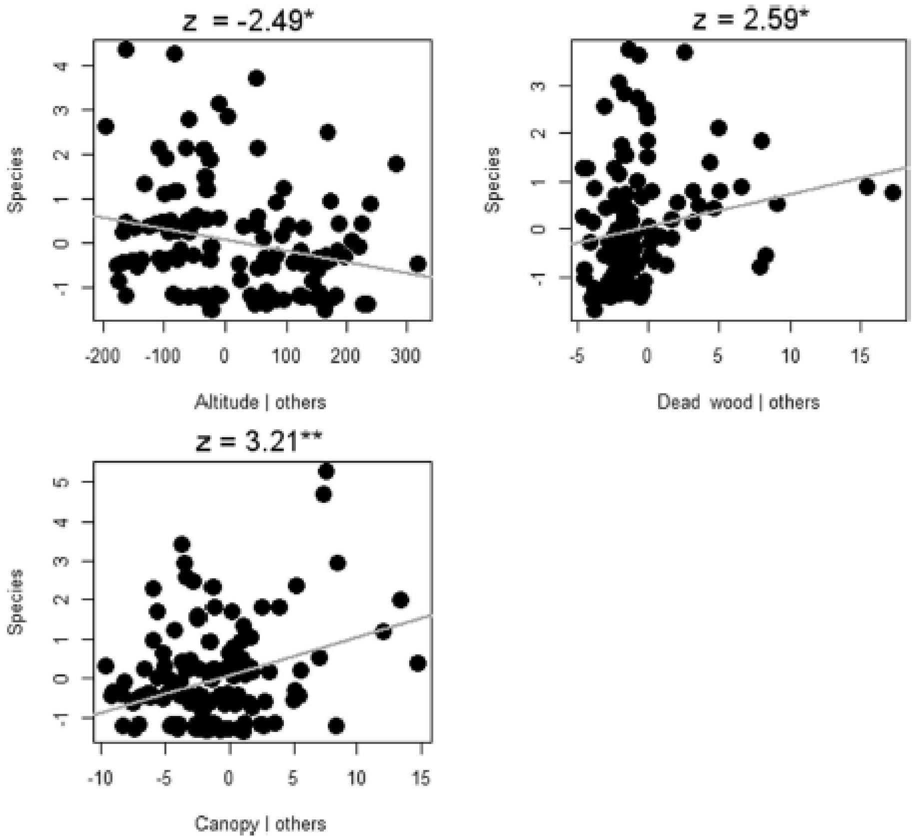


Figure 5. Aculeata Hymenoptera species richness response to the environment in Krkonoše National Park in the Czech Republic. The results of partial regression of the best subset of the GLM are visualized by Pearson residuals and gray regression lines for significant responses; z-values together with significant P-values of the GLM are indicated by *For $P < 0.05$ and **For $P < 0.01$.

parameters, spruce cover was present eight times, and canopy openness and dead wood were present seven times. Tree-level characteristics were included only three times for DBH and twice for the target tree species (Table 1).

The best subset model indicated a significant influence of increasing altitude on the number of species of lichens. The cover of spruce also stayed in the best subset model, but it had no significant effect (Fig. 3). Beetles were negatively affected by increasing elevation and spruce cover, while rising dead wood amounts and openness in the canopy had positive effects (Fig. 4). Aculeate hymenopterans had the same response as beetles, except there was influence from spruce only on beetles (Fig. 5).

Thresholds. Altitude was the only factor that indicated a threshold value for lichen species richness. The threshold was 821.1 m a.s.l., above which the number of species was significantly higher than below. The mean number of species above this altitude was 6.28 at 60 sites, while the mean below this altitude was 3.74 species at 68 sites. The majority of bootstrapped thresholds (95% confidence interval) were between 800 and 825 m a.s.l. (Fig. 6a). The dead wood gradient indicated thresholds for insect taxa. Beetles had a threshold value of 3.8 m^3, and the mean species value above this threshold was 17.74 in 17 sites, while the mean under this value was 13.74 at 111 sites. Aculeate hymenopterans had a lower threshold, at 3.4 m^3 of deadwood, with a mean species value of 3.05 in 19 sites above and a mean of 1.55 below this threshold value at 109 sites. Density plots of bootstrapped thresholds and 95% confidence intervals are visualized in Fig. 6b for beetles and in Fig. 6c for aculeate hymenopterans.

Discussion

We studied the response of biodiversity to the environment in natural beech islands using a multi-taxa approach. Insect taxa were negatively affected by increasing elevation, while lichens showed the opposite response. Given that lichens are highly sedentary and sensitive to changes in the environment, our results suggest that they can become threatened by the future climate change scenario. However, high elevation areas in mountains without forest cover still represent some possible chance for survival of these lichen forest associates. It is questionable whether the shift of their habitat (i.e., beech forest) toward higher elevations would respond to climate change

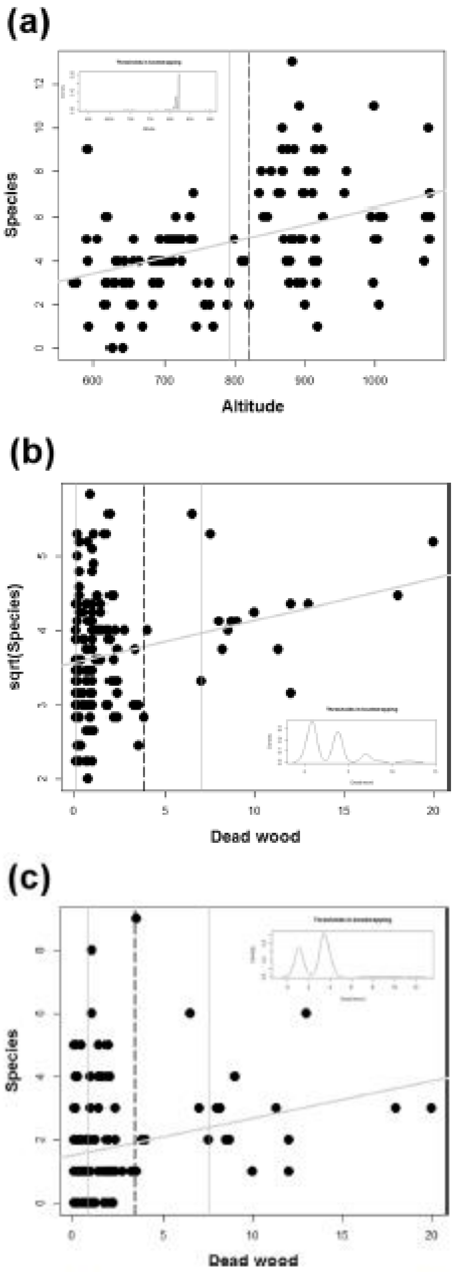


Figure 6. Multi-taxa species richness response to the most important predictor in Krkonoše National Park in the Czech Republic. The results of conditional inference tree methods and bootstrapping are visualized for (**a**) Lichenes, (**b**) Coleoptera, and (**c**) Aculeata; black dashed vertical lines are significant threshold values; thin gray vertical lines are 95% confidence intervals; thick gray lines are linear regressions; and inset frames are the density plots of all thresholds found using bootstrapping.

as quickly as needed for the migration of the lichens. The problem is that some species (e.g., *Graphis scripta* and *Trapelia corticola*) depend on the presence of old trees and sometimes also ancient woodland structures[40]. Thus, their migration lags at least hundreds of years behind the establishment of forest vegetation[41]. Because the dispersal rates of lichens are highly limited, the only chance for their survival in the future appears to be shifts in the ecological requirements of individual species, which is not common but has been observed even in species close to extinction[42]. Nevertheless, because the lichens were significantly influenced only by elevation, we can conclude that this highly isolated mountain ridge might be a good natural laboratory for the study of the possible effects of climate change in the future. Moreover, the threshold value for altitude corresponds with the mean altitude in this study and is also an approximate border between the sub-montane and montane forests in Krkonoše and elsewhere in Central Europe.

Insects were negatively affected by the increasing altitudinal gradient and may not be directly threatened by the ongoing climatic change scenario. Insect taxa were mainly influenced by the patchy structure of beech islands. Thus, they are potentially mainly affected by the increase in changes in patch structure of isolated beech islands. The main potential threat for insects probably comes from a decrease in dead wood connectivity. The observed threshold values (converted per hectare) for dead wood amounts (108.3–121.0 m^3/ha) were relatively optimistic from the point of view of similar forest habitats in Europe[43], yet they were still lower than in the oldest Czech forest reserves[35]. The need for higher dead wood amounts for saproxylic insects in higher elevations is well known[44]. In our case, dead wood amounts reflected natural disturbances and the sustainable development of forests rather than habitat availability, as we did not study only the saproxylic guild. However, it was surprising to observe a positive response to higher canopy openness combined with higher dead wood amounts[44] for both studied insect taxa. The interconnection of the positive effect of increasing dead wood amounts together with the increase of canopy openness (i.e., disturbance causing an increase of local temperatures) is more surprising, since these two environmental variables were not collinear.

The contamination of beech islands by spruce is very important information from the European perspective. This question was important for our research due to the possible influence of spruce on biota in medium and lower altitudes, where this tree is not indigenous. This species is indigenous to the highest parts of mountain forests in Krkonoše[31]. However, its artificial planting in the past makes this species the most important and widespread forest tree in the majority of the country, and the same situation is found in Central Europe. Moreover, Norway spruce is one of the most endangered tree species regarding local increases in temperature[45]. Hence, one of the possible problems is its ongoing planting in lower altitudes[46]. Thus, the management activities intended to decrease the amount of spruce (i.e., artificial interventions in the unmanaged beech forest islands) are important due to the affectation of beetles to increasing spruce cover.

