Česká zemědělská univerzita v Praze

Fakulta lesnická a dřevařská

Katedra ochrany lesa a entomologie

VLIV RŮZNÝCH TYPŮ NARUŠENÍ LESNÍCH EKOSYSTÉMŮ NA HMYZ

Dizertační práce

Autor: Adam Véle

Školitel: Jakub Horák

Praha 2019

Prohlašuji, že jsem disertační práci na téma „Vliv různých typů narušení lesních ekosystémů na hmyz“ 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 4. 8. 2019

Adam Véle

Poděkování

Za neutuchající výpomoc, cenné rady a připomínky vznesené v průběhu celé práce děkuji svému školiteli doc. Jakubu Horákovi. Za významnou pomoc při psaní rukopisů děkuji také prof. Jaroslavu Holušovi. Za podporu a shovívavost děkuji své rodině.
Práce byla finančně podpořena granty CIGA ČZU 20154301, CIGA ČZU 20174307, IGA ČZU B/02/18, MZE-RO0115, MZE-RO0116, MZE-RO0118.

Seznam publikací

Předkládaná disertační práce je sepsána na základě čtyř publikovaných článků, jež jsou citovány v textu a uvedeny v přílohách 1-4.

1. Véle A, Holuša J, Horák J (2016): Ant abundance increases with clearing size. Journal of Forest Research, 21, 110–114.
2. Véle A, Holuša J (2017): Microclimatic conditions of *Lasius flavus* ant mounds. International Journal of Biometeorology, 61, 957–961.
3. Véle A, Horák J (2018): The importance of host characteristics and canopy openness for pest management in urban forests. Urban Forestry & Urban Greening, 36, 84–89.
4. Véle A, Horák J (2019): Space, habitat and isolation are the key determinants of tree colonization by the carpenter ant in plantation forests. Forests, 10, 630.

Prohlášení

Prohlašuji, že na jednotlivých článcích jsem se podílel následujícím způsobem:

Příloha 1: spoluautor nápadu, terénní práce, spoluautor textu

Příloha 2: autor nápadu, terénní práce, spoluautor textu

Příloha 3: spoluautor textu

Příloha 4: spoluautor textu

Véle A (2019): Vliv různých typů narušení lesních ekosystémů na hmyz. Doktorská disertační práce, Katedra ochrany lesa a entomologie, Česká zemědělská univerzita v Praze, Praha, 62 s., Příloha 1-4.

Abstrakt

Předložená dizertační práce se zabývá vlivem různých typů narušení lesních ekosystémů (holosečné lesní hospodaření, fragmentace, změna druhové skladby dřevin, změna korunového zápoje v důsledku působení větru na zapojené lesní porosty) na hmyz. Za modelové taxony, na nichž byly studie provedeny, jsme zvolili mravence a brouky. Z výsledků všech provedených studií vyplývá, že množství dopadajícího světla významně ovlivňuje výskyt a početnost všech zkoumaných druhů. Pro udržení vyšší druhové pestrosti mravenců ve smrkových lesích je důležité vytvářet větší světliny, na nichž žije signifikantně více druhů než na drobných světlinách či v zapojeném lese. Na slunečním záření jsou závislí také na lesních okrajích a pasekách žijící mravenci *Lasius flavus*, kterým významně napomáhává zvýšit teplotu v jejich z hlíny vystavěných hnízdních kupách. Opačnou závislost jsme zjistili u mravence *Camponotus ligniperdus*, který se častěji vyskytoval v uzavřených lesích. Možným vysvětlením tohoto neočekávaného jevu může být snaha vyhnout se konkurenci ostatních druhů mravenců či početnější výskyt stromů napadených hnilobou, které využívá ke stavbě svých hnízd. Závislost na hnilobou napadených stromech ukazuje, že tento druh mravence není lesním škůdcem, za kterého byl doposud pokládán. Otevřené porosty nevyhovují ani bělokazu dubovému (*Scolytus intricatus*), který se v nich vyskytuje v menších početnostech a dosahuje menších velikostí těla. Pro své rozmnožování tento druh preferuje tlustší kmeny stromů, využívá však i tenké větve. Získané výsledky lze využít v rámci lesního managementu k podpoře či naopak omezení výskytu druhů, jejichž přítomnost je z pohledu ochrany lesa žádoucí (mravenci) či nežádoucí (bělokaz dubový).

Klíčová slova: bělokaz dubový, fragmentace, hmyz, les, mravenci, narušení

Véle A (2019): Impact of different forest disturbances on insects. Doctoral dissertation, Department of Forest Protection and Entomology, Czech University of Life Sciences Prague, Prague, 62 pp., Appendices 1–4.

Abstract

The presented dissertation thesis deals with the influence of various types of forest ecosystem disturbances (forest management, change of species composition of trees, change of the crown canopy affected by the wind, fragmentation) on insects. We chose ants and beetles as model organisms on which the studies were conducted. The results of all studies have shown that the amount of incident light directly or indirectly affects the occurrence and abundance of all investigated taxa. To maintain higher species diversity in spruce forests, it is important to create larger clear-cuts where live significantly more ant species. The yellow meadow ant, *Lasius flavus* also depend on the direct solar radiation, which helps to raise the temperature in their soil mounds. The opposite dependence was found in carpenter ant *Camponotus ligniperdus*, which is more common in closed forests. A possible explanation for this unexpected result may be to avoid competition from other ants, or the more frequent occurrence of trees affected by rot, which it uses for nest building. Dependence on rot-infected trees show that this species is not a forest pest. The open stands do not even suit the oak bark beetle, which there occurs in smaller numbers and has smaller body sizes. For its reproduction, this beetle prefers thicker tree trunks, but it also uses thin branches. The obtained results can be used within the forest management to support or reduce the occurrence of species whose presence is desirable (ants) or undesirable (oak bark beetle).

Key words: ants, disturbance, forest, fragmentation, insect, oak bark beetle

OBSAH

PŘÍLOHA 1 Ant abundance increases with clearing size.

PŘÍLOHA 2 Microclimatic conditions of *Lasius flavus* ant mounds.

PŘÍLOHA 3 The importance of host characteristics and canopy openness for pest management in urban forests.

PŘÍLOHA 4 Space, habitat and isolation are the key determinants of tree colonization by the carpenter ant in plantation forests.

CÍLE PRÁCE

Během zpracování dizertační práce byly hledány odpovědi na čtyři stanovené cíle:

Zjistit, zda je výskyt mravenců ve smrkových lesích ovlivněn přítomností světlin, příp. jejich velikostí.

Určit faktory, které ovlivňují termoregulaci hnízd mravence *Lasius flavus*.

Vyhodnotit faktory prostředí ovlivňující početnost bělokaza dubového v městských lesích a navrhnout metody jejich ochrany.

Popsat faktory, kterými je ovlivněn výskyt mravence dřevokaze v hospodářských lesích.

ÚVOD

Lesy pokrývají více než 30 % zemské souše a obdobnou rozlohu (33,8 %) zaujímají také lesy na našem území. V Evropě stejně jako v České republice dochází v posledních desetiletích k mírnému, ale neustálému nárůstu rozlohy lesů i množství dřeva v nich ponechaném (MacDicken et al., 2015; MZe, 2018). I přesto se nelze na lesy dívat, jako na plynule se rozvíjející stabilní ekosystém. Struktura produkčních lesů se totiž výrazně liší od struktur lesů původních (Gossner et al., 2013). Evropské lesy jsou navíc pravidelně narušovány přírodními i antropogenními silami (Wohlgemuth et al., 2002; Angelstam, Kuuluvainen, 2004; Seidl et al., 2011). Významnou roli mezi narušeními způsobenými přírodními silami zaujímají někteří zástupci hmyzu, kteří dokáží zcela zásadním způsobem a na velkých plochách měnit charakter přírodních i hospodářských lesů (Müller et al., 2008; Seidl et al., 2011; Grodzki, Fronek, 2017).

Hmyz tvoří podstatnou součást lesních ekosystémů, v nichž zastává mnoho důležitých funkcí (Weisser, Siemann, 2008; Yang, Gratton, 2014). Ovlivňuje koloběh živin i jejich dynamiku (Hunter, 2001; Véle et al., 2010). Rozšiřuje i konzumuje houby a rostliny, svojí činností dokáže oslabit stromy či zcela změnit charakter vegetace (Schowalter, 1981; Jardon et al., 1994; Pletscher, Klepzig, 2004; Lemoine et al., 2017). Hmyz je také podstatnou součástí potravních řetězců, v nichž zaujímá roli predátorů i kořisti (Laakso, Setälä, 2000; Fayt et al., 2005; Moya-Laraño, Wise, 2007). Mezi jednotlivými zástupci hmyzu existují složité mezidruhové vztahy (Adlung, 1966; Pennacchio, Strand, 2006).

Výskyt a abundance hmyzu v lesích jsou silně ovlivňovány působením přírodních i antropogenních faktorů. Významným abiotickým faktorem s dopadem na celé lesní ekosystémy je v našich podmínkách vítr. Významnými antropogenními faktory ovlivňující hmyz jsou např. lesní hospodaření či urbanizace spojené s úbytkem dřevní hmoty, změnou druhového i věkového spektra stromů a s fragmentací lesů (Niemelä, 2001; Nilsson et al., 2001; Hunter, 2002; Gaublomme et al., 2008; Véle et al., 2011; příloha 1,3). Vliv přírodních a antropogenních narušení lesů na hmyz se může, ale také nemusí od sebe odlišovat či může docházet k jejich synergickému působení (Bengtsson et al., 2000; Hanson, Lorimer, 2007; Laurance, Curran, 2008). Vzhledem k předpokládanému nárůstu v počtu a intenzitě disturbancí v důsledku nastávající klimatické změny, lze v následujících desetiletích předpokládat i zvýšený tlak na populace hmyzu v lesích (Seidl et al., 2017).

Studium vlivu narušení lesních ekosystémů na hmyz je aktuální společensky i hospodářsky významné téma, které může napomoci nejen ochraně před působením hospodářsky nežádoucích druhů, ale také k udržení biodiverzity hmyzu v lesích. Porozumění dynamice přírodních disturbancí a jejich srovnání s hospodářskými zásahy je nezbytné k ochraně a managementu biodiverzity a ekosystémových funkcí v člověkem silně ovlivněných evropských lesích (Nilsson, Ericson, 1997). Vysoká diverzita hmyzu je žádoucí mimo jiné i z důvodu ochrany lesa (Hooper et al., 2005). Návrh a aplikace metod pro udržení biodiverzity a nových metod ochrany lesa v hospodářských lesích (v nichž je potlačena funkce přírodních procesů), při současném zachování produkčních schopností lesů jsou jedním z cílů a pilířů moderního lesnictví (Ferris, Humphrey, 1999; Führer, 2000; Wohlgemuth et al., 2002; Kuuluvainen, 2009). Ekosystémy s vyšší biologickou diverzitou totiž bývají méně náchylné k narušením a tudíž vyžadují méně intenzivní zásahy vykonávané za účelem ochrany lesa (Hooper et al., 2005; Jactel et al., 2005; Mori et al., 2017).

NARUŠENÍ LESNÍCH EKOSYSTÉMŮ

Lesní disturbance jsou výkyvy prostředí a destruktivní události, které narušují zdraví a/nebo strukturu lesa a/nebo mění zdroje nebo prostředí v jakémkoli prostorovém nebo časovém měřítku (FAO, 2005). Disturbance silně ovlivňují druhové složení, strukturu i fungování lesních ekosystémů, koloběh živin a určují prostorové i časové procesy v dynamice lesů, čímž ovlivňují také populace hmyzu (Forman et al., 1995; Oliver, Larson, 1996; Foster et al., 1998; Bebi et al., 2009; Hicke et al., 2012; Bradford et al., 2013). Jejich dopad se liší v závislosti na vývojové fázi lesa (Dale et al., 2000; Hilszczański et al., 2005). Na hmyz disturbance působí přímo (např. úhyn jedinců) i nepřímo prostřednictvím změn v podmínkách prostředí či v mezidruhových vztazích (Roland, 1993; Bentz et al., 2010).

Disturbance jsou významné také z ekonomických důvodů. Narušení lesních ekosystémů ovlivňují jejich produktivitu např. prostřednictvím snížené schopnosti zachytit zdroje v důsledku snížené listové plochy či sníženou schopností získané zdroje využívat (Peters et al., 2013). Výsledky teoretických modelů i empirických studií ukazují, že frekvence a intenzita disturbancí silně ovlivňují, prostřednictvím změn v environmentálních parametrech, biodiverzitu zasažených oblastí (Petraitis et al., 1989; Wohlgemuth et al., 2002; Schowalter, 2012). Ta je přitom důležitá pro dlouhodobou stabilitu lesních ekosystémů (Hooper et al., 2005).

Ve střední Evropě se můžeme podle Wohlgemuth et al. (2002) setkat se třemi typy disturbancí. Endogenní (graduální) disturbance jsou způsobené silami uvnitř stanoviště (stárnutí a rozpad stromů, jehož výsledkem je vznik mezer v porostu, mírný tlak zvěře). Exogenní (episodické) disturbance jsou způsobené silami, jejichž původ se nachází vně stanoviště: vítr, oheň, laviny, záplavy, sesuvy půdy, škůdci. Člověkem způsobené (periodické) distrubance: lesní hospodářství (těžba dřeva, výsadba a pěstování dřevin), pastva, sběr dřeva, hrabanky a dalších lesních produktů). V nedávné době začalo být mezi disturbance řazeno i sucho (jakožto důsledek vzájemného působení srážek, biomasy, teploty, rychlosti větru a relativní vlhkosti) dříve považované za perturbaci (Hanson, Weltzin, 2000; Peters et al., 2011). Mezi nejvýznamnější abiotické disturbance v evropských lesích patří vítr, sucho a požáry (Schelhaas et al., 2003; Jactel et al., 2012; Allen et al., 2015). Významná biotická narušení zde způsobují např. kůrovcovití brouci, podstatná je ale zejména činnost člověka (intenzivní lesní hospodaření, narůstající fragmentace a urbanizace lesů apod.) (Punttila et al., 1991; Schiegg, 2001; Keller et al., 2004; Zapata, Robledano, 2014).

Vítr

Ve střední Evropě je vítr nejdůležitější exogenní disturbancí v lesích (Wohlgemuth et al., 2002; Schelhaas et al., 2003). V ČR i okolních zemích je příčinou přibližně 70 % nahodilé těžby způsobené abiotickými faktory (Šrámek, Novotný, 2019). Význam větru spočívá především ve tvorbě časové i prostorové heterogenity ve struktuře lesů, v důsledku čehož ho lze považovat za hlavní přírodní sílu sukcese lesa (Bouget, Duelli, 2004). Silně ovlivňuje regionální biodiverzitu hmyzu i výskyt hospodářsky nežádoucích druhů (Bouget, Duelli, 2004; Grodzki, Fronek, 2017). Vítr mimo jiné napomáhá šíření hmyzu na nová stanoviště, vytváří či ničí biotopy vhodné pro jeho výskyt, ovlivňuje chemickou komunikaci hmyzu (Bayers, 2000; Cardé, Willis, 2008; Mezei et al., 2014; Chase et al., 2017; příloha 4). Hmyz se často vyhýbá stanovištím se silnou intenzitou větru, na nichž nedochází ke kladení vajíček (Bonsignore, Bellamy, 2013). Za zcela zásadní lze vliv větru hodnotit ve vztahu ke vzniku polomů a následným změnám v gradačním cyklu podkorního hmyzu (Wermelinger, 2004; Grodzki, Fronek, 2017).

Sucho

V Evropě dochází k nárůstu sucha od poloviny minulého století (Dai et al., 2004). Na našem území je sucho příčinou téměř čtvrtiny nahodilé těžby způsobené abiotickými faktory (Šrámek, Novotný, 2019). Doba trvání sucha je důležitější než jeho intenzita (Fay et al., 2000). Silná nebo dlouhotrvající období sucha mohou vyvolat častější nebo závažnější napadení stromů hmyzem. Obecně je známo, že ze sucha profituje zejména podkorní, dřevokazný a savý hmyz, který lépe prosperuje na suchem oslabených stromech (Koricheva et al., 1998; Jactel et al., 2012). Opak platí např. pro hálkotvorný hmyz (Koricheva et al., 1998). Jednoznačně pozitivně na sucho reagují sekundární škůdci. Jimi způsobená poškození vzrůstají s intenzitou sucha, které se odráží ve snížené obranyschopnosti stromů (Bultman, Bell, 2003; Jactel et al., 2012; Colangelo et al., 2018; příloha 3). Interakce sucha a vyšší početnosti hmyzu může mít závažné důsledky na přežívání stromů, které by nebyly způsobeny pouze suchem či samotným působením hmyzu (Anderegg et al., 2015).

Lesní hospodaření

Lesní hospodaření narušuje lesy vícero způsoby. Hmyz je ovlivňován již samotnou těžbou dřeva (Punttila et al., 1991; Schiegg, 2001). Snaha o vysoké výnosy dřeva, způsobuje nepřirozenou strukturu lesů, čímž mění i složení společenstev hmyzu (McGee et al., 1999; Müller et al., 2007). Pěstováním hustých a zapojených porostů může být hmyz ovlivněn negativně i pozitivně (příloha 1, 3, 4). Dalším typickým jevem intenzivního lesního hospodaření je odstraňování starých a uschlých stromů, jež se odráží v poklesu biodiverzity zejména saproxylických druhů (Schiegg, 2001; Siitonen, 2001). Kromě věkové skladby může lesní hospodaření také ovlivňovat i druhou skladbu lesů. V druhově pozměněných lesích často nachází příhodné podmínky a do vysokých početností se dokáží namnožit druhy schopné způsobovat značné hospodářské ztráty (Wigley, Roberts, 1997; Hansen et al., 2001; Berryman, 2013). Lesní hospodaření ovšem může také simulovat přírodní disturbance a tím přispívat k nárůstu druhové diverzity hmyzu v lesích (Niemelä et al., 1996; Nitschke, 2005). Typickým příkladem je např. již zmíněné holosečné lesní hospodaření, díky němuž vznikají, obdobně jako díky působení některých exogenních disturbancí v lesích mozaiky různě starých porostů s odlišným složením hmyzích společenstev (Wigley, Roberts, 1997; Palladini et al., 2007; Véle et al., 2011).

Je zřejmé, že mezi intenzitou hospodářských zásahů a strukturou hmyzích společenstev neexistuje jednoduchá závislost, což je dobře patrné na příkladu mravenců. Při tvorbě holosečí dochází k přímému poškozování hnízd i nepřímému ovlivňování populací v hnízdech (Rosengren, Pamilo, 1978; Niemelä et al., 1996; Sorvari, Hakkarainen, 2007). Intenzivně obhospodařované lesy přesto mohou být díky většímu zastoupení mladých a prosvětlených porostů osídleny početněji než lesy obhospodařované extenzivně či vůbec (Punttila et al., 1991; Yi et al., 2005; příloha 1). V nejmladších lesních porostech žijí především druhy s r-stretegií a druhy vázané na otevřená stanoviště, zatímco ve starších porostech převažují druhy teritoriální (Punttila et al., 1991, 1996; Maeto, Sato, 2004). Kolonizace těmito druhy je poměrně rychlá a již do dvaceti let dosahuje diverzita mravenců svého vrcholu (Niemelä et al., 1996; Véle et al., 2011).

FRAGMENTACE

Fragmentace krajiny je dle Fahrig (2003) definována jako rozdělení přírodního krajinného pokryvu na několik menších oblastí nacházejících se v člověkem pozměněné krajině. Fragmentaci lesů způsobuje nejen lesní hospodaření, nýbrž je důsledkem i dalších lidských činností např. pokračující urbanizace (Zapata, Robledano, 2014). Vliv fragmentace spočívá ve snížení rozlohy původního biotopu a nárůstu rozlohy lesních okrajů, v důsledku čehož dochází ke změnám v intenzitách působení environmentálních faktorů. Ty se opět projevují v nárůstu i poklesu abundance hmyzu. Výsledky našich studií ukazují, že na většinu druhů mravenců obývajících smrkové lesy má fragmentace kladný vliv (příloha 1). Větší množství slunečního záření, dopadajícího na hnízdo díky fragmentaci souvislých lesních celků, může mravencům rodu *Lasius* usnadňovat termoregulaci jejich hnízd (příloha 2). Jiným druhům, např. mravencům rodu *Camponotus*, změněné parametry prostředí nevyhovují (příloha 4). Kromě změny environmentálních podmínek hraje důležitou roli v odezvě hmyzu na fragmentaci také vzrůstající izolace jejich populací (Hunter, 2002). Fragmentace ovlivňuje hmyz také prostřednictvím změny ekologických procesů, přičemž i tyto nesnadno pozorovatelné jevy mohou mít na populace hmyzu dalekosáhlé důsledky (Roland, Taylor, 1997; Tscharntke, Brandl, 2003). Konkrétně lze zmínit např. gradace defoliátorů v boreálních lesích, jež nastaly v důsledku nevhodnosti fragmentovaných lesů pro výskyt parazitoidů (Roland, 1993). K takovýmto gradacím přispívá dle Roland (1993) i skutečnost, že většina motýlů klade svá vajíčka na lesní okraje raději než do tmavých částí lesa, a že lesní okraje i silně fragmentované lesy se vyznačují vyšší teplotou, která umožňuje rychlejší vývoj hmyzu. Vliv může mít také nevhodnost fragmentovaných biotopů např. pro ptačí predátory hmyzu (Fayt et al., 2005). Na druhou stranu může fragmentace lesů kladně působit na taxony hmyzu, jejichž přítomnost je vzhledem k jejich možnému využití v ochraně lesa přínosná. Jedná se např. o predátory, kteří preferují prosluněné lesní plochy či některé parazitoidy v dospělosti sbírající potravu na vegetaci, jejíž větší množství roste na lesních světlinách (Hilszczański et al., 2007; Klapwijk et al., 2016).

