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Biodiverzita ptáků a její ochrana v rozptýlené zeleni Střední Evropy – význam biotopu, krajinné mozaiky a managementu

Bird biodiversity and its conservation in Central European non-forest woody vegetation – the importance of habitat, landscape mosaic and management

Disertační práce

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Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

Poděkování

Téma ochrany ptáků v rozptýlené zeleni mě provázelo celou érou vysokoškolského studia. Přineslo mi úžasné zážitky z terénu, ornitologické zkušenosti, větší porozumění krajině, ve které žijeme, a upřímnou lásku k ní. Přineslo mi také mnohé výzvy, fyzické i psychické vyčerpání a poznávání vlastních limitů, a to nejen při velkém množství dlouhých a dalekých terénních výjezdů za sběrem dat. Největší výzva mě však čekala v posledním roce mého studia, kdy jsem se stala kromě šťastné doktorandky, ekoložky a manželky také šťastnou maminkou. To, že jsem se zvládla plně do této nové role ponořit, a přitom publikovat poslední články a napsat tuto disertaci, je bez nadsázky mým dosavadním největším životním úspěchem. Odnáším si z něho utvrzení, že ochrana přírody bude vždy mým tématem, bez ohledu na to, jak se změní můj život nebo role ve společnosti. Tohoto úspěchu bych však nikdy nedosáhla bez svých kolegů a blízkých lidí, kteří při mně stáli. Je to i jejich úspěch. Na tomto místě bych jim proto ráda poděkovala.

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Obsah

Abstrakt

Rozptýlená zeleň je nedílnou součástí krajiny střední Evropy. Zahrnuje všechny možné podoby dřevin rostoucích mimo les, zemědělskou kulturu a lidská sídla, a představuje tak neprodukční biotop klíčový při ochraně biodiverzity v zemědělské krajině. V této disertační práci hledám odpověď na otázku, jaké faktory biodiverzitu v rozptýlené zeleni ovlivňují a jakým způsobem, přičemž sleduji vliv především na ptáky jako na indikační skupinu citlivou na změny v zemědělské krajině. V celkem čtyřech publikacích jsme se zaměřili na bílá místa v dosavadním výzkumu – na podobu biotopu rozptýlené zeleně, na podobu krajinné mozaiky a na aplikovaný management. Ukázali jsme, že všechny tyto faktory významně ovlivňují biodiverzitu ptáků, a tím i úspěšnost ochranářských opatření a zemědělských dotací na rozptýlenou zeleň orientovaných. Zatímco zeleň v podobě vzrostlých a druhově pestrých porostů původních dřevin podpoří spíše druhy lesní a zároveň vysoký celkový počet druhů ptáků, porosty obohacené o různá časnější sukcesní stadia podpoří spíše druhy zemědělské krajiny. Dále, že v krajinném kontextu je pro vysoký počet druhů ptáků klíčová biotopová diverzita, pro ohrožené druhy je však přínosná zejména jemnozrnnost mozaiky rozptýlené zeleně. Ukázali jsme, že takovouto cennou jemnozrnnou mozaiku rozptýlené zeleně najdeme na příklad ve vojenských prostorech díky zvláštnímu disturbančnímu režimu vznikajícímu jako druhotný efekt armádního výcviku. Po ukončení těchto disturbancí mozaika rozptýlené zeleně postupně zaniká nejen přeměnou na urbánní prostředí, ale také přirozenou sukcesí. Působení přirozené sukcese lze zvrátit vhodně zvoleným managementem – podle našich výsledků se jeví pro ochranu biodiverzity ptáků vhodná zejména ochranářská, ale i zemědělská pastva. Nicméně srovnání ptáků s jinými taxony odhaluje značné rozdíly v managementových preferencích, z čehož vyvozujeme, že význam ptáků jako indikátorů dalších složek biodiverzity je třeba brát s rezervou. Výsledky této práce akcentují fakt, že rozptýlená zeleň hostí široké spektrum druhů s různými ekologickými nároky a že klíčem k ochraně biodiverzity je tedy kromě zajištění jejího dostatečného množství v krajině především zajištění její různorodosti, a to v lokálním i krajinném měřítku.

Abstract

Non-forest woody vegetation is an integral part of the Central European landscape. It includes all possible forms of woody vegetation growing outside of forests, agricultural production, and human settlements; it thus represents a non-productive habitat crucial to the conservation of farmland biodiversity. In this dissertation, I am looking for an answer to the question of what factors affect biodiversity in non-forest woody vegetation and in what way, observing the effect mainly on birds as an indicator group sensitive to changes in the agricultural landscape. In a total of four publications, we focused on the white spots in research to date – habitat characteristics of non-forest woody vegetation, characteristics of the landscape mosaic, and applied management. We have shown that all these factors significantly affect bird biodiversity and, thus, the success of conservation measures and agricultural subsidies oriented towards non-forest woody vegetation. While woody vegetation in the form of mature and species-variegated stands of native trees will rather support forest species and, at the same time, a high total number of species, stands enriched by various earlier stages of succession will rather support farmland species. Furthermore, we show that in the landscape context habitat diversity is key for a large number of bird species, but for endangered species the fine-grained mosaic of non-forest woody vegetation is especially beneficial. We show that such a valuable fine-grained mosaic of non-forest woody vegetation can be found, for example, in military training areas thanks to the special disturbance regime arising as a secondary effect of military training. When these disturbances end, the mosaic of non-forest woody vegetation gradually disappears by transformation into urban areas, as well as by natural succession. The effect of natural succession can be reversed by suitably chosen disturbance management - based on to our results, conservation grazing (but also agricultural grazing) appears to be particularly suitable for the protection of bird biodiversity. However, comparisons of birds with other taxa reveal considerable differences in management preferences. The results of this work emphasize the fact that non-forest woody vegetation hosts a wide range of species with different ecological requirements and that the key to protecting biodiversity is, in addition to ensuring its sufficient quantity in the landscape, above all ensuring its diversity, both on a local and landscape scale.

Přehled článků a podíl autora

Článek 1

Dvořáková, L., Kuczyński, L., Rivas-Salvador, J., & Reif, J. (2022). Habitat characteristics supporting bird species richness in mid-field woodlots. *Frontiers in Environmental Science*, *10*, 816255. https://doi.org/10.3389/FENVS.2022.816255

LD přispěla k designu studie, provedla většinu terénních prací a většinu statistických analýz, napsala rukopis; podíl 80%.

Článek 2

Dvořáková, L., Hernová, J., Bušek, O., & Reif, J. (2023). Relationships between bird species richness and different facets of landscape heterogeneity – insights from a military area. *Journal of Vertebrate Biology*, *72*, 23012. https://doi.org/10.25225/jvb.23012

LD zanalyzovala data a napsala rukopis; podíl 60%.

Článek 3

Dvořáková, L., Hanzelka, J., Romportl, D., & Reif, J. (2024). Habitat changes explain shifts in bird community composition in abandoned military training areas: Lessons for conservation. *Journal for Nature Conservation*, *79*, 126612. https://doi.org/10.1016/j.jnc.2024.126612

LD se podílela na designu studie, koordinovala terénní práce a zároveň se na nich z velké části podílela, přispěla ke statistickým analýzám, napsala rukopis; podíl 50%.

Článek 4

Reif, J., Chajma, P., Dvořáková, L., Koptík, J., Marhoul, P., Čížek, O., & Kadlec, T. (2023). Biodiversity changes in abandoned military training areas: relationships to different management approaches in multiple taxa. *Frontiers in Environmental Science*, *11*, 1243568. https://doi.org/10.3389/fenvs.2023.1243568

LD přispěla k designu studie, podílela se na sběru dat a přispěla ke psaní rukopisu; podíl 30%.

Školitel potvrzuje, že uvedené podíly studenta na jednotlivých publikacích odpovídají skutečnosti.

Dne 8. 9. 2024 v Praze prof. Jiří Reif, školitel

Úvod

Pojem „rozptýlená zeleň“ označuje dřevinnou vegetaci, která se nachází mimo intravilány obcí a není ani lesem ani zemědělskou kulturou (Kolařík, 2003). Z této definice je patrné, že jde do velké míry o pojem „sběrný“, který v sobě ukrývá pestrou paletu krajinných prvků různé velikosti, původu i účelu. Může jít o zbytky lesů, které se dochovaly na zemědělsky nevýnosných a nedostupných místech, o dřeviny náhodně zavlečené, o plochy opuštěné s různými stadii sukcesní vegetace, či o dřeviny člověkem záměrně vysazované z nejrůznějších důvodů (Kavka & Šindelářová, 1978). Rozptýlená zeleň je nedílnou součástí volné krajiny střední Evropy – vyskytuje se v podobě solitérních dřevin, doprovodné vegetace cest a vodních toků, remízků, zarostlých mezí, křovin, větrolamů, lesíků atd. – a má tak klíčový význam při utváření krajinného rázu (Baudry et al., 2000; Hanuš et al., 1979).

Rozptýlená zeleň nemá pro člověka primárně produkční funkci, není tedy vystavena takovému tlaku lidského působení jako produkční biotopy a je jí zachován alespoň do určité míry přirozený (tzv. polopřírodní) charakter. Právě proto je, spolu s ostatními neprodukčními biotopy, klíčová pro zachování biodiverzity a pro funkčnost krajiny v ekologickém slova smyslu (Montgomery et al., 2020; Šálek et al., 2022). V současné intenzivně obdělávané zemědělské krajině potýkající se s drastickým propadem biodiverzity (Stoate et al., 2009) rozptýlená zeleň poskytuje vhodné podmínky k životu řadě organismů, včetně mnoha ohrožených druhů – ať už jde o lišejníky a houby (Horak et al., 2014), rostliny (Bergmeier et al. 2010), hmyz (Sebek et al., 2016) nebo obratlovce (Fuller et al., 2004). Díky pestré škále stanovištních podmínek zde najdeme druhy s různými biotopovými preferencemi od druhů otevřené krajiny až po druhy lesní (Haslem & Bennett, 2008; Sebek et al., 2016; Takkis et al., 2018). Mnoho z nich je dokonce na rozptýlenou zeleň svým výskytem úzce vázáno, neboť ta představuje v podstatě jedinou alternativu k jejich přirozenému, dnes již člověkem zcela potlačenému prostředí lesostepi (Wright et al., 2011). Rozptýlená zeleň umožňuje i migraci organismů krajinou, neboť funguje jako tzv. koridory či nášlapné kameny v intenzivně modifikovaném, těžko prostupném antropogenním prostředí (Gauffre et al., 2022; Mehlman et al., 2005; Wehling & Diekmann, 2009). Také poskytuje organismům možnost úkrytu před predátory, zemědělskými stroji či nepříznivým počasím působícími na otevřených zemědělských plochách (Doherty & Grubb, 2000), představuje klíčový zdroj potravy, a to i po sklizni a v zimním období (Hinsley & Bellamy, 2000), a dále plní řadu specifických funkcí ve vztahu k ekologickým potřebám konkrétních druhů organismů. Například slouží jako nepostradatelná součást teritoria pro strnada lučního (*Emberiza calandra*), který ji využívá k přednesu zpěvu – tzv. song post (Ceresa et al., 2012), nebo pro ťuhýka obecného (*Lanius collurio*), který ji potřebuje jako vhodné „čihadlo“ pro lov (Morelli et al., 2016).

Nicméně za poslední půlstoletí byla rozptýlená zeleň v evropské krajině výrazně potlačena, a s ní i biodiverzita na ni vázaná. Hlavní podíl na tom měla intenzifikace zemědělství, která nastoupila po konci druhé světové války a vyústila ve výraznou homogenizaci krajiny (Benton et al., 2003). Rozloha polí se díky novým možnostem těžké techniky zvětšovala na úkor neprodukčních biotopů. Rozptýlená zeleň byla odstraňována, neboť ubírala produkční plochu a snižovala výnos z okolo pěstovaných plodin (Huth & Possingham, 2007; MacDonald & Johnson, 2000). Naopak v okrajových oblastech došlo k zániku tradičního zemědělství a opuštění krajiny, což vedlo k postupnému zarůstání otevřených ploch a přeměně rozptýlené zeleně v souvislé křovinné či lesní porosty (Bengtsson et al., 2000; Foley et al., 2011).

V současnosti jsou již negativní dopady tohoto vývoje všeobecně známy, jeho definitivní zvrácení je však palčivou výzvou pro vědce, ochranáře i politiky. Pro efektivní dotační politiku i ochranářskou péči je nejprve potřeba pomocí empirického výzkumu zjistit, jaké faktory biodiverzitu v rozptýlené zeleni ovlivňují.

Díky období, kdy vědeckou komunitou silně rezonovala ostrovní teorie biogeografie (MacArthur & Wilson, 1967) a s ní související tzv. species-area relationship (Connor & McCoy, 1979), je poměrně dobře popsán vztah mezi počtem druhů a rozlohou, případně izolovaností jednotlivých ostrůvků rozptýlené zeleně (Mason, 2001; McCollin, 1993; Opdam et al., 1985). Pozornost byla věnována i tvaru, respektive členitosti ostrůvků rozptýlené zeleně a projevu tzv. okrajového efektu (Bellamy et al., 1996; Villard et al., 1999). Krajinná ekologie se pak zabývala otázkou, jak ovlivňuje biodiverzitu vzájemná konfigurace ostrůvků zeleně v krajinném měřítku (tzv. diskuse SLOSS – single large or several small; např. Loman & Von Schantz, 1991). Častým nedostatkem studií z této doby bývá, že se primárně zabývaly problematikou lesní fragmentace a neuvažovaly rozptýlenou zeleň jako svébytný biotop se specifickým složením společenstva, tudíž interpretace výsledků často nejsou pro ochranu biodiverzity v rozptýlené zeleni aktuální.

Méně pozornosti bylo věnováno tomu, jak biodiverzitu ovlivňuje podoba vlastního biotopu rozptýlené zeleně, heterogenita krajinné mozaiky, případně aplikovaný management (Sebek et al., 2016; Takkis et al., 2018). Situaci komplikuje i fakt, že míra dosavadního poznání se velmi liší mezi jednotlivými typy rozptýlené zeleně. Nejvíce pozornosti bylo doposud věnováno liniové zeleni podél polí (Forman & Baudry, 1984; Hinsley & Bellamy, 2000; Montgomery et al., 2020). Méně je známo o biodiverzitě ostrůvkovitých, tzv. plošných porostů (např. Hinsley et al., 1995; Kujawa, 2002; Vanhinsbergh et al., 2002) a ještě méně o drobných, tzv. bodových prvcích rozptýlené zeleně, jako jsou solitérní dřeviny (Fischer et al., 2010; Prevedello et al., 2018; Pustkowiak et al., 2021). Stejně tak jsou poměrně vzácné studie, které se věnují rozptýlené zeleni v krajinném měřítku (Bennett et al., 2006; Wuczynski, 2016). Tato disertační práce se proto zabývá významem podoby vlastního biotopu v jednotlivých ostrůvcích rozptýlené zeleně, významem heterogenity krajinné mozaiky a dopady různých typů managementu, a to především u plošné a bodové zeleně na různých prostorových škálách.

Za tímto účelem je potřeba zmapovat biodiverzitu v rozptýlené zeleni a podívat se, jaké parametry biotopu, krajinného kontextu či lidských aktivit ji významně ovlivňují. Protože ale není reálně možné mapovat všechny taxony biodiversity, pracovali jsme především s taxonem, který se běžně užívá jako indikátor celkové biodiverzity – s ptáky. Ptáci se nabízí jako modelový taxon již proto, že jsou z ekologického a taxonomického hlediska dobře prozkoumanou skupinou, v přírodě jsou snadno detekovatelní a rozpoznatelní, metody při jejich sčítání jsou již osvědčené a nenáročné na finance či materiálové vybavení, a v neposlední řadě existuje v našem prostředí mnoho zkušených ornitologů, které lze do monitoringu zapojit (Fraixedas et al., 2020). Ptáci se nachází na konci potravního řetězce, a tak nepřímo odráží i biodiverzitu taxonů nacházejících se v potravním řetězci níže. Zároveň díky schopnosti letu tak činí na velkých prostorových škálách (Eglington et al., 2012). V neposlední řadě jsou ptáci skupinou velmi citlivě reagující na změny spojené s intenzifikací zemědělství a často jsou užíváni jako jeden z indikátorů při vyhodnocování účinnosti opatření na ochranu biodiverzity v zemědělské krajině (Gottschalk et al., 2010; Morelli et al., 2014). Všechny tyto vlastnosti z nich činí vhodný modelový taxon pro náš výzkum.

Nejjednodušší a zároveň nejčastěji používanou metodou, jak kvantifikovat biodiverzitu společenstva ptáků, je zjistit celkový počet druhů (druhové bohatství) ptáků na dané lokalitě či v regionu (Magurran, 2004; Whittaker, 1972). Počet druhů je srozumitelný i široké veřejnosti, politikům a úředníkům, a je tak důležitou informací při implementaci výsledků ochranářských studií (Weber et al., 2004). V této práci jsme použili prostý počet druhů k porovnání lokální druhové diversity uvnitř různých ostrůvků rozptýlené zeleně (článek 1) a k porovnání krajinné diversity ptáků uvnitř a vně vojenského újezdu (článek 2). Uvažování pouze v rámci celkového počtu druhů má však určitá omezení – empirický výzkum opakovaně upozornil na to, že tento údaj může vypovídat spíše o počtu běžných a široce rozšířených druhů, tzv. generalistů, a naopak opomíjet trendy ochranářsky významných druhů (Lennon et al., 2004), stejně tak mohou celkový počet druhů navyšovat zavlečené nepůvodní druhy (Leroy et al., 2023). Zároveň celkový počet druhů postrádá informaci o druhové skladbě společenstva, skrze kterou můžeme nahlédnout dopadu hospodaření a změn v krajině (Fleishman et al., 2006). Proto jsme se zaměřili i na počet druhů v rámci dílčích ekologických podskupin ptáků – lesních druhů a druhů zemědělské krajiny (článek 1) a chráněných druhů (článek 2). Ještě komplexnější informaci o druhové diverzitě společenstva získáme, pokud použijeme některý z indexů diversity, které v sobě kombinují počet druhů s informací o jejich početnosti. Pro potřeby našeho výzkumu jsme využili široce rozšířený Shannon index (článek 1; Gotelli & Colwell, 2001). Pro vyjádření změny biodiverzity společenstva v čase se jeví místo počtu druhů jako vhodnější použít změnu jejich početnosti (abundance) (Storch et al., 2023). Proto jsme použili změnu početnosti druhů při modelování dopadu biotopových změn v krajině a různých typů managementu, kdy jsme porovnávali stav ptačí biodiverzity na stejných místech s odstupem dvanácti let (článek 3 a 4). Ani v tomto případě jsme nesledovali pouze změny celkové početnosti, ale také početnosti ohrožených druhů a šesti ekologických podskupin klasifikovaných na základě preference sukcesního stadia a vlhkosti stanoviště (článek 4).

Tato disertační práce hledá odpověď na otázku, jaké faktory biodiversitu ptáků v rozptýlené zeleni ovlivňují a jakým způsobem. Jinými slovy, jak by měla rozptýlená zeleň ideálně vypadat, aby co nejvíce podpořila biodiversitu ptáků v krajině. Podle ekologické teorie by měla být jedním z klíčových faktorů podoba vlastního habitatu rozptýlené zeleně (Guisan & Thuiller, 2005) (článek 1). Podle dosavadní literatury lze očekávat, že více druhů ptáků se bude nacházet v porostech s vyvinutější strukturou dřevinné vegetace (tj. vegetace vyšší a/nebo s hustším zápojem jednotlivých vegetačních pater), neboť zde bude více dostupného biotopu, který druhy mohou využít (Hinsley & Bellamy, 2000). Také předpokládáme, že více druhů ptáků se bude nacházet v porostech s vyšší biotopovou diverzitou, neboť zde bude více různých ekologických nik, díky čemuž zde najde životní prostor více různých druhů s odlišnými ekologickými nároky (Fuller et al., 2004). A nakonec předpokládáme, že druhovou diverzitu ptáků může ovlivnit i přítomnost nepůvodních druhů dřevin, které mohou určitým způsobem měnit charakter stanoviště a nabídku zdrojů v rozptýlené zeleni (J. Reif et al., 2016).

Přesuneme-li pozornost od lokálního ke krajinnému měřítku, druhovou diverzitu ptáků v krajině s rozptýlenou zelení bude pravděpodobně ovlivňovat nejen celková rozloha a izolovanost ostrůvků, ale také jejich celkový počet vypovídající o jemnosti krajinné mozaiky. Zároveň bude hrát nejspíš velkou roli i celková biotopová diverzita v krajině (Haslem & Bennett, 2008) (článek 2). Neboť čím více se v krajině o dané rozloze nachází ostrůvků rozptýlené zeleně, tím více biotopových příležitostí zde mohou nacházet druhy ptáků specializované na kombinaci otevřených a dřevinných biotopů, mezi které se řadí i velká část ohrožených druhů zemědělské krajiny. Zároveň krajina může být prostupnější pro druhy lesní (Hinsley et al., 1995; Pustkowiak et al., 2021). Vyšší biotopová diverzita zas umožňuje, podobným mechanismem jako na lokální úrovni, koexistenci více druhů ptáků s odlišnými nároky na biotop (Evans et al., 2005).

Velký prostor tato práce věnuje i otázce, zda hraje roli, jakým způsobem je rozptýlená zeleň formována a udržována. Rozptýlená zeleň je pro ptáky (a organismy obecně) de facto člověkem uměle vytvořená alternativa k původní lesostepní mozaice, která byla formována dynamicky a nahodile prostřednictvím přírodních disturbancí (požáry, polomy, pastva, sešlap velkých kopytníků aj.) (Ložek, 2007; Vera, 2000). V současnosti je rozptýlená zeleň spojena především se zemědělskou krajinou, kde jsou plochy přirozených otevřených biotopů (stepí, mokřadů, slatin, písků, skalních úbočí apod.) nahrazeny zemědělsky obdělávanými půdními bloky (poli, loukami, pastvinami), které vzhledem k intenzivnímu způsobu hospodaření často v krajině naprosto dominují. Porosty rozptýleného charakteru můžeme ale najít i v chráněných územích, kde jsou v zájmu ochrany biodiverzity simulovány tradiční zemědělské zásahy nebo přirozené disturbanční procesy tak, aby otevřené biotopy zůstaly zachovány navzdory sukcesním procesům (Fuller et al., 2017). Tato snaha o co největší přirozenost disturbancí má však značné limity, neboť se ukazuje, že současné paradigma ochrany přírody o tom, co je v krajině „přirozené“, může být poněkud zavádějící (Fuller et al., 2017) a zároveň že ochranářské zásahy selhávají v zajištění dostatečně heterogenního prostředí (Prevedello et al., 2018). Jsou totiž dopředu plánované, naráží na byrokratická omezení a často probíhají (či naopak neprobíhají) nárazově a plošně, což plyne z limitace časem, financemi či lidskými zdroji (Konvicka et al., 2008). Zajímavou alternativou pro výzkum přírodě blízké rozptýlené zeleně jsou vojenské výcvikové prostory, kde mozaika otevřených biotopů a dřevin vzniká jako vedlejší produkt vojenských aktivit (přemisťování pěších jednotek, hloubení zákopů, výbuchy ostré munice, pojezdy těžké techniky aj.). Vojenské disturbance se totiž podobají těm přírodním tím, že jsou nahodilé v prostoru, čase i intenzitě (Warren et al., 2007). Ukazuje se, vojenské výcvikové prostory jsou v Evropě významným refugiem biodiverzity a že klíčem k této biodiversitě je často právě heterogenní mozaika otevřených biotopů a rozptýlené zeleně (Bušek & Reif, 2017; Harabiš & Dolný, 2018; Warren & Büttner, 2008).

V posledních desetiletích došlo však na mnoha vojenských prostorech v Evropě k ukončení armádních aktivit (Cizek et al., 2013; Ellwanger & Reiter, 2019; Jiří Reif & Marhoul, 2010) a je otázkou, jak se změní charakter krajinné mozaiky a její biodiversita po vymizení armádního disturbančního režimu (článek 3). Místa opuštěná armádou mohou být ponechána přirozené sukcesi, velmi často je zde však dříve či později zaveden jiný způsob využití – nejčastěji jde o zemědělské využití, výstavbu fotovoltaických elektráren či rekreačních areálů nebo ochranářskou péči (Beleco, 2024). Ta k udržení otevřeného charakteru biotopů využívá různých nástrojů od klasických jako je výřez křovin, seč a oplůtková pastva až po novátorské jako je rewilding nebo pojezdy motorovými vozidly (Marhoul et al., 2024). Porovnání dopadu různých způsobů využití včetně různých typů ochranářského managementu opuštěných vojenských prostorů s rozptýlenou zelení (článek 4) je zásadní nejen pro doplnění mezery ve vědeckém výzkumu, ale také klíčové pro aplikovanou ochranu přírody, kdy nové poznatky mohou výrazně zefektivnit rozhodování státní správy i nevládních organizací. Ač je tato disertační práce především o ptácích, v této poslední části zjištěné dopady managementu na ptáky porovnáváme se třemi dalšími taxony – rostlinami, rovnokřídlým hmyzem a motýly. Toto porovnání je jistě z ochranářského hlediska zajímavé a zároveň velmi potřebné – neboť ptáci jsou zcela určitě klíčovým indikačním (a proto výzkumem často upřednostňovaným) taxonem, je však otázkou, do jaké míry odráží managementové preference i dalších, ekologicky tolik odlišných taxonů.

Cíle práce

- Zjistit, jaké vlastnosti biotopu ovlivňují biodiverzitu ptáků v porostech rozptýlené zeleně (článek 1).
- Zjistit, jak různé složky heterogenity ovlivňují biodiverzitu ptáků v krajinné mozaice s rozptýlenou zelení (článek 2).
- Zjistit, zda se krajinná mozaika formovaná armádním disturbančním režimem v různých složkách heterogenity liší oproti běžné zemědělské krajině (článek 2).
- Vyhodnotit změny v krajině s rozptýlenou zelení a její biodiversitě ptáků po vymizení armádního disturbančního režimu (článek 3).
- Vyhodnotit dopad různých typů následného managementu na biodiversitu ptáků v této krajině a zjištěné porovnat s preferencemi jiných taxonů (článek 4).

Vliv rozlohy, izolovanosti a tvaru rozptýlené zeleně

I když vliv rozlohy rozptýlené zeleně, jejího tvaru a izolovanosti není předmětem této práce, považuji za důležité ho zde alespoň stručně představit, neboť jde o vlastnosti, které diverzitu ptáků významně ovlivňují. Často se mohou do podoby společenstva promítat i silněji než všechny další faktory, které v této práci zkoumám. Především rozloha hraje u tohoto biotopu, který je z podstaty věci na plochu omezený, klíčovou roli, a proto se na její efekt budu v průběhu textu několikrát odkazovat.

Z pohledu ostrovní teorie biogeografie lze rozptýlenou zeleň považovat za ostrůvky „lesního" biotopu nacházející se v matrici otevřené krajiny, přičemž pro organismy, které rozptýlenou zeleň osidlují, je tato okolní matrice (alespoň do určité míry) nehostinné a těžko překonatelné prostředí. Podle této úvahy je počet druhů v ostrůvku rozptýlené zeleně dán především jeho rozlohou a izolovaností od okolního „lesního" prostředí (Loman & Von Schantz, 1991; Tworek, 2002). Platnost tohoto teoretického modelu však v praxi pokulhává, neboť zdaleka ne všechny organismy v rozptýlené zeleni – ptáky nevyjímaje – jsou vázané striktně na dřevinnou vegetaci. Kromě těchto lesních druhů – např. budníčka malého (*Phylloscopus collybita*), pěnkavy obecné (*Fringilla coelebs*) nebo dlaska tlustozobého (*Coccothraustes coccothraustes*) – je zde i významná část druhů zemědělské krajiny využívající ve větší či menší míře i otevřené biotopy – např. stehlík obecný (*Carduelis carduelis*), zvonek zelený (*Chloris chloris*) nebo strnad luční (Fuller et al., 2004).

Dosavadní výzkum skutečně potvrdil, že s rostoucí rozlohou rozptýlené zeleně roste i počet druhů ptáků v ní (Mason, 2001), i když nárůst počtu druhů zemědělské krajiny je s přibývající rozlohou mnohem mírnější oproti druhům lesním (Bellamy et al., 1996; McCollin, 1993). Vyšší izolovanost může snižovat celkový počet druhů, zejména však ovlivňuje druhovou skladbu společenstva – zatímco druhy zemědělské krajiny výrazně nelimituje, může snižovat počet lesních druhů, které se otevřeným biotopům více vyhýbají (Batáry et al., 2012; Bellamy et al., 1996; McCollin, 1993). Druhovou skladbu společenstva ovlivňuje i tvar ostrůvku – členitější ostrůvky mají totiž větší podíl okraje ku interiéru porostu a díky tomu se zde projevuje ve větší míře tzv. okrajový efekt, díky čemuž se zde vyskytuje více druhů zemědělské krajiny vyhledávajících tato ekotonální stanoviště (Bellamy et al., 1996).

Z tohoto stručného shrnutí vyplývají dva poznatky, které ovlivnily směr mého vlastního výzkumu rozptýlené zeleně, a tedy i obsahu následujících kapitol. 1) mezi zelení plošnou (velká rozloha s menším podílem okraje), liniovou (malá rozloha s větším podílem okraje) a bodovou (minimální rozloha zcela bez jádrového biotopu) budou co do diverzity a druhového složení avifauny – a tedy i co do podoby vhodného managementu – značné rozdíly. 2) Ptačí společenstvo rozptýlené zeleně tvoří téměř výhradně dvě skupiny druhů[1] – ptáci lesní a ptáci zemědělské krajiny – jejichž ekologické preference jsou však výrazně odlišné, v některých případech až protichůdné. Jak přesně se tyto poznatky do výzkumného designu promítly, je vysvětleno v následující kapitole.

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[1] Je na místě zde zmínit, že ekologické preference organismů obecně netvoří jasně odlišitelné kategorie, ale spíše souvislý gradient sahající od jednoho extrému po druhý. Vždy tu budou druhy s nároky kolem pomyslného středu tohoto gradientu, které nelze přiřadit do jedné nebo druhé skupiny bez výhrad. Konkrétně rozlišení na druhy lesní a druhy zemědělské krajiny vychází z jejich preference biotopu o určité míře sukcese, přičemž stanoviště může nabývat podob od samého jádra pralesa po holou planinu a rozptýlená zeleň představuje průnik „obou světů“ lesa a bezlesí právě někde uprostřed. Rozřazení ptáků rozptýlené zeleně na druhy lesní a zemědělské krajiny může proto zvláště u některých nevyhraněných druhů, jako je např. kos černý (*Turdus merula*) vyvolávat odborné debaty. Přesto jsme tuto klasifikaci použili, neboť zůstává srozumitelným a stále přijatelně zjednodušujícím způsobem, jak interpretovat vztahy mezi prostředím a druhovou diverzitou ptáků.

Vliv podoby biotopu rozptýlené zeleně *(článek 1)*

Zatímco vliv rozlohy, tvaru a izolovanosti rozptýlené zeleně na ptačí biodiverzitu je poměrně dobře popsaný, o významu vlastní podoby biotopu toho víme poměrně málo. Jednak vlastnostem biotopu nebyla věnována taková pozornost, jednak v případech, kdy byly zahrnuty do modelů, byly pravděpodobně často upozaděny vlivem rozlohy a izolovanosti, které mívají majoritní efekt (Bellamy et al., 1996; McCollin, 1993). Výjimku představuje výzkum především celkového počtu druhů ptáků v liniové rozptýlené zeleni (Hinsley & Bellamy, 2000; Montgomery et al., 2020; Walker et al., 2005). Ovšem jak je zmíněno v závěru předchozí kapitoly, mezi ptačím společenstvem různých typů rozptýlené zeleně lze očekávat významné rozdíly (Fuller et al., 2001; Šálek et al., 2022), takže pouhá extrapolace těchto znalostí na jiné typy zeleně by byla chybná. Proto jsme první část výzkumu věnovali tomu, jaké vlastnosti biotopu ovlivňují biodiverzitu ptáků v porostech plošné rozptýlené zeleně. Stejně tak z předchozí kapitoly vyplynulo, že u druhů lesních a druhů zemědělské krajiny lze očekávat odlišné preference, a proto jsme se zaměřili nejen na celkovou diverzitu, ale i na obě skupiny zvlášť.

Abychom odhalili význam vlastního biotopu rozptýlené zeleně pro druhovou diverzitu ptáků, studovali jsme malé izolované remízky kompaktního tvaru obklopené intenzivně obhospodařovanými zemědělskými plochami. V každém remízku jsme zjistili výšku porostu, zápoj keřového a stromového patra, celkový počet druhů dřevin, zastoupení nepůvodních dřevin a diverzitu mikrobiotopů. Zároveň jsme provedli ornitologický průzkum po celé ploše remízku, zjistili celkový počet druhů ptáků a na základě jejich početností vypočítali pomocí Shannon indexu i celkovou druhovou diverzitu. Na základě biotopových preferencí zjištěných Reifem et al. (2010) jsme následně druhy rozdělili do dvou kategorií na druhy lesní a druhy zemědělské krajiny a stanovili počet a diverzitu těchto druhů v každém remízku.

Význam a podobu vztahu mezi vlastnostmi remízků a počtem, resp. diverzitou druhů jsme modelovali pomocí zobecněných lineárních modelů, přičemž jsme otestovali všechny možné kombinace prediktorů (s omezeními viz článek 1). Výsledky pro počet druhů a druhovou diverzitu byl ve všech případech shodný, proto dále budu mluvit o druhové diverzitě i ve smyslu počtu druhů. Celková druhová diverzita ptáků i druhová diverzita pouze lesních ptáků rostly s výškou porostu a s počtem druhů dřevin v remízkách, naopak negativně byly ovlivněny dominancí nepůvodního trnovníku akátu v porostu. Druhová diverzita ptáků zemědělské krajiny závisela pouze na diverzitě mikrobiotopů v remízkách, a to pozitivně.

Naše výsledky ukazují, že vztah mezi podobou biotopu a biodiverzitou ptáků jsou principiálně shodné u liniové i plošné zeleně, neboť naše výsledky s výzkumem v liniové zeleni korespondují. Některé studie také našly více druhů ptáků v liniovém porostu s vyššími dřevinami (Green et al., 1994; Sauerbrei et al., 2017), s vyšší diverzitou dřevin (Green et al., 1994; MacDonald & Johnson, 1995) nebo obohacených o mikrobiotopy polních cest (Walker et al., 2005), příkopů (Arnold, 1983), travnatých okrajů apod. (Hinsley & Bellamy, 2000; Parish et al., 1995). Naše studie nově ukázala na nebezpečí nepůvodních druhů dřevin, pokud získají v porostu převahu. Jak ukázal Reif et al. (2016), jejich negativní dopad na celkovou biodiverzitu ptáků je pravděpodobně dán sníženou nabídkou potravy, přičemž zasaženy jsou především potravně specializovanější druhy.