This appears to be an important issue not only from the perspective of mountain ridges but also for other similar tree species through the world. First, Norway spruce is a possible biological contaminant elsewhere in Central Europe; second, spruce might be negativelly affected by the possible increase of temperatures and decrease in precipitation; and third, this could be an example of how important the influence of non-indigenous species on native biota can be. From the first perspective, we can conclude that the spread of spruce might be a threat to beetles. Based on the second perspective, spruce admixture and the creation of mixed mountain forests in the future is probably the only option to preserve the native spruce-associated biota, since stands with a dominance of spruce may disappear in the future climate scenario[47,48]. From the point of view of the third perspective, the removal of the non-indigenous trees in areas of high conservation interest may help biodiversity and conservation.

We did not observe any effect of the subject (i.e., influence of the characteristics of target tree), which is a relatively surprising issue regarding future methodological possibilities. We used only those trees that do not bear any visible microhabitats as target trees[20,37], which probably led to this result. This also showed us the suitability of tree trunk traps instead of those used outside the tree. Specifically, it can be seen that the recorded tree factors did not bias the results. This is also important, as it is known that tree trunk traps are suitable for communities of insects that are less mobile and more specialized, namely, often-trapped flightless species[38,39], which have a strong ability to indicate forest fragmentation[49]. No effect from the subject is also important for future studies that may show us possible temporal change due to climate change, especially because beech trees in mountainous areas will probably grow faster (i.e., increase their DBH) in the future, allowing the use of the same sites for comparison. Nevertheless, it seems that the DBH would play a role even when the tree dies, thereby increasing the amount of dead wood (i.e., during the afterlife of a tree)[50].

Implications for management. From the point of view of the two insect taxa studied, it seems that future climate change, together with low-intervention forest management, would have a positive impact on their species richness. This result needs to be taken with caution, as the response of lichens is not so optimistic.

We can conclude that the most suitable management would be the selective cutting of spruce trees. In addition to lowering the amount of spruce, this option would increase the canopy openness and dead wood amount. This management option should be implemented with the leaving of beech dead wood inside the islands. The natural decline of spruce in the future is also one of the possible options, effectively a hands-off management of beech islands. A majority of spruce trees would die, the canopy would be more open, and the amounts dead wood would increase. Thus, the interaction of hands-off management and climate change might have a positive effect on insects. However, this is a solution only from the point of view of the insect taxa. The solution for lichens is not so simple, and probably, the only management should be based on the resignation of cutting of carefully selected trees, allowing them to reach the proper conditions of veteran trees.

References

1. Messier, C., Puettmann, K. J. & Coates, K. D. Managing forests as complex adaptive systems: building resilience to the challenge of global change (eds Messier, C., Klaus, J. & Puettmann, K.) (London, Routledge, 2013).
2. Bauhus, J., van der Meer, P. & Kanninen, M. Ecosystem goods and services from plantation forests (eds Bauhus, J., van der Meer, P., & Kanninen, M.) (Routledge, 2010).
3. Kotecký, V. Contribution of afforestation subsidies policy to climate change adaptation in the Czech Republic. *Land Use Policy* **47**, 112–120 (2015).

4. Leban, V., Malovrh, Š. P., Stirn, L. Z. & Krč, J. Forest biomass for energy in multi-functional forest management: insight into the perceptions of forest-related professionals. *Forest Policy Econom.* **71**, 87–93 (2015).
5. Simeonova, K. Policies and measures to address climate change in Central and Eastern European Countries. *Appl. Energ.* **56**, 445–461 (1997).
6. Grove, S. J. Saproxylic insect ecology and the sustainable management of forests. *Annu. Rev. Ecol. Syst.* **33**, 1–23 (2002).
7. FOREST EUROPE & UNECE, FAO State. *State of Europe's Forests. Status and Trends in Sustainable Forest Management. Forest EUROPE Liaison Unit Oslo, Aas* (2011).
8. Loskotová, T. & Horák, J. The influence of mature oak stands and spruce plantations on soil-dwelling click beetles in lowland plantation forests. *PeerJ* **4**, e1568 (2016).
9. Mladenović, S. *et al.* The effects of within stand disturbance in plantation forests indicate complex and contrasting responses among and within beetle families. *Bull. Entomol. Res.* **108**, 750–764 (2018).
10. Humphrey, J. W., Ferris, R., Jukes, M. R. & Peace, A. J. The potential contribution of conifer plantations to the UK biodiversity Action Plan. *Bot. J. Scotl.* **54**, 49–62 (2002).
11. Holuša, J. *et al.* Combined effects of drought stress and *Armillaria* infection on tree mortality in Norway spruce plantations. *Forest Ecol. Manage.*, **427**, 434–445 (2018).
12. Fanta, J. Krkonošský národní park 50 let. *Živa* **4**, 157–159 (2013).
13. Bauhus, J., Puettmann, K. & Messier, C. Silviculture for old-growth attributes. *Forest Ecol. Manage.* **258**, 525–537 (2009).
14. Parviainen, J. & Schuck, A. Maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems. *In state of Europe's forests 2011 status and trends in sustainable forest management in Europe* (eds FOREST EUROPE & UNECE, FAO State) 65–97, (2011).
15. Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biol. Conserv.* **81**, 221–231 (1997).
16. Paillet, Y. *et al.* Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* **24**, 101–112 (2010).
17. Jakub H., *et al.* Green desert?: Biodiversity patterns in forest plantations. *Forest Ecology and Management* **433**, 343–348 (2019).
18. Niemelä, J., Koivula, M. & Kotze, D. J. The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. *J. Insect Conserv.* **11**, 5–18 (2007).
19. Uliczka, H. & Angelstam, P. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography* **22**, 396–405 (1999).
20. Horák, J. Insect ecology and veteran trees. *J. Insect Conserv.* **21**, 1–5 (2017).
21. Horák, J. *et al.* Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. *Forest Ecol. Manage.* **315**, 80–85 (2014).
22. Esseen, P. A., Renhorn, K. E. & Pettersson, R. B. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecol. Appl.* **6**, 228–238 (1996).
23. Gauslaa, Y. & Solhaug, K. A. Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forest stands. *Funct. Ecol.* **10**, 344–354 (1996).
24. Dittrich, S., Jacob, M., Bade, C., Leuschner, C. & Hauck, M. The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. *Plant Ecol.* **215**, 1123–1137 (2014).
25. Stokland, J. N., Siitonen, J. & Jonsson, B. G. *Biodiversity in Dead Wood* (eds Stokland, J. N., Siitonen, J. & Jonsson, B. G.) (Cambridge, Cambridge University Press, 2012).
26. Moning, C. *et al.* Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *Forest Ecol. Manage.* **258**, 745–751 (2009).
27. Gibb, H. *et al.* Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scand. J. Forest Res.* **20**, 213–222 (2005).
28. Hilszczański, J., Gibb, H. & Bystrowski, C. Insect natural enemies of Ips typographus (L.)(Coleoptera, Scolytinae) in managed and unmanaged stands of mixed lowland forest in Poland. *J. Pest. Sci.* **80**, 99–107 (2007).
29. Brunet, J., Fritz, O. & Richnau, G. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. *Ecol. Bull.* **53**, 77–94 (2010).
30. Uliczka, H. & Angelstam, P. Assessing conservation values of forest stands based on specialised lichens and birds. *Biol. Conserv.* **95**, 343–351 (2000).
31. Flousek, J., Hartmanová, O., Štursa, J. & Potocki, J. Krkonoše, příroda, historie, život. Miloš Uhlíř – Baset, Praha (2007).
32. Hirzel, A. & Guisan, A. Which is the optimal sampling strategy for habitat suitability modelling. *Ecol. Model.* **157**, 331–341 (2002).
33. Horák, J. Response of saproxylic beetles to tree species composition in a secondary urban forest area. *Urban For. Urban Gree.* **10**, 213–222 (2011).
34. Bässler, C. *et al.* Estimation of the extinction risk for high-montane species as a consequence of global warming and assessment of their suitability as cross-taxon indicators. *Ecol. Indic.* **10**, 341–352 (2010).
35. Horák, J., Kout, J., Vodka, Š. & Donato, D. C. Dead wood dependent organisms in one of the oldest protected forests of Europe: investigating the contrasting effects of within-stand variation in a highly diversified environment. *Forest Ecol. Manage.* **363**, 229–236 (2016).
36. Seibold, S. *et al.* Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *J. Appl. Ecol.* **53**, 934–943 (2016).
37. Horak, J. & Pavlicek, J. Tree level indicators of species composition of saproxylic beetles in old-growth mountainous spruce–beech forest through variation partitioning. *J. Insect Conserv.* **17**, 1003–1009 (2013).
38. Buse, J., Entling, M. H., Ranius, T. & Assmann, T. Response of saproxylic beetles to small-scale habitat connectivity depends on trophic levels. *Landscape Ecol.* **31**, 939–949 (2016).
39. Horák, J., Vodka, Š., Pavlíček, J. & Boža, P. Unexpected visitors: flightless beetles in window traps. *J. Insect Conserv.* **17**, 441–449 (2013).
40. Fritz, Ö., Niklasson, M. & Churski, M. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Appl. Veget. Sci.* **12**, 93–106 (2009).
41. Moning, C. & Müller, J. Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (Fagus sylvatica L.) dominated forests. *Ecol. Indic.* **9**, 922–932 (2009).
42. Horák, J. Threatened or harmful? Opportunism across spatial scales apparently leads to success during extralimital colonisation. *Insect Conserv. Divers.* **9**, 351–357 (2016).
43. Müller, J. & Bütler, R. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *Eur. J. Forest Res.* **129**, 981–992 (2010).
44. Müller, J. *et al.* Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography* **38**, 499–509 (2015).
45. Ge, Z. M. *et al.* Impacts of changing climate on the productivity of Norway spruce dominant stands with a mixture of Scots pine and birch in relation to water availability in southern and northern Finland. *Tree Physiol.* **31**, 323–338 (2011).
46. Röder, J. *et al.* Arthropod species richness in the Norway Spruce (*Picea abies* (L.) Karst.) canopy along an elevation gradient. *Forest Ecol. Manage.* **259**, 1513–1521 (2010).