Odezva hmyzích taxonů na fragmentaci se liší mimo jiné v závislosti schopnostech jejich rozptylu (Ribas et al., 2005). Fragmentací pozměněné okolí zůstavších ploch může sloužit jako bariéra pro šíření úzce specializovaných druhů, zatímco generalisté mohou z takovýchto zásahů profitovat a lesní okraje využívat jako nášlapné kameny (Punttila et al., 1996; Maeto, Sato, 2004; Müller et al., 2007; Sobrinho, Schoereder, 2007). Ve fragmentovaných biotopech tak může postupně docházet k náhradě specialistů druhy s širokou ekologickou valencí (Tscharntke et al., 2002). Zajímavý jev související s fragmentací byl popsán v lesích severní Evropy. Polygynní druhy mravenců lépe přežívají v rozlehlejších a méně izolovaných fragmentech, zatímco monogynní druhy dominují v malých a značně izolovaných fragmentech lesů (Vepsäläinen, Pisarski, 1982; Mabelis, 1994; Punttila et al., 1996).

Vliv fragmentace se odvíjí také od uspořádání zbývajících porostů, které ovlivňuje migraci živočichů a tím i druhové složení a početnost hmyzu (Mabelis, 1994; Schoereder et al., 2004; Eggleton et al., 2005; Sobrinho, Schoereder, 2007; Summerville, Crist, 2008). U mravenců bylo zjištěno, že jejich společenstva jsou silně ovlivněna přítomností optimálních habitatů až 300 m vzdálených (Véle et al., 2011). Rozlehlejší stanoviště zase mají schopnost přijmout více imigrantů (Kawecki, 2004).

BIOTIČTÍ ČINITELÉ

Biotičtí činitelé včetně hospodářsky nežádoucích druhů jsou integrální součástí lesních ekosystémů (Müller et al., 2008; Svoboda et al., 2012). V hospodářských lesích je však početná přítomnost druhů způsobujících jejich rozsáhlé narušení (např. kůrovcovitých brouků) nežádoucí (Schelhaas et al., 2003; Mezei et al., 2014; Grodzki, Fronek, 2017). Významné poškození smrkových lesů způsobuje lýkožrout smrkový (*Ips typographus*), který byl během uplnulých dvou století opakovanou příčinou rozsáhlých narušení smrkových lesích v podmínkách střední a severní Evropy (Wermelinger, 2004). Z čistě ekologického hlediska se však i na něho lze dívat jako na klíčový druh smrkových porostů umožňující jejich regeneraci a zvyšující počty mezidruhových vazeb, spojené s vyšší diverzitou mnoha zástupců nejen hmyzu (Müller et al., 2008).

Na listnatých stromech je důležitým zástupcem kůrovcovitých brouků bělokaz dubový (*Scolytus intricatus*), který způsobuje značná poškození dubových porostů (Marković, Stojanović, 2011). Ta mohou být citelná především v příměstských lesích, u nichž jsou vysoce ceněny i jejich mimoprodukční funkce (Konijnendijk, 2003). Početnost bělokaza dubového lze snižovat odstraňováním těžebních zbytků včetně tenkých větví, ve kterých se může vyvíjet (Galko et al., 2012; příloha 3), ale také preventivně změnou v uspořádání a druhovém složení porostů. Duby rostoucí v prostředí s vysokým jarním korunovým zápojem (způsobeným např. pěstováním jehličnanů v jejich blízkosti) jsou oslabené, čehož bělokaz dubový využívá. Takovéto stromy častěji napadá, úspěšně se zde rozmnožuje a vylíhlí brouci dosahují větších tělních rozměrů (příloha 3).

Ekosystémovými inženýry s významným vlivem na lesní ekosystém jsou také mravenci (Toro et al., 2012). Mnoho z nich pozitivně ovlivňuje půdní vlastnosti (Frouz, Jílková, 2008). Mravenci přemísťují semena rostlin, chrání rostliny před herbivory, ale také je oslabují chovem mšic (Adlung, 1966; Gorb, Gorb, 1999). Z pohledu potravního řetězce jsou mravenci důležitou kořistí i predátory (Adlung, 1966; Horstmann, 1970). Rovněž dokáží měnit složení živočišných společenstev (Laakso, Setälä, 2000; Hawes et al., 2002). Na rozdíl od kůrovců je jejich přítomnost hodnocena kladně i v hospodářských lesích, neboť mohou snižovat populace hospodářsky nežádoucích druhů či indikují nevhodnost pěstovaných dřevin na stanovišti (Adlung, 1966; příloha 4). Ani mravenci dřevokazové dříve považovaní za lesní škůdce, nezpůsobují hospodářské škody, neboť ke stavbě hnízd využívají stromy napadené hnědou hnilobou (příloha 4). Výskyt většiny druhů mravenců lze podpořit udržováním mozaiky dostatečně velkých lesních světlin, jež zajišťují mravencům vhodné environmentální podmínky (Véle et al., 2011; příloha 1, 2).

PARAMETRY PROSTŘEDÍ

Vliv narušení lesa můžeme pozorovat ve změnách abiotických i biotických parametrů prostředí. Důležitými environmentálními parametry ovlivňujícími výskyt i abundance mnoha živočišných taxonů jsou dopadající sluneční záření a s ním spojená teplota vzduchu a půdy (Carlson, Groot, 1997; Forrester et al., 2012; příloha 1, 3). Na živočichy množství dopadajícího slunečního záření působí i nepřímo např. ovlivňováním vegetace a množství potravních zdrojů (Punttila et al., 1991; Palviainen et al., 2005; Yi et al., 2005).

Množství dopadajícího slunečního záření se silně odlišuje i v drobných mikrohabiatech (Velde et al., 2011) a ovlivňuje mnoho živočišných taxonů. Namátkou lze jmenovat např. půdní živočichy, motýly, brouky a mravence (Selås Vidar et al., 2004; Salmon et al., 2008; Velde et al., 2011; Battisti et al., 2013; Vodka, Cizek, 2013; příloha 1,3). Druhová bohatost hmyzu na lesních světlinách může být díky vyššímu množství dopadajícího záření až o 50 % vyšší než ve vzrostlém lese (Duelli et al., 2002).

Kombinace teploty a slunečního záření je často používána k vysvětlení distribuce a abundance hmyzu (Bryant, Shreeve, 2002). Teplota je jedním z nejdůležitějších faktorů ovlivňujících fyziologické funkce ektotermálních živočichů, jejich vývoj a přežívání a tedy i úspěch populací (Battisti et al., 2013). V teplejším prostředí živočichové dosahuji větších tělních velikostí (Atkinson, 1994). U mravenců je změna v dotaci prostředí slunečním zářením příčinou změn struktury jejich společenstev během stárnutí lesních porostů (Niemelä et al., 1996; Véle et al., 2011). Oslunění totiž zvyšuje také vnitřní teplotu mravenčích hnízd, čímž zkracuje fyziologický čas nutný pro vývoj následující generace (Kipyatkov, Lopatina, 2002; příloha 2). Zajištění dostatečně vysoké teploty vhodné pro vývoj plodu je jednou z hlavních funkcí hnízdních kup a jednou z příčin úspěšnosti mravenců (Hölldobler, Wilson, 1990). Zatímco např. u lesních mravenců je teplota zajišťována působením vícero zdrojů (kromě teploty vzduchu a přímého slunečního záření se jedná např. o rozklad organického materiálu, z něhož je kupa postavena), u druhů stavících si hnízda pouze z půdy hraje primární roli právě sluneční záření (Frouz, 2000; příloha 2).

Velké množství slunečního záření dobře snáší zejména agresivní druhy (Punttila et al., 1996). Na lesních světlinách se však častěji nacházejí i další taxony mravenců, např. zástupci rodů *Lasius*, *Myrmica* i *Formica* (Niemelä et al., 1996; Mabelis, Korczyńska, 2001; Véle et al., 2011). Hnízda lesních mravenců na světlinách lépe přežívají (Mabelis, Korczyńska, 2001), což se odráží v dlouhodobém výskytu hnízd především ve světlejších porostech (Punttila et al., 1994; Niemelä et al., 1996; příloha 1). Na světlejších plochách se také nachází více vegetace v podrostu a s ní spojené vyšší množství potenciální potravy mravenců (Gorham et al., 2002; Jeffries et al., 2006).

Pozitivní závislost výskytu hmyzu na teplotě prostředí však neplatí vždy. Pineau et al. (2017) zjistili, že lýkožrout borový (*Ips sexdentatus*) má vyšší obsah lipidů v těle pokud se nevyvíjí v prostředí s příliš vysokou teplotou. Větší tělesná velikost u kůrovců značí jejich lepší kondici (Reid, Roitberg, 1995). Problémem pro kůrovce může být také skutečnost, že intenzivní sluneční záření snižuje účinnost, ke komunikaci hojně využívaných feromonů (Wood, 1982; Seybold et al., 2000; Artyushenko et al., 2017). Rovněž mravenci rodu *Camponotus* častěji osídlují stinná místa (příloha 4). Vzhledem ke skutečnosti, že mravenci patří mezi teplomilné živočichy (Hölldobler, Wilson, 1990) spočívá možné vysvětlení v existující nepřímé vazbě. Je možné, že se umístěním hnízd daleko od světlin snaží snížit konkurenci s jinými druhy mravenců, jejichž většina se vyskytuje na světlinách (Alinvi et al., 2008; příloha 1, 4). Mravenci dřevokazové nepatří mezi příliš agresivní a bojovné druhy (Savolainen, Vepsäläinen, 1988). Možným vysvětlením je jejich preference ke stojícímu mrtvému dřevu s velkým obvodem (Westerfelt et al., 2015), které se na světlinách většinou nenachází. Dalším důvodem může být vyrovnanější klima vhodné pro výskyt hnědé hniloby, kterou je napadena většina mravenci osídlených stromů a která usnadňuje mravencům tvorbu jejich hnízd (Gooding et al., 1966; příloha 4).

ZÁVĚR

Výsledky studie o vlivu velikosti lesních světlin na výskyt a početnost mravenců (příloha 1) ukazují, že disturbance a fragmentace způsobené lesním hospodařením nemusí na hmyz působit pouze negativně. Větší druhové zastoupení i vyšší abundance mravenců na rozsáhlejších světlinách jsou odpovědí na změnu v množství dopadajícího slunečního záření a s ním spojené změny dalších environmentálních parametrů. Sluneční záření a s ním spojená teplota vzduchu jsou také hlavními faktory ovlivňující teplotu v hnízdních kupách mravence *Lasius flavus* (příloha 2). Fragmentace lesů naopak nesvědčí mravenci *Camponotus ligniperdus*, který preferuje uzavřené smrkové porosty. Jeho absenci na prosvětlených plochách lze vysvětlit únikem z konkurenčního prostředí, v němž dominují agresivnější druhy mravenců. Roli pravděpodobně hraje i početnější výskyt dostatečně tlustých hnědou hnilobou napadených stromů v zapojených porostech, v nichž si buduje svá hnízda (příloha 4). Parametry prostředí spojené s množstvím slunečního záření ovlivňují také výskyt bělokaza dubového. V zastíněných stromech se bělokaz vyvíjí ve vyšších početnostech a zde vylíhlí jedinci se vyznačují větší velikostí těla (příloha 3).

Cílem současného lesního hospodářství je podpora biodiverzity a prevence činností, jež mohou vést k vysokým populačním hustotám hospodářsky nežádoucích organismů (Ferris, Humphrey, 1999; Führer, 2000; Wohlgemuth et al., 2002; Kuuluvainen, 2009). K těmto cílům může dopomoci i aplikace námi získaných výsledků. Přítomnost mravenců v lesích je žádoucí z vícero důvodů. Pro podporu většiny druhů mravenců lze vytvářet dostatečně rozsáhlé světliny (příloha 1, 2). Stromy osídlené mravenci dřevokazi není nutné odstraňovat, neboť tito mravenci nejsou lesními škůdci. V ochraně lesa lze naopak využít jejich predačních schopností. Jejich četný výskyt lze rovněž využít jako indikaci podmínek nevhodných pro pěstování smrků (příloha 4). Početnost bělokaza dubového v příměstských lesích lze snížit pěstováním dubů ve světlých porostech a odstraňováním i tenkých těžebních zbytků (příloha 3).

LITERATURA

Adlung KG (1966): A critical evaluation of the European research on use of red wood ants (formica rufa group) for the protection of forests against harmful insects. Zeitschrift für Angewandte Entomologie, 57, 167–189.

Alinvi O, Bohlin J, Ball JP (2008): Interspecific competition among ants in the boreal forest. Insectes Sociaux, 55, 1–11.

Allen CD, Breshears DD, McDowell NG (2015): On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere, 6, 1–55.

Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK, McDowell N, Pan Y, Raffa K, Sala A, Shaw JD, Stephenson NL, Tague C, Zeppel M (2015): Tree mortality from drought, insects, and their interactions in a changing climate. New Phytologist, 208, 674–683.

Angelstam P, Kuuluvainen T (2004): Boreal forest disturbance regimes, successional dynamics and landscape structures: A European perspective. Ecological Bulletins, 117–136.

Artyushenko PV, Tomilin FN, Kuzubov AA, Ovchinnikov SG, Tsikalova PE, Ovchinnikova TM, Soukhovolsky VG (2017): The stability of the pheromones of xylophagous insects to environmental factors: An evaluation by quantum chemical analysis. Biophysics, 62, 532–538.

Atkinson D (1994): Temperature and organism size—a biological law for ectotherms? In: Begon, M, Fitter, AH (ed): Advances in ecological research. Academic Press, pp. 1–58.

Battisti A, Marini L, Pitacco A, Larsson S (2013): Solar radiation directly affects larval performance of a forest insect. Ecological Entomology, 38, 553–559.

Bayers JA (2000): Wind-aided dispersal of simulated bark beetles flying through forests. Ecological Modelling, 125, 231–243.

Bebi P, Kulakowski D, Rixen C (2009): Snow avalanche disturbances in forest ecosystems - state of research and implications for management. Forest Ecology and Management, 257, 1883–1892.

Bengtsson J, Nilsson SG, Franc A, Menozzi P (2000): Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management, 132, 39–50.

Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL, Hicke JA, Kelsey RG, Negrón JF, Seybold SJ (2010): Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. BioScience, 60, 602–613.

Berryman AA (2013): Dynamics of forest insect populations: patterns, causes, implications. Springer Science & Business Media. New York.

Bonsignore CP, Bellamy C (2013): Daily activity and flight behaviour of adults of *Capnodis tenebrionis* (Coleoptera: Buprestidae). European Journal of Entromology, 104, 425–431.

Bouget C, Duelli P (2004): The effects of windthrow on forest insect communities: A literature review. Biological Conservation, 118, 281–299.

Bradford JB, Jensen NR, Domke GM, D'Amato AW (2013): Potential increases in natural disturbance rates could offset forest management impacts on ecosystem carbon stocks. Forest Ecology and Management, 308, 178–187.

Bryant SR, Shreeve TG (2002): The use of artificial neural networks in ecological analysis: estimating microhabitat temperature. Ecological Entomology, 27, 424–432.

Bultman TL, Bell GD (2003): Interaction between fungal endophytes and environmental stressors influences plant resistance to insects. Oikos, 103, 182–190.

Cardé RT, Willis MA (2008): Navigational strategies used by insects to find distant, wind-borne sources of odor. Journal of Chemical Ecology, 34, 854–866.

Carlson DW, Groot A (1997): Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. Agricultural and Forest Meteorology, 87, 313–329.

Chase KD, Kelly D, Liebhold AM, Bader MK-F, Brockerhoff EG (2017): Long-distance dispersal of non-native pine bark beetles from host resources. Ecological Entomology, 42, 173–183.

Colangelo M, Camarero JJ, Ripullone F, Gazol A, Sánchez-Salguero R, Oliva J, Redondo MA (2018): Drought decreases growth and increases mortality of coexisting native and introduced tree species in a temperate floodplain forest. Forests, 9, 205.

Dai A, Trenberth KE, Qian T (2004): A global dataset of palmer drought severity index for 1870–2002: Relationship with soil moisture and effects of surface warming. Journal of Hydrometeorology, 5, 1117–1130.

Dale VH, Joyce LA, McNulty S, Neilson RP (2000): The interplay between climate change, forests, and disturbances. Science of The Total Environment, 262, 201–204.

Duelli P, Obrist MK, Wermelinger B (2002): 2002: Windthrow-induced changes in faunistic biodiversity in alpine spruce forests. Forest Snow and Landscape Research, 77, 117–131.

Eggleton P, Vanbergen AJ, Jones DT, Lambert MC, Rockett C, Hammond PM, Beccaloni J, Marriott D, Ross E, Giusti A (2005): Assemblages of soil macrofauna across a Scottish land-use intensification gradient: Influences of habitat quality, heterogeneity and area. Journal of Applied Ecology, 42, 1153–1164.

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

FAO (2005): Global Forest resources assessment. Terms and definitions. 1. Ed. Food and Agriculture Organization of the United Nations, Rome.

Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL (2000): Altering rainfall timing and quantity in a mesic grassland ecosystem: Design and performance of rainfall manipulation shelters. Ecosystems, 3, 308–319.

Fayt P, Machmer MM, Steeger C (2005): Regulation of spruce bark beetles by woodpeckers—a literature review. Forest Ecology and Management, 206, 1–14.

Ferris R, Humphrey JW (1999): A review of potential biodiversity indicators for application in British forests. Forestry: An International Journal of Forest Research, 72, 313–328.

Forman RT, Forman RTT, Forman RTT (1995): Land mosaics: the ecology of landscapes and regions. Cambridge University Press. Cambridge.

Forrester JA, Mladenoff DJ, Gower ST, Stoffel JL (2012): Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. Forest Ecology and Management, 265, 124–132.

Foster DR, Knight DH, Franklin JF (1998): Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems, 1, 497–510.

Frouz J (2000): The effect of nest moisture on daily temperature regime in the nests of *Formica polyctena* wood ants. Insectes Sociaux 47, 229–235.

Frouz J, Jílková V (2008): The effect of ants on soil properties and processes (Hymenoptera: Formicidae). Myrmecological News, 11, 191-199.

Führer E (2000): Forest functions, ecosystem stability and management. Forest Ecology and Management, 132, 29–38.

Galko J, Nikolov C, Vakula J, Rell S (2012): The european oak bark beetle scolytus intricatus (ratz.) (Coleoptera: Curculionidae, Scolytinae) galleries analysis. Forestry Journal, 58, 166–170.

Gaublomme E, Hendrickx F, Dhuyvetter H, Desender K (2008): The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. Biological Conservation, 141, 2585–2596.

Gooding GV, Hodges CS, Ross EW (1966): Effect of temperature on growth and survival of fomes annosus. Forest Science, 12, 325–333.

Gorb SN, Gorb EV (1999): Dropping rates of elaiosome-bearing seeds during transport by ants (*Formica polyctena* Foerst.): Implications for distance dispersal. Acta Oecologica, 20, 509–518.

Gorham LE, King SL, Keeland BD, Mopper S (2002): Effects of canopy gaps and flooding on homopterans in a bottomland hardwood forest. Wetlands, 22, 541–549.

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

Grodzki W, Fronek WG (2017): Occurrence of *Ips typographus* (L.) after wind damage in the Kościeliska Valley of the Tatra National Park. Forest Research Papers, 78, 113–119.

Hansen AJ, Neilson RP, Dale VH, Flather CH, Iverson LR, Currie DJ, Shafer S, Cook R, Bartlein PJ (2001): Global change in forests: responses of species, communities, and biomesinteractions between climate change and land use are projected to cause large shifts in biodiversity. BioScience, 51, 765–779.

Hanson JJ, Lorimer CG (2007): Forest structure and light regimes following moderate wind storms: implications for multi-cohort management. Ecological Applications, 17, 1325–1340.

Hanson PJ, Weltzin JF (2000): Drought disturbance from climate change: Response of United States forests. Science of The Total Environment, 262, 205–220.

Hawes C, Stewart A, Evans H (2002): The impact of wood ants (Formica rufa) on the distribution and abundance of ground beetles (Coleoptera: Carabidae) in a Scots pine plantation. Oecologia, 131, 612–619.

Hicke JA, Allen CD, Desai AR, Dietze MC, Hall RJ, (Ted) Hogg EH, Kashian DM, Moore D, Raffa KF, Sturrock RN, Vogelmann J (2012): Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Global Change Biology, 18, 7–34.

Hilszczański J, Gibb H, Bystrowski C (2007): Insect natural enemies of Ips typographus (L.) (Coleoptera, Scolytinae) in managed and unmanaged stands of mixed lowland forest in Poland. Journal of Pest Science, 80, 99.

Hilszczański J, Gibb H, Hjältén J, Atlegrim O, Johansson T, Pettersson RB, Ball JP, Danell K (2005): Parasitoids (Hymenoptera, Ichneumonoidea) of saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest. Biological Conservation, 126, 456–464.

Hölldobler B, Wilson EO (1990): The Ants. Springer-Verlag, Berlin Heidelberg.

Hooper DU, Chapin FSI, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S (2005): Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs, 75, 3–35.

Horstmann K (1970): Untersuchungen über den nahrungserwerb der waldameisen (*Formica polyctena* Foerster) im Eichenwald. I. Zusammensetzung der nahrung, abhängigkeit von witterungsfaktoren und von der tageszeit. Oecologia, 5, 138–157.

Hunter MD (2001): Insect population dynamics meets ecosystem ecology: Effects of herbivory on soil nutrient dynamics. Agricultural and Forest Entomology, 3, 77–84.

Hunter MD (2002): Landscape structure, habitat fragmentation, and the ecology of insects. Agricultural and Forest Entomology, 4, 159–166.

Jactel H, Petit J, Desprez-Loustau M-L, Delzon S, Piou D, Battisti A, Koricheva J (2012): Drought effects on damage by forest insects and pathogens: a meta-analysis. Global Change Biology, 18, 267–276.