Dalším velmi důležitým zjištěním je, že podoba biotopu rozptýlené zeleně ovlivňuje i složení ptačího společenstva, a že snaha o maximalizaci celkové diverzity, která je častou ochranářskou praxí i cílem zemědělských dotací, podporuje spíše běžně rozšířené lesní druhy. Této maximalizace počtu druhů lze dosáhnout prostřednictvím rozptýlené zeleně, která bude prakticky představovat fragmenty klimaxového lesního porostu s komplexní a heterogenní strukturou dřevin. Je otázkou k diskusi, do jaké míry by měla být při ochraně biodiverzity v rozptýlené zeleni věnována pozornost lesním druhům, neboť rozptýlená zeleň představuje pro tyto druhy spíše suboptimální biotop (Loman, 2003). Na druhou stranu i ostrůvky suboptimálního biotopu jsou v rámci metapopulační dynamiky důležité pro dlouhodobé přežití druhu (Foppen et al., 2000). Prioritou ochrany rozptýlené zeleně by však jednoznačně měly být zde se vyskytující druhy zemědělské krajiny, neboť jsou na tento biotop úzce vázané a spadá mezi ně řada ohrožených a specializovaných druhů. Jak ukázal náš výzkum, jejich diverzita (resp. počet druhů) neroste s heterogenitou v rámci „lesního“ biotopu, ale s heterogenitou neprodukčních biotopů obecně. V našem případě remízků se více těchto druhů nacházelo tam, kde se kromě vzrostlého dřevinného porostu nacházely i husté či řídké křoviny, paloučky, mokřady nebo otevřené plochy s obnaženou půdou. Chceme-li tedy podpořit biodiverzitu ptáků rozptýlené zeleně, je potřeba uvažovat ne v rámci jednoho prvku, ale v rámci celé krajiny a zajistit v ní pestrou nabídku různých ostrůvků zeleně s odlišnou podobou biotopu, včetně časnějších stadií sukcesního vývoje (Wuczynski, 2016).

Stručně shrnuto, podoba vlastního biotopu má neopomenutelný vliv na celkový počet druhů ptáků v rozptýlené zeleni, ale i na poměr zastoupení lesních druhů versus druhů zemědělské krajiny. U druhů zemědělské krajiny se nám podařilo vysvětlit o poznání méně variability než u lesních druhů a všech druhů dohromady, což naznačuje, že zde zůstává další významný prediktor, který jsme nepodchytili. Pravděpodobně jde o vlastnosti okolních biotopů a jejich heterogenitu v širším prostorovém měřítku (Bennett et al., 2006). V další studii jsme se tedy podívali na to, jaký význam má pro biodiverzitu ptáků heterogenita krajinné mozaiky.

Vliv heterogenity krajinné mozaiky s rozptýlenou zelení *(článek 2)*

Heterogenita krajiny velmi významně ovlivňuje biodiverzitu napříč taxony – ať už jde o rostliny (Waldhardt et al., 2004), bezobratlé (Reynolds et al., 2018) či obratlovce včetně ptáků (Atauri & De Lucio, 2001). Dosud se však nepodařilo uspokojivě rozklíčovat, jakou roli v tomto vztahu mají její jednotlivé složky (Reynolds et al., 2018). V zásadě jsou rozlišovány dvě základní složky krajinné heterogenity – kompozice a konfigurace biotopů. Kompozice vypovídá o tom, jaké typy různých biotopů se v krajině nachází a v jakém relativním zastoupení. Konfigurace pak vypovídá o tom, jak jsou tyto biotopy v krajině prostorově uspořádány (Bennett et al., 2006). Empirický výzkum ve většině případů nachází větší dopad na druhovou diverzitu u kompoziční heterogenity (Gámez-Virués et al., 2015). Nicméně je nezpochybnitelné, že její efekt závisí i na kontextu prostorového uspořádání (Bennett et al., 2006), a že jemnost zrna krajinné mozaiky (dalo by se také říci „míra rozdrobení“ biotopů v prostoru) je pro biodiverzitu také velmi důležitá (Prevedello et al., 2018).

Heterogenitu krajiny výrazně navyšuje právě rozptýlená zeleň. Co se ptáků týče, zvyšuje jejich početnosti i celkový počet druhů v zemědělské krajině disproporčně více než jiné biotopy, a je tedy klíčovým biotopem ovlivňujícím skrze vlastnosti krajinné mozaiky jejich druhovou diverzitu (Culmsee et al., 2021; Fahrig et al., 2011; Šálek et al., 2022). Proto jsme se v této práci zaměřili na to, jak obě složky krajinné heterogenity ovlivňují počet druhů a počet ohrožených druhů ptáků v krajině s rozptýlenou zelení.

Jako vysvětlující proměnné jsme měřili dva faktory krajinné mozaiky: diversitu biotopů vyjádřenou Shannon indexem (vypovídající o kompoziční heterogenitě) a počet ostrůvků rozptýlené zeleně (vypovídající o konfigurační heterogenitě; Bennett et al., 2006). Vysvětlovanými proměnnými byl celkový počet všech druhů ptáků zjištěný na výzkumných plochách a počet ohrožených druhů ptáků (Act No.114/1992 Coll. on Nature Conservation and Landscape Protection, 1992, https://www.zakonyprolidi.cz/cs/1992-114; Šťastný & Bejček, 2003).

Pro obě vysvětlované proměnné jsme sestavili čtyři zobecněné lineární modely uvažující v různé kombinaci vliv diverzity biotopů a počtu ostrůvků: jejich lineární vztahy, vzájemnou interakci a případné nelinearity reprezentované kvadratickými členy proměnných. Z těchto čtyř jsme pak v obou případech vybrali nejlepší model na základě hodnoty Akaikeho informačního kritéria (AIC). Zjistili jsme, že na celkový počet druhů ptáků měla průkazný vliv pouze diverzita biotopů – zprvu pozitivní, ale po překročení určitého prahu diverzity naopak negativní. Počet ohrožených druhů ptáků byl vyšší na studijních plochách s vyšším počtem ostrůvků rozptýlené zeleně. Tento vztah byl lineární, nicméně při logaritmizovaném počtu ostrůvků.

Stejně nelineární pozitivní vliv počtu ostrůvků zeleně v podobě solitérních stromů na počet druhů ptáků odhalili i Fischer et al. 2010 nebo Carrasco et al. 2018. Vyšší počet ostrůvků rozptýlené zeleně (za předpokladu konstantní celkové rozlohy) znamená pro ptáky menší rozlohu ostrůvků, menší průměrnou vzdálenost mezi ostrůvky a větší podíl okrajového biotopu zeleně (Bennett et al., 2006). Takové prostředí vyhovuje k hnízdění mnoha ptákům lesostepní mozaiky, z nichž pochází i většina námi zaznamenaných ohrožených druhů. Zároveň však může v krajině podpořit i ohrožené druhy lesní, a to tím, že usnadňuje jejich pohyb otevřenou krajinou mezi lesními porosty. Náš výzkum ze své empirické podstaty sice neumožňoval zajistit konstantní celkovou rozlohu rozptýlené zeleně, takže počet ostrůvků do určité míry souvisel i s celkovým množstvím biotopu, to je však nedokonalostí většiny studií popisujících strukturu krajiny a je potřeba s ní počítat (Bennett et al., 2006).

Naše výsledky ukazují, že pokud chceme v zemědělské krajině podpořit ohrožené druhy ptáků, není nejlepším řešením založit co největší kompaktní porost mimoprodukční dřevinné zeleně (viz vliv rozlohy výše), ale naopak co nejvíce malých ostrůvků včetně solitérních dřevin rozptýlených v krajině. V kontextu jiného výzkumu může být vhodné zakládat tzv. souostroví, tedy vždy několik ostrůvků ve vzájemné blízkosti (Loman & Von Schantz, 1991). Soudě podle námi modelovaného tvaru vztahu pak bude mít největší přínos založit rozptýlenou zeleň tam, kde je jí zatím naprosté minimum.

Na druhou stranu, jak ukázal negativní trend počtu druhů u příliš vysokých hodnot biotopové diverzity, tento princip nelze použít u jiných typů biotopů jako jsou lesy, louky, mokřady nebo vodní plochy. I když i u těchto biotopů je vysoká heterogenita také obecně žádoucí (Tews et al., 2004), při diverzifikaci nad určitou mez se zřejmě začne projevovat negativní efekt limitované rozlohy biotopů a s tím související limitované možnosti disperze (the “area-heterogeneity trade-off”; Allouche et al., 2012). Jinými slovy biotopové ostrůvky jsou pro některé druhy ptáků už příliš malé, než aby pro ně byly využitelné. Je na místě upozornit, že samotná rozptýlená zeleň z pohledu druhů orientovaných na zcela otevřené biotopy (např. louky, stepi, vřesoviště apod.) způsobuje fragmentaci jejich prostředí (Besnard & Secondi, 2014; Ellison et al., 2013). Krajinná mozaika by tedy měla vypadat tak, že určitý prostor je dán rozptýlené zeleni, a to (kromě liniové vegetace) ve formě vyššího počtu malých ostrůvků porostu, a zároveň se zde nachází pestrá škála jiných biotopů, ovšem v dostatečně velkých nefragmentovaných plochách. Co přesně znamená dostatečně velká nefragmentovaná plocha, nechť posoudí výzkum zaměřený na tyto typy biotopů.

Pro ochranu biodiverzity ptáků je tedy důležitá jemnozrnnost mozaiky rozptýlené zeleně v kombinaci s přiměřeně vysokou mírou celkové biotopové diverzity v krajině. Další kapitola se zaměřuje na otázku, zda má na tyto vlastnosti krajiny vliv charakter disturbančního režimu.

Krajinná mozaika formovaná armádním disturbančním režimem *(článek 2)*

V poslední době se ukazuje, že vojenské výcvikové prostory (nejen) střední Evropy ukrývají vzácné otevřené biotopy typu suchých nebo naopak podmáčených travin, písčin apod., které v kombinaci s rozptýlenou zelení vytváří velmi pestrou krajinu (Warren et al., 2007). Tyto biotopy zde přetrvávají a prosperují právě díky vojákům, kteří svými aktivitami narušují půdu a vegetaci neboli působí tzv. disturbance (Aunins & Avotins, 2018).

Krajina vojenských prostorů je formována disturbancemi, které jsou vedlejším produktem armádních aktivit a které se od procesů v běžné krajině diametrálně liší. Vznikají náhodně v prostoru i čase a mohou nabývat široké škály intenzity od sešlapu půdy přes průjezd tanku až po výbuch granátu nebo neřízený požár. Přestože lze očekávat, že takové zásahy budou organismy ovlivňovat negativně a skutečně se tak i děje (Hirst et al., 2005; Lindenmayer et al., 2016; Valente et al., 2020), vojenské prostory jsou doslova oázami biodiverzity všech možných taxonů včetně ptáků, přičemž kromě výrazně vyšší druhové bohatosti vykazují i nezvykle vysoký podíl ohrožených druhů (Bušek & Reif, 2017; Harabiš & Dolný, 2018; Warren & Büttner, 2008). Podle teorie Warrena et al. (2007) je právě heterogenita tohoto disturbančního režimu a z něj plynoucí heterogenita krajiny klíčem k tak enormně vysoké biodiverzitě. Ačkoliv ochranářská praxe v našem prostředí podle mé zkušenosti z této premisy běžně vychází, není mi znám výzkum, který by se ji pokusil potvrdit či vyvrátit. Proto jsme v této části disertační práce zjišťovali, zda se heterogenita krajinné mozaiky liší mezi vojenským prostorem a běžnou zemědělskou krajinou.

Pro tento účel jsme zkoumali krajinu s rozptýlenou zelení v největším vojenském prostoru České republiky, Vojenského újezdu Hradiště (Skokanová et al., 2017), a v sousední oblasti běžné zemědělské krajiny. V obou oblastech jsme sledovali kompozici a konfiguraci krajinné mozaiky s rozptýlenou zelení prostřednictvím počtu ostrůvků zeleně a celkové biotopové diverzity, stejně jako v předchozí kapitole. Tentokrát však byly tyto vlastnosti vysvětlovanými proměnnými v našich modelech, zatímco na pozici vysvětlující proměnné figuroval typ krajiny.

Analýza pomocí zobecněných lineárních modelů ukázala, že v krajině uvnitř vojenského prostoru se nachází průkazně více ostrůvků rozptýlené zeleně než v běžné zemědělské krajině. To je zcela jistě dáno odlišností disturbančního režimu, který rozptýlenou zeleň formuje, neboť v zemědělské krajině je rozsah rozptýlené zeleně dán především rozparcelováním půdy a rozsahem zemědělské produkce, zatímco ve vojenském prostoru disturbance působí více nahodile, jako druhotný efekt bez krajinotvorného záměru. Zatímco v zemědělské krajině tedy najdeme hlavně kontinuální doprovodnou liniovou zeleň podél cest, vodních toků či okrajů polí nebo velké, jasně ohraničené remízky, ve vojenském prostoru najdeme rozptýlenou zeleň nahodile „rozdrobenou“, v různých stadiích narušení a opětovného zarůstání, často na poměrně rozsáhlých plochách. Výsledná mozaika rozptýlené zeleně je tak mnohem jemnějšího zrna. Podle našich výsledků z předchozí kapitoly by ve vojenském prostoru mělo být díky tomu i více ohrožených druhů ptáků – a skutečně, Bušek a Reif (2017), kteří na stejných studijních plochách zkoumali avifaunu, vyšší druhovou bohatost ohrožených druhů ptáků ve vojenském prostoru potvrdili.

Oproti tomu v biotopové diverzitě se krajiny uvnitř a vně vojenského prostoru nelišily. Zřejmě vojenské disturbance nevytváří více druhů biotopů než lidská činnost v zemědělské krajině, alespoň ne na prostorové škále relevantní pro ptáky. Pro úplnost dodejme, že kromě námi zkoumaných složek heterogenity tu bude ještě další významný faktor, který promlouvá do počtu druhů ptáků uvnitř a vně vojenského prostoru, avšak který jsme nepodchytili, a to vlastní podoba – tedy typ a kvalita – biotopů, které tvořily krajinnou mozaiku. Typ a kvalita biotopů se mezi vojenským prostorem a zemědělskou krajinou jistě také významně liší a je na budoucím výzkumu tyto odlišnosti popsat.

Na základě výsledků naší studie tedy můžeme shrnout, že krajina s rozptýlenou zelení formovaná armádními disturbancemi se liší oproti běžné zemědělské krajině vyšší heterogenitou, konkrétně jemnějším zrnem mozaiky rozptýlené zeleně. Tato odlišnost zřejmě přispívá k vyššímu podílu ohrožených druhů ptáků ve vojenských prostorech. Protože mnoho vojenských prostorů střední Evropy bylo od 90. let minulého století až do současnosti postupně opuštěno, dále jsme se zaměřili na to, jaké změny v krajině a její biodiversitě ptáků probíhají po vymizení armádního disturbančního režimu.

Změny krajinné mozaiky po vymizení armádního disturbančního režimu *(článek 3)*

Od 90. let minulého století v souvislosti s koncem studené války byly v Evropě armádou opuštěny stovky až tisíce výcvikových vojenských prostorů, přičemž přesné číslo není veřejně známo. Jde často o rozsáhlá území o stovkách někdy až tisících hektarů. Velmi hrubým odhadem jde o 1,5 milionu hektarů půdy, přitom největší část se nachází právě ve střední a východní Evropě (Ellwanger & Reiter, 2019). Jak jsme ukázali v předchozí kapitole, biodiverzita ptáků, především ohrožených druhů, je úzce spjata s armádními disturbancemi a s heterogenní krajinnou mozaikou, která je těmito disturbancemi formována. Co tedy znamená ukončení armádní činnosti pro krajinu, resp. konkrétně rozptýlenou zeleň a její biodiverzitu ptáků? Tato otázka zůstávala až doposud nezodpovězena, neboť dosavadní výzkum (nijak rozsáhlý) věnoval pozornost biodiverzitě téměř výhradně v prostorech, které se po opuštění dostaly mezi chráněná území (Ellwanger & Reiter, 2019; Hagen et al., 2022; Jentsch et al., 2009). Proto jsme se v následující části práce zaměřili na vyhodnocení dlouhodobých změn v biotopovém složení krajiny a v početnosti ptáků u třiceti bývalých vojenských prostorů, představujících vypovídající vzorek různorodého po-armádního vývoje a využití.

Náš studijní soubor představoval 30 opuštěných vojenských výcvikových prostorů s převážně otevřenou krajinou rozmístěných po celé České republice. V těchto prostorech jsme spolu s našimi předchůdci (Reif et al., 2013) uskutečnili jednak monitoring biotopového složení, jednak detailní monitoring ptáků, při kterém jsme zaznamenali každého detekovaného jedince a jeho přesnou polohu, a to vše v roce 2009 a následně znovu v období 2020–21. Pomocí RDA analýzy jsme se podívali na to, 1) jak se změnilo zastoupení jednotlivých typů biotopů ve vojenských prostorech, 2) jak se změnila početnost druhů ptáků, 3) jak změna početností druhů souvisí se změnou biotopů. Ve druhém kroku analýzy jsme se pak pomocí zobecněného lineárního modelu podívali na to, zda a do jaké míry lze změnu početností druhů vysvětlit jejich ekologickými vlastnostmi, konkrétně biotopovými preferencemi na sukcesním gradientu od lesa po traviny, mírou biotopové specializace a stupněm ohrožení.

Během jedné dekády v opuštěných vojenských prostorech s převážně otevřeným charakterem krajiny ubylo travin a řídkých křovin, naopak se rozšířily husté křoviny, les, zástavba a plochy obnažené půdy. Stejně tak změna početností druhů ptáků byla mezi oběma obdobími významná. Mezi druhy s největším úbytkem v početnosti patřily bramborníček hnědý

(*Saxicola rubetra*), cvrčilka zelená (*Locustella naevia*) nebo zvonek zelený. Naopak největší nárůst jsme zaznamenali u skřivana lesního (*Lullula arborea*), dlaska tlustozobého nebo červenky obecné (*Erithacus rubecula*). Druhý krok analýzy odhalil, že změny početnosti druhů ovlivňuje jejich biotopová preference a roli hraje i jejich stupeň ochrany. Obecně lze konstatovat, že oslabily populace druhů využívající otevřené biotopy, tento trend však zmírňuje pozitivní efekt stupně ohrožení. Do jaké míry byly druhy úzce specializovány na preferovaný biotop, nehrálo významnou roli.

Z výsledků vyplývá, že mozaika rozptýlené zeleně a otevřených biotopů dlouhá desetiletí udržovaná armádními disturbancemi z naší krajiny pomalu, ale jistě mizí. Někde ji nahrazují již zastavěné plochy nebo navážky odpadového materiálu, staveniště a jiné urbánní projekty zachycené v našich datech jako místa s obnaženou půdou. Jinde se vlivem absence disturbancí mění v zapojené křovinné a lesní porosty. Tento neblahý trend zmírňují ta území, na kterých se ochrana přírody aktivně zasazuje o zachování původní podoby biotopů. Naše výsledky také naznačují, že tato ochranářská péče úspěšně podporuje mnohé druhy ptáků s vysokou mírou ohrožení, které figurují v ochranářských strategiích jako cílové druhy – např. skřivan lesní, krutihlav obecný (*Jynx torquilla*), strnad luční. Neplatí to však pro všechny ohrožené druhy – viz velký úbytek bramborníčka hnědého a bramborníčka černohlavého (*Saxicola rubetra* a *S. rubicola*), kteří oproti výše jmenovaným druhům vyžadují ještě více otevřená stanoviště. Zároveň je patrné, že daná péče možná udržuje populace konkrétních cílových druhů, nikoliv však širšího spektra druhů zemědělské krajiny – viz silný pokles zvonka zeleného, konopky obecné (*Linaria cannabina*) nebo zvonohlíka zahradního (*Serinus serinus*). Stávající rozsah a způsob ochrany přírody tedy nestačí k tomu, aby udržel biodiverzitu ptáků v celostátním měřítku v takové míře, v jaké se se nacházela ve vojenských prostorech krátce po opuštění.

Abychom z nebývalé biodiverzity ptáků, tohoto odkazu opuštěných vojenských prostorů, zachovali co největší podíl, je potřeba zefektivnit management na chráněných místech a zároveň hledat možnosti, jak sladit podporu biodiversity s jinými způsoby využití. Následující poslední kapitola je proto věnována otázce, jak biodiverzitu ptáků v krajině s rozptýlenou zelení ovlivňují různé typy managementu od zemědělství přes zájmové aktivity po ochranu přírody.

Vliv různých typů managementu v krajině s rozptýlenou zelení *(článek 4)*

Ještě začátkem nového tisíciletí byla většina opuštěných vojenských prostorů ponechána bez využití přirozenému vývoji přírody – což znamená v současných podmínkách střední Evropy, potlačujících přírodní disturbance, pozvolné zarůstání směřující ke klimaxovému stavu souvislého lesa (Bengtsson et al., 2000). V současnosti je (alespoň podle našich dat z České republiky) takto přirozenému vývoji vegetace ponechána jen menší část bývalých vojenských prostorů, zatímco na většině jsou ustanovena chráněná území různého stupně ochrany (Dvořáková et al., 2021; Ellwanger & Reiter, 2019) nebo různý komerční způsob využití (ve smyslu za účelem generace finančního příjmu). Nejčastěji jde o zemědělskou produkci, energetickou produkci, zástavbu nebo volnočasové aktivity jako offroad, paintball atd (Dvořáková et al., 2021; Dvořáková & Reif, 2023).

Úkolem ochrany přírody v opuštěných vojenských prostorech je zachovat přírodní bohatství otevřených biotopů a rozptýlené zeleně tak, jak je po dlouhá desetiletí formoval armádní disturbanční režim – nebo v tomto případě spíše disturbanční chaos. Je to nelehká výzva, neboť to znamená chránit a uchovat něco, co musí být ze své podstaty proměnlivé (Jentsch et al., 2009). Navíc často na extrémně rozsáhlých plochách stovek i tisíců hektarů, přitom s omezeným finančním rozpočtem (Ellwanger & Reiter, 2019). Ochrana přírody využívá k tomuto účelu různých nástrojů. Mezi klasické, avšak poměrně nákladné, patří výřez dřevin, seč a oplůtková pastva (tedy pastva typicky menších kopytníků jako jsou ovce a kozy v ohraničeném prostoru a po omezenou dobu) (Marhoul et al., 2024). Tyto způsoby péče mají v evropském prostředí dlouholetou tradici v ochraně otevřených biotopů a rozptýlené zeleně simulujíce tradiční zemědělské postupy, byly mnohokrát vyhodnocovány v rámci ochranářských projektů i experimentálních výzkumů (Dunn et al., 2016; Staley et al., 2012; Westbury et al., 2017) avšak ne přímo ve vojenských prostorech. Panuje obava, že především seč a oplůtková pastva nejsou pro ochranu biodiverzity opuštěných vojenských prostorů vhodné, neboť i přes veškerou snahu směřují více či méně k nežádoucí unifikaci ploch (Marhoul et al., 2024). Alternativní možností je jednak rewilding neboli celoroční pastva odolných velkých kopytníků jako jsou exmoorští koně, zubři a pakoně v přírodě blízkých podmínkách (Konvička et al., 2021), jednak pojezdy těžkou technikou (Dvořáková et al., 2022b), offroad vozidly (Dvořáková et al., 2022a) a podobné metody strhávání drnu (Řehounková et al., 2021), které lze často zajistit prostřednictvím zájmových a sportovních spolků. Tyto způsoby péče jsou z finančního hlediska lépe dlouhodobě udržitelné a velká rozloha bývalých vojenských prostorů pro ně není překážkou, spíše výhodou. Zároveň poskytují disturbance nahodilejší v čase a prostoru, díky čemuž by měly zajišťovat vyšší heterogenitu biotopů (Marhoul et al., 2024). Avšak i když se právě v opuštěných vojenských prostorech staly rychle téměř ochranářskou „módou", o účincích těchto způsobů péče zatím výzkum přinesl jen málo informací a ty se omezují pouze na ochranu rostlin a hmyzu (Konvička et al., 2021; Riesch et al., 2020; Salek et al., 2019). Dopady jiného způsobu využití, než ochranářského managementu nebyly, pokud je nám známo, zkoumány vůbec.

Proto jsme následující a zároveň poslední část výzkumu věnovali komplexnímu vyhodnocení dopadu různých typů managementu na krajinu s rozptýlenou zelení v opuštěných vojenských prostorech a její biodiverzitu ptáků. Díky spolupráci s dalšími výzkumnými týmy jsme měli možnost výsledky pro ptáky porovnat s jinými taxonomickými skupinami: cévnatými rostlinami, rovnokřídlými a motýli, abychom výsledky mohli interpretovat v širším kontextu biodiverzity napříč taxony a zhodnotit, zda ptáci při vyhodnocení managementu fungují pro celkovou biodiverzitu jako spolehlivý indikátor.

Výzkum jsme uskutečnili na 42 opuštěných vojenských výcvikových prostorech v České republice (soubor 30 lokalit studovaných v předchozí kapitole obohacený o dalších 12 odpovídajícího charakteru). Pro tato území jsme zjistili použití různých typů managementu od roku 2009 po rok 2021, s rozlišením následujících kategorií: výřez dřevin, zemědělská seč, ochranářská seč, zemědělská pastva, ochranářská pastva (včetně rewildingu) a pojezdy motorovými vozidly. Zároveň jsme na lokalitách provedli sčítání ptáků v období 2020–21 a porovnali ho s výsledky sčítání v roce 2009. Zjištěné druhy jsme pro obě období rozdělili do šesti dílčích ekologických skupin podle jejich biotopových preferencí: druhy otevřených vlhčích biotopů, polootevřených vlhčích biotopů, lesních vlhčích biotopů, otevřených sušších biotopů, polootevřených sušších a lesních sušších biotopů. Jako vysvětlovanou proměnnou jsme použili změny početnosti v rámci těchto skupin.

Analýza ukázala, že na ptáky polootevřených biotopů, tedy druhy vázané úzce na rozptýlenou zeleň, měl příznivý vliv jediný management, a to ochranářská pastva. Zároveň na ni reagovali příznivě i ptáci vlhčích lesních biotopů, kteří také tvoří část biodiverzity rozptýlené zeleně, i když pro ně nepředstavuje optimální biotop k hnízdění (Loman, 2003). Pokud se podíváme na odpovědi ostatních taxonů, na ochranářskou pastvu reagovaly už jen dvě skupiny rovnokřídlých – jedna pozitivně, druhá negativně, což z tohoto managementu činí, v porovnání s jinými, velmi vhodný a široce aplikovatelný způsob péče.

Vhodně dimenzovaná pastva kopytníků obecně vytváří pestrou mozaiku mikrobiotopů, kterou ptáci rozptýlené zeleně potřebují k úspěšnému hnízdění a sběru/lovu potravy: silně sešlapávané, často bahnité plochy kolem bran a napajedel, na krátko spasený trávník v kombinaci s vysokou vegetací a stařinou v místech, kterým se zvířata vyhýbají, řídké křoviny limitované okusem i husté vysoké porosty dřevin (Ceresa et al., 2012; Morelli et al., 2016; Tälle et al., 2016). Navíc má přítomnost zvířat i další pozitiva, pro ptáky je to zejména produkce trusu, který znamená rozšířenou potravní nabídku hmyzu (Tälle et al., 2016), důležitou zejména pro některé druhy jako je např. dudek chocholatý (*Upupa epops*; Hudec & Šťastný, 2005). Oba popsané přínosy by teoreticky měly být ještě výraznější u rewildingu v porovnání s klasickou oplůtkovou pastvou koz a ovcí (Perino et al., 2019; Villada-Bedoya et al., 2019), rozsah statistického souboru nám však neumožnil oba typy ochranářské pastvy odlišit. Na jejich srovnání by se měl proto zaměřit budoucí výzkum.

Pro ptáky vlhčích lesů byla kromě ochranářské pastvy přínosná i zemědělská seč. Zřejmě jsou pro ně oba tyto managementy přínosné z hlediska pestřejší nabídky a snadnějšího hledání potravy, neboť tyto druhy sice hnízdí v lese, potravu však mohou sbírat i na otevřených plochách (Hudec & Šťastný, 2005; Šťastný & Hudec, 2011). Jde o pozitivní zprávu, že i zemědělské využití může být cestou (byť ne optimální), jak udržovat rozptýlenou zeleň, a zároveň alespoň částečně podpořit ptáky v krajině. Na druhou stranu měl však tento způsob péče o otevřené plochy negativní dopad na většinu rovnokřídlého hmyzu.

Naše výsledky dále ukázaly, že k potlačení postupného zarůstání a zániku rozptýlené zeleně lze využít i výřez dřevin. Ten ptákům z dlouhodobého hlediska nevadí, stejně tak ostatním taxonům, na některé rostliny a rovnokřídlý hmyz měl dokonce pozitivní dopad. Naopak ochranářská seč a pojezdy motorovými vozidly vyšly z našeho multitaxonového vyhodnocení nejhůře, neboť měly pouze negativní dopad (seč na rovnokřídlý hmyz a rostliny, offroad na motýly), což je zejména u ochranářské seče alarmující. Nakonec jen poznamenejme, že dalším typem managementu, který by bylo jistě zajímavé i potřebné do srovnání zařadit, je řízené vypalování. To však bylo naší legislativou povoleno teprve nedávno, a proto jsme neměli ke srovnání dostatek dat.

Závěr

Rozptýlená zeleň představuje refugium biodiverzity v současné zemědělské krajině Evropy. V souladu s tím, jak různorodých může nabývat podob, hostí široké spektrum druhů od lesních po stepní, přičemž mnoho z těchto druhů je na rozptýlenou zeleň úzce vázáno. Odstraňování a zarůstání rozptýlené zeleně, které se dělo a stále děje s postupující intenzifikací zemědělství, je jedním z významných faktorů, které přispěly ke strmému poklesu biodiverzity v zemědělské krajině. Na druhou stranu rozptýlená zeleň mizí i vlivem sukcesního vývoje, kdy se původně řídké porosty zapojují a postupně mění v souvislý les. V zájmu ochrany biodiverzity je potřeba najít efektivní způsob obnovy rozptýlené zeleně v krajině a zároveň dlouhodobě udržitelný způsob péče o ni. K tomu přispívá tato disertační práce. Zkoumá vliv podoby vlastního biotopu rozptýlené zeleně, vliv podoby krajinné mozaiky a vliv různých způsobů managementu na počet druhů, druhovou diverzitu a na druhové složení společenstva ptáků. Pracuje s ptáky jako indikátorem celkové biodiverzity, avšak nabízí srovnání i s jinými, ekologicky odlišnými taxony.

Z dosavadního výzkumu je zřejmé, že celkový počet druhů ptáků i podoba společenstva v jednotlivých ostrůvcích rozptýlené zeleně jsou z velké části určovány jejich rozlohou a izolovaností, z menší části i jejich tvarem. Náš výzkum ukázal, že významný vliv má také podoba vlastního biotopu (článek 1). Skrze vzrostlejší porosty, vyšší diverzitu dřevin a zabránění dominance invazních druhů dřevin lze podpořit celkový počet druhů a diverzitu ptáků stejně jako počet a diverzitu druhů lesních. Ptáky zemědělské krajiny lze podpořit zajištěním vysoké diverzity (mikro)biotopů, zejména časnějších sukcesních stadií jako jsou plochy holé půdy, travin, mokřadů nebo řídkých křovin. Pokud opustíme měřítko dílčího krajinného prvku a zaměříme se na krajinu s rozptýlenou zelení jako celek, více druhů ptáků obecně se bude nacházet v krajině s vysokou diverzitou biotopů (ovšem při zachování dostatečné rozlohy biotopů, která bude pro ptáky stále využitelná). Pro podporu ohrožených druhů ptáků je však klíčová jiná složka krajinné heterogenity, a to vysoký počet ostrůvků (jinými slovy jemnozrnnost) rozptýlené zeleně v krajině. Při porovnání vlastností zemědělské krajiny a vojenského výcvikového prostoru jsme zjistili, že otevřená krajina formovaná armádním disturbančním režimem nevykazuje v měřítku adekvátním pro ptáky vyšší biotopovou diverzitu, má však jemnozrnnější mozaiku rozptýlené zeleně (článek 2). Tento krajinný rys zřejmě přispívá k vyššímu podílu ohrožených druhů ptáků ve vojenských prostorech. Celkově vyšší počet druhů ve vojenských prostorech však se zkoumanými vlastnostmi krajiny nesouvisel a pravděpodobně je zapříčiněn kvalitativními vlastnostmi biotopů, jako např. jejich neprodukční povahou. U dlouhodobě opuštěných vojenských prostorů, po vymizení specifického disturbančního režimu, se biotopová skladba posouvá jednak k většímu podílu urbánních stanovišť, jednak k většímu podílu lesů a hustých křovin, na úkor otevřených biotopů a „jemnozrnné“ rozptýlené zeleně (článek 3). Adekvátně tomu dochází k posunu druhové skladby ptačího společenstva od druhů otevřených biotopů k druhům lesním. Vyhodnocení dopadu různých typů disturbančních managementů, které se nabízejí po ukončení armádních disturbancí, ukázalo, že biodiverzitu ptáků rozptýlené zeleně lze nejlépe podpořit ochranářskou pastvou (článek 4). Porovnání přínosu různých přístupů v rámci ochranářské pastvy (zejména oplůtkové pastvy a rewildingu) by mohlo být náplní dalšího výzkumu. K udržení rozptýleného charakteru zeleně může být využita i zemědělská seč nebo vyřezávání dřevin. Vyhodnocení zároveň ukázalo na nevhodnost některých ochranářských nástrojů, zejména klasické seče, napříč taxony. Toto zjištění volá po výzkumu ve spolupráci s ochranáři, který by navrhl a implementoval účinnější podobu ochranářské praxe.

Tato práce vyzdvihuje mimo jiné fakt, že ochrana druhové diverzity rozptýlené zeleně se bude vždy odehrávat formou „něco za něco“. Na jedné straně tu máme lesní druhy ptáků, pro které rozptýlená zeleň nepředstavuje optimální hnízdní biotop, a i přesto je pro ně biotopem důležitým, umožňujícím mimo jiné disperzi krajinou a potřebnou metapopulační dynamiku. Na druhé straně máme druhy, které jsou na rozptýlenou zeleň v období hnízdění úzce vázány – ať už je označujeme jako druhy zemědělské krajiny, polootevřených biotopů, lesostepní mozaiky či jiným termínem. Zatímco nejvyšší celkové druhové bohatosti ptáků a zároveň i lesních druhů dosáhneme rozptýlenou zelení podobající se fragmentům vzrostlého lesního porostu, druhy úzce vázané na rozptýlenou zeleň podpoříme časnějšími sukcesními stadii porostů v kombinaci s otevřenými biotopy. Stejně tak porovnání dopadu různých typů managementu na ptáky, motýly, rovnokřídlý hmyz a rostliny ukázalo až protichůdné preference mezi taxony. Ptáci sice do určité míry mohou fungovat jako indikátory celkové biodiverzity, jejich preference jsou však méně vyhraněné a projevují se na mnohem větší, a tedy i hrubší prostorové škále než např. preference rostlin nebo hmyzu. Ve výsledku tedy není až tak překvapivé ani naše zjištění, že managementy prospívající ptákům do velké míry naopak potlačují biodiverzitu rovnokřídlého hmyzu. Východiskem pro aplikovanou ochranu přírody je s těmito dilematy vědomě počítat a dělat zásahy (především ty velkoplošné) se znalostí místního společenstva nejen ptáků, ale i dalších taxonů a plánovat je na míru dané situaci a místním prioritním druhům.