47. Ge, Z. M., Kellomäki, S., Peltola, H., Zhou, X. & Väisänen, H. Adaptive management to climate change for Norway spruce forests along a regional gradient in Finland. *Clim. Change* **118**, 275–289 (2013).
48. Hlásny, T., Holuša, J., Štěpánek, P., Turčáni, M. & Polčák, N. Expected impacts of climate change on forests: Czech Republic as a case study. *J. Forest Sci.* **57**, 422–431 (2011).
49. Buse, J. "Ghosts of the past": flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. *J. Insect Conserv.* **16**, 93–102 (2012).
50. Bobiec, A., Gutowski, J. M., Zub, K., Pawlaczyk, P. & Laudenslayer, W. F. *The Afterlife of a Tree* (Poland, Warszawa, World Wildlife Fund, 2005).

Acknowledgements

Patrik Rada helped with formatting and Jiří Trombik with map. This study was supported by the grant NAZV KUS QJ1520197 and partly supported by CIGA ČZU 20174307.

Author Contributions

J.H. and J.M. designed the study, J.H. did the analyses, J.H., J.M., J.P.H., P.B. and P.P. discussed the results, S.M. and J.H. wrote the paper, and all authors reviewed the paper.

Additional Information

Competing Interests: The authors declare no competing interests.

Jaké jsou hlavní faktory ovlivňující larvěnku obrovskou? Vliv stromových charakteristik se může lišit na různých prostorvých škálách

What are the most important factors influencing the Giant Springtail? The effect of tree level characteristics could differ at different spatial scales

Strahinja Mladenović, Jan Materna, Tereza Loskotová, Jakub Horák

2019

Insect Conservation and Diversity

Manuskript před odesláním

Insect Conservation and Diversity

What are the most important factors influencing the Giant Springtail? The effect of tree level characteristics could differ at different spatial scales

Strahinja Mladenović[1], Jan Materna[2], Tereza Loskotova[1], Jakub Horak[1*]

[1]Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Department of Forest Protection and Entomology, Kamycka 1176, CZ-165 21, Czech Republic

[2]Krkonoše Mountains National Park, Dobrovského 3, 543 01 Vrchlabí, Czech Republic

*Author for correspondence, e-mail: jakub.sruby@gmail.com

Abstract

1. The Giant springtail, *Tetrodontophora bielanensis*, dwells in litter and higher soil layers, and is also known for its chemical defenses. These blind arthropod, usually lives in humid litter or in soil itself, but also climbs on tree trunks due to search for food. Giant springtail prefers cold climate with ideal temperatures between 8-11 ºC. This is the main reason why its natural habitats are mountain forests and it is considered to be a facultative saproxylic organism.

2. We were interested what are the main factors influencing the Giant Springtail at two spatial scales, namely: What are the most important environmental factors influencing the Giant Springtail at landscape scale? And how is the distribution of the species influenced by tree factors at the site level?

3. We used passive trunk-tree window traps. These traps are highly effective for sampling of even flightless fauna. We used 128 traps in Giant Mts. and 17 traps in Eagle Mts.. in the Czech Republic

4. The Giant springtail was significantly and positively influenced by the presence of Norway spruce at the landscape level. Its distribution in the Giant Mts. was, furthermore, more influence by spatial distribution of samplig sites than other factors of the environment.

5. Even though, it is not obligate saproxylic, it had shown strong deadwood connection and preference. The negative influence of bark coverage and presence of fungi were completed by the positive influence of increasing circumference of particular tree on abundance at the site level.

Introduction

Springtails (Collembola) are considered to be organisms mainly inhabiting soil and litter layers, however it was observed that also forests collembolans compose around a 25% of all canopy faunal density (Ozanne, 1996). Springtails are also found in deadwood which provides nutrients from which these detritivores can benefit. This also includes predators such as ground beetles (Carabidae) and spiders (Araneae) (Chen and Wise, 1999).

The Giant springtail, *Tetrodontophora bielanensis* (Waga, 1842), inhabits mainly litter together with higher soil layers. This species is relativley known for its chemical defenses (Dettner et al. 1996). This blind arthropod usually climbs on tree trunks in search for food, but only when there is sufficient moisture. It prefers cold temperature, ideal temperature between 8-11 ºC. This is the main reason why its natural habitat are mountain ranges. It lives also in the lowlands, but only in close proximity to the watercourses where it has been brought by water from the upper areas and where in valleys can find suitable living conditions (Materna, 2006). It is likely that soil humidity affects the distribution of collembolans at smaller scales (Grear & Schmitz, 2005). In Europe, its common range extends from southern Carpathians in Romania through Ukraine up to the northern mountain ranges in Poland and Czechia (Rusek, 1998). Considered to be marginal saproxylic organisms, living in dead wood, with its soft body, springtails are usually eaten by other predators and this collembolan has an important role in litter decomposition and nutrient cycling (Hopkin, 1997; Rusek, 1998; Addison et al., 2003; Horák, 2016).

As mentioned above decomposed wood debris and dead wood in general represent an important habitat for number of forest organisms (Dynesius et al. 2010). The whole process of decomposition in forest ecosystems is from huge significance to understand what other processes influence forest arthropod communities, including those spaces which are managed by humans (Plewa et al., 2017). Collembola subclass, to which belongs the studied Giant springtail, due to their lower dispersal ability can be used to examine if species level is good unit to obtain valid spatial distribution analysis. (Widenfalk et al., 2018).

Studies dealing with marginal, or rather neglected, saproxylic organisms are still not common, even if these organisms could play improtant role within this highly studied guild. Springtails are one of those most ommited. The most important informations as derived from this study are interconection of two topics. The first is a conspicuous member of a weakly studied saporxylic taxa. The second is combination of two approaches of influence of environment on this taxon, i.e. landscape and site level parameters.

Aims

We were interested what are the main factors influencing the Giant Springtail at two spatial scales, namely:

1. What are the most important environmental factors influencing the Giant springtail at landscape scale?
2. How is the distribution of the species influenced by tree factors at the site level?

We were also interested, if the influence of some factors is different between these two scales.

Methods

Trapping method

We used passive (i.e. non-attractive) window traps. They were placed on tree trunks (i.e. trunk traps). Trunk traps are highly effective for sampling of even flightless fauna (Horak et al. 2013). Each trap consisted of crossed transparent plastic panes (400 × 500 mm), a protective top cover and a funnel leading down into a container holding a solution of water and salt with a detergent. Each trap was placed at a height of 1.3 m facing the south. We used 128 traps in Giant Mts. (one half in 2013 and the rest in 2014) and 17 traps in Eagle Mts. in vegetation season 2009.

Study areas

Giant Mountains (Krkonose)

Study area of nearly 454 sq. km is located mainly in the area of the National Park Krkonose (KRNAP). KRNAP is the oldest national park in the Czech Republic, founded in 1963. From historical perspective, Krkonose Mountains were generally covered by European beech stands, however in last century most of its original tree species were converted into commercially more attractive Norway spruce, which is native to the area, but formerly present only in higher altitudes. All 128 traps were sparsely and randomly placed through the area of the Giant Mts. (50°40'N, 15°48'E). There were 8 locations, each location contained 8 traps, whereas 4 were located in stand where Norway spruce was the most dominant and other 4 in the stand where European beech was the most dominant species.

Eagle Mountains (Orlicke hory)

All traps were placed in the core area of Bukacka (50°20'N, 16°22'E), a very old mountainous spruce-beech forest. This forest had of more than 50 ha and is situated approximately in 1,000 m a. s. l. The area of Bukacka has recently been unmanaged, except of several salvage cuttings over the past decades due to bark beetle (mainly *Ips typhographus*) outbreaks. A smaller part this forest consists of orchid grassland (Hájek & Kučera, 2002).