Jactel J, Brockerhoff E, Duelli P (2005): A test of the biodiversity-stability theory: Meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors In: Forest diversity and function: Temperate and Boreal Systems. pp. 235–262.

Jardon Y, Filion L, Cloutier C (1994): Long-term impact of insect defoliation on growth and mortality of eastern larch in boreal Québec. Écoscience, 1, 231–238.

Jeffries JM, Marquis RJ, Forkner RE (2006): Forest age influences oak insect herbivore community structure, richness, and density. Ecological Applications, 16, 901–912.

Kawecki TJ (2004): 16 - Ecological and evolutionary consequences of source-sink population dynamics In: Hanski, I, Gaggiotti, OE (ed): Ecology, genetics and evolution of metapopulations. Academic Press, Burlington, pp. 387–414.

Keller I, Nentwig W, Largiadèr CR (2004): Recent habitat fragmentation due to roads can lead to significant genetic differentiation in an abundant flightless ground beetle. Molecular Ecology, 13, 2983–2994.

Kipyatkov VE, Lopatina EB (2002): Reaction norm in response to temperature may change to adapt rapid brood development to boreal and subarctic climates in Myrmica ants (Hymenoptera: Formicidae). European Journal of Entomology, 99, 197-208.

Klapwijk MJ, Bylund H, Schroeder M, Björkman C (2016): Forest management and natural biocontrol of insect pests. Forestry, 89, 253–262.

Konijnendijk CC (2003): A decade of urban forestry in Europe. Forest Policy and Economics, 5, 173–186.

Koricheva J, Larsson S, Haukioja E (1998): Insect performance on experimentally stressed woody plants: a meta-analysis. Annual Review of Entomology, 43, 195–216.

Kuuluvainen T (2009): Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: the complexity challenge. AMBIO: A Journal of the Human Environment, 38, 309–315.

Laakso J, Setälä H (2000): Impacts of wood ants (Formica aquilonia Yarr.) on the invertebrate food web of the boreal forest floor. Annales Zoologici Fennici, 37, 93–100.

Laurance WF, Curran TJ (2008): Impacts of wind disturbance on fragmented tropical forests: a review and synthesis. Austral Ecology, 33, 399–408.

Lemoine NP, Burkepile DE, Parker JD (2017): Insect herbivores increase mortality and reduce tree seedling growth of some species in temperate forest canopy gaps. PeerJ, 5, e3102.

Mabelis AA (1994): Flying as a survival strategy for wood ants in a fragmented landscape (Hymenoptera, Formicidae). Memorabilia Zoologica, 48, 147–170.

Mabelis AA, Korczyńska J (2001): Dispersal for survival: some obesrvations on the trunk ant (Formica truncorum, Fabricius). Netherlands Journal of Zoology, 51, 299–321.

MacDicken KG, Sola P, Hall JE, Sabogal C, Tadoum M, de Wasseige C (2015): Global progress toward sustainable forest management. Forest Ecology and Management, 352, 47–56.

Maeto K, Sato S (2004): Impacts of forestry on ant species richness and composition in warm-temperate forests of Japan. Forest Ecology and Management, 187, 213–223.

Marković Č, Stojanović A (2011): Phloemophagous and xylophagous insects, their parasitoids, predators and inquilines in the branches of the most important oak species in Serbia. Biologia, 66, 509–517.

McGee GG, Leopold DJ, Nyland RD (1999): Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. Ecological Applications, 9, 1316–1329.

Mezei P, Grodzki W, Blaženec M, Jakuš R (2014): Factors influencing the wind–bark beetles' disturbance system in the course of an *Ips typographus* outbreak in the Tatra Mountains. Forest Ecology and Management, 312, 67–77.

Mori AS, Lertzman KP, Gustafsson L (2017): Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. Journal of Applied Ecology, 54, 12–27.

Moya-Laraño J, Wise DH (2007): Direct and Indirect Effects of Ants on a Forest-Floor Food Web. Ecology, 88, 1454–1465.

Müller J, Bußler H, Goßner M, Rettelbach T, Duelli P (2008): The European spruce bark beetle *Ips typographus* in a national park: From pest to keystone species. Biodiversity and Conservation, 17, 2979.

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.

MZe (2018): Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2017. 1. Ed. Ministerstvo zemědělstí, Praha.

Niemelä J (2001): Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. European Journal of Entomology, 98, 127–132.

Niemelä J, Haila Y, Punttila P (1996): The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography, 19, 352–368.

Nilsson SG, Ericson L (1997): Conservation of plant and animal populations in theory and practice. Ecological Bulletins, 117–139.

Nilsson SG, Hedin J, Niklasson M (2001): Biodiversity and its assessment in boreal and nemoral forests. Scandinavian Journal of Forest Research, 16, 10–26.

Nitschke CR (2005): Does forest harvesting emulate fire disturbance? A comparison of effects on selected attributes in coniferous-dominated headwater systems. Forest Ecology and Management, 214, 305–319.

Oliver CD, Larson BC (1996): Forest stand dynamics. 1. Ed. Wiley, New York.

Palladini JD, Jones MG, Sanders NJ, Jules ES (2007): The recovery of ant communities in regenerating temperate conifer forests. Forest Ecology and Management, 242, 619–624.

Palviainen M, Finér L, Mannerkoski H, Piirainen S, Starr M (2005): Changes in the above- and below-ground biomass and nutrient pools of ground vegetation after clear-cutting of a mixed boreal forest. Plant and Soil, 275, 157–167.

Pennacchio F, Strand MR (2006): Evolution of developmental strategies in parasitic hymenoptera. Annual Review of Entomology, 51, 233–258.

Peters DP, Lugo AE, Chapin III FS, Pickett ST, Duniway M, Rocha AV, Laney C, Jones J (2011): Cross-system comparisons elucidate disturbance complexities and generalities. Ecosphere, 2, art81.

Peters EB, Wythers KR, Bradford JB, Reich PB (2013): Influence of disturbance on temperate forest productivity. Ecosystems, 16, 95–110.

Petraitis PS, Latham RE, Niesenbaum RA (1989): The maintenance of species diversity by disturbance. The Quarterly Review of Biology, 64, 393–418.

Pineau X, David G, Peter Z, Sallé A, Baude M, Lieutier F, Jactel H (2017): Effect of temperature on the reproductive success, developmental rate and brood characteristics of Ips sexdentatus (Boern.). Agricultural and Forest Entomology, 19, 23–33.

Punttila P, Haila Y, Niemelä J, Pajunen T (1994): Ant communities in fragments of old-growth taiga and managed surroundings. Annales Zoologici Fennici, 31, 131–144.

Punttila P, Haila Y, Pajunen T, Tukia H (1991): Colonisation of clearcut forests by ants in the southern finnish taiga: A quantitative survey. Oikos, 61, 250–262.

Punttila P, Haila Y, Tukia H (1996): Ant communities in taiga clearcuts: habitat effects and species interactions. Ecography, 19, 16–28.

Reid ML, Roitberg BD (1995): Effects of body size on investment in individual broods by male pine engravers (Coleoptera: Scolytidae). Canadian Journal of Zoology, 73, 1396–1401.

Ribas CR, Sobrinho TG, Schoereder JH, Sperber CF, Lopes-Andrade C, Soares SM (2005): How large is large enough for insects? Forest fragmentation effects at three spatial scales. Acta Oecologica, 27, 31–41.

Roland J (1993): Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. Oecologia, 93, 25–30.

Roland J, Taylor PD (1997): Insect parasitoid species respond to forest structure at different scales. Nature, 386, 710–713.

Rosengren R, Pamilo P (1978): Effect of winter timber felling on behaviour of foraging wood ants (Formica rufa group) in early spring. Memorabilia Zoologica, 143–155.

Salmon S, Artuso N, Frizzera L, Zampedri R (2008): Relationships between soil fauna communities and humus forms: Response to forest dynamics and solar radiation. Soil Biology and Biochemistry, 40, 1707–1715.

Savolainen R, Vepsäläinen K (1988): A Competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos, 51, 135–155.

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.

Schiegg K (2001): Saproxylic insect diversity of beech: Limbs are richer than trunks. Forest Ecology and Management, 149, 295–304.

Schoereder JH, Sobrinho TG, Ribas CR, Campos RBF (2004): Colonization and extinction of ant communities in a fragmented landscape. Austral Ecology, 29, 391–398.

Schowalter TD (1981): Insect herbivore relationship to the state of the host plant: biotic regulation of ecosystem nutrient cycling through ecological succession. Oikos, 37, 126–130.

Schowalter TD (2012): Insect responses to major landscape-level disturbance. Annual Review of Entomology, 57, 1–20.

Seidl R, Schelhaas M-J, Lexer MJ (2011): Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biology, 17, 2842–2852.

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D, Petr M, Honkaniemi J, Lexer MJ, Trotsiuk V, Mairota P, Svoboda M, Fabrika M, Nagel TA, Reyer CPO (2017): Forest disturbances under climate change. Nature Climate Change, 7, 395–402.

Selås Vidar, Hogstad Olav, Kobro Sverre, Rafoss Trond (2004): Can sunspot activity and ultraviolet–B radiation explain cyclic outbreaks of forest moth pest species? Proceedings of the Royal Society of London Series B: Biological Sciences, 271, 1897–1901.

Seybold SJ, Bohlmann J, Raffa KF (2000): Biosynthesis of coniferophagous bark beetle pheromones and conifer isoprenoids: Evolutionary perspective and synthesis. The Canadian Entomologist, 132, 697–753.

Siitonen J (2001): Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecological Bulletins, 11–41.

Sobrinho TG, Schoereder JH (2007): Edge and shape effects on ant (Hymenoptera: Formicidae) species richness and composition in forest fragments. Biodiversity and Conservation, 16, 1459–1470.

Sorvari J, Hakkarainen H (2007): Wood ants are wood ants: deforestation causes population declines in the polydomous wood ant Formica aquilonia. Ecological Entomology, 32, 707–711.

Šrámek V, Novotný R (2019): Povětrnostní podmínky a abiotická poškození v roce 2018. Zpravodaj ochrany lesa, 22, 9–13.

Summerville KS, Crist TO (2008): Structure and conservation of lepidopteran communities in managed forests of northeastern North America: a review. The Canadian Entomologist, 140, 475–494.

Svoboda M, Janda P, Nagel TA, Fraver S, Rejzek J, Bače R (2012): Disturbance history of an old-growth sub-alpine Picea abies stand in the Bohemian Forest, Czech Republic. Journal of Vegetation Science, 23, 86–97.

Toro DT, Ribbons R, Shannon P (2012): The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecological News, 17, 133–146.

Tscharntke T, Brandl R (2003): Plant-insect interactions in fragmented landscapes. Annual Review of Entomology, 49, 405–430.

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002): Characteristics of insect populations on habitat fragments: A mini review. Ecological Research, 17, 229–239.

Velde LV, Turlure C, Dyck HV (2011): Body temperature and territory selection by males of the speckled wood butterfly (Pararge aegeria): What makes a forest sunlit patch a rendezvous site? Ecological Entomology, 36, 161–169.

Véle A, Frouz J, Holuša J, Kalčík J (2010): Chemical properties of forest soils as affected by nests of *Myrmica ruginodis* (Formicidae). Biologia, 65, 122–127.

Véle A, Holuša J, Frouz J, Konvicka O (2011): Local and landscape drivers of ant and carabid beetle communities during spruce forest succession. European Journal of Soil Biology, 47, 349–356.

Vepsäläinen K, Pisarski B (1982): Assembly of island ant communities. Annales Zoologici Fennici, 19, 327–335.

Vodka Š, Cizek L (2013): The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. Forest Ecology and Management, 304, 33–41.

Weisser WW, Siemann E (2008): The various effects of insects on ecosystem functioning in: Weisser, WW, Siemann, E (ed): Insects and ecosystem function. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 3–24.

Wermelinger B (2004): Ecology and management of the spruce bark beetle Ips typographus—a review of recent research. Forest Ecology and Management, 202, 67–82.

Westerfelt P, Widenfalk O, Lindelöw Å, Gustafsson L, Weslien J, Leather SR, Jonsell M (2015): Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. Insect Conservation and Diversity, 8, 493–504.

White PS, Jentsch A (2001): The search for generality in studies of disturbance and ecosystem dynamics in: Esser, K, Lüttge, U, Kadereit, JW, Beyschlag, W (ed): Progress in botany: genetics physiology systematics ecology. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 399–450.

Wigley TB, Roberts TH (1997): Landscape-level effects of forest management on faunal diversity in bottomland hardwoods. Forest Ecology and Management, 90, 141–154.

Wohlgemuth T, Bürgi M, Scheidegger C, Schütz M (2002): Dominance reduction of species through disturbance—a proposed management principle for central European forests. Forest Ecology and Management, 166, 1–15.

Wood DL (1982): The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology, 27, 411–446.

Yang LH, Gratton C (2014): Insects as drivers of ecosystem processes. Current Opinion in Insect Science, 2, 26–32.

Yi H, Moldenke A, Yi H (2005): Response of ground-dwelling arthropods to different thinning intensities in young douglas fir forests of western Oregon. Environmental Entomology, 34, 1071–1080.

Zapata VM, Robledano F (2014): Assessing biodiversity and conservation value of forest patches secondarily fragmented by urbanisation in semiarid southeastern Spain. Journal for Nature Conservation, 22, 166–175.

Příloha 1

Ant abundance increases with clearing size

Adam Véle, Jaroslav Holuša, Jakub Horák

2016

Journal of Forest Research 21: 110-114

J For Res (2016) 21:110–114
DOI 10.1007/s10310-016-0520-y

SHORT COMMUNICATION

Ant abundance increases with clearing size

Adam Véle[1,2] · **Jaroslav Holuša**[2] · **Jakub Horák**[2]

Received: 23 September 2015 / Accepted: 4 January 2016 / Published online: 8 February 2016

Abstract Ants are an important part of biodiversity and are useful bioindicators. Our aim was to determine whether ant species richness and composition differ among large clear-cuts (ca. 3000 m^2), small forest gaps (ca. 400 m^2), and areas of mature forest. The research was conducted in a large plantation of *Picea abies* in the Jizerske Mountains in the Czech Republic at an elevation of ca. 900 m a.s.l. Ants were sampled using pitfall traps in three areas, each of which had a large clear-cut, mature forest, and gaps; a randomized complete block design was used. Species richness and composition of ant assemblages differed significantly among plots in the three treatments. The results showed that ant abundance and diversity were similarly low in small gaps and in closed-canopy mature stands; in comparison, large clear-cuts supported significantly higher species richness, more complex species composition, and a higher abundance of ants. Six species were found in large clear-cuts, but only one and two species were collected in small gaps and mature forests, respectively. Our findings suggest that small-scale forest management is not suitable for maintaining ant diversity.

Keywords Abundance · Ant · Diversity · Forest management · Gap

Introduction

A goal of modern forestry is to protect ecosystem biodiversity and functionality while maintaining current wood production (Decocq et al. 2004; Nagai and Yoshida 2006; Newmaster et al. 2007). Achieving this goal in managed spruce monocultures is difficult, because such forests are characterized by increased soil acidity and nutrient deficiency (Emmer et al. 1998), high susceptibility to damage by abiotic (Hlásny et al. 2011) and biotic agents (Overbeck and Schmidt 2012), and low diversity of other organisms (see Felton et al. 2010). Secondary stands of Norway spruce (*Picea abies* (L.)) Katrs. account for 51 % of the forested area (Ministerstvo Zemědělství 2014) in the Czech Republic, and the number of ant native species is low (Czechowski et al. 2002).

Clear-cutting is a widespread type of management, and the sizes of clear-cuts vary considerably in different regions. In Sweden, for example, the average size of clear-cuts is 6.3 ha, and the legal maximum is 20 ha (Eckerberg 1987; Mc Dermott et al. 2010). In Czech Republic, the average size is 0.3 ha (calculated from forest inventory data from 2005 to 2012, Kristek pers. comm.), and the legal maximum is 1 ha (Kupka 2006). Despite the small clear-cut area, there is ongoing debate in the Czech Republic about the harmful effects of clear-cuts on biodiversity (Baláž et al. 2008).

Ants constitute an important component of forest ecosystems because they improve soil properties (Véle et al. 2010) and directly or indirectly affect herbivorous insects (Maňák et al. 2013; Wynhoff et al. 2015); moreover, ant nests provide a habitat for other organisms (Härkönen and Sorvari 2014). In general, ants can be considered as a surrogate indicator of biodiversity (Alonso 2000). The occurrence of ants is strongly affected by the

---

✉ Adam Véle
adam.vele@centrum.cz

[1] Forestry and Game Management Research Institute, Strnady 136, 252 02 Jíloviště, Czech Republic

[2] Department of Forest Protection and Entomology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamycka 1176, 16521 Prague 6, Czech Republic

type of forest management (Maeto and Sato 2004). The removal of wood decreases nesting possibilities for red wood ants (Punttila et al. 1994; Punttila and Haila 1996), and nests on clear-cuts have relatively low survival rates (Sorvari and Hakkarainen 2007). On the other hand, harvesting of wood creates sunlit areas. In such areas, many ant species occur in higher abundances than in mature forests (Punttila 1996; Véle et al. 2011). The increase of abundance in these cleared areas persists until the shading increases again. Well-lit areas also serve as source points for the spread of ants into shaded stands that provide more suboptimal conditions (Véle et al. 2011).

Research to date has not taken into account the size of clearings necessary for increasing ant abundance and species richness. Although studies have indicated that small-scale harvesting can be regarded as ecologically beneficial (Phillips et al. 2006), it may not always be an ideal solution for sustaining biodiversity in large plantations. Our objective was to determine whether ant assemblages differ in small vs. large clearings surrounded by large mature stands of commercially managed forest.

Materials and methods

The study was conducted in a large plantation of Norway spruce, *Picea abies* (L.) Karts., in the Jizerske Mountains near the Josefuv Dul (annual temperature 4.4 °C, 1323 mm precipitation, ca. 900 m a.s.l.) in the Czech Republic. Three study areas were located 0.5–1.0 km from one another. Each area was composed of four study plots: one in a large clear-cut (ca. 3000 m^2), one in a mature forest (plot area ca. 3000 m^2), and two in gaps (ca. 400 m^2 each). All gaps and clear-cuts were approximately 3 years old. Plots were situated in a secondary spruce monoculture with equal age structure. The individual plots within a study area were ca. 100 m apart. The clear-cuts and gaps were the product of commercial clear-cut forest management, and approximately 30 % of their surface was covered by undergrowth. Pitfall traps, which are a proven method for sampling ants in spruce plantations (Véle et al. 2009), were placed in an elliptical configuration, ca. 2 m from one another. The plastic traps (10 cm deep and 7 cm in diameter) were filled with 3 % formaldehyde. Fourteen pitfall traps were placed in each of the plots in the clear-cuts and the mature forest, and seven traps were placed in each of the plots in the gaps. The traps were deployed at each plot for 2 weeks/month in June, July, and August in 2009.

For the analysis of total ant species richness, we computed stand-based rarefactions (Mao Tau function) with 95 % confidence intervals and the Chao function (Gotelli and Colwell 2001; Horák and Rebl 2013). The same analysis was used to compare the studied habitats: large clear-cut (clear-cut), gaps (gap), and mature forest (forest). The number of randomizations was set at 1000. Analyses were computed using EstimateS 8.2 (Colwell 2006). Statistical significance among the studied habitats was tested using ANOVA with 999 permutations as implemented in the vegan package in R. As recommended by Gotelli et al. (2011), we made occurrence-based analyses of identifying species composition and individual species responses to the three habitats. Canonical correspondence analysis (CCA) was used as the most appropriate method (Horák et al. 2014). A The Monte-Carlo permutation test with 999 permutations under the full model was used. Permutation type was restricted for split-plot design with whole plot freely exchangeable. Statistical significance of associations between species and habitat was tested using T value biplots with Van Dobben circles in CANOCO (ter Braak and Smilauer 2002).

Results

In total, six ant species were captured: *Myrmica rubra* (Linnaeus, 1758), *Myrmica ruginodis* (Nylander, 1846), *Formica fusca* (Linnaeus, 1758), *Formica sanguinea* (Latreille, 1798), *Camponotus herculeanus* (Linnaeus, 1758), and *Lasius platythorax* (Seifert, 1991) (Table 1). The species rarefactions reached an asymptote for the entire data set (Fig. 1), suggesting that most of the species in the study areas were represented in the analysis and that the number of plots was sufficient. Ant species richness was significantly influenced by the studied habitat ($F = 14.73$; $P < 0.01$), and significantly more species were collected in the clear-cuts than in the gaps or mature stands (Fig. 2). This result was also confirmed by the results for species composition based on species occurrences ($F = 8.92$; $P < 0.001$).