Souhrnem lze říci, že podoba biotopu, krajinné mozaiky i managementu rozptýlené zeleně má významný vliv na biodiverzitu ptáků, přičemž nelze doporučit jediný optimální způsob zakládání a péče, neboť preference různých druhů jsou odlišné. Klíčem k ochraně biodiverzity je uvažovat ne v rámci jednoho prvku zeleně, ale v rámci celé krajiny a zajistit v ní především heterogenitu na různých prostorových škálách. Je tedy třeba zajistit v krajině vysoký počet ostrůvků různé velikosti, tvaru i různé míry vzájemné izolovanosti, kombinující různou skladbu biotopů a mikrobiotopů různého stupně sukcesního vývoje. Zároveň je nutné usilovat o vysokou diverzitu původních dřevin, a naopak potírat invazní druhy, které by jinak vytvářely homogenní jednodruhové porosty. Je třeba zajistit otevřené plochy s rozptýlenou zelení v jemnozrnné mozaice, na druhou stranu ale ponechat v krajině dostatek místa i pro jiné biotopy a pamatovat na to, že pro některé druhy otevřených biotopů může rozptýlená zeleň představovat naopak nežádoucí fragmentaci. Věříme, že toto doporučení je platné nejen pro ptáky, ale i pro mnohé další složky biodiverzity střední Evropy.

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Příloha: články

Článek 1

Dvořáková, L., Kuczyński, L., Rivas-Salvador, J., & Reif, J. (2022). Habitat characteristics supporting bird species richness in mid-field woodlots. *Frontiers in Environmental Science*, *10*, 816255. https://doi.org/10.3389/FENVS.2022.816255

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Habitat Characteristics Supporting Bird Species Richness in Mid-Field Woodlots

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Farmland biodiversity has undergone drastic declines due to agricultural intensification during the last decades. To prevent further biodiversity loss, the maintenance and restoration of non-productive habitats is essential. Woodlots, small patches of woody vegetation in agricultural landscapes, are one such habitat that are currently subsidized by the European Union's Common Agricultural Policy (EU's CAP). For effective implementation, however, it is necessary to assess what habitat characteristics are the most beneficial for biodiversity. Our study performs such an assessment using birds as model organisms. Specifically, we related characteristics of various woodlots to (I) the species richness of all birds, and (II) the species richness of both forest and farmland birds–groups with different ecological requirements. For this purpose, we counted birds (27 farmland and 26 forest species) and measured habitat characteristics (describing vegetation structure, diversity and nativeness) and spatial characteristics (area, shape and isolation) in 82 mid-field woodlots (0.76–1.25 ha, average 0.46 ha) in the Czech Republic (Central Europe). After accounting for the effects of spatial characteristics, overall bird species richness increased with vegetation height and woody plant species richness. In addition, richness showed a non-linear decrease with the cover of an invasive tree, the Black Locust *Robinia pseudoaccacia*. Interestingly, forest bird species richness was related to the same habitat characteristics as the overall bird species richness. By contrast, farmland bird species richness was positively related to the diversity of woodlot microhabitats, which reflects mainly enrichment by non-forest sites such as grassland or sparse shrubs. Our results indicate that the ecological performance of habitat characteristics (and not only the woodlot area) is important for the restoration of bird diversity in woodlots, and as such should be taken into consideration by the EU's CAP subsidy system. Moreover, if woodlot management aims to maximize the overall bird diversity—a common practice in biodiversity conservation—our results show that current practices may favor widespread forest bird species, but not the farmland birds that are more threatened in Europe. To manage the woodlot habitat for farmland birds, we suggest that microhabitat heterogeneity should be maximized.

Keywords: farmland birds, greening measures, habitat quality, non-productive habitat, non-native plants, species richness, woodlot

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INTRODUCTION

During the last decades, farmland has undergone drastic changes due to ongoing agricultural intensification (Foley et al., 2011). These changes have caused a rapid decline of farmland biodiversity and threatened the ecosystem services important for global food production (such as pollination or soil functioning) over the long-term (Stoate et al., 2001, 2009). This is particularly the case in Europe, where agricultural landscapes currently account for about half of the area of the continent (Food and Agriculture Organization of the United Nations, 2014). Moreover, a large proportion of European biodiversity is associated with farmland habitat due a long co-evolution of biota and agriculture (Batáry et al., 2015). Thus, preventing further losses of biodiversity and sustaining the ecosystem services of agricultural landscapes has become one of the most urgent challenges the European Union (EU) currently faces (Stoate et al., 2009). In order to address this issue, the EU's Common Agricultural Policy (CAP) has incorporated various environmental measures, but their effectiveness varies considerably (Batáry et al., 2015; Gamero et al., 2017). Of the various measures in place, the restoration of non-productive habitats was found to be the most promising in promoting biodiversity and ecosystem services (Batáry et al., 2015; European Commission, 2017). Nevertheless, their conservation potential remains still largely untapped, as the system is designed to subsidize non-productive habitats according to just their area, without taking their other characteristics or future management into account (European Commission, 2017).

This is also the case of woodlots, small non-productive patches of woody vegetation, which are subsidized within both pillars of the CAP to some extent ("tree clusters" up to an area of 0.3 ha in the case of Ecological Focus Areas) (Pe'er et al., 2017). However, even though woodlots could serve as key refuges for farmland biodiversity, the impacts of their ecological characteristics on biodiversity remain largely unknown. According to ecological theory, habitat quality is an important aspect for habitat selection decisions of particular species (Guisan and Thuiller, 2005), suggesting that this aspect of woodlots is an overlooked but crucial predictor of their ecological performance.

To fill this critical knowledge gap, here we focused on investigating different aspects of the habitat of woodlots in relation to the species richness of the organisms they host. We used birds as model organisms since they are currently one of the groups most severely affected by agricultural intensification (Reif and Hanzelka, 2020). Moreover, they often serve as state of nature indicators reflecting conditions at large spatial scales and higher trophic levels (Fraixedas et al., 2020). Previous research has shown that woodlots are inhabited primarily by two bird groups with largely opposite habitat requirements: forest and farmland birds (Bellamy et al., 1996; Fuller et al., 2001, 2004). However, previous studies focused on effects of woodlot characteristics have mostly considered larger woodland patches (0.02–30 ha in Bellamy et al., 1996 and Hinsley et al., 1995; 0.3–302 ha in Lorenzetti and Battisti, 2006; 0.7–14.5 in McCollin, 1993), and investigated them rather from the perspective of forest fragmentation, focusing mainly on the effects of woodlot spatial characteristics – size, isolation or shape (McCollin, 1993; Hinsley et al., 1995; Lorenzetti and Battisti, 2006). The importance of habitat characteristics has generally not been recognized (but see Bellamy et al., 1996 and Mason, 2001). Since there has been little effort to study woodlots as a specific habitat for farmland biodiversity, their importance for the farmland birds remains to be assessed.

In this study, we surveyed birds in 82 woodlots scattered over 3,000 km^2 of farmland in the Czech Republic, central Europe. These woodlots showed high variability in their habitat characteristics, which we sorted into three groups: 1) the structure of woodland vegetation (i.e., tree height and the density of the tree and shrub layers), 2) the habitat diversity (i.e. the diversity of microhabitats and richness of woody plant species in the woodlot), and 3) the nativeness of woodlot vegetation (i.e., the proportion of coniferous trees, which are not native in woodlots in the study area, and the proportion of the exotic Black Locust *Robinia pseudoaccacia*). The aim of our study was to discover which of these characteristics are linked to overall bird species richness, as well as forest and farmland bird species richness separately (**Table 1**).

STUDY AREA AND METHODS

Study Area and Woodlot Selection

The study was carried out in central Bohemia, the Czech Republic, in a lowland area of circa 3,000 km^2 (**Figure 1**). This area is dominated by an intensive agriculture landscape (covering about 70% of the area) with a considerable proportion of human settlements and industrial areas (20%), and a small amount of forests (10%) (Ložek et al., 2003).

For the purposes of this study, we defined a mid-field woodlot as a woody patch smaller than 1.25 ha, approximately circular or rectangular in shape, with continuous tree vegetation higher than 4 m on at least part of its area (i.e., we did not consider patches of small shrubs or herbaceous vegetation). Such a definition corresponds to the typical character of mid-field woody vegetation in the region, and avoids the inclusion of forests. Moreover, we considered only woodlots fully surrounded by intensively cultivated agricultural land with no other woody vegetation or urban areas present within 100 m of each woodlot. In addition, these selection rules aimed to minimize the variability in woodlots' spatial characteristics (area, shape and isolation) since our primary research interests were the effects of habitat characteristics. We considered all woodlots in the study area meeting these criteria, with the resulting dataset containing 82 woodlots (**Figure 1**, **Supplementary Table S1**). Woodlots were surrounded by large homogenous agricultural blocks composed of fields of cereals, oilseed rape and maize, and less frequently by other crops. Distance between the nearest neighboring woodlots varied from 360 m to 11.5 km (average 2 km).

Woodlot Characteristics

Woodlots were characterized by several variables reflecting their structure, diversity and nativeness (see **Table 1**). The structure of

TABLE 1 | Variables describing habitat and spatial characteristics of woodlots and their expected relationships with bird species richness (↗ stands for positive and ↘ for negative relationship).

		Explanatory variables (units)	Abbreviation	Characterization	Expectation	Justification	References
HABITAT CHARACTERISTICS	STRUCTURE	Tree height (m)	HEIGHT	Maximum height of tree vegetation	↗	More available habitat can support more species	Sparks et al., (1996); Hinsley and Bellamy, (2000)
		Shrub layer density (%)	DENSE_SHRUB	Percentage of a woodland patch covered by shrubs (up to 4 m in height)	↗	More available habitat can support more species	Doherty and Grubb, (2000); Hinsley and Bellamy, (2000)
		Tree layer density (%)	DENSE_TREE	Percentage of woodland habitat covered by tree foliage (higher than 4 m)	↗	More available habitat can support more species	Bellamy et al., (1996); Hinsley and Bellamy, (2000)
	DIVERSITY	Woody plant species richness	PLANTS	Total number of tree and shrub species in the woodlot	↗	More diverse breeding and feeding resources provide more opportunities for species' coexistence	Green et al., (1994); Ampoorter et al., (2020)
		Microhabitat diversity	HABITAT_DIV	Shannon diversity index of five microhabitat types • Grassland • Wetland • Sparse shrubland (= walk-through shrubs) • Dense shrubland (= impassable shrubs) • Woodland (= vegetation with trees > 4 m)	↗	More microhabitats provide more opportunities for species' coexistence	Mason, (2001); Fuller et al., (2004)
	NATIVENESS	Proportion of Black Locust (%)	ROBINIA	Proportion of the Black Locust *Robinia pseudoacacia* in the tree canopy	↘	Exotic tree suppressing native plants (allelopathy) and insects (phytophagous species are not adapted to its leaves) resulting in more homogenous habitat and less food sources for birds	Reif, Hanzelka, et al., (2016); Štrobl et al., (2019)
		Proportion of coniferous (%)	CONIFERS	Proportion of coniferous vegetation in the tree canopy	↘	Not naturally occurring in study area and thus birds adapted to their stands may be missing	Reif, Hanzelka, et al., (2016); Štrobl et al., (2019)
SPATIAL CHARACTERISTICS		Area (ha)	AREA	Total area of the woodlot	↗	Larger woodlots have a higher carrying capacity for species richness	Mason, (2001); Lorenzetti and Battisti, (2006)
		Shape	SHAPE	Woodlot perimeter divided by the perimeter of a circle with the same area	↗	More complex shapes provide more ecotones and thus more opportunities for species' coexistence	Hinsley et al., (1995); Bellamy et al., (1996)
		Isolation	ISOLATION	The 1st axis of the principal component analysis ran on five isolation parameters • Woodlot distances to the nearest forest • Woodlot distances to the nearest urban area • Relative coverage of forests in a 1,000 m buffer • Relative coverage of urban areas in a 1,000 m buffer • Cumulative hedgerow length in a 1,000 m buffer	↘	Due to dispersal limitation, more isolated woodlots are less likely to be occupied	McCollin, (1993); Bennet et al. (2004)

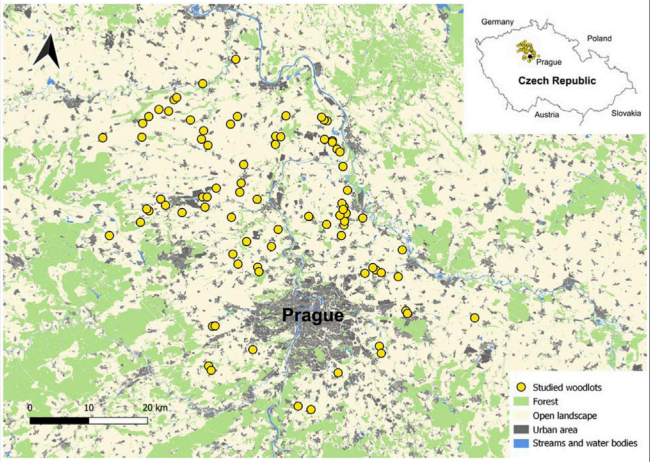

FIGURE 1 | Studied woodlots (yellow dots) on a map showing the main landcover types in the Czech Republic. Inset shows the position of the study area within the Czech Republic.

the continuous woody vegetation of each woodlot was expressed using three variables: the *tree height* was the maximal height of the tree canopy; the *shrub layer density* (vegetation up to 4 m above the ground) and *tree layer density* (higher than 4 m) were estimated as the percentages of the area covered by the respective vegetation. For describing habitat diversity, the total number of tree and shrub species was used as a measure of *woody plant species richness*; the *microhabitat diversity* was assessed by estimating the proportions of five microhabitat types (grassland, wetland, sparse shrubland, dense shrubland and woodland) and calculating the Shannon diversity index. Finally, for describing the nativeness of vegetation, we estimated the *proportion of Black Locust* (an exotic tree species of North American origin) and the *proportion of conifers* in the tree canopy. (Although the coniferous trees present are a part of the native Czech flora, they are not natural vegetation in the study area and were all planted by humans.) Because the woodlots were relatively small, all characteristics were measured over the whole area, without using any survey plots.

In addition, we used aerial photographs (scale 1:1,000) and QGIS 2.18 (QGIS Development Team, 2019) to estimate the *area*, *shape* and *isolation* of each woodlot. The area of the woodlots varied from 0.076 to 1.25 ha (average 0.46 ha). The shape was expressed as the ratio of a woodlot perimeter divided by the perimeter of a hypothetical circular woodlot with the same area–the lower the ratio, the closer the shape is to circular (Bellamy et al., 1996). This ratio varied from 1.004 to 1.627 (average 1.189) in our woodlots. To express the isolation of each woodlot, we used the first axis of a principal component analysis (PCA) ran using the R-package "vegan" (Oksanen et al., 2019) with five isolation parameters: a woodlot distance to the nearest areas of forest and urban habitat, the relative coverage of these habitats in a 1,000 m buffer around a given woodlot, and the cumulative hedgerow length in the same buffer. All these habitat types can host some of the bird species observed in our woodlots (Šťastný and Hudec, 2011) and it is thus necessary to take them into account. The PCA showed a gradient from the least to the most isolated woodlots (**Supplementary Figure S1**).

Bird Survey

Birds were counted in 2017 (in 12 woodlots) and 2018 (in the remaining 70 woodlots). Each woodlot was visited twice per breeding season in a given year (in the second half of April and in the second half of June) to cover both early- and late-breeding species. During each visit, the whole area of each woodlot was explored systematically by a slow walk and all birds detected either visually or acoustically were recorded except for individuals flying over the woodlot. All surveys were conducted at the time of the highest bird activity from 6:00 to 10:00 under favorable weather conditions (i.e. no rain or strong wind). The time devoted for a single visit of a woodlot was 5–30 min depending on its area, so that small and large woodlots were given approximately the same effort per unit area.

All nocturnal species were excluded from further analysis because the field technique was not suitable for their detection. The Common Pheasant *Phasianus colchicus* and the Grey Partridge *Perdix perdix* were excluded as well because both species are bred in captivity and occasionally released by hunters, and thus their abundance may not represent local environmental conditions.

For each woodlot, we expressed the species richness of all birds (hereafter called "overall bird species richness"), forest birds ("forest bird species richness") and farmland birds ("farmland bird species richness") as the total number of species in the respective groups across both visits. To correct the data for sample size bias, we also calculated a rarefied version of these variables (using the R-package iNEXT; Hsieh et al., 2020). In addition, we calculated the Shannon diversity index for all birds, forest birds and farmland birds separately, taking the numbers of recorded individuals (as a maximum count of each species across both visits) into account. To categorize species as forest or farmland, we followed the classification of Reif et al. (2010), who performed a multivariate analysis of birds' habitat preferences based on breeding bird monitoring data of country-wide coverage (for recorded species and their categorization see **Supplementary Table S2**).

Statistical Analyses

Before building statistical models, we assessed the collinearity between all explanatory variables using Pearson's correlation coefficient and the variance inflation factor (VIF) with the R package "usdm" (Naimi et al., 2014). We did not detect any signs of collinearity in the data (**Supplementary Table S3**). Exploratory searching for possible non-linear relationships revealed non-linearity for the proportion of Black Locust. We applied generalized linear modelling in two distinctive steps to uncover both the more general effects of the spatial variables, vegetation structure, diversity and nativeness as well as the specific effect of each explanatory variable.

Firstly, for each of the nine response variables (i.e., species richness, rarefied species richness and the Shannon index for all birds, forest birds and farmland birds) we composed six

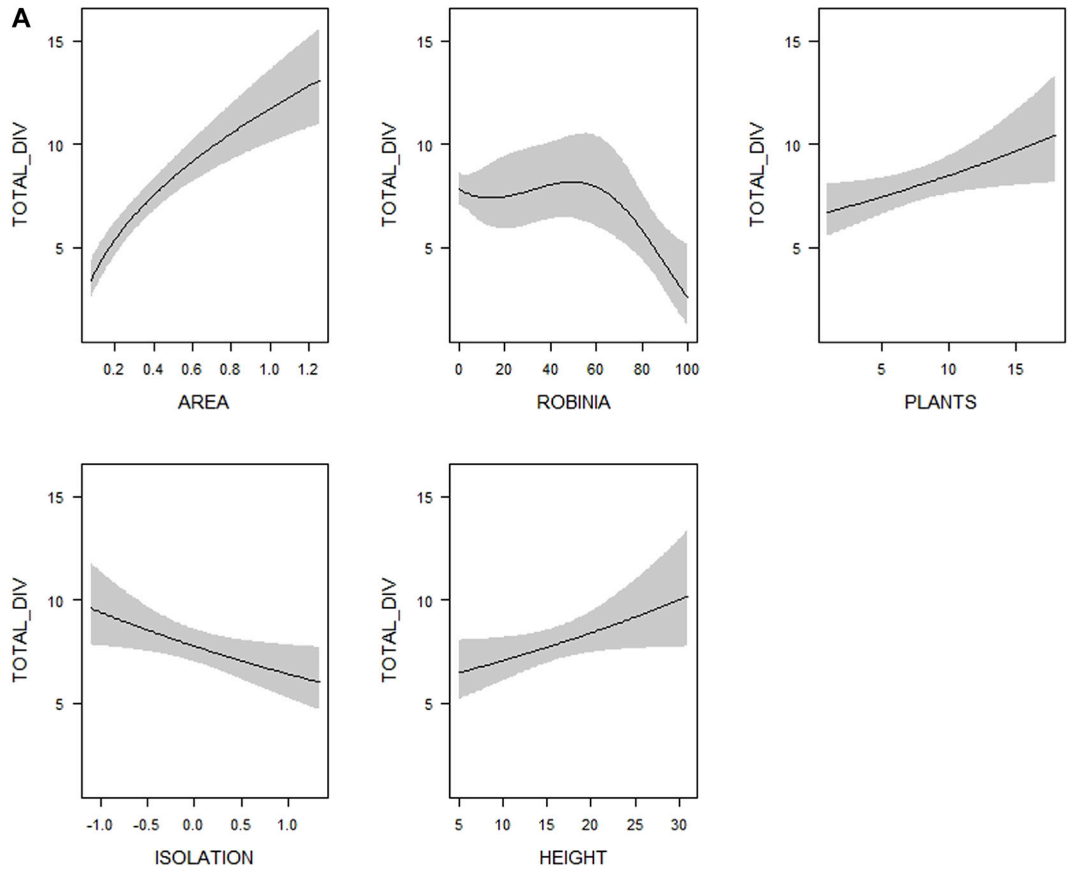

FIGURE 2 | Visualization of the relationships between (A) overall bird species richness (TOTAL_DIV–number of all bird species), (B) forest bird species richness (FOREST_DIV–number of forest bird species) and (C) farmland bird species richness (FARMLAND_DIV–number of farmland bird species), respectively, and woodlot characteristics (see **Table 1** for their definitions and abbreviations) included in the most supported generalized linear models (see **Supplementary Table S4**). Shaded areas correspond to 95% confidence intervals. The estimates from the best model for each response variable are shown.

generalized linear models (GLMs): a null model, a model containing solely spatial variables, one model for each of the three general habitat characteristics (i.e., vegetation structure, diversity and nativeness) that also included the spatial variables, and a full model including all ten variables (i.e., tree height, tree layer density, shrub layer density, woody plant species richness, microhabitat diversity, the proportion of Black Locust, the proportion of conifers, area, shape and isolation). The area was log-transformed and the proportion of Black Locust was modeled using b-splines to accommodate the non-linear relationship using the R package "splines" (Perperoglou et al., 2019). The rarefied species richness was log-transformed. For modeling of species richness variables, we used the Poisson distribution and log link function; for modeling rarefied species richness and the Shannon diversity index we used the Gaussian distribution and identity link function.

Secondly, for each response variable, each of the full GLMs was processed in the "MuMIn" R package (Bartoń, 2019) to assess all possible combinations of explanatory variables' main effects using the Akaike Information Criterion corrected for small sample sizes (AICc). We did not consider interactive effects because they were not justified by the hypotheses and the sample size did not enable such complex models. To avoid model overfitting given the sample size of 83 woodlots, the maximum number of explanatory variables included in a single model was set to eight following the recommendation of Burnhan and Anderson (2002). The variable of woodlot area was included in every candidate model in order to fully account for the species-area relationship (Rosenzweig, 1995). For each response variable, the top set of models with ΔAICc < 4 were used for inference as recommended by recent reviews on model selection (e.g., Harrison et al., 2018). For this purpose, we performed conditional model averaging of the parameter estimates across the top models.

We then plotted the relationships between the respective response variables and their predictors estimated by the single best-supported model for each response variable. In the main manuscript, we present plots with the original values of the response variable (**Figure 2**), but the individual study sites cannot be visualized in such plots; plots showing the study sites are shown as partial residual plots in the Supplementary Online Material (**Supplementary Figure S2**). For each of the top

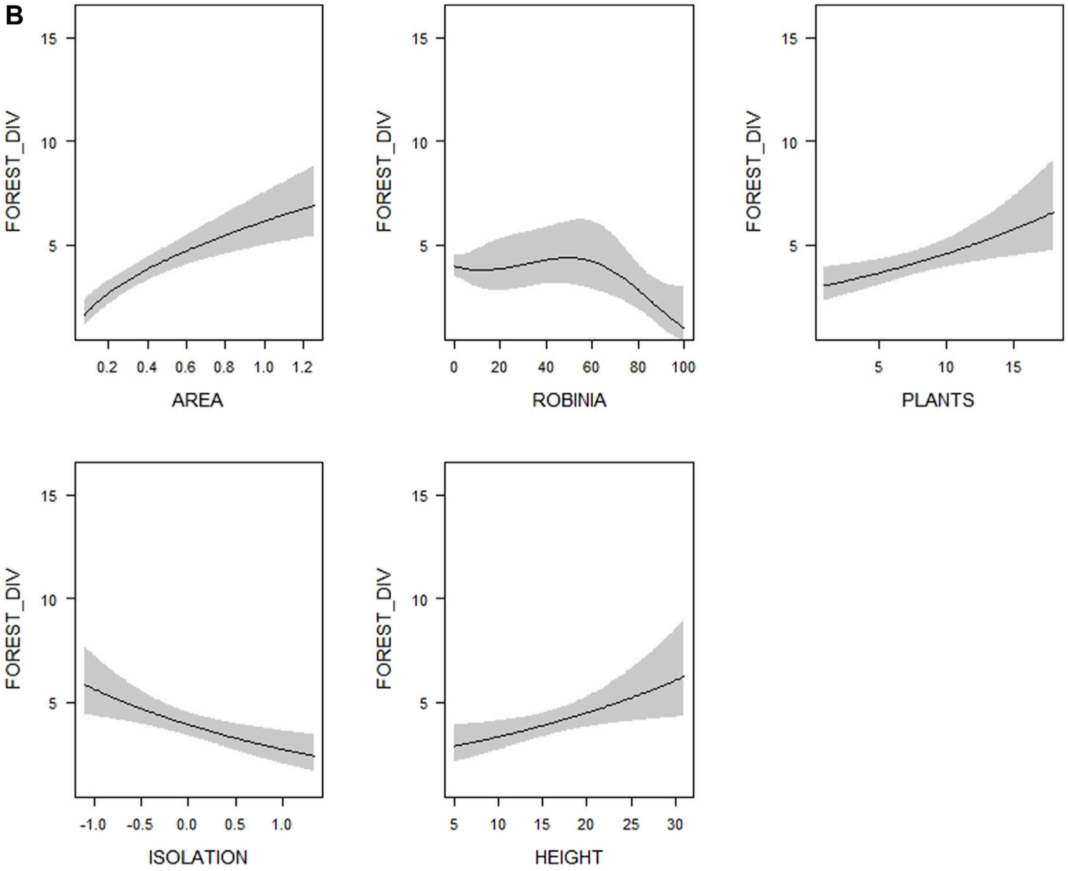

FIGURE 2 | (Continued)

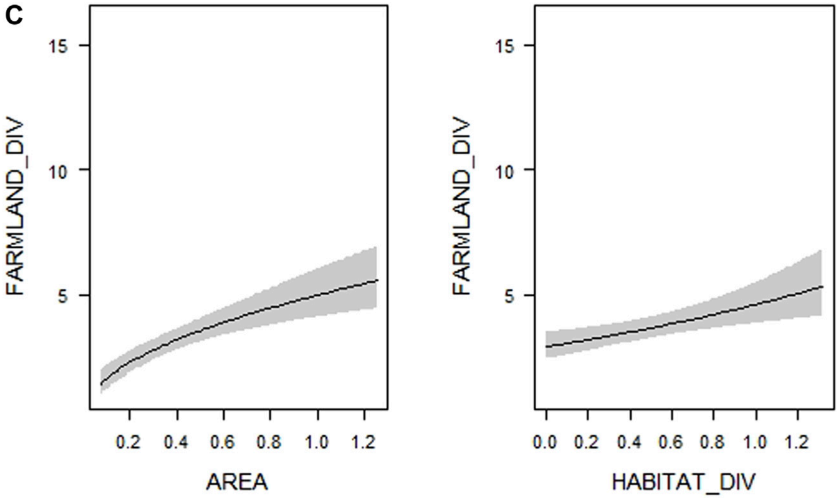

FIGURE 2 | (Continued)

TABLE 2 | Explained deviance and AICc of six generalized linear models explaining (A) species richness, (B) rarified species richness, and (C) the Shannon diversity index for all, forest and farmland bird species. For specific variables categorized as spatial, habitat structure, diversity and nativeness see **Table 1**.

	All birds		**Forest birds**		**Farmland birds**	
	Deviance	**AICc**	**Deviance**	**AICc**	**Deviance**	**AICc**
(A)						
Null model	0.000	486.848	0.000	396.731	0.000	347.985
Spatial variables model	56.652	389.671	47.811	329.200	32.790	319.352
Spatial variables and habitat structure variables model	58.146	393.933	49.896	332.968	33.632	325.444
Spatial variables and habitat diversity variables model	59.934	388.269	54.824	322.946	42.984	313.039
Spatial variables and habitat nativeness variables model	64.380	384.986	54.761	327.898	37.315	323.960
Full model	69.811	388.430	63.693	327.453	50.103	323.651
(B)						
Null model	0.000	206.503	0.000	216.964	0.000	180.920
Spatial variables model	43.114	166.882	47.222	171.198	27.612	161.061
Spatial variables and habitat structure variables model	46.348	169.265	52.062	170.493	31.136	164.151
Spatial variables and habitat diversity variables model	45.323	168.359	52.056	168.044	36.700	154.784
Spatial variables and habitat nativeness variables model	53.147	160.681	53.231	170.996	32.743	164.743
Full model	59.445	162.6128	61.708	168.3664	44.609	162.5954
(C)						
Null model	0.000	168.368	0.000	169.346	0.000	157.822
Spatial variables model	50.708	116.999	51.210	117.137	34.125	130.231
Spatial variables and habitat structure variables model	52.249	121.577	55.286	117.167	36.162	134.838
Spatial variables and habitat diversity variables model	54.633	114.917	56.550	112.356	47.486	116.368
Spatial variables and habitat nativeness variables model	62.108	105.140	56.832	116.808	39.812	132.539
Full model	67.759	105.667	65.713	111.6894	54.170	123.960

models, we checked for the possible presence of spatial autocorrelation in residuals using smoothed nonparametric functions (spline.correlog function from the R package "ncf"; Bjornstad, 2019) with 95% confidence intervals computed using a bootstrap with 1,000 replications. No significant autocorrelation was indicated in any model (results not shown). All analyses were run using R 3.6.0 (R Core Team, 2019).

RESULTS

In 82 surveyed woodlots we detected 53 bird species; 26 of them were classified as forest birds and 27 as farmland birds. On average, one woodlot hosted seven bird species (range 0–18 species), five forest bird species (0–12) and three farmland bird species (0–10). The most frequently recorded species were the Common Blackbird *Turdus merula*, the Yellowhammer *Emberiza citrinella*, the Great Tit *Parus major*, the Eurasian Blackcap *Sylvia atricapilla* and the Common Chaffinch *Fringilla coelebs*. For the complete list of recorded species see **Supplementary Table S2**.

Zero deviance explained by the respective null models, i.e. the models without predictors containing solely the intercept, indicated that our focal explanatory variables were important predictors of bird species richness in woodlots (**Table 2**). Indeed, spatial characteristics models, i.e. the models containing woodlots' area, shape and isolation, but not their habitat characteristics, improved the explained deviance considerably and led to a marked decrease in AIC$_c$ compared to the null models (**Table 2**). These patterns were observed for overall bird species richness, as well as for the species richness of forest and farmland birds (**Table 2**). Moreover, in all these bird groups, the spatial characteristics model was not the best performing model, indicating that habitat characteristics play an important role in explaining the variation of bird species richness across woodlots (**Table 2**). However, the roles of respective habitat characteristics differed among the bird groups.

All Birds

Overall bird species richness was best explained by the model containing the spatial characteristics together with the variables describing the nativeness of the woodlot vegetation–represented by the proportions of Black Locust and coniferous trees (**Table 2**). When we used the variables describing vegetation structure (tree height, tree layer density and shrub layer density) instead of the nativeness variables, model performance decreased and was lower than in the spatial characteristics model (**Table 2**). The performance of the model containing the diversity variables (microhabitat diversity and woody plant species richness) was similar to the spatial characteristics model (**Table 2**). Multimodel inference of the top models (22 out of 502 candidate models meeting the ΔAICc < 4, **Supplementary Table S4**) uncovered the importance of particular explanatory variables: the proportion of Black Locust, woody plant species richness, tree height and isolation (together with the woodlot's area included in all models by default). These variables were also the only explanatory variables with 95% confidence intervals not

TABLE 3 | Relationships of (A) overall bird species richness, (B) forest bird species richness and (C) farmland bird species richness to woodlot characteristics (see **Table 1** for their definitions and abbreviations) estimated by generalized linear models. The model-averaged coefficients together with their confidence limits (CL) across the top models (defined by $\Delta AIC_c < 4$; see **Supplementary Table S4**) are shown. Variables with confidence limits not including zero are in bold. For results for rarefied species richness and the Shannon index see **Supplementary Table S5**.

	Explanatory variable	Coefficient	2.5% CL	97.5% CL	Variable importance (sum of Akaike weights)	No of models[a]
(A)						
HABITAT CHARACTERISTICS	**HEIGHT**	**0.01853**	**0.000**	**0.037**	**0.74**	**14**
	DENSE_SHRUB	0.00052	−0.002	0.003	0.11	3
	DENSE_TREE	0.00014	−0.004	0.004	0.10	3
	PLANTS	**0.02519**	**0.002**	**0.048**	**0.90**	**19**
	HABITAT_DIV	0.14934	−0.076	0.374	0.35	8
	bs (ROBINIA)1[b]	−0.23820	−1.094	0.617	1.00	22
	bs (ROBINIA)2[b]	0.77265	−0.368	1.913		
	bs(ROBINIA)3[b]	**−1.06876**	**−1.777**	**-0.361**		
	CONIFERS	0.00061	−0.003	0.004	0.11	3
SPATIAL CHARACTERISTICS	**log(AREA)**	**0.49283**	**0.345**	**0.641**	**1.00**	**22**
	SHAPE	0.08564	−0.582	0.754	0.10	3
	ISOLATION	**−0.18194**	**−0.350**	**−0.014**	**0.90**	**19**
(B)						
HABITAT CHARACTERISTICS	**HEIGHT**	**0.02749**	**0.003**	**0.052**	**0.89**	**12**
	DENSE_SHRUB	−0.00015	−0.004	0.004	0.10	2
	DENSE_TREE	−0.00026	−0.006	0.006	0.11	2
	PLANTS	**0.04481**	**0.014**	**0.076**	**1.00**	**14**
	HABITAT_DIV	−0.22276	−0.544	0.098	0.43	7
	bs (ROBINIA)1[b]	−0.41523	−1.589	0.759	0.90	12
	bs (ROBINIA)2[b]	1.08258	−0.569	2.734		
	bs(ROBINIA)3[b]	**−1.39184**	**−2.491**	**−0.293**		
	CONIFERS	0.00043	-0.004	0.005	0.11	2
SPATIAL CHARACTERISTICS	**log(AREA)**	**0.53662**	**0.337**	**0.736**	**1.00**	**14**
	SHAPE	0.10486	−0.802	1.012	0.11	2
	ISOLATION	**−0.35234**	**−0.585**	**−0.120**	**1.00**	**14**
(C)						
HABITAT CHARACTERISTICS	HEIGHT	0.01387	−0.012	0.040	0.29	10
	DENSE_SHRUB	0.00116	−0.003	0.005	0.13	5
	DENSE_TREE	0.00351	−0.002	0.009	0.33	10
	PLANTS	0.00876	−0.023	0.041	0.15	6
	HABITAT_DIV	**0.49820**	**0.203**	**0.793**	**1.00**	**30**
	bs (ROBINIA)1[b]	0.18575	−1.033	1.405	0.05	2
	bs (ROBINIA)2[b]	0.50743	−1.098	2.113		
	bs (ROBINIA)3[b]	-0.73644	−1.661	0.189		
	CONIFERS	0.00236	−0.003	0.008	0.23	9
SPATIAL CHARACTERISTICS	**log(AREA)**	**0.46346**	**0.276**	**0.651**	**1.00**	**30**
	SHAPE	−0.04929	−1.077	0.978	0.10	4
	ISOLATION	0.07542	−0.167	0.318	0.17	7

[a] *Number of models containing a given variable, see* ***Supplementary Table S4****.*

[b] *Fitted as a nonlinear relationship using b-splines (see Methods section for more details).*

overlapping zero (**Table 3**). The overall bird species richness was positively related to tree height and woody plant species richness. More isolated woodlots and woodlots with a higher coverage of Black Locust hosted a lower number of bird species (**Figure 2A**, **Supplementary Figure S2A**). In case of Black Locust, this negative effect was non-linear and bird species richness tended to drop after it reached about 60% of the woodlot cover (see **Figure 2A**). Results of the multimodel inference were similar in case of the overall bird species richness adjusted by the rarefaction, showing qualitatively the same effects of the Black Locust cover and tree height (**Supplementary Table S5**). These two variables were also the only ones related to the Shannon index of overall bird diversity according to the confidence intervals (**Supplementary Table S5**).