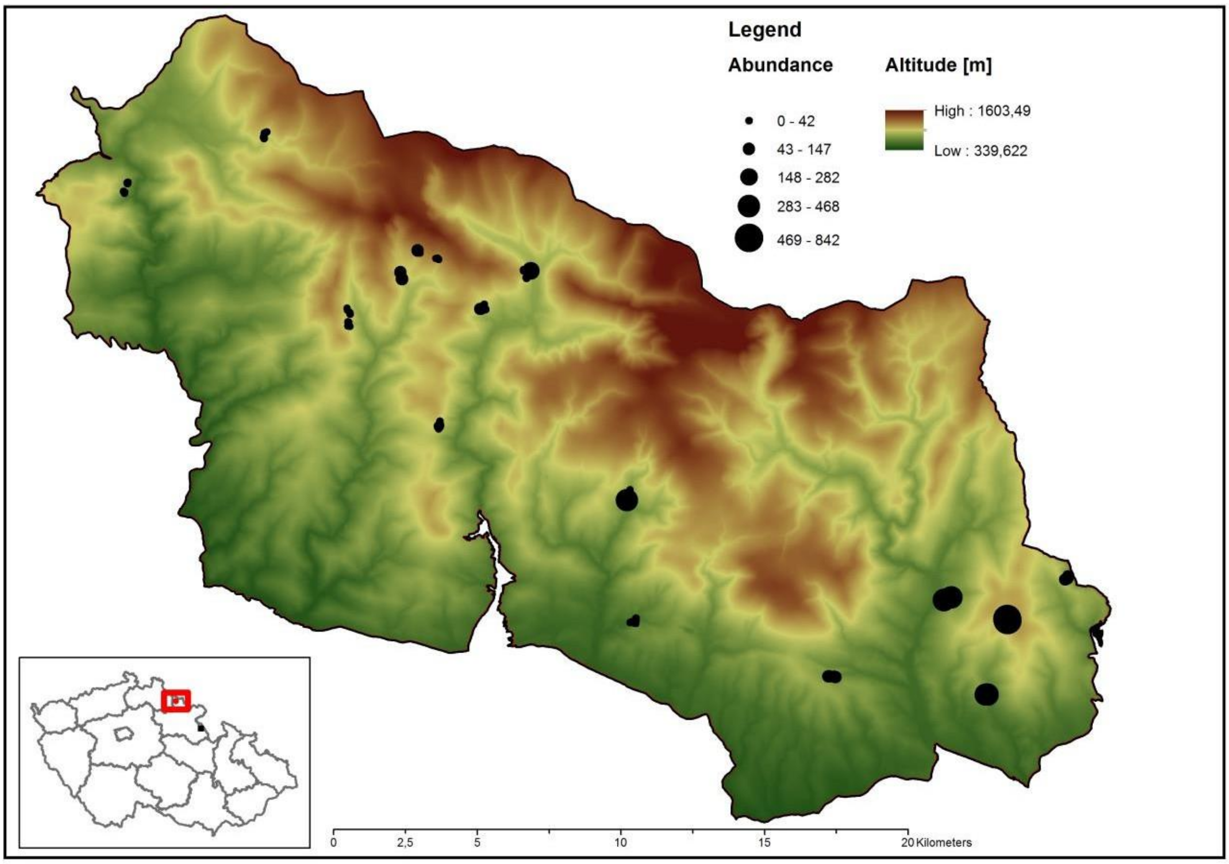


Fig. 1. The studied sites of the Giant Springtail. The frame illustrates the Giant Mts. (red) and Eagle Mts. (black square) and the large area of the Giant Mts. indicates the spatial distribution of studied sites and trapping success (black dots).

Study predictors

Giant Mountains (Krkonose)

We were interested in five environmental predators that were supplemented by two other predictors. Due to standardization of our data, we sampled only living trees without conspicuous presence of microhabitats.

We studied the difference in choice between two *tree species*. Namely, we used paired design – i.e. trap on spruce (n = 64) and beech (n = 64) in each studied forest patch. *Circumference,* as a traditional predictor that reflects DBH, of particular tree was also of our interest (mean = 154.92 ± SE 3.46 cm). Due to highly diversified topography of mountainous area, we were interested in influence of topography reflected by *altitude* (800.80 ± 12.32 m a.s.l.). Each trap was also photographed at the top for the effect of *canopy openness* by fish eye Canon EF-8-15mm f/4L FishEye USM under the full foliage. Photographs were evaluated using Gap Light Analyser 2.0 (16.11 ± 0.53 %). One predictor was also based on character the nearest surrounding of particular sampled tree (i.e. 5 m radius). Namely, we estimated the amount of *dead wood* (2.17 ± 0.31 m^3). As we studied the Giant Springtail in Krkonose during two consequent years, we used the *year of study* as a control for potential temporal bias. *Autocovariate* was used as a control for potential influence of spatial autocorrelation (see *Statistical analyses* section).

Eagle Mountains (Orlicke hory)

We evaluated five tree level predictors that well reflect forest tree microhabitats. Namely, we discriminated *tree species* between spruce (n = 8) and beech (n = 9). *Stage of decay* of the trunk was the second tree level predictor. We have traps on dying trees (n = 5), dead trees (n = 5) and snags (n = 7). We also checked if the trunk was significantly inhabited by wood-inhabiting *fungi* (i.e. presence of fruiting bodies; n = 13). Then we estimated the percentage of *bark coverage* (74.71 ± 5.89 %) on each tree. Finally, we measured the circumference of the tree (161.59 ± 10.14 cm) at 1.3 m above ground.

Statistical analyses

All analyses were done in R 3.0.2.

Data about abundance of the Giant Springtail from the Giant Mts. were cubic-root transformed to reach Gamma distribution and data from the Eagle Mts. were square-root transformed to reach Gaussian distribution.

Both dependent variables were first tested for spatial autocorrelation using Geary’s C test. Abundance of the Giant Springtail was spatially dependent in the Giant Mts. ($C = 0.48$; $P < 0.001$), while not in Eagle Mts. ($C = 0.68$; $P = 0.09$). For a control of a potential spatial bias, we implemented *Autocovariate* of dependent variable in the data set from the Giant Mts. as mentioned above in *Study predictors*.

Temporal bias was controlled using particular year of sampling in the case of Giant Mts. dataset.

For analysis on influence of environmental predictors on the Giant Springtail in the Giant Mts., we used Generalized Linear Mixed-Effect Model (GLMM) using pair of traps (beech and spruce) as a random factor. We used package MASS.

The influence of tree indicators on the Giant Springtail in the Eagle Mts., we used Generalized Linear Model (GLM). Furthermore, we used predictor selection using packages nlme, pgirmes and MASS. The Δ AICc < 2 was used as the criterion for the final GLM selection.

The explained variance of the finally selected tree predictors was analyzed by hierarchical partitioning using package hier.part.

Results

In total, we trapped 18,252 individuals of the Giant springtail (7,592 in Giant Mts. and 10,660 in Eagle Mts.).

Table 1. Influence of environmental predictors on the Giant Springtail in the Giant Mts. using Generalized Linear Mixed Effects Model (significant P-values appear in bold).

Predictor	**t**	**P**
Altitude	1.18	0.24
Tree species (Spruce)	2.61	**0.0114**
Circumference	-1.73	0.09
Dead wood	-0.99	0.33
Canopy openness	0.23	0.82
Year	1.23	0.22
Autocovariate	-4.24	**0.0001**

The giant springtail was significantly and positively influenced by the presence of spruce. Its distribution in the Giant Mts. was, furthermore, influenced by spatial distribution of the study sites (Fig. 1; Table 1). The influence of space is now modern topic, and in fact it means that the distribution of this kind has more influence than the factors of the environment itself, the only one who has been able to hurt the barrier is the influence of the tree, which somewhat confirms the suitability of our design

Table 2. Influence of tree indicators on the Giant Springtail in the Eagle Mts. using Generalized Linear Model (significant P-values appear in bold).

Predictor	**t**	**P**
Tree species (Spruce)	-0.92	0.38
Stage	0.28	0.78
Fungi	-2.26	**0.0448**
Bark	-2.54	**0.0275**
Circumference	1.82	0.10

The results indicated that the Giant Springtail was in the Eagle Mts. significantly negatively affected by presence of fruiting bodies of wood-inhabiting fungi and increasing bark coverage (Table 2).