Myrmica ruginodis was detected in both types of clearings as well as in the mature forest, but it was more

Table 1 Total number of individual ants captured in pitfall traps in three habitats (clear-cut, gap, and forest) in Norway spruce plantations (Jizerske Mts)

Species	Habitat		
	Clear-cut	Gap	Forest
Myrmica rubra	2	0	0
Myrmica ruginodis	237	94	14
Formica fusca	**163**	0	2
Formica sanguinea	**257**	0	0
Camponotus herculeanus	**9**	0	0
Lasius platythorax	**16**	0	0

For each species, a value in bold is significantly different from the other two values

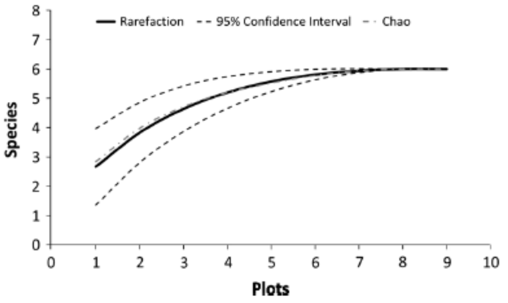

Fig. 1 Species rarefaction and estimate of total species richness of the trapped ants (Formicidae) in the Norway spruce plantation (Jizerske Mts). The *black solid line* shows the sample-based rarefaction, the two surrounding *black dashed lines* are Mao Tau estimates with 95 % confidence intervals, and the *gray dash* and *dotted line* is the Chao 1 estimate of the total number of species

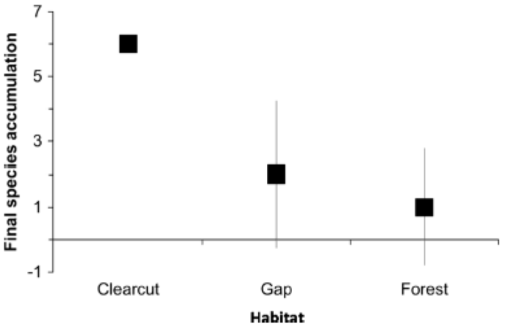

Fig. 2 Final ant species accumulations (with 95 % confidence intervals) in the three habitats in the Norway spruce plantation (Jizerske Mts)

abundant in the clear-cuts than in the gaps or mature forests. *Formica fusca* was significantly more abundant in the clear-cuts, while only two specimens were captured in mature forests, and no specimens were captured in the gaps. A significantly higher abundance of *F. sanguinea*, *L. platythorax*, and *C. herculeanus* was collected in the clear-cuts, while only two specimens of *M. rubra* were collected, and both were collected from clear-cuts.

Discussion

In the present study, ants were substantially more abundant and diverse in the clear-cuts than in the gaps or in the mature forest. These differences cannot be explained by insufficient time for colonization of the small gaps and mature forests. Clearings, for example, are colonized by ants within 1 year (Véle et al. 2011). A possible explanation for the low numbers (only 16 individuals) of ants in the mature forest was that the spruce plantation was located on a cold plateau, which is an unsuitable environment for a number of ant species (Czechowski et al. 2002). Removal of wood within the mature forest also limits nesting opportunities (Punttila and Haila 1996). In addition, the low abundance and diversity in the mature forest might be explained by the insufficient number of clearings and therefore the limited opportunities for ant dispersal in even-age plantations (see Véle et al. 2011). In general, these results are not surprising, because the diversity is known to be lower in managed forests than in unmanaged forests (Kone et al. 2014), and degraded forests may be characterized by the absence of wood ants (Torossian and Roques 1984).

Most studies show that anthropogenic changes in forests have a negative influence on ants and especially on *Formica* species (Domisch et al. 2000; Sorvari and Hakkarainen 2007). Zmihorski (2010) stated that the negative impact of cutting may result from the increased variability of abiotic conditions (sunlight, temperature, and humidity), as described by Aussenac (2000), Palviainen et al. (2005), and Olchev et al. (2009). Negative effects of changes in microclimate were also highlighted by Rosengren and Pamilo (1978), and by Domisch et al. (2000). We suspect that in closed forests, the increased amount of sunlight caused by clear-cuts may benefit ants, because light increases soil temperature and thus the rate of ant brood development and other ant activities (López et al. 1992; Banschbach et al. 1997; Kipyatkov and Lopatina 2002). Moreover, light is likely to affect the amount of understory vegetation (Cogliastro and Paquette 2012), which again can affect the abundance of invertebrates that may serve as food for ants (Gorham et al. 2002). The change in environmental conditions can be regarded as a factor causing an increase in ant species diversity in conifer forests after clear-cutting (Palladini et al. 2007; Véle et al. 2011).

Because only diverse ecosystems can sustain ecological functions (Bonn and Gaston 2005), diversity in managed forests cannot be ignored (Nelson and Halpern 2005). Quite the contrary, we must develop methods for maintaining biodiversity in managed forests (Ferris and Humphrey 1999), where natural processes have commonly been inhibited (Kirby and Watkins 1998). Our findings suggest that small-scale forest management is not suitable for maintaining ant diversity. Because ants are important indicators of biodiversity (Alonso 2000), we suggest that the creation of larger clearings of at least 1000 m^2 will help generate biodiversity in even-aged coniferous plantations.

Acknowledgments This work was supported by a project of Ministry of Agriculture of the Czech Republic (Resolution RO0115; Reference number 5774/2015-MZE-17011), by the grants from

Ministry of Agriculture of the Czech Republic (QJ1330233 and NAZV KUS QJ1520197), and partly by CIGA ČZU 20154301. The authors thank Dr. Bruce Jaffee for linguistic and editorial improvements.

References

Alonso LE (2000) Ants as indicators of diversity. In: Agosti D, Alonso LA, Schultz TR (eds) Ants—standard methods for measuring and monitoring biodiverzity. Smithsonian Institution Press, Washington DC, pp 80–88

Aussenac G (2000) Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. Ann For Sci 57:287–301

Baláž E, Kotecký V, Machalová L, Poštulka Z (2008) Vliv holosečného hospodaření na půdu, vodu a biodiverzitu. Hnutí Duha, Brno

Banschbach VS, Levit N, Herbers JM (1997) Nest temperatures and thermal preferences of a forest ant species: is seasonal polydomy a thermoregulatory mechanism? Insect Soc 44:109–122

Bonn A, Gaston KJ (2005) Capturing biodiversity: selecting priority areas for conservation using different criteria. Biodivers Coserv 14:1083–1100

Cogliastro A, Paquette A (2012) Thinning effect on light regime and growth of underplanted red oak and black cherry in post-agricultural forests of south-eastern Canada. New Forest 43:941–954

Colwell RK (2006) EstimateS: statistical estimation of species richness and shared species from samples. Version 8. Persistent URL http://purl.oclc.org/estimates

Czechowski W, Radchenko A, Czechowska W (2002) The ants (Hymenoptera, Formicidae) of Poland. Museum and Institute of Zoology PAS, Warszawa

Decocq G, Aubert M, Dupont F, Alard D, Saguez R, Wattez-Franger A, De Foucault B, Delelis-Dusollier A, Bardat J (2004) Plant diversity in a managed temperate deciduous forest: understory response to two silvicultural systems. J Appl Ecol 41:1065–1079

Domisch T, Finér L, Laiho R, Karsisto M, Laine J (2000) Decomposition of Scots pine litter and the fate of released carbon in pristine and drained pine mires. Soil Biol Biochem 32:1571–1580

Eckerberg K (1987) Environmental protection in Swedish forestry: a study of the implementation process. Doctoral thesis, University of Umea, Umea

Emmer IM, Fanta J, Khobus AT, Kooijman AM, Sevink J (1998) Reversing borelization as a means to restore biodiversity in Central-European mountain forests—an example from the Krkonose Mountains, Czech Republic. Biodiv Conserv 7:229–247

Felton A, Lindbladh M, Bruneta J, Fritz Ö (2010) Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. For Ecol Manag 260:939–947

Ferris R, Humphrey JW (1999) A review of potential biodiversity indicators for application in British forests. Forestry 72:313–328

Gorham LE, King SL, Keeland BD, Mopper S (2002) Effects of canopy gaps and flooding on homopterans in a bottomland hardwood forest. Wetlands 22:514–549

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Gotelli NJ, Ellison AM, Dunn RR, Sanders NJ (2011) Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. Myrmecol News 15:13–19

Härkönen S, Sorvari J (2014) Species richness of associates of ants in the nests of red wood ant *Formica polyctena* (Hymenoptera, Formicidae). Insect Conserv Diver 7:485–495

Hlásny T, Kristek S, Holuša J, Trombik J, Urbancova N (2011) Snow disturbances in secondary Norway spruce forests in Central Europe: regression modeling and its implications for forest management. For Ecol Manag 262:2151–2161

Horák J, Rebl K (2013) The species richness of click beetles in ancient pasture woodland benefits from a high level of sun exposure. J Insect Conserv 17:307–318

Horák J, Vodka S, Kout J, Halda JP, Bogusch P, Pech P (2014) Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. For Ecol Manag 15:80–85

Kipyatkov VE, Lopatina EB (2002) Reaction norm in response to temperature may change to adapt rapid brood development to boreal and subarctic climates in Myrmica ants (Hymenoptera: Formicidae). Eur J Entomol 99:197–208

Kirby JK, Watkins CH (1998) The ecological history of European forests. CAB International, New York

Kone M, Konate S, Yeo K, Kouassi PK, Linsenmair KE (2014) Effects of management intensity on ant diversity in cocoa plantation (Oume, centre west Côte d'Ivoire). J Insect Conserv 18:701–712

Kupka I (2006) Recreational load as a driving variable for urban forests. J Forest Sci 52:324–328

López F, Serrano JM, Acosta FJ (1992) Temperature-vegetation structure interaction: the effect on the activity of the ant *Messor barbarus* (L.). Plant Ecol 99–100:119–128

Maeto K, Sato S (2004) Impacts of forestry on ant species richness and composition in warm-temperate forests of Japan. For Ecol Manag 187:213–223

Maňák V, Nordenhem H, Björklund N, Lenoir L, Nordlander G (2013) Ants protect conifer seedlings from feeding damage by the pine. Agr Forest Entomol 15:98–105

Mc Dermott C, Cashore BV, Kanowski P (2010) Global environmental forest policies: an international comparison. Earthscan, London

Ministerstvo Zemědělství (2014) Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2013. Ministerstvo Zemědělství, Praha

Nagai M, Yoshida T (2006) Variation in understory structure and plant species diversity influenced by silvicultural treatments among 21- to 26-year old *Picea glehnii* plantations. J For Res 11:1–10

Nelson CR, Halpern CB (2005) Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Can J Bot 83:610–620

Newmaster SG, Parker WC, Bell FW, Paterson JM (2007) Effects of forest floor disturbances by mechanical site preparation on floristic diversity in a central Ontario clearcut. For Ecol Manag 246:196–207

Olchev A, Radler K, Sogachev A, Panferov O, Gravenhorst G (2009) Application of a three-dimensional model for assessing effects of small clear-cuttings on radiation and soil temperature. Ecol Model 220:3046–3056

Overbeck M, Schmidt M (2012) Modelling infestation risk of Norway spruce by *Ips typographus* (L.) in the Lower Saxon Harz Mountains (Germany). For Ecol Manag 266:115–125

Palladini JD, Jones MG, Sanders NJ, Jules ES (2007) The recovery of ant communities in regenerating temperate conifer forests. For Ecol Manag 242:619–624

Palviainen M, Finér L, Lauren A, Piirainen S, Starr M (2005) Changes in the above- and below-ground biomass and nutrient pools of ground vegetation after clear-cutting of a mixed boreal forest. Plant Soil 275:157–167

Phillips ID, Cobb TP, Spence JR, Brigham RM (2006) Salvage logging, edge effects, and carabid beetles: connections to conservation and sustainable forest management. Environ Entomol 35:950–957

Punttila P (1996) Succession, forest fragmentation, and the distribution of wood ants. Oikos 75:291–298

Punttila P, Haila Y (1996) Colonisation of a burned forest by ants in the southern Finnish Boreal Forest. Silva Fennica 30:421–435

Punttila P, Haila Y, Niemelä J, Pajunen T (1994) Ant communities in fragments of old-growth taiga and managed surroundings. Ann Zool Fenn 31:131–144

Rosengren R, Pamilo P (1978) Effect of winter timber felling on behaviour of foraging wood ants (*Formica rufa* group) in early spring. Mem Zool 29:143–155

Sorvari J, Hakkarainen H (2007) Wood ants are wood ants: deforestation causes population declines in the polydomous wood ant *Formica aquilonia*. Ecol Entomol 32:707–711

Ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York

Torossian C, Roques L (1984) The answers of the ant *Formica lugubris* Zett to anthropic degenerative process of french subalpine forests. Bull Ecol 15:77–90

Véle A, Holuša J, Frouz J (2009) Sampling for ants in different-aged spruce forests: a comparison of methods. Eur J Soil Biol 45:301–305

Véle A, Frouz J, Holuša J, Kalčík J (2010) Chemical properties of forest soils as affected by nests of *Myrmica ruginodis* (Formicidae). Biologia 65:122–127

Véle A, Holuša J, Frouz J, Konvička O (2011) Local and landscape drivers of ant and carabid beetle communities during spruce forest succession. Eur J Soil Biol 47:349–356

Wynhoff I, Bakker RB, Oteman B, Arnaldo PS, van Langevelde F (2015) *Phengaris (Maculinea) alcon* butterflies deposit their eggs on tall plants with many large buds in the vicinity of *Myrmica ants*. Ins Conserv Diver 8:177–188

Zmihorski M (2010) Distribution of red wood ants (Hymenoptera: Formicidae) in the clear-cut areas of a managed forest in Western Poland. J For Res 15:145–148

Příloha 2

Microclimatic conditions of *Lasius flavus* ant mounds

Adam Véle, Jaroslav Holuša

2017

International Journal of Biometeorology 61:957–961

Int J Biometeorol (2017) 61:957–961
DOI 10.1007/s00484-016-1275-z

ORIGINAL PAPER

Microclimatic conditions of *Lasius flavus* ant mounds

Adam Véle[1,2] **· Jaroslav Holuša**[2]

Received: 9 May 2016 / Revised: 3 October 2016 / Accepted: 7 November 2016 / Published online: 23 November 2016

Abstract Like other organisms, ants require suitable microclimatic conditions for their development. Thus, ant species inhabiting colder climates build nest mounds that rise above the soil surface, presumably to obtain heating from solar radiation. Although some ant species construct mounds of organic materials, which generate substantial heat due to microbial metabolism, *Lasius flavus* mounds consists mostly of soil, not organic material. The use of artificial shading in the current study demonstrated that *L. flavus* depends on direct solar radiation to regulate the temperature in its mound-like nests. Temperatures were much lower in shaded mounds than in unshaded mounds and were likely low enough in shaded mounds to reduce ant development and reproduction. In areas where *L. flavus* and similar ants are undesirable, they might be managed by shading.

Keywords Ants · Management · Mound · *Lasius* · Temperature · Radiation

Introduction

Ants build nests to maintain microclimatic conditions (temperature, humidity) suitable for the development of their brood (Hölldobler and Wilson 1990). The ability to regulate temperature is a key contributor to ant ecological success and may help explain social development among insects in general (Wilson 1971). The aboveground parts of ant nests are sometimes 23% warmer than the belowground parts (Tschinkel 2006). With this increase in temperature, the time required for brood development decreases (Kipyatkov and Lopatina 2015), which increases colony reproduction (Abril et al. 2010).

Ants often build their nests under stones because stones provide better and more stable thermal conditions than other habitats (Dean and Turner 1991; Fernández-Escudero et al. 1993; Thomas 2002). Ants may also help control temperatures in the nest by orienting mounds in a south-north direction (Vogt et al. 2008). Moreover, ants often migrate to habitats with more convenient microclimatic conditions (Smallwood and Culver 1979). Migration is rather typical for *L. flavus* and other ants with small nests and therefore with relatively poor thermoregulation (Coenen-Staß et al. 1980; Rosengren et al. 1987). Although construction of a new nest is difficult and time consuming, such construction is worth it (Mikheyev and Tschinkel 2004) because relocation can enhance reproduction (Smallwood 1982).

The type of material used for the nest construction influences nest temperature (Banschbach et al. 1997). Thermal conductivity of soil *Lasius* nest is much higher than thermal conductivity of *Formica* nest (Frouz 1996). In nest mounds made of organic material, the ant *Formica* s. str. is able to maintain more or less stable microclimatic conditions (Rosengren et al. 1987; Frouz 2000; Lenoir et al. 2001). The primary sources of the thermal energy in these nests are considered to be (i) the metabolic heat of ants, (ii) the metabolic heat of the microorganisms decaying the organic material, (iii) the temperature of the air surrounding the nest, (iv) solar radiation and (v) the humidity of the nest material (see Kadochová and Frouz 2014).

The yellow meadow ant, *L. flavus* (Fabricius, 1781), inhabits non-forested areas in Central Europe, Asia, Northern

---

✉ Adam Véle
adam.vele@centrum.cz

[1] Forestry and Game Management Research Institute, Strnady 136, 252 02 Jíloviště, Czech Republic

[2] Faculty of Forestry and Wood Sciences, Department of Forest Protection and Entomology, Czech University of Life Sciences Prague, Kamycka 1176, 16521 Prague 6, Czech Republic

Africa and the Northeastern USA (Czechowski et al. 2002). In some habitats, the density of *L. flavus* mounds can be as high as 52 per 100 m^2 (Dostál et al. 2005). The microclimate in these mounds, which consist largely of soil rather than organic material, is likely to be affected by a variety of factors. Because organic material is absent or scarce in *L. flavus* mounds, the thermal contribution of microorganisms is probably negligible.

The temperature of a nest mound will be affected by ant number and size. For example, a nest's self-warming ability is likely to be lower in a nest containing 2000 to 3000 *L. flavus* ants that are 2–4 mm long (Odum and Pontin 1961) than in a nest containing >1,000,000 red forest ants that are 4–9 mm long (Czechowski et al. 2002; Rosengren et al. 1987). The thermoregulation characteristics of *Lasius* nests, however, have yet to be investigated, even though *Lasius* ants are considered to affect humans in both negative and positive ways. Although *Lasius* ants improve soil quality (Holec and Frouz 2006), they can also make it more difficult to use the colonized land (Lopéz et al. 2000), and non-native *Lasius* species have invaded and colonized Europe (Boer and Vierbergen 2008). The main objective of this study was to assess the effect of solar radiation on the temperature of *L. flavus* ant mounds. A method for the easy and environmental-friendly management of *L. flavus* and similar species is also discussed.

Materials and methods

The study was conducted on a meadow with northern exposure near Zelezny Brod, the Czech Republic (50°37′55.179″ N, 15°15′4.009″ E). The meadow is at 400 m altitude, and the area has a mean annual temperature of 7 °C and a mean annual precipitation of 1000 mm (Culek 1995).

Eight *L. flavus* mounds that were 5 m apart and in a line were selected. All of the selected mounds had the same size and volume (50 cm in diameter, 30 cm high). Four of the eight mounds were randomly selected and were artificially shaded with a piece of light-blocking textile; the remaining four hills were left unshaded. Each piece of textile was tightly attached to four stakes so that it was 5–50 cm above the mound and so that it shaded the mound throughout the day but did not block rain or air flow. While unshaded mounds remained unshaded throughout the study, the shaded mounds were shaded for a 10-day period and were then left unshaded for 14 days until another 10-day shading period was initiated. From May to August 2008, the mounds were examined in seven periods: one unshaded period before any mounds were shaded, three periods with shading of designated mounds and three periods without shading. Air temperature was measured 25 cm above the soil surface. A data logger with a sensory receptor was carefully inserted in the central part of each mound to record the temperature every hour on every day of the study. To sum the temperature effect, the accumulated hours with temperatures >17 °C (accumulated degree hours, ADH values) were determined for each period. A base temperature of 17 °C was used because this is the lowest temperature that is suitable for development of all ant stages (Kipyatkov et al. 2004). Although the average nest temperature will differ depending on the type of ant and the geographical location (Kipyatkov et al. 2004; Kadochová and Frouz 2014), *L. flavus* and *L. niger* are related species of similar size and with similar behaviours. Nonetheless, the average nest temperature may not be the temperature that the brood is exposed to because workers may carry the brood to those parts of nests with temperatures most conducive to development (Penick and Tschinkel 2008; Anderson and Munger 2003). The Kruskal-Wallis test was used to compare ADH values in each period for periodically shaded and always unshaded mounds.

Results

During the circadian rhythm, temperatures fluctuated by up to 14 °C in unshaded mounds. In shaded mounds, fluctuations were lower (Fig.1). In both shaded and unshaded mounds, temperatures were highest near midday and then slowly declined until the next morning (Fig. 1). The same pattern was observed for air temperature (Fig. 1). Described circadian temperature rhythm was same during all periods in shaded and unshaded mounds. During periods when nests were shaded, the shaded mounds temperature declined. During periods without shading, the temperature of shaded mounds approached to temperature of unshaded mounds, but did not reached the same levels (Fig. 2).

In May, June and July, the average temperature was always higher for unshaded mounds than for periodically shaded mounds during the time when they were shaded (Table 1).

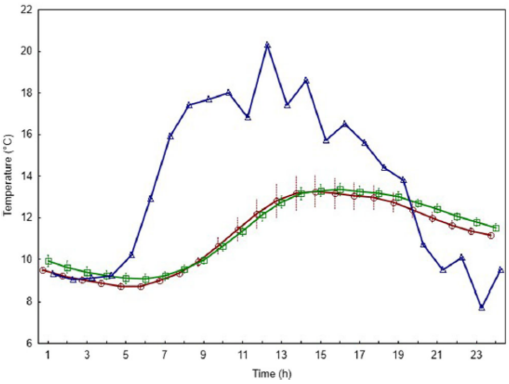

Fig. 1 Hourly temperatures in unshaded mounds (*circles*) and shaded mounds (*squares*) of *L. flavus* nests and in the surrounding air (*triangles*). The values are means ± SE for first (unshaded) period

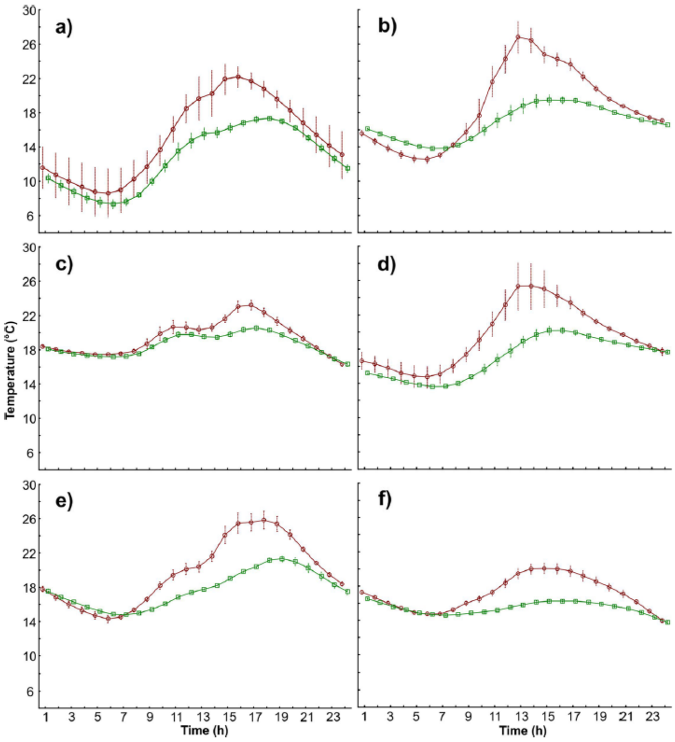

Fig. 2 Hourly temperatures in unshaded mounds (*circles*) and shaded mounds (*squares*) of *L. flavus* nests. The values are means ± SE for 2–7 periods. **a)** 2–shaded. **b)** 3–unshaded. **c)** 4–shaded. **d)** 5–unshaded. **e)** 6–shaded. **f)** 7–unshaded period

During periods with shading (periods 2, 4 and 6), the ADH values were significantly lower in the shaded mounds than in the unshaded mounds (Tables 1 and 2). During periods without shading (periods 1, 3, 5 and 7), the ADH values tended to lower in periodically shaded mounds, but the differences in periods 1 and 5 were not statistically significant (Table 2).