Forest Birds

The species richness of forest birds was best explained by the model containing both spatial and diversity variables (**Table 2**), while the model containing both spatial and vegetation structure variables was the worst performing (**Table 2**). Adding the nativeness variables into the spatial variables model did not considerably improve its performance (**Table 2**). In the multimodel inference, 14 models met the $\Delta AICc < 4$ threshold (**Supplementary Table S4**). The important explanatory variables were the same as in the case of overall species richness: tree height, woody plant species richness, the proportion of Black Locust and isolation (**Table 3**). The 95% confidence intervals of these variables did not overlap zero (**Table 3**). The direction and shape of their effects were the same as in the case of overall species richness, i.e. more species were found in woodlots with higher trees, a higher number of woody plant species, a lower coverage of Black Locust and lower isolation (**Figure 2B**, **Supplementary Figure S2B**). Using the rarified richness and Shannon diversity index as respective response variables provided the same patterns (**Supplementary Table S5**).

Farmland Birds

In the case of farmland bird species richness, the model containing both diversity and spatial variables was the only one outperforming the model with solely spatial variables (**Table 2**). According to multimodel inference, the top models (30 models which met the $\Delta AICc < 4$ threshold) explained 42.5–48% of the deviance, considerably less than top models for overall and forest bird species richness, which explained 56.2–69.6% (**Supplementary Table S4**). Only one variable–microhabitat diversity–was of considerable importance, and its 95% confidence interval did not overlap zero (**Table 3**). More farmland bird species were recorded in woodlots with higher microhabitat diversity (**Figure 2C**, **Supplementary Figure S2C**). The same variable was the only one supported by the model selection procedure in the case of rarified farmland bird richness (**Supplementary Table S5**). However, the results somewhat differed in the analysis of the Shannon index of farmland bird diversity. In addition to microhabitat diversity, both the tree layer density and the proportion of coniferous vegetation had slightly positive effects on values of this index, with their lower confidence limits only slightly overlapping zero (**Supplementary Table S5**).

DISCUSSION

Mid-field woodlots are small non-productive elements in agricultural landscapes that may serve as important biodiversity refuges (e.g., Tryjanowski et al., 2014; Štrobl et al., 2019; Pustkowiak et al., 2021). However, their role as distinctive landscape features has been largely overlooked (but see Gottschalk et al., 2010; Aue et al., 2014), since previous studies have included mostly all semi-natural landscape features together at the regional scale (Billeter et al., 2008; Doxa et al., 2010; Sasaki et al., 2020) or considered larger woodland patches from the perspective of forest habitat fragmentation (McCollin, 1993; Bellamy et al., 1996; Doherty and Grubb, 2000; Bennett et al., 2004; Lorenzetti and Battisti, 2006). Such studies mainly focused on the effects of area, shape and isolation (e.g. Hofmeister et al., 2017) for the purposes of forest bird conservation (McCollin, 1993; Lorenzetti and Battisti, 2006). If the effects of some habitat characteristics were tested, they mostly proved insignificant (McCollin, 1993; Hinsley et al., 1995; Bellamy et al., 1996; Mason, 2001; Lorenzetti and Battisti, 2006) most likely due to strong area effects driven by the large ranges of woodlot sizes in studied samples.

As a consequence, the importance of woodlot habitat characteristics for supporting farmland biodiversity has remained insufficiently explored (Vanhinsbergh et al., 2002). Our results begin to address this issue, showing that habitat characteristics, namely vegetation structure, diversity and nativeness, shape bird species richness and the proportions of forest vs. farmland birds in woodlots. A comparison of the performance of models containing different groups of habitat variables indicated that overall bird species richness was best explained by nativeness variables, whereas forest and farmland bird richness was better explained by diversity variables (see **Table 2**). However, each variable group contained both good and poor predictors of bird species richness, so it is necessary to focus on the individual habitat characteristics instead on their groups. In this respect, the importance of different habitat characteristics varied among bird groups: overall and forest bird species richness increased with the height of trees and with the species richness of woody plants and decreased with the increasing proportion of a non-native tree, the Black Locust. In contrast, farmland bird species richness was positively related only to the diversity of microhabitats. These results are comparable to some extent to those obtained by research focused on linear landscape features–hedgerows–where the positive effects of vegetation height, plant species richness and microhabitat diversity, as well as vegetation density on overall bird species richness have been observed (for example Green et al., 1994; Sparks et al., 1996; Hinsley and Bellamy, 2000).

In total, we recorded 53 bird species in 82 woodlots with areas up to 1.25 ha. This number of species is comparable to the bird species richness of woodlots studied in the United Kingdom. For example, the same number of species was recorded in sixteen woodlots (McCollin, 1993), whereas Mason (2001) recorded 46 species in 35 wood forest fragments, and Bellamy et al. (1996) found 64 species breeding in 151 fragments (in all cases without considering predators, owls, or feathered game). Besides the considerably wider range areas (which probably leads to a wider scale of habitat types), these studies also did not limit the selection of woodlots according to their isolation from different habitats, while we specifically focused on isolated ones. Therefore, a number of species that were missing in our woodlots were recorded in those studies–for instance, water birds such as the Mute Swan (*Cygnus olor*), Mallard (*Anas platyrhynchos*) and Common Moorhen (*Gallinula chloropus*); synanthropic species such as the House Sparrow (*Passer domesticus*) and Western Jackdaw (*Corvus monedula*), or species dependent on larger forest areas such as the Stock Dove (*Columba oenas*), Coal Tit (*Parus ater*), and Eurasian Treecreeper (*Certhia familiaris*). On the other hand, we recorded 12 species not reported in the studies from the United Kingdom including the Eurasian Wryneck (*Jynx torquilla*), Red-backed Shrike (*Lanius collurio*), Great Grey Shrike (*Lanius excubitor*), Common Grasshopper Warbler (*Locustella naevia*) and Western Yellow Wagtail (*Motacilla flava*). It is possible that our woodlots contained a higher proportion of grasslands, providing habitat for the Yellow Wagtail, and sparse shrubs preferred by the Common Grasshopper Warbler. Moreover, some of the above mentioned species, such as shrikes and the Eurasian Wryneck, are still commonly breeding in Central European landscapes, but are rare or even absent in the United Kingdom (Keller et al., 2020).

Habitat Characteristics

The only habitat characteristic related to farmland bird species richness was microhabitat diversity. This characteristic expressed the proportion of each habitat in a woodlot, reflecting its enrichment by sparsely vegetated habitats to a large extent. The strong and positive relationship with the number of farmland birds implies that many such species need sparsely vegetated non-productive habitats even within our very small woodlots, most likely for foraging and nesting (Bellamy et al., 1996; Bennett et al., 2004). In addition, this pattern could reflect the importance of a heterogeneous habitat mosaic for some farmland birds. For example, some bunting species such as the Corn Bunting *Emberiza calandra* need a high proportion of grasslands in their territory for foraging but also need high trees suitable as song posts (Altewischer et al., 2015). Similarly, the Red-backed Shrike *Lanius collurio* uses sparse shrubs for its sit-and-wait foraging strategy, but also requires dense shrubs for nesting and cover from predators (Ceresa et al., 2012). The Song Thrush *Turdus philomelos* requires a habitat mosaic providing song posts and nesting opportunities on trees and shrubs and simultaneously foraging sites in grassy patches for gleaning insects on the ground (Peach et al., 2004).

We found a positive linear relationship between the maximal height of woodlot tree vegetation and the species richness of all birds as well as forest birds. Higher vegetation is related to a higher volume of available habitat, and due to the presence of multiple vegetation layers also to a wider supply of different habitat niches, and thus can support more species (Sparks et al., 1996). Furthermore, height is supposed to positively correlate with the age of trees and may also reflect the presence of dead trees and cavities (Guby and Dobbertin, 1996). As our results indicate, such mature vegetation may be beneficial for many forest bird species such as woodpeckers, which forage and/or nest in the tree layer (Lorenzetti and Battisti, 2006). In addition, higher and older tree vegetation may attract larger-bodied species (e.g. corvids and birds of prey) for perching (Hinsley and Bellamy, 2000) and their presence can thus increase the total number of bird species recorded in a woodlot.

A similar positive effect of tree height has previously been reported for overall bird species richness in hedgerows (Hinsley and Bellamy, 2000), but not in studies focusing on woodland fragments (e.g., Nol et al., 2005). The reason for the absence of this effect may be due to the focus on forest fragmentation of those studies, which considered much larger woodlots where the tree height contribution to the overall habitat amount and dimensionality was presumably small. This implies that vegetation structure for birds may be more important in smaller woodlots, indicating the need for the appropriate management of such habitats.

Bird species richness in our study also increased with woody plant species diversity (see also Osborne, 1984; Green et al., 1994), and as in the case of tree vegetation height this overall positive effect was driven by forest birds. Generally, more woody plant species create more diverse breeding and feeding resources for birds and thus provide more opportunities for their coexistence (Ampoorter et al., 2020). In addition, a higher diversity of woody plants may provide food supply for birds over a larger part of the year (Arnold, 1983). Forest birds probably respond to this resource provision more strongly because they largely depend on woody vegetation, whereas farmland birds may partly satisfy their needs in open landscapes (Bellamy et al., 1996) and thus they are not limited by the woody plant composition within woodlots.

Finally, the proportion of an invasive exotic tree, the Black Locust, had a negative effect on both overall and forest bird species richness. The shape of this relationship was nonlinear: species richness stagnated up to ca 60% of Black Locust cover and then steeply decreased (see **Figure 2**). This non-linear response of bird species richness to Black Locust cover was also found in central European forests (Kroftová and Reif, 2017). It seems that there may be a certain threshold proportion of this exotic tree, over which bird species richness becomes limiting, possibly due to the homogenization of the tree stand composition. In addition, Black Locust hosts fewer insect species and changes the composition of the insect community, which may limit the food supply for birds (Kadlec et al., 2018; Štrobl et al., 2019). This is particularly likely to be important for the specialized insectivorous species foraging on trees (Reif, Hanzelka, et al., 2016) that correspond to the forest species in our study.

Spatial Characteristics

In addition to the habitat characteristics that were of our primary research interest, the area and isolation of woodlots were also related to bird species richness. Indeed, they explained a higher proportion of the variability in bird species richness than the habitat characteristics (see **Table 2**). But this was largely driven by area effects, with area positively affecting overall, forest as well as farmland bird species richness. Even though the variation of woodlot area was kept as small as possible, this was to be expected, considering that area is the main driver of species richness in habitat fragments at the landscape scale (De Camargo et al., 2018). In contrast, increasing isolation (a composite measure expressing the connection of a given woodlot with various types of landscape features and land cover classes in its surroundings including woodlands, hedgerows and urban areas) had a negative effect only on overall species richness and on forest birds, whereas no effect was found on farmland birds. These results are consistent with previous findings from forest fragmentation studies in England, where forest bird species richness decreased with isolation, whereas so called "edge species", largely corresponding to our farmland birds, tended to occupy more isolated fragments (McCollin, 1993; Bellamy et al., 1996; Bennett et al., 2004). This suggests that small mid-field woodlots may be a suboptimal habitat for forest birds (Loman, 2003; Nol et al., 2005) but a suitable habitat for many farmland birds. As woodlots have been found to possibly function as ecological traps for some bird species under some circumstances (Loman, 2003), another question is whether this also applies to those in our study area. In addition, future studies should go beyond the species richness we focused on here and test whether the bird populations occupying woodlots are viable long-term.

Forest Birds Drive Overall Species Richness

Interestingly, even though the total number of forest and farmland bird species recorded in woodlots was almost equal, the variability in bird species richness was explained by exactly the same set of characteristics for overall species richness and for the species richness of forest birds, suggesting that forest bird distribution accounts for overall species richness variation across woodlots. This can be explained by the relative commonness of forest bird species because spatial patterns in species richness are formed mainly by common species rather than rare ones (Lennon et al., 2004). Indeed, forest species found in our woodlots are rather widespread generalists, such as the Great Tit, Eurasian Blackcap, Chaffinch and Common Chiffchaff *Phylloscopus collybita* (Reif, Hořák, et al., 2016), whose requirements for a minimum area of habitat can be satisfied even in our small and highly isolated forest patches. On the other hand, farmland birds tend to be more rare and specialized species (Reif, Hořák, et al., 2016) deviating from the overall richness pattern. Even though some of these species may not use only woodlots exclusively but also take advantage of surrounding agricultural lands (Bellamy et al., 1996), woodlots represent an indispensable part of their territories (Pustkowiak et al., 2021). This invokes an important message for conservation practice. The development of measures for woodlot habitat management should be not based on findings arising from overall species richness, but rather be specifically customized in respect to the needs of farmland birds, assuming these species are intended to benefit from such management. Future research should assess how to compensate for the trade-offs between the demands of both groups and maximize bird species richness at the landscape scale (Simberloff, 2001).

At the same time, our classification of species as forest or farmland birds may mask subtle ecological preferences because species habitat selection usually follows a continual gradient rather than discrete categories (Knick et al., 2008). On the other hand, some kind of categorization is necessary to infer general insights, and our classification was based on the best available objective data, i.e. a multivariate analysis of bird habitat preferences based on country-wide breeding bird monitoring taking potential regional variations into account (Reif et al., 2010). This makes us confident that the observed differences between forest and farmland birds in relation to woodlot habitat characteristics reflect their genuine ecological requirements.

Rarified Species Richness and the Shannon Diversity Index

Patterns provided by rarified species richness were very similar to those obtained by the analysis of raw species richness. We suggest that this similarity is driven by including woodlot area into all models. Because the rarefaction analysis corrects for unequal sample size (Gotelli and Colwell, 2001) and the sample size, in terms of the number of species or individuals sampled, is strongly influenced by woodlot area, we have indeed taken the woodlot area into account when analyzing the raw species richness. Moreover, the similarity of the raw and rarified richness results suggests that our sampling was adequate for the purposes of our study provided that the differences in woodlot area were carefully considered.

Although the Shannon diversity index also provided very similar findings to those obtained for the species richness, the pattern for farmland birds shows that this index increases not only with higher microhabitat diversity (as was observed for species richness) but also tended to increase with increasing tree layer density and the higher proportion of coniferous trees. The Shannon diversity index reflects the dominance of individual species together with their number (Jost, 2006). We suggest that higher values of this index in woodlots with a denser tree layer and more coniferous trees may result from the preference of some farmland bird species for these habitats, such as Eurasian Tree Sparrow or the Yellowhammer. Such a preference may be too weak to affect the raw species richness but could be reflected in the Shannon index.

CONCLUSION

Our study shows that besides the spatial characteristics of woodlots (i.e., area, isolation and shape) previously studied from a forest fragmentation perspective (for example McCollin, 1993; Bellamy et al., 1996; Doherty and Grubb, 2000), various characteristics of local habitat are important predictors of woodlot bird species richness. Moreover, we show that woodlots should be not considered as a sort of small forest with impoverished biodiversity. Instead, they represent a specific farmland habitat that is important for specific farmland species.

Our findings thus allow the formulation of clear recommendations for woodlot management. However, it should be kept in mind that our findings concern a single study area and a limited spectrum of variables, so our recommendations should be always considered in respect to local circumstances. Further studies in different areas are needed to corroborate our results; for instance, we can imagine that woodlots located in High Nature Value farmland, i.e. not surrounded by intensively managed large arable fields, may show different relationships to bird species richness and diversity (Doxa et al., 2010). In addition, recommendations for woodlot management strongly depend on the species being targeted. If the aim is to improve the habitat for overall species richness, management should support high trees of diverse woody plant species. These trees should be native, but the inclusion of non-native Black Locust may not necessarily be harmful if its coverage remains relatively low. A reduction of woodlot isolation would also bring more bird species. However, these guidelines would improve conditions specifically for common generalist forest birds. Since populations of such generalist forest birds are increasing in Central Europe and the amount of their preferred forest habitats has been expanding due to both intentional and spontaneous afforestation (Schulze et al., 2019), we do not find these species an appropriate target of woodlot habitat management. Instead, we recommend focusing on improving the habitat characteristics beneficial for farmland birds, whose populations are declining at an unprecedented rate, at least in Central Europe (Reif and Vermouzek, 2019). Moreover, those species using woodlots as a breeding habitat in farmland have only a few alternatives (Rajmonová and Reif, 2018). Thus, woodlots should be managed to increase the diversity of various microhabitats, such as dense and sparse shrubs, grasslands or marshes. Although it may be possible to reconcile the different needs of forest and farmland birds in individual woodlots (e.g. increasing the proportion of open areas for farmland birds may be offset by tree maturation for forest birds that benefit from increasing tree height), we suggest that accommodating these diverse management targets for overall (and forest) bird species richness and for farmland birds is not feasible within individual woodlots due to their small size. Such reconciliation can be realized at the landscape scale, however, with a heterogeneous agricultural landscape including a mosaic of woodlots with different habitat characteristics. To target forest birds, several woodlots situated into clusters can be used to lower the effects of isolation (Loman and Von Schantz, 1991).

DATA AVAILABILITY STATEMENT

Dataset used for the analyses is available as **Table S1** in **Supplementary Online Material**. Raw data from bird counts are available upon request to the authors.

AUTHOR CONTRIBUTIONS

JR conceived the idea; LD and JR designed the study; LD and JR-S. carried out the fieldwork; LD analysed the data with inputs from LK and JR; LD led writing with contributions from all co-authors. All authors gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.816255/full#supplementary-material

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Článek 2

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RESEARCH PAPER

Relationships between bird species richness and different facets of landscape heterogeneity – insights from a military area

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Abstract. Military areas often host extraordinary biodiversity compared to the typical agricultural landscape in Europe. It has been suggested that this is due to the high landscape heterogeneity caused by disturbances from military training. This study aimed to test this hypothesis using data from the military area Hradiště and nearby farmland in the Czech Republic (Central Europe). Here, we measured two facets of landscape heterogeneity – the number of woody vegetation patches and habitat diversity – and supplemented these measures with previously published data from bird point counts performed on the same sites. The number of woody vegetation patches was higher in the military area than in the farmland and was positively related to the species richness of birds of conservation concern. Habitat diversity did not differ between both regions. It showed, however, a hump-shaped relationship with total bird species richness. Our results indicate that open landscapes of military areas host a higher number of birds of conservation concern than the farmland due to a finer grain of woodland-grassland mosaic. To support more bird species, it is essential to keep habitat diversity high in open landscapes but at a level that does not harm bird populations by area limitation.

Key words: biodiversity conservation, habitat diversity, woodland mosaic, disturbance, anthropogenic habitats, farmland

Introduction

European biodiversity has declined sharply over the last few decades (Stoate et al. 2009). This decline has become a problem not only for nature conservation but also more broadly, as biodiversity is closely linked to the sustainability of agricultural production and food security (Hautier et al. 2015). In a European environmental context, farmland currently accounts for about half of the area of the continent (FAO 2014), and more than half of European species are associated with it (Sutcliffe et al. 2015). The main driver of biodiversity loss is the intensification of agriculture, with habitat diversity loss and landscape homogenisation as a result (Stoate et al. 2009).

Some modern anthropogenic habitats, such as unreclaimed post-mining sites (Šálek 2012), brownfields

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(Meffert & Dziock 2012) or military areas (Warren et al. 2007), have been recognised as refuges of biodiversity, as they may offer conditions that have disappeared from the intensified agricultural landscape. Military areas represent a huge potential for nature conservation, as they are present in all major global ecosystems, and their estimated total area is up to 5-6% of the Earth's surface (Zentelis & Lindenmayer 2014). They host unusually high numbers of plant species (Čížek et al. 2013), insects (Warren & Büttner 2008, Čížek et al. 2013, Harabiš & Dolný 2018) and birds (Reif et al. 2011, Bušek & Reif 2017, Culmsee et al. 2021) with disproportionately large numbers of threatened and endangered species (Warren et al. 2007). The uniqueness of military areas lies in the absence of intensive agriculture, urbanisation, and military activities. The effect of military training activities on species and ecosystems have been examined in various studies (e.g. Milchunas et al. 2000, Lindenmayer et al. 2016, Fish et al. 2019), which mostly recognised their contribution to the maintenance of early successional habitats and to reducing competitive pressure in favour of less competitive species (Leis et al. 2005, Warren & Büttner 2008, Jentsch et al. 2009, Aunins & Avotins 2018).

On the other hand, surprisingly little attention is paid to the question of what environmental conditions of military areas are behind such enormous species biodiversity. The answer to this question is vital for the guidance of management in active military areas (Woodcock et al. 2005) as well as in those that have already been abandoned by the army and gained the status of a protected area (Hagen & Evju 2013, Ellwanger & Reiter 2019). Following the middle disturbance hypothesis (Connell 1978), Warren et al. (2007) suggested that biodiversity in military areas is high due to the high heterogeneity of disturbances causing high landscape heterogeneity. However, as far as we are aware, there is no study which would test this suggestion. In this article, we aim to fill this knowledge gap, test the difference in landscape heterogeneity inside and outside the military area, and test the importance of landscape heterogeneity for biodiversity. We use birds as model organisms since they often serve as state-of-nature indicators reflecting conditions at large spatial scales and higher trophic levels (Fraixedas et al. 2020). In addition, we focus specifically on open areas because the high conservation values of European military areas for birds are mainly due to their open (i.e. non-forest) habitats (Reif et al. 2013, Bušek & Reif 2017, Aunins & Avotins 2018, Culmsee et al. 2021, Šálek et al. 2022).

We express landscape heterogeneity using two measures: the number of woody vegetation patches and habitat diversity. They represent two complementary factors reflecting different mechanisms of how landscape heterogeneity might affect bird species richness. While the number of woody vegetation patches increases the availability of ecological space for bird species adapted to mosaic habitats and the landscape connectivity for bird species using woody vegetation (Pustkowiak et al. 2021), high habitat diversity provides different kinds of habitats facilitating the coexistence of species with different habitat requirements (Evans et al. 2005).

Our study uses data from a large military area and its surroundings in the Czech Republic (Central Europe) to test the following hypotheses. First, we hypothesise that landscape heterogeneity (i.e. the number of woody vegetation patches and habitat diversity) is higher in an open landscape of the military training area than in the nearby typical farmland landscape. Second, we predict that this difference accounts for a higher bird species richness recorded in the military area by Bušek & Reif (2017).

Material and Methods

Study area and selection of study plots

Our research occurred in the Hradiště military area and its nearby landscape in western Bohemia, the Czech Republic, Central Europe. The Hradiště military area is the largest military area in the Czech Republic, covering an area of about 300 km^2, with a cold climate and hilly relief from 334 to 933 m a.s.l. The open landscape with woodland-grassland mosaic is the area's dominant land cover type (Skokanová et al. 2017). From the management perspective, about one-third of the area is used by the army, which creates disturbances resulting in heterogeneous early succession habitats; the other parts are left with no disturbance or just extensive management (grazing or mowing), resulting in a higher proportion of shrub and tree enclaves (Vojta et al. 2010, Skokanová et al. 2017). Only a minor part of the military area is covered by commercially managed forests (Matějů 2010). The nearby landscape mainly consists of commercial forests (approximately 30%), pastures (25%) and arable land (20%), as well as other various agricultural habitats (18%). Unlike the military area, there are human settlements, industrial areas and water bodies; on the other hand, natural grasslands and scattered woody vegetation are found here sporadically.

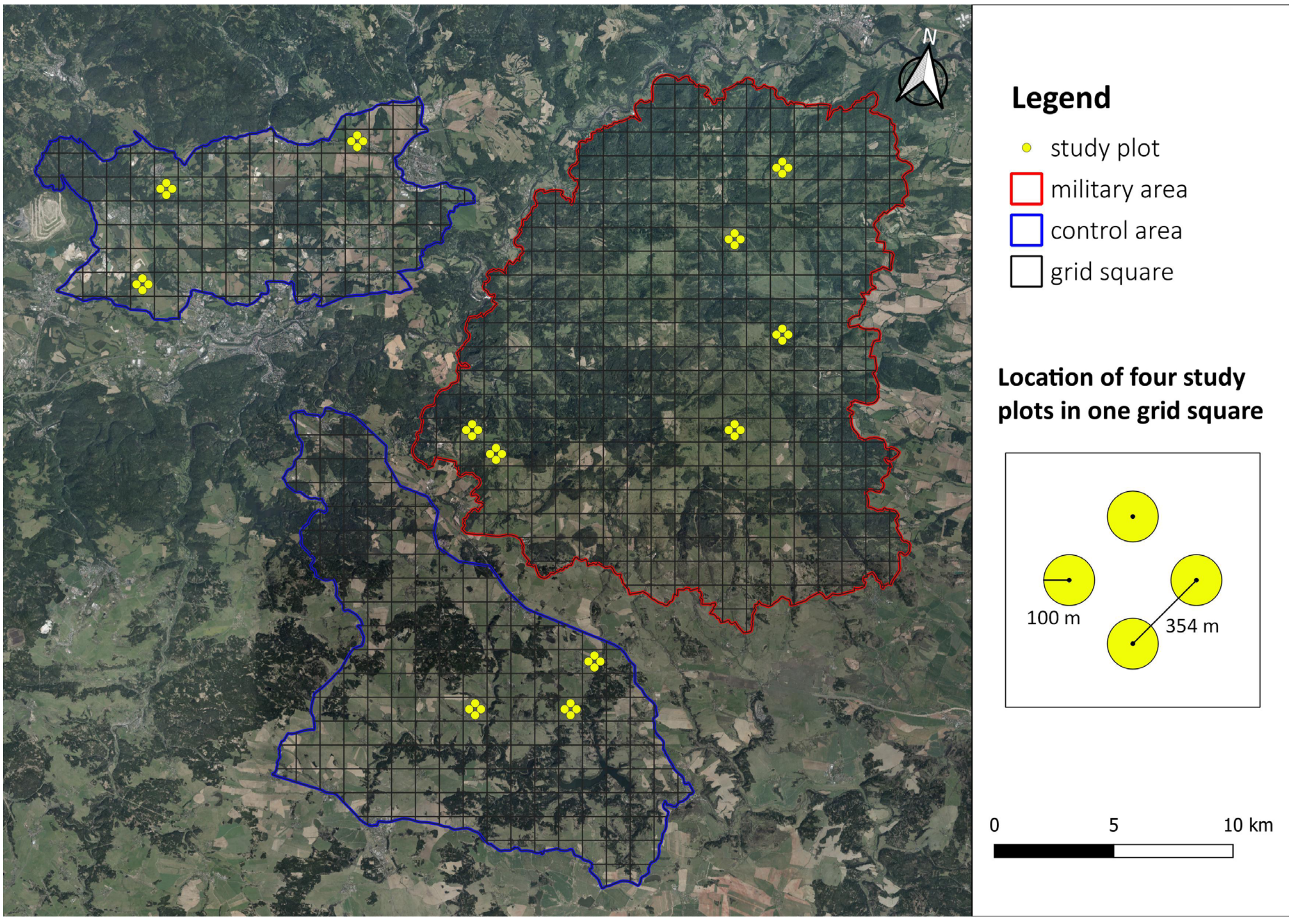

Fig. 1. Map of the study area overlapped by a grid of 1 × 1 km squares used to select study plots. Four study plots were located in each of the squares selected by stratified random approach. The aerial photograph is from 2018.

For this study, we used bird data from Bušek & Reif (2017), who studied birds in the Hradiště military area and nearby landscape as a control area and provided full details on the study design. In brief, Bušek & Reif (2017) sampled the military and control areas. As a control area, they selected a nearby agricultural landscape holding similar proportions of the main land cover types to the military training area (Bušek & Reif 2017). To establish the study plots, Bušek & Reif (2017) applied a stratified random approach using a grid with cells of 1 × 1 km randomly selecting six grid cells in the military area and six in the nearby control area from the pool of the open-habitat cells in respective areas. Open-habitat cells were considered those with more than 50% of the area covered by open habitats (Bušek & Reif 2017). Each cell contained four study plots with a radius of 100 m established in a regular design with the centres of the nearby plots being 354 m apart (see Bušek & Reif 2017, their Fig. 3). In total, the number of study plots was 24 in the military area and 24 in the control area. Habitat mapping and bird census were performed on these circular plots (Fig. 1).

Data collection

We extracted data on bird species richness on individual study plots from Bušek & Reif (2017). They performed point counts in the spring of 2014 at the points located at the centres of respective study plots. Each study plot was surveyed twice per the breeding season in the early morning hours under favourable weather conditions within a fix-radius distance of 100 m around each point (Bibby et al. 2000). See Bušek & Reif (2017) for more details on bird counts.

For each study plot, Bušek & Reif (2017) expressed the total bird species richness and the species richness of birds of conservation concern (CC). As species of conservation concern, Bušek & Reif (2017) considered species deserving special protection by national legislation (Act No. 114/1992 Coll. on Nature Conservation and Landscape Protection 1992, https://www.zakonyprolidi.cz/cs/1992-114) and species listed in the Czech national bird Red List (Šťastný & Bejček 2003). Therefore, we used these two measures of bird species richness for further analysis.

Table 1. Characteristics of linear mixed models testing difference in A) the number of woody vegetation patches and B) the habitat diversity between military area and nearby farmland (expressed as a variable "region").

A) Model	AIC	Deviance	df	*P*
log (patches) ~ 1	177.99	171.99		
log (patches) ~ region	164.10	156.10	1	0.00007
B) Model	AIC	Deviance	df	*P*
diversity ~ 1	66.58	60.58		
diversity ~ region	65.90	57.90	1	0.10130

In 2018, we collected data on landscape heterogeneity on each study plot. Landscape heterogeneity was expressed by two measures: the number of woody vegetation patches and habitat diversity. The number of woody vegetation patches was counted for each study plot using detailed aerial photographs in ArcGIS (ESRI 2013) with a 1 m resolution. The single patch of woody vegetation was defined as a single shrub/tree or cluster of shrubs/trees covering at least 1 m^2 and being isolated by at least a 1 m large gap from another woody vegetation. We set these rules assuming that 1) shrubs/trees smaller than 1 m^2 have a limited ecological function for birds and 2) shrubs/trees located closer than 1 m to each other ecologically function as a continuous block of vegetation and do not increase the landscape heterogeneity.

To measure habitat diversity, we mapped the areas of 14 habitat types (listed below) in the field from April to June. Coniferous or deciduous forests were considered as stands formed solely by coniferous or deciduous tree species. Mixed forest was represented by stands containing a mixture of deciduous and coniferous trees. Non-native forest was represented by stands of exotic trees (irrespective of whether coniferous or deciduous), usually the horse chestnut *Aesculus hippocastanum* and the northern red oak *Quercus rubra*. Forest clearing was a patch of short vegetation (up to 2 m in height) in a forest created by natural or human disturbance. Shrubs were any woody vegetation outside the forest. Grasslands were classified as either managed (represented by regularly cut meadows or active pastures) or unmanaged. As wetland vegetation, we considered all humid areas covered by herbs. Gardens and orchards were woody vegetation patches with human cultivation, typically containing fruit trees. As human settlements, we considered any buildings recorded at study plots. Note that gardens, orchards and human settlements had only marginal representation in the study plots because Bušek & Reif (2017) avoided these habitat types for sampling birds. Streams and ponds were running and still water bodies, respectively, both natural and man-made. Paved and unpaved roads were at least two meters wide, permitting the movement of cars and similar vehicles; we did not recognise footpaths. The area of individual habitat types was calculated using ArcGIS (ESRI 2013). Subsequently, habitat diversity expressed as the Shannon diversity index was calculated across these areas for each study plot.

Statistical analyses

We used linear and generalised linear mixed models (R package "lme4"; Bates et al. 2015), where the identity of the grid cell (each containing four study plots, see Study area and selection of study plots) always acted as a random effect. If the random effect

Table 2. Characteristics of the generalised linear models testing the effects of the number of woody vegetation patches (in Model terms referred to as "patches") and the habitat diversity (in Model terms referred to as "diversity") on total bird species richness and conservation concern (CC) bird species richness. AIC value and deviance of the most supported models are in bold.