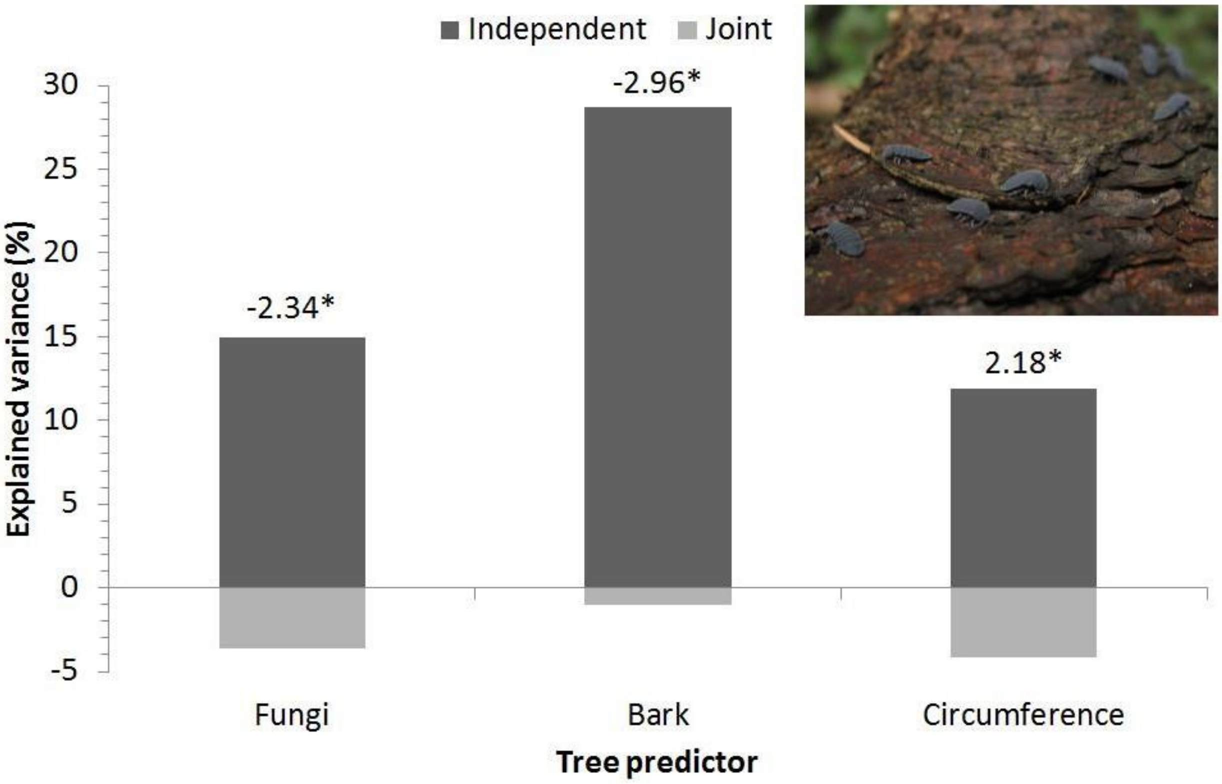


Fig. 2. The influence of tree predictors on the Giant Springtail in the Eagle Mts. after predictor selection. Captions are t-values and * is for P < 0.05. Individuals of the Giant Springtail on the bark of spruce are shown in the frame.

The negative influence of bark coverage and presence of fungi were completed by the positive influence of increasing circumference of particular tree on abundance of the Giant Springtail in the Eagle Mts. (Figure 2).

Discussion

We found that the effect of the space on the Giant springtail was the most importnat at the landscape level, followed by the effect of the tree species. The effect of the site level paramaters was a bit different, partly due to different design, the effect of presence of fungi, bark coveragand also the circumference of tis he tree were the most influnetal tree characteristics. Although we were at the beginning to get a information for the macro- to micro-scale issues affecting saproxylic sprintails, the information on preference to the tree level characteristics at landscape and site level could bring us important informatio regarding ecology of saproxylics. Another facti s that there still occurs a gap, whilst many studies have been carried out that examine the impact of tree diameter and a few studies dealt with microhabitats (Irmler et al., 1996) the impact of tree age is still highly understudied.

It was found out that giant springtail prefers spruce trees on macroscale. In combination with the results from the site level, in the same time those forest stands should have tree microhabitat characteristics of the forest stands after the bark beetle calamity, since they have preferred tree trunks without bark and bracket fungi. However, these results are in contradiction if we compare Giant springtails to some saproxylic beetles, whereas beetles act as vectors for fungi and fungi serve as food for the beetles, which i salso true for some invertabrate predators (Gilbertson, 1984; Wermelinger, 2002). Neverthless, for example Horák and Pavliček (2013) found in the same sites that click beetle, *Ampedus auripes,* prefered dead spruce stems without presence of wood-decaying fungi. The example that is in concordance with the preference of majority of threatened saproxylic beetles is another example that *Hapalaraea pygmaea* in Orlické Mts. prefered high diameter trees. This could be expected for majority of saproxylics since trees with high diameters are known to have positive impact on their diversity (Alexander, 2008).

Besides the Giant springtail, majority of Collembola species can be also assigned as primary decomposers (e.g. *Morulina verrucosa, Seira domestica, Parisotoma notabilis, Folsomia quadrioculata, Isotoma anglicana, Hymenaphorura* sp., *Isotomiella minor*). Keystone processes as nutrient cycling and decomposing, which means mechanically degrading and feeding on dead organic matter (mainly litter and the adhering fungi and bacteria) (Fiera, 2014; Anderson et al. 1981). regarding the avoidance of concks of fungi, Matic and Koledin (1985) found out that Giant springtail, fed on a greater spectrum of fungi in accordance to its availability in soil, however did not feed on bacteria and other groups of soil microorganisms (Matic & Koledin 1985). According to the De Ruiter et al. (1993) in the soil food web, collembolans are considered to be only fungivores. Raschmanová et al. (2008) found out that springtails, including the Giant springtals preffer forest habitat in comparison to the open habitat (pasture) and other forest plots, mainly at the humid sites which are often fungi rich.

Regarding the respinse of springtails at macroscale levels, land use intensification transects set up within eight pan-European countries, and six different bioclimatic zones, in work of Sousa et al. (2006) was found that collembolan taxonomic diversity (including species richness) had not decreased along the intensification gradient, from the unmanaged forest sites to agricultural areas. In fact, the losses in collembolan species within forest habitats, which were becoming fragmented along the gradient, were compensated by the increase in species richness of collembolan species adapted to open areas. This trend was significant along the different European transects across bioclimatic regions (Sousa et al., 2006). This is important information regarding the management possibilities of forests and might reflected the spatial aggregation of abundance of the Giant springtail observed at the landscape level.

One of the proble of comparison of our study with other studies on forest dwelling springtails is the fact, taht we studied the characteristics that are important for saproxylics. Majority of studies on springtails were focused on differences between forest sites, or comparison with open habitats. Another fact is that collembolan richness was negatively correlated with pH, mostly due to the higher richness values found in forest sites which comprised in general more acidic (Da Silva et al., 2016) and such forest soils are also important for some other collembolan species such as *Lipothrix lubbocki* and *Willemia anophthalma* as mentioned in literature (Ponge, 1993; Salmon & Ponge, 1999) and also regarding our result on preference for spruce at the landscape level.

The study with the Collembola species (Anslan et al., 2016) revealed their capability to transport viable spores on body surface and in guts. This is in coincidence with their affinity to fungi as mentioned above, but not to the avoidance to the conks of fungi in our study. As predicted, collembolans' fungal diet consisted mainly of saprotrophic fungi. Neverthless, majority of observed wood-inhabiting fungi species were could be also classified as saportropihic. Although we did not perform spore germination and inoculation trials, our results suggest that the high diversity of Collembola-fungal associations may provide a powerful alternative to aerial dispersal of fungal propagules. Therefore, these soil arthropods should be considered as important biological factors that may have a significant impact on fungal communities, which further influence litter decomposition and nutrient cycling and moderate plant and fauna health (Anslan et al, 2018). One of possible reasons of different response of our study species is the fact of its overabundance in comparison of other sprintails. This means that this species was absolutely dominant and regarding its body mass and population density, this species could act as supressor on other springtails which are more or less dispersers of fungi.

The focus on landscape scale should be of higher importance regarding the future management of forests in Europe. However, regarding the information of response of the studied springtail to the microbabitats, we partly fill the gap of knowlegde of response of saproxylics to this veteran tree characteristic – even if some studied trees were dead.

Conclusion

The Giant springtail was significantly and positively influenced by the presence of the Norway spruce atthe landscape level, which is important information as this species is affected by future climate change (Pretzsch et al., 2014; Schlyter et al., 2006) and also lowering of its representation in conservation oriented forests (Mladenović et al., 2018). Its distribution in the Giant Mts. was, furthermore, influenced by spatial distribution of the study sites, which was the most probaly caused by the different managemtn regimes of studied sites in the past. The negative influence of bark coverage and presence of fungi were completed by the positive influence of increasing circumference of particular tree on abundance of the Giant Springtail in the Eagle Mts., which indicated the preference for highly diversified tree-habitat. These results might be improtant arguments for more diversified management in studied mountain forests, especially for management of spruce stands in protected areas.

Acknowledgement

This study was supported from the project grants CIGA 20154301 CULS Prague and NAZV KUS QJ1520197 ENREFO. We are grateful to the Mr Jan Pavlíček for help with data collection in Bukačka Area (Eagle Mts.), Ms Veronika Špidlenová (KRNAP) for GLA and Mr Patrik Rada for counting individuals of Giant Springtails from KRNAP location.

References

Addison, J.A., Trofymow, J.A., Marshall, V.G. (2003) Functional role of Collembola in successional coastal temperate forests on Vancouver Island. *Canadian Journal of Applied Soil Ecology*, **24**, 247–261.

Alexander, KNA (2008) Tree biology and saproxylic Coleoptera: issues of definitions and conservation language. *Revue d Ecologie,* **63**, 1–5.

Anderson, R.V., Coleman, D.C., Cole, C.V. (1981) Effects of saprotrophic grazing on net mineralization – Role of soil fauna. In: Clark, F.E., Rosswall, T. (eds) Terrestrial nitrogen cycles: processes, ekosystém strategies and management impacts. *Ecological Bulletins,* **33**, 201–216.

Anslan, S., Bahram, M., Tedersoo, L. (2016) Temporal changes in fungal communities associated with guts and appendages of Collembola as based on culturing and highthroughput sequencing. *Soil Biology and Biochemistry,* **96**, 152–159.

Anslan, S., Bahram, M., Tedersoo, L. (2018) Seasonal and annual variation in fungal communities associated with epigeic springtails (Collembola spp.) in boreal forests. *Soil Biology and Biochemistry,* **116**, 245–252. In Q. B. Wheeler, M., editor. Fungus-insect relationships: Perspectives in ecology and evolution. Columbia University Press, New York, pp. 130-165.