Discussion

During periods 2, 4 and 6, when periodically shaded mounds were shaded, ADH values were lower in shaded mounds than in unshaded mounds (Tables 1 and 2).

Table 1 Temperatures (°C, means ± SD) in shaded and unshaded *L. flavus* mounds. These means are based on temperatures recorded during periods 2, 4 and 6, when periodically shaded mounds were shaded

Treatment	May	June	July	August
Unshaded mounds	13.9 ± 4.5	17.3 ± 4.5	17.6 ± 4.0	16.4 ± 3.6
Shaded mounds	13.2 ± 4.1	16.1 ± 3.4	16.8 ± 3.3	16.5 ± 3.5

Accumulated degree hours in the current study were reduced by shading of *L. flavus* mounds, which has also been observed for nests of *Leptothorax*, *Formica* and *Myrmica*

Table 2 Accumulated degree hours (*ADH*) and their comparison (both base temperature of 17 °C) in *L. flavus* mounds that were always unshaded and in mounds that were shaded during shaded periods but unshaded during unshaded periods. The values are means ± SD for each period. ADH values were compared with the Kruskal-Wallis test (Kw-H)

Period	ADH		ADH comparison	
	Always unshaded nests	Periodically unshaded nests	Kw-H	*p*
1–Unshaded	20.5 ± 2.6	20.2 ± 2.4	0.01	0.9220
2–Shaded	22.4 ± 3.7	19.1 ± 1.3	**18.31**	**<0.0001**
3–Unshaded	21.8 ± 3.4	20.3 ± 2.2	**5.42**	**<0.05**
4–Shaded	22.1 ± 3.5	18.9 ± 1.4	**25.28**	**<0.0001**
5–Unshaded	21.9 ± 4	20.6 ± 3.0	1.51	0.2190
6–Shaded	20.2 ± 2.8	19.0 ± 1.6	**14.72**	**0.0001**
7–Unshaded	22.0 ± 3.5	20.6 ± 2.5	**7.73**	**<0.05**

Significant differences are in bold

species (Brian and Brian 1951; Higgins and Lindgren 2012). As a consequence, the shading prolongs the larval stage and reduces the larval size as well as the size of the whole population (Brian and Brian 1951).

The lower temperatures in shaded vs. unshaded *L. flavus* mounds confirms that direct solar radiation is important for the thermoregulation of *L. flavus* nests, whose mounds consist largely of soil rather than organic matter. This is consistent with the general understanding that the temperature of ant mounds or hills consisting of soil can significantly differ depending on time of day and location. The aboveground parts of ant nests can heat up faster than belowground parts because aboveground parts benefit from direct solar radiation (Penick and Tschinkel 2008). The importance of solar radiation has also been confirmed with small nests made of organic material (Brandt 1980; Kilpeläinen et al. 2008). A strong dependence on direct solar radiation by ants that construct hills consisting largely of soil can be explained by (i) the small quantity of metabolic heat generated by the small quantity of organic material in the mound and (ii) the low number of ants.

The results reported here demonstrate the dependence of *Lasius* ants on the meteorological conditions of the habitat. Furthermore, the results suggest environmentally friendly methods for managing ants with soil mounds. On the one hand, the shading of such nests may cause them to decline or even vanish. For instance, the absence of pasture management causes open-habitat species of ants to disappear (Dahms et al. 2010). This can be explained by the growing vegetation, which will shade ant mounds in unmanaged pastures (Andersen 1995). Other thermophilic ant species similar to those of *L. flavus* are likely to be suppressed by overgrowing vegetation in Central Europe. These include *Formica clara Forel*, 1886 and *Lasius carniolicus Mayr*, 1861 (Bezděčka and Bezděčková 2011).

Conclusions

L. flavus, which builds aboveground nests, is strongly influenced by solar radiation. Shading significantly lowered the nest temperature and would probably slow ant development and reproduction. The high dependence on solar radiation for the thermoregulation of the nest demonstrates the susceptibility of *L. flavus* to weather conditions. Shading can be used to manage *L. flavus* and similar species in locations where they are undesired.

Acknowledgements This work was supported by the project of the Ministry of Agriculture of the Czech Republic—Resolution RO0116 (reference number 10462/2016-MZE-17011). The authors thank Dr. Bruce Jaffee for linguistic and editorial improvements.

References

Abril S, Oliveras J, Gómez C (2010) Effect of temperature on the development and survival of the Argentine ant, Linepithema humile. J Insect Sci 10:97. doi:10.1673/031.010.9701

Andersen AN (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. J Biogeogr 22:15–29. doi:10.2307/2846070

Anderson KE, Munger JC (2003) Effect of temperature on brood relocation in *Pogonomyrmex salinus* (Hymenoptera: Formicidae). West N Am Naturalist 63:122–128

Banschbach VS, Levit N, Herbers JM (1997) Nest temperatures and thermal preferences of a forest ant species: is seasonal polydomy a thermoregulatory mechanism? Insect Soc 44:109–122. doi:10.1007/s000400050034

Bezděčka P, Bezděčková K (2011) Ants in the collections of Czech, Moravian and Silesian museums. Muzeum Vysočiny, Jihlava

Boer P, Vierbergen B (2008) Exotic ants in the Netherlands (Hymenoptera: Formicidae). Entomol Ber 68:121–129

Brandt CJ (1980) The thermal diffusivity of the organic material of a mound of *Formica polyctena* forest in relation to the thermoregulation of the brood (Hymenoptera, Formicidae). Neth J Zool 30:326–344

Brian MV, Brian AD (1951) Insolation and ant population in the west of Scotland. Trans R ent Soc Lond 102:303–330. doi:10.1111/j.1365-2311.1951.tb00751.x

Coenen-Staß D, Schaarschmidt B, Lamprecht I (1980) Temperature distribution and calorimetric determination of heat production in the nest of the wood ant, *Formica polyctena* (Hymenoptera, Formicidae). Ecology 61:238–244. doi:10.2307/1935180

Culek M (1995) Biogeografické členění České republiky. Enigma, Praha

Czechowski W, Radchenko A, Czechowska W (2002) The ants (Hymenoptera, Formicidae) of Poland. Museum and Institute of Zoology PAS, Warszawa

Dahms H, Lenoir L, Lindborg R, Wolters V, Dauber J (2010) Restoration of seminatural grasslands: what is the impact on ants? Restor Ecol 18:330–337. doi:10.1111/j.1526-100X.2008.00458.x

Dean WRJ, Turner JS (1991) Ants nesting under stones in the semi-arid Karoo, South Africa: predator avoidance or temperature benefits. J Arid Environ 21:59–69

Dostál P, Březnová M, Kozlíčková V et al (2005) Ant-induced soil modification and its effect on plant below-ground biomass. Pedobiologia 49:127–137. doi:10.1016/j.pedobi.2004.09.004

Fernández-Escudero I, Tinaut A, Ruano F (1993) Rock selection for nesting in Proformica Longiseta Collingwood, 1978 (Hymenoptera, Formicidae) in a Mediterranean high mountain. Int J Biometeorol 37:83–88. doi:10.1007/BF01214386

Frouz J (1996) The role of nest moisture in thermoregulation of ant (*Formica polyctena*, Hymenoptera, Formicidae) nests. Biologia 51:541–547

Frouz J (2000) The effect of nest moisture on daily temperature regime in the nests of *Formica polyctena* wood ants. Insect Soc 47:229–235. doi:10.1007/PL00001708

Higgins RJ, Lindgren BS (2012) The effect of manipulated shading on the colony abundance of two species of ants, *Formica aserva* and *Leptothorax muscorum*, in dead wood. Entomol Exp Appl 143:292–300

Holec M, Frouz J (2006) The effect of two ant species *Lasius niger* and *Lasius flavus* on soil properties in two contrasting habitats. Eur J Soil Biol 42:213–S217. doi:10.1016/j.ejsobi.2006.07.033

Hölldobler B, Wilson EO (1990) The ants. Belknap/Harvard University Press, Cambridge

Kadochová Š, Frouz J (2014) Thermoregulation strategies in ants in comparison to other social insects, with a focus on red wood ants (Formica rufa group). F1000Research 2:280. doi: 10.12688/f1000research.2-280.v1

Kilpeläinen J, Punttila P, Finér L, Niemelä P, Domisch T, Jurgensen MF, Neuvonen S, Ohashi M, Risch AC, Sundström L (2008) Distribution of ant species and mounds (Formica) in different-aged managed spruce stands in eastern Finland. J Appl Entomol 132: 315–325. doi:10.1111/j.1439-0418.2007.01244.x

Kipyatkov VE, Lopatina EB (2015) Comparative study of thermal reaction norms for development in ants. Entomol Sci 18:174–192. doi:10.1111/ens.12098

Kipyatkov VE, Lopatina EB, Imamgaliev AA, Shirokova LA (2004) Effect of temperature on rearing of the first brood by the founder females of the ant *Lasius niger* (Hymenoptera, Formicidae): latitude-dependent variability of the response norm. J Evol Biochem Physiol 40:134–141. doi:10.1023/B:JOEY.0000033808.45455.75

Lenoir L, Persson T, Bengtsson J (2001) Wood ant nests as potential hot spots for carbon and nitrogen mineralisation. Biol Fertil Soils 34: 235–240. doi:10.1007/s003740100405

Lopéz R, Held DW, Potter DA (2000) Management of a mound-building ant, *Lasius neoniger* Emery, on golf putting greens and tees using delayed-action baits or fipronil. Crop Sci 40:511–517

Mikheyev AS, Tschinkel WR (2004) Nest architecture of the ant *Formica pallidefulva*: structure, costs and rules of excavation. Insect Soc 51: 30–36. doi:10.1007/s00040-003-0703-3

Odum EP, Pontin AJ (1961) Population density of the underground ant, *Lasius flavus*, as determined by tagging with P32. Ecology 42:186–188

Penick CA, Tschinkel WR (2008) Thermoregulatory brood transport in the fire ant, *Solenopsis invicta*. Insect Soc 55:176–182. doi:10.1007/s00040-008-0987-4

Rosengren R, Fortelius W, Lindström K et al (1987) Phenology and causation of nest heating and thermoregulation in red wood ants of the *Formica rufa* group studied in coniferous forest habitats in southern Finland. Ann Zool Fennici 24:147–155

Smallwood J (1982) The effect of shade and competition on emigration rate in the ant *Aphaenogaster rudis*. Ecology 63:124–134. doi:10.2307/1937038

Smallwood J, Culver DC (1979) Colony movements of some north American ants. J Anim Ecol 48:373–382

Thomas ML (2002) Nest site selection and longevity in the ponerine ant *Rhytidoponera metallica* (Hymenoptera, Formicidae). Insect Soc 49:147–152. doi:10.1007/s00040-002-8294-y

Tschinkel WR (2006) The fire ants. Belknap Press of Harvard University Press, Cambridge

Vogt JT, Wallet B, Freeland TB (2008) Imported fire ant (Hymenoptera: Formicidae) mound shape characteristics along a north-south gradient. Environ Entomol 37:198–205. doi:10.1603/0046-225X

Wilson EO (1971) The insect societies. Belknap Press of Harvard Uviversity Press, Cambridge, Massachusets

Příloha 3

The importance of host characteristics and canopy openness for pest management in urban forests

Adam Véle, Jakub Horák

2018

Urban Forestry & Urban Greening 36: 84–89

Urban Forestry & Urban Greening 36 (2018) 84–89

Contents lists available at ScienceDirect

Urban Forestry & Urban Greening

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

The importance of host characteristics and canopy openness for pest management in urban forests

Adam Véle, Jakub Horák*

Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Department of Forest Protection and Entomology, Kamýcká 1176, CZ-165 00 Prague, Czech Republic

ARTICLE INFO

Keywords:
Disturbance
DBH
Oak bark beetle
Quercus
Scolytus intricatus

ABSTRACT

Urban forests are important for the health of cities. These forests face high anthropogenic pressure, including demands on their multi-functional role. Therefore, the impact of pests-induced disturbances may be greater for urban forests than forests outside of cities. Monitoring of pests in their native environment is an important tool for the management of urban forests. To better understand how pest population density is affected by the forest environment, we used the Oak bark beetle, *Scolytus intricatus*, as a model organism. The study was carried out in 2014–2015 in the urban forests of Pardubice City, Czech Republic. Pest population density was studied at three levels: branch, tree and patch. The increasing branch diameter was identified as an important variable with a threshold of 70 mm for entrance holes and 45 mm for emergence holes. Increasing host tree diameter at breast height with a threshold of 46.8 cm was statistically significant at the tree level in terms of the number of entrance holes. Increasing spring canopy openness was identified as an important variable at the patch level with a threshold of 50.78% and had a decreasing trend for the number of reared adults and their total body size. Big oak trees with thick branches under closed spring canopy are the most susceptible to attack by *S. intricatus*. Based on our findings, we propose that the maintenance of mature oaks under open canopies is important for urban forest management. Avoiding mixed plantings of oaks and conifers should promote these open canopies and lead to multiple advantages regarding oak silviculture.

1. Introduction

Oaks (*Quercus*) are important economically, ecologically, and culturally for humans (Costello et al., 2011; Haneca et al., 2009; Johnson et al., 2009). Oak stands cover a substantial portion of the forested area in Eurasia and America (Johnson et al., 2009). Significant loss of oak stands as a result of the combination of abiotic and biotic (including anthropogenic) factors has occurred over the last century (Sallé et al., 2014). Oaks are threatened by multiple factors, including attack by potential pests, such as the Oak bark beetle, *Scolytus intricatus* (Ratzeburg, 1837).

The Oak bark beetle is distributed throughout Europe, North Africa and the Near East (Bright and Skidmore, 2002). This species is common in forests with presence of oaks in majority of the Central Europe. *Scolytus intricatus* appears to be a less significant pest for oaks compared with, for example, the Spruce bark beetle, *Ips typographus* L., for Norway spruce, *Picea abies,* in Europe or the North American Mountain pine beetle, *Dendroctonus ponderosae* Hopkins, for pines, *Pinus* spp. (Klutsch et al., 2009; Wermelinger, 2004). Nevertheless, *S. intricatus* can cause significant damage to oak forests (Markovič and Stojanovič, 2011). This bark beetle is frequently found in dying oaks (Jurc et al., 2009), and is often the most frequently encountered insect pest of oaks (Markovič and Stojanovič, 2003; Kunca, 2011). Furthermore, this beetle is a vector of fungi (e.g., *Ophiostoma* and *Ceratocystis*) and the nematode, *Bursaphelenchus eremus*, which negatively affect the health of oaks (Čížková et al., 2005; Marianelli et al., 2011; Yates, 1984). It can cause significant damage, especially in weakened or depleted oak stands (Führer, 1992; Markovič and Stojanovič, 2011). *Scolytus intricatus* also colonizes recently cut trees (Švestka et al., 1998), thus damaging oak timber. Urban forests in lowland areas appear to be an ideal habitat for this bark beetle.

The Oak bark beetle attacks the twigs, branches, limbs, and narrow diameter portion of trunks of oak trees (Galko et al., 2007; Markovič and Stojanovič, 2011; Švestka et al., 1998). Its females build maternal galleries in which they oviposit several tens of eggs. The species overwinters as larvae and mating occurs during the maturation feeding or during the construction of maternal galleries (Galko et al., 2007; Markovič and Stojanovič, 2011; Sallé et al., 2014; Yates, 1984) – up to

---

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

https://doi.org/10.1016/j.ufug.2018.10.012
Received 6 June 2018; Received in revised form 5 September 2018; Accepted 26 October 2018

almost 2800 maternal galleries and up to 50,000 adults can be reared from a single oak tree (Galko et al., 2012). *Scolytus intricatus* has mostly one generation per year (Švestka et al., 1998).

Oaks in pure or mixed stands are an important part of the urban landscape (Costello et al., 2011). Urban forests are characterized by a specific multi-functional environment (Blum, 2016) and often require specialized forest management (Poleno, 1985; Horák, 2018). In Europe, urban forests occupy nearly 20% of the forested area (Konijnendijk, 2003; Konijnendijk et al., 2007). Furthermore, urbanization has led to the decline of oaks (Kromroy et al., 2007).

Here we aimed to evaluate the effect of *S. intricatus* on oaks growing in urban forests and suggest ways to protect the impacted oaks. To better understand how *S. intricatus* population density affects the urban forest environment, we measured this pest's population density at the branch, tree, and patch levels in the urban forests of Pardubice City, Czech Republic.

We focused on (a) the preference of adult beetles for available breeding materials (based on the number of entrance holes); (b) the success of larval development (based on the number of emergence holes), which was controlled by (c) the number of reared adults; and (d) the suitability of the breeding material for the next generation (based on the total and mean body size of the reared adults).

2. Methods

2.1. Study area

The study area comprised of urban forest fragments (795 ha) within the city of Pardubice (50.0337 N; 15.7679 E), Czech Republic. This city is located in the flat lowland area without rugged topography at the confluence of the Labe and Chrudimka rivers with mean altitude of 220 m a.s.l. The climate is warm with mean temperature of 8.4 °C and the precipitation of 599 mm per year. The city agglomeration has approximately 100,000 inhabitants, and it is the tenth most populated city in the Czech Republic.

Former forest vegetation was consisted of oak dominated woodlands with European hornbeam, *Carpinus betulus* (Neuhauselová, 2001). More recently, native oak vegetation was partly replaced by Scots pine (*Pinus sylvestris*) plantations. Majority of forest area is used as commercial stands for timber production. Due to studied species preferences indicated in scientific literature, we used stands older than pole-stage (i.e., with trees thicker than 20 cm; Table 1).

2.2. Study design and variables

We used 40 bundles of freshly cut twigs and branches of Sessile oak (*Quercus petraea*). Each bundle consisted of four to six twigs and branches, to have an approximately consistent volume in all bundles. Branches were pooled using wire (Fig. 1). These bundles were randomly distributed in an equal-stratified design. We randomly placed four bundles in each of ten forest fragments (mean = 79.49; 11.34–376.10 ha) in Pardubice. Each bundle was hung from an oak tree (south facing; Fig. 1) on March 19, 2014, and was collected on September 4, 2014. Ten bundles were stolen and, thus, in our analyses we used 30 bundles consisting of 141 fresh twigs and branches.

Table 1
Description of variables sampled at branch, tree and patch levels in urban forests of Pardubice, Czech Republic.

Level	Variable	Measure	Mean	Min	Max	VIF
Branch	Length	cm	65.71	50.00	86.00	1.00
	Diameter	mm	51.70	3.00	170.00	1.00
Tree	DBH	cm	41.60	20.00	65.90	1.08
Patch	Canopy openness non-vegetation	%	51.44	33.14	60.46	1.06
	Canopy openness vegetation	%	17.10	9.14	30.99	1.04
	Representation of oak	%	27.33	5.00	60.00	1.02

Fig. 1. Methods used for this study of Oak bark beetle (*Scolytus intricatus*) in the urban forests of Pardubice. Bundles made of twigs, limbs, and wire (upper left), emergence cages used for rearing (lower left), and two examples of the placement of bundles on Sessile oak (*Quercus petraea*) host trees – the forest interior, under a closed canopy (upper right) and the forest edge, under the open canopy (right).

Immediately after collection of bundles, we counted the number of *S. intricatus* entrance holes on the bark surface of each twig and branch. The holes made by ambrosia beetles (e.g. *Platypus cylindrus*, *Xyleborus* spp.) were excluded after verification of their depth using a thin wire. Emergence holes of parasitic organisms were also excluded, following their recognition by their small diameter and almost aggregated pattern on the bark surface. Each entrance hole was marked by using a permanent marker to avoid it being re-counted as an exit hole.

After this, all bundles were placed separately into emergence cages (Fig. 1). They were stored indoors but without artificial heating. The cages consisted of metal cylinders with the top closed by using blackout fabric fixed with rubber. Emergence cages had two openings, one at the top and one at the bottom. Each opening was closed by using transparent bottles with a saturated saline solution and detergent for preservation of reared adults. All reared adults were taken out fortnightly until the end of the year 2015, counted, and stored in a refrigerator in a solution made of 1:1 commercial vinegar and 50% ethanol. Each individual was measured (width of its pronotum, which reflects the body size of beetles; Přikryl et al., 2012). We used a calibrated electronic microscope and Nikon NIS Elements to make the measurement. All emergence holes were counted at the end of the year 2015.

We studied five dependent variables, namely: The number of entrance holes that should reflect available breeding material; the number of emergence holes that should reflect the success of larval development; this was controlled by the number of reared adults; and the body size of the reared adults (total and mean) that should reflect the suitability of breeding material.