		Total bird species richness		CC bird species richness	
Model terms	df	AIC	Deviance	AIC	Deviance
diversity + log (patches)	2	253.733	56.916	**114.607**	**42.738**
diversity + diversity^2 + log (patches)	3	**242.383**	**43.566**	116.439	42.570
diversity + log (patches) + diversity × log (patches)	3	248.761	49.945	116.302	42.434
diversity + diversity^2 + log (patches) + diversity × log (patches) + diversity^2 × log (patches)	5	244.144	41.328	119.941	42.072

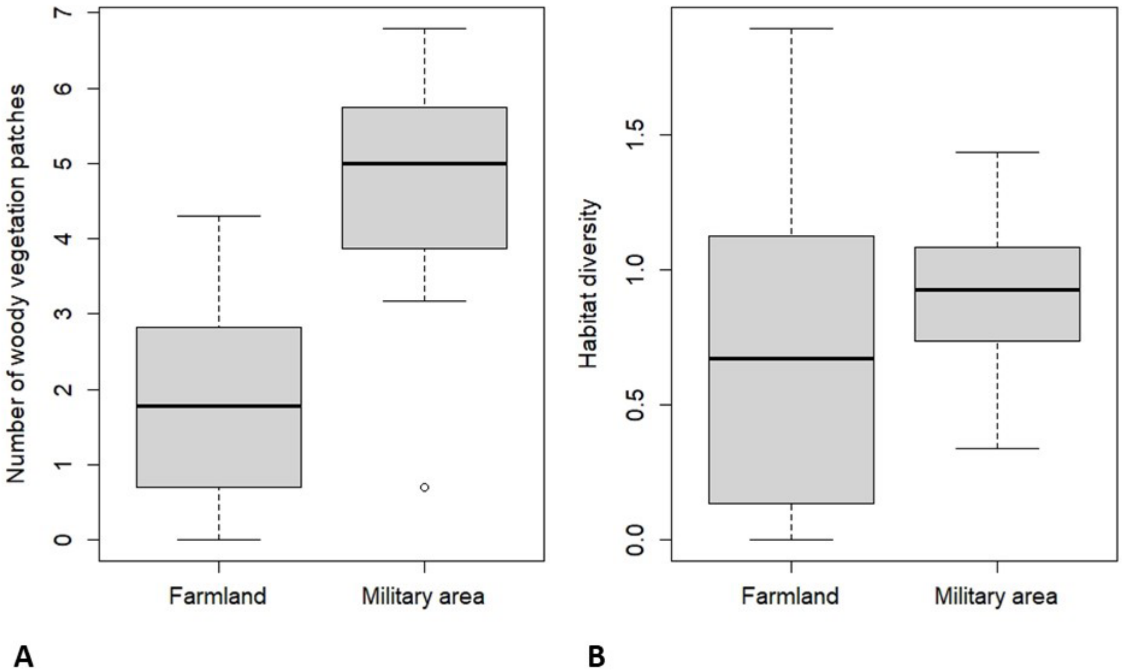

Fig. 2. Boxplot comparing A) the number of woody vegetation patches (log-transformed) and B) habitat diversity between the military area and nearby farmland. The median is the bold line, the box is the interquartile range (IQR), and the whiskers are 1.5 the IQR.

showed zero variance, we used a linear model instead. To achieve the goals of our study, we performed two sets of analyses.

First, we tested hypotheses that the military area and the farmland, expressed as a two-level explanatory categorical variable called "region", differ in the number of woody vegetation patches or habitat diversity. These latter two variables were used as respective response variables. We constructed two linear mixed models (LMMs) for each response variable with a normal distribution – a model containing the region as the explanatory variable and a null model (containing only the random effect; see Table 1). The hypothesis was not supported if the model with the explanatory variable did not have a lower AIC value (delta AIC ≤ 2) than the null model.

Second, we tested hypotheses that the total bird species richness and the CC bird species richness were related to habitat diversity or the number of woody vegetation patches on study plots. The study design intended to include cluster as a random effect. However, due to its zero variance when fitting generalised linear mixed models (GLMMs), we excluded it and used generalised linear models (GLMs) instead. For each of the response variables, i.e. the total bird species richness and the CC bird species richness, we constructed four generalised linear models explaining their variability by the number of vegetation patches and habitat diversity in different combinations: 1) linear main effects of both explanatory variables, 2) linear main effects of both explanatory variables + quadratic term of habitat diversity, 3) linear main effects of both explanatory variables and their interaction, and 4) linear main effects of both explanatory variables + quadratic term of habitat diversity and the interactions between the linear term of the number of woody vegetation patches and both linear and quadratic term of habitat diversity (see Table 2). Based on comparing AIC values of respective models, we chose the best model for each response variable and used that model for inference. The Poisson distribution with log link function was used for all those models because none showed significant overdispersion.

As diagnostic graphs of tested models recommended a logarithmic transformation of the number of vegetation patches, this variable was logarithmic in all models described above. The variables used in the models showed no signs of collinearity according to the variance inflation factor (VIF; the R package "usdm"; Naimi et al. 2014). After log transformation, the number of woody vegetation patches was weakly correlated with the habitat diversity according to Pearson's correlation coefficient, but the correlation (r = 0.43) was considerably lower than the value of r = 0.7 suggested as a threshold for the collinearity becoming an issue (Dormann et al. 2013). For all models described above, we checked for the possible presence of spatial autocorrelation in residuals using smoothed

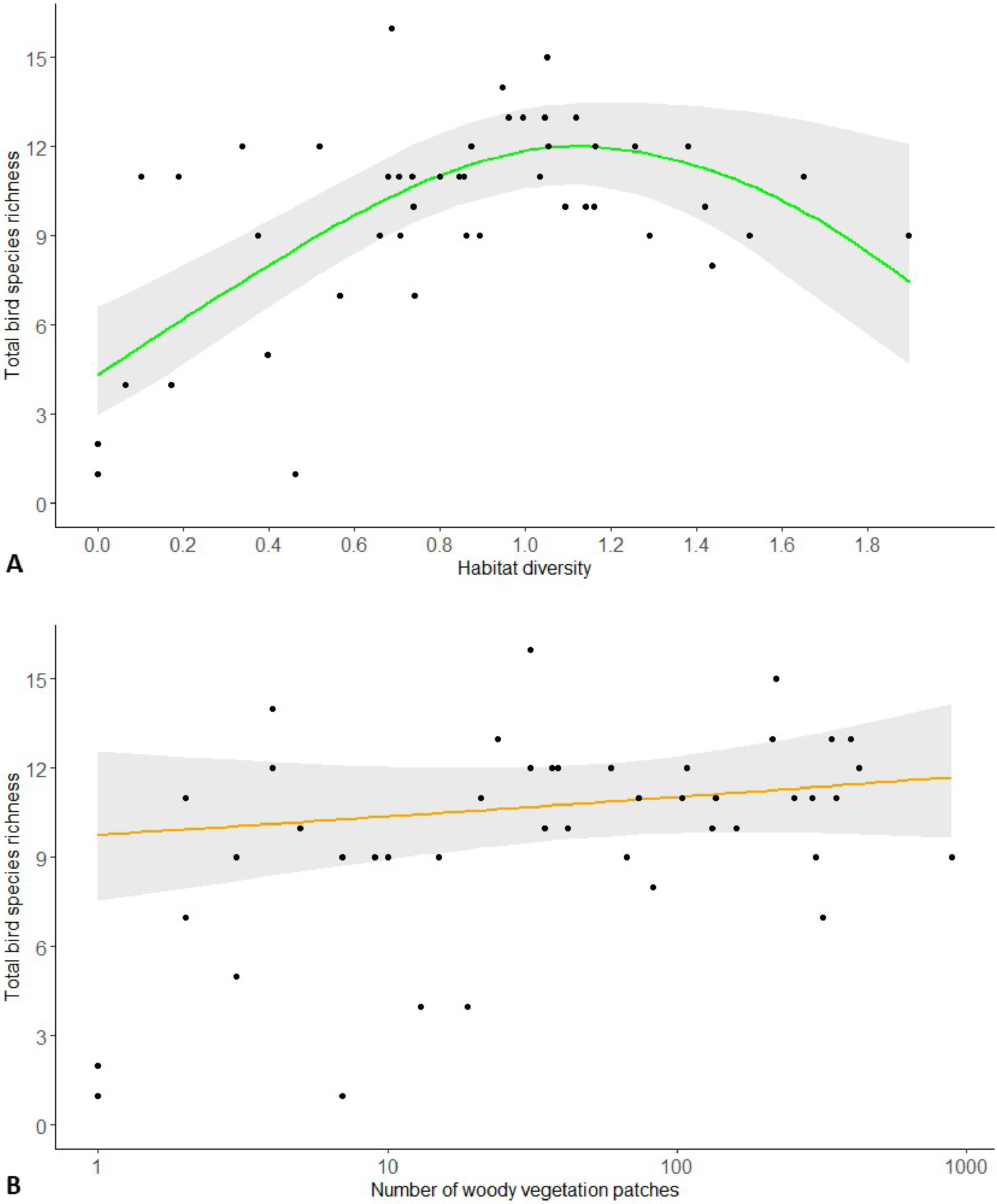

Fig. 3. Visualisation of the relationships between total bird species richness and A) habitat diversity, resp. B) the number of woody vegetation patches according to the best-supported generalised linear model. Shaded areas correspond to 95% confidence intervals. In addition, the estimates from the best model for each response variable are shown.

nonparametric functions (spline.correlog function from the R package "ncf"; Bjornstad 2019) with 95% confidence intervals computed using a bootstrap with 1,000 replications. No significant autocorrelation was indicated in any model. All analyses were performed in software R (version 4.1.0; R Core Team 2021).

Results

Landscape heterogeneity

The median number of woody vegetation patches for study plots in the military area was 147 patches (mean = 206, SD = 37, range 1-892). In nearby

Table 3. Coefficients of the explanatory variables in the model that best explains variation in total bird species richness (see Table 2).

	Coefficient	SE	*P*
diversity	1.76924	0.42161	0.00003
diversity^2	–0.78521	0.22586	0.00051
log (patches)	0.02669	0.02881	0.35421

farmland (the control area), the median was five patches (mean = 13, SD = 20, range 0-73; see Fig. 2A). Statistical models supported the hypothesis that there is a higher number of woody vegetation patches in the military area. Specifically, the deviance of the model explaining the number of woody vegetation patches by the variable region was significantly lower than the deviance of the null model, and the models also differed in AIC when the model with the variable region showed a considerably lower value (delta AIC = 5.71; see Table 1A).

At study plots in the military area, habitat diversity (expressed as Shannon diversity index, see Material and Methods) varied from 0.337 to 1.436, with a mean = 0.926 (SD = 0.266). In nearby farmland (the control area), it varied from 0 to 1.898, with a mean = 0.681 (SD = 0.584; see Fig. 2B). For habitat diversity, a comparison of the null model and the model with the region as an explanatory variable did not support the hypothesis that there is higher habitat diversity in the military area. The models did not differ significantly in deviance and had similar AIC values (delta AIC = 0.68; see Table 1B).

Bird species richness

According to the data of Bušek & Reif (2017), the bird population showed higher species richness in the military area compared to the surrounding agricultural landscape, both for all species and for CC birds. Specifically, the average number of species in military plots was 11.2 (SD = 1.8), and in control plots 7.8 (SD = 4.2). On the other hand, the average number of CC species in military plots was 1.3 (SD = 1.1) and in control plots 0.6 (SD = 0.8). For the list of recorded species, see Table S1.

Testing four models representing different combinations of the effects of the number of woody vegetation patches and habitat diversity on the total bird species richness partly confirmed our hypothesis that landscape heterogeneity affects total bird species richness. The best model with the lowest AIC contained a linear effect of the number of woody vegetation patches and a quadratic effect of habitat diversity without interactions (Table 2). According to this model, the relationship between habitat diversity and total bird species richness was hump-shaped (Table 3, Fig. 3). The other models had considerably worse performance (Table 2): two models had much higher AIC values (delta AIC > 6), and one model had a similar AIC value but a higher number of parameters, so it must be considered as less competitive.

The four models aiming to explain variation in the CC bird species richness by landscape heterogeneity partly confirmed our hypothesis. The best model with the lowest AIC value was the simplest one containing only linear main effects of habitat diversity and the number of woody vegetation patches (Table 2). According to this model, CC bird species richness significantly increased with an increasing number of woody vegetation patches but not with habitat diversity (Table 4, Fig. 4). The other models had higher or similar AIC values but contained a higher number of parameters (Table 2).

Discussion

Military areas have been recognised as biodiversity refuges with an unusually high proportion of protected species (Warren et al. 2007). Bušek & Reif (2017) confirmed this pattern specifically for birds and showed a higher species richness of CC birds in the military area compared to the nearby landscape. Warren et al. (2007) suggested that the reason for such an unusually high conservation value of military areas is the higher landscape heterogeneity due to the specific disturbance regime underpinned by the army's activities. To test this idea, our study has linked two measures of landscape heterogeneity with bird species richness data collected by Bušek & Reif (2017). Our results showed that the species richness of CC birds was greater with an increasing number of woody vegetation patches. At the same time, this aspect of landscape heterogeneity was higher in the military area than in nearby farmland. Interestingly, the second aspect of landscape heterogeneity, habitat diversity, was unrelated to CC bird species richness and did not differ between the military area and nearby farmland. Nevertheless, it showed a hump-shaped relationship with total bird species richness. Below we discuss these findings.

Birds of conservation concern benefit from woody vegetation patches

The number of patches of woody vegetation was significantly higher in the open landscape of the

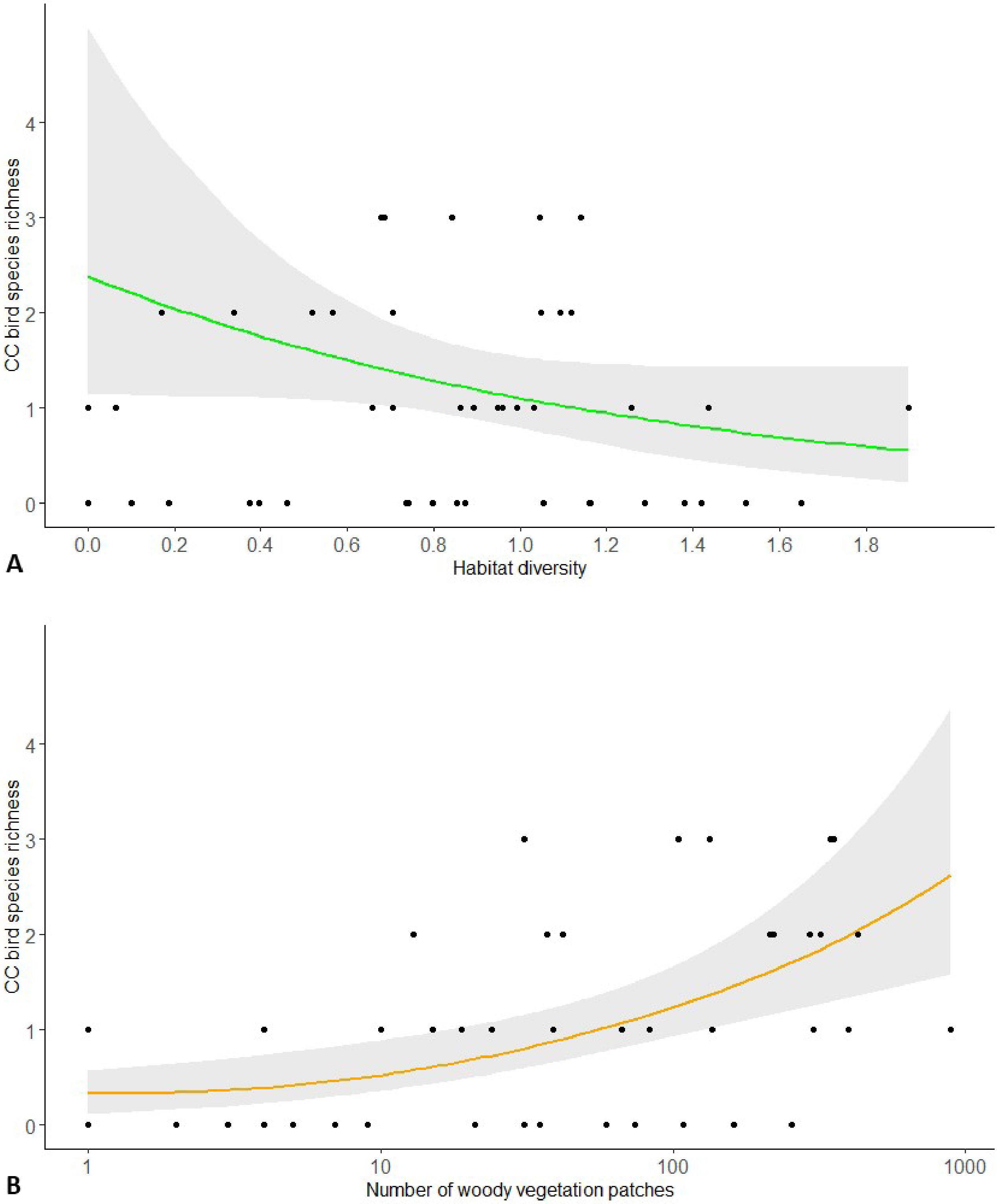

Fig. 4. Visualisation of the relationships between conservation concern (CC) bird species richness and A) habitat diversity, resp. B) the number of woody vegetation patches according to the best-supported generalised linear model. Shaded areas correspond to 95% confidence intervals. The estimates from the best model for each response variable are shown.

military area compared to the nearby farmland. This military area and farmland do not differ in their land cover composition from other such areas in the Czech Republic (Bušek & Reif 2017), so we can reasonably assume that the observed difference is a general feature characterising these kinds of landscapes, and some specific conditions in our study region were not responsible. The number of woody vegetation patches indicates how the woody vegetation is fragmented into a woodland-grassland matrix (Marcolin et al. 2021). Our findings, therefore, indicate that military areas have a finer-grained landscape mosaic in their

Table 4. Coefficients of the explanatory variables in the model that best explains conservation concerns for bird species richness (see Table 2).

	Coefficient	SE	*P*
diversity	–0.76832	0.42460	0.07040
log (patches)	0.34216	0.08769	0.00010

non-forest parts than agricultural landscapes. This phenomenon is most likely caused by military training disturbances and their high spatial heterogeneity (Warren et al. 2007). In contrast, in an intensively used agricultural landscape, a fine-grained mosaic of open and woodland habitats is undesirable, as it complicates the mechanised cultivation of soil blocks and reduces their profitability (Huth & Possingham 2007). Therefore, this mosaic has been significantly suppressed with increasing intensification in recent decades (Stoate et al. 2009).

The number of woody vegetation patches was positively related to the CC bird species richness, which explains the high number of CC bird species in the military area found by Bušek & Reif (2017). The reason why CC birds prefer environments with many woody vegetation patches can probably be attributed to their habitat preferences. CC bird species found in the open landscape of Central Europe (where our data were collected) are mostly the species adapted to the traditional extensive farmland. Many of these species need a combination of trees and shrubs with open habitats for nesting, foraging, defending territory or protecting against predators – whether in the form of individual trees (Pustkowiak et al. 2021), smaller or larger shrub patches (Tryjanowski et al. 2014), hedgerows (Morelli 2013) or woodlots (Dvořáková et al. 2022). With the advancing intensification of agriculture, these non-productive landscape elements were largely removed. Therefore, military areas with many woody vegetation patches represent a much-needed living space for these bird species, to which they do not typically have access in the current intensive agricultural landscape (Culmsee et al. 2021, Šálek et al. 2022). Indeed, CC birds recorded in the military area were mainly associated with a mosaic of woody vegetation and grasslands (e.g. corn bunting *Emberiza calandra*, red-backed shrike *Lanius collurio*, barred warbler *Sylvia nisoria*, Eurasian wryneck *Jynx torquilla*). This reasoning is confirmed by Reif et al. (2011), who showed that military areas are critical refuges for the species of early succession stages.

The positive relationship between the number of woody vegetation patches and the CC bird species richness was linear. However, it is worth mentioning that the number of patches was logarithmically transformed for the analysis. Therefore, the CC bird species richness increases with the non-transformed number of woody vegetation patches following a logarithmic function. It means that in homogeneous open landscapes, where no or only a few woody vegetation patches are present, even a small increase in their number may benefit CC birds. At the same time, in areas where the landscape mosaic is already relatively fine-grained, a further increase in the number of woody vegetation patches would not have such a strong effect. Similar patterns were found in birds' relationships to other types of woody vegetation elements in open landscapes, such as the number of solitary trees (Fischer et al. 2010, Carrasco et al. 2018) and the number of hedgerows or isolated bushes (Ceresa et al. 2012).

Total bird species richness is hump-shaped related to habitat diversity

Habitat diversity was the only factor (from those that we considered in our models) which affected the total bird species richness. This relationship was hump-shaped: habitat diversity increased the total bird species richness, but the number of bird species decreased above a particular habitat diversity value. This finding is not surprising in the context of recent research, which has revised the view on habitat diversity-species richness relationships: although originally these relationships were considered positive (Tews et al. 2004, McMahon et al. 2008), they may be absent (Hortal et al. 2009, Šálek et al. 2018) or negative under some circumstances (Chocron et al. 2015, Carrasco et al. 2018, Heidrich et al. 2020).

Increasing species richness with increasing habitat diversity is a well-known pattern in community ecology: multiple habitats represent different niches that different species can occupy. Increased niche availability reduces interspecies competition and thus allows the coexistence of more species in the same area. However, the existence of a quadratic relationship between species richness and habitat diversity is supported by the theory of Kadmon & Allouche (2007), who combined niche theory and island biogeography into one model. According to them, niche theory predicts a positive relationship between species richness and habitat diversity following the reasoning explained above, but area and dispersion limitations may create this relationship unimodal and even negative. Under these conditions, further diversification of habitats lowers their carrying capacity because their limited areas are too small to provide enough habitat for species (the "area-heterogeneity trade-off"; Allouche et al. 2012).

Consistent with this theoretical background, it can be assumed that in a relatively homogeneous landscape, increasing habitat diversity allows more bird species to coexist, but too high habitat diversity reduces the effective area available per species, leading to the absence or stochastic extinction of some species. Indeed, in recorded total bird species richness prevailed non-CC species with diverse requirements on specific (even though not rare) habitats — e.g. black woodpecker *Dryocopus martius*, mistle thrush *Turdus viscivorus*, and red crossbill *Loxia curvirostra*, which need non-fragmented forests or Eurasian skylark *Alauda arvensis* and meadow pipit *Anthus pratensis* which need large open space with fields and grasslands. To some extent of habitat diversity, these species can coexist, but the overall small area of their habitats can limit their co-occurrence.

Interestingly, we did not find a higher habitat diversity in the military area compared to the nearby agricultural landscape indicating that habitat diversity is not the factor responsible for high bird biodiversity in military areas. The absence of difference between the habitat diversity of the military area and the nearby landscape also informs about the environmental consequences of the disturbance regime associated with military activity. Although this regime increases landscape heterogeneity in terms of the number of woody vegetation patches (this study) and some other landscape elements such as ponds or surface heterogeneity (Aunins & Avotins 2018, Harabiš & Dolný 2018), it does not increase the number of different habitats, at least in categories we recognised here. Instead, habitat diversity seems to result from other kinds of human activities, such as different land uses and settlements.

Caveats

Two caveats can be identified concerning the data we used in this study. First, the data were collected in a single military area and nearby farmland. Therefore, the patterns we report here may be confined to the specific conditions in the study region and not valid for the other areas in Central Europe. Although we cannot exclude this possibility given our data, we consider it improbable. The land cover composition of the Hradiště military area corresponds well to the composition of the other large military areas in the Czech Republic (Bušek & Reif 2017), and the military training activities creating the landscape heterogeneity are similar to those performed elsewhere (Skokanová et al. 2017). Therefore, we suggest that the environmental conditions and biota observed in the Hradiště military area represent similar areas, at least in the Czech Republic.

Second, a time lag exists between the year of bird data collection (2014) and the year of data collection on landscape heterogeneity (2018). If the landscape heterogeneity experienced major changes, its measures might not correspond to the bird data. This caveat is highly unlikely because no such changes were observed on the study plots (O. Bušek, J. Hernová, pers. observ.). Theoretically, vegetation succession could slightly alter the number of woody vegetation patches. Some previously isolated patches might become connected, while some new patches could arise due to the growth of shrubs or trees that were previously not detectable. However, the four-year period was relatively short regarding the successional changes that would be important for birds. Significant changes in bird species richness in response to vegetation succession are reported at the time scale of tens of years in the Northern temperate zone (Wesołowski & Tomiałojć 1997, Holmes & Sherry 2001), while the time lag is only four years in our case. Therefore, although we cannot exclude subtle changes in patch numbers due to vegetation succession on the study plots, these changes are unlikely to alter the patterns in our data.

Conclusions and conservation implications

The results show that different aspects of landscape heterogeneity affected the total bird species richness and CC bird species richness of our studied open landscapes. Specifically, CC bird species richness was related to the number of woody vegetation patches but not habitat diversity. This finding is probably because the CC bird species richness was represented by a specific subset of species with similar habitat preferences to a woodland-grassland mosaic (as described above). Thus, it was related to the amount of one specific habitat (scattered woody vegetation patches), and other habitats probably did not matter for those species. On the contrary, the total bird species richness was related to habitat diversity but not to a higher number of woody vegetation patches, which means that the preference of the CC bird subset was not reflected in the preference of the whole bird community. Indeed, it has been reported that the spatial patterns of species richness are driven mainly by common generalist species rather than by rare ones (Lennon et al. 2004, Dvořáková et al. 2022), which may also explain the differences between the total species richness and the CC bird species richness patterns because the CC birds are typically rare.

Our study shows that open landscapes of military areas may host an exceptionally high number of birds of conservation concern compared to the typical agricultural landscape due to fine-grained woodland-grassland mosaic with patchy or singular point woody vegetation. As this fine-grained mosaic is a by-product of the disturbances caused by military training, it is therefore beneficial from the conservation perspective to maintain the continuity of these training activities or, in the case of military areas that have already been abandoned, to replace the activities of the army with conservation management, which will have a similar ecological impact. To this end, the established conservation management should be adequately heterogeneous in the intensity, time and space to achieve grain fineness and effective in maintaining early succession habitats to ensure the persistence of an open matrix.

Our study also provides general recommendations for protecting biodiversity in military areas and the typical agricultural landscape. Although environmental heterogeneity is generally considered desirable in nature conservation, it should be remembered that heterogeneity has several facets, each of which can affect the community differently. For example, to promote birds of conservation concern in a landscape with an open character, providing a fine-grained landscape mosaic with a high number of shrub and tree patches in an open matrix is beneficial. Especially in the homogenous open landscape, such as intensively managed farmland, adding even a small amount of these woody patches can have a tremendous impact. On the other hand, to enhance total bird species richness, the habitat diversity should be increased, but just to a particular value which does not harm populations by area limitation. Further research is needed to specify what rate of habitat diversity is still beneficial for what taxa and how it is affected by the spatial arrangement of habitats in the landscape.

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Author Contributions

J. Reif conceived the idea, J. Reif with O. Bušek and J. Hernová designed the study, O. Bušek and J. Hernová carried out the fieldwork for bird and landscape data, respectively. L. Dvořáková analysed the data and led writing with inputs from J. Reif.

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Supplementary online material

Table S1. List of recorded species (https://www.ivb.cz/wp-content/uploads/JVB-vol.-72-2023-Dvorakova-et-al.-Table-S1.xlsx).

Článek 3

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Habitat changes explain shifts in bird community composition in abandoned military training areas: Lessons for conservation

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ABSTRACT

Military training areas are important biodiversity refuges and may serve as viable components of regional conservation networks, mainly due to the blocking of ecological succession by the disturbance regime creating a heterogeneous open habitat mosaic hosting many threatened species. However, European armies have undergone downsizing over the past decades and numerous military training areas have been abandoned. The assessment of the consequences of this abandonment for biodiversity would show us whether these abandoned areas still provide conservation benefits. For this purpose, we carried out bird surveys in 30 abandoned military training areas in Czechia. The surveys were performed in two periods (2009 and 2020–2021) to track small-scale changes in land cover and bird abundance after the areas were abandoned in the 1990s. We tested (i) whether changes in bird abundance were related to land cover changes and (ii) whether the observed bird species' responses to the land cover changes can be explained by species-specific characteristics. Multivariate spatial analyses uncovered significant shifts in land cover composition towards a higher representation of dense shrub, forest and built-up areas at the expense of open areas represented by grassland and sparse shrub. These land cover changes explained a small but significant part of bird abundance variation across the areas. Correspondingly, species benefiting from these land cover changes were associated with dense scrub or forest, such as the Common Chiffchaff, Willow Warbler, or Eurasian Blackcap, whereas species suffering from these changes were associated with grassland, such as the European Stonechat and Eurasian Skylark. Phylogenetically informed interspecific analysis aiming to explain changes in bird abundance between periods confirmed that population declines were linked to open habitat preference, while population increases were linked to the preference for dense shrub and forest. In addition, we found that protected species increased their abundance, most likely due to the existence of conservation management that kept their habitats available. These patterns indicate that military training areas transform toward later successional stages after their abandonment with corresponding changes in bird community composition. However, these changes may not necessarily be negative provided that species of conservation concern enjoy the support of conservation management.

1. Introduction

One of the most pressing global problems is the biodiversity crisis (Hautier et al., 2015), largely caused by the loss of natural habitats and the homogenization of the environment (Newbold et al., 2015). In Europe, these adverse impacts often concern farmland which has deteriorated due to intensive exploitation or abandonment of once extensively cultivated semi-natural habitats (Stoate et al., 2009). These habitats are common in traditional farmland but rare in intensively used modern agricultural landscapes (Tryjanowski et al., 2011). In such landscapes, they act as biodiversity refugia that are usually of small spatial extent and contribute to mitigating the biodiversity crisis (Dvořáková, Kuczyński, et al., 2022; Pustkowiak et al., 2021). Apart from original natural hotspots such as calcareous grasslands (Habel et al., 2013) such refugia include various anthropogenic installations such as unreclaimed post-mining sites (Šálek, 2012), brownfields (Meffert & Dziock, 2012) or military training areas (Warren et al., 2007).

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Military training areas (MTAs) provide a great potential for nature conservation due to mutual benefits from military and conservation actions (Warren et al., 2007). They are found in all major ecosystems (e.g. Cummings et al., 2018; Valente et al., 2020; Wolff et al., 2018) with a total area estimated at up to 5–6 % of the Earth's land surface (Zentelis & Lindenmayer, 2014). In Europe, MTAs sustain various early successional, nutrient-poor habitats of high conservation importance such as grasslands, pet bogs, heaths or sand dunes, often on extraordinarily large scale (Aunins & Avotins, 2018; Ellwanger & Reiter, 2019; Grzywaczewski et al., 2014; Hirst et al., 2005). European MTAs were not affected by intensive agriculture and urbanization that took place in surrounding landscape in the second half of 20th century (e.g. Havlíček et al., 2018). The existence of military activities resulted in fine-scale disturbance regime creating heterogeneous landscape mosaic with high habitat and microhabitat diversity where numerous species with different ecological requirements coexist (Dvořáková et al., 2023; Warren et al., 2007). Unsurprisingly, many studies report that European MTAs hosts rich biodiversity and extraordinarily high number of species of conservation concern, often disturbance-dependent specialists (Culmsee et al., 2021; Harabiš & Dolný, 2018; Lindenmayer et al., 2016; Warren & Büttner, 2008).

However, many European MTAs have been abandoned by the army since the 1990s (Ellwanger & Reiter, 2019). With the disappearance of military disturbances, other factors that shape the landscape come into play – be it natural succession or various human activities such as construction, recreation or active nature protection (Reif et al., 2023). A still unanswered question is how the impacts of these land use types are reflected in the habitat composition of abandoned MTAs over time and what is the response of local communities to this change. Here we address this question by studying the changes of habitat composition in abandoned MTAs in Czechia (Central-Eastern Europe) and showing how these changes affect the composition of their avifauna. For this purpose, we mapped habitats and bird occurrence in 30 abandoned MTAs in two survey periods separated by a 12-years interval.

Specifically, the aims of this study are (i) to describe the changes in habitat composition between periods; (ii) to investigate the impact of these habitat changes on changes in bird community composition; and (iii) to determine the bird species characteristics associated with these changes. We hypothesize that the proportion of forest and dense shrubs increased at the expense of open habitats due to the dominance of ecological succession as a principal driver of habitat change (Jentsch et al. 2009). Moreover, we predict that these habitat changes resulted in the strongest declines of species that use open habitats (Bystřický et al., 2023), are habitat specialists (Le Viol et al., 2012) and are of higher conservation concern at the national level (Koleček et al., 2014a).

2. Material and methods

2.1. Study sites

The research took place in Czechia, a Central-Eastern European country, in 30 abandoned MTAs scattered throughout the country (Fig. 1). They form a representative sample of all abandoned MTAs present in Czechia (Reif et al., 2011). These abandoned MTAs are rather smaller in size (mean = 0.95 km^2, range = 0.21–3.51 km^2), and located at lower or mid altitudes (mean = 318 m, range = 200–625 m). They

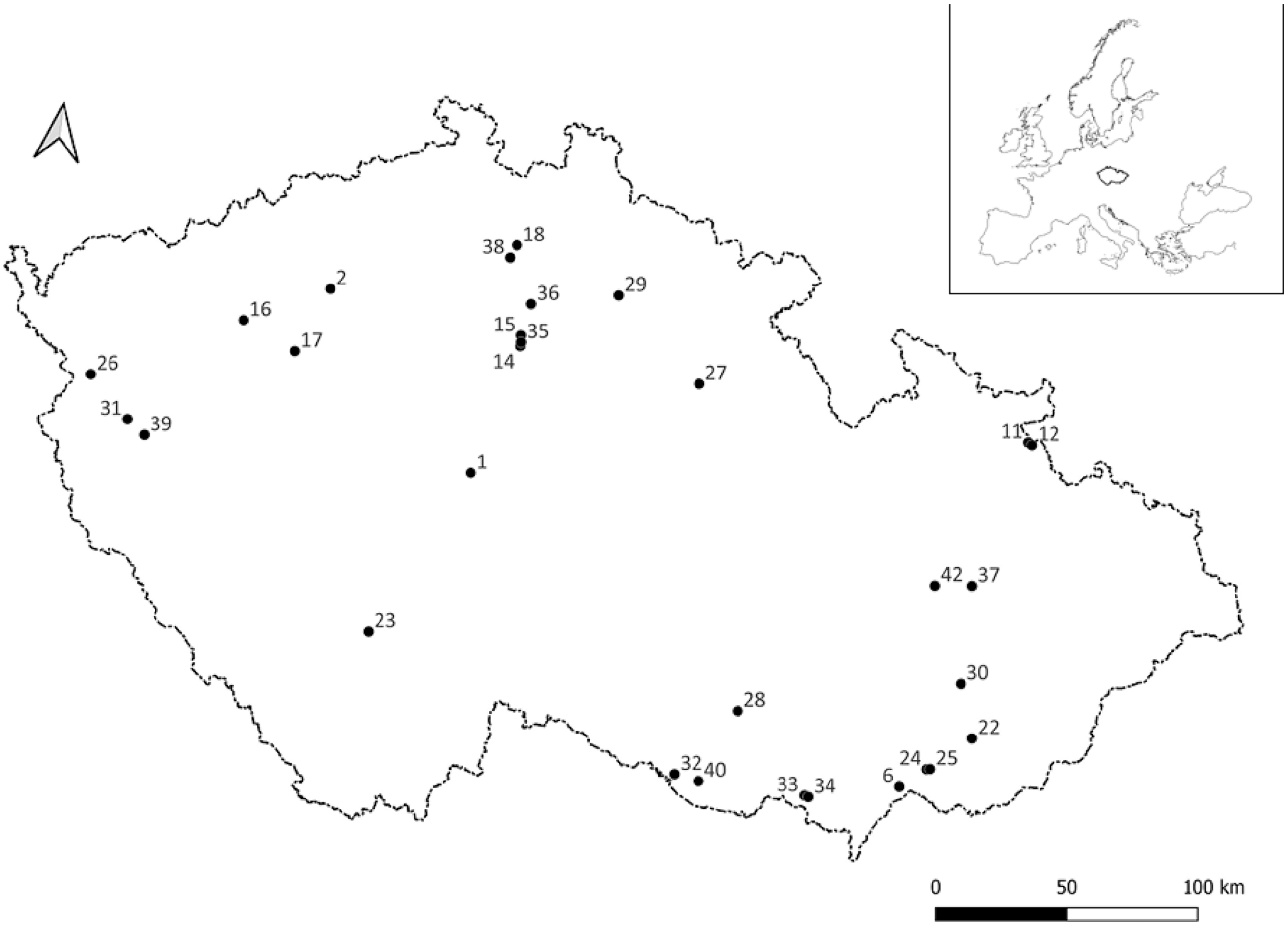

Fig. 1. Abandoned military training areas surveyed in 2009 and 2020–2021 in Czechia. Inset shows position of Czechia in Europe.

were abandoned by the army in mid-1990s (Reif et al., 2023), and are covered by open or semi-open habitats (grasslands, sometimes with scattered shrubs and trees) with enclaves of spontaneously formed woodlands (scrublands, woodlots, riparian forests). See Reif et al. (2023) for more details on environmental conditions in the study sites.