Da Silva, P.M., Carvalho, F., Dirilgen, T., Stone, D., Creamer, R., Bolger, T., Sousa, J.P. (2016) Traits of collembolan life-form indicate land use types and soil properties across an European transect. *Applied Soil Ecology,* **97**, 69–77.

De Ruiter, P. C. Van Veen, J. A. Moore, J. C., Brussaard, L. Hunt, H. W. (1993) Calculation of nitrogen mineralization in soil food webs. *Plant and Soil,* **157/2**, 263–273.

Dettner, K., Scheuerlein, A., Fabian, P.,Schultz, S., Francke, W. (1996) Chemical defense of giant springtail Tetrodontophora bielanenesis (Waga) (Insecta: Collembola). *Journal of Chemical Ecology*, **22**, 1051–1074.

Dynesius, M., Gibb, H., Hjalten, J. (2010) Surface Covering of Downed Logs: Drivers of a Neglected Process in Dead Wood Ecology. *PLOS ONE,* **5/10**, e13237.

Fiera, C. (2014) Application of stable isotopes and lipid analysis to understand trophic interactions in springtails. *North-Western Journal of Zoology,* **10/2**, 227-235.

Gilbertson, R. L. (1984) Relationships between insects and wood-rotting Grear, J.S., Schmitz, O.J., 2005. Effects of grouping behavior and predators on the spatial distribution of a forest floor arthropod. *Ecology,* **86**, 960–971.

Hájek J., Kučera J. et al. (2002) *Orlické hory*. – In: Faltysová H., Mackovčin P., Sedláček M. (eds.), *Chráněná území ČR,* **5**, 273–315. Agentura ochrany přírody a krajiny ČR a Ekocentrum Brno, Praha.

Hopkin, S.P. (1997) *Biology of the Springtails*. Oxford University Press, Oxford.

Horák J., Pavliček, J. (2013) Tree level indicators of species composition of saproxylic beetles in old-growth mountainous sprucebeech forest through variation partitioning. *Journal of Insect Conservation*, **17**, 1003–1009.

Horák, J. (2016) Organismy vázané na mrtvé dřevo III. Marginální skupiny bezobratlých/Saproxylic organisms III. Marginal groups of invertebrates. *Lesnická práce,* **2016/3**, p. 36.

Chen, B., Wise, D.H. (1999) Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology,* **80**, 761–772.

Irmler U, Heller K, Warning J (1996) Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). *Pedobiologia,* **40**, 134–148.

Lonsdale, D (2013) *Ancient and other veteran trees: further guidance on management*. The Tree Council, London.

Materna, J., (2006) Larvěnka obrovská - obr mezi chvostoskoky. *Časopis Krkonoše - Jizerské hory,* **10-11**, 2006/10.

Matic, R., Koledin, D. (1985) Preference and feeding specificity of tetrodontophora-bielanensis (Collembola, Insecta) under laboratory conditions. *Revue d´Ecologie et de Biologie du Sol.*

Mladenović, S., Loskotová, T., Boháč, J., Pavlíček, J., Brestovanský, J., Horák, J. 2018. The effects of within stand disturbance in plantation forests indicate complex and contrasting responses among and within beetle families. *Bulletin of Entomological Research*. doi:10.1017/S0007485317001304.

Ozanne, C.M.P. (1996) Arthropod communities of coniferous forest trees. *Selbyana,* **17**, 43–49.

Plewa, R., Jaworskia, T., Hilszczańskia, J., Horák, J. (2017) Investigating the biodiversity of the forest strata: The importance of vertical stratification to the activity and development of saproxylic beetles in managed temperate deciduous forests. *Forest Ecology and Management,* **402**, 186–193.

Ponge, J.F., (1993) Biocenoses of Collembola in Atlantic temperate grass-woodland ecosystems. *Pedobiologia,* **37**, 223–244.

Pretzsch, H., Biber, P., Schutze, G., Uhl, E., Rotzer, T. (2014) Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Communications,* **5**, 4967.

Raschmanová, N., Kováč, L., Miklisová, D. (2008) The effect of mesoclimate on Collembola diversity in the Zádiel Valley, Slovak Karst (Slovakia). *European Journal of Soil Biology,* **44**, 463–472

Rusek J. (1998) Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity and Conservation,* **7**, 1207-1219.

Salmon, S., Ponge, J.F. (1999) Distribution of Heteromurus nitidus (Hexapoda, Collembola) according to soil acidity: interactions with earthworms and predator pressure. *Soil Biology and Biochemistry,* **31**, 1161–1170.

Schlyter, P., Stjernquist, I., Barring, L., Jonsson, A.M., Nilsson, C. (2006) Assessment of the impacts of climate change and weather extremes on boreal forests in Northern Europe, focusing on Norway spruce. *Climate Research,* **31**, 75-84.

Sousa, J.P., Bolger, T., da Gama, M.M., et al. (2006) Changes in Collembola richness and diversity along a gradient of land-use intensity: A pan European study. *Pedobiologia,* **50/2**, 147-156.

Wermelinger, B. (2002) Development and distribution of predators and parasitoids during two consecutive years of an Ips typographus (Col., Scolytidae) infestation. J. *Applied Entomology*, **126**, 521–527.

Widenfalk, L. A., Leinaas, H. P., Bengtsson, J., Birokemoe, T. (2018) Age and level of self-organization affect the small-scale distribution of springtails (Collembola). *Ecosphere,* **9(1),** e02058.

5. DISKUZE, ZÁVĚR A DOPORUČENÍ PRO PRAXI

Integrovaný přístup k zachování krajinné mozaiky je mnohem účinnější než zastaralý systém ochrany přírody, který je založený pouze na různých kategoriích chráněných území (Bennett, 2003).

Při pěstování lesů se stejnověkým porostem obvykle dochází k tomu, že se část mrtvého dřeva obvykle ponechává při holoseči. Následně dojde k velmi malému zvýšení objemu mrtvého dřeva, a to až do okamžiku, kdy dochází k prořezávce (až 40-70 let po holoseči). Během tohoto období je mrtvé dřevo téměř nedostupné (Stenbacka et al., 2010).

Lesní hospodaření napodobující přirozené disturbance by mělo posílit heterogenitu porostu, čímž by mělo dojít ke zvýšení biologické rozmanitosti (Kuuluvainen, 2009). Výše popsané lesní hospodářství by mohlo být prováděno v lesích s nízkou ochranou, což by mohlo přispět ke zlepšení jejich funkce z hlediska biologické rozmanitosti (Horák et al., 2016).

Horák et al. (2016) dále ve své práci uvádí, že saproxyličtí brouci upřednostňuji vyšší úrovně expozice slunečního záření, zatímco kvalita a množství mrtvého dřeva byly méně důležitým parametrem. To naznačuje jejich vyšší adaptabilitu k malým disturbancím ve starých lesních porostech. Každopádně, zranitelnost saproxylických brouků na fragmentaci lesů ukazuje, že některé druhy se vyskytují výhradně v místech s vysokou konektivitou mrtvého dřeva a reagují na jeho prostorovou konektivitu v okruhu 150 metrů (Schiegg, 2000b). Ulyshen (2011) obecně doporučuje, že udržovat rozmanitost rostlinných společenstev je velice důležité, a to včetně eliminace a kontroly invazních rostlin.

Smrk a biodiverzita

Jehličnaté hospodářské lesy jsou přirozeným prostředím pro některé druhy brouků, a proto by měly být použity specifické nástroje lesního hospodářství (např. podpora diverzifikované druhové skladby dřevin), aby se nejen zabránilo úbytku biologické rozmanitosti, ale také přispělo k ochraně vzácných a ohrožených druhů. Jedním z příkladů jsou kovaříkovití, kteří preferují smrkové monokultury před dubovými porosty (to se nevztahuje na tesaříkovité, kteří byly negativně ovlivněny přeměnou porostů listnatých lesů na jehličnaté monokultury). I když larvěnka obrovská nepatří do taxonů brouků, svým chováním významně napodobuje některý saproxylický hmyz, zároveň byla pozitivně ovlivněna přítomností smrku ztepilého v úrovni krajiny, což je důležitá informace pro tento klimatickými změnami ohrožený druh.

Velikost porostu

Když vezmeme v úvahu schopnost regenerace přírody, jednou z důležitých otázek týkajících se budoucnosti holosečných porostů je skutečnost, že heterogenita skladby dřeva je potenciálně vyšší ve větších oblastech, ve srovnání se těžbou menšího rozsahu. Parametry jako jsou abundance, velikost těla a míra ohroženosti tesaříkovitých se zvyšovala se zvětšením plochy porostu. Zvětšující se plocha porostu také měla pozitivní vliv na rozmanitost a délku těla drabčíkovitých. S ohledem na množství mrtvého dřeva, kterého je v hospodářských lesích obecně málo, (Kirby et al., 1998) dospěl k závěru, že velikost porostu by mohla snadno přispět ke zvětšení množství a objemu mrtvého dřeva, které by bylo stanovištěm saproxylických organismů v hospodářských lesích.

Dalším důležitým bodem je skutečnost, že právní omezení lesního hospodářství se zdají být ve většině zemí ve střední Evropě velice přísná. Například holoseče v České republice mohou být provedeny ve většině případů pouze do 1 ha, zatímco některé čeledi brouků a jejich studované vlastnosti reagovaly na rostoucí plochu lesního porostu, kde největší plocha překročila 3 ha. Například ve Skandinávii jsou povoleny holoseče většího rozsahu. Jsou však regulovány konkrétními nástroji ochrany (např. udržování zelených stromů a mrtvého dřeva), které by mohly ochránit biodiverzitu lesa.