We measured six independent variables: The length of each twig and branch, as well as the diameter of its center as predictors were measured at the branch level (Table 1). We also measured the diameter at the breast height (DBH) for each host tree as a predictor at the tree level (Table 1). Finally, for the patch level (i.e. surrounding of the host tree; e.g. Horák et al., 2016), we measured canopy openness during the dormant season (when broadleaved trees are without foliage) on March 19, 2014. We also measured canopy openness during the growing season on July 27, 2014. Photographs were taken by using a circular fisheye camera (Sigma 4.5 mm 1:2.8 DC HSM with Canon EOS 600D), 1 m from the bundle, on the south side of the host tree, at breast height (1.3 m). All pictures were then evaluated in GLA 2.0 and canopy openness was recorded as the percentage of clear sky. The third variable, which was evaluated at the patch level, was the presence of other native oaks in the surroundings (radii of 20 m; Loskotová and Horák, 2016) of the host tree (Table 1).

2.3. Statistical analyses

All analyses were done in R 3.0.2.

For computation of our results, we first used control analyses of potential multicolinearity (situation when one independent variable in a model can be linearly predicted from the others with a substantial degree of accuracy) between and among the studied independent variables based on criterion VIF ≤ 2 (package HH; Table 1). We did not observe multicolinearity between and among studied variables and also the volume of wood in the bundle was not correlated with the DBH of the host tree ($r = 0.11$; $P = 0.95$). Thus, we did not hang bulkier bundles on larger trees.

We were interested in response of the studied bark beetle in more detail. Thus, we had searched for and used the most suitable statistical methods. Namely, we searched for possible thresholds of independent variables that should help to the practice in evaluation of the most appropriate pest management.

We were also interested in potential shifts of thresholds of independent variables using confidence intervals and, in more detail, also illustration of frequencies of species response using density plots. We computed the density diagrams as plots of all thresholds found in the bootstrapping (package boot). Bootstrapping ($N = 1000$) was used as a method that allows measures of accuracy to be assigned (defined in terms of density diagrams and confidence intervals) to sample estimates. Then, we computed statistically significant thresholds for independent variables using the conditional inference tree method (package party). The conditional inference tree is a method from the family of recursive partitioning based on maximally selected rank statistics. Confidence intervals (95%) for predictors were computed also by bootstrapping.

3. Results

In total, we observed 1047 entrance holes, with a mean of 7.43 holes per branch, and 4197 emergence holes, with a mean of 29.77 holes per branch. We reared a total of 3263 adult beetles with a mean of 108.77 adults per bundle.

3.1. Branch level

The diameter of the branch was the significant independent variable that influenced the Oak bark beetle. We did not detect a significant influence for length of branch.

The number of *S. intricatus* entrance holes was significantly influenced by increasing diameter. The threshold value was identified as 70 mm (95% confidence interval 35–80 mm). The density plot identifies an initial peak for 40 mm, the greatest preference for 60 mm, and three decreasing peaks for 70, 80 and 105 mm (Fig. 2).

The number of emergence holes was also significantly influenced by increasing diameter. In this analysis, the diameter threshold value was 45 mm (95% confidence interval 35–105 mm). Using a density plot, we identified an initial noticeable peak at 45 mm, the greatest preference between 60 and 70 mm, and a late peak at 105 mm (Fig. 3).

We did not detect a significant influence of the studied independent variableson number of adults and body size.

3.2. Tree level

The number of entrance holes was significantly influenced by increasing DBH of the host tree. In this analysis, the threshold value was identified at 46.8 cm (95% confidence interval from 32.1 to 54.7 cm). Using a density plot, we identified a single significant peak at the threshold value (Fig. 4).

The number of emergence holes, adults, and body size were not significantly influenced by the DBH of the host tree.

3.3. Patch level

Canopy openness in spring was the significant predictor on the number of reared adults and their total body size at the patch level. We did not detect an effect of canopy openness during the summer and the presence of oaks in the surrounding area.

The number of adults was significantly influenced by decreasing canopy openness in the spring. In this analysis, the threshold value was 50.78% (95% confidence interval from 45.82 to 53.90%). The density plot indicated two noticeable peaks at ≈47 and 52% (Fig. 5).

The body size of adults was significantly influenced by decreasing canopy openness in spring. For this, the threshold value was 50.78% (95% confidence interval from 45.82 to 53.90%). The density plot indicated two noticeable peaks at ≈47 and 52% (Fig. 6).

We did not identify the response on entrance and emergence holes and mean body size of adults at the patch level.

4. Discussion

We found that the studied Oak bark beetle was influenced at all studied levels in the urban forests. Diameter was the important factor at both the branch and tree levels, and canopy openness during the non-vegetation season was the most important factor at the patch level.

Entrance holes were found in greater numbers on branches with a diameter of 7 cm or more – this is the minimum diameter of economically used wood mass (Simon and Vacek, 2008). Thus, *S. intricatus* can be regarded as possible economic pest. Also, we detected significantly more emergence holes on branches with a diameter greater than 4.5 cm compared to branches with a diameter ≤4.5. These findings indicate that *S. intricatus* prefers thicker branches and limbs, but is able to develop even in relatively small-diameter branches. Yates (1984) reports a minimum diameter of 5 cm for *S. intricatus* breeding, while Galko et al. (2012) also reported larger minimum diameters. Jurc et al. (2009) found that beetles prefer branches with a diameter of 2.8 cm. Markovič and Stojanovič (2001) detected *S. intricatus* on a wide range of branch diameters (i.e., 1–10 cm). Thus, our findings are in line with the literature. A preference for branches with a maximum diameter of 7 cm has been reported in most of the literature. This can be given by the maximum diameter of the logging residues with high attention in forest protection (Švestka et al., 1998). Our findings for preference of branch diameter are consistent with the knowledge that more imagoes may develop from thicker material – mainly due to longer maternal galleries, in which females can lay more eggs (Galko et al., 2012). However, branch thickness (as a reflection of habitat quantity) is surely not the only decisive factor in the density-area relationship – the preference for a particular quality of the attacked tree might be more important during the initial searching (Jackson et al., 2013). Observed thresholds are important regarding the monitoring of species. Namely, significant thresholds indicate the optimal branch diameter for monitoring of *S. intricatus*.

In addition to the branches, *S. intricatus* also inhabits trunks. Markovič and Stojanovič (2001) report that trees with trunk diameters of 25–30 cm are suitable for *S. intricatus*, which is less than our findings (trunk diameters of 30–60 cm). These differences might be because of the different selection criteria used here and those used by Markovič and Stojanovič (2001). Trunks of a suitable diameter might attract beetles but then not be attacked by further beetles, for example, if they have an infection history from the previous year (Yamasaki and Futai, 2008). Nevertheless, the two observed peaks in density plot (Fig. 2) indicated that there was nearly no preference for diameters between 45–55 mm. The most probable reason was that branches with these diameters had clumped distribution in environment that was not

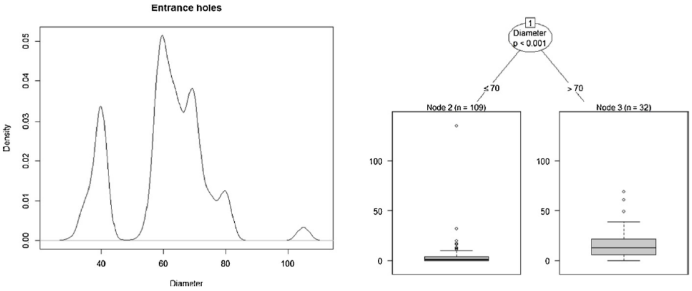

Fig. 2. Density diagram for the identification of threshold values using a bootstrapping method (left) and identification of threshold value using conditional inference tree method (right) for the number of *Scolytus intricatus* entrance holes at the branch level in urban forests of Pardubice, Czech Republic.

suitable for development. This is illustrated by the importance of environmental variables at patch level – mainly by spring canopy openness (Figs. 5 and 6).

The spring canopy openness was identified as a significant variable influencing S. *intricatus* abundance (Fig. 5). This variable was measured before the leaves of oak and other broadleaved trees sprouted. Canopy openness, and thus greater insolation (i.e. sun-exposure), can account for the frequent occurrence of many saproxylic beetles (Ranius and Jansson, 2000; Horák and Rébl, 2013; Müller et al., 2015). In the conditions of the Central Europe, majority of conifers do not lose foliation, while broadleaved trees do and the most abundant conifer tree species was Scots pine. The importance of a lower spring canopy openness regarding the success in the development of Oak bark beetle may be related to the higher stress of oak trees caused by permanent canopy closure by conifers in the surroundings (Vizoso-Arribe et al., 2014). This might be caused by a lower incidence of solar radiation and, thus, lower temperature (Forrester et al., 2012; Muscolo et al., 2014). It is known that oaks growing in a darker environment have worse vitality and regenerate poorly (Kelly, 2002; Ostrogović et al., 2009; Martiník et al., 2014). However, higher spring temperatures are associated with higher tree-ring width increases (Matisons et al., 2012). This can be explained by a longer growing period, greater accumulation of assimilates, and better frost resistance (Dickson and Tomlinson, 1996; Morin et al., 2007; White et al., 1999; Matisons et al., 2012). Water availability is another limiting element of oak growth (Matisons et al., 2012). Higher canopy closure is an indication of greater tree biomass. Trees have a high water usage, which increases with their dimensions (see Wullschleger et al., 1998). *Quercus petraea* has an intermediate tolerance to water stress (Dickson and Tomlinson, 1996). It is also possible that the oaks growing under a closed canopy were overshadowed, which was reflected in their vitality.

Therefore, the above conditions are advantageous for bark beetles, which prefer weakened trees (Groot et al., 2018). Oaks weakened by environmental factors, such as the competition of fast-growing conifers, are less resistant (Coulson and Witter, 1984) and produce weaker morphological and biochemical responses when attacked by insects (Urbanek Krajnc, 2009). Therefore, a shady environment can provide additional benefits for Oak bark beetle. The temperature requirements of *S. intricatus* are unknown (Sallé et al., 2014), but Pineau et al. (2017) found that another bark beetle *Ips sexdentatus* has a higher lipid content when it is not breeding in too high temperatures (Pineau et al., 2017). Furthermore, in bark beetles, a large body size indicates greater fitness (Reid and Roitberg, 1995). Another issue is that higher solar radiation might reduce the efficiency of pheromone-based communication (Artyushenko et al., 2017). Bark beetles use the aggregation pheromone to attract other individuals (Seybold et al., 2000; Wood, 1982). It is likely that *S. intricatus* can produce this pheromone (Vrkočová et al., 2003). Nevertheless, the detection of larger individuals in less irradiated trees reflect the rule that smaller adult body sizes result from development at higher temperatures (Atkinson, 1994).

We found that the most responsible dependent variables were the number of entrance and emergence holes. Although the counting of holes methods has many drawbacks (e.g., confusion of species origin), it is widely used to monitor pests (Dubois et al., 2004), as well as to monitor threatened beetles (Albert et al., 2012). Their use appears to be very simple for practice. Furthermore, we observed a non-equal number of adults and exit holes, which is likely because, even if we closed the extractors, it was still possible for a proportion of the adults to escape.

Regarding the monitoring, we concluded that the Oak bark beetle was attracted by possible breeding material at the branch and tree levels (as reflected by the number of entrance holes). The success of larval development was influenced at the branch level (as reflected by the number of emergence holes) and at the patch level (as reflected by the number of reared adults). The suitability of breeding material was

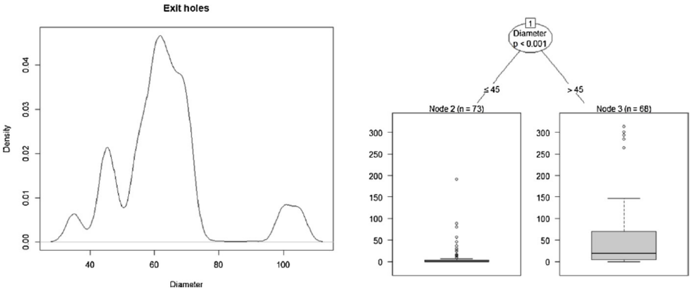

Fig. 3. Density diagram for the identification of threshold values using a bootstrapping method (left) and identification of threshold value using conditional inference tree method (right) for the number of *Scolytus intricatus* emergence holes at the branch level in urban forests of Pardubice, Czech Republic.

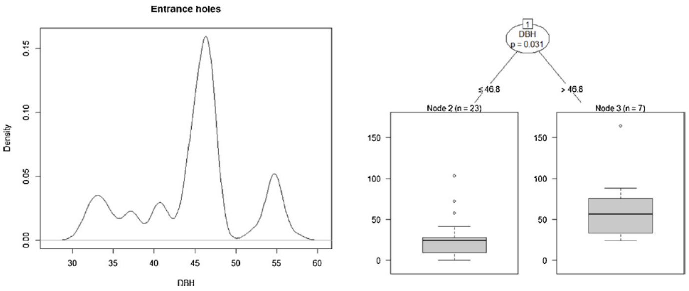

Fig. 4. Density diagram for the identification of threshold values using a bootstrapping method (left) and identification of threshold value using conditional inference tree method (right) for the number of *Scolytus intricatus* entrance holes at the tree level in urban forests of Pardubice, Czech Republic.

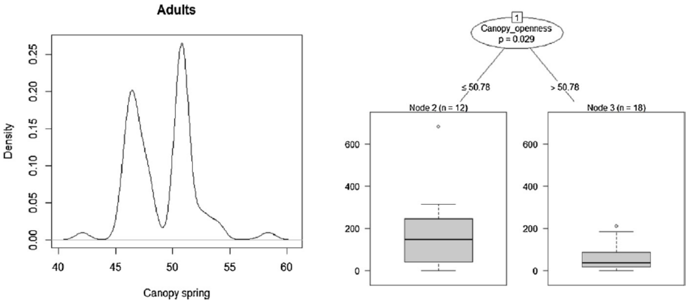

Fig. 5. Density diagram for the identification of threshold values using a bootstrapping method (left) and identification of threshold value using conditional inference tree method (right) for the number of *Scolytus intricatus* adults at the patch level in urban forests of Pardubice, Czech Republic.

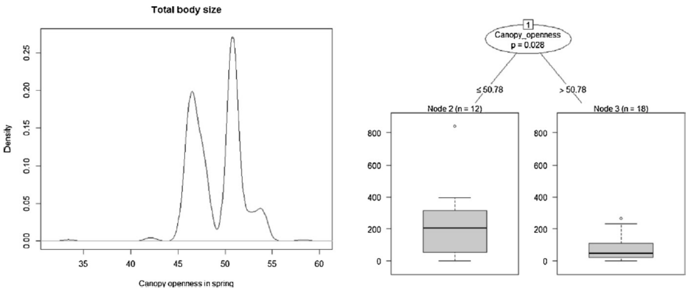

Fig. 6. Density diagram for the identification of threshold values using a bootstrapping method (left) and identification of threshold value using conditional inference tree method (right) for the total body size of *Scolytus intricatus* at the patch level in urban forests of Pardubice, Czech Republic.

influenced at the patch level (as reflected by the total body size).

4.1. Management implications

Oaks are threatened by *S. intricatus* from the early stages of their development and this threat does not decrease with increasing age. We found that large trees under a closed spring canopy are highly susceptible to *S. intricatus* attack. Therefore, forest managers cannot focus only on the avoidance of logging residuals. Based on our findings, the most important management implication is the maintenance of mature oaks under open canopies. This can be done by avoiding conifers that are mainly non-native to the lowland forests in central Europe. Open canopies also lead to better fructification and longer tree age. Thus, this kind of management would lead to multiple advantages regarding oak silviculture.

Acknowledgements

We would like to thank Iveta Karásková for help in the field and with the counting of entrance holes, Tereza Brestovanská helped in the field and Patrik Rada helped with measuring of adults. This paper was supported by grants CIGA ČZU 20174307 and IGA FLD ČZU B/02/18.

References

Albert, J., Platek, M., Čížek, L., 2012. Vertical stratification and microhabitat selection by the Great Capricorn Beetle (*Cerambyx cerdo*) (Coleoptera: Cerambycidae) in open-grown, veteran oaks. Eur. J. Entomol. 109, 553–559.
Artyushenko, P.V., Tomilin, F.N., Kuzubov, A.A., Ovchinnikov, S.G., Tsikalova, P.E.,

Ovchinnikova, T.M., Soukhovolsky, V.G., 2017. The stability of the pheromones of xylophagous insects to environmental factors: an evaluation by quantum chemical analysis. Biophysics 62, 532–538.

Atkinson, D., 1994. Temperature and organism size – a biological law for ectotherms? Adv. Ecol. Res. 3, 1–58.

Blum, J., 2016. Urban Forests: Ecosystem Services and Management. Apple Academic Press, Waretown.

Bright, D.E., Skidmore, R.E., 2002. A Catalogue of Scolytidae and Platypodidae (Coleoptera), Supplement 2 (1995–1999). NRC Research Press, Canada.

Čížková, D., Šrůtka, P., Kolařík, M., Kubátová, A., Pažoutová, S., 2005. Assessing the pathogenic effect of Fusarium, Geosmithia and Ophiostoma fungi from broad-leaved trees. Folia Microbiol. 50, 59–62.

Costello, L.R., Hagen, B.W., Jones, K.S., 2011. Oaks in the Urban Landscape: Selection, Care, and Preservation. University of California, Agriculture and Natural Resources, Oakland CA.

Coulson, R.N., Witter, J.A., 1984. Forest Entomology: Ecology and Management. Wiley-Interscience, Hoboken.

Dickson, R.E., Tomlinson, P.T., 1996. Oak growth, development and carbon metabolism in response to water stress. Ann. Sci. For. 53, 181–196.

Dubois, T., Li, Z., Jiafu, H., Hajek, A.E., 2004. Efficacy of fiber bands impregnated with Beauveria brongniartii cultures against the Asian longhorned beetle,*Anoplophora glabripennis* (Coleoptera: Cerambycidae). Biol. Control 31, 320–328.

Forrester, J.A., Mladenoff, D.J., Gower, S.T., Stoffel, J.L., 2012. Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. For. Ecol. Manage. 265, 124–132.

Führer, E., 1992. Der Zusammenhang zwischen der Dürre und Traubeneichenbestände in Ungarn. Forstw. Cb. 111, 129–136.

Galko, J., Nikolov, Ch., Rell, S., Vakula, J., Gubka, A., 2012. The European Oak Bark Beetle *Scolytus intricatus* (Ratz.) (Coleoptera: Curculionidae, Scolytinae) galleries analysis. For. J. 58, 166–170.

Galko, J., Pavlík, Š., Zach, P., 2007. Floeo- und xylopfagen Käfern Coleoptera) im Eichennützresten und ihre naturliche Insektenfeinde. Acta Inst. For. Zvolenensis 49, 31–42.

Groot, N., Ogris, N., Kobler, A., 2018. The effects of a large-scale ice storm event on the drivers of bark beetle outbreaks and associated management practices. For. Ecol. Manage. 408, 195–201.

Haneca, K., Cufar, K., Beeckman, H., 2009. Oaks, tree-rings and wooden cultural heritage: a review of the main characteristics and applications of oak dendrochronology in Europe. J. Archaeol. Sci. 36, 1–11.

Horák, J., 2018. The role of urban environments for saproxylic insects. In: Ulyshen, M.D. (Ed.), Saproxylic Insects. Springer, Germany, pp. 835–846.

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

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. For. Ecol. Manage. 363, 229–236.

Jackson, H.B., Zeccarias, A., Cronin, J.T., 2013. Mechanisms driving the density–area relationship in a saproxylic beetle. Oecologia 173, 1237–1247.

Johnson, P.S., Shifley, S.R., Rogers, R., 2009. The Ecology and Silviculture of Oaks, 2nd edition. CAB International, Wallingford, UK.

Jurc, M., Bojovic, S., Komjanc, B., Krč, J., 2009. Xylophagous entomofauna in branches of oaks (*Quercus* spp.) and its significance for oak health in the Karst region of Slovenia. Biologia 64, 130–138.

Kelly, D.L., 2002. The regeneration of *Quercus petraea* (Sessile Oak) in Southwest Ireland: a 25-year experimental study. For. Ecol. Manage. 166, 207–226.

Klutsch, J.G., Negron, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., Caissie, R., 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. For. Ecol. Manage. 258, 641–649.

Konijnendijk, C.C., 2003. A decade of urban forestry in Europe. For. Policy Econ. 5, 173–186.

Konijnendijk, C.C., Nielsen, A.B., Schipperijn, J., Rosenblad, Y., Sander, H., Sarv, M., Mäkinen, K., Tyrväinen, L., Donish, J., Gundersen, V., Akerlund, U., Gustavsson, R., 2007. Assessment of urban forestry research and research needs in Nordic and Baltic countries. Urban For. Urban Green. 6, 297–309.

Kromroy, K., Ward, K., Castillo, P., Juzwik, J., 2007. Relationships between urbanization and the oak resource of the Minneapolis/St. Paul Metropolitan area from 1991 to 1998. Landsc. Urban Plann. 80, 375–385.

Kunca, A., 2011. Výskyt škodlivých činiteľov v lesoch Slovenska za rok 2010 a ich prognóza na rok 2011. Národné lesnícke centrum - Lesnícky výskumný ústav, Zvolen.

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.

Marianelli, L., Marziali, L., Carletti, B., Pennacchio, F., Cotroneo, A., Roversi, P.F., 2011. Association *Scolytus intricatus*– Bursaphelenchus Erasmus on oak in Italy. Silva Lusit. 19, 101–104.

Markovič, Č., Stojanovič, A., 2001. Bionomics of *Scolytus intricatus* in Serbia. Plant Prot. 52, 183–197.

Markovič, Č., Stojanovič, A., 2003. Significance of parasitoids in the reduction of oak bark beetle *Scolytus intricatus* Ratzeburg (Col., Scolytidae) in Serbia. J. Appl. Entomol. 127, 23–28.