2.2. Habitat mapping

The habitat composition of each abandoned MTA was assessed prior to each bird survey period, i.e., in 2008 and 2019, respectively. We recognized six habitat types (Table 1): bare ground (unvegetated patches of soil or sand), grassland (herbaceous vegetation without woody plants), sparse shrub (grassland with low density of shrubs; it is possible to walk through easily), dense shrub (shrubs forming continuous stands; walking is not possible), forest (stands of continuous tree vegetation) and built-up areas (areas of human infrastructure such as buildings and paved surfaces). The entire area of each abandoned MTA was divided into unique habitat polygons, each formed by one of the habitat types listed above, i.e., none of the habitat polygons overlapped (Fig. 2). We used aerial photographs followed by field validation to create maps of habitat types in individual abandoned MTAs.

2.3. Bird data

Bird surveys were performed in two periods, first in 2009 and second in 2020–2021. In the second period, part of the abandoned MTAs was surveyed in 2020 and the rest in 2021 for logistic reasons, i.e., none of the MTAs were surveyed in both years of that period. During the survey, an observer walked throughout the whole area of a given abandoned MTA and recorded position of every bird individual into a map (aerial photograph). We used paper maps (scale 1:2600) in the first period and electronic maps in the ObsMapp smartphone survey application (https://observation.org/apps/obsmapp/) in the second period. In each abandoned MTA, we performed two bird mapping visits during the peak breeding season (April – June) in each period, separated by 3–5 weeks, to cover both early and late breeders. The visits took place at a time of the peak of bird vocal activity (5:00 – 10:00) because the recorded individuals are typically singing males. See Bystřický et al. (2023) for more details on bird occurrence mapping.

For further analysis, we only considered birds for whose we could assume a relationship to the areas. Thus, we excluded overflying individuals and species for which there are no or very few breeding records in Czechia, indicating that their occurrence in our records was probably the case of migration or vagrancy: Ortolan Bunting (*Emberiza hortulana*) and Redwing (*Turdus iliacus*). Moreover, we excluded species for which the field survey technique, designed to cover mainly small territorial passerines (Bibby et al., 2000), was not suitable to reliably assess their occurrence. That concerned raptors, waterfowl, aerial plankton feeders, and nocturnal species.

For each species, we collected information on their ecological traits and conservation status from national literature (Supplementary Table S1). Specifically, we expressed (i) the habitat preference for successional stage as a position of each species along a gradient from forest to grassland extracted from Koleček et al. (2014b). They assigned one or more habitats from forest interior (value = 1) to open treeless landscape (value = 7) to each species according to the literature information and calculated a mean across the habitat values for every species. (ii) We used habitat specialization from Reif et al. (2010) who used country-wide common bird monitoring data (consisting of 2555 sampling sites) and calculated species specialization index for every bird species as a coefficient of variation of its abundance across eight habitat types following Julliard et al. (2006). (iii) As a measure of conservation status, we used classification of conservation concern according to the national legislation on protected species (Act No.114/1992 Coll. on Nature Conservation and Landscape Protection, 1992, https://www.zakonyprolidi.cz/cs/1992–114) recognizing species as unprotected (value = 0), endangered (1), highly endangered (2) and critically endangered (3). We used the conservation status as an ordinal variable following Juslén et al. (2013).

Table 1
Habitat types recognized in military training areas, their abbreviations and representation in respective survey periods (2009 and 2020–2021).

Habitat type	Abbreviation	Number of grid cells	
		2009	2020–2021
Bare ground	Ground	49	74
Grassland	Grassland	493	369
Sparse shrub	Shrub_spar	1277	1291
Dense shrub	Shrub_dense	474	733
Forest	Forest	599	659
Built-up area	Built-up	0	43

Changes in bird populations observed in MTAs may be underpinned not only by local habitat changes, but also by large-scale drivers such as climate change, regional land use changes or population dynamics at the landscape scale. To take these drivers into account, we used national population trend of each species (Supplementary Table S1). The trends were calculated on data collected within a national breeding bird monitoring scheme in Czechia (Jednotný program sčítání ptáků, JPSP) coordinated by the Czech Society for Ornithology. JPSP is based on standardized fieldwork of skilled volunteers covering the area of the whole country, see Reif et al. (2013) for more details. The trends provided for purposes of this study cover the period 2009–2021 corresponding to our survey years and were estimated using log-linear models ran in RTRIM (Bogaart et al., 2020).

2.4. Spatial data processing

After obtaining habitat and bird data, i.e., habitat polygons and localized bird records, we covered each abandoned MTA by a squared grid with cells of 100 x 100 m size (Fig. 2). Using this approach even very local habitat and bird abundance changes can be detected. At the same time, this cell size broadly corresponds to breeding territory sizes of small territorial passerines, accounting for the majority of species in our dataset, in the northern temperate zone (e.g., Storch, 1998; Jones, 2011; Skorupski et al., 2018). For each grid cell, we calculated the relative areas of individual habitat types and the abundances of respective bird species in each period. For the bird abundance estimation, we took the maximum count of individuals of a given species from both visits performed in a given grid cell. Finally, we calculated the change in relative areas of respective habitat types between periods in each grid cell by subtracting the data of the second period from the data of the first period. In the same way, we calculated the change of abundance of every bird species between periods.

For further analysis, we considered only the cells fully covered by MTAs (n = 1,930), i.e., we excluded all cells overlapping MTAs' borders to avoid possible effects of altered conditions near edges and effects of unequal grid cell size. Also, we excluded all cells (n = 11) where overall bird abundance was zero in both periods. Thus, the final number of considered cells was 1,919.

2.5. Statistical analyses

We performed multivariate redundancy analyses (RDAs) to assess: (i) changes of habitat composition between periods; (ii) changes in bird community composition between periods; (iii) an effect of changes in habitat composition on the changes in bird community composition between periods; (iv) the difference between species of conservation concern and the other species in responses to habitat composition changes between periods. For this purpose, we ran four RDA models with grid cells as statistical units. Model 1 used relative covers of individual habitat types in respective grid cells as response variables, period

Fig. 2. Example of a studied abandoned military training area with habitat types and all bird observations recorded in 2020. The area is overlaid by a square grid with cell size 100 x 100 m. Note that only three out of six habitat types were recognized in this military training area.

as a categorical explanatory variable with two levels (first and second) and identity of the studied abandoned MTAs as a conditioning variable. Model 2 had the same structure, but bird abundances in respective grid cells were the response variables instead of habitat types. Model 3 included changes in bird abundances in individual grid cells between periods as response variables and related them to the changes in relative covers of habitat types as the explanatory variables. Model 4 also included changes in bird abundances and habitat types between periods, but we summed the changes for species of conservation concern and for the other species before this analysis. In this model, we tested whether changes in abundance of species of conservation concern are associated with habitat types being different from those associated with the changes in the other species. Bird abundance data were transformed by a natural logarithm as log(x) + 1 prior to the analysis to conform model assumptions, but zero abundances were kept as zero (Anderson et al., 2006).

Before running the RDAs, we investigated the presence of spatial autocorrelation in our data. We adopted the distance-based Moran's eigenvector maps (dbMEM) approach (Legendre & Legendre, 2012). First, we constructed a combined staggered matrix of dbMEM spatial eigenvectors based on the coordinates of centers of individual grid cells, using a function *create.dbMEM.model()* from an R-package 'adespatial' (Dray et al., 2023). In the next step, we performed three auxiliary RDAs where the responses (the same as defined above) were detrended via the coordinates of centers of individual grid cells and the explanatory variables were dbMEM spatial eigenvectors, using a function *rda()* from an R-package 'vegan' (Oksanen et al., 2022). If the subsequent permutation tests of these auxiliary models were significant, spatial autocorrelation needed to be taken into account (Borcard et al., 2018). We found a significant spatial autocorrelation for Models 1 (ANOVA like permutation test: $F_{177,3660} = 3.3$, $p = 0.001$) and Model 2 (ANOVA like permutation test: $F_{177,3660} = 1.8$, $p = 0.001$), but not for Model 3 (ANOVA like permutation test: $F_{543,1375} = 1.0$, $p = 0.495$) and Model 4 (ANOVA like permutation test: $F_{543,1375} = 1.1$, $p = 0.172$). To fix this problem, we detrended the response variables via the coordinates of centers of individual grid cells (Borcard et al., 2004) and included statistically significant ($p < 0.05$) spatial eigenvectors, chosen by forward selection, as additional conditioning variables. In case of Model 3 and 4, the variable sparse shrub was removed from the explanatory variables as it was causing multicollinearity according to the VIF analysis run by a function *vif.cca()* in R-package 'vegan'. The statistical significances of constrained axes and explanatory variables in respective Models were derived using ANOVA like Monte Carlo permutation tests considering model-specific design of plots and blocks. Model 1 and 2: plots = grid cell identity, no permutations, blocks = MTAs identity, free permutations (n = 999); Model 3 and 4: blocks = MTAs identity, free permutations (n = 999). The share of variability explained by individual predictors was derived using a function *rdacca.hp* from an R-package 'rdacca.hp' (Lai et al., 2022).

To identify the species characteristics associated with changes in bird abundance between periods, we used the bird species scores along the first canonical axis obtained in Model 2 (Supplementary Table S1). These scores quantify how much the abundance of a given species changed across the individual grid cells between periods controlling for the effect of spatial autocorrelation – the more positive scores signify the greater population increase of a given species, while the more negative scores the greater population decrease. Then we related these scores as a response variable to the explanatory variables including species' habitat preference, habitat specialization, conservation status, and national population trend in a generalized least squares model (GLS) with phylogenetic correlation structure *corPagel()*, using *gls()* function from 'nlme' R-package (Pinheiro et al., 2023). To allow for the phylogenetic correlation structure in the GLS, we included a consensus phylogenetic tree constructed using a function *consensus.edges()* from 'phytools' R-package (Revell, 2012). This consensus tree was based on 1000 random phylogenetic trees of all 85 observed bird species, generated at BirdTree.

org (Jetz et al., 2014) from “Stage 2 MayrParSho Ericson” backbone tree. In order to obtain comparable model parameter estimates, we standardized the explanatory variables to zero mean and unit variance prior to the analysis. The model met the assumptions in terms of multicollinearity and non-independence of residuals, examined by plots produced by a function *check_model()* from ‘performance’ R-package (Lüdecke et al., 2021).

All statistical analyses were performed in R software 4.3.1 (R Core Team, 2023). All data and code linked to this study are available in Dvořáková et al. (2024).

3. Results

In total, we recorded 85 species during our survey after excluding the species unsuitable for the analysis: 75 species and 8,834 individuals in the first period, and 81 species and 8,914 individuals in the second period.

According to the RDA Model 1, the changes in relative cover of individual habitat types in the abandoned MTAs were modest – the first canonical axis, representing the difference between periods, explained only 0.5 % of the total variability in habitat composition across all grid cells. However, the change in habitat cover was significant (ANOVA like permutation test: $F_{1,3777} = 20.8$, $p = 0.001$) indicating that some habitats expanded, while some others retreated. In this respect, relative cover of grasslands and sparse shrub decreased, whereas the relative cover of dense shrub, forest, bare ground and built-up areas increased (Fig. 3a).

Similar to the habitat composition, bird community composition also showed relatively small, but significant changes (ANOVA like permutation test: $F_{1,3800} = 7.8$, $p = 0.001$) in the abandoned MTAs between periods as indicated by the RDA Model 2. Here, the first canonical explained 0.2 % of the total variability in bird community composition across grid cells. The species with the most negative scores along this axis, indicating the greatest decrease of abundance in grid cells between periods, were Whinchat (*Saxicola rubetra*), Grasshopper Warbler (*Locustella naevia*), and European Greenfinch (*Chloris chloris*). On the contrary, the species with the most positive scores, indicating the greatest increase in abundance, were Woodlark (*Lullula arborea*), Hawfinch (*Coccothraustes coccothraustes*) and European Robin (*Erithacus rubecula*) (Fig. 3b).

The effect of habitat changes on changes in bird abundance in grid cells was evaluated by the RDA Model 3. Habitat changes explained ca 0.5 % of the variability in changes in bird species composition in five canonical axes, where first two axes explained a significant portion of variance (0.2 % and 0.1 %, respectively, Fig. 4). The highest share of the total variability in changes in bird abundance was explained by MTA identity (88.2 %), followed by the cover of dense shrub (6.1 %), grasslands (2.4 %), forest (2.2 %), built-up areas (0.6 %) and bare ground (0.4 %). The first RDA axis (ANOVA like permutation test: $F_{1,1889} = 4.0$, $p = 0.001$) showed that the key driver was the increase in dense shrub cover (ANOVA like permutation test: $F_{1,1889} = 3.4$, $p = 0.001$) and, to lesser extent, in forest cover (ANOVA like permutation test: $F_{1,1889} = 2.5$, $p = 0.001$). The species most benefiting from these increases were Willow Warbler (*Phylloscopus trochilus*), Blackcap (*Sylvia atricapilla*), Eurasian Blackbird, Common Chiffchaff (*Phylloscopus collybita*), and Common Chaffinch (*Fringilla coelebs*) as indicated by their position at the positive part of this axis (Fig. 4). In contrast, European Stonechat (*Saxicola rubicola*), Eurasian Linnet (*Linaria cannabina*), and Eurasian Skylark (*Alauda arvensis*) were associated with the negative part of the first RDA axis indicating that they suffered from these habitat changes (Fig. 4). In addition, increasing relative area of bare ground (ANOVA like permutation test: $F_{1,1889} = 0.9$, $p = 0.598$) and built-up areas (ANOVA like permutation test: $F_{1,1889} = 1.4$, $p = 0.033$) were associated with the negative part of this axis. The second axis (ANOVA like permutation test: $F_{1,1889} = 2.2$, $p = 0.020$) depicted a gradient from increasing relative cover of forest and grassland (ANOVA like permutation test: $F_{1,1889} = 1.5$, $p = 0.001$) (in the negative part) to increasing relative cover of dense shrub and bare ground (in the positive part).

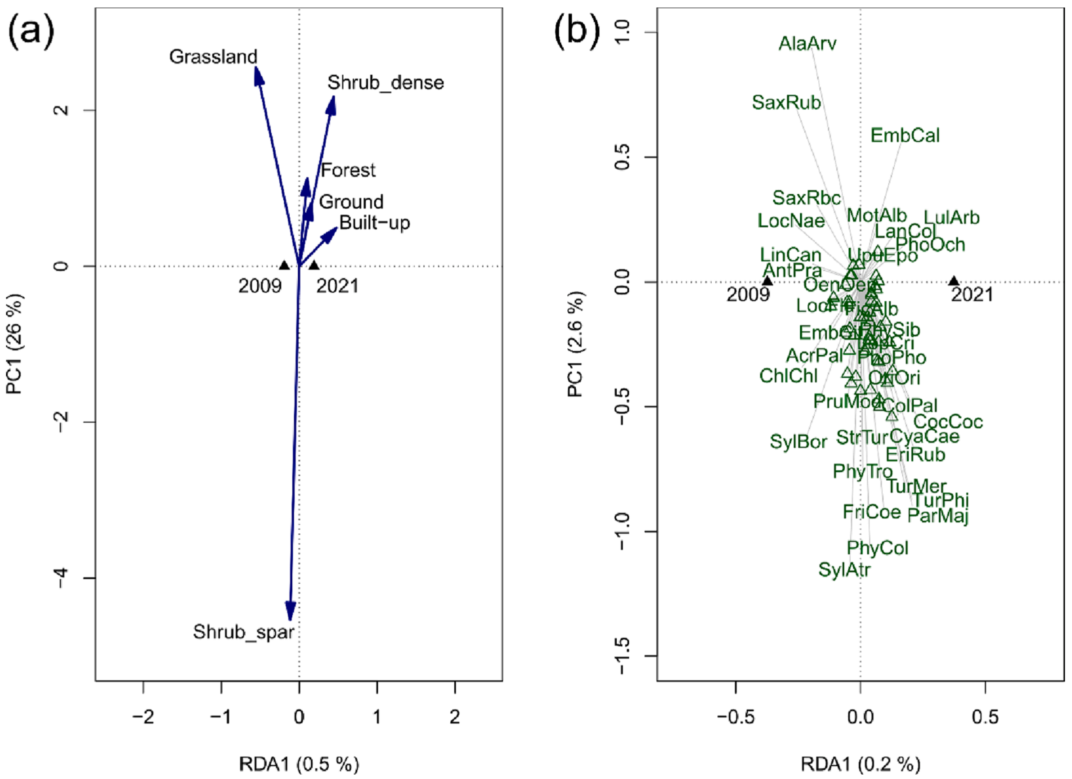

Fig. 3. Results of the RDAs showing changes in (a) relative cover of respective habitat types and (b) bird species’ abundance between two survey periods (2009 and 2020–2021) in abandoned military training areas. See Table 1 for abbreviations of habitat types. See Supplementary Table S1 for abbreviations of bird species.

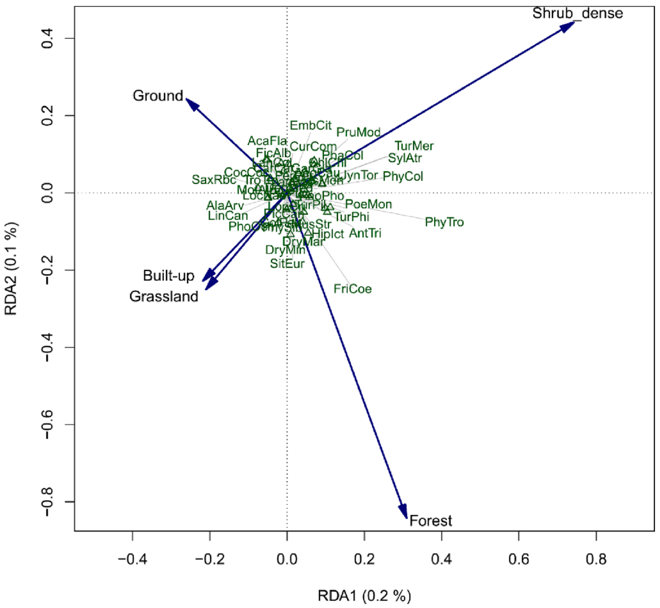

Fig. 4. Results of the RDA relating changes in abundance of respective bird species to changes in relative cover of individual habitat types between two survey periods (2009 and 2020–2021) in abandoned military training areas. See Table 1 for abbreviations of habitat types, and Supplementary Table S1 for abbreviations of bird species.

While the Nuthatch (*Sitta europaea*) and European Robin were associated with the negative part (Fig. 4) and likely benefited from increasing forest cover, the Yellowhammer (*Emberiza citrinella*) and Corn Bunting (*Emberiza calandra*) showed the opposite (Fig. 4) and were likely supported by increases of dense shrub and bare ground.

The RDA Model 4 model focused on the effects of changes in cover of respective habitat types between periods on the species of conservation concern in comparison with the other species (Fig. 5). Besides MTA identity explaining 84.1.% of variability, the habitat types most involved in these effects were dense shrub (9.6 %), built-up areas (2.1 %), forest (1.9 %), and grassland (1.7 %). The first RDA axis (2.4 % of variance explained, ANOVA like permutation test: $F_{1,1892} = 46.9$, $p = 0.001$) showed that increasing abundance of species that are not of conservation concern is associated with increasing cover of dense shrub (ANOVA like permutation test: $F_{1,1889} = 35.0$, $p = 0.001$) and forest (ANOVA like permutation test: $F_{1,1889} = 9.7$, $p = 0.001$) between periods. Changes in abundance in species of conservation concern were associated with the second RDA axis which was, however, insignificant (explained 0.3 % of variance, ANOVA like permutation test: $F_{1,1892} = 5.2$, $p = 0.180$). Decreasing abundance of these species between periods was associated with increasing cover of forest (ANOVA like permutation test: $F_{1,1889} = 9.7$, $p = 0.001$), build-up areas (ANOVA like permutation test: $F_{1,1889} = 3.9$, $p = 0.011$) and grassland (ANOVA like permutation test: $F_{1,1889} = 4.1$, $p = 0.016$).

Generalized least squares model that took the effect of national population trend into account revealed that species' habitat preference and conservation status were significantly related to changes in bird abundance between periods (Table 2). Specifically, preference for earlier successional stages showed a negative relationship indicating that this characteristic predicts population declines. On the contrary, higher conservation status showed a positive relationship with the

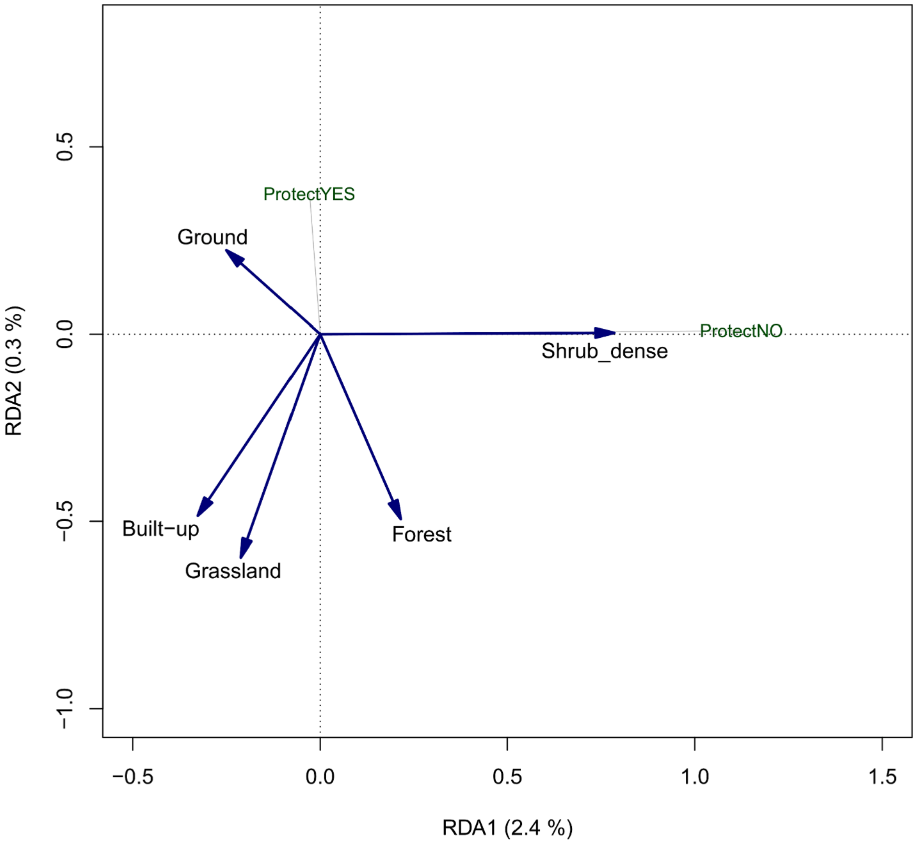

Fig. 5. Results of the RDA relating changes in abundance of bird species of conservation concern (ProtectYES) and the other species (ProtectNO) to changes in relative cover of individual habitat types between two survey periods (2009 and 2020–2021) in abandoned military training areas. See Table 1 for abbreviations of habitat types.

Table 2
The standardized effects of species characteristics and national population trends of species on bird population change (expressed as scores obtained from RDA Model 2, see Fig. 3b) between two survey periods (2009 and 2020–2021) in abandoned military training areas estimated by a phylogenetic GLS model. Statistically significant results are in bold.

Model term	Estimate	SE	t	p
Intercept	0.009	0.005	1.7	0.096
Habitat preference	**−0.043**	**0.010**	**−4.3**	**<0.001**
Habitat specialization	−0.012	0.011	−1.1	0.272
Conservation status	**0.043**	**0.010**	**4.3**	**<0.001**
National population trend	**0.038**	**0.010**	**3.7**	**<0.001**

abundance change indicating that conservation concern is associated with population increase between periods. Habitat specialization was not significantly related to changes in bird abundance, but national population trend showed a positive relationship (Table 2). The model explained 32 % of the variability in bird species scores.

4. Discussion

Between the two survey periods (2009 and 2020–2021), local habitat composition in the Czech abandoned MTAs changed slightly, but significantly towards the expansion of built-up areas and the increasing dominance of later successional stages, i.e., dense shrubs and forest patches, while the cover of the early successional stages, grassland, and sparse shrubs, decreased. These changes corresponded with the changes in abundance of bird species inhabiting the above-mentioned habitat types: the abundance of arboreal and forest-dwelling species increased, whereas the abundance of species of open habitats declined. Changes in forest, grassland and dense shrub cover were also drivers of changes in bird community composition, as confirmed by statistical analysis showing a significant, but small proportion of explained variance. Birds of conservation concern increased their abundance, but suffered from local expansion of forest, built-up areas and grassland. National population trends were positively related to changes in bird abundance in MTAs indicating that other drivers than local habitat changes may be involved in shaping bird abundance between periods.

At the beginning of the 21st century, the conservation potential of the abandoned MTAs has been clearly recognized (Cizek et al., 2013; Culmsee et al., 2021; Reif et al., 2011) and these areas are often the target of conservation management (Dvorský et al., 2022). This also applies to some of the areas included in our study that are protected and managed. As the encroachment of woody plants on open habitats is one of the most widespread land cover changes in Czechia and elsewhere (Kupková et al., 2021; Ratajczak et al., 2012), the management is typically represented by activities that block these successional changes (Prach & Řehounková, 2006). These activities are necessary if the open habitats are left without use and their value for conservation deteriorates (Ratajczak et al., 2012). In the abandoned MTAs, these activities include woody plant cutting, pasture, mowing and vehicle rides (Reif et al., 2023). Our results indicate that this effort is not sufficient to prevent the overall advancement of ecological succession. This may be caused by insufficient protected area coverage in the abandoned MTAs. In our sample, only 48 % grid cells of abandoned MTAs have been legally protected, and the unprotected areas are exposed to various threats, most notably spontaneous encroachment of woody vegetation.

As an alternative, but not mutually exclusive explanation we suggest that the current level of management effort may not be sufficient to reverse the successional changes even in the protected areas. Funding for conservation is inevitably limited and conservation managers need to select the most valuable sites that deserve the highest effort (Sutherland, 2000). This means that some other areas are left unmanaged even though they are formally protected. This problem may concern the larger abandoned MTAs with a considerable proportion of forest patches. In these areas, the management effort concentrates on the largest open parts and small areas adjacent to the forest are exposed to encroachment (L. Dvořáková, *pers. obs.*). Moreover, conservation management is not always linked to the protection status of a given abandoned MTA. In some areas, the management is performed by non-governmental stakeholders (livestock keepers, off-road riders and fans of military history), typically in agreement with local conservation authorities (Dvořáková et al., 2022a, 2022b). These efforts are often locally effective but may diminish when the preferences of a given stakeholder change.

Changes in bird abundance and community composition mirrored the changes in the relative cover of individual habitat types. Species that showed the highest abundance increases were those with a preference for late successional stages. They obviously benefited from woody vegetation maturation in the abandoned MTAs as their preferred habitat expanded. This concerned common forest species such as the Eurasian Blackbird, Great Tit, Hawfinch or European Robin, as well as shrub-dwelling species such as the Common Chiffchaff and Eurasian Blackcap. Such population increases of forest birds are in line with general trends in bird populations at the country level (Storch et al., 2023), where these species increase not only due to woody plant encroachment, but also due to active forest management towards longer rotation periods and the creation of more heterogeneous stands (Reif et al., 2022a). Therefore, we suggest that the observed increase in the abundance of the forest species may not only result from changes that occur directly in the abandoned MTAs where we collected the bird data, but also from wider landscape changes whose consequences may spill over into our study areas (de Souza Leite et al., 2022).

Encroachment and maturation of woody habitat types are also likely drivers of the observed increase in the total number of species and individuals in the abandoned MTAs between periods. As forest and dense scrubland are the richest habitat types in terms of bird diversity and abundance in Czechia, whereas grasslands are typically species-poor (Reif et al., 2022b), it is possible that the gain of forest and dense shrub patches at the expense of grassland and sparse shrub underpinned the observed pattern in the total species richness and abundance in our study sites. The high number of species and individuals in habitats of the later successional stages is probably a result of the higher structural complexity and vertical heterogeneity of these habitats (Di Cecco et al., 2022), which provide more resources and thus increase opportunities for species coexistence (Remeš & Harmáčková, 2023).

Abundance of open habitat bird species declined, which may result from the open habitat loss in the abandoned MTAs. The above-discussed successional changes are an obvious candidate, but we can also speculate about additional problems that the open habitat species may face in the study areas. First, the loss of habitat cover *per se* may not be particularly problematic as the observed changes in relative areas were modest. However, the habitat structure may change considerably, but our data were not capable of capturing such changes. It may concern, for example, the herbaceous vegetation height that is required to be short in some species, such as the Eurasian Skylark (see Donald, 2004) whose abundance decreased, and the absence of management might underlie growth of herbs (Prach et al., 2001) even if the shrubs have not yet encroached the site. At the same time, management aiming to block successional changes may also be problematic for some species: woody plant cutting can remove some important habitat features that are used by some open habitat species (e.g. European Stonechat, Eurasian Linnet) for perching (Morelli et al., 2016); cattle pasture or mowing can result in nest destruction of grassland breeders (e.g. Grasshopper Warbler, Meadow Pipit *Anthus pratensis*) if carried out during their breeding season (Sharps et al., 2015).

Some of our observations of decreasing abundance between periods may also partly result from the national long-term trends in their populations, similarly to the increasing bird species. This may concern the Whinchat, which typically breeds in grassland and has declined since the 2010s in Czechia, likely due to the intensification of the use of upland meadows and pastures (Šťastný et al., 2021). More notably, the population change in the European Greenfinch, one of the species with the most precipitous decline in our data, may not be linked to habitat changes at all because this species is seriously affected by the spread of infectious *Trichomoniasis* disease (Lehikoinen et al., 2013). Indeed, this species is rather associated with dense shrubby habitats (Reif et al., 2010), so it may even benefit from their observed expansion, and thus habitat-driven population changes are quite unlikely in its case.

Built-up areas were the most expanding habitat type according to the RDA Model 1. It means that parts of the original semi-natural cover of the abandoned MTAs were transformed into paved areas, buildings and most notably photovoltaic power plants. Our data do not indicate that these changes were linked to increases in abundance in bird species nesting on buildings (e.g., Black Redstart *Phoenicurus ochruros*) or in suburban paved areas (e.g., Crested Lark *Galerida cristata*) (Šťastný et al., 2021). However, photovoltaic installations may have further contributed to declines in open habitat species such as Eurasian Skylark, Grasshopper Warbler, or Stonechat because these installations were built in open grassy sites that would provide habitat for such species (Kubelka et al., 2015).

Although habitat change explained a significant part of the variability in changes of bird abundance between periods, this part was small in absolute numbers. This may be a product of a large sample size to some extent (we used almost 2000 spatial replicates, and the explained variance decreases with sample size), and the high spatial resolution of our data, in which some records of individual bird presence/absence in grid cells may result from behavioural processes (e.g., foraging visits into or outside the cell) and not from habitat preferences. However, it is also possible that the reduced explanatory power of habitat composition in our data may simply result from the importance of other unrecorded forces shaping changes in bird abundance between periods. One possibility is climate change that influences bird populations through several mechanisms (Dunn & Møller, 2019). Among the affected species, long-distance migrants are often the most negatively impacted (Koleček et al., 2020; Telenský et al., 2020). Therefore, declines of Grasshopper and Riverine Warbler (*Locustella fluviatilis*), Whinchat, Garden Warbler (*Sylvia borin*), or Marsh Warbler (*Acrocephalus palustris*) may be at least partly driven by climate, and not only by local habitat change.

Indeed, factors acting irrespective to habitat changes in MTAs were most likely important drivers because bird population changes observed in MTAs were positively correlated with national populations trends estimated over the period 2009–2021. Besides the climate change mentioned above, agricultural intensification and urbanization are obvious candidates (Rigal et al., 2023; Rosin et al., 2021). They may contribute to declines of species breeding in grassland (e.g. Eurasian Skylark, Meadow Pipit) and increases of some urban species (e.g. House Sparrow, *Passer domesticus* and White Wagtail, *Motacilla alba*). On the other hand, the observed correspondence of trends may also result from the same habitat changes occurring both within and outside MTAs (Grešlová et al., 2023).

Interestingly, the change in abundance was more positive in birds of a higher conservation concern. This pattern implies that, even though the land cover of the abandoned MTAs generally changes towards more encroached or built-up habitats and the species that are a primary concern of conservationists suffer from these changes locally, these local effects, fortunately, did not result in decreasing overall trends. We suggest that such species benefited from the improvement of habitat quality, possibly due to management interventions, although these interventions did not reverse the general trend of land cover changes driven by ecological succession. For example, the Corn Bunting, a critically endangered and declining species at the national level, might benefit from the rewilding of large herbivores that took place in several sites (Konvička et al., 2021). This management option improved the quality of grasslands by supporting numerous plant and insect species providing important food resources for the Corn Bunting (Golawski & Dombrowski, 2002). Similarly, the nationally endangered Woodlark, that showed one of the greatest population increases from all species between periods on our study sites, requires patches of bare ground that are created by vehicle rides in abandoned MTAs (Dvořáková et al., 2022b). It is worth mentioning that improvement of habitat quality is likely the key aspect of the conservation management as local increases of grasslands were associated with local decreases of birds of conservation concern. We speculate that such grasslands are unmanaged and likely of a low quality, so they show the negative effects.

On the other hand, several species of conservation concern declined in the abandoned MTAs, which was the case of European Stonechat and Whinchat. This suggests that the currently applied management is not sufficient to support populations of these species. As these species show decreasing population trends at the national level, improvement of their local population status in MTAs would require particularly high management effort. Indeed, we think that the current management efforts (such as mowing, grazing, or woody plant cutting) might be unable to generate the fine-scale habitat heterogeneity maintained by the disturbance regime resulting from military training performed at a time when the MTAs were active. It is possible that both of these species require such heterogeneity. The plausibility of this explanation supports another recent study from the abandoned MTAs we sampled here, which showed a considerable decline of the diversity and abundance of butterflies (Reif et al., 2023), a taxon that is critically dependent on the small-scale co-occurrence of very different habitat patches (Konvicka et al., 2008).