Otevřenost zápoje

Většina velkých hospodářských lesů byla podrobena lesnímu hospodaření s nízkou otevřeností zápoje za předpokladu, že budou odolnější proti větru. Jak už bylo zmíněno, kovaříkovití preferovali smrkové monokultury před dubovými porosty. Tento překvapivý výsledek lze vysvětlit pozitivním vlivem rostoucí otevřenosti zápoje v porostu. Čtyři z pěti druhů tesaříkovitých, které významně reagovaly na otevřenost zápoje, jsou více spojovány s rostoucí otevřenosti zápoje, na rozdíl od drabčíkovitých, kteří na otevřenost zápoje nereagovali.

Původní a nepůvodní dřeviny

Původní vegetace plní důležitou roli stanovištního ostrova v hospodářských lesích. Tyto fragmenty by mohly poskytovat zázemí většímu počtu jedinečných a mnohdy i chráněných druhů. Hospodářské lesy nepůvodních stromů nejsou vždy považované za zelené pouště. Podobné modely biologické rozmanitosti můžeme pozorovat i v jiných ekosystémech. Na základě výzkumu osmi skupin s rozlišnými disperzními schopnostmi, taxonomickými příslušnostmi a ekologickými požadavky a kombinovali je s různými environmentálními charakteristikami reflektující podmínky monokultur po celém světě. První klíčovou otázkou pozměňovacích návrhů týkajících se biologické rozmanitosti pro výsadbu lesa při očekávané budoucí expanzi je udržení a obnovení původní vegetace.

Doporučení pro lesní hospodářství je přinejmenším zachovat původní listnaté druhy dřevin, které by pomohly obnovit, vytvořit a propojit nové ostrovy listnatých stromů (Webb et al., 2008). Navzdory tomu, že je přirozená regenerace dubů mnohdy považována za složitý a komplikovaný proces (Annighöfer et al., 2015), její výhodou je zachování rozmanitosti brouků. Stav prostředí v přírodních bukových ostrovech s využitím přístupu založeného na multi-taxe naznačuje, že nejvhodnějším řešením by bylo selektivní kácení smrků. Tato možnost by zvýšila otevřenost zápoje a množství mrtvého dřeva. Bezzásahové hospodaření v bukových ostrovech spočívá v tom, že většina smrků by odumřela a následně by se zápoj více otevřel, což by vedlo ke zvýšení množství mrtvého dřeva v těchto porostech.

Do budoucna bude velmi důležité navrhnout složení a péči o hospodářské lesy tak, aby lépe poskytovaly sociálně-ekonomické benefity (například rekreační, sportovní a relaxační aktivity), mimoprodukční funkce lesa (například snižování emisí prachu a produkce hub a ovoce) i ekologické služby (biodiverzita).

6. LITERATURA A REFERENCE

Albuquerque F.S., Rueda M. 2010. Forest loss and fragmentation effects on woody plant species richness in Great Britain. Forest Ecology and Management 260, 472–479

Alexander, K.N.A. 2008. Tree biology and saproxylic Coleoptera: issues of definitions and conservation language. Revue d'Ecologie (la Terre et la Vie), 63, 1-5.

Annighöfer, P., Beckschäfer, P., Vor, T. & Ammer, C. 2015. Regeneration patterns of European oak species (Quercus petraea (Matt.) Liebl., Quercus robur L.) in dependence of environment and neighborhood. PLoS ONE 10(8), e0134935.

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., … Winter, M. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proceedings of the Royal Society B: Biological Sciences, 281(1780).

Bauhus, J., Van der Meer, P. & Kanninen, M. 2010. Ecosystem. Goods and Services from Plantation Forests. Earthscan, Oxon, s. 1–240.

Bennett, A.F., 2003. Linkages in the Landscape: the Role of Corridors and Connectivity in Wildlife Conservation. IUCN, Gland, Switzerland and Cambridge, UK, Margate, UK.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132, 39-50.

Boháč, J., Matějíček, J. 2003. Katalog brouků Prahy, svazek IV, Drabčíkovití – Staphylinidae. Flóra, Praha, 256 pp.

Bonan, G.B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444-1449.

Bouchard, P., Grebennikov, V.V., Smith, A.B., Douglas, H. 2009. Biodiversity of Coleoptera. Insect Biodiversity: Science and Society. Willey Interscience.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vie, J.C., Watson, R. 2010. Global biodiversity: indicators of recent declines. Science 328, 1164-1168.

Bütler, R., Angelstam, P., Ekelund, P., Schlaepfer, R. 2004. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biological Conservation 119, 305-318.

Della Rocca, F., Stefanelli, S., Pasquaretta, C., Campanaro, A., Bogliani, G. 2014. Effect of deadwood management on saproxylic beetle richness in the floodplain forests of northern Italy: some measures for deadwood sustainable use. Journal of Insect Conservation 18, 121-136.

Dettner, K., Scheuerlein, A., Fabian, P.,Schultz, S., Francke, W. 1996. Chemical defense of giant springtail Tetrodontophora bielanenesis (Waga) (Insecta: Collembola). Journal of Chemical Ecology 22, 1051–1074.

Di Filippo, A., Biondi, F., Maugeri, M., Schirone, B., Piovesan, G. 2012. Bioclimate and growth history affect beech lifespan in the Italian Alps and Apennines. Global Change Biology 18, 960-972.

Druhá ministerská konference o ochraně lesů v Evropě, 1993. Ministerská konference o ochraně lesů v Evropě, 16.-17. Června 1993. Dokumenty. Ministerstvo zemědělství a lesnictví, Finsko. Helsinki.

Ewers, R.M., Didham, R.K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81, 117–142.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34, 487-515.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management. 61, 603-610.

FAO, 2007. State of the World’s Forests 2007. Food and Agriculture Organization of the United Nations, Rome. Online: http://www.fao.org/3/a-a0773e.pdf , cit. 01.05.2017.

Forest Europe, 2015: State of Europe’s Forests 2015. Online: http://foresteurope.org/state-europes-forests-2015-report/, cit. 01.06.2018.

Forman, R.T.T. 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge. 632 s. ISBN: 9780521479806

Geburek, T., Myking, T. 2018. Evolutionary consequences of historic anthropogenic impacts on forest trees in Europe. Forest Ecology and Mangement 422, 23-32.

Gessler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H. 2007. Potential risks for European beech (Fagus sylvatica L.) in a changing climate. Trees 21 (1), 1–11.

Gossner, M.M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W., Müller, J. 2013. Current near-to-nature forest management effects on functional trait composition of saproxylic beetles i n beech forests. Conservation Biology 27, 605-614.

Grove, S. 2002a. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation 104, 149-171

Grove, S.J. 2002b. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology, Evolution, and Systematics 33, 1–23.

Hannah, L., Carr, J.L., Lankerani, A. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation 4, 128-155.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133–302.

Hofmeister, J., Hošek, J., Brabec, M., Kocvara, R. 2017. Spatial distribution of bird communities in small forest fragments in central Europe in relation to distance to the forest edge, fragment size and type of forest. Forest Ecology and Management 401, 255-263.

Holuša, J. 2004. Health condition of Norway spruce Picea abies (L.) Karst stands in the Beskid Mts. Dendrobiology 51(Suppl.), 11-17.

Horák J, Kout J, Vodka Š, Donato D.C. 2016. Dead wood dependent organisms in one of the oldest protected forests of Europe: Investigating the contrasting effects of within-stand variation in a highly diversified environment. Forest Ecology and Management 363, 229-236.

Horak J. 2014. Fragmented habitats of traditional fruit orchards are important for dead-wood dependent beetles associated with open canopy deciduous woodlands. Naturwissenschaften 101, 499-504.

Horák, J., Chumanová, E., Hilszczanski, J. 2012. Saproxylic beetle thrives on the openness in management: a case study on the ecological requirements of Cucujus cinnaberinus from Central Europe. Insect Conservation and Diversity 5, 403-413.

Horák, J. 2017. Insect ecology and veteran trees. Journal of Insect Conservation 21, 1–5.

Horák, J., Vodka, S., Kout, J., Halda, J.P., Bogusch, P., Pech, P. 2014. Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. Forest Ecology and Management 315, 80-85.

Horák, J. 2016. Threatened or harmful? Opportunism across spatial scales apparently leads to success during extralimital colonisation. Insect Conserv. Divers. 9, 351–357.

Humphrey, J., Bailey, S. 2012. Managing deadwood in forests and woodlands. Forestry Commission Practice Guide. Forestry Commission, Edinburgh. i–iv, 1–24 s.

Chapin, III F.S., Zavaleta E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper D.U., Lavorel S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S. 2000. Consequences of changing biodiversity. Nature 405, 234-242.

Janssen, P., Fortin D., Hébert C. 2009. Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales. Ecography 32:423–432.

Kirby, K.J., Reid, C.M., Thomas, R.C., Goldsmith, F.B. 1998. Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. Journal of Applied Ecology 35(1), 148-155.

Knight, E.C., Mahony, N.A., Green, D.J., 2014. Crop type influences edge effects on the reproduction of songbirds in sagebrush habitat near agriculture. Avian Conservation Ecology 9 (1), 8s.

Kraus, D., Krumm F. 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute.