Markovič, Č., Stojanovič, A., 2011. Phloemophagous and xylophagous insects, their parasites, predators and inquilines in the branches of the most important oak species in Serbia. Biologia 66, 509–517.

Martiník, A., Dobrovolný, L., Palátová, E., 2014. Tree growing space and acorn production of *Quercus robur*. Dendrobiology 71, 101–108.

Matisons, R., Elferts, D., Brumelis, G., 2012. Changes in climatic signals of English oak tree-ring width and cross-section area of earlywood vessels in Latvia during the period 1900–2009. For. Ecol. Manage. 279, 34–44.

Morin, X., Améglio, T., Ahas, R., Kurz-Besson, C., Lanta, V., Lebourgeois, F., Miglietta, F., Chuine, I., 2007. Variation in cold hardiness and carbohydrate concentration from dormancy induction to bud burst among provenances of three European oak species. Tree Physiol. 27, 817–825.

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I.M.M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L., Gossner, M.M., 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography 38, 499–509.

Muscolo, A., Bagnato, S., Sidari, M., Mercurio, R., 2014. A review of the roles of forest canopy gaps. J. For. Res. 25, 725–736.

Neuhauselová, Z., 2001. Map of Potential Natural Vegetation of the Czech Republic. Academia, Praha.

Ostrogović, M.Z., Sever, K., Anić, I., 2009. Influence of light on natural regeneration of pedunculate oak (*Quercus robur* L.) in the Maksimir forest park in Zagreb. Šumar. List 134, 115–123.

Pineau, X., David, G., Peter, Z., Sallé, A., Baude, M., Lieutier, F., Jactel, H., 2017. Effect of temperature on the reproductive success, developmental rate and brood characteristics of *Ips sexdentatus* (Boern.). Agric. For. Entomol. 19, 23–33.

Poleno, Z., 1985. Příměstské lesy. SZN, Praha.

Přikryl, Z.B., Turčáni, M., Horák, J., 2012. Sharing the same space: foraging behaviour of saproxylic beetles in relation to dietary components of morphologically similar larvae. Ecol. Entomol. 37, 117–123.

Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol. Conserv. 95, 85–94.

Reid, M.L., Roitberg, B.D., 1995. Effects of body size of investment in individual broods by male pine engravers (Coleoptera: Scolytidae). Can. J. Zool. 73, 1396–1401.

Sallé, A., Nageleisen, L.M., Lieutier, F., 2014. Bark and wood boring insects involved in oak declines in Europe: current knowledge and future prospects in a context of climate change. For. Ecol. Manage. 328, 79–93.

Seybold, S.J., Bohlmann, J., Raffa, K.F., 2000. Biosynthesis of coniferophagous bark beetle pheromones and conifer isoprenoids: evolutionary perspective and synthesis. Can. Entomol. 132, 697–753.

Simon, J., Vacek, S., 2008. Výkladový slovník hospodářské úpravy lesů. Mendelova zemědělská a lesnická univerzita v Brně, Brno.

Švestka, M., Hochmut, R., Jančařík, V., 1998. Praktické metody v ochraně lesa. Lesnická práce, Kostelec nad Černými lesy.

Urbanek Krajnc, A., 2009. A temporal analysis of antioxidative defense responses in the phloem of *Picea abies* after attack by *Ips typographus*. Tree Physiol. 29, 1059–1068.

Vizoso-Arribe, O., Díaz-Maroto, I.J., Vila-Lameiro, P., Díaz-Maroto, M.C., 2014. Influence of the canopy in the natural regeneration of *Quercus robur* in NW Spain. Biologia 69, 1678–1684.

Vrkočová, P., Kalinová, B., Valterová, I., Koutek, B., 2003. Analysis of European oak bark beetle (*Scolytus intricatus*) extracts using hyphenated and chiral chromatography techniques. Talanta 59, 107–114.

Wermelinger, B., 2004. Ecology and management of the spruce bark beetle Ips typographus—a review of recent research. For. Ecol. Manage. 202, 67–82.

White, M.A., Running, S.W., Thornton, P.E., 1999. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. Int. J. Biometeorol. 42, 139–145.

Wood, D.L., 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Ann. Rev. Entomol. 27, 411–446.

Wullschleger, S.D., Meinzer, F.C., Vertessy, R.A., 1998. A review of whole-plant water use studies in trees. Tree Physiol. 18, 499–512.

Yamasaki, M., Futai, K., 2008. Host selection by *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae) before and after flying to trees. Appl. Entomol. Zool. 43, 249–257.

Yates, M.G., 1984. The biology of the oak bark beetle, *Scolytus intricatus* (Ratzeburg) (Coleoptera: Scolytidae), in southern England. Bull. Entomol. Res. 74, 569–579.

Příloha 4

Space, habitat and isolation are the key determinants of tree colonization by the carpenter ant in plantation forests

Adam Véle, Jakub Horák

2019

Forests 10: 630

forests

MDPI

Article

Space, Habitat and Isolation are the Key Determinants of Tree Colonization by the Carpenter Ant in Plantation Forests

Adam Véle [1,2] **and Jakub Horák** [1,3,*]

[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] Forestry & Game Management Research Institute, Strnady 136, CZ-252 02 Jíloviště, Czech Republic
[3] Department of Biology, Faculty of Science, University of Hradec Králové, Rokitanského 62, CZ-500 03 Hradec Králové, Czech Republic
* Correspondence: jakub.sruby@gmail.com

Received: 27 June 2019; Accepted: 25 July 2019; Published: 27 July 2019

Abstract: Forest plantations are still often considered the antithesis of real nature. However, plantations can host many organisms. The problem is that some of the hosted species are regarded ad hoc as pests. The main aim of our paper was to study the carpenter ant (*Camponotus ligniperdus*) in windstorm habitats. We studied forests in East Bohemia, Czech Republic, and focused on the spatial distribution of snapped trees and the influence of selected forest characteristics on the incidence of ant nests. We found that the nests in the study area mainly occurred in Norway spruce, which is the most commercially important tree in the majority of Central Europe. More than one quarter of the snapped trees were inhabited by the ants. We found that nests exhibited a spatially autocorrelated pattern that differed on spatial scales. The most important characteristic of the host tree for determining carpenter ant nests was the presence of brown rot, and the majority of tree nests were isolated from forest openings. The presence of carpenter ants in forest plantations is, therefore, not harmful. Their presence could be used by forest managers as an indication of unsuitable stand conditions for the successful growth of the Norway spruce and other coniferous plantation trees.

Keywords: *Camponotus ligniperdus*; Norway spruce; rot type; sanitation cuttings; wind disturbance

1. Introduction

Forest plantations are often grown as monocultures, with clear cut harvest as the dominant management type. In addition to the composition of one dominant, often non-indigenous tree species, this forest land use type can negatively influence soil chemistry, moisture, and physical attributes, together with vegetation. It can also influence other abiotic factors such as solar radiation, air, and soil temperatures [1–3]. The response of insects, as the most abundant and biodiverse group of organisms, to the management of plantation forests can be highly varied. For example, saproxylic insects, in general, often have lower diversity, but, more particularly, bark beetle populations can reach outbreak levels [4,5]. The dominant tree species in plantation forests in Central Europe is the Norway spruce (*Picea abies* (L.) Karst.). This tree is highly susceptible to the attack of spruce bark beetles, drought, and wind. Plantation forests, as monocultures, are therefore often less resilient to disturbances caused by insect pests [6]. Current research has indicated that the protection of forests against such pests is a complex issue.

Plantation forests are not only a place for timber products, but also provide ecological functions such as water retention, soil conservation, and biodiversity maintenance [7–10]. Many forests with high commercial importance for the timber industry are located in areas with specific biodiversity [11].

Research has indicated that such land use is important for the survival of many different species, including some threatened species [7,12,13]. A high population density of species that are beneficial for forestry is also important. For example, parasitoids are used in biocontrol and fungi help with the decay process of wood residuals [14,15].

Several insect species have two opposing functions, and are often considered, at least potentially, pests. However, evidence of their damage is often lacking, or the damage they cause is negligible. For example, aphids tended by red wood ants can reduce tree growth, but they protect trees against herbivorous pests [16]. Woodpeckers can reduce the population of bark beetles, but they sometimes damage trees while hunting and nesting [17]. Another example of a taxon often referred to as a pest is the carpenter ants of the genus *Camponotus*. The two ant species that are most typical in forests dominated by Norway spruce in Europe are *C. herculeanus* and *C. ligniperdus* [18,19]. Both species build nests in the lower part of tree trunks. Their nests form a typical lamellar structure, with summer wood being almost untouched [20,21]. Whereas *C. herculeanus* is often part of the insect communities of indigenous spruce forests at higher elevations, *C. ligniperdus* is most common in lowland spruce plantations. The literature indicates that *C. ligniperdus* is a forest species. Besides coniferous stands, this species often occurs in mixed and deciduous forests or in habitats sparsely overgrown with woody plants. Typical places of its occurrence include stone banks and sunlit forest edges [20,22]. Carpenter ant nests are built in stumps and rarely in living trees; regardless, this species is often regarded as a pest that is damaging the wood of the most commercially important part of the tree (i.e., the lower part of the stem). The average population of a nest is approximately 3000 individuals. Ants collect food on bushes and trees, and less often in deeper soil layers or from vegetation [22]. They partly feed on honeydew, but they are also effective predators of insects [23]. This is one of the contrasting indications of the situation of this neglected big insect species—is it a pest or a beneficial predator? Highly unstable spruce plantations need beneficial species that can help combat insect outbreaks. Thus, information about the requirements of carpenter ants in plantation forests has a high potential to help foresters with successful protection.

In this study, we focused on the characteristics of plantation forest that influence the distribution of the carpenter ant, *Camponotus ligniperdus* (Latreille, 1802). Namely, we were interested in the spatial distribution of their tree nests, and the influence of the habitat, patch, stand, and isolation forest characteristics.

2. Materials and Methods

2.1. Study Area

We studied plantation forests in East Bohemia, Czech Republic, with a total area of more than 800 ha. The elevation was from approximately 300 to 350 meters above sea level. The dominant tree species in the area was Scots pine (*Pinus sylvestris* L.). Some stands were dominated by the Norway spruce (*Picea abies*) and sessile oak (*Quercus petraea* (Matt.) Liebl.)), with the occasional dominance of introduced European larch (*Larix decidua* Mill.) and white pine (*Pinus strobus* L.).

The study was conducted during the winter of 2017–2018 and early spring 2018. This area was affected by the windstorm caused by cyclone Xavier in early October 2017. The windstorm reached a peak speed of 202 km/h at Sněžka, the highest point in the Czech Republic. The effect of the windstorm was not the same as that of previous windstorms caused by Kyrill (2007) and Emma (2008). This means that the wind disturbance did not cause large areas of damaged trees with a clumped distribution, but rather individual (in the case of spruce) or small group disturbances (in pine) scattered throughout the whole study area.

2.2. Data Collection

Carpenter ants more often inhabit weakened trees, which are less resistant to wind. For this reason, we searched for all snapped trees in our study area. We carefully investigated all stands older than 40 years old. This is the approximate age at which trees start being damaged by windstorms in the study area. We observed no damage in the younger stands. This means that all stands were walked along their entire length in 50 m distant transects (i.e., two transects in stands that were wider than 100 m). In cases of the presence of natural regeneration, we performed individual visits to places that could not be observed from transects.

The sanitation cuttings by forest mechanization started immediately after the end of the climate conditions that caused the poor accessibility to the stands. This means that in the late spring, there were nearly no residual snapped trees (except for stumps), and only a few of them stayed in roundwood timber stocks until the late spring. The main reason for snapped tree removal was sanitation, mainly for the suppression of potential bark beetle outbreaks. This led to the relatively short period of the study (early October–early April).

2.3. Studied Variables

Our dependent variable was the presence of carpenter ant, *Camponotus ligniperdus* (Latreille, 1802) nests where trees had snapped (Figure 1). The presence of the studied species is easily recognized due to its galleries through the spring annual rings and the summer rings left nearly untouched (Figure 2). Other species of the genus *Camponotus* that can create their nests in trees have not been observed in the study area in the past during spring. Therefore, we confirmed that the nests were of *Camponotus ligniperdus* origin without the observation of adults. Furthermore, adults are not present in galleries outside the vegetation period.

Figure 1. Distribution of all snapped trees (**left**) and the presence of nests of carpenter ant, *Camponotus ligniperdus* (Latreille, 1802), (**right**) in our study area in the Czech Republic.

Figure 2. Snapped Norway spruce (*Picea abies* (L.) Karst.) tree (**a**). Structure of wood affected by the carpenter ant (*Camponotus ligniperdus*) in the snapped stem of the Norway spruce (**b**). Worker of the carpenter ant with its prey, observed in the late spring (**c**). Cut snag of the Norway spruce infested with a large nest of carpenter ant (**d**) in the East Bohemian woodlands, Czech Republic.

1. The first two independent variables collected were regarding the spatial distribution of nests. Each snapped tree was localized using a geographical positioning system (GPS) using geographical coordinates of (a) northing and (b) easting in WGS84 format (center: 50.0058; 16.1780).
2. We searched for four habitat characteristics. We identified (a) the tree species of the snapped tree, and five tree species were snapped. All were coniferous: the Norway spruce ($N = 102$), Scots pine ($N = 17$), larch ($N = 9$), white pine ($N = 1$), and silver fir (*Abies alba*; $N = 1$). We also searched for (b) the presence of rot in the place of the snap. We divided the type of rot into two commonly used categories: white ($N = 8$) and brown ($N = 69$) rot. The white rot was most probably caused by *Armillaria* and brown by *Heterobasidion* [24]. The rest of the trees were without any indication of the presence of rot. We also checked for (c) the presence of resin on the stem, but this was highly correlated with the presence of rot ($R_s = 0.37$; $p < 0.001$). This has been confirmed by current research [25], and we thus did not use resin indication for further analyses. We measured (d) the height of the breakage on the stem (mean = 246.57 ± 1.63 cm SE), and the height of snapped of trees inhabited by carpenter ant nests was 93.71 ± 12.20 SE (5–230) cm.
3. We also collected two patch-based characteristics. We estimated (a) the canopy closure as a percentage (80.04% ± 1.63%). (b) The composition of the same tree species as the snapped tree was also investigated (57.81% ± 2.66%).
4. The stand-based characteristic was the age of the stand (73.83 ± 1.93 years).
5. Two characteristics that reflected isolation were measured. The first was (a) the distance to the forest track (67.36 ± 5.31 m) as a permanently open area. (b) The second variable was the distance

to clear-cut or non-forest land (93.65 ± 12.57 m)—the gaps created by actual windstorm were not measured.

2.4. Statistics

The spatial distribution of the nests was analyzed using Moran's *I*, which is the measure of spatial autocorrelation in SAM v4.0 [26]. Regarding this analysis, we used coordinates (northing and easting) of the snapped trees. The number of geographic distance classes in SAM was manually set to six. Class size in SAM was set to an equal number of pairs and symmetric distances. The test for significance had 199 permutations.

Multicollinearity of independent variables was reflected by variance inflation factor (VIF) and computed using package HH in R 3.5.1. Tree species were removed from the generalized linear model (GLM) with forest characteristics due to multicollinearity (VIF > 2).

We computed a GLM with a binomial distribution of the dependent variable (presence and absence of the studied species) for analysis of the influence of the space and the forest environment. The global test for spatial autocorrelation was not significant ($I = -0.01$; $p = 0.08$). However, due to the significant influence of space on more particular distances, we used the autocovariate of the dependent variable as the control of the influence of spatial autocorrelation [27]. It was computed using package spdep in R. The differences among types of rot were analyzed by GLM and visualized by observed weighted means with 95% confidence intervals.

As the tree species was removed from GLM due to multicollinearity, we independently analyzed the possible relationship of the carpenter ant to tree species by Kruskal–Wallis ANOVA in R.

3. Results

We found 34 snapped trees that were inhabited by the carpenter ant, representing 26.15% of all snapped trees found.

Positive values on short distances (up to 1.5 km) between nests indicated their statistically significantly positive autocorrelation; thus, they had a clustered distribution and nests were attracted. Negative values for longer distances indicated that the nests were significantly negatively autocorrelated; this means that they switched to uniform distribution and were repulsed. Finally, there was no significant autocorrelation at the longest distance (over five kilometers) and the distribution of nests started to be random. This means that space had, in this case, no effect (Figure 3).

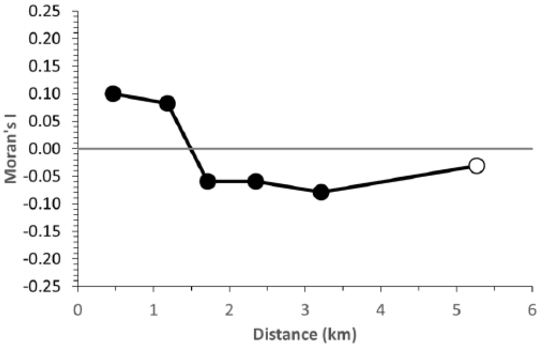

Figure 3. The influence of geographic distances in kilometers using the computed Moran's *I* from the observed incidence of the carpenter ant in the Czech Republic. Full circles represent $p < 0.05$, empty denote non-significant values.

The number of snapped trees inhabited by the carpenter ant significantly increased toward the east. The number of nests was the highest in the north-eastern part of the studied area (Figure 4).

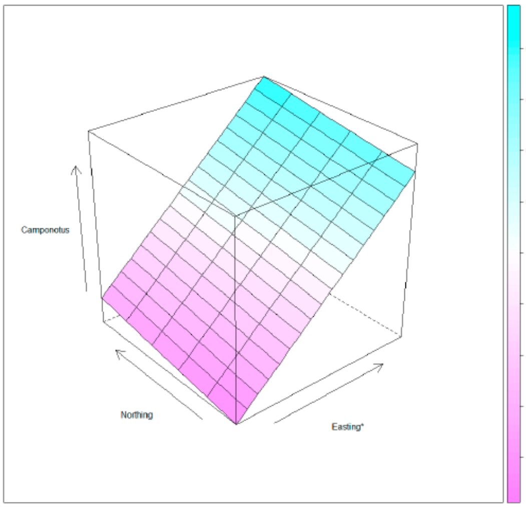

Figure 4. Influence of distribution of snapped trees on the incidence of the carpenter ant in the Czech Republic. * denotes $p < 0.05$.

The incidence of carpenter ant was statistically significantly positively related to the presence of rotten wood in snapped trees. The second significant positive relationship was with the increasing distance from clear-cut and non-forest land. The other studied characteristics showed no significant influences (Figure 5).

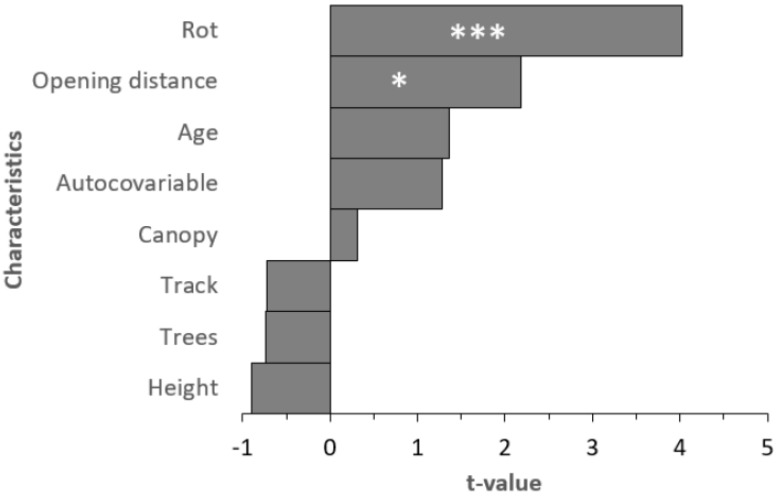

Figure 5. Influence of forest characteristics on the incidence of the carpenter ant in the Czech Republic. * denotes $p < 0.05$ and *** denotes $p < 0.001$.

Five tree species were found to be snapped in the study area. Only two were inhabited by the carpenter ant (Figure 6). We did not observe a significant difference in the incidence of the carpenter ant regarding the tree species ($H = 8.18$; $p = 0.085$).

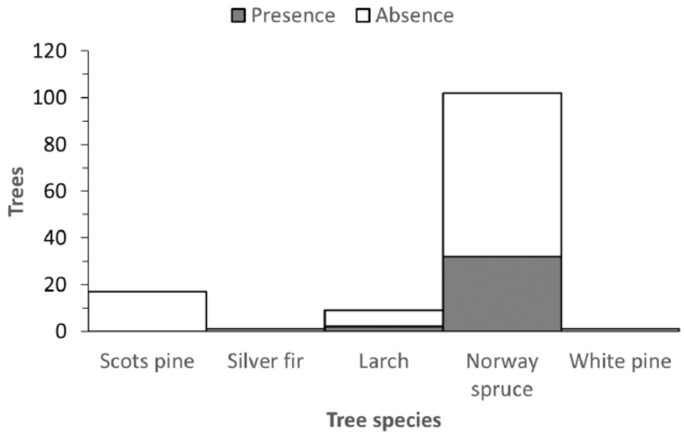

Figure 6. Incidence of carpenter ant nests with respect to tree species in the Czech Republic.

The trees preferred by the carpenter ant were rotten (Figure 5). The presence of brown rot had a positive effect on incidence of the nests ($t = 4.22$; $p < 0.001$), whereas the absence of rot had a significantly opposite effect ($t = -4.44$; $p < 0.001$). White rot had no effect ($t = 0.35$; $p = 0.725$; Figure 7).