Taken together, our results showed that the abandoned MTAs in Czechia undergo successional changes towards dense shrub and forest at the expense of grassland and sparse shrub. These land cover changes explained only a small part of variance in changes in bird abundance, but their effect was statistically significant and corresponded to the observed patterns when species of woodland habitats increased, while species of open habitats declined. As these changes occurred despite the performance of conservation actions in some of the abandoned MTAs, one may conclude that these actions were not sufficient to effectively block the general successional changes. However, the increasing abundance of bird species of conservation concern indicates that the management of the abandoned MTAs indeed supported populations of the species that were at the highest risk. Although the management is not able to help all species, our results indeed show that the conservation of the abandoned MTAs is important, and its current form delivers conservation benefits.

CRediT authorship contribution statement

Lenka Dvořáková: Writing – original draft, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jan Hanzelka:** Formal analysis, Writing – original draft. **Dušan Romportl:** Writing – original draft, Data curation, Formal analysis. **Jiří Reif:** Conceptualization (equal), Formal analysis (supporting), Investigation (supporting), Writing – original draft (equal), Funding acquisition (equal), Supervision (lead).

Declaration of competing interest

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

Data availability

All data and code associated with this study are freely available at https://doi.org/10.5281/zenodo.10784689

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Appendix A. Supplementary data

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Biodiversity changes in abandoned military training areas: relationships to different management approaches in multiple taxa

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Introduction: Abandoned military training areas are biodiversity strongholds, and this is particularly true for open-habitat and threatened species in Central Europe. Such species benefited from a specific disturbance regime created by military activities that maintained small-grained environmental heterogeneity. However, the disturbance regime no longer occurs after abandonment and the biodiversity is at risk due to forest and shrub encroachment if the areas are left unmanaged. To combat these adverse changes, several management options are used. As these options are not always applied for conservation purposes and substantially differ in their implementation, it is essential to assess their impacts on biodiversity.

Methods: We performed repeated standardized surveys (first in 2009–2010, second in 2020–2022) of vascular plants, grasshoppers, butterflies and birds in 42 abandoned military training areas in Czechia, a Central European country. We calculated changes of species richness and abundance between periods for each taxon and related these changes to six different management types (woody plant cutting, mowing for conservation, mowing for agriculture, grazing for conservation, grazing for agriculture, vehicle movement) performed in these areas between periods.

Results: Vascular plants and grasshoppers showed generally positive changes, whereas the reverse was true for butterflies, and birds experienced mixed changes. Although beta-diversity increased between periods in plants, grasshoppers and butterflies, this increase was driven by extirpation of common species. Management impacts greatly different between respective types and between taxa. Woody plant cutting showed solely positive impacts (on plants and grasshoppers), while the impacts of both types of grazing were mixed (positive on plants and birds, negative on butterflies, mixed on grasshoppers). Mowing for agriculture supported plants and birds but had negative effects on grasshoppers. Mowing for conservation and vehicle movement were linked solely to negative biodiversity changes (former in plants, latter in butterflies).

Discussion: Some components of biodiversity, i.e. plants and grasshoppers, indicate that abandoned military training areas still serve as their strongholds and the management most likely contributes to this favourable state. In contrast, the pattern found for butterflies is worrying since the management performed up to now apparently does not meet their requirements, likely because they are based on smaller-scale habitat mosaic than currently occurs in the areas. Our results may serve as a guide for future prioritization of environmental management, and we urge for development of more nuanced approaches to save the butterflies.

KEYWORDS

vascular plants, grasshoppers, butterflies, birds, ecological succession, environmental management, threatened species, Europe

Introduction

Biodiversity loss is one of the most serious global environmental problems (Chase et al., 2020). Such losses, e.g., the "insect apocalypse" (Goulson, 2019), could have pertinent impacts on the functioning of trophic relationships, with the overlap into human economy (Cardoso et al., 2020). In European lowlands, this loss is particularly severe in open habitats that have been maintained by extensive agriculture for millennia (Ellis et al., 2021). Such habitats are a part of European cultural landscape that is protected under the EU's Habitats Directive in some regions (Maes et al., 2012). Traditional management maintained high species diversity in these landscapes including some Red List taxa (Spulerova et al., 2017). Nowadays, open habitats are rapidly deteriorating due to eutrophication, intensive agricultural use or, if not managed, they become encroached by shrubland or forest (Bardgett et al., 2021). It is therefore important to find solutions on how to stop the further deterioration of the biodiversity of the open habitats in Europe.

One solution is offered by the areas with exceptionally high biodiversity of open habitat species. Such areas may serve as regional biodiversity refuges—they maintain the level of regional diversity in a plausible state and provide propagules for the potential re-colonization of the surrounding landscape (Habel et al., 2013; Tropek et al., 2013; Šálek et al., 2022). In this respect, abandoned military training areas play an important role (Zentelis and Lindenmayer, 2015). They have been widely recognized as regional open habitat biodiversity refuges, supporting a high number of threatened species and showing species richness values comparable to strictly protected nature reserves (Reif et al., 2011; Čížek et al., 2013; Bušek and Reif, 2017). Conservation of these biodiversity refuges is therefore of the utmost importance.

At the same time, abandoned military training areas are exposed to various threats that have arisen after the end of military activity (Herčik et al., 2014; Ellwanger and Reiter, 2019). Although these areas were saved from transformation to intensive forms of cultural landscape for a long time, they may recently face habitat loss due to construction activities or conversion into intensively cultivated farmland, and the quality of their open habitats may deteriorate due to changes driven by ecological succession in the absence of management (Gaertner et al., 2010; Dvořáková et al., 2023). Therefore, to secure the key role of abandoned military training areas in supporting European open habitat biodiversity, it is important to implement the appropriate active management in these areas.

Up to now, abandoned military training areas have experienced several different management approaches. These include traditional management measures such as cutting of shrubs and trees to create open habitats and slow down the encroachment, as well as mowing and cattle grazing to mitigate grassland eutrophication and suppress nutrient-demanding competitive superior species (Ellwanger and Reiter, 2019). In some areas, these management approaches are carried out to obtain economic profit rather than for conservation purposes (Wang et al., 2014), but it is possible that biodiversity may still enjoys some benefits. Besides traditional management types, novel approaches have recently been introduced. These include semi-wild horse or cattle rewilding (Konvička et al., 2021; Dvorský et al., 2022), and prescribed or free-range rides of off-road and military vehicles (Jentsch et al., 2009). They may provide different types of conservation benefits but their impact on different taxa occurring in abandoned military areas remains unclear. Therefore, knowledge of ecological impacts of respective management types on the temporal biodiversity dynamics (sensu Volery et al., 2023) is urgently needed.

To fill this knowledge gap, we explore a unique dataset based on repeated biodiversity surveys in 42 abandoned military training areas in Czechia, a country in Central Europe. The surveys focused simultaneously on multiple taxa that differ in their lifestyle and trophic position: vascular plants—primary producers with low vagility, being highly sedentary and responding slowly to management (Diekmann, 2003); grasshoppers (species of the insect order Orthoptera)—primary and secondary consumers and dietary generalists, indicators of small-scale habitat changes (Fartmann et al., 2012); butterflies—primary consumers and important pollinators, short-lived species highly sensitive to changes in habitat quality (Warren et al., 2021); birds—secondary consumers, long-lived habitat generalists with high dispersal capacity (Fraixedas et al., 2020). Simultaneous focus on such different taxa can provide a complex insight into biodiversity responses to different types of management (Hilty and Merenlender, 2000).

In the focal abandoned military training areas, we conducted a baseline survey of the above-mentioned taxa in 2009–2010 (Reif et al., 2011; Čížek et al., 2013) and repeated the survey using the same methodology in 2020–2022. While the areas were unmanaged at time of the first survey, the above-listed management approaches were applied at multiple sites during the period between surveys. In this study, we express the change in representation of the respective taxa between surveys and relate these changes to the respective management types. Since each of the focal taxa contains numerous species with different ecological characteristics that may influence these relationships, we define several ecological groups of species within each taxon.

The aim of this study is to examine the relationships between biodiversity and different management approaches across taxa and species groups. We predict that species richness of all taxa will

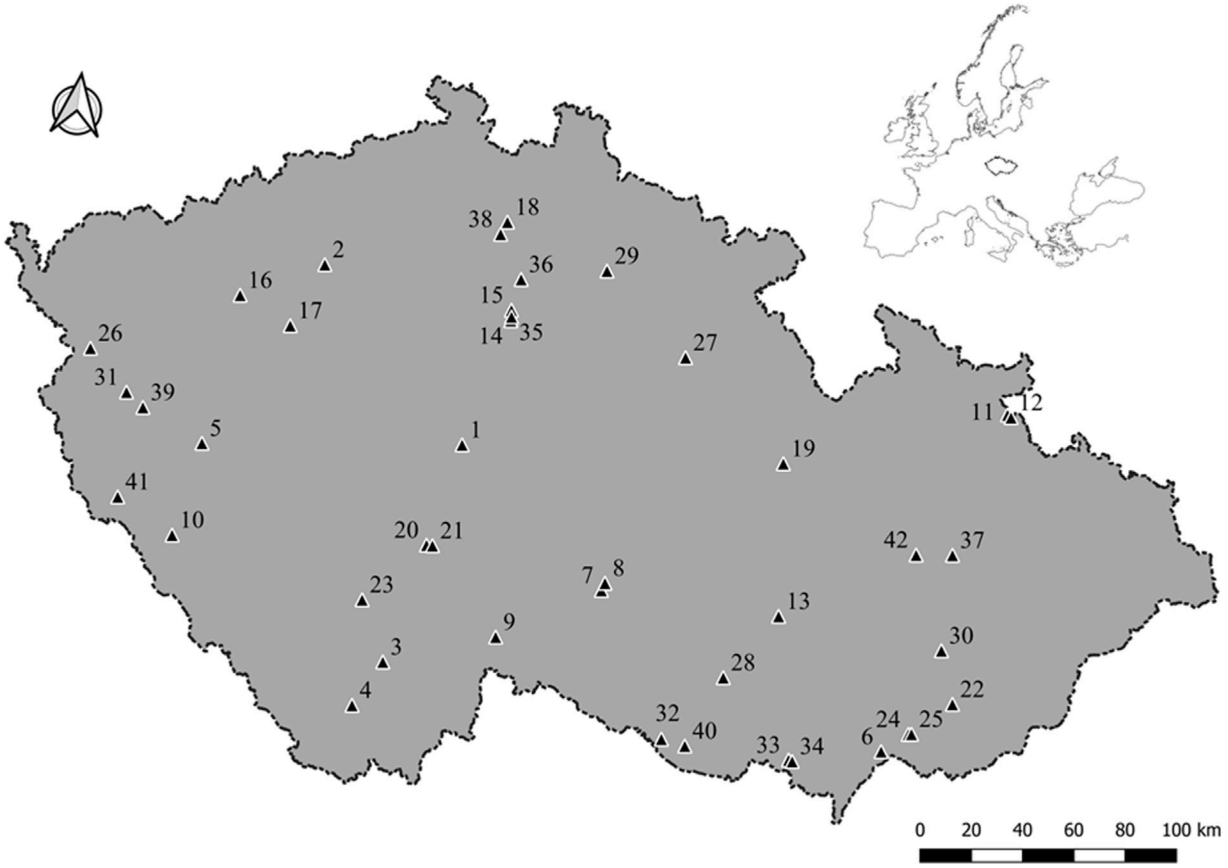

FIGURE 1
Map of the surveyed abandoned military training areas in Czechia. Inset shows position of Czechia in Europe.

increase between survey periods because management application should create specific habitats that host unique species that elevate species richness. We further predict that the management should be most beneficial for species associated with open habitats across all taxa because creating and conserving such habitats is a general management target. In addition, we predict that the management types conducted for conservation purposes should result in more positive outcomes than the management types conducted for economic profit. Finally, we predict that invertebrate taxa, i.e., grasshoppers and butterflies, will be more responsive to the management types applied in the focal military training areas than plants and birds because invertebrates have faster life styles.

Materials and methods

Study area and study sites

We focused on 42 abandoned military training areas scattered throughout Czechia (Figure 1), a central European country situated in the northern temperate zone at the transition from Atlantic to continental climate. The size of the areas varied from 21 to 351 ha (mean 91 ha), and all were located at low to mid elevations (200–625 m asl., mean 364 m). Our selection of the 42 areas used in this study was based on their regional availability and forms a representative sample of all abandoned military training areas in Czechia (Reif et al., 2011).

The areas were used by the army until 1990s and then gradually abandoned due to the downsizing of troops after the end of the Cold War (Tagarev, 2004). Military activities created a heterogeneous fine-scale mosaic of different habitats that were maintained by disturbances (shell explosions, fires, rides of tanks and other vehicles, movement of troops) that were variable in space and time (Warren et al., 2007). After abandonment, the disturbance regime ceased, and the habitats underwent changes due to ecological succession (Skokanová et al., 2017). However, as previous disturbances varied greatly within the respective areas, habitat heterogeneity was still considerable even in 2009 (Čížek et al., 2013) and included a wide range of successional stages from sparsely vegetated bare ground (on the impacted sites being most intensively used by the army) through grassland with varying degrees of shrub encroachment, to woodland (on sites already covered by woody vegetation at the time when the areas were actively used for military training). Therefore, the areas retained considerable biodiversity even 10–15 years after abandonment (Reif et al., 2011; Čížek et al., 2013).

We mapped the habitat composition of each area prior to the respective biodiversity surveys were conducted, i.e., in early 2009 and 2020, respectively, discriminating five major habitat types: bare ground (sites where bare ground dominates over herbaceous vegetation), grassland (sites dominated by herbaceous vegetation without woody plants), sparse shrubland (sites where grassland is encroached by shrubs and small trees but the woody vegetation is discontinuous), dense shrubland (heavily encroached sites consisting of continuous shrub stands), and forest (tall trees with a continuous canopy). These habitat maps (1:2600) were used in subsequent biodiversity surveys.

Biodiversity surveys

We surveyed four major taxa, i.e., vascular plants (hereafter referred to as "plants"), species of the insect order Orthoptera ("grasshoppers"), diurnal butterflies and burnet moths of Zygaenidae family ("butterflies"), and birds in the respective areas in 2009–2010 (first period) and 2020–2022 (second period). The spread of the respective periods over several years was dictated by our capacity to cover all taxa in all areas, with no annually repeated surveys within each period. The respective taxa were surveyed by trained experts to ensure correct identification of individual species.

In both periods, survey techniques were kept the same to facilitate comparability. At the same time, survey techniques varied between taxa corresponding to their biological characteristics:

Plants were surveyed by visiting the respective major habitat types (see their definitions above) in each area and recording the presence of individual plant species (Čížek et al., 2013). The effort was proportional to the size of the respective abandoned military training areas (areas up to 50 ha were surveyed for 4 h, areas 50–100 ha for 8 h, areas 100–200 ha for 16 h, and areas larger than 200 ha for 24 h), and the time spent by surveying the respective habitat types in a given area corresponded to their relative coverage in that area. For plant surveys, each area was visited once during each period between June and August.

Grasshoppers were counted at regularly spaced points in each area, and the number of points corresponded to the size of the area (from 21 in the smallest area to 116 in the largest). Point locations remained the same in both periods. In each of both periods, every point was visited once between the mid-July and the end of August at the time of the highest grasshopper diurnal activity (between 10:00 and 17:00) under suitable weather conditions (warm sunny days with no wind). Surveys combined two methods widely used for grasshopper monitoring, i.e., sweeping (e.g., Racz et al., 2013) and acoustic detections (e.g., McNeil and Grozinger, 2020). Specifically, at each point, the observer made exactly 20 sweeps with a sweep net followed by a 2-min long acoustic detection of stridulating individuals. The records of both types of detections were summed to obtain the number of individuals of each species at a given point. These point-level data were then summed over the entire abandoned military training areas in the respective periods.

Butterflies were recorded using repeated, time-limited visits (*sensu* Kadlec et al., 2012). The effort during one visit corresponded to the size of the abandoned military training area (areas up to 25 ha were surveyed for 60 min, areas of 25–50 ha for 90 min, areas of 50–100 ha for 120 min, areas of 100–200 ha for 240 min, and areas larger than 200 ha for 300 min). In each period, the visits were repeated five times in each area covering the entire butterfly flying season from the end of April to the mid-September, to record species with different phenology and activity phases. Visits were conducted under suitable weather conditions (warm sunny days with no wind) between 9:00 and 16:00. During each visit, the observer surveyed all five major habitat types mentioned above present in a given abandoned military training area by a slow zigzag walk, and the time spent in the respective habitat types corresponded to their relative coverage in that area. During this walk, all observed species and their abundances were recorded. In the case of less distinguishable species, individuals were captured with an insect net, identified in hand, and released. Only in the case of species complexes indeterminable based on external morphology (accounting for a maximum of five individuals per habitat type and visit), the captured individuals were euthanised and identified later by genital dissection in laboratory.

Birds were surveyed during their breeding season using the spot mapping technique (Bibby et al., 2000), in which the observer walked slowly through the entire abandoned military training area early in the morning (between 5:00 and 10:00) and recorded every bird individual on a map. In each period, every area was visited twice (firstly from the late April to mid-May, secondly from mid-May to early June, with at least a two-week break between visits in an area) to cover both early and late breeders. The maximum count of a given species across the visits was considered to be its abundance in a given abandoned military training area in a given period.

Ecological group definition for the respective taxa

The perception of management approaches is likely to be different for species with different ecological traits. To address this issue, we defined several ecological groups of species for each taxon based on literature information on species ecology (plants—Chytrý et al., 2018; grasshoppers—Kočárek et al., 2013; butterflies—Beneš et al., 2002; birds—Hudec and Šťastný, 2005; Šťastný and Hudec, 2011). The groups were non-exclusive, i.e., a species classified in one group can also be classified in another. These ecological groups were delimited based on the position of species along successional and wetness gradients (for all taxa) and along a nutrient gradient (for plants) as follows:

Plants were sorted into 11 groups (Supplementary Table S1): shade-dwelling species, light-dwelling species, and generalists in respect to light conditions; hygrophilic species, mesophilic species, xerophilic species, and generalists in respect to wetness; nutrient-undemanding species, nutrient-demanding species, nutrient-intensive species, and generalists in respect to nutrients.

Grasshoppers were sorted into 5 groups (Supplementary Table S2): open-habitat hygrophilic species, open-habitat mesophilic species, semi-open/woodland-habitat mesophilic species, open-habitat xerophilic species, and semi-open/woodland-habitat xerophilic species.

Butterflies were sorted into 7 groups (Supplementary Table S3): open-habitat hygrophilic species, semi-open/woodland-habitat hygrophilic species, open-habitat mesophilic species, semi-open-habitat mesophilic species, woodland-habitat mesophilic species, open-habitat xerophilic species, semi-open/woodland-habitat xerophilic species.

Birds were sorted into 6 groups (Supplementary Table S4): species of open-wetter habitats, species of semi-open-wetter habitats, species of woodland-wetter habitats, species of open-drier habitats, species of semi-open-drier habitats, species of woodland-drier habitats.

In addition to the ecologically defined groups, we defined the group of threatened species for each taxon as the species listed in the currently valid national Red List (plants—Grulich, 2017; grasshoppers and butterflies—Hejda et al., 2017; birds—Šťastný et al., 2017) in the categories Near Threatened, Vulnerable, Endangered or Critically Endangered.

Processing of biodiversity data

The data were processed at the level of individual military training areas. For each taxon, we expressed the total number of species recorded in each area in the respective periods. Similarly, we expressed the abundance of the threatened species and the abundance of the respective ecological groups for each animal taxon. We decided to focus on the abundance data due to the low number of species in some groups and due to a higher sensitivity of abundance to environmental factors compared to the species richness (e.g., Sutcliffe et al., 2014; Dornelas et al., 2023). For plants, we used the number of species instead of abundance because data on the number of individuals were not available for this taxon (see above).

Although the identity of the abandoned military training areas and the effort devoted to the surveys were kept the same in both periods, the raw data were not fully comparable due to the loss of some parts of several areas between periods. These parts were inaccessible due to private construction activities without the possibility to collect biodiversity data. To solve this problem, we divided the raw biodiversity data (i.e., the number of species or individuals of the respective taxa or their groups) by the size of the surveyed area in each period in every abandoned military training area. Therefore, all numbers of species or individuals are further expressed as relative per hectare values. Since we were interested in possible impact of the management on the change of biodiversity, we calculated the change in these relative values between periods for each abandoned military training area. The change was calculated by subtracting the value in the first period from the value in the second period. The resulting positive value indicates an increase in the relative number of species or individuals between periods, while the negative value indicates a decrease. These changes between periods for the respective taxa and species groups within taxa were used as response variables for further analyses.

Management data

We distinguished the following six types of management that were carried out in the focal abandoned military training areas between the periods:

Woody plant cutting—removal of shrubs or trees from grasslands or shrublands to reduce encroachment on open habitats or to create new open habitat patches.

Mowing for conservation—extensive mowing of grasslands to improve their quality for biodiversity (preventing encroachment by woody plants, limiting nutrient demanding highly competitive plant species, and promoting less competitive, stress tolerant plant species and animals associated with extensively used grasslands).

Mowing for agriculture—mowing of grasslands to extract biomass for hay or silage.

Grazing for conservation—extensive grazing by domestic (sheep, cows) or semi-wild animals (Exmoor pony, European bison, aurochs-like cattle) to improve the quality of open habitats for biodiversity (creating bare ground patches, limiting nutrient-demanding highly competitive plant species and promoting less competitive stress-tolerant plant species and animals associated with extensively used grasslands).

Grazing for agriculture—grazing by domestic animals (sheep, cows) for agricultural production (meat, milk).

Vehicle movement—movement of civilian (motor bikes, off-road cars, trucks) or military (tanks, troop carriers) vehicles to reduce woodland encroachment on open habitats, to create bare ground patches and to promote stress tolerant plant species and animals associated with regrowth on such sites. This management type included both prescribed (for conservation purposes) and free-range rides due to their unclear distinction (e.g., some rides were free under the supervision of conservation managers) and the relatively small number of abandoned military training areas that experienced this type of management.

The influence of each management type on each abandoned military training area was expressed by two measures: i) the size of the area where it was applied and ii) the number of years of application (Table 1). The information on these measures was obtained from local stakeholders, nature conservation authorities and a public land use database (LPIS: https://eagri.cz/public/app/lpisext/lpis/verejny2/plpis/). We then converted these numbers into relative values (from 0 to 1), i.e., the coverage of a given abandoned military training area by a given management type and the proportion of years when this management type was applied (relative to the number of years between periods). For each abandoned military training area, these proportions were multiplied by each other to obtain a single measure of "management effort" for each management type, ranging from 0 to 1. The higher the value, the larger the area where that management type has been applied or the longer the period of its application in a given abandoned military training area. These management effort scores were used as explanatory variables in further analyses.

Statistical analysis

To assess changes in biodiversity between periods in the focal abandoned military training areas, we fitted intercept-only linear models (LM) for the change in the relative number of species or individuals of respective taxa or species groups. These changes illustrate the development of biodiversity over time (see above). Since the abandoned military training areas are rarely located randomly, and thus the location of the area may affect the species distribution, we used Moran's test using the 'Moran.I' function from the 'ape' package (Paradis and Schliep, 2019) to test the residuals of each model for spatial autocorrelation. When significant, we remodelled the relationship using generalized least

TABLE 1 Management effort in the surveyed abandoned military training areas. The effort is expressed as the mean relative area (%) and the mean number of years of application (application time) across all areas.

Management type	Relative area (%)	Application time (years)
Woody plant cutting	9.1	0.3
Mowing for conservation	6.6	2.4
Mowing for agriculture	2.1	1.5
Grazing for conservation	15.0	1.8
Grazing for agriculture	9.1	1.9
Vehicle movement	12.2	3.8

squares models (GLS) using the 'gls' function from the 'nlme' package (Pinheiro and Bates, 2022). The spatial autocorrelation structure was selected from linear, exponential, Gaussian, spherical or ratio quadratic correlation structures, based on the Akaike information criterion corrected for small sample sizes (AIC_c) calculated by the 'AIC_c' function from the 'MuMIn' package (Bartoń, 2022).

We then tested the effects of respective management types on the observed biodiversity changes between periods. For each biodiversity variable, i.e., the change in the relative number of species or individuals of a given taxon or a given group of species within a taxon, we fitted a separate LM or GLS relating this variable to the respective management types (quantified as "management effort", see above) applied in individual abandoned military training areas. In addition to the influence of management, changes in biodiversity could be driven by the habitat structure of the area, or by interactions between management and habitat structure. Habitat structure was expressed as the relative cover of two habitat types, grassland and sparse shrubland. Information on the relative cover of these types was obtained by mapping of habitat composition in the abandoned military training areas prior to the 2009 biodiversity survey (see above). Although five habitat types were recognized during this mapping, only the two above-mentioned types were selected for the analysis based on results of the pilot modelling investigating their non-independence and representation.

Ideally, all possible combinations of management type, habitat structure and their interactions would be considered for each response variable. However, this approach was not feasible due to the limited sample size, i.e., the number of abandoned military training areas relative to the number of possible variable combinations, and the resulting potential statistical power issues. Therefore, to keep the model composition simple and comprehensive, we constructed three types of models:

i) models containing only the main effect of each management type;
ii) models containing the main effect of each management type and the main effects of habitat structure;
iii) models containing the main effect of each management type, the main effects of habitat structure, and their relevant two-way interactions. We considered relevant interactions to be those involving a habitat type in which a given management was most likely conducted assuming that the relative area of that habitat type may influence the impact of that management approach on biodiversity. Specifically, we included the following interactions: sparse shrubland x woody plant cutting, grassland x mowing for conservation, grassland x mowing for agriculture, grassland x grazing for conservation, and grassland x grazing for agriculture.

To make inference about the effect of management on a given response variable, we selected the best-fitting model from the three above mentioned possibilities based on the AIC_c, using $\Delta AIC_c < 2$ as the criterion for model selection. However, we always used only the main effects of respective management types for interpretation because we were interested in the "pure" effect of management and not in the effect of habitat structure or its interaction. All models were tested for spatial autocorrelation and adjusted if necessary; using the same procedure as for the intercept-only models described above.

All model assumptions were checked visually using residuals vs. fitted plots, and Q-Q plots of standardized residuals. All statistical analyses were performed in R 4.2.1 (R Core Team, 2022).

To gain further insights into biodiversity dynamics in the focal areas and to provide a general overview of the processes involved in the observed changes, we calculated temporal beta-diversity for the respective taxa following Tatsumi et al. (2021). Temporal beta-diversity informs about spatiotemporal biodiversity changes by decomposing the presence-absence data collected at spatial replicates (i.e., individual abandoned military training areas in our case) and at different temporal occasions (i.e., our two survey periods) into the processes of extirpation and colonization (Tatsumi et al., 2021). Therefore, for each taxon, we can learn whether extirpation or colonization leads to homogenization or heterogenization of the ecological communities in the focal areas between survey periods, which can be translated into losses and gains of common and rare species, respectively. For this purpose, we quantified for each taxon (i) extirpation leading to homogenization, (ii) extirpation leading to heterogenization, (iii) colonization leading to homogenization, (iv) colonization leading to heterogenization, (v) total extirpation, (vi) total colonization, and (vii) total beta-diversity change. These measures could only be expressed for all abandoned military training areas together, and thus could not be related to management data at the level of individual areas.

Results

Combining data from both periods and all abandoned military training areas, we recorded 1089 species of plants, 64 species of

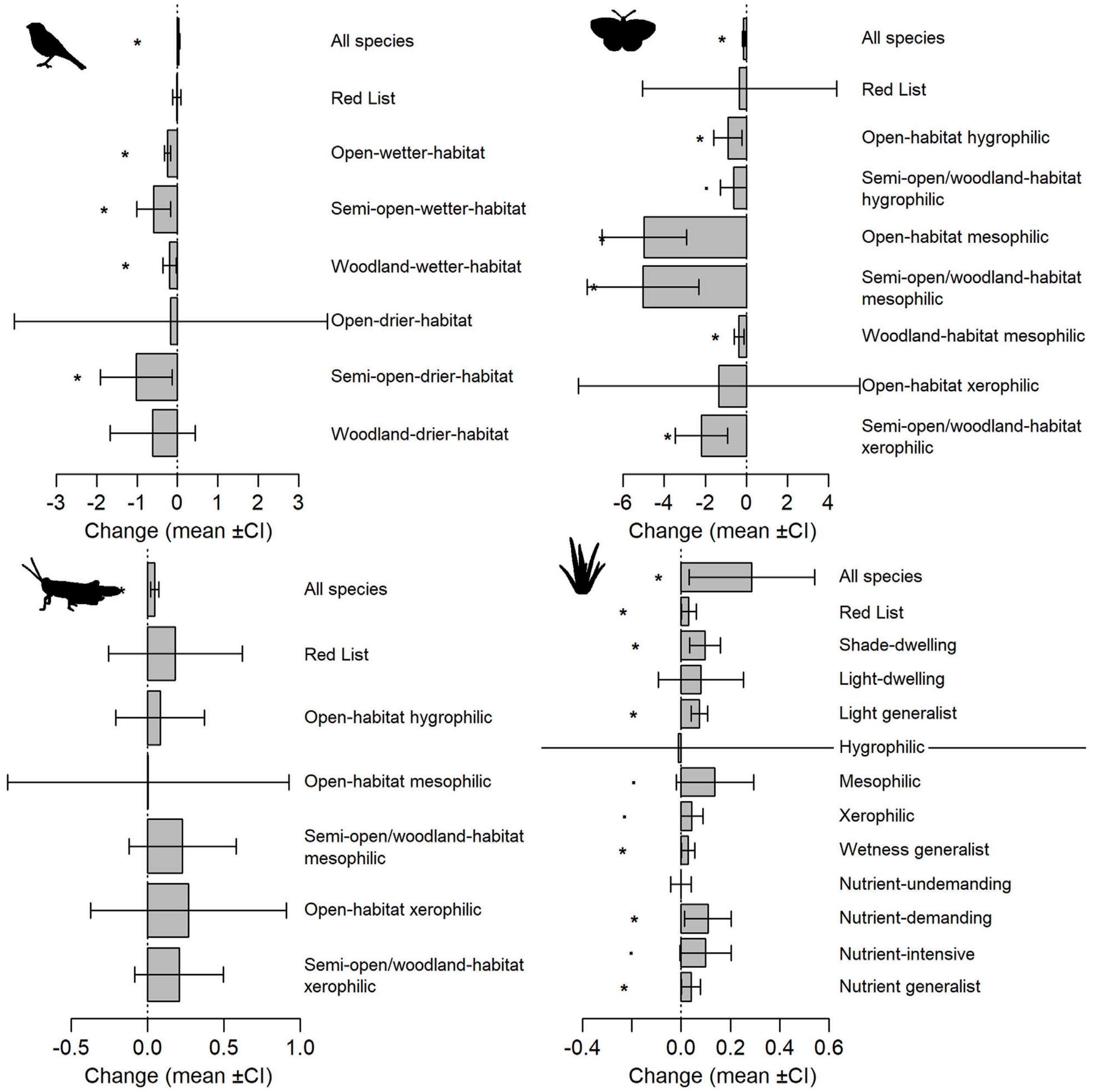

FIGURE 2
Changes in biodiversity of respective taxa (plants, grasshoppers, butterflies, and birds) in the surveyed abandoned military training areas between periods (2009–2010 and 2020–2022) estimated by linear or generalized least squares models. Mean changes (grey bars) together 95% confidence intervals (whiskers) in species richness (for plants groups and for all species in grasshoppers, butterflies and birds) or abundance (for respective groups of grasshoppers, butterflies and birds) are shown. Asterisk marks a significant change. Change is a relative value based on a difference in the per hectare number of species (or individuals) between periods (see the Materials and methods section for details).

grasshoppers, 121 species of butterflies and 86 species of birds. Of these species, 244 plants, 17 grasshoppers, 58 butterflies and 24 birds were listed in the actual national Red List.

Biodiversity changes between periods

In plants, biodiversity changes were generally positive. Overall, the number of plant species recorded per hectare of an abandoned military training area increased by 0.29 (±SE = 0.13) and the same pattern applied to Red List species, shade-dwelling species and nutrient-demanding species (Figure 1). Furthermore, increases were observed in all three groups of generalists, i.e., species indifferent to light conditions, wetness and nutrient gradients (Figure 2). None of the plant species groups showed a significant decrease in species richness (Figure 2).

For grasshoppers, the total number of species recorded per hectare increased significantly, similar to plants (Figure 2), but to

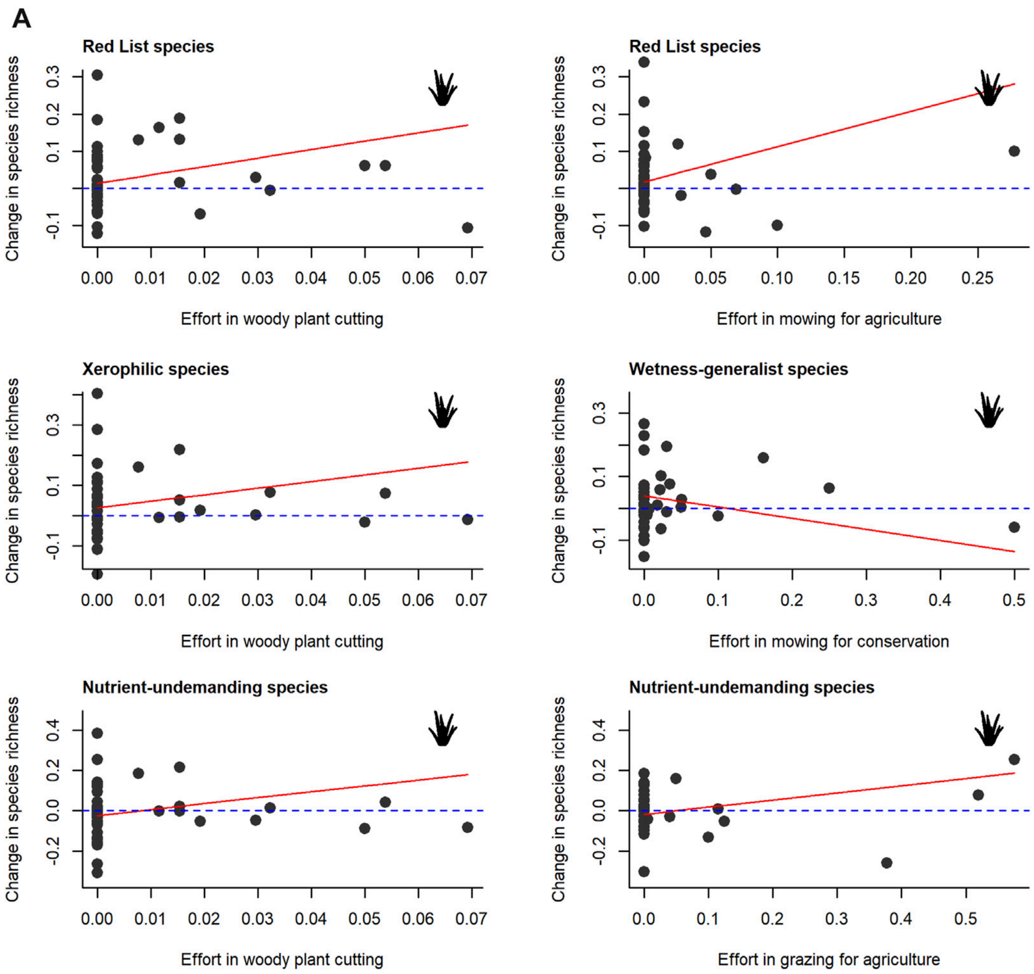

FIGURE 3
(Continued).

a lesser extent, i.e., by 0.05 (±0.01). Focusing on changes in the abundance of respective species groups, we observe a general pattern of increases across the groups defined by various combinations of habitat openness and wetness, as well as in the Red List species (Figure 2). However, none of these changes was statistically significant (Figure 2).