Kruys, N., Fries, C., Jonsson, B.G., Lämås, T., Ståhl, G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (Picea abies) trees in managed Swedish boreal forests. Canadian Journal of Forest Research 29,178-186.

Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity c hallenge. Ambio 38, 309-315.

Laibner, S. 2000. Elateridae of the Czech and Slovak Republics. Kabourek Nakladatelstvi, Praha. ISBN-13: 978-8090146624.

Lachat, T., Wermelinger B., Gossner M.M. Bussler, H., Isacsson, G., Muller, J. 2012. Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. Ecological Indicators 23:323–331.

Langor, D.W., Hammond, H.E.J., Spence, J.R., Jacobs, J., Cobb, T.P. 2008. Saproxylic insect assemblages in Canadian forests: diversity, ecology, and conservation. Canadian Entomologist 140, 453–474.

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C. 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators 11, 1027-1039.

Lee, S., Spence J.R., Langor D.W., Pinzon, J. 2015. Retention patch size and conservation of saproxylic beetles in boreal white spruce stands. Forest Ecology and Management 358 (2015) 98–107.

Lehmkuhl, J.F., Gould, L.E., Cazares, E., Hosford, D.R. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management 200, 49-65.

Lindenmayer, D.B., Franklin, J.F. 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington, D.C.

Lindenmayer, D.B., Cunningham, S.A. & Young, A., editors. 2012. Land use intensification: effects on agriculture, biodiversity and ecological processes . CSIRO Publishing, Melbourne.

Lindhe, A, Asenblad, N., Torenson H-G. 2004. Cut logs and high stumps of spruce, birch, aspen and oak- nine years of saproxylic fungi succession. Biological Conservation 119, 443–454.

Linke, J., Betts, M.G., Lavigne, M.B., Franklin, S.E. 2007. Structure, function and change of forest landscapes. In: Wulder, M.A., Franklin, S.E. (Eds.), Under-standing Forest Disturbance and Spatial Pattern: Remote Sensing and GIS Approaches. Taylor and Francis, Boca Raton, FL, s. 1–29.

Lord, J.M., Norton, D.A., 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4 (2), 197-226.

MacArthur, R.H., Wilson, E.O. 1976. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

Materna, J. 2006. Larvěnka obrovská - obr mezi chvostoskoky. Časopis Krkonoše - Jizerské hory, 10-11, 2006/10.

Mather, A.S. 2001. Forests of Consumption: Postproductivism, Postmaterialism, and the Postindustrial Forest. Environment and Planning C: Politics and Space 19, 249-268.

Mladenović, S., Loskotová, T., Boháč, J., Pavlíček, J., Brestovanský, J., Horák, J. 2018. The effects of within stand disturbance in plantation forests indicate complex and contrasting responses among and within beetle families. Bulletin of Entomological Research. doi:10.1017/S0007485317001304.

Moilanen A., Hanski I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79:2503–2515.

Müller J., Büssler H., Bense U., Brustel, H, Flechtner, G, Fowles, A, Kahlen, M, Möller, G, Mühle, H, Schmidl, J, Zabransky, P. 2005. Urwald relict species – Saproxylic beetles indicating structural qualities and habitat tradition. Waldökologie Online 2:106–113.

Müller, J., Hothorn, T., Pretzsch, H. 2007. Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech, Fagus sylvatica L. Forest Ecology and Management 242:297–305.

Neuhauselova Z et al. 2001. Map of potential natural vegetation of the Czech Republic. Academia, Praha.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45-50.

Nieto, A., Alexander, K.N.A. 2010. European Red List of Saproxylic Beetles. Publications Office of the European Union, Luxembourg.

Parisi, F., Lombardi, F., Sciarretta, A., Tognetti, R., Campanaro, A., Marchetti, M., Trematerra, P. 2016. Spatial patterns of saproxylic beetles in a relic silver fir forest (Central Italy), relationships with forest structure and biodiversity indicators. Forest Ecology and management 381, 217-234.

Parviainen, J. 2005. Virgin and natural forests in the temperate zone of Europe. Forest Snow and Landscape Research 79, 9-18.

Perlin, J. 1988. A Forest Journey. Norton, NY. ISBN-10: 0881506761

Polyakov, M., Majumdar, I., Teeter, L. 2008. Spatial and temporal analysis of the anthropogenic effects on local diversity of forest trees. Forest Ecology and Management 255, 1379-1387.

Rosson, J.F., Jr., Amundsen, C.C. 2004. Monitoring tree species diversity over large spatial and temporal scales. In: Gen. Tech. Rep. SRS–75. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, 335–345s (Kapitola 28).

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B., Walker, M., Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. Science 287 (80-), 1770-1774.

Sargent, C., Bass, S. 2013. Plantation Politics: Forest Plantations in Development. Routledge Press, London. ISBN 9781138939219

Seibold, S., Bässler, C., Brandl, R., Gossner, M.M., Thorn, S., Ulyshen, M.D., Müller, J. 2015. Experimental studies of deadwood biodiversity-A review identifying global gaps in knowledge. Biologiocal Conservation 191, 139-149.

Seidl, R., Rammer, W., Spies, T. 2014. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecological Applications 24, 2063-2077.

Schelhaas, M.-J., Nabuurs, G.-J., Schuck, A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology 9, 1620-1633.

Sláma, E.F. 1998. Cerambycidae of the Czech and Slovak Republics (Beetles-Coleoptera). Milan Sláma, Krhanice. ISBN 8023826271 (váz.).

Scherer-Lorenzen, M., Körner C., Schulze E.-D. 2005. Forest diversity and function: temperate and boreal systems. Springer. ISBN 978-3-540-26599-3

Schiegg, K. 2000a. Effects of dead wood volume and connectivity on saproxylic insect species diversity. Ecoscience 7:290-298.

Schiegg, K., 2000b. Are there saproxylic beetle species characteristic of high dead wood connectivity? Ecography 23, 579-587.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms. Fennoscandian boreal forests as an example. Ecological bulletins 49, 11-41.

Speight, M. 1989. Saproxylic invertebrates and their conservation. Council of Europe. ISBN 13: 9789287116802.

Spiecker, H. 2000. Growth of Norway spruce (Picea abies [L.] Karst.) under changing environmental conditions in Europe. In: Klimo, E., Hager, H., Kulhavy, J. (Eds.), Spruce Monocultures in Central Europe: Problems and Prospects, EFI Proceedings 33,11–26.

Spiecker, H. 2003. Silvicultural management in maintaining biodiversity and resistence of forests in Europe-temperate zone. Journal of Environmental Management 67, 55-65.

Spiecker, H., Hansen, J., Klimo, E., Skovsgaard, J.P., Sterba, H., von Teuffel, K. 2004. Norway spruce conversion – options and consequences. Brill Academic Publishers, Leiden – Boston. ISBN: 90 04 13728 9.

Stephens, S.S., Wagner,M.R. 2007. Forest plantations and biodiversity: a fresh perspective. Journal of Forestry 105, 307-313.

Stenbacka, F., Hjältén, J., Hilszczanski, J., Dynesius, M. 2010. Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. Ecological Applications 20, 2310-2321.

Šálek, L., Zahradnik, D., Marušák, R., Jeřábková, L., Merganič, J. 2013. Forest edges in managed riparian forests in the eastern part of the Czech Republic. Forest Ecology and Management 305, 1-10.

Thomaes A. 2009. A protection strategy for the stag beetle (*Lucanus cervus*, (L., ;1758), Lucanidae) based on habitat requirements and colonisation capacity. In: Buse J., Alexander K., Ranius T. et al. (eds.). Saproxylic Beetles – their role and diversity in European woodland and tree habitats. Pensoft Publishers. 149–160 s.

Uliczka, H., Angelstam, P. 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. Ecography 22, 396–405.

Ulyshen, M.D. 2011. Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. Forest Ecology and Management 261, 1479-1489.

Varasteh Moradi, H., Zakaria, M. 2009. Insectivorous bird community change along an edge-interior gradient in an isolated tropical rainforest in peninsular Malaysia. Malaysian Nature Journal 61(1):48-66.

Vogel, S., Alvarez, B., Bässler C., Müller, J., Thorn, S. 2017. The Red-belted Bracket (*Fomitopsis pinicola*) colonizes spruce trees early after bark beetle attack and persists. Fungal Ecology 27, 182-188.

Von Teuffel, K., Heinrich, B., Baumgarten, M. 2003. Present distribution of secondary Norway spruce in Europe. In: Spiecker, H., Hansen, J., Klimo, E., Slovsgaard, J.P., Sterba, H., von Teuffel, K. (Eds.), Norway Spruce Conversion-Options and Consequences, EFI Res Report 18, s. 63–96.

Wade, T.G., Riitters, K.H., Wickham, J.D., Jones, K.B., 2003. Distribution and causes of global forest fragmentation. Conservation Ecology 7.

Webb, A., Buddle, C.M., Drapeau, P.&Saint-Germain, M. 2008. Use of remnant boreal forest habitats by saproxylic beetle assemblages in even-aged managed landscapes. Biological Conservation 141(3), 815-826.

Weber, N. 2005. Afforestation in Europe: lessons learned challenges remaining. In: Stanturf, J.A., Madsen, P. (Eds.), Restoration of Boreal and Temperate Forests. CRC Press, Boca Raton, 121–135 s.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48, 607-615.

Winter S. 2012. Forest naturalness assessment as a component of biodiversity monitoring and conservation management. International Journal of Forestry 85, 293–304.