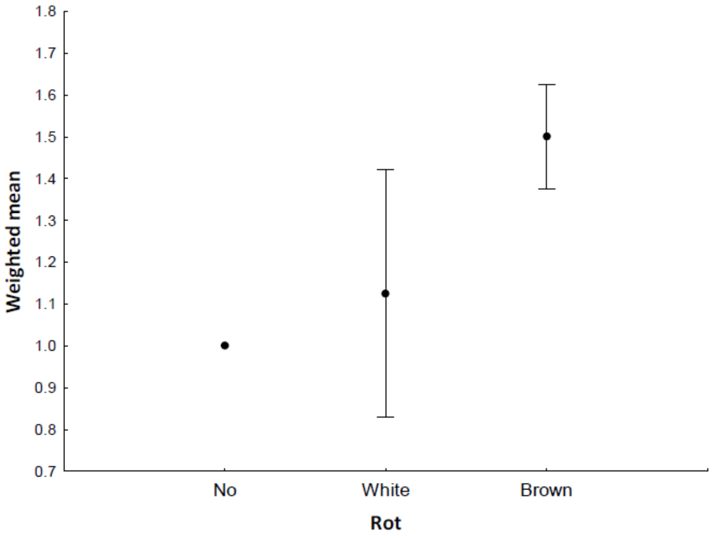

Figure 7. Influence of rot type on incidence of the carpenter ant in the Czech Republic.

4. Discussion

We observed that the nest distribution in the study area was most influenced by space, habitat, and isolation characteristics. More than one quarter of the trees broken by the windstorm were inhabited by carpenter ants. We found that the nests exhibited a clumped distribution on small scales, but had the opposite spatial pattern across larger distances. Nests were more frequent in the eastern part, although the forest structure was nearly the same in the whole study area. The most important tree parameter for the ants' nests being present was the presence of brown rot of the core wood. Ant nests were less frequent close to the forest openings.

Focusing on nest distribution, one of the main causes for the pattern could be the carpenter ant manner of breeding. After the mating flight, fertile queens build new nests. New queens sometimes occupy existing nests, and rarely the maternal nests [28,29]. The distances found between nests indicate that nests close to each other are related. The queen's dispersal ability after swarming is limited [30,31]. The observed distance between the nests, 1.5 km, mainly corresponds to the flying distance of wood ants. Their queens are able to fly a few kilometers. However, in 80% of flight incidences, the distance is less than 2 km [30,31]. This distance mainly corresponds to our results. Larger queens are able to disperse greater distances. Several morphological differences (such as a large and heavy abdomen) may limit dispersal [32]. One of the important aspects of our information about the aggregated distribution of nests over short distances is that the nest of one *C. ligniperdus* colony can be placed in several trees [33]. Some nests may have up to three queens, but they do not tolerate one another, and maintain territories within the diffused nests [28]. This also appears to be the cause of our finding of aggregation of inhabited trees, as closely inhabited trees could be inhabited by one ant colony. As the nest aggregation decreased with increasing geographical distance between them, a mosaic structure of transition from aggregated to segregated spatial structure was created. A similar pattern of ant nest distribution was noted by [34], who attributed it to several species-specific factors, as well as stochastic processes. Competition is an example of a relationship with a strong effect on nest distribution [35]. It is possible that only kinship nests exist in one clump. The subterranean species *Camponotus cruentatus* establishes new colonies near maternal ones, and the foraging areas of colonies overlap [36]. *Formica exsecta* nests that produce new queens supply nearby nests as well [37]. *Formica truncorum* ants hibernate in shared winter nests, which causes homogenizing of the population from several nests [38]. Conversely, strong interspecies animosity exists among unrelated ant colonies [39].

Our finding of a north-eastern aggregated distribution of snapped trees with nests could be caused by the prevailing direction of the wind. The wind direction in the Czech Republic is generally from the west. However, Reference [40] stated that the direction of the wind does not affect the direction of spread of the queens. However, a relatively high altitude of adult flight, which reaches up to 40 m, indicates that they could use the wind to obtain sufficient altitude [40]. The spread of ants with the help of wind corresponds to ant queens sometimes trying to establish new nests in unsuitable locations, which confirms their low active dispersion ability [22]. This fact could explain the observations of non-forest nest habitats mentioned in the literature.

The significant relationships of carpenter ant colonies with increasing distance from clear-cut and non-forest land were relatively surprising, considering the information known from the majority of entomological and forestry literature. The majority of ant species in spruce forests occur in or close to clearings. Their numbers in these habitats are also higher [41]. One possible reasons for the carpenter ants' distance from more sunny places is the reduction of competition with other ant species. One of the indications that can explain our results is that carpenter ants encounter species that do not defend their territory [42] and avoid forests with wood ants with large territories [43]. It is possible that carpenter ants can compensate for poorer temperature conditions due to their endosymbiosis with the *Blochmannia* bacteria, which improves colony growth and immune defense [44,45]. They have a good ability to heat their nests using metabolic heat [46]. One possible support for open habitats is that *C. ligniperdus* apparently prefers standing dead wood with a large perimeter [47]. Large-diameter dead wood is scarce in dense forest plantations. Thus, this situation mainly occurs in old or conservation forests [48]. Due to the type of damage, we were unable to measure the tree diameter, though the majority of trees were of average diameter in comparison to the surrounding trees in the stands. Information about ant preferences for clearings may be based on observations of nest remainders in stumps, because the discovery of nests is easier in open areas. However, the prime nests were located in tree trunks in the forest. Therefore, we cannot support that *C. ligniperdus* is associated with sunlit forest conditions and stumps.

Closed forests, the prevailing habitat in our case, have a more balanced microclimate than clearings [49,50]. This is an advantage for brown rot occurrence [51], as the probability of trees being inhabited by fungi is greater in darker forests than in gaps. For example, the mycelium of *H. annosum* does not grow if the temperature exceeds 35 °C, and fungi are destroyed at temperatures exceeding 45 °C [51,52]. We found that *C. ligniperdus* only built nests in trees that were inhabited by brown rot. Brown rot fungi preferentially decompose wood cellulose and hemicellulose, whereas white rot fungi are able to use lignin as well as cellulose and hemicellulose [53]. The presence of brown rot causes softer wood [54], but the remaining lignin ensures the maintenance of the wood structure [55]. This means that nest creation is easier in trees which are inhabited by rot, but only the wood with brown rot was suitable for nesting. Nests were mainly found in spruce trees. Spruce is an economically advantageous, highly productive species [56]. However, in Central Europe, it is often grown under unsuitable climatic conditions, which is reflected in its susceptibility to abiotic and biotic damage. Therefore, considerable attention has been paid to its damage [57–59] and the fungi associated with the species [25]. As *C. ligniperdus* inhabits fungus-infected trees, it can be seen as an indicator of weakened trees. Its numerous occurrences in the forest may indicate the unsuitability of growing spruce at lower altitudes. The number of nests in the study area was probably not so high due to the Scots pine dominance. Pines find more favorable conditions here, and they are therefore more resistant to fungal infections. Nevertheless, we observed a 1.5 km distance between the nests, which shows that not all suitable trees could be used for nest building.

Another important fact is that herbivorous insects are the diet of carpenter ants. For example, Reference [60] described successful hunting of *Malacosoma* larvae. During laboratory studies, it was found that workers attacked and killed 98% of the submitted arthropods, and they were able to catch a large number of taxa [23]. Although we have no specific data, we assume that their predation pressure is unlikely to be as strong as that of wood ants. These ants intensively hunt up to 30 m away from the nest [16]. The size of the *Camponotus* population is about 1/100th of the nest population of forest ants [22], which approximately corresponds to the ability to protect one tree. However, due to nest distribution, carpenter ants can protect entire forest patches against insect pests. Therefore, considering *C. ligniperdus* a pest species could be a serious mistake.

5. Conclusions

Carpenter ants are large and conspicuous ants, but they live a relatively hidden life. We found that carpenter ants are often found in coniferous trees, namely the Norway spruce. Regarding our results, ant presence in forest plantations appears not to be harmful, because the possible damage to the wood of stems occurs, in the majority of cases, to already rotten wood. As they often prey on insects that are potential pests, we concluded that the populations of carpenter ants in plantation forests are beneficial. Even when their nests indicated a clustered distribution pattern, we did not observe their damage to many neighboring trees, which would be typical for a bark beetle outbreak. Observation of aggregated incidences of the carpenter ants in trees would indicate to forest managers the unsuitable climatic stand conditions for the Norway spruce, due to the high possibility of damage by pathogens.

Author Contributions: J.H. generated and analyzed the data. The manuscript was written by J.H. and A.V.

Funding: This research was funded by grant IGA FLD ČZU (grant number B_02_18) and by the Ministry of Agriculture of the Czech Republic, institutional support (grant number MZE-RO0118).

Acknowledgments: Both reviewers are acknowledged for their valuable comments and suggestions, which greatly improved the paper.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Messenger, A.S. Spruce plantation effects on soil moisture and chemical element distribution. *For. Ecol. Manag.* **1980**, *3*, 113–125. [CrossRef]
2. Prévost, M.; Raymond, P. Effect of gap size, aspect and slope on available light and soil temperature after patch-selection cutting in yellow birch–conifer stands, Quebec, Canada. *For. Ecol. Manag.* **2012**, *274*, 210–221. [CrossRef]
3. Schelker, J.; Kuglerová, L.; Eklöf, K.; Bishop, K.; Laudon, H. Hydrological effects of clear-cutting in a boreal forest—Snowpack dynamics, snowmelt and streamflow responses. *J. Hydrol.* **2013**, *484*, 105–114. [CrossRef]

4. Jactel, H.; Brockerhoff, E.G. Tree diversity reduces herbivory by forest insects. *Ecol. Lett.* **2007**, *10*, 835–848. [CrossRef] [PubMed]
5. Hlásny, T.; Turčáni, M. Persisting bark beetle outbreak indicates the unsustainability of secondary Norway spruce forests: Case study from Central Europe. *Ann. For. Sci.* **2013**, *70*, 481–491. [CrossRef]
6. Drever, C.R.; Peterson, G.; Messier, C.; Bergeron, Y.; Flannigan, M. Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res.* **2006**, *36*, 2285–2299. [CrossRef]
7. Brockerhoff, E.G.; Jactel, H.; Parrotta, J.A.; Quine, C.P.; Sayer, J. Plantation forests and biodiversity. *Biodivers. Conserv.* **2008**, *17*, 925–951. [CrossRef]
8. Heiskanen, J.; Mäkitalo, K. Soil water-retention characteristics of Scots pine and Norway spruce forest sites in Finnish Lapland. *For. Ecol. Manag.* **2002**, *162*, 137–152. [CrossRef]
9. Dai, W.; Fu, W.; Jiang, P.; Zhao, K.; Li, Y.; Tao, J. Spatial pattern of carbon stocks in forest ecosystems of a typical subtropical region of southeastern China. *For. Ecol. Manag.* **2018**, *409*, 288–297. [CrossRef]
10. Horák, J.; Brestovanská, T.; Mladenović, S.; Kout, J.; Bogusch, P.; Halda, J.P.; Zasadil, P. Green desert?: Biodiversity patterns in forest plantations. *For. Ecol. Manag.* **2019**, *433*, 343–348. [CrossRef]
11. Hartley, M.J. Rationale and methods for conserving biodiversity in plantation forests. *For. Ecol. Manag.* **2002**, *155*, 81–95. [CrossRef]
12. Gjerde, I.; Sætersdal, M.; Nilsen, T. Abundance of two threatened woodpecker species in relation to the proportion of spruce plantations in native pine forests of western Norway. *Biodivers. Conserv.* **2005**, *14*, 377–393. [CrossRef]
13. Gittings, T.; O'Halloran, J.; Kelly, T.; Giller, P.S. The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. *For. Ecol. Manag.* **2006**, *237*, 290–300. [CrossRef]
14. Lonsdale, D.; Pautasso, M.; Holdenrieder, O. Wood-decaying fungi in the forest: Conservation needs and management options. *Eur J. For. Res.* **2008**, *127*, 1–22. [CrossRef]
15. Kenis, M.; Hurley, B.P.; Hajek, A.E.; Cock, M.J.W. Classical biological control of insect pests of trees. *Biol. Invasions* **2017**, *19*, 3401–3417. [CrossRef]
16. Adlung, K.G. A Critical Evaluation of the European Research on Use of Red Wood Ants (*Formica rufa* Group) for the Protection of Forests against Harmful Insects. *Z. Für Angew. Entomol.* **1966**, *57*, 167–189. [CrossRef]
17. Vélová, L.; Véle, A. The importance of woodpeckers in forest protection: Review. *Rep. For. Res.* **2019**, *64*, in press.
18. Bezděčka, P.; Bezděčková, K. *Ants in the Collections of Czech, Moravian and Silesian Museums*, 1st ed.; Muzeum Vysočiny Jihlava: Jihlava, Czech Republic, 2011; ISBN 978-80-86382-38-8.
19. Křístek, J.; Urban, J. *Lesnická Entomologie*; Vyd. 2., upr.; Academia: Praha, Czech Republic, 2013; ISBN 978-80-200-2237-0.
20. Czechowski, W.; Radchenko, A.; Czechowska, W.; Vepsäläinen, K. *The Ants of Poland*, 1st ed.; with reference to the myrmecofauna of Europe; Natura Optima dux Foundation: Warszawa, Poland, 2012; ISBN 83-930773-4-6.
21. Hansen, L.; Klotz, J. *Carpenter Ants of the United States and Canada*, 1st ed.; Comstock Publishing Associates: Ithaca, NY, USA, 2005; ISBN 978-0-8014-4262-9.
22. Seifert, B. The ecology of Central European non-arboreal ants—37 years of a broad-spectrum analysis under permanent taxonomic control. *Soil Org.* **2017**, *89*, 1–67.
23. Ayre, G.L. Feeding Behaviour and Digestion in Camponotus Herculeanus (L.) (hymenoptera: Formicidae). *Entomol. Exp. Et Appl.* **1963**, *6*, 165–170. [CrossRef]
24. Černý, A. *Parazitické Dřevokazné houby*, 1st ed.; SZN: Praha, Czech Republic, 1989; ISBN 80-209-0090-X.
25. Holuša, J.; Lubojacký, J.; Čurn, V.; Tonka, T.; Lukášová, K.; Horák, J. Combined effects of drought stress and Armillaria infection on tree mortality in Norway spruce plantations. *For. Ecol. Manag.* **2018**, *427*, 434–445. [CrossRef]
26. Rangel, T.F.; Diniz-Filho, J.A.F.; Bini, L.M. SAM. *Ecography* **2010**, *33*, 46–50. [CrossRef]
27. De Frutos, Á.; Olea, P.P.; Vera, R. Analyzing and modelling spatial distribution of summering lesser kestrel: The role of spatial autocorrelation. *Ecol. Model.* **2007**, *200*, 33–44. [CrossRef]
28. Hoelldobler, B. Zur Frage der Oligogynie bei *Camponotus ligniperda* Latr. und *Camponotus herculeanus* L. (Hym. Formicidae). *J. Appl. Entomol.* **1961**, *49*, 337–352.
29. Gadau, J.; Gertsch, P.J.; Heinze, J.; Pamilo, P.; Hölldobler, B. Oligogyny by Unrelated Queens in the Carpenter Ant, *Camponotus ligniperdus*. *Behav. Ecol. Sociobiol.* **1998**, *44*, 23–33. [CrossRef]

30. Mabelis, A.A. Flying as a survival strategy for wood ants in a fragmented landscape (Hymenoptera, Formicidae). *Memorab. Zool.* **1994**, *48*, 147–170.
31. Mabelis, A.A.; Chardon, J.P. Survival of the trunk ant (*Formica truncorum* Fabricius, 1804; Hymenoptera: Formicidae) in a fragmented habitat. *Myrmecol. Nachr.* **2006**, *2006*, 1–11.
32. Helms, J.A. The flight ecology of ants (Hymenoptera: Formicidae). *Myrmecol. News* **2018**, *26*, 19–30.
33. Kloft, W.; Haisch, A.; Haisch, B. Traceruntersuchungen mr Abgrenzung von Nestarealen holzzerstorender Rossameisen *Camponotus herculeanus* L. und *C. ligniperda* Latr.). *Entomol. Exp. Et Appl.* **1965**, *8*, 20–26. [CrossRef]
34. Markó, B.; Kiss, K.; Gallé, L. Mosaic structure of ant communities (Hymenoptera: Formicidae) in Eastern Carpathian marshes: Regional versus local scales. *Acta Zool. Acad. Sci. Hung.* **2004**, *50*, 77–95.
35. Ribas, C.R.; Schoereder, J.H. Are all ant mosaics caused by competition? *Oecologia* **2002**, *131*, 606–611. [CrossRef]
36. Boulay, R.; Cerdá, X.; Simon, T.; Roldan, M.; Hefetz, A. Intraspecific competition in the ant *Camponotus cruentatus*. *Anim. Behav.* **2007**, *74*, 985–993. [CrossRef]
37. Seppä, P.; Johansson, H.; Gyllenstrand, N.; Pálsson, S.; Pamilo, P. Mosaic structure of native ant supercolonies. *Mol. Ecol.* **2012**, *21*, 5880–5891. [CrossRef] [PubMed]
38. Elias, M.; Rosengren, R.; Sundström, L. Seasonal polydomy and unicoloniality in a polygynous population of the red wood ant *Formica truncorum*. *Behav. Ecol. Sociobiol.* **2005**, *57*, 339–349. [CrossRef]
39. Mabelis, A.A. Wood Ant Wars the Relationship Between Aggression and Predation in the Red Wood Ant (Formica Polyctena Forst.) by. *Neth. J. Zool.* **1978**, *29*, 451–620. [CrossRef]
40. Mabelis, A.A.; Korczyńska, J. Dispersal for survival: Some obesrvations on the trunk ant (*Formica truncorum*, Fabricius). *Neth. J. Zool.* **2001**, *51*, 299–321. [CrossRef]
41. Véle, A.; Holuša, J.; Horák, J. Ant abundance increases with clearing size. *J. For. Res.* **2016**, *21*, 110–114. [CrossRef]
42. Savolainen, R.; Vepsäläinen, K. A Competition Hierarchy among Boreal Ants. *Oikos* **1988**, *51*, 135–155. [CrossRef]
43. Alinvi, O.; Bohlin, J.; Ball, J.P. Interspecific competition among ants in the boreal forest. *Insectes Sociaux* **2008**, *55*, 1–11. [CrossRef]
44. Blochmann, F. Über das Vorkommen von bakterienähnlichen Gebilden in den Geweben und Eiern verschiedener Insekten. *Zentbl. Bakteriol.* **1892**, *11*, 234–240.
45. De Souza, D.J.; Bézier, A.; Depoix, D.; Drezen, J.-M.; Lenoir, A. Blochmannia endosymbionts improve colony growth and immune defence in the ant *Camponotus fellah*. *BMC Microbiol.* **2009**, *9*, 29. [CrossRef]
46. Sanders, C.J. Seasonal and daily activity patterns of Carpenter ants (Camponotus spp.) in northwestern Ontario (Hymenoptera: Formicidae). *Can. Entomol.* **1972**, *104*, 1681–1687. [CrossRef]
47. Westerfelt, P.; Widenfalk, O.; Lindelöw, Å.; Gustafsson, L.; Weslien, J.; Leather, S.R.; Jonsell, M. Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. *Insect Conserv. Divers.* **2015**, *8*, 493–504. [CrossRef]
48. Horák, J.; Rébl, K. The species richness of click beetles in ancient pasture woodland benefits from a high level of sun exposure. *J. Insect Conserv.* **2013**, *17*, 307–318. [CrossRef]
49. Aussenac, G. Interactions between forest stands and microclimate. *Ann. For. Sci.* **2000**, *57*, 287–301. [CrossRef]
50. Olchev, A.; Radler, K.; Sogachev, A.; Panferov, O.; Gravenhorst, G. Application of a three-dimensional model for assessing effects of small clear-cuttings on radiation and soil temperature. *Ecol. Model.* **2009**, *220*, 3046–3056. [CrossRef]
51. Gooding, G.V.; Hodges, C.S.; Ross, E.W. Effect of Temperature on Growth and Survival of *Fomes annosus*. *For. Sci.* **1966**, *12*, 325–333.
52. Ross, E.W. Thermal inactivation of conidia and basidiospores of Fomes annosus. *Phytopathology* **1969**, *59*, 1798–1801.
53. Rayner, A.D.M.; Boddy, L. *Fungal Decomposition of Wood. Its Biology and Ecology*, 1st ed.; John Wiley & Sons Ltd.: Chichester, UK, 1988; ISBN 0-471-10310-1.
54. Edman, M.; Jönsson, M.; Jonsson, B.G. Fungi and wind strongly influence the temporal availability of logs in an old-growth spruce forest. *Ecol. Appl.* **2007**, *17*, 482–490. [CrossRef]

55. Abreau, H.S.; Nascimento, A.M.; Maria, M.A. Lignin structure and wood properties. *Wood Fiber Sci. J. Soc. Wood Sci. Technol.* **1999**, *31*, 426–433.
56. Spiecker, H. Silvicultural management in maintaining biodiversity and resistance of forests in Europe—Temperate zone. *J. Environ. Manag.* **2003**, *67*, 55–65. [CrossRef]
57. Schelhaas, M.-J.; Nabuurs, G.-J.; Schuck, A. Natural disturbances in the European forests in the 19th and 20th centuries. *Glob. Chang. Biol.* **2003**, *9*, 1620–1633. [CrossRef]
58. Holuša, J. Health condition of Norway spruce *Picea abies* (L.) Karst. stands in the Beskid Mts. *Dendrobiology* **2004**, *51*, 11–15.
59. Jactel, H.; Nicoll, B.C.; Branco, M.; Gonzalez-Olabarria, J.R.; Grodzki, W.; Långström, B.; Moreira, F.; Netherer, S.; Orazio, C.; Piou, D.; et al. The influences of forest stand management on biotic and abiotic risks of damage. *Ann. For. Sci.* **2009**, *66*, 701–719. [CrossRef]
60. Green, G.W.; Sullivan, C.R. Ants Attacking Larvae of the Forest Tent Caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Lasiocampidae). *Can. Entomol.* **1950**, *82*, 194–195. [CrossRef]