Butterflies, in contrast to plants and grasshoppers, showed remarkably different patterns of change in species richness and abundance per hectare. Specifically, their total species richness significantly decreased by 0.14 (±0.03), and five out of seven groups defined by various combinations of habitat openness and wetness showed significant decreases in abundance (Figure 2). These decreases included semi-open/woodland-habitat xerophilic species, open-, semi-open- and woodland-habitat mesophilic species, and open-habitat hygrophilic species (Figure 2). The remaining groups, as well as Red List species, showed a tendency to decline, but this was not statistically significant (Figure 2).

Bird biodiversity expressed a mixed pattern of change. The total number of bird species recorded per hectare of an abandoned military training area slightly (0.03 ± 0.01), but significantly increased (Figure 2). However, the changes in abundance per hectare of the respective species groups were exclusively negative. Specifically, significant decreases were observed in all groups on wetter habitats regardless of their position along the open-woodland habitat gradient, and in semi-open-drier-habitat species (Figure 2). The abundance of the remaining groups including the Red List species also tended to decrease, but not significantly (Figure 2).

Relationships between biodiversity changes and management types

For plants (Supplementary Table S5), the change in richness of Red List species was positively related to woody plant cutting and mowing for agriculture (Figure 3A). Mowing for conservation was negatively related to the change in richness of generalists with respect to wetness (Figure 3A). Changes in the number of xerophilic and nutrient undemanding species were both positively related to woody plant cutting (Figure 3A). The latter group also responded positively to grazing for agriculture (Figure 3A).

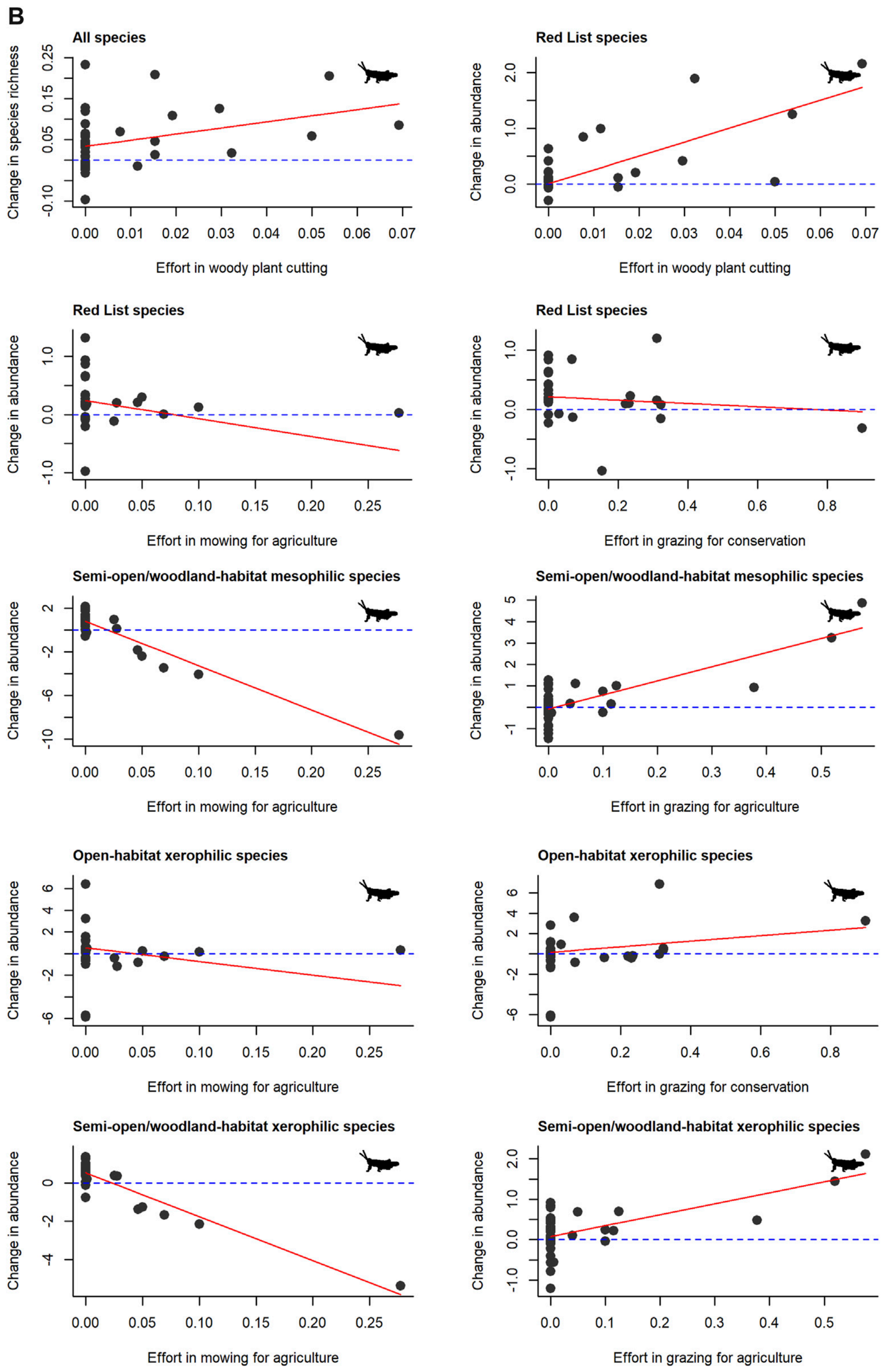

FIGURE 3
(Continued).

Grasshoppers showed partly different relationships to the respective management types than plants (Supplementary Table S6). Here we also observed a positive response to woody plant cutting, as indicated by the increase of species richness of all species and abundance of Red List species (Figure 3B). However, we detected four negative relationships to mowing for agriculture: in the case of abundance of Red List species, open-habitat xerophilic species, semi-open/woodland habitat

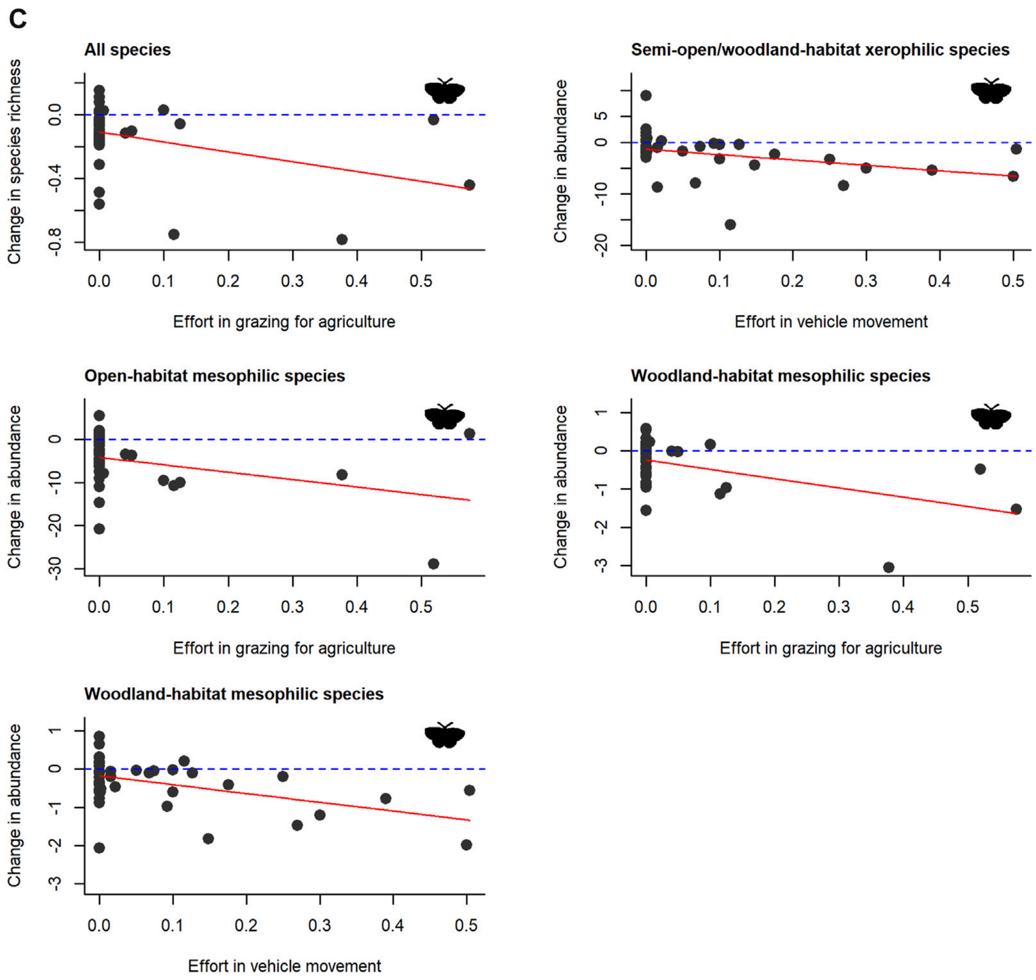

FIGURE 3
(Continued).

xerophilic and mesophilic species (Figure 3B). Grazing for conservation was positively related to the change in abundance of open-habitat xerophilic species, but negatively related to the change in abundance of Red List species (Figure 3B). Abundance of semi-open/woodland-habitat xerophilic and mesophilic species increased with increasing effort devoted to grazing for agriculture (Figure 3B).

For butterflies (Supplementary Table S7), the change in their total species richness was negatively related to grazing for agriculture, as was the change in abundance of open- and woodland-habitat mesophilic species (Figure 3C). In addition, the change in abundance of semi-open/woodland-habitat xerophilic and woodland-habitat-mesophilic species was negatively related to vehicle movement (Figure 3C).

For birds, the change in their total species richness was unrelated to any of the management types, and the same applied to the abundance of Red List species (Supplementary Table S8). The change in abundance of woodland-wetter-habitat species was positively related to both mowing for agriculture and grazing for conservation (Figure 3D). Finally, the abundance of semi-open-drier-habitat species increased with increasing effort in grazing for conservation (Figure 3D).

In summary across all taxa and species groups (Table 2), woody plant cutting was associated with an increase in biodiversity in five cases (three for plants, two for grasshoppers) and it did not show any negative relationships. Mowing for conservation showed a single negative relationship (in plants), whereas mowing for agriculture two positive (one for plants, and one for birds) and four negative relationships (all in grasshoppers). Grazing for conservation showed three positive (one for grasshoppers, two for birds) and one negative relationship (for grasshoppers), while grazing for agriculture showed three positive (one for plants and two for grasshoppers) and three negative (all in butterflies) relationships. Vehicle movement was linked to two negative responses (both in butterflies).

Temporal change in beta-diversity

In plants, grasshoppers and butterflies we observed an increase in beta-diversity, i.e., their communities across abandoned military training areas became more dissimilar between periods, although the increase was modest in grasshoppers (Table 3). In birds, beta-diversity decreased, i.e., bird communities became increasingly

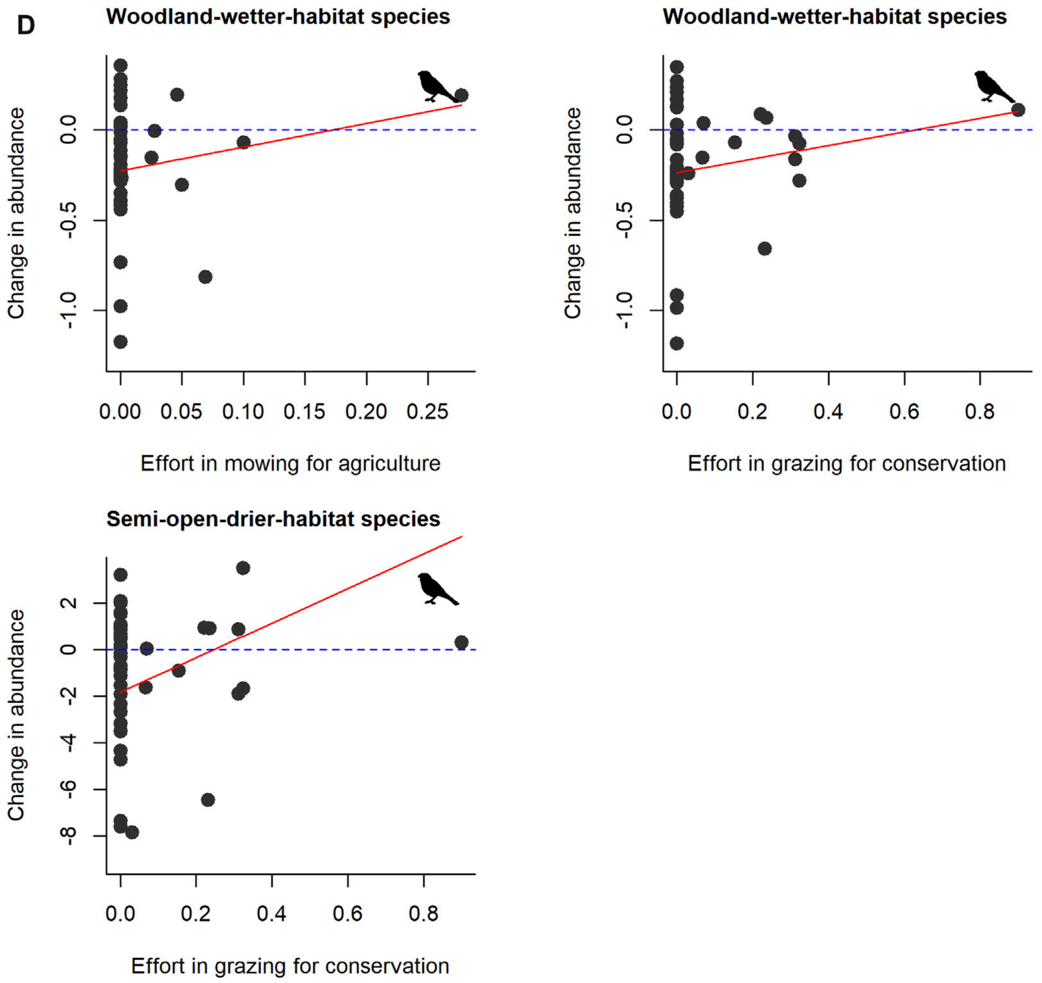

FIGURE 3
(Continued). Effects of respective management types on changes in biodiversity of respective taxa in the surveyed abandoned military training areas between periods (2009–2010 and 2020–2022) estimated by linear or generalized least squares models: **(A)** plants, **(B)** grasshoppers, **(C)** butterflies, **(D)** birds. Change is a relative value based on a difference in the per hectare number of species (or individuals) between periods (see the Materials and methods section for details). Only the significant relationships are shown (see Supplementary Tables S5–S8 for full results).

similar between periods, but the value was close to zero, meaning the change was small (Table 3).

The extirpation of common species (leading to heterogenization) was always greater than the extirpation of rare species (leading to homogenization) and it was the main driver of the overall beta-diversity change in plants, grasshoppers and butterflies (Table 3). However, this does not mean that colonization did not occur in these taxa. In fact, both plants and grasshoppers showed high levels of colonization (Table 3), but since the colonization processes were symmetric between common and rare species (Table 3), their net impact on beta-diversity change was negligible in these taxa. In butterflies, colonization of common species was much greater than colonization of rare species (Table 3). However, extirpation of common butterflies was even higher, so that it outweighed the effect of colonization on beta-diversity change in this taxon (Table 3). The situation was somewhat different in birds, where colonization was slightly greater than extirpation for both common and rare species (Table 3). As colonization of common bird species dominated among the processes, total bird beta-diversity decreased between survey periods (Table 3).

Discussion

Four major taxa selected to represent the biota of abandoned military training areas showed strikingly divergent trajectories of biodiversity change according to our standardized-effort surveys repeated after 10–12 years. Plant species richness generally increased, and the increase typically involved ecological generalists and nutrient-demanding and shade-dwelling species. However, national Red Listed plant species increased richness as well, and none of the plant ecological groups declined. Positive changes were also observed in grasshoppers whose total species richness increased and abundance of all species groups tended to increase, although not significantly. This optimistic picture contrasts

TABLE 2 Summary of the impacts of respective management types on individual taxa in the surveyed abandoned military training areas: A) plants, B) grasshoppers, C) butterflies, D) birds. ↓↑ denote significantly positive and negative relationship, respectively.

Species group	Woody plant cutting	Mowing for conservation	Mowing for agriculture	Grazing for conservation	Grazing for agriculture	Vehicle movement
A) plants						
All species						
Red List species	↑		↑			
Shade-dwelling species						
Light-dwelling species						
Generalists to light species						
Hygrophilic species						
Mesophilic species						
Xerophilic species	↑					
Generalists to wetness species		↓				
Nutrient-undemanding species	↑				↑	
Nutrient-demanding species						
Nutrient-intensive species						
Generalists to nutrients species						
B) grasshoppers						
All species	↑					
Red List species	↑		↓	↓		
Open-habitat hygrophilic species						
Open-habitat mesophilic species						
Semi-open/woodland-habitat mesophilic species			↓		↑	
Open-habitat xerophilic species			↓	↑		
Semi-open/woodland-habitat xerophilic species			↓		↑	
C) butterflies						
All species					↓	
Red List species						
Open-habitat hygrophilic species						
Semi-open/woodland-habitat hygrophilic species						
Open-habitat mesophilic species					↓	
Semi-open-habitat mesophilic species						
Woodland-habitat mesophilic species					↓	↓

(Continued on following page)

TABLE 2 (*Continued*) Summary of the impacts of respective management types on individual taxa in the surveyed abandoned military training areas: A) plants, B) grasshoppers, C) butterflies, D) birds. ↓↑ denote significantly positive and negative relationship, respectively.

Species group	Woody plant cutting	Mowing for conservation	Mowing for agriculture	Grazing for conservation	Grazing for agriculture	Vehicle movement
Open-habitat xerophilic species						
Semi-open/woodland-habitat xerophilic species						↓
D) birds						
All species						
Red List species						
Open-wetter-habitat species						
Semi-open-wetter-habitat species						
Woodland-wetter-habitat species			↑	↑		
Open-drier-habitat species						
Semi-open-drier-habitat species				↑		
Woodland-drier-habitat species						

TABLE 3 Decomposition of temporal changes in beta-diversity for respective taxa (plants, grasshoppers, butterflies, and birds) in the surveyed abandoned military training areas. Temporal change in beta-diversity (first column) can be expressed as the sum of extirpation and colonization processes (second and third columns) among focal areas between survey periods. Extirpation is the sum of local extinction of rare species leading to homogenization (fourth column) and local extinction of common species leading to heterogenization (fifth column). Colonization is the sum of the spread of rare species leading to heterogenization (sixth column) and the spread of common species leading to homogenization (seventh column). The sign of beta-diversity change shows its increase (positive values, i.e., higher dissimilarity of assemblages represented by a given taxon across areas) or decrease (negative values) over time. The sign of extirpation and colonization shows the dominance of homogenization (negative values, i.e., assemblages became increasingly homogenous in terms of species composition, leading to a decrease in beta-diversity) or heterogenization (positive values, leading to an increase in beta-diversity) in a given process.

Taxon	Beta-diversity change	Extirpation	Colonization	Extirpation => homogenization	Extirpation => heterogenization	Colonization => heterogenization	Colonization => homogenization
Plants	0.20	0.18	0.02	−0.85	1.02	1.18	−1.16
Grasshoppers	0.10	0.24	−0.15	−0.21	0.45	0.63	−0.78
Butterflies	0.31	0.47	−0.17	−0.35	0.83	0.23	−0.39
Birds	−0.07	0.32	−0.39	−0.21	0.53	0.23	−0.62

deeply with the patterns found for butterflies. Their total species richness decreased, as did the abundance of most of their species groups, regardless of their position along gradients of habitat openness and wetness. Birds showed a mixed pattern containing increase in total species richness and decreases in the abundance of species associated with semi-open drier habitats and various types of wetter habitats. Beta-diversity increased between periods in all but one taxon (birds), driven by extirpation of common species. In contrast, colonization of common species was responsible for the decrease in beta-diversity in birds.

Regarding management effort, we found a complex picture of highly variable biodiversity impacts of different approaches. The cutting of woody plants was beneficial for national Red Listed, xerophilic and nutrient undemanding plants, as well as for overall grasshopper richness and for grasshoppers listed in the national Red List. Mowing for conservation showed only negative relationship with biodiversity change, but this may not necessarily be a sign of conservation failure, as we discuss below. Mowing and grazing for agriculture provided both conservation benefits (for plants, birds and some grasshoppers) and costs (for butterflies and some other grasshoppers). Grazing for conservation had positive effects on open-habitat xerophilic grasshoppers and woodland-wetter-habitat birds, but was negatively related to abundance changes in national Red Listed grasshoppers. Vehicle movement was negative for butterflies of later successional stages.

The patterns observed in plants, i.e., the increase in the richness of shade-dwelling and nutrient-demanding species, indicate some progress in ecological succession (sensu Poorter et al., 2023) leading to habitat closure and eutrophication (e.g., Pruchniewicz, 2017). On the other hand, these processes do not seem to endanger the sensitive plant species, since no decrease in biodiversity was observed in any of the plant species groups. Moreover, the increase in richness of Red Listed plant species suggests that abandoned military training areas maintain their position as strongholds of plant biodiversity in the region (Čížek et al., 2013). One reason for these patterns may be the positive effects of management. The cutting of woody plants supported Red List species, nutrient undemanding and xerophilic species, i.e., groups that should be negatively affected by shrub or forest encroachment and eutrophication (Teleki et al., 2020). Grazing, although for agricultural purposes, could have also contributed to mitigating these impacts (Pykälä, 2003; Elias et al., 2018), as it supported nutrient undemanding species, too.

Mowing is another management tool that is considered to counteract successional changes and eutrophication (Lepš, 1999). However, its effects on plants were mixed in our study areas. Interestingly, plant species (those listed in the national Red List) seem to benefit from mowing for agriculture, but suffer from mowing for conservation (generalists to wetness). Although surprising, these patterns can be explained by species' ecological characteristics. Many species listed in the Red List originally occur in steppe habitats that are highly exposed to natural disturbances (Chytrý et al., 2007). Therefore, disturbance represented by mowing is beneficial for them as it keeps their habitats open. In contrast, generalists, that include many woody plants and expansive species (such as *Calamagrostis epigeios*) in our data, are often targeted for reduction by management (Těšitel et al., 2018) because they trigger deterioration of open habitats (Somodi et al., 2008). Thus, the negative impact of mowing for conservation on these species can be perceived as a positive outcome.

Similar to plants, grasshoppers are a taxon showing predominance of positive biodiversity changes, and management accounts for at least part of them. Cutting of woody plants proved to be beneficial for total species richness of grasshoppers and abundance of national Red List species. Since grasshoppers generally prefer open habitats (Latchininsky et al., 2011) and the threatened species like grasshopper *Dociostaurus brevicollis* or bush-cricket *Montana montana* are typically those with the highest habitat specialization (Engelhardt et al., 2022), reducing woody plant encroachment seems to be a vital strategy to support them. Xerophilic and mesophilic species in semi-open and woodland habitats were supported by grazing for agriculture that may maintain the conditions created by the cutting of woody plants, even though it is unlikely to improve the quality of the habitat *per se*. Instead, habitat quality can be improved by grazing for conservation that was associated with increased abundance of open-habitat xerophilic grasshopper species like grasshopper *Calliptamus italicus* and bush-cricket *Platycleis albopunctata*. The surprisingly negative impact of grazing for conservation on Red List grasshopper species was driven by large increases of these species in localities where this management type was absent and their modest increases in localities with a high effort devoted grazing for conservation. Such a difference resulted in an apparently negative relationship, but it would be premature to consider this management type as harmful.

In contrast to plants, where we found both positive and negative effects of mowing, this management approach had solely negative effects on grasshoppers. The abundance of open-habitat xerophilic species, semi-open/woodland habitat xerophilic and mesophilic species, as well as of Red List species decreased with increasing effort devoted to mowing for agriculture. Due to mowing, plant individuals are cut which results in high mortality of grasshoppers (Humbert et al., 2010). If mowing occurs too often, as may be the case for this management type in some of our localities, such frequent mortality events limit population recovery and result in population declines. Mortality is probably less severe in the case of grazing, even though it is performed for agricultural purposes as it had a positive effect on semi-open/woodland-habitat xerophilic grasshoppers. We suggest that the benefit may lie in preventing woodland habitat closure. Although these species are associated with woody plants (Latchininsky et al., 2011), they require open and not closed woodland (Rösch et al., 2019) which may be maintained by grazing.

Butterflies are organisms that seem to be at particular risk in abandoned military training areas. Their total species richness and the abundance of several groups show negative changes over time, and we did not detect any positive effects of management. Instead, two types of management showed negative effects. Specifically, butterflies suffered from grazing for agriculture and from vehicle movement. Management by intensive and long-term grazing results in uniform and low sward height which reduces butterfly breeding and shelter opportunities (Bussan, 2022), as well as in destruction of plant-pollinators interactions by reduction of nectar food supply for butterflies (Rakosy et al., 2022). These results suggest that butterflies may be negatively affected by the management type that simultaneously provides benefits to some other taxa (i.e., plants and grasshoppers in our dataset). Such sensitivity of butterflies can be explained by the high ecological specialization of many species, such as *Euphydryas aurinia* or hairstreaks (species of subfamily Theclinae), coupled with their complex habitat requirements—species often require the simultaneous presence of several different kinds of ecological conditions on a small area (e.g., both tall and short herbs, both grassland and woodland) that are very difficult to create or even support by a single management type (e.g., Hůla et al., 2004). The fine mosaic of variable habitat types in military training areas a few years after their abandonment was most likely the reason of the high richness and abundance of butterflies recorded at time of our first survey (Čížek et al., 2013) and it seems that subsequent homogenization of this mosaic was not prevented by management despite considerable effort. This probably resulted in the observed butterfly biodiversity decline. Therefore, butterflies appear to require a more nuanced approach to the management of abandoned military training areas.

Butterflies bound to the later successional stages were also negatively affected by vehicle movement. This result is driven by the extensive top-soil removal by military vehicles carried out as part of planned management on several abandoned military training ranges, which occurred just before our second survey period (Dvořáková et al., 2002a; Dvořáková et al., 2002b). Such an extensive disturbance inevitably resulted in habitat loss for many butterfly species, particularly those associated with forest-steppe or light forests, as *Callophrys rubi* or *Lasiommata maera*, which show significant population decreases. However, this apparent negative effect may not be permanent, since the experience from other areas that underwent such kind of disturbance indicates that, if these disturbances are not too frequent, butterfly populations recover after a few years (Zografou et al., 2017) and the community may become even more diverse compared to pre-disturbance conditions (Tropek et al., 2012). Therefore, although it is unclear whether such recovery will occur in our study areas, the observed negative impacts of vehicle movement may not be as fatal as our results suggest.

Birds showed a mixture of positive and negative changes as their total species richness increased, while the abundance of several species groups decreased between study periods. Some of these increases can be attributed to management options. Such options were represented by grazing for conservation to which birds associated with semi-open, drier habitat types responded positively. This type of disturbance blocks successional changes and maintains habitat openness, i.e., creates conditions that exactly match the habitat preferences of these bird species (Reif et al., 2013; Aunins and Avotis, 2018), such as the Stonechat (*Saxicola rubicola*) or Woodlark (*Lullula arborea*) in our dataset. At the same time, woodland birds in wetter habitats responded positively to both mowing for agriculture and grazing for conservation. We suggest that these associations can be attributed to their foraging habits—even though these species breed in woodland, they forage on the ground in grasslands (Hudec and Šťastný, 2005; Šťastný and Hudec, 2011), and reduction of herb height makes their food more accessible (Hoste-Danylow et al., 2010). In addition, large mammalian herbivores used for conservation grazing serve as a bird food source *per se*, attracting various kinds of flying insects (e.g., species of the order Diptera) and hosting their larvae (Musitelli et al., 2016).

Regarding the changes in beta-diversity, it is interesting that common species drove the pattern in all taxa, regardless of whether their species richness increased or decreased. This is consistent with the important role of common species in the ecosystems which has recently been recognized from both theoretical (Sizling et al., 2009) and applied perspectives (Gaston, 2010). In this respect, it is particularly worrying that the increasing beta-diversity of plants, grasshoppers and butterflies in the studied abandoned military training areas was driven by the extirpation of the common species. Such species may suffer from being overlooked by the current management efforts, which are typically prescribed on the basis of the needs of the most threatened species (Scheele et al., 2018) which are usually also rare (Mace et al., 2008). Birds contrasted somewhat with the other taxa, as their beta-diversity decreased due to a slight dominance of colonization by common species over extirpation. As the most common bird species prefer later successional stages (Bystricky et al., 2023), it is possible that they benefited from the lack of management in some areas.

Although at least some of the observed changes in biodiversity can be explained by management, there may be other drivers that could not be included in our analysis given the data we have. In this respect, climate change is the hottest candidate. Indeed, the increase in species richness due to climate change has been documented in Central European grasshoppers (Fartmann et al., 2022) and birds (Leroy et al., 2023), as well as the decrease in plant (Wesche et al., 2012) and butterfly richness (Eskildsen et al., 2015). However, the effects of this global driver are usually recorded at large scales, whereas the local-level data we focus on here reflect the effects of local habitat changes (see e.g., Jandt et al., 2022). Thus, we do not think that it would be strong enough to affect the reported relationships with management types at the study sites.

Our simultaneous focus on four different taxa uncovered various taxon-specific patterns in biodiversity-management relationships. If we had studied only a single taxon, e.g., birds which are often considered reliable state-of-nature indicators (Fraixedas et al., 2020), we would have obtained a seriously biased view of the system showing increasing species richness (not true for butterflies), decreasing beta-diversity (not observed in plants, grasshoppers and butterflies), and the lack of response to several management options, such as woody plant cutting (supporting plants and grasshoppers) and vehicle movement (negatively affecting butterflies). Therefore, we recommend conducting multitaxonomic studies to gain complex insights into the effects of various management types on biodiversity in open habitats. Considering such complexity is important for setting appropriate conservation targets (e.g., Boetzl et al., 2021).

Conclusions and conservation implications

Our study demonstrated a dynamic change of biodiversity in abandoned military training areas, sites considered to be biodiversity strongholds. At least some of these changes can be explained by the management. To that end, we propose the following recommendations for practitioners:

1) We observed both positive and negative biodiversity responses to the focal management types across taxa. It often happens that the benefits of one management approach for a given group of organisms are offset by costs to another one. Environmental management of abandoned military training areas thus must be based on setting the priorities for conservation.
2) As one such priority that can be considered the most urgent, we propose the conservation of butterflies. Butterflies are the only taxon to have a consistent pattern of biodiversity loss, negative management impacts and no benefits. We believe that these patterns arise from the specific ecology of this taxon, requiring smaller-scale habitat heterogeneity than any other taxa studied. To reverse the negative trends, we suggest that butterflies need combination of different management approaches that would increase small-scale habitat heterogeneity. Finding the optimal management combinations for the most declining butterflies should be the most urgent research priority.
3) The cutting of woody plants seems to be widely positive with benefits for both plants and grasshoppers and did not have any negative impacts on the other species groups. Therefore, it seems that it is an important management tool for blocking woody plant encroachment and it is currently applied in biologically plausible. Its current form can be further supported.
4) The effectiveness of mowing for conservation should be thoroughly investigated. According to our data, it did not increase the biodiversity of any groups of organisms. Although the observed negative effect can be perceived as advantageous for biodiversity (i.e., suppression of generalist plants), the absence of positive relationships is worrying. More detailed studies with an experimental design are needed to identify the aspects of this type of management that should be improved.
5) Both mowing and grazing for agriculture showed a mixture of biodiversity benefits and costs. Overall, plants and birds were more

likely to enjoy the benefits, while grasshoppers and butterflies were more likely to experience the costs. We suggest that these different effects may be explained by the differences in the lifestyle of these organisms. As both types of agricultural management are relatively intensive, the organisms that could perceive their benefits should also exhibit some form of ecological generalisation (birds) or resilience (plants). In contrast, both invertebrate taxa are relatively specialized and thus more sensitive to the negative consequences of this management approach which particularly concerns butterflies. Therefore, we suggest that mowing and grazing for agriculture can be applied on some abandoned military training areas, but not on sites where they can harm the sensitive taxa. This particularly applies to mowing for agriculture in grasshoppers and to grazing for agriculture in butterflies.

6) Grazing for conservation brought more benefits than costs, which seems encouraging. On the other hand, the benefits are modest at best, since none were observed for plants and butterflies. At the same time, these taxa are often considered to be those for which this management type is most frequently prescribed (Bubová et al., 2015). We therefore urge detailed experimental studies (such as Konvička et al., 2021) in areas of application to identify the aspects of this management approach that can be improved to maximize its positive influence.
7) Vehicle movement resulted in costs for butterflies. Although this effect may be temporary as we discuss above, we suggest that vehicle movement should be applied in a more spatially restricted manner that would prevent such negative impacts.
8) Extirpation of common species was a main driver of biodiversity changes in plants, grasshoppers and butterflies. Such species do not appear to be supported by current management efforts, and the development of specific management types to satisfy their requirements may be needed.

In conclusion, our study is the first to investigate the consequences of various managements approaches on different representatives of biodiversity in abandoned military training areas. Based on this investigation, we identified several knowledge gaps and provide management recommendations and suggestions for further research. It is important to recognize that our data collected at the level of whole areas cannot reveal more detailed relationships that require experimental design. Such experimental studies should be a research priority in the future.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://osf.io/9j6ya/.

Ethics statement

Data were obtained by standardly used methodology conforming to the national legislation. No specific permissions for manipulation with living objects were required given the observational nature of the study.

Author contributions

PM, JR, JK, OČ, and TK conceived the idea. TK, JR, PM, JK, OČ, and LD designed the research. LD, JK, PM, TK, OČ, and JR collected the data. PC conducted the analysis. JR led writing with inputs from all co-authors. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Authors LD, JK, and PM are employed by Beleco, Z.S.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2023.1243568/full#supplementary-material

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